

Invertebrates inhabiting temporary ponds found in the Tambo-Puquíos wet pasture (Andes of north-central Chile), and the physicochemical characteristics of their habitat

Invertebrados de pozas efímeras de la vega Tambo-Puquíos (Andes del norte-centro de Chile) y las características fisicoquímicas de su hábitat

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ABSTRACT

The physical-chemical features of four temporary shallow ponds and their invertebrate fauna were studied during the summer months of three consecutive years. Invertebrate sampling was conducted by suction of pond water with a pump. From the physical-chemical point of view, the study ponds were heliotoxic, mesotrophic and mesopoikilohaline microlimnotopes. Their thermal stratification is monomictic, with few degrees of difference in water temperature between surface and bottom. The chemical characteristics of pond water were in between those of freshwater and truly saline ponds. The study ponds exhibited high content of phosphate, Ca, and sulfate content, followed by fluoride, Fe, K, Mg, Cl, nitrate, and total suspended solids. They were low in bicarbonate and CN content. Apparently, the geochemical properties of the surrounding mountains play a role in the hydrochemistry of these water bodies. Total abundance per taxon was mostly low. We recorded five higher taxa. Cladocerans (e.g., *Alona* spp.), followed by dipterans (e.g., chironomid flies), and copepods (e.g., cyclopoids and harpactoids) were the dominant groups. Less abundant groups were amphipods (e.g., *Hyperia* spp.), and ostracods (e.g., Cyprididae). Some of the taxa reported in this work are recorded for first time in this type of habitat. Nevertheless, given the habitat characteristics, studies at finer taxonomic resolution are needed to search for site-specific genera or species. We obtained lower taxonomic richness compared to lotic systems found in the area. This result may be due to differences in the dynamics of abiotic conditions observed between the two habitats. The variability in abundance among ponds was high for most of the recorded taxa. This variability may be a reflection of the general condition of the wet pasture we studied, suggesting that the ponds are important sources of the high biodiversity found in these landscape units. As the wet pastures of the area are networked, also contribute to biodiversity of the entire mountain system. From this, it is clear that conservation strategies of Andean wet pastures need to include these small landscape units.

Key words: zooplankton, macroinvertebrates, temporary ponds, arid Andes, aquatic fauna, lentic habitats.

RESUMEN

*Durante los meses de verano de tres años consecutivos se estudiaron las características fisicoquímicas de cuatro pozas efímeras, de poca profundidad y su fauna de invertebrados. El muestreo de los invertebrados se llevó a cabo por succión del agua con una máquina de bombeo. Desde el punto de vista fisicoquímico, las pozas estudiadas resultaron ser microlimnotopos heliótópicos, mesotróficos y mesopoikilohalinos. Su estratificación térmica resultó ser de carácter monomictico, con pocos grados de diferencia térmica entre la superficie y el fondo. Se encontró que sus características químicas las sitúan entre hábitats dulceacuicolas y verdaderamente salinos. Las pozas mostraron alto contenido de fosfato, Ca y sulfato, seguido por los niveles de fluoruro, Fe, K, Mg, Cl y nitrato. El contenido de los sólidos totales suspendidos fue igualmente alto. Por el contrario, el contenido de bicarbonato y CN fue bajo. Al parecer, las propiedades geoquímicas de las montañas que rodean a la vega juegan un papel importante en la hidroquímica de estos cuerpos de agua. En general, las abundancias totales por taxón fueron bajas. Se registraron cinco taxones superiores. Cladóceros (e.g., *Alona* spp.), seguido por los dípteros quironómidos y los copépodos ciclopoideos y harpacticoideos fueron los grupos dominantes. Grupos menos abundantes fueron los anfípodos (e.g., *Hyperia* spp.) y los ostrácodos Cyprididae. Algunos de los taxones reportados en este trabajo se registran por primera vez en este tipo de hábitat. Sin embargo, debido a sus características, se necesitan estudios con una resolución taxonómica más fina con el fin de dilucidar la presencia de géneros o especies propias de estos sistemas. En comparación con los cuerpos lóticos encontrados en la zona, las pozas arrojaron una menor riqueza taxonómica. Este resultado puede deberse a diferencias en la dinámica de las condiciones abióticas observadas entre los dos hábitats. La variabilidad entre pozas, asociada a la abundancia, fue alta para la mayoría de los taxones registrados. Esta variabilidad puede ser un reflejo de la condición general de la vega estudiada, lo que sugiere que estas pozas son fuente importante de la alta biodiversidad observada en estas unidades de paisaje. Como las vegas de la zona están conectadas en red, también contribuyen a la biodiversidad de todo el sistema de montaña. A partir de este argumento, resulta claro que las estrategias de conservación de las vegas andinas necesitan incluir a estas pequeñas unidades de paisaje.*

Palabras clave: zooplankton, macroinvertebrados, pozas efímeras, Andes áridos, fauna acuática, hábitats lénticos.

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Introduction

The geomorphologic heterogeneity of the highlands of northern Chile creates a mosaic of environmental conditions favorable for formation of habitats with highly contrasting features. In flat terrain, for instance, wet pastures (“vegas”) ranging from less than one hectare to hundreds of hectares originate in places where water accumulates or emerges to the surface. Recently, the conservation status of these landscape units has triggered public awareness. This concern is because they are important water reservoirs and hotspots of local biological diversity in a rather poor mountain landscape. Presently, they are subjected to intense water consumption, heavy grazing, and exposed to possible effects of climate change (Fiebig-Wittmaack, 2014). To improve strategies for the conservation of these Andean landscape units it is necessary to broaden our knowledge about them. Their vegetation is relatively well known (e.g., Squeo *et al.*, 1993, 2006a, 2006b), however knowledge about their fauna is much less. In the case of invertebrates, so far the available studies have focused on insects (e.g., Cepeda-Pizarro, 2013; Cepeda-Pizarro *et al.*, 2015).

According to their levels of moisture and their plant characteristics, the wet pastures of the Andean transitional desert of Chile can be a continuous and semi dry carpet of short and cespitose vegetation, a semi-flooded wetland or a mixture of lawn, raised plant-cushions, small arroyos and ponds (Squeo *et al.*, 2006b). These ponds are generally shallow, small, and ephemeral. Recently, water scarcity and biodiversity conservation have sparked considerable interest in the study of pond ecology all over the world (Oertli *et al.*, 2009). Although preservation of large-scale wetlands seems to be warranted, it has led to a general neglect of small-scale landscape elements such as ponds. These environments may largely contribute to regional biodiversity because of their high local biological diversity, mainly by the compositional dissimilarity among sites (Jeffries, 2011). This contribution gains special importance in wetlands of arid lands (Williams, 1999). Despite this fact, knowledge about ecology of ephemeral and shallow Andean ponds remains scanty. For instance, one of the few available studies is that of Coronel *et al.* (2007), carried out in the Bolivian plateau.

The Tambo-Puquíos wet pasture is one of the better-known wet pastures of the Andes of north-central Chile. It is considered as a study

case (Cepeda-Pizarro *et al.*, 2006a, 2006b). The aims of the present study are to describe the ponds of the Tambo-Puquíos wet pasture as habitats for invertebrates and the invertebrate assemblage itself. This work is based on two ideas: (1) the ponds represent small aquatic islands surrounded by a carpet of vegetation in a rather poor mountain system (Coronel *et al.*, 2007), and (2) they are usually temporary water bodies, subject to weather vagaries (Schwartz & Jenkins, 2000).

Materials and Methods

Study site and ponds

The Tambo-Puquíos wet pasture (henceforth VTP) is located in the Andean section of the Elqui River basin at 3850-4000 m elevation (29°45' S, 69°59' W) (Figure 1). The VTP gets its water from small streams that drain downslope from the surrounding arid mountains, from its own snow cover formed during wintertime and from subterranean water (Zavala, 2006). Located in a narrow valley, the VTP extends for ~6 km, with an area of ~10 km². Its vegetation is mainly composed of cespitose species such as *Calandrinia compacta* (Portulacaceae), *Carex maritime* (Cyperaceae), *Pucinellia oresigena* (Gramineae), *Deschampsia caespitosa* (Gramineae) and *Deyeuxia velutina* (Gramineae). This array of vegetation includes several small and shallow ponds, some of them temporary water regimes (Figure 2). The aquatic vegetation is represented by the microalgae *Cryptomonas* and *Rhodomonas* and the filamentous algae *Oscillatoria* and *Microthamnion*. Common aquatic vascular plants are *Potamogeton strictus* (Potamogetonaceae), *Myriophyllum quitense* (Haloragaceae) and *Ranunculus chilensis* (Ranunculaceae). Organic debris, including fecal pellets from aquatic birds, is usually present in the pond bed (Cepeda-Pizarro *et al.*, 2006a). These ponds lack fish and amphibians (Cepeda-Pizarro *et al.*, 2006b). The avifauna are for the most part summer visitors. The most commonly found aquatic birds are the crested duck (*Lophonetta specularioides*), the Chilean teal (*Anas flavirostris*) and the Andean goose (*Chloephaga melanoptera*) (Tabilo, 2006). To carry out the study we selected four ponds as replicates (Figure 3, Table 1). Sampling for both the invertebrate assemblage and for the physical-chemical characterization of the ponds was done in summer (January or February).

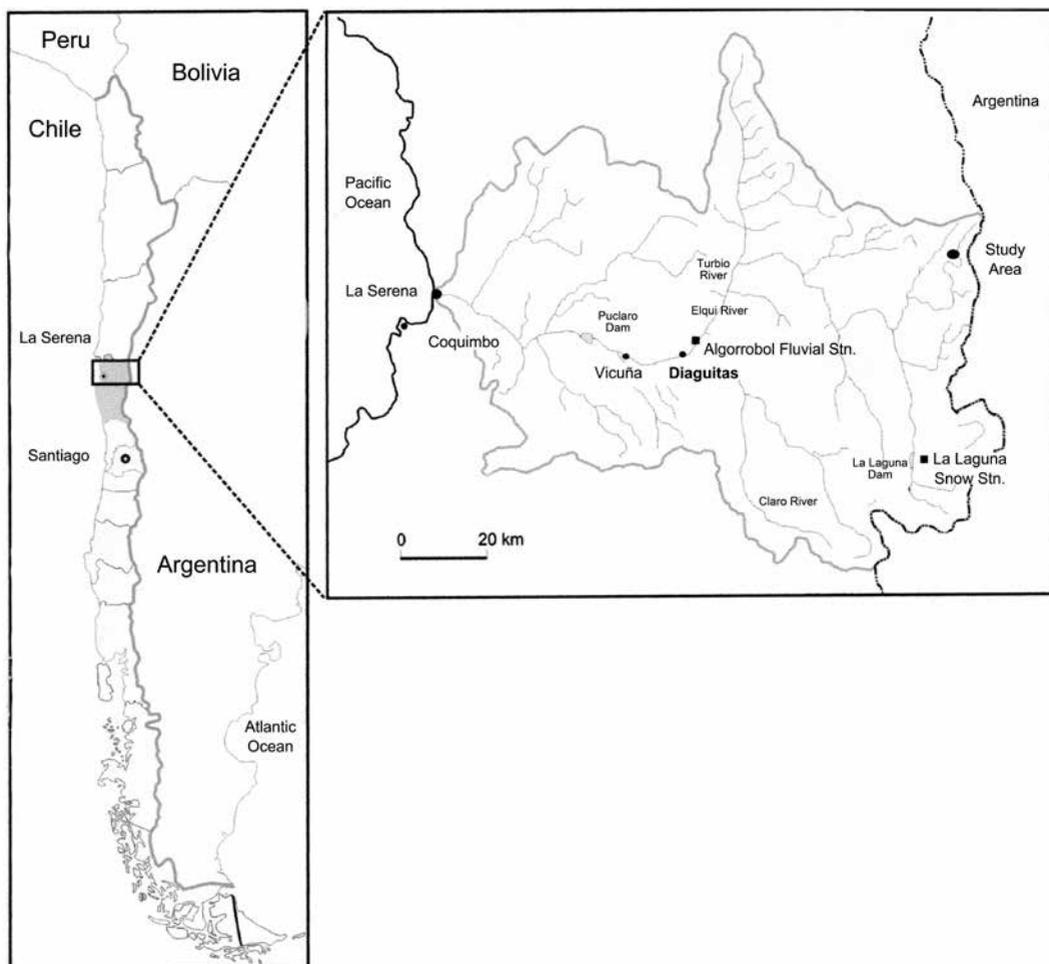


Figure 1. Geographic location of the study site () ($29^{\circ}45' S$, $69^{\circ}59' W$).



Figure 2. General view of study wet-pasture (3850 m elevation). The darker patches correspond to shallow temporary ponds. The clear spots in the peatland and its margins are sulfate crusts.



Figure 3. Close-up of one of the study ponds, with sulfate deposits on its borders.

Table 1. Some characteristics of the study ponds. For vegetation description see the paragraph study site and ponds (material and methods section).

Feature	Pond 1	Pond 2	Pond 3	Pond 4
Shape	elongated	ovoid	L-shaped	ovoid
Length	18.5 m;	12.3 m	Length large arm: 27.5 Length short arm: 14.0 m	58.7 m
Maximum width	4.0 m	58.0 m	as above	27.3 m
Mean depth	0.3 m	0.5 m	0.2 m	0.3 m
Surface (approx.)	43.8 m ²	43.7 m ²	162.5 m ²	1250.0 m ²
Bottom	without vegetation, muddy-black	without vegetation, muddy-black	covered by aquatic vegetation	covered by aquatic vegetation
Vegetation	scarce presence of filamentous algae and some vascular plants.	scarce presence of filamentous algae and some vascular plants	abundance of filamentous algae and vascular plants; borders of pond with abundant fecal depositions of aquatic birds.	abundant presence of filamentous algae and vascular plants.

Invertebrate habitat characterization

Water sampling and analyses were conducted by a specialized contractor in accordance with standard techniques (APHA *et al.*, 1985). The physical parameters examined were total hardness, electrical conductivity, turbidity, alkalinity, total dissolved solids, total suspended solids, and total solids. The chemical parameters examined were

pH, dissolved metals, inorganic nonmetallic ions and the trace elements Al, total As, Ba, Cu, B, Cd, Co, Cr, Fe, Pb, Li, Ni, Zn, and CN.

Invertebrate assemblage

Invertebrate sampling was conducted for three consecutive years (1997-1999). Two samples (50 L each) per pond were collected in each sampling

period. Samples were obtained by sucking water by means of a 2-in pump connected to a hosepipe (5 cm in diameter and 7 m long) that acted as a sucker. During suction, the water intake was moved throughout the pond to insure a homogenous sampling effort. The trapped water was then deposited in *ad hoc* containers until the required volume (50 L) was obtained. The water was filtered through a 1-mm mesh in order to remove algal clots and organic debris. The specimens trapped in algal clots and organic debris were separated by washing the clots and the debris with boiled tap water. The sample was concentrated by filtering it through a 45- μm mesh. The remaining material was removed from the mesh and preserved in a mixture of 1:9 glycerin-ethanol (70°), transported to the laboratory and stored at <10 °C until isolation, identification, and counting. Before isolating the specimens, each sample was filtered through a series of meshes of different pore sizes (i.e., 800, 600, 300, 125, 100, and 45 μm) following Makoto & Tsutomu (1976), to obtain subsamples sorted by specimen size. The sub-sampling was done using tap water. Counting was done without dilution for the first two subsamples; afterwards, the subsamples were taken to a volume of 50 ml, split into four aliquots and then quantified. Counting was conducted using both a Bogorov-open chamber and a reticular grid. Taxonomic identification was made following Villalobos (2006) and De los Ríos-Escalante *et al.* (2013). In all cases, density is expressed as individuals per liter (ind L⁻¹).

Results

Habitat characterization

Although they were considered temporary, none of the ponds dried up during the study; their depths changed slightly by 0.2-0.3 m. According to the time of day, the air mean temperature of pond water varied from 5 °C in the mid-morning, when it was 2-3 °C below air-temperature, to 15 °C in the mid-afternoon, when it was 2-3 °C above air-temperature. The water temperature tended to be slightly higher near the bottom than at the surface. Details of physical and chemical features of the pond water are provided in Table 2. Pond water was generally transparent, very hard, strongly saline, high in TDS and moderately high in oxygen. The dominant metal ions were Ca, Na, Mg, and K. The

Table 2. Mean (mg L⁻¹ \pm s.e.) of some limnetic parameters of study ponds.

Parameter	Mean \pm s.e.	
1. Physical variables		
Total hardness (mg L ⁻¹ CaCO ₃)	556.5	\pm (490.0)
Conductivity (μScm^{-1})	1678	
Turbidity (n.t.u.)	8.9	\pm (4.2)
Alkalinity (mg CaCO ₃ L ⁻¹)	130.9	\pm (19.9)
TDS (mg L ⁻¹) (a 105° C)	1229.5	-
Total solids (mg L ⁻¹)	1806.0	\pm (134.8)
Suspended solids (mg L ⁻¹)	127.7	\pm (23.1)
2. Chemical variables		
pH	8.5	\pm (0.5)
Dissolved O ₂ (mgO ₂ /L ⁻¹)	9.7	-
Al (mg L ⁻¹ Al)	0.5	-
Total As (mg L ⁻¹ As)	0.3	-
Cd (mg L ⁻¹ Cd)	<0.0	-
Ca (mg L ⁻¹ Ca)	204.8	\pm (45.7)
Total CN (mg L ⁻¹ CN)	0.1	-
Bicarbonate (mg CaCO ₃ L ⁻¹)	10.9	\pm (4.6)
Cu (mg L ⁻¹ Cu)	<0.0	-
Total Cr (mg L ⁻¹ Cr)	0.1	-
Fe (mg L ⁻¹ Fe)	0.3	-
Mn (mg L ⁻¹ Mn)	2.4	-
Mg (mg L ⁻¹ Mg)	59.7	-
Fl (mg L ⁻¹ F)	1.3	\pm (0.3)
Sulfate (mg L ⁻¹ SO ₄)	975.6	\pm (36.3)
Ba (mg L ⁻¹ Ba)	0.5	-
Be (mg L ⁻¹ Be)	0.1	-
B (mg L ⁻¹ B)	1.9	-
Co (mg L ⁻¹ Co)	0.0	-
Cl (mg L ⁻¹)	34.2	-
Zn (mg L ⁻¹ Zn)	<0.0	-
Mo (mg L ⁻¹ Mo)	<0.0	-
Hg (mg L ⁻¹ Hg)	<0.0	-
Ni (mg L ⁻¹ Ni)	0.1	-
Pb (mg L ⁻¹ Pb)	<0.0	-
Li (mg L ⁻¹ Li)	0.8	-
Ag (mg L ⁻¹ Ag)	<0.0	-
V (mg L ⁻¹ V)	0.1	-
K (mg L ⁻¹ K)	12.8	\pm (3.6)
Na (mg L ⁻¹ Na)	159.5	-
Na (%)	47.5	-
Se (mg L ⁻¹ Se)	0.0	-
Nitrate (mg N L ⁻¹)	3.3	\pm (2.6)
Nitrite (mg L ⁻¹)	<0.0	-
Phosphate (mg L ⁻¹)	22.4	\pm (30.9)

Table 3. Mean abundance (ind/L-1) of taxonomic groups of invertebrates in study ponds*.

Taxon	Mean \pm s.e.	Relative (%)
Cladocera:		
<i>Daphnia</i> spp. (Daphniidae)	3.6 \pm 1.8	3.8
<i>Alona</i> spp. (Chydoridae)	53.4 \pm 12.4	56.9
Copepoda:		
<i>Eucyclops</i> spp. (Cyclopidae)	11.9 \pm 9.6	12.7
<i>Attheyella</i> spp. (Canthocamptidae)	1.7 \pm 2.4	1.8
Amphipoda:		
<i>Hyalella</i> spp. (Hyallellidae)	0.3 \pm 0.2	0.3
<i>Hyperia</i> spp. (Hyperiididae)	1.0 \pm 1.4	1.0
Ostracoda:		
<i>Hemicypris</i> spp. (Cyprididae)	0.1 \pm 0.0	0.1
Insecta:		
Corixidae	3.4 \pm 0.52	3.6
Chironomidae (larvae)	18.4 \pm 12.6	19.8
Mean	93.8 \pm 26.4	100.0

*Taxonomic nomenclature follows Villalobos (2006) and De los Ríos-Escalante et al. (2013). Mean obtained from four ponds, three years of sampling. Percent dominance = mean taxon *i*/ grand mean.

dominant inorganic non-metal ions were sulfate, chloride, phosphate, and bicarbonate. The content of sulfate + Ca accounted for 96% of total dissolved solids. The Mg/Ca relationship was close to 0.3. Ponds showed the presence of Al, As, Ba, Be, B,

Cd, Co, Cr, Fe, Pb, Li, Mn, Mo, Ni, Ag, V, and Zn, but no Hg, Se or nitrite. The sequence of trace element content was B > Li > Al=Ba > As=Fe > Cr=Ni > Co > Pb > Cu > Cd=Zn > CN.

Invertebrate assemblage

The abundance and richness of invertebrates were rather low (Table 3). No mollusks (e.g., snails) were found. Dominant higher taxa were represented by five taxa of Arthropoda, clearly dominated by Cladocera (60.7 %), followed by Insecta (23.3 %) and Copepoda (14.5%). Less abundant taxa were Amphipoda (1.3%) and Ostracoda (0.1%). At lower taxonomic resolution, the highest abundance corresponded to *Alona* sp. (56.9%), followed by Chironomidae (19.7 %) and *Eucyclops* sp. (12.7 %) Dominance of these taxa remained stable across the study years (Table 4).

Discussion

Typologically, the study ponds are heliotoxic, mesotrophic, and mesopoikilohaline microlimnetopes (Ringuelet, 1962). Their thermal stratification is monomictic, with few degrees difference between surface and bottom. The frequent strong winds and convective currents that occur during nocturnal cooling facilitate water overturn (Cepeda-Pizarro & Novoa, 2006). The characteristics of pond water are in between those of freshwater and truly saline

Table 4. Annual variation and variability among samples (CV) of relative abundance* of invertebrates inhabiting temporary ponds located in the Tambo-Puquíos wet pasture (29°45' S, 69°59' W; Andean transitional desert of Chile).

Taxon	1997			1998			1999		
	Mean	s.e.	CV	Mean	s.e.	CV	Mean	s.e.	CV
<i>Alona</i> spp.	57.4	\pm 45.4	126.3	83.4	\pm 55.0	151.6	81.6	\pm 51.7	158.0
<i>Daphnia</i> spp.	0.1	\pm 0.1	86.5	0.3	\pm 0.2	129.5	0.4	\pm 0.4	120.0
<i>Hyperia</i> spp.	10.4	\pm 26.1	40.0	38.9	\pm 46.6	83.3	29.2	\pm 30.2	96.9
<i>Hyalella</i> spp.	0.3	\pm 0.3	110.5	0.5	\pm 0.4	129.9	0.8	\pm 0.7	113.8
<i>Hemicypris</i> spp.	0.1	\pm 0.2	35.4	0.1	\pm 0.3	43.6	0.4	\pm 0.7	55.4
<i>Eucyclops</i> spp.	11.9	\pm 17.9	66.2	14.8	\pm 21.6	68.6	8.8	\pm 6.3	140.4
<i>Attheyella</i> spp.	1.7	\pm 3.2	53.8	2.2	\pm 4.0	54.5	1.4	\pm 2.4	55.3
Corixidae	2.4	\pm 1.4	175.0	3.5	\pm 1.4	241.7	4.2	\pm 2.3	178.9
Chironomidae	18.4	\pm 13.0	141.1	16.8	\pm 11.1	151.3	47.1	\pm 20.2	233.7

*Mean abundance as ind/L-1.

ponds. Compared to data reported in the literature for natural lentic fresh-waters (e.g. Chapman, 1996), the study ponds are much higher in phosphate, Ca, and sulfate content, and higher in fluoride, Fe, K, Mg, Cl, nitrate and total suspended solids, but lower in bicarbonate and CN content. Apparently, the geochemical properties of the surrounding mountains play a role in the hydrochemistry of these water bodies as documented by early work conducted in the area (Veit, 1993), in accordance with studies carried out in other latitudes (e.g., López *et al.*, 1999). In our case, the high content of sulfate in the study ponds can be explained by the abundance of native sulfur in the area and the active hydrothermal mineralization (Oyarzún *et al.*, 2004).

Chile currently lacks taxonomic expertise for most of the groups of invertebrates inhabiting the Andean waters, and taxonomic resolution of the studies is frequently low (Villalobos, 2006; De los Ríos-Escalante *et al.*, 2013; Alvial *et al.*, 2014). The present study faced this problem as well. Therefore, the presence of the genera communicated in this report should be viewed with caution until confirmed by further taxonomic work, which is currently being carried out. The literature indicates that freshwater ponds are usually dominated numerically by microcrustaceans and insects of the orders Coleoptera (e.g., Dytiscidae, Hydrophilidae), Diptera (Chironomidae), Hemiptera (Corixidae) and Trichoptera (Flores *et al.*, 2009; Jeffries, 2011). Except for Chironomidae and Corixidae, we did not find the remaining taxa of Insecta reported as common in fresh waters. Similarly, compared to streams of the area (Alvial *et al.*, 2014) our study ponds were quite low in insect richness. Chironomidae is a conspicuous family of Diptera found in freshwater lentic habitats, both at low and highlands (Jeffries, 2011). They can become an abundant and diverse group in harsh environments (Oliver & Dillon, 1997). For example, Márquez-García *et al.* (2009) report the presence of Chironomidae in saline water bodies of the southern Altiplano, and Alcocer *et al.* (2001) for a saline lake of Central Mexico. In the wet pastures we studied, Chironomidae is one of the most abundant families of Insecta (Cepeda-Pizarro *et al.*, 2006b). Despite its conspicuousness, taxonomic knowledge of the Andean Chironomidae is quite poor at the specific level (Cepeda-Pizarro *et al.*, 2015).

Inland waters of north-central Chile appear to have low microcrustacean richness (De los

Ríos-Escalante *et al.*, 2013). Our study ponds and the small streams of the area repeat this pattern (Alvial *et al.*, 2014). We did not find Anostraca in our study ponds; however, we report the presence of Daphnids and Chidoriids as representatives of Cladocera: *Alona* sp. is probably *Alona affinis*, the dominant species. Another dominant taxon found in the study ponds was Copepoda, probably represented by *Eucyclops* sp. (Eucyclopidae) and *Attheyella* sp. (Canthocamptidae). Less abundant taxa were *Hyperia* sp. (Hyperiididae), *Hyalella* spp. (Hyalellidae), and *Hemicypris* spp. (Cyprididae). Márquez-García *et al.* (2009) have reported the genus *Alona* from Altiplano ponds, De los Ríos (2005) from northern Andean Chile and Echaniz *et al.* (2006) from saline lakes of the Argentinean Pampa. Moreover, although Amphipoda is reported as dominant group in oligosaline wetlands (500-5000 mg L⁻¹ TDS) (Hart & Loworn, 2005), the literature on Andean saline ponds does not mention it as a common taxon except for Dejoux (1993), who reports Amphipoda as one of dominant taxa in freshwater tributaries of saline lakes in the Bolivian Altiplano. De los Ríos (2005) also mentions the presence of cyclopoid copepods in water bodies located in the Andes of northern Chile. The invertebrate fauna of specific habitats such as our study ponds can diverge from patterns found in most fresh waters. For instance, although taxonomic richness is low in saline ponds, they are richer in specialized fauna (De los Ríos & Crespo, 2004; De los Ríos, 2005; Echaniz *et al.*, 2006; Márquez-García *et al.*, 2009). For the time being we are unfortunately unable to inform whether the ponds host site-specific forms of insects and microcrustaceans.

Given the characteristics of the Andes Range of north-central Chile (Cepeda-Pizarro & Novoa, 2006), the ponds may represent a rather harsh environment for the inhabiting biota. As pointed out by Dorador *et al.*, (2003), the ponds' hydroperiod and the physical-chemical characteristics of the water are expected to be the most important environmental factors shaping the assemblage of invertebrates. The effects of the physical-chemical characteristics have been more widely reported in the literature than the effects of hydroperiods (Flores *et al.*, 2009). For instance, Timms (1983), studying shallow saline waterbodies of Western Australia, reported that many groups contribute to the standing crop at low to moderate salinities, but crustaceans become important at high salinities. At higher salinities,

the invertebrate fauna becomes depauperate, with dominance of a few well-adapted species (De los Ríos & Crespo, 2004). However, salinity is not the only factor mentioned to play a role. Indeed, López *et al.* (1999) showed that salinity along with total dissolved solids, electrical conductivity, and pH explained a high proportion of abundance of plankton community inhabiting ponds found in salt flats of northern Chile. Dissolved oxygen, pH, ionic composition, water transparency, total N, inter-site distances and pond depth are also mentioned (Echaniz *et al.*, 2006; Márquez-García *et al.*, 2009). On the same grounds, the physical-chemical features of mountain streams found in two watersheds of the southern Atacama Desert have been used to explain the differences observed in their aquatic invertebrate communities (Alvial *et al.*, 2014). We believe that the low abundance and taxonomic poorness of invertebrates observed in our study ponds are due to both physical and chemical factors. Among these are the environmental temperature fluctuations (both daily and seasonal), the relative isolation of the wet pasture and the physical-chemical features of pond water, in accordance with studies conducted in nearby watersheds (Ginocchio *et al.*, 2008).

Although the four ponds we studied were in the same wet pasture, they were relatively separated from each other. As documented by former work (Alvial *et al.*, 2014 Cepeda-Pizarro & Armijo, 2014), the water bodies of the area show high spatial variability in their physical-chemical characteristics. This high spatial variability is a phenomenon commonly found in water bodies of arid and semiarid zones (Williams, 1996). This variability may be responsible for the spatial variability in abundance of invertebrates observed in this research. Recently, Briers & Biggs (2005) pointed out that both the spatial pattern in physical-chemical conditions and the physical distance between ponds influence the spatial pattern of community composition, reflecting larger features of the landscape. Following Jeffries (2008), we suspect that the environmental heterogeneity of the system of wet pastures present in the Andean transitional desert of Chile (Squeo *et*

al., 2006b; Osorio *et al.*, 2006) must be very high, where it can become the most important generator of biodiversity. Unfortunately, there is no previous work on this line of reasoning to document this assertion. Declerck *et al.* (2011) advanced the idea that in ecosystems such as those studied here there is scale dependency in the processes that structure meta-communities such as the ones found in the network of wet pastures found in the highland of the Elqui river basin, with environmental control stronger at the smallest spatial scale. From above, it becomes clear that to preserve the biota at a landscape level, it is necessary to draw attention to these small-scale systems for their own specific characteristics (Schwartz & Jenkins, 2000).

In summary, we recorded few invertebrate taxa. This may be a general case for ponds of the Andean transitional desert of Chile. High contents of total solids, sulfate, and Ca characterize the water of the ponds located in the Tambo-Puquíos wet pasture system. Spatial variability in water quality is also high. Along with vagaries of the arid mountain climate, these features can set severe restrictions on the colonizers of ponds. Based on these characteristics, many of these ponds seem to be in a permanent state of immaturity. This scenario forces invertebrates to be in a constant state of recolonization (Frisch & Green, 2007). Given the arid climate and altitude of the site, this process takes place in a temporal framework dominated by not only significant intra-annual variations but also by strong inter-annual variations (Florencio *et al.*, 2009). The low diversity and reduced abundance of invertebrates observed in this study, with clear dominance of few well adapted taxa, may reflect this dynamics.

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