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# Hypersaline Lagoons from Chile, the Southern Edge of the World

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## Abstract

Hypersaline lagoons distributed in arid and semiarid regions are unique ecosystems with unique value stemming from their extremophile biodiversity, limnological properties and services, like mining and waterbird habitat. They are natural laboratories to understand how life evolved in extreme environments and how simple ecosystems function to provide waterbird habitat, an essential noneconomic service. Policymakers need this knowledge to protect these ecosystems increasingly affected by climatic change and human-driven perturbations. Hypersaline lagoons from contrasting latitudinal conditions in Chile provide a study case to evaluate how such conditions affect their microscopic and macroscopic diversities. Those in the hyperarid Atacama Desert in northern Chile are an integral part of mineral-rich salars, whereas Patagonian lagoons are unique among freshwater lakes of glacier origin. Despite latitudinal differences, prokaryotic diversity tends to be similar in both extremes. However, genetically distant brine shrimp (*Artemia*) species, *A. franciscana* (north) and *A. persimilis* (Patagonia), inhabit them. This crustacean is a keystone taxon in the food web, and its abundance indicates ecosystem quality and attracts waterbirds. This chapter stresses the need to systematically monitoring *Artemia* abundance and all factors affecting its fitness (gut microbiota, parasites, environmental conditions). Finally, the need to conserve these unique and extreme ecosystems is highlighted.

**Keywords:** hypersaline ecosystems, extremophile biodiversity, waterbird habitat, natural laboratories, Atacama Desert, Patagonia, Chile

## 1. Introduction

Hypersaline lakes or brines (over 40 g/L) [1] are unique ecosystems with unique extremophile biodiversity and scientific value, which also have economic, esthetic, cultural, and recreational value [2, 3]. They represent a significant volume (~45%) of inland waters [4] and hence are essential components of the biosphere, mostly located in arid and semiarid regions around the world where high evaporation rates exceed rainfall. However, they also occur in unusually cold places such as Tibet in China and Patagonia in southern Chile and Argentina [5, 6]. Due to their wide ecological diversity related to their coastal (thalassohaline) or inland origin (athalassohaline) [7, 8], altitude, salinity, and island-like distribution, these lagoons display unique extreme biodiversity and limnological features. Besides, hypersaline lagoons are also affected by the combined effect of multiple stressors such as UV exposure, temperature, pH, low nutrient, and oxygen availability [8], which means these lagoons are polyextremophile environments. As a consequence, the microscopic and

macroscopic biodiversity reflects their evolution to cope with multiple stresses that are unbearable for most organisms.

Since biodiversity declines as salinity increases, hypersaline lagoons are relatively low-diversity ecosystems with simple food webs [9] and hence are considered suitable natural laboratories [10] to address fundamental questions of biology. Due to the multiple stressors shaping such unique biodiversity and the potent mutagenic role variation in ionic strength has on DNA-protein interactions, and protein structure, the biodiversity of these lagoons exhibits an accelerated rate of evolution, at least as demonstrated for brine shrimps (*Artemia*) [11]. Among the relevant biological questions salty ecosystems allow to investigate are those related to the origin of life from simple forms, and what are the limits and prominent features of life in extreme environments, topics addressed by the new discipline of astrobiology [12]. Likewise, what is the microbiological and macroscopic (zooplanktonic) diversity salty lagoons harbor, and how latitudinal, climatic, lagoon-specific conditions, or anthropic perturbations modulate such diversity? Their microbiological diversity has received significant attention due to the potential economic benefits attached to the metabolic responses evolved to cope with extreme conditions (antioxidant pigments, hydrolytic enzymes) [13–15]. While the stress response in the prokaryotic world tends to be unidimensional, multicellular systems experience critical life conditions at all levels of functionality; in other words, adaptation takes place at different domains, from the individual (molecular-cellular-physiological) to the population level. As discussed later on in this chapter, the brine shrimp *Artemia* is a relevant extremophile model to understand what means to survive and reproduce under harsh conditions [6].

From a more practical perspective, hypersaline lagoons are considered low-diversity natural laboratories to understand how simple ecosystems function to provide economic services like mining salt and brine shrimp (*Artemia*) biomass, like in the Great Salt Lake in Utah, an example of a well-managed lake to allow the coexistence of economic and noneconomic services like waterbird habitat. The lake is the main source of *Artemia* cysts for world aquaculture [16], but the *Artemia* biomass required to harvest tonnes of cysts also attracts local and migratory waterbirds that need to be protected, some of which are endangered [17, 18]. Hypersaline lakes and lagoons around the world are, however, shrinking at an alarming rate due to climate oscillations and water or brine diversion for mining [19]; hence, there is a need to conserve their unique biodiversity, properties, and services to comply with international treaties on biodiversity, ecosystem, and wetland conservation. The lack of systematic and long-term spatial and temporal studies on most hypersaline ecosystems that are often in remote places and tend to exhibit high seasonal variation in their biodiversity [9] makes difficult to understand or predict how they will respond to climate oscillations and increased anthropic pressures.

The importance of saline lakes and lagoons in the twenty-first century was highlighted by Williams [3], who in 2003 predicted they would be shrinking by 2025. Other reviews have also highlighted the fragility of these unique ecosystems [2, 4], while recent literature pinpoints the biotechnological importance of the microbiological diversity they harbor [12–15] as an argument to protect them [14]. This chapter focusses on Chilean hypersaline lagoons (or Lagunas) located at contrasting latitudinal and altitudinal settings at the southern edge of the world, i.e., southwest of South America (below 18° latitude south). In the north, inland (athalassohaline) lagoons are an integral part of mineral-rich evaporitic basins or salars (salt crusts) scattered at different altitudes in the hyperarid Atacama Desert. The aridity of the desert has raised the question if life can persist in water-less environments, and because of this and other soil characteristics, the desert is considered a terrestrial model of Mars and hence a target of astrobiological research as already mentioned.

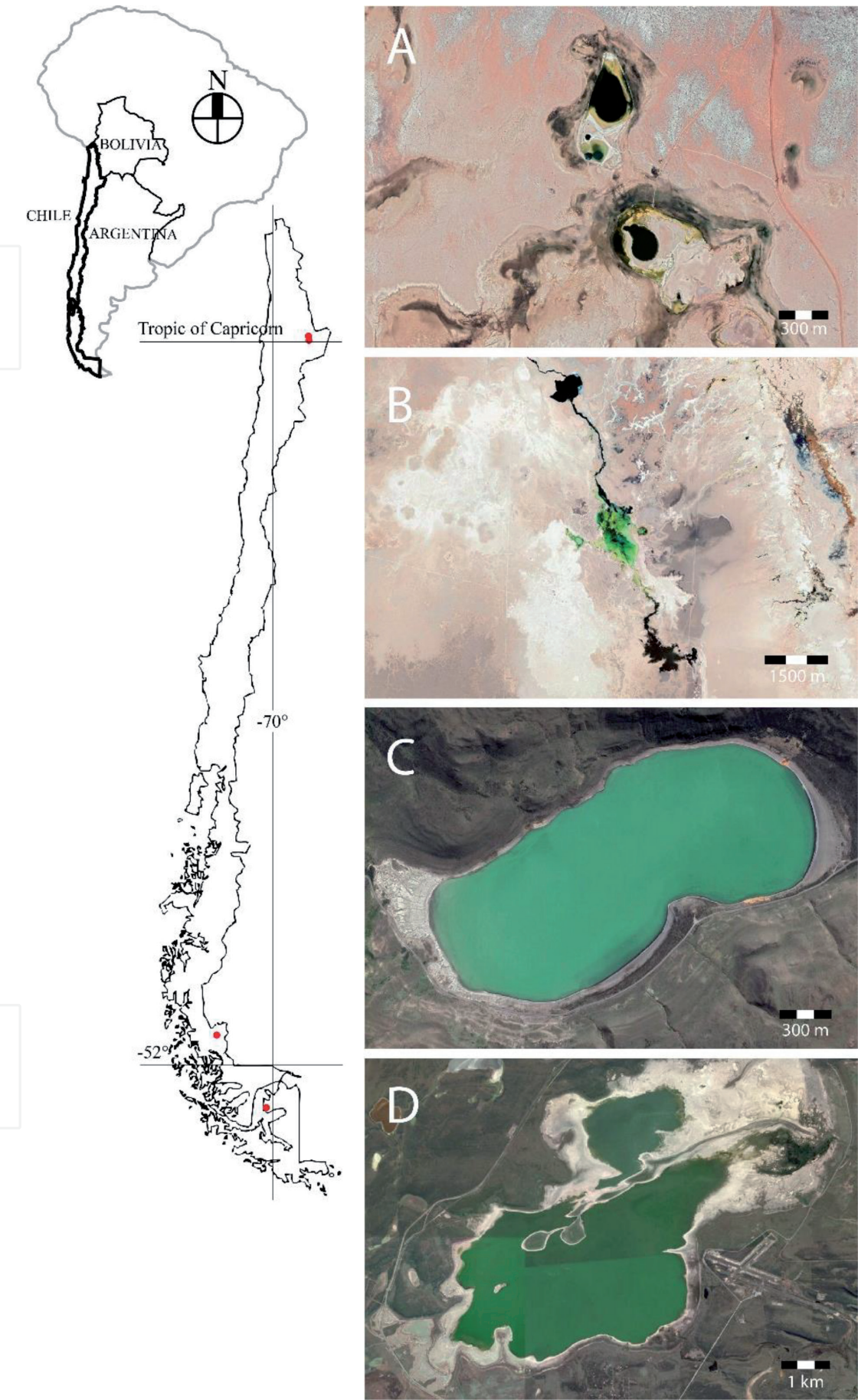
Instead, in Patagonia, there are subantarctic low-altitude lagoons, some of which are relatively close to the Pacific coast but cannot strictly be considered thalassohaline. The unique feature of these hypersaline lagoons is their location in an area where freshwater lakes of glacier origin abound. Both contrasting latitudinal settings represent useful case studies to address how their prokaryotic and eukaryotic diversity evolved. The brine shrimp *Artemia*, a key taxon in the food web of these salty lagoons, becomes relevant in the discussion on how these lagoons function to provide suitable habitat for waterbirds, as the abundance of this crustacean seems to be a good predictor of their presence [17] and the animal is also considered an indicator of environmental quality. In this context, some of the remarkable animal's adaptations are discussed, including the sort of symbiotic *Artemia*-bacteria relationship and other factors affecting *Artemia* fitness and hence the abundance of this crustacean. The aims of this chapter are as follows: (1) To provide a glimpse to the ecological characteristics of hypersaline lagoons of Chile, which are unique ecosystems located at contrasting latitudinal edges. They are a natural heritage harboring unique extremophile biodiversity that provides conditions to host a significant waterbird diversity. (2) To review studies on their microbiological communities that coexist with *Artemia*. (3) To get insights on *Artemia* species inhabiting such contrasting environments, and their ability to tolerate high salt concentration (salt-lover), and to perceive ecosystem quality. The *Artemia*-bacteria interaction is also discussed as it contributes to *Artemia* fitness and abundance. (4) To highlight the need to monitoring hypersaline lagoon dynamics on a long-term basis to predict waterbird presence. (5) To alert on the fragility of these ecosystems increasingly affected by climatic oscillations and human-driven perturbations like mining.

## 2. Hypersaline lagoons from Chile: natural heritage at the southern edge of the world

Chile is a sort of biogeographical island at the southern edge of the world, isolated by the hyperarid Atacama Desert on the north, the Antarctic ice on the south, the Andes Mountains on the east, and the Pacific Ocean on the west. This long and narrow land (**Figure 1**) exhibits a wide latitudinal ( $18^{\circ}$ – $56^{\circ}$ S latitude, excluding the Antarctic) and altitudinal range, from sea level to the high Andes. Natural hypersaline lagoons or brines exist at both latitudinal and climatological extremes. The Atacama Desert ( $17^{\circ}$ – $27^{\circ}$ S latitude) is the driest, oldest, and most extreme world environment [20, 21], well-known as a terrestrial Mars analog, as already mentioned, with microbial life similar to what could be expected to exist in the red planet [21, 22]. This desert contains numerous inland athalassohaline lagoons (**Figure 1A and B**), i.e., with salt proportions different from seawater [7, 8], which are an integral part of different evaporitic basins, salars, or salt crusts, located at different altitudes, just to name a few: Salar de Llamará ( $21^{\circ}18'S$ ,  $69^{\circ}37'W$ ) at 850 m; Salar de Atacama ( $23^{\circ}30'S$ ,  $68^{\circ}15'W$ ) over 2300 m, the largest in the Altiplano-Puna region of the Central Andes ( $\sim 3000\text{ km}^2$ ); Salar de Huasco ( $20^{\circ}18'S$ ,  $68^{\circ}50'W$ ), a protected National Park and Ramsar site at 4000 m; and Salar de Surire ( $18^{\circ}48'S$ ,  $69^{\circ}04'W$ ) at 4245 m. Only Andean countries like Perú, Bolivia, Argentina, and Chile share the geomorphological, climatic and hydrological conditions that originated these salars and hypersaline lagoons [7, 20–23].

The Chilean Patagonia belongs to the administrative region of Magallanes and Chilean Antarctica. This steppe-like landscape with cold, semi-humid climate and very windy condition are characteristic of this region where few lagoons exist. Although some are close to the coast such as Laguna Cisnes (**Figure 1D**), it is difficult to classify it as thalassohaline (marine origin) [8] due to mineral runoff from agriculture and other sources.





**Figure 1.**  
*Hypersaline lagoons from contrasting latitudinal environments in Chile, the southern edge of the world. Atacama Desert: (A) Piedra and Céjar lagoons. (B) Los Flamencos National Reserve, from north to south: Chaxa lagoon (0.37 km<sup>2</sup>), Canal Burro Muerto (0.1 km<sup>2</sup>), Barros Negros lagoon (1.03 km<sup>2</sup>), and Puilar (0.84 km<sup>2</sup>). Patagonia: (C) Amarga and (D) Cisnes lagoons.*



**Figure 2.** Cisnes (left) and Amarga lagoons in the Chilean Patagonia, the former was declared a national monument to protect waterbird diversity. Both are unique hypersaline ecosystems in an area where freshwater lakes of glacier origin abound. Bacterial diversity and the brine shrimp *Artemia persimilis* coexist, a subsample of wild bacteria diversity represented in the *Artemia*-gut microbiota.

These are (1) Laguna Amarga (Bitter lagoon, 50°29'S, 73°45'W) (**Figures 1C** and **2**), located in the province of Última Esperanza at 80 m above sea level, close to the eastern border of the Torres del Paine National Park; (2) Cisnes lagoon (53°15'S, 70°22'W) (**Figures 1D** and **2**), close to the city of Porvenir in the northeast of Tierra del Fuego (fireland) and the Magellan Strait; and (3) Laguna de la Sal (salt lagoon, 53°17'S, 70°23'W), a small and shallow lagoon located southern to Los Cisnes lagoon. The lagoon's salinity varies highly year-round and so its biological composition. Minor quantities of salt are extracted during the dry season (December) time at which salinity peaks to the maximum. At that time, the population of the most conspicuous planktonic inhabitant disappears (the brine shrimp *Artemia persimilis* in Patagonia). However, *Artemia* cysts abound, the mechanism that permits population continuity once suitable conditions recover [6, 24]. Although no systematic and long-term studies exist on these subantarctic lagoons, some literature allows getting a glimpse to their basic characteristics. Amarga lagoon is mesohaline [25], shallow (maximum depth: 4.1 m), and alkaline (pH 9.1), whereas the average annual temperature was 11.7°C when authors sampled the lagoon. About the same period, Saijo et al. [26] confirmed that water was strongly alkaline (pH 9.4), salinity was 77 g/L, and the significant ions were sodium and sulfate. Fuentes-González and Gajardo [27] sampled Cisnes lagoon in December, the dry period, when the UV index is the highest ( $6.84 \pm 0.63$ ) and temperatures range from  $15.18 \pm 1.31$  to  $6.25 \pm 0.85^\circ\text{C}$  according to the 14-year search they report. The salinity was 51 g/L, the water cold (9°C), and the lagoon was considered eutrophic, according to the high concentrations of phosphorous ( $0.30 \pm 0.73 \text{ mg L}^{-1}$ ), nitrate ( $0.66 \pm 0.14 \text{ mg L}^{-1}$ ), and chlorophyll-a ( $44.25 \pm 2.52 \mu\text{g L}^{-1}$ ). The microalga *Spirogyra* sp. and the crustacean *Artemia* were the predominating plankton. The salinity of both lagoons was recently reported in 2 consecutive years with values of 55 and 51 g/L in Cisnes lagoon and 86 and 81 g/L in Amarga lagoon, for spring 2017 (November) and autumn 2018 (April), respectively [28].

### 3. Microscopic and macroscopic biodiversity

Hypersaline lagoons contain the three domains of life, Archaea, Bacteria, and Eukarya [29], and this section provides a glimpse to the prokaryotic and eukaryotic diversity of lagoons located at the latitudinal extremes already described. As a representative eukaryotic, the brine shrimp *Artemia* is the obvious choice taking into account its key role in the food web of hypersaline lagoons [17] and because it is a model extremophile for studies of evolution and adaptation [10, 6]. Some adaptations explain *Artemia* abundance and the ability of females to perceive forthcoming



environmental conditions. Although both domains have coexisted and evolved under similar environmental pressures, the historical trend has been to consider them independently. However, later in this chapter, the *Artemia*-bacteria (microbiota) interaction is considered as an example of a symbiotic relationship.

### 3.1 Microbial communities

Studies on the microbiology of hypersaline lagoons in Chile are biased to lagoons in the Atacama Desert for various reasons. On the one hand, these lagoons provide a unique diversity of habitats to study microbial ecology and diversity as they spread in salt flats (Salars) at different altitudes, with varying salinities and ionic compositions [7, 23, 30]. On the other hand, and as previously said, the desert is a terrestrial Mars analog, and so a study case for researchers exploring the origin and limits of life on earth as a potential analog to life on Mars [21, 22]. Such diversity of microbial ecosystems (soil and brines) provides an opportunity to understand the physiological adaptations of microorganisms to extreme environmental conditions. A more practical argument has to do with the lithium richness of Salar de Atacama, the largest salt flat in the Atacama Desert, and so interest exists in evaluating the microbial diversity associated with this economically important mining process. The bacteria found in pools where brines are evaporated to concentrate lithium are expected to exhibit a range of unique molecular and metabolic capabilities to cope with high lithium concentration [31]. In a more general context, extremely salty lagoons both in Chile [32] and around the world are the source of metabolites and enzymes of biotechnological interest [12, 13]. Microbial mats are another bacterial ecosystem reported in Salar de Atacama, consisting of flat laminated communities with unicellular cyanobacteria (*Synechococcus* and *Cyanothece*), and filament forms (*Microcoleus*, *Oscillatoria*, *Gloeocapsa*, and *Gloeobacter*) [33].

The advent of culture-independent techniques such as the 16S rRNA gene sequencing has improved biodiversity studies in hypersaline lagoons, revealing hidden diversity not previously discovered by culturable-dependent techniques. This technique combined with the metagenomics [34] and other “omics” (transcriptomics, proteomics, metabolomics) has facilitated to get an integrated picture of the adaptive microbial response to extreme conditions and other aspects of microbial evolution such as antimicrobial resistance, pathogenesis, and the underlying genetic determinants of these capabilities [12].

Demergasso et al. [23] compared lagoons in Salars with strong altitude gradient (Llamará, Ascotán, and Atacama), qualitative differences in ionic compositions, and subject to different UV influence, finding predominance of phylum *Cytophaga-Flavobacterium-Bacteroides* (CFB) (now Bacteroidetes) and few Proteobacteria at high salinity and altitude (Salar de Ascotán), whereas diversity decreased in Salar de Atacama (in the pre-Andean Depression) and Llamará. Archaeal assemblages corresponded to uncultured haloarchaea distantly related to cultured strains obtained from thalassohaline environments. The study considered samples from 19 different environments of Céjas (or Céjar) (**Figure 1A**), Burro Muerto (**Figure 1B**), and Tebenquiche lagoons to conclude that athalassohaline environments are excellent sources of new microorganisms that are different from their counterparts in thalassohaline environments. A spatiotemporal study (three sites; summer and winter season) in Tebenquiche lagoon (**Figure 3**), the largest water body in Salar de Atacama [7], found abundance of genera belonging to phylum Bacteroidetes and Gammaproteobacteria, such as *Vibrio*, *Halomonas*, *Acinetobacter*, *Alteromonas*, *Psychrobacter*, and *Marinococcus*. The authors highlighted the remarkable novelty found as 16S rRNA gene sequences of Bacteroidetes. Another study on Bacteroidetes [35] evaluated brine and sediment samples from lagoons in Salar de Huasco, Salar



**Figure 3.**  
 Laguna Tebenquiche, the largest water body in Salar de Atacama harbors rich prokaryotic diversity varying spatiotemporally and coexisting with the brine shrimp *Artemia franciscana*.

de Ascotán, and also in Tebenquiche lagoon, finding high microbial diversity in Tebenquiche and Salar de Ascotán, whereas diversity decreased in Salar de Huasco. Most of the 16S rRNA gene sequences corresponded to the following genera (Flavobacteriaceae): *Psychroflexus*, *Gillisia*, *Maribacter*, *Muricauda*, *Flavobacterium*, and *Salegentibacter*. The most abundant phylotype was related to *Psychroflexus* spp. A study of hypersaline wetlands in salars of the Altiplano at a higher altitude than those previously mentioned [36, 37], including Salar de Huasco and Salar de Ascotán, also showed significant differences in their microbial community attributed to habitat type and physicochemical properties of the lagoons. Bacteroidetes and Proteobacteria predominated with a smaller contribution of Firmicutes, Actinobacteria, Planctomycetes, Verrucomicrobia, Chloroflexi, Cyanobacteria, Acidobacteria, *Deinococcus-Thermus*.

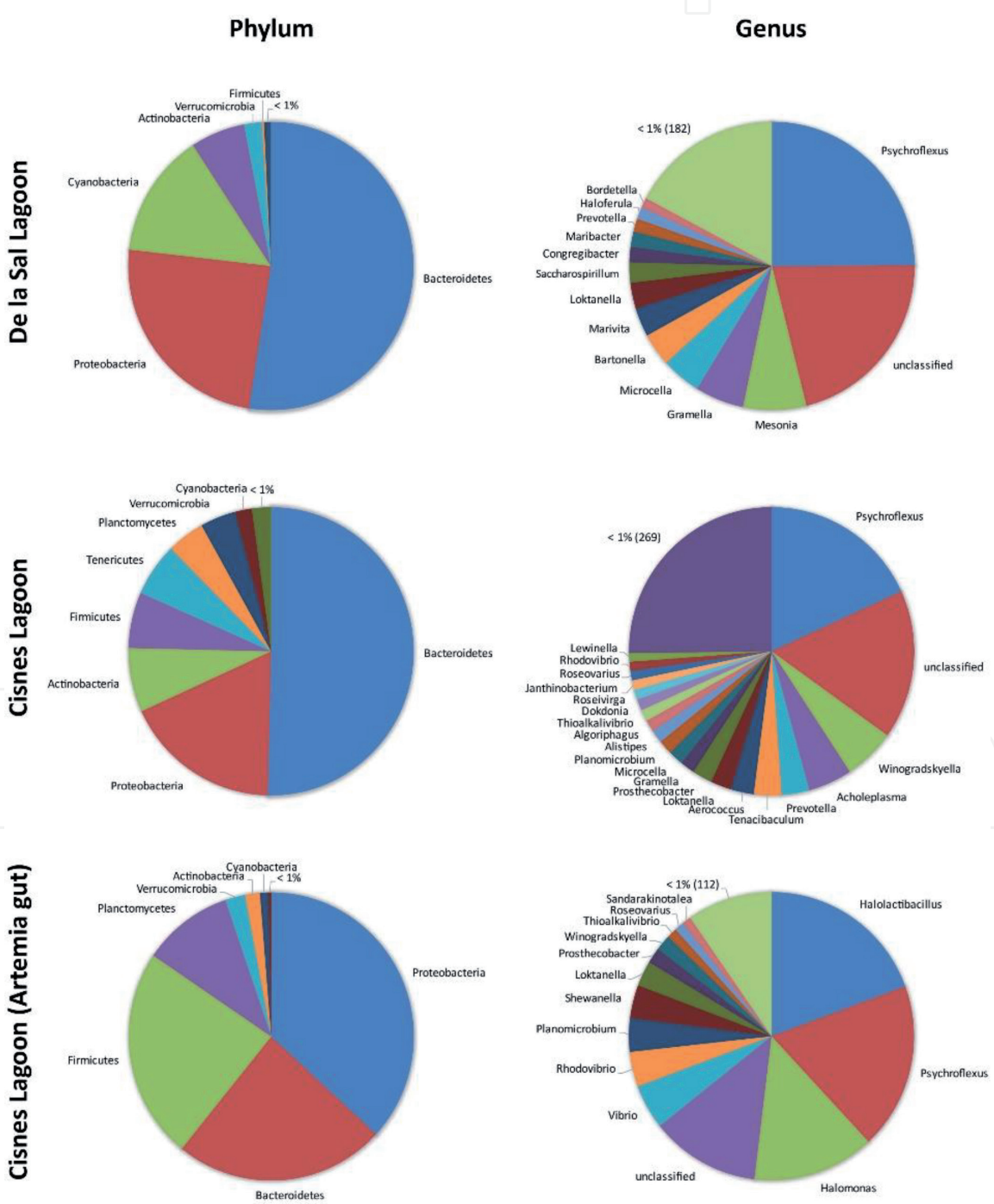
The study of Azua-Bustos et al. [21] took advantage of unusual rain events in the hyperarid core of the Atacama Desert, which created temporal lagoons for some time. The authors observed that surface bacteria died due to osmotic stress but were able to isolate a newly identified species of *Halomonas* metabolically active and reproducing in the lagoon. Another study took soil samples at 2 m of depth in the core of the Atacama Desert [22], where life was not expected to exist, analyzed the samples with a life detector chip containing 300 antibodies, and found bacteria, Archaea, DNA, and exopolysaccharides. They identified members of the alpha, beta, gamma, and epsilon—Proteobacteria, Actinobacteria, Firmicutes, Acidobacteria, *Deinococcus*, Bacteroidetes, and Euryarchaeota. Back to hypersaline lagoons, the study of Cubillos et al. [31] assessed microbial communities in evaporating pools where lithium-rich brines pumped from beneath the Salar surface are concentrated (55.6% salinity) by lithium-exploiting companies. They found the archaeal family Halobacteriaceae and genera *Halovenus*, *Natronomonas*, *Haloarcula*, and *Halobacterium*. Instead, abundant families in natural brines were Rhodothermaceae and Staphylococcaceae. As these concentrated brines represent one of the most saline environment described, the authors concluded that the microorganisms found should shed further light on the adaptive response to such extreme conditions.

### 3.2 Microbial communities of Patagonian lagoons

A study in our laboratory (Quiroz and Gajardo unpublished) (**Figure 4**) compared the microbial diversity of two Patagonian lagoons (Cisnes and de la Sal) with



the *Artemia*-gut microbiota composition. The phylum Bacteroidetes was the most common in brines of both lagoons in agreement with the study described earlier [30]. Proteobacteria and Cyanobacteria (de la Sal lagoon) were less represented. At the genus level, the diversity is high, *Psychroflexus* predominating, though a significant diversity remains unidentified. The microbiota of individuals collected in Cisnes lagoon contains a reduced amount of Bacteroidetes, whereas the proportion of Proteobacteria and Firmicutes is higher. The most frequent genera in the *Artemia* gut of Cisnes lagoon individuals are *Halolactobacillus*, *Psychroflexus*, *Halomonas*, and *Vibrio*, a pattern similar to that previously described [30]. The observation that some bacteria present in the gut of *Artemia* individuals are in low frequency in the environment, or not found, supports the idea that in some polyextremophile environments like Salar de Atacama, microbial habitats are serving as a refuge, i.e.,



**Figure 4.** Bacterial diversity in brines of Patagonian lagoons De la Sal and Cisnes and bacterial communities in the *Artemia* gut of individuals from Cisnes lagoon (bottom).

the so-called endolithic habitats [38]. From data in **Figure 4**, it is possible to think that the *Artemia*-gut microbiota could also serve as a refuge to bacteria uncommon in natural brines such as *Halomonas* and *Halolactobacillus*.

#### 4. The salt-lover brine shrimp *Artemia*: adapted to critical life conditions

The brine shrimp *Artemia* is a branchiopod crustacean well adapted to the harsh conditions of hypersaline environments impose on survival and reproduction and hence is considered a model extremophile or a salt-lover sensu Wharton [39]. It displays remarkable adaptations at different domains, one of the most striking being a highly efficient osmoregulatory system to withstand high salinities (up to 340 g/L) [6]. Also, *Artemia* females can perceive when the environment becomes suboptimal, an ability that makes *Artemia* an indicator of ecosystem quality. Under suboptimal conditions, i.e., when a shallow lagoon dries up, females switch to produce encysted offspring (oviparity), in other words, cysts or diapause embryos highly resistant to extreme conditions. Instead, offspring in the form of free-swimming nauplii (ovoviviparity) allows rapid population expansion under optimal environmental conditions. The cyst shell protects from UV irradiation, large temperature fluctuations, osmotic pressure, dryness, and other stresses, so cysts remain viable practically dehydrated [40–42]. Such evolutionary solution for populations to escape extinction when conditions become unfavorable suggests that cysts contain a memory of the past [6] that can be retrieved when cyst resurrect (sensu [43]) either naturally or experimentally, i.e., resume metabolic activity and hatch once the environment returns to normal. Since cysts deposited in saline lagoons at different times accumulate at shores and all have the chance to hatch at the same time when the environment allows it, females face a critical mating decision of choosing the right male to maximize their reproductive output. They can mate either contemporary males (hatched from cysts of the same age), males from the past (hatched from older cysts), or males from the future (hatched from more recent cysts). Females tend to select contemporary males, which would be a demonstration of male-female coevolution [44]. The sophisticated mate choice behavior of *A. franciscana* would be a consequence of such coevolution [45]. The question of how females perceive in advance when conditions will become unfavorable remains unclear, but it would be reasonable to advance the hypothesis that bacterial communication (quorum sensing) to maintain their functional diversity in extreme ecosystems could be involved. This is possible as bacteria interact with all kind of life forms in a given ecosystem, and such interaction may affect the adaptation of other species. For example, the microalgae *Dunaliella salina*, commonly found in saline environments, responds to quorum sensing [46].

In Chile, two out of the six regionally endemic and highly divergent sexual species co-occur, *A. franciscana* Kellogg, 1906 and *A. persimilis* Piccinelli and Prosdoci, 1968 [6, 24]. The latter was previously thought endemic to Argentina, though it is now clear that inhabits Chilean Patagonia lagoons [47, 48]. Both species are segregated by a latitudinal barrier coincidently with their differential ability to colonize and cope with different environments, which is the case of *A. franciscana*, the most widely distributed of all, and considered a younger species in evolutionary expansion [24]. The species inhabits lagoons of the Atacama Desert in northern Chile, which is the southern limit of a broad north-south distribution in the Americas (North, Central, South). Instead, *A. persimilis* is restricted to Patagonia, with a probable hybrid zone between both species in solar saltworks of central Chile [49, 50]. Other sexual species are restricted to the Mediterranean area (*A. salina*), Lake Urmia and some lakes in Ukraine (*A. urmiana*), China (*A. sinica*), and Tibetan Plateau

(*A. tibetiana*). The situation in Asia seems now to be a bit complex as a mix of sexual and asexual *Artemia* species, including the invasive *Artemia franciscana* coexist as shown with mitochondrial (COI) and nuclear DNA markers (ITS) [51]. The species has also invaded and even displaced local species in Europe [52]. Such evolutionary plasticity depends on the species overall high genetic variability, which is heterogeneously distributed over the populations [49, 53]. As Gajardo and Beardmore put it [6], the species gene pool is distributed over different safety baskets.

With the advent of massive sequencing and transcriptomics, new information has been reported on the genetics of sex differentiation [54–56] and stress or adaptation-related genes [41]. A transcriptomic study in *A. franciscana* identified genes responding to salt stress by experimentally comparing *Artemia* individuals reared under hypersaline and marine conditions [57]. Authors found ~100 genes differentially expressed under hypersaline conditions controlling critical biological functions such as signal transduction, gene regulation, lipid metabolism, transport, and stress response (Heat shock 70 kDa), all contributing to maintaining homeostasis-repairing mechanisms in *Artemia*.

#### 4.1 The *Artemia*-bacteria relationship

The brine shrimp *Artemia* and bacteria coexist and interact in hypersaline lagoons, as demonstrated by Quiroz et al. [30]. One evident expression of this interaction is that *Artemia* gets energy grazing on bacteria [58–60], which also provide enzymes to digest the algae and yeasts that are also *Artemia* food items. Additionally, environmental bacteria colonize and establish in the *Artemia* gut conforming the microbiota, which is known to provide multiple functional benefits to the host such as protection against pathogens, energy balance, immunological enhancement, and behavior [61]. Thus, imbalances (i.e., reduced diversity) in the microbiota composition due to environmental or other factors such as pathogens seriously affect the performance of the host in a given environment. The *Artemia*-microbiota is an example of facultative symbiosis in which mutual benefits are provided [62]. The most evident benefit for *Artemia* is fitness, which can be constrained or expanded depending on salinity in such a way that under optimum salinity, fitness should be maximized. Therefore, the *Artemia*-gut microbiota interaction influences *Artemia* abundance, which is a good predictor of waterbird presence in hypersaline wetlands. This would explain why not all hypersaline lagoons attract the same amount of waterbirds. The importance of *Artemia* in this regard was experimentally demonstrated [17] with the introduction of *A. sinica* in a Tibetan hypersaline lake where the species did not exist. Such introduction created the conditions to attract waterbirds not previously present in the lake. Another case was the introduction of *A. franciscana* in Godolphin lakes, an artificial hypersaline wetland created to attract flamingos and charadriiform birds in Dubai [63]. The flamingo species *Phoenicopterus roseus* is a regular visitor in that habitat, as well as other bird groups such as sandpipers, plovers, avocets, grebes, ducks, and gulls, and their presence is correlated with *Artemia* blooms.

The study of Quiroz et al. [30] assessed the microbial diversity of natural brines and those present in the gut microbiota of adult individuals collected in the same environment in lagoons of the Atacama Desert, solar saltworks in Central Chile, and Patagonian lagoons. The microbiota of animals collected in natural brines contains a subsample of environmental diversity, and the authors evaluated some reported functions of the bacterial communities of the gut microbiota to test the hypothesis that they should contribute to *Artemia* fitness. For example, the genus *Sphingomonas* (Alphaproteobacteria), found in the gut of wild *Artemia* individuals, contains a species (*S. wittichii*) reported to degrade polycyclic aromatic



hydrocarbons (PAHs) that are persistent pollutants accumulated in the food chain [64]. The genus *Chromohalobacter* (Gammaproteobacteria), also identified in the gut of wild individuals collected both in northern and southern lagoons, contains the species *C. salexigens* that produce ectoine (or hydroxyectoine), a compound protecting proteins from degradation, and other environmental stressors such as salinity changes, oxidative stress, and high UV radiation [65]. Ectoine and other compatible solutes also act as osmoprotectants facilitating bacteria establishment in the saline environment. The authors were surprised to find psychrophilic bacteria known to produce antifreeze proteins in C  jar (north) and Amarga lagoons (south). Moreover, some bacteria found in the Atacama Desert are phylogenetically closer to some types found in the Antarctic, similarity that tells about convergent environmental conditions or a similar adaptive pattern despite the latitude difference. Such similarity includes the Great Salt Lake in Utah, where bacterial sequences most closely related to genera *Halomonas*, *Psychroflexus*, and *Alkalilimnicola* were found in the water [66].

## 5. The need to monitoring hypersaline lagoons dynamics to predict waterbird presence

The food web of these lagoons is simple and sensitive to environmental conditions such as salinity changes caused by water or brine diversion. The main ecosystem components are bacteria, microalgae, and different zooplankters (Ostracoda, Copepoda, Branchiopoda); among the latter the brine shrimp *Artemia* plays a key ecological role in the ecosystem grazing on bacteria and phytoplankton (such as the halotolerant unicellular green algae *Dunaliella*) and hence modulate their biomass. Studies in the Mediterranean [67], Crimean lakes in Ukraine [17], and Dubai [63] have evidenced the *Artemia* role to predicting waterbirds presence. Besides, *Artemia* is an intermediate host for avian helminth parasites, particularly cestodes and nematodes [68–70], also providing useful information on waterbird abundance and diversity in hypersaline ecosystems. In turn, *Artemia* abundance is controlled by copepods and amphipods species that are common at lower salinities but can also tolerate high salinities, particularly copepods [71, 72].

Waterbirds inhabiting hypersaline wetlands, particularly flamingos, disperse *Artemia* by carrying cysts in their feathers or in the digestive tube which are released to the environments with their feces [52, 53]. This service provided by flamingos would favor the colonization of new suitable habitats and would explain *Artemia* distribution to some extent [73]. The knowledge on the halophilic biodiversity of hypersaline lagoons is, therefore, a first step toward understanding why local and long migratory waterbirds use them as a source of energy and as breeding sites. Lagoons in Salar de Atacama are essential habitats for flamingos and shorebirds [74–76], some of them with conservation problems according to the IUCN Red List of Endangered Species. The Chilean flamingo and the Puna flamingo are both near threatened; meanwhile, the Andean flamingo is recognized as a vulnerable species. Lagoons from Salar de Atacama (particularly Puillar) represent the most important breeding site in the world for the Andean flamingo (Figure 5). In addition, these lagoons are important for migrating interhemispheric species such as Baird's sandpiper *Calidris bairdii* and Wilson's phalarope *Steganopus tricolor*, among others, despite there is no quantitative data for these species in the area. Charadriiformes and Anseriformes such as the Andean gull *Larus serranus*, and the Andean Goose *Chloephaga melanoptera* (Anatidae) are also present in the Salar.

Patagonian saline lagoons also hold a great diversity of waterbirds, including flamingos, swans, grebes, and shorebirds [77]. Among the most abundant birds in



**Figure 5.**

Saline lagoons in northern Chile (Salar de Atacama) provide waterbird habitat, a relevant noneconomic service. (A) Flamingos. (B) Nests. (C) Nestlings. (D) Salar de Atacama is the epicenter of the world's largest lithium exploitation from brine pumped from beneath the Salar. The challenge ahead is how will both services coexist in a scenario of soaring lithium demand, and hence brine diversion, to support electromobility.

Amarga lagoon are the Black-necked swan *Cygnus melancoryphus*, Coscoroba swan *Coscoroba coscoroba*, upland goose *Chloephaga picta*, white-tufted grebe *Rollandia rolland*, and silvery grebe *Podiceps occipitalis* and several species of dabbling ducks. Cisnes lagoon is used mainly as feeding places by sandpipers and plovers (Charadriiformes) such as the White-rumped sandpiper *Calidris fuscicollis*, the Baird's sandpiper, Two-banded plover *Charadrius falklandicus*, Rufous-chested plover *Charadrius modestus*, and the Magellanic plover *Pluvianellus socialis*, a species near threatened at a global scale. Both lagoons include representatives of Anseriformes, such as the shelducks (Tadorninae) *Chloephaga rubidiceps* and *C. picta* and dabbling ducks (Anatinae) such as *Specularia specularis* (near threatened), *Anas georgica*, *Lophonetta specularioides*, *Tachyeres patachonicus*, and *Mareca sibilatrix* [78]. Among Phoenicopteridae, the Chilean flamingo is abundant in Patagonian saline lagoons, being one of the main *Artemia* predators, and such abundance is likely to explain the abundance of flamingo parasites recorded in the *Artemia* population from Los Cisnes lagoon [28].

## 6. Current threats and future perspective

A serious problem to conserve the biodiversity of hypersaline lagoons in Salar de Atacama or Patagonia is to make it visible to policymakers, miners, ecotourists, birdwatchers, and even to people from the local communities controlling the access to lagoons, as it is the case in the north. However, a practical way of raising awareness on the relevance of these lagoons is aquatic birds' conservation [73]. That is why we have emphasized the relationship between hypersaline

lagoons dynamic, *Artemia*, and waterbird abundance. Indeed, particularly charismatic species like flamingos inhabit hypersaline wetlands in the Altiplano (**Figure 5**), some of which are considered endangered [74–76]. Three South American flamingo species occur associated with these wetlands: Puna flamingo (*Phoenicoparrus jamesi*), Andean flamingo (*Phoenicoparrus andinus*), and Chilean flamingo (*Phoenicopterus chilensis*), the latter species is also abundant in hypersaline lagoons from the Chilean Patagonia [77].

As mentioned in the previous sections, hypersaline lakes and lagoons produce commercial services like salt extraction and brine shrimp cysts, as in the Great Salt Lake in Utah, the major cyst producer for aquaculture in the world. The lake is an example of good management to combine economic and noneconomic services like waterbird habitat [18]. However, mining is the cause of water and brine diversion and, together with climate oscillations, is the main driver accounting for the actual shrinking of hypersaline ecosystems around the world [19]. Lagoons of the Atacama Desert are indeed highly sensitive to the water budget in such a way that little changes can result in significant and amplified response in the physicochemical, ionic, and biological properties of the lagoons [8]. These lagoons are an integral part of the world largest lithium exploitation from brine (**Figure 5D**) [18, 37] pumped from beneath the surface of Salar de Atacama, the largest salt flat in Chile. The water and brine diversion associated with lithium exploitation represent a significant volume per day and is expected to increase as lithium demand has soared to support the growing fleet of electric cars. Because of this, we have alerted on the need to protect these highly fragile ecosystems [18]. In this chapter, the role as a bioindicator of the ecosystem health of the brine shrimp *Artemia* has been highlighted, as this crustacean is also a predictor of waterbirds abundance. *Artemia* abundance or fitness depends on the combined effect of the environment (salinity or brine quality) [8], the microbial diversity in the *Artemia* gut and in brines [30], and controllers like copepods [71, 72], depending on the salinity, parasites [68–70], and waterbird grazing pressure. This is a delicate cascade of events that need to be monitored regularly to be understood in order to advance science-based management decisions.

## 7. Conclusions

1. Hypersaline lagoons from north and south of Chile hold unique prokaryotic and eukaryotic biodiversity adapted to cope with extreme conditions. Microbiological studies are, however, biased to lagoons in the Salar de Atacama for various reasons. They provide a diversity of habitats, ideal for studies of microbial ecology. The fact that the Atacama Desert is considered a terrestrial analog of Mars makes it a target area for astrobiologists.
2. Chilean hypersaline lagoons are a natural heritage as they contain a unique halophile biodiversity and provide waterbird habitat, a relevant noneconomic service, to local aquatic birds and some endangered long-distance, migratory species like flamingos and so are a matter of global concern and a flagship to raise awareness on the need to protect these ecosystems. Several Ramsar sites exist in the north, and Laguna Cisnes in Patagonia has been declared a natural monument to protect waterbirds.
3. Hypersaline lagoons have relatively simple food web and so are kind of natural laboratories to understand how the ecosystem functions to attract waterbirds.



This knowledge is useful for policymakers to take science-based management decisions in relation to these ecosystems.

4. The brine shrimp *Artemia*, a keystone taxon of hypersaline lagoons, is a model extremophile to study adaptation to critical life conditions, and some of these adaptations explain why the animal is an indicator of environmental quality and a predictor of waterbirds abundance. Thus, all the factors affecting *Artemia* fitness (gut microbiota, copepods, parasites, birds grazing pressure, and environmental quality) should be monitored. *Artemia* abundance depends on a delicate cascade of events that require careful long-term spatiotemporal monitoring.
5. Two regionally endemic *Artemia* species occur in Chilean hypersaline lagoons separated by a latitudinal barrier, *A. franciscana* in Atacama Desert and *A. persimilis* in Patagonia. The former is widely distributed in the Americas (North, Central, South) and considered a species in expansion, whereas *A. persimilis* is restricted to southern latitudes in Chile and Argentina. Given the importance of *Artemia* as an indicator of environmental quality and a predictor of waterbirds abundance, these species need further studies.
6. Climatic oscillations in the hyperarid Atacama Desert along with water and brine diversion due to the large lithium exploitation based in Salar de Atacama are severe threats to hypersaline lagoons stability and hence to waterbird presence. Moreover, in a scenario of increased lithium demand to support electromobility how will Chile combine lithium exploitation with agreements on biodiversity and wetlands conservation?
7. The Patagonian lagoons are yet less intervened but very sensitive to climatic conditions. They represent a special case of hypersaline lagoons where freshwater lakes of glacier origin abound.

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