



**Fig. 6.**—PCA of codon usage in deep-Mediterranean Thaumarchaeota and GII/III-Euryarchaeota pangenomes. (A) Genes colored as a function of their thaumarchaeal or euryarchaeal origin. (B) GII/III-euryarchaeal genes colored as a function of their class of origin. (C) Thaumarchaeal genes colored as a function of their class of origin.

significant for all COG distributions and for all the KEGG distributions except that of late HT-transfers (supplementary table S1, Supplementary Material online). As expected, archaeal core (including universal) genes in the two lineages contained the most important fraction of genes involved in storage and processing of genetic information, together with an equivalent (or slightly smaller) fraction of genes involved in metabolism. Early and late HT-genes also displayed a remarkable similarity. Their COG classes were clearly dominated (ca. 60%) by metabolism-related genes, although also included a few informational and signaling-related genes. Whenever classifiable, their KEGG superclasses were also largely dominated by metabolism-related genes; their levels were very similar in Thaumarchaeota (ca. 50%), although a slight difference was observed between early HT-genes (ca. 55%) and late HT-genes (ca. 35%) in GII/III-Euryarchaeota. However, the most striking difference corresponded to the patterns displayed by Thaumarchaeota- and GII/III-Euryarchaeota-specific core genes, which were clearly dominated by genes that could not be attributed to existing COG classes (70–80%) or KEGG superclasses (ca. 90%), the remaining fraction being dominated by metabolism-related genes.

At finer scale, some differences were observed between early and late HT-genes and between Thaumarchaeota and GII/III-Euryarchaeota in COG categories (supplementary figs. S8 and S9, Supplementary Material online). However, the general functional categories most affected by HGT were similar in the two lineages: Nucleotide, coenzyme, carbohydrate, lipid and amino acid transport and metabolism, inorganic ion transport, energy production and conversion, and cell wall/membrane biogenesis. Late HT-genes contained more genes with general prediction only. GII/III-Euryarchaeota appeared more impacted by HGT and contained more HT-genes affecting transcription/signal transduction and posttranslational modifications than Thaumarchaeota.

The distribution of HT-genes that could be assigned to KEGG pathways also revealed that early and late HGT events distributed similarly in each of the lineages, with ancient HT-genes being more represented than recent HT-genes in the identified pathways. The only exceptions were the import of lysine and streptomycin biosynthesis in GII/III-Euryarchaeota (supplementary fig. S10, Supplementary Material online). Likewise, there were some similarities between the global distribution of HT-genes in Thaumarchaeota and GII/III-Euryarchaeota, which were high in functions such as benzoate degradation, phenylalanine metabolism, folate biosynthesis, fatty acid biosynthesis, ABC transporters, oxidative phosphorylation, or the metabolism of glyoxylate and dicarboxylate, cysteine, methionine and, to some extent, other amino acids (although with variations in percentages), and cofactors. However, there were also important differences. Thaumarchaeota seem to have imported more genes related to sugar metabolism (fructose, mannose, galactose, aminosugar, and nucleotide sugar metabolism), whereas GII/III-Euryarchaeota seem to have acquired more genes involved in amino acid and nucleotide metabolism (HT-genes related to streptomycin and lysine biosynthesis; the pentose phosphate pathway; and the metabolism of thiamine, pyruvate, or nitrogen, fatty acids, alanine, aspartate and glutamate, and pyrimidine).

## Discussion

HGT is an important force in evolution, contributing to innovation and adaptation to changing or new environments through the expansion of gene families and the import of radically different metabolic functions (Ochman et al. 2000; Gogarten et al. 2002; Treangen and Rocha 2011). Our work shows that this likely applies to two different lineages of planktonic mesophilic archaea whose members remain largely