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Cold Arid Microbiomes: An Insight into Biodiversity, Adaptation Strategies, and Potential Applications

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Abstract: Cold-arid deserts, among the most extreme ecosystems on Earth, are characterized by persistently low moisture availability and extremely low temperatures. Despite the extreme harsh conditions, this particular terrestrial ecosystem harbors, highly specialized microbial species of bacteria, archaea, fungi and viruses. The microbial community thriving in the extreme cold and driest habitat plays a pivotal role in the functioning of ecosystem by maintaining the biogeochemical cycles. The microbial diversity in cold-arid deserts have ability to withstand the freezing and desiccation stress through multiple adaptative strategies which includes production of anti-freeze proteins, enzymes and other biomolecules. The cold-arid microbiomes have wide range of biotechnological application in agriculture, environment and industrial sector, in which they can be used for the alleviation of plants stresses (nutrients, biotic and abiotic stress), bioremediation of various pollutants, and production of industrial products used in food processing, textile and pharmaceutical industries. The study of microbial diversity in freezing and desiccation stress is an important aspect which could be done through culture-dependent, culture-independent and omics techniques. This review highlights the, biodiversity of cold-arid microbiomes along with their adaptation strategies, and techniques and methods to study microbial diversity and emerging ecological and biotechnological applications.

Key words: Cold-arid deserts, microbial diversity, adaptation strategies, biotechnological significance, ecological resilience.

Cold-arid deserts, an extreme terrestrial ecosystem of Earth is shaped by the combination of mainly two stresses i.e. extreme low temperature (subzero) and severe limitation of water (annual precipitation typically <250 mm). The ecosystem is more worsen by the other stresses like elevated levels of UV radiation, low atmospheric pressure, and strong winds. Moreover, the region exhibits the extreme variability in the climate, with strong diurnal and seasonal temperature fluctuations (Fortt *et al.,* 2025). On Earth, across high-altitude and latitude, eight major cold-arid deserts are known that includes Antarctic Desert, Gobi Desert, Arctic Desert, Taklamakan Desert, Patagonian Desert, Great Basin Desert, Karakum Desert, and Kyzylkum Desert. On the other hand, Atacama Desert, Trans-Himalayan Cold Desert, Altiplano Desert, and Iranian Plateau are also sometime denoted as cold-arid deserts as some zones of these region shows cold desert conditions. Among all the cold-arid deserts listed, Antarctic Desert is often regarded as the dry valley due to its coldest and driest region on the planet (Abd El-Ghani *et al.,* 2017; Doran *et al.,* 2002).

The soil of this terrestrial ecosystem is coarse-textured, poorly developed, low in bioavailable nutrients and organic carbon, due to which vegetation is absent or sparse. Besides the cold stress, water limitation, high UV radiations low availability of nutrients, and apparent barrenness, microhabitat is protected (Fortt *et al*., 2025). Cold arid deserts niches, including permafrost layer, subsurface soil, translucent rocks, cryoconite holes and snow patches are home to number of microbes. Archaea, bacteria, fungi, algae and viruses are found to inhabit this extreme terrestrial Earth's ecosystem (Chauhan and Anita, 2024). The microbes surviving in the cold arid deserts play a significant role in biogeochemical cycling i.e. mineral weathering, nitrogen transformation, carbon turnover and ecosystem stability. The microbes opt various adaptation strategies which includes production of extracellular polymeric substances, UV-protective pigments, and enzyme, reduces metabolic rate, flexible membrane lipid composition and DNA repair system (Collins and Margesin, 2019; McCann *et al.,* 2016; Russell, 2007).

Microbes, inhabiting the cold arid microbial reservoir consisting unique and important biomolecules, may have ecological, agricultural and biotechnological advantages. Among all the biomolecules, cold active enzymes (lipases, proteases, cellulases, amylases, xylanases, and β-galactosidases), antifreeze proteins, pigments, osmoprotectants, antimicrobial compounds and exopolysaccharides are various important molecules for several ecological and biotechnological applications (Cavicchioli *et al.,* 2011; Collins and Margesin 2019). As microbiome residing in the cold-arid habitat has significant biotechnological applications, therefore, biodiversity study is very significant. Traditionally, the biodiversity of microbes residing in cold-arid environment relied culture-dependent methods. The culture-dependent methods help in capturing only a fraction of the complete biodiversity. However, the culture-independent and high-throughput omics techniques i.e. metatranscriptomics, metaproteomics and metagenomics have been found to be effective to reveal the hidden functional and taxonomic diversity across the cold-arid terrestrial system (Datta *et al.,* 2026). In the present manuscript compiles the details on biodiversity, their adaptative strategies, techniques and methods to study microbial biodiversity and biotechnological applications.

Biodiversity of Cold Arid Microbiome

Earth contains eight major cold-arid deserts, along with several other regions that possess similar habitats and support diverse microbial communities. These environments harbor a wide range of microbial phyla belonging to bacteria, archaea, algae, and fungi, including Pseudomonadota, Bacillota, Bacteroidota, Actinomycetota, Acidobacteriota, Chloroflexota, Gemmatimonadota, Verrucomicrobiota, Planctomycetota, Nitrospirota, Deinococcota, Ascomycota, Basidiomycota, Chytridiomycota, Mortierellomycota, Cyanobacteriota, Bacillariophyta, Chlorophyta, Euryarchaeota, Thaumarchaeota, and Woesearchaeota (Fig. 1).

The remarkable diversity of microbial communities inhabiting cold-arid deserts is sustained by specialized physiological and biochemical adaptations that enable survival under extreme environmental stress. These adaptations include regulation of ion-channel permeability, alteration of enzyme kinetics, modulation of membrane fluidity, and seasonal dormancy through various mechanisms. Maintaining cellular membrane fluidity is a critical requirement for psychrophilic microbes, as decreasing temperature reduces membrane fluidity and consequently affects cellular functionality (Suyal *et al*., 2021).

The ability of cold-tolerant or cold-adapted microbes to survive at extremely low temperatures is attributed to unique molecular attributes such as antifreeze proteins (AFPs), cold shock proteins (CSPs), ice-nucleating proteins

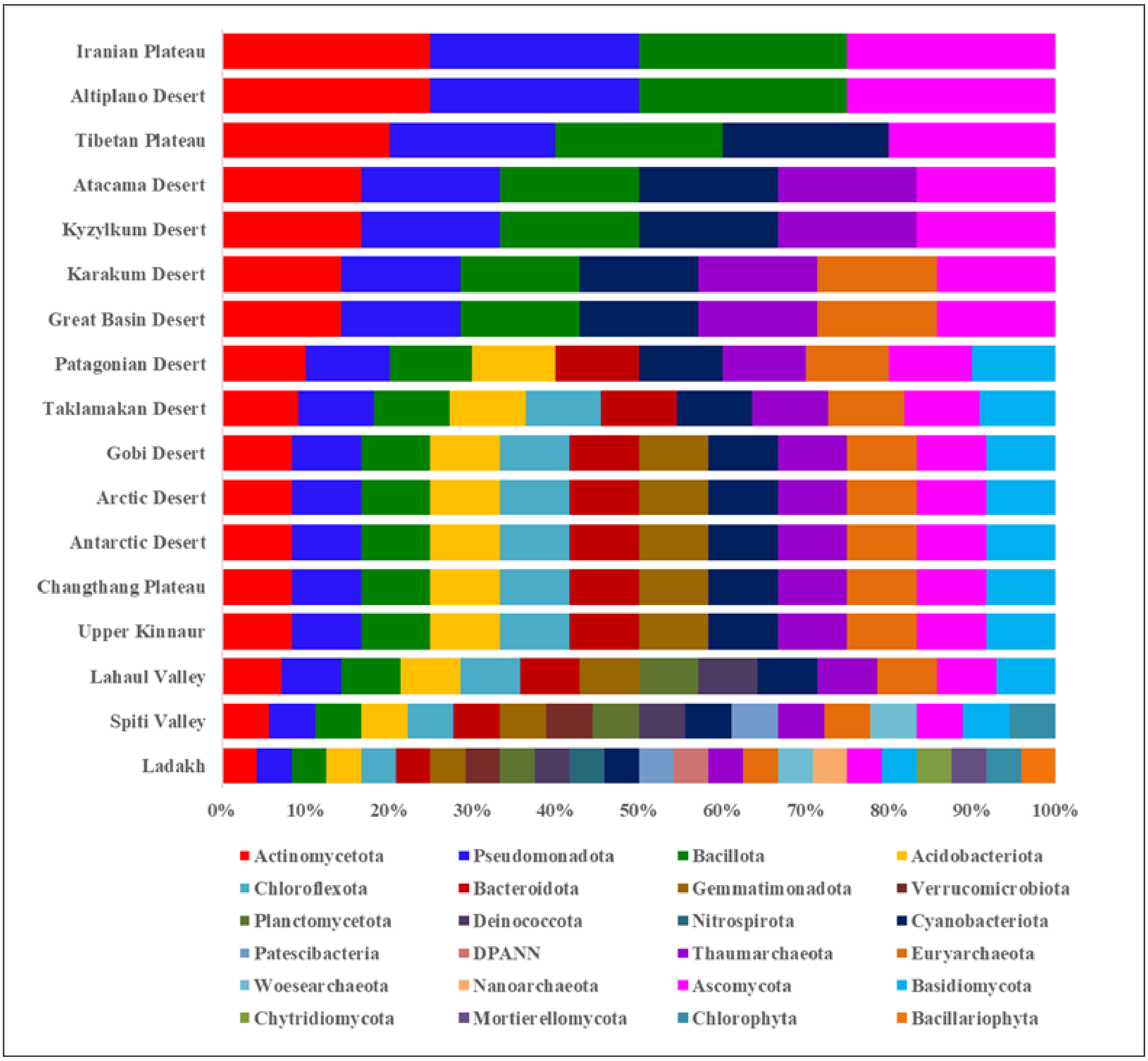

Fig. 1. Relative distribution of microbial phyla among cold-arid deserts.

(INPs), and cold-acclimated proteins (CAPs), which facilitate survival in cold environments. Additionally, osmolytes, pigments, and lipopeptides play significant roles in enhancing microbial tolerance to extreme environmental conditions (Choudhary *et al*., 2024).

Antifreeze proteins: The production of antifreeze proteins (AFPs) represents an important survival strategy adopted by microbial communities inhabiting icy environments (Pathania *et al*., 2022). These proteins bind to ice crystal surfaces and inhibit further crystal growth by depressing the freezing point without significantly altering the melting point (Celik *et al*., 2010). Cold-adapted microbes therefore exhibit measurable thermal hysteresis (TH), defined as the difference between freezing and melting temperatures, arising from the adsorption of AFPs onto ice crystals. This interaction generates convex ice fronts between adjacent AFP molecules, increasing surface energy and thereby preventing continued ice growth (Muñoz *et al*., 2017). Proteins exhibiting thermal hysteresis (TH) and ice recrystallization inhibition (IRI) activities are broadly classified as ice-binding proteins (IBPs) (Kim *et al*., 2014). AFPs have been isolated from diverse organisms including sea-ice diatoms, bacteria, snow algae, and snow-mold fungi (Hoshino *et al*., 2003; Raymond, 2011). Bacterial genera reported to possess AFP activity include *Enterobacter*, *Marinomonas*, *Pseudomonas*, *Psychrobacter*, *Rhodococcus*, and *Stenotrophomonas* (Santiago *et al*., 2016). The Afp1 antifreeze protein has been characterized from the psychrophilic yeast *Glaciozyma antarctica* PI12 (Hashim *et al*., 2013). In a recent study, AFP-producing microbes were screened from environmental isolates; among 215 isolates, 24 exhibited freeze resistance, and protein extracts prepared from 131 isolates were evaluated for ice recrystallization inhibition, of which 14 demonstrated AFP activity, including species of *Acinetobacter*, *Arthrobacter*, *Cryobacterium*, and *Pseudomonas* (Lopes *et al*., 2024).

Ice nucleating proteins: Ice nucleating proteins (INPs) represent another important class of ice-interacting biomolecules produced by certain microorganisms inhabiting cold environments. Several bacterial species synthesize ice crystal–modulating substances, including ice-nucleating proteins, antifreeze proteins (AFPs), and anti-nucleating compounds (Kawahara, 2017). Although AFPs and INPs both bind to ice surfaces, they perform opposite biological functions: AFPs inhibit ice crystal growth, whereas INPs promote controlled ice formation.

INPs are large, membrane-associated proteins that facilitate heterogeneous ice nucleation by organizing water molecules into an ice-like lattice structure (Pandey *et al*., 2016). This organization reduces the activation energy required for freezing and enables ice formation at relatively high subzero temperatures, often between 0°C and −10°C (Collins and Margesin, 2019). By promoting extracellular ice formation, INPs help prevent intracellular freezing, thereby minimizing cellular damage. Additionally, the release of latent heat during crystallization temporarily buffers further temperature decline (Pummer *et al*., 2015).

Ice-nucleating activity has been documented in bacteria, fungi, insects, and plants from cold environments, although most mechanistic studies have focused on bacterial systems (Cid *et al*., 2016). Bacterial ice nuclei are typically active within temperature ranges of 0°C to −10°C (Cochet and Widehem, 2000). Based on heterogeneous nucleation threshold temperatures, bacterial INPs are classified into Type I (0°C to −4°C), Type II (−5°C to −7°C), and Type III (−8°C to −10°C) categories (Schmid *et al*., 1997). These activity classes are associated with differences in protein aggregation states, including monomeric and higher-order oligomeric assemblies.

The ice-nucleation-active (Ina+) phenotype in bacteria is encoded by specific structural genes that express outer membrane proteins capable of catalyzing ice formation at high subzero temperatures (Wu *et al*., 2009). Numerous INP-producing bacterial species have been reported, although many of these proteins remain insufficiently characterized at the molecular level (Białkowska *et al*., 2020).

Cell membrane fluidity: Bacterial communities inhabiting cold environments encounter several physiological challenges at sub-zero temperatures, including reduced enzymatic reaction rates, protein destabilization, increased water viscosity, decreased membrane fluidity, and limited availability of liquid water for metabolic processes (Hassan *et al*., 2016). Temperature stress significantly alters the physical properties of membrane lipids, thereby influencing overall membrane fluidity (Los and Murata, 2004). The bacterial cell membrane serves as a critical interface between the cell and its environment, functioning as the primary site for nutrient transport, environmental sensing, and energy generation.

A decline in temperature reduces membrane fluidity, promoting a transition from the biologically active liquid-crystalline phase to a rigid gel phase, which impairs membrane functionality. Membrane fluidity refers to the degree of molecular motion and structural disorder within the lipid bilayer (Chintalapati *et al*., 2004). To counteract cold-induced rigidity, microorganisms employ homeoviscous adaptation, a conserved physiological strategy that maintains optimal membrane viscosity under changing environmental conditions (Mansilla *et al*., 2004). Both Gram-positive and Gram-negative bacteria, as well as archaea possessing distinct membrane architectures, respond differently to temperature fluctuations. Many bacteria modify endogenous fatty-acid composition to prevent phase transition into the gel state (Flegler, 2022). Psychrophilic microorganisms typically increase the proportion of unsaturated and polyunsaturated fatty acids relative to saturated fatty acids in membrane phospholipids. Additional adaptive mechanisms include reduction in lipid head-group size and charge, alteration of lipid class composition, and conversion of trans- to cis-fatty acids (Guan *et al*., 2013; Sharma *et al*., 2022). These modifications introduce steric constraints that disrupt tight lipid packing, thereby enhancing membrane flexibility and maintaining functionality at low temperatures (D'Amico *et al*., 2006).

Omics-based studies further support these adaptive responses. Transcriptomic analyses demonstrate cold-induced up-regulation of genes associated with membrane biogenesis (Gao *et al*., 2006), while comparative genomic studies reveal enrichment of membrane-related genes in psychrophilic genomes (Lauro *et al*., 2008). Proteomic and transcriptomic investigations also indicate increased expression of membrane transport proteins, facilitating nutrient acquisition under cold stress (Cacace *et al*., 2010).

Cold-adapted eukaryotic microbes exhibit similar strategies. The Arctic yeast *Rhodosporidium diobovatum* is considered psychrotolerant due to its relatively high membrane fluidity. Likewise, *Aureobasidium* species isolated from Arctic glaciers display elevated membrane fluidity with moderate temperature-dependent variation, reflecting specialization to glacial habitats (Turk *et al*., 2011). Comparative studies of Antarctic *Flavobacterium* species have shown greater diversity in membrane fatty-acid composition than mesophilic and thermophilic counterparts, highlighting enhanced biochemical flexibility under cold stress.

Overall, maintaining membrane stability together with sufficient fluidity is essential for microbial survival in extreme cold environments, making membrane fluidity a key physiological indicator of successful adaptation to cold-arid ecosystems.

Cold shock proteins: Cold conditions induce a set of cold inducible proteins, some of which are vital for cell growth under low temperature stress. Microbes produce cold shock proteins (CSPs) when exposed to cold stress. These are nucleic acid binding proteins with an approximate molecular weight of 7.4 KDa and possess a cold shock domain (Horn *et al.,* 2007). CSPs have been extensively studied in *E. coli*, these act as molecular chaperons and regulate DNA replication, transcription and translation (Chattopadhyay 2006). Most studied CSPs include *csp*A of *E. coli* and *csp*B of *Bacillus subtilis*. Both of these proteins contain RNA binding motif and also function as RNA chaperones that minimize secondary folding of RNA molecules at low temperatures (Wouters *et al.,* 2000).

Nine CSPs have been identified in *E. coli* named *csp*A to *csp*I. Out of these, *csp*A, B, G, and I are cold inducible whereas, *csp*D is generally expressed under nutrient stress (Nakashima *et al.,* 1996; Yamanaka and Inouye, 1997). CSPs are found to have five antiparallel β strands, forming β barrels. Most of the CSPs bind to single stranded DNA and RNA (Ermolenko and Makhatadze, 2002). Besides CSPs, another set of proteins known as cold acclimation proteins differ from the former as their expression increases gradually and lasts longer than CSPs which are expressed immediately after cold shock (Kuhn, 2012). In a study, four species of psychrotrophic *Pesudomonas* were found to have *csp*A protein with conserved DNA/RNA binding motif. Exposing them to cold shock and incubating all the four species at 4°C led to expression of *csp*A protein, which explains protective mechanism of cold shock proteins at low temperatures (Bisht *et al.,* 2014).

Pigments: Pigments are important secondary metabolites produced by microbes surviving in stressful environments as a protective strategy to combat stress conditions, provide protection from UV damage, photooxidation, and freeze-thaw cycles (Silva *et al.,* 2021). Some of these coloured secondary metabolites are utilized for the process of photosynthesis, while others act as a source of energy. Pigment molecules also have antimicrobial properties that provide protection to the producing organism (Sajjad *et al.,* 2020). Pigment production has been reported in psychrophilic algae, bacteria, molds, and yeast (Cavalcante *et al.,* 2023). Carotenoids are most common microbial pigments produced under cold stress. Shen *et al.,* (2018) obtained pigmented bacteria of orange, red-range, yellow, pink and white colour from core of Yuzhufeng Glacier in Tibetan Plateau.

Enzymes: The drop in reaction rates and enzyme activity has been observed with decreasing temperatures. Psychrophiles for their survival and metabolic activities in cold ecosystems possess psychrozymes which are cold-active enzymes, that perform optimally and with high specific activity even at low temperatures (0-20°C) (Hamid *et al.,* 2022). This can be attributed to structural adaptation of the entire proteins or certain regions of protein to increase the flexibility, decrease thermal stability to surpass the freezing effect (Al-Maqtari *et al.,* 2019). Psychrozymes show high catalytic activity at temperatures where other organisms would barely survive. Higher structural flexibility is the major reason for higher catalytic efficiency of these enzymes. Structural composition of cold adapted enzymes however renders them heat labile (Tronelli *et al.,* 2007). Psychrozymes have higher K_{cat} due to decreased activation energy and negative value of entropy. Besides, enhanced flexibility in their architecture allows easy accommodation of the substrate and reduced cost of confirmational changes required during enzyme-substrate interaction which explicate high K_m values (D'Amico *et al.,* 2006). Various cold active enzymes including amylases, ligases, lipases, cellulase, proteases, xylanases, laccases, pectinases and galactosidases are produced by psychrophiles (Gupta *et al.,* 2023). Alkaline protease producers belonging to actinobacteria and proteobacteria, were isolated from glaciers and soils of Lahaul and Spiti (Salwan *et al.,* 2010). The study observed the production of high levels of enzymes between 15 to 25°C by microbes. *Bacillus pumilus* was isolated from Thajwas glacier produced a cold active enzyme showing km value of 1.0 mg mL^{-1} and V_{max} 10.0

Fig. 2. Applications of cold-arid microbiomes in various sectors.

Table 1 Potential applications of cold-arid microbes

Microbes	Source	Biotechnological applications	References
Arthrobacter phenanthrenivorans	Siberian permafrost	Ability to tolerate heavy metal stress	Zhang *et al.* (2013)
Arthrobacter sulfonivorans	Ladakh	Exhibits P-solubilization, IAA production, Siderophores production PGP traits	Yadav *et al.* (2015)
Arthrobacter sulfureus	Ladakh	Exhibits IAA production, ACC deaminase activity PGP traits	Yadav *et al.* (2015)
Bacillus anthracis	Ladakh	Exhibits P-solubilization, IAA production, PGP traits	Yadav *et al.* (2015)
Bacillus cereus	Ladakh	Exhibits IAA production PGP traits	Yadav *et al.* (2015)
Bacillus firmus	Ladakh	Exhibits P-solubilization, IAA production, Siderophores production PGP traits	Yadav *et al.* (2015)
Bacillus muralis	Ladakh	Exhibits IAA production, Siderophores production PGP traits	Yadav *et al.* (2015)
Bacillus pumilus	Ladakh	Exhibits P-solubilization, IAA production, Siderophores production PGP traits	Yadav *et al.* (2015)
Bacillus simplex	Ladakh	Exhibits IAA production PGP traits	Yadav *et al.* (2015)
Bacillus subtilis	Lahul and Spiti	Improve growth of tomato	Kumar *et al.* (2015a)
Brevundimonas sp.	Patagonian Desert	Exhibits nitrogen fixation PGP traits and promoted the growth of tomato	Vega-Celedón *et al.* (2021)
Candidatus Nitrososphaera	Gobi Desert	Ability to tolerate drought stress	Wang *et al.* (2024)
Desemzia incerta	Ladakh	Exhibits P-solubilization, IAA production, Siderophores production PGP traits	Yadav *et al.* (2015)
Exiguobacterium antarcticum	Ladakh	Exhibits P-solubilization, IAA production, PGP traits	Yadav *et al.* (2015)
Exiguobacterium undae	Ladakh	Exhibits IAA production PGP traits	Yadav *et al.* (2015)
Flavobacterium sp.	Patagonian Desert	Exhibits N_2-fixation and P-solubilization PGP traits, and promoted the growth of tomato	Vega-Celedón *et al.* (2021)
Gemmatirosa kalamazoonesis	Atacama Desert	Exhibits nitrogen fixation, and chitinolysis PGP traits	Contreras *et al.* (2023)
Glaciimonas immobilis	Siberian permafrost	Ability to tolerate heavy metal stress	Zhang *et al.* (2013)
Lysinibacillus fusiformis	Ladakh	Exhibits P-solubilization, IAA production, Siderophores production PGP traits	Yadav *et al.* (2015)
Paenibacillus terrae	Ladakh	Exhibits P-solubilization, PGP traits	Yadav *et al.* (2015)
Planococcus donghaensis	Ladakh	Exhibits P-solubilization, IAA production, Siderophores production PGP traits	Yadav *et al.* (2015)
Priestia aryabhattai	Lahaul and Spiti	Improve growth and productivity of garlic and potato	Gulati *et al.* (2024)
Pseudomonas geniculata	Lahaul and Spiti	Improve growth and productivity of garlic and potato	Gulati *et al.* (2024)
Pseudomonas migulae	Lahaul and Spiti	Improve growth and productivity of garlic and potato	Gulati *et al.* (2024)
Pseudomonas panacis	Antarctic desert	Ability to tolerate heavy metal stress	Barrientos-Díaz *et al.* (2008)
Pseudomonas sp.	Atacama Desert	Exhibits ACC deaminase activity PGP traits	Gaete *et al.* (2020)
Pseudomonas tolaasii	Antarctic desert	Ability to tolerate heavy metal stress	Barrientos-Díaz *et al.* (2008)
Pseudomonas trivialis	Antarctic desert	Ability to tolerate heavy metal stress	Barrientos-Díaz *et al.* (2008)
Rhizobium nepotum	Lahaul and Spiti	Improve growth and productivity of pea	Gulati *et al.* (2024)
Sanguibacter antarcticus	Ladakh	Exhibits P-solubilization, IAA production, Siderophores production PGP traits	Yadav *et al.* (2015)
Solibacter usitatus	Atacama Desert	Exhibits nitrogen fixation, chitinolysis PGP traits	Contreras *et al.* (2023)
Subtercola frigoramans	Siberian permafrost	Ability to tolerate heavy metal stress	Zhang *et al.* (2013)

µmol/mL/min at 20°C and pH 9 (Farooq *et al.,* 2021).

Ecological and Biotechnological Applications

Cold temperature stress is one of the prominent environmental stresses encountered by cold arid microbiomes. In order to survive an extreme and inhospitable environmental conditions, the psychrotrophic microbes develop obvious adaptative attributes towards several abiotic factors namely freezing temperatures, sea ice, salinity, high radiation (in Antarctic region), nutrients limitation, low humidity and strong winds. Their distinct adaptiveness is due to the expression of various biological molecules including proteins and enzymes, which can be utilized for different ecological and biotechnological applications (Choudhary *et al*., 2024; Feller and Gerday, 2003; Puranik *et al.,* 2022) (Fig. 2).

Agricultural applications: In extreme cold temperature regions, the biological processes become sluggish owing to the constrains in nutrients and water supply, which significantly reduces the yield of agricultural and commercial crops (Collins and Margesin, 2019). Psychrotrophic microbes were found to positively impact the soil health and plant growth by solubilizing various micro-nutrients including potassium, phosphorus, zinc etc., and biological N_2 fixation (Table 1). They also play a major role in combating cold induced environmental stress in plants. Phosphorus solubility and cold-induced stress adaptability is favored by *Serratia*, *Arthrobacter*, *Pseudomonas*, and *Bacillus* genera of psychrotrophic microbes (Kumar *et al.,* 2015b; Kumar *et al.,* 2016; Yadav *et al.,* 2019). Similarly, the fixation of atmospheric nitrogen in cold-arid environmental conditions is facilitated by the genera *Arthrobacter*, *Azoarcus*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Gluconoacetobacter*, *Herbaspirillum*, *Rhizobium*, and *Serratia* (Kumar *et al.,* 2019; Yadav *et al.,* 2017). Additionally, certain genera of these microbes like *Rhizobium*, *Enterobacter*, *Acinetobacter*, *Achromobacter*, *Azospirillum,* etc., also produce plant hormones under abiotic stress conditions which further helps in plant adaptation. For instance, they produce 1-amino cyclopropane-1-carboxylate deaminase (ACC deaminase) and helps in regulating the levels of ethylene hormone in plants (Cai *et al.,* 2017; Xu *et al.,* 2014). Psychrotrophic bacterium *Pseudochrobactrum kiredjianiae* A4 are reported to produce stress induced siderophores, ACC deaminase, and indoleacetic acid (IAA). Furthermore, this strain was found to assist plants against various plant pathogens like *Rhizoctonia cerealis*, *Botrytis cinerea*, *Fusarium oxysporum*, *Fusarium graminearum*, and *Magnaporthe grisea* under *in-vitro* conditions (Qin *et al.,* 2017). The psychrophilic microbes can be employed to nurture and enhance the plant growth and crop yield in cold-arid regions both in normal conditions and under biotic and abiotic stress. The consortium of psychrophilic microbes can be make use of as bioinoculant, and biofertilizers to promote sustainability in production of food and commercial crops in cold-arid regions.

Environmental applications: The effectiveness of thermophilic and mesophilic enzymes in colder environments is feeble or, very limited. Therefore, psychrophilic microbes with cold-active enzymes can play very crucial role in biodegradation of organic wastes in cold and cold temperate regions. There have been successful attempts to develop microbial consortium of psychrophiles (including *Bacillus sp.*, *Bacillus atrophies*, *Paceliomyces* sp., *Eupenicillium crustacean*, etc.,) for converting agricultural wastes into compost thereby enriching the soil nutrients, fertility and negating the environmental pollution caused by burning of these wastes (Shukla *et al.,* 2016). It has also been observed that the direct use of cold-active enzymes like xylanase, proteases, lipases etc., for bioremediation purposes is more feasible and worthy option as the optimal growth of bacterial cells requires various other parameters which can be challenging to meet in harsh cold conditions. Psychrophilic microbes like *Sphingomonas* spp., *Oleispira antarctica*, *Rhodococcus* sp., and *Pseudomonas* sp., are also found to be efficient in degrading petroleum hydrocarbons (Aislabie *et al.,* 2006; Kumar and Bharadvaja, 2019; Miri *et al.,* 2019).

Industrial applications- Cold active enzymes: The psychrophilic microbes can thrive in harsh cold environments because their physiology is regulated by cold-adapted enzymes which are responsible for reduced thermal stability, higher flexibility and catalytic efficiency (Bruno *et al.,* 2019). The cold-active enzymes extracted from psychrophilic microbes can be classified into three groups based on their heat sensitivity and catalytic activity in comparison to mesophilic enzymes. The 'group 1' cold-active enzymes are heat sensitive with catalytic activity similar to mesophilic enzymes, 'group 2' cold-active enzymes are heat sensitive with higher catalytic activity at low temperature, and 'group 3' cold-active enzymes have same thermal characteristics as mesophilic enzymes but exhibit higher catalytic activity at low temperature. The cold-active enzymes are required for low-temperature industrial operations in the sectors like food and beverage, textile, molecular biology, detergents, and bioremediation (Javed and Qazi 2016; Kuddus 2015; Kuddus 2018). Some of the cold-active enzymes derived from psychrophilic microorganisms with high industrial demands include hydrolase, protease, pectinase, lipase, cellulase, amylase, **β**-galactosidase, β-glucosidase, cellulase, xylanase, and chitinase (Hamid *et al*., 2022). In a study, *Klebsiella* sp. from cold deserts of Ladakh was reported for producing the cold adapted endocellulase that was having ability to hydrolyse the carboxymethyl cellulose (Bhat *et al.,* 2013). In a similar report, microfungi, *Aspergillus sydowii, A. uvarum,* and *Nodulisporium verrucosum,* was reported for exhibiting α-amylase activities and *Penicillium fellutanum,* and *P. griseofulvum* was found to exhibits protease activity (Khajuria and Nonzom 2025).

Industrial applications- Nanobiotechnology: The psychrophilic microbes, particularly Antarctic bacteria have been explored in recent years for the bio-fabrication of inorganic nanoparticles. The biomineralization process of fabricating nanoparticles is environment friendly and cost-effective approach without using harsh and toxic chemicals. The metal nanoparticles synthesized by employing cold adapted bacterial strains for various biomedical applications exhibited exceptional stability (Javed and Qazi 2016; John *et al.,* 2020; John *et al.,* 2021). The gold nanoparticles fabricated using Antarctic bacteria *Bacillus* sp. GL1.3 at varying temperature range (4°C to 37°C) have shown effective bactericidal activity against *Desulfovibrio* sp., which is a sulphate reducing bacteria (Das *et al.,* 2020). Extracellular biosynthesis of AgNPs using Antarctic bacteria *Yersinia kristensenii*, *Psychrobacter* sp., *Pseudomonas veronii*, and *Aeromonas salmonicida* has been reported at different temperatures (4°C and 30°C), and it was observed that the Ag nanoparticles synthesized at lowest temperature (4°C) exhibited higher stability and bactericidal property. The fabricated Ag nanoparticles remained stable for more than ten months despite incubating under light (Javani *et al.,* 2015). Cadmium sulphide (CdS) and Cadmium telluride (CdTe) quantum dots were successfully fabricated using Antarctic bacteria *Shewanella*, *Psychrobacter*, and *Pseudomonas* which are resistant to cadmium and tellurite induced toxicity (Plaza *et al.,* 2016). The CdS and CdTe quantum dots are known to exhibit size dependent multi-colour emissions and are used in various industries dealing with optical devices (da Costa *et al.,* 2024). Silver nanoparticles synthesized using bacterial strains of Antarctic region namely *Bacillus*, *Brevundimonas*, and *Rhodococcus* exhibited very effective activity against nosocomial pathogens and can be used as an alternative to traditional antibiotics in order to combat these pathogens (John *et al.,* 2022). The psychrophilic microbes remain largely underexplored for their true potential to be used in fabricating different kinds of nanomaterials for industrial applications, nonetheless they provide an assuring platform towards greener nanotechnology.

Techniques and Methods Relevant to Analysis of Cold Adapted Microbes

Psychrophilic microbes are studied and analyzed using physiology, ecology and omics tools. The foremost step for studying microbial diversity of cold environment is isolation done by culture dependent and independent techniques. Culture-based approaches provide understanding of physiological potential of isolated microorganisms, but do not essentially provide complete information on composition of microbial community (Orphan *et al.,* 2000). The use of culture-based approaches for studying the microbes of extreme environments still remains a challenge such as oceans that are among the harshest environment on Earth where temperatures can drop below down the freezing in the abyssal zone (Fulke *et al.,* 2025).

Limitations with the conventional/traditional methods to study the behavior of microbes at molecular level shifted the focus of the researchers to advanced "omics" tools and techniques. The growth of microorganisms and the interpretation of their kinetics is a core skill for studying microbial communities so that the essential skills are not lost (Fernández-Martínez *et al.,* 2024). The information gathered from bacterial growth curve is of great value to field of microbiology. The physiological strategies that recompense for low-temperature metabolism remain poorly known. Growth and metabolism are limited in colder environments as of membrane fluidity, thermal energy, reaction rates and affinity of enzymes for their substrates reduces, and aqueous viscosity increases.

Metagenomics approach is used to study communities of uncultured microorganisms at the genetic level (Nam *et al.,* 2023) (Vieites *et al.,* 2008). Applications of 'omics' approaches have improved the psychrophilic adaptation mechanisms understanding, un-veiling the versatility and adaptability of cryosphere life (Aliyu *et al.,* 2017). Metagenomics is revolutionizing the ability to explore functional potential, and ecological roles of the microbes. The methodologies for metagenomic study cover sample collection, library preparation, nucleic acid extraction, sequencing, and data analysis (Rajpurohit *et al.,* 2026). Identification of the microbes by phenotypic method is done by microscopic techniques. Fluorescence microscopy and cryo-electron microscopy can be used to expose membrane adaptations (Brzozowski *et al.,* 2019; Khanna and Villa 2022).

Combination of electron microscopy, epifluorescence microscopy, and nanoscale secondary ion mass spectrometry with steady isotope probing was used for studying cellular features involved in the cold phenotype expression in *Clostridium psychrophilum* exposed to cold stress under anoxic conditions. The study observed a temperature dependent change in morphology. Inhibition of cell division below −10 °C pre-dominance of filamentous growth. Bacterial cells showed thick cell wall and of long exopolysaccharide (EPS) fibres formed a capsule. Bacteria were also seen to be embedded in dense matrix extracellularly suggesting role in cryo-protection and nutrient cycling. Extracellular DNA strings, release of membrane vesicles, and transient cell membrane permeability were also observed suggesting that evolution via genetic material transfer may be particularly active under frozen conditions (Perfumo *et al.,* 2014).

Another emerging research is the use of cold adaptive microbes in fabrication of the nanoparticles for which different techniques such as ultraviolet-visible spectroscopy, X-Ray Diffraction (XRD), Fourier transformed infrared spectroscopy (FTIR), and dynamic light scattering (DLS) can be used to characterize synthesized nanoparticles. Further, the microscopic techniques used are transmission electron microscopy (TEM), scanning electron microscopy (SEM), atomic force microscopy (AFM), scanning tunneling microscopy (STM). The physio-chemical properties can be studied by mass spectroscopy (MS), fluorescence correlation spectroscopy (FCS), X-ray photoelectron spectroscopy (XPS), Raman scattering (RS), circular dichroism (CD), and inductively coupled plasma atomic emission spectroscopy (ICP/AES), were used (Mageswari *et al.,* 2016).

16S rRNA gene sequencing is used for identification and classification of bacteria and the technique uses highly conserved 16S ribosomal RNA (rRNA) gene present in all prokaryotes but exhibits enough sequence variation to distinguish between species (Poretsky *et al.,* 2014). Whole-genome sequencing of microbes is helping in mapping genome mapping of novel organisms, finishing genomes of known microbes, or comparing genomes of multiple samples (Aminu *et al.,* 2024). Further, transcriptomics, metabolomics and proteomics, have greatly enhanced our understanding of the adaptations at sub-zero temperatures (Datta *et al*. 2026). Future research could be focused on single-cell omics, machine learning (ML), and advanced sequencing for discovering untapped microbial diversity of extreme ecosystems.

Conclusions

Biologically intriguing ecosystem i.e. cold-arid deserts which are shaped with three severe environmental stresses including extreme low temperature, water scarcity and intense radiation, are very significant for the planet Earth. It harbors the substantial taxonomic and functional diversity of microbes that are reservoirs of the various novel metabolites and biomolecules. Microbes from these niches are capable of producing specialized metabolites and biomolecules such as cold-active enzymes, secondary metabolites, pigments, and antimicrobial compound which may have promising applications in the agricultural, industrial and environmental sector. Till the time, many cold-adapted taxa have been cultured and identified using culture-dependent and culture independent studies, however many taxa are yet to be discovered with their functional potentials. In future, some advanced computational, molecular, and system level approached could be used for translating the microbial biodiversity into potential practical applications. Moreover, conservation efforts are required to preserve this unique extreme ecosystem as it is being threatened by climate change, human disturbance and glacial retreat.

Competing Interests

The authors declare no competing interests.

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