# Microbial Diversity and Biogeochemical Cycling in Red Sea Hydrothermal Vents: A Comprehensive Review of an Iron-Rich, Low-Temperature Hydrothermal System

#### Mahshad Abazari

Department of Biology, Science and Research Islamshahr Branch, Islamic Azad University, Tehran, Iran

#### **Abstract**

Hydrothermal vents are globally significant ecosystems that host diverse microbial communities responsible for driving major biogeochemical cycles. While most known vent systems are characterized by high-temperature sulfide-rich emissions, the Red Sea presents a uniquely oligotrophic and iron-dominated hydrothermal environment. Recent discoveries at the Hatiba Mons volcano, the first active hydrothermal vent field identified in the central Red Sea, have revealed extensive iron-oxide mounds, warm vent fluids (~40°C), and abundant microbial mats. This review synthesizes current knowledge on the microbial diversity and metabolic capabilities of Red Sea hydrothermal vents, integrating recent findings from metagenomics, metabarcode analyses, and comparative genomics with global literature on vent microbiology. Microbial communities in this region are dominated by novel and deeply branching taxa from Chloroflexi, Bathyarchaeia, Pseudomonadota, and Thermoproteota, many of which remain unclassified at the genus level. Iron cycling emerges as the central metabolic axis, with widespread distribution of genes involved in Fe(II) oxidation (cyc2, cyc1, foxEYZ) and Fe(III) reduction (mtrABC, DFE 04xx family, flavin-mediated extracellular electron transfer). Unlike sulfur-rich vents, sulfur metabolism appears fragmented and taxonomically dispersed, reflecting the low sulfur availability in Red Sea vent deposits. Nitrogen cycling involves a decentralized network of nitrifiers, denitrifiers, and DNRA-capable microbes, while carbon fixation is predominantly mediated via the Wood Ljungdahl pathway in both bacterial Chloroflexi and archaeal Bathyarchaeia. Comparative analyses show that Red Sea vents differ markedly from Pacific and Atlantic systems in community composition, metabolic architecture, and geochemical constraints. Collectively, the Red Sea hydrothermal vents represent a unique model for studying metal-driven microbial ecosystems, extremophilic adaptation, and biogeochemical cycling in nutrient-poor, iron-rich marine environments.

#### **Keywords**

Hydrothermal vents, Hatiba Mons, microbial diversity, metagenomics, iron cycling, sulfur metabolism, nitrogen cycling

#### Introduction

Hydrothermal vent systems are among the most dynamic microbial habitats on Earth, hosting communities that contribute substantially to global elemental cycling and primary production in the deep ocean. Since their discovery in the late 1970s, deep-sea vents have been recognized as engines of chemosynthesis, where microorganisms harness reduced chemicals such as H<sub>2</sub>S, Fe(II), CH<sub>4</sub>, and H<sub>2</sub> to fix carbon and sustain complex ecosystems independent of sunlight (Dick, 2019) Microbial processes at these sites regulate fluxes of iron, sulfur, nitrogen, methane, and other elements, influencing ocean chemistry and potentially shaping early Earth analog environments(Altalhi et al., 2025). Most of our understanding of hydrothermal microbiology derives from high-temperature, sulfide-rich systems in the Pacific Atlantic (Mid-Atlantic Ridge), and Indian Oceans(Fisher et al., 2007). In these settings, sulfur-oxidizing Campylobacterota, Gammaproteobacteria, and Zetaproteobacteria dominate metabolism through sulfur and iron transformations. However, the Red Sea represents a fundamentally different hydrothermal regime (Keffer et al., 2021). As one of the youngest ocean basins on Earth, the Red Sea is characterized by persistent high temperatures (21-22°C at depth), elevated salinity (~40%), oligotrophic waters, and the presence of unique brine pools enriched in metals and gases(Altalhi et al., 2025).

# The Red Sea Rift as a Distinctive Geodynamic System

The Red Sea spreading center exhibits slow seafloor spreading, extensive rifting, and geochemical signatures influenced by evaporitic deposits. Hydrothermal fields here are rare compared to other ocean basins, and only recently have active systems been discovered. Unlike classic black smoker environments, Red Sea vent fluids are typically warm (≤40°C), metalrich, and depleted in sulfide, generating iron-oxyhydroxide mounds rather than sulfide chimneys(Augustin et al., 2021).

# Discovery of the Hatiba Mons Hydrothermal Vents

The identification of active hydrothermal fields at Hatiba Mons marked a significant milestone. These fields contain expansive Fe-oxide deposits, Mn-rich layers, microbial mats, and low-temperature venting. Metagenomic analyses revealed extraordinary microbial novelty over 300 MAGs, most representing previously unknown taxa. This microbial novelty, combined with the unusual iron-dominated geochemistry, positions Hatiba Mons as a globally important analog for metal-rich early Earth environments(Van der Zwan et al., 2023).

# **Unique Ecological Constraints in Red Sea Vents**

Red Sea hydrothermal vents function under an unusual combination of physical and geochemical conditions that sharply distinguish them from classical deep-sea vent systems. The region's exceptionally high salinity imposes substantial osmotic pressure on resident microorganisms, selecting for taxa capable of producing specialized osmoprotectants and salttolerant enzymes. In addition, the elevated ambient deep-water temperature (~21°C) far warmer than typical abyssal waters reduces thermal gradients around venting sites and influences reaction kinetics, diffusive fluxes, and microbial thermal tolerances(DiBattista et al., 2016). The ecosystem is also strongly shaped by extreme oligotrophy, which limits the availability of dissolved organic carbon and essential nutrients, forcing microbes to rely on low-energy metabolic pathways. Perhaps the most defining constraint is the combination of low sulfide and high iron, a geochemical signature that suppresses sulfur-based chemolithoautotrophy while strongly favoring iron oxidation and reduction as central energy-yielding processes(Allioux, 2021). These conditions collectively create a metabolic landscape dominated by metal-driven redox reactions rather than the sulfur-driven cycles typical of most hydrothermal vents. As a result, Red Sea vents serve as natural laboratories for understanding

microbial adaptation to multi-stress environments, revealing metabolic flexibility, unique genomic innovations, and ecological strategies that challenge existing paradigms of hydrothermal microbiology(Van der Zwan et al., 2023).

### Scope

This review synthesizes the most recent genomic and ecological findings from the Hatiba Mons hydrothermal field and places them in the broader context of global hydrothermal microbiology. Our objective is to provide an integrated overview of microbial diversity within Red Sea vents and to evaluate how these communities drive key biogeochemical processes under metal-rich, low-temperature conditions. We compare the metabolic and ecological characteristics of Red Sea microorganisms with those from well-studied vent systems worldwide, highlighting both shared features and fundamental differences. In doing so, we aim to identify major evolutionary and geochemical implications of life in such atypical environments. Finally, this review outlines key knowledge gaps and prioritizes future research directions needed to advance our understanding of metal-dominated vent ecosystems(Altalhi et al., 2025).

### Geological and Geochemical Setting of Red Sea Hydrothermal Systems

#### **Tectonic Evolution and Rift Structure**

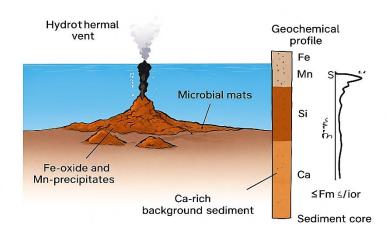
The Red Sea is an active divergent plate boundary where the African and Arabian plates are slowly rifting apart. This region is considered one of Earth's youngest ocean basins and represents an early-stage analog of mature mid-ocean ridge systems. Unlike fast-spreading ridges such as the East Pacific Rise, the Red Sea is characterized by slow spreading, significant continental influence, and geochemical signatures shaped by the interaction between magmatic fluids and thick evaporitic deposits (Bowman, 2019). These features lead to brine pools,

metalliferous sediments, and unique hydrothermal manifestations that differ from classic high-temperature venting systems. The Red Sea's deep waters maintain unusually high temperatures (~21–22°C) and salinity (~40‰), creating a warm, dense water mass that influences hydrothermal fluid mixing and mineralization patterns. Such conditions facilitate the formation of iron-oxyhydroxide mounds, rather than sulfide-rich chimneys typical of other ocean basins(Bosworth, 2015).

### **Low-Temperature Venting and Iron-Oxide Precipitates**

Recent surveys using remotely operated submersibles have identified several active, low-temperature vent fields on the Hatiba Mons dome volcano, where clear hydrothermal fluids with exit temperatures of up to 40 °C are discharged. These areas are marked by extensive accumulations of iron-oxide and manganese-rich precipitates, along with widespread microbial mats coating vent orifices(Augustin, 2023). Hydrothermal sediment sequences reach up to three meters in thickness, indicating long-term deposition. Geochemical profiles reveal high concentrations of Fe, Mn, and Si in the precipitates, accompanied by very low sulfide levels. The increase in iron content with depth in sediment cores reflects prolonged fluid sediment interaction and sustained metal precipitation. In contrast, calcium-rich zones represent background sediment input rather than hydrothermal influence. The scarcity of sulfur is a defining geochemical feature of Red Sea vents, limiting the proliferation of classical sulfur-oxidizing taxa and creating ecological opportunities for novel iron-driven microbial metabolisms(MARCHAN HERNANDEZ, 2023).

#### Low-Temperature Venting and Iron-Oxide Precipitates



**Figure 1.** Schematic representation of low-temperature hydrothermal venting at the Hatiba Mons dome volcano, illustrating clear 40 °C fluid discharge, extensive Fe-oxide and Mn-rich precipitates, and surface microbial mats. The diagram highlights the vertical structure of hydrothermal sediments, including increasing iron concentration with depth, minimal sulfide availability, and calcium-enriched background sediment layers characteristic of Red Sea vent geochemistry(Altalhi et al., 2025).

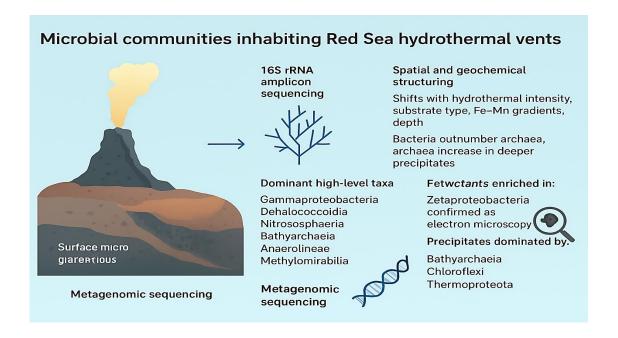
### **Comparison with Global Hydrothermal Systems**

Red Sea hydrothermal systems, when compared with other iron-rich environments such as Loihi Seamount in Hawai'i and the Southern Mariana Trough, share certain traits including abundant iron cycling and the presence of Zetaproteobacteria, yet they also display key distinctions(Cremer, 1994). These differences include markedly lower temperatures, much higher salinity, stronger oligotrophy, the absence of sulfide-driven chimney formation, and the involvement of a broader array of microbial lineages in iron cycling. Together, these characteristics place Red Sea vents in a uniquely defined ecological niche among global hydrothermal ecosystems and offer valuable opportunities to investigate metal-rich, low-energy microbial communities that serve as compelling analogs for early Earth environments(Emerson & Moyer, 2010).

# Microbial communities inhabiting Red Sea hydrothermal vents

exhibit striking spatial and geochemical structuring, as revealed by 16S rRNA amplicon sequencing of both surface mats and subsurface Fe-oxide precipitates. Community omposition shifts markedly with hydrothermal intensity, the nature of the sampled substrate, steep Fe–Mn geochemical gradients, and depth within sediment cores(Van der Zwan et al., 2023). Across all samples, bacteria outnumber archaea in abundance, yet archaeal representation increases substantially in deeper precipitates, reflecting adaptation to low-energy, anoxic niches. Dominant high-level taxa consistently include Gammaproteobacteria, Dehalococcoidia, Nitrososphaeria, Bathyarchaeia, Anaerolineae, and Methylomirabilia, with surface microbial mats additionally enriched in Zetaproteobacteria particularly Mariprofundus confirmed through electron microscopy. However, unlike Loihi Seamount, where Zetaproteobacteria overwhelmingly dominate Fe-oxidizing communities, Hatiba mats host a far more taxonomically diverse consortium of Fe oxidizers and reducers, highlighting a broadened metabolic network(Altalhi et al., 2025). Alpha diversity peaks in upper layers, suggesting higher environmental heterogeneity or fluctuating energy fluxes at the sediment-water boundary. Metagenomic sequencing provides even deeper insight, yielding 314 non-redundant MAGs, comprising 250 bacterial (34 phyla) and 64 archaeal (11 phyla) genomes. Notably, over half of bacterial MAGs and more than 60% of archaeal MAGs lack genus-level assignments, and nearly all remain unclassified at the species level, underscoring the exceptional novelty of the Red Sea microbial biosphere. Dominant MAG lineages span Pseudomonadota, Chloroflexota, Thermoproteota, Acidobacteriota, Methylomirabilota, Desulfobacterota, Hydrothermarchaeota, and Halobacteriota, many of which exhibit close phylogenomic links to microbes from Fe-Mn deposits in the Pacific, Fe-rich chimneys of the Mid-Atlantic Ridge, oligotrophic abyssal sediments from the Mariana Trench and South China Sea, and methaneor petroleum-influenced seeps(Veloso et al., 2023). These evolutionary affinities point to a

microbial community highly adapted to metal-rich, low-energy, and geochemically extreme conditions, positioning Hatiba Mons as an important analog for globally distributed deep-ocean ecosystems and potentially early Earth habitats(Dasgupta et al., 2021).



**Figure 2.** Abstract visualization of the spatially structured microbial communities inhabiting Red Sea hydrothermal vents, highlighting major bacterial and archaeal lineages, iron-driven metabolic pathways, and the contrasting diversity between surface microbial mats and deeper Fe-oxide precipitates.

# **Microbial Mats Versus Precipitates**

Microbial mats in the Red Sea hydrothermal vents constitute the most metabolically dynamic zone, hosting dense populations of Fe-oxidizing microorganisms, microaerophilic chemoautotrophs, and a wide array of extracellular electron transfer (EET) capable taxa that thrive at the sediment—water interface(Zhao et al., 2025). These mats capitalize on steep redox gradients generated by the mixing of oxygenated seawater with Fe-rich hydrothermal fluids, enabling rapid metal oxidation and energy harvesting(Dasgupta et al., 2021). In contrast, the deeper Fe-oxide precipitates support communities that are metabolically slower but ecologically crucial for long-term sediment transformation. Bathyarchaeia, Anaerolineae and

Dehalococcoidia within Chloroflexi, and several Thermoproteota lineages dominate these lower layers, where oxygen is scarce and energy availability is minimal. Their metabolic roles center on anaerobic carbon turnover, the reduction of metal oxides, and the progressive diagenesis of Fe-rich deposits over extended timescales. Together, the stark contrast between the oxygen-tolerant, rapidly cycling metabolisms in surface mats and the deeply anaerobic, low-energy processes in subsurface precipitates highlights a vertically stratified ecosystem tightly governed by redox conditions, hydrothermal fluid flux, and sediment geochemistry(Freches & Fradinho, 2024).

# **Comparison with Other Hydrothermal Microbiomes**

Table1:Red Sea microbial communities differ from those of classical vents:

Feature	Typical Vents (Pacific,	Red Sea Vents
	Atlantic)	
Dominant	Sulfur oxidation	Iron oxidation & reduction
metabolism		
Key taxa	Campylobacterota,	Chloroflexi, Bathyarchaeia, novel
	Gammaproteobacteria	lineages
Temperature	250–400°C fluids	≤40°C fluids
Chimney type	Sulfide-rich	Iron-oxide
Novelty	Moderate	Extremely high (hundreds of novel taxa)

These differences highlight the unique ecological strategies of Red Sea vent microorganisms, shaped by metal-rich and sulfur-poor geochemistry(Alamoudi et al., 2025).

# Iron Cycling as the Dominant Metabolic Driver in Red Sea Vents

Iron cycling forms the dominant metabolic engine of the Hatiba Mons hydrothermal vents, where high concentrations of dissolved Fe(II), extremely low sulfide levels, and lowtemperature fluid discharge create a uniquely metal-driven ecosystem unlike sulfur-dominated vent fields elsewhere. Strong redox gradients arise as Fe(II)-rich hydrothermal fluids mix with oxygenated deep water, favoring microaerophilic Fe(II) oxidation at the sediment-water interface. Here, diverse Fe-oxidizing microorganisms catalyze rapid mineral precipitation, generating the characteristic rust-colored Fe-oxyhydroxide deposits that blanket the vent field. Beneath these surface layers, anaerobic microenvironments support active Fe(III) reduction, establishing a vertically coupled redox loop in which Fe-oxidizers and Fe-reducers continuously regenerate each other's substrates(Altalhi et al., 2025). Metagenomic surveys reveal that hallmark Fe-oxidation genes such as cyc2, cyc1, and foxEYZ are distributed across a broad taxonomic spectrum including Zetaproteobacteria, Gammaproteobacteria, Chloroflexi, Thermoproteota, and multiple candidate phyla, demonstrating that iron oxidation is a community-wide trait rather than a lineage-restricted capability(McAllister et al., 2020). Likewise, Fe-reducing metabolisms are encoded by Bathyarchaeia, Anaerolineae, Dehalococcoidia, and Desulfuromonadales-like organisms, many of which possess multiheme cytochromes, mtr-type complexes, and flavin-based electron transfer pathways adapted for extracellular metal respiration. Archaea contribute significantly through distinct mechanisms, relying on metal reduction, hydrogen oxidation, and potentially acetogenic pathways linked to Fe cycling. The unusually high microbial novelty of Hatiba Mons combined with the lowenergy, metal-rich, and sulfur-poor conditions produces one of the most phylogenetically diverse and metabolically complex Fe-driven ecosystems known. Compared with iron-rich systems such as Loihi Seamount or the Southern Mariana Trough, the Red Sea stands out for its broader taxonomic distribution of Fe metabolisms, lower operating temperatures, stronger archaeal involvement, and far weaker sulfur cycling, positioning it as an unparalleled natural laboratory for understanding metal-based life in extreme environments(Altalhi et al., 2025).

# Sulfur Cycling in Red Sea Hydrothermal Vents

Sulfur cycling in the Hatiba Mons hydrothermal vents is remarkably limited compared with most global vent systems, where sulfur transformations typically dominate primary productivity. Instead, the Red Sea hosts a highly fragmented and taxonomically dispersed sulfur network, a consequence of the exceptionally low sulfide content of both hydrothermal fluids and surrounding sediments. Metagenomic analyses identify key sulfur-related genes including sdo, sat, dsrAB, and scattered sox cluster fragments yet these genes are distributed across diverse lineages such as Gammaproteobacteria, Acidobacteriota, Chloroflexi, Bathyarchaeia, and Thermoproteota rather than concentrated within specialized sulfur oxidizers(Altalhi et al., 2025). Classical sulfur-oxidizing groups typical of high-temperature vents, including Sulfurimonas, Thiomicrospira, Sulfurovum, and the SUP05 clade, are nearly absent, aligning with the scarcity of reduced sulfur substrates in the system(Dede et al., 2022). In their absence, certain Gammaproteobacteria appear to fill the functional gap, using partial sox operons and sdo genes to carry out limited thiosulfate and elemental sulfur oxidation as well as sulfite detoxification(Dahl, 2020). However, these metabolic activities remain secondary to iron cycling, which dominates the energetic landscape of the vent field. Environmental constraints including minimal sulfur availability, predominantly oxidizing conditions, and rapid abiotic removal of sulfide through reaction with abundant Fe(III) minerals collectively restrict the development of classical sulfur-based chemosynthesis. Consequently, sulfur cycling in the Red Sea plays only a supporting role within a broader metal-centric metabolic architecture, distinguishing Hatiba Mons from sulfur-rich hydrothermal ecosystems worldwide(Altalhi et al., 2025).

# Conclusion

Hydrothermal vent ecosystems host highly diverse and metabolically versatile microbial communities shaped by extreme geochemical gradients. Advances in sequencing and metagenomics reveal extensive metabolic novelty, particularly in iron, sulfur, and methane cycling pathways. Despite major progress, large portions of the vent microbiome remain unclassified, underscoring the need for deeper multi-omics exploration. Overall, vent systems represent key natural laboratories for understanding microbial evolution, biogeochemical processes, and life's adaptability in extreme environments.

#### References

- Alamoudi, R., Barozzi, A., Michoud, G., Van Goethem, M. W., Odobel, C., Chen, Y., Marasco, R., & Daffonchio, D. (2025). Metabolic redundancy and specialisation of novel sulfide-oxidizing Sulfurimonas and Sulfurovum along the brine-seawater interface of the Kebrit Deep. *Environmental Microbiome*, 20(1), 19.
- Allioux, M. (2021). *Physiological and multi-omics studies of microbial sulfur metabolisms* present in hydrothermal ecosystems Université de Bretagne occidentale-Brest].
- Altalhi, S., Schultz, J., Jamil, T., Diercks, I., Sharma, S., Follmann, J., Alam, I., Raman, K., Augustin, N., & Van der Zwan, F. M. (2025). Decoding microbial diversity, biogeochemical functions, and interaction potentials in red sea hydrothermal vents. *Environmental Microbiome*, 20(1), 118.
- Augustin, N. (2023). The Effect of Spreading Rate on the Volcanic Activity and Frequency Distribution of Hydrothermal Vent Sites in the Red Sea Rift, RV METEOR cruise M194 HEXPLORES, Jeddah (SA)—Piraeus (GR), 10.09. 2023—07.11. 2023.
- Augustin, N., Van der Zwan, F. M., Devey, C. W., & Brandsdóttir, B. (2021). 13 million years of seafloor spreading throughout the Red Sea Basin. *Nature communications*, 12(1), 2427.
- Bosworth, W. (2015). Geological evolution of the Red Sea: historical background, review, and synthesis. *The Red Sea: The formation, morphology, oceanography and environment of a young ocean basin*, 45-78.
- Bowman, E. E. (2019). *North-south variations in structure, topography, and melting regime along the ultra-slow spreading Red Sea Ridge* Massachusetts Institute of Technology].
- Cremer, M. D. (1994). Geochemistry of Hydrothermal Deposits from the Summit Region of Loihi Seamount, Hawai'i. University of Hawai'i at Manoa.
- Dahl, C. (2020). A biochemical view on the biological sulfur cycle. *Environmental technologies to treat sulfur pollution: principles and engineering*, *2*, 55-96.
- Dasgupta, S., Peng, X., & Ta, K. (2021). Interaction between microbes, minerals, and fluids in deep-sea hydrothermal systems. *Minerals*, 11(12), 1324.
- Dede, B., Hansen, C. T., Neuholz, R., Schnetger, B., Kleint, C., Walker, S., Bach, W., Amann, R., & Meyerdierks, A. (2022). Niche differentiation of sulfur-oxidizing bacteria (SUP05) in submarine hydrothermal plumes. *The ISME Journal*, *16*(6), 1479-1490.
- DiBattista, J. D., Roberts, M. B., Bouwmeester, J., Bowen, B. W., Coker, D. J., Lozano-Cortés, D. F., Howard Choat, J., Gaither, M. R., Hobbs, J. P. A., & Khalil, M. T. (2016). A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. *Journal of Biogeography*, *43*(3), 423-439.
- Dick, G. J. (2019). The microbiomes of deep-sea hydrothermal vents: distributed globally, shaped locally. *Nature Reviews Microbiology*, *17*(5), 271-283.
- Emerson, D., & Moyer, C. L. (2010). Microbiology of seamounts: common patterns observed in community structure. *Oceanography*, *23*(1), 148-163.
- Fisher, C. R., Takai, K., & Le Bris, N. (2007). Hydrothermal vent ecosystems. *Oceanography*, 20(1), 14-23.
- Freches, A., & Fradinho, J. C. (2024). The biotechnological potential of the Chloroflexota phylum. *Applied and Environmental Microbiology*, *90*(6), e01756-01723.
- Keffer, J. L., McAllister, S. M., Garber, A. I., Hallahan, B. J., Sutherland, M. C., Rozovsky, S., & Chan, C. S. (2021). Iron oxidation by a fused cytochrome-porin common to diverse iron-oxidizing bacteria. *MBio*, *12*(4), 10.1128/mbio. 01074-01021.

- MARCHAN HERNANDEZ, S. F. (2023). The potential of the Hydrothermal Vents from the Galapagos Ridge for clean and sustainable energy production.
- McAllister, S. M., Polson, S. W., Butterfield, D. A., Glazer, B. T., Sylvan, J. B., & Chan, C. S. (2020). Validating the Cyc2 neutrophilic iron oxidation pathway using meta-omics of Zetaproteobacteria iron mats at marine hydrothermal vents. *Msystems*, *5*(1), 10.1128/msystems. 00553-00519.
- Van der Zwan, F. M., Augustin, N., Petersen, S., Altalhi, S. M., Schultz, J., Peixoto, R. S., Follmann, J., Anker, A., Benzoni, F., & Garcia Paredes, E. R. (2023). Widespread diffuse venting and large microbial iron-mounds in the Red Sea. *Communications Earth & Environment*, *4*(1), 496.
- Veloso, M., Waldisperg, A., Arros, P., Berríos-Pastén, C., Acosta, J., Colque, H., Varas, M., Allende, M., Orellana, L., & Marcoleta, A. (2023). Diversity, taxonomic novelty, and encoded functions of salar de ascotán microbiota, as revealed by metagenomeassembled genomes. Microorganisms. 2023. In.
- Zhao, N., Ding, H., Zhou, X., Guillemot, T., Zhang, Z., Zhou, N., & Wang, H. (2025).

  Dissimilatory iron-reducing microorganisms: The phylogeny, physiology, applications and outlook. *Critical Reviews in Environmental Science and Technology*, 55(2), 73-98.