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Current Opinion in Microbiology

Review

Cave microorganisms: hidden players in global greenhouse gas cycling and climate regulation

Tamara Martin-Pozas[1], Soledad Cuezva[2], Angel Fernandez-Cortes[3], Janez Mulec[4,5] and Marcela Hernández[6]

Caves are unique among ecosystem types because of their physical structures and biological functions. Embedded in rocks, the geological setting defines the boundaries of caves and dictates how energy and matter move through them. General features of caves, compared to surface ecosystems, include absence of light, relatively stable temperature and humidity, and oligotrophic conditions. Despite these conditions, caves are highly diverse ecosystems whose environmental properties are shaped by geological, hydrological, and climatic factors. Cave microbiomes metabolize atmospheric trace gases, such as methane, nitrous oxide, and carbon dioxide, contributing to greenhouse gas (GHG) cycling dynamics. In some cases, these microbes also form biominerals, such as calcium carbonate, highlighting critical gaps in our understanding of subterranean biogeochemical processes. Some of these gaps include the limited genomic data and geographic bias in the literature. Herein, we review the current state of knowledge surrounding the potential of cave microorganisms, including those capable of biomineralizing calcium carbonate, as agents for sustainable GHG sequestration and climate change mitigation, with emerging strategies for developing novel sustainable biotechnological solutions. By revealing the hidden microbial activity beneath the Earth's surface, this review proposes integrating subterranean ecosystems into global climate models, reframing caves as metabolically and functionally active contributors to the planet's climate system rather than isolated geological features.

Addresses
[1] Instituto de Recursos Naturales y Agrobiología de Sevilla, IRNAS-CSIC, Avda. Reina Mercedes, 10, 41012 Sevilla, Spain
[2] Museo Nacional de Ciencias Naturales, MNCN-CSIC, José Gutiérrez Abascal, 2, 28002 Madrid, Spain
[3] Departamento de Biología y Geología, Universidad de Almería, Ctra. Sacramento, s/n, 04120 Almería, Spain
[4] Karst Research Institute, Research Centre of the Slovenian Academy of Sciences and Arts, Titov trg 2, SI-6230 Postojna, Slovenia
[5] UNESCO Chair on Karst Education, University of Nova Gorica, Glavni trg 8, SI-5271 Vipava, Slovenia
[6] School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

Corresponding authors: Martin-Pozas, Tamara (tmpozas@csic.es), Hernández, Marcela (marcela.hernandez@uea.ac.uk)

Current Opinion in Microbiology 2026, **90**:102707

This review comes from a themed issue on **Environmental Microbiology**

Edited by **Chris Greening** and **Cornelia Welte**

For complete overview of the section, please refer to the article collection, "Environmental Microbiology (2025)"

Available online 27 January 2026

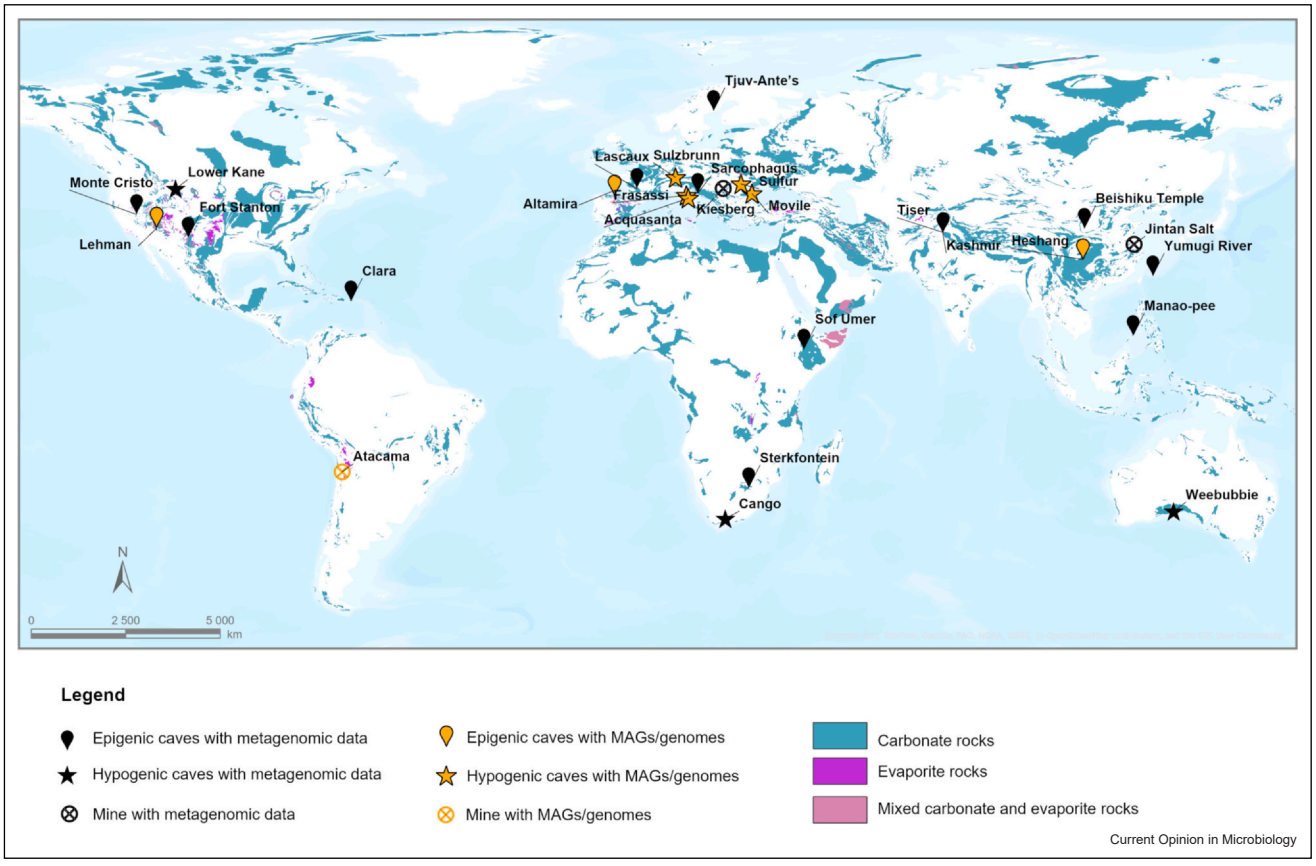
https://doi.org/10.1016/j.mib.2026.102707

Introduction

Subterranean ecosystems, such as caves, are increasingly recognized as dynamic components of global biogeochemical cycles [1], yet their role in greenhouse gas (GHG) regulation remains largely understudied. These subterranean environments exchange trace gases, such as carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), with the atmosphere at seasonal and daily scales, playing an essential role as dynamic regulators of carbon and nitrogen fluxes. In the karst subsurface, several abiotic and biotic processes are involved in GHG regulation. Carbonate weathering and mineral formation occur through purely abiotic reactions [2,3] and microbially mediated mechanisms [4]. Additional microbially driven processes include CH_4 oxidation [5], CO_2 fixation [6], respiration, and nitrogen-cycle transformations such as denitrification and nitrification [7]. While the global extent of cave systems remains uncertain, karst areas — formed on soluble bedrock substrates such as limestone, dolomite, and gypsum, and excluding those from volcanic or mechanical origin — cover approximately 15–20% of the terrestrial surface [8,9] (Figure 1).

The karst vadose zone globally stores between 2 and 53 petagrams of carbon (PgC) in the form of CO_2. This 'ground air' reservoir represents the second largest

Figure 1



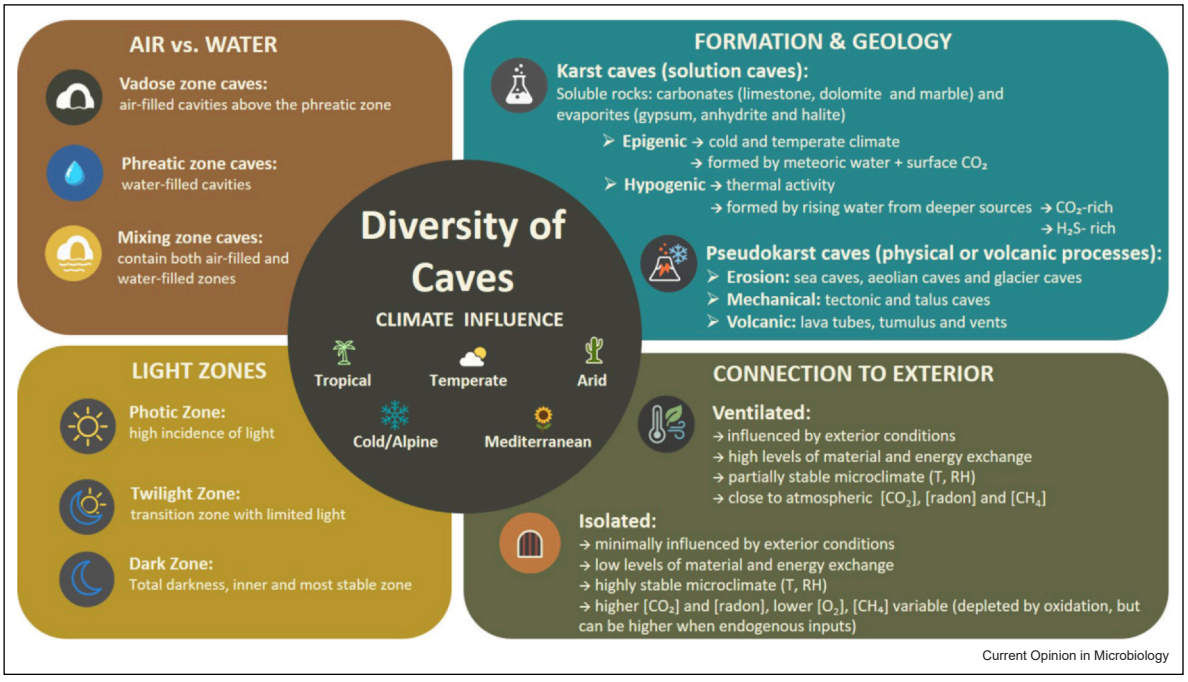
World map showing the main areas underlain by soluble rocks (carbonates, evaporites, and gypsum), as well as caves and mines with metagenomic data (see Supplementary Table S2 for additional information). Caves with MAGs and genomes are shown in Figure 3.

natural store of atmospheric CO_2 on the planet [10]. In addition to its role in carbon storage, this subterranean system also functions as a major CH_4 sink [11], with an estimated consumption of up to 106 teragrams (Tg) of CH_4 per year — more than twice the 49 Tg CH_4 per year typically attributed to terrestrial soils [5,12]. These findings underscore the potential significance of cave systems in global carbon–GHG balances. There is an imbalance between the estimated sources and sinks of CH_4 [13], which should produce a higher atmospheric growth rate than observed, indicating either an overestimation of sources or an underestimation of sinks. The role of subterranean atmospheres should be considered separately to refine global CH_4 budgets and reduce the underestimation of the terrestrial sink. Current subsurface estimations probably overstate the global subterranean sink, so better scaling-up measurements and models are needed based on real whole-cave or whole-karst CH_4 consumption studies.

Additionally, potential contributions of karst landscapes to N_2O cycling are caused by varying redox conditions during surface water–groundwater exchange [14]. Therefore, the cave atmospheres in the vadose zone closer to the water table (on gaseous equilibrium with the underground air) may represent a hotspot for N_2O production and emissions, particularly in karst agricultural areas with extensive irrigation (high surface water–groundwater exchange) and use of nitrogen fertilizers.

Caves host abundant, specialized microbial communities adapted to oligotrophic, dark, and geochemically distinct conditions. They are of particular interest in the context of GHGs due to their ability to consume and transform them. This review synthesizes current knowledge on cave microbial contributions to GHG dynamics, including methanotrophy, nitrogen transformation, CO_2 production and fixation, and biomineralization of calcium carbonate, highlighting the potential of these microbes as biotechnological tools for sustainable GHG sequestration and climate change mitigation.

Figure 2



Scheme representing the diversity of cave ecosystems and their role in GHG dynamics. T: temperature; RH: relative humidity.

Diversity of cave ecosystems and their role in GHG dynamics

Caves can be entirely air-filled, water-filled, or contain both phases, and this strongly determines their capacity for gas exchange with the external atmosphere (Figure 2). From the perspective of GHG dynamics, the most relevant systems are in the vadose zone, above the water table, where intense exchanges occur between the subterranean and surface atmosphere, with key implications for global GHG balances [10,15]. In the vadose zone, the gas dynamics are controlled by local climate, cave morphology, and the number of entrances and their locations [16,17]. Cave ventilation at diurnal and seasonal scales depends on external factors. A main driver of advective airflow between the outside and the cave atmosphere is the temperature difference between external and internal air masses [16–20]. Well-ventilated areas are more strongly influenced by external conditions and exhibit higher rates of gas and matter exchange. In contrast, poorly ventilated areas accumulate CO_2, while CH_4 concentrations decline below atmospheric levels due to microbial oxidation, a typical pattern of epigenic caves where the main source of subterranean CH_4 comes from the surface [20,21]. However, in hypogenic systems with endogenous CH_4 inputs [7,22], concentrations can remain above atmospheric levels. In addition to the entry of CH_4 from the outside atmosphere, potential *in situ* sources of cave CH_4 include methanogenesis, which is anaerobic respiration of microbes that generate CH_4, primarily by archaea, in anoxic conditions within sediments and groundwater, commonly by decomposition of organic matter (e.g. large deposits of bat guano or surface originating organic pollution). Methanogenesis can be triggered within water-filled pores and fissures of the vadose zone, where seepage enriched in organic matter promotes microbial CH_4 production [23]. Furthermore, contributions from deep soils, sewage, and outgassing swamp water connected to the cave environment can introduce additional CH_4 inputs [24]. These processes indicate that caves may host both methanogenic and methanotrophic communities, whose relative balance determines the net CH_4 budget in subterranean systems.

At cave entrances, sunlight availability defines different ecological zones: a photic entrance zone with abundant photosynthetic communities, an ecotone twilight zone, and the dark zone with the absence of surface colonization of algae and cyanobacteria. In deeper cave zones with stable conditions, chemoautotrophic bacteria dominate as primary producers, converting inorganic carbon into organic matter [25]. External climate, vegetation, and surface geomorphology dictate water flow, air circulation, and nutrient transfer that control the internal environmental conditions of caves and consequently determine the distinctive cave habitats along a gradient of light, temperature, humidity, and gaseous composition of underground air. The productivity and nutrient storage capacity of the overlying soils determine the available energy for subsurface microbial colonization. Therefore, the decomposition processes based on

these nutrients influence biogeochemical cycling in the subterranean environment, which in turn provides habitat structures that shape the diversity patterns of microbial taxa in caves.

Geological processes, such as speleogenesis driven by geological, hydrological, chemical, and biological factors, further contribute to cave diversity and evolution. On a global scale, epigenic karst carbonate caves predominate, representing 80–90% of known systems [26]. These caves develop in soluble rocks through meteoric recharge enriched with soil-derived CO_2, producing weak carbonic acid. Less common are hypogenic caves, formed by deep-sourced fluids rich in dissolved CO_2 and/or H_2S and associated with activity of hydrothermal systems. These caves represent more than 10% of karstic networks worldwide [27].

Both cave types play a key role in the regulation of CH_4, regardless of the origin or source of the gas. In epigenic caves, methanotrophs consume atmospheric methane entering from the exterior, whereas in hypogenic systems with geogenic sources of CH_4, methanotrophs contribute to a partial decrease of the elevated concentrations of CH_4 that are in these environments [7,11,23].

Regarding CO_2, caves behave mainly as temporary reservoirs of atmospheric carbon [2,20,28]. While overlying soil CO_2 is generally considered the main source of cave CO_2, studies have also shown contributions from cave sediments and deeper aquifers [15,29,30]. Under conditions of limited ventilation, CO_2 from topsoil and cave sediments accumulates in cave air in the vadose zone and is released back to the atmosphere during ventilation periods, when caves act as gas emitters. However, part of this subterranean CO_2 remains dissolved in underground water and can be transformed into carbonates, forming a stable carbon sink [2,28,29]. These characteristics make caves complex systems, in which it is challenging to quantify their contribution to global carbon balances.

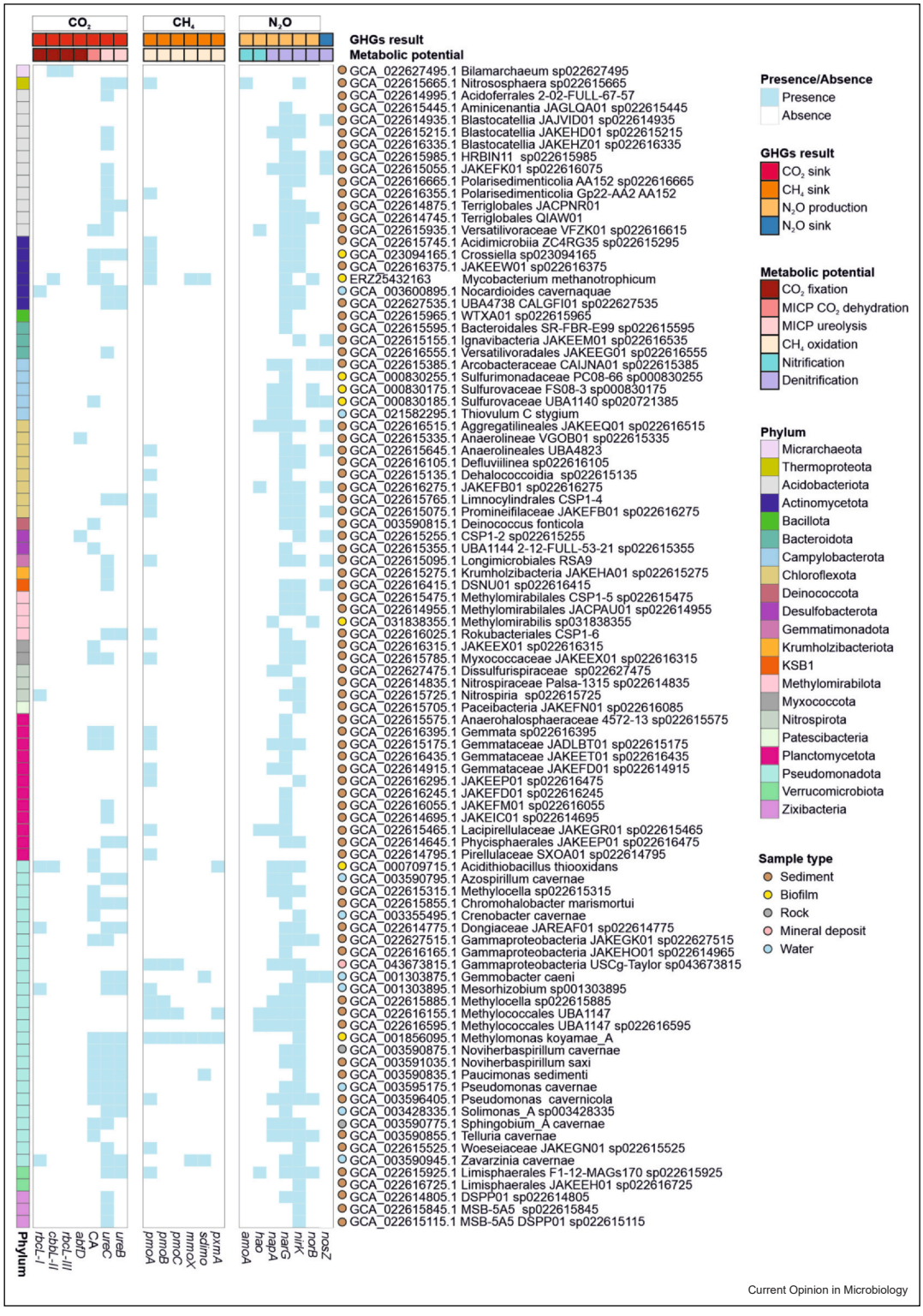
In contrast to CO_2 and CH_4, the role of caves in N_2O dynamics remains poorly understood. Evidence suggests that N_2O in cave atmospheres often reflects a strong soil and groundwater imprint, acting in some cases as a conservative tracer of external inputs rather than as the product of *in situ* processes [21]. However, variability across ecosystems is likely: shallow, well-ventilated epigenic caves tend to mirror atmospheric N_2O, whereas isolated caves often reflect soil-derived N_2O. In contrast, systems with stronger hydrological connectivity and well-developed conduits may promote denitrification and transient N_2O accumulation [7,14]. Recent evidence from karst waters also shows that local recharge events strongly shape the potential of N_2O production by modifying the structure of microbial communities and nitrogen transformation processes [31]. This highlights the need to explore how contrasting cave types — from well-ventilated karst cavities to hypogenic settings with deeper groundwater influence — modulate N_2O storage and potential release, and to assess whether caves represent overlooked sources or sinks in global nitrogen cycling.

Microbial community composition and GHGs

One of the key challenges in understanding the contribution of cave microbiomes to GHG dynamics is identifying the key microbial actors and quantitatively assessing their role in modifying the composition of the subterranean atmosphere and regulating GHG fluxes across rocks, sediments, water, and air. Metagenomic and genomic analyses offer powerful approaches to address this challenge, providing valuable insights into the genetic potential of microbial communities involved in GHG cycling in caves. However, only a limited number of microbial cave–derived genomes are currently available in public databases. Additional data mining and new sequencing efforts give new, valuable findings. To assess the current state of knowledge, we conducted a literature search in Scopus (early in July 2025) for cave metagenomes/genomes. Our search revealed that most studies have relied on targeted amplicon sequencing, while only 33 have employed shotgun metagenomics. Of these, only 17 mention the potential role of microorganisms in GHG dynamics, and only 12 provide genome or metagenome-assembled genome (MAG) accession numbers, covering just eight caves worldwide [32–43]. Genomes and metagenomes were retrieved from public repositories (see Supplementary Tables S1 and S2), taxonomically reclassified using the Genome Taxonomy Database (GTDB), and functional genes of interest were identified using BLAST searches against custom databases and hidden Markov model (HMM)-based approaches. Based on our cave genome search, the following results summarize the available genomic evidence on microbial communities involved in GHG cycling. The current genomic evidence across cave environments, linking specific MAGs with their metabolic potential for GHG transformations, is summarized in Figure 3. Notably, most of the MAGs come from sediments of Movile Cave (Romania), with a few additional samples from water, sediments, and biofilms. The heatmap shows the presence/absence of genes related to CH_4 oxidation, CO_2 fixation, N_2O production and consumption, denitrification, nitrate/nitrite reduction, nitrification, and microbially induced carbonate precipitation (MICP).

Several MAGs harbor pathways for nitrite oxidoreductase, which is responsible for the oxidation of nitrite to nitrate. Genes for ammonia assimilation, denitrification, and dissimilatory nitrate reduction were also well represented across cave-associated MAGs, highlighting

Figure 3



Heatmap of the presence/absence of genes related to CH_4 oxidation (*pmoA*, *pmoB, pmoC, mmoX, sdimo, pxmA*), CO_2 fixation (*rbcL-I, cbbL-II, rbcL-III*), N_2O consumption (*nosZ*) and production (*norB*), denitrification (*narG, napA, nirK, norB, nosZ*), nitrification (*amoA, hao*), and biomineralization pathways (carbonic anhydrase (CA, *ureC, ureB*) in eight caves. The analysis is based on MAGs and genomes retrieved from the literature (Additional details, including accession numbers and references, are provided in Supplementary Table S2). Functional genes were identified by BLAST searches against custom databases for each gene and further validated using HMM-based approaches.

the importance of redox gradient and nitrogen cycling in these subsurface ecosystems. Moreover, evidence for MICP, urea hydrolysis, and CH_4/CO_2 metabolism underscores the role of cave microbiomes as active players for sinks of atmospheric GHGs and as drivers of carbonate mineral formation.

Methane cycling

Recent metagenomic studies have shown that methanogenic archaea generally occur at low relative abundances in caves when compared to methane-oxidizing bacteria (MOB) [44,45]. This pattern suggests that methanotrophy predominates over methanogenesis in these environments, which aligns with the absence of methanogenic genomes in our dataset. Typical MOB in karst and volcanic caves are dominated by high-affinity upland soil cluster gamma (USCγ) and alpha (USCα) methanotrophs [21,43–46]. Our search revealed numerous potential MOB MAGs ranging from assemblies containing *pmoA*-like sequences to MAGs encoding a more complete set of methane-metabolism genes. Phylogenetically, they group within USCγ (*Methylomonas*, *Methylococcaceae*, USCγ-Taylor/Chromatiales wb1-p19), USCα (*Methylocella*), and *Actinomycetota* (*Candidatus* Mycobacterium methanotrophicum). USCγ methanotrophs have been detected in hypogenic, epigenic karstic, and volcanic caves, whereas USCα taxa, though typically dominant in volcanic environments, have also been reported from karstic and sulfur-rich caves [22,32,43,44,47].

Both biological and physicochemical perspectives have been explored to understand the mechanisms of cave CH_4 oxidation. Analyses based on isotopic methods [4,48–50], molecular biology [21,22,32,44–46,49], and mesocosm simulation experiments [51,52] have consistently shown that CH_4 oxidation in caves is predominantly driven by MOB, ruling out abiotic processes such as radiolysis. One of the first studies on methanotrophic activity in subterranean environments was the DNA-stable isotope probing experiment conducted in Movile Cave [22]. However, its broader implications were underestimated at the time of discovery but later became an example of an underground sulfidic chemoautotrophic ecosystem. Subsequent research on bacterial CH_4 oxidation in natural subterranean environments proved that microbial methanotrophy is the primary mechanism for *in situ* CH_4 removal from cave air [21,48,52,53]. These studies mainly used isotopic proxies such as $\delta^{13}C$-CH_4 and $\delta^{2}H$-CH_4. Several studies have since confirmed that CH_4 consumption varies seasonally and that MOB are chiefly responsible for the widespread depletion of CH_4 in subterranean environments [4,20,21,53]. However, observations of CH_4 concentrations in cave air were first limited to localized studies in caves from Gibraltar, Spain, Romania, Indiana (USA), Vietnam, and Australia, often with incomplete isotopic datasets. Webster et al. [24] expanded this scope by analyzing cave air from 33 caves in the USA and three in New Zealand, demonstrating that caves act as a global CH_4 sink.

The first study to investigate the presence and spatiotemporal distribution of cave methanotrophs used the bacterial methane monooxygenase gene *pmoA* as a functional marker [21], showing that methanotrophic bacteria were predominantly located in cave sediments. Real-time PCR quantification revealed that methanotrophs comprised a high proportion (2–12%) of the total bacterial community in these sediments. In addition, methane oxidation has been shown in cave biofilms. The first direct measurements of biological CH_4 oxidation in cave ecosystems were conducted through *in situ* field mesocosm experiments in Vietnamese caves. These experiments estimated CH_4 oxidation rates of 1.3–2.7 mg CH_4 m^{-2} day^{-1} by microbial biofilms on limestone rocks [51]. Quantitative PCR assays targeting the *pmoA* gene confirmed that methanotrophic bacteria were abundant on cave rocks, with relative abundances ranging from 0.16% to 1.48% of the total microbial community. An extrapolation to Vietnam's entire karst region (29 000 km^2) suggests a potential CH_4 sink of approximately 1.5×10^8 kg CH_4 per year [54]. These oxidation rates are comparable to — or even exceed — those reported in other ecosystems, including agricultural soils, grasslands, deciduous forests, and Arctic tundra. More recent investigations in other caves have provided complementary data that can also be used for global estimates. In Heshang Cave (China), potential methane oxidation rates measured in microcosms ranged from 0.63 ng CH_4 g^{-1} DW h^{-1} in sediments to 11.02 ng CH_4 g^{-1} DW h^{-1} in weathered rock, values comparable to or higher than those of surface soils, while CH_4 production by methanogens was undetectable [45]. In Pindal Cave (Spain), *in situ* real-time monitoring of diffusive fluxes also revealed a continuous uptake of CH_4 by sediment microorganisms and bioprecipitates of calcite (known as moonmilk deposits). Methane consumption rates ranged from –1.5 nmol m^{-2} s^{-1} during the ventilation stage to –1.9 nmol m^{-2} s^{-1} during the stagnation stage, equivalent to daily fluxes of approximately 1.7–2.6 mg CH_4 m^{-2} day^{-1} [4]. These values fall within the same order of magnitude as those reported in Vietnamese caves, supporting the paradigm that subterranean environments function as effective methane sinks.

Carbon dioxide fixation and carbonate precipitation

Our review revealed that beyond methane metabolism, several MAGs encode RuBisCO and Wood–Ljungdahl pathways, supporting the potential role of chemolithoautotrophy as a key metabolic strategy sustaining subsurface primary production. These pathways are represented across diverse bacterial and archaeal lineages such as Pseudomonadota, Nitrospira, Anaerolineae, Desulfobacterota, Actinomycetota, and Thaumarchaeota. Previous studies have demonstrated that cave microorganisms create favorable chemical conditions for calcium carbonate precipitation through urease and carbonic anhydrase activity, as well as through extracellular polymeric substances (EPS) formation [4,55–57]. Genes associated with MICP, mainly discussed here — carbonic

anhydrase and urease — were also detected across several MAGs. Recent cave studies highlight their occurrence across diverse bacterial lineages, including Pseudomonadota (*Pseudomonas*, *Acinetobacter*, *Stenotrophomonas*), Bacillota (*Bacillus*, *Sporosarcina*), and Actinomycetota (*Crossiella*), among others. This widespread process of carbonate precipitation has been reported in many different types of caves, suggesting a phylogenetically broad potential for carbonate mineral formation in subterranean environments.

The first metagenomic study of cave microbial communities linked to GHG cycling was conducted in the Frasassi Caves (Italy), a limestone karst cave system formed by sulfuric acid derived from gypsum/anhydrite reduction [58]. The study revealed that the extremely acidophilic (pH 0–1) snottite biofilms were dominated by the sulfur-oxidizing bacterium *Acidithiobacillus thiooxidans*. The microbe oxidizes sulfur to sulfuric acid, which is responsible for carbonate dissolution, while it fixes CO_2 autotrophically (through the Calvin cycle).

The first study to pair CO_2 flux measurements directly with microbial community analyses was conducted in Altamira Cave (Spain) [59], an epigenetic limestone cave. This work demonstrated that Actinobacteria-rich biofilms on cave walls acted as biological sinks of CO_2, with measurable net uptake from the cave atmosphere. Along with CO_2 fixation by chemolithoautotrophic *Acidithiobacillus* in Frasassi Caves [58], these studies provided the first direct evidence that cave microorganisms can function as biological sinks for CO_2.

Microbial activity transforming carbon-GHG (CO_2 and CH_4) has also been detected on wet rock surfaces and in moonmilk deposits [4,60]. Based on these observations, Martin-Pozas et al. [4] proposed a biogeochemical model in which cave bacterial consortia, particularly those that inhabit moonmilk deposits, are the main contributors to CH_4 consumption, CO_2 sequestration, and calcium carbonate ($CaCO_3$) formation. Using a soil-flux chamber system, carbon isotope tracing, and microbial sequencing analysis, the authors measured *in situ* GHG fluxes and showed that the observed CH_4 consumption and CO_2 uptake were attributed to bacterial activity. The high rate of CH_4 consumption was attributed to the most abundant MOB identified, belonging to the USCγ pmoA cluster (upland soil cluster gamma). The fluxes and the isotopic signatures of carbon indicated that CO_2 was being captured by cave bacteria and subsequently transformed into carbonate minerals.

Nitrous oxide cycling

Commonly detected genes related to nitrification and denitrification, including nitrite oxidoreductase and nitrous oxide reductase, suggest that N_2O production and consumption are widespread and mediated by phylogenetically diverse taxa spanning Pseudomonadota, Desulfobacterota, Chloroflexota, Bacillota, Acidobacteriota, and Methylomirabilota, among others.

Compared to the knowledge on microbial role of dynamics of CH_4 and CO_2, the role of cave microbiomes in the regulation of N_2O fluxes remains poorly characterized. Early studies suggested that the N_2O observed in cave atmospheres mainly represents an external soil-derived signal [21]. However, growing evidence indicates that subterranean microbial processes can also contribute to N_2O dynamics, particularly in zones of elevated hydrological connectivity and redox gradients. In the mixing zone caves (Figure 2), where the water table of the karst aquifer is in contact with the upper cave atmosphere, ammonia-oxidizing microorganisms and denitrifying communities can generate transient N_2O accumulation [4,14]. Recent studies in karst waters also highlight the importance of recharge events in modulating the structure of nitrogen-transforming microbial communities, thereby affecting the potential for N_2O production or consumption [31]. Metagenomic surveys have revealed that genes related to nitrification, denitrification, and dissimilatory nitrate reduction are widespread across cave microbiomes (Figure 3) [61]. Importantly, many cave microorganisms possess incomplete denitrification pathways, lacking the terminal *nosZ* reductase, which catalyzes the reduction of N_2O to dinitrogen gas (N_2). As a result, these taxa may act as net N_2O producers [7]. Despite this known potential, the quantitative contribution of cave microbiomes to N_2O fluxes remains largely unquantified at the moment.

Overall, the large diversity of cave types and internal microhabitats highlights niche differentiation as a key control on CO_2, CH_4, and N_2O dynamics in cave ecosystems. Shallow cave sediments and surface-attached biofilms, which favor aerobic methane oxidation, CO_2 fixation, and carbonate mineralization, are likely to be more relevant for GHG consumption linked to the overlying atmosphere. In contrast, less ventilated microhabitats, such as subterranean rivers, pools, deeper sediments, and active hypogenic systems, often develop micro-oxic to anoxic conditions, where denitrification and other anaerobic nitrogen transformations may be more prominent and can be coupled to anaerobic methane oxidation. Although the micro-oxic/anoxic habitats play an important role in transforming GHGs derived from deeper sources, they would play a secondary role to the atmosphere GHG fluxes since they are usually isolated from the lower troposphere layer.

Conclusions and future challenges

The integration of isotopic flux measurements with metagenomic and genomic data suggests that cave bacterial communities — particularly MOB and CO_2-fixing lineages — play a central role in subterranean carbon cycling. They metabolize GHGs while simultaneously

promoting the precipitation of carbonate minerals, such as $CaCO_3$. Biofilms formed by methanotrophic and chemoautotrophic microbes can oxidize CH_4 and fix CO_2, enabling stable long-term carbon storage through biomineralization. In addition, because N_2O has a much higher greenhouse effect than CO_2 and CH_4, understanding its dynamics in caves, where it can accumulate or be microbially transformed, is particularly crucial and globally important. These findings point to a more dynamic role of caves in the nitrogen cycle than previously assumed, emphasizing the need to distinguish passive transport of soil-derived N_2O from active microbial transformations within the subterranean environment. These processes position caves as natural biofilters with potential applications in climate mitigation. Current knowledge is still limited by the small number of genomic datasets and the lack of standardized flux measurements. Future challenges include quantifying global cave GHG fluxes and integrating field data with omics and isotopic analyses. Experimental designs using microcosms or mesocosms to test whether some cave microbes are more efficient than others in mineralizing CO_2 and consuming CH_4 may help in this regard. Expanding the cave genomic catalog will be essential to refine microbial contributions and to develop biomineralization-based, low-energy strategies for long-term carbon capture and storage.

Funding

This research was supported by the Spanish Ministry of Science and Innovation through a coordinated project, PID2023-146299OB-C21, funded by MICIU/AEI/10.13039/501100011033. TMP was supported by a Juan de la Cierva Fellowship JDC2023-051909-I. MH was supported by a Royal Society Dorothy Hodgkin Research Fellowship, UK (DHF\R1\211076).

Author contributions

TMP, SC, AFC, and MH: Writing – original draft. TMP, SC, AFC, MH, and JM: Writing – review & editing. TMP, and MH: Resources, Investigation, and Visualization. TMP and MH: Conceptualization and Funding acquisition. All authors read and approved the final manuscript.

Data Availability

All data are shared in the Supplementary Information.

Declaration of Competing Interest

The authors declare no competing interests.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.mib.2026.102707.

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- •• of outstanding interest

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The authors introduce the concept of 'aerotrophs' and highlight cave microbial communities as key providers of ecosystem services. It emphasizes their role in nutrient cycling, pollutant degradation, and climate regulation.

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