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Importance of extremophilic microorganisms in biogeochemical cycles

Arlette Galván González ¹ and Rocío Pérez y Terrón ^{2,*}

¹ *Academic Unit of Agriculture, Autonomous University of Nayarit, Jalisco, Nayarit, Mexico.*

² *Faculty of Biological Sciences, Meritorious Autonomous University of Puebla, Puebla de Zaragoza, Puebla, Mexico.*

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Abstract

Extremophilic microorganisms are organisms capable of proliferating under extreme conditions that are generally detrimental to most life on Earth. They are organisms considered of importance in different areas of research, due to their ability to produce proteins and enzymes under inhospitable conditions. Therefore, in the present work, the information on their participation in the processes of biogeochemical cycles was collected and analyzed in order to demonstrate their ecological importance. Recent studies on the metabolic pathways of the Extremophilic microorganisms and their environment have shown that most of the archaea, some bacteria and cyanobacteria carry out metabolic activities essential for the biogeochemical cycles of sulfur, carbon and nitrogen. Archaea and bacteria being one of the main microorganisms that participate in a variety of processes such as sulfidogenesis, methanogenesis, ANAMMOX (anaerobic ammonium oxidation), among others. This has suggested that Extremophilic microorganisms and extreme ecosystems have a significant impact on global biogeochemical cycles.

Keywords: Extremophilic microorganisms; Biogeochemical cycles; Sulfur; Carbon; Nitrogen

1. Introduction

"Extremophilic microorganisms are organisms that thrive physically or geochemically in extreme conditions that are generally harmful to most life on Earth" [1]; such as very high or very low temperatures, high or low pH levels, high pressures, low availability of nutrients or high concentrations of salt. Extreme environments are defined as those environments or ecosystems that exceed the limits of the ranges of the physical-chemical environmental parameters suitable for most living beings [2, 3]. These ecosystems are cold polar lands and seas, alpine glaciers, underwater vents, saline lakes, hot springs, volcanic areas, ecosystems on the seabed or under the earth's crust (where pressure values are very high), among others [3,4]

Extremophiles are found in the three domains of life: Archaea, Bacteria, and Eukarya; but most of the Extremophiles belong to the domain of Archaea [1]. In general, these organisms are classified according to the environmental conditions in which they grow optimally; thus we have: acidophiles (pH ≤ 3), alkaliphiles (pH ≥ 9), halophiles (high salt concentration), hyperthermophiles (temperatures > 80 ° C), thermophiles (temperature between 42-122 ° C), piezophiles (high pressures), psychrophiles (temperatures ≤ -15 ° C), radiophiles (UV radiation, cosmic rays, X-rays) and xerophiles (drying conditions; $\leq 50\%$ relative humidity) [1, 5]. Those who can thrive in more than one extreme condition are called polyextremophiles [6].

The main elements that make up living beings, such as carbon (C), nitrogen (N), hydrogen (H), oxygen (O), sulfur (S), phosphorus (P), among others, are also found in oceans and in different deposits or reservoirs of these chemical elements [7]. The circulation of these nutrients between the ecosystem and living beings is known as the biogeochemical

* Corresponding author: Rocío Pérez y Terrón

Faculty of Biological Sciences, Meritorious Autonomous University of Puebla, Puebla de Zaragoza, Puebla, Mexico.

cycle or nutrient cycle [8]. Offre *et al.* in 2013 mention that this cycle arises from geophysical processes and the combined metabolisms of life forms. Biogeochemical cycles are influenced by anthropogenic activities and climate change and global warming, for this reason, it is important to understand the magnitude of the effects that these factors have on the response of ecosystems on these cycles [1].

Microorganisms are the main drivers of biogeochemical cycles in the biosphere [9], therefore, it is deducible that extremophilic microorganisms also play an important role in these cycles. In the case of archaea, they play an important role in these cycles because they participate in at least three of them, in the carbon, nitrogen and sulfur cycle. "At least two essential metabolisms for these cycles are carried out exclusively by archaea and the third metabolism by archaea and bacteria" [7]. Considering that these cycles are driven mainly by microorganisms, more studies should be carried out to try to understand their physiology, metabolism and their role in mediating cycles in extreme environments [1].

Extremophiles have been considered important organisms in different areas of research due to their ability to produce functional proteins and enzymes under extreme conditions. They are used in biotechnological studies, in bioremediation, in studies on adaptations to hostile conditions, in the search for the possible existence of life in other planetary bodies and in biogeochemical cycles. In this work, information on the participation of some extremophiles was collected and analyzed, relating them to the processes of biogeochemical cycles, to try to understand their ecological importance, and that this analysis serves as support when making measurements and predictions resulting from their metabolic activity in a natural environment.

2. Material and methods

In order to demonstrate the importance of extremophilic microorganisms in biogeochemical cycles in this retrospective and documentary research, information on the participation of extremophiles in these cycles was collected. First, a literature search was carried out on the main biogeochemical cycles in which they participate. The research was carried out through a retrospective documentary analysis. Extremophiles that are part of these cycles were analyzed. Any extremophilic microorganisms, whether fungi, algae, archaea or bacteria, were taken into account. Later, the cycles and the points of these were described together, where the extremophiles carry out some important metabolic activity for the processes of the cycles.

3. Results and discussion

The biogeochemical cycle or nutrient cycle is that circulation and redistribution of nutrients (elements) between living beings and the ecosystem [7, 10]. These elements are found in oceans, atmosphere, rocks and in some extreme ecosystems (salty lakes, sea ice and polar regions, shallow and deep-water hydrothermal vents, hyperacidic lakes and volcanoes, among others) [3, 5, 4].

In recent years, studies have been carried out on the metabolic pathways of the extremophilic microorganisms and their environment, and they have shown that the majority of archaea, some bacteria and cyanobacteria participate in the processes of the biogeochemical cycles of sulfur, carbon and nitrogen [7]. The role that extremophilic fungi play in biogeochemical cycles is still not well understood, however, it is believed that if they could play an important role, due to their ability to survive in extremely oligotrophic conditions, they could be suppliers of H₂ to autotrophic organisms. in deep water [11].

3.1. Sulfur cycle (S)

The sulfur cycle is primarily driven by the metabolic activities of microorganisms, most of which reside in the ocean. There are several sulfur reservoirs, but the ocean represents the largest reservoir; there it is found in the form of dissolved sulfate and sedimentary minerals [12].

Archaea and bacteria are one of the main microorganisms that influence the sulfur cycle; they use this inorganic element to form organic compounds (assimilation, energy-dependent process) and to produce energy (dissimilar sulfur metabolism). They are essential processes for the global sulfur cycle [12]. These microorganisms participate in a variety of processes in the cycle, which result in the production or oxidation of sulfidic compounds [7].

3.2. Sulfidogenesis

Sulfidogenesis is the production of sulfur through dissimilatory reduction of oxidized sulfur compounds, such as sulfate (SO₄²⁻), sulfite (SO₃²⁻), thiosulfate (S₂O₃²⁻) and sulfur [13].

Some members of the bacteria *Deltaproteobacteria* and *Epsilonproteobacteria* are capable of reducing elemental sulfur to hydrogen sulfide (H_2S); and archaea belonging to the phylum *Euryarchaeota* and *Crenarchaeota* produce H_2S , through the dissimilatory reduction of elemental sulfur, sulfite, thiosulfate or sulfate [7]. Sulfidogenesis is an important biogeochemical process in saline lakes, some species of bacteria belonging to the genera *Desulfonatronum*, *Desulfonatronovibrio*, and *Desulfonatronospira* (deltaproteobacteria), represent sulfate reducing lithotrophic bacteria (SRB) in saline lakes [13].

3.3. Sulfur oxidation

Sulfur oxidation can produce elemental sulfur or sulfate [13]. Archaea and bacteria are the main involved in this reaction and it is believed that they have an important role in the formation of sulfur deposits [14, 7].

Some examples of sulfur oxidizing bacteria (SOB) are: the chemolithotrophic bacteria *Bacillus* and *Acidithiobacillus*, as well as the phototrophic bacteria *Chlorobium*, *Allochrochromatium*, *Rhodobacter*, *Rhodovulum* [14, 7, 13]. " In saline lakes, the bacteria that carry out this process are purplish sulfur anoxic bacteria, including some haloalkaliphilic species of the genera *Ectothiorhodospira* and *Halorhodospira* in high salinity, and of the genera *Thiorhodospira*, *Thioalkalicoccus* and *Ectothiorhodosinus* in low salinity" [13]. In these lakes, chemotrophic SOBs belong to four genera of haloalkaliphilic Gammaproteobacteria: *Thioalkalimicrobium* and *Thioalkalispira*, moderately salt tolerant aerobic alkalines; *Thioalkalivibrio* and *Thioalkalibacter* can grow in high salt concentrations [13].

Oxidizing archaea capable of oxidizing sulfur belong to some genera and orders of the phylum *Crenarchaeota* (*Sulfolobus*, *Desulfurococcus*, *Acidianus*, *Ferroglobus*, *Metallosphaera*) and *Thermoplasmatales* (*Euryarchaeota*) [14, 7]. Some *Acidianus* strains can also grow on carbon disulfide (CS_2), a component of volcanic exhalations, converting CS_2 to hydrogen sulfide (Offre et al, 2013). *Crenarchaeota* have the ability to oxidize elemental sulfur, but can only grow at temperatures above 65°C , and *Thermoplasmatales* include mesophiles that can withstand extreme acidity with a $\text{pH} = 0$ [7].

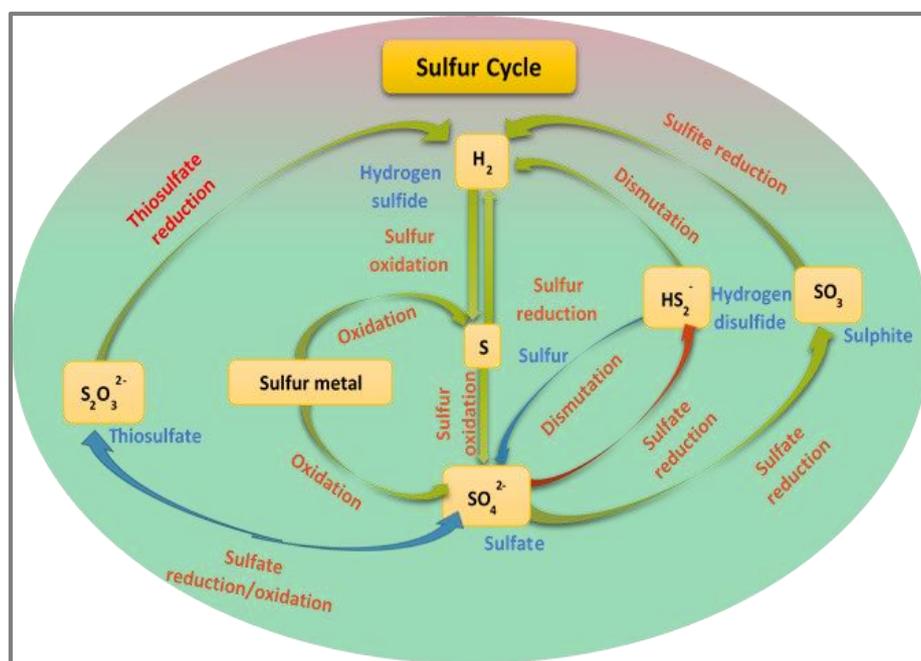


Figure 1 Scheme of the participation of archaea and bacteria in the sulfur cycle (modified from Offre *et al* [7]).

Figure 1. Schematically represents the metabolic processes of archaea and bacteria in the sulfur cycle (green arrows), metabolic processes present only of archaea (red arrows) and metabolic processes present only of bacteria (blue arrows).

3.3.1. Metabolic processes of archaea and bacteria

Oxidation of sulfur metal to sulfur or sulfate (SO_4^{2-}); the oxidation of hydrogen sulfide (H_2S) to sulfur; the reduction of sulfur to H_2S ; sulfur oxidation to SO_4^{2-} ; reduction of thiosulfate ($\text{S}_2\text{O}_3^{2-}$) to H_2S ; reduction of SO_4^{2-} to sulfite ($\text{S}_2\text{O}_3^{2-}$); and the reduction of SO_3^{2-} to H_2S .

3.3.2. Metabolic processes only in archaea

Reduction of SO_4^{2-} to hydrogen disulfide (HS^-).

3.3.3. Bacteria-only metabolic processes

Reduction / oxidation of SO_4^{2-} to $\text{S}_2\text{O}_3^{2-}$ or vice versa; dismutation from HS^- to SO_4^{2-} .

3.4. Carbon cycle (C)

Carbon is a fundamental element for life and is key in the biotic and abiotic processes of the Earth [15]. The carbon cycle is a series of carbon reservoirs on Earth and they are connected by carbon exchange fluxes. These reservoirs consist of carbon in the atmosphere, the ocean, in surface ocean sediments, vegetation, rocks, and other sediments [16].

The oceans are of great importance in the carbon cycle, because the coupling between the upper part of the ocean and the atmosphere results in high concentrations of dissolved CO_2 at the surface of seawater. In the ocean, the carbon cycle is largely driven by bacteria and archaea. Bacteria mediate a significant flow of organic matter, from dissolved organic matter (DOM) to particulate organic matter (POM) and represent a substantial fraction of heterotrophic respiration in the oceans [17].

3.4.1. Carbon fixation

Carbon fixation is carried out mainly by archaea, bacteria, algae and cyanobacteria [7, 13, 18]. With respect to archaea, various members of *Crenarchaeota*, *Thaumarchaeota* and *Euryarchaeota* are autotrophic, due to the fact that they assimilate carbon through oxidized inorganic compounds (carbon dioxide or bicarbonate). However, there are some archaea that are mixotrophic, that is, they are capable of changing their nutritional form and can be autotrophic or heterotrophic, or co-assimilate small organic compounds under suitable conditions [7].

It is believed that the archaea belonging to *Thaumarchaeota* could be contributing approximately 1% of the annual production of carbon in the ocean, and could also provide in some cases, most of the reduced carbon for heterotrophic microorganisms in zones of minimal oxygen (OMZ) [7]. In the case of sea ice algae, although annual carbon production is relatively low, they play an important role in the polar biogeochemical carbon cycle; because they are a fixed carbon source for higher trophic levels in ice-covered waters [18].

In salt lakes, the autotrophic primary producers capable of fixing CO_2 in organic polymers are some oxygenic and anoxygenic haloalkaliphilic phototrophs, and some chemolytoautotrophs. In most of these lakes, primary production is high due to the dense population of haloalkaliphilic cyanobacteria [13].

3.5. Methane cycle

Methane CH_4 is an important greenhouse gas in the global carbon cycle. Anaerobic methane oxidation (AOM) is a unique metabolism of extremophiles and is mediated primarily by anaerobic methanotrophic archaea (ANME) and sulfate-reducing bacteria [7, 19, 20, 21]. AOM represents 2% of the methane released into the atmosphere and consumes approximately 80% of the methane that arises from hydrocarbon seeps on the seabed; and the reduction of CO_2 represents the rest of the contribution of archaea to atmospheric methane, with small amounts of methane produced by the dismutation of methyl compounds [7, 19].

The methanogenic archaea that have been characterized are found among five classes belonging to *Euryarchaeota*: *Methanopyri*, *Methanococci*, *Methanobacteria*, *Methanomicrobia*, and *Thermoplasmata*. Methanogens are found in various types of ecosystems, such as: rice fields, pipelines, hydrothermal vents, subsurface habitats, freshwater, marine and hypersaline sediments, and even in the gastrointestinal tract of some animals [7].

Methanotrophs are gram-negative aerobic bacteria and generally only grow in methane or methanol as a carbon and energy source [20]. In salt lakes, the main aerobic methanotrophs are: *Methylococcaceae* family of *Gammaproteobacteria*; and the main haloalkaliphilic ones are: *Methanobolus taylorii* (in moderate salinity) and *Methanosalsum zhilinae* (in high salinity), and the lithotroph *Methanocalculus natronophilus* (highly tolerant to salt) [13, 20].

Offre *et al.* (2013) [7] show some methanogenic pathways (carried out by methanogens) that depend on various substrates, which:

- Hydrogenotrophic methanogens: reduction of CO₂ with hydrogen
- Formatotrophic methanogen: CO₂ reduction with formate
- Acetoclastic methanogens: acetate fermentation
- Methylotrophic methanogens: dismutation of methylated compounds (methanol, methylamine, dimethylsulfide or methanethiol).

Acetate fermentation is performed by only a few methanogens, but could account for up to 2/3 of the methane released into the atmosphere through archaea methanogenesis [7].

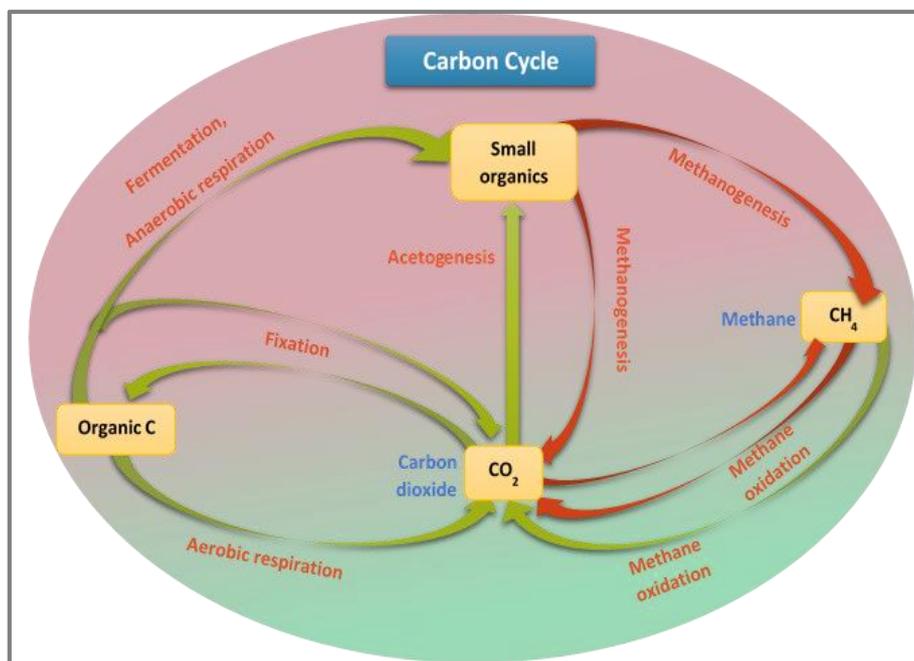


Figure 2 Scheme of the participation of archaea and bacteria in the carbon cycle (modified from Offre *et al* [7]).

In Figure 2, metabolic processes of archaea and bacteria are schematically represented (green arrows) and metabolic processes present only of archaea (red arrows).

3.5.1. Metabolic processes of archaea and bacteria:

- Oxidic environment Oxidation of methane to CO₂ and aerobic respiration.
- Anoxic environment: Fermentation and anaerobic respiration take place from organic C, which results in small organics or CO₂; the fixation of CO₂ to organic C; and Acetogenesis from CO₂ resulting in small organics.

3.5.2. Exclusive metabolic processes of archaea:

- Anoxic environment Methanogenesis by hydrogenotrophic methanogens reduces CO₂ with hydrogen to methane (CH₄); Methanogenesis by formatotrophic, acetoclastic, and methylotrophic methanogens degrades formate, acetate, and methylated compounds, respectively, to CO₂; oxidation of methane to CO₂.

3.6. Nitrogen cycle (N)

The nitrogen (N) cycle is one of the most important biogeochemical cycles in nature, because it is found in various forms such as ammonium (NH₄⁺), organic nitrogen, nitrate (NO₃⁻), among others, circulating in large flows in the atmosphere, land and water through various biological processes [1, 22]. Nitrogen is part of the main building blocks of life (found in DNA, RNA, and proteins); it is the dominant gas on Earth; it is stored in all geological deposits on Earth (the crust, mantle and core); and plays an important role in the biogeochemistry of the ocean [1]. In the ocean, its main sources of N are the biological fixation of N₂ and atmospheric deposition, and in the sinks, the main sources are denitrification and anaerobic oxidation of ammonia [22].

Microorganisms are the main ones in mediating the redox transformations of N and change the concentrations of N compounds in the environment. For this reason, it is possible to suppose that Extremophilic microorganisms play an

important role in catalyzing reactions of the N cycle in extreme environments such as salty lakes, mining sites, hot springs, volcanoes, among others [1, 22].

3.6.1. Fixation of nitrogen

Atmospheric nitrogen mainly enters the food chain through nitrogen fixation, which consists of the reduction of N_2 to NH_3 . This process is carried out naturally by bacteria and archaea [1, 7].

The assimilation of nitrate and ammonium is characterized in symbiotic microorganisms, mesophilic bacteria, algae, plants and fungi [1, 7]. The ability to fix N_2 gas or diazotrophy “metabolic capacity to fix atmospheric nitrogen in a biologically useful form” [23], is a generalized characteristic of methanogenic archaea, although it is also present in the oxidizing anaerobic euriarchaeotes (or euriotes) of methane, in some species of bacteria, and cyanobacteria [7, 22].

In saline lakes, ammonia produced during nitrogen fixation can be oxidized to nitrate via nitrite by haloalkaliphilic nitrifiers. In these lakes and on saline soils, the oxidation of ammonium to nitrite is carried out by a subpopulation of *Nitrosomonas halophila* extremely tolerant to alkalis, while the oxidation of nitrite can be carried out by *Nitrobacter alkalicus* which are moderately tolerant to alkalis [13].

Information on nitrogen fixation in extreme environments is scarce and is limited to a few members of the *Haloferacaceae* family (halophilic archaea) or some thermophilic bacteria [1]. In the case of saline lakes, there is very little information about the nitrogen fixation that occurs in these, however, it is believed that there is a group of heterocyst alkaliphilic cyanobacteria with low tolerance to salt from the *Anabaena* group (*Anabaenopsis* and *Nodularia*) that possibly carry out this activity [13].

3.6.2. Nitrification

The nitrification process has a global impact on the form of inorganic nitrogen (ammonia or nitrate) in ecosystems. This process consists of two steps, and each step is catalyzed by different groups of microorganisms: (1) oxidation of ammonia (NH_3) to nitrite (NO_2^-) and (2) its subsequent conversion to nitrate (NO_3^-) [7].

Anaerobic ammonium oxidation (ANAMMOX) is the process of oxidation of ammonium (NH_4^+) through the reduction of NO_2^- . Extremophilic microorganisms capable of carrying out the ANAMMOX process have recently been described in natural ecosystems, such as some extreme freshwater environments, hot springs, and deep-sea hydrothermal vents [1]. Lithoautotrophic archaea (thrive in oxidic and moderate habitats) have the ability to oxidize ammonia (NH_3) to nitrite (NO_2^-) and their high numbers in marine and fresh waters, soils and surface sediments, and warm environments suggest an important role in the global nitrogen cycle [7].

Aerobic oxidation of ammonium (NH_4^+) is the process of converting ammonium to nitrate. It is essential for the nitrogen cycle and is currently believed to be driven by two main groups of microorganisms, the chemolithotrophic ammonia oxidizing bacteria (AOB) and the ammonia oxidizing archaea (AOA) [1].

3.6.3. Denitrification

Denitrification is an anaerobic airway where nitrate (NO_3^-) is reduced to nitrogen compounds such as N_2 , nitric oxide (NO) and / or nitrous oxide (N_2O) [1, 7]. Extremophilic microorganisms that have been reported to carry out this process are some species of thermophilic bacteria of the genus *Thermus*, some species of halophilic archaea, the thermophilic archaea *Pyrobaculum aerophilum* and some moderately halophilic bacteria [1].

Denitrification occurs in various environments, both in fresh and marine waters, as well as in soils, and is generally carried out by facultative anaerobes that grow in microaerophilic or anoxic conditions (some bacteria, archaea and eukaryotes) [7]. In salty lakes, this process is carried out by some species of the genus *Halomonas* (extremely salt-tolerant alkaliphiles), by several facultative anaerobic lithotrophs of the genus *Thioalkalivibrio* and the *Alkalilimnicola* – *Alkalispirillum* group of Gammaproteobacteria [13].

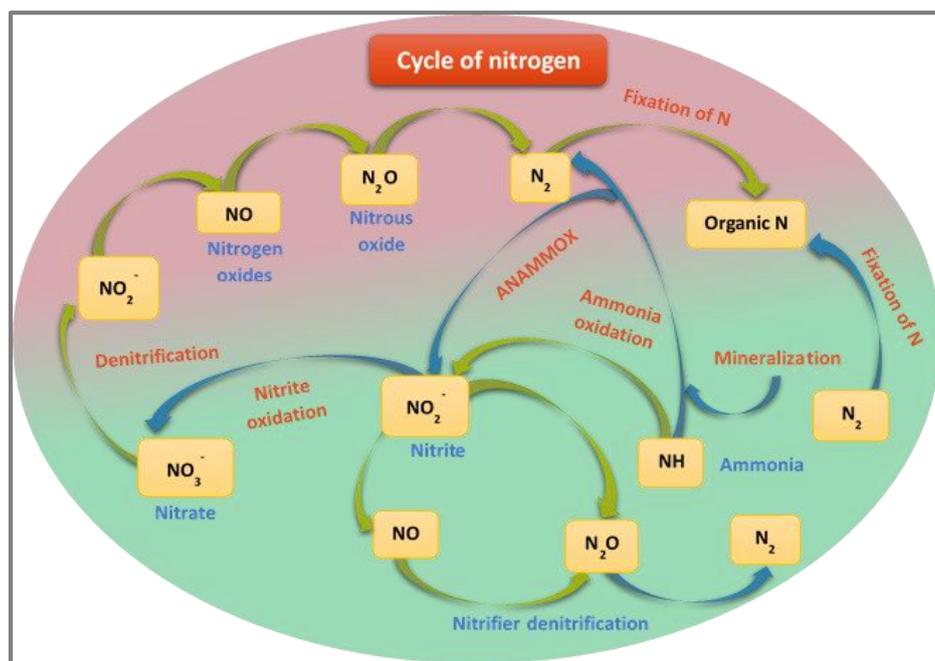


Figure 3 Scheme of the participation of archaea and bacteria in the nitrogen cycle (modified from Offre *et al* [7]).

Figure 3 schematically represents the metabolic processes of archaea and bacteria in the nitrogen cycle (green arrows) and metabolic processes present only of bacteria (blue arrows).

3.6.4. Metabolic processes of archaea and bacteria

- Oxidic environment: Mineralization of organic nitrogen to ammonia (NH_3) and vice versa; oxidation of NH_3 to nitrite (NO_2^-); "Nitrous oxide, N_2O , can be a direct product of the oxidative pathway of ammonia"; denitrification of NO_2^- to nitric oxide (NO).
- Anoxic environment: Denitrification of nitrate (NO_3^-) to nitrite (NO_2^-); denitrification of NO_2^- to NO ; denitrification of NO to N_2O ; denitrification of N_2O to N_2 ; and fixation of N_2 to organic nitrogen.

3.6.5. Bacteria-only metabolic processes

- Oxidic environment: Fixation of N_2 to organic nitrogen; mineralization; denitrification of N_2O to N_2 ; and oxidation of NO_2^- to NO_3^- .
- Anoxic environment: ANAMMOX process.

Examples of Extremophilic Microorganisms Participating in the Biogeochemical Processes of Sulfur (S), Carbon (C), and Nitrogen (N)

Extremophilic microorganisms inhabit a wide variety of ecosystems, both on the surface of the Earth and below it, and by regulating these ecosystems they present one or more extreme physical or chemical conditions [3, 4, 5]. A great variety of microorganisms can be found in these ecosystems, such as archaea, bacteria, algae, fungi and eukaryotes; However, most of the Extremophiles belong to the Archaea domain, and through research it has been shown that they are essential in the biogeochemical cycles, because some metabolic processes in the sulfur and carbon cycles are carried out exclusively by archaea [7]. Archaea have a significant biogeochemical impact, for example, their syntrophic interactions (obligatorily mutualistic metabolism) [47], allow the degradation of complex organic molecules to CO_2 and CH_4 in methanogenic habitats; and through methanogenesis, they produce around 1 Gt (gigaton) of methane each year, representing approximately 74% of the annual net emissions of methane to the atmosphere [7].

Recent research has suggested the importance of extreme ecosystems in biogeochemical cycles, such as salty or saline lakes, polar ecosystems, and glaciers [13, 48]. In salty lakes, groundwater is rich in CO_2 , poor in magnesium and calcium; They are highly productive and functional ecosystems for a great diversity of communities of haloalkaliphilic microorganisms, responsible for the sulfur, carbon and nitrogen cycles [13]. In glacial and polar ecosystems, a great diversity of communities of microorganisms capable of sequestering nitrogen from the atmosphere has been found,

particularly in cryoconite holes, where a great variety of microorganisms such as bacteria, algae, tardigrades, among others have been found [49].

Table 1 Some examples of Extremophilic microorganisms that participate in the biogeochemical cycles of sulfur (yellow), carbon (green) and nitrogen (blue) are shown; sulfur and carbon (light brown), nitrogen and carbon (purple), sulfur and nitrogen (pink); and the type of Extremophile [1, 5, 7, 12, 13, 14, 20, 22, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46].

	Microorganism	Extremophilic type
Bacterium	Proteobacteria:	
	<i>Acidithiobacillus</i>	Acidophilic
	<i>Allochromatium</i>	Halophilic
	<i>Ectothiorhodospira</i>	Haloalkaliphilic
	<i>Halorhodospira</i>	Haloalkaliphilic
	<i>Ectothiorhodosinus</i>	Haloalkaliphilic
	<i>Thiorhodovibrio</i>	Halophilic
	<i>Nitrosomonas halophila</i>	Haloalkaliphilic
	<i>Nitrobacter alkalicus</i>	Alkaliphilic
	Deltaproteobacteria:	
	<i>Desulfobulbus alkaliphilus</i>	Haloalkaliphilic
	<i>Desulfonatrobacter acidivorans</i>	Haloalkaliphilic
	<i>Desulfonatrovibrio hydrogenovorans</i>	Alkaliphilic
	<i>Desulfonatrovibrio magnus</i>	Haloalkaliphilic
	<i>Desulfonatrovibrio thiodismutans</i>	Haloalkaliphilic
	<i>Desulfatronospira thiodismutans</i>	Haloalkaliphilic
	<i>Desulfatronum cooperativum</i>	Haloalkaliphilic
	<i>Desulfatronum thiosulfatophilum</i>	Haloalkaliphilic
	<i>Desulfatronum thioautotrophicum</i>	Haloalkaliphilic
	<i>Desulfatronum thiodismutans</i>	Haloalkaliphilic
	<i>Desulfatronum buryatense</i>	Haloalkaliphilic
	<i>Desulfatronum lacustre</i>	Haloalkaliphilic
	Gamma proteobacteria:	
	<i>Thioalkalimicrobium</i>	Haloalkaliphilic
	<i>Thioalkalispira</i>	Haloalkaliphilic
	<i>Thioalkalivibrio</i>	Haloalkaliphilic
	<i>Thioalkalibacter</i>	Haloalkaliphilic
	<i>Thiorhodospira</i>	Haloalkaliphilic
	<i>Methylomicrobium alcaliphilum</i>	Haloalkaliphilic
	<i>Methylomicrobium sp.</i>	Haloalkaliphilic
	<i>Methanobolbus taylorii</i>	Haloalkaliphilic
	<i>Methanosalsum zhilinae</i>	Haloalkaliphilic
	<i>Methanocalculus natronophilus</i>	Haloalkaliphilic
	<i>Halomonas sp. AIR-2</i>	Haloalkaliphilic
	<i>Halomonas sp. Z-7009</i>	Haloalkaliphilic
	<i>Thioalkalivibrio denitrificans</i>	Alkaliphilic
	<i>Alkalilimnicola halodurans</i>	Haloalkaliphilic
	<i>Alkalilimnicola ehrlichii</i>	Haloalkaliphilic

	<i>Alkalispirillum</i>	Haloalkaliphilic
	Firmicutes:	
	<i>Bacillus</i>	Alkalophilic
	<i>Clostridium alkalicellum</i>	Alkalophilic
	<i>Anoxyratronum sibiricum</i>	Alkalophilic
	<i>Anaerobranca gottschalkii</i>	Thermoalkaliphilic
	<i>Anaerobacillus alkalilacustris</i>	Alkalophilic
	<i>Dethiobacter alkaliphilus</i>	Alkalophilic
	Chlorobi:	
	<i>Chlorobium</i>	Thermophilic
	Deinococcus-Thermus:	
	<i>Thermus thermophilus</i>	Thermophilic
	Thermotogae:	
	<i>Thermotoga maritima</i>	Hyperthermophilic
	Leptospirillum:	
	<i>Leptospirillum ferriphilum</i> ML-04	Acidophilic
	Cyanobacteria:	
	<i>Arthrospira</i>	Alkalophilic
	<i>Anabaenopsis</i>	Alkalophilic
	<i>Cyanospira</i>	Alkalophilic
	<i>Nodularia</i>	Alkalophilic
Archaea	Euryarchaeota:	
	<i>Termoplasmatales</i>	Thermophilic
	<i>Methanopyri</i>	Thermophilic
	<i>Methanococci</i>	Thermophilic
	<i>Methanobacteria</i>	Thermophilic
	<i>Methanomicrobia</i>	Thermophilic
	<i>Haloferacaceae</i>	Halophilic
	<i>Archaeoglobales</i>	Hyperthermophilic
	<i>Halobacteriales</i>	Halophilic
	<i>Thermococcales</i>	Hyperthermophilic
	<i>Nanohaloarchaea</i>	Hyperhalophilic
	Crenarchaeota:	
	<i>Sulfolobus</i>	Thermophilic
	<i>Desulfurococcus</i>	Thermophilic
	<i>Acidianus</i>	Thermophilic
	<i>Ferroglobus</i>	Hyperthermophilic
	<i>Metallosphaera</i>	Thermophilic
	<i>Pyrobaculum aerophilum</i>	Hyperthermophilic
	Thaumarchaeota	Thermophilic

The sequestration of NH_4 by microorganisms is an important component of the annual nitrogen fluxes of the glacial surface, representing around 50% of the atmospheric NH_4 deposited in the snow cover [49]. Regarding the carbon cycle in the polar regions, sea ice algae play an important role in carbon fixation, fixing approximately between 2-10% (in the Arctic) and 1-3% (in the Antarctic) of total annual production [18].

4. Conclusion

Because the first extremophilic microorganisms on the planet were the ones that modified the environmental conditions of the Earth, transforming it into a planet with oxygen, it is highly probable that extremophilic microorganisms currently have an important role in global biogeochemical cycles.

Recent research has suggested the importance of these microorganisms and their habitat in biogeochemical cycles, and has shown that some members of archaea, bacteria and cyanobacteria perform essential metabolic activities for the sulfur, carbon and nitrogen cycles. Archaea and bacteria being one of the main microorganisms that influence these cycles, participating in a variety of processes such as sulfidogenesis, methanogenesis, ANNAMOX, among others. This has suggested that extremophilic microorganisms and extreme ecosystems have a significant impact on global biogeochemical cycles. In addition, the study of their function in these cycles could provide information so that in the future measurements and predictions of the biogeochemical fluxes resulting from their metabolic activity in a natural environment can be made.

Compliance with ethical standards

Disclosure of conflict of interest

The authors declare not to have any interest conflicts.

References

- [1] Martínez-Espinosa RM. Microorganisms and Their Metabolic Capabilities in the Context of the Biogeochemical Nitrogen Cycle at Extreme Environments. *International Journal of Molecular Sciences*. 2020; 21(2): 4228.
- [2] Boyd R, Krell NT, Rajakaruna N. Extreme Environments. En D. Gibson (ed.). *Oxford Bibliographies in Ecology*. 2016.
- [3] Gómez F. *Life in extreme environments*. 2016.
- [4] Oliart-Ros RM, Manresa-Presas A, Sánchez-Otero M. Use of microorganisms from extreme environments and their products in biotechnological development. *Ciencia UAT*. 2016; 11(1): 79-90.
- [5] Merino N, Aronson HS, Bojanova DP, Feyhl-Buska J, Wong ML, Zhang S, Giovannelli D. Living at the Extremes: Extremophiles and the Limits of Life in a Planetary Context. *Frontiers in Microbiology*. 2019; 10: 780.
- [6] Rothschild LJ, Mancinelli RL. Life in extreme environments. *Nature*. 2001; 409(6823): 1092-101.
- [7] Offre P, Spang A, Schleper C. Archaea in Biogeochemical Cycles. *The Annual Review of Microbiology*. 2013; 67(1): 437-357.
- [8] Hameed A. *Ecology Class Notes – Biogeochemical Cycle (Nutrient cycle)*. 2019.
- [9] Zheng B, Zhu Y, Sardan J, Peñuelas J, Su J. QMEC: a tool for high throughput quantitative assessment of microbial functional potential in C, N, P, and S biogeochemical cycling. *Sci. China Life Sci*. 2018; 61: 1451-1462.
- [10] Summons RE. Biogeochemical Cycles. En M. H. Engel., S. A. Macko (eds.) *Organic Geochemistry. Topics in Geobiology*, 11. Boston, MA.: Springer. 1993.
- [11] Drake H, Ivarsson M. The role of anaerobic fungi in fundamental biogeochemical cycles in the deep biosphere. *Fungal Biology Reviews*. 2017; 32(1): 20-25.
- [12] Sievert SM, Kiene RP, Schulz-Vogt HN. *The sulfur Cycle*. The Oceanography Society. 2007; 20(2).
- [13] Sorokin DY, Berben T, Melton ED, Overmars L, Vavourakis CD, Muyzer G. Microbial diversity and biogeochemical cycling in soda lakes. *Extremophiles*. 2014; 18(5).
- [14] Kumar U, Panneerselvam P, Gupta VVSR, Majunath M, Priyadarshinee P, Sahoo A, Dash SR, Kaviraj M, Annapurna K. Diversity of Sulfur-Oxidizing and Sulfur-Reducing Microbes in Diverse Ecosystems. En T. K. Adhya et al (eds.), *Advances in Soil Microbiology: Recent Trends and Future Prospects*. 2018; 65-89.
- [15] Zhang C, Dnag H, Azam F, Benner R, Legendre L, Passow U, Polimene L, Robinson C, Suttle CA, Jiao N. Evolving paradigms in biological carbon cycling in the ocean. *National Science Review*. 2018; 5: 481-499.

- [16] Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, Canadell J, Chhabra S, DeFries R, Galloway J, Heimann M, Jones C, Le Quéré C, Myneni RB, Piao S, Thronston P. Carbon and Other Biogeochemical Cycles. En T. F. Stocker., D. Qin., G.-K. Plattner., M. Tignor., S. K. Allen., J. Boschung., A. Nauels., Y. Xia., V. Bex., P. M. Midgley (eds.). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. 2013.
- [17] Fang J, Li Z, Li J, Kato C, Tamburini C, Yuzhong Z, Hongyue D, Guangyi W, Fengping W. The POM-DOM piezophilic microorganism continuum (PDPMC)—The role of piezophilic microorganisms in the global ocean carbon cycle. *Science China: Earth Sciences.* 2015; 58(1): 106–115.
- [18] Dawson HM, Heal KR, Boysen AK, Carlson LT, Ingalls AE, Young JN. Potential of temperature- and salinity-driven shifts in diatom compatible solute concentrations to impact biogeochemical cycling within sea ice. *Elem Sci Anth.* 2020; 8(1): 25.
- [19] Marlow JJ, Steele JA, Case DH, Connon SA, Levin LA, Orphan VJ. Microbial Abundance and Diversity Patterns Associated with Sediments and Carbonates from the Methane Seep Environments of Hydrate Ridge, OR. *Frontiers in Marine Science.* 2014; 1(44).
- [20] Nazaries L, Murrells JC, Millard P, Baggas L, Singh BK. Methane, microbes and models: Fundamental understanding of the soil methane cycle for future predictions. *Environmental Microbiology.* 2013; 15(9).
- [21] Rathour R, Gupta J, Mishra A, Rajeev AC, Dupont CL, Thakur Shekhar IS. A comparative metagenomic study reveals microbial diversity and their role in the biogeochemical cycling of Pangong lake. *Science of the Total Environment.* 2020; 731.
- [22] Pajares S, Ramos R. Processes and Microorganisms Involved in the Marine Nitrogen Cycle: Knowledge and Gaps. *Frontiers in Marine Science.* 2019; 6: 739.
- [23] Peretó J. Diazotrophy. En M. Gargaud., R. Amils., J. C. Quintanilla., H. J. CleavesII., W. M. Irvine., D. L. Pinti., M. Viso. (eds) *Encyclopedia of Astrobiology.* Berlin, Heidelberg: Springer. 2011.
- [24] Boltianskaia I, Kevbrin VV, Lysenko AM., Kolganova TV, Turova TP, Osipov GA, Zhilina TN. *Halomonas mongoliensis* sp. nov. and *Halomonas kenyensis* sp. nov., new haloalkaliphilic denitrifiers capable of reducing N₂O, isolated from soda lakes. *Mikrobiologiya.* 2007; 76(6): 834–843.
- [25] Brochier-Armanet C, Gribaldo S, Forterre P. Spotlight on the Thaumarchaeota. *The ISME Journal.* 2012; 6: 227–230.
- [26] Garnova ES, Zhilina TN, Tourova TP, Lysenko AM. *Anoxynatronum sibiricum* gen.nov., sp.nov. alkaliphilic saccharolytic anaerobe from cellulolytic community of Nizhnee Beloe (Transbaikal region). *Extremophiles.* 2003; 7(3): 213-20.
- [27] Hocking WP, Roalkvam I, Magnussen C, Stokke R, Steen IH. Assessment of the Carbon Monoxide Metabolism of Hyperthermophilic Sulfate-Reducing Archaeon *Archaeoglobus fulgidus* VC-16 by Comparative Transcriptome Analyses. *Archaea.* 2015; 2015(16): 1-12.
- [28] Hoefft SE, Blum JS, Stolz JF, Tabita FR, Witte B, King GM, Santini JM, Oremland RS. *Alkalilimnicola ehrlichii* sp. nov., a novel, arsenite-oxidizing haloalkaliphilic gammaproteobacterium capable of chemoautotrophic or heterotrophic growth with nitrate or oxygen as the electron acceptor. *International Journal of Systematic and Evolutionary Microbiology.* 2007; 53(3): 504-512.
- [29] Holmes DE, Risso C, Smith JA, Lovley DR. Anaerobic Oxidation of Benzene by the Hyperthermophilic Archaeon *Ferroglobus placidus*. *Applied and Environmental Microbiology.* 2011; 77(1): 5926-5933.
- [30] Kalyuzhnaya MG, Khmelenina V, Eshinimaev B, Sorokin D, Fuse H, Lidstrom M, Trotsenko Y. Classification of halo(alkali)philic and halo(alkali)tolerant methanotrophs provisionally assigned to the genera *Methylomicrobium* and *Methylobacter* and emended description of the genus *Methylomicrobium*. *International Journal of Systematic and Evolutionary Microbiology.* 2008; 58: 591–596.
- [31] Maezato Y, Johnson T, McCarthy S, Dana K, Blum P. Metal Resistance and Lithoautotrophy in the Extreme Thermoacidophile *Metallosphaera sedula*. *Journal of Bacteriology.* 2012; 194(24): 6856-6863.
- [32] Melton ED, Sorokin DY, Overmars L, Lapidus AL, Pillay M, Ivanova N, Del Rio TG, Kyrpides NC, Woyke T, Muyzer G. Draft genome sequence of *Dethiobacter alkaliphilus* strain AHT1T, a gram-positive sulfidogenic polyextremophile. *Standards in genomic sciences.* 2017; 12: 57.

- [33] Panda MK, Sahu MK, Tayung K. Isolation and characterization of a thermophilic *Bacillus* sp. with protease activity isolated from hot spring of Tarabalo, Odisha, India. *Iranian journal of microbiology*. 2013; 5(2): 159–165.
- [34] Prowe SG, Antranikian G. *Anaerobranca gottschalkii* sp. nov., a novel thermoalkaliphilic bacterium that grows anaerobically at high pH and temperature. *Int J Syst Evol Microbiol*. 2001; 51(Pt 2): 457-465.
- [35] Ramírez-DN, Serrano-R JA, Sandoval-T H. Microorganismos extremófilos. Actinomicetos halófilos en México. *Revista Mexicana de Ciencias Farmacéuticas*. 2006; 37(3): 56-71.
- [36] Sorokin DY, Muyzer G, Brinkhoff T, Gijs Kuenen J, Jetten MSM. Isolation and characterization of a novel facultatively alkaliphilic *Nitrobacter* species, *N. alkalicus* sp. nov. *Arch Microbiol*. 1998; 170: 345-352.
- [37] Sorokin DY, Tourova TP, Henstra AM, Stams AJM, Galinski EA, Muyzer G. Sulfidogenesis under extremely haloalkaline conditions by *Desulfonatospira thiodismutans* gen. nov., sp. nov., and *Desulfonatospira delicat* sp. nov. - A novel lineage of Deltaproteobacteria from hypersaline soda lakes. *Microbiology*. 2008; 154(Pt 5): 1444-53.
- [38] Sorokin DY, Tourova TP, Kolganova TV, Detkova EN, Galinski EA, Muyzer G. Culturable diversity of lithotrophic haloalkaliphilic sulfate-reducing bacteria in soda lakes and the description of *Desulfatronum thioautotrophicum* sp. nov., *Desulfatronum thiosulfatophilum* sp. nov., *Desulfatronovibrio thiodismutans* sp. nov., and *Desulfatronovibrio magnus* sp. nov. *Extremophiles*. 2011; 15(3): 391-401.
- [39] Sorokin DY, Tourova TP, Panteleeva AN, Muyzer G. *Desulfatronobacter acidivorans* gen. nov., sp. nov. and *Desulfobulbus alkaliphilus* sp. nov., haloalkaliphilic heterotrophic sulfate-reducing bacteria from soda lakes. *Int J Syst Evol Microbiol*. 2011; 62(Pt 9): 2107-2113.
- [40] Vuilleumier S, Khmelenina VN, Bringel F, Reshetnikov AS, Lajus A, Mangenot S, Rouy Z, Op den Camp HJM, Jetten MSM, Dispirito AA, Dunfield P, Klotz MG, Semrau JD, Stein LY, Barbe V, Médigue C, Trotsenko YA, Kalyuzhnaya MG. Genome Sequence of the Haloalkaliphilic Methanotrophic Bacterium *Methylophilum alcaliphilum* 20Z. *Journal of Bacteriology*. 2011; 194(2): 551-552.
- [41] Wahlund TM, Madigan MT. Nitrogen fixation by the thermophilic green sulfur bacterium *Chlorobium tepidum*. *Journal of Bacteriology*. 1993; 175(2): 474–478.
- [42] Zavarzina GG, Tourova TP, Kolganova TV, Boulygina ES, Zhilina TN. Description of *Anaerobacillus alkalilacustre* gen. nov., sp. nov.—Strictly Anaerobic Diazotrophic *Bacillus* Isolated from Soda Lake and Transfer of *Bacillus arseniciselenatis*, *Bacillus macyae*, and *Bacillus alkalidiazotrophicus* to *Anaerobacillus* as the New Combinations *A. arseniciselenatis* comb. nov., *A. macyae* comb. nov., and *A. alkalidiazotrophicus* comb. nov. *Microbiology*. 2009; 78(6): 723-731.
- [43] Zhilina TN, Kevbrin VV, Tourova TP, Lysenko AM, Kostrinkina NA, Zavarzin GA. *Clostridium alkalicellum* sp. nov., an Obligately Alkaliphilic Cellulolytic Bacterium from a Soda Lake in the Baikal Region. *Microbiology*. 2005; 74: 557–566.
- [44] Zhilina TN, Zavarzin GA, Rainey FA, Pikuta EN, Osipov GA, Kostrikina NA. *Desulfatronovibrio hydrogenovorans* gen. nov., sp. nov., an Alkaliphilic, Sulfate-Reducing Bacterium. *International journal of systematic bacteriology*. 1997; 47(1): 144-9.
- [45] Zhilina TN, Zavarzina DG, Kuever J, Lysenko AM, Zavarzin GA. *Desulfatronum cooperativum* sp. nov., a novel hydrogenotrophic, alkaliphilic, sulfate-reducing bacterium, from a syntrophic culture growing on acetate. *International Journal of Systematic and Evolutionary Microbiology*. 2005; 55(Pt 3): 1001-6.
- [46] Sorokin DY, Kuenen JG, Jetten MS. Denitrification at extremely high pH values by the alkaliphilic, obligately chemolithoautotrophic, sulfur-oxidizing bacterium *Thioalkalivibrio denitrificans* strain ALJD. *Arch Microbiol*. 2001; 175(2): 94-101.
- [47] Morris BEL, Henneberger, R., Huber, H., Moissl-Eichinger, C. Microbial syntrophy: interaction for the common
- [48] good. *FEMS Microbial Rev*. 2013; 37(3): 384-406.
- [49] Maccaroi L, Sanguino L, Vogel TM, Larose C. Snow and ice ecosystems: not so extreme. *Research in Microbiology*. 2015; 166(10): 782-795.
- [50] Anesio AM, Hodson AJ, Fritz A, Psenner R, Sattler B. High microbial activity on glaciers: importance to the global carbon cycle. *Global Change Biology*. 2009.