Extremotolerant pioneer species for cold, arid, oligotrophic, low-pressure environments

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Abstract. Cold deserts, high mountains, glacier forefields, and volcanic craters represent the closest terrestrial analogues to early extraterrestrial environments, particularly those expected on Mars. These systems impose convergent selective pressures, including chronic water limitation, subzero or near-freezing temperatures, extreme oligotrophy, high radiation, and reduced atmospheric pressure. This review synthesizes recent experimental and field-based evidence identifying extremotolerant pioneer plants, fungi, and bacteria capable of colonizing mineral, humus-poor substrates under such conditions. We highlight bryophytes, especially desert and alpine mosses (*Syntrichia caninervis*, *Grimmia* spp.), as leading plant-level pioneers due to their exceptional tolerance to desiccation, freezing, irradiation, and simulated Martian atmospheres. Pioneer vascular plants from volcanic and high-altitude deserts further illustrate how shrubs and grasses establish under acidic, nutrient-poor, and highly irradiated substrates through close associations with stress-adapted rhizosphere microbiomes. Cold-adapted fungi, including psychrophilic soil taxa and extreme endophytes from polar and hyperarid deserts, emerge as primary colonizers and key facilitators of plant survival under combined cold, drought, low oxygen, and high UV stress. Similarly, bacterial pioneers, dominated by Actinobacteria and other metabolically versatile oligotrophs, drive early soil development, nitrogen cycling, and organic matter accumulation in newly exposed cold mineral soils. Across systems, evidence consistently demonstrates that multi-stress tolerance is an emergent property of integrated plant–fungal–bacterial consortia rather than isolated taxa. These terrestrial pioneer assemblages provide experimentally supported models for designing early-stage biotic systems capable of functioning in cold, arid, oligotrophic, and low-pressure extraterrestrial environments.
Key Words: Actinobacteria, astrobiology, bryophytes, cold deserts, glacier forefields, Mars analog environments, microbial consortia, oligotrophic soils, plant-microbe interactions, psychrophilic fungi, volcanic soils.

Introduction. Cold deserts, high mountains, glacier forefields and volcanic craters provide the closest terrestrial analogues of early extra terrestrial habitats. Work in these systems has identified plant, fungal and microbial pioneers combining tolerance to aridity, subzero or near freezing temperatures, nutrient poor mineral substrates and intense radiation, all highly relevant for a Martian context.

The aim of this work is to identify and synthesize experimentally supported terrestrial models of extremotolerant pioneer organisms (plants, fungi, and bacteria) capable of colonizing cold, arid, oligotrophic, and low-pressure environments analogous to early extraterrestrial habitats. By integrating evidence from desert, polar, alpine, and volcanic systems, the study seeks to define key taxonomic groups, functional traits, and plant-microbe consortia that underpin early ecosystem assembly on mineral substrates, with particular relevance to Mars analog conditions and long-term astrobiological and bioengineering applications.

Pioneer Plants and Bryophytes. The strongest plant level evidence for multi stress tolerance comes from desert mosses and high altitude bryophytes.

The desert moss *Syntrichia caninervis* (Mohave, Tibetan and other cold deserts) shows extreme desiccation tolerance, recovering full photosynthetic activity within seconds after rehydration even after losing >98% of its cellular water content (Li et al 2024). Intact plants tolerate ultra low temperatures, remaining viable after 5 years at −80 °C or 1 month in liquid nitrogen (Li et al 2024). *S. caninervis* also withstands very high γ irradiation and survived 7 days under simulated Mars conditions combining 95% CO_2, anoxia, extreme desiccation, low temperature and strong UV, then regenerated branches after 15 days of recovery (Li et al 2024). These traits make it a leading candidate pioneer for colonizing mineral, humus poor substrates under cold, dry, thin atmospheres.

Mosses from high altitude, high UV sites also show remarkable stress resistance. Plantlets of *Grimmia* spp. from the Swiss Alps were exposed in the BIOMEX/EXPOSE R2 pre flight tests to combinations of extreme temperatures, vacuum and Mars like UV in various atmospheres. All stressors except UV had negligible impact on vitality; even high UV doses only reduced photosynthetic activity by ~36–37 %, and mosses remained viable after doses equal to or exceeding those expected on the ISS mission (Huwe et al 2019). These bryophytes naturally colonize thin, poorly developed soils and rock surfaces at low temperatures and high radiation, mirroring key Martian constraints.

In volcanic settings with acidic, nutrient poor soils, a small set of pioneer vascular plants establish first vegetation cover. In the crater of the active El Chichonal volcano, three pioneers were documented on acidic, oligotrophic substrates: *Tibouchina longifolia* (dominant shrub), Poaceae (co dominant grasses) and *Palhinhaea cernua* (non-dominant lycophyte) (Rios-Reyes et al 2025). These species tolerate low organic matter and high abiotic stress; their rhizospheres harbor diverse extremotolerant microbes (see below), illustrating integrated plant microbiome pioneer systems for harsh, humus poor substrates.

In the Andean Altiplano and Atacama Desert, among the driest, high radiation regions on Earth, the shrub *Parastrephia quadrangularis* grows on volcanic slopes under low nutrient availability, high solar irradiation, water scarcity and often saline soils. It acts as a pioneer species, and its rhizosphere recruits distinctive, stress adapted rhizobacterial communities that support colonization of these extreme sites (Zhang et al 2021).

Together, these results point to bryophytes (*Syntrichia*, *Grimmia*) and a limited set of shrubs/graminoids from cold, high elevation deserts and volcanic terrains as realistic taxonomic pools for first wave pioneer vegetation in Mars analog conditions.

Fungal pioneers and Endophytes from Extreme Environments. Cold and drought adapted fungi are key primary colonizers of mineral or humus poor substrates, often forming cryptogamic crusts or living as endophytes.

A recent review of cold adapted fungi emphasizes that psychrophilic yeasts and filamentous fungi dominate in polar regions, alpine ecosystems and glaciers, where they experience low temperatures, high UV, freeze–thaw cycles and oligotrophic conditions (Jodłowska & Białkowska 2024). They persist via multiple adaptations: membrane and envelope modifications, production of cryoprotectants and chaperones, cold active enzymes (e.g. proteases, lipases) and metabolites such as pigments and osmolytes (Jodłowska & Białkowska 2024). Fungal communities in oligotrophic Antarctic soils are diverse and include highly specialized, slow growing taxa able to mineralize organic matter under extremely low nutrient and temperature regimes (Jodłowska & Białkowska 2024). These traits fit the profile of fungal pioneers for cold, nutrient poor regoliths.

Experiments with extreme fungal endophytes directly under "exoplanetary" conditions show practical colonization potential. Two endophytic fungi isolated from the Atacama Desert were inoculated into lettuce, chard and spinach, then plants were grown for 30 days under combined stresses: high UV radiation, low temperature, limited water and low oxygen (Molina-Montenegro et al 2023). Inoculation increased survival by roughly 15–35 % and biomass by ~30–35% across crops, with the strongest effects in polyculture plantings (Molina-Montenegro et al 2023). Nutritional quality and antioxidant content (flavonoids, phenolics) also increased (Molina-Montenegro et al 2023). These results demonstrate that Atacama endophytes can substantially enhance plant performance in a laboratory simulation of low pressure, high radiation, cold, arid "exoplanetary" agriculture.

Cold adapted fungi in Antarctic mosses and soils contribute to early ecological succession, tolerating oligotrophy, low temperatures and freeze–thaw cycles while participating in nutrient recycling (Jodłowska & Białkowska 2024). Such cryptogamic assemblages, moss plus fungal community, represent a self-organizing pioneer consortium capable of slowly building organic matter on mineral substrates under severe climatic stress.

Bacterial Pioneers in Cold, Arid, Oligotrophic Soils. Several lines of evidence identify specific bacterial taxa as pioneers in newly exposed, nutrient poor, cold environments.

In continental Antarctic glacier forefields, early successional soils are extremely dry and oligotrophic. Along a chronosequence of newly deglaciated soils in the Larsemann Hills, Actinobacteria were consistently abundant at all stages, while Chloroflexi, Gemmatimonadetes and Proteobacteria thrived in the most extreme, nutrient poor sites (Amen et al 2025). The earliest stages featured co colonization by nitrogen fixing bacteria, green algae (Trebouxiophyceae) and cryophilic fungi, forming the first pro and eukaryotic microbial networks in bare mineral soils (Amen et al 2025). These communities initiate soil development under cold, dry, humus free conditions directly comparable to early regolith colonization scenarios.

Detailed source tracking in an alpine glacier retreat system showed that microbial pioneers in initial mineral soils originate predominantly from endogenous glacial habitats, not from atmospheric deposition (Rime et al 2016). Bacterial communities in barren soils closely resembled those in glacier ice, sub and supraglacial sediments and glacial streams, whereas atmospheric inputs carried mostly plant epiphytic microbes (Rime et al 2016). Indicator bacterial OTUs from genera such as *Bradyrhizobium*, *Hyphomicrobium*, *Methylibium* and *Rhodoplanes* were shared between these endogenous habitats and newly exposed soils, consistent with metabolically versatile, oligotroph capable bacteria being selected as pioneers (Rime et al 2016). These taxa can use diverse organic compounds and may exploit very limited carbon sources, an essential trait for colonizing fresh mineral surfaces.

At the single strain level, *Arthrobacter agilis* Ant EH 1, isolated from nutrient poor, cold arid Antarctic mineral soils, shows true subzero growth and respiration (Wood et al 2025). Cell division occurs from at least −5 °C to 30 °C, while respiration is optimal at 5 °C, indicating adaptation to persistently cold, oligotrophic conditions where fast growth would be maladaptive (Wood et al 2025). The genome encodes genes for cold, osmotic and oxidative stress, pigment biosynthesis and scavenging of necromass components, all beneficial in exposed mineral matrices with high radiation and scarce nutrients (Wood et al 2025). *Arthrobacter* and related Actinobacteria are frequent in polar deserts and glacier forefields (Amen et al 2025; Wood et al 2025), reinforcing their role as prokaryotic pioneers.

From high altitude, cold Himalayan farmland, *Dyadobacter aurulentus* was isolated and characterized as a cold adaptive, metabolically versatile bacterium (Yadav et al 2025). It grows from 5–30 °C (optimum 30 °C), tolerates a broad pH range (6-11) and salinity up to 4% NaCl, and carries multiple cold adaptation genes (cold shock proteins, fatty acid desaturases) plus pathways for nitrate assimilation and degradation of aromatic compounds such as sodium benzoate (Yadav et al 2025). This combination suggests capacity to function in low temperature, nutrient limited and chemically variable soils, similar to those expected from weathered basaltic regolith.

In the crater of El Chichonal volcano, 311 microbial isolates, predominantly bacteria, were obtained from acidic, nutrient poor soils and plant tissues of the pioneer vegetation (Rios-Reyes et al 2025). Among them, *Bacillus cereus* and *Priestia megaterium* (formerly *Bacillus megaterium*) showed plant growth promoting traits: nitrogen fixation, auxin production and antagonism toward fungal pathogens (Rios-Reyes et al 2025). These PGPR thrive under acidic, oligotrophic conditions and establish intimate associations with pioneers on fresh volcanic substrates, offering a model for bacterial partners facilitating plant establishment on Martian regolith analogues.

Finally, the rhizosphere of *P. quadrangularis* in the Atacama Desert hosts abundant Actinobacteria, Proteobacteria, Acidobacteria and Bacteroidetes, with many operational taxonomic units (OTUs) unique to each plant, implying host specific recruitment of stress adapted rhizobacteria under extremely dry, irradiated, nutrient poor conditions (Zhang et al 2021). Functional predictions highlight chemoheterotrophy and nitrogen cycling (nitrate reduction, denitrification) as dominant, indicating that these communities sustain plant growth through nutrient transformations in harsh volcanic desert soils (Zhang et al 2021).

Integrated Plant-Microbe Pioneer Consortia and Stress Mitigation. Several studies show that microbial partners greatly expand plant tolerance to drought, cold, low nutrients and other stresses, suggesting that pioneer assemblages should be designed as plant-fungal-bacterial consortia rather than single species.

Broad reviews of plant associated bacteria and fungi document mechanisms by which PGPR, arbuscular mycorrhizal fungi (AMF), endophytes and even plant associated viruses enhance drought and heat tolerance: osmotic adjustment, antioxidant enzyme up regulation, altered phytohormone balances, improved water and nutrient uptake, biofilm formation and induction of plant stress responsive genes (Poudel et al 2021; Hanaka et al 2021; Iqbal et al 2023). These mechanisms are independent of crop identity and reflect general microbiome functions that could be co opted in extremophile hosts.

In horticultural systems, drought tolerant PGPR and mycorrhizal fungi are highlighted as a "relatively cheap, easy to apply and efficient" strategy for alleviating water deficit in crops, via phytohormone production, antioxidant and xeroprotectant synthesis, and induction of systemic resistance (Hanaka et al 2021). Under combined drought and heat, microbial symbionts modulate hormonal and metabolic pathways to maintain growth and photosynthesis (Iqbal et al 2023). Although these works use mesic crops, the underlying mechanisms are directly relevant to exploiting desert and polar microbiomes in Mars analog pioneers.

Tree and perennial systems show that microbiome shifts themselves can confer climate tolerance. Inoculating tree seedlings with microbial communities from drier or colder sites improved seedling survival under drought, heat or cold stress, respectively. Drought tolerance correlated with increased arbuscular mycorrhizal fungal diversity, whereas cold tolerance was associated with reduced overall fungal richness, presumably by pruning maladapted taxa (Allsup et al 2023). Along aridity gradients in Pinus radiata forests, specific bacterial and fungal taxa become conditionally present under higher aridity, supporting host resilience to water limitation (Addison et al 2025). These results suggest that selecting and transferring whole microbial consortia from cold deserts, high mountains or polar soils may be as important as choosing extremophile host plants.

Under simulated exoplanetary conditions, Atacama endophytic fungi improved survival, biomass and antioxidant status of multiple leafy crops as discussed above (Molina-Montenegro et al 2023). In a similar vein, combined inocula of AMF, helper bacteria and PGPR in crops like rice significantly increased cold tolerance through improved antioxidant defense, osmolyte accumulation, hormonal balancing and up regulation of cold responsive genes (Shi et al 2025). Such microbial consortia design provides a clear experimental framework for assembling pioneer plant-microbe systems tailored to Martian analog stresses.

Microbial Networks and Ecosystem Level Resilience. Beyond individual taxa, the architecture of microbial co-occurrence networks under stress informs how pioneer communities might behave on new planets.

In an agricultural drought experiment, fungal communities were more resistant to drought but less resilient after rewetting than bacterial communities at the level of composition (Gao et al 2022). Drought generally disrupted microbial co-occurrence networks, yet networks among arbuscular mycorrhizal fungi and some rhizosphere fungi and leaf bacteria were strengthened, and positive correlations became more frequent (Gao et al 2022). This supports the "stress gradient hypothesis" at the microbiome level: under high abiotic stress, facilitative interactions among microbes increase, potentially stabilizing pioneer communities on harsh substrates.

In Antarctic glacier forefields, microbial succession proceeds from "single pioneers" to complex networks of bacteria, algae and fungi as soils age and minimal organic matter accumulates (Amen et al 2025). Nitrogen fixing bacteria and algae/fungi are prominent early, indicating that N inputs and primary production are crucial first steps in functional ecosystem assembly (Amen et al 2025). A similar sequence could be expected on Martian regolith once water and minimal energy sources are available.

Synthesis: **Taxonomic Candidates and Traits**. Although no terrestrial organism fully matches Martian surface conditions, the literature converges on several taxonomic groups and traits relevant for cold, arid, humus poor, low pressure contexts:

• Bryophyte pioneers:
  - *Syntrichia caninervis*: extreme desiccation, freezing and irradiation tolerance; survival under simulated Mars conditions (Li et al 2024).
  - *Grimmia* spp.: high resistance to combined vacuum, temperature extremes and UV in Mars like atmospheres (Huwe et al 2019).

• Pioneer vascular plants in extreme soils:
  - Shrubs and grasses such as *Tibouchina longifolia*, Poaceae and *Palhinhaea cernua* on acidic, oligotrophic volcanic crater soils (Rios-Reyes et al 2025).
  - *Parastrephia quadrangularis* on high elevation, hyper arid, nutrient poor Andean volcanic slopes (Zhang et al 2021).

• Bacterial pioneers:
  - Actinobacteria (including *Arthrobacter agilis* Ant EH 1) and other oligotrophs (Chloroflexi, Gemmatimonadetes, Proteobacteria) dominating early Antarctic and alpine mineral soils (Rime et al 2016; Amen et al 2025; Wood et al 2025).
  - Metabolically versatile cold adapted species such as *Dyadobacter aurulentus* from high altitude cold soils (Yadav et al 2025).
  - PGPR like *Bacillus cereus* and *Priestia megaterium* from volcanic pioneer systems (Rios-Reyes et al 2025).

• Fungal pioneers and endophytes:
  - Psychrophilic and oligotrophic fungi from polar and alpine soils and mosses (Jodłowska & Białkowska 2024).
  - Atacama Desert endophytes that enhance crop performance under combined low temperature, low water, high UV and low oxygen (Molina-Montenegro et al 2023).

In all cases, multi stress tolerance arises from consortia: plants (or mosses) together with drought, cold and radiation tolerant bacteria and fungi, often with nitrogen fixation, mycorrhiza, endophytism and oxidative stress mitigation as core functions (Hanaka et al 2021; Poudel et al 2021; Zhang et al 2021; Allsup et al 2023; Iqbal et al 2023; Molina-Montenegro et al 2023; Jodłowska & Białkowska 2024; Amen et al 2025; Addison et al 2025; Wood et al 2025). These terrestrial systems provide concrete, experimentally supported models for designing pioneer biota in early extra-terrestrial habitats, even if direct Martian deployment remains a long-term prospect.

Conflict of Interest. The authors declare that there is no conflict of interest.

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