

# A global atlas of subsurface microbiomes reveals phylogenetic novelty, large scale biodiversity gradients, and a marine-terrestrial divide

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## Abstract

Marine and terrestrial subsurface sediments, rocks, and water may represent the largest habitat for microbial life on Earth. Despite the global importance of subsurface ecosystems for biogeochemical cycling and microbial diversity, essential questions remain unanswered. These concern the abundance of novel microbial clades in the subsurface, the difference between marine and terrestrial microbiomes, as well as between subsurface and surface microbiomes, and the adaptation of specific clades to environmental conditions of the subsurface. Here, we analyzed 523 archaeal and 1,211 bacterial 16S rRNA gene amplicon sequence datasets and 146 shotgun metagenomes from surface, interface, and subsurface ecosystems worldwide, including lakes, saltmarshes, hot springs, caves, mines, methane seeps, hydrothermal vents, and seafloor sediments. We found that archaeal and bacterial alpha diversity (per sample richness and evenness) and beta diversity (community differentiation) varied continuously between surface and subsurface biomes, but differed abruptly between marine and terrestrial subsurface ecosystems. Bacterial alpha diversity tended to be lower in subsurface than surface ecosystems. However, subsurface archaeal alpha diversity often exceeded that of surface ecosystems suggesting that the subsurface holds a considerable and largely underestimated fraction of Earth's archaeal diversity. Overall, microbial communities of marine subsurface ecosystems exhibited greater alpha diversity, while gamma diversity (total richness and evenness) was higher in the terrestrial subsurface, potentially due to greater habitat diversity. We identify diagnostic clades, especially for the archaea, that are widespread in marine (e.g., Lokiarchaeia, Bathyarchaeia) and terrestrial (e.g., Hadarchaeia, Methanococci) subsurface ecosystems. The substantial community overlap along depth transects and between surface, interface and subsurface realms suggests a global

gradient between the surface and subsurface rather than a discrete and defined subsurface biosphere. Finally, none of the included subsurface ecosystems seem to be exhaustively sampled, leaving much biodiversity and metabolic capability yet to be discovered.

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## **Conflicts of interest**

The authors have declared that no competing interests exist.