GII-euryarchaeote (see examples in fig. 4). This implies that they were acquired by HGT from distant donors recently, after the diversification of Thaumarchaeota and GII/III-Euryarchaeota, respectively. Surprisingly, HGT events that occurred at the base of these two archaeal lineages were also abundant (fig. 3; see examples in fig. 5). Clear HGT affecting these archaeal genes could be inferred even if some cases of HGT among bacteria could sometimes be observed; the latter appears inevitable given the large phylogenetic scales considered. In Thaumarchaeota, they were as abundant (11.5%) as late HT-genes (12.6%). In GII/III-Euryarchaeota, they accounted for 8.6% (compared with 21.1% late HT-genes), although this proportion corresponds to a high number of genes (416) that might increase when representative true complete genomes become available for this lineage. Because our reconstructed thaumarchaeal pangenome included basal fosmids branching earlier than soil Thaumarchaeota, we would expect finding shared HT-genes in soil members. To test it, we looked for homologs of the HT-genes identified in our thaumarchaeal pangenome in *N. gargensis* (Spang et al. 2012) and reconstructed the corresponding phylogenetic trees. *Nitrososphaera gargensis* shared 196 HGTs out of the 290 genes that had been identified as early HT-genes in the Thaumarchaeotal pangenome (table 1).

Which were the distant donors of HT-genes? The majority were bacteria: 94% and 93% of early HT-genes and 81% and 96% of late HT-genes for deep-Mediterranean Thaumarchaeota and GII/III-Euryarchaeota, respectively (fig. 3). A very minor fraction came from eukaryotic donors or from other archaeal phyla (Euryarchaeota for the Thaumarchaeota or Crenarchaeota/Thaumarchaeota for the Euryarchaeota). Only recent HT-genes in Thaumarchaeota had a significant fraction of euryarchaeal donors (17%). Among the bacterial donors, between one-fourth and one-third of the HGT events could be ascribed to specific bacterial phyla, the remaining cases could not be confidently assigned to particular phyla. Proteobacteria, Actinobacteria, Firmicutes, and Cyanobacteria were the most frequently identified donors (fig. 3).

We checked that the high level of HGT in thaumarchaeal and GII/III-euryarchaeal fosmids from bacterial donors was not due to the inclusion in our analysis of chimeric archaeal/bacterial fosmids artificially produced during the fosmid library construction. First, our fosmids were carefully verified and lacked frameshifts that might be indicative of chimerism. Second, when we mapped the genes on fosmid-cloned genome fragments as a function of their origin class (archaeal core, lineage-specific core, early HT-genes, late HT-genes, and others), both early and late HT-genes were scattered among typical archaeal genes from the other classes. As a proxy to quantify this, we computed the mean synteny block length per gene class. In general, synteny blocks (here broadly defined as arrays of contiguous genes of same origin class) were small for all gene classes but those including early and late HGT events had the shortest average lengths (supplementary fig. S6, Supplementary Material online), indicating that HT-genes were transferred mostly as single genes and/or that HT-genes interspersed after transfer into host genomes. We also analyzed the class of origin of their flanking genes. Interestingly, the distribution patterns observed were very similar for the same gene classes defined independently of the archaeal phylum considered. Thus, early Thaumarchaeota HT-genes displayed a flanking pattern more similar to the corresponding class in GII/III-Euryarchaeota than to any other gene class in Thaumarchaeota, and so on (supplementary fig. S6, Supplementary Material online). This observation may be suggestive of similar histories for each gene class and/or similar evolutionary processes involved. We also looked for the presence of potential insertion elements, transposons, or viral sequences flanking HT-genes, but we failed to detect a clear association of such elements with HT-genes.

Because differences in codon usage may be indicators of HGT (Garcia-Vallve et al. 1999), we looked for potential signatures of codon usage differences in recent HGT events when compared with other gene classes in deep-Mediterranean pangenomes. There were marked differences in codon usage between Thaumarchaeota and GII/III-Euryarchaeota pangenomes (fig. 6*A*) in agreement with manifest differences in GC content (table 1). However, differences in codon usage for recent HT-genes when compared with late HT-genes, lineage-specific core, or archaeal core genes in Thaumarchaeota (fig. 6*B*) or Euryarchaeota (fig. 6*C*) were not seen. Similar observations could be made from the CAI of the different gene classes considered. CAI measures the deviation of protein codon usage with respect to reference, highly expressed genes. All thaumarchaeal and GI/III-euryarchaeal gene classes had similar high CAI values when compared with their own reference data set (ribosomal proteins) (supplementary fig. S7, Supplementary Material online). This suggests that recent HGT events occurred sufficiently long ago for the corresponding genes to adapt to their host genomic environment.

Functional Classes of Transferred Genes

We looked for potential functional differences between late and early HT-genes to Thaumarchaeota and GII/III-Euryarchaeota pangenomes, and between these and the corresponding archaeal core and lineage-specific core genes. Shell non-HGT genes were not included in this analysis, because they correspond to predicted genes with one to a few homologs only in fosmids and lacking clear homologs in the database (hence, nonannotated). Overall differences were already seen at a very general level of functional classification in COG classes and KEGG superclasses between gene origin classes. However, there were remarkable similarities in the functional patterns observed for the different gene origin classes between Thaumarchaeota and GII/III-Euryarchaeota (fig. 7), suggesting similar underlying processes and/or mechanisms of adaptation by gene acquisition. These similarities were