

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 Ktedonobacteraceae 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

36 The Atacama Desert is located on the driest part of the South American dry diagonal, which extends from 5°S on the west
 37 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
 38 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
 39 Andes Cordillera represents a physical barrier that directly modulates climatic conditions and water availability in the Atacama
 40 Desert (Garreaud et al., 2003). Particular environmental conditions of the Atacama, such as high solar radiation, low
 41 atmospheric humidity, and other pressures associated with the natural composition of the desert, directly influence life
 42 occurring in these ecosystems (Demergasso et al., 2008; Albarracín et al., 2020; Kurth et al., 2021; Kereszturi et al., 2020;
 43 Borsodi et al., 2022). Thus, the Atacama Desert water bodies are truly natural laboratories for understanding evolutionary
 44 processes, not only of the geomorphology of the landscape but also of different life forms promoted by environmental forces,
 45 such as climate changes at different time scales (Adrian et al., 2009).

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

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

64 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
 65 River, in the San Francisco de Chiu-Chiu village, northern Chile. It is a karstic sinkhole developed during the Quaternary
 66 period by the dissolution of calcareous layers of the Chiu-Chiu Formation (El Loa Group). The Atacama Desert and its
 67 surroundings have a particular geological history; metals and metalloids found in the Inka-Coya area include Ti, Al, Fe, Ni,
 68 and Cr; also, As and Sb are associated with the local geological activity (Aszalós et al., 2020; Borsdorf and Stadel, 2015;
 69 Pérez-Portilla et al., 2024), that directly influence the chemical composition of the underground water (Vignale et al., 2021).
 70 The central Atacama Desert, specifically the Antofagasta Region, holds large porphyry copper deposits that support the great
 71 metal-mining industry (Dittmar, 2004; Salvarredy-Aranguren et al., 2008). In 2021, Chile was the world's top copper producer,
 72 producing 5,508,084 tons -26.6% of the world's production- (Rodríguez-Luna et al., 2022). The mining industry in the
 73 Antofagasta region has developed extensively since the 19th century (Dittmar, 2004; Salvarredy-Aranguren et al., 2008) with
 74 increasing impacts on the national economy and development, but also on the health of ecosystems, which have triggered

75 social and environmental conflicts, affecting especially relevant groups such as ancient Indigenous communities from Quechua
76 and Lickan Antay people (see Ramírez et al., 2005; Tapia et al., 2019).

77 Previous studies aimed to assess mining pollution records on environmental matrices have included the sediment records of
78 different longitudes from the Inka-Coya Lake, showing variation through the geochemistry and magnetic properties (Cerde et
79 al., 2019; Aránguiz-Acuña et al., 2020; Pérez-Portilla et al., 2024). Analyzed variables have allowed us to identify episodes
80 associated with changes in water availability, flash flooding, and evidence of perturbations induced by mining activities.
81 Overall, the lake is polluted at different degrees of severity with Cu, Sb, Mo, and As, and some elements like Cu and Ni have
82 been enriched in the most recent periods (Cerde et al., 2019; Pérez-Portilla et al., 2024). Additionally, some biological proxies,
83 such as macroinvertebrates and diatom communities, were found to be directly influenced by the accumulation of metal(loid)
84 as observed by changes in assembly composition (Aránguiz-Acuña et al., 2020). Surrounding metal-mining exploitation,
85 which has been maintained and even increased through the last 200 years, in addition to aridity stable conditions, makes Inka-
86 Coya Lake an excellent site for understanding biological adaptations of aquatic populations to these anthropic pressures
87 (Aránguiz-Acuña et al., 2018; 2020).

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

95 This study aimed to characterize the microbial community along a lacustrine sediment core, capturing the depositional history
96 of the Inka-Coya Lake over the last 600 years. We hypothesize that the microbial community assemblage of Inka-Coya Lake
97 is strongly associated with sediment attributes shaped by autochthonous and allochthonous processes, particularly
98 anthropogenic contributions from the metal-mining industry that has operated near the lake for the past century. To our
99 knowledge, this is a pioneering study in the microbial characterization of a sedimentary core of this length (136 cm) and date
100 (600 years) from a lake sediment in the Atacama Desert. Results show that the microbial communities have changed through
101 time, identifying three clear periods in which alpha and beta diversity has been associated with organic matter content,
102 magnetic susceptibility, and metals and metalloid concentrations. Additional studies of the metabolic functions of the
103 microorganisms inhabiting these sediments are required to understand the interactions between microbial life and the
104 geochemical components of the Inka-Coya Lake further.

105 1. METHODS

106 2.1 Study site and sampling

107 Inka-Coya Lake (San Francisco de Chiu Chiu village, Antofagasta; 22° 20.300' S; 068°35.981' W, Chile) has a surface area of
108 500 m² and a maximum depth of 18 m, is located in the Pre-Andean Depression of the Antofagasta Region at an elevation of

109 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
110 pre-Puna zone, strongly associated with the hydric variability of the emerging groundwaters.

111 **2.2 Sediment Core Sampling**

112 A fieldwork campaign was driven in August 2021. The topography of the lake bottom was modeled using the Echo-Map Plus
113 42CV from Garmin. Afterward, three sediment cores from the depocenter of Inka-Coya Lake, where maximum sedimentation
114 rates are expected, were obtained. The cores were obtained using a 9.0 cm diameter Uwitec gravity corer. This study shows
115 the most extended core analysis results, measuring 136 cm (labeled LIC-SHC03). X-ray and photography images were
116 captured before obtaining sections of sediment subsamples from the core. For subsampling, the frozen core was sliced every
117 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
118 for molecular analysis were first taken from each segment center within a laminar flow hood and using ethanol-sterilized tools.
119 These sub-samples were collected in sterile 15 ml tubes, labeled and kept frozen. Other sub-samples were also taken for the
120 geochemical analyses. Additionally, sub-samples for every 1 cm interval were obtained to develop the magnetic susceptibility
121 analysis. The cores' detailed treatment, geochemical analysis, and magnetic properties can be reviewed by Pérez-Portilla et al.
122 (2024).

123 **2.3 Sediment Core Dating**

124 The geochronology of the sediment core from Inka-Coya Lake was determined through radiocarbon dating (^{14}C) on the
125 remaining macroscopic carbon along the record. The measurements were done using accelerator mass spectrometry (AMS),
126 and the results were corrected for isotopic fractionation with an unreported $\delta^{13}\text{C}$ value. Subsequently, the age-depth model
127 for this sedimentary core was established using the Bayesian radiocarbon chronology package *Bechron* in R, using the 'shcal20'
128 as the calibration curve (Hogg et al., 2020; Haslett and Parnell, 2008). A detailed description of the procedure is available in
129 Pérez-Portilla et al. (2024).

130 **2.4 Magnetic and Geochemical Properties Analysis**

131 Five grams of each sediment sub-sample were placed into paleomagnetic boxes of 8 cm³ to measure the mass magnetic
132 susceptibility (χ) using a Kappabridge MFK1_FA instrument (AGICO Co) under environmental conditions (22–24°C) and a
133 magnetic field of 200 A/m. The samples were measured at a low frequency of 976 Hz (χ_{lf} or simply χ) and a high frequency
134 of 15,616 Hz (χ_{hf}). The magnetic susceptibility dependent on the frequency was calculated using both measurements, as
135 described by Pérez-Portilla et al. (2024). The $\chi_{\text{fd}}\%$ parameter is used to indicate the presence of magnetic particles near the
136 limit of the superparamagnetic/single domain (SP/SD) magnetic size (Verosub and Roberts, 1995), which can be linked to the
137 presence of magnetic particles of authigenic origin (Dearing et al., 1996). Additionally, sub-samples of each 1 cm slice were
138 dried in an oven at 50°C. Afterwards, they were homogenized using an agate mortar in the Geochemistry Laboratory of
139 Universidad Católica del Norte (UCN), Antofagasta, Chile. The sediments were then digested using reverse aqua regia (4 mL
140 HCl + 12 mL of HNO₃ + 300 mg of sediment sample) and a microwave digester (Perkin Elmer MPS 320; EPA 3052 method),
141 following Tapia et al. (2022) in Centro de Investigación Tecnológica del Agua en el Desierto (CEITSAZA-UCN). The
142 elements aluminum (Al), titanium (Ti), vanadium (V), manganese (Mn), iron (Fe), nickel (Ni), Cu, zinc (Zn), arsenic (As),
143 molybdenum (Mo), and antimony (Sb) were measured by the inductively coupled plasma atomic emission spectroscopy (ICP-
144 OES) Perkin Elmer Optima 7000 in the digested residue at CEITSAZA. The organic, inorganic matter, and carbonate contents
145 were estimated using the loss on ignition (LOI) method, which was assessed at a contiguous 1 cm interval following Heiri et
146 al. (2001). This procedure involved drying 1 cm³ of each sediment sample in crucibles at 105°C for two hours and weighing

147 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
148 cool. The samples were weighed, then the crucibles were transferred to the flask and burned at 925°C. Finally, the crucibles
149 were weighed again once they cooled.

150 2.5 Sediment sample processing and DNA extraction

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

158 2.6 Taxonomic Composition Analysis

159 This analysis was conducted in R v4.0.3 and RStudio v1.3.1093 following the DADA2 v1.16.0 R package pipeline (Callahan
160 et al., 2016) to infer amplicon sequence variants (ASVs) for each sub-sample. Briefly, the reads were evaluated for quality
161 control and subsequently trimmed (Ns=0, length ≥ 150 bp, expected errors ≤ 2), followed by dereplication, denoising, and
162 merging of paired reads. Following, an ASV table was built to allow a maximum of two expected errors, removing chimeras
163 and assigning taxonomy using the Silva v138 database (Quast et al., 2012). Also, all ASVs identified as Eukarya, Chloroplast,
164 and Mitochondria were removed. A multi-sequence alignment was created to infer phylogeny using FastTree v2.1.10 (Price et
165 al., 2009), and phyloseq-object (containing the ASVs, taxonomy assignment, phylogenetic tree, and the samples meta-data)
166 was created using the R package Phyloseq v1.34.0 (McMurdie et al., 2013) and the variance stabilizing transformation was
167 used for normalization. Finally, taxa relative abundance and taxonomic composition at different ranks were visualized using
168 the ggplot2 v3.3.3 (Wickham, 2016), Fantaxtic v0.2.0 (Teunisse, 2022), and ampvis2 v2.7.4 (Andersen et al., 2018) R
169 packages.

170 2.7 Diversity Analysis

171 Alpha diversity metrics (Shannon, Chao, phylogenetic diversity, and Simpson indexes) were calculated for each segment along
172 the core using the microbiome v1.24.0 (Lahti et al., 2017) and btools v0.0.1 R packages. Also, Wilcoxon statistical tests to
173 compare means with Bonferroni correction were carried out between the identified zones and visualized using the DESeq2
174 v1.42.0 (Love et al., 2014) and ggpubr v0.6.0 (Kassambara, 2017) packages. Moreover, beta diversity was evaluated by
175 principal coordinates analysis using Hellinger transformed Bray Curtis distances based on the ASV abundance matrix were
176 calculated using Phyloseq v1.34.0 (McMurdie et al., 2013) and ampvis2 v2.4.5 (Andersen et al., 2018) R package. Also,

177 redundancy analysis (RDAs) was calculated using depth gradient and zone parameters to constrain the multivariate space, and
178 ANOVA tested the statistical significance of the selected geochemical variables.

179 2.8 Functional Predictions

180 Functional potential signatures and metabolic pathways abundances were inferred based on the ASV abundance and taxonomy
181 matrices using PICRUST2 v2.4.1 software (Douglas et al., 2020) with the Kyoto Encyclopedia of Genes and Genomes (KEGG)
182 (Kanehisa et al., 2012) and MetaCyc (Caspi et al., 2018) pathway databases. We used the three identified zones along the core
183 that present significant differences at the of taxonomic composition level and then Differential Abundance of inferred pathways
184 was tested with the Kruskal-Wallis test (confidence interval = 0.95) and the Benjamini-Hochberg correction false-discovery
185 rate using ggpicrust2 v1.7.2 R package (Yang et al., 2023). Also, we use the Functional Annotation of Prokaryotic Taxa
186 (FAPROTAX) database v1.2.7 (Louca et al., 2016) to map the identified ASVs and quantify changes in established
187 ecologically relevant functions.

188 1. RESULTS

189 The samples analyzed correspond to a sediment core from Lake Inka-Coya, located in the Atacama Desert, with a water depth
190 of 18.5 meters (Fig. 1). The sediment core age-depth model was constructed based on six charcoal sample dates, where the
191 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).

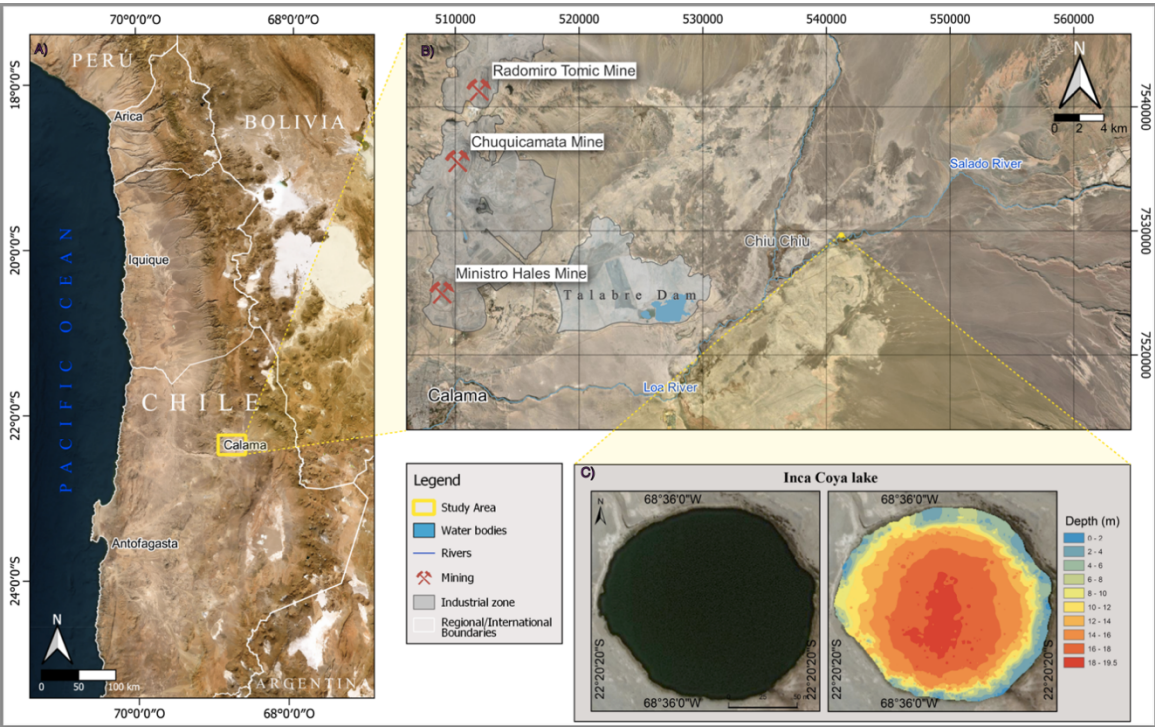


Figure 1. Sampling site location in Northern Chile (A), Inka-Coya Lake, and important surrounding mining and urban centers (B) and the bathymetry of the lake (C).

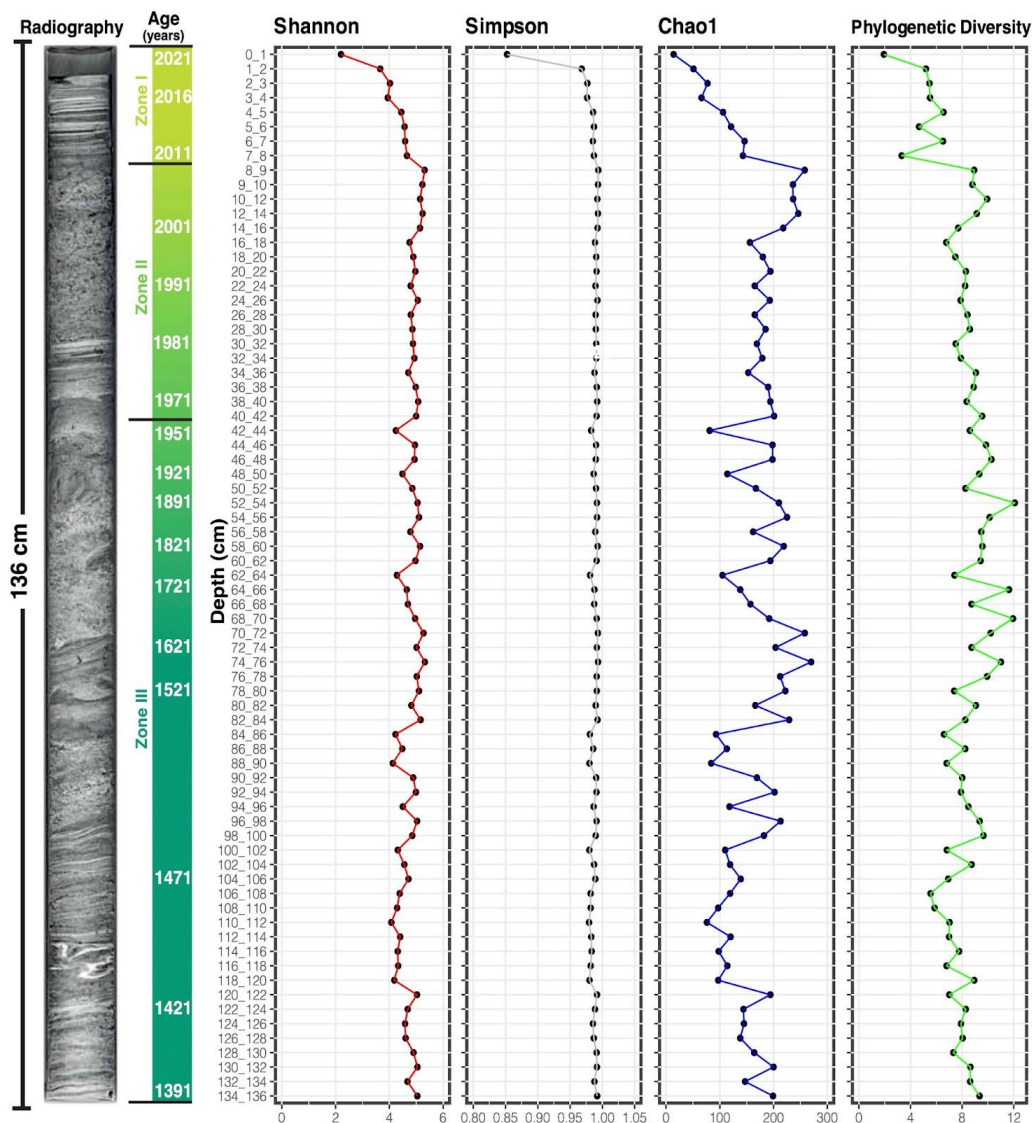


Figure 2. Diversity of the microbial community of the Inka-Coya sediment core. The core sedimentary radiography, dating, and alpha diversity indices variation along the core depth are displayed.

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

205 phylogenetic history of the species (Fig. 2). The diversity increases in all cases at two cm long, and maximum values were
206 observed between 8 and 86 cm, with minor peaks at 96, 120, and 130 cm near the bottom samples.

207 Three distinct zones in terms of microbial taxonomy could be identified and are statistically different for the four evaluated
208 diversity indices, except between Zone II and III in the context of phylogenetic diversity (Fig. 3A). These three disjunct
209 clustering zones of microbial community diversity along the sediment core were also identified in the beta diversity analysis,
210 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).

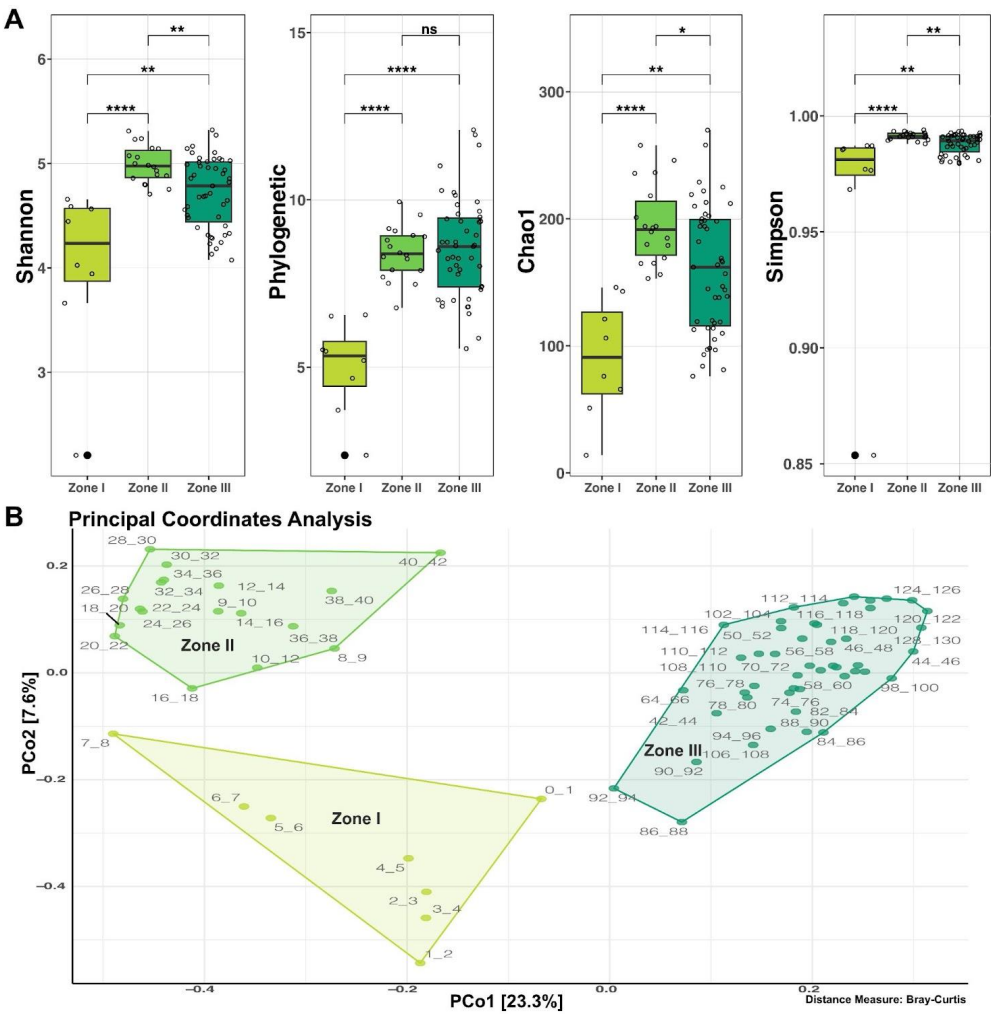


Figure 3. Clustering of the microbial communities inhabiting the deep sediment of Inka-Coya Lake A) Statistical differences in alpha diversity between depth zones. B) Principal Coordinates Analysis (PCoA) with the ASVs relative abundance using Bray-Curtis as distance metric; each point corresponds to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

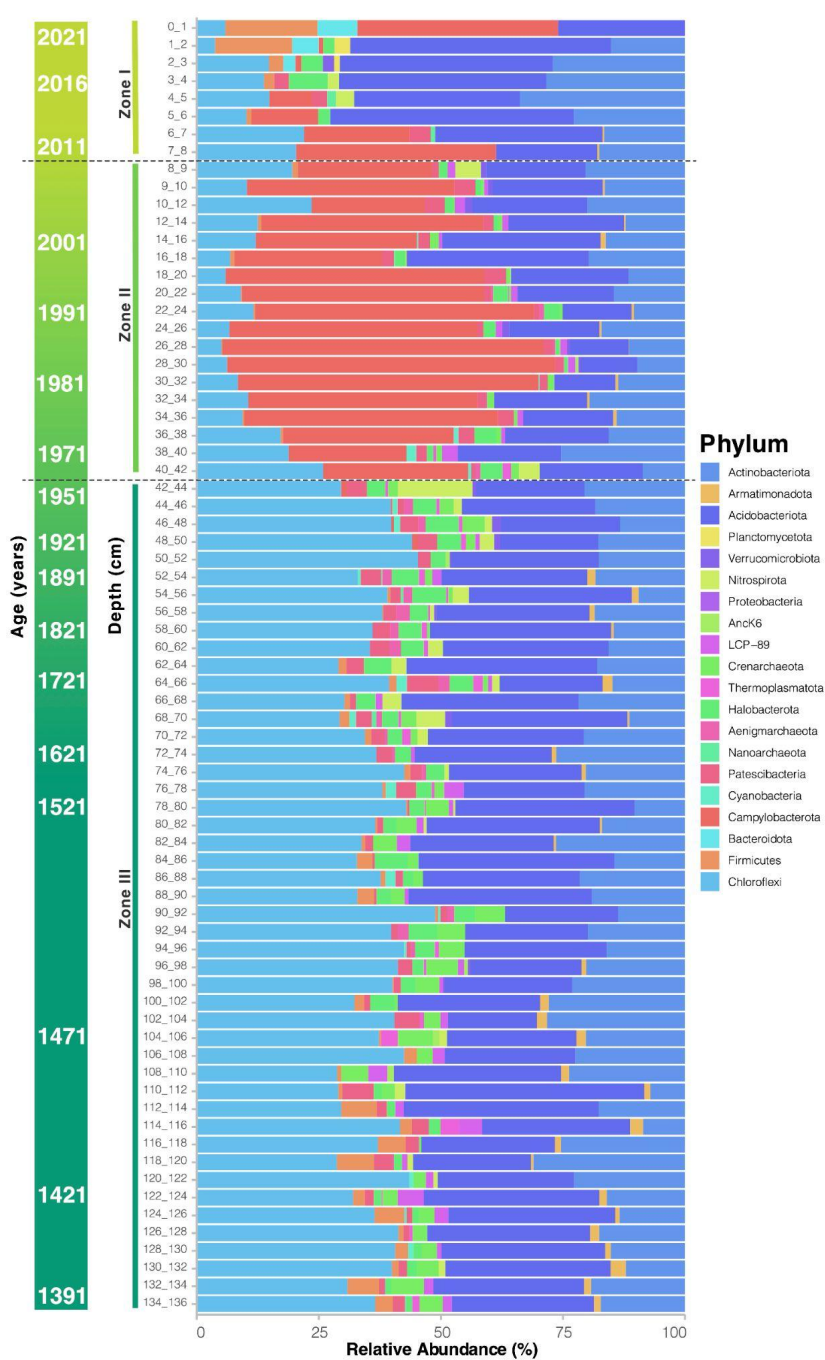
The taxonomic composition and abundance along the communities at phylum rank also reflect the clustering on three distinct zones, where zone I is dominated by Actinobacteriota and includes a great abundance of Firmicutes in the top layers, and Campylobacterota, there is also the presence of Bacteroidota, Halobacteriota, and Plantomycetota. Zone II is more diverse and

221 composed mainly of Campylobacterota, Chloroflexi, Acidobacteriota, and Actinobacteriota. While zone III is the largest and
222 more homogeneous, composed of several low-abundance taxa, dominated by Chloroflexi, Acidobacteriota, and
223 Actinobacteriota, there is also a higher representation of Crenarchaeota, Nitrospira, Aenigmarchaeota, and Armatimonadota
224 that in the rest of the zones (Fig. 4).

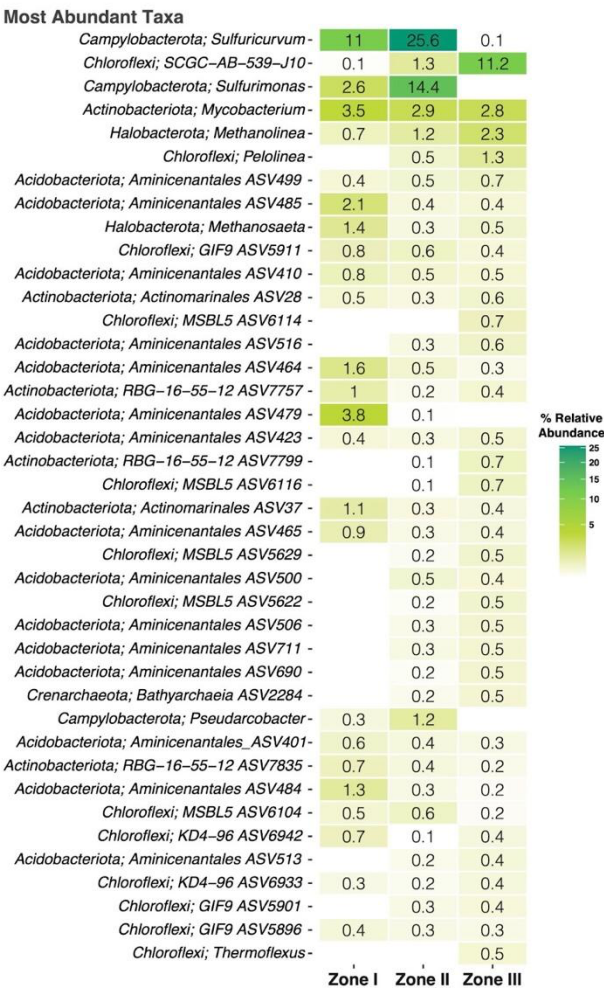
225 Notably, 76.6% of the taxa could not be identified at the genus level (0% matched any known species). Thus, Figure 5 shows
226 the abundance at the “best hit,” where Campylobacterota (*Sulfuricurvum*, *Sulfurimonas*), *Mycobacterium*, and *Methanolinea*

dominated the overall community. While in each zone, there are particular taxa associated; for instance, species belonging to the Aminicenantaes Phyla are very common in Zone I; *Pseudarcobacter* is prevalent in Zone II as *Pelolinea* is in Zone III.

229



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



232

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

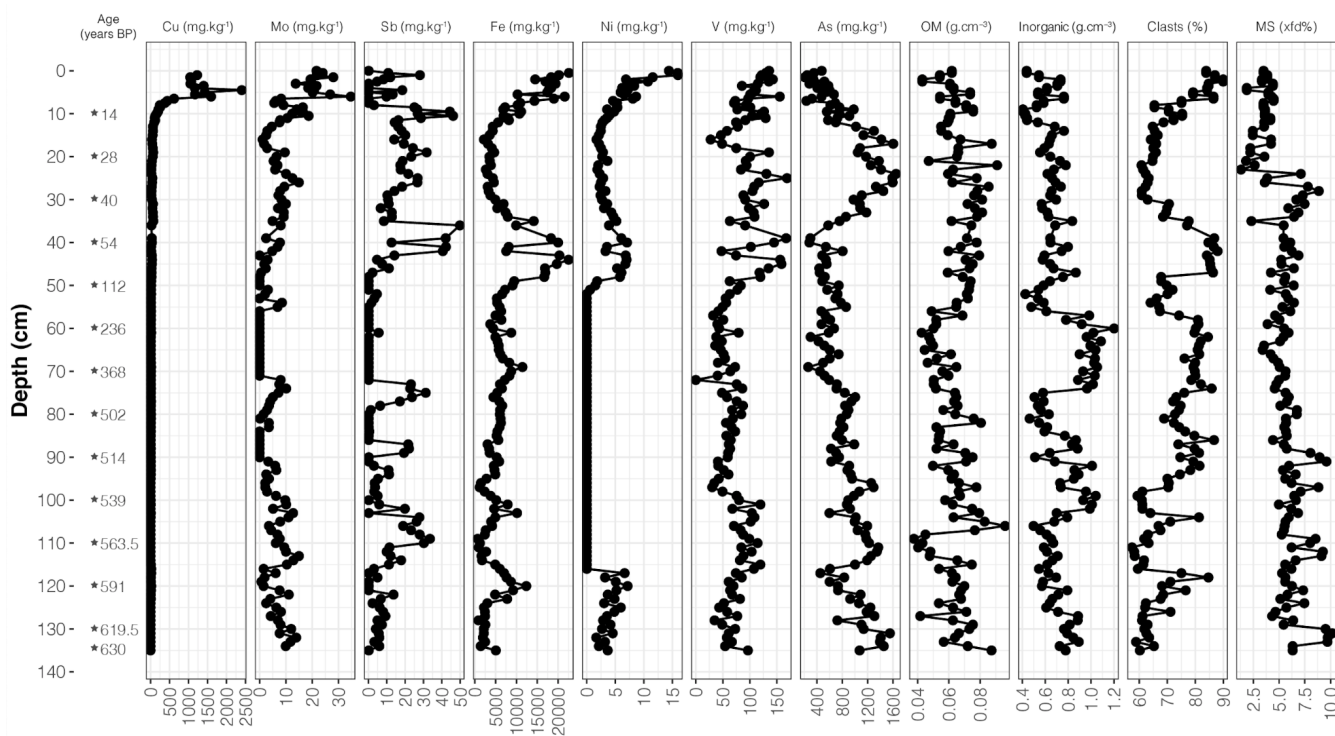


Figure 6. Depth variation of metals and metalloids concentrations ($\text{mg}\cdot\text{kg}^{-1}$), organic matter (OM) and inorganic concentrations ($\text{g}\cdot\text{cm}^{-3}$), clasts percent, and magnetic susceptibility (MS) measured in Inka-Coya Lake sediment core (modified from Pérez-Portilla 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 ($0.71 \text{ g}\cdot\text{cm}^{-3}$). 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 -6.09×10^{-9} to $8.13 \times 10^{-7} \text{ m}^3\cdot\text{kg}^{-1}$, with an average value of $2.77 \times 10^{-7} \text{ m}^3\cdot\text{kg}^{-1}$. Frequency-dependent susceptibility ($\chi_{fd}\%$) 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 $\chi_{fd}\%$, while Zone II shows the lowest χ values and intermediate $\chi_{fd}\%$ values. Zone III presents intermediate χ values and the highest $\chi_{fd}\%$ 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).

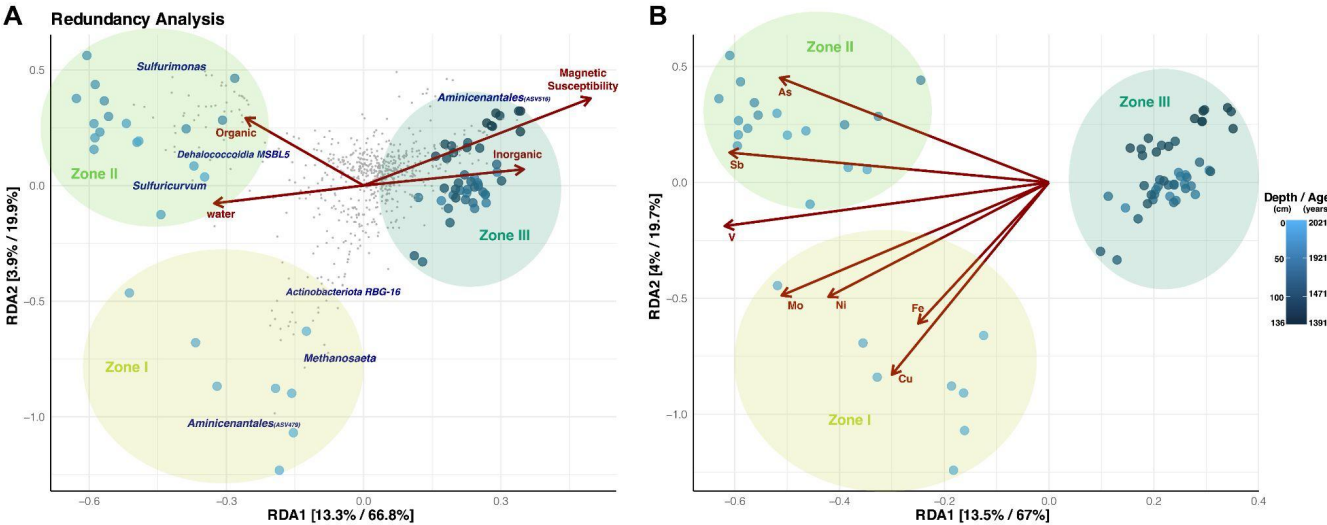


Figure 7. Redundancy analysis on Hellinger transformed Bray-Curtis distances (corrected by unobserved species) for the microbial communities along the core distance. A) Influence of physicochemical parameters and B) Elemental composition. Depth gradient and Zone parameters were chosen to constrain the 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, *Methanoregulaceae*, *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 $\chi_{fd}\%$, 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 (Fariás 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 (Fariás 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 (Fariás 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),

317 Actinobacteriota (*Mycobacterium*), and Campylobacterota (*Sulfuricurvum* and *Sulfurimonas*), sharing some similarities and
318 taking into account changes in taxonomy (Oren and Garrity, 2021).

319 At the lower taxonomic rank, the community is dominated by microorganisms with a broad repertoire for mineral interactions,
320 e.g., there is experimental evidence of organomineralization in extracellular S⁰ formation by a species of the sulfur-oxidizing
321 bacteria *Sulfuricurvum* (Cron et al., 2019). Another remarkable microorganism found along the lacustrine sediment is the
322 cosmopolitan and highly diverse *Sulfurimonas*, which can grow using sulfur, hydrogen, nitrogen, oxygen, and organic
323 compounds, suggesting it is critical in maintaining trophic dynamics (Han and Perner, 2015). Additionally, *Mycobacterium* is
324 a saprophytic bacterium commonly found in lakes, rivers, and other water sources (Falkinham et al., 2015), there are some
325 species representatives of this genus that have bioremediation potential for polycyclic aromatic hydrocarbons (Deng et al.,
326 2023), suggesting adaptability and a broad range of metabolic capacities. There are extensive studies on Mycobacteriaceae
327 representatives that cause human disease, as reviewed by Falkinham (2009). However, environmental representatives with the
328 capacity to inhabit poly-extreme environments have yet to be determined.

329 Furthermore, several representatives of the candidate phylum Aminicenantes are common in current sediments from Zone I,
330 i.e., recently deposited sediments during the last ten years. So far, these microorganisms are associated with a fermentative
331 saccharolytic lifestyle that does not have an isolated representative yet (Kadnikov et al., 2019). Zone II, comprising the period
332 between 10 and 50 years ago approximately, is mainly represented by microorganisms classified as the *Pseudarcobacter* genus,
333 that was recently separated from the *Arcobacter* genus (Pérez-Cataluña et al., 2018) and are characterized as mesophilic
334 bacteria that can grow in microaerophilic conditions (Collado et al., 2011). Finally, in the deeper and older sediments, where
335 anaerobic (or facultative anaerobes) microorganisms can thrive, there is a particular abundance of an ASV from the *Pelolinea*
336 genus that has only one described species that was isolated from the subseafloor sediment (Imachi et al., 2014), and an unknown
337 Chloroflexi species that is associated with Dehalococcoidia class a common sub-seafloor bacterium (Wasmund et al., 2014).
338 This finding suggests past conditions of higher salinities for the lake than the current conditions of around 5 g·L⁻¹ (Aránguiz-
339 Acuña et al., 2020), close to marine salinity. Archaea representatives found inhabiting the lacustrine sediments include the
340 hydrogenotrophic methanogen *Methanolinea* (Imachi et al., 2008; Rainey et al., 2015), which is distributed along the length
341 of the core with an abundance ranging from 0.7-2.3% and is very abundant towards the older and more anoxic environment
342 (since 1400 until 1950, zone III), where methanogenesis is the central predicted metabolism at play. These results suggest that
343 the microbial community in Inka-Coya Lake is potentially heterotrophic with a special enrichment in methanogenic organisms
344 in the oldest deposits, where oxygen levels are lower as evidenced by the metabolic approximation done in this study. Another
345 kind of metabolism, depending on CO₂ concentrations, could have dominated during this period.

346 Overall, our results suggest a great taxonomic and potential metabolic diversity is associated with the microbial community
347 from this lacustrine sediment. There is a vast taxonomic novelty harbored in Inka-Coya Lake sediment; over 70% of taxa
348 cannot be identified to the genus level, indicating there is a significant amount of “microbial dark matter” a term associated
349 with unknown microbial representatives that can potentially harbor novel bioactive compounds with numerous applications
350 (Zha et al., 2022; Jiao et al., 2021).

351 The main drivers for microbial community composition in the sinks-Coya sediments were As, Sb, V, Mo, Mn, Fe, and Cu,
352 which suggest that there are numerous strategies that microorganisms use to resist high concentrations of metals and metalloids
353 that thrive in this ecosystem (Rahman, 2020; Mathivanan et al., 2021), as observed in the Atacama and Altiplano area (Orellana
354 et al., 2018; Donati et al., 2019; Aszalós et al., 2020; Castro-Severyn et al., 2019). Additionally, microorganisms can use oxido-
355 reduction processes to obtain energy from metal ions (Raab and Feldman, 2003; Staicu and Stolz, 2021). Given the known
356 geochemical characteristics of the area, it is expected to find strong relationships between the microbial life and inorganic
357 compounds, as they can dissolve and precipitate ores and influence metal(loid)s transformations (Raab et al., 2003; Zhou et
358 al., 2022). In this extreme environment where competition is strong and abiotic pressures are constant, organic matter and

359 water availability -both parameters critical for most life forms- govern community abundance and composition, suggesting a
360 delicate dynamic balance reached between abiotic and biotic entities at play. It is important to remark that with the number of
361 unclassified taxa, many novel resistant or usage mechanisms remain to be characterized.

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

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

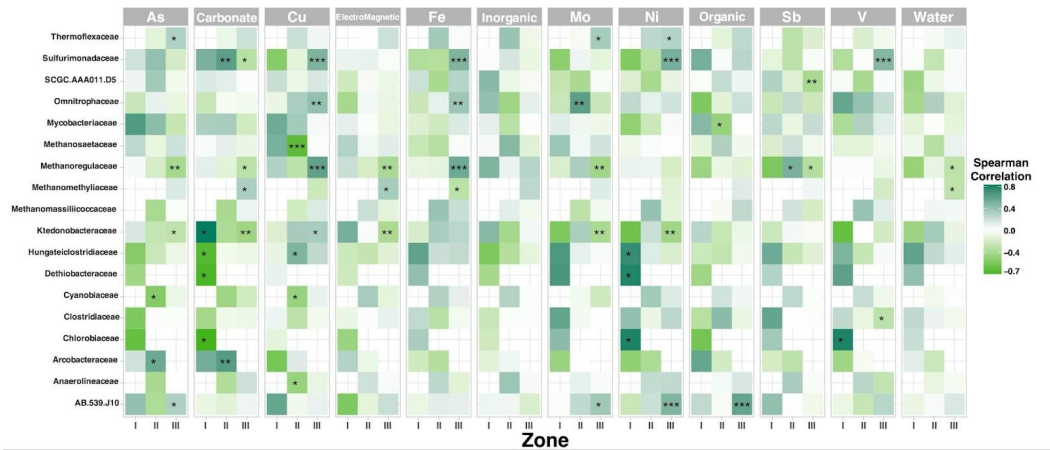
380 There are statistically significant correlations between some particular taxa and the geochemical composition along the
381 sediment gradient in Inca-Coya Lake suggesting that each element directly influences the metabolic capabilities of the
382 microorganisms and shapes the community selecting taxa that can resist metal(loid)s toxicity (Yao and Gao, 2007; Laplante
383 et al., 2013; Stankevica et al., 2020; Kostka and Leśniak, 2021; Yan et al., 2020). Further studies that elucidate the functional
384 properties using shotgun metagenomics will enhance our understanding in terms of the mechanisms used to resist and survive
385 in environments with high metal(loid)s concentrations and the use of different electron acceptors for energy production.

386 Finally, increasing metal(loid)s exploitation in the region during the last 100 years has directly influenced their mobility and
387 the local geochemistry. In this context, microorganisms from these extreme environments are known to be highly adaptive and
388 have developed several resistance mechanisms and the ability to use these compounds to their benefit. Hence, some bacteria
389 (and their genes) can be used as biomarkers for the bioavailability of such metals and contamination of soils (Li and Wong,
390 2010; Roosa et al., 2014). In Inka-Coya Lake, a selective process could be evidenced along the sediment record, in which the
391 recent period is characterized by a marked increase in chemical elements and microbial composition, which could be associated
392 with the increasing mining activity and other anthropological activities, as water extraction or aridity increase by climatic
393 changes, that also would increase the disturbance of this relevant area in the core of the most arid non-polar Desert.

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

406 Appendix A.

407



408
409 **Figure A1.** Pearson correlation between the top microbial families and geochemical parameters. Asterisks show the level of
410 significance (* p value < 0.05, ** p value < 0.01, Pearson correlation). Purple, blue, and white indicate positive, negative, and
411 no correlation, respectively.

412

413 Appendix B

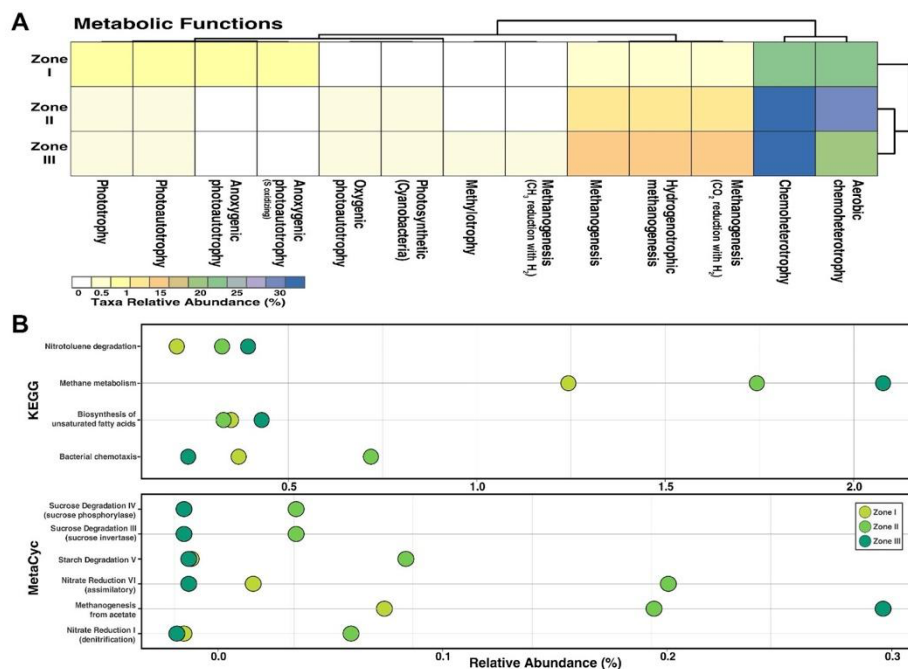


Figure B1. Metabolic pathways prediction of the microbial community inhabiting sediments along a depth gradient in Inka-Coya Lake. The predictions are based on the identified taxonomic composition according to the comparison with different databases, such as: A) FAPROTAX; B) KEGG and MetaCyc. Categories 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.

FUNDING

ANID 2020 FONDECYT Regular 1200423 (AA-A; FR), UTA-Mayor 9738-24 (AA-A)
 ANID 2022 FONDECYT Regular 1220902 (FR)
 ANID 2023 FONDECYT postdoctoral 3230189 (CPE)

434 ANID 2021 FONDECYT postdoctoral 3210156, ANID-Anillo ATE 220007 (JCS)

435 ANID 2022 MILENIO-NCS2022_009 (AA-A, AM)

436

437 **COMPETING INTERESTS**

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

439

440 **ACKNOWLEDGMENTS**

441 Likan antay Community of San Francisco de Chiu-Chiu.

442 MAINI-UCN (Kappabridge)

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