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Special Issue Article

Astrobiology of life on Earth

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Summary

Astrobiology is mistakenly regarded by some as a field confined to studies of life beyond Earth. Here, we consider life on Earth through an astrobiological lens. Whereas classical studies of microbiology historically focused on various anthropocentric sub-fields (such as fermented foods or commensals and pathogens of crop plants, livestock and humans), addressing key biological questions via astrobiological approaches can further our understanding of all life on Earth. We highlight potential implications of this approach through the articles in this *Environmental Microbiology* special issue 'Ecophysiology of Extremophiles'. They report on the microbiology of places/processes including low-temperature environments and chemically diverse saline- and hypersaline habitats; aspects of sulphur metabolism in hypersaline lakes, dysoxic marine waters, and thermal acidic springs; biology of extremophile viruses; the survival of terrestrial extremophiles on the surface of Mars; biological soils crusts and rock-associated microbes of deserts; subsurface and deep biosphere, including a salticle formed within Triassic halite; and interactions of microbes with igneous and sedimentary rocks. These studies, some of which we highlight here, contribute to our understanding of the spatiotemporal reach of Earth's functional biosphere, and the tenacity of terrestrial life. Their findings will help set the stage for future work focused on the constraints for life, and how organisms adapt and evolve to circumvent these constraints.

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The astrobiology of Earth

The field of astrobiology includes the search for life beyond Earth. However, no traces of extraterrestrial life have yet been found despite missions dedicated to its detection on Mars, starting with the 1976 Viking landers (Soffen and Snyder, 1976) and extending to the currently active Curiosity and Perseverance rovers (Gómez-Elvira *et al.*, 2014; Voosen, 2021). In addition, there have been searches for evidence of life elsewhere in the Solar System and in relation to exoplanets but as yet have no evidence of life in these locations either. We might therefore forgive sceptics who consider astrobiology somewhat esoteric, or even an oxymoron. Here, we take the view that, in addition to the value of the astrobiology field in relation to considerations of life in extraterrestrial locations, astrobiological approaches augment traditional biological studies even when used with the sole purpose of understanding life on Earth. This *Environmental Microbiology* special issue 'Ecophysiology of Extremophiles' explores the value of astrobiology as a lens through which to understand present-day terrestrial life. Indeed, astrobiology gives rise to novel scientific questions, technologies and experimental approaches; unexplored theoretical frameworks; and other insights into life on Earth that we otherwise would not have (Prasad *et al.*, 2021).

With the exception of many remarkable extremophiles (some of which are showcased in this special issue), historically the science of microbiology has revolved around cultivatable microbes that are unremarkable in their stress biology, grow well at high nutrient concentrations and/or are not lithosphere-dwelling taxa. These include human commensals and pathogens, such as *Escherichia coli* and *Salmonella* species; microbes used as model systems for studies of biochemistry (e.g. *Saccharomyces cerevisiae*); microbial pathogens of crop plants or livestock; and microbes in fermented foods, such as lactic acid bacteria. Such microorganisms are, in general, of the greatest concern to the daily lives of humans.

However, to address some of the most-profound questions in biology, we often need to take on a mindset that is rooted outside Earth's biosphere (as if we are looking in); a mindset that is interdisciplinary - rather than employing an approach that is anthropocentric and/or more narrow. Here, we argue that this mindset is, in essence, provided by and is best described as astrobiology.

Some of the (long-standing) biological questions yet to be properly resolved are:

- i. what is life (Schrödinger, 1944; Cleland, 2019);
- ii. what permits and what constrains active life;
- iii. where is life on Earth and when is it active/inactive;

- iv. how do microbes determine planetary health and how does planetary health impact the biosphere (Cavicchioli, *et al.*, 2019);
- v. how long can cells and communities persist through geological time;
- vi. how and where did life originate;
- vii. could life plausibly occur beyond Earth; and
- viii. do the laws of chemistry and physics dictate the same basic biochemistry for life everywhere it is found in the universe, or even beyond?

These are lines of enquiry that generally cannot be addressed via laboratory-based experiments using canonic microbes that are copiotrophic, mesophilic, aerobic and heterotrophic. Instead, we need to look at the spatiotemporal fringes of Earth's biosphere represented by the biology of microorganisms that are atypical and extreme in their nutrition (e.g. chemolithotrophs) and/or their stress biology, such as halophiles, psychrophiles and polyextremophiles. Even higher-ranked taxa that are widely known as mesophiles (for temperature and water activity) can have extremophilic members; for example, the extremely halophilic genus *Wallemia* within the fungal division Basidiomycotina (Zalar *et al.*, 2005; Stevenson *et al.*, 2015). These extremophilic microbes colonize habitats that are too hostile for the vast majority of life and are among those organisms at an interface where active biology must wrestle with the thermodynamic constraints on cellular biochemistry and structures.

'Ecophysiology of Extremophiles' special issue

This special issue includes studies on diverse types of extremophile systems and extreme environments. Life on Earth (and, presumably, putative life beyond our planet) is usually exposed to multiple, concomitant stresses (or stressful events) such as those in polyextreme environments (Johnson *et al.*, 2015; Hallsworth, 2019). Martínez *et al.* (2021) carried out a study of low water-activity and osmotically stressful chaotropic brines located at high altitude in the Salar de Uyuni salt pan (Andes Mountains). At the surface, microbes are also exposed to high ultraviolet radiation (primarily UV-A) and considerable fluctuations in temperature and relative humidity. At the surface and in the subsurface, *Archaea* and *Bacteria* occur in brines or thin, briny films that consist of dissolved NaCl and the chaotropic salts MgCl₂, LiCl and NaBr (and lower concentrations of other substances). Environmental samples from the surface and subsurface (to a depth of 80 m) were used to characterize spatial and temporal variations in microbial communities. Intriguingly, the water activity of the Salar-de-Uyuni system (0.856–0.618; Martínez *et al.*, 2021) straddles the

currently recognized limit for cellular activity of halophilic prokaryotes (0.635; Stevenson *et al.*, 2015). Consistent with this finding, Martínez *et al.* (2021) identified taxa that are known to be capable of proliferating at water activities lower than that of saturated NaCl (which is about 0.755). The Martínez *et al.* study provides the first insights into the microbiology of an underground chaotropic habitat and reveals marked differences between surface and subsurface communities.

Durán-Viseras *et al.* (2021) used a culturomics-based approach (Bilen *et al.*, 2018) to isolate novel microbial taxa from hypersaline environments; two solar salterns in southwest Spain. They identified four halophile strains belonging to a thus-far undiscovered haloarchaeal genus that they named *Halosegnis*. The analyses of Durán-Viseras *et al.* (2021) revealed these to be heterotrophic aerobes containing halorhodopsin and that they represent two new species, for which they proposed the names *Halosegnis longus* sp. nov. and *Halosegnis rubeus* sp. nov. By searching previously published metagenomic datasets obtained from saline and hypersaline lakes, salterns and deep-sea brines (in North America, Europe and Asia), the authors found evidence of the genus *Halosegnis* in geographical locations worldwide. In habitats with intermediate salinities (from 18% to 27%, wt./vol.), these *Archaea* reached the highest abundance, up to 8% of the prokaryotic communities. Metagenomics and other culture-independent techniques used in studies of environmental microbiology have revealed a vast gap between the number of microorganisms we are able to cultivate and the numbers of taxa actually present *in situ*; the latter are orders of magnitude greater than the former (Whitman *et al.*, 1998; Lloyd *et al.*, 2018). However, culture-independent techniques can also be prone to errors, including those caused by contamination; incomplete gene databases or faulty data inputs within such databases; lack of insight into metabolic activity, phenotype, or physiological and phenotypic plasticity/capability; and ecological interactions. Durán-Viseras *et al.* (2021) used diverse culture conditions (either rich organic or oligotrophic medium) and new protocols to combine metagenomics with culturing techniques, demonstrating that culture-based approaches are crucial for understanding the evolutionary, metabolic and ecological importance of individual species. We anticipate that similar studies will become increasingly important in the near future, for various microbial systems.

In a comprehensive review of athalassohaline deep-sea hypersaline anoxic brines, Fisher *et al.* (2021) point out that the art of extrapolating chaotropicity values can be imprecise. We agree with this finding and believe that this is because, beyond specific concentrations of highly chaotropic salts, the chaotropicity limit has been

surpassed in terms of both biological tolerance of the cell and biophysical tolerance of some biomacromolecules. Therefore, additional amounts of salt do not add to the chaotropic activity, and any values derived by extrapolating beyond this point are only hypothetical, as described by Hallsworth *et al.* (2007) and Yakimov *et al.* (2015). Therefore, the apparent limitation of the chaotropicity-quantification technique (Cray *et al.*, 2013) at high molar concentrations of MgCl₂ is in reality a biologically pertinent indication that there is no further chaotropic activity. The authors of Fisher *et al.* (2021) were also involved in a study by Klempay *et al.* (2021), which analysed *Archaea* and *Bacteria* and water chemistry, in salterns hosting a range of evaporated seawater from San Diego Bay (southern California, USA). The Klempay *et al.* study has implications for interactions of chaotropicity and water activity in relation to biophysical constraints on cellular activity, an issue pertinent to diverse microbial systems (Hallsworth *et al.*, 2007; Alves *et al.*, 2015; Cray *et al.*, 2015). Klempay *et al.* (2021) also used geochemical modelling to speculate that even brines saturated with respect to epsomite (MgSO₄) and carnallite (KMgCl₃·6H₂O) can potentially be inhabited by active halophiles; that is, at less than ~0.600 water activity which is a value consistent with empirical data for cell division of halophilic/xerophilic *Aspergillus penicillioides* at high glycerol concentration (Stevenson *et al.*, 2017). The work of Klempay *et al.* makes a strong case that the search for life on Mars should focus on past saline environments.

Although any putative life in our Solar System beyond Earth is likely to be anaerobic (as was early life on Earth), we cannot know whether terrestrial-type life on exoplanets - or, in a multiverse scenario, beyond our universe (Adams and Grohs, 2017) - would necessarily be anaerobic. This would depend on the longer-term conditions of habitability on extraterrestrial rocky planets (Westall *et al.*, 2015; Gebauer *et al.*, 2018). That said, terrestrial anaerobes are highly pertinent to astrobiology research (Westall *et al.*, 2015; Beblo-Vranesevic *et al.*, 2020). In the current special issue, Sorokin *et al.* (2021) conceptually defined an independent and self-sufficient hypersaline anoxic ecosystem based solely on sulphur-respiring haloarchaea. The authors isolated neutrophilic haloarchaea from hypersaline salt lakes, and a natronoarchaeon from soda lakes, of Russia. These halophiles represent analogues of 'primary' anaerobes, a functional subgroup of sulphur-respiring haloarchaea that was thus-far unknown in culture. The neutrophilic haloarchaea are carbohydrate-fermenting, and produce H₂ in the absence of electron acceptors but switch to respiration in the presence of sulphur, thiosulphate, or dimethylsulphoxide (DMSO). The non-fermentative, saccharolytic natronoarchaeon is able to grow anaerobically

only in the presence of sulphur compounds as electron acceptors. The discovery of the metabolic capabilities of these microorganisms demonstrates that a self-sufficient community consisting of three subgroups of sulphur-respiring haloarchaea could completely mineralize organic carbon in anoxic sediments, starting from carbohydrates.

A minireview by van Vliet *et al.* (2021) explores microbe-mediated sulphur cycling in dysoxic marine waters where oxygen levels fall below the usual limits of detection ($<1 \mu\text{M}$). Over the past 60 years, dysoxic marine waters - a hotspot for anoxic metabolic cycling - increased more than fourfold (by volume) due to global warming. A network of phylogenetically and ecophysiologicaly diverse microorganisms mediates redox reactions between sulphate (SO_4^{2-}) and hydrogen sulphide (HS^-), including their sulphur-bearing intermediates. The biochemical sulphur cycle is an important component of the global biogeochemical cycling of Earth's oceans. Knowledge of sulphur cycling is also pertinent to models designed to evaluate the biological potential of aquatic environments beyond Earth. One example is ancient lakes on Mars, whose remnant sediments are currently being explored by NASA's Curiosity and Perseverance rovers (sulphur-bearing minerals and organics have already been discovered by Curiosity, providing tantalizing hints of a possible sulphur cycle on ancient Mars). Other, more distant examples are the dark oceans that lie beneath some icy moons in the outer Solar System, such as Saturn's moon Enceladus, where sulphur-bearing compounds are known to be present. The complex web of sulphur-cycling reactions in Earth's oceans, which has been carefully disentangled by van Vliet *et al.* (2021), appears to depend ultimately on a supply of oxidized compounds. Although oxidative power is thought to be a limiting commodity in the subsurface oceans of icy moons, new discoveries are already revealing new or unexpected sources of oxidative power, such as the potential oxidation and reduction of pyrite, a mineral often associated with hydrothermal chimneys thought to exist on the seafloor of Europa (Altair *et al.*, 2018). In addition, recent geochemical models point to new or unexpected sources of oxidants in the ocean of Enceladus (Ray *et al.*, 2021), thereby propelling Earth-based models of biochemical sulphur-cycling to the forefront of 'extraterrestrial' astrobiology research.

Recent studies of the Earth's deep biosphere have revealed biodiverse communities in both deep-ocean sediments and the Earth's crust (e.g. Lloyd *et al.*, 2018; Daly *et al.*, 2019 and, in the current issue, Karnachuk *et al.*, 2021; Orcutt *et al.*, 2021). Indeed, some of the most-remote environments on Earth host microbial communities fed by carbon and nutrients present in the

fluids that move through fractures in crustal rocks. The deep biosphere is actively involved in global nutrient cycles, pollutant degradation, and the formation and weathering of rocks. Orcutt *et al.* (2021) report a study carried within the oxic oceanic crust on a flank of the Mid-Atlantic Ridge. Minerals were inserted into boreholes and microbial colonization was assessed over time. These minerals were 'igneous silicates (basalts, fayalite, olivine), metal sulphides (pyrite, pyrrhotite, sphalerite, chalcopyrite), metal oxides (haematite, goethite), metal carbonate (siderite) and less-reactive surfaces including glass beads, glass wool and plastic' (Orcutt *et al.*, 2021). Remarkably, microbial growth (determined by factors such as water/rock ratios, fluid temperature and oxygenicity) did not correlate with mineral type. One of the most-abundant microbial taxa present was the bacterial family *Rhodobacteraceae* (Orcutt *et al.*, 2021). During the study period (several years), biodiversity of biofilm-forming microbes that colonized the mineral surfaces increased. One of the taxa that became more abundant was *Thiopfundum*, which the authors speculate could be used as an indicator of the stage of colonization. The presence of all these microbes is evidence that there has been an intimate interrelationship between microbes and volcanic substrates that dates back to the earliest terrestrial life forms more than 3.5 billion years ago (Westall *et al.*, 2015). It is biofilm-forming microbes (i.e. *Archaea* and *Bacteria* similar to those in the Orcutt *et al.* study) that dominated the rocky habitats of the young Earth prior to the appearance of photosynthesis, especially oxygenic photosynthesis. The longevity of the oligotrophic, low-biomass habitat provided by the crust, along with the tenacity of microbial systems, has permitted the persistence of life over several billions of years.

A different kind of subsurface habitat was studied by Cirigliano *et al.* (2021); Iron-Age tombs hewn out of a calcarenite and a sandstone rock. The study focused on the microbiology of moonmilk (a layer of precipitated CaCO_3 in the form of nanofibers) on the walls of these 'anthropogenic caves' that are located in central Italy at depths of 1–10 m below ground level. They are home to an ecophysiologicaly and phylogenetically diverse microbiome that the authors described as 'primarily bacteria mesophilic for temperature and xerotolerance (including Actinobacteria, Bacteroidetes and Proteobacteria);...photosynthetic Cyanobacteria exhibiting heterotrophic nutrition (*Calothrix* and *Chroococcidiopsis*);...[and taxa known to be] psychrotolerant (*Polaromonas*), acidotolerant or acidophilic (members of the *Acidobacteria*), or resist to ionizing radiation (*Brevundimonas* and *Truepera*)' (Cirigliano *et al.*, 2021). The authors determined the kinetics of moonmilk

formation (occurring over one to several decades) and discussed the paradox that this underground ecosystem, that lacks primary production, is apparently highly active.

Other special issue articles also focus on interactions of microbes with minerals and igneous or sedimentary rocks (Kang *et al.*, 2021; Wu *et al.*, 2021). There is interest in biomineralization of rare earth elements beyond Earth (McLeod and Krekeler, 2017), and bacteria have been proposed previously for this purpose (Cockell *et al.*, 2020). In the current special issue, Kang *et al.* (2021) now examine the influence of *Aspergillus niger* on the weathering of monazite, a phosphate-mineral source of rare earth elements such as Ce, La and Nd. Culture-based studies that involved addition of monazite to the growth medium were used to unravel the biophysical/biogeochemical process of rock degradation by this ascomycete, including the production of organic acids such as citric acid and oxalic acid. Kang *et al.* (2021) provides fundamental knowledge on the microbial processing and potential utilization of these important elements on Earth and potentially on other planetary bodies in the future.

A number of the special issue articles focus on life at low temperatures in the Arctic or Antarctic (Coleine *et al.* 2021; Mudge *et al.*, 2021; Pavankumar *et al.*, 2021; Magnuson *et al.*, 2021). These habitats are typically poly-extreme due to combinations of extreme cold, low water-activity, long-term desiccation and freezing, salt(s), ultra-violet radiation, low-nutrient conditions, and/or events that can be traumatic for the cell such as desiccation–rehydration (in some cases, caused by salt deliquescence–efflorescence) and freeze–thaw cycles (Hallsworth, 2018). To date, studies of cryptoendolithic communities of the Antarctic were concentrated on the McMurdo Dry Valleys and the Transantarctic Mountains of Victoria Land. Coleine *et al.* (2021) report on cryptoendolithic microbes in sedimentary rock (sandstone) in a newly explored area (Helliwell Hills, North Victoria Land). The authors conducted a comparative study of biodiversity data from these rocks and data from previous studies of sandstones located at more than 30 other sites in Victoria Land. This revealed that both alpha- and beta-diversity were strongly correlated to geography and that the most-remote region of Helliwell Hills hosts an uncommon type of microbial community including *Archaea* and lichen such as *Lecidella grenii* (Coleine *et al.*, 2021). Such investigations, on pristine Antarctic environments, can provide insights into the ecology and evolution of early life on Earth and can inform investigations into the habitability of extraterrestrial environments (Cockell *et al.*, 2016). Sandstones and other rocky substrates on early Mars may have supported putative Martian life (Wierzchos *et al.*, 2012), since cryptoendolithic life forms

would have found refuge within the rock's gas spaces during the cooling and drying of the planet.

Pavankumar *et al.* (2021) analyse the molecular biology of the cold-active bacterium *Pseudomonas syringae* that is a model for unravelling the effects of low temperature on the molecular infrastructure of cells and uses the full suite of biochemical and genetic tools now available. Their review focuses on the effects of cold on membrane-mediated and enzymatic activities, in particular enzymes that catalyse replication and transcriptional events. One insightful concept, considered for the first time, is how changes in the density of water that occur around 4°C appear to impact the biology of the cell. Not only membranes but also cytoplasmic viscosity, protein structure and enzymatic catalysis can be affected by density changes in the biophilic solvent, water. Given that temperature is one of the most significant environmental controls on microbial growth, this review brings the reader up to speed on cold-related molecular barriers to life and known mechanisms for overcoming them.

Several *Bacteria* are capable of subzero growth, and microbial communities may exist in some of Earth's coldest environments, such as the interior of Antarctica (Madigan *et al.* 2017; Hayward *et al.* 2021). This indicates that extreme cold is not an insurmountable barrier for terrestrial (and presumably extraterrestrial) life. The special issue article by Mudge *et al.* (2021) probes physiological features of *Colwellia psychrerythraea*, a polyextremophilic bacterium isolated from subzero marine sediments that can grow at a salinity up to 18% (wt./vol.) and at temperatures as low as −12°C. As such, and because its genome and many unusual biochemical features are already known, *C. psychrerythraea* has risen to become a model marine psychrophile for the study of carbon cycling in cold marine sediments, and a relevant subject for assessing growth and survivability under simulated Martian conditions. Using radiotracer methods, previous studies of this bacterium revealed protein synthesis in unamended cell suspensions at −20°C and in those supplemented with additional extracellular polymeric substances at −80°C. Mudge *et al.* (2021) now utilize proteomic tools to reveal metabolic pathway-specific proteins produced by *C. psychrerythraea* in response to variations in temperature, salinity and nutrient status. In addition, useful new tools emerge from their research including a novel approach for life detection that identifies over 500 very short peptides whose sequences could be determined by either lander-based or in-orbit mass spectrometers and used as potential biosignatures of cold- or hypersaline metabolisms.

Also on the topic of life at subzero temperatures, Magnuson *et al.* (2021) present a comprehensive, multi-phase study of a microbial community thriving in a

perennial system of (hypersaline, low-temperature) springs located in the Canadian High Arctic. This unusual ecosystem is underlain by permafrost, with water temperatures consistently close to zero, and is anoxic, oligotrophic and rich in reduced sulphur compounds. These waters are dominated by a sulphide-oxidizing chemolithoautotrophic bacterium of the genus *Thiomicrothabodus* which is present within streamers (made up of microbial biomass), while Actinobacteria, Bacteroidetes and Cyanobacteria make up the rest of the community. Multiphase-omic tools, supported by an isotopic approach, have deciphered the contribution of this (apparently new) species of *Thiomicrothabodus* to sulphur cycling and primary production. It is very likely that this CO₂-fixing organism is responsible for the functioning of the entire streamer ecosystem. The microbial community and biogeochemistry of the Magnuson *et al.* springs are qualitatively different from those of spring systems located in other cold regions (Roy *et al.*, 2020; Knuth and Potter-McIntyre, 2021). The light-independent chemolithoautotrophic microbial community flourishing in the High Arctic (Magnuson *et al.*, 2021) has implications for the possibility of life existing in cold places beyond Earth.

Also relating to a cold location, a research paper by Hallsworth (2021) examines whether the surface/near-surface of Mars is biocidal to all life. He gives an overview of the suite of Mars surface conditions that are often considered incompatible with the survival of terrestrial extremophiles. This article coaxes the reader to consider a putative (Mars-based) terrestrial microbe from a Mars-centric point of view. The Earth, that appears in general to be hospitable for humans, is highly oxidative so may be a challenging place for putative microbial life that has evolved elsewhere. Oxygen is extremely toxic to strict anaerobic microbes and requires special adaptations to evolve over a long timescale to be tolerated, detoxified and utilized (indeed, life could never have emerged in an oxidized environment). A major environmental change on Earth was caused by the evolution of oxygenic photosynthesis in Cyanobacteria about 3 billion years ago (Blankenship and Hartman, 1998). Anaerobic life forms that were unable to evolve mechanisms to deal with slowly rising oxygen levels likely either died off or retreated to the anoxic niches where they remain today. For other microbes, an oxygenated planet provided an opportunity for life to diversify through the evolution of powerful energy-conservation mechanisms based on aerobic respiration. The analysis elaborated by Hallsworth (2021) indicates that Mars' surface may not be lethal to all kinds of terrestrial microbes; this emphasises the necessity of planetary protection measures during exploration missions.

An environment that is widely used as an analogue for the Mars' surface is the Atacama region in Chile (Aerts *et al.*, 2020; Nagy *et al.*, 2020). In the current special issue, Uritskiy *et al.* (2021) give a comprehensive overview of an extremophile community on halite nodules at the surface of the Atacama Desert. The NaCl-saturated brine films here are exposed to intense ultraviolet radiation and prone to cycles of salt efflorescence–deliquescence (Hallsworth, 2020). Combining metagenomic and metatranscriptomic analyses (in both light and dark conditions), Uritskiy *et al.* (2021) identify microbes responsible for the essential metabolic functions. One important finding was that the only eukaryote of the community, a novel *Dolichomastix* alga, is the major contributor of photosynthetic transcripts. An additional key finding was that new halophile viruses exhibit transcriptional activity, indicating an active role in infecting their hosts in the halite-associated brines of this dry desert region (mainly Halobacteria and *Salinibacter*). Another study that raises intriguing questions about Mars is that of Thompson *et al.* (2021), which focuses on the microbiology of a subsurface NaCl stalactite within a Triassic halite deposit. The study reveals the microbiome of this structure, located in Northern Ireland (North West Europe). It also reveals ecophysiological functions of the resident microbes, and describes the habitat as one of stable in temperature (17°C) and water activity (0.755), and consistent water supply. The authors convincingly argue that saline speleothems (structures formed of precipitated salt) located in the Mars subsurface could potentially host ancient Martian life at depths where temperatures permit.

A special issue study of a different kind of extreme (aqueous) environment used comparative genomics to study *Archaea* of the order *Sulfolobales* and identified characteristics that enable life, in thermal acid springs (Counts *et al.*, 2021). Evidence is presented by the authors that, collectively, these microbes have diverse oxygen-consuming protein complexes; are able to detoxify sulphur and utilize it lithotrophically (for energy generation); and are capable of pH homeostasis under highly acidic conditions. Their metabolic versatility in these ways is consistent with their thermo- and acidophilic phenotype and their ability to colonize geothermal habitats that can be abundant in H₂S and S⁰. Given the recent interest in the question of habitability in the sulphuric acid clouds of Venus, the acid-, temperature- and xerotolerance of terrestrial polyextremophiles has become a resurgent topic (Greaves *et al.*, 2021; Hallsworth *et al.*, 2021).

Two papers in this special issue describe the structure of genomes in taxonomic orders within the Euryarchaeota and reflect on how genome structure may

contribute to the success of archaeal lineages. Zhong *et al.* (2021) retrieved whole-genome sequences for 30 species within the order Thermococcales from the public sequence databases. A core group of functional genes were found to be present in all 30 species, as well as 'accessory' and 'unique' genes present in only some member species of the order that serve diverse functions relating to habitat and lifestyle, among them extremotolerance. Zhong *et al.* suggest that common adaptation mechanisms within the Thermococcales hint at survival strategies for extreme conditions likely to have been present on the early Earth and possibly also present in extraterrestrial environments.

Hu *et al.* (2021) performed whole-genome environmental sequencing on samples retrieved from a black-odorous river in China, a habitat containing pollutants that can cause cellular stress/toxicity by various mechanisms (e.g. Bhaganna *et al.*, 2010). Sequencing was carried out after disaggregating the samples into slurry and allowing the sedimentary structure to re-form in the laboratory. This approach represents a successful compromise between sequencing environmental samples immediately after collection, when organisms of interest may be rare, and the laboratory culture in which an ecological community is disaggregated into the component members and only those able to grow in isolation are studied. From the environmental sequences obtained, Hu *et al.* assembled nearly complete genomes for four new species within the taxonomic class Thermoplasmatales, members of which are known for acid tolerance. They identified a further five partial genomes assembled from environmental sequences available in public sequence databases and propose that these genomes are sufficiently divergent to represent a new candidate order, *Candidatus* Gimiplasmatales. Within these genomes, Hu *et al.* identify consistent groups of genes that could be capable of metabolizing complex organic compounds as well as *de-novo* synthesis of nucleic acids and mevalonate.

Zhong *et al.* (2021) report the expansion of accessory genes in the genomes of Thermococcales, and Hu *et al.* (2021) provide evidence that one mechanism for such expansion is lateral gene transfer. The genomes of *Candidatus* Gimiplasmatales include genes for arsenic detoxification and cell motility. A set of genes involved in the Wood–Ljungdahl carbon-fixation pathway appears to have been obtained from the Firmicutes. This evidence for gene transfer between *Archaea* and *Bacteria*, two different domains of Earth life, raises important questions around planetary protection and appropriate precautions to take when studying extraterrestrial life should we find it. For instance, could Earth organisms take up DNA from extraterrestrial organisms (assuming that the latter also use DNA as genetic material) and gain novel, potentially hazardous functions. Alternatively, could extraterrestrial organisms that use DNA take up genes from Earth

organisms, and thereby gain functions that improve their survival or invasiveness on Earth?

Concluding remarks

Both the current article and the other articles in this special issue focus mainly on studying life on Earth but, importantly, include approaches from astrobiology. In some cases, they also discuss issues pertaining to life beyond Earth. Although astrobiology has always included studies of terrestrial life (whether past, present or future), the latter have not always included the former. Indeed, the etymology of the term *astro-* (star or celestial) *-biology* (the story/study of life) is somewhat misleading. Nevertheless, we believe that astrobiology utilizes its own set of approaches and that studying Earth's biology from an astrobiology-inspired perspective can give rise to novel scientific questions and scientific findings. For example, the Coleine *et al.* (2021) paper focused on sandstone in Antarctica a Mars analogue site to reveal aspects of the terrestrial endolithic ecosystem. Another study, of biophysical limits for biotic activity of terrestrial extremophiles that focused on the question of habitability of Venus' atmosphere, discovered that the ecophysiological constraints of the ultimate acidophile are apparently determined by xerotolerance (Hallsworth *et al.*, 2021).

Modern science has become more specialist (and more reductionist) as scientific fields fragment into distinct sub-fields. This trend does not favour syncretistic approaches that integrate disparate lines of evidence (Ehrenzweig, 1970)); approaches that might help to address key questions in biology. We believe that the interdisciplinary and cross-cutting field of astrobiology can enhance our understanding of terrestrial life by acting counter to an excessively narrow focus. In addition, new and miniaturized technologies have been created by the field of astrobiology, and these can have important applications for studying life on Earth. These include miniaturised bioreactors, sequencers, spectrophotometers (Castro-Wallace *et al.*, 2017; Massaro Tieze *et al.*, 2021); sterilisation methodologies (Craven *et al.*, 2021); a water-activity sensor (Desai *et al.*, 2021); and protocols for life detection (Kminek *et al.*, 2014; Abrahamsson *et al.*, 2021). The articles presented in this special issue also contribute to our understanding of the nature and tenacity of life on Earth. They also help set the stage for future exploration of the various constraints on terrestrial life and how organisms strive to circumvent these constraints.

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