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Diversity of planktonic and benthic communities in the high-altitude Salar de Pedernales basin, Atacama Desert, Chile

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ABSTRACT

Diversity of planktonic and benthic communities in the high-altitude Salar de Pedernales basin, Atacama Desert, Chile.

Salar de Pedernales basin is located at 3370 meters above sea level in the Atacama Desert, Chile, covering an area of 3620 km^2. This ecosystem is characterized by high exposure to ultraviolet radiation, low humidity, huge variations in ion content and extreme thermal gradients. Despite these extreme conditions, it has a rich fauna and flora. However, the aquatic biodiversity in the basin remains poorly documented. Our study assessed compositional changes of planktonic and benthic communities across several salt flats (Pedernales S-O, Piedra Parada, La Laguna), natural water courses (wetland and creeks), an artificial stream and lagoon (Pedernales N-E), and their relationship with local physicochemical parameters. Our results show that the Salar de Pedernales basin is a highly heterogeneous ecosystem principally influenced by conductivity, pH, and major ions. Community diversity was high at all locations except for the artificial stream. Microalgae were spatially similar with major changes observed in the disturbed habitats. The composition of the invertebrate communities strongly varied among habitats but displayed distinct composition in the perturbed ones (Salar Pedernales N-E). Distance-based redundancy analysis revealed that phytoplankton and benthos composition were driven by changes in trace metals and nitrate, whereas zooplankton community composition was mainly related to osmotic stress. Our data highlight the remarkable biodiversity of the natural water bodies of the Salar de Pedernales basin and the potential effects of anthropogenic perturbations on the biota in these extreme habitats.

KEY WORDS: hypersaline ponds, microalgae, invertebrates, extreme environment.

RESUMEN

Diversidad de comunidades planctónicas y bentónicas en la cuenca de gran altitud del Salar de Pedernales, Desierto de Atacama, Chile.

La cuenca del Salar de Pedernales está situada a 3370 metros sobre el nivel del mar en el desierto de Atacama (Chile) y ocupa una superficie de 3620 km^2. Este ecosistema se caracteriza por una alta exposición a la radiación ultravioleta, baja humedad, enormes variaciones en el contenido de iones y gradientes térmicos extremos. A pesar de estas condiciones extremas, posee una rica fauna y flora. Sin embargo, la biodiversidad acuática de la cuenca está poco documentada. Nuestro estudio evaluó los cambios composicionales de las comunidades planctónicas y bentónicas en varios salares (Pedernales S-O, Piedra Parada, La Laguna), cursos de agua naturales (humedales y arroyos), un canal artificial y una laguna (Pedernales N-E), y su relación con los parámetros fisicoquímicos locales. Nuestros resultados muestran que la cuenca del Salar de Pedernales es un ecosistema altamente heterogéneo influenciado principalmente por la conductividad, el pH y los iones principales. La diversidad de la comunidad fue alta en todas las localidades excepto en el canal artificial. Las microalgas fueron espacialmente similares, observándose cambios importantes en los hábitats alterados. La composición de las comunidades de invertebrados varió fuertemente entre hábitats, pero mostró una composición distinta en las perturbadas (Salar de Pedernales N-E). El análisis de redundancia basado en la distancia reveló que la composición del fitoplancton y bentos estaban impulsados por cambios en los metales traza y el nitrato, mientras que la composición de las comunidades de zooplancton estuvo relacionada principalmente con el estrés osmótico. Nuestros datos ponen de relieve la notable biodiversidad de las masas de agua naturales de la cuenca del Salar de Pedernales y señalan los posibles efectos de la perturbación antropogénica sobre la biota de estos hábitats extremos.

PALABRAS CLAVE: *posas hipersalinas, microalgas, invertebrados, hábitats extremos.*

INTRODUCTION

Hypersaline biotopes, ranging from subtropical high-altitude lagoons in the Atacama Desert to sub-Antarctic lagoons in Patagonia, encompass diverse environments, including permanent inland and coastal lagoons or temporary salterns (Cabello, 2021; McGenity & Oren, 2012). High-altitude wetlands known as "salars" are distinct ecosystems composed of very diverse aquatic habitats, such as wetlands (Squeo et al., 2006), creeks (Uribe et al., 2015), ponds, and salt flats (Alvarez, 1984). These habitats are exposed to extreme environmental conditions, including intense ultraviolet radiation, minimal precipitation, high evaporation rates, high salinity, and significant daily temperature variations (Cabello, 2021; Ericksen & Salas, 1990; Payano-Almánzar et al., 2020). Despite these severe conditions they support a unique diversity of microorganisms, plants, and invertebrates, many of which exhibit specialized adaptations (Saccò et al., 2021).

The Salar de Pedernales basin is characterized by its low precipitation levels (120 to 140 mm / year) (Risacher et al., 2003) and an evaporation rate of 1075 mm/year (de la Fuente et al., 2021). It is notable for the accumulation of various minerals and metals (Cabello, 2021), making it a zone of significant economic importance. The system has a history of anthropogenic disturbance; for instance, a pipe was deployed in the northwestern of the Salar in the 1930s to obtain water for industrial purposes (Risacher et al., 1999), thereby lowering the level of the phreatic zone in the basin.

Salar de Pedernales exhibits strong spatiotemporal variability in vegetation and water coverage (de la Fuente et al., 2021) leading to local variations in soil moisture and salinity that likely promote habitat heterogeneity. The high environmental variability of these ecosystems supports diverse communities of organisms, including prokaryotes, microalgae, invertebrates, and vertebrates such as migratory birds (Gajardo & Redón, 2019). Despite their ecological distinctness and economic importance, the biodiversity of aquatic organisms in the Salar de Pedernales basin has been scarcely studied (Codelco Chile División Salvador, 2024).

High Andean systems face increasing threats, such as water extraction for productive economic purposes (Acosta, 2018; Kesler et al., 2012;

Liu et al., 2019). These activities pose a risk to biodiversity, particularly considering Salar de Pedernales is one of the largest basins in the southern Atacama Desert (de la Fuente et al., 2021), representing an ecological hotspot that has been scarcely studied. The objective of this study was to describe spatial variations in physicochemical properties and their associated biodiversity. We assessed changes in the composition of microalgae and invertebrate communities across natural and anthropogenically impacted habitats. Additionally, we examined for the first time, the relationship between these communities and local physicochemical parameters in the Salar de Pedernales basin.

METHODOLOGY

We studied the microalgae and invertebrate communities and physicochemical parameters in the Salar de Pedernales basin, located in northern Chile (26.23° S, 69.12° W), between April and May 2023. We defined the Salar de Pedernales basin as a system comprising Salar Pedernales, Salar La Laguna, Salar Piedra Parada, and adjacent habitats. This endorheic basin covers 3620 km² and its located at approximately 3370 m altitude in the Atacama Desert (Risacher et al., 1999). The basin exhibits heterogeneous morphological, climatological, and geological characteristics, with sedimentary, volcanic, and plutonic rocks (Chong, 1988; Johnson et al., 2010). To cover the natural heterogeneity across the basin, several habitats were sampled (Fig. 1): Salar Piedra Parada (n=3), Salar La Laguna (n=1), Creeks (n=6), wetlands (n=3), Salar Pedernales SO (n=5). We also included two cases of anthropogenically disturbed habitats, as they are the result of direct modification of the basin: the artificial lagoon (excavated) Salar Pedernales NE (n=5), and a long-term artificial stream (n=5), cement constructed for water channeling (Alvarez, 1984), with an estimated flow of 51 L/s (Risacher et al., 1999).

At each sampling station, the environmental conditions were assessed by deploying a 50 m transect with subsamples at intervals of 0, 25, and 50 m. Temperature and conductivity (TetraCon 325 sensor) were measured at each sampling site using a portable WTW Multi 3320 multimeter. Dissolved oxygen (% saturation) was quantified with a Hanna HI 98193. For pH quantification, a Hanna HI 98129 pH meter was used. Samples for the determination of metals (Cu, Fe, Li, V), met-

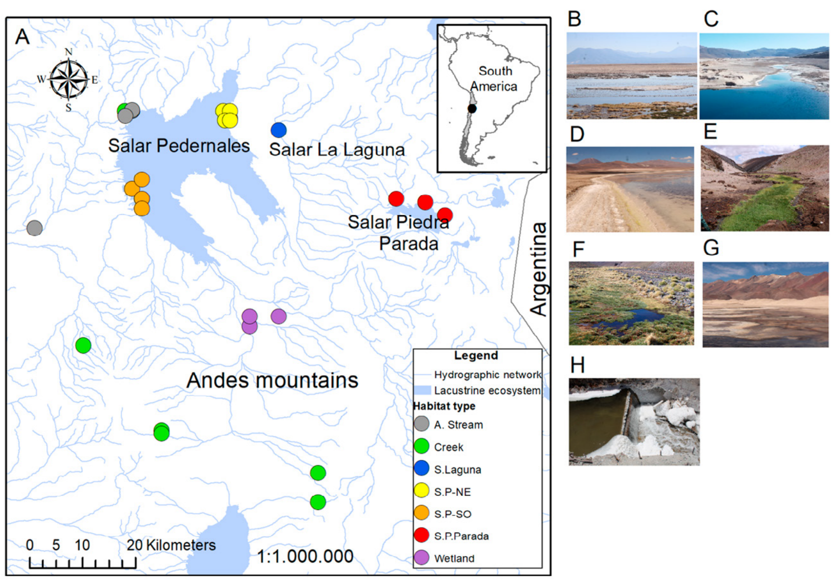

Figure 1. A) Zone of study. Salar Pedernales Basin and habitat types (B-H). B) Salar Pedernales SO, C) Salar Pedernales NE, D) Salar La Laguna, E) Creek, F) Wetland, G) Salar Piedra Parada, and H) Artificial stream. *A) Zona de estudio. Cuenca del Salar de Pedernales y tipos de habitats (B-H). B) Salar Pedernales SO, C) Salar Pedernales NE, D) Salar La Laguna, E) Arroyo, F) Humedal, G) Salar Piedra Parada, y H) Canal artificial.*

alloids (As, Bo), ions (Cl^-, Mg^{2+}, Ca^{2+}, Na^+, SO_4^{2-}, and K^+), total dissolved solids (TDS) and nitrate (NO_3-) were maintained at dark conditions at 4°C until analysis at the certified HIDROLAB LTDA laboratory, following the Chilean guidelines for water quality (NCh 411/3 Of .96).

Microalgae identification

For the identification of planktonic microalgae, triplicate 1 L water samples were collected from the water column using a 60-µm net at each sampling site. For the collection of benthic microalgae, samples were taken in triplicate using a 10 cm² scraping area at sites with rocky substrates. The samples were immediately fixed with Lugol for later taxonomic identification and abundance estimation. Morphological identification was performed using the Utermöhl methodology (Utermöhl, 1958) on an Olympus CKX42 inverted phase contrast microscope. For each sample, individuals were counted until the most abundant species reached 100 individuals or 300 fields. We followed the taxonomic identification guidelines from Biggs & Kilroy, 2000; Cox, 1996; Parra & Bicudo, 1996; Rivera et al., 1982; Round et al., 1990; Sant'Anna, 2006. Microalgae compositional data are presented as relative abundance.

Invertebrate identification

Zooplankton samples were obtained in triplicate at each sampling site. Sampling was conducted by filtering 20 L of water through a sieve of 58 µm mesh size. To collect zooplankton in running waters with a depth of less than 20 cm, a cone attached to a 58 µm mesh was deployed current-oriented for 15 min. Zoobenthos was sampled using a core of 10 cm internal diameter to obtain surface sediments. Collected sediments were sieved (500 µm mesh size) and fixed with 70% ethanol. Zooplankton density was expressed as the number of individuals per cubic meter (ind/m^3), while zoobenthos density was expressed as individuals per square meter (ind/m^2). Taxonomic identification was conducted using Araya & Zúñiga, 1985; Bayly, 1992; Dominguez et al., 1992, 2009; Fernandez & Dominguez, 2001; Lopretto & Tell, 1995; Lugo-Ortiz & McCafferty, 1996; Palma, 2013. For downstream analysis, all compositional data are presented as relative abundance.

Statistical analysis

All the statistical analyses were performed with R (v4.2.3), using the libraries vegan (Oksanen et al., 2022), dplyr (Wickham et al., 2022), and microbiome (Lahti & Shetty, 2017). A t-test was performed to evaluate overall differences in alpha diversity indices (Pielou evenness and richness) between the microalgae and invertebrates. To evaluate differences in alpha diversity between communities dependent on sampling habitat, a two-way ANOVA was performed when assumptions of normality and homoscedasticity were fulfilled. Normality and homoscedasticity were tested by applying the Kolmogorov–Smirnov and Levene tests, respectively. For the post hoc evaluation of differences between treatments a Tukey test was applied.

Principal component analysis (PCA) on environment variables was performed using the function "princomp" in the vegan package (Oksanen et al., 2022). We calculated the Bray-Curtis distance matrix of the square root-transformed relative abundances. A PERMANOVA was performed to evaluate the compositional differences between the station types. Distance-based redundancy analyses (dbRDA) (Legendre & Anderson, 1999) were performed on the dissimilarity matrix of diatom abundances to elucidate the relationship between environmental variables that influence community composition. The pH, temperature, conductivity, alkalinity, oxygen saturation, metals, and minerals were used in this analysis. The selection of the most important variables explaining community composition was conducted by a forward selection method on the dbRDA results (Blanchet et al., 2008).

RESULTS

Salar de Pedernales basin environmental variability

The habitats of the basin featured distinct conditions, as shown by PCA (Fig. 2A). The first prin-

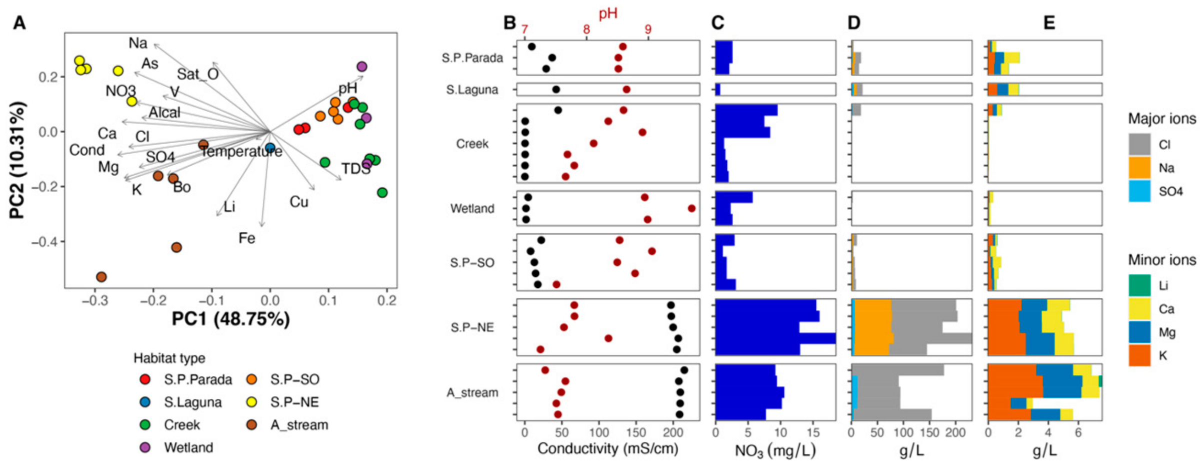

Figure 2. Environmental variables of Salar Pedernales Basin and main contributors to brine variability. A) Principal components analysis (PCA) with the habitat type, B) Conductivity and pH, C) NO_3- concentration, D) major (Cl^-, Na^+ and SO_4^{2-}) and E) minor ions (Li^+, Ca^+, Mg^{2+} and K^+). *Variables ambientales de la cuenca del Salar de Pedernales y principales contribuyentes a la variabilidad de la salmuera. A) Análisis de componentes principales (PCA) con el tipo de hábitat, B) Conductividad y pH, C) Concentración de NO_3-, D) Iones mayores (Cl^-, Na^+ y SO_4^{2-}) y E) menores (Li^+, Ca^+, Mg^{2+} y K^+).*

cipal component (PC1) represented 48.75% of the variability, principally influenced by changes in conductivity, pH, and cations, such as Mg^{2+}, Ca^+, K^+, and SO_4^{2-}. The second principal component (PC2) explained 10.31% comprising variations in Na, As, Fe, V, and Li changes. Stations were distributed mainly along PC1, depending on their disturbance status (Fig. 2A). Undisturbed habitats were characterized by a high and variable pH and lower conductivity than the disturbed ones (Fig. 2B). Disturbed habitats (Salar Pedernales-NE and the artificial stream) had extreme values: the highest conductivity (~200 mS/cm), NO_3- (~10 mg/L), and 100-fold ion concentrations compared to the rest of the habitat types (Fig. 2B-E).

Diversity at Salar de Pedernales Basin

No organisms were found at all in the artificial stream (Fig. 3). Both, the planktonic and benthic microalgae community richness was significantly different among habitats (Two-way ANOVA, $p<0.05$). Phytoplankton richness ranged from 6 to 44 taxa (Fig. 3A), Salar Pedernales-SO being more diverse than the creek and Salar Pedernales-NE habitats (Tukey-test $p<0.05$). Phytobenthos richness varied from 6 to 30 taxa, with Salar Pedernales-SO featuring higher richness than the Salar Piedra Parada (Tukey-test $p<0.05$). The microalgae were characterized by exhibiting highly even communities in all habitats (Pielou's evenness > 0.8; Fig. 3C).

The richness of invertebrate communities was significantly lower than microalgae (t-test, $p<0.001$). Zooplankton and zoobenthos communities displayed similar richness (Two-way ANOVA, $p>0.05$; Fig. 3B), but were variable in terms of community evenness (Two-way ANOVA, $p<0.05$; Fig. 3D). Evenness in Salar Pedernales-NE was significantly different in zoobenthos from Salar Pedernales-SO and the creek communities (Tukey-test, $p<0.05$), and so were the creek, Salar La Laguna and the wetland communities (Tukey-test, $p<0.05$).

The microalgae communities of the Salar de Pedernales Basin were compositionally similar with little differences between habitat types (Fig. 4A). A species cluster was observed in the stations located in Salar Pedernales-NE that differed in composition from the other habitats (Fig. 4B). The microalgae community was largely dominated by diatoms, with *Nitzschia* and *Navicula* genera being the most abundant in Salar Piedra Parada, creeks, and wetlands habitats. *Amphora* spp.,

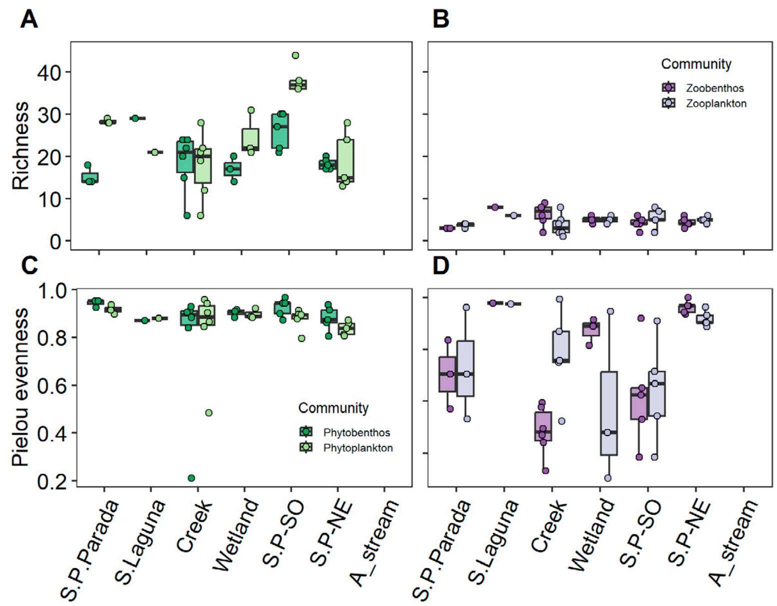

Figure 3. Richness (A, B) and Pielou evenness (C, D) of microalgae and invertebrate communities of Salar Pedernales Basin. *Riqueza (A, B) y equitatividad de Pielou (C, D) de las comunidades de microalgas e invertebrados de la cuenca del Salar de Pedernales.*

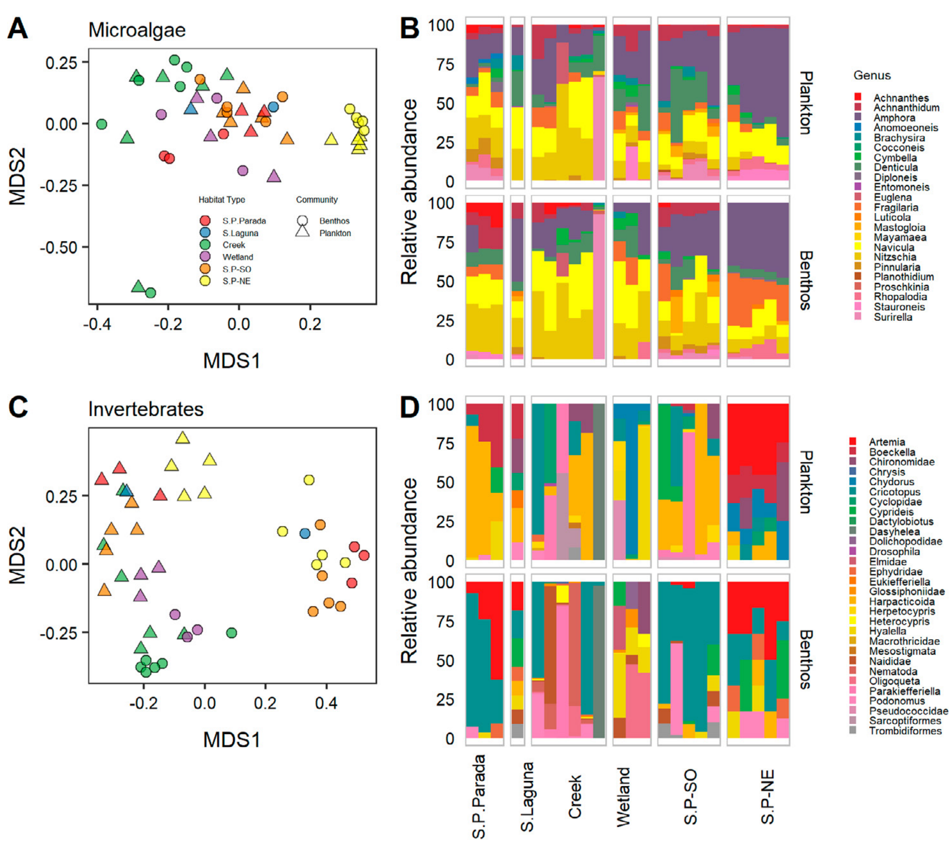

Figure 4. Beta diversity of microalgae (A), invertebrates (C) of Salar de Pedernales Basin. Relative abundances of microalgae (B) and invertebrates (D). *Beta diversidad de microalgas (A), invertebrados (C) de la cuenca del Salar de Pedernales. Abundancia relativa de microalgas (B) e invertebrados (D)..*

while widespread, was only abundant in the Salar Pedernales-SO and -NE, whereas *Fragilaria* spp. strongly proliferated in Salar Pedernales-NE (Fig. 4B).

The invertebrate community exhibited higher variability than the microalgae (Fig. 4A, 4C). The planktonic and benthic communities in lentic habitats had great taxonomic variability. They differed from each other, except for the creek and wetland stations, where both, zooplankton and zoobenthos were highly similar (Fig. 4C). Benthic communities tended to cluster together, possibly related to the presence of the Branchiopoda crustacea *Artemia* and the Chironomidae diptera *Cricotopus*, with *Artemia* standing out in the Salar Pedernales-NE (Fig. 4D).

Major variables influencing communities in the Salar de Pedernales Basin

dbRDA analysis illustrated how the different environmental variables were structuring local communities according to trophic level and life history (Table 1). The phytoplankton communities were related to temperature, NO_3-, As, Fe, and Li^+ (Table 1, Forward selection, $p<0.05$), whereas the phytobenthos was mainly affected by K^+, Fe was one of the most important variables for structuring the invertebrate communities, followed by Na, temperature and Li (Table 1, Forward selection, $p<0.05$).

DISCUSSION

This study shows that Salar de Pedernales basin presents a high biodiversity of microalgae and invertebrates. Moreover, anthropogenic impacts on habitats lead to remarkable differences in local diversity at different trophic levels. The Salar de Pedernales is an isolated and heterogeneous ecosystem that historically has faced anthropogenic pressure, including water extraction, mineral and metal mining.

Diversity of Salar de Pedernales Basin

Studies on the diversity of eukaryotic organisms in salar ecosystems are scarce, especially in the Salar de Pedernales (Codelco Chile División Salvador, 2024). Changes in phytoplanktonic communities were mainly bottom-up driven, as reflected by the significant effects of trace metal concentrations, nutrient availability and temperature in the dbRDA results (Table 1). Phytobenthic organisms, however, were influenced by changes in potassium. While potassium has been considered to be unrelated to growth rates (Jaworski et al., 2003), osmotic stress may act as a selective force on the community, as supported by studies on transcriptional regulation in euryhaline dia-

Table 1. Distance-based RDA (dbRDA) using the Bray- Curtis distances of the different community types with environmental variables selected with a forward selection. *RDA basado en distancias (dbRDA) utilizando distancias Bray- Curtis de diferentes tipos de comunidades con variables ambientales seleccionadas con un “forward selection”.*

Community type	Life history	Variable	R^2	F	*p*-value
Microalgae	Plankton	As	0.18	4.68	0.001**
		Fe	0.13	3.76	0.048*
		Temperature	0.07	2.21	0.008*
		Li^+	0.07	2.16	0.032*
		NO_3^-	0.07	2.36	0.029*
	Benthos	K^+	0.12	2.87	0.005**
Invertebrate	Plankton	Na^-	0.12	2.72	0.010*
		Fe	0.11	2.71	0.012*
	Benthos	Fe	0.13	3.15	0.006**
		Li^+	0.08	2.07	0.034*
		Temperature	0.08	2.03	0.047*

**: $p<0.01$; *: $p<0.05$

toms (Nakov et al., 2020). Invertebrate communities for both, planktonic and benthonic life histories responded to trace metal variability, probably aligned with phytoplankton growth-related factors. In addition, we observed that the planktonic invertebrate communities responded to osmotic stress in agreement with experiments demonstrating its constraining negative effect on zooplankton biomass and body size (Ersoy et al., 2022).

Both microalgae and invertebrate communities are recognized as important components of the local trophic web, sustaining for example local and migratory flamingo populations (Gajardo & Redón, 2019; Tobar et al., 2012). The microalgae community was mostly represented by Bacillariophyta, organisms known for their high saline tolerance (Balycheva et al., 2023) and zoochory (Quevedo-Ortiz et al., 2024). To date, the majority of studies on microalgae in Chilean salars are related to either new species description, new isolates (i.e., Rivera et al., 2018; Rivera & Cruces, 2009, 2015), indirect assessment of ecosystem productivity (quantified as chlorophyll-a) and cyanobacteria (Dorador et al., 2008, 2013). Surprisingly, invertebrate communities were heterogeneous and diverse, characterized by the presence of crustaceans, nematodes, dipterans, and coleopterans (Fig. 4D). These results contrast with observations on other hypersaline habitats, such as Laguna La Brava (Salar de Atacama), about 180 km north of the Pedernales basin, where only few common species of amphipods, gastropods and brine flies were detected (Dorador et al., 2018).

Anthropogenic perturbations in the Salar de Pedernales Basin

The survey through the Pedernales Basin revealed high natural variability among the sampled habitats, with a clear distinction between undisturbed and anthropogenically disturbed habitats (Fig. 2A). Both disturbed habitats (Salar Pedernales-NE and the artificial stream) showed increased conductivity, NO_3- concentration and salinity, differing from the natural variability registered across the undisturbed habitats (Fig. 2). While in Salar Pedernales-NE, the community differed from undisturbed habitats (principally microalgae communities), the artificial stream revealed a drastic absence of organisms (Fig. 3, Fig. 4). Our findings are consistent with observations in other anthropogenically disturbed habitats, where activities like water irrigation for agriculture, coal or salt mining were found to alter local hydromorphology and to cause importance changes in the properties of water bodies and on aquatic communities (Cañedo-Argüelles et al., 2013; Stenger-Kovács et al., 2023). For instance, increasing mineral weathering has been shown to cause an increase in dissolved salt content, alkalinity, nitrate levels (Montross et al., 2013), and a decrease in pH (Kaushal et al., 2018).

The factors influencing the species composition in the Salar de Pedernales basin differed between the organismic groups according to trophic position and life history. While compositional changes were observed across habitats, the response of communities varied depending on the level of disturbance (Fig. 4). At Salar Pedernales NE, environmental conditions led to significant shifts in species composition. In contrast, in the artificial stream, severe conditions, i.e., high conductivity and low pH (Fig. 1; Fig. 2) might be unsuitable for the sustainment of microalgae and invertebrate lifeforms (Fig. 3). This particular case can be taken as an example of the magnitude of the anthropogenic effect on communities when compared to the overall diversity of the basin.

The mining industry poses a risk to the biodiversity of salars due to potential habitat loss (Sonter et al., 2018). For instance, the extraction of economically valuable minerals, such as lithium, involves pumping groundwater into a series of evaporation ponds, resulting in the flooding of large areas. In addition, this process can lower phreatic water levels, disrupting the natural water balance and reducing water availability (Flexer et al., 2018). Overall, it is expected that the effects of increasing lithium extraction pressure (Liu et al., 2019), accompanied by desiccation exacerbated by water extraction, could lead to even more severe water scarcity (Parker et al., 2024). Since the Salar de Pedernales basin is an geographically isolated area, a reduction in habitats size could negatively impact not only on local species but also on emblematic species, such as flamingos (Gutiérrez et al., 2022).

Biological indicators

Microalgae in the perturbed habitats were characterized by a dominance of the genera *Amphora* and *Fragilaria* (Fig. 4B). *Amphora* is known to be dominant in benthic freshwater systems related to increasing nitrogen and phosphorus availability (Cvetkoska et al., 2018). Indeed, *Amphora* spp. has been isolated and grown at eutrophic conditions, such as municipal wastewater (Harini et al., 2023). Similarly, the *Fragilaria* genus has been described as highly adaptable (Vidal et al., 2021), serving as an important water quality indicator, particularly in the context of organic pollution (Saros et al., 2005), as also supported by paleolimnological records (Stoermer, 1993).

In the invertebrate communities, *Artemia* spp. dominated at disturbed conditions (Fig. 4D). This increase in abundance might be related to its remarkable tolerance to hypersaline conditions (Gajardo & Beardmore, 2012) and the capacity to enter a state of dormancy at unfavorable environmental conditions (Hand et al., 2016). These characteristics make *Artemia* one of the most widely used live commercial diets in aquaculture (Lavens & Sorgeloos, 2000).

CONCLUSION

This study shows the biodiversity of aquatic microalgae and invertebrate communities of the Salar de Pedernales basin. By collecting data from different habitats, we found pronounced changes in the ionic composition in the anthropogenically perturbed habitats which caused shifts in biodiversity and community composition. Our investigation thus sheds light on the vulnerability of the Salar de Pedernales basin and its associated biodiversity to anthropogenically driven habitat deterioration.

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AUTHOR CONTRIBUTIONS

F.G.S.: Data Curation, Formal Analysis, Writing - Original Draft Preparation. A.R.F.: Data Curation, Formal Analysis, Writing - Original Draft Preparation. J.P.: Visualization, Review & Editing. J.G.: Visualization, Review & Editing. J.Á.: Investigation, B.B.: Investigation. L.F.F.: Investigation, Supervision, Project Administration, Funding Acquisition, Review & Editing.

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