

Review Paper

Macroinvertebrate community structure in an extreme altiplanic environment from Chile: The Ascotán salt pan



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ABSTRACT

The Ascotán salt pan is an extreme freshwater system in the Southern Altiplano of Chile (17°–22°S). Its origin has been traced to the presence of the paleolake Minchin approximately 0.0117 Ma. Currently, this system has been experiencing important changes such as seasonal temperature increase, higher water evaporation and water depletion. The eastern side of the Ascotán salt pan is conformed by twelve isolated springs that host a unique biodiversity in the Altiplano. The aim of this research has been to characterize the composition and structure of benthic macroinvertebrates community in relation to the environmental characteristics in five springs of the Ascotán salt pan. We found significant differences in the community structure and composition among the springs (PERMANOVA: Pseudo-F = 8.417; $P < 0.01$). These results were related to differences in the salinity concentrations of several anions and cations of the springs. Regarding benthic fauna 24 families were identified. The most abundant taxa were the Elmidae, Hydrozetidae, Hyalellidae, and Cyprididae. Recently the uncontrolled water and Boron extraction due to mining could affect freshwater biodiversity. Therefore, legal measures need for conservation of this extreme ecosystem in the Southern Altiplano.

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1. Introduction

The Southern Andean Altiplano is characterized by having one of the driest climates on Earth and the presence of isolated endorheic aquatic systems and extensive salt pans such as Uyuni, Coipasa, Atacama, Carcote and Ascotán, with altitudes between 3000 and 6000 m above sea level (Ochsenius, 1986; Montgomery et al., 2003; Risacher et al., 2003). The intense volcanic activity and the historical climate changes have created salt pans and salt lakes in the Southern Altiplano (Vila, 1975; Ochsenius, 1986; Risacher and Bertrand, 2008). The effects of continuous droughts and high evaporation (1630 mm yr⁻¹, Márquez-García et al., 2009) have promoted a negative water balance in the basins, resulting in extreme conditions such as higher concentration of salts, electrical conductivities higher than 100 µmhos cm⁻¹ and pH of approximately 8.0–9.5 (Vila et al., 2007a).

The Ascotán salt pan (21°29'S; 68°15'W), is located at the Southern Altiplano, in the Antofagasta region of Chile (Fig. 1). This is part of an endorheic basin with an area of 18 km² (Risacher et al., 2003). The Ascotán salt pan was part of the Minchin paleolake that extended north along the present Titicaca Lake and Ascotán basin, during Quaternary period, roughly 0.0117 Ma ago (Keller and Soto, 1998; Placzek et al., 2006). The current climate is cold and dry, with large daily and seasonal

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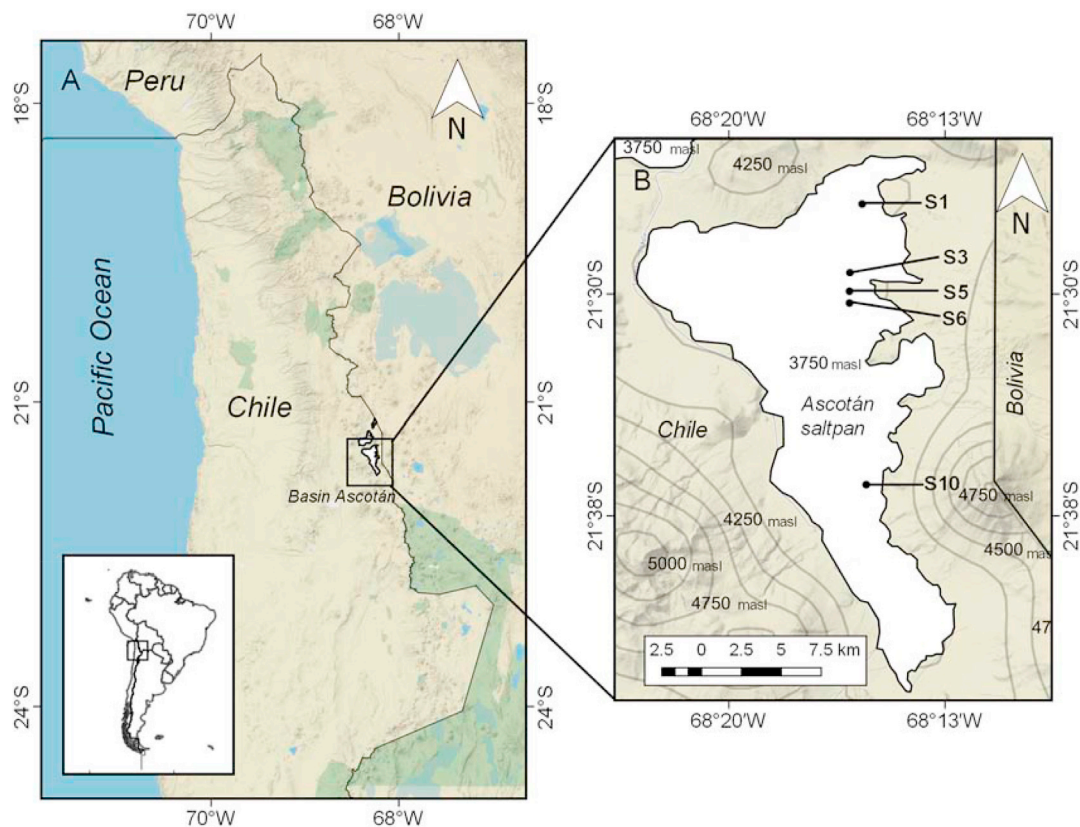


Fig. 1. The geographic location of Ascotán and the five springs studied. A, General location of Southern Altiplano. B, Ascotán salt pan and S1 to S10 indicate springs. C, Photograph of the spring system S1. D, Photograph of the spring system S3. Photograph of the spring system S5. F, Photograph of the spring system S6. G, Photograph of the spring system S10.

temperature variations (up to 40 °C), and rainfall is usually less than 100 mm yr⁻¹, which occurs from December to March, corresponding to The Altiplano Winter (Risacher et al., 2003; Sáez et al., 2007; Placzek et al., 2009; Rondanelli et al., 2015).

The water resides on the eastern side of the Ascotán salt pan with twelve springs and rivulets that at the western side generate evaporite deposits (Keller and Soto, 1998; Hermosilla et al., 2019). Physical and chemical studies have displayed that the electrical conductivity of water decreases from north to south varying from 14 to 2.5 mS/cm, and with pH fluctuating between 8.2 and 8.4, as slightly alkaline, containing high concentrations of carbonates (Risacher et al., 1999; Hermosilla et al., 2019).

The particular environmental conditions of the Ascotán salt pan have generated an isolated system with confined populations, potentially diversified by evolutionary processes (Vila et al., 2013; Victoriano et al., 2015; Valladares et al., 2018). The Ascotán springs biota is composed of microalgae such as *Surirella wetzeli* var. *dubia* Hustedt (1927); hydrophyte such as *Ruppia filifolia* (Phil.) Skottsb and *Lilaeopsis macloviana* (Gand.) A.W.Hill (Lopez, 1997; Teillier and Becerra, 2003), endemic macroinvertebrates as the gastropods; *Heleobia ascotanensis* (Courty, 1907), and *Biomphalaria crequii* (Courty, 1907), and also as the endemic fish, *Orestias ascotanensis* Parenti (1984) a generalist predator of zooplankton and benthic macroinvertebrates (Guerrero et al., 2015).

The benthic macroinvertebrate community is the most important for the processing of organic matter in freshwater ecosystems, due to its taxonomic diversity and its functional role in the different trophic levels (Hauer and Resh, 1996; Giller, 2005). At the Altiplano basins such as Titicaca Lake and Pastos Grandes located in Bolivia, several articles have demonstrated the predominance of Coleoptera and Gastropods which feed of organic matter associated with rocky substratum and macrophyte. The macroinvertebrates are the base of the trophic structure of the high Andean systems (Dejoux and Iltis, 1992; Dudgeon, 2000; Jacobsen and Dangles, 2017; Nieto et al., 2016).

In this context, it has been of interest to establish the current composition and structure of macroinvertebrate community of the Ascotán springs to study trophic interactions and their conservation. Regrettably, since the 20th century, the system is under threat by Boron extraction and water usage in major copper mining, which take place mainly on the southern springs of the Ascotán salt pan, affecting the hydrological balance of the basin and the aquatic communities (Romero et al., 1997).

The objective of this research has been to characterize the composition and structure of the current benthic macroinvertebrates community in relation to the environmental characteristics of the Ascotán salt pan. We hypothesized differences in the composition and structure of the benthic macroinvertebrate communities in response to the physical-chemical properties of the springs. The results of this study could contribute to a better understanding of the structure of macroinvertebrates present in the high Andean salt pans for effective management in biodiversity conservation.

2. Material and methods

The study was developed in five freshwater springs (S1, S3, S5, S6, S10) from Ascotán salt pan (21°29'54"S; 68°15'25"W) located at the Southern Altiplano, Chile (Fig. 1; Table 1). Four sampling processes were carried out during March 2016 and September 2017, corresponding to pre and post rainfall periods to associate the taxa presence with its habitat (Poff and Ward, 1989; Poff et al., 1997; Poff and Zimmerman, 2010). Ten quantitative samples from benthic macroinvertebrates were collected from each one of the five springs, using a Surber net (0.09 m²; 250 µm). All samples collected were fixed in 70% ethanol for later identification in the laboratory. Identification of macroinvertebrates was done at a family and genus level with a stereoscopic microscope following Dejoux and Iltis (1992); Merrit and Cummins (1996); Fernández and Domínguez (2001) and Domínguez and Fernández (2009), Collado et al. (2011); Collado and Méndez (2012). (Table 2). The richness, relative abundance, Shannon-Weaver diversity and the Pielou evenness index were calculated for each spring community.

The water quality parameters measured in the five springs were pH, electrical conductivity, Sodium, Potassium, Magnesium, Calcium, Total Nitrogen, Total Phosphorus, Sulphates, Total Hardness, and Alkalinity. The analytical methods followed the methodology established by the Standard Methods for the Examination of Water and Wastewater (APHA-AWWA-WEF, 2012), (Table 3).

PERMANOVA (permutational multivariate analysis of variance), based on Bray-Curtis similarity of fourth-root transformed data was used to determine the community structure differences in the springs and periods (pre and post rainfall) as factors. All PERMANOVA tests were based on 9999 permutations (Anderson, 2001, 2005). Significant terms were investigated with a posteriori pairwise comparisons using the PERMANOVA t statistic. Monte-Carlo P-values were used to detect significant variations among the springs. A multidimensional non-parametric scaling analysis (NMDS; Clarke and Green, 1988), was carried out to graph the differences among the communities.

Additionally, the relationship of benthic macroinvertebrate communities with environmental variables was estimated. This was done through RDA (redundancy analysis) using the CANOCO 4.5 (Ter Braak and Smilauer, 2002). This analysis allows determining linear combinations between environmental variables and abundance of benthic macroinvertebrates communities. The Monte-Carlo test was carried out to verify which variables exerted a significant effect on macroinvertebrates distribution.

3. Results

In general, a higher presence of macrophytes was observed in the spring S1, S5 and S6 (Fig. 1 D and 1E). The springs' waters revealed differences in most of the physical-chemical properties analysed (Table 3). The parameters with the highest variation

Table 1
Locality and descriptors of structure of macroinvertebrate benthic communities of Ascotán springs.

Ascotán Springs	Geographical coordinates	Richness S (Families)	Abundance total (ind/m ²)	Shannon H'	Evenness J'
S1	21° 27' 01"S/68° 15' 10"W	16	774.1	2.4	0.9
S3	21° 29' 28"S/68° 15' 26"W	14	2803.7	1.8	0.7
S5	21° 29' 48"S/68° 15' 25"W	13	4737	1.8	0.7
S6	21° 29' 51"S/68° 15' 25"W	19	1114.8	2.8	0.9
S10	21° 36' 34"S/68° 15' 01"W	14	14996.3	1.6	0.6

Table 2
Taxonomic diversity and abundance (ind/m²) of benthic macroinvertebrates in the Ascotán springs.

Macroinvertebrates	mean \pm SD Abundance ind/m ²				
	S1	S3	S5	S6	S10
Platyhelminthes					
Turbellaria					
Tricladida					
Dugesidae					
<i>Dugesia</i> sp.	11.1 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	77.8 \pm 47.1	0.0 \pm 0.0
Nematoda					
Adenophorea					
Plectida					
Plectidae	27.8 \pm 23.6	0.0 \pm 0.0	0.0 \pm 0.0	44.4 \pm 47.1	0.0 \pm 0.0
Annelida					
Clitellata					
Rhynchobdellida					
Glossiphoniidae					
<i>Haementeria</i> sp.	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	5.6 \pm 7.6	0.0 \pm 0.0
<i>Helobdella</i> sp.	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	50.0 \pm 70.7	0.0 \pm 0.0
Haplotaxida					
Naididae					
<i>Nais</i> sp.	33.3 \pm 31.4	0.0 \pm 0.0	0.0 \pm 0.0	11.1 \pm 0.0	0.0 \pm 0.0
Mollusca					
Bivalvia					
Sphaeriida					
Sphaeriidae					
<i>Pisidium</i> sp.	0.0 \pm 0.0	5.6 \pm 0.0	0.0 \pm 0.0	5.6 \pm 0.0	0.0 \pm 0.0
Gastropoda					
Hygrophila					
Planorbidae					
<i>Biomphalaria crequii</i>	5.6 \pm 0.0	72.2 \pm 39.3	22.2 \pm 0.0	16.7 \pm 7.9	105.6 \pm 23.6
Physidae					
<i>Physa</i> sp.	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	638.9 \pm 322.1
Littorinimorpha					
Cochliopidae					
<i>Heleobia Ascotánensis</i>	5.6 \pm 0.0	61.1 \pm 7.9	216.7 \pm 23.6	16.7 \pm 7.9	1172.2 \pm 259.3
Arthroproda					
Ostracoda					
Podocopida					
Cyprididae					
<i>Amphicypris</i> sp.	22.2 \pm 15.7	33.3 \pm 13.4	33.3 \pm 5.6	33.3 \pm 15.3	83.3 \pm 55.0
Malacostraca					
Amphipoda					
Hyalellidae					
<i>Hyalella</i> sp.	22.2 \pm 15.7	94.4 \pm 117.9	333.3 \pm 62.9	33.3 \pm 15.7	127.8 \pm 23.6
Arachnida					
Oribatids					
Hidrozetidae					
<i>Hydrozetes</i> sp.	22.2 \pm 0.0	166.7 \pm 62.9	700.0 \pm 125.7	22.2 \pm 15.7	3577.8 \pm 722.8
Trombidiformes					
Arrenuridae					
<i>Arrenurus</i> sp.	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	27.8 \pm 23.6	0.0 \pm 0.0
Hydryphantidae					
<i>Euwandesia</i> sp.	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	5.6 \pm 7.9	0.0 \pm 0.0
Limnocharidae					
<i>Limnochares</i> sp.	5.6 \pm 7.9	22.2 \pm 31.4	16.7 \pm 7.9	0.0 \pm 0.0	466.7 \pm 157.1
Entognatha					
Collembola					
Collembola	0.0 \pm 0.0	0.0 \pm 0.0	22.2 \pm 15.7	0.0 \pm 0.0	0.0 \pm 0.0
Insecta					
Coleoptera					
Elmidae					
<i>Austrelmis</i> sp.	5.6 \pm 7.1	705.6 \pm 495.0	700.0 \pm 282.8	33.3 \pm 0.8	1055.6 \pm 267.1
Dystiscidae					
<i>Liodessus</i> sp.	0.0 \pm 0.0	55.6 \pm 62.9	44.4 \pm 47.1	0.0 \pm 0.0	55.6 \pm 31.4
Diptera					
Aphididae	0.0 \pm 0.0	88.9 \pm 2.2	138.9 \pm 3.7	11.1 \pm 0.0	33.3 \pm 0.0
Ceratopogonidae	11.1 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Ephydriidae	5.6 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	16.7 \pm 62.9	0.0 \pm 0.0
Chironomidae					
<i>Chironomus</i> sp.	0.0 \pm 0.0	5.6 \pm 7.4	55.6 \pm 30.7	5.6 \pm 4.3	44.4 \pm 4.6
<i>Cricotopus</i> sp.	38.9 \pm 39.3	0.0 \pm 0.0	0.0 \pm 0.0	16.7 \pm 7.5	0.0 \pm 0.0
<i>Polypedilum</i> sp.	22.2 \pm 17.5	0.0 \pm 0.0	0.0 \pm 0.0	16.7 \pm 0.0	0.0 \pm 0.0

Table 2 (continued)

Macroinvertebrates	mean \pm SD Abundance ind/m ²				
	S1	S3	S5	S6	S10
Odonata					
Aeschnidae					
<i>Aeschna</i> sp.	27.8 \pm 39.3	27.8 \pm 18.4	33.3 \pm 30.4	11.1 \pm 0.0	27.8 \pm 23.6
Coenagrionidae					
<i>Protallagma</i> sp.	5.6 \pm 0.0	33.3 \pm 3.3	33.3 \pm 0.0	50.0 \pm 55.0	83.3 \pm 70.7
Tricoptera					
Hydroptilidae					
<i>Neotrichia</i> sp.	88.9 \pm 62.9	27.8 \pm 23.6	0.0 \pm 0.0	11.1 \pm 0.0	11.1 \pm 15.7

were Sodium (min = 468.67 mg L⁻¹; max = 1935.3 mg L⁻¹), Calcium (min = 130 mg L⁻¹; max = 703.5 mg L⁻¹) and Sulfate (min = 51.47 mg L⁻¹; max = 1085.87 mg L⁻¹).

The benthic macroinvertebrate fauna recorded 24 families in the studied areas (Table 2). The spring with the highest richness was S6 with 20 families, while the lowest richness was recorded in S5 with 13 families (Table 1). The Insects showed the highest richness, represented by 5 Orders and 10 Families. The Coleoptera order presented the highest abundance with 265.5 ind/m², constituting 22.2% of the total abundance. The Shannon-Weaver index showed the highest diversity in S6 with 2.8 and the lowest one in S10 with 1.6 (Table 1). The Pielou evenness index showed a maximum of 0.9 in S1 and S6, whereas the minimum was recorded in S10 with 0.6 (Table 1).

The macroinvertebrate families with the highest relative percentage abundance in S1 were Hydroptilidae (29%) and Naididae (11%); in S3 Elmidae (50%) and Hydrozetidae (12%); in S5 Hydrozetidae (30%) and Elmidae (30%); in S6 Hyalellidae (7%), Elmidae (7%) and Cyprididae (7%); in S10 Hydrozetidae (45%) and Cochliopidae (15%) (Fig. 2).

Communities composition was different among springs (PERMANOVA: Pseudo-F = 8.417; P < 0.01). Instead, pre and post rainfall significant differences in the composition were not found among springs (PERMANOVA: Pseudo-F = 1.45; P > 0.05). The pairwise comparisons (Table 4) detected differences among the spring S1 versus S10 (P < 0.05), S5 versus S6 (P < 0.05), S5 versus S10 (P < 0.05) and S6 versus S10 (P < 0.05). The multidimensional scaling analysis (NMDS) of benthic macroinvertebrate abundances showed two groups. The first group consisted of springs S1 and S6 and the second group consisted of springs S3, S5, and S10 (Fig. 3).

The RDA explains 74.1% of the total variability of the results (Axis 1 = 52.7%, Axis 2 = 21.3%). The physical-chemical properties; Calcium, Magnesium, Sodium, Sulfate, Chloride, pH, Hardness, total Nitrogen and Phosphorus, were positively associated with axis 1 and to the springs S1 and S6; opposite to this tendency are the springs S3, S5, and S10 (Fig. 4). Among the strongest associations, we found that the families Ceratopogonidae, Naididae, Ephydriidae, Dugesidae, and Chironomidae were associated with Magnesium, Sodium, and Calcium in S1. Glossiphoniidae, Arrenuridae, Hydriphantidae, and Sphaeriidae were associated with Chloride in S6. There is also a clear grouping of families Aphididae, Aeschnidae and order Colembola with Potassium in the springs S3 and S5, as well as families Cyprididae, Physidae, Hydriphantidae were associated with Silicate and Total Phosphorus in S10 (Fig. 4). According to the results and RDA analysis (Table 5), macroinvertebrate communities in the reservoir were influenced by Magnesium (p = 0.004), Sodium (p = 0.012), Chloridere (p = 0.016), Silicate (p = 0.036) and Calcium (p = 0.02).

4. Discussion

The analysed springs support low and unique biodiversity being adapted historically to the extreme environmental factors and current lack of connectivity among them (Dejoux and Iltis, 1991; Jacobsen and Dangles, 2017). The water quality parameters determined differences among environmental conditions for each spring in the Ascotán salt pans due to the higher ion concentrations in the southern springs. High conductivities were found, due to concentrations of Na⁺ and Cl⁻ ions as well as Ca⁺², and SO₄²⁻, typical of these Altiplano systems (Risacher et al., 2011).

The springs maintained 24 macroinvertebrates families showing a low yet unique biodiversity. These results have also been reported in other high-altitude freshwater systems in Bolivia and Peru such as Lake Titicaca (Dejoux and Iltis, 1992; Jacobsen and Dangles, 2017). Diptera larvae were not dominant, showing a low abundance compared to other macroinvertebrates in the studied springs. Although these taxa have been considered tolerant to different environmental conditions as the family Chironomidae (Figueroa et al., 2003; Hauer and Resh, 2007) the Ascotán salty conditions let us consider them as secondary elements of the benthic fauna of the Altiplano in comparison to other high Andean systems of South America (Muñoz-Quesada, 2004; Jacobsen, 2008).

When comparing diversity and richness among springs, S1 and S6 registered the higher indexes. Furthermore, an important similarity in the composition between these springs was found. The families Elmidae, Hydrozetidae, and Hyalellidae were the most abundant in the springs S1 and S6, being mainly associated with macrophytes, which were mostly observed in S1 and S6. These taxa have also been dominant in macrophyte habitat systems in trans-Andean highland systems, possibly providing as resources and refuge for insects (Moya et al., 2009; Nieto et al., 2016). S3 and S5 also present an important similarity, these springs are geographically close, which may be explained by their connections during the rainfalls

Table 3

Mean values and standard deviations (\pm) the physical-chemical properties obtained in the Acotán springs. CE- Electrical conductivity (mS cm⁻¹); PT- Total Phosphorus (mg L⁻¹); N - Total Nitrogen (mg L⁻¹); Si - Silicate (mg L⁻¹); WH - Hardness (mg L⁻¹); AT-Total Alkalinity (mg L⁻¹); Na⁺- Sodium (mg L⁻¹); K⁺- Potassium (mg L⁻¹); Mg²⁺- Magnesium (mg L⁻¹); Ca²⁺- Calcium (mg L⁻¹); SO₄ - Sulfate (mg L⁻¹); Cl⁻ - Chloride (mg L⁻¹).

	Ascotán springs				
	S1	S3	S5	S6	S10
CE	3.93 \pm 0.01	3.87 \pm 0.07	3.93 \pm 0.01	4.10 \pm 0.17	5.67 \pm 0.57
PT	0.33 \pm 0.06	0.32 \pm 0.03	0.30 \pm 0.01	0.3 \pm 0.1	0.17 \pm 0.06
N	0.40 \pm 0.1	0.45 \pm 0.1	0.52 \pm 0.03	0.47 \pm 0.21	0.18 \pm 0.08
Si	309.50 \pm 6.66	302.57 \pm 0.51	308.00 \pm 8.54	286.80 \pm 32.99	412.33 \pm 15.53
WH	1758.90 \pm 97.59	1860.07 \pm 2.0	1764.07 \pm 99.9	528.83 \pm 36.6	475.00 \pm 20.07
AT	4.01 \pm 0.5	4.40 \pm 0.1	4.45 \pm 0.1	8.17 \pm 0.29	9.77 \pm 1.55
Na ⁺	1935.30 \pm 6.51	468.67 \pm 5.51	481.33 \pm 3.21	967.40 \pm 11.83	686.97 \pm 21.57
K ⁺	28.17 \pm 12.1	45.67 \pm 0.58	46.33 \pm 1.15	3.13 \pm 0.15	6.47 \pm 0.45
Mg ²⁺	94.87 \pm 3.5	56.00 \pm 10.0	58.67 \pm 4.73	84.23 \pm 3.64	71.77 \pm 4.14
Ca ²⁺	703.50 \pm 0.95	130.00 \pm 2.0	130.33 \pm 1.53	213.60 \pm 4.86	223.33 \pm 43.06
SO ₄	1085.87 \pm 5.29	223.30 \pm 6.66	205.33 \pm 4.51	62.87 \pm 0.93	51.47 \pm 0.93
Cl ⁻	1316.37 \pm 21.91	1073.00 \pm 0.01	1071 \pm 10	989.30 \pm 56.53	584.50 \pm 9.99
pH	8.10 \pm 0.11	8.10 \pm 0.07	8.80 \pm 0.05	8.33 \pm 0.06	7.59 \pm 0.01

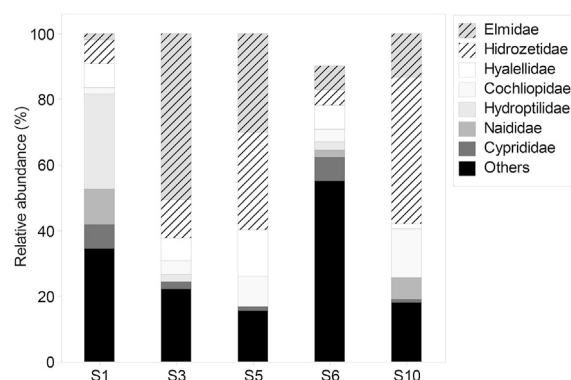


Fig. 2. The relative abundance of benthic macroinvertebrates in the five Ascotán springs (S1; S3; S5; S6; S10).

Table 4

Multivariate PERMANOVA followed by post hoc tests (PERMANOVA pairwise comparisons). The degrees of freedom in the source = df; F-statistic = F; t-statistic = t; permutation P-value = P(perm); Monte Carlo P-value = P(MC). Springs = S1, S3, S5, S6, S10.

Main test	df	MS	F	P(perm)
Springs	4		8.4169	0.001
Period	1		1.4479	0.2697
Pairwise test	df	t	P (MC)	
S1 x S3	1	6.37	0.066	
S1 x S5	1	11.68	0.059	
S1 x S6	1	1.66	0.283	
S1 x S10	1	13.59	0.030	
S3 x S5	1	2.55	0.182	
S3 x S6	1	4.80	0.077	
S3 x S10	1	7.57	0.058	
S5 x S6	1	10.29	0.037	
S5 x S10	1	15.28	0.025	
S6 x S10	1	13.46	0.027	

of “Altiplano winter” (usually between December and March). On the other hand, the southernmost spring (S10) was significantly different in composition when compared to the northern springs (S1, S3, S4 and S6), possibly the isolation and the greater distance between these springs may explain these differences.

The RDA analysis showed that environmental variables explained differences variation in the composition of benthic macroinvertebrate communities in the springs. These variables were Magnesium, Sodium, Chloride, Silicate and Calcium. These results are in line with the physical-chemical properties of the Ascotán salt pan (Risacher et al., 1999). The high

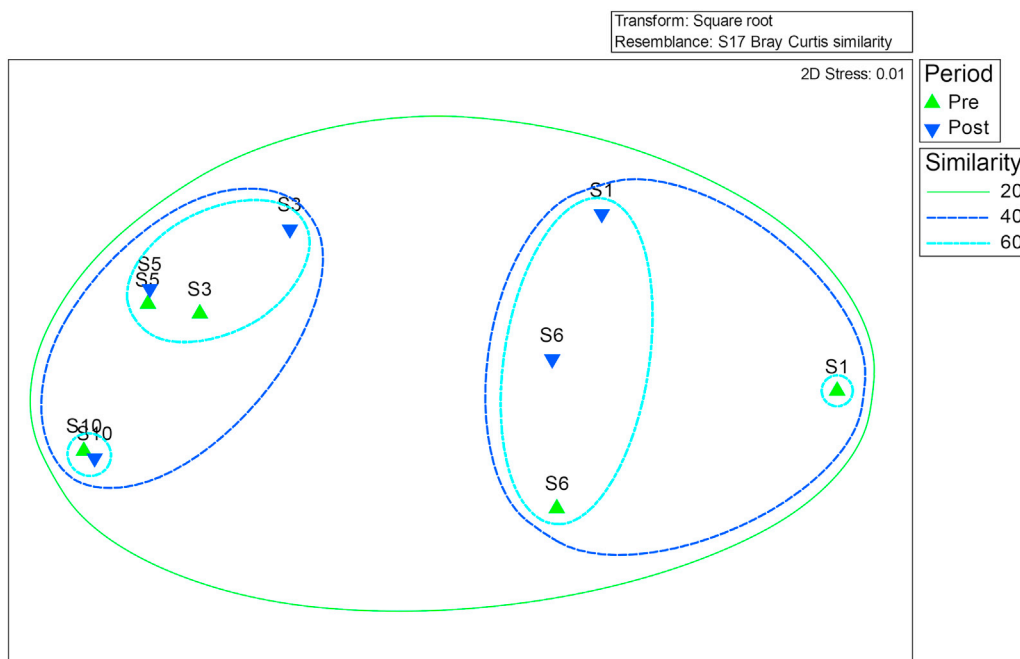


Fig. 3. MDS plots showing distribution of macroinvertebrate communities the Asotán springs, in the pre and post rainfall periods.

concentrations of cations and anions determine the current structure and the composition in the macroinvertebrate communities in the springs. The only exceptions were springs S3 and S5, which had a strong association with each other. On the other hand, there is low temporal variation (pre and post rainfall) at this latitude due to the origin of the Ascotán springs water, in which physical-chemical properties are similar for every spring (Keller and Soto, 1998).

Another distinctive feature observed in the Ascotán salt pan is the predominance of a collector group and the absence of shredder functional feeding groups taxa (e.g., moth larvae and caddisflies); this has been observed in systems associated to the Lake Titicaca in Bolivia and Nevado de Pastos Grandes in Argentina (Dudgeon, 2000; Nieto et al., 2016). The absence of border vegetation implies the possibility that the Ascotán microbiota has a fundamental role in maintaining functional stability and the integrity of the ecosystem in the analysed springs (Irons et al., 1994; Nieto et al., 2016). Besides, recent researches in Ascotán revealed new taxa for the composition of the microbiota community, dominated by the groups: Bacteroidetes, Deltaproteobacteria, and Halobacteriales (Dorador et al., 2009, 2013).

Endemic gastropods collected were from the families Cochliopidae and Planorbidae; *Heleobia ascotanensis* and *Biophalaria crequii*, respectively, mainly at the springs S5 and S10, and were associated essentially to a hard substrate. Genetic studies have shown that *Heleobia ascotanensis* populations present in the springs are in a process of genetic and morphological diversification in response to the genetic and geographic isolation of Ascotán (Valladares et al., 2018). This fact would allow projecting that other taxa with low dispersion present a similar pattern as amphipods and other gastropods at Ascotán (Murphy et al., 2015; Collado et al., 2011; Collado and Méndez, 2012; Collado and Méndez, 2013; Collado et al., 2013; Collado et al., 2011; Valladares et al., 2018).

The extreme characteristics observed in the salt pans and the lack of border vegetation have generated a direct and simple trophic chain with a top predator and lower richness of primary and secondary producers as observed in other systems of the southern Chilean Altiplano (Guzmán and Sielfeld, 2009; Riveros et al., 2012; Scott et al., 2015). Although the lack of some nutrients, especially nitrogen compounds, is constant, the simple trophic network has been sustained by a low number of primary producers, such as diatoms, and a low number of hydrophyte macrophytes (Teillier and Becerra, 2003). Additionally, previous works have registered a higher abundance of *Orestias ascotanensis* in the springs with higher coverage of macrophytes and nutrient concentration (Keller and Soto, 1998).

The permanent mining activities for Boron extraction and water extraction from the springs (Romero et al., 1997; Keller and Soto, 1998; Placzek et al., 2006) are drying and deteriorating the ecosystem where lately the abundance of an important and endemic fish *O. ascotanensis* has diminished significantly (Ministerio del Medio Ambiente, 2018). This is extremely relevant because the Ascotán salt pan is the only habitat described for *O. ascotanensis* (Vila et al. 2006; Vila et al. 2007b; Guerrero et al., 2015; Vila and Quezada-Romegialli, 2018).

Climate change has caused a significant decrease in precipitation for this area. The historical precipitation recorded an average of 188–210 mm per year (Klohn, 1972). Currently, climatic data shows that the average rainfall reaches about 80 mm (Teillier and Becerra, 2003) decreasing the water level and consequently increasing salinity in the southern springs, damaging organisms from primary producers to macroinvertebrates.

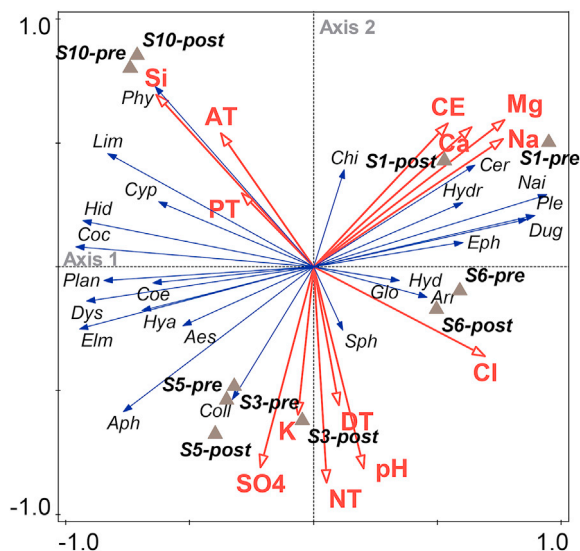


Fig. 4. Redundancy analysis (RDA) triplot diagram (pre and post rainfall period), showing all species of benthic macroinvertebrate the Ascotán springs. The red vectors represent physical-chemical properties. CE- Electrical conductivity; PT- Total Phosphorus; N - Total Nitrogen; Si - Silicate; WH - Hardness; AT- Total Alkalinity; Na- Sodium; K- Potassium; Mg- Magnesium; Ca- Calcium; SO4 - Sulfate; Cl - Chloride. The blue vectors represent taxa the Ascotán springs. Sphaeriidae (*Sph*); Planorbidae (*Pla*); Physidae (*Phy*); Cochliopidae (*Coc*); Hidrozetidae (*Hid*); Arrenuridae (*Arr*); Hydryphantidae (*Hyd*); Limnocharidae (*Lim*); Hyalellidae (*Hya*); Dugesiidae (*Dug*); Glossophoniidae (*Glo*); Naididae (*Nai*); Elmidae (*Elm*); Dystiscidae (*Dys*); Chironomidae (*Chi*); Ceratopogonidae (*Cer*); Ephyridae (*Eph*); Aphididae (*Aph*); Coenagrionidae (*Coe*); Hydroptilidae (*Hydr*); Aeschnidae (*Aes*); Plectidae (*Ple*); Cypridae (*Cyp*); Collembola (*Coll*). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 5

Results of redundancy analysis (RDA) and Monte-Carlo permutations for testing the significance physical-chemical properties obtained in the Ascotán springs in relation to distribution patterns of benthic macroinvertebrates. F statistic = F; P- value were generated by 999 permutations).

Explanatory variables	Variance Explained %	F	P
Mg (mg/L)	39.8	5.3	0.004
Na (mg/L)	38.9	5.1	0.012
Cl-(mg/L)	32.5	3.8	0.016
Si (mg/L)	30.5	3.5	0.036
Ca (mg/L)	30.1	3.4	0.02
CE (mS/cm)	24.3	2.6	0.08
AT (mg/L)	16.3	1.6	0.16
SO4-2(mg/L)	13.4	1.2	0.266
pH	12.7	1.2	0.28
NT (mg/L)	11.3	1	0.344
PT (mg/L)	10.9	1	0.376
DT (mg/L)	9.8	0.9	0.462
K (mg/L)	9.7	0.9	0.378

In conclusion, a benthic macroinvertebrate community was found which has been developing historically in an extreme environment. The analysed springs displayed differences in the community dominated by insects and a low similarity in the structure and composition as a response to the physical-chemical properties and geographic isolation among springs. Although this ecosystem has evolved in different geological and climatic stages, recently the uncontrolled water and Boron extraction must be taken into account. Legal measures are needed to ensure future protection and conservation of such unique ecosystem as the Ascotán salt pan biota.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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