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REVIEW

Extremophiles and their expanding biotechnological applications

Manvi Rawat[1] · Mansi Chauhan[2] · Anita Pandey[1]

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Abstract
Microbial life is not restricted to any particular setting. Over the past several decades, it has been evident that microbial populations can exist in a wide range of environments, including those with extremes in temperature, pressure, salinity, and pH. Bacteria and Archaea are the two most reported types of microbes that can sustain in extreme environments, such as hot springs, ice caves, acid drainage, and salt marshes. Some can even grow in toxic waste, organic solvents, and heavy metals. These microbes are called extremophiles. There exist certain microorganisms that are found capable of thriving in two or more extreme physiological conditions simultaneously, and are regarded as polyextremophiles. Extremophiles possess several physiological and molecular adaptations including production of extremolytes, ice nucleating proteins, pigments, extremozymes and exopolysaccharides. These metabolites are used in many biotechnological industries for making biofuels, developing new medicines, food additives, cryoprotective agents etc. Further, the study of extremophiles holds great significance in astrobiology. The current review summarizes the diversity of microorganisms inhabiting challenging environments and the biotechnological and therapeutic applications of the active metabolites obtained as a response to stress conditions. Bioprospection of extremophiles provides a progressive direction with significant enhancement in economy. Moreover, the introduction to omics approach including whole genome sequencing, single cell genomics, proteomics, metagenomics etc., has made it possible to find many unique microbial communities that could be otherwise difficult to cultivate using traditional methods. These findings might be capable enough to state that discovery of extremophiles can bring evolution to biotechnology.

Keywords Extremophiles · Extreme environments · Bioremediation · Medicine · Extremozymes

Introduction

Scientists have been fascinated by organisms that thrive in extreme ecological niches that would be deadly to most other life on Earth. Extremophiles include plants, insects, animals, bacteria, fungi and algae (Zhu et al. 2020). They have been vastly reported as a boon to biotechnology (Rampelotto 2013). The word Extremophiles denotes "extreme-lovers" in Latin. They are distributed in several classifications viz., psychrophiles, thermophiles, alkaliphiles, acidophiles, peizophiles etc., based on how their environmental niche varies from mesophilic circumstances. Figure 1 represents the pioneer microorganisms belonging to the various classes and discovered from their selective extreme environment. An extremophile can exist outside the normal distribution of a minimum of one environmental substance. This criterion, however, is not rigorous enough since many species may survive beyond their usual range even while their ideal development circumstances are within it; commonly denoted as polyextremophiles (Bowers et al. 2009). Thus, polyextremophiles are extremophilic microorganisms that fit into more than one category; for instance, *Thermococcus barophilus* (Marteinsson et al. 1999).

The vast literature suggests that extremophiles are indispensable in biotechnology by providing unique biological resources. They offer a vast reservoir of genetic diversity, producing a plethora of specialized enzymes, metabolites, and biomolecules with extraordinary properties.

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✉ Anita Pandey
anitapandey333@gmail.com; anitapandey@geu.ac.in

[1] Department of Biotechnology, Graphic Era (Deemed to be University), Dehradun, Uttarakhand 248002, India

[2] Department of Microbiology, Graphic Era (Deemed to be University), Dehradun, Uttarakhand 248002, India

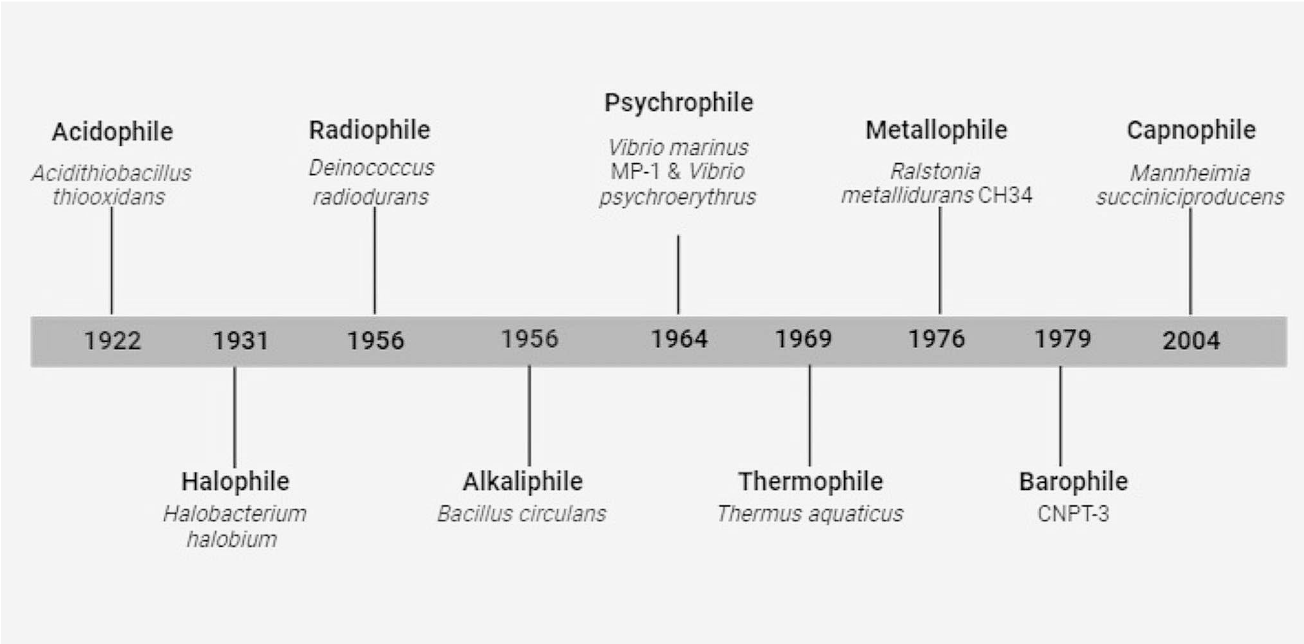

Fig. 1 Some of the pioneer microorganisms along with their year of discovery from each class of extremophiles

Extremozymes, being the most significant, find extensive use in various industrial processes (Al-Ghanayem et al. 2022). Moreover, the large number of studies mentions the role of extremophiles in bioremediation efforts and cleaning up polluted environments by metabolizing contaminants (Thathola et al. 2022; Choi et al. 2023). Their metabolic pathways also yield bioactive compounds with pharmaceutical potential, paving way to novel drug discovery and development (Chatterjee et al. 2020; Das et al. 2022). Extremophiles are flexible, therefore can be used for the purpose of optimization in order to induce high product yield (Bowers et al. 2009). The report by Scoma et al. (2019) on *Clostridium paradoxum* (a haloalkalophile and thermophile) is an example of one such study. In the cited study, the effect of hydrostatic pressure was hydrolyzed and it was demonstrated that *Clostridium paradoxum* attained a moderate peizophilic trait when grown at high temperature and alkaline pH (10). Furthermore, extremophiles serve as valuable model organisms for studying adaptation to extreme environments and offer insights into the limits of life, contributing to astrobiology and origin-of-life research.

In essence, extremophiles represent a treasure trove of biological resources with remarkable implications for biotechnology, environmental sustainability, and our understanding of life itself. The review aims to provide insights into the growing significance of extremophiles in biotechnology. It also throws light on their potential to address key challenges in industry, medicine, and environmental sustainability.

Extremophiles in different environments: diversity, classification and research limitations

Understanding the constraints and richness of life on Earth, as well as the potential for significant insights into the Origin of Life on Earth, depend heavily on our knowledge of microbial life. In context to the ubiquitous nature of microorganisms, there is a hypothesis saying "everything is everywhere – but the environment selects" which implies although everything is present everywhere, microbial species have preferred habitats (Bass Becking 1934; Keller and Hettich 2009; Müller et al. 2013; Fig. 2). However, the hypothesis has several limitations (De Wit and Bouvier 2006) as in the case of polyextremophiles. The major limiting factors includes osmotic and hydrostatic pressure, sun, earth, and cosmic radiation, oxidative stress, and the availability of nutrients (D'Amico et al. 2006).Therefore, some of the notable adaptations may include devised techniques to tolerate high temperatures, whether blazing hot or freezing cold, by using specialized proteins and membranes of lipids that protect cellular integrity (Chauhan et al. 2023a; De Maayer et al. 2014). They may also withstand very alkaline or acidic pH values by producing pH-buffering chemicals. Extremophiles have systems to control osmotic pressure in saltwater settings, avoiding cellular dehydration or rupture (De Maayer et al. 2014). The adaptive ability of extremophiles pave way to numerous applications and in turn supports the world's economy (Table 1).

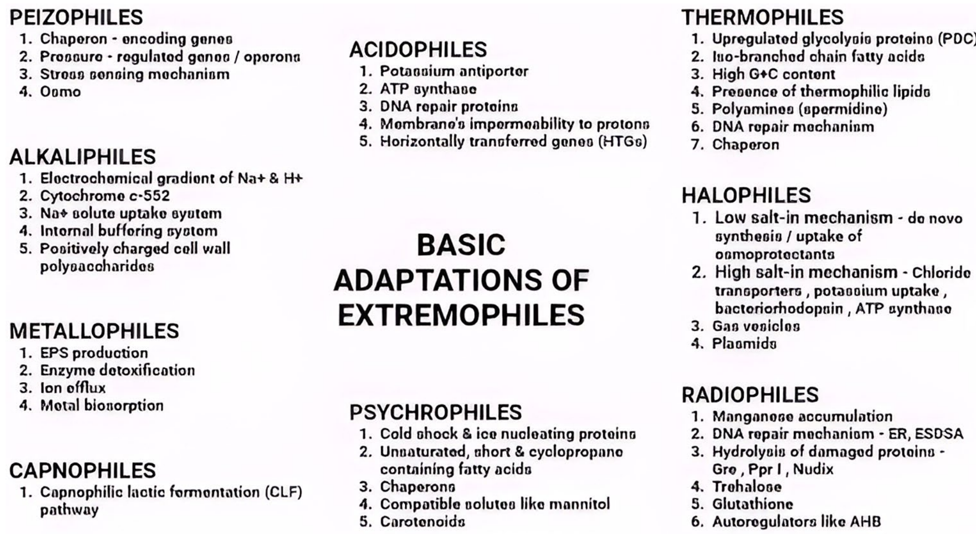

Fig. 2 General adaptation mechanism exhibited by each class of extremophiles in order to survive various extreme conditions

Temperature

Temperature poses a number of difficulties, ranging from the structural destruction caused by crystals of ice at one extreme to the denaturation of proteins at the other. The solubility of gases in water varies with temperature, posing challenges for aquatic species that require O_2 or CO_2 (Bowers et al. 2009). Based on the review by Merino et al. (2019), microbial life may withstand temperatures as low as -25 °C (*Deinococcus geothermalis*) and as high as 130 °C (*Geogemma barossii*). It was also observed for a general trend of temperature with microbial community that the community complexity generally declines with rising temperature. Based on the temperature range, microorganisms are majorly classified as psychrophiles, mesophiles and thermophiles. Since, mesophiles are not considered as extremophiles; they are not included as a part of this manuscript.

Psychrophiles

Psychrophiles inhabit extremely cold environments, such as deep sea (except for black smokers) and large areas of water on Earth's surface including the high altitude mountains, Arctic, Antarctica, and glaciers (Chattopadhyay et al. 2014; Dhakar and Pandey 2020). Numerous studies suggest that psychrophiles have successfully adapted to two major environmental challenges: low temperature, where the rate of biochemical reactions is affected exponentially by a drop in temperature, and the viscosity of aqueous environments, which rises by a factor larger than two between 37 °C and 0 °C (D'Amico et al. 2006).

Although research on psychrophiles has made significant advancement in understanding their adaptations and biotechnological potential; however, several research gaps still persists. There is a need for an insight on the intricate interplay of genetic, metabolic and structural mechanisms responsible for framing their survival strategies. Discovering the interactions with other organisms, community dynamics and nutrient cycling could provide valuable information into ecosystem functioning. Lastly, there seems to be a scarcity of studies exploring the genomic diversity and biogeography of psychrophiles across different cold environment hindering the understanding of their distribution and evolution.

Thermophiles

The Earth's surface is home to a variety of thermophile and hyperthermophile habitats, such as deep-sea hydrothermal vents, volcanic settings, hot springs, mud pots, fumaroles, and geysers. They can also be found in artificial settings like spray dryers, reactors, and hot composting facilities (Kushkevych et al. 2019; Urbieta et al. 2015). Based on their ideal development temperatures, these bacteria may be divided into hyperthermophiles (≥76°C) and thermophiles (46-75°C). As an alternative, thermophiles used dissimilatory metal reduction to respire by extracellularly moving their electrons to insoluble electron acceptors (Lusk 2019). The biogas fermenters and compost has been an ideal site for the growth of thermophiles, as supported by Kushkevych et al. (2019). They isolated a variety of thermophilic microorganisms including *Syntrophaceticus*, *Oceanotoga*, *Thermogymnomonas* and *Gelria* from a number of biogas fermenters plant in Czech Republic. Besides, thermophiles possess certain survival factors including permeability and chemical stability of fatty acyl ester lipid membrane, higher G + C content, presence of thermophilic lipids (caldarchaeol and cyclic archaeol) and more charged aminoacids in the surface membranes. Thermophiles possess evolutionary significant pressure to remove heat-sensitive amino acids, offload polar

Table 1 Different classes of extremophiles stating their growth attributes along with the applications they possess in several arenas

Class	Growth condition	Applications	References
Thermophiles	Hyperthermophile => 76 °C Thermophile = 46°-75 °C	Involved in marine and other geographical explorations, molecular studies (Taq polymerase), biorefining, hydroelectricity generation, biogas production, bioremediation, cancer diagnosis	Müller et al. 2013; Turner et al. 2007; Sekar et al. 2017; Luo et al. 2018; Chatterjee et al. 2020
Psychrophiles	-20° to 20 °C	Food additives, meat tenderness, bioformulation to promote agriculture, cold active enzymes and lipids for industries, cryoprotective agents, aerosol degradation, involved in astrobiology related studies	Margesin and Feller 2010; Cavicchioli et al. 2011; Ali et al. 2022; Chauhan et al. 2023b
Mesophiles	25° – 45 °C	Produces industrially important enzymes (proteases, lipases), involved in fermentation processes (making of bread, beer, wine, cheese), biofuel production	Singh et al. 2011; Tamaru et al. 2010
Halophiles	Borderline extreme halophiles = 1.5–4.0 M salt Extremely halotolerant = above 2.5 M salt Moderate halophiles = 0.5–2.5 M salt	Preparation of fermented foods, releases various substances such asectoine, β-carotene, bacteriorhodopsin, carotenoids and exopolysaccharides that are well known substrates for many industrially manufactured products, biosurfactants, marine bioremediation	Oren 2008; Neifar et al. 2019; Daoud and Ben Ali 2020; Yu et al. 2022; Kauth and Trusova 2022; Choi et al. 2023
Alkaliphiles	pH > 9	Preparation of detergents, biomineralization, biological bleaching (paper and pulp), raw material for bioplastics	Mamo and Mattiasson 2019; Khalikova et al. 2019
Acidophiles	pH < 5	Polymer-hydrolysis, bioleaching, mineralization	Johnson and Quatrini 2020; Li et al. 2020
Piezophiles	up to 80 MPa	Food processing and sterilization, biofilm formation, cure to pressure-induced injuries, antimicrobial and antioxidant properties	Malik et al. 2020; Das et al. 2022
Metallophiles	High metal concentration	Metal detoxification, bioleaching, mining, bioremediation, biomarker for cancer diagnosis	Chatterjee et al. 2020
Radiophiles	Extreme = 5000 J/m2 for sunlight, ionizing radiation = 1500–6000 Gy	Outer shields of spaceships, Radiotherapy, anticancer drugs, bioremediation of heavy metals	Tian et al. 2018; Jin et al. 2019
Capnophiles	CO_2 concentration between 1–10%	Production of biodegradable polymers, additives and resins, fermentation processes	Hong et al. 2004

amino acids that destabilize chains, and lower the entropy (Meruelo et al. 2012).

There exists a lack of research studies on extremophiles comprising of certain problems such as exploring the genetic variations and evolutionary adaptations of thermophiles across different habitats could provide insights into their ecological niche specialization and evolutionary history. Although, some mechanisms of thermotolerance in thermophiles have been elucidated, there is a need for further investigation into the development and mechanisms of heat shock proteins, chaperones, membrane stabilization methodology, and DNA repair processes. Additionally, there is a lack of comprehensive knowledge about the metabolic pathways and regulatory networks governing the metabolism of thermophiles.

pH

Microbes typically live in communities made up of several distinct species that interact with one another. Microbes alter the environment by consuming nutrients and excreting metabolites which impacts both, their own and other microbes' development. This is how microorganisms' modifications and responses to their surroundings shape interactions both within and across populations of the same species. Changing the pH of the surrounding environment is a very frequent environmental adjustment. Microbes developed a number of strategies to keep their internal pH balanced (Ratzke and Gore 2018). Secondary proton absorption through membrane-associated antiporters is one of the active methods for maintaining internal pH (Dhakar and Pandey 2016). However, because protons are often exchanged during biological events, bacteria also change the pH of the environment in which they live (Jin and Kirk 2018; Tran et al. 2021). This concept initiates new applications [for e.g., Tran et al. (2021) assessed the effect on the corrosive nature of sulphate-reducing bacteria] for such microorganisms, thus broadening the horizons.

A phenomenon known as ecological suicide has been developed assessing the behaviour of microorganisms exhibited during the modification of surroundings in ways that are detrimental to them; for instance, *Pseudomonas veronii*, which favors a lower pH, actually causes its own extinction by alkalizing the medium (Ratzke and Gore 2018). As the concentration of protons and hydroxyls impact geochemical events and nutrient solubility that result in an increase or reduction in the nutrient for bacterial growth, similarly pH can also alter the concentration of nutrients (Tran et al. 2021). It was also observed by Jin and Kirk (2018) that environmental pH had a significant impact on bacterial growth rates, with a one-unit variation from the ideal pH causing a 50% reduction in bacterial growth rate and a 50% reduction in microbial metabolism. On the basis of sustaining pH levels, microorganisms are divided as: alkaliphiles (pH > 9), neutrophiles (pH 5–9) and acidophiles (pH < 5) (Jin and Kirk 2018).

Alkaliphiles

Alkaliphilic microorganisms may thrive in alkaline conditions with pH levels exceeding 8. They inhabit harsh settings like alkali eutrophic soda lakes, high-carbonate soil and oligotrophic $Ca(OH)_2$-dominated water table (Mandal and Jawed 2023). The most common microorganisms belong to Archaebacteria and Cyanobacteria. Some of the examples of bacterial acidophiles include *Alkalibacter, Pseudomonas, Bacillus, Clostridium, Natranorubrum*, while fungi are *Cladosporium, Fusarium, Penicillium, Sodiomyces, Thielavia* (Dhakar and Pandey 2016). Alkaliphiles have evolved an array of adaptations to thrive in these extreme environments. Notwithstanding the high pH in their surroundings, they must keep their cells at a near-neutral pH. They accomplish this by employing transporters and enzymes that deliver protons into the interior of cells and metabolically generating acids (Krulwich 1995). Alkaliphile's cell surface layers also undergo modifications including positively charged cell-wall polysaccharides, peculiar bioenergetics, permeability qualities, surface charges, internal buffering capacity, amplification of hydrogen ions export digestive enzymes, and unique transporter are examples of passive mechanisms that aid in the retention of protons within the cell (Madigan 2000). A chapter written by Kevbrin (2019) suggested various isolation and cultivation techniques for alkaliphiles.

Besides, the regulatory pathways governing alkaliphile metabolism are still not fully elucidated. Investigating how alkaliphiles acquire, metabolize, and conserve energy under alkaline conditions could lead to the discovery of novel enzymes and metabolic networks. They are well known for developing biotransformed products therefore, research based on optimization and technology transfer can provide a potential boost to circular economy. Further research is needed to unravel the ecological roles of alkaliphiles in alkaline environments. Also highlighting their interactions with other organisms can be a potential contribution to the studies related to biogeochemical cycles and ecosystem functioning.

Acidophiles

These organisms may be found in both natural settings such as boiling springs, volcanic vents, and acidic soils, as well as man-made settings such as mine drainage systems (Johnson and Quatrini 2020). Common acidophilic bacteria and fungi are *Acidithiobacillus, Acidiphilium, Sulfolobus, Scytalidium, Ferroplasma, Picrophilus, Bacillus* and *Acidothrix, Aspergillus, Cryptococcus, Phialophora, Trichoderma, Trichosporon* respectively (Dhakar and Pandey 2016). These acidophiles release acid outside of the cell to sustain a pH gradient across the plasma membrane allowing biological processes to take place between a pH of 5.0 and 7.5 in order to live in low pH settings. The selection of medium can induce the growth of novel acidophiles as documented by Yamazaki et al. 2010. In the cited study, an acidic enrichment culture of microbial mats and biofilms obtained from an exceptionally acidic and hot spring resulted in the isolation of a new acidophilic fungus. It was identified that this fungus produces ascomycetous teleomorph structures and is a novel species of *Teratosphaeria acidotherma*. The genomic analysis of *Acidiphilium* revealed the presence of a vast array of horizontally transferred genes (HTGs) including those that confer CO_2 assimilation (rbc), utilization of sulfur compounds (sox, psr, sqr), photosynthesis (puf, puh) etc., that support metabolic expansion and environmental adaptation (Li et al. 2020).

One of the primary limitations in the studies related to acidophiles is the scarcity of diverse and well-characterized acidophile cultures from natural environments. Since, acidophiles are difficult to isolate and cultivate in laboratory settings, it affects the expedition of their genomic diversity, metabolic capabilities, and ecological roles. Furthermore, the lack of comprehensive genomic and metagenomic studies on acidophile communities in acidic habitats limits our understanding of their genetic makeup and functional potential. Without a robust database of acidophile genomes and metagenomes, researchers face challenges in identifying novel genes, metabolic pathways, and biotechnological applications. Additionally, the majority of acidophile research has focused on extreme acidophiles inhabiting highly acidic environments, such as acid mine drainage sites, while acidophiles in moderate pH environments remain relatively unexplored. Consequently, there is a need for more research on acidophiles across a broader range of habitats to elucidate their diversity, physiology, and ecological significance, as well as to unlock their full biotechnological potential.

Pressure

The deep sea, subseafloor, and continental subsurface which are less accessible represents the greatest habitats for microorganisms on Earth in terms of volume, after the well-studied continental and oceanic surface settings. Pressure is the most peculiar physical characteristic in these dark and isolated locations. High pressure produces detrimental impacts on life, including the inhibition of chemical processes, the damage of cell exteriors and membranes, and the disruption of protein-protein interactions. Marietou and Bartlett (2014) assessed the response of marine bacterial communities to pressure that were selective to deep-sea conditions. A variety of temperatures (3–16 °C) and hydrostatic pressure (0.1 to 80 MPa) were used. The findings include that the cell variety increases while the cell quantity decreases. The colonies were dominantly modified to tiny cocci. Also, pressure led to alterations in the microbial diversity with a rise in the relative abundance of *Gammaproteobacteria*, *Actinobacteria*, *Epsilonproteobacteria*, *Flavobacteria*, and *Alphaproteobacteria*. Smedile et al. (2022) worked on an epsilonproteobacterium *Nautilia* sp. PV-1 thriving in a deep sea hydrothermal vent. The research group stated that pressure induced adaptations are not only limited to the cell membrane and lipids but also affect the release or activity of enzymes (e.g., hydrogenases) that are involved in various metabolic cycles.

Peizophiles

They can be found in deep-sea vents, mountainous regions, and areas with a lack of oxygen. The term barophiles was replaced by peizophiles, since in Greek translation, the words are meant as weight and pressure, respectively (Yayanos 1995). Phylogenetic analyses have demonstrated that significant fractions of the peizophilic bacteria present in culture collections are members of the unique subgroup of the genus *Shewanella* (Kato and Bartlett 1997). Piezophiles have developed an array of adaptations to deal with these obstacles including the capacity to modulate the expression of genes, chaperon-encoded genes, presence of pressure-regulated genes or operons, stress-sensing mechanisms on their membranes inside their cells, and osmotolerance in response to the species or the pressure settings (Merino et al. 2019). Some piezophiles e.g., contain genes that create proteins that are less volatile or active under high pressure while others have genes that create proteins that aid in the protection of cell wall and membranes (Morozkina et al. 2010).

Research on peizophiles has significant challenges; firstly, accessing pressure induced sites for research purpose requires specialized training along with high-tech equipment and vessels. Their slow growth rates and specialized nutritional requirements hinder the establishment of pure cultures and large-scale cultivation, limiting researchers' ability to study their physiology and metabolism. Another limitation is the lack of suitable model organisms for piezophiles. Unlike thermophilic microorganisms, which have well-established model organisms for genetic manipulation and functional studies, piezophiles often lack tractable model systems for experimental research. Revealing the hidden mechanisms behind the adaptation of peizophiles by using omics becomes difficult due to technical limitations and resource constraints.

Salinity

The need for salt is typical in marine microbes, which exist in an environment with 30–35 g/L salts. Salinity may result in stress condition and causes cell drying and lysis, primarily due to the low osmotic potential of their surroundings (Yan and Marschner 2012). Two methods employed by halophilic bacteria allow them to maintain an osmotically balanced cytoplasm with their medium. First includes the accumulation of KCl which requires the modification of intracellular enzymatic setup while the other follows accumulation of organic compatible solutes such as glycine, ectoine that do not obstruct enzyme action while keeping salt out of the cytoplasm (Oren 2008).This concept was first determined in model organism, a eukaryote – *Dunaliella* sp (green algae; Oren 2005).

Halophiles

Extremely halophilic bacteria may tolerate substantially greater salt level up to 300 g/L salt. Compared to bacteria from originally non-saline environment, those from saline areas do not exhibit greater tolerance to elevated salt concentration (DasSarma and Arora 2002). Archaebacteria has gained most attention in terms of salt tolerance. A characteristic feature of halophilic archaebacteria is the excess ratio of acidic to basic aminoacids that help in regulating their homeostasis. Other features include presence of purple membrane (specific regions in cell membrane with chromoproteins- bacteriorhodopsin), halophilic proteins (halorhodopsin), carotenoids, gas vesicles and dynamic plasmids (DasSarma and Arora 2002). Halophilic archae e.g., *Haloferax alexandrinus* has been one of the most reliable and efficient halophile that has been exploited for their industrial applications (Alvares and Furtado 2021). *Haloterrigena salifodinae* sp. nov., *Natrinema halophilum* sp. nov., *Haloterrigena alkaliphila* sp. nov., *Natrinema salinisoli* sp. nov., *Natrinema amylolyticum* sp. nov. etc., belong to the novel archaeon species reported from halophilic environments (Bao et al. 2022; Chen et al. 2019).

The fungi, which have been overlooked in halophile studies for a long time and fulfill the criteria for being real halophiles, including their insistence on high salt concentrations and their capacity to grow up to nearly saturation levels of salt. Example include, the black yeast *Hortaea werneckii*, *Aureobasidium pullulans, Phaeotheca triangularis* (Gunde-Cimerman et al. 2000) and the meristematic fungus *Trimmatostroma salinum* (Zalar et al. 1999) which are native to hypersaline habitats. Several reports stated the presence of halophiles including novel genera in a large number of fermented foods, for instance, *Haloterrigena jeotgali* sp. nov., isolated from shrimp *jeotgal* (a Korean fermented food dish; Roh et al. 2009).

The research area focused on halophiles has several challenges including the difficulty in culturing the halophilic microorganisms, lack of comprehensive genomic and metagenomic studies conducted in response to halophile's taxonomic diversity and scarcity of the databases containing information about the characterization of metabolites derived by halophiles.

Radiation

Extreme exposure to radiation such as UV, X-rays, and gamma rays results in the development of cytotoxic and mutagenic DNA modifications that may be cancerous at later stages (Gabani and Singh 2012). In relevance to this, radiation-resistant microorganisms (e.g. *Deinococcus hohokamensis, D. radiodurans*, *Halomonas* sp., *Psychrobacter pacificensis, Thermococcus gammatolerans*) is a wide collection of organisms that have acquired the ability to survive high radiation doses (Musilova et al. 2015; Merino et al. 2019) due to the release of several extremolytes. They are also reported for the development of autoregulatory factors that resembles alkylhydroxybenzene (AHB), Rec pathway, excision repair (ER), synthesis-dependant strands annealing (ESDSA), mycosporin-like aminoacids, accumulation of manganese complexes, hydrolysis of damaged proteins and trehalose production (Musilova et al. 2015; Ghosh et al. 2023). Pitonzo et al. (1999) stated the incidence of converting the indigenous radiation resistant microorganisms into VBNC (viable but non-culturable) state when exposed to gamma radiations (2.33 kGy for 96 h). A significant correlation was found between radiation resistance and desiccation by Musilova et al. (2015), who suggest that a microbe sustaining desiccation for 5days at room temperature develops an irradiation resistance of 1 kGy. A relationship based study dealing with sunlight and radiation was evaluated by Ragon et al. (2011) who reported that the microbes capable of forming biofilm were much resistant to the radiation levels noted during Chernobyl disaster. Their exposure duration to sunlight (UV radiation) and desiccation were one of the major factors responsible for such remarkable resistance.

The foremost limitation to radiophiles is the accession to their habitats; that is logistically complex. The studies highlighting the underlying mechanisms of existence of radiophiles is much challenging due to limited resources and technology. Moreover, research based on radiophiles requires compliance with strict regulatory guidelines that can be resource-intensive.

Capnophiles

High concentration of CO_2 is toxic to most microorganisms since the molecule interferes with intracellular functions (Santillan et al. 2013). Thus, the sequestration of anthropogenic CO_2 by pumping into deep saline aquifers creates a new environmental subsurface conditions (Little and Jackson 2010). On the other hand, these novel conditions serve as a home for CO_2-tolerant bacteria that further favor a different group of microbes resistant to CO_2 toxicity known as Capnophile; e.g. *Mannheimia succiniciproducens* (Hong et al. 2004; Santillan et al. 2015) and widely inhabit animal rumen. Such microbes have the ability to efficiently fix CO_2 from sugar enriched substrates and produces high concentration of H_2 and lactic acid; this unique pathway is known as Capnophilic lactic fermentation (CLF) (Hong et al. 2004). Recently, CLF pathway was reported in the survival of *Themotoga neapolitana* (Nuzzo et al. 2019).

Several capnophilic namely *Proteus mirabilis*, *E. coli* and *Streptococcus pneumonia* have been reported from the urine samples of severe pyelonephritis, urinary tract infection (UTI; Karahan et al. 2023), bacteremia (Gao et al. 2022) and pediatric with pneumococcal disease (Kobayashi et al. 2023) patients, respectively. But their cultivation is quite challenging due to sensitive growth requirements. Despite their potential biotechnological relevance, such as in CO_2 capture and utilization, microbial fuel production, and bioremediation of CO_2-rich environments, there is a paucity of research on harnessing capnophiles for practical applications.

Metallophiles

Metals in limited concentrations possess a significant contribution in various enzyme regulated reactions. Iron, cobalt, nickel, manganese, zinc, molybdenum, copper etc., behaves as cofactors (Kanekar and Kanekar 2022; Muro-González et al. 2020). Metallophiles are metal-resistant microorganisms inhabiting metal-rich environments and can withstand high metal concentrations. Deep-sea or terrestrial thermal sources are natural homes for metallophiles; however, they are also reported from man-made habitats (mainly industrialized area) (Nies 2000; Uqab et al. 2020). Some of the metal resistant microbial species includes *Cupriavidus metallidurans*, *Rhodobacter sphaeroides*, *Gloeophyllum sepiarium, Aspergillus luchuensis*, mycorrhizae, *Methanobacterium bryantti, Pyrobaculumis landicum, Thiobacillus ferrooxidans*, *Bacillus thuringenesis, B. safensis*, *Pseudomonas* sp., *Ralstonia* sp., *Staphylococcus warneri*, *Micrococcus* sp. (Muro-González et al. 2020; Nies 2000; Tovar-Sánchez et al. 2023; Uqab et al. 2020). Metallophiles adopt several mechanisms including sequestration, precipitation, conversion, and efflux (Kanekar and Kanekar 2022). They produce metallothioneins (MTs) that are intracellular metal binding protein and smt genes which are involved in shielding these cells from harmful metals (Chatterjee et al. 2020; Naik et al. 2012). Keeping aside the applications of metallophiles, there are certain problems that reduces the research outcome. Studying metallophiles requires careful consideration of the toxic effects of metals on cell viability, growth, and metabolism. To deal with it, the researchers must develop appropriate cultivation techniques and growth media to mitigate metal toxicity while maintaining physiological relevance.

Biotechnological applications

Extremophiles are regarded as primitive cells from an evolutionary perspective, having evolved to survive in the harsh conditions of the early Earth's history. These extremophiles, and especially their bioactive chemicals, have numerous well-established and beneficial applications (Fig. 3).These microbes, which have been the subject of extensive research over the past 30 years (Fig. 4), are invaluable sources of biomolecules and bioprocesses. Microorganisms have been isolated from high altitudes and characterized for their various functional aspects (Adhikari et al. 2021; Dhakar and Pandey 2020; Pandey et al. 2019a; Pandey and Sharma 2021; Yadav et al. 2019). The role of extremophiles in different arena is discussed further with suitable examples.

Extermophiles as drivers of circular economy

Extremophiles play a crucial role in the circular economy by offering innovative solutions for waste management and resource recovery. These resilient microorganisms thrive in extreme environments and possess unique metabolic capabilities that enable them to degrade, detoxify, and transform various pollutants and waste materials. Extremophiles are harnessed for bioremediation of contaminated sites, conversion of organic waste into valuable bioproducts, and bioleaching of metals. Their ability to operate under extreme conditions makes extremophiles as valuable assets in closing the loop of resource utilization, reducing environmental impacts, and advancing the principles of circular economy.

Biodegradation

Researchers are continuously finding a suitable strategy of biodegradation at extreme conditions. Hydrocarbon degradation at low temperature has been a great concern since 1980s. Whyte et al. (1997) reported the significance of two specific catabolic pathways viz., *nah* and *alk* adopted for biodegradation. They can also coexist together for an enhanced effect. Furthermore, Margesin and Schinner (2001) summarized various findings reported at initial research stages. Now-a-days, the degradation of xenobiotics has gained much attention since they are released as a major component of industrial effluent. Thathola et al. (2021) observed 93% caffeine degradation using psychrotolerant *Pseudomonas* sp., up to 4 days while Thathola et al. (2022) studied biodegradation of Bisphenol A by another psychrotolerant species of *Pseudomonas –P. palleroniana* GBPI_508 at variable conditions. Piterina et al. (2012) showed the importance of capnophiles such as *Clostridium* for treating wastewater sludge in autothermal thermophilic aerobic digester (ATAD) system. Neifar et al. (2019) stated that halophile-*Halomonasdesertis* G11can be utilized to decompose oil spills in marine water. The bioactive metabolites released in response to extreme conditions have dominated the published literature. Some examples of thermophilic molds used in the bioremediation of contaminated water and dye decolorization are *Talaromyces emersonii*, *Thermomucorindica eseudaticae*, *Mucor* sp., *Rhizopus* sp. (Singh et al. 2016). Certain psychrotolerants,

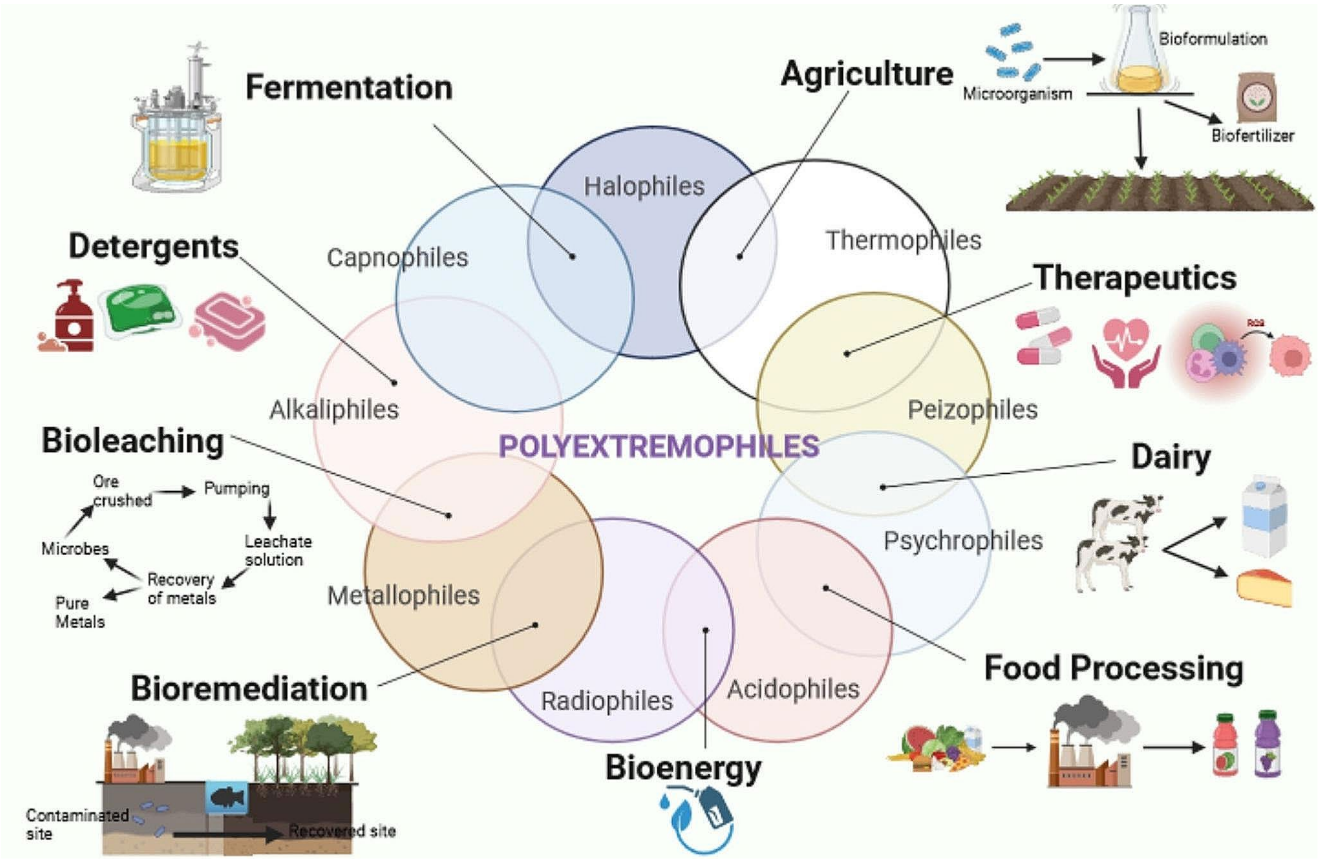

Fig. 3 Diverse applications of extremophiles in various sectors

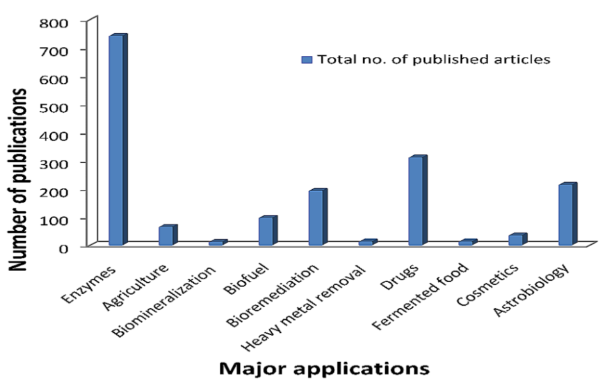

Fig. 4 Representation of the publication status of extremophiles with reference to the total number of articles published in the specific application area. (*Source*: The data has been generated via Scopus database using keywords and logical expression "Extremophiles" AND "Enzymes"; "Extremophiles" AND "Agriculture"; "Extremophiles" AND "Biomineralization"; "Extremophiles" AND "Biofuel"; "Extremophiles" AND "Bioremediation"; "Extremophiles" AND "Heavy metal removal"; "Extremophiles" AND "Drugs"; "Extremophiles" AND "Fermented food"; "Extremophiles" AND "Cosmetics"; "Extremophiles" AND "Astrobiology"; Accessed on 19th January 2024)

when used in consortia, has been reported for soot aerosol biodegradation that plays a pivotal role in the modification of biogeochemical cycles (Ali et al. 2022). Dominance and laccase production with respect to cold adapted bacteria and fungi of Himalayan region and relevant to various industrial applications have been studied in last two decades (Dhakar et al. 2014; Kaira et al. 2015; Pandey et al. 2019b).

Removal of heavy metals

Acidophiles are especially useful in such cases, because they can bioleach a wide spectrum of metallic ions including elements that are hazardous to most species. These heavy metals possess low mobility and longer residence time, therefore may harm the ecosystem by polluting soil, water supplies and wreaking havoc on the lives of animals and plants. The methodology opted by extremophiles in heavy metals such as cobalt, nickel, manganese, vanadium, lead, titanium, and copper removalhas beenthrough bioaccumulation and biosorptive mechanisms reported in *Pseudomonas putida* (Kamika and Momba 2013).Lead and cadmium were efficiently removed through biosorptionby *Bacillus barbaricus* when used in consortium (Sen et al. 2014). Copper was also observed to be eliminated by *Acinetobacter* *guillouiae* through the process of biosorption (Majumder et al. 2015). Lacerda et al. (2016) reported the properties of many genes and proteins existing in *Chromobacterium violaceum* linked to the metabolism of arsenic, iron, zinc etc. *Anoxybacillus* sp. enzymes have the potential to decrease heavy metal contaminants from the waste generated by food industry (Jardine et al. 2018). Radiation-resistant *Deinococcus* finds application in removing heavy metals. They follow a combination of mechanisms including adsorption, precipitation, and transformation (Jin et al. 2019). In addition to this, *Deinococcus radiodurans* has the potential to shield spaceships and astronauts from radioactive harm (Jin et al. 2019). The metallophiles such as *Lactobacillus rhamnosus*, *Pediococcus acidilactici*, *Bifidobacterium* sp., has been successfully reported for human metal (e.g., mercury, arsenic, lead) detoxification.

Biomineralization

Alkaliphiles have already had a significant influence on the use of biotechnology in the production of mass-market consumer goods via detergents. Microbially induced calcite precipitation is one of the biomineralization technologies that have shown promise as a substitute for the current chemical-based concrete crack healing approach. Since concrete is highly alkaline in nature, alkaliphiles and alkalitolerants play a key role in biomineralization. Moreover, such microbes have been explored for the production of self-healing concrete and protective surface coatings for concrete buildings, in addition to their ability to fix pre-existing fissures in the material (Mamo and Mattiasson 2019). Alkaliphiles are also involved in the biological bleaching methods employed on wood pulp to form papers and notebooks. *Halogranum amylolyticum* and *Haloferax mediterranei*, extreme halophilic archae that has been observed to produce biopolymer PHBV (Poly 3-hydroxybutyrate–co-3-Hydroxyvalerate) in order to support the environment sustainability as well as circular economy approach (Bairwan et al. 2024). Several capnophiles possess the ability of forming a good amount of intermediates such as succininc acid involved during TCA cycle which is used for the production of biodegradable polymers, additives and resins (Hong et al. 2004). Metallophiles have also been utilized in order to extract rare earth metals (lanthanides, scandium, yttrium) which are known for their potential in development of high technology products.

Extremophiles for energy generation

A large number of reports suggest that extremophiles can be employed to create new renewable energy sources. Extremophilic algae, for example, *Galdieria sulphuraria*can be utilized to make biofuels (Perez Saura et al. 2022). Extremophilic bacteria *Pyrococcus furious*, isolated from a hydrothermal vent, was reported to generate power from both carbon and hydrogen dioxide (Sekar et al. 2017). This procedure is being researched as a potential method of producing pure electricity from renewable resources. Eukaryotic halophile-*Dunaliella salina* is known to produce bacteriorhodopsin that is used for energy conversion (Daoud and Ben Ali 2020; Oren 2008). The expression of *irr*E gene extracted from *Deinococcus* and incorporated with *Pseudomonas aeruginosa* induced the cell power density by 70%. Thus, suggesting their ability in bioelectricity generation, stress response and substrate utilization (Luo et al. 2018). Extremophilic bacteria may be utilized to manufacture biofuels like ethanol and biodiesel from renewable resources like plant biomass and algae. *Clostridium thermocellum*, for example, may be utilized to create ethanol from cellulose, which is the major component of plant biomass.

Extremophilic enzyme production

Extremophiles create a wide range of proteins that are durable and functional in harsh environments. Extremozymes exhibit several structural differences than mesophilic enzymes that are responsible for their success story. The modifications in thermophilic enzyme include the lesser number of amino acid replacements and enhanced hydrophobic core. Similarly, halophilic enzymes have acidic residues and salt bridges, incorporation of alanine within helices and presence of more negatively charged amino acids in NH_2 terminal (Kumar 1998). Psychrophilic metabolites can be utilized to manufacture additives for food and enzymes that extend the shelf life and improve the quality of food items, for example, the ice-nucleating proteins are used in the production of ice cream or artificial snow, cold-active enzymes are useful in detergent and food industries and contact lens cleaning fluids and lowering the lactose content of milk (Cavicchioli et al. 2011; Margesin and Feller 2010). However, lipids are useful as dietary supplements in the form of polyunsaturated fatty acids. Proteases are a great instance of a product that allows mesophiles to live. They are commonly employed in medical applications and can rapidly adjust to cold temperature variations (Singh et al. 2011). They can also be utilized in conjunction with other extremophiles. Thermophilic bacteria are incapable of growing on the frigid sea floor, therefore environmental selection does not affect their dormant spores. Taq polymerase developed from *Thermus aquaticus* is widely utilized for the crucial investigations involving PCR (polymerase chain reaction) technique. Thermophiles are also essential target for many biorefining processes (Turner et al. 2007). Dhakar and

Pandey (2016) summarized various applications revealed by the microorganisms' wide pH tolerance.

The use of extremophiles as model organisms for astrobiology

Their ability to survive and even thrive in conditions once considered inhospitable offers crucial insights into the potential for life elsewhere in the universe. For example, extremophiles such as thermophiles, found in hot springs and deep-sea hydrothermal vents, provide analogs for potential life in the subsurface oceans of icy moons like Europa and Enceladus. Similarly, halophiles, thriving in salt flats and hypersaline lakes, offer insights into the possibility of life in briny environments on Mars or the subsurface ocean of Saturn's moon Titan (Thombre et al. 2020). Moreover, extremophiles such as acidophiles, living in acidic environments like mine drainage sites, inform our understanding of potential acidic habitats on Venus or in volcanic regions on other planets. The report by Hoover and Pikuta (2009) demonstrated that psychrophiles may survive when cryopreserved in ancient ice based on the finding of living microbes from the deep Fox Tunnel and Vostok Ice, Alaska. It is also suggested that one of the promising candidate for life that may exist on comets or in the polar caps of Mars is the psychrophilic lithoautotrophic homoacetogen isolated from the deep anoxic trough of Lake Untersee. Furthermore, the ice geysers that shoot from the tiger-striped areas of Saturn's moon Enceladus may be explained by the gas that spontaneously released from the Anuchin Glacier above Lake Untersee. Polar extremophile studies offer new insights into astronomy, as they are crucial for locating life in the universe, as most other planets are frozen.

Extremophiles in food processing and preservation

Several halophiles have been implemented as starter-culture in the preparation of fermented dishes and have successfully reported for enhanced flavor and sensory traits as compared to the food prepared using traditional methods. The presence of this flavour may be due to the increased levels of benzaldehyde, 3-methylbutyraldehyde and phenylethylaldehyde (Yu et al. 2022). *Rhodothermus marinus* RD is shown to exhibit thermohalophile GDSL lipase-encoding gene which was cloned and expressed in *Escherichia coli*. It was found that the enzyme exhibited the maximum hydrolytic activity (1055.3 U/mg) towards p-nitrophenyl butyrate at 70 °C/pH 8.5 and after 60 min of incubation at this temperature it maintained 78.6% of its initial activity (Memarpoor-Yazdi et al. 2017). Thus, it can be used during methods like lipid processing and organic synthesis. Haloarchae has been reported to produce halocins (proteinaceous antimicrobial substances) that has been used for the preservation of salted food (Kumar et al. 2021).Eukaryotic halophiles were effectively employed to generate ectoine and β-carotene from *Dunaliella* sp. Additionally, they are said to be creating osmotic solutes as stabilizers, carotenoids from *Salinibacter ruber*, and exopolysaccharides from *Aphanothece halophytica* (cyanobacteria) as emulsifiers (Daoud and Ben Ali 2020; Oren 2008).

Extremophiles as regulators of ecological homeostasis

Despite the fact that millions of people rely on agriculture for their daily needs, environmental constraints such as uncertain weather, low soil fertility, water scarcity and rough terrain severely restrict crop productivity. However, the pressure induced on the environment by growing population, necessitates an even greater intensification of crop production (Pandey and Yarzábal 2019). Moreover, social concerns about the environment and legislative restrictions are coming together to support more sustainable agriculture that relies on soil preservation and organic compounds. These developments are contributing to the proliferation of biofertilizers which are advantageous solutions enriched with microorganisms that improve a plant's capacity to absorb vital nutrients (Ibáñez et al. 2023). A large number of studies illuminating the success of biofertilizers dominate the published literature. Some of the latest findings include-Mukhtar et al. (2019) evaluated plant growth promoting effects of halophytes belonging to the genera *Bacillus*, *Halobacillus*, and *Pseudomonas* in maize. These were used as inoculants in the form of seed coat and enriched soil-based phosphate biofertilizers. The findings were more than 90% of the strains exhibited IAA generation and P-solubilization activity, 50% of the strains were able to create ACC deaminase, 30% of the strains had positive nitrogen fixation output, 40 and 20% of the strains were able to make siderophores and HCN, respectively. Moreover, 90% of the strains produced several hydrolytic enzymes and possessed antifungal activity. Santos et al.(2022) assessed plant growth and development under salt stress by halophiles from the genera *Exiguobacterium* and *Stanotrophomonas.* There was an approximate 45% increased germination rate, twice the root length and biomass of soybean in compared to non-inoculated seeds. Several applications of cold adapted *Pseudomonas* spp., are well mentioned by Chauhan et al. 2023a); Pandey and Yarzábal (2019), thereby supporting their significance to agricultural sustainability. Endophytic microorganisms possessing PGP traits, associated with high altitude plants, are increasingly receiving attention in this regard (Adhikari and Pandey 2020). Dark septate endophytes from high mountains, particularly, are emphasized in the present climate change scenario (Dasila et al. 2020; Pandey 2019). A recent term "plant probiotics" has been provided to such plant growth promoting microorganisms that possess a range of necessary factors responsible to enhance the development of plants mediated by plant-microbe interactions. A haloarchae *Haloferax alexandrinus* have been reported to combat silver stress; it was demonstrated through genomic transcription (Buda et al. 2023). Upadhayay et al. (2023) provided a detailed overview of synergistic effect exhibited between nanomaterials and microorganisms, therefore, discovering novel applications of extremophiles. Müller et al. (2013) used endospores from thermophiles as tracers to investigate the impact of ocean current dispersal on the biogeography of marine microorganisms which are passively deposited by sedimentation to the cool bottom. 81 distinct maritime sediment types from around the globe revealed 146 species-level 16 S rRNA phylotypes of thermophilic endospore-forming *Firmicutes.*

Unveiling the therapeutic potential of extremophiles

These days, extremophiles are making waves in the pharmaceutical sectors with their unique extremolytes, e.g., scytonemin, palythine, mycosporine, biopterin, shinorine, phlorotanninandporphyra-334. Researchers are already looking at the possible uses of extremolytes for human medicines, such as anticholesteric, antioxidants, anticancer medications, cell cycle inhibitors, skincare products etc. (Gabani and Singh 2012). Extremophiles create a wide range of chemicals that may have medical benefits, for instance ectoine- a chemical generated by halophilic extremophiles used to protect the epidermis from harm in various skincare products. Thus, it has been demonstrated to have antioxidant and anti-inflammatory properties (Kauth and Trusova 2022). SalinosporamideA produced by the oceanic extremophile *Salinispora tropica*, has been scientifically demonstrated to be effective against a range of cancer cells and is now being tested in clinical studies for cancer therapy (Gulder and Moore 2010). Halocins from haloarchae has been supported by studies to protect the myocardium from ischemia and reperfusion injury, besides dealing with cardiac arrest and cancer (Kumar et al. 2021). Many reports suggested the therapeutic potential of thermophiles which is due to their distinct cell membranes. They are being exploited to create cancer therapies that require extreme heat. Furthermore, thermophiles can transform carbohydrate-rich compounds into hydrogen; they might aid in the prevention of harmful organism growth and the development of therapies for neurological illnesses. Consequently, thermophiles might also be exploited to create novel antiviral medications as well as large-scale therapeutic manufacture. The MTs produced by metallophiles plays a significant role in carcinogenesis. They are used as a biomarker in cancer diagnosis (Chatterjee et al. 2020). The production of optically pure enantiomers has garnered significant attention for pharmaceuticals since they are more target-specific and have fewer adverse effects than racemic mixtures. For instance, Memarpoor-Yazdi et al. (2017) utilized lipolytic enzymes from *Rhodothermus marinus* DSM4252 to obtain enantiopure ibuprofen.

Keeping in mind, the pressure-induced injuries such as during concussions and sports, scientists discover novel remedies by examining peizophiles. Such injuries can cause considerable harm to human cells. Another major therapeutic application of peizophiles includes their sensitive mechanotransduction (method by which cells perceive and respond to stimuli) systems. Researchers are now able to design novel medications and treatments that target mechanical transfer pathways (Malik et al. 2020). Das et al.(2022) observed the release of various pharmacologically active compounds such as prenylxanthones, diketopiperazine, brevianespiroditerpenoids, hydroxyphenyl acetic acid, sorbicillin-type compounds etc., from several peizophilic fungi. These compounds have shown promising antimicrobial, antiviral, anticancer and antioxidant properties during preclinical investigations. It is hypothesised that most microorganisms resistant to ultraviolet radiation (UVR) can be exploited to generate anticancer medications to prevent UVR-induced skin damage. This may be evident by Tian et al. (2018) by synthesizing gold nanoparticles using hydroxyl tetraterpenoid deoxyxanthine (formed by *Deinococcus*) that was functional in producing ROS thereby resulting in the cancer cell apoptosis.

Extremophiles in the conservation of cultural heritage

The degradation of cultural artifacts and monuments due to microbial colonization is a significant challenge faced by conservationists (Pyzik et al. 2021). Extremophiles, with their remarkable ability to survive and thrive in harsh conditions, offer unique solutions to mitigate microbial-induced deterioration and preserve cultural heritage for future generations. One of the primary ways extremophiles contribute to the conservation of cultural heritage is through bioprospecting for extremozymes. For example, extremozymes such as proteases and lipases sourced from extremophiles can be used to develop eco-friendly cleaning agents for the removal of microbial biofilms and organic contaminants from stone, metal, and ceramic surfaces without causing damage to the underlying substrate (Ranalli and Zanardini 2021). Extremophiles also play a crucial role in biomineralization processes, which can be harnessed for the consolidation and protection of deteriorated cultural materials (Mamo and Mattiasson

2019). Some extremophiles are capable of precipitating minerals such as calcite, silica, and iron oxides, which can fill pores, cracks, and voids in archaeological artifacts and architectural structures, strengthening them and inhibiting further deterioration. Extremophile-mediated bioremediation techniques involve the use of microbial consortia or genetically engineered extremophiles to degrade organic pollutants, detoxify heavy metals, and restore environmental balance at heritage sites (Jin et al. 2019). Additionally, extremophiles contribute to the development of sustainable preservation methods for organic materials such as parchment, textiles, and wooden artifacts. Extremophile-derived enzymes, such as cellulases and hemicellulases, can be utilized to safely and efficiently remove biological contaminants, such as fungi and bacteria, from organic substrates, preventing further degradation and preserving the integrity of cultural artifacts (Cirone et al. 2023). However, despite the promising applications of extremophiles in cultural heritage conservation, several challenges remain. These include the identification and isolation of extremophiles with specific enzymatic activities tailored to the conservation needs of different materials, the optimization of enzymatic treatments for maximal efficacy and minimal damage, and the integration of extremophile-based conservation strategies into existing conservation practices.

Solutions to the limitations of research for extremophiles

Recent research has employed a comprehensive methodology that combines culture-dependent and culture-independent techniques. It possess the potential of exploring the interactions among genetic and metabolic mechanisms, revealing the entire microbial community inhabiting the extreme environments and discovering the novel psychrophilic lineages. The results have clearly supported this fact that there is far more unexplored microbial diversity thriving in extreme conditions (Kajale et al. 2020; Sharma et al. 2018). Recently, scientists are implementing omics approach to elucidate the possible microbial contaminants in monuments, cultural artworks and heritage sites (Pyzik et al. 2021). However, one of the greatest challenges faced by microbiology and microbial biotechnology today is figuring out the taxonomic and metabolic traits of microbial diversity. This issue has been much resolved with the development of next-generation sequencing technology and computational techniques for NGS data analysis. However, it has also been discovered that metagenomic techniques must work in concert with single-cell genomics to optimize the utilization of the genetic and metabolic variety of extremophilic microbial diversity (Chen et al. 2017; Stepanauskas 2012). The use of such multi-omics tools has potential to shed light on biotechnological breakthroughs.

Maintaining a robust database can be induced by foster international collaboration and partnerships to facilitate data sharing, resource exchange, and joint research initiatives. Collaboration across geographical boundaries enhances the diversity and scope of research studies on extremophiles and promotes global scientific advancement. An example of a successful attempt of database is Halophile protein database (HProtDB) that is a collection of physicochemical characteristics of proteins derived from halophiles (Sharma et al. 2014).

Advances in protein engineering and structural biology have facilitated the development and characterization of cold adaptive metabolites (Bhatia et al. 2021). Scientists have turned attention to more experimental based studies as well as relating climate change impacts to elucidate ecological dynamics. Mead et al. (2023) innovated a Hollow-fibre infection model (HFIM) to successfully culture the fastidious microorganisms that can be used as in vitro models for testing other antimicrobial resistant microorganisms.

Future prospects

Extremophiles have been a research hotspot in recent years. They have attained this attention with their astonishing versatility and unusual adaptations to severe settings. Moreover, they hold enormous potential for both basic and practical study. The metabolic mechanisms responsible for their survival as well as amazing persistence in the harsh environment have offered vital insights into the limitations of life and the possibility of its existence beyond the cosmos. Extremophiles are hypothesized as the remnants of primordial creatures based on their survival to physicochemical characteristics of life on Earth; gaining insight into the origin of life and hence are considered as models of early life. As discussed in the review, extremophiles and the bioactive compounds, they show enormous promise for use in biotechnology and medicine. Extremozymes and extremolytes have shown great economic promise in a variety of industrial activities spanning from agriculture to chemistry to medicines. The continuing genomic and microbiological revolution is set to further uncover extremophiles' immense genetic resources, perhaps pushing the bounds of life even further. The era of high throughput sequencing including whole genome techniques demonstrates the potential in discovering many novel microbial communities that may be uncultivable when using conventional techniques. However, there are certain key limitations that still need attention. As compared to bacteria and eukaryotes, archaea appear to have a distinct genetic inheritance. Despite the fact that numerous archaea have been found to date, there are currently few practical applications for them. Furthermore, continued interdisciplinary research efforts are essential to further unravel the mysteries of extremophiles. These discoveries have the potential to revolutionize biotechnology.

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Declarations

Competing interests The authors declare no competing interests.

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