SOIL MICROBIOME OF THE COLD HABITATS

Trends and Applications

EDITED BY

Puja Gupta

Mohd. Shahnawaz

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Soil Microbiome of the Cold Habitats

This book focuses on cold habitat microbes as a potential source of elite enzymes and secondary metabolites to meet the growing demands of the pharmaceutical, food and biotechnological industries. Microbes living in such extremely cold conditions are reported to produce various biomolecules with potential biotechnological applications.

The book overviews recent research trends to discover such important biomolecules and also suggests future research directions to discover such elite novel biomolecules.

Salient features:

- Covers studies on various biotic communities and abiotic components of the soil of terrestrial habitats, with a focus on cold habitats
- Discusses various 'Omic' approaches: metagenomics and meta-transcriptomics
- Lists adaptation strategies adopted by cold-adapted microbes
- Highlights various biotechnological and industrially important biomolecules produced by cold-adapted microbes
- Explores the role of microbial biofilm in the degradation of microplastics in cold habitats

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Each editor dedicates this book to their respective parents, better halves and kids for their kind support and trust

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Preface

Microbes are present everywhere, from extreme cold to hot environments. Depending upon the type of environmental stress resisted by microbes, these are grouped according to temperature (high temperature: thermophilic, low temperature: psychrophiles), pH (acidic: acidophiles), salinity (high salinity: halophiles), etc. Among the various harsh habitats mentioned here, the microbes surviving at low temperatures, i.e., cold habitats, have attracted special attention from researchers for study. Cold habitats cover the majority of the Earth. Polar habitats like Antarctica and the Arctic, the Tibetan region and the Great Himalayas are among the cold habitats. These extreme environments are not very appropriate for the survival of human beings. Despite such extreme cold conditions, microbes thrive and occupy every corner. It is quite surprising how these microbes survive in such extreme environmental conditions. It has been documented in the literature that most microbes are the same everywhere; it is only a fraction of microbes that are endemic to a specific environment. The literature survey reveals that microbes have developed some adaptational features to withstand harsh environmental conditions. The adaptations are at the structural and functional levels. At the structural level, it could be a change in the percentage and abundance of certain amino acids. At the functional level, it could be the production of specific enzymes, secondary metabolites or other biomolecules. Such biomolecules can be exploited for various pharmaceutical and biotechnological industries.

Microbial diversity is a huge topic, and recent high-throughput sequencing techniques have played a vast role in generating data and exploring this hidden treasure. There is a need to dispense the data generated by the researchers to other scientists under the following lines: (i) to cover studies on various biotic communities and abiotic components of the soil of the terrestrial habitats, with much focus on cold habitats; (ii) to highlight various methods/techniques employed to explore microbial diversity, as well as the various biogeochemical pathways that regulate the soil microbial processes; (iii) to broaden the scope of the soil microbiome of cold habitats with various approaches already reported in the literature, i.e., metagenomics, metatranscriptomics and meta-proteomics, to get a better idea about active communities.

So, various subject experts at the international level were contacted, and the most important chapters were screened and accepted based on peer-reviewed reports. Accordingly, only 16 chapters were finalized to cover the major theme of the book. The chapter-wise synopsis of the book is as follows.

The opening chapter (Chapter 1) of the book overviews the physicochemical and biological properties of soil in cold habitats and the adoption of different strategies for maintaining soil health. Chapter 2 mentions soil as a host to various biotic communities. Chapter 3 discusses the effect of soil characteristics on soil microbial biomass and diversity. Chapter 4 highlights mainly the microbial diversity of five major cold deserts of the world, namely, the Gobi Desert; the

Taklamakan of Eurasia; the Namibian Desert in Africa; the Drass Desert of India; and the Atacama Desert of South America. Chapter 5 discusses the diversity of potassium and iron solubilising bacteria in trans-Himalayan soil. Chapter 6 discusses the potential and responses of microfungi to the dynamics of cold environments. Chapter 7 mentions the microbial diversity of rhizosphere soils of the Indian Himalayan regions. Chapter 8 mentions the soil microbiome responsible for enhanced crop productivity. Chapter 9 reports the impact of microbial biofilm community shifts on the degradation of microplastics in cold habitats. Chapter 10 portrays varied adaptive strategies employed by psychrophilic bacteria to live in cold habitats alongside their diversity in various spheres of planet Earth. Chapter 11 pools the studies on the production of secondary metabolites by some of the important psychrophilic soil microbes to report the important drug molecules. Chapter 12 describes the application of 'Omics' technologies to study soil microbiomes. Chapter 13 describes the ecological role of psychrophiles and the mechanism of adaptation in various cold ecozones. Chapter 14 describes the ecology and remediation of soil as a step toward modern soil biotechnology. Chapter 15 presents a new approach to explore the psychrophilic soil microbiome through machine learning. Chapter 16 mentions mass spectrometry as an emerging analytical technique for agriculture in a changing climate.

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Introduction

Soil contains a vast number of microbes that work cooperatively to hold *nutrients* in the soil. Different edaphic factors are responsible for modifying the soil microbial communities, thereby influencing soil quality and plant health. Various adaptations allow these microbes to cope in different environments, enabling them to survive even in hostile conditions that may not be suitable for human beings to live. One such harsh environment is extremely cold habitats. The adapted microbes produce various biomolecules for adaptation. These biomolecules can be exploited for various pharmaceutical and biotechnological industries.

Experts from different parts of the world have contributed 16 chapters in the current volume as follows:

1. Chapters 1 and 2 overview the physicochemical, biological properties, soil health and biotic communities of soil in cold habitats.
2. Chapters 3 and 4 highlight the impact of soil characteristics on the soil microbial biomass and microbial diversity of five major cold deserts of the world (the Gobi Desert; the Taklamakan Desert, Eurasia; the Namibian Desert, Africa; the Drass Desert, India; and the Atacama Desert, South America).
3. Chapters 5 and 6 discuss the diversity of potassium and iron solubilising bacteria in trans-Himalayan soil and the responses of microfungi to the dynamics of cold environments.
4. Chapters 7 and 8 document the microbial biodiversity of the rhizosphere soils in the Himalayan (Indian part) regions and report the soil microbiome for enhanced crop productivity.
5. Chapters 9 and 10 report the impact of microbial biofilm community shifts on the degradation of microplastics in cold habitats and portray varied adaptive strategies employed by psychrophilic bacteria to live in cold habitats.
6. Chapters 11 and 12 pool the studies on the production of secondary metabolites by some of the important psychrophilic soil microbes to report the important drug molecules and application of 'Omics' technologies to study soil microbiomes.
7. Chapters 13 and 14 describe the ecological role of psychrophiles' adaptation in various cold ecozones and the remediation of soil as a step toward modern soil biotechnology.
8. Chapters 15 and 16 present a new approach to exploring the psychrophilic soil microbiome through machine learning and mass spectrometry as an emerging analytical technique for agriculture in a changing climate.

13 Ecological role of psychrophiles and mechanism of adaptation in various cold ecozones

Osikemekha Anthony Anani, Mohd. Shahnawaz, Puja Gupta, Osayomwanbo Osarenotor and Frances Ngozi Olisaka*

CONTENTS

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13.1 INTRODUCTION

Microorganisms (viruses, Eukarya, Archaea and Bacteria) play a significant role in the recycling of nutrients and are considered as important indicators of a well-balanced and unperturbed ecosystem.[1] Microorganisms having the natural ability to conquer extreme environmental conditions like cold are termed *psychrophiles*, from the Greek: *psukhros* (cold) and *philein* (love).[1,2] The ability to overcome biogeographic limitations, responses to different abiotic and biotic parameters, and tropism (lifestyle) are other features psychrophiles also possess to conquer their immediate environment.[1]

Psychrophiles can tolerate a wide range of environmental temperatures below 30 °C because as temperature rises, the rate of enzymatic activities increases, which leads to kinetic heat effects, cellular activities and the swift growth of the microorganisms.[1,2] However, several studies have reported tolerances of microbes in varied temperatures, e.g., *Methanococcoides burtonii* and *Methanogenium frigidum* (15 °C, 18 °C, 23 °C, 28 °C),[1] *Chusquea subtessellata* (4–25 °C),[3] *Sphingopyxis alaskensis* and haloarchaea (4–10 °C–20 °C).[4,5]

As per studies, climate change poses a serious biological threat to animal diversity, distribution, forced migration, loss and biological change as well as ecological threats: cold, heat, nutrient deficiencies, drought and salinity.[6,7] Microbiomes and microbial symbionts impact negatively or positively on their host(s), which in turn has been found to modify the ecosystem severely. This can be seen in the relationship between the severity and incidence of diseases caused by microbes in plants.[8,9] Some studies[10–12] have recounted the impacts of global warming occasioned by climate change on the rise of sea temperatures, which has impacted *Symbiodinium*, the algal coral endosymbiont, although not the bacterial form. In addition, plants with this form of association have been shown to possess a high level of resistance and adaptation toward drought-abiotic conditions.

Global warming impacts on biodiversity have recently revealed how microbes can either acclimatise or adapt to severe conditions or migrate from them. Some studies have reported[13–15] how symbionts of microbes and mycorrhiza conquer their immediate environment (high temperature) and suggested that psychrotrophic fungi can thrive better at 10 °C and 20 °C.

In the present chapter, an attempt will be made to discuss the ecological role and adaptive mechanism of psychrophiles in various cold ecozones in the following aspects: (1) to highlight the ecological role and mode of action of psychrophiles, (2) to list the genes used by psychrophiles to adapt in the cold environment, (3) to discuss the biotechnological potential of psychrophiles and (4) to overview the metagenomic properties of psychrophiles in soil.

13.2 PSYCHROPHILES: THEIR ECOLOGICAL ROLE AND MODE OF ACTION

D'Amico et al.[2] evaluated the challenges faced by the psychrophiles to proliferate and survive at very low environmental temperatures. Psychrophiles' adaptability in various cold ecozones is portrayed in Figure 13.1.

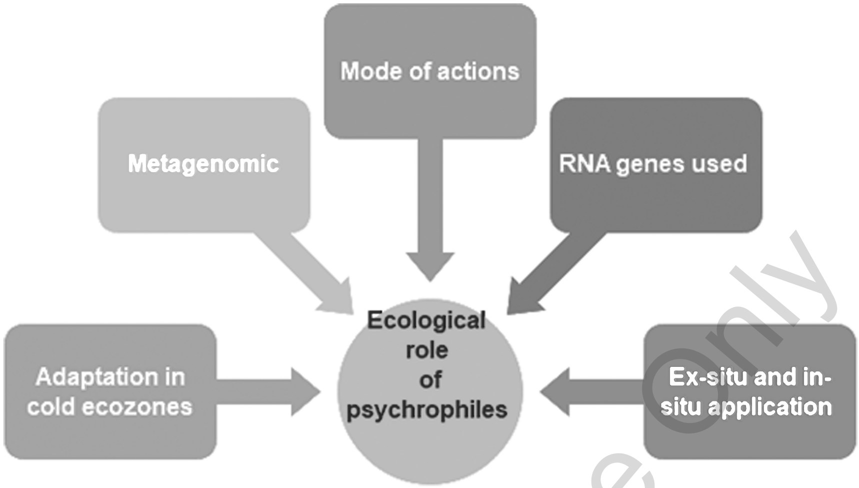

FIGURE 13.1 Ecological role of psychrophiles and mechanism of adaptation in various cold ecozones.

Psychrophiles thrive in extreme abiotic conditions – cold, even at 0 °C – in the presence of active enzymes, which aid in the sustenance of their biological cell cycle.[16] Feller[16] showed that temperature dependence is usually at a low state during the cold period, and the catalytic action is reduced moderately.

Cavicchioli et al.[17] stated that about 90% of the biosphere is covered with water (temperature ≤5 °C), which sustains several microbial diversities. These water bodies span the polar, alpine and deep-sea regions, ecosystems that are always cold and harbour psychrophiles. A study[18] evaluated the survival tactics used by psychrophiles to cope with the severe cold environment. Ecological factors like soil-microbial physiological actions affect the soil composition and structure, and a decrease in environmental temperature is one of the leading consequences of commercial plant losses globally.[19] However, severe cold ecosystems have been reported to be a good habitat for psychrotolerant and psychrophilic PSB (phosphate solubilising bacteria) that can tolerate several ranges of low-temperature settings while still keeping their metabolic activities intact. The production and expression of proteins that have antifreeze properties and stress-induced DNA segments at reduced temperatures encourage their survival instinct during severe cold stress. Psychrophiles can elicit plant development and growth by providing phosphorus and essential nutrients to soil that is highly deficient, which is a new functional feature of psychrophilic PSB. Plants require rhizosphere bacteria while growing under intense or severe environmental conditions. By contrast, it aids to improve their biological performance. In addition, the utilisation of psychrophilic PSB mixtures in the form of formulations has been reported to be effective in the optimisation of plants in low-temperature settings.[19] Psychrophiles are also adapted to the cold environment by using biomolecules like enzymes and proteins from cell factories characterised by heat lability.[20] These properties make it essential for psychrophiles' biomolecules to be utilised in cosmetics, detergents, industrial feed and food technologies, and molecular and biomedical research. Cold temperature has been known to affect biochemical and nucleic processes, folding of proteins, the rate of diffusion and porosity of membranes, and the growth of organisms. Psychrophiles are conformers with many enzymes that possess crystallographic materials that have been widely reported to enable them to adapt to the cold. These structures or materials are also characterised to have moderate and low-temperature specificity and stability, which improves the flexibility to prevent freezing effects during temperature changes.[21]

Hassan et al.[22] isolated 42 strains of bacteria from a glacier region in Pakistan and reported that the fluidity of the *Chryseobacterium frigidisoli* PB4T's membrane was significantly affected by exposure to the environment with varied temperature. For the analysis of fatty acids and methyl esters, GC-MS (gas chromatography/mass spectrometry) was used to characterise them by the liberation of the acid-catalysed methanolysis. Gram −ve and Gram +ve groups were cultivated at temperatures 5, 15, 25 and 35 °C to ascertain the effect of temperature on the fatty acid and cell membrane distribution, like the br-FAs and n-MUFAs (branched fatty acids and straight-chain monounsaturated fatty acids), which accounted for over 70% of the total analysed fatty acid components.

13.3 HIGHLIGHTS OF THE VARIOUS RNA GENES USED BY THE PSYCHROPHILES TO ADAPT TO THEIR ENVIRONMENT

Psychrophiles acclimatise to cold environments through certain adaptations, e.g., production of cold shock proteins, RNA chaperones, RNA helicases, oxidative and osmotic stress, synthesis of carotenoids and transformation factors, and peptidoglycan and membrane modifications in compatible solutes.[23] The presence of these genes is not unique to psychrophiles, but an abundance of such genes has been reported in microbes confronting low temperatures. The above-mentioned adaptations are discussed briefly in the following.

13.3.1 Cold shock proteins

Bacteria contain numerous cold shock protein (CSP) gene homologs, e.g., ribonuclease, RNA helicase (RNase, DEAD-box) and CSP.[8] It is worth stating that not all CSP genes are induced by cold.[23] CspI, G, CspE, B and CspA of *Escherichia coli* are among the few examples that are stimulated by cold.[24] An extremely preserved biological component – the nucleic acid acting as a bond region known as the cold shock domain (CSD) – is found in CSP.[25] CSD has two ribo-nucleoprotein binding subjects that aid its binding to bull's eye DNA and RNA.[26] CSP avoids the establishment of hairpin structures, thereby weakening two-degree structures in bull's eye RNA at a reduced temperature, and enables transcription and translation at low temperatures.[27] CSPs were initially identified as vital cold-induced proteins involved in tolerance to cold stress and playing an important role in controlling a wide variety of gene expressions and physiological responses in bacteria. However, it has been hypothesised that a few of them participate in several cellular functions that support healthy growth and stress adaptation. It has been demonstrated that a few CSPs also promote host cell invasion and ethanol, osmosis, oxidation, pH, starvation and stress tolerance.

The effects of heat and cold shock on psychrophilic lactic acid microbes were studied by Duru.[28] The cspA (cold shock protein A) gene was noted as the major protein in the genes of the microbes. Besides, cshB and cshBA, the DEAD-box ribonucleic acid helicase genes, were also reported to play an important part in the response of the psychrotrophic lactic acid bacteria, while the DEAD-box ribonucleic acid helicase contributes to the unwinding and degradation of the ribosome and RNA biosynthesis all through the cold shock.[28] Some of the CSPs detected in mesophiles are expressed constitutively in psychrophiles as cold-acclimation proteins (CAPs) to adapt to extremely low temperatures.[2]

13.3.2 RNA chaperones

Chaperones aid in the efficient folding of proteins. Low temperature appears to elevate the synthesis of RNA chaperones.[4] Cold-adapted chaperones such as DnaK,[29] GroEL[30] and the molecular chaperone IbpA[31] when expressed in *E. coli* increase the mesophilic bacterium's ability to grow at low temperatures. Co-chaperonin GroES, chaperonin GroEL, molecular chaperone DnaK, molecular chaperone IbpA, molecular chaperone HSP90 and molecular chaperone GrpE were noted among the chaperones elicited at reduced temperature.[32]

The TF (ribosome-bound-trigger factor) assists in protein folding.[33] The vast majority of nascent polypeptides generated by the ribosome interact with TF during co-translational processes. TF assists in the folding of the majority of proteins (about 70% of all proteins) quickly after synthesis. Interestingly, the remaining chaperones were noted to be heat shock proteins (HSPs), but TF is a cold shock protein in *E. coli*.[34] Cold-adapted bacteria have been found to overexpress TF at low temperatures, whereas HSP chaperones are downregulated.[35] The downregulation of chaperones' HSP in the cold implies that the majority of these are produced at transitorily higher ambient temperatures.[35] Certain bacterial species produce the chaperonins Cpn10 60, which aid in their adaptation to the evironment.[36] The chaperone proteins Hsc66 and TF played an important part in the cold shock response,[37] with the presence of other proteins important for trehalose, cellular metabolism and the biological manufacturing of lipids.

A study on the TRiC chaperonin in the psychrophilic yeast *Glaciozyma antarctica* revealed that the genes are consistently produced irrespective of cold or heat shock. TRiC chaperonin is known to transport denatured luciferase back to its active state at low temperatures.[38] Reduced ion pair electrostatic interactions are required for efficient protein folding by such chaperones. Besides, non-polar amino acids like isoleucine, phenylalanine, leucine, tryptophan and cysteine are involved in hydrophobic residues and are modified in the TRiC and TCP1-1 ring chaperonin and complex subunits, respectively, as an adaptation to low temperatures. The hydrophobic residues are substituted with hydrophilic residues like glutamine, histidine, lysine, aspartic acid, arginine and serine, increasing the residue distance, which eventually assists in cold adaptation; e.g., isoleucine is substituted for valine at TRiCa at location 372 in *G. antarctica*. The isoleucine is put into hydrophobic compartments formed by the distanced residues. Interactions with aromatic amino acids are also involved that aid in cold adaptation.[38] A few psychrophile genomes are reported to have the gene for proline, an osmolyte that is known to support the cell's viscosity and maintain structural integrity. A higher concentration of lysine is observed in the genomes of psychrophiles, which retains protein flexibility at reduced temperatures.[39]

13.3.3 RNA helicases

RNA helicases are mostly associated with abiotic stress. Low temperature is among the most studied biotic stresses. RNA helicases are engaged in the establishment of cold-adapted ribosomes and RNA degradosomes.[40] Such helicases are reported to be important for the weakening of RNA and DNA secondary assemblies.[2] They might help to slow down the RNA secondary assemblies for effective transformation in the cold.[41] SrmB and CsdA are among the DEAD-box RNA helicase family members that are encoded by *E. coli*. These appear to be involved in the adaptation of cells to the cold.[42] SrmB contributes to the biosynthesis of ribosomes. CsdA is more strongly required at low temperatures than SrmB. The deletion of the csdA gene drastically affects growth at low temperatures.[43] Numerous biological processes, including mRNA degradation, translation initiation and ribosome synthesis, have been attributed to CsdA. It is involved in mRNA degradation, which is the primary mechanism through which it contributes to cold acclimatisation. CsdA's helicase activity is essential at low temperatures. It was demonstrated that helicase-deficient CsdA mutants do not complement cold sensitivity.[42] The RNA helicases have also been seen to be overexpressed in many psychrophiles, like *Exiguobacterium sibiricum*,[44] *Psychrobacter arcticus arcticus*,[45] *Pseudoalteromonas haloplanktis*, *Sphingopyxis alaskensis*[4] and *Shewanella denitrificans*[46], at low temperature.[47] These underpin that the microbes have evolved adaptive strategies at reduced temperatures by the production of proteins. Therefore, RNA helicases increase the interactive crosstalk between helicase and protein cofactors, modifying the arrangement of functional protein complexes under various environmental conditions.[40]

13.3.4 Oxidative stress and osmotic stress

Increased heat and respiration in cold conditions give rise to oxidative stress. This results in the creation of the catalase-peroxidase (KatG) and the biogenesis of the proline use protein (PutA). As a result of these molecules, H_2O_2 synthesis gradually increases, activating proteins that inhibit reactive oxygen species (ROS).[36] Some other examples of molecules that are produced in response to OS (oxidative stress) are β-lactamase superfam II, catalase peroxiredoxin, glyoxylase or related hydrolase, glutathione peroxidase, spermidine synthase, thioredoxin reductase, ABC glycine/proline-betaine messenger, ATPase constituent, choline glycine-betaine transporter, choline-trehalose-6-phosphate synthase, osmoprotectant binding protein, trehalose-6-phosphatase and maltooligosyl trehalose synthase. Na^+/proline-symporter, Na^{+}/H^+-antiporters dehydrogenase or related flavoprotein are some of the osmotic regulators that are also produced in response to oxidative stress. Genes related to osmotic stress like vicR and vicK are thought to be in control for coping with ecological pressure; resD and resE for oxygen stress; narGHIJ and nreABC operon genes for respiration; and ompR and envZ for osmotic operon and upshift genes osmVW and osmXY.[48]

Gas solubility and harmful ROS generation both greatly increase at low temperatures. The presence of many genes encoding dismutases, superoxidase and catalases in *Colwellia psychrerythraea* and *Pseudoalteromonas haloplanktis* has improved the antioxidant capability to combat harsh environmental conditions.[2] LCPFAs (long-chain polyunsaturated fatty acids) like eicosapentaenoic, docosahexaenoic and arachidonic acid are formed at enhanced rates at lower temperatures.[49] Long-chain polyunsaturated fatty acids defend the cell membrane against ROS, thereby functioning as a shield from OS at a reduced temperature.[50]

13.3.5 Carotenoid synthesis enzymes

Psychrophiles synthesise carotenoid pigments in response to fluctuating temperatures to preserve the fluidity and viscosity of the cell-protective structure/membrane.[18] At very low temperatures, the cell membrane is stabilised by the carotenoids. The carotenoid biosynthetic pathways in psychrophiles contain genes such as crtB, idi, crtZ, crtY and crtI (phytoene synthase, isopentenyl-diphosphate delta isomerase, beta-carotene hydroxylase, lycopene beta cyclase and phytoene dehydrogenase).[39] Non-polar and polar carotenoid pigments are formed by a variety of Antarctic microbes to control membrane fluidity and help maintain homeoviscosity during temperature variations.[44] Many research groups have co-related the presence of carotenoids with the cold adaptation of microbes.[51] These pigments are known to serve a variety of important functions: light harvesting (photosynthesis by microbes), photoprotection (against UV rays) and antimicrobial.

13.3.6 Transcription and translation

Psychrophilic microorganisms adapt to low temperatures by controlling the activity of certain enzymes, e.g., peptidyl-prolyl *cis-trans* isomerase, extension factor and RNA polymerase. These enzymes are shown to retain action at extremely low temperatures in several psychrophilic microorganisms. Protein-folding rates may need to be maintained at low temperatures through overexpression at these temperatures.

Previous investigations have demonstrated that microbes control translation at low temperatures through the translation initiation factors (IF-3, IF-2 and IF-1).[26] Initiation factors IF-3 greatly favour CSP translation in *E. coli*.[52] Other examples of translation factors that are regulated are tRNA-dihydrouridine synthase, threonyl carbamoyl adenosine dehydratase (tRNA A37), GTPase translation initiation factors IF-2 and IF-3, GTPase translation elongation factor EF-Tu and EF-G, transcription-blocking protein NusA, transcription-related element helicase of the NusB superfamily II RNA and DNA, SNF2 superfamily II RNA helicase, and RNA or DNA helicase.[32]

13.3.7 Membrane and peptidoglycan modifications

Certain microbes enhance their peptidoglycan production, which eventually thickens the peptidoglycan layer, allowing it to withstand low temperatures. For instance, *Planococcus halocryophilus* has an unusual process that results in a thickened outer cell wall made of peptidoglycan, choline and calcium carbonate.[53] Some microbes additionally have LPS (lipopolysaccharide) structures in the outside layer of the cell to adapt to the cold habitat. Short-chain unsaturated fatty acids included in the LPS component further increase the fluidity in cold settings. Recent transcriptome research revealed that some organisms had larger quantities of outer-layer proteins and glycosyltransferases.[54] Benforte et al.[55] demonstrated impaired growth at reduced temperatures in an Antarctic microbe due to a transmutation in the glycosyltransferase wapH gene of LPS. It resulted in a decreased ability of Antarctic bacteria to thrive at cold temperatures. Other examples of proteins engaged in membrane modification are glycosyltransferases, reductase, 3-oxoacyl-[acyl-carrier-protein]-synthase III (KASIII) and 3-oxoacyl-[acyl-carrier-protein]. Lower growth temperatures also result in a complex content of polyunsaturated and unsaturated anteiso-branched fatty acids, *cis*-unsaturated double-bonds, acyl-chain and methyl-branched fatty acids.[2] By adding steric limitations that alter the packing order or decrease the number of contacts in the membrane, this changed composition is expected to play a crucial part in improving membrane fluidity. In addition, increasing levels of the big pigments of non-polar carotenoids, proteins and lipid groups contribute to increased fluidity of membrane structures.[56]

13.3.8 Compatible solutes and related compounds

Osmoprotection and cryoprotection are significantly aided by the presence of certain solutes, e.g., betaine, glycine, glycerol, mannitol, sucrose, sorbitol and trehalose. Additionally, these solutes act as suppliers of carbon, nitrogen and energy.[57] Compatible solutes stabilise cellular membranes at cold temperatures, lower the cytoplasm's freezing point, and stop and scavenge free radicals and macromolecule accumulation.[58] Nunn et al.[59] studied the genome of *Colwellia psychrerythraea* and reported the genes that code for proteins involved in the degradation and synthesis of polymers, nitrogen and polyamides. Such genes can be viewed as a possible special adaptation to cold conditions.[59] Ghobakhlou et al.[60] evaluated the metabolomic scrutiny of the Arctic strain N33 (*Mesorhizobium* sp.) and reported elevated accumulation of valine, threonine and sarcosine when cultivated at 4 °C. The microbe was found to behave like a cryoprotectant.

Many bacteria that are native to the cold ecosystem are found to manufacture PHAs (polyhydroxyalkanoates). These are stand-in polymers with significant physiological functions. They operate as an active sink of carbon, thus accumulating and reducing imbalanced growth conditions, nitrogen, and other macro- or micronutrients.[61] PHAs have ecological significance and give bacteria increased survival and resilience to a range of environmental stressors.[62] The DNA analysis of *C. psychrerythraea* showed the capacity to produce PHA, which is connected to synthesising and breaking down fatty acids.[59] Several gene duplications in the families of enoyl-CoA hydratase and acyl-CoA dehydrogenase were found, likely suggesting the diversity of the PHAs that can be produced.[57] The capacity of freshwater alpha-, beta- and gammaproteobacterial isolates from Antarctica to synthesise PHA was thought to be a common trait at early sites.[62] PHB synthesis was discovered to be essential for freezing and cold survival and growth, respectively.[62] PHB accretion boosted movement and prolonged planktonic cells' ability to survive in the bacteria's cold-adapted biofilms, indicating that having the ability to accumulate PHB may provide an adaptive benefit for attachment in those environments.[62]

13.3.9 Antifreeze proteins (AFPs)

The AFPs are a structurally varied set of proteins that are crucial in preventing the production of intracellular and extracellular ice crystals, which would otherwise cause cell death.[63] These proteins prefer ice and can lower a solution's freezing point without changing the temperature of the solution's melting point.[63] The process, termed TH (thermal hysteresis), also changes the ice shape foundation, reliant on the protein binding site and the level of ice formation.[64] The antifreeze and ice-binding proteins allow the cells of microbes to thrive in severe cold settings.[48] AFPs play distinct functions in various organisms. These function by either preventing freezing or increasing tolerance to freezing. Mostly, AFPs attach to frozen crystals, impede their growth, and help to prevent ice formation and re-crystallisation, which keeps the organism from freezing. According to Davies et al.,[65] the AFPs isolated from microorganisms display a typical triangular helical fold paired with a stretch of °-helical assembly. The previously indicated pattern differs noticeably from AFPs produced by other organisms.[65] Gilbert et al.[66] showed that the Antarctic lake bacterium *Marinomonas primoryensis* contains AFPs.[66]

Muryoi et al.[67] reported antifreeze proteins from rhizobacterium strain GR12-2 (*Pseudomonas putida*) in Arctic plants.[67] Nine AFP-encoding genes were reported by several research teams working on *G. antarctica*. The gene expression analysis showed that each AFP has a range of expression levels contingent on the environment, temperature and organism.[63] It's interesting to note that just two AFP-encoding genes were found in the expressed sequence tags (EST) studies, one transcript for AFP7 (GaAFP7) being found in the −12 °C library and the other for AFP9 (GaAFP9) being found in the 0 °C library. Additionally, quantitative PCR (qPCR) analysis was used to support the data and revealed similar expression levels.[67]

13.4 BIOTECHNOLOGICAL APPLICATION OF PSYCHROPHILES

Margesin and Feller[20] examined the use of psychrophiles for environmental purposes. Low environmental temperature is common in temperate parts of the world. Organisms like microbes that live at this temperature can tolerate and conquer their immediate habitat. Such organisms can be employed for the manufacture of biological cell factories or biological molecules for the remediation of wastewater and pollutants *ex situ*.[20] These biological molecules include mostly enzymes and proteins with good catalytic actions and definite heat lability, which have been found important and useful in industrial applications in different areas like cosmetics, detergents, feed and food technologies, and medical and biological research. Hamid et al.[68] reviewed the potential use of psychrophilic yeast for biotechnology. About 7% of the global area is covered with cold ecological systems, which are colonised by microbes that are cold tolerant. Psychrophilic microorganisms like yeast are important assets in such an ecosystem because they have the potential to adapt to a very low temperature due to their varied physiological activities that could generate cold shock proteins and enzymes. So, psychrophilic yeast could be a potential source for biotechnological use for the production of industrial food, chemicals, pharmaceutical and medical products, and textiles. They can also be used for ecological applications to manage environmental stress in plants. Hamid et al.[68] recommend further studies on enzymes and cold proteins for better applications in other fields like bioengineering.

The microbes that inhabit the frozen or cold environment possess exopolysaccharides, polyunsaturated lipids, and proteins in their membranes that enable them to conquer the environment successfully.[69] Psychrophiles have a great pool of cold enzymes that enable them to tolerate a wide range of environmental temperatures. Due to their biotechnological potential, cold enzymes could be employed in a wide range of environmental and industrial uses, like the textile, domestic, agricultural, cosmetic, biosensor and bioremediation industries, and in the manufacture of enzymes and pharmaceutical products.[69] In addition, the components of their enzymes could also be employed in distant satellite planets monitoring to explore the possible existence of life therein through the evidence of the presence of gases. The biopotential of psychrophiles in the food and manufacturing industry using cold enzymes like β-mannanases, lipases, pullulanases, xylanases, amylases, proteases, pectinase and β-galactosidase is highly recommended.[70] These enzymes are used to improve the quality of certain catalytic effects in food production processes. Biocatalysts or enzymes sourced from microbes have been stated to possess potential use for industrial applications in the waste management, pharmaceutical, chemical, agriculture and food sectors.[71] The enzymes from psychrophiles possess strong biochemical efficiency that will help to lower the time of reaction of the substrate and the inputs of energy in the industrial process. The process is cheap, non-toxic and eco-friendly, and the use of such biological enzymes from microbes in the industrial production of food has also highlighted the need for collaboration between industry and academia for the production of an engineered biocatalyst that has the potential to take part in a reaction without altering its initial process.[71]

13.5 SOIL PSYCHROPHILES' METAGENOMIC PROPERTIES

Low available nutrient contents, low annual precipitation, extreme temperatures, low soil moisture and freeze-thaw cycles are all factors that limit microbial activity in Arctic soils.[72] The Bacteroidetes and Proteobacteria are the main taxa in all metagenomes involving psychrophiles in the soil of Antarctic lakes.[73] In studying the consortia of microbes, various CASPs, CIPs and C-RSGs (cold-associated general stress-responsive proteins, cold-induced proteins and cold-responsive stress genes) in soil, sediment and Antarctic lake metagenomes were also studied. It was observed that in all samples investigated, *Gloeobacter*, *Haliangium*, *Anaeromyxobacter* and *Myxococcus* were dominant in the soil and lake sediment metagenomes. However, genes for exopolysaccharide biosynthesis were dominant in Lake Untersee soil metagenomes. In conclusion, it was found that although different consortia of microbes are found in many metagenomes, they share similar C-RSGs needed for their sustenance and survival in severe Antarctic settings. In Finnish Lapland, a study[74] reported that Gram-negative bacteria (Alpha-, Beta- and Gammaproteobacteria phyla) are dominant, and 60% of all isolates from Arctic tundra soils are Pseudomonads, while the phylum Acidobacteria was rich in soils having low pH.[75]

The Actinobacteria, Bacteroidetes and Proteobacteria were also reported as the predominant phylogenetic groups of the glacier ice on topsoil in Northern Schneeferner, Germany,[76] with some important genera like *Stenotrophomonas*, *Cryobacterium*, *Sphingomonas* and *Polaromonas.* After comparison of all pyrosequencing-derived sequences of efficient diversity of the Northern Schneeferner glacier, it was observed that some microbial species were reported to have similar homologies, such as dicarboxylate metabolism, glyoxylate, sucrose, starch, butanoate propanoate and pyruvate. However, some of the homologous sequence genes take part in the phosphate-pentose cycle, citrate cycle and gluconeogenesis/glycolysis pathway. It was observed that the genes responsible for growth specifically under anaerobic settings were detected when the microbe utilised nitrite and/or nitrate as an electron acceptor. In addition, several enzymes and compounds essential for a psychrophilic lifestyle and adaptation to living in a low-nutrient environment were also detected. It has also been recorded that in cold soil environments, ammonia oxidisers are known to be present.[77] Shen et al.,[78] in a metagenomic data comparison, investigated the linkage between physiological and genomic characteristics of the psychrophilic bacteria Arthrobacter. The analyses showed that the Arthrobacter family comprises a clade with associates having genomic characteristics with a strong capacity to reproduce faster due to the possession of an amino acid that is projected to reduce the rigidity of a great number of proteins by improving enzyme action at reduced temperatures. Together, the genomic and physiological traits compel adaptation for a psychrophilic clade of Arthrobacter. The metagenomics of bacterial communities in Antarctica, using the CRISPR spacer content, revealed that the genus *Flavobacterium* was a major bacterium in all sampling sites,[79] whereas another study[80] on the cold desert soils reported *Acinetobacter* and *Streptomycetes* as major phylogenetic groups. A group of researchers suggested that soil nutrients, global warming/climate change and reduced atmospheric pressure have resulted in a significant decline in biodiversity.[81] As a consequence of this, the bacterial and physio-chemical properties of soil within cold regions of the world, like the cold desert of the Himalaya, face severe ecological stress that prompts an environmental and biological strategy to survive. In soil at low altitudes and extremely cold conditions, *Firmicutes* and *Bacteroidetes* were dominant, while *Bacteroides*, *Flavobacterium* and *Cytophaga* were found in large quantities at the altitude. A similar study by Joshi et al.[82] revealed the presence of the species *Pseudomonas helmanticensis*, *Pseudomonas mandelii*, *Brevibacillus invocatus* and *Arthrobacter humicola* in the high altitude of the western Indian Himalaya. Actinobacteria were reported to be the major phylum in the Antarctic tundra soil, and their synergistic relationship with the genera *Streptomyces*, *Streptosporangium* and *Amycolatopsis* was also documented.[83] These microbes also possess cellular and cold-active catabolic enzymes with potential for catabolic breakdown of lignocellulose.[83]

13.6 PSYCHROPHILES' ADAPTABILITY IN VARIOUS COLD ECOZONES

The mechanisms used by psychrophilic PSB in cold ecozones to conquer their environment include enzymes, nucleic acids, phospholipids and phytin.[19] For example, organisms like *Pseudomonas azotoformans*, *Pseudomonas proteolytica*, *Pseudomonas palleroniana* and *Pseudomonas aeruginosa*. can grow

TABLE 13.1
Psychrophiles' adaptability in various cold ecozones

Sr. No.	Species	Type of acids used for adaptability	Ecozone(s)
1	Fluorescent *Pseudomonas* sp.	Malic, citric, formic, succinic, lactic, 2-ketogluconic, oxalic and gluconic acids	The Himalayan cold desert[86]
2	Strain BIHB 723 (*Acinetobacteria rhizosphaerae*)	Formic, malic, lactic, 2-ketogluconic, oxalic and gluconic acids	The trans-Himalayan cold desert[87]
3	Strain BIHB 783 (*Ralmella* sp.)	Iso-citric, citric and gluconic acids	*Hippophae rhamnoides* rhizosphere[88]
4	*Pseudomonas* sp.	Gluconic acid	In samples of glacial ice[89]
5	Strain AZ17 (*Bacillus* sp.) and strain AZ5 (*Pseudomonas* sp.)	Lactic, citric, acetic, gluconic and oxalic acids	The rhizosphere of chickpea[90]
6	*Bacilli* sp.	Propionic, succinic, malic, citric, lactic and gluconic acids	Phosphate rocks in mine region and rhizospheres of wheat plants[91]
7	*Enterobacter*, *Serratia*, *Pseudomonas* and *Pantoea*	Fumaric, succinic, gluconic, citric and oxalic acids	Rhizospheres of wheat plants[92]
8	*Paenibacillus* sp., *Burkholderia* and *Bacillus*	Acetic, formic, succinic, tartaric, citric, oxalic and gluconic acids	Paddy rice field[93]
9	*Serratia plymuthica*	Acetic acid	Soils[94]
10	*Pseudomonas azotoformans*, *Pseudomonas proteolytica*, *Pseudomonas palleroniana* and *Pseudomonas* sp.	Succinic, citric, malic and lactic acids	High-altitude region of Himalayan soil – Indian[84]

and survive at the temperature range between 15 and 25 ° by the production of malic and oxalic acids in the wild, while laboratory-cultured organisms released succinic, citric and lactic acids (Table 13.1).[19,53] In addition, enzymes released by their membranes, such as GED (glucose dehydrogenase), can mediate the released acids, such as gluconic acid, which is an important solubilisation effect in soil microbiomes.[85] The adaptive features are possibly linked to the study of the metagenomics, ecozones, climate warming surrounding the microbes, and the ecological factors as well as the genes responsible for their tolerance limits towards self-preservation and conservation of their innate ability (Figure 13. 2).

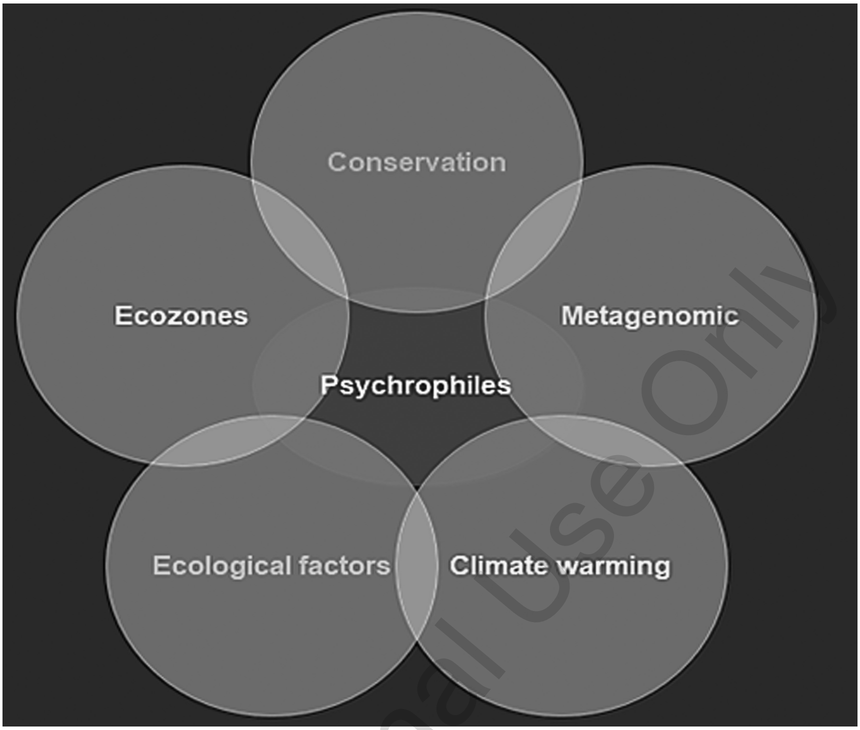

FIGURE 13.2 Strategies for psychrophiles' survival in cold ecozones.

13.7 CONCLUSIONS

Based on the preceding discussion, the following conclusions can be drawn:

- Psychrophiles have a natural ability to conquer extreme environmental conditions like cold. As the temperature rises, the rate of enzymic activities increases, which leads to kinetic heat effects, cellular activities and the swift growth of the microorganisms.
- The mechanism of action and the ecological role of psychrophiles show that they can proliferate and survive at very low environmental temperatures.
- Psychrophiles acclimatise to cold environments through certain adaptations, e.g., production of cold shock proteins, RNA chaperones, RNA helicases, oxidative and osmotic stress, synthesis of carotenoids, transformation factors, peptidoglycan and membrane modifications in compatible solutes.
- The cold enzymes could be employed in a wide range of environmental and industrial uses, such as the textile, domestic, agricultural, cosmetic,

biosensor and bioremediation industries and in the manufacture of enzymes and pharmaceutical products.

- Low available nutrient contents, low annual precipitation, extreme temperatures, low soil moisture and freeze-thaw cycles are all factors that limit microbial activity in Arctic soils.

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