



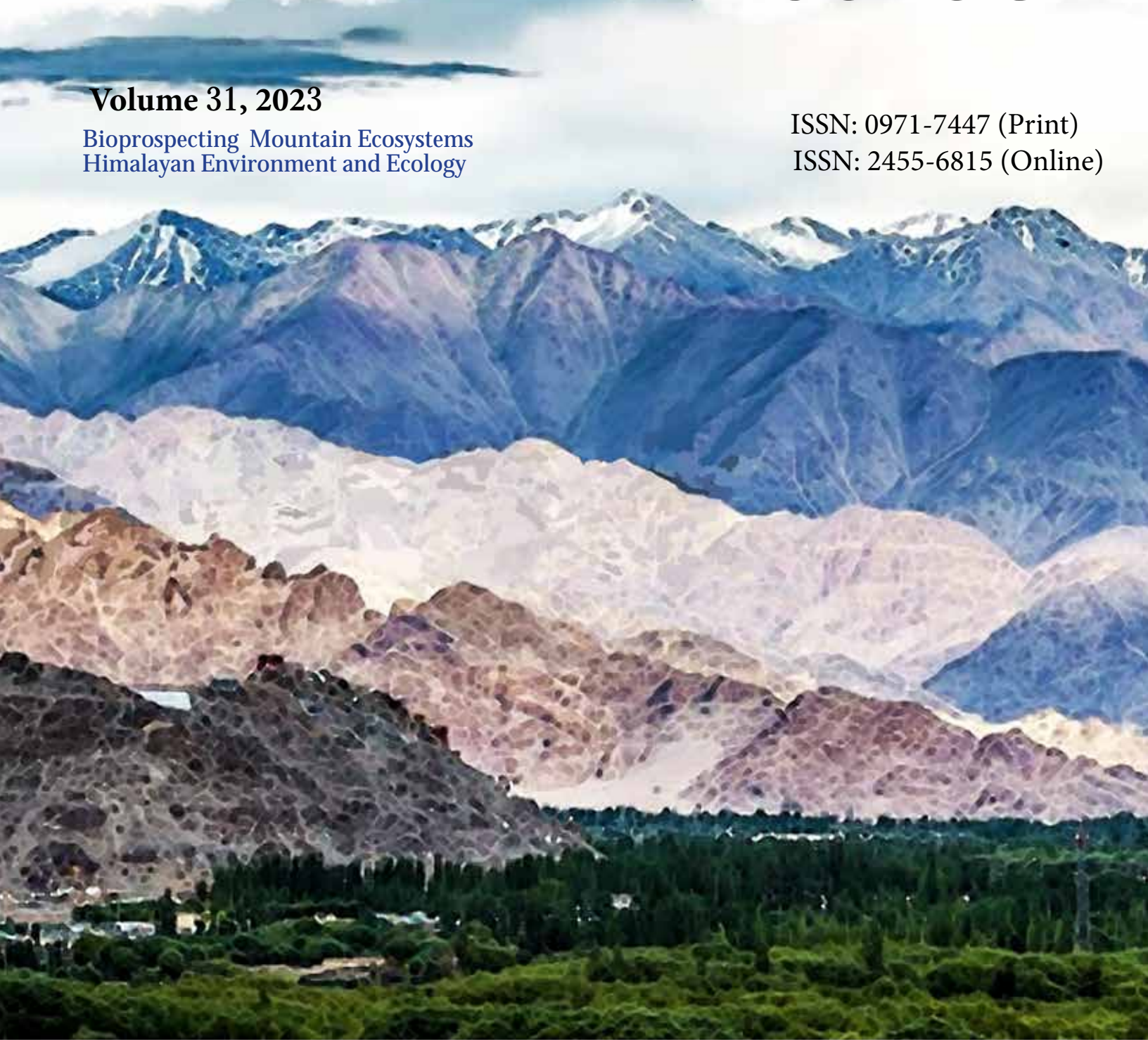
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(An Autonomous Institute of Ministry of Environment, Forest and Climate Change, Government of India)

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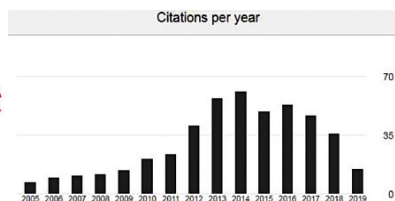
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MICROBIAL BIODIVERSITY IN THE COPAHUE GEOTHERMAL REGION-AN EXTREME ENVIRONMENT DOMINATED BY AN ACTIVE VOLCANO IN CORDILLERA DE LOS ANDES

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ABSTRACT

The Copahue geothermal area is located on the Northwest of Neuquén province in Patagonia, Argentina, on the Cordillera de los Andes, one of the world's most important mountain systems. This naturally acidic extreme environment is dominated by the still active Copahue volcano, a stratovolcano of approx. 2965 m.a.s.l., whose cyclic eruptive periods have shaped the landscape, the geo-physicochemical characteristics of the place and the microbial diversity that inhabits it. The Copahue geothermal area, of approx. 250 Km², has two different parts, both extreme environments: the Copahue volcano-Río Agrio system and the geothermal ponds. Río Agrio is a natural acidic river that originates at two geothermal ponds a few meters below the volcano crater and runs down its hill maintaining the low pH values for almost its entire path, despite receiving many tributary neutral water courses. On the other hand, the geothermal manifestations, pools, ponds and hot springs with a wide range of temperature and pH, are a constantly changing environment, highly dependent on the volcanic activity.

In this work we discuss the rich biodiversity and complex community structure of the microbial species, bacteria and archaea, that inhabit the Copahue geothermal area, and their correlation with the geology and physicochemical characteristics. The Copahue-Caviahue geothermal system is a clear example of how the environmental and geochemical condition defined by a mountain, in this particular case, the Copahue volcano, determines the shape and dynamics of the native microbial communities.

INFLUENCE OF THE COPAHUE VOLCANO IN ITS SURROUNDINGS AND DESCRIPTION OF THE COPAHUE CAVIAHUE GEOTHERMAL SYSTEM

The Copahue Geothermal region is in the Northwest corner of the Neuquén province, in Cordillera de los Andes. Cordillera de los Andes occupies the western part of South America, bordering its entire coastline on the Pacific Ocean. It is 8500 kilometres long, making it the longest continental mountain system on Earth. It has the highest mountains outside Himalayas and presents many active volcanoes, among them, the Copahue volcano, which dominates the Copahue geothermal system. The Copahue Volcano is an imposing stratovolcano, characterized by its towering height of approximately 2,997 meters above sea level. Its distinct geological composition consists of alternating layers of volcanic ash, lava flows, and pyroclastic deposits, reflecting its complex history of past eruptions. Geographically, the volcano's coordinates are approximately 37.85°S latitude and 71.17°W longitude. The particular geology associated with the volcanic activity and the condensation of gases such as HCl (hydrogen chloride), H₂S (hydrogen sulfide), SO₂ (sulfur dioxide), make the

Copahue geothermal region an environment rich in sulfur and iron compounds. Over the last few decades, Copahue has been a subject of heightened scientific interest due to a series of significant eruptions that have generated ash plumes that blanketed nearby areas, temporarily disrupting air travel and also generating ejection of pyroclastic material and volcanic gases, contributing to temporary shifts in atmospheric composition. These eruptions have led to alterations in local physicochemical conditions, including fluctuations in temperature, with hydrothermal springs reaching temperatures of up to 90°C during eruptive periods, a temperature that is close to boiling point of water at the area's height. Additionally, the release of volcanic gases during these eruptions has influenced pH levels, causing acidification of the water bodies of all the system. These environmental and landscape characteristics as well as the perturbations caused by the volcanic activity have had direct impact in the diversity and dynamic of the microbial communities that inhabit the different geothermal water bodies and the waters of Río Agrio. For studying purposes, the Copahue-Caviahue geothermal region is divided in two areas: the Copahue volcano - Río Agrio system and the geothermal field. Fig 1 shows the location of the region in the map and images of both areas. In the crater of the Copahue

volcano there is a very acidic lake with pH varying between 1.1 and 2.0 and temperatures ranging from 4°C to near the boiling point of water during eruptive periods. In fact, the lake disappeared after the eruption of the year 2000 and it has only been possible to sample from it in 2018. Río Agrio originates approximately 100 metres below the Copahue volcano crater as a very narrow course at two highly acidic geothermal affluents. The physicochemical conditions of these hot springs vary greatly with the volcanic activity; with temperatures fluctuating from 70 to 30°C and pH values from 0.5 to 2. After emerging from its geothermal source, the Upper Río Agrio (URA) rapidly cools down to approx. 15°C, a temperature that maintains all through its path. Regarding pH, waters remain acidic all through the course of the river, in spite of receiving many tributary courses mostly of snowmelt origin. The URA then flows down through a series of very beautiful water falls until it discharges in the Cavi-

ahuelake. The lake is from glacier origin, the waters are acidic (measured pH around 3), however due to the discharge of fluids from Cavihue village, emplaced in its west side, it is contaminated. After emerging from Cavihue lake, Lower Río Agrio (LRA) is wider and the borders are covered by red-orange rocks and sediments due to the precipitation of iron minerals produced by the rise in pH above 3 caused by the massive input of tributary courses of waters. Approximately 5 Km down the lake LRA has a spectacular waterfall, named Salto del Agrio. Then, the river continues its course slowly raising its pH for more than 40 Km when it finally reaches neutrality and merges with another mayor river. The other study area, the geothermal field, is even more influenced by the volcanic/geothermal activity. They are a series of pools, ponds and hot springs, some of them used for recreational or therapeutic purposes. Geological studies have determined

MICROBIAL BIODIVERSITY IN THE COPAHUE GEOTHERMAL SYSTEM

Our research group has studied the microbial diversity of this area for many years, using a variety of approaches, including enrichment cultures, high throughput molecular ecology techniques, and other culture-independent methods. This has allowed us to gain a comprehensive understanding of the microbial communities and their interactions with the environment.

- Copahue volcano - Río Agrio system

The natural acidic waters of Río Agrio are inhabited by a quite diverse community of acidophilic, sulfur and/or iron oxidising prokaryotes that is richer near the origin of the river, where the environmental conditions are more extreme. As the river flows down the Copahue volcano hill and the environment gets more stable, the microbial community also stabilises and the better adapted species endure. According to microscopic cells recount done using fluorescence in situ hybridisation (FISH) with specific probes for bacteria and archaea and high throughput ampliconsequencing of the 16S rRNA gene, Archaea represent between a 20 and 40% of the prokaryotes of Río Agrio, nevertheless they have not been detected in the highly acidic crater lake of the Copahue volcano. At the Phylum level the archaeal diversity was represented by four phyla with a clear dominance of the genus *Ferroplasma*, comprised of extremely acidophilic, moderately thermophilic, iron oxidising, pleomorphic species, from the domain Euryarchaeota. Thanks to high throughput sequencing it was also possible to detect all over the URA *Acidianus copahuensis*, a thermoacidophilic crenarchaeota autochthonous of the Copahue geothermal system. Regarding Bacteria, the diversity was described by twenty-four phyla, with Proteobacteria being the most abundant phylum along the Copahue volcano-Río Agrio system, followed by Firmicutes. In order to gain deeper insights into the relationships among microbial species, their metabolic activities, and the interplay of physicochemical and geochemical factors, we conducted various biostatistical analyses to establish correlations within these variables. For instance, a canonical correspondence analysis between the points in the system, their physicochemical variables and microbial species showed in Fig. 2 B, clearly separated the Copahue volcano-Río Agrio system in three different habitats. One group is the URA, which positively correlates with temperature, organic matter, conductivity, iron, and sulphate concentrations and negatively correlate with pH. The points of the URA as well as the microbial

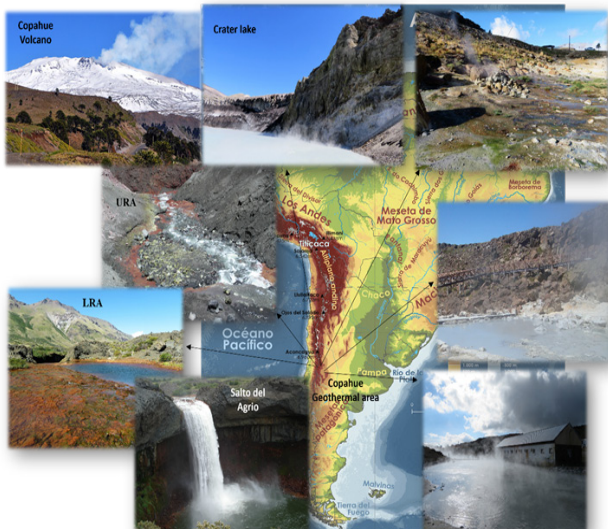


Fig.1: Location of Copahue Geothermal field in Cordillera de los Andes (Argentina, South America). Left side: images of the Copahue volcano and the Río Agrio. Right side: images of the different geothermal manifestations

ahuelake. The lake is from glacier origin, the waters are acidic (measured pH around 3), however due to the discharge of fluids from Cavihue village, emplaced in its west side, it is contaminated. After emerging from Cavihue lake, Lower Río Agrio (LRA) is wider and the borders are covered by red-orange rocks and sediments due to the precipitation of iron minerals produced by the rise in pH above 3 caused by the massive input of tributary courses of waters. Approximately 5 Km down the lake LRA has a spectacular waterfall, named Salto del Agrio. Then, the river continues its course slowly raising its pH for more than 40 Km when it finally reaches neutrality and merges with another mayor river. The other study area, the geothermal field, is even more influenced by the volcanic/geothermal activity. They are a series of pools, ponds and hot springs, some of them used for recreational or therapeutic purposes. Geological studies have determined

species that inhabit there (represented by the blue dots) are very close together meaning that all the upper river is very similar in both environmental characteristics and biodiversity. On the other hand, the crater lake is clearly separated from the points of the URA, especially by its negative correlation with temperature, organic matter, conductivity, iron, and sulphate concentrations; it also shows its own biodiversity with only a few species shared with the other groups. Salto delAgrio, in LRA, is also separated from the URA, it correlates positively with pH and negatively with the other variables and, like in the other groups, the microbial species are very close together, sharing almost no taxa with the crater lake or the URA. These three environments are inhabited by different microbial communities, the relative abundances with the most representative species highlighted can be seen in Fig. 2 A. The crater lake is dominated by species related to *Sulfuriferula*, a neutrophilic and mesophilic genus able to oxidise a variety of sulfur compounds. The remaining species presented lower abundances and were mostly acidophiles, mesophiles, or moderately thermophiles related to sulphur or iron metabolism and found in other acidic environments including Río Agrio. Among them, *Ferrithrix*, extremely acidophilic, moderate thermophilic and obligate heterotrophic iron oxidisers, and *Thiomonas*, moderate acidophilic, mesophilic, quimioheterotrophic sulfur oxidisers, were only detected at the crater lake. The occurrence of species at pH and temperature conditions that are apparently distant from their optimum for growth can be explained by considering the changing nature of the lake. It could also be expected that the relative abundances of species vary greatly with pH and temperature modifications favouring the better adapted ones. In the particular case of *Sulfuriferula* and *Ferrithrix*, they have been detected by high-throughput sequencing in other environments with conditions similar to the crater lake and distant from their optimum. On the other hand, in the URA the microbial community is more stable. It is dominated by acidophilic, mesophilic or moderately thermophilic, sulphur and/or iron oxidising species, including *Acidithiobacillus*, *Sulfobacillus*, *Leptospirillum*, *Acidibacillus* and the archaeon *Ferroplasma*. Among these genera, some of the sequences retrieved have the peculiarity of being distantly related to cultivated species (97% or less) but being 99–100% similar to different uncultured sequences found in other acidic environments such as Río Tinto, hot springs, and mine tailings. Particularly, all the OTUs affiliated with the genus *Acidibacillus* were 99% similar to uncultured clones retrieved from Río Agrio but distantly related to cultivated species. In the same way, the archaeal sequences affiliated with the family *Thermoplasmataceae* were 99–100% similar to sequences retrieved from the Copahue-Caviahue system and from an acid mine drainage in China; however, they were around 90% similar to cultivated species of the genus *Thermoplasma*. These findings suggest that there may

be potential indigenous novel species or even new genera yet uncultured but ubiquitous and characteristic of acidic environments. Finally, the surroundings of the big waterfall Salto delAgrio had a completely different, much more diverse microbial community with no clear dominant members. There was a higher abundance of anaerobic species and no significant occurrence of the acidophiles found in the URA or the crater lake. Such differences could be explained considering the higher pH, lower Eh and iron concentration at this site. Despite the low abundances of the most common acidophiles in the high throughput sequencing data analysed, species related to iron and/or sulfur oxidising species like *Acidithiobacillus*, *Acidiphilium*, and *Leptospirillum* have been cultured from samples collected from Salto delAgrio.

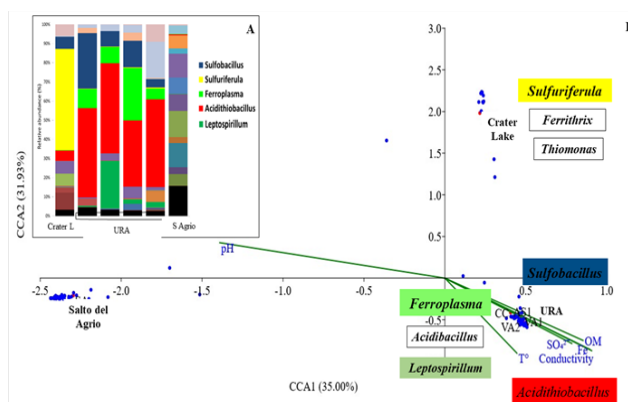


Fig 2.: (A). Relative abundance of bacteria and archaea in the Copahue volcano-Río Agrio system. (B). Canonical correspondence analysis of microbial diversity and environmental parameters in the sampling points of the Copahue volcano-Río Agrio system.

Agrio system. B. Canonical correspondence analysis of microbial diversity and environmental parameters in the sampling points of the Copahue volcano-Río Agrio system. Connecting the environmental and biodiversity results we were able to outline a geomicrobiological model of the URA, schematised and summarised in Fig 3A: the geothermal origin of the river and its closeness to the Copahue volcano provide a variety of sulfur and iron compounds, and work also as the reservoir of the bacterial and archaeal species that inhabit all the URA. The oxidation of these iron and sulfur compounds catalysed by the acidophilic bacteria and archaea helps to maintain the low pH all through the URA, in spite of the constant input of snowmelt and other neutral waters. Also, the metabolically catalysed sulfur oxidation justifies the great amount of sulfate measured in the waters of Río Agrio. Among cations, Fe(II) is the most relevant, its concentration is quite high at the origin of the river, where the diversity of iron oxidisers is higher and then the concentration decreases, in part for the dilution but mostly because the slight increase in pH produces the hydrolysis and precipitation of Fe(III) compounds, that can be seen in the margins of the river. Such

chemical process also releases H⁺ contributing to the maintenance of the acidic pH.

GEOTHERMAL FIELD

The geothermal manifestations are a much more complex environment, more dependent on the volcanic activity and with a wider range of ecological niches. The unrooted phylogenetic tree of Fig. 4A shows the main species found in the water, sediments and biofilms of the geothermal ponds. The species marked in green, most of them photosynthetic, were detected exclusively on the biofilms. On the other hand, archaea were dominant in the higher temperature niches, represented by species of thermoacidophilic genera such as *Sulfolobus* and *Vulcanisaeta* and the autochthonous *Acidianus copahuensis*. This distribution was confirmed by comparing the universal DAPI stain, in blue, with the images of the FISH assay using the archaea specific probe in the ponds of different temperatures. Figure 4 A and B, respectively, shows the charts with the cell's recounts using probes specific for Bacteria and Archaea domains and the hybridisations with the fluorescent probe specific for archaea and DAPI images for different ponds and hot springs of high temperature. The moderate temperature pools were inhabited by sulfur and/or iron oxidising bacterial species, similar to those found in Río Agrio, such as *Acidithiobacillus*, *Acidiphilium* and *Thiomonas* and other species very common in geothermal environments like *Hydrogenobaculum*.

Based on the geological and volcanic characteristics of the area that led to the accumulation of different sulfur compounds and our findings that all ponds, pools and hot springs were inhabited by acidophilic, sulfur and/or iron oxidising species, either strict or facultative autotrophs, we proposed two geomicrobiological models. One for the moderate temperature niches (Fig. 3B) and other for the ones with high

temperatures (Fig. 3C), both specially focused on the carbon and sulphur cycles. Basically, in both niches the metabolic processes and reactions are the same, the aerobic oxidation of sulfur compounds, autotrophically or at the expenses of organic matter, releases H⁺ contributing to the maintenance of the acidic conditions of ponds and pools and also releasing sulphate, which explains the high concentrations measured. In the sediments the sulphate reducing microorganisms (SRM) take care of the anaerobic reduction of such sulphate. Various SRM have been found in anaerobic sediments collected from different ponds and pools from the Copahue geothermal field, including potential novel species, like *Desulfotomaculum copahuensis*, *Desulfosporosinus* sp. and *Desulfotomaculum* sp. At certain pools and ponds with less extreme conditions, where the waters are quieter, biofilms and mats develop, and they are inhabited by photosynthetic species that contribute to carbon fixation.

CONCLUSION

In conclusion, our comprehensive study of the Copahue geothermal system over more than twenty years, with a particular focus on the influence of the Copahue volcano's activity, has shed light on the remarkable microbial diversity within this unique environment. The frequent eruptions of the volcano have not only disrupted local atmospheric conditions but have also significantly altered the properties of geothermal water bodies, including temperature, pH, and chemical composition.

Within the Copahue volcano - Río Agrio system, we observed distinct microbial communities inhabiting different habitats. The crater lake, characterized by extreme acidity and fluctuating temperatures, harbours sulfur-loving species and a minority of iron-oxidisers. In contrast, the Upper Río Agrio maintains a stable microbial community dominated

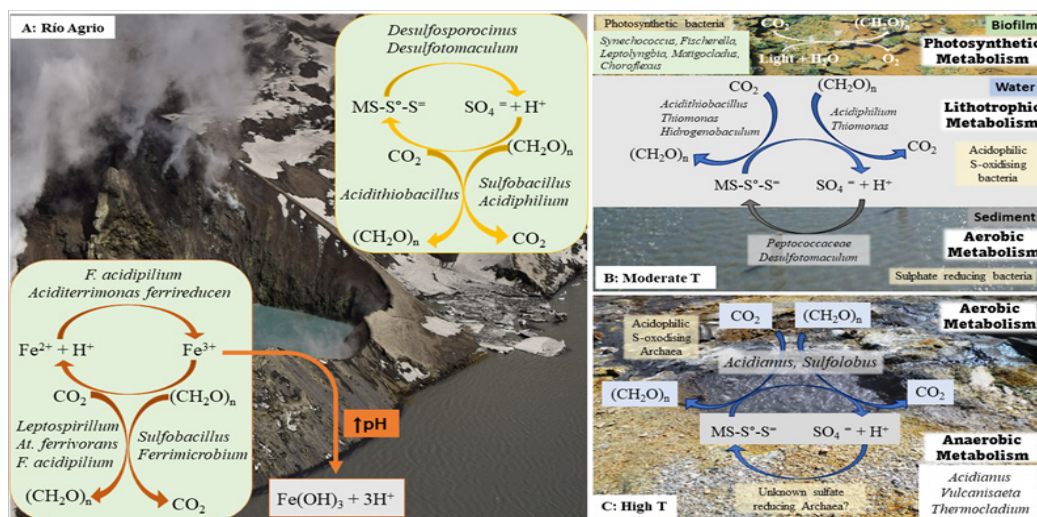


Fig. 3. Geomicrobiological models of the Río Agrio (A). Geothermal ponds of moderate temperature (B). geothermal ponds and hot springs of high temperature (C).

EIACP Centre on Himalayan Ecology

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