The Multifaceted Life of Microbes: Survival in Varied Environments

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Abstract

The world of microorganisms comprises a vast diversity of living organisms, each with its individual set of genes, cellular components, and metabolic reactions that interact within the cell and communicate with the environment in many different ways. Microbes perform several key ecosystem functions. They provide a number of ecological services like soil formation, nutrient cycling, plant growth, bioremediation, source for pharmaceuticals, etc. Earth may be a home for more than 10^{12} microbial species. These species are present in varied environments, many of which for other life forms are extremely hostile. Microbes have been found in varied environments ranging from the tropics to the Arctic and Antarctica, from underground mines and oil fields to the stratosphere and the top of great mountains, from deserts to the Dead Sea, from aboveground hot springs to underwater hydrothermal vents. They can survive at pressures up to 110 MPa, at extreme acid (pH 0) to extreme alkaline (pH 12.8) conditions, at temperatures as high as 122 °C to as low as −20 °C, in toxic wastes, in organic solvents, heavy metals, guts of insects, roots of plants, low oxygen conditions, etc. These microorganisms are classified according to their habitats such as thermophiles/hyperthermophiles, psychrophiles, acidophiles and alkaliphiles, barophiles, and halophiles. Studies on microbial life, their diversity, physiology, genetics, ecology, and biochemistry can reveal a lot in terms of the characteristics of biological processes, such as biochemical limits to macromolecular stability and genetic

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instructions for constructing macromolecules. These organisms have also provided a number of clues to the origin and evolution of life. Further, a study of microbes in conflict environments has become vital in the field of research in astrobiology, since the microbes found in extreme environments may be analogous to potential life forms in other planets. In the present times of climate change, the study of microbes living at the edge of life has become even more important.

Keywords
Extremophiles · Varied environment · Genes · Ecology

1.1 Introduction

During the history of earth's evolution, microbes have played a vital role in changing and maintaining the environments on earth. An environment that was initially anoxygenic was transformed and has been maintained till today in the present state by microorganisms. Since their evolution on earth at about 3–4 million years ago, microbes have occupied every nook and corner of the earth that one can think of. The earliest microorganisms were anaerobic heterotrophic, since the atmosphere was free of oxygen. The enormous microbial biodiversity that we find today is the result of a balance between evolution, extinction, and colonization. Microbial species have been found in varied environments, many of which for other life forms are extremely hostile or not "normal," with normal being those environments where temperature is between 4 and 40 °C, pH between 5 and 8.5, and salinity between that of freshwater and that of seawater. Many microbes have the ability to survive in extreme conditions, whereas others cannot survive and die in these conditions. The study of microorganisms in varied environments allows us to get a glimpse of the environment that must have been present on the earth before the rise of eukaryotes and the role microbes must have played in making the conditions feasible for the higher life forms. Their study can also provide vital clues that can be used by humans for adapting to the changing environment.

Many microorganisms can survive in multiple extreme conditions, e.g., cyanobacterium *Chroococcidiopsis* can survive in a variety of extreme conditions such as acidity, salinity, dryness, and high and low temperatures. *Salinibacter ruber* is a red obligatory aerobic chemoorganotrophic extremely halophilic Bacterium, related to the order Cytophagales. It was isolated from saltern crystallizer ponds and requires at least 150 g l^{-1} salt for growth. Microbes, present everywhere, play an important role in the cycling of carbon, hydrogen, oxygen, nitrogen, sulfur, etc. However, archaea is the main microbial group to thrive in most of the extreme environments.

1.2 Microbes in Varied Environments

1.2.1 Microbes in High Salt Concentration

Halophiles are found in all three domains of life. Within the Bacteria, we know halophiles are found within the phyla Cyanobacteria, Proteobacteria, Firmicutes, Actinobacteria, Spirochaetes, and Bacteroidetes. Within the archaea the most salt-requiring microorganisms are found in the class *Halobacteria*. Members of the *Halobacteria* are characteristic inhabitants of salt lakes at or approaching halite saturation, saltern crystallizer ponds, and other high salt environments (i.e., the Dead Sea, the Great Salt Lake, etc.). Halophilic organisms can also be found in man-made saline environments such as salted foods and tanned hides (Antranikian 2009). Most of its relatives are obligate halophiles and require over 150–200 g L^{-1} of salts for growth and structural stability. Further, they cannot survive under lower concentrations. The halophilic species are also found within the order Methanococci. Halophiles adopt different strategies for survival in high salt concentrations and thus maintain the cytoplasmic balance with the medium. One of the widely adopted strategies is the accumulation of compatible organic osmotic solutes which do not interfere with the enzymatic activity. These compatible osmolytes include glycine betaine, glycerol, ectoine, and other amino acid derivatives, sugars and sugar alcohols, etc. These are uncharged molecules and their concentrations are adjusted to the outside salinity. Halophiles commonly contain cell membrane proteins with high ratio of acidic to basic amino acid, thus giving the surface of the proteins a negative charge (DasSarma and Arora 1997). These organisms have a highly acidic proteome. Their protein surfaces have excess of negatively charged amino acids such as aspartate and glutamate, when compared to the positively charged amino acids like lysine and arginine.

1.2.2 Microbes in Low-Temperature Environments

A number of microorganisms can grow optimally at less than 15 °C (upper limit of 20 °C) and are called psychrophiles, whereas some others are able to survive at temperatures below 0 °C and grow optimally at 20–25 °C and are called psychrotolerant organisms. The psychrophiles usually inhabit marine ecosystems, where the temperatures are permanently lesser than 5 °C. In contrast, the psychrotolerant organisms are usually isolated from terrestrial environments, which are prone to extreme temperature fluctuations (Deming 2002). Cold temperature usually limits the cell function since it has negative impact on the cell integrity, water viscosity, membrane fluidity, and macromolecular interactions. Therefore, the organisms adopt a number of adaptive strategies to maintain vital cellular functions at cold temperatures and associated stress factors, such as desiccation, radiation, excessive UV, high or low pH, high osmotic pressure, and low nutrient availability. These microorganisms contain polyunsaturated and fatty acids and cold shock proteins to help in fluidity and nutrient transportation (Feller 2013).

1.2.3 Microbes in High-Temperature Environments

The microorganisms growing optimally at temperature between 60 and 80 °C are designed as thermophiles. In contrast to this, some non-photosynthetic prokaryotic can grow at >100 °C or even more are referred as hyperthermophilic (Scambos et al. 2018). These are found in the three domains of life, Archaea, Bacteria, and Eukaryotes. There are two major types of thermophiles: the microbes that grow in geothermal sites and that grow in self-heating materials such as composts. The thermophiles contain a variety of mechanisms that allow them to survive at higher temperature no other organisms can thrive (Weigal. 2000). These microorganisms have evolved several traits including novel membrane lipid composition (saturated fatty acids with more branches), thermostable membrane proteins, and higher rates of the synthesis of various enzymes (Sterner and Liebl 2001). Apart from having thermostable membrane proteins, these microorganisms also contain stabilized proteins, DNA, and RNA (Ladenstein and Ren 2006). Further, genomic studies of thermophiles have demonstrated that the evolution of thermophiles depends on the level of heritable variation (i.e., genomic size, gene mutations, transcriptional and proteome regulations) (López-García 1999).

1.2.4 Microbes in the Atmosphere

The atmosphere of the earth is comprised of different layers, i.e., troposphere, stratosphere, mesosphere, and thermosphere. These layers are based on the temperature. The troposphere, which is the lowest layer, begins at the surface of the earth and extends up to 10 km above sea level. It is the wettest layer of the atmosphere and has almost all types of clouds and all types of weathers. The layer immediately above the troposphere is the stratosphere. The bottom of the stratosphere is at 10 km above sea level and extends up to 50 km above sea level. Ozone is abundant in this layer and heats this layer as it absorbs the energy from the incoming UV radiations. This layer is dry and thus contains very few clouds. The temperature increases as the altitude increases. The layer above the stratosphere is the mesosphere. It extends from 50 to 85 km above sea level. The temperature decreases with altitude in this layer and the coldest temperature on earth (−100 °C) can be recorded in this layer. The thermosphere extends from about 90 km to between 500 and 1000 km above our planet, and the temperatures can range from about 500 °C to 2000 °C. This is followed by the ionosphere, the part of the atmosphere ionized by solar radiation. The uppermost layer is the exosphere (up to 10,000 km), which merges with space. Diverse and viable communities of bacteria reside high in the troposphere despite the extreme cold, high UV irradiation, and thin air, suggesting adaptive mechanisms. Surprisingly, viable bacteria form up to 20% of the total number of particles found in the troposphere (DeLeon-Rodriguez et al. 2013). Some atmospheric regions have extreme conditions, but microorganisms already live under even harsher environments with extremes of pH, temperatures, and radiation

(Pikuta et al. 2007). The roles of high-altitude dwelling bacteria are not well understood. It is likely that these microbes affect meteorological events, such as cloud formation, precipitation, or atmospheric chemistry. Microbes are often considered passive inhabitants of the atmosphere, dispersing via airborne dust particles. However, recent studies suggest that many atmospheric microbes may be metabolically active (Bowers et al. 2009), even up to altitudes of 20,000 m (Griffin 2004). Some airborne microbes may alter atmospheric conditions directly by acting as cloud condensation nuclei (Bauer et al. 2003; Mohler et al. 2007) and/or ice nuclei (IN) (Pouleur et al. 1992; Mohler et al. 2007); this hypothesis is supported by the observation that most ice nuclei in snow samples are inactivated by a 95 °C heat treatment (Christner et al. 2008). However, the overall contribution of airborne microbes to atmospheric processes such as ice nucleation remains unclear.

1.2.5 Microbes in Varied pH Environments

Extremely low and high pH habitats have been observed for different ecosystems contaminated by mining waste on earth. Acidophiles thrive at low pH and come from bacteria, fungi, algae, protozoa, and archaea. Currently, the most extreme acidophiles and alkaliphiles can thrive at pH 0 and pH 12. These microorganisms thrive in hot springs, marine vents, sulfuric pools and geysers, coal mines, and metallic ores. In order to maintain the internal pH, acidophiles either actively excrete protons or use them in various metabolic reactions such as the reduction of oxygen in the membrane. Acidophiles utilize both energies derived and non-energy processes to maintain internal pH. On the other hand, the alkaliphiles thrive in environments with a pH between 10 and 12 with an optimum growth pH of about 9 (Padan et al. 2005; Singh et al. 2016; Li et al. 2017). These microorganisms are distributed worldwide like hypersaline lakes, soda lakes, industrial effluents, and alkaline soil microenvironments (Fujisawa et al. 2010). In order to survive at these extreme conditions, these microorganisms have novel adaptations to cell wall structure such as a variety of acidic compounds (i.e., phosphoric acid, aspartic acid, galacturonic acid, glutamic acid, and gluconic acid).

1.2.6 Microbes in High-Pressure Environments

These microorganisms (piezophiles/barophiles) have the capability to thrive at high-pressure area, especially higher than normal (from 0.1 MPa to 112 MPa), or they need increased pressure for their normal growth and survival. They thrive in deep sea location, hydrothermal vents, trenches, sediments, and water samples from depths (Certes 1884). *S. benthica* and *M. yayanosii* have different strains which are extremely barophilic and barophilic with optimal growth at 50–80 MPa (Kato et al. 1998). *S. violacea* and *Photobacterium profundum* and *M. japonica* strains come in the category of moderate barophilic bacteria thriving at pressures of 10–50 MPa (Kato et al. 1995). *Sporosarcina* sp. strains belong to the category of barotolerant capable of growing at 0.1 MPa pressure (Kato et al. 1995). These microbes have adapted to such extreme environments because of various modifications like secretion of polyunsaturated fatty acid (PUPA) and eicosapentaenoic acid (EPA) (Nogi et al. 1998; DeLong et al. 1997; Kato et al. 1998). Such microbes have gene expression under the control of pressure-regulated promoter sequences (Nakasone et al. 1998). There are reports of pressure-inducible proteins (Jaenicke et al. 1988) and elevated levels of heat shock protein GroES (Lin and Rye 2006). These extremophiles can be exploited for the industrial and high-pressure fermenters because genes and proteins are accustomed to high-pressure conditions; also the barophilic origin proteases and glucanases can be used for detergents and DNA polymerases in PCR amplification. The research is being extended to mesophilic piezophiles apart from commonly explored psychrophilic and thermophilic piezophiles. The yeast *S. cerevisiae* is converted into a piezophile by manipulating the genome and by introducing genes that control high-pressure growth in yeast. Tryptophan permease gene TAT2 confers high-pressure growth in *S. cerevisiae* (Abe and Horikoshi 2000). The mesophilic organisms with piezophilic applications may help industrial applications. Similarly, novel antibiotics may be produced from mutants grown under high-pressure conditions. Piezophiles/barophiles have a unique membrane composition or structure that would allow them to survive at the greatly increased pressure.

1.2.7 Microbes in Radiation Environment

These extremophiles can withstand and survive the presence of ionizing and UV radiations such as *Deinococcus radiodurans* (Sandigursky et al. 2004), *D. radiophilus* (Yun and Lee 2004), *Thermococcus piezophilus* (Jolivet et al. 2004), and Cyanobacteria like *Nostoc muscorum* and *Microcoleus vaginatus* (Singh 2018). *Acinetobacter radioresistens* (Jawad et al. 1998) are few examples of radiophiles. They thrive in various radioactive places like dry climate soil, nuclear reactors like *D. radiodurans*, and Mars Analog Antarctic Dry Valleys (Musilova et al. 2015). They have various adaptations to withstand radiation stresses like Nudix hydrolase enzyme superfamily and the homologs of plant desiccation resistance-associated proteins contributing to extreme radiation and desiccation resistance of *Deinococcus* sp. (Makarova et al. 2001). PprA protein helps in DNA ligation after DNA fragmentation due to radiation exposure reported in *D. radiodurans* (Narumi et al. 2004), increased metal concentration (i.e., Mn/Fe) ratios in protection of *D. radiodurans* cellular proteins from oxidative damage (Daly 2009), and accumulation of MnII. It helps in resistance toward gamma radiation exposure (Daly et al. 2004), production of mycosporine-like amino acids (MAAs) in cyanobacteria due to exposure of solar UV-B radiations (Sinha et al. 2001), etc. As far as applications of radiophile are concerned, they are helpful in the management of nuclear waste-polluted environments (Brim et al. 2003; Appukuttan et al. 2006).

1.2.8 Microbes in Metallic Environment

These extremophiles (metallophiles) have the capability to grow in the presence of heavy metal waste. They thrive in industrial sediments, soil, and waste effluents containing heavy metals (Mergeay et al. 2003). These metallophiles possess heavy metal resistance due to the presence of megaplasmids conferring genes for resistance by efflux mechanisms (Gomes and Steiner 2004). These microorganisms remove toxic metals via change in redox potential of metals by aiding in bioleaching of contaminants and precipitation (Lovley and Coates 1997; Wani et al. 2007; Pal and Rai 2010). These extremophiles can be exploited as bioremediation/bioleaching for different metal ores (i.e., Cu, Fe, Zn, etc.) from toxic compound removal from various industrial/mining waste effluents.

1.2.9 Microorganisms in Xerophilic Environment

These microorganisms (xerophiles) are able to thrive in low water environments and resist high desiccation, i.e., water activity below 0.8. Endolithic and halophilic microbes come under xerotolerant. Some xerophiles such as Cyanobacteria, *Nostoc commune*, were recovered from dry area after 13 years and from herbarium storage after 55 years (Shirkey et al. 2003), from dry storage conditions of herbarium after 87 years (Lipman 1941), and after 107 years from dry soil sample (Blank and Cameron 1966). There are reports of synthesis of extracellular polysaccharides (EPS) which withstand dry environment (De Philippis and Vincenzini 1998); cell component stabilization by buildup of compatible solutes like trehalose (Welsh 2000); upregulation of genes related to osmotic, salt, and low-temperature stress, osmoprotectant metabolisms, K^+ transporting system, and heat shock proteins; and downregulation of genes involved in photosynthesis, nitrogen transport, RNA polymerase, and ribosomal proteins (Katoh et al. 2004). The proteins like catalases, peroxidases, and superoxide dismutase expression are increased to neutralize ROS due to desiccation (Shirkey et al. 2000).

1.3 Future Prospective

All the three domains of life (thermophiles, halophiles, acidophiles, alkaliphiles, and piezophiles) take life to the extreme. By studying the biology of these unique microorganisms, we can gain deep insight into how life evolve on earth and even infer as to how life would be able to exist elsewhere in the universe. As for the origins of life on earth, some scientists are looking to the extremophile microbes such as *D. radiodurans* as model organisms when exploring the existence of extraterrestrial life of the solar system and beyond. This microorganism has the unique ability to survive radiation at several thousand times the lethal dose for humans.

With these groundbreaking research work and recent development in the field of extremophiles, which have been directly applicable in different branches of life sciences, our understanding about the biosphere has grown and the putative boundaries of life have expanded. However, due to the recent growth and advancement, we are just at the beginning of exploring the world of extremophiles. In this chapter, we have discussed the several aspects of these fascinating microorganisms, exploring their habitats, biodiversity, ecology, evolution, biochemistry, as well as applications.

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