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Editorial: Living on the edge: biodiversity, adaptation, and evolution in extreme groundwater habitats

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Editorial on the Research Topic

Living on the edge: biodiversity, adaptation, and evolution in extreme groundwater habitats

Groundwater ecosystems exist below the Earth's surface in diverse environments, including cold polar and circumpolar regions, hot springs, and areas with salt, gypsum, or volcanic rocks. These ecosystems are characterized by extreme environmental conditions that encompass freezing (0°C) and hot (> 45°C) temperatures, hypersaline waters, and elevated levels of toxic gases such as hydrogen sulfide and methane. Despite these inhospitable environmental factors, extreme groundwater ecosystems are vibrant with an "unseen" life consisting of an astonishing array of diverse organisms (e.g., Jacobsen et al., 2012; Galassi et al., 2016; Brad et al., 2021; Culver et al., 2021). Extreme groundwater ecosystems present both challenges and opportunities for studying the intricate interplay between organisms and their environment (Di Lorenzo et al., 2023; Iepure et al., 2023), shedding light on the mechanisms of adaptation and evolution in extreme conditions (Fiser et al., 2012). Within the Research Topic "Living on the Edge: Biodiversity, Adaptation, and Evolution in Extreme Groundwater Habitats", we embarked on a scientific journey into these habitats, striving to unlock the mysteries of these extraordinary ecosystems. This editorial emphasizes the importance of investigating extreme groundwater ecosystems and their relevance in grasping the dynamics of their biodiversity. The Research Topic features a concise report on a newly discovered specialized species in an anchialine cave, alongside four in-depth research articles spanning from microorganisms to microinvertebrates, and a comprehensive review paper on groundwater invertebrate assemblages. Collectively, these contributions enhance our understanding of the boundaries of life, the adaptive mechanisms employed, and the factors that influence biodiversity in extreme groundwater environments and emphasize the importance of interdisciplinary approaches in studying extreme groundwater habitats.

Allenby et al. shed light on the diversity and distribution of methane-oxidizing bacteria (MOB) and methanogens in karst cave ecosystems. The taxonomic analysis unveiled the predominance of MOB, with *Gammaproteobacterial* MOB emerging as the most abundant group. Additionally, the potential for biogenic methane production in caves was

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predominantly related to the archaeal genus Methanosarcina. The authors also generated a database based on protein level assembly of cave metagenomes (doi: 10.5281/zenodo.5987029) that represents a key resource to profile genes of interest. Karwautz et al. enhanced our understanding of microbial communities, food web interactions, and carbon flow in oligotrophic groundwater ecosystems. Their findings indicated that most of the dissolved organic carbon in oligotrophic alpine aquifers remains unaffected by uptake processes, while only a small portion is transformed by prokaryotes. They also demonstrated that microbial food webs of oligotrophic alpine aquifers are likely bottom-up controlled. However, to improve our understanding of energy flows in extreme groundwater ecosystems, it is crucial to conduct cross-disciplinary investigations that focus on unraveling the trophic structures of these ecosystems and their dependence on carbon inputs originating from aboveground sources. Sacco et al. employed stable isotope analysis, radiocarbon fingerprints, and DNA metabarcoding to investigate organic flows and diet preferences of metazoan assemblages in calcrete aquifers located in an arid zone of Australia. The data presented uncovered fascinating insights into the dietary preferences of primary consumers (copepods) and secondary consumers (amphipods). During the dry season, the diet of amphipods heavily depended on root inputs from perennial trees. However, during the wet season, both amphipods and copepods expanded their diets to incorporate organic material from various shallow-rooted shrubs, ephemeral herbs, and grasses. The unique hydrographic conditions in subtidal blue holes (mature karst landscapes formed by the dissolution of carbonate platforms throughout Quaternary sea-level oscillations), provided an excellent opportunity to study the response of benthic foraminiferal communities to extreme environmental conditions, including low pH and dysoxia. Little et al. compared recent benthic foraminiferal distributions in shallow Carbonate Tidal Flats (CTF) and two subtidal blue holes (BH) on Great Abaco Island in the Bahamas. They identified distinct foraminiferal assemblages in the two habitats, however dominated by porcelaneous miliolid taxa like Triloculina and Quinqueloculina. The assemblages in the two BH consisted of small-sized miliolids and other taxa known to tolerate brackish, oxygen-depleted, and organic-rich conditions. These differences may be attributed to short-term population blooms driven by hydroclimate changes or storm activity. Blue holes are deep underwater sinkholes that often connect to underlying cave systems. Belmonte made an exciting discovery of a new copepod species, Stygocyclopia badinoi sp. nov., belonging to the Pseudocyclopiidae family (Copepoda, Calanoida) in the anchialine Zinzulùsa cave in Italy. It represents the first recorded instance of a Pseudocyclopiidae copepod species in the Italian fauna and only the second one reported in the Mediterranean area. Stygocyclopia badinoi sp. nov. possesses distinct characteristics that set it apart from other closely related species. These findings provide evidence supporting the hypothesis of an ancestral distribution of Pseudocyclopiidae along the coastlines of the ancient Tethys Ocean. Finally, Pop et al. delved into the world of groundwater invertebrates by presenting a fascinating synthesis of the invertebrate diversity of extreme groundwater habitats encompassing glacierized landscapes, ice caves, thermal springs, lava tubes and volcanic caves, and sulfidic aquifers. They also expanded on the symbiotic relationships between bacteria and invertebrates, providing valuable insights into how these biological interactions can function as adaptive strategies for various groundwater invertebrates to survive and thrive in challenging environmental conditions.

The contributions in this Research Topic underscored the captivating nature and biological importance of extreme groundwater ecosystems. Nevertheless, these ecosystems confront an uncertain future due to the profound impact of human activities worldwide (Kretschmer et al., 2023). Such activities exert substantial pressure on groundwater habitats, posing a threat to the survival of their highly specialized organisms. It is our projection that, without proactive conservation measures, several of these exceptional species may face the risk of extinction soon. To protect these invaluable ecosystems and their inhabitants, it is imperative to address existing knowledge gaps and embrace innovative research approaches moving forward (Mammola et al., 2022). To this end, we remark the importance of collaboration among researchers from various disciplines, including microbiology, ecology, hydrology, and geology, to gain a comprehensive understanding of extreme groundwater habitats. By doing so, we can work towards safeguarding these unique ecosystems for generations to come.

Author contributions

SI: Conceptualization, Data curation, Writing – original draft, Writing – review & editing. TD: Conceptualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

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