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Extremophiles of Polluted Environments: Mechanisms of Surviving Extreme Pollution Settings

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ABSTRACT

Diverse microorganisms survive harsh environments that are beyond the limits of life. Environmental pollution has contributed to the unprecedented discharge of waste beyond the acceptable limit for microbial survival. Microbes surviving in environments with extreme/diverse pollution levels have learnt to thrive in all physiological, metabolic, and genomic senses. Extremophiles surviving in environments of extreme pollution have been described, and bioprospecting for such continues to be key to revolutionising discoveries in microbial diversity and biotechnology/industrial applications. Microorganisms with polyextremophilic characteristics have the added advantage of being able to adapt to highly polluted environments. Examples of such microorganisms include *Caldibacillus*, *Geobacillus*, *Mycolicibacterium*, *Bacillus*, *Chelatococcus*, and *Aeribacillus* spp. The current paper provides consolidated key highlights on diversity, adaptation, bioremediation potential, bioprospection, and recent developments in the microbiology of extreme and polluted environments. These details will help reveal the study's progress in understanding the diversity and adaptation mechanisms for surviving toxic and harsh pollution settings, enabling bioremediation and other prospective and beneficial biotechnological applications.

Keywords: Extremophiles, Environmental pollution, Bioremediation, Bioprospection, Microbial diversity.

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INTRODUCTION

Extremophiles are microbes possessing the potential to survive and proliferate under extreme harsh environments. The various harsh environments that extremophiles can survive include environments with extreme temperatures (cold or hot), pH (acidic or alkaline), high pressure, and environments with toxin levels capable of inhibiting the proliferation and survival of other microorganisms (Giovanella et al., 2020). Based on the extreme environment, extremophiles are classified as acidophiles (those surviving at extreme low pH) (Jeong and Choi, 2020), alkaliphiles (those surviving at high pH) (Naykodi et al., 2024), halophiles (those surviving at high salt environment) (Gunde-Cimerman et al., 2018), psychrophiles (those surviving at temperature below 0°C) (Collins and Margesin, 2019), thermophiles (those surviving above 60°C) (Ranawat and Rawat, 2017), and radiophiles (those surviving at high dose radiation) (Tanner et al., 2020).

According to the United Nations Food and Agriculture Organisation (FAO), environmental pollution is increasing due to agricultural activities, industrialisation, and urbanisation, and is expected to affect 90% of the global soil by 2050 (FAO, 2015; 2022). These polluted environments alter the microbial ecosystem, leading to the growth of extremophiles capable of surviving in the environment. The study done by Köhler et al. (2025) in the copper mine in Germany underscores the role of copper contamination in the growth of extremophilic bacteria, particularly halophiles. Their study highlights how the highly saline and sulfidic environment of the copper ore shapes microbial diversity, leading to a high prevalence of sulfur-related metabolisms. Climatic changes that result in extreme cold and hot environments also contribute to the growth and abundance of diverse extremophiles. The study done by Doytchinov et al. (2024) in Antarctica unveiled the abundance of bacterial taxa such as *Oxyphotobacteria*, *Bacteroidia*, and *Gammaproteobacteria*,

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and archaeal groups such as *Woesearchaeales* and *Candidatus nitrosopumilus*. According to the authors, psychrophiles can proliferate in the extremely cold environment due to their ability to secrete enzymes and biomolecules that enhance their adaptation and survival. Microbial communities in extremely polluted environments tend to adapt through diverse mechanisms, which include changes in metabolic pathways that promote breakdown of contaminants, as well as their survival (Abdelfattah et al., 2020). According to Koul et al. (2021), this adaptive capacity of these extremophiles in harsh environments makes them good candidates for bioremediation of environmental pollutants under extreme conditions and elevated concentrations of pollutants. The bioremediation of environmental pollutants by the extremophiles can occur through processes such as bioleaching and biomining, oil recovery/remediation, water treatment, and biopolymers degradation (Koul et al., 2021).

Rawat et al. (2024) highlighted that extremophiles inhabiting environments with extreme and diverse pollution levels exhibit physiological, metabolic, and genomic changes to ensure their survival. According to Tan et al. (2022), microbial adaptation is a gradual change in microbes that plays a crucial role in their survival in stressful environments. The authors further highlighted that during the adaptation processes in microbial communities, microorganisms adopt diverse strategies that promote their survival and proliferation in the environment (Tan et al., 2022). Sheppard et al. (2018), as well as several other studies (Sun et al., 2021; Naykodi et al., 2024), indicated that genomic mutation is a mechanism of adaptation in extremophiles that could result in their ability to survive stress. A novel stress-induced, error-prone Okazaki fragment was identified and explained by Sun et al. (2021) as the reason behind mutations, counteraction of replication defects, and promotion of cell evolution and survival in many microorganisms, as well as extremophiles.

The adaptation of extremophiles has also made them models for studying evolution and changes in the molecular structures of microbial communities. Hence, they have now emerged as a tool for biotechnological applications, especially in the field of medicine, industry, environmental management, and even space exploration (Schröder et al., 2020; Aulitto and Gallo, 2025). In a study by Doytchinov et al. (2024), psychrophiles were found to secrete arrays of cold-adapted enzymes and biomolecules. This implies that these enzymes and biomolecules are active in extremely cold weather, making them potentially useful substances that could be applied in medicine, food preservation, and industrial processes. Arredondo-Nuñez et al. (2023) discovered that a halotolerant strain of *Bacillus subtilis* CH11 isolated from Chilca salterns in Peru was able to secrete a novel type II L-asparaginase. L-asparaginases have been known for their application in cancer therapy and the food industry. This made the discovery of type II L-asparaginase more desirable because of its ability to withstand high environmental temperatures and salinity. The presence of these enzymes in extremophiles highlights them as potential sources of industrially relevant enzymes.

Halobacterium salinarum (a halophile) is known for its ability to secrete stable proteins in an extremely saline environment (Eichler, 2023). This stable protein can be applied in drug formulation and marine biotechnology, making this bacterium essential in the medicinal and industrial fields. Rastädter et al. (2021) reported that the enzymes secreted by *Sulfolobus acidocaldarius* (an acidophile and thermophile) are stable at low pH and high temperature. These characteristics of the enzymes made them suitable for the synthesis of drugs and chemical degradation in industrial settings. For molecular diagnosis advancement, the enzymes (KOD polymerase) secreted by *Thermococcus kodakarensis* have been reported to be useful due to their high fidelity and precision in the DNA replication processes (Scott et al., 2021). In biofuel production, extremophiles have been applied and have shown great promise in biofuel production. *Geobacillus thermoglucosidasius* (a thermophile) has been genetically engineered for ethanol production at high temperature from biomass, which allows more efficient biofuel production through saccharification and fermentation processes' enhancement (Cripps et al., 2009). Genetically engineered *Halomonas* sp. (a halophile) has been reported to produce more polyhydroxyalkanoates (PHAs) (a type of bioplastic) in an extremely saline environment (Van Doan and Nguyen, 2012). These genetic modifications of extremophiles promote production processes and enhance sustainability in industrial productions. Understanding extremophiles is crucial for advancing biosystems and bioprocesses and for gaining insights into their roles in global material cycles and ecosystem responses to human activity. In addition, the knowledge of their mechanisms in surviving extreme environmental conditions provides further insights into their applications in medical, industrial, food, and other biotechnological processes. The current review study provides information on extremophiles of contaminated environments surviving under diverse metabolic and toxic settings.

Microbial Communities in Polluted Environments

Pollutants present in any polluted environment play a pivotal role in dictating the functioning and any alteration of the ecosystem of the environment, and their presence and persistence determine the microbial communities that can thrive well in such environments (Kachienga et al., 2018). Sharma et al. (2021) examined the microbial communities associated with heavy metals in polluted pulp and paper industrial waste. The authors observed that the heavy metal present in the industrial waste promotes the proliferation of members of bacterial communities belonging to the phyla Proteobacteria, Bacteroidetes, Firmicutes, Chloroflexi, Actinobacteria, Spirochetes, Patesibacteria, Acidobacteria and other unknown bacterial communities. In acidic environments, Zouch et al. (2018) indicated that the acidified industrial wastewater promoted the growth of members of bacteria belonging to the family *Flavobacteriaceae*. In extreme acidic environments, bacteria such as *Acidithiobacillus ferrooxidans*, *Ferrovum* sp., *Fervidacidithiobacillus caldus*, were noted as dominant strains that could play roles in pollutant degradation (Watkin et al. 2024). Diverse wastewater sources released into terrestrial and aquatic environments are characterised by different pollutants, which select for the microbial communities that can proliferate in the polluted environment (Wang et al., 2022). The study of Wang et al. (2022) showed the proliferation of bacterial communities that include *Georgfuchsia*, *Thauera*, and *Gp4* in wastewater with petrochemical pollutants; *Phaeodactylibacter* and *Hyphomicrobium* in domestic wastewater; and *Otheakwangia*, *Terrimonas*, *Gimesia*, *Rhodopirellula*, *phenylobacterium*, *Dokdonella* and *Haloferula* in mixed domestic and industrial wastewater. Table 1 provides more information on microbial diversities as impacted by different extreme pollutant levels in the environment.

Extremophiles and Extreme Toxic Pollutant Concentrations Degradation

Extremophiles are categorised into groups that include acidophiles (surviving under low pH), alkaliphiles (adapted to high pH), halophiles (thriving under high-salt environment), psychrophiles (surviving under temperature range of 1-4 ^{o}C), thermophiles (proliferating well at temperatures above 45 ^{o}C), and radiophiles (thriving well in environments with high level of radiations) (Arora and Panosyan, 2019; Jeong and Choi, 2020). Through diverse, unique physiological, metabolic and genomic processes and mechanisms, these categories of extremophiles have adapted to the harsh environment. Jeong and Choi (2020) highlighted that these extremophiles, during their adaptation to the harsh environment with high toxic pollutants, tend to convert the unstable toxic pollutants into resources that can be used for their cellular metabolisms and promote their ability to tolerate the toxic pollutants at any concentrations.

Acidophiles

Acidophiles survive very low pH conditions by controlling proton permeation via a unique homeostatic process (Jeong and Choi, 2020). Studies have shown that members of microbial communities belonging to the genera *Thermoplasma*, *Ferroplasma*, and *Sulfolobu*s adapt to low pH conditions via structural/morphological modification that promotes the development of a highly impermeable cell membrane that comprises tetraether lipids (Rastädter et al., 2020; Naykodi et al., 2024). These modifications promote their ability to regulate proton permeation. In *Ferroplasma* type II and *Leptospirillium* group II, enzymes such as H^{+}-ATPase and proteins known as symporters and antiporters enhance proton influx modulation, thereby promoting their ability to survive in a low pH condition and maintain the pH homeostasis (Golyshina et al., 2017; Vergara et al., 2020).

Acidophiles have been employed in the detoxification of toxic heavy metals via bioleaching and bio-oxidation, processes known as biomining (Gumulya et al., 2018; Jafari et al., 2019; Saavedra et al., 2020). *Acidothiobacillus ferrooxidans*, an acidophile, has been applied in bioleaching at an industrial level (Zhang et al., 2018). Other studies have also demonstrated the heavy metal bioremediation potential of *At. Ferrooxidans* NCIMB 8455 (Romero-González et al., 2016) as well as *At. Ferrooxidans* and *Acidothiobacillus ferrivorans* strains (Jameson et al., 2010) under acid conditions. The studies done by Chakravarty and Banerjee (2012) and Okibe et al. (2016) demonstrated the efficient biosorption of cadmium cations and reduction of vanadium ions by *Acidiphilium symbioticum* H8 and *Acidocella aromatica* PFBC, respectively, under highly acidic conditions. A summary of the mechanisms adopted by the acidophiles to survive in an extreme condition and to remediate the environment is presented in Fig. 1.

Alkaliphiles

Alkaliphiles survive high pH conditions through different biological mechanisms that include the following:

➢ Increase in the generation of hydrogen ion motive force via secondary acidic membrane synthesis as observed in alkaliphilic *Bacillus* spp. (Aono, 1995; Aono et al., 1999; Seyedi et al., 2020). Among the benefits of the increase in proton motive force in the alkaliphiles under high pH conditions is the generation of energy as well as the promotion of pH balance within the microbes (Kitada et al., 2000; Calamita et al., 2001; Padan et al., 2005; Seyedi et al., 2020).

Table 1: Polluted environment and some associated microbial communities

Environment of high pollution levels	Pollutants	Microbial communities detected	References
Soil	Heavy metal	Proteobacteria, Chloroflexi, and Acidobacteria (Bacterial phyla); Crenarchaeota and Euryarchaeota (Archaeal phyla)	Li et al. (2017)
River (Sediments)	Heavy metal	Firmicutes, Chloroflexi, Crenarchaeota, Proteobacteria and Actinobacteria	Yin et al. (2015)
Mine tailings	Heavy metals	Proteobacteria and Firmicutes	Zhao et al. (2019)
River (Sediments)	Arsenic (As) and antimony (Sb)	*Anaerolinea*, *Sphingomonas*, and *Opitutus*	Sun et al. (2019)
Soil	Oil	*Rubrivivax*, *Nitrospira*, *Methylotenera*, *Methyloversatilis* and *Acidaminobacter*	Jiao et al. (2016)
Soil	Cadmium (Cd)	Proteobacteria, Sulfuricella and Thiobacillus	Feng et al. (2018)
River (Sediments)	Microplastic (polyethylene, polyvinyl chloride, polyurethane foam or polylactic acid)	Bacteriodes and Proteobacteria	Seeley et al. (2020)
River	Heavy metals	*Gallionella, Acidovorax, Arenimonas, Curvibacter, and Sideroxydans*	Wang et al. (2021)
River (sediments)	Nitrogen, heavy metals, acidic water	Proteobacteria, Acidobacteriota, Chloroflexi, Actinobacteriota, Bacteroidota, Firmicutes and Nitrospirota	Shu et al. (2023)
River (sediments)	Heavy metals	*Rhodobacter, Nocardioides, Sphingomonas, Pseudarthrobacter, Kouleothrix, Dechloromonas, Gaiella, Pedomicrobium, and Hyphomicrobium*	Yang et al. (2023)
Soil	Heavy metals (Lead)	*Perlucidibaca, Limnobacter, Delftia, Hydrogenophaga, Thiobacillus, Sulfurifustis and Sphingopyxi*	Wu et al. (2024)

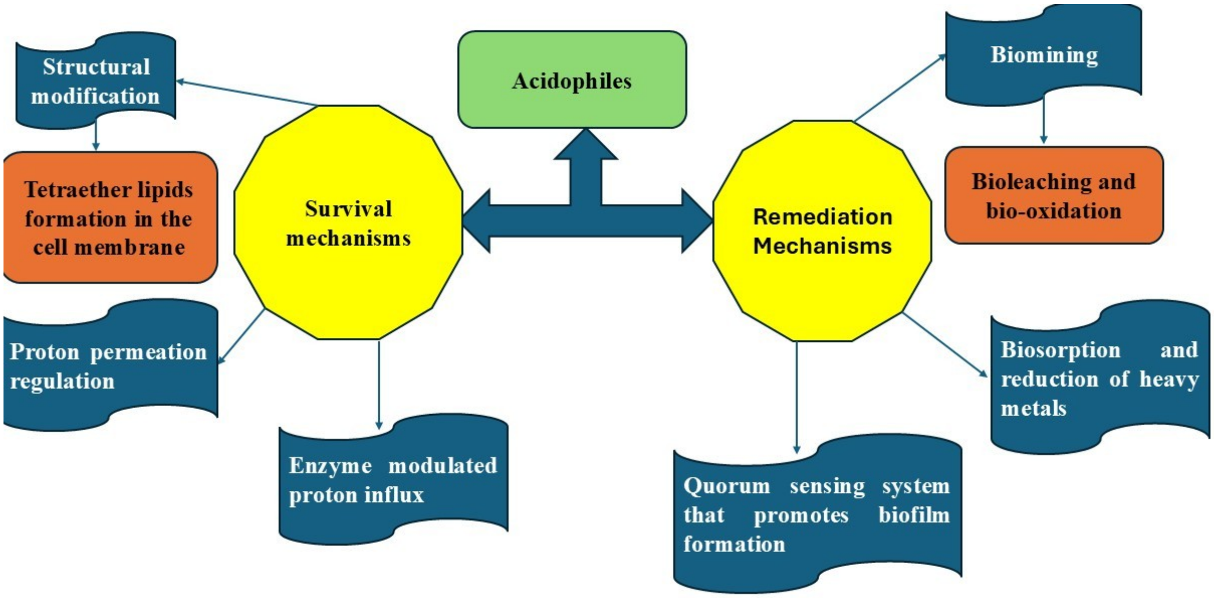

Fig. 1: Overview of survival and remediation mechanisms of acidophiles in low pH environments.

- Activation of the sodium motive force, which tends to control the amount of sodium ions, thereby promoting the activation of bioenergetic processes and regulation of internal pH (Stancik et al., 2002; Matsuno et al., 2018; Fang et al., 2018; Rawat et al., 2024) and
- Organic acid production serves the purpose of pH calibration in the maintenance of internal pH balance via metabolic processes (Slonczewski et al., 2009; Wernick et al., 2016; Rawat et al., 2024).

Naykodi et al. (2024) undertook a study to evaluate the potential of alkaliphiles in the detoxification and bioremediation of bauxite residue (red mud) in the bauxite-contaminated environment. The authors observed that *Evansella cellulosilytica*, *Halalkalibacterium halodurans* and *Sutcliffiella cohnii* showed great tolerance for Al^{3+}, Cr^{6+}, and Co^{2+}respectively. Furthermore, the authors observed that *Alkalihalobacillus* sp. exhibited great tolerance to 10% red mud through their ability to produce mixed acids capable of neutralising the pH within 24 hours. This indicates the potential of these species in the remediation of red mud. *Salipaludibacillus agaradhaerens* AK-R was isolated from a soda lake in Egypt by Ibrahim et al. (2019), and the strain *S. agaradhaerens* NRC-R was further identified and noted to play a crucial role in the reduction of chromium in the same lake (Ibrahim et al., 2020). Naykodi et al. (2024) provided a detailed mechanism of metal tolerance and remediation by bacteria, including alkaliphiles as well as halophilic bacteria, as shown in Fig. 2. Rapid Annotation using Subsystem Technology (RAST) analysis was used by the authors to provide insight into the role of metal reduction proteins, transporter proteins, production of organic acid and siderophores' presence in multi-metal tolerance in haloalkanes (Naykodi et al., 2024). They further observed that some of the identified strains contain genes that enable them to produce extracellular polymeric matrix, which aids them in the adsorption of metals and metalloids (Naykodi et al., 2024).

Alkaliphiles have been reported to bioremediate azo-dyes present in textile wastewater. For example, *Bacillus flexus* VITS6 displayed more than 90% dye removal (Reactive Orange 16 dye) at pH and temperature of 9 and 37°C respectively, within 24 hours of inoculation (Saha and Rao, 2020). *Bacillus* sp. strain CH12 was reported to cause the decolourisation of Reactive Orange 16 dye when the pH increased from 6 to 10 (Guadie et al., 2017). Bhattacharya et al. (2017) and Kapoor et al. (2021) also reported that the alkaliphile *Nesterenkonia lacusekhoensis* EMLA3 was able to degrade 97 % of methyl red dye from industrial dye effluent. Wadhawan et al. (2024) provided detailed information on the alkaphiles discovered in azo-dye remediation of textile wastewater, mode of actions (enzymatic mechanisms and associated genes), and their adaptive features that promote their survival and remediation. NADH-ubiquinone oxidoreductase and the associated encoding genes have been reported to be abundant in a halophilic alkali-thermophilic bacterial consortium capable of degrading and discolourising azo dye Metanil Yellow G (MYG) (Guo et al., 2020; Chaieb et al., 2022).

Halophiles

Microorganisms in a high-salt environment face the challenge of osmotic imbalance as well as metabolic problems; however, halophiles survive through this challenge through various metabolic and structural strategies that enhance their adaptations (Gunde-Cimerman et al., 2018). One of the strategies is the "salt-in" strategy, which involves the accumulation of KCl (known as inorganic osmoprotectants) inside the cell to ensure the maintenance of both internal and external osmotic homeostasis as observed in *Halobacterium salinarum* (Engel and Catchpole, 2005; Coker et al., 2007; Strahl and Greie, 2008; Gunde-Cimerman et al., 2018; Corral et al., 2019). Halophiles possess large amounts of aspartate and glutamate with negative charge on protein surfaces

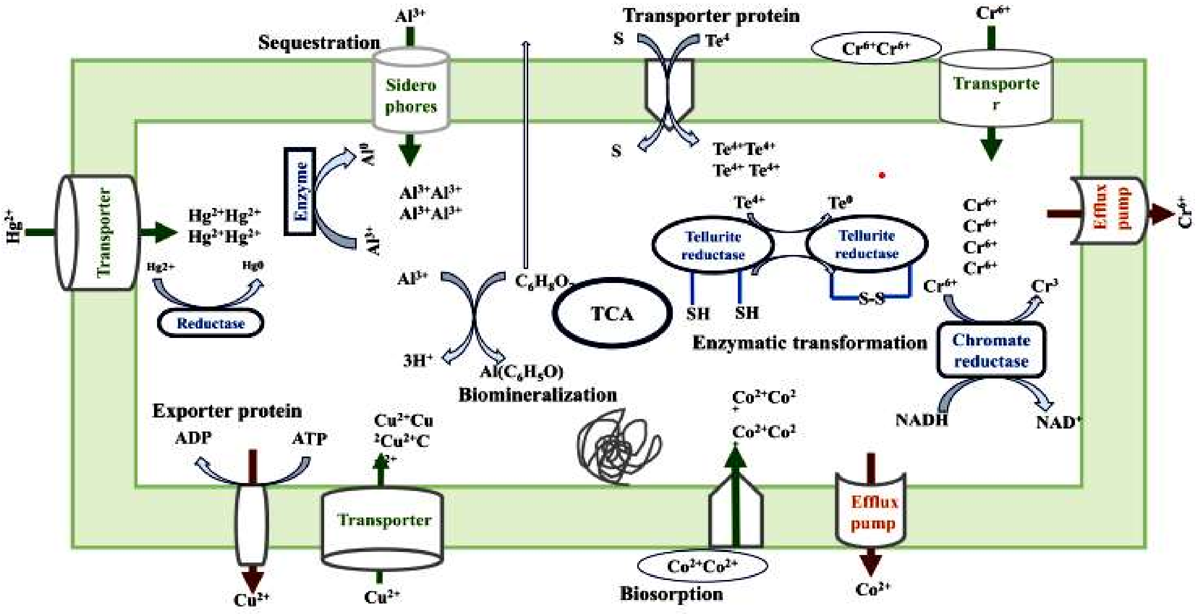

Fig. 2: Metal tolerance mechanisms in alkaliphiles and haloalkiliphiles (Source: Naykodi et al. (2024)).

capable of interacting with molecules of water, producing a protein precipitation and dehydration protection cage called a water cage, a mechanism that further ensures their survival in a salt environment (Reed et al., 2014; Brininger et al., 2018; Corral et al., 2019). Compatible solute adaptation is another strategy adopted by halophiles for survival under high-salt conditions. This strategy involves the use of polyols, glucosylglycerol, sucrose, trehalose, ectoine, and betaine (known as compatible solutes) to ensure that osmotic homeostatic balance is maintained via diverse metabolic approaches (León et al., 2018). According to León et al. (2018), *Spiribacter salinus* M19-40 (a halophile), under high salt concentration, produced high levels of compatible solutes such as ectoine and trehalose to ensure its survival. Vandrich et al. (2020) underscore the importance of these compatible solutes as molecules that provide homeostatic balance in the environment.

Halophiles play a crucial role in the detoxification of toxic pollutants in high-salt conditions. Several reports on the bioremediation of toxic heavy metals using halophiles from the marine environment have been provided. For example, Abd-Elnaby et al. (2011) reported that *Vibrio harveyi* can build up Cd^{2+} within the cell with a high absorption capacity. *Enterobacter cloaceae* has been reported to possess the ability to chelate Cd, Cu, and Co from mixed-salt solutions (Iyer et al., 2005). Halophiles can also degrade hydrocarbons. Studies have shown the transformation of phenanthrene, anthracene, biphenyl, and naphthalene as carbon sources by *Marinobacter sedimentalis*, *Marinobacter falvimaris*, and *Marinobacter nanhaiticus* D15-8W in hypersaline environments (Gao et al., 2013; Al-Mailem et al., 2013). Jeong and Choi (2020) further indicated that extracellular polymeric substances (EPS) and exopolysaccharides secreted by halophiles play an essential role in the bioremediation of organic pollutants and act as biosurfactants (which enhance the emulsification of hydrocarbons as well as the aggregation of oil, respectively). *Halobacillus* sp. *EG1HP4QL* was reported to break down crude, naphthalene, polycyclic aromatic hydrocarbons, mono- and bicyclic aromatic hydrocarbons, and alcohol–benzene resins (Ibrahim et al., 2020).

Yang et al. (2024) investigated the polycyclic aromatic hydrocarbons (PAHs) degradation mechanisms by halophiles belonging to the genus *Pontibacillus*. The authors observed that in most strains of *Pontibacillus*, cytochrome P450 monooxygenases initiated the degradation pathways for benzo[*a*]pyrene (BaP) and phenanthrene under high-salt (5% NaCl) stress. BaP and phenanthrene are representative of PAHs that are hazardous to human health and the environment (Yang et al., 2024; Qian et al., 2024). Qian et al. (2024) reported that in saline environments, *Pontibacillus chungwhensis* HN14 demonstrated high potentials in the degradation of BaP through various pathways that include chrysene, phenanthrene, and naphthalene pathways that aid in the conversion of BaP to 4,5-epoxide-BaP. The role of halophiles in the bioremediation of azo-dye from textile wastewater, including the mechanisms controlled by enzymatic activities and the associated genes, has been documented by Wadhawan et al. (2024). Enzymes such as laccase, azo reductase, and NADH-DCIP reductase have been reported to be abundant in extreme halophilic/halotolerant bacteria and play a crucial role in the degradation of azo-dye like Direct Black G via redox reactions (Qiu et al., 2022).

Psychrophiles

Psychrophiles thrive at temperatures below 0ºC, and this is possible because of various physiological adaptation mechanisms adopted by them. Among the physiological adaptation mechanisms are molecular chaperones' action, membrane fluidity control, and antifreeze molecules' synthesis (De Maayer et al., 2014; Collins and Margesin, 2019). Modulation of membrane fluidity is done via the alteration of the psychrophiles' lipid composition (Collins and Margesin, 2019). Yoshimune et al. (2005) reported that diverse temperature-induced enzymes (cold-shock proteins (Csps) and heat-shock proteins (Hsps)) play a pivotal role in the psychrophiles' cold-shock resistance through the regulation of cascades of signals that protect damaged proteins and cofactors.

At very low temperatures, psychrophiles change various molecular pathways and mechanisms. Some of these pathways and mechanisms affected by low temperature in psychrophiles include oxidative metabolism process, pathways that has to do with metal ions and molybdopterin metabolism (glycolysis, the pentose phosphate pathway, the TCA cycle, and/ or the electron transport chain). Studies have reported downregulation of the above-mentioned pathways and mechanisms by psychrophiles under very low temperatures to promote their survival and adaptation (Médigue et al., 2005; Piette et al., 2011; Tribelli et al., 2015; Bharali et al., 2024). Psychrophilic hydrocarbonoclastic bacteria (PHcB) have been reported to play a crucial role in the bioremediation of petroleum hydrocarbons in an extreme cold environment (Bharali et al., 2024). Bharali et al. (2024) further highlighted the mechanisms of survival and adaptation of PHcB in extremely cold environments as: 1) modification of the cell membrane, which includes fatty acid levels modification within the cell membrane and reduction of membrane-hopanoids; 2) lipid substances extrusion, enhancing the removal of hydrophobic substances from the membrane and cytoplasm; and 3) extracellular metabolites synthesis. More information on the degradation of hydrocarbons in extremely cold environments by PHcB, including examples of the psychrophiles, has been documented by Bharali et al. (2024).

Thermophiles

Thermophiles can survive temperatures above 60 °C by adopting similar mechanisms of survival of the psychrophiles. Ranawat and Rawat (2017) revealed that *B. Acidocalidus* resists high temperature conditions via the modulation of membrane lipid fluidity promoted by increased hopanoids (a subclass of triterpenoids) synthesis. Other studies have demonstrated that *Metahnocaldococcus jannaschii* (thermophilic archaea) tend to regulate membrane lipid composition (such as decrease and increase in the synthesis of diether lipid and caldarchaeol-based/cyclic archaeol-based lipids, respectively) under high temperature to ensure their survival (Sprott et al., 1991; Mansilla et al., 2004). Through the synthesis of biomolecules, thermophiles have developed thermal stability (Valenti et al., 2011). Furthermore, thermophiles possess rich ribosomal proteins as well as a well-developed shock response that promotes normal metabolic processes that lead to protein synthesis at extremely high temperatures (Sieck, 2015; Wang et al., 2015).

Geobacillus thermantarcticus and *Anoxybacillus amylolyticus* have been identified as potential bioremediation microbes due to their heavy metal biosorption capacity (Özdemir et al., 2013). Some studies have pointed out that some thermophiles, such as *Bacillus*, *Thermus* and *Geobacillus* strains isolated from oil-contaminated environments, could decontaminate aromatic hydrocarbons and long-chain alkanes (Nazina et al., 2001; Feitkenhauer et al., 2003; Feng et al., 2007; Sood and Lal, 2008; Sun et al., 2015). Through metagenomic analysis, Peng et al. (2024) were able to unveil the ability of the following thermophiles under high temperature to degrade petroleum hydrocarbons: *inter alia*, *Caldibacillus*, *Geobacillus*, *Mycolicibacterium*, *Bacillus*, *Chelatococcus*, and *Aeribacillus* spp. The authors further highlighted the importance of alkane hydroxylase genes (*alkB* and *ladA*) released by the thermophiles in various metabolic pathways during the degradation of petroleum hydrocarbons under an extremely hot environment (Peng et al., 2024). *Geobacillus stearothermophilus* has been reported to resist the toxicity of many metals in electroplating, battery industrial discharge, with the ability to remediate arsenic and cadmium at a temperature of 80°C (Puopolo et al., 2020). Swaminaathan et al. (2024) provided significant information on different remediation mechanisms in microorganisms, including thermophiles, as shown in Fig. 3.

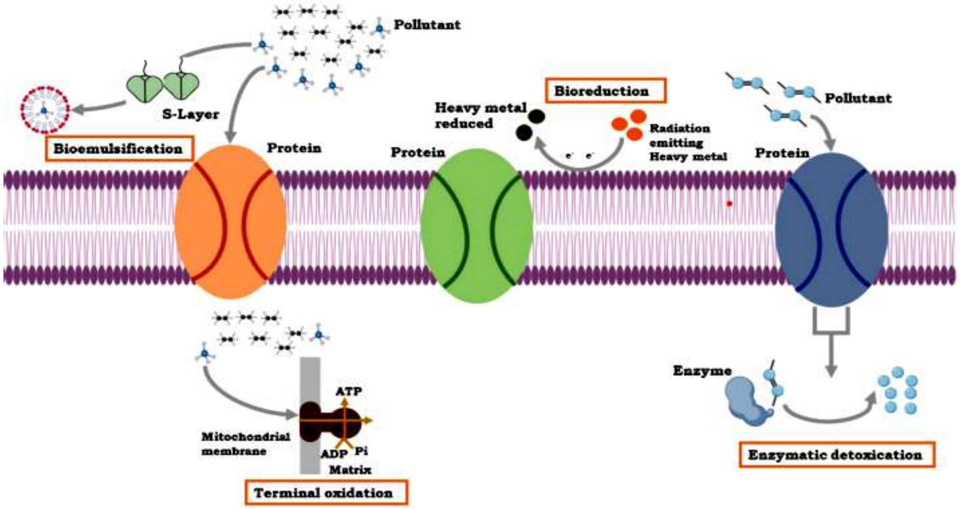

Fig. 3: Remediation approaches/mechanisms in microbial communities including thermophiles (Source: Swaminaathan et al. (2024)).

Radiophiles

The ability of radiophiles to survive high-dose radiation as well as oxidative stress is traced to their strong DNA repair systems and antioxidation mechanisms (Liu et al., 2017; Srinivasan et al., 2017; Park et al., 2018; Tanner et al., 2020). Under gamma ray irradiation, *Deinococcus radiodurans* R1 show an increase in the synthesis of RecA proteins that promote the repair of damaged DNA (Slade and Radman, 2011; Rajpurohit et al., 2016). Other studies have shown that *Deinococcus radiodurans* R1 further synthesises novel proteins such as PprA, PprM, PprI, and DdrABCDO and DNA damage response regulons under high doses of irradiation to promote DNA repair as well as the reconstruction of the damaged genome (Tanaka et al., 2004; Lim et al., 2019; Jin et al., 2019; Floc'h et al., 2019). The synthesis of antioxidant enzymes by radiophiles promotes their ability to scavenge reactive oxygen species under high dose irradiation (ROS) as observed in *D. radiodurans* (Slade and Radman, 2011; Jeong et al., 2016). In addition to their ability to scavenge ROSs and protection against protein damage is the synthesis of non-enzymatic factors (Choi et al., 2019; Maqbool et al., 2020). Radiophiles adopt the following strategies in the detoxification of radioactive waste: biomineralisation, biotransformation, and biosorption (Prakash et al., 2013; Shukla et al., 2017). Studies have proposed that biomineralisation is the main strategy radiophiles adopt in radionuclide removal (Wildung et al., 2000; Istok et al., 2004). *Shewanella* and *Geobacter* strains were reported to possess the ability to detoxify alpha nuclides (Wildung et al., 2000).

D. radiodurans is a well-known radioresistant bacterium mostly applied in the remediation of radioactive contaminated environments; however, under acidic radioactive wastewater, the bacterium's performance has been minimal due to its inability to withstand acid conditions (Razia et al., 2023). *Rhodotorula taiwanensis* MD1149, an environmental yeast, has been reported to possess the ability to resist radiation and acidic conditions. This ability could be linked to their biofilm formation ability under high-level radiation and low pH value (Tkavc et al., 2018). The ability of these extremophiles, that have the properties of radiophiles and acidophiles, possess unique structures as shown in Fig. 4. Llorens et al. (2012) reported the presence of s-layer proteins on the cell surface of *Cupriavidus metallidurans* that aid the bacterium in its ability to adsorb uranium at a pH of 1. *A. Ferroxidans*, an acidophile, has also been reported to possess extracellular polymer substances (EPS) that make it easy for the bacterium to absorb radioactive materials and heavy metals (Marques, 2018). Among the physiological changes that help these radiophiles with acidophilic properties is the one that promotes the release of extremozymes. These enzymes tend to catalyse many mechanisms or metabolic pathways that promote the solubilisation of heavy metals and radioactive materials through oxidation processes, as well as the precipitation of heavy metals and radioactive materials through reduction processes (Das et al., 2016). Enzymatic activity of inorganic phosphates granule has been reported to enhance the remediation of heavy metals and radioactive materials via bioaccumulation in *Caulobacter crescentus*, *Acidithiobacillus* sp. and archaea such as *Sulfolobus metallicus* (Navarro et al., 2009; Marques, 2018).

Progress in Studies of Extremophiles of Contaminated Environments

Rapid industrialisation and urbanisation globally have consequently resulted in the production and release of toxic pollutants contaminating the environment. To better protect the environment, various physicochemical-based remediation strategies have been adopted (Muddemann et al., 2019; Xiang et al., 2019; Gebreeyessus, 2019; Ouyang et al., 2019). However, due to high cost and secondary contamination, bioremediation using the microbial communities present, adapted, and proliferating in the contaminated environment becomes a promising tool in the remediation of the toxic pollutants (Kumar Mishra, 2017; Abdelfattah et al., 2020). In an extremely harsh environment, the extremophiles that are capable of surviving and proliferating in microhabitats thereof offer a suitable approach in the bioremediation of the toxic pollutants (Kiadehi et al., 2018). In view of establishing a sustainable green technology for the remediation of toxic pollutants, studies have been done and are still on-going in the identification of diverse extremophiles in different environments, their adaptive mechanisms, metabolic pathways, enzymatic activities, and various applications in different fields of study and life.

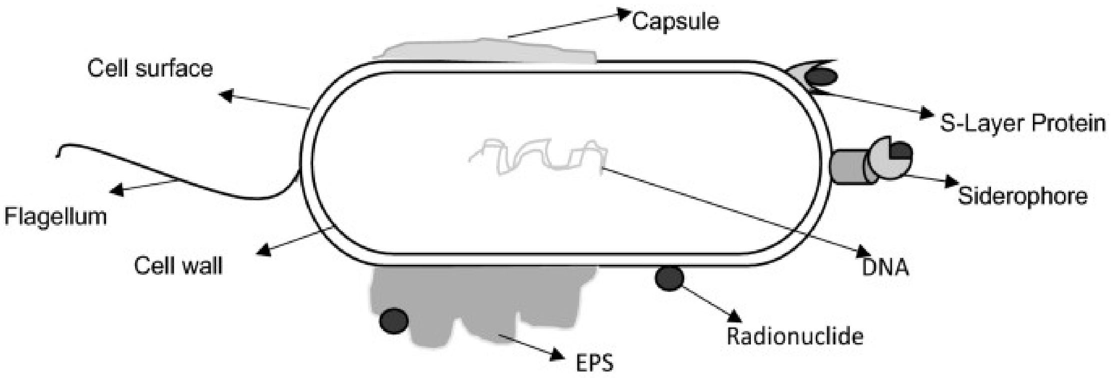

Fig. 4: Structural and physiological modification at cellular level of microorganisms with radiophilic and acidophilic properties (Source: Razia et al., 2023).

In toxic heavy metal-polluted environments, studies have been done in unveiling the diverse extremophiles proliferating and surviving there, as well as diverse metabolic pathways and enzymes associated with the extremophile's survival and possibly, remediation of the environment (Gallo et al., 2021). Through genome analysis, heavy metal resistance systems in thermophiles have been identified, which provided an insight into individual putative molecular determinants that enhanced their survival (Panyushkina et al., 2019; Aulitto et al., 2021). Extracellular barrier, active transport of metal ions (efflux), enzymatic reduction of metal ions, and intracellular sequestration are the heavy metal resistance mechanisms of thermophiles and other extremophiles (Cazorla et al., 2002; Lin et al., 2006). Ranawat and Rawat (2018) highlighted that during intracellular sequestration of heavy metals by thermophiles, the proteins that are rich in cysteine residues form complexes with metals via thiol groups. This is made possible because of the molecular adaptation that involves the irreversible folding of the proteins, laying bare the hydrophobic cores that can enhance their aggregation with metals and other substances (Basak et al., 2020). Studies have also demonstrated the ability of acidophiles to detoxify and remediate toxic heavy metals in a contaminated environment through the synthesis of biomolecules. For example, the synthesis of extremely stable and active biomolecules by *Lactobacillus plantarum* YW11 promoted Pb adsorption properties (Kirillova et al., 2017). The interaction of the S-layer proteins of *Lactobacillus kefiri* CIDCA 8348 and *Lactobacillus kefiri* JCM 5818 enhanced the adsorption of heavy metal cations (Cd^{2+}, Zn^{2+}, Pb^{2+}, and Ni^{2+}) in a heavy metal-contaminated environment (Jeong and Choi, 2020).

For the remediation of organic pollutants in contaminated environments, a lot of progress has been made in the characterisation of extremophiles capable of degrading or detoxifying different pollutants. Psychrophiles have been reported to play crucial roles in the treatment of organic hydrocarbon pollutants. *Pseudoalteromonas* sp. P29 and *Oleispira antarctica* RB-8^T (psychrophiles) have been observed to degrade hydrocarbon mixtures comprising diesel, military jet fuel, and crude oil with high efficiency (Lin et al., 2009; Gentile et al., 2016).

Notable progress has been made in the microbiology of extremely polluted environments, leading to the identification of diverse extremophiles, as well as their roles in the bioremediation of toxic pollutants. The advent of "omics" technologies provided a platform for this progress. Through "omics" technologies (meta-genomics, meta-transcriptomics, metabolomics, and meta-proteomics) diverse extremozymes have been identified that can be industrially applied in biorefinery, hence promoting sustainable biofuel production (Krüger et al., 2018; Zhu et al., 2020; Chettri et al., 2021). Zhu et al. (2020) identified through genomic studies thermophiles such as *Thermotoga*, *Thermoplasma*, *Pyrococcus*, and *Thermus* and their ability to synthesise enzymes for biorefinery. Furthermore, genomic studies provided more insights into transport mechanisms, metabolic pathways, substrate biotransformation, and enzymatic mechanisms that enhanced the survival and adaptation of extremophiles in extremely contaminated environments (Kochhar et al., 2022). Modification of protein via proteomics and gene recombinant techniques further enhanced the progress made in the study of extremophiles, as they promote the solvent tolerance, higher specificity, pH tolerance, thermal stability, and extremozymes activities of the extremophiles that enhance their bioremediation potentials (Zhu et al., 2020).

Recently, the application of nanotechnology in extremophiles has become a promising tool or strategy in the remediation of a polluted environment. This has led to the advent of a nano-biotechnology which involves the combination of extremophiles with nanomaterials (nano-adsorbents and reductants) for bioremediation of the polluted environment. Few studies have reported the biosynthesis of diverse nanomaterials using extremophiles (Kulkarni et al., 2015; Beeler and Singh, 2016; Li et al., 2016; Choi et al., 2017; Chen et al., 2017). Choi et al. (2017) reported the removal of radioactive iodine (^{125}I) by *D. radiodurans* in combination with biogenic Au nanoparticles. Kitjanukit et al. (2019) reported the reduction of Cr(IV) by thermo-acidophilic archaeon *S. tokodaii* 7^T (NBRC 100140) capable of producing biogenic Pd(0) nanoparticles.

Future Direction

Toxic pollutants present in a contaminated environment select the microbial communities that can thrive well in that environment. The presence of pollutants in extreme microbial habitats is acknowledged, and extreme concentrations of pollutants create extreme microhabitats that exert extremism in microorganisms that thrive there. Due to setbacks of conventional methods of treatment, both biological and physicochemical methods, it becomes pertinent to continue discovering diverse microbial communities present in extreme and synthetic contaminated environments, identifying their mechanisms of survival, metabolic pathways, and enzymatic processes, which can serve as better tools for rapid remediation of contaminated environments (Crini and Lichtfouse, 2019). Furthermore, the advent of advanced biotechnology in combination with extremophiles in this omic era has provided more insight into developing promising bioremediation techniques through extremophiles' genetic reprogramming (Marques, 2018; Giovanella et al., 2020). Application of advanced biotechnology in combination with nanotechnology in improving the extremophiles for environmental remediation, development, as well as improvement of tools in bioengineering will unveil more potential of extremophiles that can provide sustainable toxic pollutant removal and environmental remediation.

Prospects of Extremophiles in Environmental Biotechnology

Application of extremophiles to contaminated environments that comprise an array of pollutants has shown great success due to their ability to undergo various chemical transformation processes that promote environmental remediation (Jeong and Choi, 2020). *Acidithiobacillus ferrooxidans* (hyper-acidophilic extremophile), through specialised metabolism, was able to oxidise Fe and S compounds and solubilise many trace elements. These characteristics have encouraged the application of this bacterium in biomining and bioleaching processes (Tonietti et al., 2024). *Pseudomonas alcaliphila* NEWG-2 showed a varied hexavalent chromium biosorption capacity (97.2% and 96.1%) at different hexavalent chromium concentrations (50 mg/L and 200 mg/L, respectively), indicating its application in green technology for the treatment of Cr-contaminated water (El-Naggar et al., 2020). Ibrahim et al. (2020) reported the ability of *Halobacillus* sp. EG1HP4QL to degrade aromatic hydrocarbons (51.2%), polycyclic aromatic hydrocarbons (43.5%), naphthalene (49.6%), paraffin (34.5%), and alcohol-benzene resins (25.5%) in a heavy metal-contaminated environment. This highlights their potential in bioremediation processes and their application in the development of various technologies that can be applied to ensure sustainable remediation of contaminated environments.

Conclusion

Extremophiles of contaminated environments have paved the way for more research into identifying their potential in surviving harsh environments and the benefits of their physiological processes, as well as the modification of those processes to provide a sustainable bioremediation tool for toxic pollutants. This is because of their ability to undergo diverse metabolic, molecular, and physiological changes in order to thrive well in such conditions. Through advanced biotechnology, diverse proteins as well as enzymes (extremozymes) and other low/high molecular weight molecules have been identified and used in different fields such as food manufacturing, pharmaceutical, agricultural, etc. The application of enzymes and biomolecules in the remediation of contaminated environments is a valuable tool. There is still a need for the combination of extremophiles biotechnology (especially, genetic engineering) and nanotechnology to provide more sustainable bioremediation pathways and platforms for the remediation of the environment contaminated with toxic pollutants.

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