Microbial communities inhabiting 600-year-old sediments in the Inka-Coya Lake located in the Atacama Desert

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Abstract. Lacustrine sediments are natural archives for the surrounding area's biogeochemical dynamics; in particular, the isolation and extreme conditions in which desert lakes are located make them ideal study models for studying perturbations in the ecosystem. We aimed to study the microbial community dynamics in Inka-Coya Lake, located in the Atacama Desert, where active geological activity and the local mining industry influence biological dynamics in this ecosystem, as suggested for macroinvertebrates and plankton communities in the lake. In this study, we aimed to characterize the microbial communities that inhabit deep lacustrine sediments and their interaction with the surrounding environment. The results show that the microbial community from lacustrine sediments contains over 70% unclassified organisms, highlighting this ecosystem's microbial taxonomic novelty. Our results indicate that the microbial communities cluster in three distinct zones: a superficial community, an intermediate and mixed community, and a more specialized anaerobic community in the deeper sediments. The microbial composition is dominated by chemoheterotrophic bacteria strongly associated with methane metabolism. Additionally, there is statistical evidence of strong correlations between particular taxa such as Sulfurimonadaceae, Metanoregulaceae, and Ktedonobacteroceae with elements like Cu, As, Fe, Ni, and V, and magnetic properties of the surrounding environment, evidencing the strong correlation between the surrounding geochemistry and microbial life that could be disrupted with the continuous mining activity in the area. Further detailed studies of the metabolic repertoire of these communities are necessary to understand the complex dynamics between microbial life and geochemical composition in this fragile and extreme environment.

KEYWORDS: desert lake, deep lacustrine sediment, microbial communities, extremophiles

1. INTRODUCTION

The Atacama Desert is located on the driest part of the South American dry diagonal, which extends from 5°S on the west coast to almost 50°S on the east coast, over 4,000 km with less than 200 mm mean annual rainfall (MAR). It is surrounded by the western slopes of the Central Andes Cordillera between 15 and 30°S at elevations between sea level and 3,500 m a.s.l. The Andes Cordillera represents a physical barrier that directly modulates climatic conditions and water availability in the Atacama Desert (Garreaud et al., 2003). Particular environmental conditions of the Atacama, such as high solar radiation, low atmospheric humidity, and other pressures associated with the natural composition of the desert, directly influence life occurring in these ecosystems (Demergasso et al., 2008; Albarracín et al., 2020; Kurth et al., 2021; Kereszturi et al., 2020; Borsodi et al., 2022). Thus, the Atacama Desert water bodies are truly natural laboratories for understanding evolutionary processes, not only of the geomorphology of the landscape but also of different life forms promoted by environmental forces, such as climate changes at different time scales (Adrian et al., 2009).

Aquatic sediments are sources and/or sinks of elements participating in biogeochemical cycles, including both allochthonous and autochthonous lake processes, influencing biodiversity and trophic dynamics of water bodies (Trolle et al., 2010; Fernández et al., 2000; Usenko et al., 2007; Bandowe et al., 2018). Aquatic sediments have an advantage over terrestrial records, and that is that they accumulate at measurable rates because they are often buffered from physical, chemical, and biotic disturbances, thus allowing the recording of past environmental conditions (Benito, 2020; Picard et al., 2022; Da Costa et al., 2023; Yan et al., 2024). A wide variety of abiotic (e.g., bulk density, dry mass, radioactive isotopes, mineralogy, chemical elements) and biotic proxies (e.g., fossils, species abundance, and presence/absence, resting structures, pigments, environmental DNA) preserved in the sediments are currently analyzed to reconstruct ecosystem change at timescales ranging from fine scale (interannual or decadal) to millennial (Cohen, 2003; Korosi et al., 2017).

The central Andes water systems have mainly originated after successive glaciations and volcanic and tectonic activity. In the Atacama Desert, lacustrine sediments are natural archives holding evidence of past precipitations, dust deposition, anthropic disturbances, and pollution, mainly due to mining activity that occurs in the area (Grosjean and Veit, 2005; Placzek, 2009; Cerda et al., 2019; Aránguiz-Acuña et al., 2020). Desert lakes are located in extremely arid and isolated areas, making them susceptible to perturbations (Valero-Garcés et al., 2003; Pueyo et al., 2011; Grosjean and Veit, 2005) and hosting extreme forms of life, especially microorganisms that have evolved physiological and life-history adaptations allowing them to thrive in challenging conditions (Dib et al., 2009; Ordoñez et al., 2009; Farías et al., 2013, 2014; Rasuk et al., 2014). Therefore, lacustrine sediments are expected to contain a great taxonomic diversity, including low-abundance and highly specialized taxa, directly influenced by small-scale conditions determining local environments (Borsodi et al., 2022).

Inka-Coya Lake (22°20’S-68°35’W, 2534 m.a.s.l.) is located at the eastern margin of the Atacama Desert, close to the Salado River, in the San Francisco de Chiu-Chiu village, northern Chile. It is a karstic sinkhole developed during the Quaternary period by the dissolution of calcareous layers of the Chiu-Chiu Formation (El Loa Group). The Atacama Desert and its surroundings have a particular geological history; metals and metalloids found in the Inka-Coya area include Ti, Al, Fe, Ni, and Cr; also, As and Sb are associated with the local geological activity (Aszalós et al., 2020; Borsdorf and Stadel, 2015; Pérez-Portilla et al., 2024), that directly influence the chemical composition of the underground water (Vignale et al., 2021). The central Atacama Desert, specifically the Antofagasta Region, holds large porphyry copper deposits that support the great metal-mining industry (Dittmar, 2004; Salvarredy-Aranguren et al., 2008). In 2021, Chile was the world’s top copper producer, producing 5,508,084 tons -26.6% of the world’s production- (Rodríguez-Luna et al., 2022). The mining industry in the Antofagasta region has developed extensively since the 19th century (Dittmar, 2004; Salvarredy-Aranguren et al., 2008) with increasing impacts on the national economy and development, but also on the health of ecosystems, which have triggered social and environmental conflicts, affecting especially relevant groups such as ancient Indigenous communities from Quechua and Lickan Antay people (see Ramírez et al., 2005; Tapia et al., 2019).

Previous studies aimed to assess mining pollution records on environmental matrices have included the sediment records of different longitudes from the Inka-Coya Lake, showing variation through the geochemistry and magnetic properties (Cerda et al., 2019; Aránguiz-Acuña et al., 2020; Pérez-Portilla et al., 2024). Analyzed variables have allowed us to identify episodes associated with changes in water availability, flash flooding, and evidence of perturbations induced by mining activities. Overall, the lake is polluted at different degrees of severity with Cu, Sb, Mo, and As, and some elements like Cu and Ni have been enriched in the most recent periods (Cerda et al., 2019; Pérez-Portilla et al., 2024). Additionally, some biological proxies, such as macroinvertebrates and diatom communities, were found to be directly influenced by the accumulation of metal(loid) as observed by changes in assembly composition (Aránguiz-Acuña et al., 2020). Surrounding metal-mining exploitation, which has been maintained and even increased through the last 200 years, in addition to aridity stable conditions, makes Inka-Coya Lake an excellent site for understanding biological adaptations of aquatic populations to these anthropic pressures (Aránguiz-Acuña et al., 2018; 2020). Regarding microbial communities, previous studies have established that methanogens are abundant in cold desert lakes, and microorganisms inhabiting these lake oases are the basis for many ecological services (Cavicchioli, 2006; Stoeva et al., 2014; Olilo et al., 2023). Additionally, salinity and pH are the major drivers determining microbial community structure in other desert lakes (Casamayor et al., 2013; Banda et al., 2021; Santini et al., 2022). Therefore, it is necessary to establish a baseline regarding the dynamics between the microbial life and geochemical conditions in Inka-Coya Lake as a model for the Atacama Desert.

While microbial life in arid ecosystems plays a key role in maintaining biogeochemical cycles (Madsen, 2011), there is a high proportion of unclassified taxa that hold great interest in poly-extreme environments from an ecological, environmental, and biotechnological point of view (Farias et al., 2014; Castro-Severyn et al., 2021; Dong et al., 2022). Nevertheless, there are scarce records in which microbial assemblage has been used as a paleolimnological proxy of the possible responses to long-term sustained anthropogenic metal stress (Da Costa et al., 2023; Yan et al., 2024). The few studies considering this aim have focused on changes in primary producers' abundance, under-interpreting the impact on other metabolic functional groups (Benito et al., 2020; Picard et al., 2022).

This study aimed to characterize the microbial community along a lacustrine sediment core, capturing the depositional history of the Inka-Coya Lake over the last 600 years, and contribute to the knowledge of geo-microbial dynamics in the underexplored desert lakes as these microorganisms are the basis for most geochemical cycling of critical nutrients. We hypothesize that the microbial community assemblage of Inka-Coya Lake is strongly associated with sediment attributes shaped by autochthonous and allochthonous processes, particularly anthropogenic contributions from the metal mining industry that has operated near the lake for the past century. To our knowledge, this is a pioneering study in the microbial characterization of a sedimentary core of this length (136 cm) and date (600 years) from a lake sediment in the Atacama Desert. Results show that the microbial communities have changed through time, identifying three clear periods in which alpha and beta diversity has been associated with organic matter content, magnetic susceptibility, and metals and metalloid concentrations. Additional studies of the metabolic functions of the microorganisms inhabiting these sediments are required to understand the interactions between microbial life and the geochemical components of the Inka-Coya Lake further.

1. METHODS

2.1 Study site and sampling

Inka-Coya Lake (San Francisco de Chiu Chiu village, Antofagasta; 22° 20.300′ S; 068°35.981′ W, Chile) has a surface area of 500 m^2 and a maximum depth of 18 m, is located in the Pre-Andean Depression of the Antofagasta Region at an elevation of 2,520 m a.s.l. (Fig. 1 A, B). Around the lake, the predominant vegetation is of vegas, a type of wetland typical of the Andean pre-Puna zone, strongly associated with the hydric variability of the emerging groundwaters.

2.2 Sediment Core Sampling

A fieldwork campaign was driven in August 2021. The topography of the lake bottom was modeled using the Echo-Map Plus 42CV from Garmin. Afterward, three sediment cores from the depocenter of Inka-Coya Lake, where maximum sedimentation rates are expected, were obtained. The cores were obtained using a 9.0 cm diameter Uwitec gravity corer. This study shows the most extended core analysis results, measuring 136 cm (labeled LIC-SHC03). X-ray and photography images were captured before obtaining sections of sediment subsamples from the core. For subsampling, the frozen core was sliced every 0.5 cm to a depth of 12 cm; then, every 1 cm until the end of the core, totaling 146 sediment samples. Sediment sub-samples for molecular analysis were first taken from each segment center within a laminar flow hood and using ethanol-sterilized tools. These sub-samples were collected in sterile 15 ml tubes, labeled and kept frozen. Other sub-samples were also taken for the geochemical analyses. Additionally, sub-samples for every 1 cm interval were obtained to develop the magnetic susceptibility analysis. The cores' detailed treatment, geochemical analysis, and magnetic properties can be reviewed by Pérez-Portilla et al. (2024).

2.3 Sediment Core Dating

The geochronology of the sediment core from Inka-Coya Lake was determined through radiocarbon dating (14C) on the remaining macroscopic carbon along the record. The measurements were done using accelerator mass spectrometry (AMS), and the results were corrected for isotopic fractionation with an unreported δ13C value. Subsequently, the age-depth model for this sedimentary core was established using the Bayesian radiocarbon chronology package Bchron in R, using the ‘shcal20’ as the calibration curve (Hogg et al., 2020; Haslett and Parnell, 2008). A detailed description of the procedure is available in Pérez-Portilla et al. (2024).

2.4 Magnetic and Geochemical Properties Analysis

Five grams of each sediment sub-sample were placed into paleomagnetic boxes of 8 cm^3 to measure the mass magnetic susceptibility (χ) using a Kappabridge MFK1_FA instrument (AGICO Co) under environmental conditions (22–24°C) and a magnetic field of 200 A/m. The samples were measured at a low frequency of 976 Hz (χlf or simply χ) and a high frequency of 15,616 Hz (χhf). The magnetic susceptibility dependent on the frequency was calculated using both measurements, as described by Pérez-Portilla et al. (2024). The χfd% parameter is used to indicate the presence of magnetic particles near the limit of the superparamagnetic/single domain (SP/SD) magnetic size (Verosub and Roberts, 1995), which can be linked to the presence of magnetic particles of authigenic origin (Dearing et al., 1996). Additionally, sub-samples of each 1 cm slice were dried in an oven at 50°C. Afterwards, they were homogenized using an agate mortar in the Geochemistry Laboratory of Universidad Católica del Norte (UCN), Antofagasta, Chile. The sediments were then digested using reverse aqua regia (4 mL HCl + 12 mL of HNO_3 + 300 mg of sediment sample) and a microwave digester (Perkin Elmer MPS 320; EPA 3052 method), following Tapia et al. (2022) in Centro de Investigación Tecnológica del Agua en el Desierto (CEITSAZA-UCN). The elements aluminum (Al), titanium (Ti), vanadium (V), manganese (Mn), iron (Fe), nickel (Ni), Cu, zinc (Zn), arsenic (As), molybdenum (Mo), and antimony (Sb) were measured by the inductively coupled plasma atomic emission spectroscopy (ICP-OES) Perkin Elmer Optima 7000 in the digested residue at CEITSAZA. The organic, inorganic matter, and carbonate contents were estimated using the loss on ignition (LOI) method, which was assessed at a contiguous 1 cm interval following Heiri et al. (2001). This procedure involved drying 1 cm^3 of each sediment sample in crucibles at 105°C for two hours and weighing them. The dry samples were weighed before heating to 550°C in a flask over 1.5 h, left at 550°C for two h, then allowed to cool. The samples were weighed, then the crucibles were transferred to the flask and burned at 925°C. Finally, the crucibles were weighed again once they cooled.

2.5 Sediment sample processing and DNA extraction

Sediment samples were obtained every 1 cm from the top to the bottom of the core under sterile conditions within a laminar flow hood and using ethanol-sterilized tools. According to the manufacturer's instructions, total DNA was extracted from the 250 mg of sediment samples using the DNeasy PowerSoil kit (Qiagen Inc., Hilden, Germany). DNA integrity, quality, and quantity were verified by 1% agarose gel electrophoresis, the 260/280nm ratio and fluorescence using a Qubit4 fluorometer and the Qubit dsDNA HS assay kit (Thermo Fisher Scientific, MA, USA). Following, DNA samples were sent to AustralOmics, Chile, for amplification of the bacterial 16S rRNA gene V4 region (~ 450 bp) using tBakt_341F and Bakt_805R primers (Herlemann et al., 2011), construction of 250 bp paired-end libraries and sequencing on a MiSeq (Illumina) platform.

2.6 Taxonomic Composition Analysis

This analysis was conducted in R v4.0.3 and RStudio v1.3.1093 following the DADA2 v1.16.0 R package pipeline (Callahan et al., 2016) to infer amplicon sequence variants (ASVs) for each sub-sample. Briefly, the reads were evaluated for quality control and subsequently trimmed ($Ns = 0$, $length \geq 150$ bp, expected $errors \leq 2$), followed by dereplication, denoising, and merging of paired reads. Following, an ASV table was built to allow a maximum of two expected errors, removing chimeras and assigning taxonomy using the Silva v138 database (Quast et al., 2012). Also, all ASVs identified as Eukarya, Chloroplast, and Mitochondria were removed. In addition, ASVs with very low abundance (<0.0005%) and those only observed in few samples (<10%) were eliminated; Samples with very few reads (<1000) were eliminated as well. Next, a multi-sequence alignment was created to infer phylogeny using FastTree v2.1.10 (Price et al., 2009), and phyloseq-object (containing the ASVs, taxonomy assignment, phylogenetic tree, and the samples meta-data) was created using the R package Phyloseq v1.34.0 (McMurdie et al., 2013) and the variance stabilizing transformation was used for normalization. Finally, taxa relative abundance and taxonomic composition at different ranks were visualized using the ggplot2 v3.3.3 (Wickham, 2016), Fantaxtic v0.2.0 (Teunisse, 2022), and ampvis2 v2.7.4 (Andersen et al., 2018) R packages.

2.7 Diversity Analysis

Alpha diversity metrics (Shannon, Chao, phylogenetic diversity, and Simpson indexes) were calculated for each segment along the core using the microbiome v1.24.0 (Lahti et al., 2017) and btools v0.0.1 R packages. Also, Wilcoxon statistical tests to compare means with Bonferroni correction were carried out between the identified zones and visualized using the DESeq2 v1.42.0 (Love et al., 2014) and ggpubr v0.6.0 (Kassambara, 2017) packages. Moreover, beta diversity was evaluated by principal coordinates analysis using Hellinger transformed Bray Curtis distances based on the ASV abundance matrix were calculated using Phyloseq v1.34.0 (McMurdie et al., 2013) and ampvis2 v2.4.5 (Andersen et al., 2018) R package. Also, redundancy analysis (RDAs) was calculated using depth gradient and zone parameters to constrain the multivariate space, and ANOVA tested the statistical significance of the selected geochemical variables.

2.8 Functional Predictions

Functional potential signatures and metabolic pathways abundances were inferred based on the ASV abundance and taxonomy matrices using PICRUSt2 v2.4.1 software (Douglas et al., 2020) with the Kyoto Encyclopedia of Genes and Genomes (KEGG) (Kanehisa et al., 2012) and MetaCyc (Caspi et al., 2018) pathway databases. We used the three identified zones along the core that present significant differences at the of taxonomic composition level and then Differential Abundance of inferred pathways was tested with the Kruskal-Wallis test (confidence interval = 0.95) and the Benjamini-Hochberg correction false-discovery rate using ggpicrust2 v1.7.2 R package (Yang et al., 2023). Also, we use the Functional Annotation of Prokaryotic Taxa (FAPROTAX) database v1.2.7 (Louca et al., 2016) to map the identified ASVs and quantify changes in established ecologically relevant functions.

1. RESULTS

The samples analyzed correspond to a sediment core from Lake Inka-Coya, located in the Atacama Desert, with a water depth of 18.5 meters (Fig. 1). The sediment core age-depth model was constructed based on six charcoal sample dates, where the more superficial at 41 cm corresponds to 75 ± 32 cal years BP, and the deepest found at 94 cm corresponds to an age value of

505 ± 22 cal years BP. Based on the age-depth model constructed, the sediment core of Inka-Coya Lake analyzed had 630 years of age (Fig. 2).

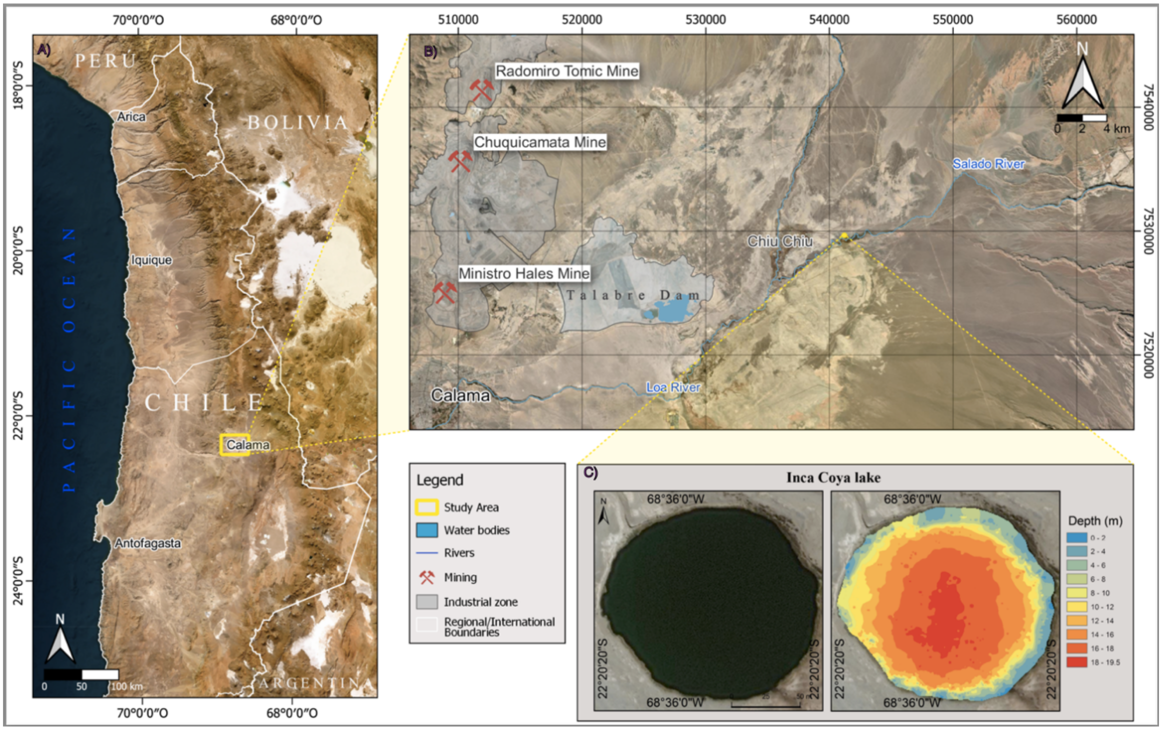


Figure 1. Sampling site location in Northern Chile (A), Inka-Coya Lake, and important surrounding mining and urban centers (B) and the bathymetry of the lake (C).

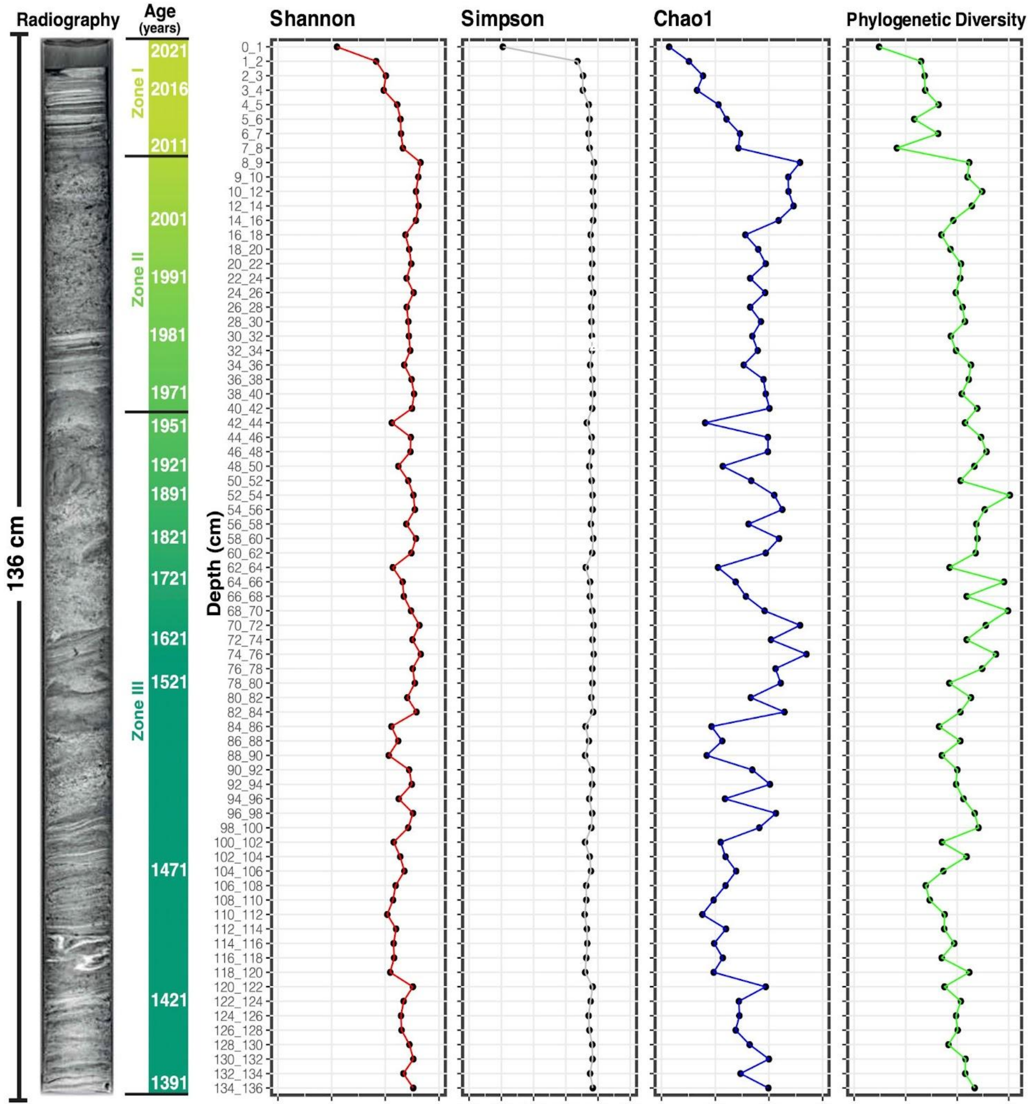


Figure 2. Diversity of the microbial community of the Inka-Coya sediment core. The core sedimentary radiography, dating, and alpha diversity indices variation along the core depth are displayed.

The variation in diversity within the sample was measured to determine the changes in the microbial community along the sediment core by calculating the Shannon, Simpson, Chao, and Phylogenetic indices as standard measures of the taxonomic diversity within a sample (Thukral, 2017). The microbial community observed along the core was diverse, based on the DNA samples analyzed. Quantification of diversity showed that it increased with depth, and the Simpson index remained stable after the 2 cm surface layer. At the same time, Chao1 considered low-abundance taxa, and the phylogenetic index based on the phylogenetic history of the species (Fig. 2). The diversity increases in all cases at two cm long, and maximum values were observed between 8 and 86 cm, with minor peaks at 96, 120, and 130 cm near the bottom samples.

Three distinct zones in terms of microbial taxonomy could be identified and are statistically different for the four evaluated diversity indices, except between Zone II and III in the context of phylogenetic diversity (Fig. 3A). These three disjunct clustering zones of microbial community diversity along the sediment core were also identified in the beta diversity analysis, where zone I includes the less diverse upper layer (0-8 cm), zone II, the middle zone of the core (9-42 cm) with significant greater diversity, and zone III the deepest are sampled in this study, depicted in three shades of green going from lighter (zone I) to darker (zone III) in the PCoA clustering analysis (Fig. 3B).

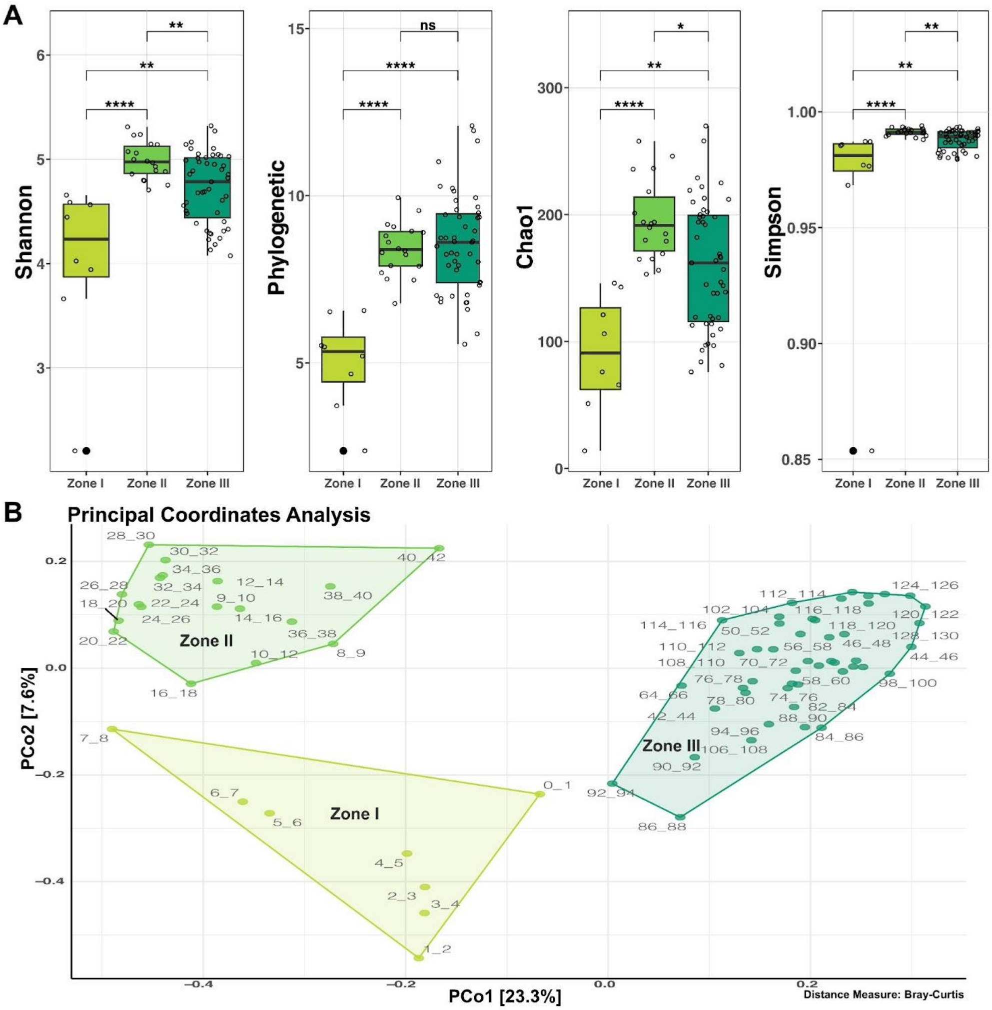


Figure 3. Clustering of the microbial communities inhabiting the deep sediment of Inka-Coya Lake A) Statistical differences in alpha diversity between depth zones. B) Principal Coordinates Analysis (PCoA) with the ASVs relative abundance using Bray-Curtis as distance metric; each point corresponds to a community, tagged by depth and colored by zone.

The taxonomic composition and abundance along the communities at phylum rank also reflect the clustering on three distinct zones, where zone I is dominated by Actinobacteriota and includes a great abundance of Firmicutes in the top layers, and Campylobacterota, there is also the presence of Bacteroidota, Halobacteriota, and Plantomycetota. Zone II is more diverse and composed mainly of Campylobacterota, Chloroflexi, Acidobacteriota, and Actinobacteriota. While zone III is the largest and more homogeneous, composed of several low-abundance taxa, dominated by Chloroflexi, Acidobacteriota, and Actinobacteriota, there is also a higher representation of Crenarchaeota, Nitrospira, Aenigmarchaeota, and Armatimonadota that in the rest of the zones (Fig. 4). The taxonomic composition along the sediment core evidenced the metabolic adaptions that occur in each layer that presents endogenous characteristics, for instance the upper layer includes generalist groups including microorganisms would break down complex organic groups and light driven-metabolic pathways as well as have the metabolic flexibility that would allow the use of different electron acceptors for energy production, supporting heterotrophic communities and mutualistic dynamics. On the other hand, zone III includes more adaptable and ancient phylogenetic lineages that also have the ability to maintain geochemical cycles (C, N, S, Fe) in low oxygen or anaerobic conditions, as those found in early Earth.

Notably, 76.6% of the taxa could not be identified at the genus level (0% matched any known species). Thus, Figure 5 shows the abundance at the "best hit," where Campylobacterota (*Sulfuricurvum*, *Sulfurimonas*), *Mycobacterium*, and *Methanolinea* dominated the overall community, where many representatives of chemo-lithotrophic, S-oxidizing and nitrate reducing capabilities would thrive. While in each zone, there are particular taxa associated; for instance, species belonging to the Aminicenantales Phyla are very common in Zone I; *Pseudarcobacter* is prevalent in Zone II as the anaerobic bacterium *Pelolinea* is in Zone III.

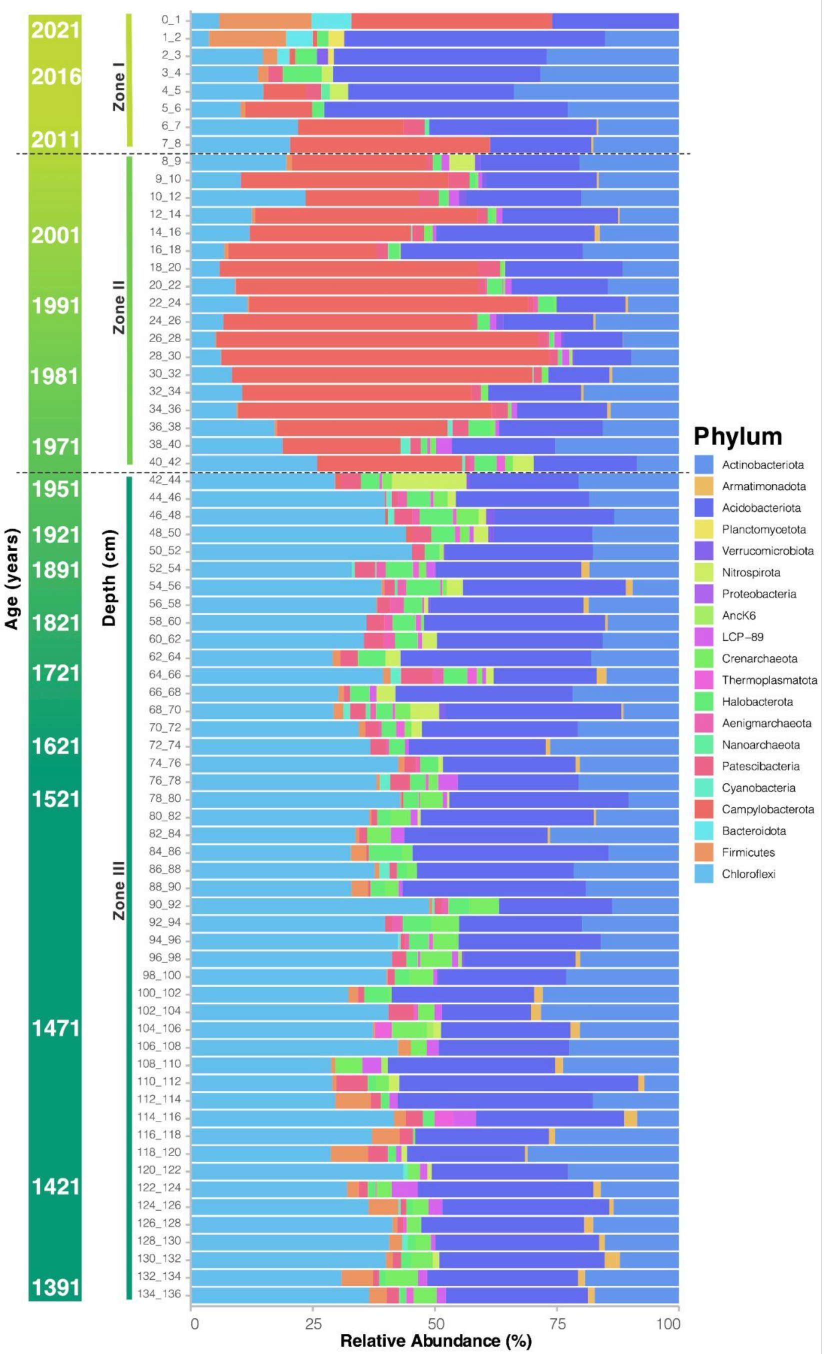
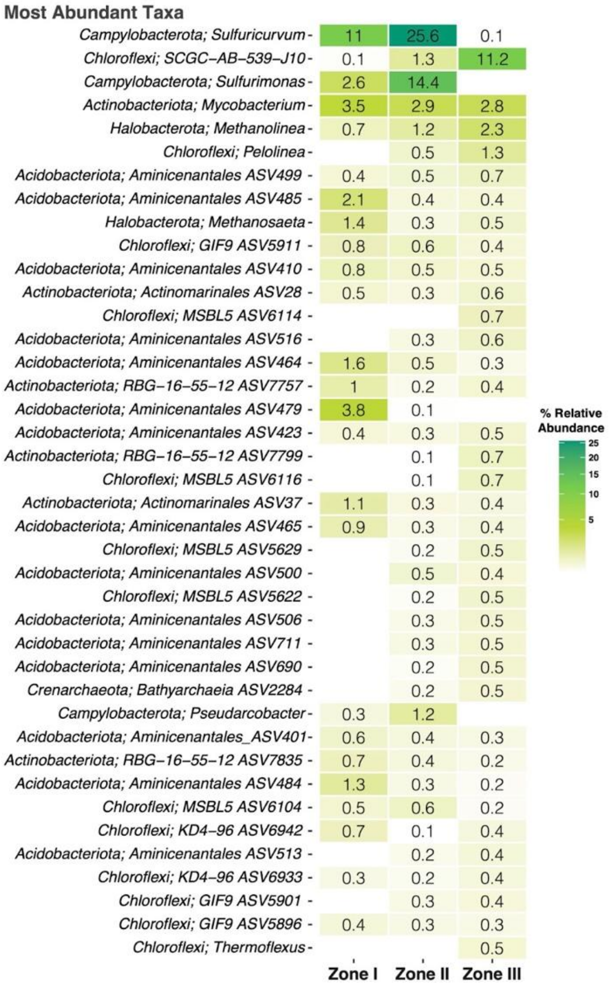


Figure 4. Taxonomic composition of the microbial community in the deep sediments of Inka-Coya Lake. Stacked bar of the taxonomic composition at the phylum level.



Most Abundant Taxa	Zone I	Zone II	Zone III
Campylobacterota; Sulfuricurvum	11	25.6	0.1
Chloroflexi; SCGC-AB-539-J10	0.1	1.3	11.2
Campylobacterota; Sulfurimonas	2.6	14.4	
Actinobacteriota; Mycobacterium	3.5	2.9	2.8
Halobacterota; Methanolinea	0.7	1.2	2.3
Chloroflexi; Pelolinea		0.5	1.3
Acidobacteriota; Aminicenantales ASV499	0.4	0.5	0.7
Acidobacteriota; Aminicenantales ASV485	2.1	0.4	0.4
Halobacterota; Methanosaeta	1.4	0.3	0.5
Chloroflexi; GIF9 ASV5911	0.8	0.6	0.4
Acidobacteriota; Aminicenantales ASV410	0.8	0.5	0.5
Actinobacteriota; Actinomarinales ASV28	0.5	0.3	0.6
Chloroflexi; MSBL5 ASV6114			0.7
Acidobacteriota; Aminicenantales ASV516		0.3	0.6
Acidobacteriota; Aminicenantales ASV464	1.6	0.5	0.3
Actinobacteriota; RBG-16-55-12 ASV7757	1	0.2	0.4
Acidobacteriota; Aminicenantales ASV479	3.8	0.1	
Acidobacteriota; Aminicenantales ASV423	0.4	0.3	0.5
Actinobacteriota; RBG-16-55-12 ASV7799		0.1	0.7
Chloroflexi; MSBL5 ASV6116		0.1	0.7
Actinobacteriota; Actinomarinales ASV37	1.1	0.3	0.4
Acidobacteriota; Aminicenantales ASV465	0.9	0.3	0.4
Chloroflexi; MSBL5 ASV5629		0.2	0.5
Acidobacteriota; Aminicenantales ASV500		0.5	0.4
Chloroflexi; MSBL5 ASV5622		0.2	0.5
Acidobacteriota; Aminicenantales ASV506		0.3	0.5
Acidobacteriota; Aminicenantales ASV711		0.3	0.5
Acidobacteriota; Aminicenantales ASV690		0.2	0.5
Crenarchaeota; Bathyarchaeia ASV2284		0.2	0.5
Campylobacterota; Pseudarcobacter	0.3	1.2	
Acidobacteriota; Aminicenantales_ASV401	0.6	0.4	0.3
Actinobacteriota; RBG-16-55-12 ASV7835	0.7	0.4	0.2
Acidobacteriota; Aminicenantales ASV484	1.3	0.3	0.2
Chloroflexi; MSBL5 ASV6104	0.5	0.6	0.2
Chloroflexi; KD4-96 ASV6942	0.7	0.1	0.4
Acidobacteriota; Aminicenantales ASV513		0.2	0.4
Chloroflexi; KD4-96 ASV6933	0.3	0.2	0.4
Chloroflexi; GIF9 ASV5901		0.3	0.4
Chloroflexi; GIF9 ASV5896	0.4	0.3	0.3
Chloroflexi; Thermoflexus			0.5

Figure 5. Heatmap of the abundance of the microbial community at the family level. The color gradient indicates the abundance of the specific taxa.

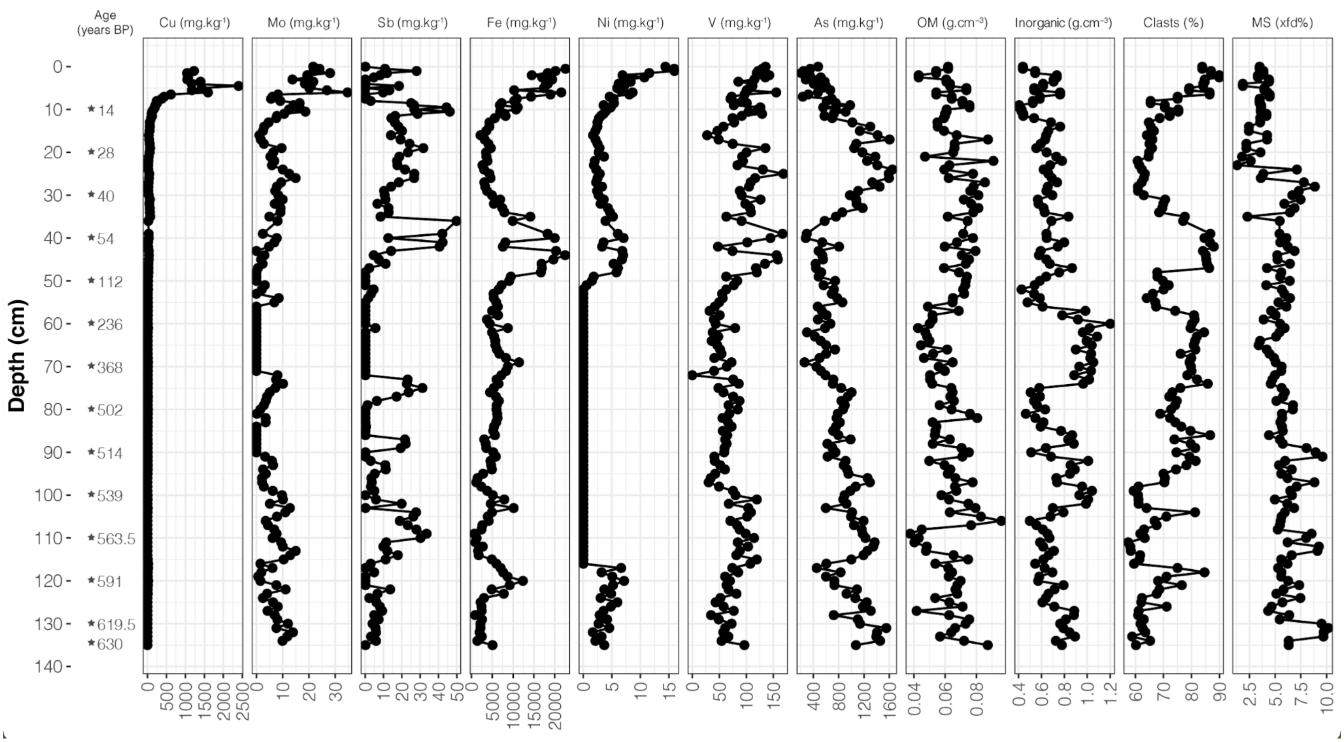


Figure 6. Depth variation of metals and metalloids concentrations (mg·kg^{-1}), organic matter (OM) and inorganic concentrations (g·cm^{-3}), clasts percent, and magnetic susceptibility (MS) measured in Inka-Coya Lake sediment core (modified from Pérez-Portilla et al. 2024).

Variations in analyzed sediment properties along the core, such as magnetic susceptibility, organic matter, and carbonates/clasts composition, are shown in Figure 6. Copper (Cu) and nickel (Ni) were in lower concentration and variability at greater depths and showed concentration peaks in surface sediments. Elements such as iron (Fe), molybdenum (Mo), and vanadium (V) also showed top sediment peaks. Still, overall, they had more variable behavior than previously mentioned elements in the middle and bottom sediments (> 40 cm). Metalloids, arsenic (As), and antimony (Sb) exhibited the highest concentrations between 10-45 cm depth.

The mean organic matter and carbonate contents are around 8.7% and 19.5%, respectively, while the inorganic density (91%) showed the highest averaged values (0.71 g·cm^{-3}). The sediment composition shifts to clay and silt from 28 cm to the top of the core. The content of clasts was predominant in the inorganic fraction, with 71.8% along the core. The carbonate peaks were observed at 10-36 cm, 46-56, and more significant and variable proportions below 96 cm, which did not exceed 40%.

Magnetic susceptibility (MS, χ) values range from -6.09x10^{-9} to 8.13x10^{-7} m^{3}·kg^{-1}, with an average value of 2.77x10^{-7} m^{3}·kg^{-1}. Frequency-dependent susceptibility (χfd%) values range between 1.31 and 10.17%, with an average of 5.62%. Zone I has the highest values of χ and the lowest values of χfd%, while Zone II shows the lowest χ values and intermediate χfd% values. Zone III presents intermediate χ values and the highest χfd% values.

Geochemical and magnetic variables are associated with microbial diversity found in the sediment of Inka-Coya Lakes, differentiated into zones (I, II, and III). Deeper and older fractions of sediments (dark blue), especially Aminicenantaes, are positively influenced by the magnetic susceptibility and inorganic elements in the sediments. Microbial assemblage found in the middle sediments (Zone II) of the core is driven by organic matter content and water availability, where taxa like *Sulfurimonas*, *Sulfuricurvum*, and *Dehalococcoidia* were the most represented. The middle zone is associated with a significant As peak, which suggests that the presence of metal(loid)positively affects the microorganisms assemblage inhabiting middle-to-superficial layers. In Zone II, microbial diversity is mainly associated with low but stable concentrations of organic matter, a more significant proportion of clasts, and the higher peak of As and Sb in the sediments, where χ values decreased. Upper Zone I is mainly characterized by metal enrichment, with elevated concentrations of Cu, Zn, Ni, Fe, and Mo, among other elements. These peaks correlate with high χ values (Fig. 7).

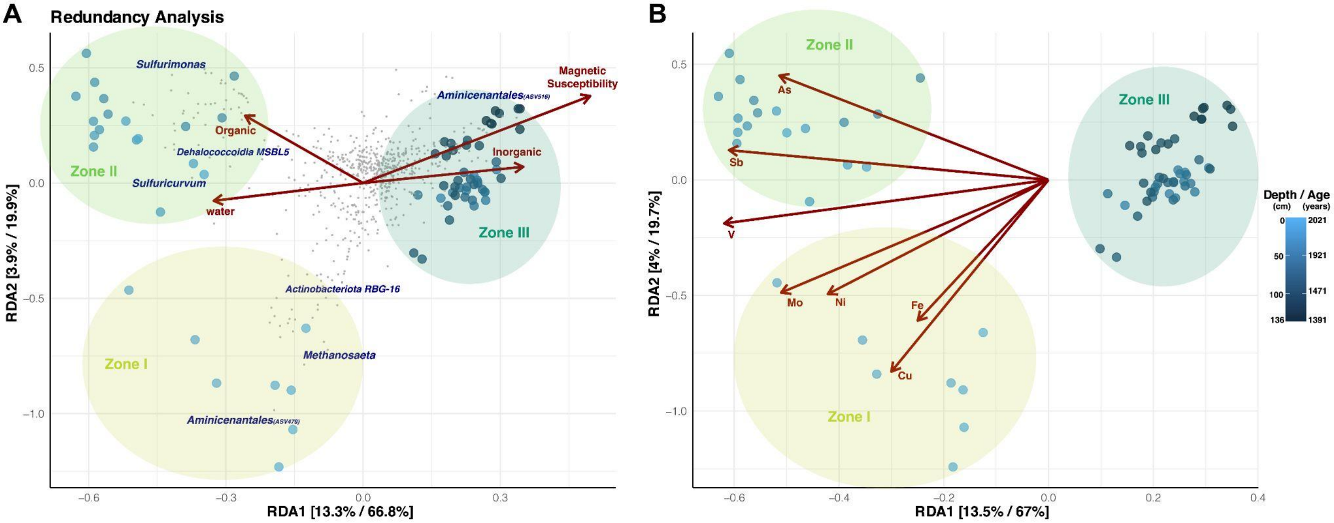


Figure 7. Redundancy analysis on Hellinger transformed Bray-Curtis distances (corrected by unobserved species) for the microbial communities along the core distance. A) Influence of physicochemical parameters and B) Elemental composition. Depth gradient and Zone parameters were chosen to constrain the multivariate space in a supervised approach. Each axis in the graph shows the percentage of variance explained in an unsupervised and supervised analysis.

There is statistical significance between some key taxa and the physicochemical and elemental composition along the sediment gradient in Inca-Coya Lake; for instance, *Methanoregulaceace*, *Ktedonobacteriaceae*, and *Sulfurimonadaceae* are some of the taxa with the strongest correlation to Cu, Fe, Ni and V presence while zones II and III are the most influenced by these dynamics (Supplementary Fig. 1).

Regarding metabolic approximation, chemoheterotrophy is the most abundant function in all three zones, while aerobic chemoheterotrophs are the most prevalent in zone II. Still, chemoheterotrophs (including several electron acceptors) thrive in zones II and III (Supplementary Fig. 2). Other functions, such as Methanogenesis, were abundant only in deep sediments (zone III). Moreover, as expected, phototrophy and photoautotrophy were present only in low abundance in zone I, where little light could reach the community (Supplementary Fig. 2). Methane metabolism is very relevant in all three zones, especially in zone III, where acetate is the primary source for this pathway (Supplementary Fig. 2). Other relevant forms of energy transformation are Nitrate reduction VI (assimilation) and starch degradation in zone II. Nitrotoluene degradation and biosynthesis of unsaturated fatty acids are also crucial in the benthic microbial community as a whole (Supplementary Fig. 2). A somewhat homogeneous prediction for metabolic ability regarding energy production among microorganisms inhabiting in sediments over than one meter deep in the Inka-Coya Lake sediments, where geochemical and magnetic dynamics directly influence microbial activities.

4. DISCUSSION

Microbial dynamics along the length of the sediment core of Inka-Coya Lake are tightly associated with analyzed sediment attributes, such as metal(loid)s concentrations and χfd%, organic compounds- and water- availability. The geochemical characteristics of the area surrounding Inka-Coya Lake, where active volcanic activity results in the enrichment of elements such as arsenic, sulfur, copper, and others (Romero et al., 2003; Tapia et al., 2018), suggests that microbial assemblages inhabiting the Atacama area (1) have showed structure changes during the last 600 years and (2) have developed broad tolerance range to this potential toxic compounds. Microbial biomarkers serve as criteria to assess anthropogenic impact (Yan et al., 2024), and microorganisms can alter the speciation and bioavailability of meta(oids) in an ecosystem (Niu et al., 2020).

Five stratigraphic zones in the sedimentary core in Inka-Coya were defined from the sediment core here analyzed by Pérez-Portilla et al. (2024). In this sedimentary core, the concentration of rock-forming elements such as Cr, Zn, and V are found in concentrations as expected for the Atacama Desert; while Cu, Mo, Sb and As are higher than expected, suggesting influence from nearby mining activities (Pérez-Portilla et al., 2024). Copper production in the region generates by-products such as Mo, As, and, to a lesser extent, Zn (Ramírez et al., 2005; Tapia et al., 2019). Also, mining wastes contain high concentrations of chemical products such as Pb, Cr, Cd, Cu, Zn, Hg, and Ni, and metalloids, which are often stored in dams or reservoirs (Csavina et al., 2012) or passed through lotic systems, making them an important source of contamination of inorganic chemical elements for the aquatic biological communities (Keller et al., 1992; Pollard et al., 2003; Pigati et al., 2011; Hamilton et al., 2017; Ritter et al., 2019). Previous studies have shown impacts and metal enrichment from the mining industry in the Antofagasta region surrounding Calama City and the Loa River basin near the Inka-Coya Lake. Cerda et al. (2019), Vargas-Machuca et al. (2021), Aránguiz-Acuña et al. (2020), and Zanetta-Colombo et al. (2022, 2024), using both abiotic and biological proxies, have evidenced an increase in the concentration of metals in different environmental matrices during post-industrial time, attributing this difference to the mining activities in the area. Additionally, changes in the composition of the zooplankton community (inferred by diapausing egg banks) and benthic diatoms could be attributed to the increase in Cu concentration evidenced in the sedimentary cores obtained in this lake (Aránguiz-Acuña et al. 2020). It is therefore to be expected that other components of the aquatic community, which are as or more sensitive than planktonic invertebrates to changes in metal concentrations in the environment, may also be affected by the impacts of increases in metals associated with the development of the mining industry.

A strong correlation between mineral composition and microbial diversity in other arid region water bodies, such as salt flats and brines, is expected (Farías et al., 2014; Castro-Severyn et al., 2021; Dong et al., 2022), as demonstrated in pre-Puna salt lakes, such as Tebenchique and La Brava (Farías et al., 2014; Ramos-Tapia et al., 2023). The diversity of microbial life in these shallow salty lakes is dominated by Bacteroidetes, Proteobacteria, and Euryarchaeota (Farías et al., 2014; Fernandez et al., 2016; Kurth et al., 2021) and hypersaline lakes are mainly composed by Bacteroidetes, Chloroflexi, Cyanobacteria and Proteobacteria (Dorador et al., 2018). Inka-Coya, one of the few brackish water lakes located in the Antofagasta Region below 3,000 m a.s.l., and its sediment communities are dominated by Phylum Acidobacteriota, Chloroflexi (*Pelolinea*, among others), Actinobacteriota (*Mycobacterium*), and Campylobacterota (*Sulfuricurvum* and *Sulfurimonas*), sharing some similarities and considering changes in taxonomy (Oren and Garrity, 2021). Overall, desert lake sediment microbial communities are very diverse, accounting for the variable conditions and different niches that microorganisms can utilize. In this study, we found great taxonomic diversity and potential metabolic richness where several electron acceptors would sustain the community, including complex carbon complexes, nitrogen, sulfur, and iron, each in different oxidation states. Heterotrophic and autotrophic aerobes and anaerobic representatives were found along the length of the sediment core, indicating that mutualistic relationships are vital for the maintenance of the ecosystem and ecological functions.

At the lower taxonomic rank, the community is dominated by microorganisms with a broad repertoire for mineral interactions, e.g., there is experimental evidence of organomineralization in extracellular S^0 formation by a species of the sulfur-oxidizing bacteria *Sulfuricurvum* (Cron et al., 2019). Another remarkable microorganism found along the lacustrine sediment is the cosmopolitan and highly diverse *Sulfurimonas,* which can grow using sulfur, hydrogen, nitrogen, oxygen, and organic compounds, suggesting it is critical in maintaining trophic dynamics (Han and Perner, 2015). Additionally, *Mycobacterium* is a saprophytic bacterium commonly found in lakes, rivers, and other water sources (Falkinham et al., 2015), there are some species representatives of this genus that have bioremediation potential for polycyclic aromatic hydrocarbons (Deng et al., 2023), suggesting adaptability and a broad range of metabolic capacities. There are extensive studies on Mycobacteriaceae representatives that cause human disease, as reviewed by Falkinham (2009). However, environmental representatives with the capacity to inhabit poly-extreme environments have yet to be determined.

Furthermore, several representatives of the candidate phylum Aminicenantales are common in current sediments from Zone I, i.e., recently deposited sediments during the last ten years. So far, these microorganisms are associated with a fermentative saccharolytic lifestyle that does not have an isolated representative yet (Kadnikov et al., 2019). Zone II, comprising the period between 10 and 50 years ago approximately, is mainly represented by microorganisms classified as the *Pseudarcobacter* genus, that was recently separated from the *Arcobacter* genus (Pérez-Cataluña et al., 2018) and are characterized as mesophilic bacteria that can grow in microaerophilic conditions (Collado et al., 2011). Finally, in the deeper and older sediments, where anaerobic (or facultative anaerobes) microorganisms can thrive, there is a particular abundance of an ASV from the *Pelolinea* genus that has only one described species that was isolated from the subseafloor sediment (Imachi et al., 2014), and an unknown Chloroflexi species that is associated with Dehalococcoidia class a common sub-seafloor bacterium (Wasmund et al., 2014). This finding suggests past conditions of higher salinities for the lake than the current conditions of around 5 $g \cdot L^{-1}$ (Aránguiz-Acuña et al., 2020), close to marine salinitiy. Archaea representatives found inhabiting the lacustrine sediments include the hydrogenotrophic methanogen *Methanolinea* (Imachi et al., 2008; Rainey et al., 2015), which is distributed along the length of the core with an abundance ranging from 0.7-2.3% and is very abundant towards the older and more anoxic environment (since 1400 until 1950, zone III), where methanogenesis is the central predicted metabolism at play. These results suggest that the microbial community in Inka-Coya Lake is potentially heterotrophic with a special enrichment in methanogenic organisms in the oldest deposits, where oxygen levels are lower as evidenced by the metabolic approximation done in this study. Another kind of metabolism, depending on CO_2 concentrations, could have dominated during this period.

Overall, our results suggest a great taxonomic and potential metabolic diversity is associated with the microbial community from this lacustrine sediment. There is a vast taxonomic novelty harbored in Inka-Coya Lake sediment; over 70% of taxa cannot be identified to the genus level, indicating there is a significant amount of “microbial dark matter” a term associated with unknown microbial representatives that can potentially harbor novel bioactive compounds with numerous applications (Zha et al., 2022; Jiao et al., 2021). This microbial dark matter is also associated with a great metabolic diversity, specially for the production of bioactive compounds with biotechnological potential, for example, we determined that there are abundant representatives of Actinobacteriota, a taxonomic group traditionally associated with the production of antimicrobial, antitumoral and anti-inflammatory compounds (Al-Shaibani et al., 2021; Taj and Chattopadhyay, 2024), thus we hypothesize there is a high probability of finding novel compounds produced by microorganisms inhabiting the sediment of Inka Coya Lake.

The main drivers for microbial community composition in the sinks-Coya sediments were As, Sb, V, Mo, Mi, Fe, and Cu, which suggest that there are numerous strategies that microorganisms use to resist high concentrations of metals and metalloids that thrive in this ecosystem (Rahman, 2020; Mathivanan et al., 2021), as observed in the Atacama and Altiplano area (Orellana et al., 2018; Donati et al., 2019; Aszalós et al., 2020; Castro-Severyn et al., 2019). Additionally, microorganisms can use oxido-reduction processes to obtain energy from metal ions (Raab and Feldman, 2003; Staicu and Stolz, 2021). Given the known geochemical characteristics of the area, it is expected to find strong relationships between the microbial life and inorganic compounds, as they can dissolve and precipitate ores and influence metal(loid)s transformations (Raab et al., 2003; Zhou et al., 2022). In this extreme environment where competition is strong and abiotic pressures are constant, organic matter and water availability -both parameters critical for most life forms- govern community abundance and composition, suggesting a delicate dynamic balance reached between abiotic and biotic entities at play. It is important to remark that with the number of unclassified taxa, many novel resistant or usage mechanisms remain to be characterized.

Observed trends in magnetic susceptibility in Inka-Coya sediment could be mainly attributed to variations in the concentration of ferromagnetic minerals, such as titanomagnetite, and authigenic origin minerals, such as sulfide (greigite), as is broadly explained in Pérez-Portilla et al. (2024) for this sediment core. In this case, the high X values would result from a high concentration of ferromagnetic minerals of detrital origin, primarily Fe oxides, while elevated xfd% values would be linked to the presence of greigite of authigenic origin (Pérez-Portilla et al., 2014). Thus, greigite formation typically occurs through the dissolution of titanomagnetite or other detrital minerals containing Fe (e.g., Chan et al., 2001; Fialová et al., 2006; Versteeg et al., 1995).

Elevated magnetic susceptibility values in the upper layers of sediments may be attributed to a recent deposition of fine Fe oxide grains, which could be originating and transported from industrial and urban sources (e.g., Chan et al., 2001); this concurs with the Fe top sediment peak, and it could be related to a diverse superficial community, while in zone II the lowest values of χ are observed, which could be associated with a mixed community. All these processes occur under a high production of Fe minerals of authigenic origin (χfd% > 3%; Dearing et al., 1996). Moreover, lower levels of χfd% could be involved in the production and assimilation of iron sulfides such as greigite (Bazylinski et al., 2001; Lins et al., 2007), promoting a microbial specialization and increasing resistance of the anaerobic community found in the deeper sediments. Microbial metabolic responses could satisfactorily support several processes associated with greigite formation. The presence of greigite in the lake sediments could be associated with reducing or low-oxygen environments (e.g., Benning et al., 2000), where additionally magnetotactic bacteria could contribute to sedimentary greigite formation through the biomineralization of magnetosomes in anoxic aqueous environments (Moskowitz et al., 2008).

There are statistically significant correlations between some particular taxa and the geochemical composition along the sediment gradient in Inca-Coya Lake suggesting that each element directly influences the metabolic capabilities of the microorganisms and shapes the community selecting taxa that can resist metal(loid)s toxicity (Yao and Gao, 2007; Laplante et al., 2013; Stankevica et al., 2020; Kostka and Leśniak, 2021; Yan et al., 2020). However, this study is restricted to metabolic approximations based on taxonomy from a single sediment core. Therefore, it would be desirable to carry our future studies including metagenomic data to explore functional potential and investigate other water bodies to identify temporal patterns of microbiological assemblages in the most exploited area of the Atacama Desert, which will enhance our understanding in terms of the mechanisms used to resist and survive in environments with high metal(loid)s concentrations and the use of different electron acceptors for energy production.

Finally, increasing metal(loid)s exploitation in the region during the last 100 years has directly influenced their mobility and the local geochemistry. In this context, microorganisms from these extreme environments are known to be highly adaptive and have developed several resistance mechanisms and the ability to use these compounds to their benefit. Hence, some bacteria (and their genes) can be used as biomarkers for the bioavailability of such metals and contamination of soils (Li and Wong, 2010; Roosa et al., 2014). In Inka-Coya Lake, a selective process could be evidenced along the sediment record, in which the recent period is characterized by a marked increase in chemical elements and microbial composition, which could be associated with the increasing mining activity and other anthropological activities, as water extraction or aridity increase by climatic changes, that also would increase the disturbance of this relevant area in the core of the most arid non-polar Desert.

5. CONCLUSIONS

This study is the first to describe a deep gradient of microbial life in a desert lake in the Atacama area, proposing a biological clustering of taxa and predicted function in three periods that stratified for over 600 years, including pre-mining period, the mining development and the most industrialized mega mining observed nowadays. A great taxonomic novelty exists among the microbial community inhabiting lacustrine sediments of Inka-Coya and mineralogical enrichment, water, organic matter availability, and magnetic susceptibility are variables that explain the changes in its abundance and composition. There are strong relationships between geochemical composition and microbial diversity, especially in Cu, Fe, Ni, and V. The first zone is less diverse and dominated by Actinobacteria; the second zone has a high abundance of Chloroflexi, Acidobacteriota, and Actinobacterota. The third zone shows more rare taxa with lower abundance and clusters the more recent sediments closer to the surface, including archaea. Overall, chemoheterotrophy is the prevalent energy production mechanism along the sediment core. This unique and fragile ecosystem depends on biogeochemical dynamics that are vulnerable to anthropogenic activities and climate change.

Appendix A.

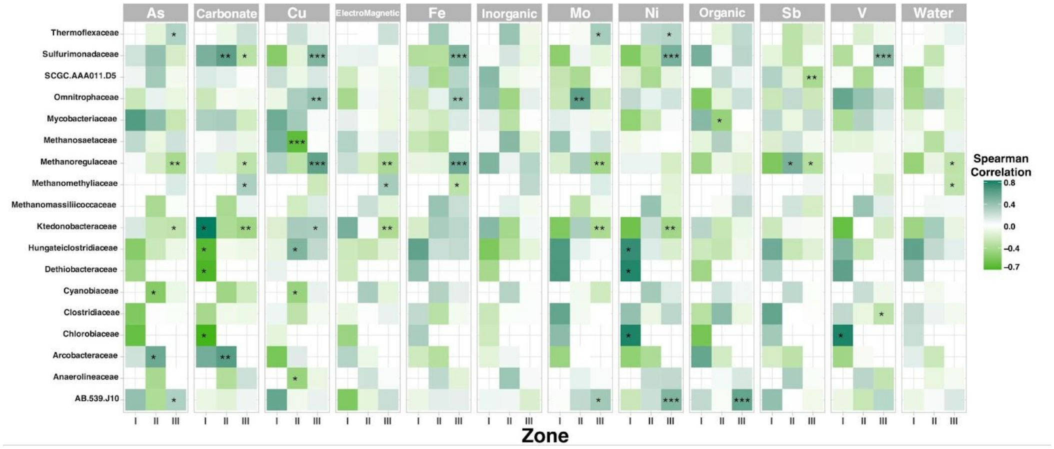


Figure A1. Pearson correlation between the top microbial families and geochemical parameters. Asterisks show the level of significance (*p value < 0.05, **p value < 0.01, Pearson correlation). Purple, blue, and white indicate positive, negative, and no correlation, respectively.

Appendix B

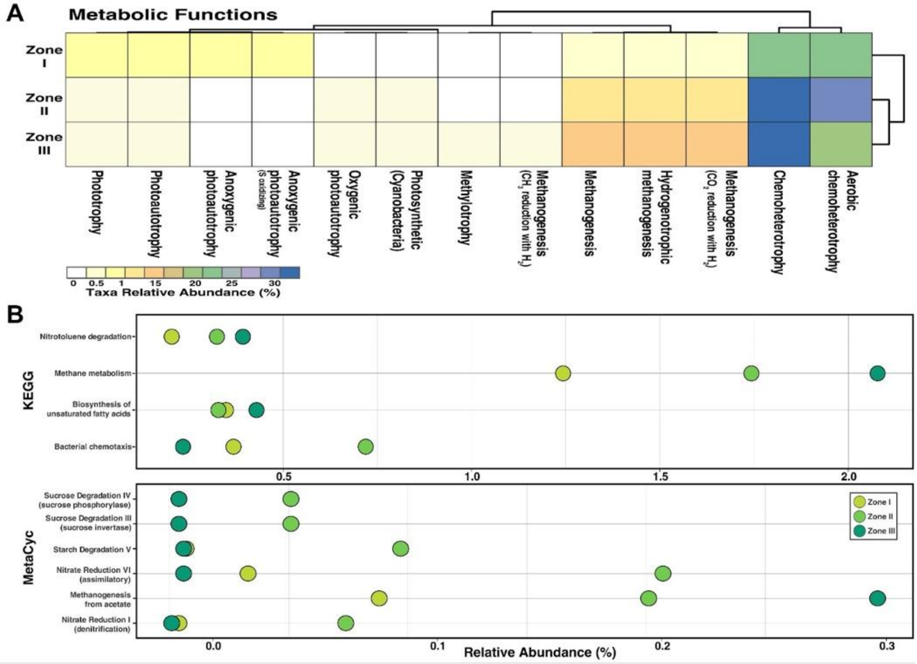


Figure B1. Metabolic pathways prediction of the microbial community inhabiting sediments along a depth gradient in Inka-Coya Lake. The predictions are based on the identified taxonomic composition according to the comparison with different databases, such as: A) FAPROTAX; B) KEGG and MetaCyC. Categories with significant differences ($p<0.05$) according to Kruskal-Wallis test are displayed.

DATA AVAILABILITY STATEMENT

The raw sequencing data presented in this study have been deposited in the DDBJ/ENA/GenBank SRA database under the BioProject: PRJNA1067596.

AUTHOR CONTRIBUTIONS

Conceptualization: AAA; FR, JCS, CPE. Data curation: CPE, JCS, FR, IHF, AAA. Formal analysis: CPE, JCS, FR, AAA, AM, HP. Funding acquisition: FR, AAA Methodology: CPE, JCS, AM, HP, FR, AAA. Supervision: AAA, FR Writing original draft: CPE, JCS. Writing review and editing: AAA, AM, HP, JCS, CPE. All authors have read and agreed to the published version of the manuscript.

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COMPETING INTERESTS

The contact author has declared that none of the authors has any competing interests.

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