

Adapting to the Changing Environment: Microbial Way of Life

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Abstract

Microorganisms are always faced with an ever-changing environment within their natural habitats both in planktonic form and/or microbial communities. Common of these changes include nutrient inadequacy, pH, temperature, osmolarity variations, radiation, heavy quantity superoxides and heavy metals. Different forms are considered when studying microbial adaptation to extreme conditions. Some specific metabolisms are equally vital for the survival of these microbes in such conditions although there is no general agreement to say that an environment is extreme for all organisms or microorganisms. This is because an environment considered extreme for an organism may be favourable for other organisms. However, due to some changes in the physicochemical conditions which have occurred from time to time in our environment, this said normal environment for some organisms has equally undergone some changes. We, therefore, tried to explore what could be considered as environmental changes and extreme environment, associated physicochemical factors and adaptation of microorganisms in these environments at their different levels of existence.

Keywords

Environment · Environmental changes · Extreme environment · Microorganisms · Adaptation · Extremophiles

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14.1 Background

Environment can be seen as a complex system due to its diverse nature and compositions. The dynamics that exist among environmental components modify the living components of the environment. In this regard, microorganisms are invariably faced with such environmental changes. This prepares some of them to adapt to and thrive in various environmental conditions which might be challenging and hostile to others. Certain levels of environmental conditions such as temperature, pH and ionic concentrations are required by microbial cells and their macromolecules for optimum functioning (Talley and Alexov 2010; Dhar 2013). To develop, life requires three basic things, namely, carbon which serves as the bedrock of all biological macromolecules, water which is confirmed as the best solvent for proper functioning of proteins and energy which is essential for biological systems to function efficiently (Franzetti 2019). The survival ability of organisms in different environments is a function of their biological molecules which gradually adapts for optimum function in their natural environment over evolutionary time (Ortega et al. 2011; Garcia-Moreno 2009; Tadeo et al. 2009; Greaves and Warwicker 2007; Rothschild and Mancinelli 2001). In a very stable environment, there is the need for organisms to be able to survive and thrive during certain environmental changes, for example, changes resulting from seasons. Inefficient functioning and/or, in some cases, total inhibition of functioning of biological molecules may result from dramatic changes in the environmental conditions; this may consequently lead to retardation of growth and in life-threatening degrees and cause death of cells or extinction of the affected organisms (Skirycz et al. 2011; Cramer et al. 2011; Fulda et al. 2010; Vermeulen et al. 2008). This discrepancy of adaptations of microorganisms in various environmental conditions led to the curiosity of scientists and researchers to investigate the propelling factors involved and the strategies used by these microbes in their microbial activities for survival in such environments. Generally, environmental conditions that are life-threatening to organisms are referred to as stressors, and they are classified into natural (occurring by nature in the environment) and man-made (evolving as aftermaths of the activities of man) (Dhar 2013).

14.2 Concept of Environmental Change

Environmental changes are caused by both natural processes and activities of its biotic components including anthropogenic activities. These changes often pose some adaptative and survival challenges to the microbes living therein either in their planktonic form or microbial communities. Hence, for improved chances of survival, every microbial cell needs to adapt to fluxes of nutrients and other environmental conditions (Katz and Springer 2016). Common environmental changes that face microorganisms in their habitats include nutrient limitation, temperature, pH and osmolarity fluctuations, radiation, drought and other harmful agents, such as the extreme amount of superoxides and heavy metals (Rampelotto

2010; Gao et al. 2011). For instance, the mammalian gut which has been identified to host numerous eukaryotic and prokaryotic microbes serves as a typical example of a changing environment which is equally characterized by some level of randomness and order (Walter and Ley 2011; Parfrey et al. 2011; Katz and Springer 2016). Although there may be stochastic fluctuations of nutrients and metabolites in the gut, such fluxes are controlled by the physiology, behaviour and diet of the host (Thaiss et al. 2014; David et al. 2014a, b). Cells that are able to adventure this kind of noisy and dynamic structure and expect fluxes in their environment would probably enjoy fitness advantage (Katz and Springer 2016).

14.2.1 Extreme Environment

Giving a single and direct explanation of what an extreme environment is all about has been a point of debate. This is because some conditions considered extreme from a normal anthropocentric view may be favourable for microbial growth and activities and vice versa. Also, among microbes, some conditions considered adversely extreme for some microbes are at the same time favourable for other microorganisms. For instance, from the anthropocentric standpoint, physicochemical factors that promote mammalian lives are considered normal, whereas those contributing otherwise are referred to as extreme (Torsvik and Øvreås 2008). Microbes live in almost all soil habitats (Torsvik and Øvreås 2008), and the clear definition of what normal and extreme environment are for microorganisms remains a point of debate as what we may suggest being extreme for microbes may not certainly be appropriate (Gorbushina and Krumbein 1999). Hence, understanding the mechanisms of adaptation of microorganisms to such extreme environments is significant for both evolutionary and ecological viewpoints (Allen and Banfield 2005; Denev et al. 2010; Li et al. 2014). Microorganisms have been identified to live and survive in a different soil environment that is considered 'extreme'; a wide range of soil types, ranging from highly dry, cold soils in the Antarctic to geothermal, humid soils near volcanic areas and from highly acidic areas to highly alkaline areas, have been identified in this regard due to their associated stressful factors like high temperature, low pH and high osmotic stress (Li et al. 2014; Torsvik and Øvreås 2008; Rothschild and Mancinelli 2001; Ghai et al. 2011; Kuang et al. 2012). Halophilic microbes (e.g. bacteria and archaea) thrive in salty environs ten times greater than saltwater, acidophiles survive in the highly acidic environment of pH level 1, and hyperthermophiles similarly thrive in high-temperature level of 85 °C and beyond. Specifically, bacteria can sense fluctuations in environmental parameters (e.g. temperature, pH, pressure, solute concentrations, ionic strength and available water) and quickly develop adaptations through the protection of their biomolecules and regulation of their biochemical reactions in response to harsh conditions (Heulin et al. 2012).

14.3 Physicochemical Factors Limiting to Life

Some physicochemical factors have been identified to affect the life of microorganisms in their environment (e.g. soils). The influences of these factors and the fluctuations in their amounts have prompted microbes to develop some adaptive strategies which support them to grow and survive in such conditions. Some of these factors are discussed as follows.

14.3.1 Water

Soil moisture (water) exists in forms that could either be adsorbed on surfaces or be available as water in the soil pores or as films between soil particles. The level of available water in the soil refers to water potential of the soil, which is defined as water held and being moved in the soil by means of energy and forces (Torsvik and Øvreås 2008). The major components of the soil water potential that control the availability of soil water are the matric potential and the osmotic potential (Vetterlein and Jahn 2004). As the matric potential and the osmotic potential decrease the free energy of water, the water potential tends to negative, and water becomes less available to organisms, thereby causing increased stress level of organisms as they require more energy to withdraw water in such condition. In most soils, this extreme soil water stress arises sporadically. Soil prokaryotes which exist in hydrological film or in saturated pores are considered to be very sensitive to water deficits, whereas soil fungi are considered to have more tolerant strength than prokaryotes with respect to water stress; soil fungi can equally thrive in drought owing to hyphal growth enabling them to cross dried pores and access water from minor pores over an extended period (Killham 1994).

Generally, for most bacteria, to sustain cell integrity when temperatures are not extreme (10–40 °C), water potential needs to be greater than -4 MPa or $0.95 a_w$ (MPa, mega Pascal; a_w , water activity) whereas $0.86 a_w$ or -22 MPa for most fungi and actinomycetes. -70 MPa ($0.60 a_w$) is generally suggested to be the lower water potential limit for life (Zvyagintsev et al. 2005); however, some recent studies observed that the spores of some actinomycetes can germinate and elongate at -96 MPa ($0.50 a_w$) (Zvyagintsev et al. 2005; Doroshenko et al. 2005). Lichen is a kind of organisms that have been identified to have the capacity of surviving on water vapour instead of liquid water (Torsvik and Øvreås 2008). In general, these microorganisms that can survive in highly arid environments (or in the condition of extremely little water content) are referred to as xerophiles; only specific genera of bacteria, algae, fungi, lichens and yeasts have been identified to possess the ability to thrive in such environmental conditions (Rothschild and Mancinelli 2001). Spoiling of dry foods including nuts, stored grains, oilseeds and spices is suggested to be an effect of xerophiles (Gupta et al. 2014). Microorganisms that fall into this category can survive optimally in such condition of water and salt stress due to their ability to counterweight a low water potential in the environment through the accumulation of highly soluble small molecules (osmolytes or compatible solutes) in the cytoplasm

(Kempf and Bremer 1998), and this solutes accumulation leads to a decrease in the internal water potential (Torsvik and Øvreås 2008).

14.3.2 Salinity

Some microorganisms have been identified to be able to grow optimally in various environments of different degree of salinity (often ranging from 0.5 to 5.2 M NaCl); these microorganisms are referred to as halophiles (Gupta et al. 2014) some of which can survive in salt crystals (DasSarma and Arora 2002). With respect to salinity, microbes are classified into non-halophiles (those that thrive in media with <0.2 M NaCl), slight halophiles (those that thrive in media with 0.2–0.5 M NaCl), moderate halophiles (those that thrive in media with 0.5–1.5 M NaCl) and extreme halophiles (those that thrive in media with 1.5–5.2 M NaCl) (Gupta et al. 2014; Kumar and Khare 2012). Halophiles are also found in all the three domains of life (Archaea, Bacteria and Eukarya) and their significance in the field of biotechnology, as potential sources of enzymes that are stable in salt and organic solvents have attracted the attention of researchers (Margesin and Schinner 2001; Karan and Khare 2010; Ventosa et al. 1998).

In the terrestrial environment, salinity is often attributed naturally to arid areas characterized by high evaporation rates; also, soil salinity may increase as a result of pollution originating from mining, chemical and metallurgical industrial sites (Torsvik and Øvreås 2008). Such soils of high alkalinity have characteristic uneven chronological and spatial distribution of water (Brown 1976). The fluctuations influence the survival and growth of microbes due to the associated osmotic stress. However, halophiles can survive such conditions by their adaptative mechanisms. Similar to xerophytes, halophytes accumulate osmolytes in their cytoplasm. Specifically, halophilic archaea are identified to store salts (NaCl and KCl) to the level of getting isotonic with the environ to sustain an osmotic balance; moreover, to survive in such high salt concentration, their enzymes are usually activated to gain a comparatively great number of anionic amino acid residues on their surfaces to avoid precipitation. The osmolytes in archaea are usually inorganic cations which they gain via passive diffusion or through selective ion transport across the membrane. In the case of halophilic bacteria, their intracellular salt level is relatively low, and they are highly capable of producing and accumulate organic osmolytes that are either zwitterions (such as glycine betaine, proline, ecotines, methylamines and hydroxyectoines) or non-ionic (such as carbohydrates, polyols, neutral peptides and amino acids) (Torsvik and Øvreås 2008; Gupta et al. 2014).

14.3.3 Temperature

The description of temperature limits as it relates to life in extreme environments often points at the water's freezing and boiling points although some microbes have been identified to thrive even beyond the normal freezing and boiling temperatures

of pure water and normal atmospheric pressure by using some special mechanisms (Torsvik and Øvreås 2008). Microorganisms that grow optimally in environments or media of high temperatures are known as thermophiles, whereas those that thrive in environments of low temperature close to the freezing temperature of pure water are referred to as psychrophiles or psychrotolerant microorganisms. Presently, it has been suggested that the temperature limits for microbial activities range between $-40\text{ }^{\circ}\text{C}$ and $+130\text{ }^{\circ}\text{C}$ (Price and Sowers 2004; Kashefi and Lovley 2003).

Thermophiles and hyperthermophiles have attracted the interest of researchers in recent times owing to their production of thermostable enzymes (Singh et al. 2011) which are of great importance in biotechnology and molecular biology (Sinha et al. 2012; Haki and Rakshit 2003; Roy et al. 2003; Van den Burg 2003; Bertoldo and Antranikian 2002). According to the temperature limits within which they have optimum growth, thermophiles can be classified into moderate thermophiles ($50\text{--}60\text{ }^{\circ}\text{C}$), extreme thermophiles ($60\text{--}80\text{ }^{\circ}\text{C}$) and hyperthermophiles ($80\text{--}110\text{ }^{\circ}\text{C}$) (Gupta et al. 2014). Studies have suggested that thermophiles (especially hyperthermophiles) isolated from different environments (such as hot springs, deep sea) of the Earth can grow optimally within a temperature range of $103\text{--}110\text{ }^{\circ}\text{C}$. The commonest in this category of thermophiles belong to the genera *Pyrobaculum*, *Pyrodictium*, *Pyrococcus* (e.g. hyperthermoanaerobic species known as *Pyrococcus furiosus*) (Lowe et al. 1993) and *Melanopyrus* for archaea, whereas the family *Ascomycete* and *Zygomycete* are for the fungi (Busk and Lange 2013) and the *Thermotoga maritima* and *Aquifex pyrophilus* for bacteria with their optimum growth temperatures as $90\text{ }^{\circ}\text{C}$ and $95\text{ }^{\circ}\text{C}$, respectively (Kumar et al. 2011; Haki and Rakshit 2003).

On the other hand, psychrophilic microbes grow in environmental temperature of as low as $15\text{ }^{\circ}\text{C}$ or below. Also, a similar subdivision known as psychrotolerants have been identified to grow at temperatures near freezing, but their optimum growth is recorded from $20\text{ }^{\circ}\text{C}$ and above (Gupta et al. 2014). Psychrophiles exist in various cold environments including the stratosphere and the deep sea (Rampelotto 2010).

The deep sea often maintains a constant temperature of $2\text{ }^{\circ}\text{C}$; however liquid seawater gets cooled even to the level below $0\text{ }^{\circ}\text{C}$ within the polar ice caps, as it is observed that the seawater salt level (usually 3.4%) decreases the freezing point to $-1.8\text{ }^{\circ}\text{C}$ (Atkins and Locke 2004). As the seawater freezes, small pockets of an increased salt content are formed, and the freezing point of the water gets decreased to about $-20\text{ }^{\circ}\text{C}$ in such conditions (Margesin et al. 2008). Natural microbial actions have been observed in such conditions, for instance, *Psychrobacter cryopegella* is able to grow in a cold environment with temperature as low as $-10\text{ }^{\circ}\text{C}$, as well as live and metabolize in environments of $-20\text{ }^{\circ}\text{C}$ temperature (Rodrigues et al. 2009). Owing to this fact, many psychrophiles are equally halophiles (Rampelotto 2010).

For psychrophiles to surpass some problems experienced in permanent cold environments, they develop some adaptative features. Such problems often experienced include enzymes becoming rigid, increase in solute concentration and toxicity (Cavicchioli 2006), as well as the likely piercing of the cell membranes and destruction of the wholeness of the cells by frozen/ice crystals (D'Amico et al. 2006). The special adaptive features of psychrophiles include possession of high

levels of unsaturated fatty acids which rise as the temperature reduces to ensure regulation of membrane fluidity (Nichols et al. 2004), production of enzymes that are effective and can enhance transcription and translation at such low temperatures (Feller and Gerday 2003) and possession of antifreeze proteins that can bind to the ice crystals by large complementary surface, thereby preventing the crystals from penetrating and damaging the cell membrane (Gilbert et al. 2004).

14.3.4 pH

pH is an important factor considered in every living environment due to its connective significance with respect to the relationship between the environment and its biotic components. Considering the pH scale, extremophiles can be grouped into two, namely, acidophiles and alkaliphiles. These will be discussed as follows.

Morozkina et al. (2010) described acidophiles as those microbes that exhibit favourable growth at pH level of 2.0. Interestingly, acidic environment (low pH) has been suggested to result from metabolic activities of microorganisms unlike other environmental factors that are commonly imposed by the system (Rampelotto 2010). Generally, prokaryotes can survive in environments where the pH ranges from 0 to 13 (Marion et al. 2003); however more prokaryotes have been recorded to grow at pH within the neutral scale. Furthermore, it is suggested that the general survival mechanism used by microbes to survive in extreme pH conditions is their ability to regulate their intracellular pH as well as sustaining it within neutral (Torsvik and Øvreås 2008). To generate energy, acidophiles oxidize the elemental sulphur in volcanic environments and sulphitic minerals in mining environments, which produces extreme acidic environments (Rohwerder and Sand 2007). Some acidophiles classified as thermoacidophiles (because they were identified in hot acidic environments) have been isolated from volcanic areas and acid mine drainages. For instance, thermoacidophilic archaea *Picrophilus torridus* and *P. oshimae* were initially isolated from dry, volcanic Japanese soils, and they exhibited the best growth level at very acidic pH (0.7) and temperature 60 °C (Schleper et al. 1995). Unlike most other acidophiles that keep their pH at 6.0, the *P. torridus* maintains low intracellular pH of 4.6 and cannot grow in pH greater than 4.0. An acidophile, *Ferroplasma acidarmanus* which was isolated from acid mine drainage in Iron Mountain, California, has been identified to grow at a pH of 0 (Dopson et al. 2004).

Environments of high acidity are associated with the problem of denaturing proteins of organisms, and to prevent the denaturation of their proteins, acidophiles and acid-tolerant microbes develop another adaptive feature which helps them to prevent such adverse effect. This feature is their ability to create acidophilic lipids with cyclic rings and alkyl side chains in their fatty acids, as well as their active pumping of protons out of their cells to keep their intracellular pH level fixed (Baker-Austin and Dopson 2007). It has also been noted that the adaptation of some acidophiles such as *Ferroplasma* and *Picrophilus* is improved by the unusual tetraether lipids in the cell membrane, while *Acidithiobacillus* adapts equally well

to lipopolysaccharides with a low fatty acid content. Protons cannot permeate the membrane of acidophilic archaea because of its tetraether lipids, and it has a proton pump that pulls protons out of the cytoplasm (Torsvik and Øvreås 2008).

On the other hand, microorganisms that show optimum growth between pH range of 9 and 11 and little or no growth at pH values close to neutral are referred to as alkaliphiles (Horikoshi 1999). Alkaline environments are often found in places characterized by a high quantity of Ca^{2+} resulting from the hydrothermal transformation of silicate minerals; some examples of such areas include the hyperalkaline spring waters in Jordan and the soda lakes; others include the high desert in the west of the United States, the East African Rift Valley and the plateaus of Mongolia, Inner Mongolia and Qinghai-Tibet (Zhang et al. 2007; Grant 2003). Most alkaliphiles are commonly found in areas with high salt (NaCl) content and therefore referred to as haloalkaliphiles (Gareeb and Setati 2009).

Generally, alkaline conditions are characterized by low hydrogen ion (H^+) concentrations which pose some challenges to cells in using ATP synthase to generate energy and vital ions like M^{2+} and Ca^{2+} which usually precipitate as salts, thereby being available in very small amounts (Krulwich et al. 1998). Krulwich et al. (1998) further stated that the cytoplasmic pH is commonly not less than two units below than the outward pH, and this is an indication that the cell membrane plays an important role in blocking OH^- ion fluxes, and there is also an effective inward proton translocation system (e.g. Na^+/H^+ or K^+/H^+ antiporters, proton-transferring ATP synthase). Horikoshi (2006) also suggested that the cell wall of alkaliphiles serves as a resistant wall against probable interfering environmental factors.

14.3.5 Radiation

Radiation has been identified as one of the significant factors affecting the microbial way of life. High dosage of ionizing and ultraviolet (UV) radiations has been suggested to be deadly to most microorganisms, while some microbes have been known to be tolerant to extreme doses of radiation. Shukla et al. (2007) suggested that there are several connections between radiation tolerance, desiccation tolerance and exposure to DNA damaging chemicals. A typical example of such microbes is *Deinococcus radiodurans* which researchers have affirmed to be the most radiation-resistant ever known and it can live within doses as high as 1000 Jm^{-2} UV light and more than 20 kGy of gamma (γ) radiation (note: Gy means grey, and $1 \text{ Gy} = 100 \text{ Rad}$), which is about 4000 times the dose that is capable of killing humans (Rainey et al. 2005; Marion et al. 2003). *Deinococcus radiodurans* is a red spherical bacterium that was found in 1957, in a piece of spoiled ground meat, despite being radioactively sterilized. Besides adaptation to very high radiation dosages, this bacterium is equally uniquely adapted to extreme conditions including drought and deficiency of nutrients (Battista 1997). It has been found in many areas including various soil environments and in granite in Antarctic dry valleys.

Also, by close observation, it is suggested that the DNA damage offered by desiccation and DNA damage by radiation are alike; for instance, high dosages of radiation or desiccation cause double-strand breaks in DNA (Torsvik and Øvreås 2008). However, the high resistance conferred on *Deinococcus radiodurans* is as a result of its possession of an effective system for DNA repair as well as its possession of four to ten copies of its chromosomes (Battista 1997) and the capacity to repair the fragments by recombination within chromosomes that reconstitutes an unbroken chromosome within a short time (usually in few hours) (Sale 2007). Certain organisms (e.g. prokaryotes and algae) that live on surfaces of barren polar soils have some adaptations that help them to avoid or abate UV damage. This protection against extreme light radiation and oxidative injury is aided by substances like pigments and amino acids (e.g. scytomin, melanoid, mycosporine-like amino acids, carotenoids) (Wright et al. 2005; Bowker et al. 2002).

14.3.6 Low Nutrients

Extreme environs are often known for having nutrient deficiency due to the various prevalent physical and chemical conditions that exist therein. For example, environments like deserts and permafrost soils commonly show a very low level of organic and inorganic nutrients. This condition leads to the identification of some microorganisms called oligotrophs that are known for their ability to survive in conditions of low or poor nutrient supply. Some oligotrophic prokaryotes are found in bogs and high organic matter containing soils, although the organic matters in such soils are mainly humus that is usually resistant to decomposition (Koch 2001; Fierer et al. 2007). Among bacteria, those in the phylum Acidobacteria are known to be oligotrophic, and they are greatly seen in soils with low nutrient availability while they diminish in abundance when amended by readily available carbon (Fierer et al. 2007). For prokaryotes, those of the K-selected category are usually considered as oligotrophs, and they have slow growth rates and are able to capture organic substrates at low saturation constants (to the levels of nM); this adaptive feature often makes them unable to grow in environments where nutrients are richly available (Bernard et al. 2007). Furthermore, another interesting adaptive feature of oligotrophs is their ability to utilize various substrates concurrently (Eichorst et al. 2007).

14.3.7 Pollution

Environmental pollution is a great factor when considering various anthropogenic activities and their associated health risks to both humans and non-humans including the microbial communities. Ajibade et al. (2021a) defined environmental pollution as the contamination of the various aspects of the environment that make up our natural resources such as soil, water, air, forests, etc. This implies that the

environment refers to all things surrounding humans, including pollution that may harm them and other organisms that live there.

Deposition of acid affects soil microbes and their activities. This deposition is usually caused by acid rain resulted from such compounds as nitrogen oxide (NO_x) and sulphur dioxide (SO_2) that are released to the atmosphere and in turn are oxidized to SO_4^{2-} and NO_3^- (Ugya et al. 2018). Also, nitrogen and sulphur present in acid may enhance the growth of some soil microbes; however, low-level lengthened acid rain leads to soil acidification which equally has adverse effects on soil bacteria; the effects on fungi have been suggested to be minor (Bååth and Anderson 2003).

Acid deposition has been noted to have some direct and indirect effects. For instance, increased acidity level and decreased concentrations of divalent cations (Ca^{2+} , Mg^{2+}) lead to mobility and heightened bioavailability of heavy metals and other toxins (Francis 1986). Soil acidification has also been identified to decrease the organic matter solubility, hence reduces substrates that would have been available for microorganisms (Torsvik and Øvreås 2008).

In general, various pollutants or contaminants that pollute the environment have various levels and kinds of adverse effects on the microbial community (Ajibade et al. 2021b, c). Commonly mentioned contaminants in this respect include heavy metals (from mines, rock weathering, sewage sludge and metal smelters), hydrocarbons (mainly from anthropogenic activities) and agrochemicals such as pesticides which are made specifically for some target pests, but in some cases, however, they become toxic to other organisms when modified by the environment. Table 14.1 summarizes the various features of extremophiles including the environmental conditions they can be found, their adaptations, variety of extremozymes and their applications in various fields such as medicine, food, pharmaceuticals, environmental remediation and pollution control, biotechnology, etc.

14.4 Soil as Habitat for Microbes

Soil can be seen as a product of the interactions among various physical, chemical and biological processes involving climatic factors (such as temperature and moisture), parent materials, time, topography and organisms. Soils are suggested to be among the habitats that support the largest number of various microorganisms (Ajibade et al. 2021d); soil habitats are differentiated from aquatic habitats by their high complexity and spatial heterogeneity (Torsvik and Øvreås 2008). Soil has a feature such as the various steep physicochemical gradients (e.g. pH, redox potential, substrate concentrations and available water) which may possibly present within short distances of a size approaching that of a soil aggregate. This is evident as even a few millimetres of aggregate can produce a wide variety of microenvironments that would attract and support various kinds of microbial communities and activities (Standing and Killham 2006).

Table 14.1 Summary of extremophiles, their associated extremozymes and their applications

Extremophiles and examples	Classes and example(s)		Condition of environment	Defining parameter of the habitat	Adaptive mechanisms	Associated extremozymes	Extremozymes applications
	Classes	Example(s)					
Thermophile	Psychrophile	<i>Psychrobacter</i>	Low temperature	Growth $\leq 0-20^{\circ}\text{C}$ $T_{\text{opt.}} < 20^{\circ}\text{C}$	Ability to produce unsaturated fatty acids that counter reduced membrane fluidity; cell size reduction	Proteases Dehydrogenases	Cheese maturation, dairy production, detergents; biotransformations, biosensors
						Amylases	Detergents
						Cellulases	Detergents, feed, textiles
						Lipases	Detergents, food, cosmetics
	Psychrotroph			Growth $\leq 5-30^{\circ}\text{C}$ $T_{\text{opt.}} > 20^{\circ}\text{C}$	Ability to increase some fraction of ordered cellular water.	Alkaline phosphatase β -galactosidase Methanogens	Molecular biology Lactose hydrolysis Methane production
	Moderate thermophile	<i>Picrophilus</i> sp.	High temperature	Growth $50-60^{\circ}\text{C}$	They can produce heat-stable biomolecules (proteins, nucleic acids, lipids); ability to produce long-chained, saturated, branched fatty acids and cyclic lipids	Amylases Xylanases Proteases	Glucose, fructose for sweeteners Paper bleaching Baking, brewing, hydrolysis in food and feed
	Thermophile	<i>Thermobaculum terrenum</i>		Growth $60-80^{\circ}\text{C}$		Lipases, esterases	Hydrolysis in food and feed
	Hyperthermophile	<i>Pyrolobus fumarii</i>		Growth $> 80^{\circ}\text{C}$		Alkaline phosphatase Glycosyl hydrolases	Detergents, stereo-specific reactions Dairy products, diagnostics starch, cellulose, chitin,

Acidophile	Acidophile	<i>Acidithiobacillus</i> ; <i>Picrophilus</i> sp.; <i>Ferroplasma</i> sp.	Low pH	$\text{pH} \leq 2-3$	Ability to perform proton exclusion and initiate effective outflow system; production of the acid-stable membrane and proton-driven secondary transporters	pectin processing, textiles; hydrolysis of starch, cellulose and related poly- and oligosaccharides Dehydrogenases DNA polymerases Amylases, glucoamylases Proteases, cellulases Sulphur oxidation Chalcopryrite concentrate	Genetic engineering Starch processing Feed component Desulphurization of coal Valuable metals recovery
Alkaliphile	Alkaliphile	<i>Natronobacterium</i> ; <i>Bacillus firmus</i> OF4	High pH	$\text{pH} \geq 9$	Possesses impermeable membrane for OH ions; exhibits effective proton uptake membrane-mediated antiporters; the presence of negatively charged cell wall polymers	Cellulases, proteases Proteases Elastases, keratinases Cyclodextrins Xylanases Pectinases	Polymer degradation in detergents, food and feed Food and feed Gelatin removal on X-ray film Hide dehairing Foodstuffs, chemicals and pharmaceuticals Pulp bleaching, fine papers and degumming

(continued)

Table 14.1 (continued)

Extremophiles and examples	Classes and example(s)		Condition of environment	Defining parameter of the habitat	Adaptive mechanisms	Associated extremozymes	Extremozymes applications
	Classes	Example(s)					
Halophile	Halophile/halotolerant	Osmophile <i>Haloarcula japonica</i> ; Cyanobacteria	High salinity	2–5 M NaCl; water potential –1.5 to –40 Mpa	Accumulation of osmolytes; salt-resistant (and salt-dependent) extremozymes	Proteases Dehydrogenases Bacteriorhodopsin Polyhydroxyalkanoates Rheological polymers Compatible solutes	Peptide synthesis Biocatalysis in organic media Optical switches Medical plastics Oil recovery Protein and cell protectants in a various industrial purpose, e.g. freezing, heating
Radiophile	High radiation resistant/tolerant	<i>Deinococcus radiodurans</i> ; <i>Rubrobacter</i> sp.	High radiation	High ionizing radiation levels	Possession of strong pigmentation (melanoids, carotenoids, etc.); exhibits effective DNA repair mechanisms	Whole microorganism	Hypersaline waste conversion and degradation; ion exchange resin regenerant disposal, producing poly (β-glutamic acid; PGA) and poly (β-hydroxy butyric acid; PHB) Bioremediation of radionuclide polluted sites

Metallophile	Metallo-resistant/ tolerant	<i>Ferroplasma acidarmanus</i>	Heavy metals	High metal concentrations	Possession of effluence pump; able to sequester and/or detoxify metals (by reduction, alkylation)	Whole microorganism	Ore bioleaching, bioremediation, biomineralization
Xerophile	Xerophile/xero- tolerant	<i>Trichosporonoides nigrescens</i> ; <i>Actinobacteria</i> such as group 1 Rubrobacteria and members of Actinomycetales, cyanobacteria, fungi	Desiccation	Water potential MPa: -4 to -10 (bacteria), -10 to -70 (actinomycetes and fungi)	Accumulates inorganic or organic osmolytes; produces extracellular polysaccharides; exhibits cell differentiation to form desiccation resistant cells (spores)		
Toxibiotolerant/ xenobiotic decomposers		<i>Ralstonia</i> sp.; <i>Pseudomonasputida</i>	Toxins and xenobiotics	High concentrations of toxic compounds including toxic reagents/ organic solvents	Possession of effectual effluence pump; ability to detoxify and decompose toxins and xenobiotics	Proteases, lipases Cyclodextrin glucanotransferase Whole microorganism	Peptide synthesis, enzymatic catalysis in nonaqueous solvents Esterification/ transesterification Synthesis of non-reducing cyclodextrins from starch, utilized in food, pharmaceutical and chemical industries Solvent bioremediation and biotransformation

(continued)

Table 14.1 (continued)

Extremophiles and examples	Classes and example(s)		Condition of environment	Defining parameter of the habitat	Adaptive mechanisms	Associated extremozymes	Extremozymes applications
	Classes	Example(s)					
Microaerophile	Aerotolerant	<i>Borrelia burgdorferi</i>	Low oxygen	Growth in <21% O ₂	Ability to metabolize energy anaerobically	Catalase, superoxide dismutase	Produce toxic substances such as superoxide free radicals and peroxides
Piezophile	Piezophile	<i>Pyrococcus</i> sp.	High pressure	Around 130 Mpa	Possesses a hydrophobic core with the preference for smaller amino acids	Whole microorganism	Formation of gels and starch granules; food processing and antibiotic production

14.4.1 Extreme Soils

Soil microbiology deals with the study of life, activities and adaptation of microorganisms in the soil, so also extreme soil microbiology deals with the adaptation of microorganisms in an extreme or stressful soil environment. Geological properties, biota and climatic factors are the significant determinants of soil properties, and these are influenced by various human activities in the environment. Concerning the controlling factors, Odum (1971) classified soils into two, namely, based on climate and vegetation types and based on ecological or geological or pedological factors such as drainage, pollution, topography, etc. Slight differences in edaphic factors (especially in areas with extreme climatic conditions) may significantly alter the activities and structure of soil microbiota. For instance, soil water and soil temperature stresses are periodic in most areas of temperate climate, and so does nutrient stress exist periodically in many soils. These periodic occurrences affect the activities of soil microbiota; hence their adaptations to such conditions become predominant.

Tundra soil and desert soil are two types of extreme soils that significantly exist on Earth. These biomes are characterized by sparse and low vegetation as well as the absence of trees.

14.4.1.1 Desert Soils

Deserts exist in areas of annual rainfall less than 250 mm (Odum 1971). Water has been identified as the most limiting factor in tellurian ecosystems. About 30% of Earth's tellurian areas are arid which is characterized by either exceedingly hot or cold (Rainey et al. 2005). Spatial patterns and heterogeneity are peculiar features of dry soil ecosystems. Similarly, spatial variability is highly determined by vegetation in temperate deserts, while in polar deserts, which lack vascular plants, physical processes control the spatial variation in soil properties. An example is the formation of frost fissure patterns. Antarctica (Ross Desert, Dry Valleys), Atacama Desert in northern Chile and central Sahara where almost no rainfall is experienced are the most extreme deserts. The low precipitation is a result of high subtropical atmospheric pressure (as in the Sahara), position in rain shadow areas (as in Chile), high altitude (e.g. Tibet and Gobi) or latitude (observed in the Antarctic Dry Valley) (Torsvik and Øvreås 2008).

Due to the various diverse extremities associated with desert areas, arguments were raised on whether organisms exist and grow in such environments. However, microbes have been isolated from even identified most extreme desert conditions. In deserts, microorganisms commonly live in sandstone pores and/or sometimes try to form biological soil crust. It is also stated that within the highly intense cold deserts, favourable state for microbial metabolic processes probably occurs only 2–10 days yearly (Torsvik and Øvreås 2008). Due to the extreme conditions experienced by soil microbes in the desert areas (e.g. drying out in the most extreme dry habitats and freeze-drying in arctic deserts), microorganisms need a special strategy to adapt and survive such harshest conditions. Such strategy is their suspension of metabolic activities and keeping dormant during such conditions and resuming their

metabolism when the conditions get better; hence many of the desert extremophiles have resting stages or spores (Barak et al. 2005).

14.4.1.2 Tundra Soils

Microbial community has been suggested to exist in tundra soils (black mucky soils with a frozen subsoil that is characteristic of Arctic and subarctic regions), and they are considered as extreme environments. Climate is a great factor that significantly affects species diversity globally. In general, biodiversity decreases as latitudes and altitudes increase. For instance, eukaryotes exhibit this trend in polar regions both in terms of species number and forms of growth. Nevertheless, on smaller spatial scales, biodiversity in the arctic tundra may be almost the same as that in temperate soils (Torsvik and Øvreås 2008). About 26% of the terrestrial soil ecosystems are considered to be permafrost which extends hundreds to thousands of metres down into the subsurface (Steven et al. 2006). The permafrost is referred to as an extreme environment owing to its nature which subjects indigenous microbes to subzero temperatures and background radiation over a long period of time. In extreme tundra, temperatures are usually low and the growing season lasts for less than 2 months.

14.5 Significance of Studying Extremophiles

Studying the existence, nature and activities of extremophiles in the environment paves way for understanding their diverse physicochemical properties. This helps in the development of model systems that could serve as a basis for discovering the interlinking factors governing diversity, microbial activities and climatic conditions (Smith et al. 2006). Also, the knowledge of the microbial components and activities in the environment can be applied in environmental cleanup, pollution control and energy production for the promotion of environmental health and sustainability. For instance, *Vibrio harveyi*, a marine microbe has been reported to have the capacity of bioaccumulating up to 23.3 mg of cadmium, Cd²⁺/g of dry cells (Abd-Elnaby et al. 2011).

In biotechnology particularly, the study of extremophiles provides insights into their acclimatization mechanisms and the possibility of using them for enzymes and other compounds which can function under certain intense physical and chemical conditions. For instance, extreme prokaryotes that have a good number of bioactive compounds which are useful in medicine, food, pharmaceutical and environmental industries can be resourceful in bioprospecting (Torsvik and Øvreås 2008).

The study of extremophiles gives a tentative comparative knowledge of existence and conditions in other planets and moons; hence, careful examination of some conditions or environments considered extreme on Earth can offer us some hints of probable life that exists on other planets. The study of extremophiles is very relevant in astrobiology as it explores nature, signs and conditions defining extraterrestrial life both at molecular and physiological levels. For instance, the discovery of some microorganisms in the ice cores reclaimed from the depth of Lake Vostok and other

perennial subglacial lakes from Antarctica may be used as a model for the search and study of life in Jupiter's moon Europa (Rampelotto 2013).

14.6 Adaptation

Microorganisms are well known for their ability to adapt to a variety of environmental conditions including the ones considered to be harsh or extreme. They adapt to diverse environmental conditions by using different mechanisms or combination of them (van der Meer 2006). The earlier section of this chapter discussed various extremophilic conditions and some extremophiles common therein. For example, halophilic microbes (bacteria and archaea) adapt to a high salt-concentrated environment of about ten times greater than that of seawater, while acidophiles can survive and thrive at a pH of 1, whereas thermophiles survive and thrive in environmental temperature of 85 °C and above. In particular, bacteria can detect any temporary or permanent alteration of various environmental factors such as pH, temperature, ionic strength, pressure, concentrations of solutes and availability of water and upon that sensing adjust, respond and adapt to such environmental condition by protecting their biological molecules and altering biochemical reactions (Heulin et al. 2012).

For the existence of cellular life in extreme conditions of temperature, pressure or salinity, maintenance of stable and functional biological membranes remains the first condition; membranes are vital during energy production and compartmentalization of biochemical activities (Franzetti 2019). Heulin et al. (2012) further stated that four major adaptation strategies including compensation, conservation, protection and damage repair are used by microbes depending on whether the extreme environmental condition is permanent or ephemeral. Compensatory responses tend to re-establish equilibrium and maintain normal functions and are often used when the condition is ephemeral; however, they sometimes apply it to adapt to some long-term conditions, for instance, the regulation of efflux pumps to squeeze out metals when there is an upsurge in heavy metal concentration. For long-term adaptation, *Helicobacter pylori*, an extremely acid-tolerant microorganism in the human stomach, give a compensatory response by its ability to produce urease in a large amount (Mobley et al. 1995). Bacteria also adopt 'nongrowth' state as a response to stress in some cases. Conservative response is often used by spore-forming bacteria when they face strong or continued stress, and they apply this by entering a nondividing state and moving into a dormancy state as a spore form. The conservative response maintains a viable reversible state of reduced elemental metabolic rate in a unit (Barer 2003). The protective response is often used when the physical integrity of an organism is threatened. For instance, desiccation possibly causes water loss leading to cell-volume collapse and impairment of cellular macromolecules like nucleic acids and proteins which in most cases prompt bacterial cells to accumulate solutes like amino acids, quaternary amines, carbohydrates and tetrahydropyrimidines (Takagi 2008). For damage repair, some microorganisms such as members of Deinococcaceae have been suggested to be highly resistant to deadly effect of

DNA-damaging agents (e.g. desiccation, gamma radiation) and to be efficient in repairing hundreds of DNA double- and single-strand breaks and other types of DNA impairments (Heulin et al. 2012).

14.7 Conclusion

Environment is a great factor both as an aspect of the ecosystem and as an object of academic research. The diverse nature of the environments and the fluctuating environmental components pose several living conditions to the microorganisms therein. Such conditions which are often extreme subject microorganisms in such areas to modification and development of some adaptation mechanisms that enable them survive and thrive. This chapter has discussed extreme environment starting from the concept of environmental change which is a result of some natural processes and anthropogenic activities. Some important physicochemical factors (pH, temperature, water, radiation, salinity, low nutrients and pollution) affecting microbial life and some extremophiles found in these environmental conditions, their adaptations, associated extremozymes and applications were discussed. Soil as a habitat supporting a large number of microbial communities and the various types of soil considered to possess extreme ecological conditions were discussed. The significance of the study of extreme environment, extremophiles and extremozymes in various fields of life including research, biotechnology and food science and technology, astrobiology, microbiology, protein engineering, agriculture, medicine, pharmaceuticals and other industries were discussed.

References

- Abd-Elnaby H, Abou-Elela GM, El-Sersy NA (2011) Cadmium resisting bacteria in Alexandria Eastern Harbor (Egypt) and optimization of cadmium bioaccumulation by *Vibrio harveyi*. *Afr J Biotechnol* 10:3412–3423
- Ajibade FO, Adelodun B, Lasisi KH, Fadare OO, Ajibade TF, Nwogwu NA, Sulaymon ID, Ugya AY, Wang HC, Wang A (2021a) Environmental pollution and their socioeconomic impacts. In: Kumar A, Singh VK, Singh P, Mishra VK (eds) *Microbe mediated remediation of environmental contaminants*. Woodhead Publishing, Elsevier. <https://doi.org/10.1016/B978-0-12-821199-1.00025-0>
- Ajibade FO, Wang H, Guadie AA, Ajibade TF, Fang Y, Sharif HMA, Liu W, Wang A (2021b) Total nitrogen removal in biochar amended non-aerated vertical flow constructed wetlands for secondary wastewater effluent with low C/N ratio: Microbial community structure and dissolved organic carbon release conditions. *Bioresour Technol*:124430. <https://doi.org/10.1016/j.biortech.2020.124430>
- Ajibade FO, Nwogwu NA, Lasisi KH, Ajibade TF, Adelodun B, Guadie A, Ugya AY, Adewumi JR, Wang HC, Wang A (2021c) Removal of nitrogen oxyanion (nitrate) in constructed wetlands. In: Oladoja NA, Unuabonah IE (eds) *Progress and prospects in the management of oxoanion polluted aqua systems*. Springer Nature, The Netherlands. https://doi.org/10.1007/978-3-030-70757-6_12

- Ajibade FO, Adelodun B, Ajibade TF, Lasisi KH, Abiola C, Adewumi JR, Akinbile CO (2021d) The threatening effects of open dumping on soil at waste disposal sites of Akure city, Nigeria. *Int J Environ Waste Manag* 27(2):127–146. <https://doi.org/10.1504/IJEW.2021.10030610>
- Allen EE, Banfield JF (2005) Community genomics in microbial ecology and evolution. *Nat Rev Microbiol* 3:489–498
- Atkins PW, Locke JW (2004) Physical chemistry, 7th edn. Oxford University Press, Oxford, UK
- Bååth E, Anderson TH (2003) Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques. *Soil Biol Biochem* 35:955–963
- Baker-Austin C, Dopson M (2007) Life in acid: pH homeostasis in acidophiles. *Trends Microbiol* 15:165–171
- Barak I, Ricca E, Cutting SM (2005) From fundamental studies of sporulation to applied spore research. *Mol Microbiol* 55:330–338
- Barer MR (2003) Physiological and molecular aspects of growth, non-growth, culturability and viability in bacteria. In: Coates AM (ed) Dormancy and low-growth states in microbial disease. Cambridge University Press, Cambridge, pp 1–35
- Battista JR (1997) Against all odds: the survival strategies of *Deinococcus radiodurans*. *Ann Rev Microbiol* 51:203–224
- Bernard L, Mougel C, Maron PA, Nowak V, Leveque J, Henault C et al (2007) Dynamics and identification of soil microbial populations actively assimilating carbon from ^{13}C -labelled wheat residue as estimated by DNA- and RNA-SIP techniques. *Environ Microbiol* 9:752–764
- Bertoldo C, Antranikian G (2002) Starch-hydrolyzing enzymes from thermophilic archaea and bacteria. *Curr Opin Chem Biol* 6:151–160
- Bowker MA, Reed SC, Belnap J, Phillips SL (2002) Temporal variation in community composition, pigmentation, and fv/fm of desert Cyanobacterial soil crusts. *Microb Ecol* 43:13–25
- Brown AD (1976) Microbial water stress. *Bacteriol Rev* 40:803–846
- Busk PK, Lange L (2013) Cellulolytic potential of thermophilic species from four fungal orders. *AMB Express* 3:47–56
- Cavicchioli R (2006) Cold-adapted archaea. *Nat Rev Microbiol* 4:331–343
- Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K (2011) Effects of abiotic stress on plants: a systems biology perspective. *BMC Plant Biol* 11:163
- D'Amico S, Collins T, Marx JC, Feller G, Gerday C (2006) Psychrophilic microorganisms: challenges for life. *EMBO J* 7:385–389
- DasSarma S, Arora P (2002) Halophiles, encyclopedia of life sciences. Nature Publishing Group, London, UK
- David LA, Materna AC, Friedman J, Campos-Baptista MI, Blackburn MC, Perrotta A et al (2014a) Host lifestyle affects human microbiota on daily timescales. *Genome Biol* 15(7):R89. <https://doi.org/10.1186/gb-2014-15-7-r89>
- David LA, Maurice CF, Carmody RN, Gootenberg DB, Button JE, Wolfe BE et al (2014b) Diet rapidly and reproducibly alters the human gut microbiome. *Nature* 505(7484):559–563. <https://doi.org/10.1038/nature12820>
- Denef VJ, Mueller RS, Banfield JF (2010) AMD biofilms: using model communities to study microbial evolution and ecological complexity in nature. *ISME J* 4:599–610
- Dhar R (2013) The genetic basis of microbial adaptations to new environments in laboratory evolution. University of Zurich, Faculty of Science, Zürich
- Dopson M, Baker-Austin C, Hind A, Bowman JP, Bond PL (2004) Characterization of *Ferroplasma* isolates and *Ferroplasma acidarmanus* sp. nov., extreme acidophiles from acid mine drainage and industrial bioleaching environments. *Appl Environ Microbiol* 70:2079–2088
- Doroshenko EA, Zenova GM, Zvyagintsev DG, Sudnitsyn I (2005) Spore germination and mycelial growth of streptomycetes at different humidity levels. *Microbiol* 74:690–694
- Eichorst SA, Breznak JA, Schmidt TM (2007) Isolation and characterization of bacteria from soil that define *Terriglobus* gen. nov., in the phylum Acidobacteria. *Appl Environ Microbiol* 73:2708–2717

- Feller G, Gerday C (2003) Psychrophilic enzymes: hot topics in cold adaptation. *Nat Rev Microbiol* 1:200–208
- Fierer N, Bradford M, Jackson R (2007) Towards an ecological classification of soil bacteria. *Ecology* 88:1354–1364
- Francis AJ (1986) Acid rain effects on soil and aquatic microbial processes. *Cell Mol Life Sci (CMLS)* 42:455–465
- Franzetti B (2019) Microbes in extreme environments. *Encyclopédie de l'Environ.* <http://www.encyclopedie-environnement.org/?p=6888>
- Fulda S, Gorman AM, Hori O, Samali A (2010) Cellular stress responses: cell survival and cell death. *Int J Cell Biol* 2010:214074
- Gao H, Weitao T, He Q (2011) Coping with the environment: how microbes survive environmental challenges. *Int J Microbiol*:379519. <https://doi.org/10.1155/2011/379519>
- Garcia-Moreno B (2009) Adaptations of proteins to cellular and subcellular pH. *J Biol* 8:98
- Gareeb AP, Setati ME (2009) Assessment of alkaliphilic haloarchaeal diversity in Sua pan evaporator ponds in Botswana. *Afr J Biotechnol* 8:259–267
- Ghai R, Pašić L, Fernández AB, Martín-Cuadrado AB, Mizuno CM, McMahon KD et al (2011) New abundant microbial groups in aquatic hypersaline environments. *Sci Rep* 1:135. <https://doi.org/10.1038/srep00135>
- Gilbert JA, Hill PJ, Dodd CE, Laybourn-Parry J (2004) Demonstration of antifreeze protein activity in Antarctic lake bacteria. *Microbiology* 150:171–180
- Gorbushina AA, Krumbein WE (1999) The poikilotrophic micro-organism and its environment. In: Seckbach J (ed) *Enigmatic microorganisms and life in extreme environments*. Kluwer Academic, Dordrecht, pp 177–185
- Grant WD (2003) Alkaline environments and biodiversity. In: Gerdsy C, Glansdorff N (eds) *Extremophiles: basic concepts*. Paris, France, Encyclopedia of Life Support Systems
- Greaves RB, Warwicker J (2007) Mechanisms for stabilisation and the maintenance of solubility in proteins from thermophiles. *BMC Struct Biol* 7:18
- Gupta GN, Srivastava S, Khare SK, Prakash V (2014) Extremophiles: an overview of microorganism from extreme environment. *IJAEB* 7(2):371–380. <https://doi.org/10.5958/2230-732X.2014.00258.7>
- Haki DJ, Rakshit SK (2003) Developments in industrially important thermostable enzymes: a review. *Bioresour Technol* 89:17–34
- Heulin T, De Luca G, Barakat M, Gommeaux M, de Groot A, Blanchard L et al (2012) Bacterial adaptation to hot and dry deserts. In: Stan-Lotter H, Fendrihan S (eds) *Adaption of microbial life to environmental extremes*. Springer-Verlag/Wien, Cham, Switzerland, pp 69–85
- Horikoshi K (1999) Alkaliphiles: some applications of their products for biotechnology. *Microbiol Mol Biol Rev* 63:735–750
- Horikoshi K (2006) *Alkaliphiles: genetic properties and applications of enzymes*. Springer, Berlin
- Karan R, Khare SK (2010) Purification and characterization of a solvent stable protease from *Geomicrobium* sp. EMB2. *Environ Technol* 31:1061–1072
- Kashefi K, Lovley DR (2003) Extending the upper temperature limit for life. *Science* 301:934
- Katz Y, Springer M (2016) Probabilistic adaptation in changing microbial environments. *PeerJ* 4:e2716. <https://doi.org/10.7717/peerj.2716>
- Kempf B, Bremer E (1998) Uptake and synthesis of compatible solutes as microbial stress responses to high-osmolality environments. *Arch Microbiol* 170:319–330
- Killham K (1994) *Soil ecology*. Cambridge University Press, Cambridge
- Koch AL (2001) Oligotrophs versus copiotrophs. *Bio Essays* 23:657–661
- Krulwich TA, Ito M, Hicks DB, Gilmour R, Guffanti AA (1998) pH homeostasis and ATP synthesis: studies of two processes that necessitate inward proton translocation in extremely alkaliphilic *Bacillus* species. *Extremophiles* 2:217–222
- Kuang JL, Huang LN, Chen LX, Hua ZS, Li SJ, Hu M et al (2012) Contemporary environmental variation determines microbial diversity patterns in acid mine drainage. *ISME J* 7:1038–1050. <https://doi.org/10.1038/ismej.2012.139>

- Kumar S, Khare SK (2012) Purification and characterization of maltooligosaccharide-forming α -amylase from moderately halophilic *Marinobacter* sp. EMB8. *Bioresourc Technol* 116:247–251. <https://doi.org/10.1016/j.biortech.2011.11.109>
- Kumar L, Awasthi G, Singh B (2011) Extremophiles: a novel source of industrially important enzymes. *Biotechnology* 10:121–135
- Li SJ, Hua ZS, Huang LN, Li J, Shi SH, Chen LX et al (2014) Microbial communities evolve faster in extreme environments. *Sci Rep* 4:6205. <https://doi.org/10.1038/srep06205>
- Lowe SE, Jain MK, Zeikus JG (1993) Biology, ecology, and biotechnological applications of anaerobic bacteria adapted to environmental stresses in temperature, pH, salinity, or substrates. *Microbiol Rev* 57(2):451–509
- Margesin R, Schinner R (2001) Potential of halotolerant and halophylic microorganisms for biotechnology. *Extremophiles* 5:73–83
- Margesin R, Schinner F, Marx JC, Gerday C (2008) Psychrophiles: from biodiversity to biotechnology. Springer, New York
- Marion GM, Fritsen CH, Eicken H, Payne MC (2003) The search for life on Europa: limiting environmental factors, potential habitats, and Earth analogues. *Astrobiology* 3:785–811
- Mobley HL, Island MD, Hausinger RP (1995) Molecular biology of microbial ureases. *Microbiol Rev* 59:451–480
- Morozkina EV, Slutskaya ES, Fedorova TV, Tugay TI, Golubeva LI, Koroleva OV (2010) Extremophilic microorganisms: biochemical adaptation and biotechnological application. *Appl Biochem Microbiol* 46:1–14
- Nichols D, Miller MR, Davies NW, Goodchild A, Raftery M, Cavicchioli R (2004) Cold adaptation in the Antarctic archaeon, *Methanococcoides burtonii*, involves membrane lipid unsaturation. *J Bacteriol* 186:8508–8515
- Odum EP (1971) Fundamentals of ecology, 3rd edn. W.B. Saunders, Philadelphia
- Ortega G, Laín A, Tadeo X, López-Méndez B, Castaño D, Millet O (2011) Halophilic enzyme activation induced by salts. *Sci Rep* 1:6
- Parfrey LW, Walters WA, Knight R (2011) Microbial eukaryotes in the human microbiome: ecology, evolution, and future directions. *Front Microbiol* 2:153. <https://doi.org/10.3389/fmicb.2011.00153>
- Price PB, Sowers T (2004) Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. *Proc Natl Acad Sci U S A* 101:4631–4636
- Rainey FA, Ray K, Ferreira M, Gatz BZ, Nobre MF, Bagaley D et al (2005) Extensive diversity of ionizing-radiation-resistant bacteria recovered from Sonoran Desert soil and description of nine new species of the genus *Deinococcus* obtained from a single soil sample. *Appl Environ Microbiol* 71:5225–5235
- Rampelotto PH (2010) Resistance of microorganisms to extreme environmental conditions and its contribution to astrobiology. *Sustainability* 2:1602–1623. <https://doi.org/10.3390/su2061602>
- Rampelotto PH (2013) Extremophiles and extreme environments. *Life* 3:482–485. <https://doi.org/10.3390/life3030482>
- Rodrigues DF, Jesus EC, Ayala-del-Río HL, Pellizari VH, Gilichinsky D, Sepulveda-Torres L, Tiedje JM (2009) Biogeography of two cold-adapted genera: psychrobacter and exiguobacterium. *ISME J* 3:658–665
- Rohwerder T, Sand W (2007) Oxidation of inorganic sulfur compounds in acidophilic prokary. *Eng Life Sci* 7:301–309
- Rothschild LJ, Mancinelli RL (2001) Life in extreme environments. *Nature* 409:1092–1101
- Roy I, Sardar M, Gupta MN (2003) Hydrolysis of chitin by PectinexTM. *Enzyme Microbial Technol* 32(5):582–588
- Sale JE (2007) Radiation resistance: resurrection by recombination. *Curr Biol* 17:R12–R14
- Schleper C, Puehler G, Holz I, Gambacorta A, Janekovic D, Santarius U et al (1995) *Picrophilus* gen. nov. fam. nov.: a novel aerobic, heterotrophic, thermoacidophilic genus and family comprising archaea capable of growth around pH 0. *J Bacteriol* 177:7050–7059
- Shukla M, Chaturvedi R, Tamhane D, Vyas P, Archana G, Apte S, Bandekar J, Desai A (2007) Multiple-stress tolerance of ionizing radiation-resistant bacterial isolates obtained from various habitats: correlation between stresses. *Curr Microbiol* 54:142–148

- Singh S, Shukla L, Khare SK, Nain L (2011) Detection and characterization of new thermostable endoglucanase from *Aspergillus awamori* strain F18. *J Mycol Plant Pathol* 41(1):97–103
- Sinha A, Pant KK, Khare SK (2012) Studies on mercury bioremediation by alginate immobilized mercury tolerant *Bacillus* sp. cells. *Int Biodeter Biodegrad* 71:1–8
- Skirycz A, Claeys H, De Bodt S, Oikawa A, Shinoda S, Andriankaja M et al (2011) Pause-and-stop: the effects of osmotic stress on cell proliferation during early leaf development in *Arabidopsis* and a role for ethylene signaling in cell cycle arrest. *Plant Cell* 23:1876–1888. <https://doi.org/10.1105/tpc.111.084160>
- Smith JJ, Tow LA, Stafford W, Cary C, Cowan DA (2006) Bacterial diversity in three different Antarctic cold desert mineral soils. *Microb Ecol* 51:413–421
- Standing D, Killham K (2006) The soil environment. In: van Elsas JD, Jansson JK, Trevors JT (eds) *Modern soil microbiology*, 2nd edn. CRC Press, Taylor and Francis, Boca Raton, FL, pp 1–22
- Steven B, Lévêillé R, Pollard WH, Whyte LG (2006) Microbial ecology and biodiversity in permafrost. *Extremophiles* 10:259–267
- Tadeo X, López-Méndez B, Trigueros T, Laín A, Castaño D, Millet O (2009) Structural basis for the amino acid composition of proteins from halophilic archaea. *PLoS Biol* 7:e1000257
- Takagi H (2008) Proline as a stress protectant in yeast: physiological functions, metabolic regulations, and biotechnological applications. *Appl Microbiol Biotechnol* 8:211–223
- Talley K, Alexov E (2010) On the pH-optimum of activity and stability of proteins. *Proteins* 78:2699–2706
- Thaïss CA, Zeevi D, Levy M, Zilberman-Schapira G, Suez J, Tengeler AC et al (2014) Transkingdom control of microbiota diurnal oscillations promotes metabolic homeostasis. *Cell* 159(3):514–529. <https://doi.org/10.1016/j.cell.2014.09.048>
- Torsvik V, Øvreås L (2008) Microbial diversity, life strategies, and adaptation to life in extreme soils. In: Dion P, Nautiyal CS (eds) *Microbiology of extreme soils*, *Soil biology*, vol 13. Springer-Verlag, Berlin, Heidelberg, pp 15–43
- Uguya AY, Ajibade FO, Ajibade TF (2018) Water pollution resulting from mining activity: an overview. *Proceedings of the 2018 Annual Conference of the School of Engineering & Engineering Technology (SEET), The Federal University of Technology, Akure, Nigeria*, 17–19 July, pp. 703–718
- Van den Burg B (2003) Extremophiles as a source for novel enzymes. *Curr Opin Microbiol* 6:213–218
- van der Meer JR (2006) Environmental pollution promotes selection of microbial degradation pathways. *Front Ecol Environ* 4(1):35–42. [https://doi.org/10.1890/1540-9295\(2006\)004\[0035:EPPSOM2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)004[0035:EPPSOM2.0.CO;2)
- Ventosa A, Nieto JJ, Oren A (1998) Biology of moderately halophilic bacteria. *Microbiol Mol Biol Rev* 62:504–544
- Vermeulen N, Keeler WJ, Nandakumar K, Leung KT (2008) The bactericidal effect of ultraviolet and visible light on *Escherichia coli*. *Biotechnol Bioeng* 99:550–556
- Vetterlein D, Jahn R (2004) Combination of micro suction cups and time-domain reflectometry to measure osmotic potential gradients between bulk soil and rhizosphere at high resolution in time and space. *Eur J Soil Sci* 55:497–504
- Walter J, Ley R (2011) The human gut microbiome: ecology and recent evolutionary changes. *Annu Rev Microbiol* 65:411–429. <https://doi.org/10.1146/annurev-micro-090110-102830>
- Wright DJ, Smith SC, Joardar V, Scherer S, Jervis J, Warren A et al (2005) UV irradiation and desiccation modulate the three-dimensional extracellular matrix of *Nostoc commune* (Cyanobacteria). *J Biol Chem* 280:40271–40281
- Zhang G, Ma X, Niu F, Dong M, Feng H, An L, Cheng G (2007) Diversity and distribution of alkaliphilic psychrotolerant bacteria in the Qinghai-Tibet Plateau permafrost region. *Extremophiles* 11:415–424
- Zvyagintsev DG, Zenova GM, Sudnizin I, Doroshenko EA (2005) The ability of soil Actinomycetes to develop at an extremely low humidity. *Doklady Biol Sci* 405:461–463