



## BIOLOGICAL SCIENCES

# Chironomidae assemblages at different altitudes in Northwest Argentina: the role of local factors.

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**Abstract:** This study aimed to examine spatiotemporal variations in chironomid assemblages and to detect how environmental variables affect their structure. We sampled seven streams at low and high altitudes in Northwest Argentina under contrasting climate conditions (Puna and Chaco Serrano) during high- and low-water periods. The environmental variables that affected Chironomidae community structure were water temperature, conductivity, hardness, current velocity and type of substrate. Fine substrates, gravel and low water temperature favoured cold stenothermal fauna, composed of Orthocladiinae, Diamesinae and Podonominae specimens in the high-altitude streams, whereas warm waters with low conductivity and higher velocity favoured increased species diversity in lowland streams, where there was greater abundance of Chironominae (which corresponds to warm eurythermal fauna). The studied environments belong to a transition zone that should be preserved where cold stenothermic and warm eurythermal Chironomidae overlap.

**Key words:** Chaco Serrano, Chironomidae larvae, cold stenothermal and eurythermal species, physical and chemical variables, Puna, spatial and temporal variations.

## INTRODUCTION

Spatiotemporal variations in Chironomidae (Diptera) assemblages have been used to assess the trophic status of rivers (Fend & Carter 1995, Paggi 2009) and examined (Jacobsen et al. 1997, Lencioni & Rossaro 2005, Acosta & Prat 2010) in order to further understand the ecological functioning of rivers and biological interactions with the environment (Allan & Castillo 2007).

The study of the Chironomidae family is important at taxonomic and ecological levels due primarily to the great density and diversity they exhibit in disparate aquatic ecosystems, as well as their great plasticity to adapt to different environmental conditions. The immature stages of Chironomidae depend on myriad environmental variables (Merritt & Cummins 1996). The variables that affect

microdistribution (Lencioni & Rossaro 2005) are: current velocity (Lindegaard & Brodersen 1995), which determines substrate composition (Ruse 1992, Wantzen & Rueda Delgado 2009); type of substrate (Ruse 1994, Sanseverino & Nessimian 2001, Hepp et al. 2012); water temperature (Maiolini & Lencioni 2001), which determines the distribution of Chironomidae species (Tokeshy 1995) and differences among cold stenothermal and warm eurythermal species (Cranston 1995); altitude (Lencioni et al. 2007, Scheibler et al. 2014); phosphorus and nitrate concentrations (Ramírez & Pringle 2006, García & Añón Suarez 2007); food resource availability (Tokeshy 1995), which is limited by temperature and velocity (Cranston 1995, Lindegaard & Brodersen 1995); the presence of macrophytes, which favours feeding and environmental aeration and contributes to the formation of refuges to avoid

predation (Velásquez & Miserendino 2003, Bazzanti et al. 2010), resistance to broad salinity ranges (Wiederholm 1983), pH and excessive concentrations of oxygen, metals and toxic substances (Pinder 1995, Fesl 2002, Jacobsen 2008, Hamerlík & Jacobsen 2012, Loayza Muro et al. 2014).

Changes in the Chironomidae community structure have been documented for different mountain aquatic systems (Lods-Crozet et al. 2001, Medina & Paggi 2004, Acosta & Prat 2010, Tejerina & Malizia 2012, Robinson et al. 2016, Hamerlík et al. 2017). However, ecological studies in Northwest Argentina mountain streams are scarce and should be increased, since in a relatively short time they could be altered by human activities due to a mining boom and livestock farming. We selected seven streams with contrasting environmental conditions, due to their differences in climate and altitude, that belong to the Puna and Chaco Serrano ecoregions. Puna streams are permanent waterbodies that flow across a highland plateau (3300-4300 m above sea level [a.s.l.]) with low annual rainfall (100-200 mm) and an arid climate. The lower aquatic systems are embedded in mountain valleys at between 700 and 2000 m elevation and belong to the dry Western Chaco subtropical forest. Streams in these systems are currently in good conservation status; this fact is reflected in the macrofauna community structure and water quality (Colla et al. 2013).

The study of spatiotemporal variations in Chironomidae assemblages should provide information on their community structure and distribution as well as on the influence of physicochemical variables on assemblages located in disparate mountain environments. This data would allow the production of informed management plans and the conservation of these areas, an especially important endeavour because water is scarce and vital for the supply

of nearby populations in these locations. Altitudinal differences influence spatial diversity patterns in chironomid communities, and cold stenothermal species (species that develop within a narrow cold-temperature range) are expected to exhibit greater richness at higher altitudes. Comparatively, warm eurythermal species (species tolerant of higher temperatures) will predominate at lower altitudes. Likewise, physical variables, specifically current velocity, type of substrate and water temperature, affect the chironomid community structure by causing species replacement and changes in relative abundance of organisms at spatiotemporal levels.

Seasonal variations modify the Chironomidae assembly. When there are high waters, there is marked environmental instability with a greater proportion of suspended solids due to storm runoff and increased water flow (Downes et al. 1998, Langton & Casas 1999). At these times, some species disappear and others will decrease in abundance (Rossaro et al. 2006). During low-water periods, the abundance and wealth of taxa is greater due to the stability of the substrate and the slower river water flow (Jacobsen et al. 1997).

Given the above factors, the goals of the present study were: 1) to determine the distribution of Chironomidae species among different altitudes and climatic conditions; 2) to assess temporal variations in Chironomidae community structure during low- and high-water periods; and 3) to establish the environmental variables that affect the community structure.

## MATERIALS AND METHODS

### Study area

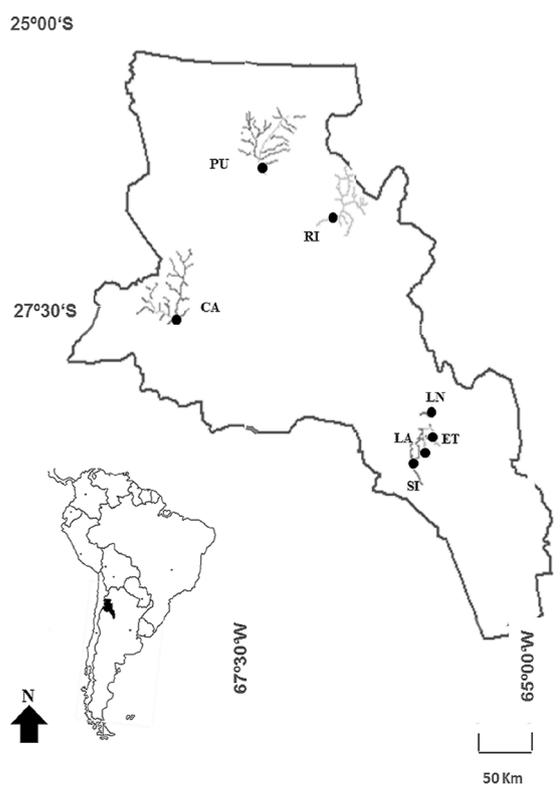
We selected diverse streams located in the Puna and Chaco Serrano ecoregions (Cabrera 1971). The study area was located between 25°12'S and 30°4'S and 69°03'W and 64°58'W, in Catamarca

province, Argentina. Puna is a highland plateau that lies between 3300 and 4300 m a.s.l., with a cold, dry climate and winds that blow all year. Rainfall is scarce (100-250 mm per year) and concentrated in the summer months, from December to March. There is a wide daily temperature range, and high solar insolation levels (Cabrera 1971, Cajal 1988). The vegetation is composed of *Ephedra breana* (Phil.), *Fabiana densa* (J. Remy Phil.), *Baccharis boliviensis* (Wedd.) Cabrera, *Acantholippia salsoides* (Griseb), *Junellia seriphioides* (Gillies & Hook. ex Hook.) Moldenke and *Maihue niopsis* sp. Along riverbanks, *Trichocereus* sp. grows, and flooding areas are populated with *Cortaderia rudi uscula* (Stapf.), *Juncus* sp., *Scirpus asper* (J. Presl. & C. Presl. var. asper.) and Poaceae (Morlans 1995, Borgnia et al. 2006).

Chaco Serrano is a subtropical dry forest that is part of the Western Chaco. Its climate is temperate and semiarid, and summer rainfall prevails, with an annual mean of 750 mm (Morrone 2014). The vegetation grows on hill slopes, in hill forests between 700 and 1600 m elevation, and comprises *Prosopis chilensi* (Molina) Stuntz, *Acacia visco* (Lorentz ex Griseb), *Celtis tala* (Gillex ex Planchon), *Zanthoxylum coco* (Gillies ex Hook. f. & Arn), *Lithraea molleoides* (Vell. Engl.), *Ruprechtia apetala* (Wedd.) and *Schinopsis haenckeana* (Engl.). There are shrubs and grasses above 1500 m a.s.l. and highland grassland above 2000 m a.s.l. At elevations above 3500 m, the vegetation becomes very sparse and High-Andean species appear (Morlans 1995).

### Sampling sites

We sampled seven streams during periods of low water (winter, June-August) and high water (summer, December-January) over an annual cycle (Figure 1). Streams from volcanoes and those formed from mountain ice melting, which drain into lakes of the Puna ecoregion, were: Del Cazadero (CA: 3457 m a.s.l., 27°25'13.9"S,



**Figure 1.** Location of Puna and Chaco Serrano streams, Catamarca, Argentina.

68°08'16.2"W), Río (RI: 3345 m a.s.l., 26°02'63.8"S, 67°24'69.2"W) and Punilla (PU: 3379 m a.s.l., 26°02'56.56"S, 67°24'43.10"W). Streams from rainfall runoff and springs located in Chaco Serrano were: El Simbolar (SI: 890 m a.s.l., 28°39'02.21"S, 66°03'11.69"W), Los Angeles (LA: 1556 m a.s.l., 28°28'51.50"S 65°57'0.19"W), Los Nogales (LN: 1330 m a.s.l., 28°11'23.17"S, 65°52'36.42"W) and El Tala (ET: 880 m a.s.l., 28°25'45.80"S, 65°57'0.19"W).

### Environmental variables

At each sampling site, we measured the following environmental variables: water temperature (°C), pH and conductivity ( $\mu\text{S cm}^{-1}$ ) with a CIBAR CORNING multimeter, wet width of the streambed (m, with a measuring tape), maximum stream depth, depth of the sampling site (m, with a calibrated stick), stream order (Strahler 1957), current velocity ( $\text{m s}^{-1}$  with the float

method; Gordon et al. 1994) and substrate type. Substrate composition was estimated from the percentages of medium blocks (0.5-1 m), small blocks (0.25-0.5 m), pebbles (6.4-25 cm), cobbles (3.2-6.4 cm), gravel (2-3.2 mm) and sand (0.6-2 mm; Cummins 1992) in the field. Measurement of fine fractions was performed in the laboratory by separating coarse material (sand) from fine material by sieving and subsequently separating fine materials (silt and clay) using the Stokes principle with the pipette method (Folk 1974).

In the laboratory, we also determined the concentration (in  $\text{mg l}^{-1}$ ) of  $\text{CO}_3^{2-}$ ,  $\text{HCO}_3^-$ , total hardness, total dissolved solids (TDS),  $\text{Cl}^-$ ,  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{PT}$ ,  $\text{SO}_4^{2-}$ ,  $\text{NO}_2^-$  and  $\text{NO}_3^-$  following standard methods (APHA 1998). The percentage of coarse particulate organic material (CPOM) and fine particulate organic material (FPOM) was examined in samples obtained with a Surber net. We used a 1000  $\mu\text{m}$  sieve to separate CPOM fractions and a 62  $\mu\text{m}$  sieve to separate FPOM. These particles were subsequently oven dried for 4 h at 500°C and weighed with a scale (APHA 1998).

### Chironomidae sampling and identification

Benthic invertebrates were sampled using a Surber net (with a 900  $\text{cm}^2$  sample area) and a 300  $\mu\text{m}$  mesh collecting net. Three replicates were obtained per sampling site; a total of 42 samples were collected. Samples were fixed *in situ* in 4% formaldehyde solution for later laboratory processing. In the laboratory, larvae were grouped into morphospecies using a stereomicroscope and then stored in 70% alcohol. Permanent microscopic slides were prepared for identification at the lowest possible taxonomic level, following Brundin (1966), Roback & Coffman (1983), Epler (1995), Wiedenbrug (2000), Paggi (2009) and Prat et al. (2012, 2014). All specimens were deposited in the Limnology Institute "Dr. Raúl A. Ringuelet"

(CONICET, UNLP, La Plata; ILPLA), and in the Centro de Investigaciones y Transferencia in Catamarca (CITCA-CONICET-UNCA).

### Data analyses

To estimate abundance and taxonomic richness for each sample, we developed a matrix of biotic (in  $\text{m}^{-2}$  per morphospecies) and abiotic data (environmental variables) per replicate, season (high and low water) and sampling site. To calculate taxonomic diversity for each sampling site and season, we used the Shannon-Wiener diversity index ( $H'$ ) with MultiVariate Statistical Package 2000 (MVSP) version 3.11.

To verify the degree of similarity between sampling sites, considering taxonomic richness and chironomid abundance, we performed a modified Morisita similarity analysis (UPGMA method, MVSP version 3.11). To examine spatiotemporal variations in biotic variables (total abundance, diversity and richness of each species), we used generalised linear models (GLMs; Genstat version 4.2, 2005) using seasons (S: winter and summer) and sampling sites (SS) as factors. Discrete data (density and richness) were analysed with a Poisson distribution, and continuous data (diversity) were analysed following a normal distribution (Crawley 1993, McConway et al. 1999).

To analyse the relationship among environmental variables, Chironomidae species and sampling sites, we performed a canonical correspondence analysis (CCA) using MVSP version 3.11. Prior to the CCA, we conducted a Spearman correlation analysis to determine the degree of correlation among environmental variables. The variables that showed high correlation values ( $p \geq 0.60$ ) were eliminated from the CCA.

To examine differences in environmental and biotic variables among sites and seasons, we used GLMs; sites and seasons were the response

variables while biotic and environmental factors were the explanatory variables. Only those environmental variables that presented low correlation with one another (based on the Spearman correlation analysis results) were analysed. Continuous data (diversity, depth, TDS, bicarbonate, nitrate, nitrite, magnesium, potassium, sodium, CPOM and FPOM) were analysed using a normal distribution. Discrete data (density and richness) were analysed by considering a Poisson distribution (Crawley 1993, McConway et al. 1999). The percentage of variation explained by the model for each environmental variable was estimated as follows: % of explained variability = (explained deviance or variance/total deviance or variance) x 100.

## RESULTS

### Environmental characterisation

High-altitude streams showed calcium bicarbonate (CA) and sodium chloride (RI) in the waters. Water temperature was relatively low; it fluctuated between 3 and 12°C (Table I). The substrate was mainly composed of sand and gravel (depending on the stream). Lower-altitude streams contained calcium bicarbonate in the waters. Water temperature fluctuated between 6 and 25.2°C. Overall, these streams had warmer waters compared to the higher-altitude streams. The substrate was dominated by gravel and cobbles (Table I).

GLM analysis revealed that pH, altitude, TDS, bicarbonate, nitrate, sulfate, calcium, magnesium, potassium, sodium, chloride, total phosphorus, FPOM, CPOM and substrate (medium blocks, small blocks and clay) exhibited greater significant differences among sites than between seasons (Table II). High-altitude streams had more alkaline waters (maximum pH was in PU; 8.50), high calcium concentrations

(maximum value was in RI; 70 mg/L), magnesium (maximum value was in CA; 73.50 mg/L), potassium (maximum value was in CA; 20.50 mg/L), a considerable TDS concentration (maximum value was in CA; 730 mg/L), higher percentage of FPOM (maximum value was in RI; 15.9%) and a substrate composed of a higher proportion of clay (maximum value was in RI; 1%) compared to lower-altitude stream sites (Chaco Serrano).

### Chironomidae assemblage composition

From a total of 42 analysed samples, we found 3986 specimens that belonged to five subfamilies and 21 genera of Chironomidae (Diptera; Table SIII - Supplementary Material). The subfamily Orthocladiinae showed high relative abundance at the highest altitudes (CA, PU and RI streams) and LN at a lower altitude (1300 m), whereas Chironominae occurred in higher proportions in the lower-altitude ET, LA and SI streams (Figure 2). Podonominae larvae predominated at the highest elevation (3300-3400 m). During low-water periods, the most abundant subfamilies were Orthocladiinae (90%) and Chironominae (63%) in Chaco Serrano streams. Comparatively the predominant subfamilies during high-water periods were Orthocladiinae (93%) in Puna streams and Chironominae (59%) and Tanypodinae (47%) in Chaco Serrano streams. The Podonominae subfamily exhibited moderate relative abundance in low waters, whereas Diamesinae specimens were highly abundant in the high waters at the highest altitude (3345 m).

Faunal composition demonstrated more differences at the spatial rather than the temporal level (Table SIV). The highest variability at the spatial level was observed at the highest altitudes.

**Table 1. Environmental parameters measured at the seven streams in Puna and Chaco Serrano ecoregions. Mean values and standard deviation (in parentheses). ND = no data.**

	LN		ET		LA		SI		CA		PU		RI	
	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW
Altitude (masl)	1333		880		1556		890		3457		3387		3345	
Strahler order	2		3		2		4		3		2		3	
Wet width (m)	3.0 (1)	7.2 (1)	4.0 (1)	5.60 (2)	5.5 (1)	6.40 (1)	5.5 (2)	5.85 (2)	3.60 (2)	3.80 (2)	6.65 (2)	4.77 (1)	6.20 (2)	7.10 (2)
Current speed (m s <sup>-1</sup> )	0.09 (1)	0.11 (2)	0.23 (5)	0.18 (4)	0.16 (5)	0.26 (6)	0.87 (10)	0.26 (12)	0.20 (20)	0.22 (10)	0.11 (10)	0.87 (5)	0.26 (4)	0.24 (8)
Depth (m)	0.14 (1)	0.23 (1)	0.16 (2)	0.26 (2)	0.15 (2)	0.23 (1)	0.17 (1)	0.16 (3)	0.30 (1)	0.27 (1)	0.17 (3)	0.21 (2)	0.18 (2)	0.27 (3)
Mean depth (m)	0.41 (2)	0.50 (9)	0.30 (5)	0.49 (2)	0.40 (1)	0.45 (1)	0.43 (1)	0.55 (2)	0.26 (1)	0.29 (1)	0.23 (1)	0.29 (3)	0.22 (2)	0.28 (1)
pH	7.3 (1)	5.7 (2)	6.8 (0.1)	5.3 (1)	8.1 (1)	6.7 (0.1)	8.23 (2)	7.97 (0.1)	7.3 (2)	6.4 (3)	8.19 (0.1)	7.63 (1)	8.18 (1)	7.71 (2)
Water temperature (C°)	10.2 (1)	18.9 (3)	16.7 (5)	21.1 (3)	6 (5)	25.2 (3)	11 (9)	22.5 (5)	6 (3)	11.7 (5)	7.5 (4)	12 (5)	3 (4)	4 (3)
Conductivity (µs/cm <sup>-1</sup> )	87.4 (3)	60.2 (1)	122.2 (2)	96.6 (5)	120.2 (4)	133.3 (2)	250 (2)	268 (3)	1089 (6)	961 (7)	360 (5)	555 (1)	997 (2)	812 (3)
TDS (mg/L)	64.64 (1)	70.23 (2)	85.12 (1)	95.32 (1)	83.2 (2)	92.13 (1)	132 (1)	153 (1)	634.88 (3)	690.2 (2)	330 (2)	250 (2)	587 (1)	549 (2)
HCO <sub>3</sub> <sup>-</sup> (mg/L)	198.2 (5)	155.92 (6)	237.86 (2)	190.3 (2)	325 (1)	174.4 (2)	68.4 (1)	75.4 (1)	683.08 (5)	634.3 (4)	63.45 (3)	118.6 (3)	101.3 (4)	78.45 (2)
CO <sub>3</sub> <sup>2-</sup> (mg/L)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	3.6 (0.1)	0.00 (0)	31.18 (0.5)	7 (0.4)	0.00 (0)	0.00 (0)	10.2 (0.3)
T. hardness (mg/L)	39 (3)	22.05 (3)	32 (2)	36.5 (1)	39 (1)	61 (1)	137 (1)	168 (2)	127 (2)	122.5 (2)	70 (1)	253 (1)	232 (1)	223 (2)
SO <sub>4</sub> <sup>2-</sup> (mg/L)	3.0 (0.1)	0.4 (0.2)	2.4 (0.2)	2.2 (0.1)	2.1 (0.1)	1.4 (0.1)	ND	0.8 (0.2)	150 (0.1)	19.8 (0.1)	ND	ND	ND	9.23 (0.1)
NO <sub>3</sub> <sup>-</sup> (mg/L)	0.234 (0.1)	0.017 (0.1)	0.191 (0.2)	0.002 (0.1)	0.184 (0.1)	0.002 (0.1)	ND	0.25 (0.2)	1 (0.1)	0.123 (0.2)	ND	ND	ND	1.1 (0.1)
NO <sub>2</sub> <sup>-</sup> (mg/L)	0.002 (0.2)	0.005 (0.2)	<0.001 (0)	<0.001 (0)	<0.001 (0)	<0.001 (0)	ND	0.006 (0.1)	0.003 (0.1)	0.003 (0.2)	ND	ND	ND	<0.001 (0)

Table I. Continuation.

	LN		ET		LA		SI		CA		PU		RI	
	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW
TP (mg/L)	0.005 (0.1)	0.039 (0.1)	0.019 (0.2)	0.014 (0.1)	0.014 (0.1)	0.016 (0.1)	ND	0.009 (0.1)	0.075 (0.1)	0.084 (0.1)	ND	ND	ND	0.08 (0.1)
Cl <sup>-</sup> (mg/L)	22.01 (0.2)	53.17 (0.1)	31.55 (0.1)	92.7 (0.1)	28.03 (0.2)	66.65 (0.1)	4 (0.1)	4 (0.1)	197.81 (0.1)	122.30 (0.1)	31.99 (0.3)	66.5 (0.2)	146 (0.1)	195.63 (0.2)
Ca <sup>2+</sup> (mg/L)	10.82 (2)	9.62 (1)	10.62 (2)	11.62 (3)	18.03 (3)	25.65 (3)	40 (4)	50.4 (4)	58.14 (4)	29.26 (3)	22.1 (2)	30 (2)	61.8 (4)	66 (4)
Mg <sup>2+</sup> (mg/L)	12.39 (3)	4.13 (1)	8.5 (1)	10.69 (2)	19.93 (2)	14.1 (3)	9.6 (2)	10.08 (1)	52.64 (4)	41.81 (3)	4.4 (2)	11.25 (2)	18.72 (1)	13.92 (3)
Na <sup>+</sup> (mg/L)	20.60 (12)	7.51 (10)	17.81 (4)	11.06 (10)	15.581 (3)	10.94 (2)	ND	1.39 (10)	148.71 (20)	121.85 (20)	ND	ND	95.3 (12)	100.56 (0.2)
K <sup>+</sup> (mg/L)	1.28 (0.2)	1.53 (0.2)	3.64 (0.3)	2.08 (0.2)	3.407 (0.2)	2.10 (0.2)	ND	8.92 (0.1)	15.73 (0.1)	17.42 (0.3)	ND	ND	7.56 (0.3)	10.34 (0.1)
CPOM (%)	16.63 (8)	17.02 (32)	6.78 (30)	4.32 (12)	10.29 (10)	9.65 (8)	12.45 (9)	16.75 (10)	1.20 (10)	1.02 (9)	1.12 (8)	1.00 (8)	2.17 (7)	1586 (0.7)
FPOM (%)	2.38 (3)	3.45 (5)	0.77 (3)	0.98 (1)	2.62 (2)	3.21 (5)	4.57 (5)	3.27 (3)	0.30 (2)	0.16 (2)	0.60 (2)	0.64 (3)	9.67 (3)	10.8 (4)
Median block %	0.5 (0.2)	0.5 (0.3)	1 (0.1)	1.5 (0.1)	1.8 (0.1)	2 (0.7)	2.0 (0.6)	3.0 (0.8)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.5 (0.1)	0.5 (0.1)
Small block %	1.6 (0.5)	1.6 (0.6)	2.5 (0.2)	3 (0.1)	2 (0.6)	3 (0.2)	9.0 (0.4)	8.7 (0.2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.5 (0.2)	0.5 (0.2)
Pebble %	2 (0.8)	3 (0.9)	7.2 (0.4)	8 (0.5)	5.9 (1)	3.7 (0.6)	10.0 (0.9)	13.0 (0.6)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	3.0 (0.6)	2.5 (0.9)
Cobble %	35.5 (2)	32.6 (2)	42.1 (2)	39.4 (1)	39.8 (0.4)	42.4 (1)	16.1 (0.4)	25.0 (1)	20.2 (3)	19.0 (1)	10.5 (0.4)	9 (0.2)	7.0 (1)	6.8 (0.9)
Gravel %	39 (1)	43.9 (2)	33.9 (3)	30.7 (1)	34.9 (2)	30 (1)	41.0 (2)	32.0 (1)	38.0 (2)	35.0 (1)	40.4 (2)	35 (0.7)	42.5 (2)	38 (2)
Sand %	18 (1)	15.5 (0.8)	10.4 (2)	13.5 (1)	12.2 (0.9)	15 (2)	20.05 (1)	17.3 (1)	39.3 (3)	41.6 (2)	43.6 (3)	50 (2)	40 (2)	46.3 (1)
Silt %	0.9 (0.3)	0.9 (0.4)	0.6 (0.3)	0.9 (0.2)	0.15 (0.1)	0.9 (0.6)	0.02 (0.2)	0.02 (0.2)	0.3 (0.1)	0.9 (0.1)	1 (0.1)	1 (0.5)	0.5 (0.1)	0.4 (0.1)
Clay %	2.5 (0.6)	2 (0.7)	2.3 (0.2)	3 (0.1)	3.25 (0.2)	3 (0.3)	1.8 (0.2)	1 (0.1)	2.2 (0.2)	3.5 (0.2)	4.5 (0.9)	5 (0.2)	6 (0.4)	5 (0.2)

**Table II. Summary of GLMs analysis used to examine differences in environmental variables among sites and seasons.**

	Site				Season			
	F/X <sup>2</sup>	df	P	% variability explained	F/X <sup>2</sup>	df	P	% variability explained
pH	48.49	6	<0.001	10.86	121.56	1	<0.001	27.22
Altitude	8.16	6	<0.001	1.52	0.02	1	1.0	0.001
TDS	720.38	6	<0.001	99.21	0.12	1	0.73	0.003
CO <sub>3</sub> <sup>2-</sup>	4.57	6	0.002	6.63	7.52	1	0.010	10.9
HCO <sub>3</sub> <sup>-</sup>	238.82	6	<0.001	96.84	12.75	1	0.001	0.86
NO <sub>3</sub> <sup>-</sup>	3.4	6	0.010	18.37	0.03	1	0.086	0.054
NO <sub>2</sub> <sup>-</sup>	8.53	6	<0.001	50.91	15.32	1	<0.001	15.24
SO <sub>4</sub> <sup>-2</sup>	9.05	6	<0.001	0.014	3277.3	1	0.032	0.0081
Ca <sup>2+</sup>	49.77	6	<0.001	89.78	0.00	1	0.945	0.0014
Mg <sup>2+</sup>	113.18	6	<0.001	94.12	8.39	1	0.007	1.16
Na <sup>+</sup>	567.67	6	<0.001	16.46	13.81	1	<0.001	0.399
K <sup>+</sup>	57.37	6	<0.001	89.29	7.25	1	0.011	1.88
Cl <sup>-</sup>	43.37	6	<0.001	14.37	7.41	1	0.010	2.45
TP	6.03	6	<0.001	7.99	5.24	1	0.028	6.95
CPOM	232.67	6	<0.001	97.61	0.10	1	0.755	0.007
FPOM	387.19	6	<0.001	98.43	2.99	1	0.093	0.13
Median block	27.70	6	<0.001	79.53	8.75	1	0.006	4.19
Small block	1221.34	6	<0.001	99.44	7.28	1	0.011	0.09
Clay	52.71	6	<0.001	90.29	0	1	0.962	6.81

### Spatiotemporal variations in the Chironomidae community structure

Taxonomic richness and diversity showed significant seasonal differences among the sampling sites. In general, richness was low; however, there was a notable increase during low-water periods for all the sampling sites (Figure 3). The highest diversity (2.88 bits) was recorded for the low-altitude SI stream during low-water periods, and the lowest diversity was observed for the CA stream at the highest

altitude (1.87 bits) during the high-water period. GLM results demonstrated that taxonomic richness was nearly similar between seasons ( $F_{4,1-1} = 25.47$ ;  $p < 0.001$ ; explained variability = 32%) and among sampling sites ( $F_{4,1-6} = 3.55$ ;  $p = 0.008$ ; explained variability = 26%). On the other hand, diversity was more variable among sampling sites ( $F_{4,1-6} = 20.68$ ;  $p < 0.001$ ; explained variability = 78%) than between seasons ( $F_{4,1-1} = 0.79$ ;  $p = 0.379$ ; explained variability = 0.5%).

Chironomidae assemblage compositions were not very similar among the streams. Morisita similarity analysis (Figure 4) revealed the existence of two groupings. The first grouping was formed by high-altitude streams (CA and RI) with 49% similarity. This grouping shared the following species in common; *Podonomus* sp., *Cricotopus (Isocladius)* sp. 2, *Cricotopus* spp., *Paracladius* sp., Genus 1, *Polypedilum* sp., *Limnophyes* sp. and *Rheotanytarsus* sp. The second grouping was linked to streams of different altitudes, namely PU (high altitude) and LN, LA, SI and ET (lower altitudes), and showed a low similarity coefficient (24%). The sampling sites that were most related in faunal composition were LA and SI, both located at lower altitudes; they shared *Cricotopus (Oliveiriella)* *almeidai*, *Pseudochironomus viridis*, *Cricotopus* spp., *Parametriocnemus* sp., Genus 1, Genus 10, *Rheotanytarsus* sp., *Pentaneura* sp. and *Polypedilum* sp.

### Influence of environmental variables on species distribution

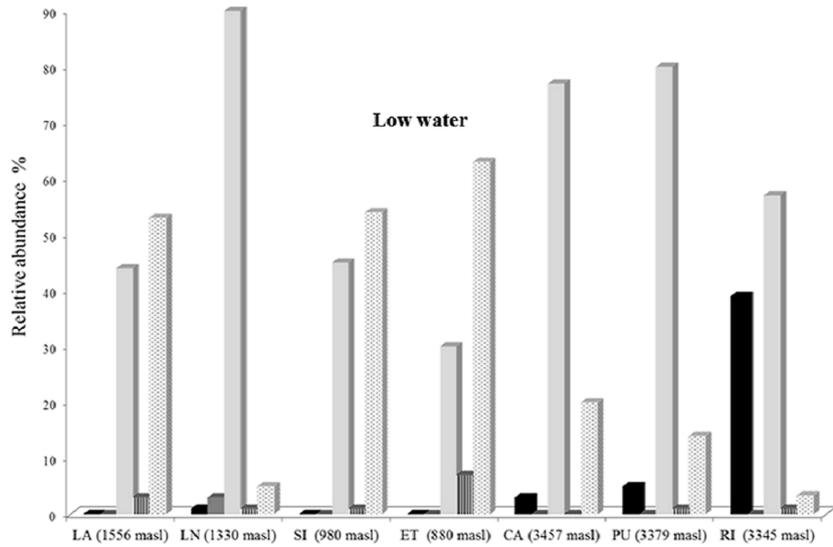
The following variables were highly correlated: carbonate, altitude, chloride, sodium, pH, nitrate, nitrite, sulfate, phosphate, TDS and clay with conductivity ( $r = 0.70$ ;  $p \geq 0.60$ ), calcium with hardness ( $r = 0.90$ ;  $p \geq 0.60$ ), TDS and pebbles with silt ( $r = 0.87$ ;  $p \geq 0.60$ ), wet width with current velocity ( $r = 0.87$ ;  $p \geq 0.60$ ), depth with water temperature ( $r = 0.93$ ;  $p \geq 0.60$ ), CPOM with gravel ( $r = 0.80$ ;  $p \geq 0.60$ ), potassium and magnesium with cobbles ( $r = 0.87$ ;  $p \geq 0.60$ ), FPOM with sand ( $r = 0.70$ ;  $p \geq 0.60$ ), bicarbonate and pebbles with carbonate ( $r = 0.70$ ;  $p \geq 0.60$ ) and medium blocks with calcium and potassium ( $r = 0.77$ ;  $p \geq 0.60$ ). Consequently, carbonate, altitude, chloride, sodium, calcium, potassium, magnesium, pH, nitrate, nitrite, sulfate, phosphate, TDS, bicarbonate, CPOM, FPOM, medium blocks, small blocks, pebbles, clay and

the width and depth of the sampling sites were excluded from the CCA. This analysis (Figure 5) showed that the first three axes explained 59.7% of the accumulated variance. The correlation of environmental variables with species was high for Axis 1 (0.94) and Axis 2 (0.95), results that indicate a close relationship among organisms and environmental variables. Water temperature, current velocity and cobbles were significantly correlated with Axis 1, whereas Axis 2 was defined by conductivity, total hardness, silt, gravel and sand (Figure 5).

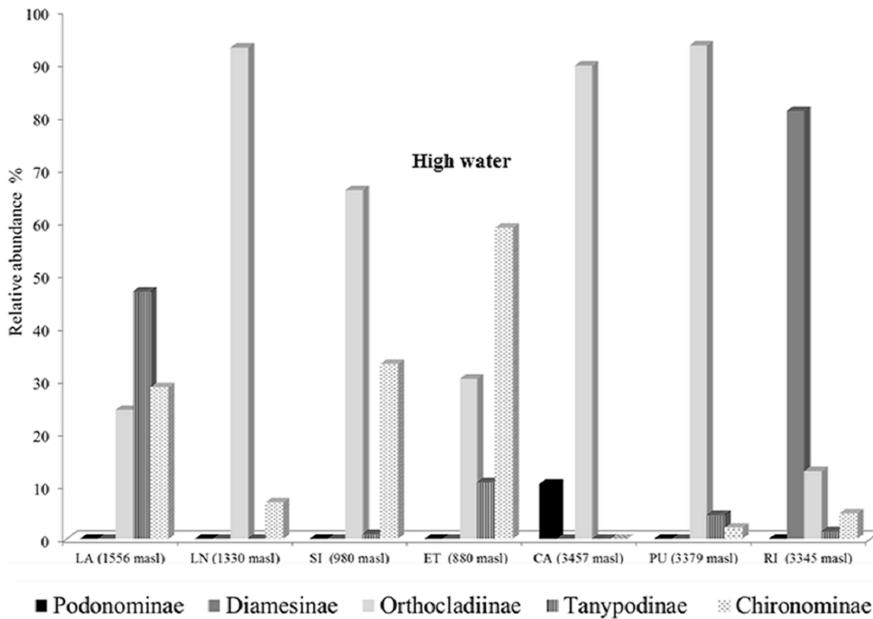
*Pentaneura* sp., *Pseudochironomus viridis*, *Rheotanytarsus* sp., *Parametriocnemus* sp., *Cricotopus* sp. 3, Genus X, Genus 10, *Polypedilum* sp. and *Larsia* sp. showed a preference for high water temperature and a substrate composed of a higher proportion of cobbles. These environmental variables characterise SI, LA and ET. *Onconeura* sp., *Corynoneura* sp., *Cricotopus (Isocladius)* sp. 2, *Cricotopus (Oliveiriella)* *almeidai*, taxon richness and diversity were associated with high flow velocities, a physical variable that defines LN and ET sampling sites. *Cricotopus (Isocladius)* sp. 1, *Cricotopus* sp. 1 var A and *Podonomus fastigians*, showed a preference for a substrate composed mostly of silt, which characterises PU. *Limnophyes* sp., *Apsectrotanypus* sp., Genus 1, *Paracladius* sp., *Cricotopus* spp., *Podonomus* sp. *Cricotopus* (C.) f.l.4, *Allocladius quadrus*, *Paraheptagyia cinerascens*, *Paraheptagyia* sp. 2, *Paraheptagyia* sp. 1 and *Stictocladius prati* presented an affinity for highly conductive, hard and cold waters and a substrate composed of gravel and sand, variables that characterise CA and RI (Figure 6).

### DISCUSSION

In the present study, the Chironomidae assemblages were composed by a dominant

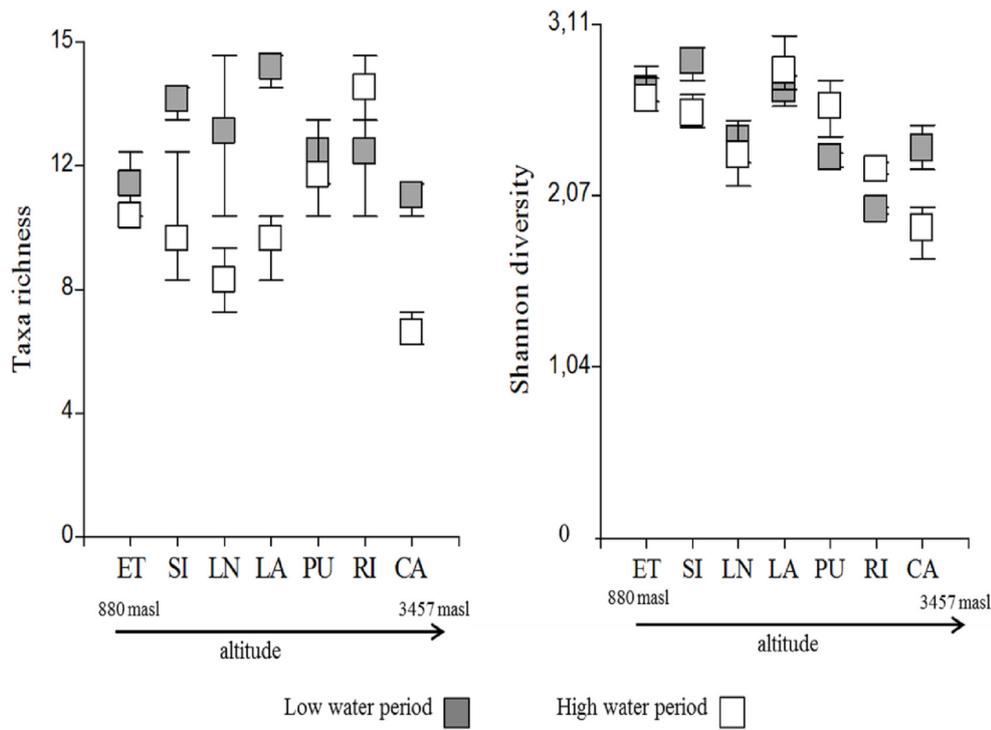


**Figure 2.** Relative abundance of subfamilies for each season in the seven reaches (Puna and Chaco Serrano streams) sampled in the study.

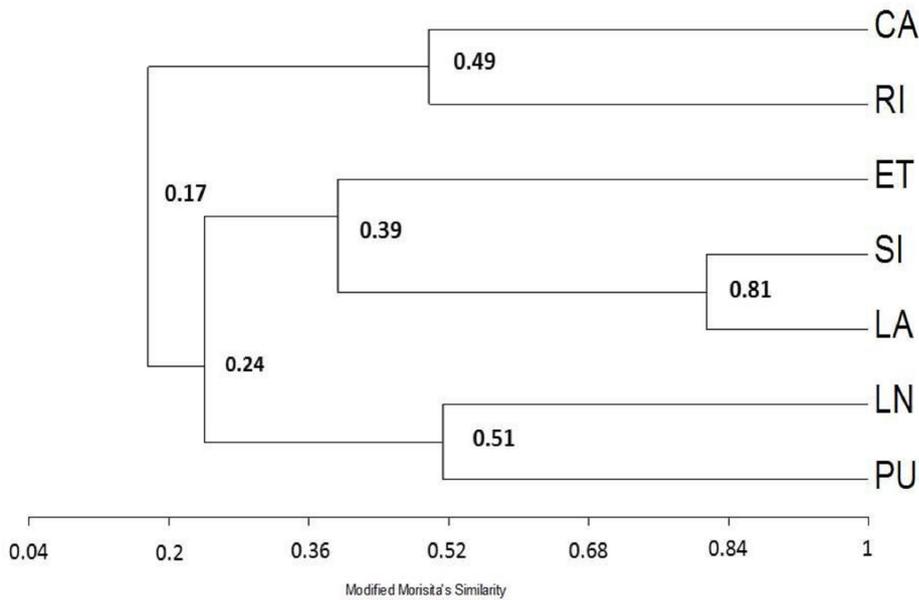


community, constituted mainly by the Orthoclaadiinae, Diamesinae and Podonominae subfamilies (Loayza Muro et al. 2014) at the highest altitudes and Chironominae in lowlands (Lods-Crozet et al. 2001, Maiolini & Lencioni 2001, Acosta & Prat 2010). Among the altitudes, Orthoclaadiinae showed the greatest diversity. This finding follows the distribution pattern proposed by Lindegaard & Brodersen (1995), who noted the predominance of Orthoclaadiinae at highland sites and their reduced abundance

in lowland areas. These findings are in agreement with research conducted at several mountain aquatic systems (Jacobsen 2008, Lencioni et al. 2011, Scheibler et al. 2014). In contrast, the Chironominae dominated at lowland sampling sites, where they exhibited low diversity. The Tanypodinae specimens were not well represented among the sampling sites, because the low temperatures typical of highland rheophilic environments favour the dominance of Podonominae and Diamesinae



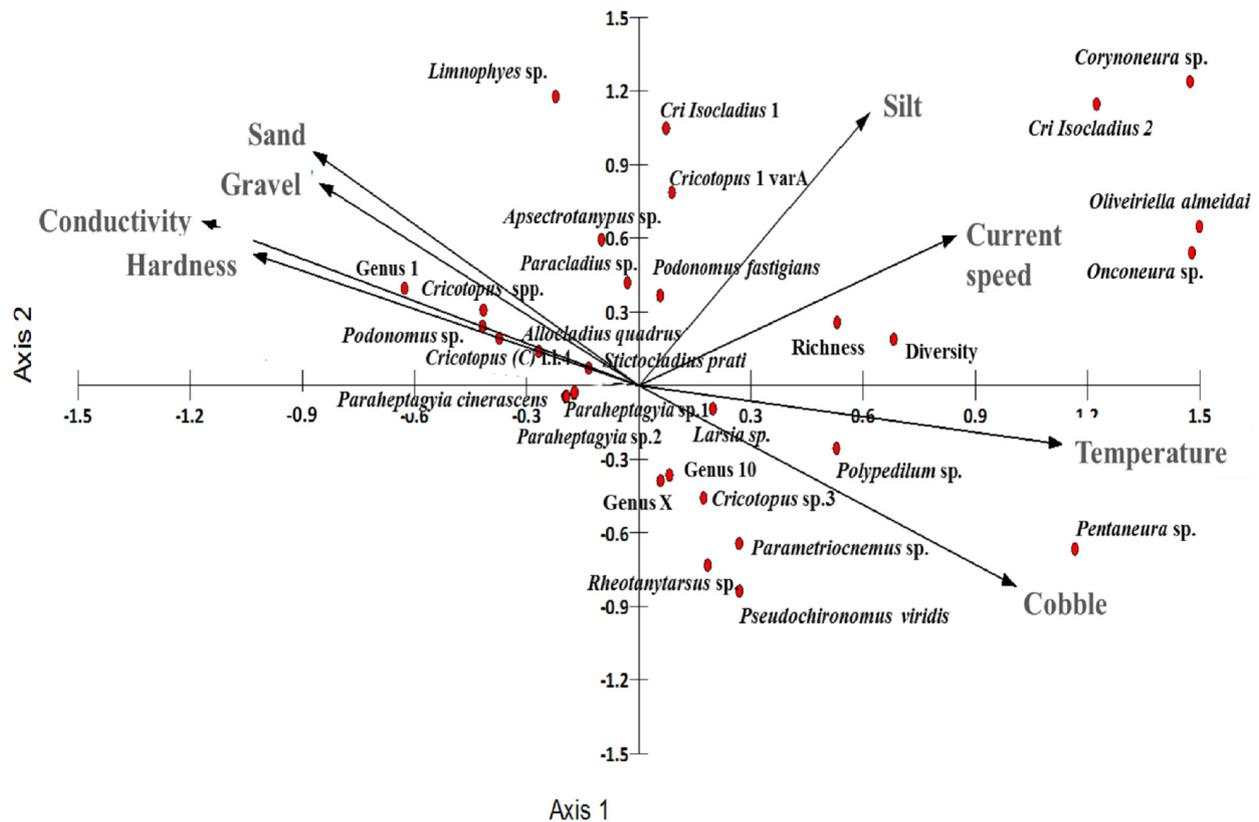
**Figure 3.** Shannon diversity index and richness of Chironomidae taxa for each sampling sites and period. Range bars show minimum and maximum values.



**Figure 4.** Modified Morisita's Cluster showing similarity between benthic communities at different altitudes.

and a nival freshwater system. Both subfamilies are representative of high Andean environments (Scheibler et al. 2014). Altitude, a variable spatially correlated with diverse environmental variables (Finn & Poff 2005), including water

temperature, plays a determining role in the distribution of these subfamilies, which are found at the headwaters of streams that originate from glaciers or snowfields. In these waters, water flow, hardness, suspended

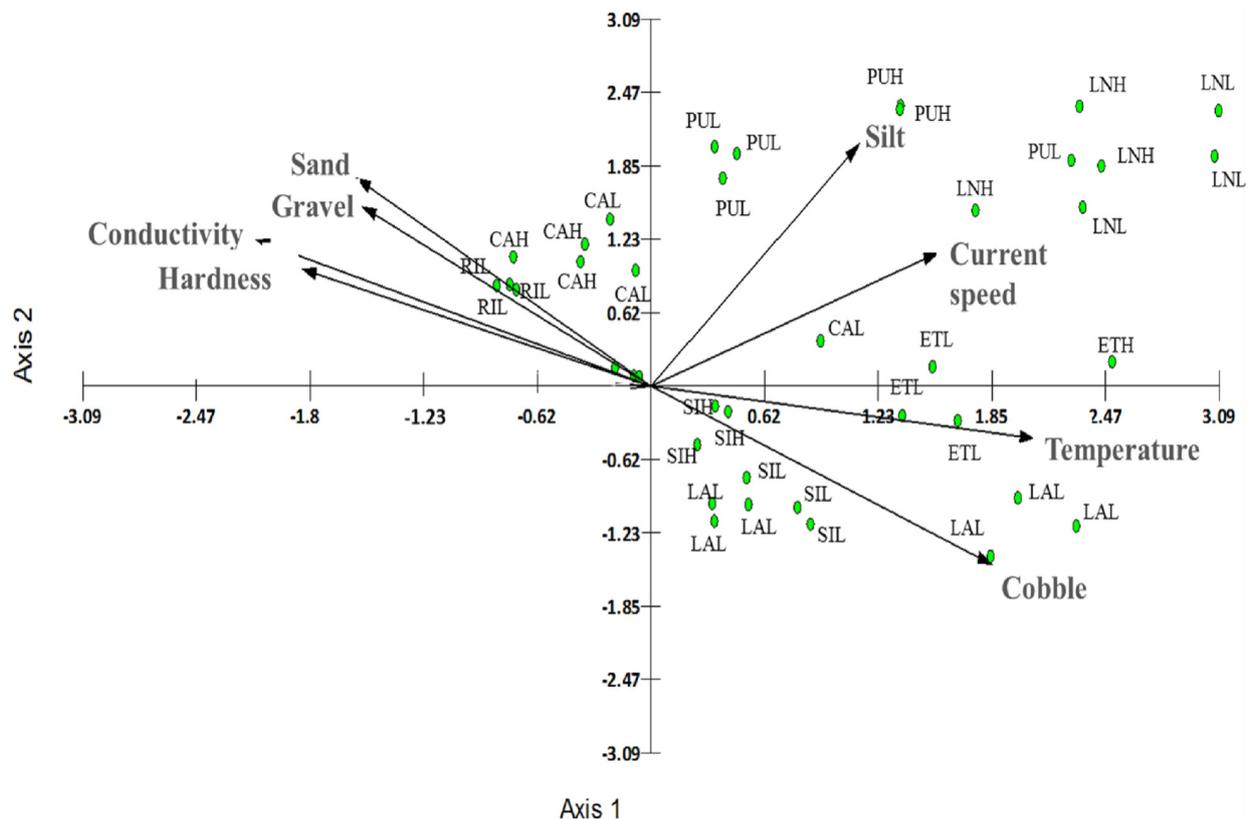


**Figure 5.** Canonical Correspondence Analysis (CCA) between Chironomidae species and environmental variables in the seven reaches of Chaco Serrano and Puna streams.

sediment load and conductivity are the most stressing variables that affect chironomid species development (Scheibler et al. 2014). The highest density and richness of Chironomidae larvae is reported in high-altitude and latitude streams (Füreder 1999, Lods-Crozet et al. 2001), and these representatives are the only insects present when environmental conditions worsen (Niedrist & Füreder 2016).

High-altitude streams were characterised by Orthoclaadiinae, Podonominae and Diamesinae subfamilies, all of which correspond to the Andean-Patagonian region. Comparatively, low-altitude streams would belong to the tropical-subtropical region due to the presence of Chironominae (Ashe et al. 1987). Moreover, taking into account the biogeographic scheme proposed by Morrone (2006), the study area

corresponds to a South American transition zone that exhibits an overlap of Andean and subtropical neotropical Chironomidae taxa, where cold stenothermal and warm eurythermal organisms coexist. Their presence reflects the intermediate area to which they belong, where temperature, snow melt and rainfall regulate species presence and distribution among regions (Richardson & Whittaker 2010, Thomas 2010), factors that in turn establish the permanence of organisms with different ecological requirements. Consequently, these transition environments are considered diversity hotspots and could function as sentinel ecosystems for climate change as well as areas for species dispersal (Reid 1998, Morrone 2014, McLaughlin et al. 2017).



**Figure 6.** Canonical Correspondence Analysis between sampling sites and environmental variables (CCA) in Chaco Serrano and Puna streams. References: LN: Los Nogales, LA: Los Angeles, SI: El Simbolar, ET: El Tala, RI: Río, CA: Del Cazadero, PU: Punilla. H: high water; L: low water.

We recorded temporal variations in species richness and abundance, with higher richness and abundance during low-water periods (winter). During this season, streamflow is low, and therefore the substrate is more stable, a phenomenon that promotes greater habitat heterogeneity (Burgherr & Ward 2001). Conversely, during high-water periods (summer), streamflow increases due to rainfall runoff and ice melting from mountain peaks, with consequent substrate removal, increased suspended solids and altered richness and abundance of immature chironomid stages (Rossaro et al. 2006). Additionally, water temperature rises in the summer, a change that favours adult emergence and reduces the zoobenthic community. These variations in zoobenthic abundance are common in mountain

streams and occur along the longitudinal profile, both at highland (Acosta & Prat 2010, Tejerina & Malizia 2012, Jacobsen et al. 2014) and lowland streamflows (Fend & Carter 1995, Príncipe et al. 2008).

The environmental variables that strongly affected Chironomidae species distribution were water temperature, conductivity, total hardness, current velocity, and substrate type (mainly silt, sand, gravel and cobbles). Conductivity is a variable that considerably affects benthic faunal composition (Nieto et al. 2017), and it is related to climate and the geology of the streambed substrate (Segnini & Chacón 2005). In the present study, the increase in conductivity modified chironomid abundance and changed the community composition among the sampling sites. Substrate also plays a key role

in chironomid microdistribution (Ruse 1994). Additionally, current velocity is a determining factor for substrate composition and stability (Ruse 1992, Lindegaard & Brodersen 1995). A coarse substrate acts as a refuge (Coffman & Ferrington 1996, Henriques-Oliveira et al. 2003) and, along with high velocities, favours the feeding of filtering larvae, such as *Rheotanytarsus* and Genus X (Sanseverino & Nessimian 2001). In general, Chironomidae species at the highest altitudes inhabited stressed environments characterised by hard waters, high conductivity values and low water temperature (3-12°C), all of which are environmental features of high mountain streams and rivers (Tejerina & Malizia 2012, Scheibler et al. 2014). In contrast, streams at lower altitudes exhibited better physical (warm water temperature, low suspended sediment load and predominance of cobbles) and chemical conditions (slightly mineralised waters and lower total hardness values). These features favour a wide ecological gradient suitable for a variety of benthic invertebrate species. Consequently, these conditions promote high diversity of aquatic insects (Colla et al. 2013, Rodríguez Garay & Paggi 2015). Our streams belong to the rhithral systems (rain/snowmelt dominate); depending of the source of stream, it can produce environmental conditions that are responsible for the variability in the water physicochemical conditions further downstream (Brown et al. 2006).

Our study reflects an altitudinal zonation pattern for chironomids, with changes in the composition of their assemblages due to altitude changes. At higher altitudes, we found cold stenothermal fauna, whereas warm eurythermal species were found at lowland sites, in accordance with Cranston (1995) and in corroboration of findings for other mountain regions in Argentina (Medina & Paggi 2004, García & Añón Suárez 2007, Príncipe et al. 2008,

Miserendino et al. 2008, Tejerina & Malizia 2012, Scheibler et al. 2014). Cold stenothermal chironomids (Podonominae, Diamesinae and some Orthocladiinae species) distributed at higher altitudes are vulnerable because they are restricted to narrow environmental ranges; they would be the first organisms required to modify their distribution and faunal composition with temperature rise from climate change. Temperature elevation would increase water evaporation, and this change, concomitant with the rainfall scarcity typical of a semiarid environment, would increase the frequency of droughts and the consequent accumulation of dry biomass, both of which are factors that trigger forest fires (Allen et al. 2010, Argañaraz et al. 2015). In turn, accumulation of ash from fires would modify the physicochemical water conditions (Temporetti 2006, Mellon et al. 2008), with the resulting disappearance of species or their displacement to other areas (Irons et al. 1993). However, how community structures would be modified is not well known (Khamis et al. 2015). Monitoring high-altitude streams as our freshwater systems may be critical for preventing a potential loss of unique and sensitive stream biota. Anthropogenic activities, including dam construction, cattle grazing and human recreation, modify habitat heterogeneity (Uieda et al. 2017) and cause mountain streams to change. These activities, combined with the pervasive effects of climate change, will likely result in biodiversity loss for many communities in snowmelt streams that are especially sensitive to environmental alterations (Milner et al. 2015, Robinson et al. 2016). As the Earth warms up, cold-adapted species retreat to even higher elevations, and so high-altitude macroinvertebrate communities will become increasingly important for conserving mountain stream biodiversity (Robinson et al. 2003, Jacobsen et al. 2012). Thus, it is critical that we

understand how these communities respond to variations in environmental conditions across wide spatiotemporal scales to improve our understanding of these sentinels of anthropogenic change.

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## SUPPLEMENTARY MATERIAL

### Tables SIII and SIV.

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