**Theory of microbial genome evolution**

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Bacteria and archaea have small genomes that are tightly packed with protein-coding genes. This genomic compactness is commonly perceived as evidence of adaptive genome streamlining caused by strong purifying selection in large microbial populations. However, by comparing predictions of population-genetic models to comparative genomic data, we show that new genes acquired by microbial genomes, on average, are adaptive. We further refine this theory by identifying the adaptive or neutral evolutionary regimes for different functional classes of genes as well as mobile elements. Evolution of bacterial and archaeal genomes is highly dynamic and is dominated by horizontal gene transfer and gene loss. Many microbes have open pangenomes, where each newly sequenced genome contains more than 10% ‘ORFans’, i.e. genes without detectable homologues in other species. A quantitative analysis of microbial genome evolution using a simple, steady-state evolutionary model reveals two sharply distinct classes of microbial genes, one of which (ORFans) is characterized by effectively instantaneous gene replacement, whereas the other consists of genes with finite, distributed replacement rates. These findings imply a conservative estimate of the prokaryotic genomic universe size, which appears to contain at least a billion distinct genes.

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