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REVIEW ARTICLE

Life on the Edge: Bioprospecting Extremophiles for Astrobiology

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Abstract | Discovering exoplanets and satellites in habitable zones within and beyond our solar system has sparked intrigue in planetary setting varieties that could support life. Based on our understanding of life on Earth, we can shed light on the origin, evolution, and future of Earth-like organisms in the galaxy and predict extinct or extant extraterrestrial life. Hence, extremophiles thriving in mimic outer space environments are particularly interesting as they exhibit traits that preponderate our comprehension regarding the possibility of life elsewhere and in situ life detection. Additionally, many extremophiles have been used for astrobiological research model organisms to unveil native alien life or possible life-produced metabolites outside Earth. Laboratory-based simulation chambers mimic this outer space condition, helping researchers study life beyond Earth in near identical conditions and understand molecular mechanisms for survival. This review summarizes relevant studies with isolated microorganisms from extreme analog Earth environments, harnessing them as promising astrobiological model candidates for pursuing life potentialities in other planetary bodies. We also highlight the necessity of environmental simulation chamber approaches for mimicking extraterrestrial habitats.

Keywords: *Extremophilic microorganisms, Analog environments, Astrobiological model, Space simulation chamber, Space exploration*

1 Introduction

Can life originate, evolve, or survive in extraterrestrial environments? Such fundamental questions motivate scientists to search for life beyond Earth. Astrobiology is a relatively new branch of space-related science merging astronomy and biology.[1] Searching for habitable environments is quintessential when investigating extraterrestrial life. Nowadays, nearly 200 planets and satellites in the solar system and more than 5000 exoplanets orbiting stars in the universe have been discovered, inspiring an exploration mission concerning planetary environment diversity that may host life. However, Earth remains the only known living planetary body that can guide us to these answers.[2,3]

Based on what we know, several planetary bodies exhibit extinct or extant life potential. Prokaryotic life dominates our planet's evolutionary history, evolving to occupy every possible environmental habitat, including various extreme environments. Common Earth life forms have traditionally taught us about terrestrial boundaries and abilities. We now appreciate living organisms' physiological and biochemical capabilities as it illuminates an extensive origin, evolution, and future for Earth-like beings in our solar system and beyond, primarily due to an ever-increasing awareness of extremophile varieties over the past 50 years.[4–6]

Extremophiles can survive in a myriad of planetary environments and present relevant characteristics advancing our understanding of potential life elsewhere and in situ life detection. Thus, extremophilic microbes, especially those thriving under multiple extremes (polyextremophiles), represent a

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vital research avenue for astrobiological and space exploration.[7] Furthermore, many extremophiles are ideal astrobiology models, aiding in finding indigenous extraterrestrial life or potential life-produced metabolites outside Earth.[8,9]

Although space missions offer essential and distinctive planetary exploration knowledge, they are expensive and time-consuming. Therefore, to overcome *in situ* planetary exploration's economic and technical limitations, laboratory simulations play a crucial role in achieving outer space conditions on Earth, establishing a critical link between the laboratory and life beyond Earth. Prominent factors for designing planetary simulation chambers include atmospheric composition, gas pressure, temperature, humidity, and UV radiation levels. Substantial model and instrumental design improvements of these simulation chambers over time enabled various simulated experiments related to Mars,[10–15] the Moon,[16] and asteroid/cometary/solar system small bodies,[17] aiding mineral analysis,[18] astrobiology,[19,20] instrument calibration/materials testing,[21] and planetary exploration studies.[22,23]

Herein, we review extremophilic microorganisms' relevance and application in astrobiology and space-related studies, discussing their potential as astrobiological models. Additionally, we cover environmental simulation chamber development and use for simulating extraterrestrial habitats. Finally, we detail prospects concerning this emerging field and priorities for the upcoming decades.

2 Life Beyond Earth: Extremophiles as Models for Astrobiology

Astrobiology's primary goal is to search for life on planetary bodies beyond Earth. Mars, Venus, and the icy moons Europa, Enceladus, and Titan offer numerous opportunities for investigating life's chemical evolution and origin. In addition, their similar biochemistry features to those that support life on Earth make them targets for extensive research.[24] To ascertain extraterrestrial life, we must first define boundary conditions where life can thrive. Outer space presents severely harsh and inhabitable environmental conditions deleterious for life growth, including high radiation doses, extreme temperatures, different gravity, pressure, pH, salinity, energy source, and nutrient scarcity.[25] Nevertheless, as microbial life can flourish within broad physicochemical spectrums and extremely inhospitable habitats on Earth, they may be capable of surviving space's harsh conditions.[4] Thus, understanding living extremophiles' molecular mechanisms and unique physiological characteristics is paramount for defining Earth's boundary life limits and identifying conditions likely to originate or support life on other planetary bodies.[4,26]

2.1 (Poly)Extremophilic Microorganisms in the Planetary Context

Environmental parameters, such as extreme temperature, pH, salinity, water availability, pressure, radiation, and nutrients, can limit microbial life. Extremophiles are microorganisms that flourish in these intense conditions, whereas polyextremophiles optimally grow under multiple extreme stresses in the habitat simultaneously.[27] Most extremophiles are affiliated with Archaea and Bacteria domains, while very few belong to Eukarya.[28,29] Despite our progress in extremophile biology, (poly)extremophiles remain a novel microorganism group in different environments distributed around the biosphere, classified relative to the physicochemical conditions in which they grow: i) psychrophiles thrive in cold habitats, such as polar regions, deep-sea, and high mountain altitudes[30]; ii) thermophiles and hyperthermophiles flourish under high temperatures in volcanoes, desert hot springs, and hydrothermal vents[31]; iii) acidophiles localize in acid-mine drainage sites and acidic lakes as they require a pH less than 5.0[32]; iv) alkaliphiles grow at high pH levels, such as in sodic lakes[33]; v) piezophiles prosper when highly pressurized deep inside the ocean[34]; vi) halophiles prefer the high salt concentrations of the sea, salars, saline lakes, and brine pools[35]; vii) xerophiles can thrive in the desert's low water availability[36]; viii) oligotrophic microbes require low nutrient concentrations[37]; ix) radioresistant microbes can tolerate a high radiation incidence[38–41]; and x) metallophiles can prosper in high metals/heavy metals concentrations.[42]

Moreover, various environments on our planet's surface—especially subsurfaces—exhibit extremes in one or more physical or chemical conditions. Mirroring Earth, other planetary bodies may have different environments with varying ranges for each condition. Even when natural terrestrial environments appear too strenuous and incompatible, such as volcanic and sulfuric hot springs, dry and hot deserts, deep-sea hydrothermal vents, acid-mine drainages, highly pressurized deep seas, cold and high UV irradiated polar environments, sub-surface caves, or supersaturated salt lakes, life still exists.[8,43]

These organisms endure selective pressure in such extremes by developing an extensive adaptation range for local survival, providing a unique perspective on fundamental biological process characteristics and exhibiting broad metabolic diversities and physiological capabilities.[44,45] These adaptations include proteins and enzymes capable of functioning under extreme conditions, microbial membrane property modifications (proton permeability, lipid structure, and composition), and genomic modifications with horizontal gene transfer of mobile genetic elements (plasmids, integrons, and bacteriophages).[46,47]

Due to these unique and versatile characteristics to thrive in hostile conditions, isolated extremophiles are highly adapted and promising candidates for astrobiology study. Most ecological extremophile habitats on Earth resemble planetary bodies in outer space regarding biogeochemistry, nutrient composition, or topological similarities.[48] Therefore, exploring modern living extremophiles on Earth is critical in understanding their adaptation mechanisms and helps identify novel biosignatures applicable in habitable zones beyond Earth.[49] Furthermore, assessing potential extraterrestrial colonizers by investigating extreme microbiomes analogous to Earth could provide clues to whether (and how) life persists on other planetary bodies. Additionally, extremophiles can provide insight into how those microbes can support the terraformation of planets constantly facing extreme conditions.[6,26] In this way, (poly)extremophiles are invaluable for predicting living organisms' boundaries and deciphering mechanisms and strategies behind survival in extreme environments.

2.2 Extremophiles as Great Candidates for Astrobiological Studies

Mars (with several ongoing missions, including Curiosity and Perseverance) and the icy moons, Enceladus and Europa, are the leading candidates for harboring microbial life in the past or extant.[50–52] However, technological restrictions, distances between planets, and time make collecting and retrieving samples for study exceptionally difficult. Thus, this hypothesis of life as we know it beyond Earth remains mysterious, which has led astrobiologists to discuss possible forms of life and their characteristics under extreme environments in our solar system.

Earth harbors a myriad of analogous terrestrial environments that can be our foundation for understanding other planetary bodies' potential habitability, including Antarctica's dry valleys,[53,54] the Atacama Desert,[55] hydrothermal vents,[56] and deactivated nuclear reactors.[38,41] These microbial-colonized environments are potential organism models in this search for life. In astrobiology, model microorganisms can survive one or more extreme environmental conditions found on planets, moons, and asteroids which may be biochemically similar. All life domains (Archaea, Bacteria, and Eukarya) present these extremophilic models[4] (Table 1). Prokaryotes are considered the oldest reported microorganisms on our planet and have survived all mass extinctions; therefore, prokaryotes are one of the most studied groups in astrobiology.

Among known extremophiles with considerable astrobiological model potential, halophilic archaea members are also promising models for space-related studies due to their evolutionarily ancient and physiologically versatile characteristics.[57] They are frequently observed in brine pools, soda lakes, salt mines, and marine solar salterns in terrestrial environments. Haloarchaea constitute polyextremophilic microbes that can withstand salinity, anaerobic conditions, high ultraviolet and ionizing radiation levels, subzero temperatures, desiccation, and toxic ions.[58] Halophilic archaea may survive in diverse planetary environments in outer space, including exposure to various extreme conditions found on Mars, such as desiccation, radiation, subzero temperatures, and perchlorate oxidizer exposure.[5]

Haloarchaea survived launches into Earth's stratosphere and exposure to space conditions similar to those observed on Mars' surface.[59,60] Several studies have elucidated how these microbes function in high ionic strengths, perchlorate salts, and substantial negative temperatures. Haloarchaea also synthesizes red–orange isoprenoid carotenoids for protection and photorepair processes against UV irradiation. Among Haloarchaea, two species are widely studied as astrobiology models: *Halobacterium* sp. NRC-1, a pigmented strain isolated from solar salterns in California (USA),[59] and *Halobacterium lacusprofundi*, a more brightly pigmented and biofilm-forming strain isolated from a hypersaline lake in Antarctica.[60]

Bacteria are easily manipulated, preserve ancient ancestors from our planet's origin, and contain various extensively studied extremophile specimens. Different studies demonstrated that *Bacillus* spores could survive arid conditions,[61] high radiation levels,[62,63] temperature fluctuations,[64] outer space conditions,[63,65,66] high perchlorate salt concentrations,[65] and also regoliths that mimic the geochemical composition of Mars' soil.[67,68] For instance, *Bacillus pumilus* SAF-032

Table 1: Notable extremophilic microbes as astrobiological planets and icy moons models.

Extraterrestrial Environment	Microorganism				
Celestial body	Phylum	Species	Sampling location	Resistance/Tolerance	References
Mars (planet)	Euryarchaeota	*Halobacterium* sp. NRC-1	Solar salterns, California, USA	High and low osmolarity and temperatures, heavy metals, UV-C radiation	5, 60, 85, 86
	Euryarchaeota	*Halobacterium lacusprofundi*	Hypersaline Deep Lake, Antarctica	Cold-adapted, high salinity and sodium or magnesium perchlorate concentrations	5, 57, 87
	Euryarchaeota	*Haloterrigena hispanica*	Fuente de Piedra Salt Lake, Spain	Desiccation, low pressure, high salinity	88
	Euryarchaeota	*Thermococcus gammatolerans* EJ3	Hydrothermal chimney, Guaymas Basin	High temperatures and salinity, UV-C radiation	89
	Deinococcota	*Deinococcus radiodurans*	Oregon, USA	UV-C and γ-rays radiation, desiccation, low pressure and pH	69–74
	Pseudomonadota	*Brevundimonas* sp. MV.7	Miers Valley, McMurdo Dry Valleys, Antarctica	Low temperatures, UV-C radiation	90
	Pseudomonadota	*Pseudomonas* sp. MV.27	Miers Valley, McMurdo Dry Valleys, Antarctica	Low temperatures, UV-C radiation	90
	Pseudomonadota	*Halomonas* spp. MVT 161, 463, 464, 468	Miers Valley Transect, McMurdo Dry Valleys, Antarctica	Low temperatures, UV-C radiation	90
	Pseudomonadota	*Psychrobacter pacificensis* L0S3S-03b	Hydrothermal vent, Rodriguez Triple Junction, Indian Ocean	Desiccation, peroxide exposure, UV-C and γ-rays radiation	91
	Bacillota	*Parageobacillus thermantarcticus*	Mount Melbourne, Antarctica	UV-C and γ-rays radiation, desiccation, low temperatures, space environment	92–94
	Bacillota	*Bacillus subtilis*	Massachusetts, USA	UV-C radiation, low pressures and temperatures, magnesium perchlorate concentrations	61, 62, 95–97
	Bacillota	*Bacillus pumilus SAFR-032*	Jet Propulsion Laboratory – spacecraft assembly facility, USA	High temperatures, low or no nutrient availability, extreme desiccation, H2O2, UV-C radiation, chemical desinfection	63, 65
	Bacillota	*Halarsenatibacter silvermanii* SLAS-1	Searles Lake, USA	High salinity and pH, desiccation, arsenic, hydrocarbons	98, 99

Table 1: (continued)

Extraterrestrial Environment	Microorganism				
Celestial body	Phylum	Species	Sampling location	Resistance/Tolerance	References
	Cyanobacteria	*Chroococcidiopsis* sp. CCMEE 029	Negev Desert, Israel	UV-C radiation, desiccation, space environment, high perchlorate concentrations	75–79, 100–102
	Ascomycota	*Exophiala* sp.	Atacama Desert, Chile	Cold temperatures, high salinity, UV-C radiation	81
	Ascomycota	*Cryomyces antarcticus*	McMurdo Dry Valleys, Antarctica	UV-C and γ-rays radiation, desiccation, low temperatures, space environment	84
	Ascomycota	*Debaryomyces hansenii DSM 3428*	Spoilt sake	High sodium perchlorate concentrations	80
	Ascomycota	*Purpureocillium lilacinum*	Sodium perchlorate contamination, Berlin, Germany	High sodium perchlorate concentrations	80
	Ascomycota	*Rhizocarpon geographicum*	Plataforma de Gredos, Spain	Extreme temperatures, desiccation, UV-C radiation	103
	Ascomycota	*Xanthoria elegans*	Peñones de San Francisco, Spain	Extreme temperatures, desiccation, UV-C radiation	103
	Ascomycota	*Circinaria gyrosa*	Zaorejas highlands, Spain	Extreme temperatures, desiccation, UV-C radiation	104
Venus (planet)	Rhodophyta	*Galdieria sulphuraria*	Sulfuric hot springs, Japan	Low pH, high temperatures	105
	Rhodophyta	*Cyanidium caldarium*	Nymph Creek, Yellowstone National Park, WY, USA	Low pH, high temperatures	106
Ceres (dwarf planet)	Pseudomonadota	*Colwellia hornerae*	Ellis Fjord, Antarctica	High aliphatic substrate, cold-adapted	107
Enceladus (icy moon)	Euryarchaeota	*Methanothermococcus okinawensis*	Iheya Ridge deep-sea hydrothermal vent field, Okinawa Trough, Japan	Extreme temperatures, anoxic conditions,	108
	Euryarchaeota	*Methanococcus villosu*	Hydrothermal system, Kolbeinsey Ridge, north of Iceland	Extreme temperatures, anoxic conditions	108, 109
	Euryarchaeota	*Methanothermobacter wolfeii*	Germany	Extreme temperatures and pH, anoxic conditions, high-pressure	110, 111
	Pseudomonadota	*Psychromonas antarcticus*	Pond sediment, McMurdo Ice Shelf, Antarctica	Cold-adapted, high salinity	112
	Pseudomonadota	*Syntrophotalea acetylenivorans* SFB93	South San Francisco Bay, USA	Extreme temperatures, high pH and salinity, acetylene	99, 113

Table 1: (continued)

Extraterrestrial Environment	Microorganism				
Celestial body	Phylum	Species	Sampling location	Resistance/Tolerance	References
Europa (icy moon)	Thermoproteota	*Saccharolobus shibatae*	Acid hot spring, Japan	Extreme temperatures, low pH, high sulfate and salt concentrations	114
	Bacillota	*Bacillus pumilus*	Jet Propulsion Laboratory—spacecraft assembly facility, USA	High temperatures, low or no nutrient availability, extreme desiccation, H2O2, UV-C radiation, chemical disinfection	63, 65, 115, 116
	Bacillota	*Candidatus* Desulforudis audaxviator	Mponeng gold mine, South Africa	Radioactive materials	117, 118
Titan (icy moon)	Pseudomonadota	*Syntrophotalea acetylenica*	Sewage treatment plants, Konstanz, Germany	Extreme temperatures, high pH and salinity, acetylene	99, 119
Io (icy moon)	Pseudomonadota	*Desulfotalea psychrophila*	Sediments, Arctic	Cold-adapted, high sulfur species concentrations	120

spores are a potential astrobiology model as they have repeatedly demonstrated an ability to survive numerous extreme conditions encountered in outer space, specifically heightened UV irradiation [63,65].

Deinococcus radiodurans is also known for its high radiation resistance; it is one of Earth's two most radiation-resistant organisms, surviving a dose of up to 10,000 Gy.[69] Unlike other bacteria that produce specialized cellular structures (spores) or remain vegetative when exposed to stress, this microorganism remains metabolically active even at exceptionally high ultraviolet radiation levels. However, this ability necessitates a carbon source and a rich amino acid environment.[70] For instance, Venkateswaran[70] reported that *D. radiodurans* could grow on a rich nutrient medium in continuous radiation (6000 rads/h) without lethality. Contrarily, when in a nutrient-limiting condition, cells did not grow and were killed by continuous radiation. In addition, this study identified prominent nutritional constituents that restored *D. radiodurans*' growth in nutritionally limiting radioactive environments, such as nicotinic acid, amino acids, and some salts.

Furthermore, *D. radiodurans* can survive prolonged desiccation under very low relative humidity and even in an ultra-high vacuum.[71] Araujo et al.[72] demonstrated that this bacterium could survive irradiation with synchrotron ultraviolet light in its dry form. In recent International Space Station (ISS) experiments, *D. radiodurans* survived three years outside the space station (in a shielded compartment), establishing it as a relevant planetary protection and panspermia model.[73] It is speculated that these forms of stress resistance are mainly associated with efficient DNA repair and antioxidant systems that protect cellular components from oxidative damage.[74]

Astrobiology also has a place for photosynthetic extremophilic organisms. Several astrobiological survival experiments have incorporated Chroococcidiopsidales members, which occupy diverse ecological niches in our planet's most diverse and extreme habitats. For example, some *Chroococcidiopsis* strains can tolerate at least four years of air drying,[75,76] up to 13 kJ m − 2 of UV-C radiation,[75–77] 15 kGy of X-rays,[78] and 12 kGy of γ radiation.[79] Although prokaryotes are common astrobiology and space-related study models, eukaryotes (yeast and mold) are promising astrobiology representatives. For instance, the fungi *Cladosporium sphaerospermum* and *Cremonium murorum* isolated from a Chernobyl nuclear reactor (Reactor 4 walls) extracted energy from the emitted ionizing radiation by the extensive radioactive material still present there.[29] Some authors describe these microorganisms as a viable life model of space bodies due to the constant cosmic radiation exposure in these places.[29,38]

Another intriguing example is the halotolerant yeast *Debaryomyces hansenii*, considered the most perchlorate-tolerant microbe described thus far. Studies have shown that this microorganism can withstand 2.4 M of sodium perchlorate. This finding is particularly relevant for determining life potential on Mars due to the planet's high concentration of this salt, which favors liquid water even at negative temperatures. In addition, species resistant to this chemical stress are pertinent for understanding possible life forms biochemistries that may be present in Mars' perchlorate brines.[80]

Still, black yeasts stand out the most among fungi as eukaryotic astrobiology models,[81,82] as their polyextremophilic nature allows these microorganisms to withstand various environmental stresses. Several studies have tested black yeast's survival in space conditions through ground facility simulations and on space missions. Black yeasts isolated from Antarctica's dry valleys (*Cryomyces antarcticus* and *C. minteri*) are the best-studied examples within this group. Onofri and collaborators[83,84] indicated that the black yeast *C. antarcticus* maintained survival, DNA integrity, ultrastructural stability, and rapid metabolic activity recovery after 18 months of exposure to space and Mars-like conditions in various ISS experiments. Many studies still require further development to fully understand terrestrial life limits and how they are applicable for astrobiology purposes. Still, with the recent years' increased extremophile research advancements, we can design new analog environments, plan new experiments, and lead the next steps in the search for life beyond Earth.

3 Extraterrestrial Environment Simulation

Numerous studies in modern astrobiology research use laboratory-based simulation facilities, demonstrating simulation chamber necessity and potential in space research. Although laboratory-based simulation chambers aid in various space research aspects, such as geology, astronomy, cosmo-chemistry, and planetology, these machines usually comprise an uncomplicated system that imitates a particular temperature and gas composition. Some sophisticated simulation chambers incorporate multiple techniques, including gas chromatography–mass spectrometry (GCMS), quadrupole mass spectrometry (QMS), and infrared spectroscopy. For example, Andromeda[121] is a planetary simulation chamber that simulates Martian conditions. At the same time, Exocam[10] and SURFRESIDE[122] help in studying physical–chemical interactions between Mars' atmosphere, surface, and sub-surface and simulating interstellar and protostellar conditions, respectively.

In the late 2000s, a simulation chamber capable of reproducing most planetary objects' atmospheric compositions and surface temperatures was constructed,[123] achieving pressures and temperatures ranging from 5 to 5×10^{-9} mbar and 4 K to 325 K, respectively. This versatile simulation chamber can also study irradiation-induced chemical changes in controlled conditions. Furthermore, a planetary environment and analysis chamber (PEACh)[18] uses in situ analytical techniques like laser Raman spectroscopy, laser-induced breakdown spectroscopy, near-IR reflectance spectroscopy, mid-IR attenuated total reflectance spectroscopy, and microscopic imaging for studying geological samples under relevant planetary environmental conditions. In addition, Sobrado et al.[12] developed a Mars environmental simulation chamber incorporating a dust generation mechanism to study Martian dust deposition while controlling temperature and UV irradiation, the two essential planetary conditions.

A research group investigated the UV irradiation processing of biomarkers adsorbed on minerals (Mars soil analog) under Martian conditions using the planetary surface simulation facility (PALLAS).[124] This study determined that these biomarkers degraded under Martian-like conditions at a substantially slower rate than terrestrial ambient conditions, indicating that current Martian conditions favor potential biomarker preservation embedded in Mars analog mineral matrices.[125] In addition, UV radiation damages extremophilic yeast more in the stratospheric atmosphere than reduced atmospheric pressure, high desiccation, and low temperatures.[81] *Chroococcidiopsis* biofilms with Martian mineral analog expressed enhanced biomarker protection when exposed to a Martian-simulated atmosphere combined with or without UV irradiation, signifying ground-based simulations' importance for interpreting space experiment data..[13,126]

Bacillus and *Paenibacillus* species are cultivable microbial communities found in spacecraft assembly facilities (SAFs)[63,65,127,128] with elevated UV irradiation and hydrogen peroxide treatment resistance due to the presence of several genes, gene orders, and proteins linked to providing extreme condition resistance.[129–131] Another study examined simulated Martian solar UV radiation effects on bacteriophage T7 and isolated T7 DNA. The UV treatment decreased biological activity and lowered PCR product levels, indicating UV radiation damage.[132,133] Recently, Li and colleagues[134] administered simulation microbial community (represented by cyanobacterial crusts microbial communities) experiments and concluded that low stratospheric temperatures (similar to Martian conditions) alter microbial community structures by modifying their genomic and transcriptomic content.

4 Future Directions

A 2015 document, the NASA Astrobiology Strategy, addressed questions and defined goals and objectives to guide and inspire astrobiology research more effectively for the next decade.[135] While a lot has improved since then, outstanding questions and challenges remain. Detecting unknown biological systems on unknown worlds is astrobiology's biggest challenge. Scientists stress that to overcome this critical and complex hurdle, we need to understand how life on Earth functions because it is our only sample to examine. Despite current advances, we have only started to characterize extreme terrestrial microbiomes and understand their tolerance to multiple environmental extremes. Furthermore, more microbial diversity exists in unexpected and unexplored Earth ecosystems that will push the current boundary of life even further. Thus, continued analog environments and microbiome experiments will provide valuable insights regarding life limits on Earth and how extremophiles can support the terraformation of planets exhibiting extreme conditions.

Additionally, extremophilic microbes may assist in designing and developing future orbiters, lander missions, and planetary protection practices.[136] Increasing the available microorganism culture collection isolated from astrobiology-relevant terrestrial environments is urgent; thus, novel microbial culture strategy customization, optimization, and development will be relevant. In addition, integrating omics-based approaches (genomics, transcriptomics, proteomics, metabolomics, and epigenetics) with customized microbial cultivation will permit us to understand adaptation mechanisms that enable extreme environment survival on Earth and in other habitats past our solar system (Fig. 1).

Astrovirology, or our understanding of viruses in astrobiology, is another avenue astrobiologists have been moving toward, yet very little is known.[137] Viruses co-occurring with archaea and bacteria on Earth's biosphere express highly diverse structural and genomic sequences. These are vital in biogeochemical cycles in terrestrial ecosystems and evolution, mediating horizontal gene transfer and influencing microbial community dynamics. Overall, astrovirologists hypothesize that viruses are as vital in other planet ecosystems as they are paramount contributors on Earth.[137,138] Furthermore, viral signatures may be pivotal in searching for life in other biospheres and understanding their evolutionary mechanics.[138] Nowadays, two main field priorities are 1) viruses that inhabit extreme analog environments characterization and 2) virus-detection experiments in ancient oceans (Europa and Enceladus) using flight instruments to detect viral particles or sequences.[137,138]

Novel biological activity signature advances shed light on future frontiers for life detection missions. Since the Viking age, the astrobiology community has gained a palpable awareness about defining experimental protocols in the search for life on other worlds and the guiding principles needed to interpret generated data.[139] In the coming years, several missions will be launched to answer fundamental astrobiology queries: how planets form, evolve, and support life. Current and planned planetary missions will examine extraterrestrial environments' physical and chemical characteristics. Furthermore, space agencies (NASA, ESA, CNSA) are expected to develop biosignature strategies for Mars, Europa, and Enceladus soon.

Mars, Titan, Europa, Enceladus, and Venus planetary missions will require specialized tools for distinguishing signs of life. As part of the ExoMars mission, ESA's and ROSCOSMO's Rosalind Franklin rover will collect subsurface (up to 2 m) samples, where radiation shielding could preserve life, encouraging the possibility of active life on Mars.[140] The Mars Organic Molecule Analyzer (MOMA) instrument cluster is on board this rover,[141] equipped with a gas chromatography system and mass spectrometry equipment. This portable laboratory will elucidate molecular species with complex chemical compositions. However, MOMA will face challenges, as the mass spectrometry system must measure complex organic molecules' induced fragmentation, an approach never attempted outside Earth until now.[142]

The Dragonfly Mass Spectrometer (DraMS), another MOMA-like instrument NASA plans to launch in 2024, will explore an even more distant and bizarre world, Titan, Saturn's largest and richly organic moon. Titan is an attractive

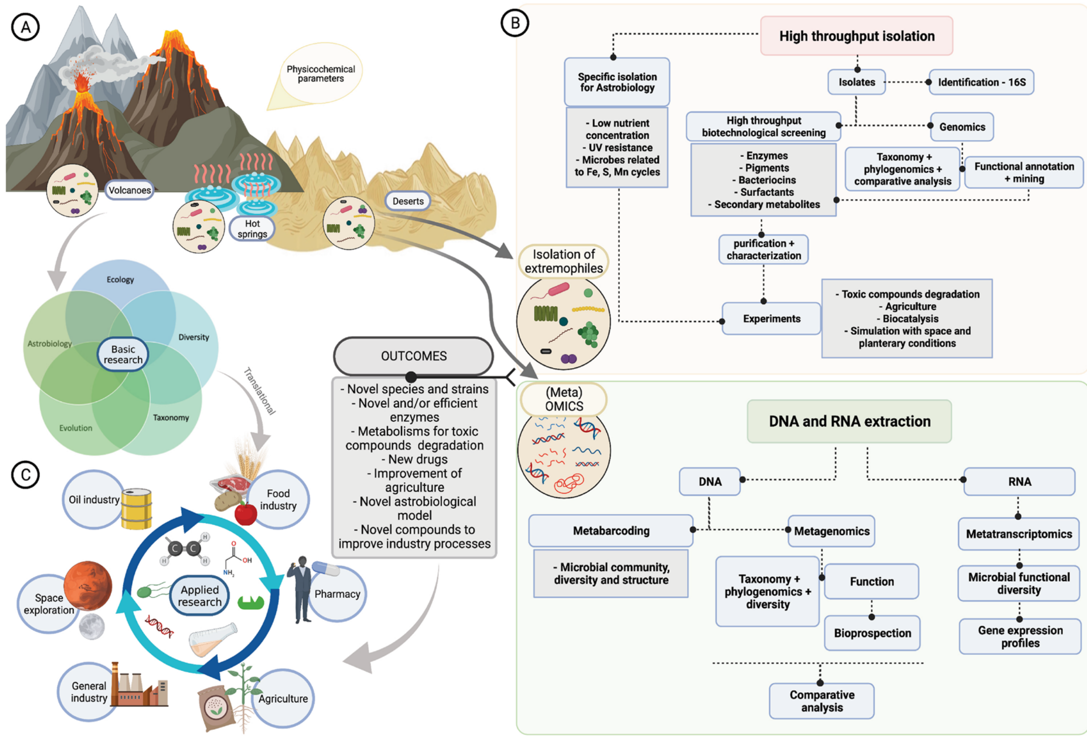

Figure 1: Strategic overview. **A** Sampling sites in extreme environments; **B** Samples processing through two strategies: i. extremophiles isolation and ii. (meta)omics approaches; **C** Both strategy outcomes are potential products for use in different biotechnological areas on Earth or space.

astrobiology target because its surface contains abundant and complex carbon-rich chemistry and presents liquid (transient) water and hydrocarbons, possibly producing a primordial prebiotic soup.[143] Other analytical instruments planned to be on board the spacecraft include the Dragonfly Gamma-Ray and Neutron Spectrometer, Dragonfly Geophysics and Meteorology Package, and the Dragonfly Camera Suite, a microscopic and panoramic camera suite for imaging Titan's terrain and exploring scientifically interesting landing sites.[144]

Jupiter's icy moons, such as Europa, Ganymede, and Callisto, will welcome a new mass spectrometer aboard an ESA orbital mission scheduled for launch in 2022. The Jupiter Icy Moon Explorer will harbor neutral gas and ion mass spectrometry (NIM), making inaugural exosphere measurements for Jupiter's three icy moons.[145,146] NIM can detect neutral and charged molecules from biosignatures in a molecular mass range, including lipids, small peptides, and some secondary metabolites. By examining their exospheres in detail, we could potentially gain insight into how life originates, necessary resources, and how these moons differ from each other and other planetary bodies in the Solar System.[147]

The strong evidence of liquid water under an icy crust denotes Europa as one of the most promising locations in our solar system for discovering currently habitable environments.[148] Scientists hope to launch the Europa Clipper mission in the mid-2030s to determine if life exists beneath Europa's surface. The spacecraft payload for this mission will include the Mass Spectrometer for Planetary Exploration/Europa instrument, a high-resolution TOF–MS for measuring trace organic compounds at parts-per-billion levels, and cameras to produce high-resolution images and compositional maps of Europa's surface and thin atmosphere.[149] Included in the Europa Clipper mission, a solid-state UV laser source is integrated into the Ocean Debris and Life Signature Characterization instrument, a candidate instrument for the Europa Lander mission. The device can obtain 2D chemical images of Europa samples using an Orbitrap mass analyzer and active beam scanning.[150] With these high-resolution instruments, it will be possible to determine if organic compounds originate from biological processes.[151]

We generally look for Earth-like life on Earth-like worlds. So, if life is rare or different from Earth's, our current extraterrestrial life and biosignature detection approaches may fail. Expanded efforts are required to develop robust quantitative approaches to remotely detect biosignatures in stellar or planetary contexts.[3] Whether or not other planetary bodies (Mars, Venus, Enceladus, Europa, or Titan) could or did support life, studying Earth's life in extreme analog environments and their associated microbiomes will further space exploration and could shed light into the origination of life on and beyond Earth. Although simulating extraterrestrial environments in laboratory conditions is challenging, many research organizations have designed new technologies to interpret outer space data. Given the importance and booming interest in extraterrestrial environment study, new and improved simulation chambers are frequently constructed around the globe guaranteeing success in astrobiological studies.

5 Concluding Remarks

Microbial life has colonized most of Earth's environments, even the most extreme and hostile. Microorganisms diversify their metabolisms and utilize available resources in habitats that may be extreme, and modify their cells' components to function at life frontiers. Hence, extremophilic microorganisms are crucial for astrobiology studies since they thrive in various terrestrial analog environments, face extreme stresses, and are relevant for in situ life detection (cells, biomolecules, or biosignatures) of planetary bodies in the Solar System and exoplanets. Furthermore, studying life on Earth's edge enables us to uncover extremophile potential and answer primary questions concerning how life originates and evolves in the universe. Lastly, these studies have provided an avenue for investigating microbe means and survival extents in extreme environmental conditions, broadening the scope of space biology.

Publisher's Note

Author Contributions

JS and ASR devised the topic, supervised manuscript structure and data collection, conducted the literature search, created figures, and wrote the manuscript. AS conducted the literature search, created figures, and wrote the manuscript. NP conducted the literature search and wrote the manuscript.

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Data availability

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

Declarations

Conflict of Interest

The authors declare that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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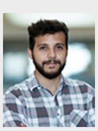

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