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THREE-DIMENSIONAL BIOGEOCHEMISTRY OF PERCHLORATE IN ANTARCTICA: ROLES OF BACTERIA, ARCHAEA, AND EUKARYA IN POLAR ECOSYSTEM SUSTAINABILITY

BIOGEOQUÍMICA TRIDIMENSIONAL DEL PERCLORATO EN LA ANTÁRTIDA: ROLES DE BACTERIAS, ARQUEAS Y EUCARIOTAS EN LA SOSTENIBILIDAD DEL ECOSISTEMA POLAR

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ABSTRACT
Antarctica, Earth's most extreme and pristine continent, hosts resilient microbial communities that sustain critical biogeochemical cycles under subzero temperatures, intense ultraviolet radiation, nutrient scarcity, and hypersaline conditions. Perchlorate (ClO_4^-), a persistent and highly oxidized chlorine oxyanion, is present in Antarctic snow, ice, soils, and saline lakes, subtly shaping microbial processes and redox dynamics. Its chemical stability and deliquescent properties enable it to persist while forming liquid microenvironments at subfreezing temperatures, supporting microbial activity in otherwise inhospitable landscapes. This review examines perchlorate biogeochemistry through a three-dimensional framework involving Bacteria, Archaea, and Eukarya. Bacteria and Archaea drive dissimilatory perchlorate reduction via cold- and salt-adapted enzymes encoded on mobile genetic elements. Archaea enhance consortium stability through osmolyte production and electron supply via methane oxidation, while Eukarya contribute organic carbon and structure biofilms, promoting redox stratification. However, climate-driven ice melt remobilizes legacy perchlorate, and anthropogenic inputs, primarily from rocket propellants, could threaten these delicate cycles by altering habitat conditions. This synthesis highlights the ecological significance of microbial perchlorate metabolism and its biotechnological potential for low-temperature bioremediation. We also evaluate strategies, including optimized combustion technologies and alternative propellants, to minimize anthropogenic perchlorate emissions and safeguard Antarctic ecosystem sustainability.
Keywords: Biogeochemistry, Perchlorate, Antarctica, Sustainability

RESUMEN
La Antártida, el continente más extremo y prístino de la Tierra, alberga comunidades microbianas resilientes que sostienen ciclos biogeoquímicos esenciales bajo temperaturas bajo cero. El perclorato (ClO_4^-), un oxianión de cloro altamente oxidado y persistente, está presente en la nieve, hielo, suelos y lagos salinos de la Antártida, influenciando los procesos microbianos y la dinámica de óxido-reducción. Su estabilidad química y propiedades delicuescentes le permiten persistir mientras forma microambientes líquidos a temperaturas bajo cero, facilitando la actividad microbiana en regiones frías. Esta revisión examina la biogeoquímica del perclorato a través de un marco tridimensional que involucra Bacterias, Arqueas y Eukarya. Las Bacterias y Arqueas impulsan la reducción disimilatoria del perclorato mediante enzimas adaptadas al frío y la salinidad, codificadas en elementos genéticos móviles. Las Arqueas mejoran la estabilidad de consorcios mediante la producción de osmolitos y el suministro de electrones a través de procesos de oxidación, mientras que los Eukarya aportan carbono orgánico y estructuran biopelículas, promoviendo la estratificación redox. El deshielo inducido por el cambio climático puede movilizar el perclorato retenido lo que, sumado a los aportes antropogénicos principalmente de propelentes de cohetes, podrían amenazar los ciclos ecosistémicos. Esta síntesis destaca la importancia ecológica del metabolismo microbiano del perclorato y su potencial biotecnológico para la biorremediación a bajas temperaturas. También evaluamos estrategias, incluyendo tecnologías de combustión optimizadas y propelentes alternativos, para minimizar las emisiones antropogénicas de perclorato y salvaguardar la sostenibilidad de los ecosistemas antárticos.
Palabras clave: Biogeoquímica, Perclorato, Antártida, Sostenibilidad

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1. INTRODUCTION

Antarctica is a continent of extremes—cold, arid, and irradiated—yet it harbors diverse and resilient microbial communities that sustain biogeochemical cycles and contribute to global environmental stability (Ortiz et al., 2020). Its vast ice sheets and permafrost serve as natural archives of Earth's climatic and geochemical history (Brook & Buizert, 2018; Chandler et al., 2025; Strugnell et al., 2022). The preservation of this unique environment has been a central objective of international agreements that restrict human activities to mitigate the risk of contamination and the introduction of non-native species, thereby safeguarding its ecological integrity (Deary & Tin, 2015). In response to the impacts of climate change, scientific research suggests that Antarctica is a priority area for global collaboration and management. In this context, strategic alliances have been established, emphasizing the importance of interdisciplinary research on global climate, political, and economic issues (Villamizar-Lamus, 2024; Baquero Valdés et al., 2024; Espinoza Arenas & Valdivia Cerda, 2024).

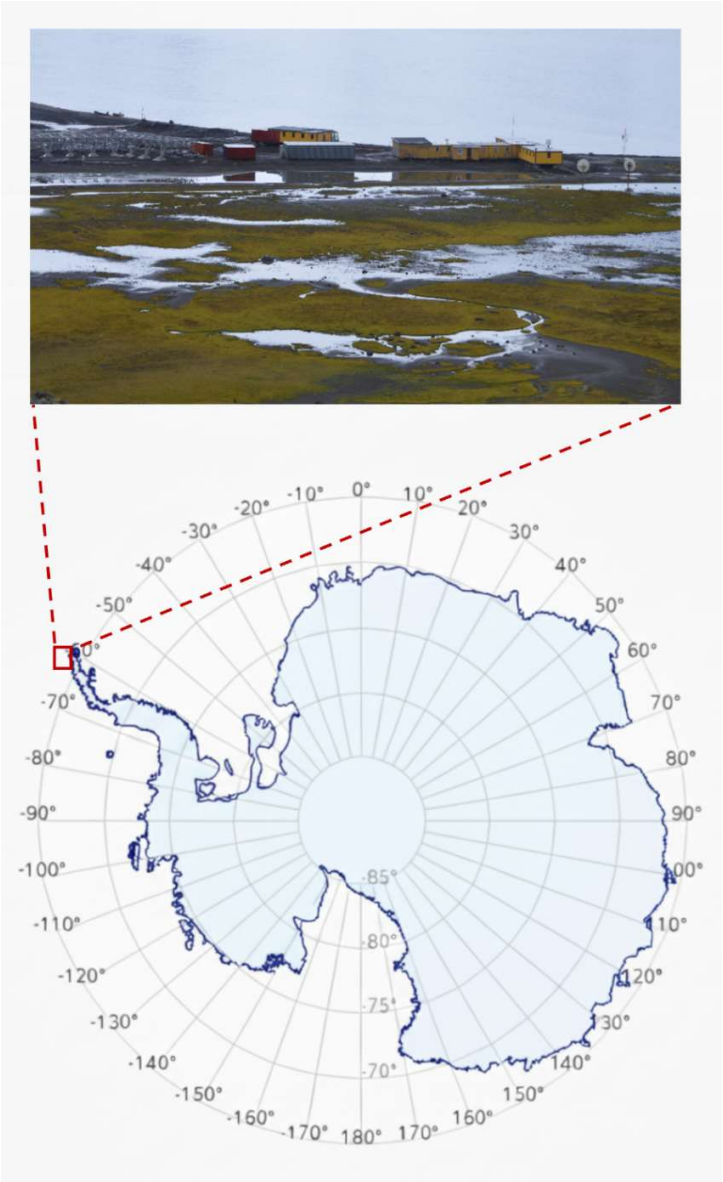

Figure 1. Antarctic Map and their landscape 2022 (obtained under License CC BY 4.0. B).

Among the chemical compounds present in Antarctic ecosystems, perchlorate (ClO_4^-) has drawn increasing scientific attention. Detected in snow, ice, soils, and saline lakes, this highly soluble and redox-active oxyanion raises important questions across biological, environmental, clinical, and biotechnological research (Acevedo-Barrios et al., 2025; Jiang et al., 2021; Kounaves et al., 2010). Perchlorate represents the most oxidized form of chlorine and can be produced naturally through successive photochemical oxidation of chloride in the atmosphere, from where it is transported to remote environments (Barnum et al., 2018; Dasgupta et al., 2005; Parker, 2009). The remarkable chemical stability of $ClO4^-$, coupled with a high activation energy for reduction, allows it to persist for millennia (Brown & Gu, 2006; Jiang et al., 2021).

Beyond natural formation, perchlorate has been widely manufactured for industrial applications, particularly in solid rocket fuels, explosives, and munitions, making anthropogenic contamination a significant concern (Jiang et al., 2021; Vega et al., 2018). Stable isotope analyses of chlorine and oxygen can help discriminate natural from anthropogenic sources (Bao & Gu, 2004; Jiang et al., 2021). Although perchlorate concentrations in Antarctica are generally low and considered ecologically insignificant under present conditions, climate-driven warming and ice melt can mobilize sequestered perchlorate, thereby enhancing its bioavailability and potential for ecosystem disruption. Notably, high concentrations have been reported in the hyperarid regions of Antarctica (Jackson et al., 2012; Jiang et al., 2016), reinforcing its significance both as a geochemical marker and as a potential target for biotechnological applications, such as the development of low-temperature perchlorate treatment methods.

Perchlorate's strong oxidizing capacity enables microorganisms to exploit it as an electron acceptor, thereby contributing to energy generation and influencing redox dynamics within Antarctic ecosystems. Indeed, perchlorate-reducing activity is considered one of the few anaerobic metabolisms implicated in Earth's atmospheric oxygenation. Byproducts and intermediates of perchlorate reduction also interact with other metabolic pathways, shaping microbial community structure and function (Barnum et al., 2018). Moreover, perchlorate's deliquescent properties allow it to absorb atmospheric water vapor and form liquid microenvironments at subzero temperatures, supporting microbial activity in niches where liquid water is otherwise absent (Gentilhomme et al., 2025; Gu et al., 2017).

Despite these ecological roles, perchlorate is also a toxic compound. Within cells, it induces chaotropic and oxidative stress (dos Santos et al., 2025; Gentilhomme et al., 2025). In mammals, perchlorate disrupts thyroid function by competitively inhibiting the sodium–iodide symporter (NIS), to which it binds with significantly higher affinity than iodide; in humans, this affinity is approximately 30-fold greater (Tonacchera et al., 2004; Vega et al., 2018).

This review examines the impact of natural and anthropogenic perchlorate in Antarctic ecosystems, with a focus on its role in microbial redox dynamics and implications for polar sustainability under climate change. We propose that functional cooperation among bacteria, archaea, and eukaryotes has enabled the recycling of perchlorate for millions of years. However, accelerating ice melt and increasing anthropogenic inputs may compromise this adaptive capacity. The objective of this article is to analyze the three-dimensional biogeochemistry of perchlorate in Antarctica, highlighting the complementary roles of microorganisms across all three domains of life, while also assessing the risks posed by human activity and environmental change.

2. METHODOLOGY

2.1 Literature Review

This article adopts a narrative review approach, integrating recent findings on perchlorate in polar environments with a particular focus on microbial processes involving Bacteria, Archaea, and Eukarya. Information in a time frame to 2025 and inclusion criteria were established to consider peer-reviewed articles published in journals indexed in Web of Science, Scopus, and PubMed, as well as technical literature from SCAR and the Antarctic Treaty System. Studies with empirical evidence in Antarctic ecosystems (ice, soils, saline lakes) or comparative studies in analogous cold climate environments were included, addressing biogeochemistry, microbial ecology, and anthropogenic impacts in Antarctica.

2.2 Genomic and Proteomic Analysis

To complement the literature review, we analyzed genomic and proteomic data from public repositories. Nucleotide and amino acid sequences of genes encoding perchlorate reductases, as well as other homologous or evolutionarily related genes, were retrieved from the NCBI database following its information use protocols. All accession codes were documented and used in graphics to ensure traceability. The *perchlorate reductase* subunit alpha (*pcrA*) gene and its corresponding protein product serve as reliable biomarkers for identifying and quantifying perchlorate-reducing bacteria (PRB) in environmental samples. The PcrA subunit functions as the catalytic component of the perchlorate reductase enzyme, which is unique to organisms capable of anaerobic perchlorate respiration. A search in the NCBI database retrieved 593 nucleotide sequences for the *pcrA* gene. From these, 194 amino acid sequences were selected based on sequence length and their correspondence to the enzyme classification number EC 1.97.1 (UniProtKB) for alignment. Aminoacid sequences (194) were aligned using MAFFT v7 with the G-INS-i refinement method and the phylogenetic tree was constructed using IQTREE2 with ultrafast bootstrap (options -m TEST -bb 1000 -alrt 1000) (Katoh et al., 2002; Minh et al., 2020). The best-fit model, LG+F+G4, was chosen according to the Bayesian Informative Criteria (BIC). The ITOL plugin was used to generate and visualise the phylogenetic inference of the *pcrA* gene (Letunic et al., 2021).

Additionally, we examined Antarctic metagenomic datasets to identify enzymatic functions involved in perchlorate reduction, but without conclusive results that connecting molecular mechanisms to ecosystem-scale processes. Among the limitations are the uneven availability of genomic and proteomic data in polar organisms, the scarcity of in situ studies that evaluate perchlorate reduction processes under real environmental conditions, as well as the lack of accuracy of the annotations of putative perchlorate reductase enzymes.

3. RESULTS AND DISCUSSION

3.1. Perchlorate in the Antarctic environment

Perchlorate in Antarctic ecosystems originates from both natural and anthropogenic sources. Naturally, its highest concentrations occur in hyperarid regions such as the McMurdo Dry Valleys, where levels can exceed 1,000 µg/kg (Kounaves et al., 2010). In most other Antarctic soils, however, concentrations are much lower, typically in the nanogram-per-kilogram range (Acevedo-Barrios et al., 2022; Jiang et al., 2023). The main natural source of ClO_4^- is atmospheric formation, promoted by the strong polar vortex that favors photochemical reactions between chlorine radicals (Cl·) and ozone (O_3) in the stratosphere (Jiang et al., 2023; Jiang et al., 2021). Local surface production may also occur in smaller amounts. As ice sheets melt and permafrost thaws due to climate warming, legacy perchlorate sequestered in ice becomes bioavailable, with the potential to disrupt delicate microbial balances(Jackson et al., 2016). Globally, perchlorate tends to accumulate in hyperarid regions but not in wetter environments, likely because microbial reduction prevents its persistence (Kounaves et al., 2010). Anthropogenic contributions, mainly linked to the use of perchlorate in fuels and propellants, are generally considered negligible in the Dry Valleys (Jiang et al., 2023; Jiang et al., 2021). Isotopic studies capable of distinguishing natural from anthropogenic origins have not yet been applied systematically across other Antarctic regions, leaving open questions about the contribution of human activity.

Perchlorate also plays a critical role in shaping Antarctic microhabitats. Its deliquescent properties allow it to absorb atmospheric moisture and form brines at relative humidities above 50%, even at temperatures well below freezing (Cesur et al., 2022; Chevrier, 2025). These brines generate localized liquid water niches in an otherwise frozen landscape, supporting microbial metabolism and geochemical processes. However, organisms inhabiting these environments must simultaneously cope with multiple stressors, including subzero temperatures, intense radiation, chaotropic stress, and high ionic strength from perchlorate salts (Heinz et al., 2020; Margesin & Collins, 2019). Chemically, perchlorate is highly stable. With a standard reduction potential (E°) of +0.79 V for the ClO_4^-/ClO_3^- couple at pH=7 and an abiotic activation barrier of approximately 80 kJ/mol, it is a strong electron acceptor but kinetically resistant to reduction (Hofbauer et al., 2014). Environmental removal occurs through interconnected physical, chemical, and biological processes that follow predictable patterns of stability and response to change, although these processes likely have thresholds beyond which they fail to function effectively. Indeed, the absence of widespread perchlorate accumulation elsewhere on Earth has been attributed to the global activity of microbial reduction (Kounaves et al., 2010; Liebensteiner et al., 2013).

3.2. Microbial perchlorate biogeochemistry

The cycling of perchlorate in Antarctic ecosystems is maintained by the cooperative activity of Bacteria, Archaea, and Eukarya, each contributing complementary functions that collectively sustain redox balance and ecosystem resilience (Diaz et al., 2021; Holmberg & Jørgensen, 2023; Youngblut et al., 2016). Cold environments harbor metabolically versatile microbial communities, yet the diversity and ecological roles of perchlorate reducers in natural extreme ecosystems remain insufficiently understood (Cadena et al., 2024). Studies from Antarctic ice-covered lakes, such as those in the McMurdo Dry Valleys, have begun to reveal how perchlorate participates in ecological, evolutionary, and geochemical processes (Jackson et al., 2012).

In the canonical pathway, perchlorate (ClO_4^-) is used anaerobically as a final electron acceptor by dissimilatory perchlorate-reducing microorganisms. Through this metabolism, microbes couple the reduction of perchlorate to the oxidation of diverse electron donors, thereby generating energy (Barnum et al., 2018; He et al., 2019). An exception is found in the genus *Arthrobacter*, which can reduce perchlorate under aerobic conditions (Vega et al., 2018). The first enzymatic step is catalyzed by perchlorate reductase (PcrA), a molybdoenzyme that reduces perchlorate to chlorate and chlorate to chlorite (Figure 2). Chlorite, a toxic intermediate, is then degraded into chloride and molecular oxygen by a chlorite dismutase (Achenbach et al., 2006). While most known perchlorate reducers belong to the Proteobacteria, this ability has also been identified in Firmicutes and Archaea (Liebensteiner et al., 2014). The genes necessary for perchlorate reduction are often carried in mobile genetic elements called perchlorate reduction islands (PRIs), which are frequently located on plasmids, together with stress-response and molybdenum cofactor biosynthesis genes (Melnyk & Coates, 2015). Recent studies highlight oxidative stress defense as a key determinant of microbial fitness during perchlorate reduction (Melnyk & Coates, 2015).

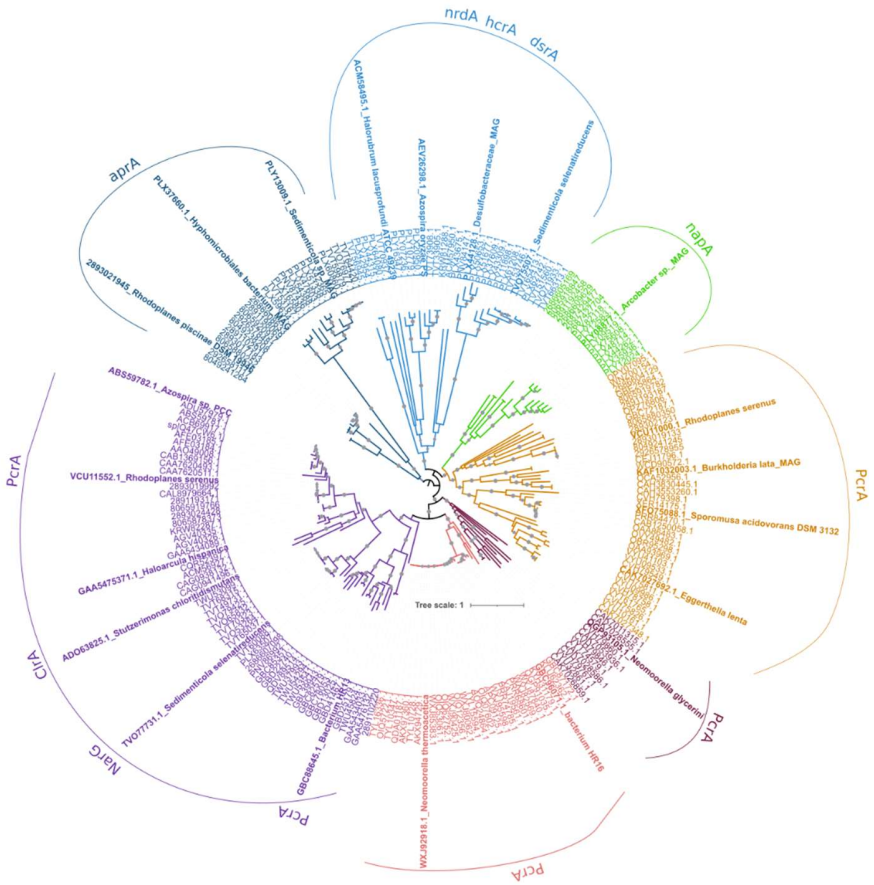

Figure 2. Phylogenetic tree to visualize phylogenetic inference of the PcrA. Aminoacid sequences were aligned using MAFFT v7 and the phylogenetic tree was constructed using IQTREE2. The best-fit model, LG+F+G4, was chosen according to the Bayesian Informative Criteria (BIC) to visualize phylogenetic inference.

Microbial communities in perchlorate-rich environments consist not only of dissimilatory perchlorate reducers but also of organisms without the enzymatic capacity for ClO_4^- reduction. Bacteria, Archaea and Eukarya, for example, contribute indirectly by regulating carbon and electron fluxes, producing osmolytes, or structuring biofilms. Such interactions enable the complete perchlorate reduction under Antarctic conditions, where symbiotic relationships help maintain electron donor availability, e.g. acetate, ethanol, glycerol, methane, hydrogen, sulfur, or iron (Anupama et al., 2015; Barnum et al., 2018; He et al., 2019).

Experimental studies reinforce this ecological picture. Microbial consortia enriched from Antarctic lake sediment follow Michaelis–Menten kinetics in perchlorate reduction, exhibiting consistent substrate affinities and reduction rates (Dong et al., 2022). Even under high perchlorate concentrations, microbial activity persists, although tolerance levels vary depending on habitat type (Cheptsov et al., 2021). Archaea and Eukarya are apparently crucial in acetate metabolism for complete ClO_4^- reduction, where the three domains of life contribute to the symbiotic reduction of perchlorate (Anupama et al., 2015; Barnum et al., 2018).

The persistence of microbial activity under chaotropic and oxidizing stress conditions suggests that perchlorate is not merely a toxicant but also a structuring force within Antarctic microbial ecosystems. By enabling anaerobic respiration, shaping community composition, and fostering inter-domain cooperation, perchlorate contributes to energy flow and ecosystem resilience in extreme polar environments. Understanding this three-dimensional microbial framework is essential not only for reconstructing the past, present, and future of ecological dynamics in Antarctica but also for informing potential biotechnological applications in perchlorate bioremediation under cold conditions.

3.2.1. Bacteria

Bacteria capable of dissimilatory perchlorate reduction (DPR) are the primary drivers of perchlorate detoxification in natural ecosystems. Perchlorate-reducing bacteria (PRB) are widespread and can use ClO_4^- as a terminal electron acceptor under both heterotrophic and autotrophic conditions (He et al., 2019). Genera such as *Dechloromonas*, *Azospira*, *Pseudomonas*, and *Psychrobacter* have been reported to couple perchlorate reduction to energy generation, producing chloride and oxygen through the sequential action of perchlorate reductase (PcrA) and chlorite dismutase (Achenbach et al., 2006; Melnyk & Coates, 2015; Miralles-Robledillo et al., 2019).

Heterotrophic PRB rely on organic electron donors—most notably acetate, but also ethanol, carbohydrates, glycerol, and methane—while autotrophic DPR can proceed with inorganic donors such as hydrogen, zero-valent iron, elemental sulfur, or anthrahydroquinone (He et al., 2019). Availability of these donors is crucial, as electron limitation strongly constrains DPR efficiency. Despite multiple isolates showing perchlorate reduction, the precise mechanisms by which ClO_4^- structures Antarctic microbial communities remain poorly understood, representing a critical gap in current knowledge (Díaz-Rullo & González-Pastor, 2025; Torres-Rojas et al., 2023).

At the genetic level, PcrA is encoded within perchlorate reduction islands (PRIs), frequently located on plasmids that also harbor genes for stress response, molybdenum cofactor biosynthesis, and occasionally chlorite dismutase (Miralles-Robledillo et al., 2019). PRIs vary widely in content and integration mechanisms, reflecting horizontal gene transfer events across phylogenetic lineages. For instance, despite divergent genomes, *Azospira* and *Magnetospirillum* genera share conserved PRI sequences, implying gene transfer within restricted taxonomic groups (Melnyk & Coates, 2015). Other cases, such as *Brucella* sp. QD19-16, *Acidovorax* sp. QD1-5, and *Citrobacter* sp. P3-1, indicate monophyletic PRI origins facilitated by transposases (Wang et al., 2024). PcrA belongs to the DMSO reductase superfamily and exhibits high affinity for perchlorate (Km = 6 μM), contrasting with the lower affinity of related nitrate reductases (Km = 1.1 mM) (Barnum et al., 2018). Experimental studies have demonstrated perchlorate reduction capacity in Antarctic microorganisms. For example, the psychrotolerant acidophile *Acidithiobacillus ferrivorans*, isolated from King George Island, exhibited a perchlorate removal rate of 19 mg/L·day at 20 °C and pH=2, comparable to performance reported

for *Dechloromonas* sp. CS-1 and *Clostridioides* sp. CS-2 (Torres-Rojas et al., 2023). The persistence and the adaptability of bacterial consortia to perchlorate stress in enrichment cultures from Antarctic saline lake sediments displayed reduction kinetics consistent with Michaelis–Menten behavior, with a maximum specific substrate reduction rate (q_{max}) of 0.5 mg/mg$_{DW}$·h and a half-saturation constant (Ks) of 16 mg/L of ClO_4^- (Dong et al., 2022).

Ecological interactions further highlight bacterial versatility. Through both direct reduction and cooperative interactions with other microbial groups, bacteria transform ClO_4^- from a chaotropic stressor into an electron acceptor. In mixed communities, perchlorate-reducing bacteria can support populations of chlorate-reducing bacteria by releasing chlorate intermediates (Barnum et al., 2020). Moreover, non-reducing bacteria may contribute indirectly by cycling key metabolites essential for community stability. Extremophilic bacteria such as *Planococcus halocryophilus* display exceptional tolerance (13.6 wt/vol% $NaClO_4$ at 25 °C), surpassed only by some fungi. Similarly, *Hydrogenothermus marinus* tolerates up to 440 mM $NaClO_4$, undergoing morphological changes from motile rods to long chains of up to 80 cells (Beblo-Vranesevic et al., 2017). Thermophilic species such as *Carboxydothermus hydrogenoformans* and *Moorella glycerini* reduce perchlorate in sulfide-dependent processes that rely on abiotic reactions due to the absence of chlorite dismutase (Liebensteiner et al., 2015).

3.2.2. Archaea

The discovery that *Archaeoglobus fulgidus* can couple (per)chlorate reduction with energy metabolism extended this metabolic trait beyond Bacteria into the archaeal domain (Liebensteiner et al., 2015; Liebensteiner et al., 2014; Liebensteiner et al., 2013). In this hyperthermophilic archaeon, perchlorate reduction involves both abiotic and biotic redox reactions with sulfur compounds. Similarly, the crenarchaeon *Aeropyrum pernix* reduces ClO_4^- using a periplasmic nitrate reductase–like enzyme (Liebensteiner et al., 2015).

The archaeal reduction pathway shares mechanistic parallels with bacterial DPR. In *A. fulgidus*, molybdoenzymes of the type II DMSO reductase family catalyze the reduction of (per)chlorate (Miralles-Robledillo et al., 2019). However, unlike bacterial chlorite dismutase, which produces oxygen and chloride, archaeal systems often rely on chemical interactions between chlorite and sulfide, yielding oxidized sulfur compounds as byproducts (Liebensteiner et al., 2013). Other archaeal species, such as *Haloferax mediterranei*, have been shown to reduce perchlorate without possessing classical pcrA genes; instead, they seem to depend on alternative pathways, demonstrating evolutionary plasticity in archaeal perchlorate metabolism (Vega et al., 2018).

In addition to direct ClO4- reduction, numerous Archaea fulfill essential indirect roles in perchlorate biogeochemistry. Within mixed microbial consortia, halophilic and psychrophilic archaea enhance ecosystem stability by synthesizing osmolytes, which protect cells against chaotropic stress. They also regulate carbon and electron fluxes by competing for organic substrates, thereby modulating community energy balance (Anupama et al., 2015). Anaerobic methanotrophic (ANME) archaea contribute additional electrons through methane oxidation, reinforcing redox cycling in perchlorate-reducing communities (He et al., 2019). These stabilizing and donor-providing functions help maintain microbial networks under fluctuating Antarctic conditions.

Some archaea also display notable tolerance to perchlorate. *Haloterrigena* sp. strain SGH1, for instance, withstands concentrations up to 0.15 M ClO_4^-, suggesting that structural and physiological adaptations enhance survival in perchlorate-rich saline habitats (Flores et al., 2020).

3.2.3. Eukarya

Eukaryotic microorganisms are integral components of Antarctic ecosystems, particularly in saline and cold environments (Hassan et al., 2016; Edwards et al., 2013). Although they do not directly reduce perchlorate, they contribute indirectly by supplying organic matter that fuels heterotrophic DPR, structuring biofilms that promote redox stratification, as well as acting as sensitive indicators of oxidative and chaotropic stress. In this way, eukaryotes provide ecological scaffolding that sustains bacterial and archaeal perchlorate metabolisms. Tolerance to perchlorate among eukaryotes is variable but, in some cases, exceeds that of bacteria and archaea. For instance, the yeast *Debaryomyces hansenii* can grow in liquid media containing up to 2.4 M $NaClO_4$, while the filamentous fungus *Purpureocillium lilacinum* tolerates approximately 1.9 M (Heinz et al.,

2020). These values exceed bacterial tolerance levels, which generally remain below 1.1 M. Physiological analyses in the fungus *Rhinocladiella similis* under magnesium perchlorate stress revealed multiple defense mechanisms, including the production of antioxidant enzymes, osmolyte accumulation, and the synthesis of protective biomolecules (dos Santos et al., 2025). In *Debaryomyces hansenii*, tolerance is mediated by intracellular glycerol accumulation and regulation through ion transporters (Heinz et al., 2022). Structural responses are also important, as seen in *Chlamydomonas reinhardtii*, where exposure to 200 mM perchlorate induces the formation of multicellular palmelloid aggregates that encapsulate cells in clonal clusters. This defensive structures against chaotropic stress enhance microbial resilience and facilitate the cooperative functioning of Bacteria and Archaea in perchlorate-rich environments (Poluri et al., 2024).

Eukaryotic microorganisms display adaptations to the combined stressors of polar environments, including low temperatures, salinity, nutrient scarcity, and low water activity. Cryoconite holes—small water-filled depressions on ice surfaces—illustrate the ecological importance of these organisms. In these microhabitats, eukaryotic phototrophs (e.g., Chlorophyta and Bangiales) and heterotrophs (e.g., Rhizaria) play central roles in carbon cycling, while fungi, rotifers, tardigrades, ciliates, and ochrophytes contribute at lower abundances (Lutz et al., 2019). Microbial activity in such niches persists at subzero temperatures, with metabolic activity detected down to −20 °C (Margesin & Collins, 2019).

3.3. Inhibition of Perchlorate Biogeochemistry and Implications for Antarctic Sustainability

The cooperative activity of Bacteria, Archaea, and Eukarya in Antarctic ecosystems demonstrates the resilience of microbial life under extreme conditions. By detoxifying perchlorate, stabilizing microbial networks, and sustaining redox and nutrient cycles, these microorganisms generate robust ecological frameworks that can withstand freeze–thaw cycles, hypersalinity, and oxidative stress. However, climate change threatens this balance by remobilizing legacy perchlorate from melting ice and altering physicochemical conditions, thereby destabilizing established microbial interactions. Safeguarding microbial perchlorate reduction is therefore critical not only for Antarctic conservation but also for understanding bioremediation strategies in cold, contaminated environments.

Although perchlorate-reducing metabolisms are versatile, their functionality depends on favorable physicochemical conditions. Stressors such as excess perchlorate, competing chemical species, unfavorable pH or salinity levels, and the presence of oxygen can inhibit the reduction process. While perchlorate reduction has been reported across diverse conditions, most studied processes occur between 20–40 °C (Dugan et al., 2009). This knowledge gap underscores the importance of studying Antarctic systems in situ to determine the proper limits of perchlorate reduction and predict the impact of ongoing environmental change.

A key challenge is the accumulation of chlorite, a toxic intermediate. Sustained perchlorate reduction requires its removal, either enzymatically via chlorite dismutase, which produces chloride and oxygen, or through abiotic–biotic interactions involving sulfur compounds (Achenbach et al., 2006; Liebensteiner et al., 2013; O. Wang & Coates, 2017). Enzymatic activity often depends on trace metals. For example, perchlorate reductase (PcrA) from *Azospira oryzae* GR-1 requires iron and molybdenum cofactors, along with [3Fe-4S] and [4Fe-4S] clusters, to catalyze the reduction of both chlorate and perchlorate (Kengen et al., 1999). However, excess ferrous iron can disrupt the reduction pathway, leading to the accumulation of chlorate (Levakov et al., 2021).

Competition with other electron acceptors is another inhibitory factor. Many PRB are also capable of respiratory nitrate reduction. In most cases, perchlorate reduction begins only after nitrate is depleted, as PcrA exhibits higher affinity but lower turnover for perchlorate compared to nitrate (Lv et al., 2020). For example, in *Azospira* sp., the Km value is 27 mM for perchlorate, while nitrate, iodate, and bromate are also reduced at significant rates, reflecting evolutionary parallels with nitrate reductases and related enzymes (Kengen et al., 1999). Microorganisms capable of utilizing multiple electron acceptors typically prefer nitrate over perchlorate due to the lower thermodynamic barriers, despite the similar reduction potentials of the NO_3^-/N_2 (+1.25 V) and ClO_4^-/Cl^- (+1.28 V) couples (Lv et al., 2020).

Dissolved oxygen is a particularly strong inhibitor. Concentrations as low as 2 mgO_2/L can completely suppress perchlorate reduction. Even after oxygen removal, residual inhibition has been observed, although some exceptions exist, such as molybdenum-independent PcrA activity in *Arthrobacter* sp., which can proceed in the

presence of oxygen (Bardiya & Bae, 2011). In addition, chaotropic stress from deliquescent perchlorate brines imposes further constraints, destabilizing biomolecules and posing a challenge to microbial survival. Some halophilic archaea, such as *Haloferax volcanii*, mitigate this stress using "salt-in" strategies, accumulating intracellular KCl to shield cellular machinery from perchlorate's chaotropic effects (Díaz-Rullo & González-Pastor, 2025; Heinz et al., 2022).

3.4. Network of strategies for anthropogenic reduction of emissions

Anthropogenic activities are major contributors to environmental perchlorate contamination worldwide (Trumpolt et al., 2005). However, long-range transport through atmospheric distillation processes has not been identified as a significant contributor to perchlorate deposition in Antarctica. Under current conditions, Antarctic perchlorate fluxes remain dominated by natural sources (Jackson et al., 2012; Jiang et al., 2016), underscoring the importance of preventing future anthropogenic inputs through sustainable management of perchlorate-generating activities. The dominant anthropogenic source of perchlorate is solid rocket propellant, released either during its manufacture or through combustion residues (Trumpolt et al., 2005). Mitigation strategies, therefore, focus primarily on this sector. Two complementary approaches have been identified: (i) replacing ammonium perchlorate-based propellant formulations with environmentally safer alternatives, or (ii) improving combustion efficiency to minimize unreacted perchlorate emissions.

Alternative propellant formulations, including paraffin-based hybrid systems and other less toxic energetic compounds, have been proposed as alternatives to ammonium perchlorate-based propellants to reduce perchlorate release and associated environmental risks (Dibdalli et al., 2025; Lopez-Telgie et al., 2023; Trache et al., 2017; Trumpolt et al., 2005). However, limitations in cost, performance, and large-scale feasibility have so far restricted their practical application in aerospace systems. Where complete substitution is not viable, three strategies have been developed to enhance the combustion efficiency of ammonium perchlorate-based propellants. First, stoichiometric optimization of the oxidizer-to-fuel ratio minimizes excess reactants and sustains optimal combustion (Jain, 1987; Azizi et al., 2024). Second, the use of catalytic additives (e.g., copper-, iron-, or ferrocene-based nanoparticles) has been widely explored to enhance thermal decomposition of ammonium perchlorate (Gaete et al., 2024; Gaete et al., 2023; Gaete et al., 2022; Molina et al., 2021; Chaturvedi & Dave, 2013; Rodriguez et al., 2022; Li et al., 2008). Third, advances in chamber design aim to maintain homogeneous fuel–oxidizer mixing, sustain optimal combustion temperatures and pressures, and improve combustion stability (Walther & Ahn, 2011; Yu et al., 2025).

4. CONCLUSION

The study of perchlorate biogeochemistry in Antarctic ecosystems reveals its critical role as a multifaceted compound influencing microbial processes, redox dynamics, and ecological resilience in one of the planet's most extreme environments. Perchlorate, originating from both natural and anthropogenic sources, occurs in varying concentrations, with significantly higher levels in hyperarid regions such as the McMurdo Dry Valleys. Its natural formation, driven by photochemical reactions in the atmosphere, and its chemical stability enable its persistence in the Antarctic environment, where it serves as an electron acceptor for microorganisms, a chaotropic agent, and a generator of liquid microenvironments under subfreezing conditions.

The functional cooperation among Bacteria, Archaea, and Eukarya forms a three-dimensional framework that sustains perchlorate cycling in Antarctica. Bacteria, as the primary agents of dissimilatory perchlorate reduction, transform this compound into an energy source, while Archaea contribute through alternative metabolic pathways and stabilizing functions, such as osmolyte production. Eukarya, though not directly reducing perchlorate, play an essential role by supplying organic matter, structuring biofilms, and serving as indicators of environmental stress. This microbial network demonstrates remarkable adaptability to Antarctica's extreme conditions but faces significant challenges due to climate change, which can mobilizes sequestered perchlorate from melting ice, disrupting microbial interactions and redox balances.

Despite the resilience of these microbial systems, factors such as chlorite accumulation, competition with other electron acceptors (e.g., nitrate), and the presence of dissolved oxygen can inhibit perchlorate reduction,

particularly in the context of environmental change. Furthermore, while anthropogenic contributions to perchlorate in Antarctica are currently negligible, human activities in proximate regions pose a potential risk, necessitating mitigation strategies. Among these, stoichiometric optimization of propellants, the use of metal catalysts, and improvements in combustion chamber design stand out as promising approaches to reduce perchlorate emissions from propellent fuels.

In conclusion, perchlorate is not only a geochemical marker and toxicological challenge but also a structuring component of Antarctic ecosystems, fostering inter-domain cooperation and microbial resilience. Preserving these biogeochemical processes is critical for polar sustainability, particularly in the face of accelerating ice melt and increasing anthropogenic influences. This knowledge not only enhances our understanding of biogeochemical cycles in extreme environments but also has direct implications for developing bioremediation strategies in low-temperature conditions, underscoring the importance of continued research into the functional limits of these microbial systems in the context of global climate change.

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