



Lithifying and Non-Lithifying Microbial Ecosystems in the Wetlands and Salt Flats of the Central Andes

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Abstract

The wetlands and salt flats of the Central Andes region are unique extreme environments as they are located in high-altitude saline deserts, largely influenced by volcanic activity. Environmental factors, such as ultraviolet (UV) radiation, arsenic content, high salinity, low dissolved oxygen content, extreme daily temperature fluctuation, and oligotrophic conditions, resemble the early Earth and potentially extraterrestrial conditions. The discovery of modern microbialites and microbial mats in the Central Andes during the past decade has increased the interest in this area as an early Earth analog. In this work, we review the current state of knowledge of Central Andes region environments found within lakes, small ponds or *puquios*, and salt flats of Argentina, Chile, and Bolivia, many of them harboring a diverse range of microbial communities that we have termed Andean Microbial Ecosystems (AMEs). We have integrated the data recovered from all the known AMEs and compared their biogeochemistry and microbial diversity to achieve a better understanding of them and, consequently, facilitate their protection.

Keywords Hypersaline lakes · AMEs · Microbialites · Endoevaporites · Microbial mats · Extremophiles

Introduction

The Central Andes of South America, which extend through southwestern Bolivia, northwestern Argentina, and northern Chile, exhibit a unique geography of closed basins at altitudes ranging from 3000 to 6000 m above sea level (masl). The Altiplano (Bolivia), Atacama Desert (Chile) (Fig. 1), and Puna (Argentina) (Fig. 2) regions are rich in salt flats (e.g., Uyuni, Atacama, Arizaro, Antofalla) (Fig. 3), active volcanoes, hot springs, fumaroles, and high-altitude Andean lakes (HAALs), most of which present diverse polyextremophilic microbial ecosystems [1–3] named Andean Microbial Ecosystems (AMEs).

Compared to other saline systems around the world, the Central Andean systems have, on the one hand, higher ultraviolet (UV) radiation expositions, higher levels of desiccation, and higher daily temperature fluctuations caused by the high altitudes; and on the other hand, a different chemical composition of the water (e.g., high arsenic concentration) attributable to the volcanic activity [5, 6]. These environmental conditions resemble the early Earth and potentially extraterrestrial conditions. Therefore, the study of the AMEs could provide information about the early evolution of life on Earth, as well as knowledge for the search of life on Mars [7].

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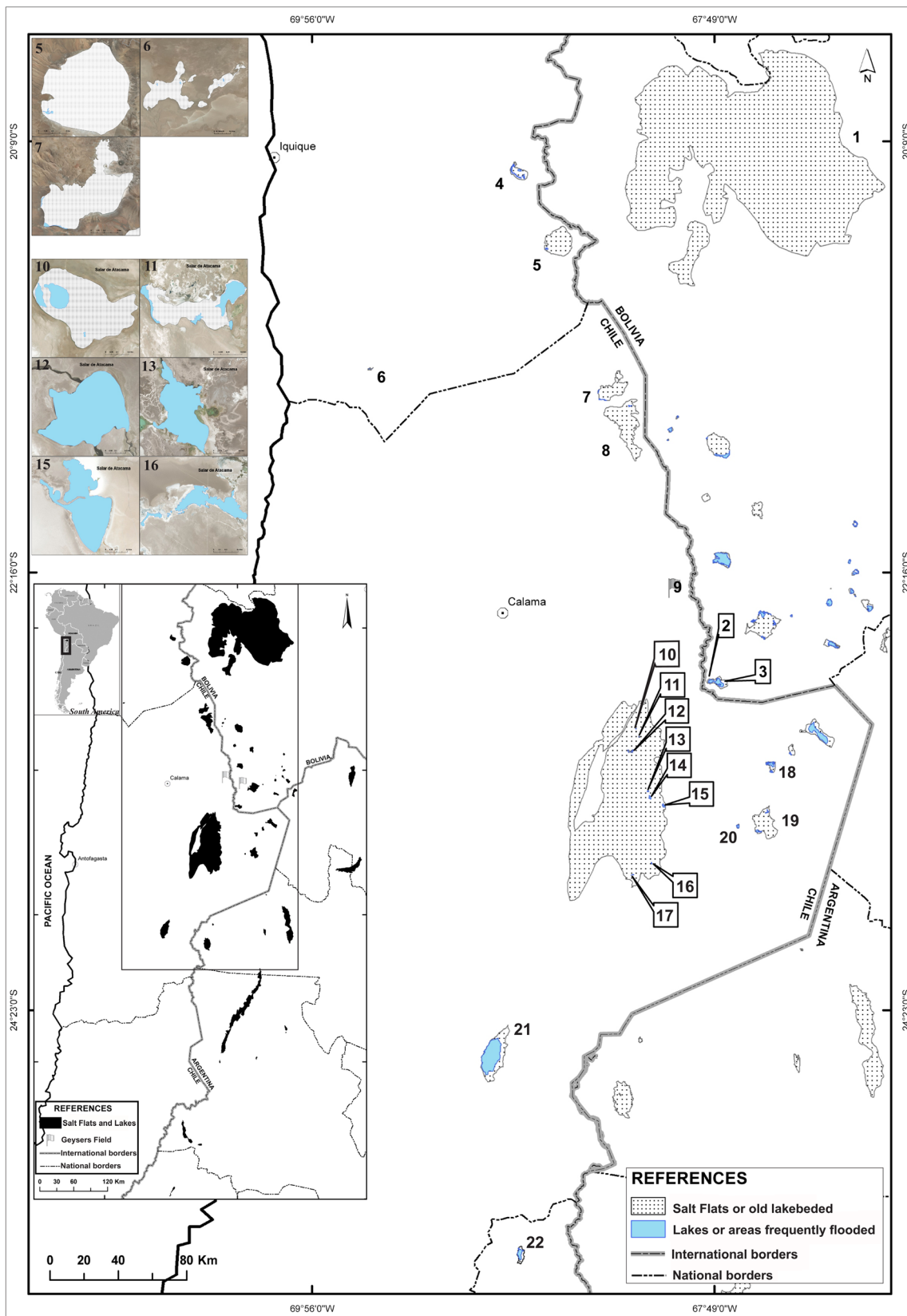
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The AMEs are complex associations of microbes with minerals, mostly halite (NaCl), gypsum (CaSO₄·2H₂O), calcite

(CaCO₃), and aragonite (CaCO₃) (Fig. 4) [3, 8–16]. For this review, we have categorized the AMEs into four distinct

◀ **Fig. 1** Map of Bolivia and Chile showing location of salt flats and lakes harboring AMEs. Bolivia: 1 Salar de Uyuni. 2 Laguna Verde. 3 Laguna Blanca. Chile: 4 Salar de Huasco. 5 Laguna Coposa. 6 Salar de Lllamará. 7 Salar de Carcote. 8 Salar de Ascotán. 9 Campo de Géiseres del Tatio. 10 Laguna de la Piedra. 11 Laguna Cejar. 12 Laguna Tebenquiche. 13 Laguna Chaxa. 14 Laguna Barros Negros. 15 Aguas de Quelana. 16 Laguna Salada. 17 Laguna Brava. 18 Laguna Pujsa. 19 Salar Aguas Calientes. 20 Laguna Lejía. 21 Laguna Punta Negra. 22 Salar Agua Amarga

groups based on community organization and extent of mineralization. These include biofilms (1), microbial mats (2), microbialites (3), and endoevaporites (4).

Biofilms (1) are communities of microbial cells associated with a solid surface and embedded in an exopolymeric substance (EPS) matrix [18]. The microbial colonization of a surface depends on the EPS matrix formation, which can trap inorganic and abiotic compounds as well as immobilize water. Microbial mats (2) are biofilms distributed in layers, defined by light, oxygen, and physicochemical requirements, which colonize both solid and sedimentary surfaces [19, 20]. The mat-constructing biota escapes burial by freshly deposited sediments migrating vertically upwards, where it can again colonize newly deposited surfaces. The thickness of living microbial mat communities can reach several centimeters, even decimeters, and they can be formed in a wide variety of shallow aquatic environments, from fresh to thalassic water conditions, and even within halite or gypsum crusts [21].

Some microbial mat communities can influence carbonate precipitation giving rise to structures named microbialites (3). These are organosedimentary deposits accreted by sediment trapping, binding and/or in situ precipitation due to the growth, metabolic activities, and EPS matrix produced by the microorganisms of the microbial mat [22–29]. Geological records indicate that microbialites first appeared more than 3.7 Ga ago and were the main evidence of life on Earth for the next 2 Ga [30–32]. As the first communities performing significant oxygenic photosynthesis, they are thought to have played a major role in the oxygenation of the Earth's atmosphere [33, 34].

Most microbialites can be classified into one of five main categories based on their mesoscopic features: stromatolites, oncoids, thrombolites, dendrolites, or leiolites [35–37]. The main structures found in AMEs are stromatolites, oncoids, and thrombolites (Fig. 4). While stromatolites exhibit a laminated mesostructure [38, 39], oncoids and thrombolites display a concentrically laminated and clotted mesostructure, respectively [40–43].

Although the most studied types of organosedimentary systems are carbonate deposits with calcium (Ca^{2+}) (calcite, aragonite) [40], calcium-magnesium (Ca^{2+} - Mg^{2+}) (magnesian calcite ($\text{Ca,Mg}(\text{CO}_3)$), dolomite ($\text{CaMg}(\text{CO}_3)_2$)) [27, 41], and magnesium (Mg^{2+}) (magnesite (MgCO_3)) [42, 43], there

are also endolithic microbial communities associated with gypsum and halite named endoevaporites (4) (Fig. 4) [44–46], which can form “stromatolite-like” domes [47, 48] or “gypsum stromatolites” [4]. The exact role of microbial metabolic activity and growth in the formation of these gypsum and halite evaporitic domes is not fully understood yet [4].

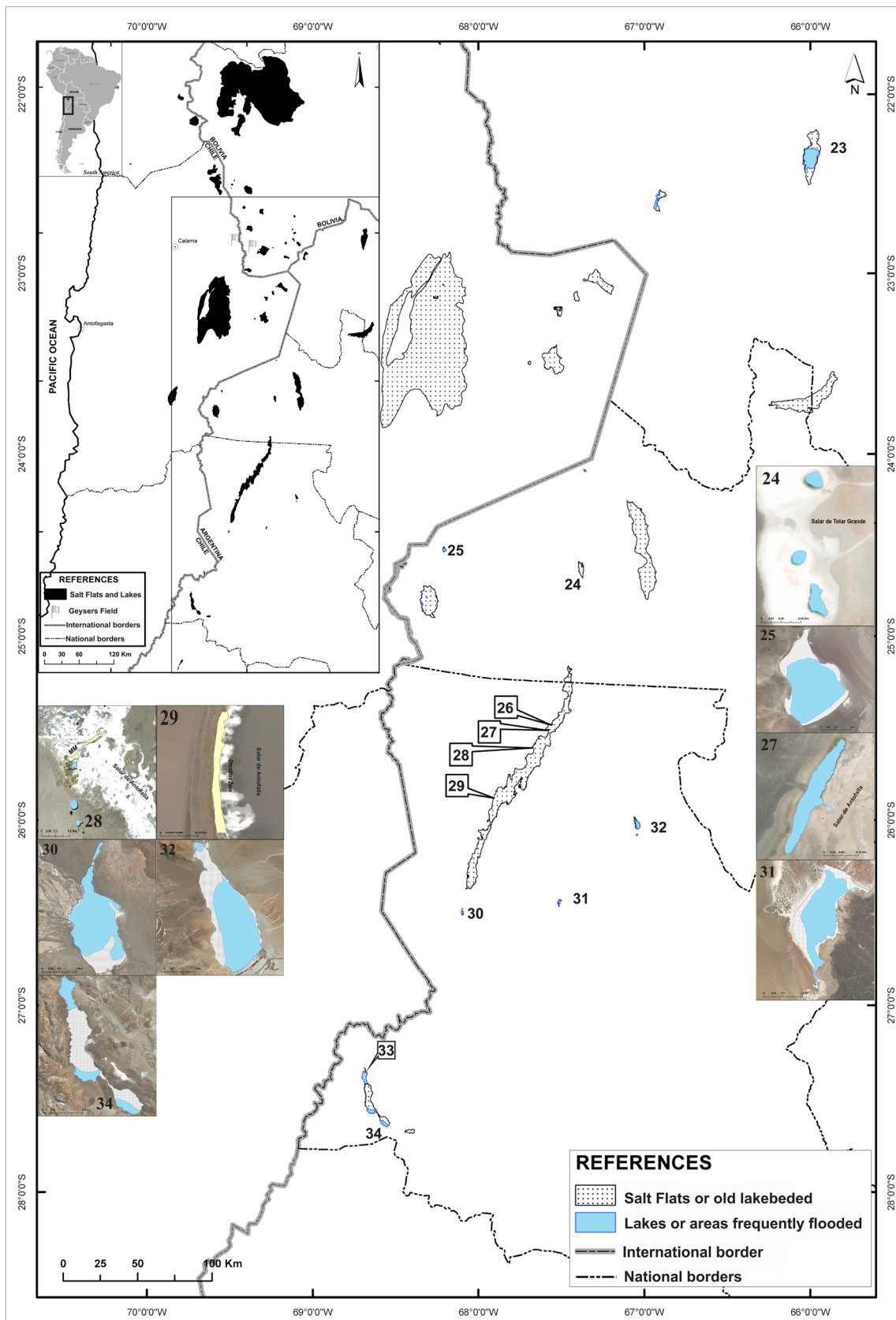
This review aims to examine the current state of knowledge of the AMEs acquired during the past decade of Andean exploration. All the data gathered from the different AME studies have been integrated into a single high-level comparative analysis to assess the microbial and mineral diversity and complexity of these polyextreme environments.

AMEs in Central Andes Region

In the past decade, extensive exploration has been carried out on salt flats, lakes, hot springs, and fumaroles of Bolivia, Argentina, and Chile to study the AMEs [2, 3]. Different AMEs were reported in these explorations, including biofilms, mats, microbialites, and endoevaporites (Fig. 4). However, not all types of AMEs were found in every prospected place. Endoevaporites were exclusive of salt flat environments, but not all the salt flats presented endoevaporitic microbial ecosystems. Similarly, not all types of microbialites were found in salt flats, hypersaline lakes, or brackish rivers [2]. Therefore, in an attempt to update all the knowledge generated until now, we have summarized the AMEs found in the Central Andes as well as their chemical conditions, geographical location, main characteristics, and references (Table 1). While some systems have only been reported, others have been described in more detail with respect to the characteristics of their habitat, composition of their mineral phase and microbiota, and certain aspects of microbial activity and physiology.

Evaporitic Gypsum-Associated Microbial Ecosystems

Evaporites are sediments formed by physicochemical precipitation of brines [78]. In endorheic basins of the Central Andes region, salt flats are common Quaternary evaporitic deposits [79–81]. They contain a great variety of evaporites such as halite, gypsum, anhydrite (CaSO_4), selenite ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$), glauberite ($\text{Na}_2\text{Ca}(\text{SO}_4)_2$), and in some cases borates (borax ($\text{Na}_2\text{B}_4\text{O}_5(\text{OH})_4 \cdot 8\text{H}_2\text{O}$), ulexite ($\text{NaCaB}_5\text{O}_6(\text{OH})_6 \cdot 5\text{H}_2\text{O}$), hydroboracite ($\text{CaMgB}_6\text{O}_8(\text{OH})_6 \cdot 3\text{H}_2\text{O}$), colemanite ($\text{CaB}_3\text{O}_4(\text{OH})_3 \cdot \text{H}_2\text{O}$), or inyoite ($\text{CaB}_3\text{O}_3(\text{OH})_5 \cdot 4\text{H}_2\text{O}$)) [80, 82–85]. However, depending on the location of the salt flat, the dominant mineralogical facies can vary between lacustrine carbonate facies, halite facies, boratiferous facies, and gypsum-boratiferous facies [79, 80]. In these salt flats, the dominant AMEs are gypsum evaporitic microbial ecosystems (GEMEs) [13, 14, 86–88]. GEMEs consist mainly of



◀ **Fig. 2** Map of Argentina showing location of salt flats and lakes harboring AMEs. 23 Laguna Vilama. 24 Salar de Tolar Grande. 25 Salar Socompa. 26 Laguna Verde and Bosques del Salar. 27 Laguna Pozo Bravo. 28 Puquio de Campo Naranja. 29 Las Quinoas. 30 Laguna El Peinado. 31 Laguna Carachipampa. 32 Laguna Diamante. 33 Salado river. 34 Laguna Negra

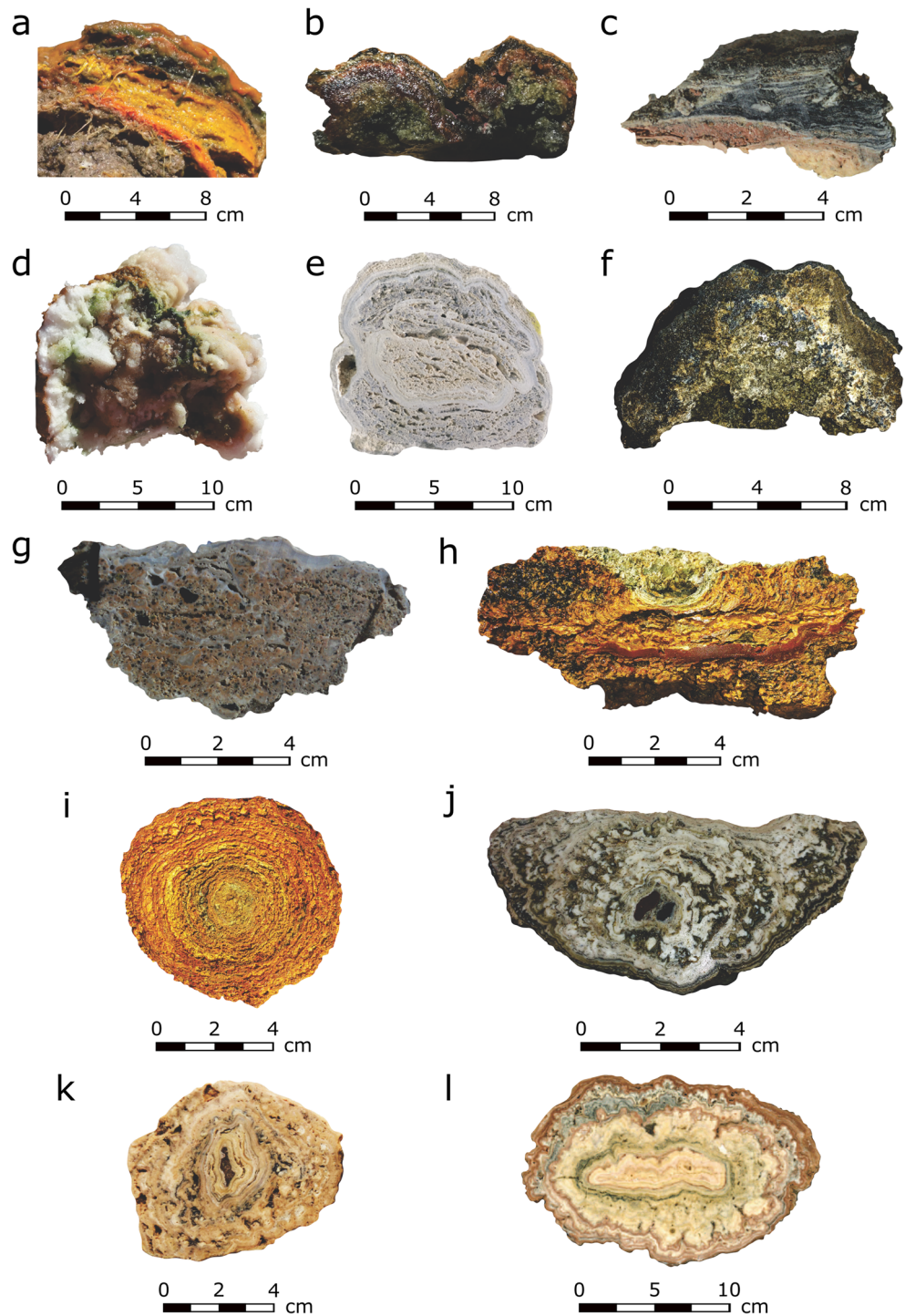
microbial communities associated with gypsum and halite. These communities can develop either as biofilms attached to the surface of minerals, where microorganisms extract

water from them [21, 44, 89, 90], or as endolithic communities (endoevaporites) where minerals provide protection against desiccation and UV-B radiation but allow photosynthetically active radiation (PAR, 400 to 700 nm) to pass through, which is important for the development of photoautotrophs. These microbes produce photosynthetic pigments and photoprotective biomolecules (chlorophyll *a* (Chl*a*), bacteriochlorophyll *a* (BChl*a*), and their respective pheophytins) which are key to maintain a balance between light-harvesting and protection against an excess of harmful

Fig. 3 Overview of Bolivian, Chilean, and Argentinian salt flats and saline lakes harboring AMEs. **a** Salar de Uyuni (1). **b** Salar de Coposa (5). **c** Puquios de Lllamará (6). **d** Laguna Verde del Salar de Carcote (7). **e** Laguna Cejar (11). **f** Laguna Tebenquiche (12). **g** Laguna Chaxa (13). **h** Laguna Barros Negros (14). **i** Laguna Salada (16). **j** Laguna Brava (17). **k** Salar Aguas Calientes (19). **l** Laguna Agua Amarga (22) [4]. **m** Laguna Vilama (23). **n** Ojos de Mar de Tolar Grande (24). **o** Laguna Socompa (25). **p** Laguna Pozo Bravo (27). **q** Puquio de Campo Naranja (28). **r** Las Quinoas (29). **s** Laguna El Peinado (30). **t** Laguna Carachipampa (31). **u** Laguna Diamante (32)



Fig. 4 The AMEs from Argentinian Puna show diverse mesostructures. **a** Non-lithifying microbial mat from Laguna Diamante hot spring. **b** Non-lithifying microbial mat from Puquio de Campo Naranja. **c** Lithifying microbial mat from Laguna Carachipampa. **d** Endoevaporite from Laguna Verde (Salar de Antofalla). **e** Thrombolitic stromatolite from Laguna El Peinado. **f** Thrombolitic stromatolite from Laguna Pozo Bravo. **g** Microbialite from Laguna Diamante. **h** Stromatolite from Laguna Carachipampa. **i** Oncoid from Laguna Carachipampa. **j** Oncoid from Salado river. **k** Oncoid from Las Quinoas. **l** Oncoid from Laguna Negra [17]



irradiation [87]. The minerals of the GEMEs preserve these biomolecules, enhancing even more the growth of photoautotrophs in these ecosystems.

The salt flats where GEMEs have been reported are Salar de Tolar Grande, Salta, Argentina (Ojos de Mar de Tolar Grande; 3510 masl); Salar Socompa, Salta, Argentina (Laguna Socompa; 3570 masl); Salar de Antofalla, Catamarca, Argentina (Laguna Verde and Bosques del

Salar; 3343 masl) (Figs. 2 and 3); Salar de Uyuni, Bolivia (3653 masl); Salar de la Laguna Verde, Bolivia (Laguna Verde; 4300 masl); Salar de Atacama, Chile (Laguna de la Piedra, Laguna Cejar, Laguna Tebenquiche, and Laguna Barros Negros; 2300 masl); Salar Agua Amarga, Chile (Laguna Agua Amarga; 3558 masl); Salar de Carcote, Chile (Laguna Verde; 3690 masl); Salar de Ascotán (Laguna Turquesa; 3722 masl) and Salar de Lllamará, Chile (Puquios

Table 1 Summary of AMEs found in the Central Andes with the geographical location, mineralogical composition and physicochemical characteristics of their habitat

Region	Salt flats and saline lakes	Associated salt flat or volcano	Global position	Altitude (masl)	Max EC (mS/cm)	pH	T (°C)	DO (%)	Arsenic (mg/L)	AMEs	Mineralogy	Position in the map	Figure References
Bolivia	Uyuni	S. de Uyuni	20° 17.74' S 67° 22.69' W	3653	147–242	5.94–6.92	10–20	NA	NA	Biofilms associated to evaporites	Halite	1	1, 3a [49–51]
	Nor Lípez (Potosí)	S. de la L. Verde	22° 47.27' S 67° 49.24' W	4300	0.0234–78.1	8.19–9	10–15	NA	NA	Biofilms associated to evaporites, microbial mats, stromatolites	Carbonates	2	1 [52, 53]
Chile	L. Blanca	S. de la L. Blanca	22° 46.89' S 67° 47.62' W	4300	0.0234–35	7.2–8.42	10–14	NA	NA	Microbial mats, stromatolites	Carbonates	3	1 [52, 53]
	L. de Huasco	S. de Huasco	23° 30' 24.27" S 67° 34' 43.44" W	3800	0.610–105	7	4.9–17.9	NA	NA	Microbial mats	NA	4	1 [54, 55]
	L. Coposa	S. de Coposa	21° 31' 30.07" S 68° 17' 51.47" W	3700	6	9.8	19.8	2.6	0.4	Biofilms associated to sediment, microbial mats	NA	5	1, 3b [56]
	Puquios de Llamará	S. de Llamará	21° 16' 14.73" S 69° 38' 1.41" W	850	143–511	7.6–8.5	36.5–27.4	0.7–1.8	2–1.2	Endoevaporites, microbial mats	Halite, gypsum	6	1, 3c [8, 56, 57]
	L. Verde del S. de Carcote	S. de Carcote	21° 22' 57.64" S 68° 21' 35.80" W	3690	200	9.01	24.8	0.5–11.5	0.005–9.0	Microbial mats, endoevaporites	Gypsum, halite	7	1, 3d [2]
	L. Turquesa	S. de Ascotán	23° 29' 55.38" S 67° 41' 40.96" W	3722	122.9	9.37	42	3.5–19.7	0.005–8.2	Microbial mats, endoevaporites	NA	8	1 [2, 55]
	Campo de Geiseres y Complejo del Taño	Pastos Grandes y Complejo Guacha Caldera	22° 20' 5.56" S 66° 59' 40.74" W	4300	NA	6.5–7.5	86	NA	NA	Microbial mats, stromatolites	Silica	9	1 [58, 59]
	L. de la Piedra	S. de Atacama	23° 3' 17.61" S 68° 12' 58.01" W	2300	224–264	7.5	25	NA	NA	Endoevaporites forming "stromatolite-like" domes	Gypsum, halite, gfauberite	10	1 [60]
	L. Cejar		23° 43' 30.79" S 68° 14' 29.38" W	2300	161	8.2	21.8	1.4	5.5	Microbial mats, endoevaporites	Halite, gypsum	11	1, 3e [56]
	L. Tebenquiche		23° 3' 35.58" S 68° 13' 0.98" W	2340	38–150	7.4–8.6	21.5–31	2.2	2.3	Microbial mats, endoevaporites forming "stromatolite-like" domes, rhizome-associated mats	Halite, gypsum, carbonates	12	1, 3f [9, 13, 61]
	L. Chaxa		29° 24.9' S 68° 10' W	2300	NA	7.32–7.99	27–36	NA	NA	Microbial mats, microbialites	Carbonates	13	1, 3g [61]
	L. Barros Negros		23° 21.7' S 68° 9.1' W	2300	175.9	7.61	30.8	47.8	NA	Endoevaporites forming "stromatolite-like" domes, microbial mats	Halite, gypsum	14	1, 3h [2]
	Aguas de Quelana		23° 24.9' S 68° 5.77' W	2300	116.0	6.6	26.6	111.4	1.3–18.56	Microbial mats	NA	15	1 [2]
	L. Salada		23° 41.1' S 68° 9.66' W	2300	26.5	8.05	18.5	104.1	2.6–17.86	Microbial mats	NA	16	1, 3i [2]
	L. Brava		23° 43' 30.79" S 68° 14' 29.38" W	2300	98–108	7.8–8.2	24.6–30.1	3.75	9–11	Microbial mats, microbialites, rhizome-associated mats	Halite, gypsum, carbonates	17	1, 3j [9, 11]
	L. Pujsa	S. de Pujsa	23° 12' 10.15" S 67° 31' 1.17" W	4500	70	10.8	NA	9.3	120	Biofilms associated to sediment	NA	18	1 [56]
	S. Aguas Calientes		23° 30' 24.27" S 67° 34' 43.44" W	4280	131.5	7.63	52	NA	0.58–55.0	Microbial mats	NA	19	1, 3k [2, 62]
	L. Lejía	S. de Lejía	24° 35' 51.95" S 68° 59' 14.78" W	4325	1.37–91.2	6.9–8.36	3–10.6	NA	NA	Microbial mats	NA	20	1 [62, 63]
	L. Punta Negra	S. de Punta Negra	23° 1' 59.40" S 67° 17' 9.98" W	2945	45	9.7	21	0.4–11.8	4.10 ⁻⁴ –1.4	Microbial mats	NA	21	1 [2]
				25° 32' 2.39" S	3558	200	2–8	NA	NA	NA	Gypsum	22	1, 3l [4]

Table 1 (continued)

Region	Salt flats and saline lakes	Associated salt flat or volcano	Global position	Altitude (masl)	Max EC (mS/cm)	pH	T (°C)	DO (%)	Arsenic (mg/L)	AMEs	Mineralogy	Position in the map	Figure References
Argentina	L. Agua Amarga	S. Agua Amarga	68° 50' 4.34" W							Endoevaporites forming "stromatolite-like" domes			
	L. Vilana	V. Vilana	22° 35' S 66° 55' W	4660	182.81	7	NA	NA	11.8	Microbial mats	NA	23	2, 3m [64]
Salta	Ojos de Mar de Tolar Grande	S. de Tolar Grande	24° 37' 23.51" S 67° 22' 14.35" W	3510	NA	6.5	14	NA	0.59	Endoevaporites	Gypsum, halite	24	2, 3n [65, 66]
	F. Socompa	S. y V. Socompa	24° 31' 43.29" S 68° 11' 53.76" W	3570	0.9	6.5	26	NA	0.05	Biofilms	NA	25	2, 3o [10, 67]
Catamarca	L. Socompa		24° 28' S 68° 17" W	3570	1.15	8.6	10–24	NA	18.5	Stromatolites, endoevaporites	Aragonite		[10, 67, 68]
	L. Verde and Bosques del Salar del Salar	S. de Antofalla	25° 28' 45.73" S 67° 33' 17.72" W	3343	222	7.44	11.4	7.1	NA	Endoevaporites forming "stromatolite-like" domes, microbial mats	Gypsum, halite	26	2, 4d [2]
	L. Pozo Bravo		25° 30' 48.55" S 67° 34' 37.18" W	3333	148	7.8	14	17.1	0.86	Stromatolites, thrombolites, microbial mats	Carbonates	27	2, 3p, 4f [2]
	Puquio de Campo Naranja		25° 36' 48.09" S 67° 40' 20.81" W	3335	33.4	7.78–8.4	22.25	6.4	0.81	Microbial mats	NA	28	2, 3q, 4b [2, 69]
	Las Quinoas		25° 52' 15.50" S 67° 54' 25.56" W	3338	256.1	8.5	18	5.18	18	Oncoids, microbial mats	Carbonates	29	2, 3r, [70]
	L. El Peinado	V. El Peinado	26° 30' 46.16" S 68° 5' 50.09" W	3748	16.28	7.9	22.5	5.3	NA	Stromatolites, oncoids, microbial mats	Carbonates	30	2, 3s, [71]
L.	Carachipampa	S. y V. Carachipampa	26° 27' 2.29" S 67° 30' 39.38" W	3018	87.31	7.8	31.3	3.8	NA	Microbial mats, oncoids, stromatolites	Carbonates	31	2, 3t, 4c, 4h, [2, 72]
	L. Diamante hot spring	Caldera del V. Galán	26° 1' 57.91" S 66° 59' 9.98" W	4828	NA	6.5	85	NA	0.05	Microbial mats	NA	32	4i, 2, 3u, [2]
	L. Diamante		26° 0' 49.75" S 67° 2' 10.08" W	4596	217.3	11	14	1.02	354	Microbialites, biofilms	Carbonates		4g [12, 73, 74]
	Salado river	Laguna Verde Complex	27° 21' 39.20" S 68° 40' 37.09" W	4100	26.4	7.42	29.9	36.3	NA	Oncoids	Carbonates	33	2, 4j [2]
L. Negra			27° 38' 34.82" S	4200	103.8	5.7	31.6	NA	NA	Microbial mats, oncoids	Carbonates	34	2, 4l [17, 75–77]

L Laguna (lake), V Volcán (volcano), S Salar (salt flat), F Fumarola (fumarole), NA not available in the literature, T temperature, EC electric conductivity, DO dissolved oxygen, and pH variables could report seasonal changes throughout the year

de Lllamará; 850 masl) [2, 4, 9, 13, 14, 49, 50, 57, 60, 91–93] (Figs. 1 and 3, Table 1). *Puquios* is the Spanish language version of the *Quechua* term “Pukyu” which means springs [94]. Local people named the springs “Puquios” or “Ojos” (eyes). GEMEs forming “stromatolite-like” domes have been reported in Laguna de la Piedra [60], Laguna Tebenquiche [9, 13], Laguna Barros Negros [2, 93], Laguna Agua Amarga [4], and Laguna Verde and Bosques del Salar (Salar de Antofalla) [2] (Fig. 3, Table 1).

Molecular diversity analyses based on the small subunit ribosomal (SSU) rRNA of *Bacteria* and *Archaea* were performed to study the GEMEs of Laguna Tebenquiche [9, 13], Laguna de la Piedra [60], Laguna Lllamará [57], and Salar de Uyuni [49, 50] (Fig. 3). These analyses revealed that *Euryarchaeota* (ca. 40–100%), *Bacteroidetes* (ca. 5–50%), and *Proteobacteria* (ca. 27–43%) are the dominant phyla in the ecosystems studied. The high halotolerance of *Euryarchaeota* and *Bacteroidetes* species might explain their great abundance [9, 49]. Within the phylum *Proteobacteria*, the most abundant classes are *Alphaproteobacteria* (ca. 8–37%) and *Gammaproteobacteria* (ca. 6–32%) [9, 13, 57, 60].

Although in Laguna de la Piedra the phylum *Cyanobacteria* was reported to be present in remarkable proportions (relative abundance not available) [60], in the rest of the evaporitic microbial ecosystems, it is underrepresented (<2%). In Laguna Tebenquiche endoevaporite [13], anoxygenic photoautotrophs from the classes *Alphaproteobacteria* (*Rhodovibrio* sp.) and *Gammaproteobacteria* (*Halorhodospira* sp.) are more abundant (relative abundance (log 10 base)) in layers 3 (ca. 2%), 4 (ca. 0.7%), and 5 (ca. 1.5%) than *Cyanobacteria* (ca. <2%, 0%, and 0.5%, respectively), suggesting that these taxa might play an important role in the inorganic carbon fixation. Metagenomic analyses of evaporitic microbial mats in Laguna Lllamará revealed that the Wood-Ljungdahl (reductive acetyl-CoA) pathway is abundant (ca. 0.04–0.08%) in the oxic layers, and even dominant (ca. 0.2–0.28%) over the Calvin-Benson cycle (ca. 0.09%) in the anoxic layers, supporting the idea that other groups different from *Cyanobacteria* may largely contribute to the carbon fixation process [57, 95].

As in microbial mats and microbialites, the accessibility to light and oxygen creates a stratified system in the endoevaporitic gypsum domes [48, 57]. In Laguna de la Piedra, for example, a green layer (0.5–1 cm thick) dominated by oxygenic photoautotrophic bacteria (*Cyanobacteria*) and heterotrophic bacteria (*Bacteroidetes*) is visible a few millimeters (ca. 5 mm) beneath the surface, followed by a purple layer of comparable thickness dominated by anoxygenic purple photosynthetic bacteria (*Alphaproteobacteria*) [60]. In Laguna Lllamará, on the contrary, a green layer is visible a few centimeters (ca. 2 cm) beneath the surface (upper part), followed by an orange-dark layer (lower part). *Bacteroidetes* (30% winter and summer), *Gammaproteobacteria* (31% winter - 21% summer), and *Alphaproteobacteria* (9% winter - 19% summer) dominate the

upper air-exposed part both in winter and summer. However, in the lower water-submerged part, substantial differences are found between these seasons. In summer, the most abundant groups are *Gammaproteobacteria* (32%), *Alphaproteobacteria* (22%), and *Verrucomicrobia* (24%), whereas in winter, the abundance of these groups reduces (12%, 8%, and <2%, respectively) and the abundance of *Bacteroidetes* (18%), *Planctomycetes* (12%), and *Firmicutes* (8%) increases, enlarging biodiversity [57].

Chao1, Shannon, Equitability, and Simpson indexes (OTUs at 97%) are normally lower in GEMEs ((242–501), (2.0–7.0), (0.58–0.85), (0.83–0.95), respectively) than in soft mats ((486–592), (6.6–6.8), (0.79–0.81), (0.96–0.97), respectively) and carbonate mats and microbialites ((358–799), (6.6–7.3), (0.79–0.86), (0.98–0.99), respectively), but the Dominance index (OTUs at 97%) is higher in GEMEs (0.02–0.40) than in soft mats (0.03–0.04) and carbonate mats and microbialites (0.01–0.03) [9–11, 13, 49, 57]. This means that GEMEs, compared to the rest of AMEs, present low diversity and large dominance of a few species (e.g., *Halonotius* sp., *Haloarcula* sp., *Halorubrum* sp.) [13, 49].

Carbonate Microbial Ecosystems: Mats and Microbialites

Carbonate precipitation can be biologically driven when microbial metabolism is the main process inducing supersaturation of CaCO_3 (by altering alkalinity, pH, and cations availability) or extrinsically driven when physicochemical processes are responsible for the carbonate supersaturation state (evaporation, salinity, CO_2 degassing, etc.) [22]. In HAALs, both processes take place [3, 75, 76].

Andean carbonate microbial ecosystems (CMEs) are generally located in water-mixed zones where fresh superficial and groundwater inputs reach the lake, promoting microbial development, as well as providing a source of carbonate/bicarbonate ions for the carbonate precipitation [17, 77]. The chemistry of the HAALs is generally thought to result from the weathering of surrounding volcanic rocks by the infiltration and passage of precipitation through them, leading to the formation of dilute inflow waters that subsequently concentrate by evaporation [97], but it is believed that the most important mineral and salinity supply comes from thermal springs that discharge into the superficial and underground waters [98]. Depending on the physicochemical conditions of the water (e.g., pH, Eh, alkalinity, temperature), carbonate, sulfate, and chloride minerals could precipitate. For instance, the abundance of Na^+ in the water allows the occurrence of gaylussite ($\text{Na}_2\text{Ca}(\text{CO}_3)_2 \cdot 5\text{H}_2\text{O}$) in Laguna Diamante [12] or pure aragonite in Laguna Socompa [10, 65].

CMEs have been reported in lakes, brackish rivers, and hot springs, characterized by three main types of mesostructures: stromatolites, oncoids, and thrombolites (Fig. 4) [99]. These include Laguna Verde stromatolites from Salar de la Laguna

Verde, Bolivia (4300 masl); Laguna Blanca stromatolites from Salar de la Laguna Blanca, Bolivia (4300 masl) [52, 53]; Laguna Brava mats and microbialites [9, 100] and Laguna Chaxa mats and microbialites (Fig. 3) [2, 93] from Salar de Atacama; Laguna Pozo Bravo mats, stromatolites, and thrombolites (Fig. 3), Puquio de Campo Naranja mats and microbialites (Figs. 3 and 4) [2, 69], and Las Quinoas mats and oncoids (Figs. 3 and 4) [70] from Salar de Antofalla; Laguna Carachipampa mats, stromatolites, and oncoids (Figs. 3 and 4) [2] from Salar Carachipampa, Argentina (3018 masl); Laguna Diamante microbialites (Fig. 4) [73] from Caldera del Volcán Galán (4596 masl); Laguna Negra mats and oncoids (Fig. 4) [75, 76, 101] and Salado river oncoids (Fig. 4) [2] from Laguna Verde Complex (4150 masl); Laguna Socompa stromatolites (3570 masl) from Salar de Socompa [10, 67]; and Laguna El Peinado mats, stromatolites (Figs. 3 and 4), and oncoids (3748 masl) [71] (Table 1).

Molecular diversity analyses based on the small subunit ribosomal (SSU) rRNA of *Bacteria* and *Archaea* were carried out to study the microbial communities from Laguna Socompa stromatolites [10, 68], Las Quinoas oncoids [70], and Laguna Brava carbonate microbialites [9, 11]. These analyses revealed that *Proteobacteria* (ca. 6–46%) and *Bacteroidetes* (ca. 4–25%) are the most abundant phyla in the majority of the ecosystems studied. Within the phylum *Proteobacteria*, the most representative classes are *Alphaproteobacteria* (ca. 7.5–25%), *Gammaproteobacteria* (ca. 4–26%), and *Deltaproteobacteria* (ca. 5–13%). *Spirochaetes* (ca. <1–15%), *Firmicutes* (ca. <1–13%), *Verrucomicrobia* (ca. <1–13%), *Chloroflexi* (ca. 1–8%), and *Deinococcus-Thermus* (ca. <1–7.5%) phyla are also well-represented, but their abundances greatly differ between ecosystems. Interestingly, in Laguna Brava [11], a hypersaline lake (98–108 mS/cm), there are microbialites covered by pink or black leathery biofilms in which the most abundant phyla are *Planctomycetes* (ca. 35–42%) and *Euryarchaeota* (*Methanomicrobia* and *Thermoplasmatales*) (ca. 16–17%). These lineages have never been reported before to dominate microbialites, which suggests that physicochemical conditions greatly influence the microbial composition of the AMEs.

Compared to low-altitude marine microbialite systems like Cuatro Ciénegas (Mexico), Shark Bay (Australia), or Highborne Cay (Bahamas), the majority of the microbialites present in the Central Andes have a low abundance (ca. <1–4%) of *Cyanobacteria*, possibly due to their high sensitivity to environmental stresses such as UV, high salt, and arsenic (As) [67, 102]. The oxygenic photoautotrophic species of this phylum play a fundamental role in inorganic carbon fixation and biologically induced and biologically influenced mineralization (organomineralization *sensu lato*) in the low-altitude microbialite systems, but in the Central Andes microbial systems other groups different from *Cyanobacteria* may largely

contribute to these processes [67]. Another characteristic of the Central Andes microbialites, absent in the low-altitude marine microbialites, is the presence of *Deinococcus-Thermus* species in the upper oxic zones (ca. 0–7 mm) [9–11, 67]. In Laguna Socompa stromatolites, this phylum even dominates (ca. 35–87%) the first two layers (0–2 mm). The high radioresistance of these species provides them a selective advantage to outcompete other microorganisms in the high-UV irradiance environment of the Central Andes microbialites, while at the same time, protects the rest of the microbial community from UV radiation.

Non-Lithifying Microbial Mats (Soft Mats)

Non-lithifying microbial mats are layered microbial communities associated with minerals that are neither part of gypsum nor part of carbonate deposits. They can vary from several decimeters to only some millimeters depending on the altitude. Thick multiple-layered mats (ca. 2–4 cm) are found mainly in hypersaline lakes located at altitudes lower than 3000 masl, such as Laguna Tebenquiche (2340 masl), Laguna Brava (2300 masl), Aguas de Quelana (Salar de Atacama; 2300 masl), and Puquios de Lllamará (850 masl) [9, 11, 56]. Over ~3000 masl, strong winds and high-temperature fluctuations seem to prevent the development of multilayered mats [2]. For this reason, thinner mats (no more than 1 cm thick) are found in Laguna Pozo Bravo (3333 masl), Laguna El Peinado (3748 masl), Laguna Negra (4200 masl), Puquio de Campo Naranja (3335 masl) (Fig. 4), Laguna Coposa (3700 masl), and Laguna Vilama (4660 masl).

Over the last few years, molecular diversity analyses based on the small subunit ribosomal (SSU) rRNA of *Bacteria* and *Archaea* were performed to study the microbial composition of non-lithifying microbial mats from Laguna Lllamará, Laguna Cejar, Laguna Tebenquiche, and Laguna Brava [9, 11, 13, 56]. These analyses revealed that *Euryarchaeota* (ca. 29–33%), *Crenarchaeota* (ca. 14–17%), *Bacteroidetes* (ca. <1–39%), *Proteobacteria* (ca. <1–38%), *Spirochaetes* (ca. 1–23%), *Deinococcus-Thermus* (ca. <1–18%), *Planctomycetes* (ca. <1–14%), *Firmicutes* (ca. <1–11%), *Chloroflexi* (ca. 2–8%), and *Verrucomicrobia* (ca. <1–6%) phyla are well-represented in the majority of the ecosystems studied. Within the phylum *Proteobacteria*, the most representative classes are *Deltaproteobacteria* (ca. <1–23%), *Alphaproteobacteria* (ca. <1–14%), and *Gammaproteobacteria* (ca. <1–6%). As in the rest of the microbial communities from the Central Andes, *Cyanobacteria* species are present in low proportion (ca. <1–2%), which means that other groups different from *Cyanobacteria* may largely contribute to the carbon fixation process [11, 95].

The arrangement of these taxa in a vertically organized structure is mainly determined by steep vertical gradients of light, UV radiation, O₂, H₂S, and pH [103]. For instance, in

Brava and Tebenquiche soft mats [11, 13], radioresistance bacteria (*Deinococcus-Thermus*), and oxygenic photoautotrophs (*Cyanobacteria*) are mostly present in the upper layers (ca. 0–1 cm depth), followed by anoxygenic green photoautotrophs (*Chloroflexi*) mainly located in the intermediate ones (ca. 1–3 cm depth). As *Cyanobacteria* and *Chloroflexi* fix inorganic carbon, they share their location with aerobic heterotrophs that consume their organic carbon exudates (*Euryarchaeota*, *Bacteroidetes*, *Planctomycetes*, *Verrucomicrobia*, and *Spirochaetes*, among others). Methanogens (*Euryarchaeota*), sulfate reducers (*Crenarchaeota*), fermenters (*Firmicutes*), and anaerobic heterotrophs are generally present in the lower layers (ca. 1–5 cm depth); however, these anaerobes have been reported close to the surface as well (0–1 cm depth). The mechanism(s) that allows them to survive under high oxygen conditions are still unknown [11, 13].

Distinctive Characteristics of AMEs

Alternative Carbon Fixation Pathways

Compared to other microbial ecosystems located at low altitudes, the AMEs contain a low abundance of *Cyanobacteria* (ca. <1–4%) which fix carbon dioxide through the Calvin-Benson cycle. This observation is supported, on the one hand, by the low amounts of *Chla* (ca. <0.1–3 µg/L) reported in Laguna Socompa stromatolites, Laguna Tebenquiche mats, Laguna Brava mats and microbialites, and Laguna Negra mats [9–11, 13, 100], and on the other hand, by the metagenomic analyses of both 16S rRNA gene amplicons and whole-genome sequencing (WGS) data sets [3]. Therefore, in the AMEs, carbon fixation might occur not only by the Calvin-Benson cycle but also through alternative cycles/pathways. To determine which carbon fixation cycle/pathway dominates each AME, metagenomic analyses of Laguna Socompa stromatolites, Laguna Diamante red biofilms, Laguna Lllamará endoevaporites, and Laguna Brava and Tebenquiche mats were carried out. In these analyses, the abundances of key enzyme genes from each carbon fixation cycle/pathway were determined. These key enzymes were the ATP-citrate lyase from the rTCA cycle, the RuBisCO from the Calvin-Benson cycle, the bifunctional enzyme carbon monoxide dehydrogenase/acetyl-CoA synthase from the reductive acetyl-CoA pathway (Wood-Ljungdahl pathway), the 4-hydroxybutyryl dehydratase from the dicarboxylate-hydroxybutyrate (DC/HB) and hydroxypropionate-hydroxybutyrate (HP/HB) cycles, and the 2-methylfumaryl-CoA isomerase from the 3-hydroxypropionate bicycle (3HP) [104]. The metagenomic analyses revealed that, in Laguna Socompa stromatolites, the dominant carbon fixation cycle/pathway is the rTCA cycle, followed by the Calvin-Benson

cycle and the Wood-Ljungdahl pathway [68]. In Laguna Diamante red biofilm, the rTCA cycle was the only one reported [12]. In Laguna Lllamará endoevaporites, the oxygen-rich upper part is dominated by the Calvin-Benson cycle, whereas the anoxic lower part is dominated by the Wood-Ljungdahl pathway [95]. Finally, in Laguna Brava and Tebenquiche mats, the Calvin-Benson cycle and the Wood-Ljungdahl pathway were reported in similar proportions [105]. All these results support the idea that carbon fixation in the AMEs might not be carried out only by the Calvin-Benson cycle, but also through alternative cycles/pathways such as the rTCA cycle and the Wood-Ljungdahl pathway.

Diatoms: Key Structural Components of AMEs

Optical microscopy and scanning electron microscopy (SEM) images of the AMEs revealed the presence of prokaryotic cells (filamentous cyanobacteria, coccoids and/or bacillus) associated with diatom frustules forming nano-globular carbonate aggregates [101]. Diatoms produce great amounts of EPS that trap and bind detrital sediments and/or provide a matrix for mineral nucleation [76, 106]. Therefore, they could be promoting carbonate precipitation in AMEs [101]. As diatoms were reported in most of the studied AMEs, and they are photoautotrophic microorganisms, they might play an important role in the primary production of these ecosystems. Moreover, they are the main source of food for the species of flamingos in the Central Andes [107, 108], representing a key component of the trophic network.

Diatoms were reported in CMEs of Laguna Negra [75, 76, 101], Laguna Brava [9, 11], and Laguna Socompa [10], as well as in GEMEs of Laguna Lllamará and Laguna Tebenquiche [13, 109]. In these studies, the genera reported were *Achnanthes* sp., *Halamphora* sp., *Navicula* sp., *Striatula* sp., *Cymbella* sp., *Hantzschia* sp., *Nitzschia* sp., *Synedra* sp., *Surirella* sp., *Rhopalodia* sp., and *Pinnularia* sp. [9–11, 13, 75, 76, 101, 109].

Besides diatoms, other microscopic eukaryotic taxa were reported in the AMEs including green algae like *Dunaliella salina* and *Chlamydomonas* spp. [110]; flagellates like *Pleurostomum flabellatum* [111]; dinoflagellates like *Ceratium hirundinella* and *Diplopsalis lebourae*; ciliates like *Caryotricha* sp., *Strombidium purpureum*, *Codonella apicata*, *Eutintinnus pectinis*, *Oxytricha elegans*, *Amphisiella magnigranulosa*, *Gonostomum strenuum*, and *Stichotrichia* sp.; fungi like *Alternaria* spp. and *Trimmatostroma salinum* [112, 113]; and the brine shrimp *Artemia* spp.

The ecological role of microscopic eukaryotic taxa in AMEs, and their participation (directly and/or indirectly) in the carbonate precipitation processes are not well understood. The main limitations to answer these interrogations are the lack of data related to the diversity and abundance of these taxa, as well as the seasonal variation of the physicochemical

parameters of the habitat. Therefore, further physicochemical and eukaryotic composition analyses should be performed to have a better comprehension of these processes.

Archaea: an Abundant Domain in AMEs

Molecular diversity analyses based on the small subunit ribosomal (SSU) rRNA of *Archaea* have revealed that this domain is well-represented in the AMEs, especially those with high salinity content (ca. 100–200 mS/cm) such as Salar de Uyuni brines (ca. 40–100%) [49, 50], Laguna Tebenquiche mats (ca. 50%) and endoevaporites (ca. 97%) [13], Laguna Diamante red biofilms (ca. 94%) [12], and Laguna Brava soft mats (ca. 43%) and microbialites (ca. 16–17%) [11]. The most abundant archaeal phyla in these AMEs are *Euryarchaeota* (ca. 16–100%) and *Crenarchaeota* (ca. 14–17%). Within *Euryarchaeota*, the most representative genera are *Halonotius* sp. (ca. 4–63%), *Halorubrum* sp. (ca. 4–55%) and *Halorhabdus* sp. (ca. 2–6%) from the *Halobacteria* class. Although the *Archaea* domain is also present in low-altitude marine microbialite systems like Shark Bay, Highborne Cay and Cuatro Ciénegas [114], its abundance is lower (ca. <2–10%) than in the AMEs. The high salt concentrations present in the AMEs are absent in the low-altitude marine microbialite systems. These concentrations are required by halophilic archaea (*Halobacteria*) to grow, which could explain the differences observed in the archaeal composition of these systems.

Arsenic Metabolism

In the HAALs, high As concentrations (ca. $4 \cdot 10^{-4}$ –354 mg/L) are naturally found in the water (Table 1) [68]. Prokaryotes that colonize the AMEs have specific metabolic pathways that allow them to resist these elevated As concentrations [68, 73, 96, 115–117], and in some cases, obtain energy from the oxidation of arsenite (As^{3+}) and/or reduction of arsenate (As^{5+}) [100]. The general mechanism of As resistance, which is present in *Exiguobacterium* sp. S17 isolated from Laguna Socompa stromatolites, consists in the cytoplasmic arsenate reduction (*ars* operon) followed by the extrusion of the resulting arsenite (*acr3* or *arsB*) to the periplasm [96, 115]. Depending on the organism, the arsenite in the periplasm could be used later for the generation of metabolic energy through an aerobic arsenite oxidase (*aioAB*) and/or a respiratory arsenate reductase (*arrAB*) [68]. This bioenergetic mechanism was proposed to be carried out by *Halorubrum* sp. AD156 and *Halorubrum* sp. DM2, isolated from Laguna Diamante red biofilms [12, 116].

To determine how extended are these As resistance and bioenergetic mechanisms in the prokaryotes that colonize the AMEs, different studies were performed in Laguna Diamante ([As]: 347 mg/L) [12, 121], Laguna Socompa ([As]: 28 mg/L) [68], and Laguna Brava ([As]: 20 mg/L) [100, 122, 123], all of

which present high arsenic concentrations. Metagenomic analysis of Laguna Diamante red biofilm revealed a high abundance of genes used for arsenite oxidation (*aioBA*) and respiratory arsenate reduction (*arrCBA*), suggesting that the haloarchaea that dominate the biofilm use arsenic compounds as bioenergetics substrates. Phylogenetic analysis of these sequences even suggested that the origin of arsenic metabolism in haloarchaea is ancient [12]. Metagenomic analysis of Laguna Socompa stromatolites also revealed a surprisingly diverse metabolism comprising all known types of As resistance and energy-generating pathways. Although the *ars* operon was the main mechanism identified, an important abundance of *arsM* genes, which encode an arsenite methyltransferase, was observed in *Bacteroidetes*, *Actinobacteria*, *Firmicutes*, *Verrucomicrobia*, *Spirochaetes*, *Cyanobacteria*, and *Euryarchaeota* phyla [68]. In Laguna Brava mats, no metagenomic analysis was carried out to study the As metabolism, but an arsenic-sulfur (As-S) cycle was suggested [100] based on the following observations: (i) the high As and S concentrations in the water column [11], (ii) the lack of O_2 in the mats, (iii) the reduction of S and As compounds through anoxygenic photosynthesis [124], and (iv) the heterogeneous distribution of arsenate and arsenite [100]. All these findings suggest that an As biogeochemical cycle is present in the AMEs, probably similar to the proposed one in ancient microbial ecosystems [125, 126].

Strains Isolated from AMEs Provide Insight into Arsenic and UV-B Radiation Resistance

Isolation and characterization of microbes from AMEs have provided knowledge on how these extremophiles deal with the diverse environmental conditions present in the Central Andes [127, 128], such as high arsenic concentration and UV-B (280–320 nm) radiation.

To study the arsenic resistance mechanisms, *Exiguobacterium* sp. S17 was isolated from Laguna Socompa stromatolites [96, 115]. This strain tolerates an arsenic concentration (10 mM As^{3+}) 20 times higher than the maximum concentration (0.5 mM As^{3+}) tolerated by other *Exiguobacterium* strains isolated from an estuarine system in Goa, India, with high arsenic content. The analysis of its genome revealed that the S17 strain presents copies of both *arsB* and *acr3* genes, which encode arsenite efflux pumps that export As^{3+} to the periplasm. The combined work of both efflux pumps might explain the enhanced tolerance of this strain to As^{3+} [115]. A proteomic analysis, carried out on the same strain, revealed that proteins involved in cellular stress responses were overexpressed under the presence of As (e.g., superoxide dismutase, heat-shock proteins, prolyl-tRNA synthetase, elongation factor TS, among others) [96]. Therefore,

such proteins have also been proposed to be involved in the arsenic resistance mechanism of the S17 strain.

To study the molecular mechanisms involved in the resistance to high-UV-B radiation, *Salinivibrio* sp. S10B, *Salinivibrio* sp. S34, and *Salinivibrio socompiensis* S35 were isolated from Laguna Socompa stromatolites [129, 130]. These strains have shown to be extremely resistant to UV-B radiation (19 KJ/m², corresponding to 240 min of exposure). The analyses of their genomes revealed several genes with a potential role in DNA repair. These include the complete set of genes for RecBCD helicase/nuclease and UvrABC endonuclease holoenzymes, homologs for *recA* and *recX* genes, and gene homologs of CPD photolyases, proteorhodopsins, and xantorhodopsins. Photolyases are enzymes that repair cyclobutyl pyrimidine dimers, which are formed between adjacent bases on the same DNA strand upon exposure to UV radiation. Proteorhodopsins and xantorhodopsins enhance the harvest of solar energy, allowing photosynthesis to occur even in periods where there is a lack of solar energy [127, 131, 132]. *Halorubrum* sp. BOL3-1, isolated from Salar de Uyuni, also contains gene homologs for photolyases and bacteriorhodopsins in its genome [133], suggesting that these genes belong to a UV-B radiation resistance mechanism shared among the Andean extremophiles.

Final Considerations

During the past decade, several explorations have been carried out to identify and study the AMEs located in the Central Andes region, which thrive under extreme environmental conditions resembling those of the early Earth. The analyses performed to these AMEs have revealed that (1) they display diverse mesostructures and mineralogical compositions; (2) they contain low abundance of *Cyanobacteria* (ca. <1–4%), and therefore, carbon fixation might occur not only by the Calvin-Benson cycle but also through alternative cycles/pathways (e.g., rTCA cycle and Wood-Ljungdahl pathway); (3) most contain high abundance of *Archaea* (*Halobacteria*) probably due to their high salinity content; and (4) they harbor prokaryotes which present high arsenic and UV-B radiation resistance mechanisms that allow them to grow under the extreme conditions of the environment.

Nevertheless, to have a complete understanding of the AMEs, further analyses need to be done to determine the abundance and diversity of viruses; their impact in the communities of the AMEs; the ecological role of microscopic eukaryotes like fungi, protists, and microinvertebrates and their participation (directly and/or indirectly) in the mineral precipitation processes. Although some analyses have been performed related to these interrogations [2, 51, 134–137], there are no clear answers to them.

The several studies performed during the last years have been of great importance to declare as protected areas Laguna Socompa, Ojos de Mar de Tolar Grande, and Laguna Tebenquiche, which demonstrate that scientific research and exploration are essential for the protection and conservation of these unique ecosystems.

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Author Contribution FAV and MEF designed and performed the review. MEF conceived the original HAAL project. FAV, AIL, TMS, MNS, LAS, DK, DG, PGV, VHA, and MEF wrote the review. FAV, AIL, TMS, JSF, DGP, and MEF revised the review. MEF, DG, and MC obtained funding for the original project idea. All authors read and approved this manuscript.

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Declarations

Competing Interests The authors declare no competing interests.

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