Microbial adaptation to different environmental conditions: molecular perspective of evolved genetic and cellular systems

Atif Khurshid Wani[1], Nahid Akhtar[1], Farooq Sher[2], Acacio Aparecido Navarrete[3], Juliana Heloisa Pinê Américo-Pinheiro[3*]

[1]Department of Biotechnology, School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, Punjab-144411, India

[2]Department of Engineering, School of Science and Technology, Nottingham Trent University, Nottingham NG11 8NS, United Kingdom.

[3] Brazil University, Street Carolina Fonseca, Number 584, São Paulo, SP, 08230-030, Brazil

*Corresponding author. Email: americo.ju@gmail.com; juliana.pinheiro@universidadebrasil.edu.br (+55) 1698249-1919

Abstract

Microorganisms are ubiquitous on Earth and can inhabit almost every environment. In a complex heterogeneous environment or in face of ecological disturbance, the microbes adjust to fluctuating environmental conditions through a cascade of cellular and molecular systems. Their habitats differ from cold microcosms of Antarctica to the geothermal volcanic areas, terrestrial to marine, highly alkaline zones to the extremely acidic areas, and freshwater to brackish water sources. The diverse ecological microbial niches are attributed to the versatile, adaptable nature under fluctuating temperature, nutrient availability, and pH of the microorganisms. These organisms have developed a series of mechanisms to face the environmental changes and thereby keep their role in mediate important ecosystem functions. The underlying mechanisms of adaptable microbial nature are thoroughly investigated at the cellular, genetic and molecular levels. The adaptation is mediated by a spectrum of processes like natural selection, genetic recombination, horizontal gene transfer, DNA damage repair, and pleiotropy-like events. This review paper provides the fundamentals insight about the microbial adaptability besides highlighting the molecular network of microbial adaptation under different environmental conditions.

Keywords: Microorganisms; Molecular mechanism; Thermophiles; Psychrophiles; Halophiles; Acidophiles

Introduction

Microorganisms are adjusted in natural environments for optimum and normal functioning. Any fluctuation in abiotic factors from the normal operating range induces stress on microorganisms (Jordan and Tomberlin 2017). The degree of shift level regulates the survival chances of a particular microorganism (Hibbing et al. 2010). The changes in abiotic environmental factors can initiate stress responses as changes are more survival-oriented than growth (Meena et al. 2017). The maximum microbial populations withstand the little environmental changes by adapting over a certain time duration. They do so by inducing cellular, genetic, and morphological modulations and thus resist the stress (Brooks et al. 2011). Often, the degree of tolerance increases by providing cells an extended time for acclimatizing in dynamic environments. Microorganisms incessantly customize in fluctuating environmental conditions (ECs). In the changing ECs where maximum organisms experience maladaptive coping, the microbial lineages exploit other microcosm opportunities by modulating physiological states, thereby adapt to the new environments via positive selection (Wadsworth 2015). The existence of microorganisms as acidophiles, halophiles, and psychrophiles is testimony of the regulated lifestyle of the microorganisms (Rampelotto 2013). Bacteria, in general, have a morphological make-up in such a way that it prepares well for the transforming environment. Their membranes, along with genetic products, can undergo alterations with a particular stimulus that emerges as a result of varying abiotic conditions like temperature, pH, pressure, and salinity (Bartlett et al. 2007; Ranawat and Rawat 2017; Zuñiga et al. 2017). These changes are well regulated and can be passed on to the next generations as well. The emergence of resistance against several anti-microbial drugs in numerous microorganisms is a good example of microbial adaptation (Américo-Pinheiro et al. 2021; Storto et al. 2021). The resistance to penicillin by *Staphylococcus aureus* was reported soon after its introduction and by 1990, 80% of *S. aureus* were reported as resistant to this drug (Lowy 2003). The adaptation to the anti-microbial agent is either driven by an inherent character like the presence of outer lipid membrane in gram-negative bacteria or it is driven by acquired (genetic) character (Brooks et al. 2011; Munita and Arias 2016). Once the adaptability is mediated by genetic make-up, it is passed on to the generations that follow. The microbial adaptation to antimicrobial drugs involves various mechanisms such as enzymatic destruction or inactivation of drugs, pumping out of drugs by efflux pumps, modification of drug target sites and limiting the uptake of drugs due to the presence of lipopolysacharidde layers, formation of biofilms and modification of porin channels (Reygaert 2018). Furthermore, regulatory RNAs such as small RNA (sRNA) have been implicated in the bacterial adaptation to antimicrobial drugs by controlling important biological processes necessary for antibiotic drug resistance such as drug uptake, drug efflux and biofilm formation (Felden and Cattoir 2018). Banerjee et al. (2021) have reported that the cell shape changes can also help in bacterial adaptation to antibiotics. The bacteria can also become resistant to antibiotics due to the mutations in their genome or by uptaking foreign DNA (Larsson and Flach 2021). The microbes can also adapt to the changing environmental condition by transforming to different cell types that help the microbes to maintain optimum growth in new environment (Freitas et al. 2020). An example of this changing environment adaptability towards the changing surrounding support is reported in *Vibrio parahaemolyticus* (Freitas et al. 2020). In a highly viscous vicinity, the bacteria form a swarmer cell that ensures motility for the process of chemotaxis (Jose and Singh 2020). The adaptation is well regulated and involves the expression or repression of many genes. This mechanism transforms intracellular, extracellular, and surface properties of the microorganism (Niño-Martínez et al. 2019). The microbes adapt to high temperature damage (unfolding of cellular proteins and production of aggregates of misfolded proteins) by activating heat shock response (Rodríguez-Verdugo et al. 2020). The heat shock response of *Escherichia coli* is a very familiar example of this kind of adaptation (Arsène et al. 2000). The bacteria sense the increase in temperature by the help of sensory biomolecules called thermosensors which then activates the heat shock response where the expression of two types of proteins namely chaperons and proteases is increased (Roncarati and Scarlato 2017; Rodríguez-Verdugo et al. 2020). Furthermore, in *E. coli* and *Zymomonas mobilis* the genes responsible for membrane transport, energy metabolism, DNA repair, tRNA modification, membrane stabilization, and cell division have been found to be important for growth under high temperature (Murata et al. 2011; Charoensuk et al. 2017). Recently, the recombinant transfer of cold shock protein, named CspL, among different bacteria has also been reported to confer resistance to high temperature (Zhou et al. 2021). Furthermore, the formation of solid surface adherent populations popularly known as biofilms have also been reported to play important role im microbial resistance to extreme environmental conditions such as UV irradiation, high pH, salinity and temperature (Yin et al. 2019; Penesyan et al. 2021). *V. parahaemolyticus* and many other bacterial species also show adaptability of environmental changes by forming biofilms (Yildiz and Visick 2009). Biofilms also provide protective environment where the cells with reduced fitness to the impacts of the environmental changes can accumulate mutations that will offset the impact and help the microbe to adapt and evolve (Penesyan et al. 2021). Adapting to the mode of biofilm formation involves a sequence of changes that include the expression of unexpressed genes or even deactivation of hyperactive genes (Wolska et al. 2016). Chemotaxis by *Bacillus subtilis* and other bacteria is the widely studied adaptation mechanism whereby bacterium senses chemical make-up and either move towards a particular compound or away from it. This is a highly regulated system and is controlled by 40 or more genes that mediate flagella synthesis (Mukherjee and Kearns 2014). There have been several comprehensive studies on evaluation of the microbial adaptation (Katarína et al. 2018; Merino et al. 2019; Ji and Wei 2020; Manriquez et al. 2021) . Still, the progress on in-depth analysis requires detailed insight into the cellular strategies adopted by microorganisms in the changing ECs. This review paper provides insight about the microbial dynamics in adapting to different environmental conditions and highlights the cellular and molecular perspective of the microbial adaptability.

Microbial adaptation to survive in different environmental conditions

Symbiosis

Symbiotic association of microorganisms are ubiquitous, and they can be mutualistic, commensal or pathogenic to the host (Moënne-Loccoz et al. 2014). The host provides nutrients and space to the microbes and they can also act as a vector for diffusing the microbes into surrounding environments (van de Water et al. 2018). At every step of the symbiosis process, the microbes experience the fluctuating ECs in which they adapt to maintain optimal fitness for symbiotic associations. The changeover parameters in these environments include temperature, host immune factors, and pH (Moënne-Loccoz et al. 2015). When a microbe resides exclusively in a single host or is passed on to the progeny via vertical transmission, it has to come up against substantial changes in ECs like ion concentration, nutrient availability, oxidative and osmotic stress (Chaguza 2020). A common example is the mammalian gastrointestinal (GI) tract that consists of several niches with persistent variations in the levels of ions, pH and sugars. A minor environment fluctuation represents a substantial environmental change for any species of microorganisms (Milani et al. 2017). The microbial adaptation in these changing environments follows a specific pattern in most of the cases. For example, the enteropathogen infection process follows the steps: a loose attachment with mucosal surface of the host, toxin and virulence factor induction, close association, and invasion (Peterson 1996). A common example of the horizontal transmission between *Xenorhabdus nematophila* and its host *Steinernema carpocapsae* is started by attachment with specific tissues, selective colonisation and then shifting towards a specialized niche within the host (Cao and Goodrich-Blair 2017). In many pathogenic bacteria, the phenotypic variation enables the adaptation between host-associated and free-living states (Bäumler and Fang 2013). The uncertain environmental changes may determine the phenotypes which stochastically switch among different conditions in such a way that a bacterial population may express a special trait suited for that environment or express traits predictably so that they are advantageous in future (Brooks et al. 2011). For example, the attachment of *Vibrio cholera* with the mammalian mucosal surfaces requires low levels of cyclic diguanylate (c-di-GMP), contrary to the persistence in aquatic environment requires higher levels of c-di-GMP (Römling et al. 2013). Microorganisms that evolve under predictable fluctuation conditions have the ability to anticipate the forthcoming environment. Such predictions allow the microorganisms to suitably regulate gene expression to pre-induce the gene profiles that are required for survival in the varying climate (Francino 2012). This predictable nature is studied in *E. coli* occupying the GI tract of mammals. For example, *E. coli*, while passing the GI tract, is initially exposed to lactose and then maltose. An *in vitro* experimental study has shown that exposing *E. coli* to lactose induces lactose gene expression and least expresses maltose gene. This summarizes the adaptive nature of *E. coli* on two different substrates (Peek et al. 2018).

Fluctuating climatic and environmental conditions

Human activities such as rampant use of various natural resources, urbanization and industrialization has deleterious effects on the environment (Tilman and Lehman 2001; Webster et al. 2018). As a result, climate change, severe pollution of the oceans, freshwater and soils generates enormous changes in the environments. Agricultural and forest activities, in turn, lead to soil degradation and erosion, while changes in land use threaten terrestrial ecosystems. The human activities such as fossil fuel burning, deforestation, change in land use, agricultural activities and cement manufacture are some of the major causes of greenhouse gases emission (Yue and Gao 2018). These human activities emit various long-lived (methane – CH_4, carbon dioxide – CO_2, nitrous oxide – N_2O) and short-lived (ozone – O_3) greenhouse gases along with aerosol and water vapor (Heshmati 2020). These greenhouse gases trap heat radiation and lead to increase in global temperature causing global warming and climate change. Furthermore, the increase in emission of CO_2 from the anthropogenic activities can also increase the acidity of the seawater (Zhang and Wang 2019). In all this situations, the microbiota role plays in the maintenance of a sustainable environment through its adaptive capacity (Vicuña and González 2021). The impact of climatic fluctuations on the biotic components of the Earth is widely accepted. In the previous century the average global temperature has increased by 0.7 °C and it is expected to continue increasing (Sintayehu 2018; Muluneh 2021). Furthermore, it has been predicted that by the end of the 21st century the global temperatures will increase by 1.1-6.4 °C (Qin et al. 2014). Hence, it is expected that the environmental perturbations due to the climate change and global warming can affect the microbial communities rapidly at a global level (Cavicchioli et al. 2019; Jain et al. 2020). During this, warming is believed to cross the optimum temperature range that most biotic components cannot withstand, especially those with low-temperature adaptability (Montoya and Raffaelli 2010). Furthermore, climate change can alter the temperature, oxygen content and pH; and also elevate CO_2 level of the microbial habitat which can affect the local microbial communities, microbial biomass, microbial abundance and diversity (Classen et al. 2015; Wettstadt 2021). The climate change can alter the microbial metabolism, microbial soil respiration and affect the ecosystem functions of microbes such as nitrification, nitrogen fixation, denitrification and carbon cycling (Classen et al. 2015; Cavicchioli et al. 2019). Climate change can also alter the interactions between microbes and the microbes' relationship with their host (Jain et al. 2020). The long term exposure of microbes to environmental fluctuations due to climate change such as elevated CO_2 level can cause irreversible genetic changes in the microbes (Cavicchioli et al. 2019). A study reported that the terrestrial ectotherms, having narrow thermal variation distribution tolerance, would be extremely sensitive to changes in the temperature (Deutsch et al. 2008). Despite increased research, biotic adaptation in changing climatic conditions, the adaptability of microorganisms in cryptic biodiversity has not received much attention. Belotte et al. 2003 and Whitaker et al. 2003 investigated local adaptation in diverse bacterial species in different environments. Both found local adaptation evidence in specialized populations indicating existence in the patchy environments. Belotte et al. 2003 designed an experiment to test the local adaptation of soil bacteria. They obtained bacterial isolates form soil samples collected from different sites of a forest located at the Gault Nature Reserve, Quebec, Canada. The bacterial isolates were identified as *Bacillus mycoides* by fatty acid composition analysis (Belotte et al. 2003). Then, the growth of these isolates were analyzed by growing them at home sites (medium made using the soil from which the isolates were obtained) and other sites. Their study indicated that some of the isolates showed indication of local adaptation where the isolates grew better at home site in comparison to their growth at other sites. Moreover, the isolates grew better at home site in comparison to the isolates from elsewhere (Belotte et al. 2003). Similarly, in the study by Whitaker et al. 2003, it was found that the genetically isolated populations of hyperthermophilic acidophiles belonging to the *Sulfolobus* strains which were isolated from the water and sediment samples collected from five different regions located in Russia, Iceland and United States of America exhibited higher potential for local adaptation to specific environmental conditions. In another study *Saccharomyces paradoxus* populations of North America was used as a representative to evaluate the local adaptation of fungi in changing climatic conditions (Leducq et al. 2014). In this study, various strains of *S. paradoxus* were studied for fitness components like growth rates at the temperature range of 10-42 °C and survival through the freeze-thaw cycle. The results favored the local adaptation of microbial fungi and thus the existence in changing climatic conditions (Leducq et al. 2014).

Temperature ranges

The submarine, subterranean and certain terrestrial areas of high-temperature harbour diverse hyperthermophiles. These are found in hydrothermal land sources heated up by volcanic exhalations forming sulfur-rich alkaline hot springs (Stetter 2002). More than 50 hyperthermophilic bacterial and archaeal species are known so far, and most of them are classified using 16S rRNA gene-based classification (Miyazaki and Tomariguchi 2019). Hyperthermophiles generally adapt to high-temperature environments by their nutritional requirements and physiological state, making their genome, cellular components stable and functional (Figure 1) (Vieille and Zeikus 2001). The cellular ingredients like nucleic acids, proteins and lipids are usually known to be heat sensitive (Casares et al. 2019); however, *Thermotoga maritima*, a bacterial hyperthermophile, contains a membrane lipid known as 15,16-dimethyl-30-glyceryloxy-triacontanedioic acid instead of the esterlipids that increases the membrane stability and prevents hydrolysis at higher temperatures (Siliakus et al. 2017). In Archaea domain, both mesophiles and hyperthermophiles contain di(biphytanyl)-diglycerol and diphytanyl-glycerol that exhibit resistance at an acidic pH and high temperature against hydrolysis (Jaenicke and Sterner 2006; Siliakus et al. 2017). For example, *Pyrolobus fumarii,* chemolithoautotrophic *Archaea,* survives at a temperature up to 113 °C, thereby representing the life of upper border temperature. The mode of nutrition in hyperthermophiles is generally chemolithoautotrophic, whereby inorganic redox reaction acts as energy sources and CO_2 is the carbon source (Stetter 2002). Besides hyperthermophiles on marine and terrestrial ecosystems, many psychrophiles are well adapted to cold environments (Barria et al. 2013). They adjust to such cold temperatures by maintaining the fluidity of membranes, structural adjustment through enzymes, cold shock protein expression and storage of cold-resistant solutes (Tribelli and López 2018). *Psychrobacter arcticus* (permafrost bacteria that survive -10°C) is devoid of a phosphotransferase system and glycolysis genes, but expresses gluconeogenic enzymes such as phosphoenolpyruvate synthase and fructose-1,6-bisphosphatase. This indicates that this bacterium is unable to metabolize sugars, but prefers other sources of oxidized carbon (Ayala-del-Río et al. 2010). One of the studies carried out to evaluate the adaptive behaviour of two strains of *Pseudoalteromonas* in Antarctica showed glutathionylspermidine and glutathione as the main agents responsible for their adaptation in such cold regions (Tribelli and López 2018). Table 1 provides the list of some hyperthermophiles and psychrophiles at different temperatures and pH ranges.

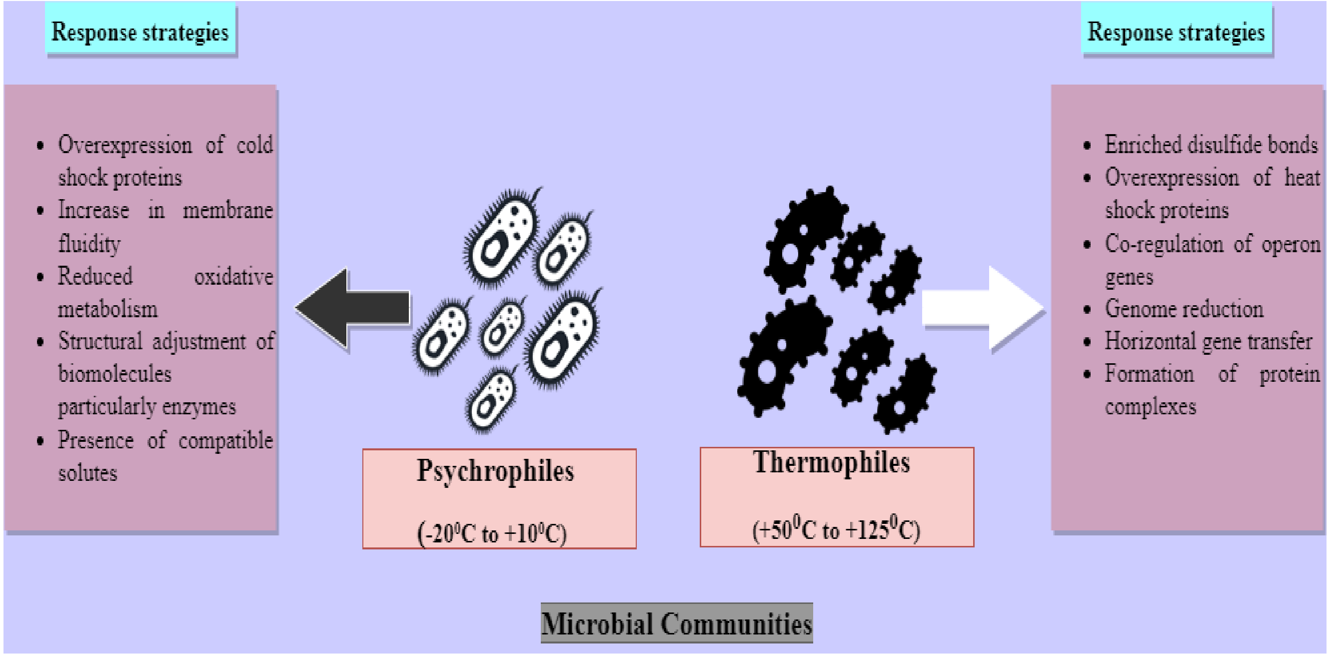

Figure 1: Response strategies of psychrophiles and thermophiles towards cold and heat respectively.

Salinity

The diversity of microbes in saline environments is very well known (Gan et al. 2020; Xue et al. 2021; Chen et al. 2021; Xing et al. 2021). The hypersaline microcosms are inhabited by halotolerant, halophilic bacteria and archaea (Oren 2006). The strategies followed by microbes to adapt in high salt concentration environments continue to gain the interest of many scientists. One attribute associated with halophiles is the isosmotic nature of the intracellular domain with the outside area (Ventosa et al. 1998). To maintain increased osmotic pressure intracellularly, the salt-in strategy is followed by maintaining osmotic balance by accumulating inorganic salts of higher concentrations (Oren 1999). Low-salt-in compatible solute strategy is also an adaptive feature of microorganisms in which a defined solute concentration allows the cellular processes to function effectively (Weinisch et al. 2018). The compounds that have been evaluated and found compatible in different microorganisms include sugars, amino acids, polyols, ectoines, and betaines (Roberts 2005). Microorganisms using organic solutes are usually more dynamic, and they easily adapt to the increasing salinity or dilution stress than those that utilise the salt-in strategy (Ma et al., 2010). In *Haloarcula marismortui*, *Halobacterium salinarum* and some related organisms, the intracellular ionic concentrations have been analysed. It is reported that cells contain sufficient salt concentration for osmotically balancing the external medium-salinity (Poidevin and MacNeill 2006). In halophilic archaea such as *H. salinarum* and *H. marismortui*, Na^+ is found in low concentration, and K^+ is present in higher concentration, whereas chloride ion balances the intracellular cations to balance the salinity (Gunde-Cimerman et al. 2018; Szatmári et al. 2020).

Another attribute associated with the halophilic archaea is the acidic proteome having increased excess to amino acids of negative charge over positively charged amino acids (Reed et al. 2013).

Acidic-alkaline environments

Microorganisms encounter fluctuating pH stress during various bioprocesses (Guan and Liu 2020). Microbial species have thus developed adaptive strategies to resist both alkaline and acidic environments (Padan et al. 2005). The damage caused in high acidic environments is mitigated by membrane fluidity and integrity, pH homeostasis, DNA repair and metabolic regulation (Yang et al. 2019). The proton influx in acid-tolerant microbes is reduced by chemiosmotic strategy (Baker-Austin and Dopson 2007). Biofilm formation is another adaptive strategy that microorganisms use to resist acid stresses (Singh et al. 2017). The pH homeostasis maintenance for acid stress resistance results from multiple transport system interactions (Padan et al. 2005). Protons are expelled from the cell by electrogenic proton pumps resulting in the generation of pH gradient and membrane potential (Palmgren and Morsomme 2019). In *Helicobacter pylori*, the urease system neutralizes H^+ by producing NH_3 (ammonia) which helps to resist the acidic environment during its culturing (Ansari and Yamaoka 2017). In alkaliphilic microorganism, pH maintenance is driven by active and passive strategies (Salwan and Sharma 2020). The low permeability of membranes and cytoplasmic polyamine pools drive passive regulation while ion channels of Na^+ mediate active regulation (Yumoto 2002). Besides, alkaliphilic compensate pH gradient mode by causing the coupling of Na^+ expulsion to transport electrons for homeostasis of pH and maintaining higher membrane potential (Krulwich et al. 1998). Table 1 gives an account of acidophilic and alkalophilic microorganisms.

Table 1: Psychrophilic, thermophilic, halophilic, and acidophilic microorganisms with optimum pH and temperatures ranges for metabolism.

Microorganism	Temperature range (°C)	pH	Metabolism	References
Acidianus infernus	60-95	1.5-5.0	Lithoautotrophs (aerobic-sulfur metabolizing)	Plumb et al. 2007
Aeropyrum pernix	70-100	5.0-9.0	Autotrophic (aerobic)	Balestrieri et al. 2011
Aquifex pyrophilus	85-95	5.4-7.5	Autotrophs (Typically uses oxygen for respiration but can also grow anaerobically by reducing nitrogen instead of oxygen)	Wäber and Hartmann 2019
Archaeoglobus fulgidus	60-95	5.5-7.5	Chemolithoautotrophs (anaerobic-sulfate reducing archaea)	Hocking et al. 2014

Bacillus psychrosaccharolyticus	-2 – 20	5.2 – 7.0	Autotrophic (facultative anaerobe)	Fresco-Taboada et al. 2013
Cryobacterium flavum	-6 – 28	5.5-10.5	Chemoautotrophic (aerobic)	Liu et al. 2012
Cryobacterium roopkundense	-10 – 20	5.0- 10.0	Autotrophic (aerobic)	Liu et al. 2020
Exiguobacterium sibiricum	-12 to 55	5.0-11.0	Chemolithoautotrophs (facultative anaerobes or aerobes)	Rodrigues et al. 2008
Halorhodospira halophila	55-70	7.5-10.6	Exhibits autotrophic growth	Antón et al. 2000
Hyperthermus butylicus	80-108	7.0	Heterotrophic (anaerobic)-sulfur reducing	Zillig et al. 1990
Metallosphaera sedula	65-85	2.0-5.0	Autotrophic (fixation of carbon dioxide in the presence of H_2) and heterotrophic (uses organic molecules except for sugars)-obligate aerobic	Maezato et al. 2012; Terrado et al. 2017
Methanocaldococcus jannaschii	50-86	5.5-6.5	Hydrogenotrophic (anaerobic)	Jones et al. 1983
Natronomonas pharaonis	20-45	7.5-9.0	Utilizes amino acids as carbon source with higher degree of self-sufficiency in nutrition.	Falb et al. 2005
Planococcus halocryophilus	-16 to 10	7.0-8.0	Chemolithoautotrphs (aerobe)	Raymond-Bouchard et al. 2017
Psychrobacter arcticus	-10 to 40	5.0-7.0	Autotrophs (aerobic)	Hinsa-Leasure et al. 2013
Pseudomonas fluorescens	4-37	5.0-7.0	Versatile metabolism (obligate aerobe-Some strains use nitrate instead of oxygen)	Rainey 1999
Pyrobaculum islandicum	65-98	4.5-8.5	Heterotrophic (anaerobic)	Huber et al. 1987

Staphylothermus marinus	65-98	4.5-8.5	Heterotrophic (anaerobic)-sulfur respiring	Jung et al. 2012
Thermoanaerobacter mathranii	50-75	4.7-8.8	Heterotroph (anaerobic)	Larsen et al. 1997
Thermococcus celer	75- 93	4.0-7.0	Chemolithoautotrophic (anaerobic)	Wong et al. 2003
Thiohalospira alkaliphila	50-60	6.5-8.3	Chemolithoautotrophic Sulphur oxidizing bacteria	Sorokin et al. 2008

Molecular perspective of microbial adaptation

Since the environment is extremely heterogeneous at different levels, microorganisms face changing biotic and abiotic components. Table 2 illustrates the different cellular adaptive strategies of the microorganism in fluctuating environments. The variables in their microcosms are generally temperature, pH, competition (intra- and interspecific), and nutrient availability (Hibbing et al. 2010). One of the examples is the *E. coli* population found in the mammalian gastrointestinal tract. Within the digestive tract, cells adapt to a series of stresses like fluctuating oxygen levels and increasing temperature, changing carbon sources (lactose and maltose) (Freter et al. 1983). One of the major factors that ensure the active adaptive mechanism in a rapidly fluctuating environment is its predictability (Bleuven and Landry 2016). The adaptation in such scenarios prefers the evolution of molecular networks that can predict the coming fluctuations like gene regulation by up regulating or down regulating an involved gene or maintaining a memory of previous encounters (Mitchell et al. 2009). An example is the prediction of seasonal changes before the variation with the help of certain signals generated from the environment (Brunke and Hube 2014). However, in unpredictable changes, the adaptability favors a bet-hedging strategy in which genotype visits phenotypes randomly and thus increases the adaptation probability (Tal and Tran 2020). Experimental studies have presented a more in-depth view of underlying molecular mechanisms in different laboratory setups under controlled conditions. *S. cerevisiae* evolved under carbon limiting conditions for more than 200 generations, leading to multiple mutations and increased HXT6/7 gene copy number that codes for a transporter protein (hexose) (Payen et al. 2016). The strains of yeast carrying amplified versions of this gene show enhanced fitness compared to the ancestral forms (Broach 2012). In the absence of a drug, the drug resisting gene may cause fitness issues that are compensated via gene amplification of that particular gene (Depardieu et al. 2007). Another potential trade-off source is the over-expressing genes (Kim et al. 2020). This strategy may also result in loss of response which can be devastating for those genes where downregulation is required (Karasov et al. 2017). Sherlock 2013) evolved some yeast strains in a chemostat deficient of nutrients and examined the evolution of adaptive response. The key to the enhanced fitness as a stress response was the loss of the cAMP/PKA pathway and environmental sensing. Still, maladaptive nature was found during starvation when nutrient availability was not constant (Kvitek and Sherlock 2013). When environmental fluctuations follow a regular pattern, the anticipation mechanism guides the adaptive strategies. The adaptability within such environment has been reported in *Candida albicans*, *E. coli* and *V. cholera* (Siavoshi and Saniee 2014). Several cells express essential genes to protect from oxidative stress during the heat shock, allowing the cells to acclimatize to the stressful ECs (Morano et al. 2012).

Table 2: Adaptation strategies of microorganisms in fluctuating environments.

Microorganisms	**Microorganism in extreme environments**	**Mechanism of Adaptation**	**References**
Acidithiobacillus ferrooxidans, Halarchaeum acidiphilum, Metallosphaera sedula, Thiobacillus prosperous, Acetobacter aceti	Acidophile (pH 0.5 to 5)	Efficient efflux system, Acid tolerant membrane, proton exclusion and secondary transporters driven by protons	Krulwich and Guffanti 1983; Baker-Austin and Dopson 2007
Chloroflexus aurantiacus	Xerotolerant/xerophile	Organic and inorganic osmolyte accumulation, synthesis of extracellular polysaccharides and regulated differentiation of cells into desiccation resistant cells like spores	Bachar et al. 2007; Lebre et al. 2017
Deinococcus radiodurans	Radiation tolerant/resistant	Strong pigmentation and efficient DNA repair system	Krisko and Radman 2013
Ferroplasma acidarmanus	Metalo-tolerant/ resistant	Detoxification and/or sequestering of metals by alkylation and/or reduction	Mangold et al. 2013
Haloarcula amylolytica, H. argentinensis, H. hispanica, H. japonica, H. quadrata	Halotolerant/Halophile (2-6 M NaCl and -1.5 to -40 Mpa water potential)	Accumulation of osmolytes and synthesis of salt-tolerant/dependent enzymes.	González-Hernández and Peña 2002; Siglioccolo et al. 2011; Hänelt and Müller 2013
Halorhodospira halochloris, Thiohalospira alkaliphila, Bacillus firmus, Natronomonas pharaonis	Alcaliphile (pH 8.5 to 11)	Efficient proton uptake system mediated by antiporters of the membrane, OH- ion	Krulwich and Guffanti 1983;

		membrane impermeability	Kulkarni et al. 2019
Leptospirillum ferriphilum	Acidophile	Active pH regulating pumps	Patel et al. 2012
Pseudomonas putida, Ralstonia solanacearum	Toxin tolerant/ resistant, Efficient xenobiotic decomposer	Effective efflux pump	Chen et al. 2006; Fernández et al. 2009; Colburn-Clifford et al. 2010
Psychrobacter adeliensis, P. aestuarii, P. alimentarius, P aquimaris, P. luti, P glacincola	Psychrophile (-10 to 40 °C)	Synthesis of unsaturated fatty acids to prevent the decrease of membrane fluidity reduces the size of the cell and elevates cellular water in an ordered fashion	Feller et al. 1997; Ayala-del-Río et al. 2010; Liu et al. 2019
P. fumarii, Thermobaculum terrenum, Picrophilus torridus	Hyperthermophile (60 – 100 °C)	Synthesis of saturated long-chain fatty acids and cyclic lipids, and heat-stable proteins, lipids and, nucleic acids	Stetter 1999; Soo et al. 2009
Serratia ureilytica	Thermophile (20-54 °C)	Modified vegetative cells into resistant structures	Filippidou et al. 2019
Streptomyces atacamensis	Xerotolerant	Dormancy and sporulation response to desiccation, and up regulation of proteins that are functional during xeric stress	Lebre et al. 2017; Orellana et al. 2018
Thermococcus litoralis	Hyperthermophile (55-100 °C)	Facultatively sulphur dependent and produces exopolysacchrides	Price and Giovannelli 2017
Pyrococcus	Piezophile	Presence of higher proportion of fatty acids in cytoplasmic membranes	Siliakus et al. 2017

Adapting via transcriptional regulation

Microbial adaptation to different environment is largely attributed to their genetic make-up and its regulation. Figure 2 illustrates the fundamentals of microbial adaptation via changing genetic and community structure and composition. It is well known that microbial genomes particularly of bacteria are diverse in size, and content with few conserved genes among the sequenced genomes. An assessment of the fraction of the genome that is associated with metabolism, transport and transcription indicated that larger genomes harbor more transcription factors (TFs) per gene than smaller ones (Cases et al. 2003). This is a strong indication that in complex conditions signal integration and gene expression regulation enable rapid adaptation to environmental signals. Transcription regulatory network (TRN) builds a response to a particular condition despite being highly diversified. While the dynamics and topology of these networks has been center of attention for research groups, the evolution of the topological features which continues to drive adaptive nature of microorganisms is still lesser known. One of the research groups studied the evolution of TRNs from reductive perspective and found that the action exerted by TFs correlate with conservation degree with dual regulators found to be more conserved than the activators and repressors in extreme reduction conditions. Besides they found that preponderant conservation of these dual regulators may be attributed to their action as nucleoid-associated proteins and global regulators (Galán-Vásquez et al. 2016). This suggests that TRNs play a pivotal role in understanding of basic principles underlying the microbial adaptability. Ma et al. 2019 studied chalcopyrite bioleaching by 2,4, and 6 acidophilic strains with similar inoculation density and found that 6-strain community adapted first to bioleaching conditions and maintained suitable function until late stage. The comparative transcriptomic analysis showed upregulation of 226 and 737 genes at early and later stage respectively (Ma et al. 2019). This strongly indicated that microbes adapt to oligotrophic environment by improving catalytic activation, cell proliferation, and binding action to maintain different life activities. Human microbiome also produces metabolites that influence the resistance and susceptibility. Colonized mice with anaerobic symbionts show that the immune responses lead to dramatic transcriptional reprogramming with negligible alterations in their abundance. The transcriptomic alterations include downregulation of carbohydrate degrading factors and induction of stress-response mediators (Becattini et al. 2021). *Mycobacterium tuberculosis*, a human pathogen, resists the unfavorable environment of phagosomes and alters dendritic cells and macrophages to prolong its survival, thus making transcriptome capture slightly difficult during infection (Rienksma et al. 2015). Extreme thermophilic bacteria belonging to the genus *Caldeloulosiruptor* degrade carbohydrates in the plant cell wall and subsequently utilize them. The mechanism of carbohydrate transcription regulation using genes and investigated the binding sites to TF and regulons with transcriptomic analysis for *C. bescii* cultivated on glucose, xylan, cellulose and cellobiose was observed (Rodionov et al. 2021)

Adapting via translational regulation

One of the vital molecular mechanisms capable of detecting and adapting to changing ECs is gene expression regulation at the translational level. The microbial communities use environmental stimuli to tune the protein concentration and translational rate (Tollerson and Ibba 2020). The fluctuations in nutrient concentration leads to translational responses like riboswitch folding, and alarmone (*ppGpp*) synthesis causing changes in cellular physiology (Wurch et al. 2019). Alarmone synthesis starts in response to stimuli like ribosome pausing during elongation phase of translation process. When cells have lesser availability of amino acids, the uncharged tRNA fraction increases that raises the chances of uncharged tRNA entering ribosomal A-site. This induces the Rel A binding of *ppGpp* synthase and alarmone synthesis begins thereby regulating wide range of cellular processes (Traxler et al. 2008; Brown et al. 2016). Cyanobacterial heat shock proteins preserve the integrity of thylakoid membranes under stress conditions like heat, light, or salt stress (Cimdins et al. 2014; Wani et al. 2021). Psychrophiles adapt to low temperature ranges through a series of structural, physiological, metabolic, and sequence adjustments. Aspartic acid, alanine, serine, and threonine are overrepresented in the coiled regions of secondary structures pertaining to psychrophilic bacteria, while as leucine and glutamic acid in helical regions are underrepresented (Metpally and Reddy 2009). Thermophilic bacteria show heat resistance through tRNA and tRNA associated enzymes mediating cascade of translational events. The combination of tRNA enzymes and modified nucleosides like, dihydrouridine, 4- thiouridine, N^2-methyl guanosine, form a network that regulates tRNA modifications at higher temperature (Hori 2019). Halophilic *Methanohalophilus portucalensis*, a methanoarchaeon, synthesizes osmolyte betaine in response to salt stress making it as an essential osmoadaptive strategy (Lai and Lai 2011). Translational regulation in *E. coli* during temperature shift from 37 °C (Optimum temperature) to 10 °C (Cold shock) has been well illustrated through the expression of thermosensing RNAs. Cell growth and protein synthesis stops during acclimation phase and thereafter grow at slower rate. Importantly, the mRNAs encoding these cold shock proteins make certain structures that ensures their regulartion at lower temperatures (Zhang et al. 2018; Lindquist and Mertens 2018).

Adapting via horizontal gene transfer

Horizontal gene transfer (HGT) entails the movement of genetic material, either DNA or RNA, between organisms via non-sexual methods where the transferred genetic material can either replace the existing genes or add new genes to the genome (Keeling and Palmer 2008). HGT is more common in prokaryotes where they play an important role in microbial evolution and adaptation to new environment (Wagner et al. 2017; Hall et al. 2020). Canonically, the HGT occurs in prokaryotes through mechanism such as conjugation, transduction and transformation (García-Aljaro et al. 2017). However, the HGT in prokaryotes can occur via other ways such as through mobile genetic elements, integrating conjugative element, membrane vesicles, and gene transfer elements (García-Aljaro et al. 2017). In archaea also other ways of horizontal gene transfer occurs such as cell fusion and a specific DNA transport system which plays an important role during DNA damage (Wagner et al. 2017). The role of HGT in helping the microbes to adapt to extreme environmental conditions such as UV irradiation has been explored in *Sulfolobus acidocaldarius* and *Sulfolobus solfataricus* (Ajon et al. 2011). *S. acidocaldarius* and *S. solfataricus*, the hyperthermophilic archaea, when exposed to DNA damaging factors like bleomycin, UV irradiation or mitomycin C showed an upsurge in the induction of species-specific cellular aggregation (Götz et al. 2007). In *S. acidocaldarius*, cellular aggregation induced by UV has been reported to mediate chromosomal exchange with a higher frequency. The recombination rates well exceeds the uninduced cultures by three times (Ajon et al. 2011). Scientists have reported that the cellular aggregation improves species specific transfer of DNA among the *Sulfolobus* cells to provide enhanced DNA damage repair system through homologous recombination (Wagner et al. 2017). This was also supported by the findings of van Wolferen et al. 2013, suggesting DNA exchange under extreme conditions in hyperthermophiles which plays an essential role in DNA repair through homologous recombination. Accurate DNA repair is important for maintaining gene functions. *Chalamydomonas* sp. *ICE-L*, a unicellular alga, thrives in cold polar sea where it withstands high salinity, low temperature and seasonal changes. Zhang et al. (2020) assembled genome sequence of ~542 Mb and reported that retrotransposon proliferation largely contributes to the genome size of ICE-L, which was hypothesized that it may support fatty acid synthesis, ionic homeostasis, ROS detoxification, DNA repair, and photoreception. The acquisition of several ice binding proteins via putative HGT likely supports the lifestyle of psychrophiles (Raymond and Remias 2019). The lesser genomic content limits the adaptive nature of thermophiles in fluctuating environment (Hickey and Singer 2004). The active HGT allows the fast spread of strain specific adaptive gene networks in the entire population. The constitutive expression of an efficient DNA transport module (DTM) is at the middle of HGT-mediated improved adaptability (Sun et al. 2019). The function of DTM is highly integrity and longevity dependent of the transformed extracellular DNA (eDNA) improved by extracellular vesicles. Blesa and Berenguer (2015) studied the contribution of vesicle protected eDNA to HGT in *Thermus spp*. and reported protection against DNAse was a resultant of eDNA association to vesicles.

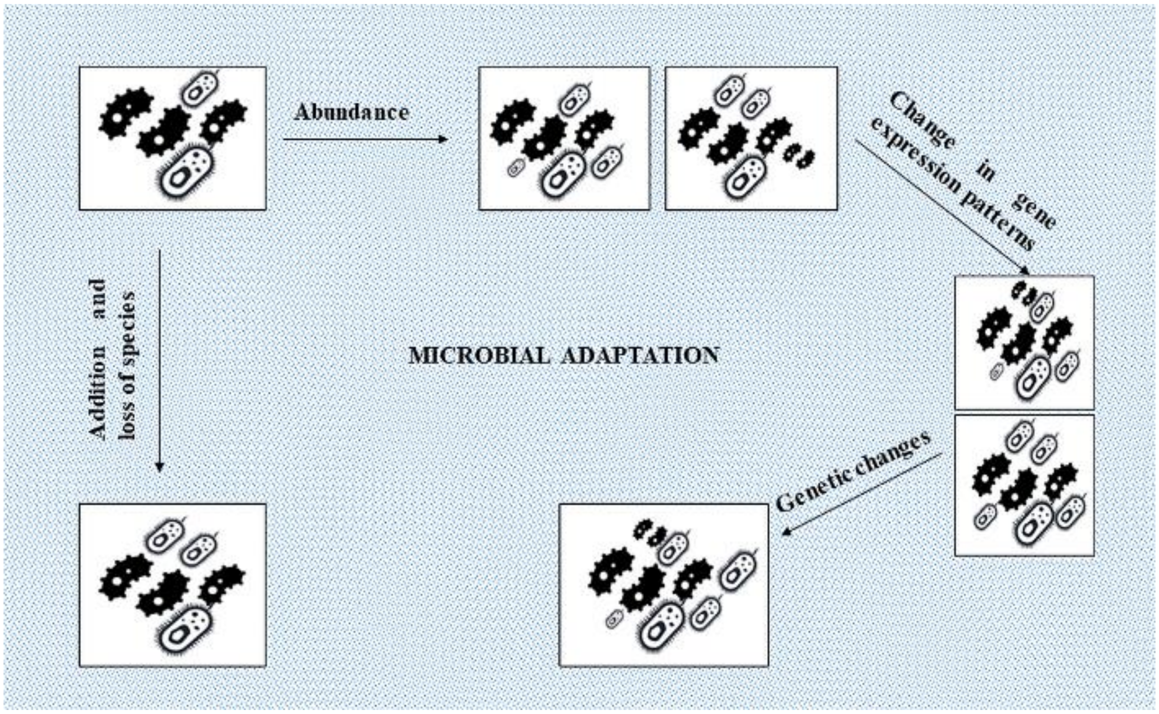

Figure 2: Changes in genetic and community structure and composition during microbial adaptation to extreme environments.

Table 3: Extremophiles and their adaptive strategies involving genes and gene products

Extremophiles	**Examples**	**Adaptive strategy**	**References**
Hyperthermophile	M*ethanopyrus kandleri*	Membrane consists of terpenoid lipid. 1B DNA topoisomerase V and the two-subunit reverse gyrase are two notable enzymes	Slesarev et al. 2002
Psychrophiles	*Arthrobacter cryoconiti, Chryseobacterium greenlandensis, Arthrobacter* sp., *Psychrobacter* sp.	Downregulation of genes translating into charged surface protein Reduced hydrophobic core	Margesin et al. 2012; Fresco-Taboada et al. 2013; Koh et al. 2019
Thermophiles	*Alicyclobacillus acidocaldarius, A. tengchongensis, A. ferrooxydans*	Upregulation of genes giving rise to proteins forming prominent hydrophobic core and least charged protein surface.	van Wolferen et al. 2013; Reed et al. 2013
Piezophiles	*Pyrococcus yayanosii, Shewanella* sp., *Moritella* sp.,	Smaller amino acids forming hydrophobic core. Presence of pressure-sensing operon system with their growth regulated by both temperature and pressure	Peoples et al. 2020
Barophiles	*Halomonas salaria*	Tight membrane lipid packing. Homoviscous adaptation through elevation of unsaturated fatty acids and robust DNA repair system.	Michoud and Jebbar 2016; Hamsanathan et al. 2021
Hyperalkaliphile	*Bacillus pseudofirmus, Alkaliphilus metalliredigens*	Intracellular pH homoeostasis. High Level of Monovalent Cation/Proton Antiporters.	Preiss et al. 2015; Mamo 2020

		Effective Proton Capturing by ATP Synthase	
Radiation resistant	*Deinococcus radiodurans, Ignicoccus hospitalis, Methylobacterium radiodurans*	Efficient repair system for disintegrated DNA. Multiple antioxidant systems. Increased genome copy number	Krisko and Radman 2013; Koschnitzki et al. 2021; Maeng et al. 2021

Conclusion

The microbial adaptation in different environmental conditions is mediated by complex cellular changes that maintain physiology and metabolism, thereby ensuring survival. These adaptable characters act in a regulated manner at cellular, genetic and molecular levels, which involves gene expression and gene silencing. Several studies elucidated discus the molecular perspective of microbial adaptations via signal proteins and transcriptional regulators. Yet, better clarity and explanations are required to tackle the harmful effects caused by adaptive behavior like infection and antibiotic resistance. Understanding and analyzing the peculiarity of microbes in different environment will ensure manipulating the environments in a useful manner that largely remains obscure. Microbial diversity exploration in extreme environments have already revolutionized molecular studies by bio-prospection of thermostable and other stable biomolecules at extreme conditions of pH, temperature, pressure, etc. So far, the topic of microbial adaptation has been explored comprehensively in various studies and helped us to identify the fundamental forces controlling this complex process but the intrinsic cellular and molecular mechanisms along with the metabolic pathways involved in these adaptations is yet to be completely understood. Hence, the studies examining microbial adaptation and evolutionary patterns under different environments are imperative and need further exploration. In future, the better understanding of how the microbes evolve and adapt to their changing environment can help in further understanding the physiology of microbes and discovering new strategies to control microbes that can be harmful to human health and agriculture. The understanding of microbial adaptation can also be useful in developing novel avenues to remove harmful pollutants from the environment efficiently.

Declarations

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