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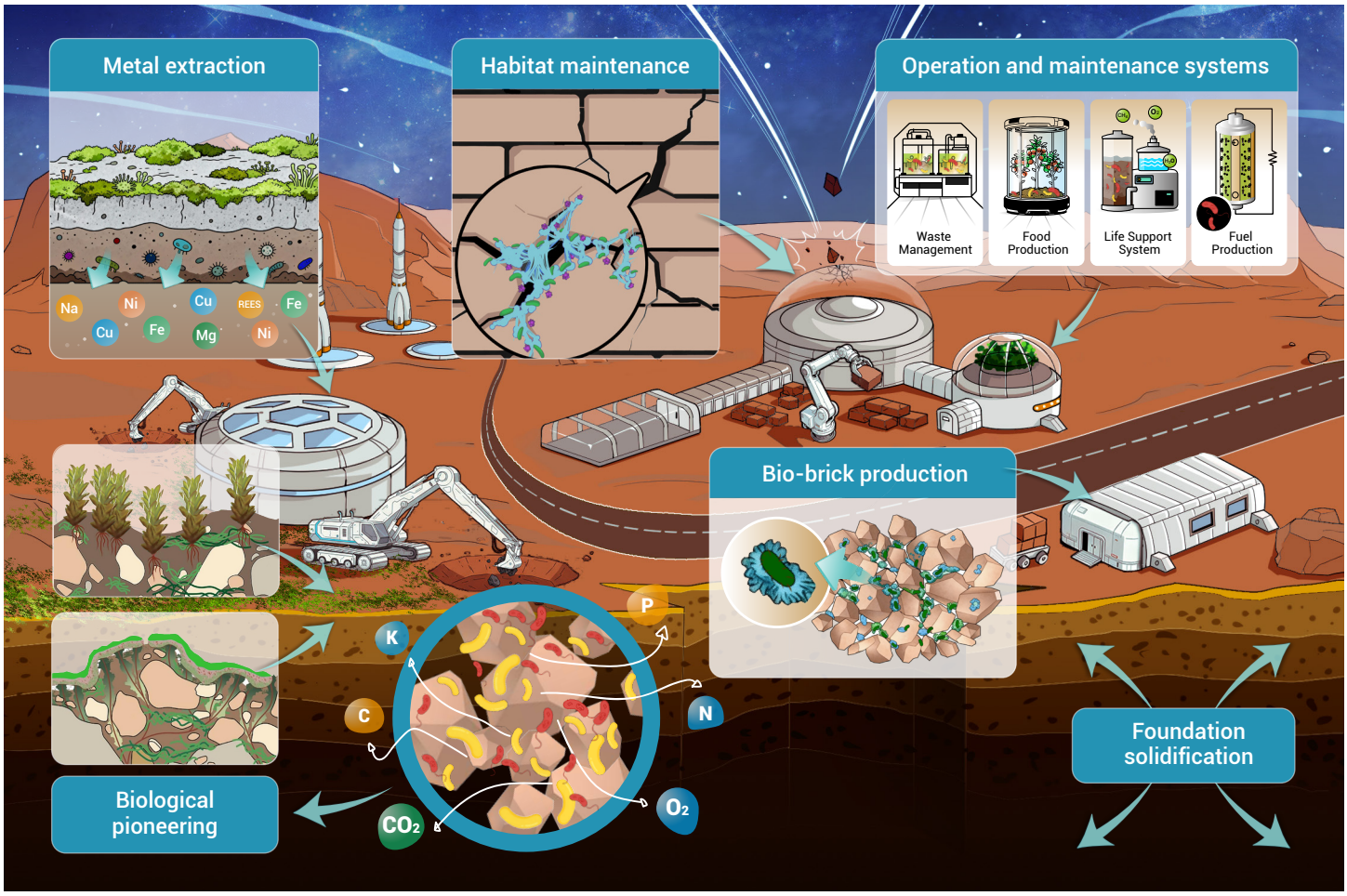
GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Microbe-driven bioconstruction offers a sustainable path for long-term human habitats in deep space.
- Systematically discusses the potential of microorganisms in extraterrestrial construction.
- Presents an 'Earth-Space Station-Extraterrestrial Object' multi-dimensional roadmap for bioconstruction.
- First proposes a full-lifecycle paradigm for extraterrestrial bioconstruction.

REVIEW Microbiology

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Extraterrestrial bioconstruction technology system: Bridging space station applications and deep-space missions

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Microbe-driven bioconstruction offers a promising approach to sustainable deep-space habitats as missions shift from short-term exploration to long-term human presence. This review presents the first full-lifecycle bioconstruction paradigm that integrates Earth-derived extremophilic microorganisms, space station validation, and in-situ utilization of Lunar and Martian resources. It addresses gaps in extraterrestrial bioconstruction strategies. The proposed four-stage paradigm begins with biological pioneering using extremophilic microorganisms to establish survival conditions. This is followed by biological conversion of extraterrestrial resources for metal extraction, thereby enabling the synthesis of building materials through biological fabrication and their in-situ assembly into integrated habitats. The final stage involves integration into a self-sustaining life support system for long-term habitation. Key challenges include limited adaptability under compound space stresses, slow screening processes, limited in-orbit validation, and uncertain material longevity. Recommended directions include AI-driven strain optimization, expanded space and lunar experiments, and predictive modeling of material behaviour to support the development of resilient and resource-efficient extraterrestrial habitats.

INTRODUCTION

With the progressive advancement of lunar exploration programs—including China's Chang'e Project, the U.S. Artemis Program, and Europe's Explore 2040—as well as Mars missions such as China's Zhurong rover and NASA's Perseverance rover,[1] new insights have been gained into the geological structures, mineral and water-ice distributions, and extreme environments of the Moon and Mars.[2,3] Nations are transitioning from conceptual planning to the practical construction of long-term lunar and Martian bases. The United States intends to establish a permanent lunar base,[4] while China and Russia are jointly planning an International Lunar Research Station.[5] Detailed plans and enabling technologies for Martian bases are also advancing rapidly.[6] Current extraterrestrial exploration, however, remains heavily dependent on Earth-based resupply, leading to prohibitive launch costs and strict launch window constraints. This dependence introduces risks of supply disruption and restricts the sustainability of long-term missions. For example, constructing a lunar base for four astronauts without in-situ resource utilization (ISRU) is projected to require an infrastructure investment of $35 billion and annual operational costs of $7.35 billion.[7] Therefore, shifting toward the use of lunar and Martian in-situ resources for construction is essential. Establishing long-term habitats on the Moon and Mars under extreme environments—characterized by vacuum, high radiation, severe temperature fluctuations, and frequent micrometeoroid impacts—constitutes a cross-disciplinary systems engineering challenge, requiring the coordination of resource utilization, environmental adaptation, and technical integration.[8] Researchers have considered using regolith as the primary raw material,[9] exploring its conversion into construction units through methods such as sintering, microwave treatment, laser melting, and geopolymer concrete production.[10] These approaches typically depend on high-energy devices (e.g., solar concentrators) or additional materials (e.g. alkaline solutions and fibers), creating demanding requirements for energy supply (e.g., stability of energy storage systems) and material circulation (e.g., consistent binder supply) in extraterrestrial environments. During long-term operation, materials are unavoidably exposed to severe thermal cycling, radiation-induced fatigue, and micrometeoroid impacts.[11] Studies indicate that the micrometeoroid flux on the lunar surface is within a range of approximately (6.19–14.74)× 10^{-13} g/m^2·s.[12] Such impacts can generate significant structural cracks and accelerate material fatigue, making rapid repair essential. While prevailing ISRU methods—such as regolith sintering and geopolymer concrete—demonstrate technical feasibility, their operational viability remains constrained by high energy consumption and short-term resource dependency. Beyond construction materials, long-term extraterrestrial habitation requires astronauts to achieve self-sufficiency in oxygen, water, and nutrients, which depends on waste recycling and resource conversion. Current space station life support systems generate oxygen and hydrogen through water electrolysis and recycle carbon using solid carbon adsorption beds.[13] Although these systems have undergone multiple in-orbit validations, they still rely on stable power supply and periodic resupply from Earth.

Bioconstruction is a rich, interdisciplinary frontier aimed at conducting engineering and construction activities by utilizing living systems themselves or by mimicking their operational principles. From the perspective of its implementation pathways and core agents, bioconstruction can be broadly categorized into four paradigms: animal construction, represented by organisms like corals and earthworms; plant construction, which modifies the engineering environment through life activities such as soil stabilization via the mechanical anchoring of tree root systems and the regulation of local microclimates by plant communities; biomimetic construction, which does not directly rely on living systems but draws inspiration from natural biological structures—such as the hexagonal pattern of honeycombs or the fiber arrangement in bamboo—to guide the optimization of engineering designs; and microbial construction, which utilizes the metabolic activities of microorganisms like bacteria and fungi.[14] In the context of extraterrestrial exploration missions, the application of bioconstruction technologies is subject to strict constraints, including payload mass limitations, energy supply shortages, and the need for adaptation to extreme environments (low temperatures, high radiation, lack of atmosphere). The complex ecosystems required for animal and plant construction are not only massive in themselves but also demand continuous maintenance of suitable temperature, humidity, and nutrient supplies, and they exhibit extremely low tolerance to harsh environments, making their direct transplantation a significant technical and logistical challenge. Meanwhile, biomimetic construction only offers design inspiration and cannot directly participate in the in-situ construction process to address the core requirement of In-Situ Resource Utilization (ISRU). In contrast, microbial construction is uniquely suited to the constraints of extraterrestrial exploration. Its core advantages are evident: microbes have negligible mass and can be stored long-term (for several years) via lyophilization (freeze-drying), significantly reducing the pressure on extraterrestrial transport payloads and offering a low-logistics-cost advantage. They can directly utilize in-situ resources (e.g., minerals from Martian regolith, atmospheric CO_2) as metabolic substrates, eliminating the need to transport large quantities of raw materials from Earth and demonstrating strong ISRU compatibility. Furthermore, some extremophilic microorganisms can maintain metabolic activity in severe environments, and the microbial construction process itself is not energy-intensive.

Therefore, this study focuses primarily on microbe-driven extraterrestrial construction, defining it as a technology that utilizes microorganisms for the in-situ modification of extraterrestrial environments to support long-term human habitation. Using in-situ resource conversion, microorganisms can

transform extraterrestrial minerals, gases, and other substances into construction materials, energy, and life-support supplies, enabling low-cost and long-term sustainable construction systems beyond Earth. This technological pathway serves as a core strategy to overcome dependence on Earth-based materials and establishes a new paradigm for extraterrestrial construction at the systems level.[15,16,17] For example, chemolithotrophic and chemoorganotrophic microorganisms secrete organic acids that promote the dissolution and enrichment of metals and silicates in regolith;[18] microbial-induced carbonate precipitation or extracellular polymer cementation can glue loose regolith particles into bio-bricks;[19] and photoautotrophic cyanobacteria convert carbon dioxide, wastewater, and organic waste into oxygen, purified water, and nutrients.[20] Additionally, microorganisms can convert elements from human metabolites into plant-available carbon and nitrogen, or serve directly as nutrients to support plant growth and food production.[21] Implementing bioprocesses for on-site resource transformation—converting minerals, water, and atmospheric components into life-support materials and engineering products while treating organic waste—enables the closure of material, energy, and nutrient cycles. Notably, some microorganisms possess dual "pioneering-repair" capabilities: Fungi and cyanobacteria in terrestrial deserts can modify arid ecosystems by retaining water, stabilizing carbon-nitrogen cycles, and securing surface soils.[22] Analogous approaches can be transferred to lunar and Martian settings, using such microorganisms as "pioneer species" to gradually modify regolith composition and enrich microbial communities, creating more habitable conditions for sustained human residence. However, extraterrestrial extreme environments represent one of the primary challenges to microbial survival. While conventional Earth conditions differ substantially from those in space, extremophilic microorganisms—microorganisms adapted to Earth's most extreme settings, such as hot springs, polar permafrost, nuclear waste sites, and deserts—have evolved unique survival strategies .[23,24] These strategies, honed over billions of years by natural selection, offer invaluable guidance for human adaptation and development in extraterrestrial environments. Furthermore, space stations, as the first long-term space habitats, provide ideal testbeds for in-orbit validation of biological manufacturing technologies under microgravity, radiation, and closed environmental conditions. For instance, U.S. aerospace companies have conducted in-orbit 3D printing experiments using human stem cells and tissue-derived proteins as "bio-inks" to fabricate functional tissue and organ models.[25] By integrating Earth-based extremophile screening platforms with in-situ space station validation, a closed-loop process can be established for microbial strain selection, functional assessment, and on-orbit validation of bioconstruction techniques, thereby laying the technical foundation for in-situ construction on the Moon and Mars.

The concept of microbe-driven "full-lifecycle extraterrestrial bioconstruction" is introduced as a new paradigm, which encompasses the entire process from bio-pioneering and in-situ resource construction to a self-sustaining microbial ecosystem. It must be recognized that this is a grand systems engineering project involving multiple disciplines and environments, and it is fraught with immense challenges. Advances in a single field are insufficient to overcome this engineering hurdle. To address this challenge, a systematic multi-dimensional spatial perspective offers a feasible technology roadmap for achieving this grand objective. This roadmap progresses from Earth, which provides the foundation and design, to the Space Station for testing and validation, and finally to extraterrestrial celestial bodies for application and implementation. The extraterrestrial application and implementation phase itself comprises several stages: and establishing baseline survival conditions through biological pioneering, extracting resources via biological conversion, synthesizing building materials through biological fabrication and their in-situ assembly into structurally and functionally integrated habitats, and ultimately, establishing a sustainable microbial ecological cycle.

EARTH: BIOLOGICAL RESOURCE BANK

The realization of extraterrestrial biological construction primarily depends on the screening, understanding and engineering design of functional microorganisms on Earth. The main challenge in realizing extraterrestrial bioconstruction systems is overcoming multiple cross-planetary survival barriers. Key limiting factors include extreme temperatures, cosmic radiation, vacuum-low pressure environments, periodic desiccation, low gravity, and high salt stress.[26,27,28] Notably, certain Earth extremophilic microorganisms exhibit survival mechanisms that appear capable of coping with these conditions, providing directly translatable models for extraterrestrial environmental adaptation research.[29] Figures 1A-B presents a comparison between extraterrestrial extreme environments and the corresponding responses of extremophilic microorganisms (Figures 1C-F). Table 1 summarizes the five principal categories of extremophilic microorganisms and 15 types of regulatory mechanisms.

Mechanisms of extremophilic microorganisms

Thermotolerance. To adapt to extraterrestrial environments, microorganisms must withstand both high and low temperatures. The main challenge at temperatures above or below their optimal range is maintaining the functional integrity of macromolecules (nucleic acids, proteins, and lipids), balancing stability (robustness) and flexibility (activity, transition states).[30] Thermophiles, a group of microorganisms capable of surviving and reproducing in high-temperature environments, thrive above 40°C and can exceed 80°C. They are commonly found in geothermal springs, deep-sea hydrothermal vents, and other high-temperature regions. Through evolution, thermophiles develop strategies to avoid heat-induced damage, primarily through membrane structure modification, nucleic acid adjustment, protein stabilization, and specialized regulatory factors.[23,31,32]

High temperatures markedly increase the fluidity and permeability of microbial cell membranes, disrupting lipid packing and causing loss of the liquid-crystalline phase.[30] Membrane phase transition depends on fatty-acid composition, so microbes rapidly remodel membrane lipids in response to temperature changes. Under heat stress, bacteria raise saturated and reduce unsaturated fatty acids, which stiffens bilayers. Archaea synthesize monolayer tetraether lipids—often with pentacyclic branches or a higher ratio of tetraethers—to decrease permeability and increase thermal stability.[33] Thermophiles typically mitigate heat-induced damage by compressing their genomes and increasing GC (guanine–cytosine, GC) content. Genomes of thermophiles thriving above 60°C are generally smaller than 4 Mbp (million base pairs, Mb), whereas those living below 45°C tend to exceed 6 Mbp, thereby reducing the energetic cost of DNA replication.[34] Triple-bonded GC pairs increase DNA rigidity, so most thermophilic strains are GC-rich.[35] However, C. hydrothermalis (35% GC) and B. burgdorferi (29.31% GC) indicate that base composition is not the only factor determining thermotolerance.[36]

Thermostable proteins are enriched in Arg, Glu, and Lys, and contain disulfide bonds, dense hydrophobic cores, and salt bridges that stabilize the folded state at high temperatures.[32,37-38] Regulatory factors and osmolytes favor native conformations, while DNA-repair enzymes and heat-shock chaperones (e.g., GroES, GroEL, Clp) and polyamines remove damage and prevent aggregation, maintaining cellular function.[32]

Low-temperature tolerance. In contrast to thermophiles, cold-tolerant microorganisms are widely distributed in extreme cold environments such as polar ice sheets and deep seas. A temperature decrease causes membrane lipids to transition to a gel phase, reducing membrane fluidity and hindering protein mobility. Increasing the proportion of low-melting-point fatty acids—including monounsaturated, polyunsaturated, and branched-chain fatty acids—helps maintain membrane fluidity at low temperatures.[39] Cells also form disordered fatty acid arrangements to further enhance fluidity in cold environments.[40] For protein adaptation, cold-tolerant bacteria synthesize highly active enzymes and increase the mobility and flexibility of enzyme active sites to accelerate reaction rates.[41] Meanwhile, reducing stable structural interactions such as hydrogen bonds, salt bridges, ion pairs, and disulfide bonds increases protein flexibility, whereas extended external loop structures decrease overall stability to adapt to low temperatures.[40] Although adaptation mechanisms differ among environments and microbial species, the core enzymatic strategy is to counteract cold effects by increasing intracellular reaction rates.

The phase change of water in cold environments also causes cellular damage. Cold-tolerant microbes address this by synthesizing various protective substances: for example, they increase compatible solutes (e.g., glycerol) to offset water loss and cell shrinkage.[42] Anti-freeze proteins (AFPs) inhibit ice recrystallization and nucleation by altering the freezing point of cellular solu-

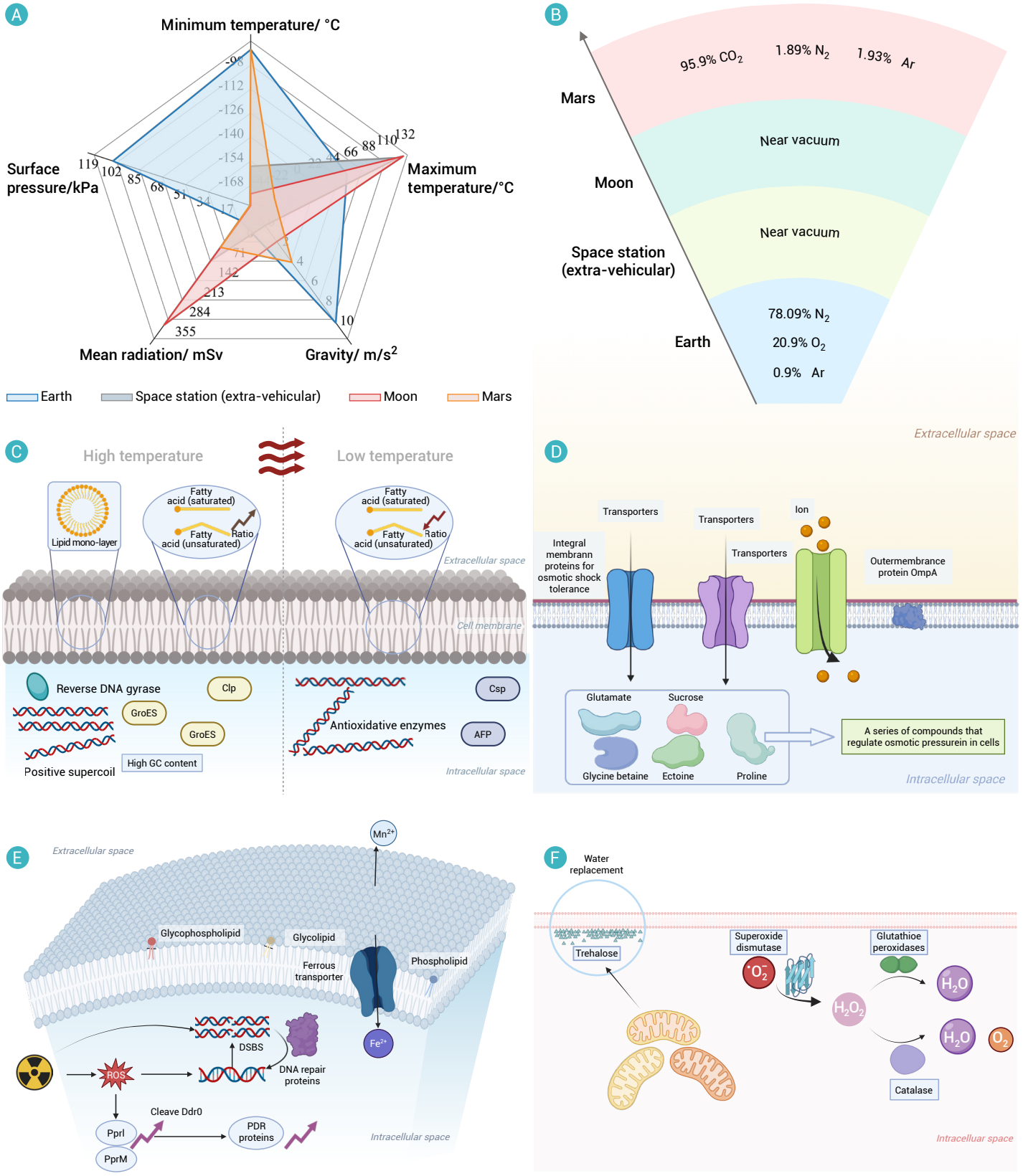

Figure 1. Extremophiles' adaptive responses to extremes extraterrestrial Extreme Conditions (A) Comparison of temperature, surface pressure, and gravity among Earth, space station, Moon, and Mars. (B) Comparison of atmospheric components of Earth, space station, Moon, and Mars. (C) Microbial responses to extreme temperatures,[39] reproduced with permission.[39] Copyright 2013, Elsevier. (D) Microbial tolerance to ions and osmotic stress,[60] reproduced with permission.[60] Copyright 2019, Frontiers Media S.A.. (E) Microbial radiation resistance, [47] reproduced with permission.[47] Copyright 2023, Elsevier. (F) Microbial desiccation tolerance,[52] reproduced with permission.[52] Copyright 2020, Frontiers Media S.A.. These images (C)-(F) were created at: https://www.biorender.com/.

tions.[43] Cold shock proteins (Csps) cooperate with induced RNA helicases to support normal DNA replication and protein synthesis.[44]

Radiation tolerance. In extraterrestrial environments, microbes are continuously exposed to ultraviolet, X-ray, and charged-particle irradiation. Radia-

Table 1. Summary of adaptation strategies of extremophilic microorganisms to extreme environments.

Environmental type	adaptation mechanism	Specific molecular/structural strategies
High Temperature	Membrane Structure regulation[30,31,32,33]	Saturated fatty acids, unsaturated fatty acids; monolayer tetraether lipid (archaea)
	Nucleic Acid Protection [34,35]	Shortened genome length, increased GC content
	Protein Stabilization [37,38]	Enrichment of Arg/Glu/Lys; enhanced disulfide bonds/hydrophobic cores/salt bridges
	Regulatory factors[32]	GroES/GroEL/Clp chaperone systems
Low Temperature	Membrane fluidity maintenance[39,40]	Mono/polyunsaturated and branched-chain fatty acids; disordered fatty acid arrangements
	Protein modification[40,41,43,44]	Csps, AFPs, extended active-site loops in enzymes, reduced weak interactions (e.g., hydrogen bonds/salt bridges)
	Cryoprotectants[42]	Compatible solutes (e.g., glycerol)
Radiation	DNA repair[48,49]	BER/NER/MMR/DSB repair pathways; redundant gene backup
	Antioxidant defense[50,51]	PprI/PprM regulatory coordination; SOD, catalase, peroxidase
	Structural barriers[47]	Multilayered cell wall, DeinoPol exopolysaccharide
Desiccation	Osmotic/membrane stabilization[53,54]	Saturated fatty acids; polyols, amino acids, glyceramides, sugar alcohols
	Protein protection[56,57]	LEA proteins; HSP20
	moisture retention barrier[58,59]	Antioxidant/hydroscopic, EPS; trehalose vitrification
High Salt/Perchlorate	Osmotic regulation	Solute accumulation or intracellular K^+
	Morphological/biofilm adaptation[62]	Viscous biofilms and highly adhesive aggregates to resist combined osmotic and oxidative stress
	Cellular morphology[61]	Reversible morphological elongation

tion causes cellular damage primarily through two mechanisms: direct induction of DNA lesions—particularly lethal double-strand breaks—and radiolysis of intracellular water, generating reactive oxygen species (ROS) that oxidize macromolecules and disrupt metabolism.[45] Effective radio-resistance therefore requires rapid detoxification of ROS and efficient DSB repair.

Deinococcus radiodurans, the benchmark organism, survives ionizing doses up to 15,000 Gy by integrating structural shielding, enzymatic defence, and multilayered repair. Its thick, tripartite envelope, enriched in the exopolysaccharide DeinoPol, serves both as a physical barrier and a radical scavenger.[46,47] Extensive gene redundancy provides functional "back-ups," allowing alternative gene copies to maintain essential pathways under mutagenic stress.[48] Four complementary repair pathways operate in parallel within the cytoplasm: base-excision repair (BER) excises oxidized or alkylated bases via AP endonucleases; nucleotide-excision repair (NER) removes bulky lesions such as UV-induced dimers, mediated by proteins like PprAd; mismatch repair (MMR), involving MutS2, corrects replication errors; and the DSB repair module, centered on RecA and RecF, reconstructs fragmented chromosomes.[49] These systems can restore genomes shattered into hundreds of fragments. Persistent ROS are eliminated by robust antioxidant enzymes—superoxide dismutase（SOD）, catalase, and peroxidase—which function at unusually high rates.[50] Two specialized regulators, PprI and PprM, coordinate the response: PprI upregulates repair and antioxidant genes, while PprM fine-tunes the network, further increasing radio-resistance.[51] Through this integrated system of shielding, detoxification, and layered DNA repair, D. radiodurans and related extremophilic microorganisms remain metabolically active under radiation levels far exceeding those expected on Mars or the Moon.

Desiccation tolerance. Liquid water is extremely scarce in extraterrestrial environments, and periodic drying presents a central challenge for bioconstruction, even in future self-sustaining ecosystems. Mechanisms from desiccation-tolerant extremophilic microorganisms provide important strategies for maintaining system viability. These microorganisms employ multifaceted approaches, including membrane structure reinforcement, osmotic regulation, oxidative stress defense, and protein protection.[52] Under desiccation, plasma membranes shrink due to water loss, leading to membrane rupture or cell death. Desiccation-tolerant microbes enhance membrane stability by modifying lipid composition, such as increasing the ratio of saturated to unsaturated fatty acids.[53] They also accumulate compatible solutes—including polyols, amino acids, glyceramides, and sugar alcohols—to regulate osmotic pressure, thus preserving cellular structure and function.[54]

Drying-induced oxidative stress exacerbates ROS accumulation, causing oxidative damage to DNA and proteins.[55,56] Microorganisms counter this with specialized proteins: late embryogenesis abundant (LEA) proteins act as molecular shields to prevent protein aggregation during water stress;[57] the heat shock protein HSP20 maintains proper protein folding and stability under desiccation.[56] Extracellular polysaccharides (EPS) retain moisture through hygroscopic properties.[58] Among these, trehalose—a non-reducing sugar—plays a crucial role in desiccation tolerance.[26] It stabilizes proteins by preventing misfolding and aggregation, preserving structural integrity and function under low water activity, while also maintaining osmotic balance in place of water.[59]

High salt/perchlorate tolerance. Martian surface environments are characterized by high concentrations of perchlorate salts (e.g., sodium perchlorate) and chloride salts, presenting microorganisms with dual stresses: the strong oxidizing nature of perchlorates generates ROS, causing DNA breaks, protein denaturation, and membrane damage; meanwhile, trans-membrane salt ion transport disrupts intracellular osmotic balance, threatening cell viability. Microorganisms have evolved two main adaptive strategies: some reduce perchlorates to gain energy (see the "Construction application blueprint" section), while others use tolerance mechanisms to survive without metabolizing perchlorates.[60]

Several perchlorate-tolerant microbes have been identified. For example, Hydrogenothermus marinus tolerates high-perchlorate environments, although perchlorate stress induces reversible morphological changes.[61] Planococcus halocryophilus forms viscous biofilms and large, highly adhesive clusters to cope with perchlorate exposure.[62]

In addition to the above factors, there are also anaerobic conditions. Some existing anaerobic microorganisms on Earth replace aerobic respiration with fermentation or anaerobic respiration, thereby reducing their reliance on oxygen. The anaerobic survival conditions can also significantly reduce energy consumption and process costs. Therefore, aerobic microorganisms with functional effects can be modified to enable them to undergo anaerobic transformation.

Applications of extremophilic microorganisms in extraterrestrial construction

Applications of extremophilic microorganisms in space construction can be categorized into two approaches: direct use of existing extremophilic microorganisms for extraterrestrial bioconstruction and the engineering of novel microorganisms with enhanced survivability and functionality in extreme environments using genetic modification, synthetic biology, and related techniques. Certain Earth extremophilic microorganisms already demonstrate high adaptability, enabling their potential use in extraterrestrial construction. Lichens, as a representative example, tolerate extreme desiccation, vacuum pressures as low as 10^{-7}–10^{-4} Pa, ionizing radiation up to 190 mGy, and wide temperature fluctuations (−196°C to 70°C) Lichen systems hold utility in extraterrestrial bioconstruction:[63,64] fungal components secrete enzymes, and their hyphae form composite biological materials suitable for construction, thereby contributing to biological building material production.[65] However, only a small fraction of natural microorganisms withstand multiple extraterrestrial stresses, such as low gravity and high perchlorate concentrations.

Current research primarily focuses on developing and reserving organisms suitable for extraterrestrial construction by applying genetic modification and related techniques to Earth extremophilic microorganisms. These engineered strains are generally developed for three purposes: remediation of extreme environments, ISRU, and establishment of ecological circulation systems. For extreme environment remediation, engineered heat- and radiation-resistant microbes perform biological nitrogen fixation and facilitate nutrient cycling processes, supporting sustainable, low-fertilizer cultivation for extraterrestrial biota.[66] For ISRU, genetic engineering endows mining-capable microorganisms with robust membrane barriers and enhanced DNA or protein repair functions to improve adaptability in extraterrestrial settings.[67] Incorporating genes that enhance iron and sulfur metabolism can also accelerate microbial mineral decomposition;[68] Biomineralization for construction has attracted increasing attention: protective biofilms formed outside living cells create favorable microenvironments, maintain microbial function under extreme conditions, improve cementation efficiency, and enhance the toughness of the resulting materials.[69,70] In establishing ecological cycles, Berepiki et al. engineered a Synechococcus strain to acquire mammalian cytochromes, increasing photosynthetic electron flow by 31% and thereby improving photosynthetic efficiency.[71]

Although the above-mentioned applications have different scenarios, they all rely on the stable extreme environmental adaptability of microorganisms. Therefore, sorting out the common mechanisms behind these applications can not only clarify the function-mechanism relationship but also provide an entry point for strain screening and modification. Extremophilic microorganisms combat convergent cellular challenges—primarily DNA damage, protein instability, and oxidative stress—using a survival toolkit of conserved core pathways and strategies developed through convergent evolution. To maintain genomic integrity, nearly all life utilizes conserved DNA repair systems like Homologous Recombination,[72,73] which is complemented by unique convergent solutions such as the protective manganese-peptide complex in Deinococcus radiodurans.[74] For protein stability, extremophilic microorganisms employ common strategies including the adjustment of molecular forces, activation of stress proteins (e.g., HSPs, CSPs), and the use of protective small molecules.[75] Oxidative stress is universally countered by a conserved enzymatic defense system (SOD, catalase),[76] supplemented by non-enzymatic alternatives like secondary metabolites in lichens and cyanobacteria. This interwoven network of ancient and evolved mechanisms reveals common principles of microbial resilience. Understanding this toolkit not only identifies high-value targets for engineering multi-resistant strains but also provides a clear design blueprint for designing bioengineered systems capable of withstanding extreme extraterrestrial environments.

However, microorganisms that perform well in Earth laboratories may not be able to adapt to the real space environment. Therefore, before the ultimate challenge of entering an extraterrestrial celestial bodies, an indispensable intermediate step is to conduct in-orbit verification on the space station.

SPACE STATION: A FRONTIER PLATFORM FOR BIOTECH DETECTION AND VALIDATION

The space station, characterized by microgravity, high vacuum, and elevated radiation, serves as a critical testbed for extraterrestrial bioconstruction. This multifactorial environment exceeds the capabilities of ground-based simulations and provides essential data for bioconstruction engineering in outer space.[77] Dedicated biological experiment facilities are established on both the International Space Station (ISS) and the Chinese Space Station. On the ISS, NASA conducts microbial trials such as the BioNutrients experiment, which produces essential nutritional substances via microorganisms.[78] China's Wentian Module features specialized biological test areas designed for investigating biological responses and functional alterations in space station environments. These areas include facilities for cell and tissue culture experiments, life-ecological research, and biological detection technologies, along with a dedicated centrifuge facility to simulate variable gravity conditions. With an operational plan exceeding 10 years, these projects systematically explore the effects of the space environment on biological systems across multiple scales and advance bioconstruction technologies.[79]

Multiple in-situ biological experiments on space stations examine real biological responses under combined environmental stressors.[80,81] The conditions of radiation, vacuum, desiccation, and microgravity, primarily affect biological traits such as cellular morphology,[82,83] growth and reproduction,[84,85] encoded proteins,[82] gene expression,[86] and molecular functional mechanisms.[87] Microgravity is the most distinctive factor affecting microorganisms in space compared to terrestrial extremes, exerting multifaceted effects, as shown in Figures 2A-E. At the cellular level, microbial biofilm morphology changes:[88] under microgravity, biofilms grow thicker,[27] adopt new structural forms (e.g., Pseudomonas aeruginosa shifts from flat to columnar and coronal shapes),[89] and accumulate more extracellular matrix.[90] However, some existing studies present conflicting findings. For instance, the Space Biofilms experiment on the ISS demonstrated that under low-shear, nutrient-rich conditions, microgravity actually led to a reduction in biofilm formation. This inhibitory effect was even more pronounced on lubricant-impregnated surfaces.[91] A recent microfluidic study also revealed that the 'direction of gravity' influences the clustering behavior of bacteria on a surface, resulting in asymmetrical differences in biofilm morphology and distribution.[92] These findings indicate that the effect of microgravity on biofilms is highly dependent on a combination of factors, including the cultivation conditions, fluid dynamics, and surface material properties. At the genetic level, microgravity impairs DNA repair gene function, reducing repair capacity and leading to DNA damage accumulation.[93] Gene regulation under microgravity displays significant time dependency: in Caenorhabditis elegans, DNA repair-related gene expression reorganizes dynamically—short-term downregulation of basic repair prioritizes MMR, mid-term activation targets double-strand break repair, and long-term adaptation fully initiates multiple repair mechanisms.[94]

Although the above studies highlight the adverse effects of space station environments on microorganisms, the station also functions as a screen for microbes with extraterrestrial application potential, particularly extremophilic microorganisms, thereby establishing a candidate functional microbial library for future research.[95] More than 50 in-situ adaptability and function tests on microalgae have been performed in space stations, which are critical for sustainable life support systems.[96] For example, Chroococcidiopsis sp. CCNEE 029 survives 1.5 years of space station exposure (desiccation, radiation, vacuum) without increased genomic mutations, indicating protective mechanisms against extreme environments.[97] Another study shows that cyanobacterial DNA shielded by minerals remains stable for millions of years.[98] The radiation-resistant Deinococcus species survive one year under combined vacuum, temperature cycles, and radiation in space station experiments.[99] Dormant Bacillus subtilis spores consistently demonstrate robust tolerance to extremes, serving as a model in space microbiology.[100] The European Space Agency (ESA)'s EXPOSE-R experiment confirms that these spores resist extraterrestrial conditions in a dormant state, recover viability post-exposure, and repair DNA damage.[101] This finding provides a dormancy-revival model of passive stress resistance, which complements the active metabolic adaptation strategies of extremophilic microorganisms. In a simulation of the ISS environment, Antarctic cryptoendolithic extremophilic fungi—tolerant to low temperature and radiation—show limited proliferation (survival rate < 10%) after 18 months of exposure, as measured by colony-forming units. Notably, more than 60% of single-cell and rock-associated communities retain intact membrane structures and highly stable genomic DNA, highlight-

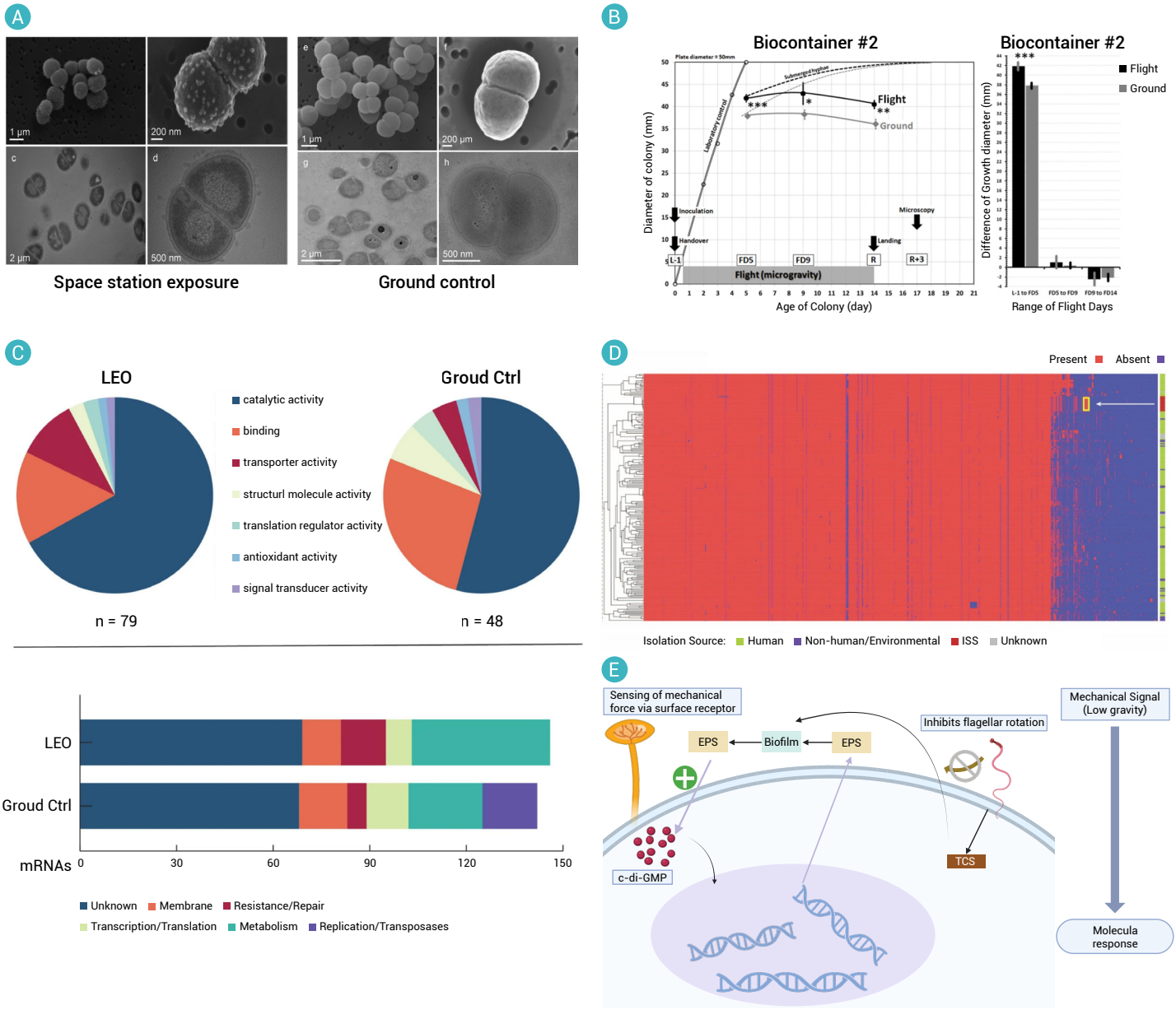

Figure 2. Multidimensional microbial responses in space station (A) Cell morphology;[82] reproduced with permission.[82] Copyright 2020, Springer. (B) Cell growth rate;[84] reproduced with permission.[84] Copyright 2013, PLOS. (C) Encoded proteins.[82] (D) Genetic changes;[86] reproduced with permission.[86] Copyright 2024, Springer. (E) Functional changes in cells.[87] reproduced with permission.[87] Copyright 2024, Elsevier.

ing molecular stability under dehydration–radiation combined stress.[102]

On-orbit biotechnology validation

A series of biotechnological validations have been performed in space environments. Recent studies on Sphingomonas desiccabilis, Bacillus subtilis, and Cupriavidus metallidurans confirm that these microbes not only survive at high rates under space station microgravity but also thrive in mineral environments resembling regolith (e.g., basalt), supporting their functional potential in extraterrestrial-like conditions. Over the 21-day test period, under different gravity conditions, the cell concentration of S. desiccabilis was 0.4–2.7 × 10^9 cells/mL and Bacillus subtilis was 2.4–8.9 × 10^7 cells/mL. Although the concentration of C. metallidurans was not on the same order of magnitude, it also lacked any statistically significant difference. This demonstrates that differences in gravity have no significant effect on growth.[103] An in-situ rare earth element (REE) mining trial under ISS microgravity showed that for Bacillus subtilis acting on basalt, the leached element concentration was 3.2 × 10^{-2}% to 4.1 × 10^{-3}% of the total available amount. Crucially, the final yield showed no significant difference across various gravity conditions. This demonstrates that microbial mining in space is feasible, with efficiency comparable to that on Earth, verifying the viability of using microbes for extraterrestrial bioconstruction.[104] Although gravity differences are expected to affect intracellular metabolism and mining efficiency, a space station experiment on vanadium ore leaching finds no significant difference in leaching rates between microgravity and Earth gravity,[105] further confirming the promise of microbial mining in space.

Potential risks in microbial-mediated construction technologies must also be considered. Fungi colonizing the Mir Space Station caused corrosion damage to aluminum–magnesium alloys, primarily through biofilm formation following microbial attachment, which accelerates material degradation.[106] The first on-orbit study of long-term microbe–material interactions by Zhang et al. reveals differences between space station and ground simulation results: microgravity further accelerates surface corrosion of materials.[107] Microorganisms not only damage aerospace equipment but, more seriously, also pose significant risks to astronauts' health. The space station, as a typical closed and special environment, features unique microgravity conditions, continuous exposure to cosmic radiation, and relatively

high carbon dioxide concentrations, all of which together form a distinctive environment. In this setting, microorganisms undergo remarkable changes in their survival strategies and metabolic behaviors, with accelerated evolutionary rates, making them more likely to develop into highly toxic bacterial strains with multidrug resistance.[108,109] In the ionizing radiation environment of the space station, the growth of Aspergillus niger is promoted, and the synthesis level of its proteins is also upregulated. This fungus can cause ear infections and may lead to invasive pulmonary aspergillosis. [110] Staphylococcus aureus, a common pathogenic bacterium that can cause pneumonia, sepsis, and other illnesses, has also been found in large quantities in on-orbit space stations. Other microorganisms that harm astronauts' health include Klebsiella pneumoniae, Bacillus, etc. .[111]

Furthermore, the microbial communities living in astronauts' bodies also pose threats to the human body as spaceflight duration increases, affecting body parts such as the skin, intestines, and oral cavity.[112] For example, a comparison of astronauts before and after spaceflight shows that viruses such as Epstein - Barr virus, varicella - zoster virus, and cytomegalovirus are reactivated and replicated after spaceflight. These viruses may cause mild infectious inflammation in astronauts and may even increase the risk of lymphoma and oral squamous cell carcinoma.[113] Additionally, Malassezia, a pathogen associated with seborrheic dermatitis that adheres to skin-related microorganisms of astronauts, proliferates during spaceflight.[114] To prevent and control the impact of microorganisms on astronauts' health, the space station has implemented a series of protective management measures. Astronauts undergo regular and rigorous cleaning and disinfection for personal hygiene; the station is equipped with a high - efficiency air filtration system, as well as water filtration and disinfection systems that meet high standards, with dynamic monitoring of microorganisms. In terms of diet, functional foods such as multivitamins and probiotics are added, and vaccines are administered, all to maximize protection for astronauts against microorganisms.[109]

It should be noted that while the space station provides an invaluable platform for validating biotechnology under microgravity conditions, it has inherent limitations as a simulation platform for the deep space environment. The station's LEO is subject to the dual shielding of both the Earth's magnetosphere and the solid body of the extraterrestrial celestial bodies itself. This significantly attenuates the flux of galactic cosmic radiation, causing its radiation environment to differ markedly from that of true deep space in terms of dose, particle energy spectrum, and composition.[115] According to monitoring data from Berger et al., the daily dose rate from galactic cosmic radiation in the ISS orbit is approximately 90–110 μGy/d, which is considerably lower than that on the lunar surface (120–240 μGy/d) and the Martian surface (approx. 140 μGy/d). The data show that under the influence of changing solar activity, the radiation dose rate on the lunar surface can be more than double that of the ISS during the same period.[116] Adding to the complexity, the deep space radiation field is not uniform. Precise data collected during the recent Artemis I mission in cislunar orbit reveal that the radiation dose exhibits pronounced dynamic variations, influenced by factors such as the spacecraft's attitude and its passage through the Van Allen belts. Critically, the shielding effectiveness varies dramatically at different locations within the spacecraft, which can lead to local dose differences of nearly fourfold.[117]

PARADIGM FOR EXTRATERRESTRIAL BIOCONSTRUCTION

The realization of long-term and full-system construction through biological means in extraterrestrial areas faces systemic challenges such as extreme environments and resource shortages. Based on the core idea of in-situ resource utilization and relying on the environmental adaptation, material transformation and autonomous construction functions of organisms, this study proposes a brand-new paradigm for the construction of extraterrestrial organisms, as shown in Figures 3A-D.

Pioneering extremophilic microorganisms initially temper the hostile extraterrestrial environment, establishing micro-niches that support subsequent biological activity. In the bioconversion stage, Microbial metabolic activities extract minerals from local regolith substrates and provide feedstock for the synthesis of structural alloys and construction materials. These products support a bio-directed fabrication phase in which engineered microbial consortia precipitate minerals and synthesize biopolymers, consolidating regolith into load-bearing composites while integrating harvested metals. All astronauts metabolic outputs are incorporated into self-sustaining life support system that recycles water, gases, and nutrients, redirecting wastes to the pioneering and fabrication stages. This approach achieves a complete chain, moving from Environmental Transformation to Resource Conversion, then to Structural Construction, and finally to Waste Recycling and life support.

Biological pioneering

Biological pioneering constitutes the initial biological intervention in extraterrestrial construction. Through synergistic physicochemical and biological processes, microbial communities transform extreme environments and regolith into primary microbial habitats capable of supporting subsequent biological functions, by establishing physical barriers that shield against extraterrestrial stressors and driving metabolic processes that provide essential nutrients for microbial growth. (Figure 4). This stage serves as a critical foundation for ecological succession and engineering on extraterrestrial surfaces such as the Moon and Mars. Its primary functions are adaptation to extreme environments and the construction of basic habitats, forming a staged division of labor with subsequent phases that are dedicated to the progression from environmental foundation-laying to structural construction.

Microbial communities including cyanobacteria, lichens, mosses, and other taxa secrete extracellular polymers (e.g., polysaccharides, proteins) that bind soil particles into cohesive biofilms and biofilaments, generating millimeter-thick biological soil crusts (BSC) at the surface.[118] Serving as ecological pioneers, these crusts provide both physical protection and biogeochemical transformation.[33] Their low water requirements and robust tolerance to extreme temperatures and intense light allow stable colonization in high-stress terrestrial environments such as deserts and polar regions. Biological crusts modulate soil physical properties, including pore structure, porosity, particle aggregation, soil stability, surface albedo, and temperature.[119] Soil structure—defined by the arrangement of solid particles and pore spaces[120]—influences water retention, nutrient storage, and microbial activity by shaping microenvironments that regulate microbial diversity and metabolism.[121] For example, biocrusts have been used to repair soil damaged by freeze-thaw cycles; the presence of the biocrust reduced the relative loss of soil stability caused by these cycles by 39.4%.[122] On a global scale, biocrusts effectively stabilize soil surfaces, which is estimated to reduce global atmospheric dust emissions by about 60%, in turn decreasing global radiative forcing by approximately 0.12 to 0.22 W/m^2.[123]

BSC promote soil aggregation through several mechanisms: chemically, EPS secreted by cyanobacteria function as natural cementing agents, binding particles into microaggregates through functional group complexation; physically, the three-dimensional networks formed by lichen hyphae and moss rhizoids directly entangle and stabilize soil particles, creating a robust composite matrix.[121] EPS and hyphal networks resist mechanical erosion by wind and micrometeorite impacts, providing protected microhabitats and stabilizing dust particles. For example, cyanobacteria and algae cultivated in a Mars-like environment in Inner Mongolia, China, formed a biological crust that prevented dust emission and withstood wind speeds of 10 m/s without structural failure.[124] Organic matter accumulation and aggregate formation gradually enhance water retention, nutrient cycling, and pore structure, thereby supporting plant root growth and microbial colonization. Owing to the small particle size of regolith, biological crusts influence complex pore networks that expand microbial habitats and facilitate direct microbial adhesion, supporting metabolic processes such as microbially induced calcium carbonate precipitation (MICP). However, large pores can increase gas and water exchange, reducing water retention under temperature fluctuations. Evidence indicates that biological crusts stabilize surface particles by limiting water exchange with the atmosphere, primarily through EPS and hydrophobic compounds that obstruct pores or form impermeable surface layers.[125]

Photosynthetic crust organisms—including cyanobacteria, lichens, and mosses—utilize pigments for energy conversion and light absorption.[126] Microbial communities in biological crusts also enhance DNA repair, countering ultraviolet radiation and desiccation.[127] BSC exhibit efficient water acquisition (e.g., fog condensation and absorption) and nutrient cycling, creating self-

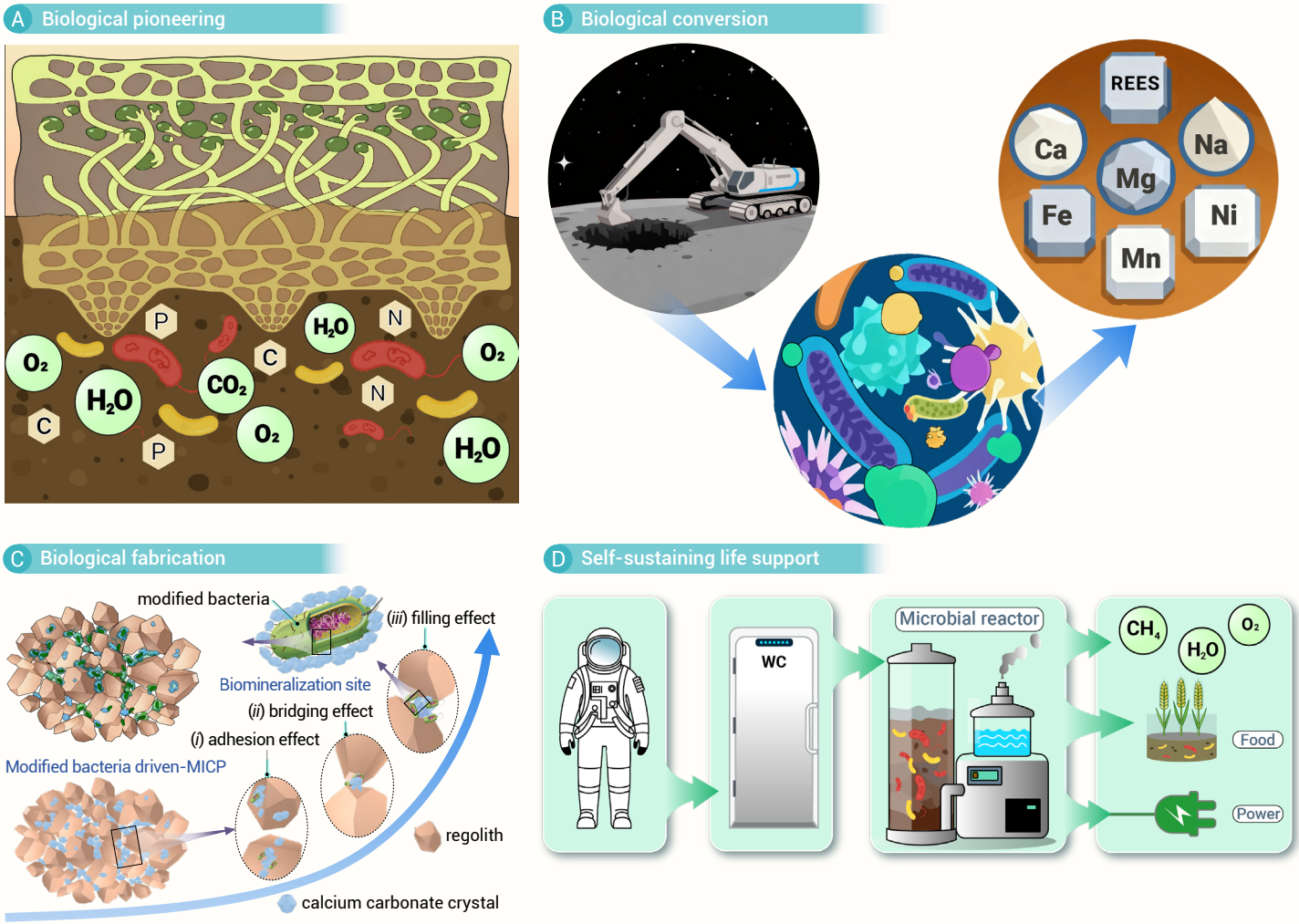

Figure 3. New paradigm for extraterrestrial bioconstruction (A) Microbial conditioning of extraterrestrial regolith to create a habitable micro-environment; (B) biogenic extraction of metallic minerals; (C) microbial cementation into structural building materials;[163] reproduced with permission.[163] Copyright 2025, Elsevier. (D) establishment of a closed-loop life-support system.

sustaining microhabitats suitable for life in extreme environments.[128] During crust formation, microbial communities modify microenvironments: lichens lower soil pH via organic acid secretion, while certain bacteria increase pH by producing alkaline metabolites.[129] For temperature regulation, the physical barrier of the crust reduces heat loss in winter and insulates against heat gain in summer.[130] Pigments produced by mosses and cyanobacteria further absorb ultraviolet radiation, resulting in lower surface reflectivity and more efficient solar energy absorption compared to bare surfaces.[131]

Extraterrestrial environments lack readily available carbon, nitrogen, phosphorus, and water—key components for cellular structure, metabolism, and survival. Therefore, biological pioneering must facilitate the extraction and recycling of these elements.[132] In such environments, two mechanisms are essential for sustained material cycling: atmospheric component cycling and microbial decomposition of regolith to access essential elements, given limited resources and high Earth resupply costs. Microbe–mineral interactions can release elements required for microbial survival.[133] On Earth, diatoms—photosynthetic microbes with high biodiversity—play a major role in the carbon–oxygen cycle by fixing carbon dioxide and releasing oxygen, contributing 20%–30% of global oxygen production.[134] Their adaptability and efficient material conversion suggest strong potential for extraterrestrial applications.[135] Biological crusts dominated by mosses and lichens release glucose through cellulose breakdown, providing carbon for heterotrophic bacteria and fungi.[136] Nitrogen- and carbon-fixing microbes introduced into regolith can supply nutrients for other microbes or plants.[137,138] Cyanobacteria, with unique metabolic advantages, drive material cycles in extreme environments by fixing carbon via photosynthesis and converting atmospheric nitrogen to bioavailable forms. For instance, they utilize Mars' CO_2-rich atmosphere (96% CO_2) for organic synthesis and convert N_2 (2.6% of the Martian atmosphere) to NH_4^+ or nitrate.[139] In simulated lunar regolith, phosphorus-solubilizing bacteria (Bacillus mucilaginosus, Bacillus megaterium, Pseudomonas fluorescens) release bioavailable phosphorus from insoluble regolith compounds.[140] Microbes obtain trace elements such as iron, zinc, and copper from regolith by secreting organic acids or mediating redox reactions. Aspergillus niger releases trace elements through organic acid synthesis,[141] while Acidithiobacillus ferrooxidans oxidizes Fe^{2+} to Fe^{3+}, destabilizing minerals and releasing copper, zinc, and other elements, thereby acquiring energy.[142] EPS secreted by cyanobacteria capture atmospheric water vapor through adsorption and network structures, creating humid microenvironments on the crust surface and reducing water loss at the system level.[58]

Biological conversion

Bio-ISRU, which refers to microbially mediated in-situ resource utilization, enables the energy-efficient conversion of local extraterrestrial materials to directly or indirectly supply construction-ready products. A key pathway within bio-ISRU is biological mining (biomining)—the extraction of metals from minerals by biological systems—which is characterized by low energy demand and minimal environmental impact and currently contributes to ~15% of global copper production.[143] Given the severe energy constraints and hostile conditions that impede conventional mining in space, biomining provides a viable route to recover metals from the abundant lunar and Martian regolith, thereby supplying critical construction feedstocks—including iron, aluminum, and nickel—for the development of off-Earth infrastructure.[18]

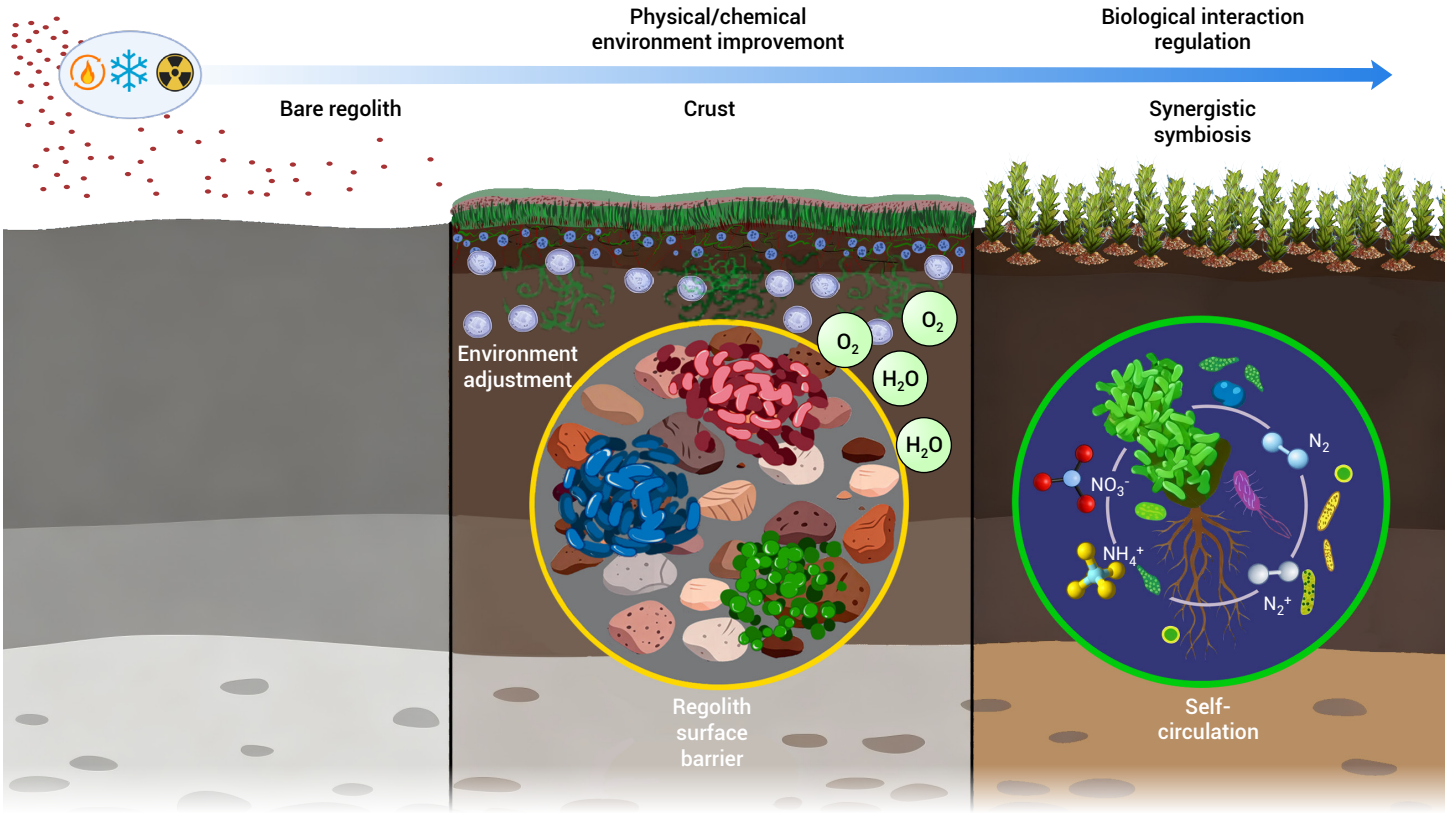

Figure 4. Biological pioneering process.

Lunar regolith primarily comprises four main mineral groups: plagioclase (anorthite end-member, $CaAl_2Si_2O_8$), pyroxene (clinopyroxene and orthopyroxene, $(Mg,Fe)Si_2O_6$), olivine ($(Mg,Fe)SiO_4$), and ilmenite ($FeTiO_3$).[144] The regional mineralogy of lunar regolith varies: maria regions are rich in the above components, whereas highland regolith is dominated by plagioclase.[145] In contrast, Martian regolith, predominantly basaltic, contains plagioclase, olivine, pyroxene, hematite, magnetite, halides (e.g., antarcticite, $CaCl_2{\cdot}6H_2O$), oxychlorides (e.g., sodium perchlorate, $NaClO_4$), sulfates (e.g., alunite, $KAl_3(SO_4)_2(OH)_6$; gypsum, $CaSO_4{\cdot}2H_2O$), phosphates (e.g., bobdownsite, $Ca_9Mg(PO_3F)(PO_4)_6$), and carbonates (e.g., ankerite, $CaFe(CO_3)_2$).[146] Martian regolith, therefore, presents a broader elemental diversity than lunar regolith. For extraterrestrial bioconstruction, the focus is on extracting iron, silicon, aluminum, and magnesium.[145] Specifically, iron and titanium are obtained from ilmenite, hematite, and magnetite; silicon from pyroxene, olivine, and silica; aluminum from plagioclase; and magnesium from magnesium-rich silicates and carbonates. Beyond regolith resources, recycling space debris is expected to become an important supplemental source of construction materials. Research demonstrates that elements such as iron, copper, zinc, and nickel can be extracted from the metallic components of space launch debris and electronic waste.[147] Elements such as zinc, often deficient for extraterrestrial biological processes, may be supplied through this route. Iron, a key construction element, accounts for 5–22 wt% of lunar regolith and up to 17 wt% in Martian regolith,[148] with recent research focusing on its extraction.

Two principal categories and four subcategories of extraterrestrial biological mining methods have been proposed,[142,148,149,150] as illustrated in Figures 5A-D. The first category, magnetic extraction, relies on the directional enrichment of dissolved iron. For example, Escherichia coli utilizes Fe^{2+} in aqueous solutions to synthesize magnetically responsive modified ferritin, while Magnetospirillum gryphiswaldense employs Fe^{3+} as a substrate for biomineralization, forming magnetosomes—both processes concentrate dispersed iron ions into magnetically separable solids via microbial metabolism. The second category, magnetic precipitation, is induced by the leaching and transformation of mineral iron: Shewanella oneidensis uses lactate to reduce solid Fe^{3+} to aqueous Fe^{2+}, promoting magnetite formation; Acidithiobacillus ferrooxidans oxidizes solid Fe^{2+} to Fe^{3+} in the presence of oxygen and CO_2, similarly generating magnetite. Among these four mining microorganisms, E. coli, M. gryphiswaldense, and S. oneidensis are heterotrophs that require organic carbon sources such as glucose or lactate for growth. To address this, Olsson et al. proposed employing the autotrophic cyanobacterium Anabaena cylindrica for mining. This strain fixes CO_2 via photosynthesis to generate energy and secretes organic acids and EPS, directly dissolving metals such as iron, aluminum, magnesium, zinc, and nickel from lunar plagioclase and Martian basalt. For example, A. cylindrica can grow on hydrated basalt at a rate of 0.315 day^{-1} while simultaneously leaching 61.48 μM of Ca^{2+} and 125.04 μM of K^+.[151] In the leaching of major elements subsystem, experiments have confirmed that specific microorganisms possess strong mineral-solubilizing capabilities. For example, methanogens can reductively dissolve pyrite under anaerobic conditions, thereby mobilizing and releasing essential industrial elements like iron and sulfur.[152] In the leaching of rare/precious metals subsystem, microbial leaching has demonstrated high efficiency in recovering rare earth elements (REEs) in the laboratory, with extraction efficiencies reaching up to 80%. Through genetic engineering (e.g., expressing REE-binding proteins), the recovery rate can be further increased to 90%, providing a validated technological pathway for the in-situ production of advanced materials off-world.[153] As natural organic carbon is scarce the lunar and Martian environments, their direct application is constrained Fortunately, the CO_2 provided by the atmosphere on Mars can serve as a source of organic carbon, while carbon sources on the Moon are relatively scarce. Biological mining technologies show clear promise in extraterrestrial resource processing. For instance, Castelein demonstrated that S. oneidensis pretreatment, combined with magnetic extraction, increases iron enrichment by 5.8 times and iron concentration by 43.6% in simulated Martian regolith. Treated samples, after 3D printing, exhibited compressive strengths up to 13 MPa, confirming the feasibility of microbial processing of construction resources under extraterrestrial conditions.[154]

In addition to metal extraction, the application of biological mining to REE development in extraterrestrial environments has gained increasing attention. In-situ experiments aboard the ISS confirm that microorganisms can extract

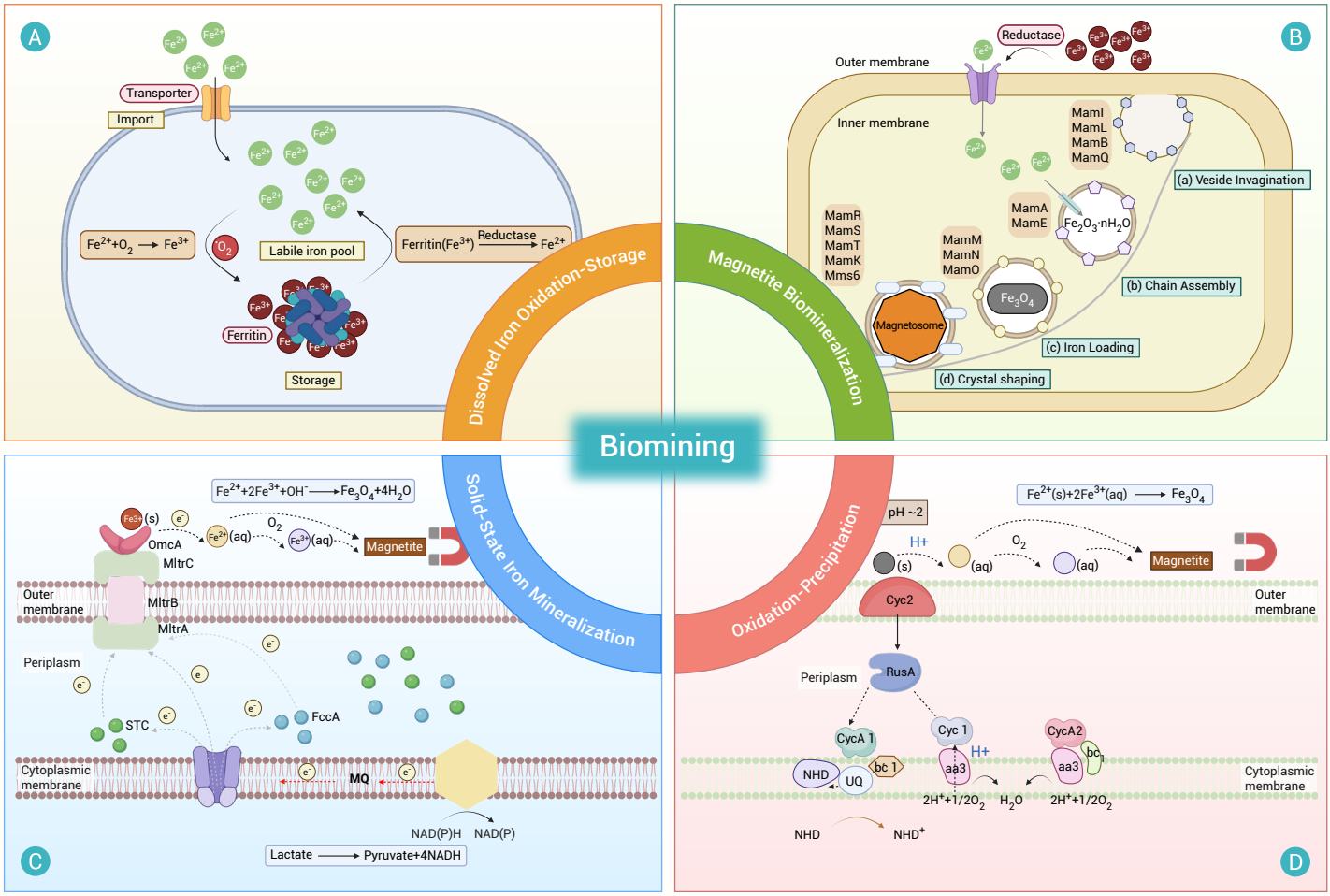

Figure 5. Biological mining mechanisms. Four potential extraterrestrial biological mining methods (A) Dissolved iron oxidation-storage;[148] reproduced with permission.[148] Copyright 2020, Elsevier. (B) Magnetite biomineralization,[149] reproduced with permission.[149] Copyright 2016, Springer. (C) Solid-Stateiron mineralization;[150] reproduced with permission.[150] Copyright 2025, Elsevier. (D) Oxidation-precipitation.[142] reproduced with permission.[142] Copyright 2022, Elsevier. The figure was created at: https://www.biorender.com/.

REE from extraterrestrial minerals, offering new opportunities for resource self-sufficiency in future bases.[104] Analysis of lunar geological samples—including regolith returned by Apollo missions and lunar meteorites—show REE enrichment in multiple minerals, such as apatite, monazite, and yttrium-rich phases (e.g., lunar rocks containing up to 4.6 wt% yttrium and 0.25 wt% neodymium).[155] The Lunar Prospector identified potential REE-enriched zones by mapping thorium distribution—while thorium is not a rare earth, its anomalous distribution is often associated with REE-rich areas—using gamma-ray spectrometry.[156] On Mars and other bodies, rare earths are present in apatite, perovskite, and yttrium-bearing minerals (e.g., xenotime.).[155,156] The Mars Perseverance rover's PIXL instrument directly detected yttrium and cerium in samples from Jezero Crater, verifying the detectability of REE on Mars.[157] REE obtained by biological mining can be applied directly in extraterrestrial bioconstruction systems as functional materials to enhance construction technology. They may be used to prepare thermal barrier coatings that withstand extreme temperature fluctuations,[158] serve as radiation shielding to protect electronic devices from deep-space particles and ultraviolet damage,[159] improve the strength, toughness, and ductility of structural ceramics, and enhance stability during particle sintering.[160] Additionally, rare earths are essential for advanced electronic devices (e.g., high-precision sensors, detectors) and functional materials (e.g., self-healing ceramics, high-efficiency solid-state fuel cells),[161,162]enabling extraterrestrial construction systems to achieve superior adaptability and reliability.

Biological fabrication

Following biological pioneering and biologival conversion, which establish environmental control, ensure nutrient availability, provide feedstocks for microbial activity, and the metal, the subsequent step is biological fabrication. In this context, it refers specifically to the use of biological processes to produce construction materials for habitat infrastructure.

Regolith's high looseness and poor cohesion prevent its direct use as a building material, making sustainable improvement necessary. Within the domain of biological fabrication, MICP provides a scalable pathway to transform in-situ resources into load-bearing, construction-ready composites. In this biological cementation process, microbial metabolism (e.g., ureolysis) generates carbonate/bicarbonate ions that react with available Ca^{2+} (native or supplied) to precipitate $CaCO_3$, forming calcite cement bridges between particles and thereby increasing stiffness and strength.[163] MICP is categorized into four types according to microbial metabolism: sulfate reduction, ureolysis, iron reduction, and denitrification,[164,165] as illustrated in Figure 6. In denitrification, microorganisms (e.g., Pseudomonas denitrificans, Thiobacillus) use nitrate (NO_3^-) as an electron acceptor, reducing it stepwise to nitrogen gas (N_2) through dissimilatory reduction while oxidizing organic carbon substrates (e.g., glucose, acetate) to inorganic carbon (CO_2) or bicarbonate (HCO_3^-). This process raises pH and facilitates $CaCO_3$ formation.[166] Denitrification-induced cementation forms a robust mineral network via cement deposition, pore filling, and surface roughening, thereby improving cyclic resistance and anti-liquefaction properties.[167] Here, acetate as a carbon source and nitrate as a nitrogen source support both energy metabolism and microbial anabolism for bacterial growth. In urea hydrolysis, urease-producing microorganisms hydrolyze urea (NH_2CONH_2) to ammonia (NH_3) and CO_2, yielding ammonium (NH_4^+) and hydroxide ions (OH^-), which increase pH and promote $CaCO_3$ precipitation.[168] In Martian environments, urea can be synthesized in situ using CO_2 and N_2 as feedstocks. By contrast, the Moon

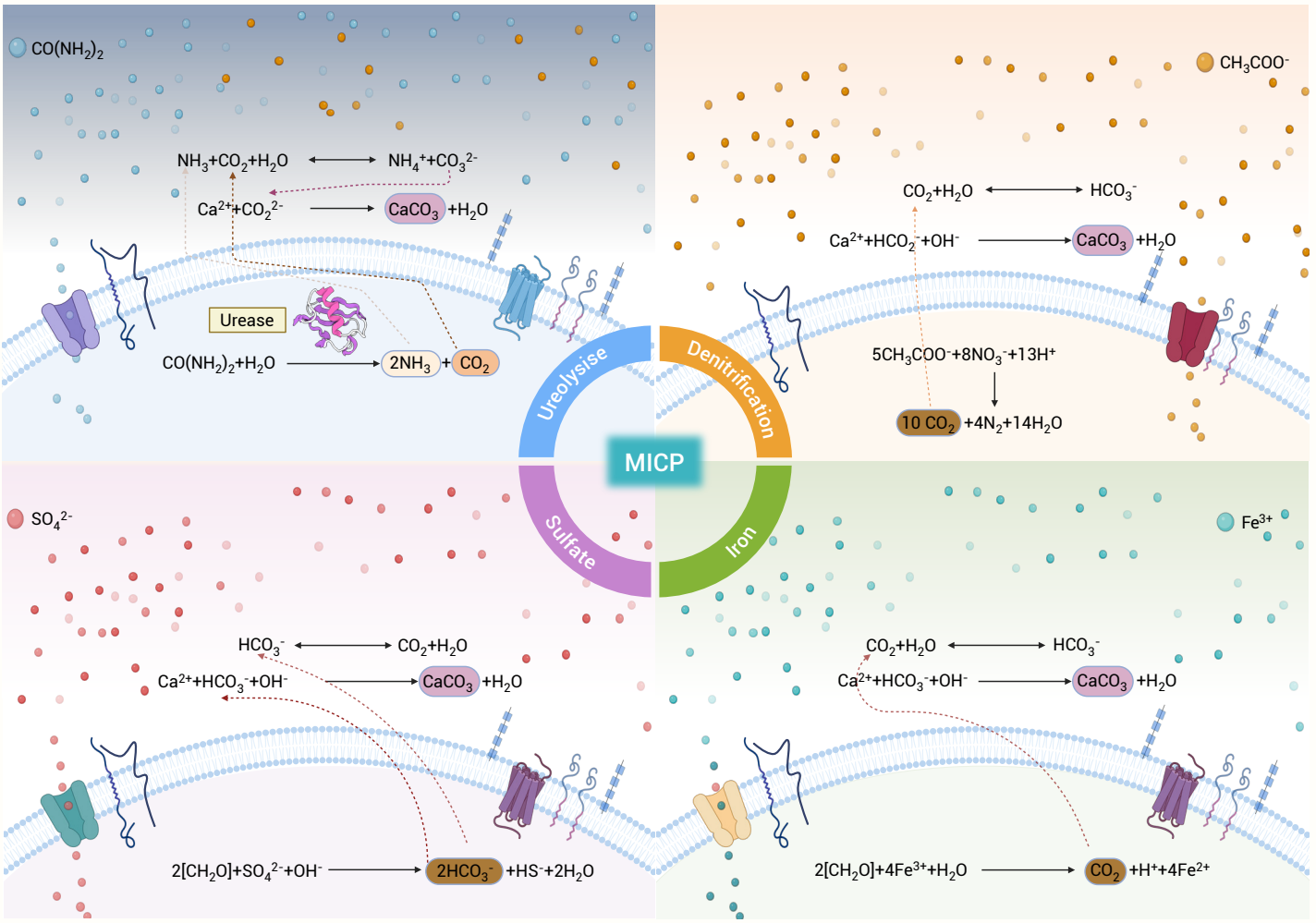

Figure 6. MICP mechanisms Four MICP mechanisms[164]: Ureolysise, Denitrification, Iron Reduction, Sulfate Reduction. Reproduced with permission.[164] Copyright 2024, KeAi. The figure was created at: https://www.biorender.com/ .

faces greater limitations in this regard due to insufficient availability of such resources. Fortunately, human urine is a stable biowaste continuously generated during space missions. Each astronaut produces about 49.7 kg of urine daily, providing a significant source of urea for MICP.[169] The feasibility of this approach for soil stabilization has been recently confirmed. For instance, the world's first urine-based bio-brick, with a compressive strength of 2.7 MPa, was created by solidifying sand with urine and calcium hydroxide.[170] Moreover, carbide sludge, a waste material, has also been effectively used as an alternative calcium source with urine for soil solidification.[171] The rapid reaction enables quick high-strength cement formation, but the release of ammonia requires careful process control. Among strains, Sporosarcina pasteurii is notable for stable urease activity at high pH and strong ammonia tolerance.[165] In sulfate reduction, sulfate-reducing bacteria (e.g., Desulfovibrio) reduce sulfate (SO_4^{2-}) to hydrogen sulfide (H_2S) and HCO_3^-, which reacts with calcium ions (Ca^{2+}) to precipitate $CaCO_3$. The high sulfate abundance in Martian soil (e.g., gypsum, jarosite) supplies substrates for this pathway, offering a potential route for in-situ Martian construction. Hydrogen sulfide by-products can be oxidized to elemental sulfur, supporting extraterrestrial sulfur cycles; however, lunar sulfate scarcity limits its utility on the Moon.[146] In iron reduction, iron-reducing bacteria (e.g., Geobacter, Shewanella) reduce ferric iron (Fe^{3+}) to ferrous iron (Fe^{2+}), generating HCO_3^-, which precipitate $CaCO_3$ with calcium.[172] Martian regolith's high iron oxide content (e.g., hematite) allows direct use of in-situ iron, reducing material transport costs and improving material cycling efficiency; in contrast, lunar regolith, although iron-rich, contains little oxidized iron and needs pre-oxidation to initiate the process. These microbial strategies provide sustainable solutions for in-situ construction in extraterrestrial environments.

In terrestrial sands, particle size and gradation determine the pore structure and permeability, significantly influencing the calcium carbonate precipitation pattern and macroscopic mechanical performance.[173] Experiments have shown that well-graded soils with a moderate content of fine particles are more conducive to forming "carbonate bridges," thereby enhancing material strength. However, when the fine particle content is excessive, pore throat clogging can occur, confining deposition to the surface layer near the injection point and leading to internal consolidation failure. At the same time, this environment hinders the survival or transport of bacteria.[174] In contrast, lunar regolith (e.g., as found in Chang'e-5 sample) is primarily composed of impact debris, glass, and agglutinates.[175] It is characterized by a unimodal particle size distribution with a mode of approximately 50 μm,[176] sharp angularity, high surface reactivity, and a significant interlocking mechanism.[177] Furthermore, under vacuum conditions, it carries a negative electrostatic charge, which creates repulsion with negatively charged mineralizing bacteria.[178] Such characteristics can lead to more complex grouting behavior. However, numerous studies have confirmed the potential of extraterrestrial bioconstruction in terrestrial laboratories by optimizing processes and adjusting the gradation of regolith simulants. Dikshit et al. extensively investigated MICP for extraterrestrial regolith solidification.[19] In 2021, their team used Sporosarcina pasteurii to solidify simulated lunar regolith, achieving a compressive strength of 0.16 MPa through bacterial induction; the addition of guar gum as a biopolymer markedly enhanced cementation, increasing compressive strength to 2.38 MPa. Glass fiber improved material toughness but reduced compressive strength. The team also tested the technology on simulated Martian regolith, finding that Sporosarcina pasteurii alone did not form a solidified structure. By optimizing additive combinations—introducing

guar gum and nickel (a crucial metal in urease active centers)—they overcame solidification bottlenecks: compressive strength increased to 3.3 MPa for simulated lunar regolith and reached 5.65 MPa for Martian regolith, verifying the synergistic effect of multi-component additives on cementation efficiency.[179] Although MICP is validated for simulated lunar and Martian regolith, improvements in solidification strength and adaptation to extreme environments remain necessary. Shi et al. proposed a bio-carbonation method for MgO using urea pre-hydrolysis, where MgO reacts with water and urea-derived carbonates to form hydrated magnesium carbonates, achieving a compressive strength of 10 MPa.[180]

Under the shared vacuum or low-pressure, high-radiation, and sub-zero conditions of the Moon and Mars, the four MICP pathways diverge in their suitability. Ureolysis achieves the fastest reaction kinetics and the highest $CaCO_3$ yield, making it optimal for engineering efficiency; however, it relies on imported urea and releases NH_3. Denitrification is clean and nearly anoxic but depends on native nitrate—abundant on Mars but scarce on the Moon. Sulfate reduction can utilize Martian sulfates but is constrained by limited sulfate on the Moon and releases H_2S. Iron reduction leverages Fe^{3+}-rich regolith on both the Moon and Mars, forming siderite, but requires organic electron donors. All four pathways require liquid water and thermal regulation.

Enzyme Induced Calcite Precipitation (EICP) holds significant potential for extraterrestrial construction. The process utilizes free urease enzymes to catalyze urea hydrolysis, forming CO_3^{2-} which precipitates with Ca^{2+} into $CaCO_3$, thus eliminating the need to sustain living cells. The enzymes can be sourced from plants (e.g., jack beans, soybeans) or bacterial lysates. Compared to MICP, which relies on aerobic growth and metabolism, EICP does not require microbial respiration or proliferation. Experimental evidence shows that the hydrolysis efficiency of purified urease is minimally affected by oxygen availability,[181] and the technique is characterized by simple operation and strong adaptability. Furthermore, freeze-dried enzymes offer an extended shelf life, facilitating remote deployment and on-site activation, and exhibit greater stability and efficacy than liquid enzymes. For instance, Ng et al. demonstrated that preserving urease at -20°C increased its activity by 326% and the shear strength of EICP-treated soil by 238.8%, proving that freeze-drying is an effective improvement method for EICP.[182] These features are highly compatible with the low-oxygen or enclosed working conditions on the Moon and Mars. The typical 12 nm size of urease enzymes,[183] over 100 times smaller than microorganisms, allows for deep penetration into micropores, preventing clogging and promoting uniform precipitation—a key advantage for fine-grained extraterrestrial regolith. However, a potential drawback of EICP is the lack of nucleation sites in pores, which can lead to inefficient precipitation and reduced cementation efficiency.[184] From a performance perspective, EICP technology is better suited for extraterrestrial construction needs. Its main potential hurdle is cost, driven by the expensive chemical extraction of high-purity urease, which is also difficult to recycle long-term in off-world environments. Therefore, cost management remains a key consideration. Notably, emerging low-cost solutions, such as extracting crude urease from plants like soybeans and jack beans, provide a new path to lower preparation expenses.[185] Continued progress in this area could enable the large-scale production of crude urease, meeting the demands of extensive EICP applications and paving the way for its implementation in extraterrestrial construction.

Mycelium-based biomaterials have received considerable attention in recent years. Compared with traditional materials, mycelium—due to its biological properties—acts as an effective adhesive, enabling low-cost and low-energy cementation of organic matrices through self-assembled dense fibril networks. During growth, mycelium secretes long fibers that invade, degrade, and colonize organic matrices, forming a three-dimensional filamentous network. As mycelium expands and crosslinks, secreted biopolymers facilitate both physical entanglement and chemical bonding between fibers and organic particles, resulting in strong, self-supporting materials.[186,187] This property has enabled researchers to develop thermal insulation materials and soundproofing materials using fungal mycelium.[188,189] The feasibility of mycelium as a building block has also been demonstrated; for example, using sugarcane molasses as a culture medium and a mixture of clay and waste coconut shells as the matrix, researchers achieved a compressive strength meeting the minimum 3.5 MPa standard for masonry bricks. This shows that mycelium can function as a fiber adhesive, biocomposite binder, or stabilizer, effectively enhancing the load-bearing capacity of mycelium-based bricks.[190] Traditional MICP relies on microbial mineralization for cementation but is limited by short microbial viability and limited internal structural control. Fungal mycelium overcomes these limitations through its three-dimensional network, which prolongs microbial activity (maintaining high viability after 4 weeks) and allows for complex geometric structures. Additionally, fungal ureolytic mineralization complements bacterial MICP, enabling the selection of self-mineralization or synergistic mineralization to balance material stiffness and long-term activity.[191] For example, embedding the photosynthetic cyanobacterium Synechococcus sp. PCC 7002 into inert sand–hydrogel scaffolds, researchers found that cyanobacterial carbonate biomineralization significantly increased the mechanical strength of the hydrogel matrix. Regulation of temperature and humidity further enhances microbial metabolic activity, resulting in long-term survival rates nearly 10-fold greater than those in conventional cement-based materials.[192]

Beyond these cementation strategies, biopolymers can also facilitate cementation. One study used human serum proteins, sweat, and urine as adhesives to cement simulated regolith, achieving compressive strengths up to 39.7 MPa.[193] This bio–mineral coupling strategy points to a new approach for creating materials with sustainability, durability, and tunable structure, advancing biological cementation from short-term function to living material systems and providing a technical foundation for extraterrestrial construction.

Self-sustaining life support

Following the completion of biological cementation and the establishment of extraterrestrial habitats, internal ecological circulation systems become essential for both short-term occupancy and long-term habitability. The Environmental Control and Life Support System (ECLSS) manages waste processing, atmospheric regeneration, water purification, and nutrient cycling, providing the foundation for human survival in extreme environments.[20] Microorganisms are central to these processes.[17,137] On average, humans consume 641 g of dry food, 3216 g of water (approximately equally divided between drinking and food moisture), and 806 g of oxygen daily, while excreting 94 g of feces, 1630 g of urine, and 943 g of carbon dioxide.[194] On Earth, the atmosphere serves as an unlimited buffer for oxygen supply and carbon dioxide regulation. However, in closed extraterrestrial habitats or spacecraft, restricted ventilation results in respiratory-derived carbon dioxide accumulation. Elevated carbon dioxide concentrations directly threaten crew health, causing symptoms such as headaches and fatigue.[195] Astronauts performing 2 hours of high-intensity activity per day require approximately 1 kg of oxygen daily,[139,196] highlighting the need for efficient biological oxygen production and gas recycling in closed systems.[197]

Photoautotrophic organisms, including cyanobacteria, microalgae, and plants, are optimal for life support due to their ability to remove carbon dioxide and produce oxygen and organic matter using sunlight, with productivity exceeding that of higher plants.[139] Their integration in life support systems has been extensively studied. Photosynthetic efficiency reached 86% of the theoretical maximum.[198] Experimental data demonstrate that a 20 L culture of Chlorella can satisfy the oxygen and water needs of a single person.[199] Beyond green algae, cyanobacteria are promising for life support because of their unique chlorophyll-f, which enables far-red photosynthesis and oxygen production in low-light or filtered-light environments, such as Martian or lunar shadowed regions.[200] Early bioregenerative life support research, such as the Soviet BIOS-3 facility, integrated an 18 L Chlorella reactor into a closed-loop system for 1–3 people, achieving 20% atmospheric closure through photosynthesis. With subsequent incorporation of air and water circulation technologies, the closure rate rose to 80–85%.[201] The recent PBR@LSR experiment on the ISS tested a hybrid system in which astronaut-exhaled CO_2 was concentrated using ESA equipment and supplied to a Chlorella reactor for oxygen and biomass production. Although the experiment was halted prematurely due to power failure and leaks, initial biomass accumulation significantly exceeded control experiments.[202] However, calculations indicate that photosynthetic oxygen production to meet one person's needs requires 1.3 kg of carbon dioxide input per day, while only about 1 kg is available from human metabolism.[139,203] Thus, it is necessary to extract additional oxygen

from excreta and regolith. The microbial metabolic pathways described in biological pioneering and mining can be adapted for resource recycling within closed environments to meet oxygen requirements.

Water is the most critical consumable for humans; astronauts need an estimated 20 liters daily for drinking and other uses (showering, laundry, dishwashing, and toilet flushing).[204] Water treatment systems, distinguished by differences in microbial oxygen requirements, can be divided into four main technical approaches: aerobic treatment (nitrification), anoxic treatment (denitrification), anaerobic treatment (methanogenic fermentation), and phototrophic bioconversion (microalgal photosynthesis).[205] The membrane bioreactor (MBR), a hybrid technology, has attracted wide attention for its high pollutant removal efficiency and resource regeneration, achieved by combining membrane separation and biological processes.[206] Biomembrane systems in space consist of biofilms, carriers, wastewater, and gas phases. Numerous studies have explored microbial waste treatment for extraterrestrial scenarios. For example, Tang et al. utilized a two-layer MBR to achieve 100% water recycling and 87% solid waste recovery, using microbial extraction of organic matter and nitrogen to support survival for six astronauts in a closed system.[207] However, biofilm thickness remains a critical parameter: insufficient thickness reduces conversion efficiency due to limited active biomass, while excessive thickness impedes substrate penetration and causes carrier blockage, thereby lowering pollutant treatment capacity.[206]

Microorganisms are also integral to nutrient cycling in extraterrestrial habitats, enabling their use as food, facilitating nutrient recycling, and supporting the production of microbial-based foods.[208] Achieving nutritional self-sufficiency for astronauts requires an adequate supply of proteins, carbohydrates, and fats. Microalgae such as Spirulina and Chlorella have unique advantages as space food: their protein content ranges from 30% to 80% by weight,[209] and they are rich in essential unsaturated fatty acids (e.g., Omega-3),[210] trace elements,[96] and antioxidants.[211] Despite their nutritional value, poor palatability and color currently limit their use as staple foods,[139] but they can serve as protein supplements or dietary additives in bread and biscuits.[212] For nutrient recycling, urine can be purified to recover water and also enables targeted extraction of nitrogen and phosphorus. For example, biobattery technology uses microorganisms in the anode chamber (e.g., Firmicutes, Proteobacteria) to degrade organic matter in urine, while the cathode chamber converts ammonia nitrogen to nitrate via nitrification; this nitrate then reacts with magnesium ions to form struvite. This process not only generates electricity but also recovers 90% of phosphorus from urine.[213] Another method used Nitrosomonas and Nitrobacter to convert ammonia nitrogen in urine to nitrate, which is then reduced to nitrogen gas by denitrifying bacteria (e.g., Pseudomonas), achieving efficient nitrogen removal.[214]

In bioregenerative systems, microorganisms play an essential role in processing decomposable solid materials, including human metabolic waste and inedible plant residues. The primary step in solid waste recycling is drying, which separates moisture from solids, retains organic matter, and removes inorganic components. The dried waste is then fermented in bioreactors containing degrading microbial communities, enabling efficient material recycling.[137] Microorganisms facilitate the conversion and cycling of key nutrients such as nitrogen and phosphorus by degrading organic waste. For example, proteases secreted by bacteria like Bacillus subtilis hydrolyze proteins in excreta into amino acids and ammonia nitrogen, which are subsequently converted to nitrates by nitrifying bacteria and made available as nitrogen sources for plants.[215] Phosphorus-solubilizing bacteria (e.g., Pseudomonas spp., Burkholderia spp., Agrobacterium spp.) secrete organic acids and phosphatases, transforming insoluble phosphorus into soluble phosphate salts that plants can absorb. The combined effect of vermicompost and phosphorus-solubilizing bacteria enhances phosphorus extraction by increasing phosphatase efficiency in converting organic phosphorus: water-soluble phosphorus concentrations increase by up to 106% compared with uninoculated controls, significantly improving the bioavailability of otherwise insoluble phosphorus.[216] Lee et al. developed the AF-ISM process using the engineered strain Rhodococcus jostii PET S6 to extract minerals such as magnesium, calcium, iron, and manganese from simulated lunar and Martian regolith. Their study also emphasizes the value of anaerobic-pretreated fecal waste: its leachate, enriched in essential nutrients and metal ions, when combined with regolith simulants, supports RPET S6 growth and enhances lycopene biosynthesis. Lycopene production using this medium matches Earth-based controls and reduces overall costs.[217]

Building on these approaches, several integrated closed-loop systems have been proposed. The ESA initiated the MELiSSA (Micro-Ecological Life Support System Alternative) program in the late twentieth century to develop a biological life support system for closed environments—the longest-running initiative of its kind.[218] The system consists of five interdependent functional compartments, each containing specific microorganisms or higher plants. Through biological conversion, human metabolic waste is transformed into oxygen, recycled water, and edible nutrients, creating a closed-loop ecosystem for material cycling. In this system, humans function as consumers, microorganisms conduct waste recycling, and plants or cyanobacteria act as producers, synergistically maintaining a stable foundation for sustaining life in closed habitats. Human-generated organic and inorganic waste is first transferred to fermenting bacteria, which preliminarily process carbon waste, nitrogenous compounds, and minerals before passing material to photoheterotrophic bacteria for further processing. The output then proceeds to nitrifying bacteria, which convert it to nitrates, minerals, and carbon dioxide—resources used by cyanobacteria and higher plants. Through photosynthesis, these organisms generate food, water, and oxygen for humans, closing the ecosystem loop. Microbial communities digest and liquefy feces, solid waste, and urine into CO_2 volatile fatty acids, and minerals (including NH_4^+). Photoheterotrophic bacteria further utilize volatile fatty acids and minerals to produce nutrients and process NH_4^+, which nitrifying bacteria convert into plant- and cyanobacteria-accessible NO_3^-. Cyanobacteria and higher plants then assimilate NO_3^-, minerals, and CO_2 via photosynthesis to supply oxygen and edible nutrients for humans. Within China's Lunar Palace 1 project, optimized plant cultivation techniques efficiently supply oxygen and nutrient-rich fruits and vegetables, while edible insect farming is being explored as a protein production strategy. Urine and condensate water treatment systems extract greywater and potable water, respectively. Initial experiments achieved a urine nitrogen recovery rate of 20.5%, a solid waste degradation rate of 41%, and a food regeneration rate of 55%.[219] Building on Lunar Palace 1, Fu et al. further optimized gas balance mechanisms in the "Lunar Palace 365" project using two strategies:[220] (1) plant photoperiod regulation, with dynamic feedback control of light duration to precisely modulate photosynthesis and balance CO_2 absorption and O_2 release rates; and (2) adjustment of solid waste reactor activity, with optimized temperature to accelerate microbial catabolism, enabling active control of CO_2 generation and O_2 consumption during fermentation. The project demonstrated strong material cycling, with urine and solid waste recovery rates reaching 99% and 67%, respectively, providing critical validation for gas stability and resource efficiency in long-term closed ecosystems.

In addition to life support, microorganisms also enable energy production through microbial fuel cells, which oxidize organic matter in urine or wastewater, root exudates from living plants, inorganic waste such as sulfides, and even certain gaseous pollutants.[221]

CONSTRUCTION APPLICATION BLUEPRINT

Building on the new paradigms of extraterrestrial bioconstruction discussed above, this section presents a consolidated application blueprint. This blueprint not only outlines specific construction scenarios—such as biological bricks, foundation solidification, crack repair, and radiation-resistant materials—but also integrates the critical pathways for overcoming planetary environmental constraints and assesses the developmental readiness of each technological component. The surface regolith of the Moon and Mars comprises silty soils with broad particle size distributions and low plasticity, lacking clay minerals and organic cements. These properties result in extremely weak interparticle bonding, with cohesion on the order of hundreds of pascals, shear strength in the range of thousands of pascals, and natural bearing capacity between tens and hundreds of kilopascals.[222,223] Constructing infrastructure such as habitats, roads, and landing pads directly on this substrate often results in settlement, instability, and dust pollution. For large-scale foundation solidification, traditional cement-based methods are costly and resource-intensive, making MICP a promising alternative with substantial advantages for extensive treatment. MICP has already been validated in large-scale experiments and engineering applications.[224] Van Paassen estab-

Table 2. TRL assessment and basis at each stage.

Phase	Subsystem	Representative Milestones	TRL
Biological Pioneering	P-1: Ecological Colonization & Surface Stabilization	*Syntrichia caninervis* can withstand simulated Mars environments (-196°C, extreme desiccation, and radiation exposure), serving as a pioneer plant for extraterrestrial colonization.[244] Lichens can tolerate extreme desiccation, vacuum pressures down to 10^{-7}–10^{-4} Pa, ionizing radiation up to 190 mGy, and wide temperature fluctuations (-196°C to 70°C).[63]	3
	P-2: Nutrient & Resource Supply	(i) Biocrusts can increase water vapor adsorption by 30%;[245] (ii) Phosphorus-solubilizing bacteria increase available phosphorus in lunar regolith simulant ;[140] (iii) Cyanobacteria cultured in a 100 hPa CO_2/N_2 atmosphere can support the growth of other organisms.[246]	3
Biological conversion	C-1: Leaching of Major Elements	Leaching of Ca, Mn, Fe, Mg, Al, etc., from regolith simulant using Penicillium simplicissimum in a simulated microgravity environment.[247]	4
	C-2: Leaching of Rare/Precious Metals	Under space station conditions, Sphingomonas desiccabilis increases the leaching of Nd/Ce;[104] Penicillium simplicissimum can leach elements like Pd and Pt from meteoritic material in a space station environment.[248]	6
Biological fabrication	T-1: Inorganic Consolidation	Sporosarcina pasteurii combined with urea and MgO solidifies lunar regolith simulant, achieving a compressive strength of ~10 MPa.[180]	4
	T-2: Fungal Composite Aggregation	A viable mycelium scaffold can be produced, with active components maintaining vitality for at least 4 weeks.[191]	3
	T-3: Bioremediation	MICP-based repair of LHS-1 lunar regolith bricks: compressive strength recovery of 28%–54% after 20 days.[233]	3
Self-sustaining life support	L-1: Nutrient Bioreactor	The Yuegong-1 (Lunar Palace 1) BLSS demonstrated that plant production could fully meet plant-based food needs, achieving 100% recovery of oxygen and water.[220]	6
	L-2: Microbial Fuel & Energy Storage	Production of rocket propellant using photosynthetic cyanobacteria, saving ~32% in power consumption.[249]	3

Table 3. Summary of key resources and utilization potential across spatial dimensions.

Environment	Applicable Microbe Types (Validated or Potential Value)	Available Local Resources/Raw Materials	Potential Synthesized Materials/Products
Earth's Surface	Diverse natural microbial consortia: (a) Bio-pioneering: Cyanobacteria, lichens; (b) Bio-conversion: Sporosarcina pasteurii, fungi; (c) Bioconstruction technologies: Sporosarcina pasteurii, fungi; (d) Self-sustaining life systems: Chlorella vulgaris (wastewater treatment), Bacteroides (biogas fermentation)	Soil, rich atmosphere (N_2, CO_2, O_2), liquid water, abundant natural biomass materials (cellulose, chitin, etc.)	Biocement/consolidated soil, mycelium composite materials, bioplastics, biofuels (biogas), environmental bioremediation (carbon sequestration, nitrogen sequestration)
Space Station	Chlorella vulgaris, Microalgae/cyanobacteria	Microgravity conditions, external exposure platforms, waste streams from life support systems (astronaut-exhaled CO_2, urea from urine, wastewater), and resupplied water and nutrients from Earth.	Food, oxygen, regenerated water, as well as synthesized pharmaceuticals and 3D-printing bio-inks.
Moon	(a) Biological pioneering: Cyanobacteria, lichens, Deinococcus radiodurans, microalgae; (b) Biological conversion: Shewanella oneidensis (c) Biological fabrication: Sporosarcina pasteurii, Pleurotus ostreatus (d) Self-sustaining life systems: Photosynthetic cyanobacteria	Anorthositic/basaltic lunar regolith (containing ilmenite), polar water ice, urea (from astronaut urine).	Bio-bricks, radiation shielding materials, metals such as Ti, Fe, Al, Mg, REEs, water, and essential biological nutrients.
Mars	(a) Biological pioneering: A. cylindrica, lichens, Deinococcus radiodurans, Dechloromonas aromatica, microalgae (b) Biological conversion: Shewanella oneidensis, Photosynthetic cyanobacteria (c) Biological fabrication: Sporosarcina pasteurii, Desulfovibrio, Pleurotus ostreatus (d) Self-sustaining life systems: Photosynthetic cyanobacteria, nitrogen-fixing cyanobacteria, Methanobacterium formicicum	CO_2, N_2, basaltic Martian regolith (containing hematite, magnetite), nitrates, sulfates, perchlorates, polar water ice, and urea (from astronaut urine).	Bio-bricks, radiation shielding materials, rocket propellant, metals such as Fe, Al

lished a 100 m^3 test site filled with poorly graded sand, equipped with three injection wells for introducing microbial and nutrient solutions and three extraction wells for recovering reaction fluids.[225] The soil's strength and stiffness had already improved, reaching a peak compressive strength of 12 MPa on the 16th day. Subsequently, this technology was scaled to treat 1000 m^3 of soil at depths between 3 and 20 meters.[226] In another large-scale MICP trial on a 2.3-meter-tall sandy slope with a 3:1 slope ratio (horizontal:vertical) in North Carolina, USA, freeze-thaw cycles had negligible effect on MICP-treated soil, demonstrating the stability of biocementation.[227] These studies confirm the feasibility of MICP for foundation solidification. However, large-scale MICP applications are challenged by spatial variability in cementation and suboptimal strength. Researchers are addressing these issues using discrete element modeling and molecular dynamics simulations to investigate calcite precipitation in porous media,[228,229] providing the foundation for scalable MICP implementation.

Under extreme extraterrestrial conditions, building materials must withstand multiple adverse factors, such as pronounced high-low temperature cycles, strong cosmic radiation, and severe dryness. These stressors cause a

notable reduction in mechanical properties, thermal conductivity, and durability.[9] Microcracks and micropores commonly develop, further compromising structural integrity and thermal stability. Microbial self-healing technology can precipitate minerals such as $CaCO_3$ within cracks, filling and cementing defects in situ, restoring the original properties, and extending service life. For example, Jongvivatsakul et al. artificially generated cracks 120 mm in length and 20 mm in depth; after 20 days of repair, the surface crack area was reduced by 85%, and the compressive strength was 43% higher than that of cracked controls.[230] In addition to direct injection of microorganisms into cracks and pores, self-healing concrete has also been proposed. There are two main mechanisms for self-healing concrete: (1) incorporating repair microorganisms during initial material formation and (2) employing carriers to protect microorganisms as a component of the starting material.[231] The first approach yields relatively high early-stage strength but environmental fluctuations during formation reduce microbial survival. The second method, which uses carriers such as capsules to shelter microorganisms, preserves viability during adverse formation conditions, enabling activation of repair functions upon crack formation. When cracks develop, microorganisms are released from the capsules and initiate repair. Roda et al. developed capsules based on bacterial powder, nutrient solution, SAP, and EPS, incorporating both aerobic and anaerobic bacteria.[232] This system avoids premature reactions during drying and enhances repair capability. The reported repair area rate for cracks between 50 and 600 μm reached 90%. Recent studies indicate that repairing sintered simulated lunar regolith cracks can restore compressive strength by 28%–54% .[233] Microbially produced EPS can form protective shells around materials, shielding them from freeze-thaw cycles, chemical exposure, and microbial erosion, thereby prolonging service life. The complex EPS matrix helps materials tolerate fluctuating humidity and extreme temperatures. Microbial polysaccharides can also spread across surfaces, creating a gelatinous barrier that isolates the matrix from the external environment. This film mitigates the effects of extreme temperatures, radiation, and sand erosion, and reduces potential microbial colonization. The polysaccharide network not only builds an efficient water vapor barrier but also adsorbs and buffers trace volatiles, substantially enhancing the long-term service performance of the extraterrestrial building envelope in complex, stress-coupled environments.[234]

The "Phoenix" Mars probe discovered high concentrations of perchlorate (0.4%–0.6% wt) in the regolith.[235,236] Perchlorate is a strong oxidant and an energy carrier. Three main strategies exist for addressing perchlorate: (1) introducing organic substances, ferric chloride, hydrochloric acid, or plants to decompose and remove perchlorate;[197,237] (2) screening perchlorate-tolerant microorganisms on Earth or employing genetic engineering to enhance tolerance in other strains ,[238] including perchlorate-resistant cyanobacteria and E. coli DH10B;[239,240] and (3) utilizing perchlorate-reducing bacteria to decompose perchlorate and remediate regolith, producing useful energy substances. The biological decomposition pathway of perchlorate consists of three key enzymatic steps. The initial reduction is catalyzed by perchlorate reductase, converting ClO_4^- to chlorite (ClO_2^-), which is the rate-limiting step. Subsequently, chlorite dismutase (Cld) rapidly converts chlorite to chloride (Cl^-) and molecular oxygen, the latter being directly utilizable by biological systems.[241,242] This process removes perchlorate toxicity, releases oxygen, and allows purified Martian soil to serve as a substrate for plant cultivation or as a microbially driven construction module. In addition, electrons released during chlorate oxidation can be harvested to power biological batteries,[243] providing a continuous energy source for extraterrestrial automated construction equipment and robotics. Mars' carbon dioxide-rich atmosphere can also be utilized by microorganisms: (1) as a carbon source to support microbial growth and self-sustaining life systems; (2) directly in MICP for material production; and (3) as an electron acceptor in microbial batteries, thereby supplying energy.[139]

To provide a clear development roadmap, this study systematically evaluates the Technology Readiness Level (TRL) for each subsystem within the proposed four-phase bioconstruction framework, as detailed in Table 2. This assessment reveals a broad spectrum of technological maturity. Foundational concepts in the Biological Pioneering phase, such as surface stabilization and initial nutrient supply, are largely at the lab-based proof-of-concept stage (TRL-3). In contrast, more advanced subsystems have achieved higher readiness. For example, the Biological Conversion of rare metals and the ground-based prototypes for Self-sustaining Life Support bioreactors have been successfully demonstrated in relevant environments, including in-orbit on the ISS, reaching TRL-6. The table summarizes the evidence supporting each TRL assignment, pinpoints the key challenges currently limiting progress, and defines the specific research required to advance each technology to the next level. In addition to assessing the technological maturity of each subsystem, it is crucial to summarize the available resources and constraints that define each operational dimension. These resource boundary conditions directly influence which technologies are feasible and how they must be adapted. Therefore, Table 3 provides a systematic overview of the key resources and their utilization potential across the Earth, LEO, and extraterrestrial dimensions (Moon/Mars). This summary clarifies the resource landscape that will shape the development and deployment of bioconstruction technologies at each stage of the roadmap.

Additionally, extraterrestrial bioconstruction must adhere to Planetary Protection principles to prevent Forward Contamination." The deployment of engineered microbes risks irreversibly altering celestial environments, compromising scientific research, and harming potential native life. These risks evolve throughout the construction lifecycle, shifting from the initial danger of ecological contamination during the pioneering phase, to challenges of industrial biosafety and permanent landscape alteration during construction, and finally to the unpredictable evolution of closed ecosystems. Addressing these challenges requires a proactive, multi-layered mitigation strategy integrated from the design phase. This approach should combine genetic safeguards, robust process-level containment with waste inactivation, and strict operational protocols involving phased progression and zonal management.

CONCLUSIONS

Establishing sustainable human habitats in extraterrestrial environments is a grand engineering endeavor in which microbe-centered bioconstruction plays a pivotal role, demanding a transition from conventional construction concepts to full-lifecycle solutions. This review presents a paradigm of full-lifecycle extraterrestrial bioconstruction and an implementation roadmap across spatial scales, encompassing foundational research on Earth, verification aboard space stations, and application on the Moon and Mars. By synthesizing the shared adaptive mechanisms and regulatory strategies of terrestrial extremophiles under multiple stresses, the roadmap provides a theoretical foundation for the engineering, screening, and utilization of functional microbial strains. In orbit, the feasibility of biomining and biocementation has been demonstrated under microgravity and radiation, elucidating environmental impacts on microbial function and metabolism and guiding risk mitigation for in-situ deployment. For target bodies such as the Moon and Mars, a four-stage scheme is outlined, comprising biological pioneering, biological conversion, fabrication, and self-sustaining life support. This scheme begins with pioneering and conversion as phases for early settlement and environmental conditioning; proceeds to resource extraction and material supply through fabrication; and ultimately aims to achieve habitat construction and closed-loop operation. Collectively, it offers a comprehensive, practicable blueprint for sustainable lunar and Martian base development.

DISCUSSIONS

Rapid multi-stress screening of pioneer microorganisms

Earth extremophilic microorganisms develop their defences—such as DNA repair pathways—within relatively simple and stable ecological niches. In contrast, lunar and Martian environments exert simultaneous, nonlinear stresses, so single-trait strains are inadequate.[250] Conventional culture-based testing cycles remain slow and low-throughput.[251] Furthermore, microgravity can alter protein abundance in radiation-resistant D. radiodurans.[252] AI-driven genome–phenotype–environment models now predict multi-resistance gene sets.[253] Deep-learning frameworks, including Transformer architectures, integrate diverse stress datasets to design customised chassis microorganisms.[254]

Beyond initial stress tolerance, a critical challenge is the genetic and func-

tional stability of natural or engineered strains during long-term exposure to extraterrestrial environments. Previous studies have indicated that conditions such as space radiation and microgravity can induce genomic structural variations and functional decay over successive passages, potentially undermining the stability of synthetic ecosystems designed for extraterrestrial construction.[95] Moreover, during adaptive evolution, strains may exhibit metabolic or performance trade-offs, such as enhancing survivability at the expense of reducing the yield of a target product.[255] Therefore, future work must focus on developing strategies that incorporate both functional performance and evolutionary robustness from the initial design stage. These strategies should be integrated with methods such as experimental evolution, omics monitoring, and modeling to investigate potential evolutionary trajectories and their associated risks, ultimately enhancing the long-term sustainability of extraterrestrial synthetic ecosystems.

High-throughput on-orbit verification and data feedback

Payload restrictions on the ISS and Tiangong limit most experiments to single-strain survival snapshots, and hardware failures may cause complete data loss. Ground-based simulators now reproduce up to nine space-related factors but still deviate from real orbital conditions.[256] Lab-on-chip (μTAS) platforms can culture multiple strains under graded,[257,258] combined stresses during flight, transmit real-time metabolic data, and—through AI-guided space–ground co-optimization—create a closed in-orbit–ground feedback loop, substantially accelerating experimental cycles.[259]

Carbon availability: A critical resource constraint for the moon

While bioconstruction strategies based on autotrophic microorganisms—such as cyanobacteria-driven metal bioleaching and photosynthetic MICP—are highly sensitive to CO_2 availability, Mars and the Moon present fundamentally different carbon source boundary conditions. The Martian atmosphere is dominated by CO_2 (~95%), and in-situ demonstrations have already proven that an ISRU pathway of "CO_2 collection, compression, and conversion" is technically viable.[260]

In stark contrast, the Moon lacks any readily available free CO_2, which implies that in a lunar context, CO_2-dependent bioconstruction strategies cannot rely on the premise of sourcing from the ambient environment and must instead shift towards engineered CO_2 supply and closed-loop management. Specifically, two primary approaches can be prioritized: first, leveraging closed-loop carbon management, which would use CO_2 recycled from astronaut respiration or established self-sustaining ecosystems as a foundational carbon source, paired with urea-driven MICP technology (where the carbon source is derived from urea decomposition rather than environmental CO_2). The second approach involves exploring the extraction of CO_2 from lunar polar volatiles,[261] which could also serve as a foundational starting point for establishing a polar resource utilization chain.

Mechanistic insight into extraterrestrial biotechnology

Macroscopic indicators such as cyanobacterial O_2 yield provide limited information about how microbes drive mineral precipitation or reprogram metabolism under combined extreme conditions. A multi-scale workflow—using omics to identify mineralisation and stress-tolerance genes, cryo-electron microscopy and molecular-dynamics simulations to examine structural resilience, and in-situ AFM–Raman spectroscopy to monitor ion migration and crystal growth—rapidly links genotype to function, expediting rational strain selection.

Long-term service performance of biobased materials

Biocements and mycelium composites must withstand vacuum, radiation, temperature fluctuations, and chemical exposure over extended periods, yet most available data come from short-duration, single-factor laboratory tests that obscure actual degradation pathways. High-fidelity exposure platforms with continuous monitoring should provide damage datasets for coupled thermal–mechanical–chemical–radiation FE/DE models, supporting sensitivity analysis and service-life prediction. Integrating these models and sensor data within a digital-twin framework enables real-time calibration, informing compositional adjustments and reliability assessments of extraterrestrial structures.

REFERENCES

1. Pulsiri N., Dobson R.R., Isckia T., et al. (2022). Ad-Astra: A bibliometric analysis of Lunar and Mars explorations. 2022 Portland international conference on management of engineering and technology. IEEE. pp:1-8. DOI:10.23919/PICMET53225.2022.9882849
2. Anand M., Crawford I.A, Balat-Pichelin M., et al. (2012). A brief review of chemical and mineralogical resources on the Moon and likely initial in situ resource utilization (ISRU) applications. *Planet. Space Sci.* **74**:42–48. DOI:10.1016/j.pss.2012.08.012
3. Liu J., Li H., Sun L., et al. (2022). In-situ resources for infrastructure construction on Mars: A review. *Int. J. Transp. Sci. Technol.* **11**:1–16. DOI:10.1016/j.ijtst.2021.02.001
4. Creech S., Guidi J., and Elburn D. (2022). Artemis: An overview of NASA's activities to return humans to the Moon. In 2022 IEEE aerospace conference (AERO). IEEE. pp:1-7. DOI:10.1109/AERO53065.2022.9843277
5. Xu L., Li H., Pei Z., et al. (2022). A brief introduction to the international lunar research station program and the interstellar express mission. *Chin. J. Space Sci.* **42**:511–513. DOI:10.11728/cjss2022.04.yg28
6. Amini K., Moradi M., Teymoori P.E.B., et al. (2022). Design of a set of habitat units and the corresponding surrounding cluster for long-term scientific missions in the pre-terraforming era on Mars. *Icarus* **385**:115119. DOI:10.1016/j.icarus.2022.115119
7. Weppler J., Sabathier V. and Bander A. (2009). Costs of an international lunar base. *Center for strategic and international studies.* https://csis-website-prod.s3.amazonaws.com/s3fs-public/legacy_files/files/publication/090923_weppler_lunar_base_costs.pdf
8. Bao C., Zhang D., Wang Q., et al. (2024). Lunar in situ large-scale construction: Quantitative evaluation of regolith solidification techniques. *Engineering* **39**:204–221. DOI:10.1016/j.eng.2024.03.004
9. Zhou C., Gao Y.Y., Zhou Y., et al. (2024). Properties and characteristics of regolith-based materials for extraterrestrial construction. *Engineering* **37**:159–181. DOI:10.1016/j.eng.2023.11.019
10. Sakamoto K. and Wajima T. (2020). Preparation of geopolymer cement from simulated lunar rock sand using alkali fusion. *Int. J. Geomate.* **18**:62–67. DOI:10.21660/2020.70.9162
11. Allende M.I., Miller J.E., Davis B.A., et al. (2020). Prediction of micrometeoroid damage to lunar construction materials using numerical modeling of hypervelocity impact events. *Int. J. Impact Eng.* **138**:103499. DOI:10.1016/j.ijimpeng.2020.103499
12. Badyukov D.D. (2020). Micrometeoroids: The flux on the Moon and a source of volatiles. *Solar Syst. Res.* **54**:263–274. DOI:10.1134/S0038094620040024
13. Seedhouse E. (2020). International space station life support system. Life support systems for humans in space (Springer Cham.), pp:151-179. DOI:10.1007/978-3-030-52859-1_5
14. Liu H. (2025). Biogenic construction: The new era of civil engineering. *Biogeotech.* **3**:100130. DOI:10.1016/j.bgtech.2024.100130
15. Berliner A.J., Lipsky I., Ho D., et al. (2022). Space bioprocess engineering on the horizon. *Commun. Eng.* **1**:13. DOI:10.1038/s44172-022-00012-9
16. Nangle S.N., Wolfson M.Y., Hartsough L., et al. (2020). The case for biotech on Mars. *Nat. Biotechnol.* **38**:401–407. DOI:10.1038/s41587-020-0485-4
17. Santomartino R., Averesch N.J.H., Bhuiyan M., et al. (2023). Toward sustainable space exploration: A roadmap for harnessing the power of microorganisms. *Nat. Commun.* **14**:1391. DOI:10.1038/s41467-023-37070-2
18. Santomartino R., Zea L. and Cockell, C. S. (2022). The smallest space miners: Principles of space biomining. *Extremophiles* **26**:7. DOI:10.1007/s00792-021-01253-w
19. Dikshit R., Dey A., Gupta N., et al. (2021). Space bricks: From LSS to machinable structures via MICP. *Ceram. Int.* **47**:14892–14898. DOI:10.1016/j.ceramint.2020.07.309
20. Sukhinov D.V., Gotovtsev P.M. and Sergeeva Y.E. (2023). Phototrophic microorganisms in bioregenerative life support systems for long-term crewed expeditions: Prospects and challenges. *Acta Astronaut.* **211**:518–538. DOI:10.1016/j.actaastro.2023.07.006
21. Langenfeld N.J., Kusuma P., Wallentine T., et al. (2021). Optimizing nitrogen fixation and recycling for food production in regenerative life support systems. *Front. Astron. Space.* **8**:699688. DOI:10.3389/fspas.2021.699688
22. Zhou X., Liang B., Zhang T., et al. (2024). Co-inoculation of fungi and desert cyanobacteria facilitates biological soil crust formation and soil fertility. *Front. Microbiol.* **15**:1377732. DOI:10.3389/fmicb.2024.1377732
23. Shu W and Huang L (2022). Microbial diversity in extreme environments. *Nat. Rev. Microbiol.* **20**: 219–235. DOI: 10.1038/s41579-021-00648-y.
24. Gostinčar C., Stajich J.E. and Gunde-Cimerman N. (2023). Extremophilic and extremotolerant fungi. *Curr. Biol.* **33**:R752–R756. DOI:10.1016/j.cub.2023.06.011
25. Moroni L., Tabury K., Stenuit H., et al. (2022). What can biofabrication do for space and what can space do for biofabrication. *Trends Biotechnol.* **40**:398–411. DOI:10.1016/j.tibtech.2021.08.008
26. Cockell C.S. (2022). Bridging the gap between microbial limits and extremes in space: Space microbial biotechnology in the next 15 years. *Microb. Biotechnol.* **15**:29–41. DOI:10.1111/1751-7915.13927
27. Prasad B., Richter P, Vadakedath N, et al. (2021). How the space environment influences organisms: An astrobiological perspective and review. *Int. J. Astrobiol.* **20**:159–177. DOI:10.1017/S1473550421000057

28. Liu J., Zhang W., He K., et al. (2022). Survival of the magnetotactic bacterium Magnetospirillum gryphiswaldense exposed to Earth's lower near space. *Sci. Bull.* **67**:1335–1339. DOI:10.1016/j.scib.2022.03.005
29. Wood C., Bruinink A., Trembath-Reichert E., et al. (2024). Active microbiota persist in dry permafrost and active layer from Elephant Head, Antarctica. *ISME Commun.* **4**:ycad002. DOI:10.1093/ismeco/ycad002
30. Siliakus M.F., van der Oost J. and Kengen S.W. (2017). Adaptations of archaeal and bacterial membranes to variations in temperature, pH and pressure. *Extremophiles.* **21**:651–670. DOI:10.1007/s00792-017-0939-x
31. Obruča S., Dvořák P., Sedláček P., et al. (2022). Polyhydroxyalkanoates synthesis by halophiles and thermophiles: Towards sustainable production of microbial bioplastics. *Biotechnol. Adv.* **58**:107906. DOI:10.1016/j.biotechadv.2022.107906
32. Somayaji A., Dhanjal C.R., Lingamsetty R., et al. (2022). An insight into the mechanisms of homeostasis in extremophiles. *Microbiol. Res.* **263**:127115. DOI:10.1016/j.micres.2022.127115
33. Sylvia D.M., Fuhrmann J.J., Hartel P.G., et al.. (2021). Bacteria and archaea. Terry Gentry, Jeffry J. F., David A.Z.(ed). Principles and applications of soil microbiology (Elsevier, Amsterdam), pp:111-148. DOI:10.1016/B978-0-12-820202-9.00005-8
34. Abath N., Ferrada E., Barve A., et al. (2013). Growth temperature and genome size in bacteria are negatively correlated, suggesting genomic streamlining during thermal adaptation. *Genome biol. Evol.* **5**:966–977. DOI:10.1093/gbe/evt050
35. Hu E.Z., Lan X.R., Liu Z.L., et al. (2022). A positive correlation between GC content and growth temperature in prokaryotes. *BMC genomics* **23**:110. DOI:10.1186/s12864-022-08353-7
36. Hurst L.D. and Merchant A.R. (2001). High guanine–cytosine content is not an adaptation to high temperature: A comparative analysis amongst prokaryotes. *Proc. Biol. Sci.* **268**:493–497. DOI:10.1098/rspb.2000.1397
37. Ahmad A., Rahamtullah and Mishra R. (2022). Structural and functional adaptation in extremophilic microbial α-amylases. *Biophys. Rev.* **14**:499–515. DOI:10.1007/s12551-022-00931-z
38. Liu L., Cai L., Chu Y., et al. (2022). Thermostability mechanisms of β-agarase by analyzing its structure through molecular dynamics simulation. *AMB Express* **12**:50. DOI:10.1186/s13568-022-01394-x
39. Lewin A., Wentzel A. and Valla S. (2013). Metagenomics of microbial life in extreme temperature environments. *Curr. Opin Biotech.* **24**:516–525. DOI:10.1016/j.copbio.2012.10.012
40. Collins T. and Margesin R. (2019). Psychrophilic lifestyles: Mechanisms of adaptation and biotechnological tools. *Appl. Microbiol. Biot.* **103**:2857–2871. DOI:10.1007/s00253-019-09659-5
41. Truongvan N., Jang S. and Lee C. (2016). Flexibility and stability trade-off in active site of cold-adapted Pseudomonas mandelii esterase EstK. *Biochemistry.* **55**:3542–3549. DOI:10.1021/acs.biochem.6b00177
42. Goordial J., Raymond-Bouchard I., Zolotarov Y.,et al. (2016). Cold adaptive traits revealed by comparative genomic analysis of the eurypsychrophile Rhodococcus sp. JG3 isolated from high elevation McMurdo Dry Valley permafrost, Antarctica. *FEMS microbiol ecol*, **92**: fiv154. DOI:10.1093/femsec/fiv154
43. Yusof N.A., Hashim N.H.F. and Bharudin I. (2021). Cold adaptation strategies and the potential of psychrophilic enzymes from the antarctic yeast, Glaciozyma antarctica PI12. *J. Fungi* **7**:528. DOI:10.3390/jof7070528
44. Casanueva A., Tuffin M., Cary C.,et al. (2010). Molecular adaptations to psychrophily: The impact of 'omic'technologies. *Trends Microbiol.* **18**:374–381. DOI:10.1016/j.tim.2010.05.002
45. Nayak T., Sengupta I. and Dhal P.K. (2021). A new era of radiation resistance bacteria in bioremediation and production of bioactive compounds with therapeutic potential and other aspects: An in-perspective review. *J. Environl. Radioactiv.* **237**:106696. DOI:10.1016/j.jenvrad.2021.106696
46. Jin M., Xiao A., Zhu L., et al. (2019). The diversity and commonalities of the radiation-resistance mechanisms of Deinococcus and its up-to-date applications. *AMB express* **9**:1–12. DOI:10.1186/s13568-019-0862-x
47. Liu F., Li N. and Zhang Y. (2023). The radioresistant and survival mechanisms of Deinococcus radiodurans. *Radiat. Med. Protect.* **4**:70–79. DOI:10.1016/j.radmp.2023.03.001
48. Makarova K.S., Aravind L., Wolf Y.I., et al. (2001). Genome of the extremely radiation-resistant bacterium Deinococcus radiodurans viewed from the perspective of comparative genomics. *Microbiol. Mol. Biol. Rev.* **65**:44–79. DOI:10.1128/MMBR.65.1.44-79.2001
49. Timmins J. and Moe E. (2016). A decade of biochemical and structural studies of the DNA repair machinery of Deinococcus radiodurans: Major findings, functional and mechanistic insight and challenges. *Comput. Struct. Biotechnol J.* **14**:168–176. DOI:10.1016/j.csbj.2016.04.001
50. Cho C., Lee G.W., Hong S.H., et al. (2019). Novel functions of peroxiredoxin Q from Deinococcus radiodurans R1 as a peroxidase and a molecular chaperone. *FEBS Lett.* **593**:219–229. DOI:10.1002/1873-3468.13302
51. Lim S., Jung J.H., Blanchard L. and de Groot A. (2019). Conservation and diversity of radiation and oxidative stress resistance mechanisms in Deinococcus species. *FEMS microbiol. Rev.* **43**:19–52. DOI:10.1093/femsre/fuy037
52. Hibshman J.D., Clegg J. S. and Goldstein B. (2020). Mechanisms of desiccation tolerance: Themes and variations in brine shrimp, roundworms, and tardigrades. *Front. Physiol.* **11**:592016. DOI:10.3389/fphys.2020.592016
53. Karlinsey J.E., Fung A.M., Johnston N., et al. (2022). Cyclopropane fatty acids are important for Salmonella enterica serovar Typhimurium virulence. *Infect. Immune.* **90**:e00479–21. DOI:10.1128/IAI.00479-21
54. Olgenblum G.I., Hutcheson B.O., Pielak, G.J.,et al. (2024). Protecting proteins from desiccation stress using molecular glasses and gels. *Chem. Rev.* **124**:5668–5694. DOI:10.1021/acs.chemrev.3c00752
55. Marks R.A., Ekwealor J.T.B., Artur M.A.S., et al. (2025). Life on the dry side: A roadmap to understanding desiccation tolerance and accelerating translational applications. *Nat. Commun.* **16**:3284. DOI:10.1038/s41467-025-58656-y
56. Claudia M.V., Javiera A.A., Sebastián N.S., et al. (2024). Interplay between desiccation and oxidative stress responses in iron-oxidizing acidophilic bacteria. *J. Biotechnol.* **383**:64–72. DOI:10.1016/j.jbiotec.2024.01.017
57. Calahan D., Dunham M., DeSevo C., et al, (2011). Genetic analysis of desiccation tolerance in Saccharomyces cerevisiae. *Genetics.* **189**: 507-519. DOI: 10.1534/genetics.111.130369
58. Colica G., Li H., Rossi F., et al. (2014). Microbial secreted exopolysaccharides affect the hydrological behavior of induced biological soil crusts in desert sandy soils. *Soil Biol. Biochem.* **68**:62–70. DOI:10.1016/j.soilbio.2013.09.017
59. Nawaz M., Hassan M.U., Chattha M.U., et al. (2022). Trehalose: A promising osmo-protectant against salinity stress—physiological and molecular mechanisms and future prospective. *Mol. Biol. Rep.* **49**:11255–11271. DOI:10.1007/s11033-022-07681-x
60. Khaleque H.N., González C., Shafique R., et al. (2019). Uncovering the mechanisms of halotolerance in the extremely acidophilic members of the Acidihalobacter genus through comparative genome analysis. *Front. Microbiol.* **10**:155. DOI:10.3389/fmicb.2019.00155
61. Beblo-Vranesevic K., Huber H. and Rettberg P. (2017). High tolerance of Hydrogenothermus marinus to sodium perchlorate. *Front. Microbiol.* **8**:1369. DOI:10.3389/fmicb.2017.01369
62. Heinz J., Waajen A.C., Airo A., et al. (2019). Bacterial growth in chloride and perchlorate brines: Halotolerances and salt stress responses of Planococcus halocryophilus. *Astrobiology* **19**:1377–1387. DOI:10.1089/ast.2019.2069
63. Kyriatzi A., Tzivras G., Pirintsos S., et al. (2021) Biotechnology under extreme conditions: Lichens after extreme UVB radiation and extreme temperatures produce large amounts of hydrogen. *J. Biotechnol.* **342**: 128-138. DOI: 10.1016/j.jbiotec.2021.10.011.
64. de la Torre Noetzel R., Miller A.Z., de la Rosa J.M., et al. (2018). Cellular responses of the lichen Circinaria gyrosa in Mars-like conditions. *Front. Microbiol.* **9**:308. DOI:10.3389/fmicb.2018.00308
65. Rokaya N., Carr E.C., Tiwari S., et al. (2025). Design of co-culturing system of diazotrophic cyanobacteria and filamentous fungi for potential application in self-healing concrete. *Mater Today Commun.* **44**:112093. DOI:10.1016/j.mtcomm.2025.112093
66. Jimenez M., L'Heureux J., Kolaya E. et al. (2024). Synthetic extremophiles via species-specific formulations improve microbial therapeutics. *Nat. Mater.* **23**:1436–1443. DOI:10.1038/s41563-024-01937-6
67. Chen J., Li, Y., and Mahadevan R. (2023). Genetic engineering of Acidithiobacillus ferridurans using CRISPR systems to mitigate toxic release in biomining. *Environ. Sci. Technol.* **57**:12315–12324. DOI:10.1021/acs.est.3c02492
68. Chen J., Liu Y., Diep P., et al. (2022). Genetic engineering of extremely acidophilic Acidithiobacillus species for biomining: Progress and perspectives. *J. Hazard. Mater.* **438**:129456. DOI:10.1016/j.jhazmat.2022.129456
69. Wang Q., Hu Z., Li Z., et al (2023). Exploring the application and prospects of synthetic biology in engineered living materials. *Adv. Mater.* **35**: 2305828. DOI: 10.1002/adma.202305828.
70. Li F., Li X., Ye L., et al. (2022) A genetically engineered composite biofilm for microbial induced calcium carbonate precipitation by synergic effect of urease, protein adhesive and xanthan gum. *J. Environ. Chem. Eng.* **10**: 108431. DOI: 10.1016/j.jece.2022.108431.
71. Berepiki A., Hitchcock A., Moore C.M., et al. (2016). Tapping the unused potential of photosynthesis with a heterologous electron sink. *ACS Synth. Biol.* **5**:1369–1375. DOI:10.1021/acssynbio.6b00100
72. Rosa L. T., Vernhes É., Soulet A.L., et al. (2024). Structural insights into the mechanism of DNA branch migration during homologous recombination in bacteria. *EMBO J.* **43**:6180–6198. DOI:10.1038/s44318-024-00264-5
73. Hertzog M., Perry T.N., Dupaigne P., et al. (2023). Assembly mechanism and cryoEM structure of RecA recombination nucleofilaments from Streptococcus pneumoniae. *Nucleic Acids Res.* **51**:2800–2817. DOI:10.1093/nar/gkad080
74. Horne W.H., Volpe R.P., Korza G., et al. (2022). Effects of desiccation and freezing on microbial ionizing radiation survivability: Considerations for Mars sample return. *Astrobiology,* **22**:1337–1350. DOI:10.1089/ast.2022.0065
75. Kochhar N., Kumar I.K., Shrivastava S., et al. (2022). Perspectives on the microorganism of extreme environments and their applications. *Curr. Res. Microb. Sci.* **3**:100134. DOI:10.1016/j.crmicr.2022.100134
76. Jomova K., Alomar S.Y., Alwasel S.H., et al. (2024). Several lines of antioxidant defense against oxidative stress: Antioxidant enzymes, nanomaterials with multiple enzyme-mimicking activities, and low-molecular-weight antioxidants. *Arch Toxicol,*

98:1323–1367. DOI:10.1007/s00204-024-03696-4
77. Elsaesser A., Burr D.J., Mabey P., et al. (2023). Future space experiment platforms for astrobiology and astrochemistry research. *npj Microgravity* **9**:43. DOI:10.1038/s41526-023-00292-1
78. Sweet P., Ball N., Vu S., Anderson L., et al. (2025). Bionutrients-1: Utilizing genomics and transcriptomics to assess the reliability of microorganisms for in situ nutrient production on long duration missions. 2025 NASA HRP IWS human research program investigator's workshop. https://ntrs.nasa.gov/citations/20250000598.
79. Zhang B., Zhong R., Shen G., et al. (2025). The space radiobiological exposure facility on the China space station. *Astrobiology* **25**:32–41. DOI:10.1089/ast.2024.0027
80. NASA. (2023). Exposed: International space station tests organisms and materials in space. https://www.nasa.gov/missions/station/iss-research/exposed-international-space-station-tests-organisms-materials-in-space/
81. Billi D. (2019). Desert cyanobacteria under space and planetary simulations: A tool for searching for life beyond Earth and supporting human space exploration. *Int. J. Astrobiol.* **18**:483–489. DOI:10.1017/S147355041800037X
82. Ott E., Kawaguchi Y., Kölbl D., et al. (2020). Molecular repertoire of Deinococcus radiodurans after 1 year of exposure outside the International Space Station within the Tanpopo mission. *Microbiome.* **8**:1–16. DOI:10.1186/s40168-020-00927-5
83. Deshevaya E.A., Fialkina S.V., Shubralova E.V., et al. (2024). Survival of microorganisms during two-year exposure in outer space near the ISS. *Sci. Rep.* **14**:334. DOI:10.1038/s41598-023-49525-z
84. Gomoiu I., Chatzitheodoridis E., Vadrucci S., et al. (2013). The effect of spaceflight on growth of Ulocladium chartarum colonies on the international space station. *PLoS One.* **8**:e62130. DOI:10.1371/journal.pone.0062130
85. Senatore G., Mastroleo F., Leys N., et al. (2018). Effect of microgravity & space radiation on microbes. *Future Microbiol.* **13**:831–847. DOI:10.2217/fmb-2017-0251
86. Sengupta P., Muthamilselvi Sivabalan S.K., Singh N.K., et al. (2024). Genomic, functional, and metabolic enhancements in multidrug-resistant Enterobacter bugandensis facilitating its persistence and succession in the International Space Station. *Microbiome.* **12**:62. DOI:10.1186/s40168-024-01777-1
87. Sowmeya V.G. and Sathiavelu M. (2024). Biofilm dynamics in space and their potential for sustainable space exploration–A comprehensive review. *Life Sci. Space Res.* **44**:108–121. DOI:10.1016/j.lssr.2024.08.006
88. Acres J.M., Youngapelian M.J. and Nadeau J. (2021). The influence of spaceflight and simulated microgravity on bacterial motility and chemotaxis. *npj Microgravity* **7**:7. DOI:10.1038/s41526-021-00135-x
89. Kim W., Tengra F.K., Young Z., et al. (2013) Spaceflight promotes biofilm formation by Pseudomonas aeruginosa. *PloS one.* **8**: e62437. DOI: 10.1371/journal.pone.0062437
90. Wilson J.W., Ott C.M., Zu Bentrup K.H., et al. (2007) Space flight alters bacterial gene expression and virulence and reveals a role for global regulator Hfq. *Proc. Natl. Acad. Sci. USA.* **104**: 16299-16304. DOI: 10.1073/pnas.0707155104
91. Flores P., McBride S.A., Galazka J.M., et al. (2023). Biofilm formation of Pseudomonas aeruginosa in spaceflight is minimized on lubricant impregnated surfaces. *npj Microgravity* **9**:66. DOI:10.1038/s41526-023-00316-w
92. Marra D., Rizzo M. and Caserta S. (2025). Microfluidics unveils role of gravity and shear stress on Pseudomonas fluorescens motility and biofilm growth. *npj Biofilms Microbi.* **11**:122. DOI:10.1038/s41522-025-00744-4
93. Moreno-Villanueva M., Wong M., Lu T., et al. (2017). Interplay of space radiation and microgravity in DNA damage and DNA damage response. *npj Microgravity.* **3**:14. DOI:10.1038/s41526-017-0019-7
94. Zhao L., Zhang G., Tang A., et al. (2023). Microgravity alters the expressions of DNA repair genes and their regulatory miRNAs in space-flown Caenorhabditis elegans. *Life Sci. Space Res.* **37**:25–38. DOI:10.1016/j.lssr.2023.02.002
95. Irby I. and Broddrick J.T. (2024). Microbial adaptation to spaceflight is correlated with bacteriophage-encoded functions. *Nat. Commun.* **15**:3474. DOI:10.1038/s41467-023-42104-w
96. Revellame E.D., Aguda R., Chistoserdov A., et al. (2021). Microalgae cultivation for space exploration: Assessing the potential for a new generation of waste to human life-support system for long duration space travel and planetary human habitation. *Algal Research.* **55**:102258. DOI:10.1016/j.algal.2021.102258
97. Napoli A., Micheletti D., Pindo M., et al. (2022). Absence of increased genomic variants in the cyanobacterium Chroococcidiopsis exposed to Mars-like conditions outside the space station. *Sci. Rep.* **12**:8437. DOI:10.1038/s41598-022-12631-5
98. Billi D., Mosca C., Fagliarone C., et al. (2020). Exposure to low Earth orbit of an extreme-tolerant cyanobacterium as a contribution to lunar astrobiology activities. *Int. J. Astrobiol.* **19**:53–60. DOI:10.1017/S1473550419000168
99. Kawaguchi Y., Yang Y., Kawashiri N., et al. (2013). The possible interplanetary transfer of microbes: Assessing the viability of Deinococcus spp. under the ISS environmental conditions for performing exposure experiments of microbes in the Tanpopo mission. *Origins Life Evol. B.* **43**:411–428. DOI:10.1007/s11084-013-9346-1
100. Cortesão M., Fuchs F.M., Commichau F.M., et al. (2019). Bacillus subtilis spore resistance to simulated Mars surface conditions. *Front. Microbiol.* **10**:333. DOI:10.3389/fmicb.2019.00333
101. Panitz C., Horneck G., Rabbow E., et al. (2015). The SPORES experiment of the EXPOSE-R mission: Bacillus subtilis spores in artificial meteorites. *Int. J. Astrobiol.* **14**:105–114. DOI:10.1017/S1473550414000251
102. Onofri S., de Vera J.P., Zucconi L. et al. (2015). Survival of Antarctic cryptoendolithic fungi in simulated Martian conditions on board the International Space Station. *Astrobiology* **15**:1052–1059. DOI:10.1089/ast.2015.1324
103. Santomartino R., Waajen A.C., De Wit W., et al. (2020). No effect of microgravity and simulated Mars gravity on final bacterial cell concentrations on the International Space Station: Applications to space bioproduction. *Front. Microbiol.* **11**:579156. DOI:10.3389/fmicb.2020.579156
104. Cockell C.S., Santomartino R., Finster K., et al. (2020). Space station biomining experiment demonstrates rare earth element extraction in microgravity and Mars gravity. *Nat. Commun.* **11**:5523. DOI:10.1038/s41467-020-19276-w
105. Cockell C.S., Santomartino R., Finster K., et al. (2021). Microbially-enhanced vanadium mining and bioremediation under micro-and Mars gravity on the International Space Station. *Front. Microbiol.* **12**:641387. DOI:10.3389/fmicb.2021.641387
106. Gu J.D. (2007). Microbial colonization of polymeric materials for space applications and mechanisms of biodeterioration: A review. *Int. Biodeter. Biodeg.* **59**:170–179. DOI:10.1016/j.ibiod.2006.08.010
107. Zhang W., Chen N., Yuan J., et al. Initial attempt: Design and application of microorganism-material interaction test on On-orbit space microgravity conditions. *Acta Astronaut.* **228**: 384-395. DOI:10.1016/j.actaastro.2024.12.006
108. Mahnert A., Verseux C., Schwendner P., et al. (2021). Microbiome dynamics during the HI - SEAS IV mission, and implications for future crewed missions beyond Earth. *Microbiome.* **9**:27. DOI:10.1186/s40168-020-00959-x
109. Cowen D., Zhang R. and Komorowski M. (2024). Infections in long - duration space missions. *The Lancet Microbe.* **5**:100875. DOI:10.1016/S2666-5247(24)00098-3
110. Romsdahl J., Blachowicz A., Chiang A.J., et al. (2018). Characterization of Aspergillus niger isolated from the international space station. *mSystems.* **3**:e00112–18. DOI:10.1128/mSystems.00112-18
111. Simoes M.F., Antunes A. (2021). Microbial pathogenicity in space. *Pathogens* **10**:450. DOI:10.3390/pathogens10040450
112. Afshinnekoo E., Scott R.T., MacKay M.J., et al. (2020). Fundamental biological features of spaceflight: Advancing the field to enable deep - space exploration. *Cell.* **183**:1162–1184. DOI:10.1016/j.cell.2020.10.050
113. Urbaniak C., Lorenzi H., Thissen J., et al. (2020). The influence of spaceflight on the astronaut salivary microbiome and the search for a microbiome biomarker for viral reactivation. *Microbiome.* **8**:56. DOI:10.1186/s40168-020-00830-z
114. Tozzo P., Delicati A. and Caenazzo L. (2022). Skin microbial changes during space flights: A systematic review. *Life* **12**:1498. DOI:10.3390/life12101498
115. Slaba T.C., Rahmanian S., George S., et al. (2025). Validated space radiation exposure predictions from earth to mars during Artemis-I. *npj Microgravity* **11**:6. DOI:10.1038/s41526-025-00459-y
116. Berger T., Matthiä D., Burmeister S., et al. (2020). Long term variations of galactic cosmic radiation on board the International Space Station, on the Moon and on the surface of Mars. *J. Space Weather Spac.* **10**:34. DOI:10.1051/swsc/2020028
117. George S.P., Gaza R., Matthiä D., et al. (2024). Space radiation measurements during the Artemis I lunar mission. *Nature* **634**:48–52. DOI:10.1038/s41586-024-07927-7
118. Maier S., Tamm A., Wu D., et al. (2018). Photoautotrophic organisms control microbial abundance, diversity, and physiology in different types of biological soil crusts. *ISME J.* **12**:1032–1046. DOI:10.1038/s41396-018-0062-8
119. Guida G., Nicosia A., Settanni L., et al. (2023). A review on effects of biological soil crusts on hydrological processes. *Earth-Sci. Rev.* **243**:104516. DOI:10.1016/j.earscirev.2023.104516
120. Hartmann M. and Six J. (2023). Soil structure and microbiome functions in agroecosystems. *Nat. Rev. Earth Env.* **4**:4–18. DOI:10.1038/s43017-022-00366-w
121. Rabot E., Wiesmeier M., Schlüter S., et al. (2018). Soil structure as an indicator of soil functions: A review. *Geoderma* **314**:122–137. DOI:10.1016/j.geoderma.2017.11.009
122. Cao Y., Xiao B. and Ghanbarian B. (2024). Biocrusts enhance soil structural stability during freeze-thaw cycles and improve soil erosion resistance in cold-winter drylands. *Catena* **243**:108206. DOI:10.1016/j.catena.2024.108206
123. Rodriguez-Caballero E., Stanelle T., Egerer S., et al. (2022). Global cycling and climate effects of aeolian dust controlled by biological soil crusts. *Nat. Geosci.* **15**:458–463. DOI:10.1038/s41561-022-00942-1
124. Liu Y., Cockell C.S., Wang G., et al. (2008). Control of Lunar and Martian dust—Experimental insights from artificial and natural cyanobacterial and algal crusts in the desert of Inner Mongolia. *China. Astrobiology* **8**:75–86. DOI:10.1089/ast.2007.0122
125. Yu X., Xiao B., Cao Y., et al. (2024). Microbial-induced extracellular polymers are fundamentally responsible for the mechanical stability of biocrusts in drylands. *Catena* **245**:108349. DOI:10.1016/j.catena.2024.108349
126. Lan S., Ouyang H., Wu L.,et al. (2017). Biological soil crust community types differ in photosynthetic pigment composition, fluorescence and carbon fixation in Shapotou region of China. *Appl. Soil Ecology* **111**:9–16. DOI:10.1016/j.apsoil.2016.11.009
127. Mackelprang R., Vaishampayan P., Fisher K. (2022). Adaptation to environmental extremes structures functional traits in biological soil crust and hypolithic microbial communities. *Msystems* **7**:e01419–21. DOI:10.1128/msystems.01419-21
128. Garcia-Pichel F. (2023). The microbiology of biological soil crusts. *Annual Rev. Microbiol.* **77**:149–171. DOI:10.1146/annurev-micro-032521-015202
129. Wang C. and Kuzyakov Y. (2024). Soil organic matter priming: The pH effects. *Global*

Change Biol. **30**:e17349. DOI:10.1111/gcb.17349
130. Xiao B., Ma S., and Hu K. (2019). Moss biocrusts regulate surface soil thermal properties and generate buffering effects on soil temperature dynamics in dryland ecosystem. *Geoderma* **351**:9–24. DOI:10.1016/j.geoderma.2019.05.017
131. Chilton A.M., Neilan B.A. and Eldridge D.J. (2018). Biocrust morphology is linked to marked differences in microbial community composition. *Plant Soil.* **429**:65–75. DOI:10.1007/s11104-017-3442-3
132. Liao K., Chen C., Ye W., et al. (2024). The adaptability, distribution, ecological function and restoration application of biological soil crusts on metal tailings: A critical review. *Sci. Total Environ.* **927**:172169. DOI:10.1016/j.scitotenv.2024.172169
133. Wild B., Gerrits R., Bonneville S. (2022). The contribution of living organisms to rock weathering in the critical zone. *npj Mat. Degrad* **6**:98. DOI:10.1038/s41529-022-00312-7
134. Armbrust E.V. (2009). The life of diatoms in the world's oceans. *Nature* **459**:185–192. DOI:10.1038/nature08057
135. Liu D. and Zhang Y.X. (2025). Diatom-driven activation of in-situ lunar resource utilization for space farming. *Biogeotech.* **3**:100162. DOI:10.1016/j.bgtech.2025.100162
136. Resl P., Bujold A.R., Tagirdzhanova G., et al. (2022). Large differences in carbohydrate degradation and transport potential among lichen fungal symbionts. *Nat. Commun.* **13**:2634. DOI:10.1038/s41467-022-30218-6
137. Koehle A.P., Brumwell S.L., Seto E.P., et al. (2023). Microbial applications for sustainable space exploration beyond low Earth orbit. *npj Microgravity* **9**:47. DOI:10.1038/s41526-023-00285-0
138. Averesch N.J., Berliner A.J., Nangle S.N., et al. (2023). Microbial biomanufacturing for space-exploration—what to take and when to make. *Nat. Commun.* **14**:2311. DOI:10.1038/s41467-023-37910-1
139. Verseux C., Baqué M., Lehto K. et al. (2016). Sustainable life support on Mars–the potential roles of cyanobacteria. *Int. J. Astrobiol.* **15**:65–92. DOI:10.1017/S147355041500021X
140. Xia Y., Yuan Y., Li C., et al. (2023). Phosphorus-solubilizing bacteria improve the growth of Nicotiana benthamiana on lunar regolith simulant by dissociating insoluble inorganic phosphorus. *Commun. Biology.* **6**:1039. DOI:10.1038/s42003-023-05391-z
141. Aung K.M.M. and Ting Y. (2005). Bioleaching of spent fluid catalytic cracking catalyst using Aspergillus niger. *J. biotechnol.* **116**:159–170. DOI:10.1016/j.jbiotec.2004.10.008
142. Jung H., Inaba Y. and Banta S. (2022). Genetic engineering of the acidophilic chemolithoautotroph Acidithiobacillus ferrooxidans. *Trends Biotechnol.* **40**:677–692. DOI:10.1016/j.tibtech.2021.10.004
143. Johnson D.B. (2014). Biomining—biotechnologies for extracting and recovering metals from ores and waste materials. *Current Opin. Biotech.* **30**:24–31. DOI:10.1016/j.copbio.2014.04.008
144. Li C., Hu H., Yang M.F., et al. (2022). Characteristics of the lunar samples returned by the Chang'E-5 mission. *Natl. Sci. Rev.* **9**:nwab188. DOI:10.1093/nsr/nwab188
145. Gumulya Y., Zea L. and Kaksonen A.H. (2022). In situ resource utilisation: The potential for space biomining. *Miner. Eng.* **176**:107288. DOI:10.1016/j.mineng.2021.107288
146. Hazen R.M., Downs R.T., Morrison S.M., et al. (2023). On the diversity and formation modes of martian minerals. *J. Geophys. Res- Planet.* **128**:e2023JE007865. DOI:10.1029/2023JE007865
147. Jaiswal M. and Srivastava S. (2024). A review on sustainable approach of bioleaching of precious metals from electronic wastes. *J. Hazard. Mater. Adv.* **14**:100435. DOI:10.1016/j.hazadv.2024.100435
148. Volger, R., Pettersson G.M., Brouns S.J.J., et al. (2020). Mining moon & mars with microbes: Biological approaches to extract iron from Lunar and Martian regolith. *Planet. Space Sci.* **184**:104850. DOI:10.1016/j.pss.2020.104850
149. Tiquia-Arashiro S. and Rodrigues D.F. (2016). Nanoparticles synthesized by microorganisms. Tiquia-Arashiro S., Rodrigues D.F. (eds). Extremophiles: Applications in nanotechnology. (Springer-International publisher), pp:1-15. DOI:10.1007/978-3-319-45215-9.
150. Yang Y., Li H., Yuan Y., et al. (2025). Microbiological mechanisms and effects of dissimilatory iron reduction on combined contaminants bio-transformation: A review. *Process Biochem.* **153**:47–65. DOI:10.1016/j.procbio.2025.03.004
151. Olsson-Francis K. and Cockell C.S. (2010). Use of cyanobacteria for in-situ resource use in space applications. *Planet. Space Sci.* **58**:1279–1285. DOI:10.1016/j.pss.2010.05.005
152. Spietz R.L., Payne D., Szilagyi R.,et al. (2022). Reductive biomining of pyrite by methanogens. *Trends Microbiol.* **30**:1072–1083. DOI:10.1016/j.tim.2022.05.005
153. Vo P.H., Danaee S., Hai H.T.N., et al. (2024). Biomining for sustainable recovery of rare earth elements from mining waste: A comprehensive review. *Sci. Total Environ.* **908**:168210. DOI:10.1016/j.scitotenv.2023.168210
154. Castelein S.M., Aarts T.F., Schleppi J., et al. (2021). Iron can be microbially extracted from Lunar and Martian regolith simulants and 3D printed into tough structural materials. *Plos one* **16**:e0249962. DOI:10.1371/journal.pone.0249962
155. McLeod C.L. and Krekeler M.P. (2017). Sources of extraterrestrial rare earth elements: To the Moon and beyond. *Res.* **6**:40. DOI:10.3390/resources6030040
156. Zhang J. and Liu J. (2024). Thorium anomaly on the lunar surface and its indicative meaning. *Acta Geochim.* **43**:507–519. DOI:10.1007/s11631-023-00670-2
157. VanBommel S.J., Sharma S., Kizovski T.V., et al. (2025). Rare earth element assessment in Jezero crater using the Planetary Instrument for X-ray Lithochemistry on the Mars 2020 rover Perseverance: A case study of cerium. *Icarus* **425**:116355. DOI:10.1016/j.icarus.2024.116355
158. Ren K., Wang Q., Cao Y., et al. (2021). Multicomponent rare-earth cerate and zirconocerate ceramics for thermal barrier coating materials. *J. Eur. Ceram. Soc.* **41**:1720–1725. DOI:10.1016/j.jeurceramsoc.2020.10.005
159. Jing H., Geng L., Qiu S., et al. (2023). Research progress of rare earth composite shielding materials. *J. Rare Earth* **41**:32–41. DOI:10.1016/j.jre.2022.06.004
160. Srikant, Sharma V.K., Kumar V., et al. (2021). A review of recent research on rare earth particulate composite materials and structures with their applications. *Trans. Indian Inst. Met.* **74**:2569–2581. DOI:10.1007/s12666-021-02338-y
161. Hossain M.K., Ahmed M.H., Khan M.I., et al. (2021). Recent progress of rare earth oxides for sensor, detector, and electronic device applications: A review. *ACS Appl. Electron. Mater.* **3**:4255–4283. DOI:10.1021/acsaelm.1c00703
162. Hossain M.K., Raihan G.A., Akbar M.A., et al. (2022). Current applications and future potential of rare earth oxides in sustainable nuclear, radiation, and energy devices: A review. *ACS Appl. Electron. Mater.* **4**:3327–3353. DOI:10.1021/acsaelm.2c00069
163. Zhang X., Wang H., He Y., et al. (2025). Application of PVA fiber-reinforced biocement for the stabilization of dispersive soil: Water stability, mechanical properties, and modification mechanism. *Mater. Today Commun.* **48**:113439. DOI:10.1016/j.mtcomm.2025.113439
164. Zhang X., Wang H., Wang Y., et al. (2024). Improved methods, properties, applications and prospects of microbial induced carbonate precipitation (MICP) treated soil: A review. *Biogeotech.* **3**:100123. DOI:10.1016/j.bgtech.2024.100123
165. Gebru K.A., Kidanemariam T.G., Gebretinsae, H. K. (2021) Bio-cement production using microbially induced calcite precipitation (MICP) method: A review. *Chem. Eng. Sci.* **238**: 116610. DOI:10.1016/j.ces.2021.116610.
166. Gao Y., Wang L., He J., et al. (2022). Denitrification-based MICP for cementation of soil: Treatment process and mechanical performance. *Acta Geotech.* **17**:3799–3815. DOI:10.1007/s11440-022-01489-6
167. O'Donnell ST, Kavazanjian E and Rittmann B.E. (2017). MIDP: Liquefaction mitigation via microbial denitrification as a two-Stage process II: MICP. *J. Geotech. Geoenviron.* **143**:04017095. DOI:10.1061/(ASCE)GT.1943-5606.0001806
168. Shivaprakash S.H. and Burns S.E. (2025). Microbial interactions during carbonate biomineralization via urea hydrolysis metabolic pathway. *Acta Geotech.* **20**:3929–3950. DOI:10.1007/s11440-025-02609-8
169. Volpin F., Badeti U., Wang C., et al. (2020). Urine treatment on the international space station: Current practice and novel approaches. *Membranes* **10**:327. DOI:10.3390/membranes10110327
170. Lambert S.E. and Randall D.G. (2019). Manufacturing bio-bricks using microbial induced calcium carbonate precipitation and human urine. *Water res.* **160**:158–166. DOI:10.1016/j.watres.2019.05.069
171. Yang Y., Chu J., Cheng L., et al.. (2022). Utilization of carbide sludge and urine for sustainable biocement production. *J. Environ. Chem. Eng.* **10**:107443. DOI:10.1016/j.jece.2022.107443
172. Fang C. and Achal V. (2024). Enhancing carbon neutrality: A perspective on the role of microbially induced carbonate precipitation (MICP). *Biogeotech.* **2**:100083. DOI:10.1016/j.bgtech.2024.100083
173. Xiao Y., Zhao C., Sun Y., et al. (2021). Compression behavior of MICP-treated sand with various gradations. *Acta Geotech.* **16**:1391–1400. DOI:10.1007/s11440-020-01116-2
174. Wilpiszeski R.L., Aufrecht J.A., Retterer S.T., et al. (2019). Soil aggregate microbial communities: Towards understanding microbiome interactions at biologically relevant scales. *Appl. Environ. Microbiol.* **85**:e00324–19. DOI:10.1128/AEM.00324-19
175. Azami M., Kazemi Z., Moazen S., et al. (2024). A comprehensive review of lunar-based manufacturing and construction. *Prog. Aerosp. Sci.* **150**:101045. DOI:10.1016/j.paerosci.2024.101045
176. Chen Y., Hu S., Li J.H., et al. (2023). Chang'e-5 lunar samples shed new light on the Moon. *The Innovation Geoscience* **1**:100014–1. DOI:10.59717/j.xinn-geo.2023.100014
177. Liu H., Xiao Y., Shi J., Cao B., et al. (2025). 3D printing lunar regolith simulant with microbial-carbonated magnesium oxide. *Biogeotech.* 100197. DOI: 10.1016/j.bgtech.2025.100197
178. Gu J., Qian X., Liu Y., et al. (2024). Charging properties and particle dynamics of Chang'e-5 lunar sample in an external electric field. *Engineering* **42**:267–277. DOI:10.1016/j.eng.2024.08.003
179. Dikshit R., Gupta N., Dey A., et al. (2022). Microbial induced calcite precipitation can consolidate martian and lunar regolith simulants. *Plos one* **17**:e0266415. DOI:10.1371/journal.pone.0266415
180. Shi J.Q., Xiao Z., Xiao Y., et al. (2024) Bio-molding of lunar regolith with bio-carbonized magnesium oxide. *Biogeotech.* **3**: 100159. DOI: 10.1016/j.bgtech.2024.100159
181. Jiang N.J., Yoshioka H., Yamamoto K., et al. (2016). Ureolytic activities of a urease-producing bacterium and purified urease enzyme in the anoxic condition: Implication for subseafloor sand production control by microbially induced

carbonate precipitation (MICP). *Ecol. Eng.* **90**:96–104. DOI:10.1016/j.ecoleng.2016.01.073
182. Ng S. and Chu J. (2024). Frozen enzyme EICP method for more effective soil improvement. *Acta Geotech.* **19**:7117–7124. DOI:10.1007/s11440-024-02348-2
183. Kidanemariam T.G., Gebru K.A. and Kidane Gebretinsae H. (2024). A mini review of enzyme-induced calcite precipitation (EICP) technique for eco-friendly bio-cement production. *Environ. Sci. Pollut. Res. Int.* **31**:16206–16215. DOI:10.1007/s11356-023-31555-9
184. Ahenkorah I., Rahman M.M., Karim M R., et al. (2021). A review of enzyme induced carbonate precipitation (EICP): The role of enzyme kinetics. *Sustain. Chem.* **2**:92–114. DOI:10.3390/suschem2010007
185. Li C., Li S., Xing J., Gao Y., et al. (2025). On-site test of fixed mobile sand dunes using combined technology of sand plants and EICP in the Ulanbuh Desert, China. *Acta Geotech.* **20**:1921–1934. DOI:10.1007/s11440-024-02524-4
186. Madusanka C., Udayanga D., Nilmini R., et al. (2024). A review of recent advances in fungal mycelium based composites. *Discover Mater.* **4**:13. DOI:10.1007/s43939-024-00084-8
187. Elsacker E., Vandelook, ., Van Wylick A., et al. (2020). A comprehensive framework for the production of mycelium-based lignocellulosic composites. *Sci. Total Environ.* **725**:138431. DOI:10.1016/j.scitotenv.2020.138431
188. Zhang X., Hu J., Fan X., et al. (2022). Naturally grown mycelium-composite as sustainable building insulation materials. *J. Clean. Prod.* **342**:130784. DOI:10.1016/j.jclepro.2022.130784
189. Bonga K.B., Bertolacci L., Contardi M., et al. (2024). Mycelium agrowaste - bound biocomposites as thermal and acoustic insulation materials in building construction. *macromol. Mater. Eng.* **309**:2300449. DOI:10.1002/mame.202300449
190. Maximino C. Ongpeng J., Inciong E., et al. (2020). Using waste in producing bio-composite mycelium bricks. *Appl. Sci.* **10**:5303. DOI:10.3390/app10155303
191. Viles E., Heyneman E., Lin S., et al. (2025). Mycelium as a scaffold for biomineralized engineered living materials. *Cell Rep. Phys. Sci.* **6**:102517. DOI:10.1016/j.xcrp.2025.102517
192. Heveran C.M., Williams S.L., Qiu J., et al. (2020). Biomineralization and successive regeneration of engineered living building materials. *Matter* **2**:481–494. DOI:10.1016/j.matt.2019.11.016
193. Roberts A.D., Whittall D.R., Breitling R., et al. (2021). Blood, sweat, and tears: Extraterrestrial regolith biocomposites with in vivo binders. *Mater. Today Bio.* **12**:100136. DOI:10.1016/j.mtbio.2021.100136
194. Sauer R.L. (1985). Metabolic support for a lunar base. In lunar bases and space activities of the 21st century. https://ntrs.nasa.gov/citations/19860045375
195. Jacobson T.A., Kler J.S., Hernke M.T. et al. (2019). Direct human health risks of increased atmospheric carbon dioxide. *Nat. Sustain.* **2**:691–701. DOI:10.1038/s41893-019-0323-1
196. Horneck G., Facius R., Reichert M., et al. (2006) HUMEX, a study on the survivability and adaptation of humans to long-duration exploratory missions, part II: Missions to Mars. *Adv. Space Res.* **38**: 752-759. DOI: 10.1016/j.asr.2005.06.072.
197. Keller R., Goli K., Porter W., et al. (2023). Cyanobacteria and algal-based biological life support system (BLSS) and planetary surface atmospheric revitalizing bioreactor brief concept review. *Life* **13**:816. DOI:10.3390/life13030816
198. Kerner M., Wolff T. and Brinkmann T. (2024). Efficient supply with carbon dioxide from flue gas during large scale production of microalgae: A novel approach for bioenergy facades. *Bioresource Technol.* **391**:129917. DOI:10.1016/j.biortech.2023.129917
199. Wagner I., Braun M., Slenzka K., et al. (2016). Photobioreactors in life support systems. *Adv. Biochem. Eng. Biotechnol.* **153**:143–184. DOI:10.1007/10_2015_327
200. Gan F. and Bryant D.A. (2015). Adaptive and acclimative responses of cyanobacteria to far - red light. *Environ. Microbiol.* **17**:3450–3465. DOI:10.1111/1462-2920.12992
201. Salisbury F.B., Gitelson J.I. and Lisovsky G.M. (1997). Bios-3: Siberian experiments in bioregenerative life support.Attempts to purify air and grow food for space exploration in a sealed environment began in 1972. *BioScience.* **47**: 575-585. DOI:10.2307/1313164
202. Detrell G., Keppler J., Helisch H., et al. (2020). PBR@ LSR: The algae-based photobioreactor experiment at the ISS–operations and results. 2020 international conference on environmental systems. https://ttu-ir.tdl.org/handle/2346/86331
203. Ellery A. (2021). Supplementing closed ecological life support systems with in-situ resources on the moon. *Life* **11**:770. DOI:10.3390/life11080770
204. Ewert M.K., Drysdale A.E., Levri J.A. et al. (2002). Advanced life support requirements, assumptions and reference missions. AE technical paper. No. 2002-01-2480. DOI:10.4271/2002-01-2480
205. Pickett M.T., Roberson L.B., Calabria J.L., et al. (2020). Regenerative water purification for space applications: Needs, challenges, and technologies towards' closing the loop. *Life Sci. Space Res.* **24**:64–82. DOI:10.1016/j.lssr.2019.10.002
206. Espinosa-Ortiz E.J., Gerlach R., Peyton B.M., et al. (2023). Biofilm reactors for the treatment of used water in space: Potential, challenges, and future perspectives. *Biofilm.* **6**:100140. DOI:10.1016/j.bioflm.2023.100140
207. Tang Y., Dong W., Ai W., et al. (2021). Design and establishment of a large-scale controlled ecological life-support system integrated experimental platform. *Life Sci. Space Res.* **31**:121–130. DOI:10.1016/j.lssr.2021.08.001
208. Llorente B., Williams T.C., Goold H.D., et al. (2022). Harnessing bioengineered microbes as a versatile platform for space nutrition. *Nat. Commun.* **13**:6177. DOI:10.1038/s41467-022-33974-7
209. Janssen M., Wijffels R.H. and Barbosa M.J. (2022). Microalgae based production of single-cell protein. *Curr. Opin. Biotech.* **75**:102705. DOI:10.1016/j.copbio.2022.102705
210. Kumar B.R., Deviram G., Mathimani T., et al. (2019). Microalgae as rich source of polyunsaturated fatty acids. *Biocatal. Agric. Biotechnol.* **17**:583–588. DOI:10.1016/j.bcab.2019.01.017
211. Coulombier N., Jauffrais T. and Lebouvier, N. (2021). Antioxidant compounds from microalgae: A review. *Mar. Drugs.* **19**:549. DOI:10.3390/md19100549
212. Williamson E., Ross I.L., Wall B.T., et al. (2024). Microalgae: Potential novel protein for sustainable human nutrition. *Trends Plant Sci.* **29**:370–382. DOI:10.1016/j.tplants.2023.08.006
213. Sharma P. and Nuri S.M. (2019). Nutrient recovery and microbial diversity in human urine fed microbial fuel cell. *Water Sci. Technol.* **79**:718–730. DOI:10.2166/wst.2019.089
214. Oishi W., Vinnerås B. and Sano D. (2023). Resource recovery technologies as microbial risk barriers: Towards safe use of excreta in agriculture. *Environ. Sci.: Water Res. Technol.* **9**:1008–1029. DOI:10.1039/D2EW00832G
215. Caballero P., Macías-Benítez S., Revilla E., et al. (2020). Effect of subtilisin, a protease from Bacillus sp., on soil biochemical parameters and microbial biodiversity. *Eur. J. Soil Biol.* **101**:103244. DOI:10.1016/j.ejsobi.2020.103244
216. Busato J.G., Lima L.S., Aguiar N.O., et al. (2012). Changes in labile phosphorus forms during maturation of vermicompost enriched with phosphorus-solubilizing and diazotrophic bacteria. *Bioresource Technol.* **110**:390–395. DOI:10.1016/j.biortech.2012.01.126
217. Lee H., Diao J., Tian Y., et al. (2025). Developing an alternative medium for in-space biomanufacturing. *Nat. Commun.* **16**:728. DOI:10.1038/s41467-025-56088-2
218. Verbeelen T., Leys N., Ganigué R., et al. (2021). Development of nitrogen recycling strategies for bioregenerative life support systems in space. *Front. Microbiol.* **12**:700810. DOI:10.3389/fmicb.2021.700810
219. Fu Y., Li L., Xie B., et al. (2016). How to establish a bioregenerative life support system for long-term crewed missions to the moon or Mars. *Astrobiology* **16**:925–936. DOI:10.1089/ast.2016.1477
220. Fu Y., Liu H., Liu D. et al. (2025). A case for supporting human long-term survival on the moon: "Lunar Palace 365" mission. *Acta Astronaut.* **228**:131–140. DOI:10.1016/j.actaastro.2024.12.002
221. Kyazze G. (2020). Four ways microbial fuel cells might revolutionise electricity production in the future. The Conversation. https://theconversation.com/four-ways-microbial-fuel-cells-might-revolutionise-electricity-production-in-the-future-152184
222. Dotson B., Valencia D.S., Millwater C., et al. (2024). Cohesion and shear strength of compacted lunar and Martian regolith simulants. *Icarus.* **411**:115943. DOI:10.1016/j.icarus.2024.115943
223. Xi B., Jiang M., Mo P., et al. (2024). Bearing capacity of lunar soil ground under extraterrestrial environmental effects. *Comp. Geotech.* **165**:105923. DOI:10.1016/j.compgeo.2023.105923
224. Zhang K., Tang C.S., Jiang N.J., et al. (2023). Microbial-induced carbonate precipitation (MICP) technology: A review on the fundamentals and engineering applications. *Environ. Earth Sci.* **82**:229. DOI:10.1007/s12665-023-10899-y
225. Van Paassen L.A., Ghose R., van der Linden, et al. (2010). Quantifying biomediated ground improvement by ureolysis: Large-scale biogrout experiment. *J. Geotech. Geoen.* **136**:1721–1728. DOI:10.1061/(ASCE)GT.1943-5606.0000382
226. Van Paassen, L. A. (2011). Bio-mediated ground improvement: From laboratory experiment to pilot applications. Han J, Alzamora D.E. (eds). Geo-Frontiers 2011: Advances in geotechnical engineering, pp: 4099-4108. DOI:10.1061/41165(397)419
227. Ghasemi P. and Montoya B.M. (2022). Field implementation of microbially induced calcium carbonate precipitation for surface erosion reduction of a coastal plain sandy slope. *J. Geotech. Geoen.* **148**:04022071. DOI:10.1061/(ASCE)GT.1943-5606.0002836
228. Xiao Y., He X., Zaman M., et al. (2022). Review of strength improvements of biocemented soils. *Int. J. Geomech.* **22**:03122001. DOI:10.1061/(ASCE)GM.1943-5622.0002565
229. Gao X., Han Z., Zhao Y., et al. (2024). Interaction of microorganisms with carbonates from the micro to the macro scales during sedimentation: Insights into the early stage of biodegradation. *J. Environ. Manage.* **356**:120714. DOI:10.1016/j.jenvman.2024.120714
230. Jongvivatsakul P., Janprasit K., Nuaklong P., et al. (2019). Investigation of the crack healing performance in mortar using microbially induced calcium carbonate precipitation (MICP) method. *Constr. Build. Mater.* **212**:737–744. DOI:10.1016/j.conbuildmat.2019.04.035
231. Zhang Y.S., Liu Y., Sun X. et al. (2024). Application of microbially induced calcium carbonate precipitation (MICP) technique in concrete crack repair: A review. *Constr. Build. Mater.* **411**:134313. DOI:10.1016/j.conbuildmat.2023.134313
232. Reda M.A. and Chidiac S.E. (2022). Performance of capsules in self-healing cementitious material. *Materis* **15**:7302. DOI:10.3390/ma15207302
233. Gupta N., Kulkarni R., Naik A.R., et al. (2025). Bacterial bio-cementation can repair space bricks. *Front. Space Technol.* **6**:1550526. DOI:10.3389/frspt.2025.1550526

234. Atmakuri A., Yadav B., Tiwari B., et al. (2024). Nature's architects: A comprehensive review of extracellular polymeric substances and their diverse applications. *Waste Dispos. Sustain. Energy* **6**:529–551. DOI:10.1007/s42768-024-00205-2
235. Chevrier V.F., Hanley J. and Altheide T.S. (2009). Stability of perchlorate hydrates and their liquid solutions at the Phoenix landing site, Mars. *Geophys. Res. Lett.* **36**:L10202. DOI:10.1029/2009GL037497
236. Hecht M.H., Kounaves S.P., Quinn R.C., et al. (2009) Detection of perchlorate and the soluble chemistry of Martian soil at the Phoenix Lander Site. *Science* **325**: 64–67. DOI: 10.1126/science.1172466
237. Rzymski P., Poniedziałek B., Hippmann N., et al. (2022). Screening the survival of cyanobacteria under perchlorate stress. Potential implications for Mars in situ resource utilization. *Astrobiology* **22**:672–684. DOI:10.1089/ast.2021.0100
238. Rzymski P., Losiak A., Heinz J., et al. (2024). Perchlorates on Mars: Occurrence and implications for putative life on the Red Planet. *Icarus* **421**:116246. DOI:10.1016/j.icarus.2024.116246
239. Fagliarone C., Fernandez B.G., Di Stefano G., et al. (2024). Insights into the chaotropic tolerance of the desert cyanobacterium Chroococcidiopsis sp. 029 (Chroococcidiopsales, cyanobacteria). *J. Phycol.* **60**: 185-194. DOI: 10.1111/jpy.13414
240. Díaz-Rullo J., Rodríguez-Valdecantos G., Torres-Rojas F. et al. (2021). Mining for perchlorate resistance genes in microorganisms from sediments of a hypersaline pond in Atacama Desert, Chile. *Front. Microbiol.* **12**:723874. DOI:10.3389/fmicb.2021.723874
241. Misra G., Smith W., Garner M., et al. (2021). Potential biological remediation strategies for removing perchlorate from Martian regolith. *New Space* **9**:217–227. DOI:10.1089/space.2020.0055
242. Ruff S.E., Schwab L., Vidal E., et al. (2024). Widespread occurrence of dissolved oxygen anomalies, aerobic microbes, and oxygen-producing metabolic pathways in apparently anoxic environments. *FEMS Microbiol. Ecol.* **100**:fiae132. DOI:10.1093/femsec/fiae132
243. Meylani V., Santri D.J. and Surahman E. (2024). Microbial electrochemical technologies: Different configurations, electrodes and working principle/microbial electrochemical eechnologies—working principle and design of biocathode. Selvasembian R., Mal J., Das S., Verma D.K., Anastopoulos I. (eds). Emerging trends in microbial electrochemical technologies for sustainable mitigation of water resources contamination (Springer, Cham.), pp:63-81. DOI: 10.1007/978-3-031-74636-9_3
244. Li X., Bai W., Yang Q., et al. (2024). The extremotolerant desert moss Syntrichia caninervis is a promising pioneer plant for colonizing extraterrestrial environments. *The Innovation* **5**:100657. DOI:10.1016/j.xinn.2024.100657
245. Sun F., Xiao B., Kidron G.J., et al. (2024). Biocrusts critical regulation of soil water vapor transport (diffusion, sorption, and late - stage evaporation) in drylands. *Water Resour Res.* **60**:e2023WR036520. DOI:10.1029/2023WR036520
246. Verseux C., Heinicke C., Ramalho T.P., et al. (2021). A low-pressure, N_2/CO_2 atmosphere is suitable for cyanobacterium-based life-support systems on Mars. *Front microbiol.* **12**:611798. DOI:10.3389/fmicb.2021.611798
247. Figueira J., Koch S., Müller D.W. et al. (2025). Biomining of lunar regolith simulant EAC-1 A with the fungus Penicillium simplicissimum. *Fungal Biol. Biotechnol.* **12**:8. DOI:10.1186/s40694-025-00201-z
248. Santomartino R., Blanco G.R., Gudgeon A., et al. (2024). Testing microbial biomining from asteroidal material onboard the International Space Station. *bioRxiv* 2024-01. DOI: 10.1101/2024.01.13.575412
249. Kruyer N.S., Realff M.J., Sun W., et al. (2021). Designing the bioproduction of Martian rocket propellant via a biotechnology-enabled in situ resource utilization strategy. *Nat. Commun.* **12**:6166. DOI:10.1038/s41467-021-26393-7
250. Rampelotto P.H. (2010). Resistance of microorganisms to extreme environmental conditions and its contribution to astrobiology. *Sustainability.* **2**:1602–1623. DOI:10.3390/su2061602
251. Putatunda C., Solanki P., Pathania S., et al. (2023). Screening strategies: . Bhatt A.K., Bhatia R.K. and Bhalla T.C. (eds). Basic biotechniques for bioprocess and bioentrepreneurship (Academic Press), pp: 23-46. DOI: 10.1016/B978-0-12-816109-8.00002-7
252. Ott E., Fuchs F.M., Moeller R., et al. (2019). Molecular response of Deinococcus radiodurans to simulated microgravity explored by proteometabolomic approach. *Sci. Rep.* **9**:18462. DOI:10.1038/s41598-019-54742-6
253. Mohseni P. and Ghorbani A. (2024). Exploring the synergy of artificial intelligence in microbiology: Advancements, challenges, and future prospects. *Comput. Struct. Biotechnology Rep.* **1**:100005. DOI:10.1016/j.csbr.2024.100005
254. Choi S.R., Lee M. (2023). Transformer architecture and attention mechanisms in genome data analysis: A comprehensive review. *Biology* **12**:1033. DOI:10.3390/biology12071033
255. Zhu M., Wang Q., Mu H., et al. (2023). A fitness trade-off between growth and survival governed by Spo0A-mediated proteome allocation constraints in Bacillus subtilis. *Sci Adv.* **9**:eadg9733. DOI:10.1126/sciadv.adg9733
256. SESRI: Bringing space to earth (2020). Nature. DOI:10.1038/d42473-020-00198-6. (2023-10-01). https://www.nature.com/articles/d42473-020-00198-6
257. Zhao C., Xiao Y., He X., et al. (2025). Influence of injection methods on bio-mediated precipitation of carbonates in fracture-mimicking microfluidic chip. *Géotechnique* **75**:153–165. DOI:10.1680/jgeot.23.00155
258. Xiao Y., He X., Stuedlein A.W., et al. (2022). Crystal growth of micp through microfluidic chip tests. *J. Geotech. Geoenviron.* **148**:06022002. DOI:10.1061/(ASCE)GT.1943-5606.0002756
259. Krakos A. (2024). Lab-on-chip technologies for space research—current trends and prospects. *Microchimica Acta* **191**:31. DOI:10.1007/s00604-023-06084-4
260. Vandaele A.C., Aoki S., Bauduin S., et al. (2024). Composition and chemistry of the Martian atmosphere as observed by Mars express and ExoMars trace gas orbiter. *Space Sci Rev.* **220**:75. DOI:10.1007/s11214-024-01109-7
261. Schorghofer N., Williams J.P., Martinez - Camacho, et al. (2021). Carbon dioxide cold traps on the moon. *Geophys. Res. Lett.* **48**:e2021GL095533. DOI:10.1029/2021GL095533

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AUTHOR CONTRIBUTIONS

C. Z., Y.Z, L.Y., D, Y.D., G and S.L. conceptualized and designed the study. S.L. and Y.D, G wrote the manuscript. C. Z., Y.Z, and L.Y., D, provided advice. C. Z., Y.Z, and S.L contributed to manuscript review and editing. C. Z., Y.D., G and L.Y., D, contributed to conceptualization, supervised the research, provided project administration and resources. All authors approved the final manuscript for submission.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

No new data were created or analyzed in this study.