

Vertical Stratification of Archaeal Communities in Lake Sediments: A Comparative Analysis of Dead and Thriving Lakes

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ABSTRACT

Archaea are influenced by environmental conditions in various ecosystems and are essential to global biogeochemical cycles. By contrasting healthy and dead lakes, this study examines the vertical stratification of archaeal populations in lake sediments. Archaea play a role in the breakdown of organic matter, the oxidation of ammonia, and the formation of methane. The study investigates the effects of temperature variations, nutrition availability, redox conditions, and oxygen gradients on archaeal diversity and distribution. The study highlights the importance of archaea in preserving ecosystem health, especially in sedimentary contexts, using DNA sequencing, community analysis, and environmental characterization. The results demonstrate that although dead lakes, which are defined by oxygen depletion and changed redox gradients, show decreased diversity and ecological services, healthy lakes sustain a variety of archaeal populations. Gaining knowledge of these microbial communities can help us better understand how resilient aquatic ecosystems are to environmental stresses like eutrophication and climate change, as well as the potential for ecological restoration. The study emphasizes how crucial archaea are to preserving the health of ecosystems and how their dispersion affects the maintenance of aquatic environments.

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1. INTRODUCTION

Over the past 200 years, human activity has had a major impact on lake ecosystems, changing biodiversity and the way biogeochemical cycles function (Tardy et al., 2021). Among the most notable changes is the pervasiveness of oxygen depletion in lake bottom waters, which can happen periodically or continuously throughout the year. However, the increased nutrient imports into lakes, primarily from human activities in the surrounding watersheds, lead to eutrophication, the primary source of this oxygen loss. Eutrophication contributes significantly to oxygen depletion, but it is not the main driver of change. Lake sediments, which are complex and dynamic environments that also play a significant role in forming microbial diversity, are home to a wide variety of microorganisms, particularly bacteria, and archaea, which are important contributors to nutrient cycling, organic matter transformation, and aquatic food webs (Jenny et al., 2016; Wurzbacher et al., 2017). In deeper lake regions, hypoxic and anoxic conditions are also formed in the sediments due to a combination of thermal stratification, lake morphology, and enhanced water column productivity. These conditions foster the development of microbial communities that can use fermentation and anaerobic respiration to break down organic molecules (Schwefel et al., 2018; Vuillemin et al., 2023). Many investigations have been conducted in the last ten years to investigate the temporal and spatial variations in the diversity of bacteria and archaea in freshwater lake sediments (Ruuskanen et al., 2018; J. Zhang et al., 2015; L. Zhang et al., 2019). In addition, environmental factors such as water depth, organic matter content and quality, nutrient levels, and the presence of pollutants have been shown to affect the structure, abundance, and diversity of these microbial communities (Xiong et al., 2015). Bacteria in lake sediments play crucial roles in the transformation of organic matter and the cycling of key elements like nitrogen, sulfur, phosphorus, and iron (L. Zhang et al., 2019). Archaea, while less studied, are also involved in essential biogeochemical processes, including methanogenesis, sulfate reduction, and ammonia oxidation (Lyu et al., 2018). Despite their relevance, the community structure and diversity of archaea in

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lake sediments have not been as fully examined as bacterial communities. Research shows that sample site and sediment depth can affect archaea diversity (Morrison et al., 2017; J. Zhang et al., 2015), and in some areas, such as the Brazilian Savanna (Rodrigues et al., 2014), seasonal impacts can be seen. Archaeal community composition in lake sediments is influenced by environmental conditions such as pollution, sediment depth, and salinity (Fan & Xing, 2016; Yang et al., 2016). Although microbiological diversity has been the subject of research, it is still unknown how diverse bacteria and archaea are concerning one another in lake sediments. According to some research, the variety of bacteria is greater than that of archaea (Nazir et al., 2019; Tardy et al., 2021), however, other research suggests the contrary. The importance of the Archaea, a unique class of prokaryotic organisms, in aquatic environments—especially in the nutrient-rich and anoxic conditions of lake sediments—is becoming more widely acknowledged. They can participate in vital biogeochemical processes such as methanogenesis, ammonia oxidation, and the breakdown of organic materials because of their capacity to flourish in harsh environments (Tang et al., 2013). Lake sediments create intricate microbial ecosystems with vertical gradients that are impacted by nutrient fluxes, oxygen penetration, organic carbon availability, and redox potential. Comprehending these trends is essential for assessing the contributions of archaea to nitrogen and methane fluxes as well as their adaptability and resilience in ecosystems impacted by pollution, eutrophication, and climate change. Understanding how archaeal communities respond to environmental pressures can be gained by comparing those in thriving lakes to those in dead lakes (Fenchel & Finlay, 2008). According to Gerphagnon et al., (2015), dead lakes show reduced microbial diversity and a collapse of ecosystem functions as a result of oxygen depletion, whereas thriving lakes usually have varied, functionally robust archaeal communities. This study compares dead and thriving lakes, focusing on the vertical stratification of archaeal communities in lake sediments. It explores taxonomic diversity, functional roles, environmental factors, and ecological functions. The study aims to understand archaeal communities' contribution to lake health and resilience.

2. THE LAKE SEDIMENTS' FUNDAMENTAL PHYSICAL AND CHEMICAL CHARACTERISTICS

Eutrophication has become a significant global issue affecting lake ecosystems, with phosphorus (P) identified as the primary limiting factor responsible for water eutrophication (Huang et al., 2005; Xiong et al., 2015; Z. bin Zhang et al., 2012). Sediments in lakes are formed through depositional processes over time, creating layers that reflect past environmental conditions. In healthy lakes, sediment profiles show clear boundaries of chemical and physical gradients that influence microbial distribution. The upper sediment layer, known as the active zone, is rich in dissolved oxygen, organic matter, and nutrients, providing an ideal environment for microbial life (Uchman & Wetzel, 2011; Xiong et al., 2015). Below this, sediments traverse redox-saturated zones, which promote methanogenesis by gradually depleting electron acceptors from oxygen to carbon dioxide. The survival of numerous archaeal communities may be restricted by these redox conditions. On the other hand, dead lakes, which have disturbed sediment profiles, display environmental degradation indicators such as altered pH, chemical pollution, nutritional imbalances, and disrupted redox gradients (Wan et al., 2024). These alterations significantly alter the makeup of microorganisms. Permanent anoxia brought on by pollution and eutrophication can disturb normal microbial communities, and chemical contaminants like heavy metals can favor resistant archaeal species (Shaibu et al., 2015, 2024; Thakur et al., 2023; Xiao et al., 2017). Moreover, excessive nutrition intake might result in harsh circumstances that change the diversity of archaea. A balance of environmental conditions is reflected in the vertical distribution of archaeal communities in flourishing lakes, where ammonia-oxidizing archaea (AOA) from the phylum Thaumarchaeota dominate surface sediment communities. These organisms, which oxidize ammonia to nitrite, are essential to the nitrogen cycle and are usually located in the highest sediment layers where circumstances change seasonally (Kimble et al., 2018). The breakdown of organic matter in microaerophilic or anaerobic environments is dominated by members of the Bathyarchaeota phylum, indicating a greater metabolic diversity in mid-depth communities (Thakur et al., 2023). Moreover, the Euryarchaeota phylum's methanogenic archaea, which generate methane as a consequence of carbon metabolism, are the main inhabitants of deep sediment levels that lack oxygen. On the other hand, the archaeal diversity is reduced in dead lakes, where species that are suited to hard conditions—such as acidophilic Thermoplasmatales in acidic environments—dominate (Baldrian, 2017). According to Zhang et al., (2024), these communities frequently exhibit changed vertical patterns, which upset the normal stratification found in healthy lakes. Dead lake archaeal species can also act as bioindicators of environmental stresses, such as metal-resistant species suggesting heavy metal contamination or halophilic archaea indicating rising salinity (Kassim et al., 2017).

2.1 Metabolic Activities and Ecosystem Functions

Archaeal communities' metabolic processes in lake sediments create a complex network that is essential to the health and functioning of ecosystems. Oxygenated sediments at the surface layer offer a home for a variety of archaea, including those engaged in ammonia oxidation, a crucial nitrification process that affects primary productivity and nitrogen balance. Additionally, by aiding in the breakdown of organic materials, these archaea change the chemistry of sediments and release nutrients for use by other living things (Diao et al., 2023).

According to Marakushev & Belonogova, (2018), some archaea can also fix carbon dioxide into organic molecules, which aids in autotrophic primary production. Archaea specialize in using particular metabolic pathways to break down more resistant organic

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molecules in the mid-depth transition zones (Morris et al., 2013). Additionally, they use new electron acceptors to participate in alternative energy metabolism and a variety of biogeochemical changes. Methanogenesis, a crucial stage in the carbon cycle, and syntrophic interactions—in which archaea collaborate with bacteria to break down challenging organic matter—are the main foci of archaeal metabolism in the anoxic deep sediments (Wallenius et al., 2021). The entire health of lake ecosystems depends on these metabolic activities, which affect carbon fluxes, microbial community health, and nutrient cycling. Knowledge of these activities provides information about the dynamics of lake ecosystems and possible restoration tactics.

2.2 Archaeal Communities and Stratification Patterns

The stratified distribution of archaeal and bacterial communities in diverse natural habitats was highlighted by Zhou et al. (2017). Understanding physicochemical and spatiotemporal aspects of microbial diversity and composition in coastal mangrove wetlands provides information about the ecological roles of microorganisms. The use of MiSeq sequencing and 16S rRNA quantitative PCR to analyze seasonal changes in microbial communities from two sediment types (intertidal mudflats and mangrove forests) at three Mai Po wetland sites showed that the abundance of bacterial 16S rRNA genes declined with depth, indicating weak seasonal changes for both bacterial and archaeal communities. Seasonality affected bacterial beta diversity more than archaeal, with sediment depth and pH influencing community composition. Stratified bacterial distribution and archaeal dominance patterns were shaped by oxygen availability and electron acceptor distribution. Thaumarchaeota Marine Group I predominated surface sediments, while Bathyarchaeota and MBG-B dominated subsurface sediments, regardless of sediment type, location, or seasonality. However, Andrei et al., (2015), discovered typical extreme hypersaline aquatic archaeal communities in the oxic zone of Fara Fund Lake, dominated by Halobacteriales phylotypes (Ghai et al., 2011; Ventosa et al., 2015). These communities exhibited vertical variation and distinct monimolimnion assemblages. Halobacteriaceae, related to solar saltern DNA, predominated in samples from depths of 0.5 and 2 meters. Hypersaline meromictic lakes, with strong physicochemical gradients and high salt concentrations, serve as valuable models for understanding microbial niche differentiation and biogeochemical cycling. Comparing prokaryotic communities in Ursu and Fara Fund lakes revealed differences in diversity, with Ursu Lake having a bacterial dominance and Fara Fund Lake hosting greater archaeal populations in oxic zones. Despite these differences, both lakes share roles in carbon degradation and sulfate reduction. Methane detection and isotope analysis indicated a new methanogenic group in hypersaline zones, while Fara Fund Lake's chemocline featured ultrasmall archaeal lineages, including the Nanohaloarchaeota phylum (Andrei et al., 2015). Rissanen et al. (2019) highlighted that while small boreal humic lakes are crucial carbon stores and greenhouse gas sources, their microbial community composition and structuring mechanisms are understudied. Analysis of vertical sediment profiles revealed that microbial biomass decreased with depth, but viable microbes (RNA and PLFA) were present throughout. Archaeal communities showed vertical stratification, with surface sediments dominated by well-known groups like Methanomicrobia and Proteobacteria, and deeper layers by lesser-known groups like Bathyarchaeota and Aminicenantes. These findings suggest that deep communities persist under low-energy conditions, contributing to methane emission and potential carbon storage changes. Similarly, Cadena et al., (2019) investigated benthic bacteria and archaea community structure and distribution in a Southern Gulf of Mexico coastal lagoon with strong physicochemical gradients affecting microbial biogeochemical activities. The study identified three distinct regions—oligohaline, marine, and mixing zones—through 16S rRNA gene Illumina sequencing. Principal coordinate and PERMANOVA analyses determined that salinity and zonation were the main environmental factors shaping microbial assemblages. The research emphasized the abundance of specific taxa in each region, such as methanogens in oligohaline sediments and Thaumarchaeota in marine zones, contributing to our understanding of microbial diversity in transitional coastal lagoons.

2.3 Taxonomic and Functional Diversity of Sediment-Dwelling Archaea

Archaea, a unique life domain first classified by Woese et al. in 1990, were distinguished from bacteria and eukaryotes based on phylogenetic and nucleic acid analyses (Offre et al., 2013; Zou et al., 2025). Initially believed to thrive primarily in extreme environments, such as high temperatures and acidic or alkaline conditions, the discovery of mesophilic archaeal groups has broadened our knowledge of their ecological distribution (Cavicchioli, 2011). Archaea play essential roles in global biogeochemical cycles, particularly in sediment ecosystems covering more than half of Earth's surface. Recent studies indicate that archaea constitute a considerable portion of benthic microbial communities, ranging from approximately 12.8% in pelagic sites to 40% in marginal regions (Zhou et al., 2017; Zou et al., 2020). Archaea inhabit a range of sediment environments, from inland regions to land-sea interfaces and open oceans. An extensive analysis of 2,063 archaeal genomes from various ecosystems, including hot springs, freshwater lakes, estuaries, and coastal sediments, by Zou et al., (2025) emphasized the taxonomic and functional diversity of sediment-dwelling archaea and their significance in carbon, nitrogen, and sulfur cycles. Major archaeal groups found in sediments are Euryarchaeota, Crenarchaeota, and Thaumarchaeota, featuring key players such as Methanogens, ammonia-oxidizing archaea (AOA), and sulfur-reducing archaea, which contribute to nutrient cycling and organic matter transformation (H. Jiang et al., 2007; Offre et al., 2013; Santoro, 2010). Methanogens, found predominantly in deeper, oxygen-free sediment layers, are key contributors to methane production, a process with implications for global greenhouse gas emissions. Ammonia-oxidizing archaea (AOA), commonly found in surface sediments, play a crucial role in ammonia oxidation, an essential part of the nitrogen cycle (Katayama

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et al., 2022; Pester et al., 2011). Emerging archaeal phyla like Bathyarchaeota and Lokiarchaeota are gaining recognition for their roles in carbon degradation within deep sediments (Meng et al., 2014). Sediment-dwelling archaea showcase functional specialization, with some carrying out anaerobic processes such as methanogenesis, while others perform aerobic processes like ammonia oxidation, emphasizing their ecological importance. Archaea in extreme environments like hypersaline lakes can utilize alternative electron acceptors, demonstrating metabolic versatility. Taxonomically, archaea are most prevalent in hot springs, seafloor sediments, and hydrothermal vents, with reduced presence in land-sea intersections due to mixed terrigenous and oceanic archaea populations (Zou et al., 2025). The majority of 2,063 representative genomes span 18 phyla, with dominant groups such as Thermoproteota, Halobacteriota, Asgardarchaeota, Nanoarchaeota, and Thermoplasmata. Some archaeal lineages, including Methanosarcinia, Methanomicrobia, Nitrososphaeria, and Bathyarchaeia, inhabit various sedimentary environments, while others, like thermophilic and halophilic extremophiles, are habitat-specific (Zou et al., 2025). This diverse distribution and functional capacity emphasize archaea's global biogeochemical significance and potential impact on ecosystem functions.

2.4 Depth-Wise Distribution and Dominant Archaeal Lineages

In a study of seasonal and depth-wise variations in bacterial and archaeal communities in the Arabian Sea oxygen minimum zone (AS-OMZ), Bandekar et al. (2018) analyzed 16S rRNA gene sequences from samples taken at different depths across three seasons. It was observed that bacterial communities dominated by *Gammaproteobacteria*, *Alphaproteobacteria*, and *Cyanobacteria*, while archaeal sequences were mostly from Marine Group II. Seasonal and depth-related shifts in bacterial communities were observed, with minimal variation among OMZ communities. Differences in dissolved oxygen and total organic carbon levels were linked to the vertical distribution of these communities. However, Zhou et al., (2017) noted that the depth-wise distribution of archaea in lake sediments is influenced by a combination of environmental factors such as oxygen availability, redox conditions, and organic matter quality. Studies have shown that archaea are stratified in sediments, with distinct communities inhabiting different sediment layers depending on the availability of electron acceptors and organic substrates (Li et al., 2012). In oxic surface sediments, archaeal communities are often dominated by ammonia-oxidizing archaea (AOA) from the Thaumarchaeota phylum, which play a key role in nitrogen cycling (Zhalnina et al., 2012; Zhao et al., 2021). As the sediment depth increases and oxygen levels decrease, methanogens from the Euryarchaeota phylum, such as *Methanosarcina* and *Methanosaeta*, dominate deeper, anoxic layers, where they facilitate methanogenesis, a process critical for methane production. In more anoxic environments, sulfur-reducing archaea and sulfate-reducing bacteria are also prevalent, contributing to sulfur cycling. Additionally, the discovery of phyla such as *Bathyarchaeota* and *Lokiarchaeota* in deep sediments highlights the functional diversity and specialization of archaea in these extreme environments, where they are involved in carbon degradation and organic matter turnover. The vertical stratification of these archaeal lineages underscores their adaptability to specific environmental niches, from surface to deep sediments, and their integral role in global biogeochemical cycles (Udousoro et al., 2015; Jørgensen & Boetius, 2007).

3. ARCHAEOAL METABOLIC PROCESSES AND THEIR ROLE IN BIOGEOCHEMICAL CYCLES

Archaeal metabolisms play a vital role in sustaining archaeal biomass and influencing biogeochemical cycles. Archaea comprise over 20% of prokaryotes in ocean waters and contribute significantly to various geochemical processes, especially in carbon cycling, where they dominate methane production and oxidation (Offre et al., 2013). Archaeal groups like Crenarchaeota, Thaumarchaeota, and Euryarchaeota participate in autotrophic growth by assimilating carbon dioxide or bicarbonate to form organic molecules. Some archaea also exhibit mixotrophic behavior, switching between autotrophic and heterotrophic lifestyles depending on environmental conditions. Thaumarchaeota, a key group of autotrophic archaea, significantly contribute to carbon cycling in marine ecosystems, supplying reduced carbon for other organisms. These archaea are vital in organic carbon mineralization, breaking down organic compounds into carbon dioxide under aerobic and anaerobic conditions. Methanogenesis, another crucial metabolic process, involves methanogens producing methane from various substrates, impacting greenhouse gas emissions as shown in Figure 1. Methanogens thrive in anoxic environments like rice paddies, peat bogs, and hydrothermal vents, sometimes forming syntrophic relationships with other microorganisms to facilitate methane production. Moreover, some archaeal species play a role in methane oxidation, converting methane to carbon dioxide in environments where methane and sulfate coexist. This process is essential for mitigating methane emissions and has important implications for climate regulation and carbon cycling in aquatic ecosystems. In addition, Archaea play a critical role in controlling methane emissions in ecosystems such as marine sediments and freshwater habitats through methane oxidation. Additionally, they impact nitrogen cycling by participating in ammonia oxidation, nitrogen fixation, and denitrification. Ammonia-oxidizing archaea (AOA) are particularly significant in ammonia oxidation to nitrite across various ecosystems, often outcompeting bacteria in certain conditions. Archaeal denitrification, though less studied, is crucial for reducing nitrate to nitrogen gas, thereby completing the nitrogen cycle. Archaeal involvement in sulfur cycling includes processes like sulfidogenesis and sulfur oxidation, impacting environments such as geothermal fields and acid drainage. Sulfidogenesis, the production of hydrogen sulfide, is common in anaerobic archaea, while sulfur-oxidizing archaea are essential in environments containing metal sulfides.

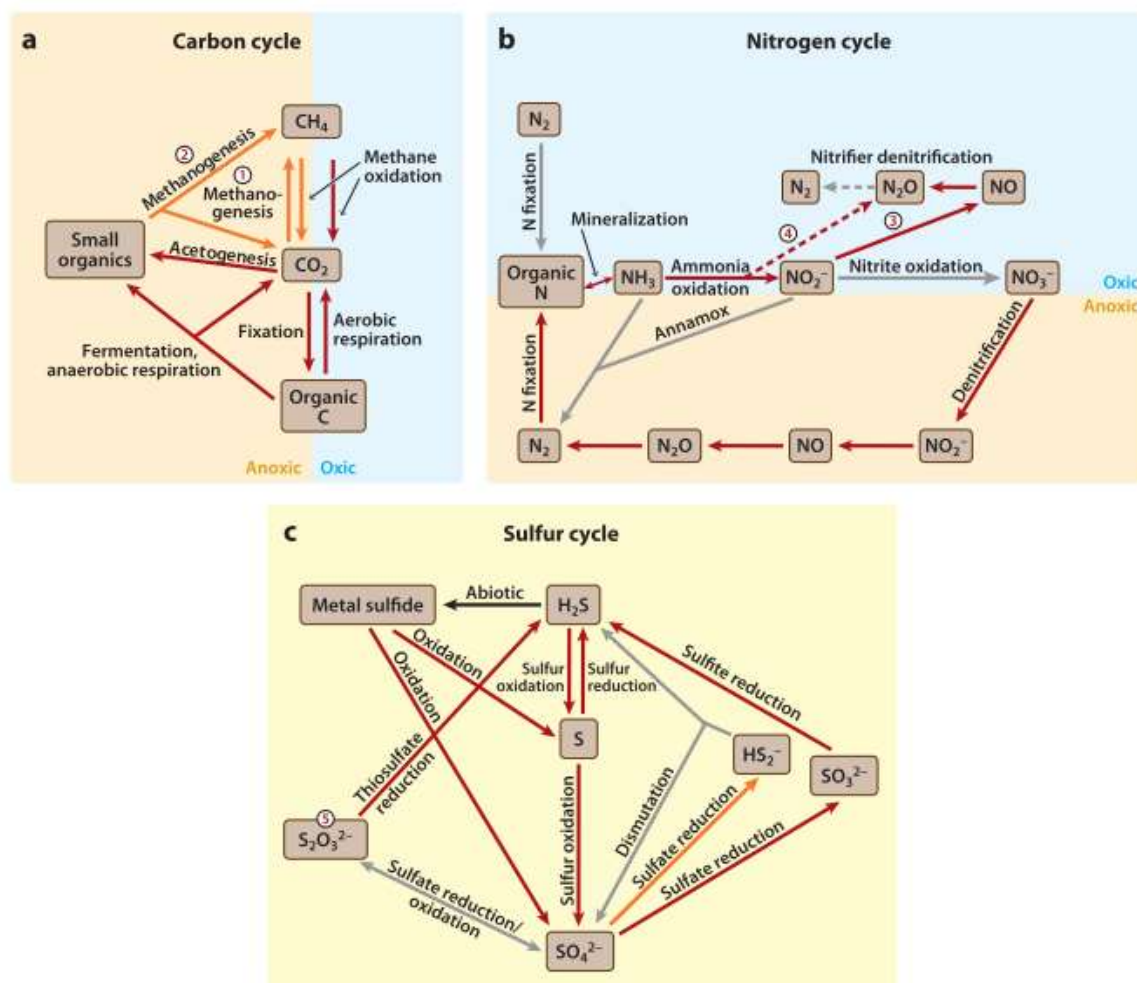


Fig. 1: A schematic illustration showing the role of archaea in (a) carbon, (b) nitrogen, and (c) sulfur cycles. Red arrows represent metabolic steps shared by archaea and bacteria, orange arrows indicate metabolic pathways unique to archaea, and gray arrows highlight processes found only in bacteria. (Offre et al., 2013).

3.1 Environmental Factors Influencing Archaeal Stratification

According to Cadena et al., (2019), numerous physical factors impact the vertical distribution of archaeal communities in lake sediments, which is crucial for comprehending how these communities react to environmental changes and can aid in the development of efficient management plans which is in accordance with several studies (Moore et al., 2017; Rissanen et al., 2019; J. Zhang et al., 2015). The availability of oxygen is one of the main elements affecting the dispersion of archaea. The organization of archaeal communities in healthy lakes is mostly determined by oxygen levels (Morrison et al., 2017; J. Zhang et al., 2015). Oxygen is the main electron acceptor in the oxic zone, which stretches a few millimeters to centimeters into the sediment. By helping to oxygenate the sediment, bioturbation fosters the growth of aerobic archaeal communities, especially those that oxidize ammonia and belong to the phylum *Thaumarchaeota* (Ruuskanen et al., 2018; Wurzbacher et al., 2017; L. Zhang et al., 2019). The formation of stratified archaeal redox communities, with methanogenic archaea occupying the deepest layers, is the result of alternate electron acceptors such as manganese, iron, and sulfate becoming increasingly significant beyond this oxic zone. Persistent anoxia or fluctuating redox conditions frequently disturb this ordered redox stratification in degrading water bodies, changing the nature of the archaeal population. Archaeal communities are significantly shaped by temperature as well. In flourishing lakes, seasonal temperature fluctuations can affect the makeup of the community and the metabolic activity of microorganisms, particularly in the upper sediment layers (Tardy et al., 2021). The growth patterns of archaeal species are temperature-dependent, and these seasonal variations influence the composition of communities. Because the temperatures in deeper sediment layers are often more constant, specialized communities that are suited to those conditions are more likely to form. But these temperature trends and lake thermal regimes can be upset by climate change, particularly in dead lakes that are stagnant or thermally contaminated, where rising temperatures can stress archaeal communities and cause a shift toward organisms that can withstand heat (Katayama et al., 2022; Lan et al., 2024; Tardy et al., 2021). The organization of archaeal communities is also greatly influenced by the availability of nutrients, especially the kind and distribution of organic matter. A wide variety of archaeal organisms are supported in healthy lakes

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by the fresh organic matter that surface sediments get. As organic matter degrades with depth, the quality of the organic material changes, creating a vertical gradient that influences archaeal distribution. In deep sediments, the organic matter is more recalcitrant, and in dead lakes, organic matter profiles are often disrupted, with altered degradation patterns or accumulation of organic material, further affecting archaeal community composition. These environmental factors together shape the dynamic structure and function of archaeal communities in lake sediments (Chen et al., 2021; Z. Jiang et al., 2024).

3.2 Adaptation and Resilience Mechanisms

In sedimentary settings, archaeal communities are highly adaptive, allowing them to flourish in the face of a wide range of chemical and physical challenges. Their molecular and physiological systems reflect these adaptations. Changing lipid saturation levels and adding specific membrane-spanning lipids are two examples of membrane changes that assist archaea in stabilizing their membranes under challenging circumstances (Pichler & Emmerstorfer-Augustin, 2018). Archaea can sustain metabolic activities in varying sediment depths thanks to enzymatic adaptations, which are particularly essential because some archaeal enzymes are designed to work best in particular environmental circumstances (Somayaji et al., 2022). In order to adjust to changing environmental conditions, archaea have also evolved stress response systems, such as metabolic flexibility, DNA repair mechanisms, and stress protein synthesis. Archaea physiologically adjust their development rates based on the circumstances of the sediment; species that live on the surface grow quickly, whereas species that live deeper grow more slowly because of scarcer supplies. Archaea change the composition of their communities in challenged situations, including dead lakes, by shifting their metabolic focus from development to survival (Wahab et al., 2023). According to Bräsen et al., (2014), archaeal communities also demonstrate exceptional resource usage methods, such as nitrogen cycling and carbon metabolism, which are critical for maintaining microbial ecosystems. As environmental changes like algae blooms and temperature fluctuations affect the composition of communities, seasonal variations also affect the distribution of archaea (Hess et al., 2024). Furthermore, metabolic activity and ecological balance may be negatively impacted by irreversible disturbances in archaeal communities brought on by long-term succession and climate change. In order to guarantee the participation of archaeal communities in post-recovery ecosystem activities, effective ecosystem restoration strategies must carefully take into account the physical and chemical conditions that support these communities (Bhaduri et al., 2022). Additionally, to comprehend archaeal diversity and function at various sediment depths, sophisticated sampling and sequencing technologies are essential.

CONCLUSION

Lake sediment archaeal populations are strongly impacted by environmental gradients such as temperature, redox conditions, oxygen availability, and the quality of organic materials. According to this study, robust and complex archaeal communities seen in healthy lakes play a major role in the nutrient cycle and overall health of the ecosystem. On the other hand, dead lakes exhibit reduced archaeal diversity and changed functional activities due to their ongoing anoxia and disturbed redox zones. The results demonstrate the ecological significance of archaea in preserving lake ecosystem balance and their potential as bioindicators for evaluating the health of lakes. Strategies for restoring ecosystems can be informed by knowledge of how archaeal populations adjust to shifting environmental conditions, particularly in lakes impacted by eutrophication and climate change.

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