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Seasonal influence and local factors affecting macroinvertebrate structure in a high-altitude Andean stream

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Abstract: Small water bodies are critical for maintaining freshwater biodiversity, but are among the least investigated aquatic environments. We examined physical and chemical variables at two reaches in Arroyo Tambillos, a small, high-elevation Andean stream, in NW Mendoza province, Argentina, across four seasons to examine how local factors and seasonality affected the structure of the macroinvertebrate community. The Arroyo Tambillos community was numerically dominated by ephemeropterans (mainly *Massartellopsis irarrazavali*) while the dipteran Chironomidae were the most species rich. Total macroinvertebrate abundance was highest in summer, driven mainly by taxa that were secondary in dominance (*Austrelmis sp.* and *Andesiops peruvianus*), while richness did not differ between seasons. However, benthic composition was different in Fall 2013 (March) compared to other seasons, largely because of the increased abundance of Chironomidae. Canonical correspondence analysis discriminated Chironomidae species distributions in Fall 2013 by substrate type (i.e., big and small boulder substrate). By contrast, discharge, velocity, and depth were the variables which most affected the macroinvertebrate abundance and distributions. Contrary to our expectations, most community changes observed occurred in fall instead of summer. Nivo-kryal stream communities like the one described here have become increasingly important for conserving mountain stream biodiversity as anthropogentic impacts and climate change increasingly impact lower stream reaches. Therefore, monitoring high-altitude streams like the Arroyo Tambillos may be critical for preventing the future loss of unique and sensitive

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Introduction

Mountain streams are highly heterogeneous systems that exhibit wide variation in physical and chemical conditions, attributes that make them ideal for understanding how environmental variation shapes biological patterns (Wellnitz et al. 2001; Finn and Poff 2005; Scheibler et al. 2014). Identifying and investigating these patterns can reveal functional processes indicative of biological integrity or stream 'health' (Heino et al. 2004; Feld and Hering 2007). Benthic macroinvertebrate communities are especially useful for discerning biological patterns because they readily respond to environmental variation at multiple scales of space and time (Füreder 1999; Beisel et al. 2000; Jacobsen 2004; Costa and Melo 2008).

Environmental variation and hydrology across time often depends on the regional climate and water sources (Richards et al. 1997; Füreder et al. 2005). Climate can affect such key environmental factors as stream temperature, discharge and current (Hawkins et al. 1997). For high mountain streams, seasonal differences in these factors are often driven by snow and glacial melt, which in turn affect a variety of biotic and abiotic factors (Burgherr and Ward 2001; Miserendino and Pizzolón 2003; Füreder 2005 et al.; Bogan and Lytle 2007; Scheibler and Debandi 2008). Previous work in large, high-elevation Andean rivers has shown macroinvertebrate richness and abundance responds to temporal variation in environmental variables linked to discharge, which markedly increases in summer as snow and glacial melt rates increase (Scheibler et al. 2014). Small Andean streams may respond similarly, but there is a lack of knowledge about the functioning of these systems.

Like other small water bodies, first- and second-order mountain streams are critical for maintaining freshwater biodiversity. They have been increasingly recognized for their role in providing ecosystem services (carbon cycling, removing excess nutrients, degrading waste and toxic substances) and their cultural value (recreation) (Biggs et al. 2016). Small streams may also respond differently to perturbations and disturbances than do large rivers. For example, Miserendino et al. (2012) found that the recovery of benthic communities in Patagonian streams affected by volcanic eruptions were more rapid in large rivers than small streams, suggesting that small streams may be more vulnerable and less resilient to environmental changes, especially when changes are unpredictable and stochastic (Poff 1997). Similarly, small streams may be more vulnerable than large rivers to climate change and other anthropogenic impacts (Haghkerdar et al. 2019). Thus, it is important that small mountain streams be monitored across seasons to understand how annual variations in environmental conditions affect their macroinvertebrate communities. Such an understanding could lead to more effective management of these systems and help managers address the threats they face (Biggs et al. 2016).

We designed a study to examine how local environmental factors and seasonality affected macroinvertebrate community structure in a high-elevation Andean stream in Central Argentina. Headwater streams in this region are poorly studied and little is known about their macroinvertebrate composition, much less how their macroinvertebrate communities respond to variations in environmental factors (Scheibler PhD Thesis 2007). We examined physical and chemical variables in two reaches of the stream for a year. We predicted that the greatest change in the macroinvertebrate community structure (abundance, richness, and composition) would occur in summer due to increased snowmelt discharge, in a manner similar to what was found in large mountain rivers.

1 Materials and Methods

1.1 Study area

The Arroyo Tambillos (channel slope: 12.16%, Strahler order 2, discharge: 0.58 $m^3 s^{-1}$) is a permanent stream that drains the Cordillera del Tigre sub-basin of the dry and arid Cordillera Frontal (Andean Frontal Range) in NW Mendoza province, Argentina (32°22'7.56" S, 69°26'9.66" W) (Figure 1). The Cordillera del Tigre lies approximately 30 km east of Cerro Aconcagua and runs parallel to the Cordillera Principal (Andean Principal Range), extending north and south. Arroyo Tambillos originates on the eastern slope of Cerro los Tambillos (5580 m) and is fed by snowmelt and glacial runoff. The stream is turbid during periods of high discharge in spring and summer, becoming clear during baseflow in fall and winter (Scheibler 2007 unpublished data). The study area has a mountain tundra climate typical of the High Andes region (Trombotto 1991). Mean annual precipitation is 127 mm, with 69% of it occurring during October and March. Mean annual temperature is 12.4°C, with a mean annual minimum of 3.8°C and maximum of 18.6°C (Servicio Meteorológico Nacional). The Tambillos flows through rangeland where livestock grazing is common, but sampling sites were located upstream of the main grazing areas.

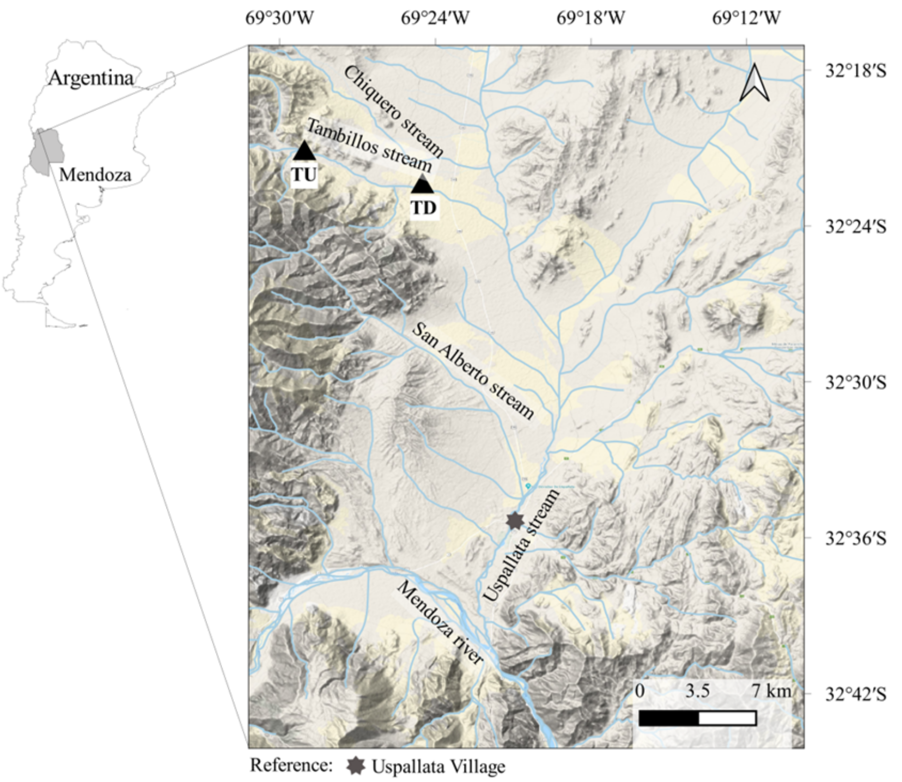

Figure 1 Location of the study sites in the Arroyo Tambillos. Reach 1 (TU) is the upstream site at 2630 m asl, Reach 2 (TD) is the downstream site at 2470 m asl elevation. The map shows Uspallata valley with Arroyo Tambillos, Arroyo San Alberto and Arroyo Uspallata draining into the Mendoza River basin. Blue lines indicate rivers and streams.

1.2 Sampling and laboratory procedures

Benthic samples of macroinvertebrates and physicochemical parameters were collected four times during the study period: in March 2012 (Fall 2012), December 2012 (Early summer 2012), February 2013 (Late summer 2013), and March 2013 (Fall 2013).

We selected two sampling sites having different streambed morphology that we called Tambillos upstream (TU) and Tambillos downstream (TD) (Figure 1). The TU site was located 2630 m above sea level (asl), and approximately 15.5 km from the source glacier that fed the stream (e.g., the nivo-kryal section, Milner et al. 2010). This reach was wide and shallow compared to TD which was deeper and narrower and located at 2470 m asl and 3.2 km downstream from TU. The TU riparian zone was dominated by *Adesmia trifuga* (40%), *Senecio Uspallatensis* (35%), and *Mulinum patagonico* (15%). TD had riparian vegetation comprised largely of *Senecio subulatus* (82%) with patches of *Stipa ichu* (7%) and *Junellia ligustrina* (7%). Wetted width for both reaches was between 2.5 and 4 m depending on the season (Table 1).

We established a 20 m study reach at each site. Each study reach had four transects running perpendicular to the stream, with sampling points at 0, 5, 10 and 15 m. Across each transect there were three locations for collecting Surber samples, one at each stream margin and one at the stream center, giving a total of 12 samples per reach. The samples were treated as replicates for analyses. Surber samples were taken with a Fieldmaster®

Table 1 Environmental parameters measured at the two reaches in Arroyo Tambillos between the 2012 Fall and 2013 Fall. Mean values and standard deviation (in parentheses). Water and air temperatures are minimum and maximum values. Temperatures for 2012 Fall were lost.

TU: Reach 1

Factor	2012 Fall	Early summer (2012)	Late summer (2013)	2013 Fall
pH	7.21 (0.46)	7.91 (0.15)	7.61 (0.06)	7.49 (0.12)
Water temperature (ºC)	-	5.1-19.1	8.0-25.4	4.8-18.5
Air temperature (ºC)	-	4.4-32.4	6.0-42.1	1.63-1.9
Conductivity (µS cm^{-1})	248 (2)	234 (6)	138 (1)	250 (3)
Wet Width (m)	2.55 (0.49)	2.13 (0.18)	2.88 (0.18)	4 (0.42)
Discharge (m^{3} s^{-1})	0.47 (0.13)	0.44 (0.02)	0.85 (0.09)	1.15 (0.35)
Depth (m)	0.21 (0.14)	0.15 (0.05)	0.18 (0.08)	0.23 (0.09)
Velocity (m^{2} s^{-1})	0.21 (0.12)	0.30 (0.14)	0.36 (0.12)	0.35 (0.13)
Big block (%)	0	0	0	0
Median block (%)	0	0	0	0
Small block (%)	0	0	0	0
Pebble (%)	54.58 (38.05)	56.25 (30.83)	59.58 (31.66)	28.33 (34.60)
Gravel (%)	41.25 (41.07)	33.33 (29.80)	31.67 (29.87)	32.08 (29.73)
Sand (%)	4.17 (11.65)	10.42 (13.05)	1.67 (5.77)	1.67 (5.77)

TD: Reach 2

Factor	2012 Fall	Early summer (2012)	Late summer (2013)	2013 Fall
pH	7.69 (0.38)	8.23 (0.03)	6.78 (0.51)	7.49 (0.12)
Water temperature (ºC)	-	5.8-19.7	11.1-22.7	5.8-18.1
Air temperature (ºC)	-	6.6-44.3	10.9-46.0	0.6-35.1
Conductivity (µS cm^{-1})	236 (3)	222 (1)	138 (1)	250 (3)
Wet Width (m)	2.43 (0.04)	2.5 (0.35)	3.6 (0.85)	2.8 (0.28)
Discharge (m^{3} s^{-1})	0.89 (0.35)	0.90 (0.14)	1.28	0.91 (0.15)
Depth (m)	0.28 (0.14)	0.27 (0.07)	0.30 (0.09)	0.23 (0.09)
Velocity (m^{2} s^{-1})	0.27 (0.13)	0.37 (0.18)	0.44 (0.18)	0.33 (0.11)
Big block (%)	0	0	0	1.67 (5.77)
Median block (%)	8.33 (28.87)	0	0	0
Small block (%)	0	2.92 (10.10)	0	55 (36.87)
Pebble (%)	37.50 (35)	56.67 (37.13)	59.58 (31.66)	28.33 (34.60)
Gravel (%)	49.17 (35.09)	33.33 (34.86)	18.75 (20.01)	9.17 (16.21)
Sand (%)	5 (14.46)	7.08 (24.54)	21.67 (35.63)	5.83 (6.34)

“mini-Surber” having a 0.023 m^{2} sample area and a 500 µm mesh collecting net.

Benthic samples were preserved in 90% ethanol and macroinvertebrates were identified to the lowest feasible taxonomic level using the keys by Dominguez and Fernandez (2009), Paggi (2009) and Prat et al. (2011, 2014). Ephemeroptera, Plecoptera, Trichoptera, and Coleoptera were identified to genus or species. Diptera were identified to family, except for Chironomidae, which were identified to genus. Water mites were grouped into the superfamily Hydracarina, and Annelida and Nematoda were identified to class.

Environmental measurements included depth, near-bed current velocity and substrate grain size using the Wentworth scale (Allan 2007). Boulder substrate were subdivided into three size categories: big block (1-2 m); median block (0.5-1 m), and small block (0.25-0.5 m). Near-bed current was measured between 11:00-14:00 during each sampling period using a MiniWater20 Micro-velocity probe (Schiltknecht Messtechnik AG, Zürich). The velocity probe was placed at each corner of the square Surber sampler frame for 6 s, and the Schiltknecht meter “rep” function was used to find the mean near-bed current velocity. The four measures were averaged to determine near-bed current for each Surber sample. We also measured pH (Hanna pH meter HI 9025), conductivity (µS cm^{-1}, Hanna conductivity meter HI 9033), water transparency (m, Secchi disk), air and water temperature (°C), and discharge (m^{3} s^{-1}). Discharge was estimated using the formula Q= maximum depth (m) × maximum current velocity (m sec^{-1}) × wetted width of the streambed (m). Wetted width was measured twice, at the upstream and downstream end of each reach and the average was calculated for each reach for each sampling period. Average maximum depth and maximum velocity were calculated from 12 measurements taken across a single transverse profile. Air and water temperatures were recorded every hour using Onset Hobo® Pendant data loggers (UA-002-08) for a period of five days.

1.3 Data analysis

1.3.1 Environmental features of the system

We used the R-Project program (version 3.3.2, R Core Team 2016) for statistical analyses, except where otherwise stated.

To examine differences in physical and chemical variables among seasons and reaches, we used Generalized Linear Models (GLMs). Reach and season were the response variables and conductivity, pH, discharge, depth, velocity, and substrate type were explanatory variables. These parameters were analyzed using a normal distribution and identity link function. Substrate type was analyzed using binomial distribution and logit link function (Binomials totals = 100). The percent variation explained by the GLMs for each environmental variable was estimated as: % of explained variability = (explained variance/total variance) (100).

1.3.2 Macroinvertebrate community patterns

GLMs were used to analyze how macroinvertebrate structure (i.e., richness, total abundance, and abundance of dominant taxa) varied among seasons and reaches. Stepwise regression (Poisson distribution with logit link function) was used to model relationships, and the best-fitted models were selected based on the Akaike Information Criterion (AIC). In the event of having multiple delta AIC values < 2, we selected the most parsimonious model. The percent variation in the data explained by the model was estimated as: % of explained variability = (model deviance/null deviance) (100) of the best model (Aydin and Tuzemen 2010).

1.3.3 Response of macroinvertebrate community

We performed Canonical Correspondence Analysis (CCA) to compare distribution of macroinvertebrates across seasons and in relation to the environmental variables measured. None of the variables were strongly correlated ($r < 0.6$) and all were included in the analysis.

An Analysis of Similarity (ANOSIM) was performed with PRIMER 6 (Clarke and Gorley 2006) to compare community composition among seasons and reaches. ANOSIM tests the null hypothesis that the similarity between groups (different seasons or reaches) is greater than or equal to the similarity within the groups. R values (i.e. the strength of the factor on the samples) varied between 0 (no separation of groups with the factor analyzed) and 1 (high separation between groups of the factor), and the *P* value denotes the significance level of the R value.

In addition, a Similarity Percentage Analysis (SIMPER) was performed with PRIMER 6 to determine which taxa best explained the differences among groups differentiated by ANOSIM. Bray-Curtis distance was used to quantify dissimilarity between groups and data were square root-transformed to decrease the influence of dominant species. To examine how environmental variables affected the distribution of common taxa, GLMs (Poisson distribution with logit link function) were performed. Response variables were taxonomic richness and abundance of total and dominant taxa. The full model included reach, season, and their interaction. Best-fitted models were selected using AIC values as stated above.

2 Results

2.1 Environmental features of the system

Table 1 shows the physical and chemical characteristics of the sites during the study period. Environmental variables changed across seasons and reaches (Table 2, Figure 2). With the exception of depth and substrate type (although small block was more abundant in Fall 2013), measured variables changed with season (Table 2). pH values were neutral in Fall (March = 6.88-7.64) and Late Summer (February 2013 = 6.08-7.69) and more alkaline in Early Summer (December = 7.72-8.27). Velocity was higher in both Early and Late Summer, and discharge was higher during Late

Summer and Fall 2013. Conductivity was higher during the fall. Reaches showed some differences in physical variables. TD had greater discharge (maximum = 2.43 $m^3 s^{-1}$, Late Summer) and was deeper than TU. Substrate type distribution was similar between reaches, with the exception of blocks of all size categories that were present only at TD.

2.2 Macroinvertebrate community patterns

Macroinvertebrate samples from Arroyo Tambillos contained 4379 individuals representing 31 taxa (Appendix 1). Four taxa accounted for over 90% of the individuals: the ephemeropterans *Massartellopsis irarrazavali* and *Andesiops peruvianus* (77%), the coleopteran *Austrelmis sp.* (6%), and dipterans of the Chironomidae family (10%) (Figure 3).

Total macroinvertebrate abundance differed across seasons and reaches, but the best model explained only 16% of the variance (Table 3), suggesting variables other than those measured could be associated with variation in macroinvertebrate abundance. Total abundance was greatest at the TU site and varied across season (Figure 3). In terms of individual taxa, we found that *M. irarrazavali* abundance tracked total macroinvertebrate abundance. By contrast, *Austrelmis sp., A. peruvianus* and Chironomidae showed only seasonal changes, with the model explaining nearly 50% of the variability for *A. peruvianus* and Chironomidae (Table 3). Higher abundances were recorded for *Austrelmis sp. and A. peruvianus* during the summer (Figure 3), whereas Chironomids reached their highest abundance in Fall 2013 (Figure 3).

We found 33 taxa in total. Diptera exhibited the greatest richness (19 taxa), and were comprised largely of Chironomidae (11 taxa). Chironomids were represented by four subfamilies, of which Orthocladiinae was the richest (7 taxa). The best model for richness explained approximately 30% of the variance and included reach, season and their interaction; however, none of these variables were significant by themselves (Table 3).

Community composition was similar between reaches and across seasons. Though we did detect differences, these were quite small as judged by R values (reaches: R = 0.14, p = 0.00; seasons: R= 0.14, p = 0.001). Pairwise tests revealed that macroinvertebrate composition in Fall 2013 differed significantly from that of all other seasons (Fall 2012: R= 0.26, p = 0.001, Early Summer: R= 0.26, p = 0.001, Late Summer: R= 0.20, p = 0.001). SIMPER analysis showed that differences in taxonomic composition were driven by groups that were secondary in abundance after the most common taxon, which in all cases was *M. irarrazavali*. Across seasons, and reaches, *M.*

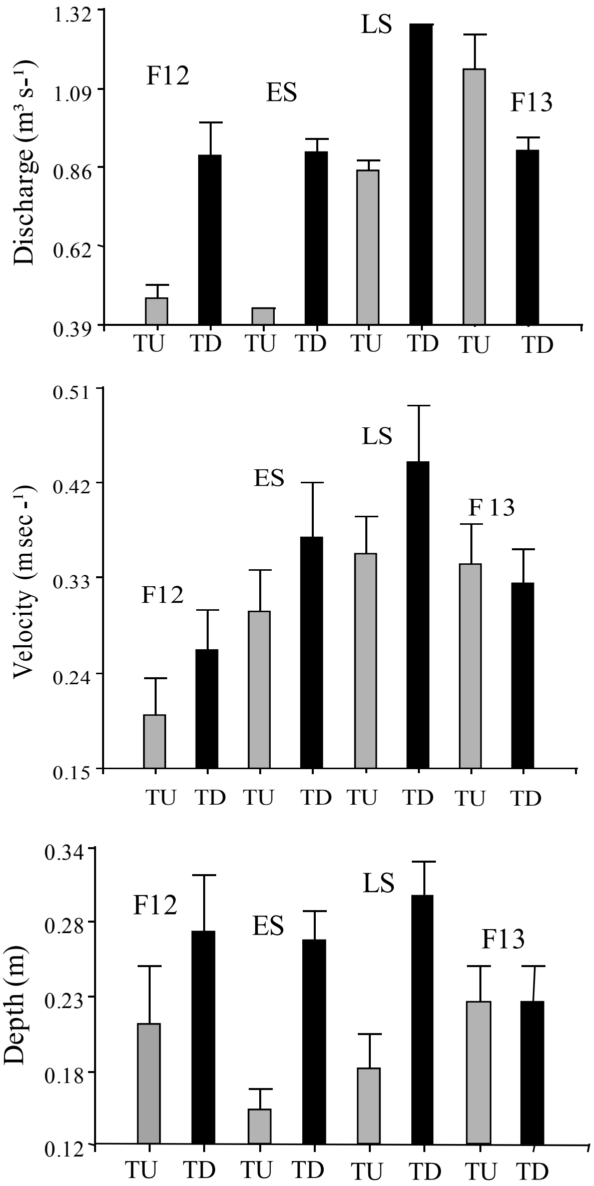

Figure 2 Mean and standard error of physical variables (discharge, velocity, and depth) at both reaches across seasons. TU: reach 1, TD: reach 2, F12: Fall 2012, ES: Early Summer 2012; LS: Late Summer 2013, F13: Fall 2013.

Table 2 Summary of Generalized Linear Model (GLMs) analysis used to examine differences in environmental variables among sampling reaches, and seasons. "%" is the percent variability explained by significant factors in the model, n/a = not applicable.

	Reach				Seasons			
	F	*df*	*p*	%	*F*	*df*	*p*	%
Velocity	3.12	1-95	0.081	n/a	5.80	3-95	0.001	15.40
Depth	15.94	1-95	<0.001	13.47	0.64	3-95	0.592	n/a
Discharge	20.00	1-95	<0.001	12.00	18.90	3-95	<0.001	34.01
Conductivity	45.09	1-95	<0.001	0.43	3449.18	3-95	<0.001	99
pH	0.01	1-95	0.925	n/a	22.03	3-95	<0.001	42
Small block	n/a	n/a	n/a	n/a	57.83	3-95	<0.001	45.38
Pebbles	4.03	1-95	0.048	4.10	1.06	3-95	0.372	n/a
Gravel	1.09	1-95	0.298	n/a	2.48	3-95	0.066	n/a
Sand	3.87	1-95	0.052	3.86	1.74	3-95	0.164	n/a

Table 3 Effect of reach and season on richness, total abundance, and abundance of the four most common taxa in response to environmental variables. Values are regression coefficients from Generalized Linear Model (GLMs) analyses. The sign and magnitude of the coefficient relate to the factors of the corresponding variable being compared. Bold coefficients were significant at $p<0.05$.

Response variables	Richness	Total Abundance	*M. irarrazavali*	*A. peruvianus*	*Austrelmis*	Chironomidae
% variability explained	28.65	16.32	16.82	47.16	22.66	53.29
Reach (TU vs TD)	-0.0834	**0.3145**	**0.5850**	0.1022	0.2392	-0.1643
Season						
F12 vs ES	-0.2638	**-0.2468**	**-0.1795**	**-0.2595**	**-1.3652**	**-1.2528**
F13 vs ES	-0.3629	**-0.7297**	**-0.6142**	**-2.5998**	**-1.3652**	-0.2412
LS vs ES	0.2767	-0.0076	0.0827	**-0.5013**	-0.2392	-0.1967
Reach*Season						
TU-F12	0.0647	0.0275	-0.1650	**1.1019**	**-1.1216**	-0.3212
TU-F13	-0.4762	**-0.6294**	-0.0803	0.6710	**-1.8319**	**-2.1337**
TU-LS	0.4834	**0.2400**	0.1888	**0.7546**	-0.4995	**1.1026**

Notes: for season, F12 = Fall 2012, ES = Early summer, LS = Late summer, and F13 = Fall 2013. TU = reach 1; TD = reach 2.

irarrazavali comprised from 46% to 62% of the individuals in the samples, whereas taxa of secondary importance varied across seasons and reaches (Table 3). Seasonally, *A. peruvianus* was the second most abundant taxon for Fall 2012 (March), Early Summer (December) and Late Summer (February), whereas three species of Chironomidae (Genus 1, *Cricotopus* sp. 3, and *Cricotopus* f. l. 6) were the second most abundant taxa for Fall 2013 (March). For reaches, *A. peruvianus* was of secondary importance in TU, whereas *Austrelmis* sp. was the second most abundant group in TD.

Some taxa were found exclusively in one reach or season (Appendix 1). For example, the dipterans Blephariceridae and Athericidae, and Hirudinea and Nematoda were only found at TU, whereas Ephydridae (Diptera) and the Acari were present only at TD. Among the Chironomidae, *Podonomus* sp. and *Bardocladius andinus* (Cranston and Krosh 2011) were present only at TU, whereas *Limnophyes* sp., *Cricotopus* sp. 1 and *Cricotopus* (*Isocladius*) were exclusive to TD. Similarly, taxa such as Hirudinea, Nematoda and Ephydridae, and the chironomids *Cricotopus* sp.1 *and Cricotopus* (*Isocladius*) were found only in one season.

The CCA ordination distinguished samples between reaches, with TD samples in Fall 2013 dispersed along axis 1, while most of the remaining samples were clustered in the center of the graph. Only axis 1 was significant at separating samples (Table 4) and the variables that significantly contributed to this axis where small and big blocks (both present only at TD) (Table 5; Figure 4a). In the species ordination graph, species of chironomids (sp. 10 to sp. 20 in Figure 4b; see Appendix 1) were the most dispersed in the environmental space delineated by the CCA axes.

Table 4 Results of Monte Carlo permutation test showing the significance of the first Canonical Correspondence Analysis (CCA) axis.

Axis	Eigenvalues (constrained)	Eigenvalues (unconstrained)	*F*	*p*
1	0.2835	0.0797	14.755	0.001***
2	0.0516	0.0569	2.689	0.43

Table 5 Significance values of environmental variables selected by the Canonical Correspondence Analysis model

Variables	*F*	*p*
Velocity	1.055	0.346
Depth	1.153	0.273
Big block	7.506	0.002 ***
Median block	0.345	0.845
Small block	8.844	0.001 ***
Pebble	0.758	0.584
Gravel	0.613	0.672
Sand	0.687	0.675
pH	0.929	0.442
Conductivity	1.293	0.192
Discharge	1.140	0.285

Note: *** significant *p* value

When analyzing how physical variables affected the richness and abundances of major taxa, GLM results revealed that only depth was associated with richness changes (approximately 19% of variance explained), whereas depth, velocity and discharge affected total abundance (28% of variance explained). In general, greater depths were associated with lower abundances and richness. Near-bed current velocity had a positive effect on total abundance, *A. peruvianus* and *Austrelmis sp.*, while *M. irarrazavali* and Chironomidae were not affected by this variable. Discharge had a negative effect on *A. peruvianus* abundance, while abundances of Chironomidae and *Austrelmis sp.* increased with discharge (Table 6).

3 Discussion

3.1 Macroinvertebrate assemblage composition

Examined in the context of other high-altitude Andean streams, the macroinvertebrate assemblage in the Tambillos was typical for small, cold water streams of the region (Miserendino and Pizzolón 2000; 2003; Scheibler and Debandi 2008; Scheibler 2007 PhD thesis). Ephemeropterans comprised approximately 80% of macroinvertebrates, and the Chironomidae

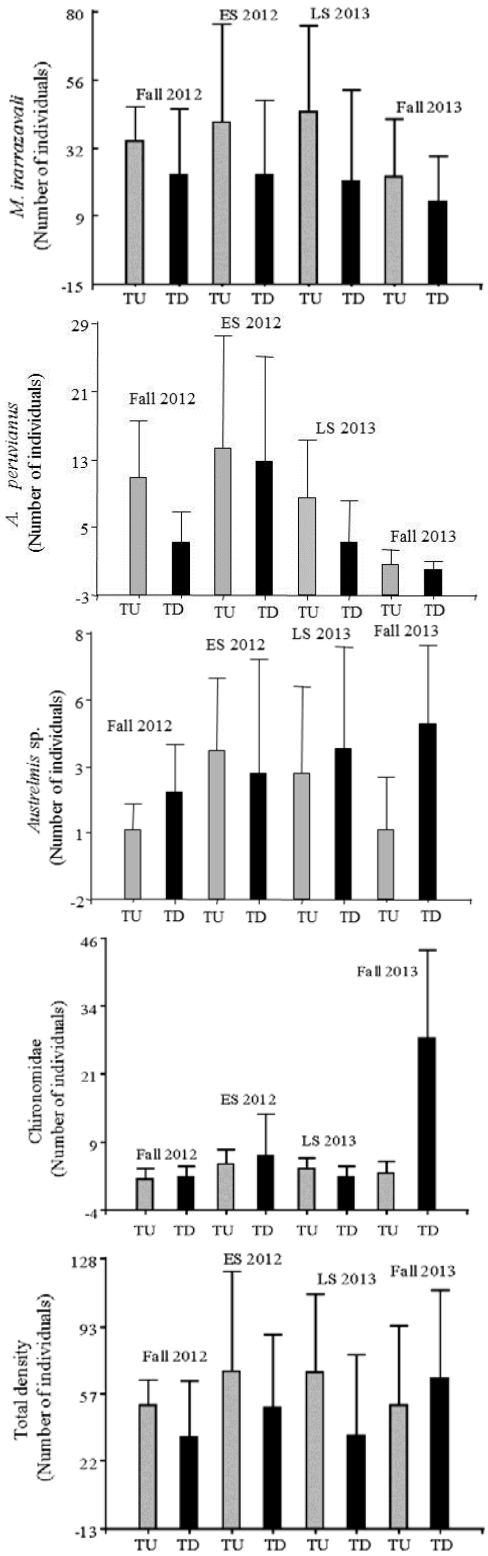

Figure 3 Mean and standard deviation of total abundance and the abundance of the major macroinvertebrate taxa at both reaches across seasons sampled in the study. TU: reach 1, TD: reach 2, F12: Fall 2012, ES: Early Summer 2012, LS: Late Summer 2013, F13: Fall 2013.

(Diptera) were the richest taxon, comprising 11 of the 33 taxa found. These orders represent more than 50% of taxa in unperturbed mountain aquatic systems (Miserendino and Pizzolón 2003; 2004). The most abundant taxa – the ephemeropterans *Massartellopsis irarrazavali* Demoulin (Leptophlebiidae), *Andesiops peruvianus* Ulmer (Baetidae) and the coleopteran *Austrelmis sp.* (Elmidae) – are important components of Central Andean desert mountain streams (Alvial et al. 2013; Scheibler et al. 2014a). Compared to large Andean rivers of the region where discharge changes are fifty times greater (Scheibler et al. 2014 a), small snow- and glacier-fed streams such as Tambillos are more stable. This is supported by the high abundance of Ephemeroptera found throughout the year. In large Andean rivers, the proportions of Chironomidae and ephemeropterans are reversed, with Chironomidae comprising 70% of total abundance whereas Ephemeroptera (mostly *M. irarrazavali* and *A. peruvianus*) make up only 6% (Scheibler et al. 2014a).

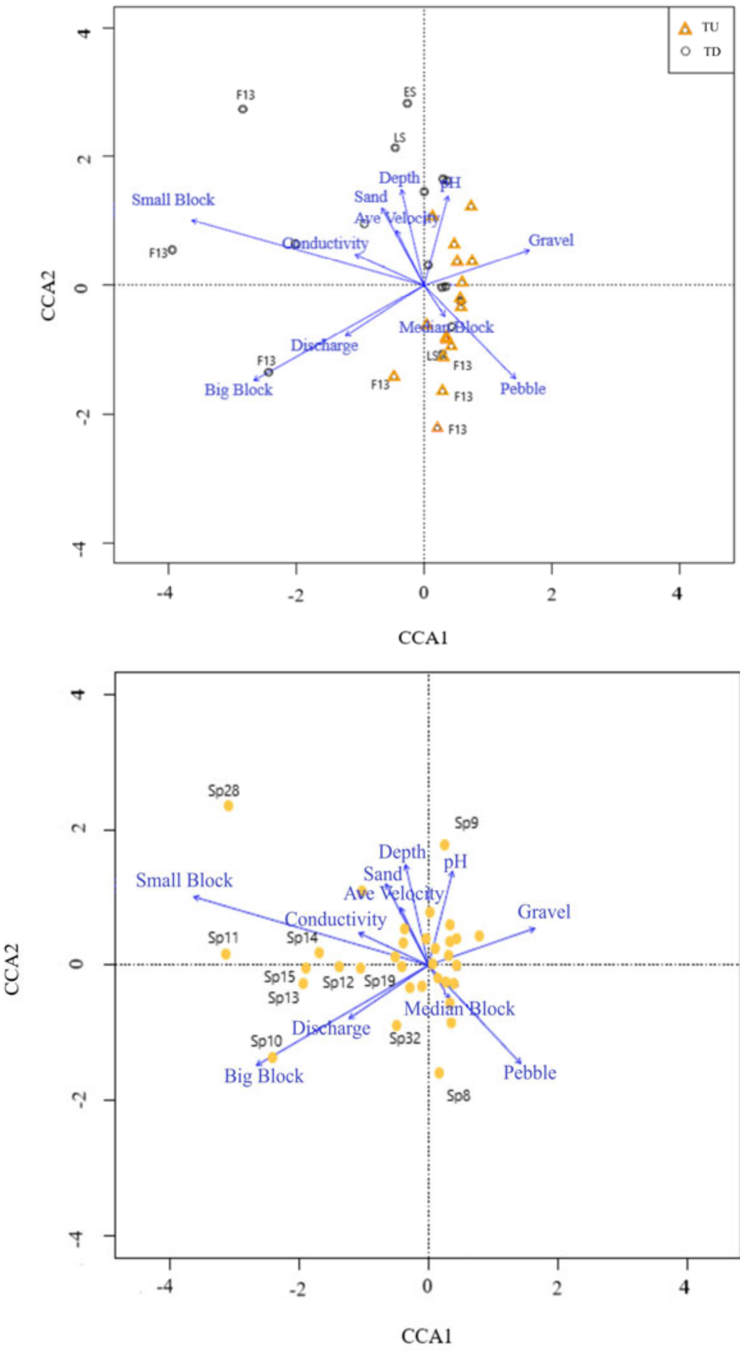

Figure 4 Canonical Correspondence Analysis (CCA) ordination of samples and species within the environmental space determined by the physical and chemical variables measured (vectors) in Arroyo Tambillos. (a) Ordination of samples by sites and seasons. (b) Ordination of species found in the present study, taxa are named following the list of taxa given in Appendix 1. Samples in the ordination are total abundances of the three Surbers per transect at each reach (TU and TD) during the four sampling periods. Notations: TU: reach 1, TD: reach 2, LS: Late Summer, ES: Early Summer, F12: Fall 2012, F13: Fall 2013.

In the context of high-altitude streams worldwide, taxonomic richness in the Tambillos was low (Maiolini and Lencioni 2001; Finn and Poff 2005; Laursen et al. 2015; Nautiyal et al. 2015). The orders Plecoptera and Trichoptera, for example, are well-represented in many mountain streams (Hynes 1970; Ward 1994), but the one stonefly (Plecoptera) and two caddisflies (Trichoptera) found in Tambillos made up < 1% of richness. Studies carried out in Equatorial Andean streams (Jacobsen and Encalada 1998; Studholme et al. 2014) found richer communities with Baetidae, Elmidae, Chironomidae and Hyalellidae as the dominant taxa; but again, Plecoptera and Trichoptera were not well represented. The lower richness seen in the Arroyo Tambillos could be due to the small amount of allochthonous input from the sparse riparian

Table 6 Change in total richness, total abundance, and abundance of the four most common taxa in response to environmental variables. Values are regression coefficients from Generalizad Linear Model (GLMs) analyses. Only variables from the best fitted model have their corresponding values shown. Bold coefficients were significant at $p<0.05$.

Response variables	Richness	Total Abundance	*M. irarrazavali*	*A. peruvianus*	*Austrelmis*	Chironomidae
% Variance explained	18.66	28.44	39.84	63.40	48.84	59.95
Velocity		**1.186**		**2.174**	**2.590**	
Depth	**-1.731**	**-3.934**	**-4.908**	**-5.594**	**-8.342**	**-2.438**
Small block		-0.016	-0.033	-0.032	-0.010	0.004
Pebble		-0.010	-0.0.13	-0.017	-0.007	
Gravel		-0.016	-0.021	-0.022		-0.019
Sand		-0.013	-0.035	-0.013		-0.031
pH		0.325	0.165	1.205		-0.800
Conductivity		0.006		-0.068	0.033	0.057
Discharge		**0.815**	0.182	**-5.662**	**3.471**	**2.098**

vegetation and high desert environment through which the Tambillos flows (Scheibler et al. 2014 a, b). Alternatively, it could be due to biogeographic filters (e.g., desiccation stress) that reduce the pool of available colonizing species (sensu Poff 1997).

Though the macroinvertebrate assemblage in Arroyo Tambillos stream showed low richness, the dipteran family Chironomidae was represented by a large number of species. Chironomid distributions in Tambillos were similar to those seen in other glacier-fed streams (Milner 2016), such as those described by Robinson et al. (2016) for Swiss alpine systems. As in Tambillos, Robinson et al. (2016) found that Orthocladiinae were common and Diamesinae were rare in streams having less glacial influence.

3.2 Seasonal changes in macroinvertebrate assemblage

We predicted that an important driver of seasonal change would be stream discharge. Discharge in Arroyo Tambillos is subject to glacier snowmelt and follows the classic pattern of high flow in late spring and summer and baseflow in fall and winter (Poff and Ward 1989; Scheibler 2007, PhD thesis). Discharge from glacial runoff and snowmelt create physical conditions (e.g., water temperature, substrate and suspended sediment load) that produce ecological gradients that allow benthic species to coexist (Füreder 2007). We found that discharge, and the related variables of current velocity and depth, were the factors that most affected the abundance and distribution of macroinvertebrates in Arroyo Tambillos. Discharge had a positive relationship to total macroinvertebrate abundance in general, and the abundance of *Austrelmis* sp., and Chironomidae in particular. *A. peruvianus,* by contrast, had a negative relationship to discharge. We also found that while velocity had positive effects on the abundance of the dominant taxa, the effects of depth were negative. Seasonal variation in discharge could be entangled with other variables such as water temperature, insect emergence, and nutrient inputs. In Tambillos stream, there is little riparian vegetation, and as a consequence allochthonous input to the stream is very limited and unlikely to be an influential factor. However, considering that samples were taken during the warmer summer months when insect emergence peaks (from December to March), macroinvertebrate life history patterns could also be important (Füreder et al. 2005). Thus, we should consider life history as well as discharge effects to explain changes in macroinvertebrate abundance.

Hydraulic conditions are critical for understanding the structure and function of stream communities. In running waters, hydraulic conditions influence species distributions because many have preferred hydraulic ranges. Any hydrological change, therefore, reduces the availability of suitable microhabitat for some species, while increasing it for others (Mérigoux and Dolédec 2004). As a consequence of climate change, temperature extremes are predicted to increase in the coming years and decades (Meade et al. 2018), leading to stochastic changes in glacier- and snow-fed water systems that include unusual increases of discharge and subsequent modifications of physical and chemical conditions in streams. Increasing the frequency and intensity of hydrological extremes may not be in accordance with the environmental conditions under which stream taxa have evolved (Boersma et al. 2013), and are likely to have important community and ecosystem level consequences (Woodward et al. 2016).

This study helps increasing our knowledge about the structure of function of small streams in the Andes mountains. It was carried out in a central Andes stream characterized by semi-arid conditions, which distinguishes it from streams studied at higher latitudes. In addition, these systems generally show fewer and lower human impacts compared to the large rivers of the region, and consequently, they have physico-chemical conditions more closely matching the stream's natural state. The Arroyo Tambillos and similar streams are also dominated by ephemeropterans, a group that is especially sensitive to environmental deterioration. Monitoring high-altitude streams like the Arroyo Tambillos may be critical for preventing the potential loss of unique and sensitive stream biota. Anthropogenic activities such as dam construction, cattle grazing and human recreation modify mountain habitats and cause mountain streams to change (Milner et al. 2015; Uieda et al. 2017). These activities in combination with the pervasive effects of climate change will likely result in biodiversity loss for many glacial-fed and snowmelt stream communities that are especially sensitive to environmental alteration (Milner et al. 2015; 2016; Robinson et al. 2016). As the Earth warms, glaciers disappear, and cold-adapted macroinvertebrates retreat to even higher elevations, the nivo-kryal communities like the one described here 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 variation in local factors across temporal scales to improve our understanding of these sentinels of anthropogenic change.

4 Conclusions

The macroinvertebrate assemblage of the high Andean stream studied was represented by nivo-kryal communities typical of small, cold water streams of the region. The community was dominated by Ephemeropterans (80% of total abundance) which are especially sensitive to environmental deterioration, while the dipteran family Chironomidae was the best represented in terms of richness. Taxonomic richness was low compared with other mountain streams, and could be due to the small amount of allochthonous input from the sparse riparian vegetation and the high altitude arid environment through which the Tambillos stream flows. Among the physical and chemical variables studied, discharge and the associated variables like current velocity and depth, were the environmental variables that most affected the abundance and distribution of macroinvertebrates in this high mountain stream. We expected the greatest change in the structure of the macroinvertebrate community during the summer as found in large mountain rivers. However, we did not find this change caused by increased snowmelt discharge. Instead, we detected some non-significant changes. This study contributes to our knowledge about the structure and function of small streams in the Andes Mountains, which generally in this kind of environments have physical and chemical conditions more closely matching the stream's natural state. In the future, it would be interesting to know the ecological status of several small Andean streams mainly because they are sentinel of clime change, host sensitive species, and serve as reservoir of these species in the event of contamination of large rivers preserving the regional biodiversity.

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References

Allan JD, Castillo MM (2007) Stream ecology: structure and function of running waters. The abiotic environment. 2nd edition. Chapman and Hall Press, New York. pp. 75-102.

Alvial IE, Orth K, Durán BC, et al. (2013) Importance of geochemical factors in determining distribution patterns of aquatic invertebrates in mountain streams south of the Atacama Desert, Chile. Hydrobiology 709: 11-25. https://doi.org/10.1515/biol-2015-0008

Aydin D, Tuzemen S (2010) A comparative study of the sum of squares and deviance in linear, additive and partial linear additive models. Journal of Applied Science 10: 919-929. https://doi.org/10.3923/jas.2010.919.929

Beisel JN, Usseglio-Polatera P, Moreteau JC (2000) The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. Hydrobiology 422: 163-171. https://doi.org/10.1023/A:1017094606335

Biggs J, von Fumetti S, Kelly Quinn M (2016) The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. Hydrobiology 793: 3-39. https://doi.org/10.1007/s10750-016-3007-0

Boersma K, Bogan M, Henrichs B, et al. (2013) Invertebrate assemblages of pools in arid land streams have high functional redundancy and are resistant to severe drying. Freshwater Biology 59: 491-501. https://doi.org/10.1111/fwb.12280

Bogan MT, Lytle DA (2007) Seasonal flow variation allows "time-sharing" by disparate aquatic insect communities in montane desert streams. Freshwater Biology 52: 290-304. https://doi.org/10.1111/j.1365-2427.2006.01691.x

Burgherr P, Ward JV (2001) Longitudinal and seasonal distribution patterns of the benthic fauna of an alpine glacial stream (Val Roseg, Swiss Alps). Freshwater Biology 46: 1705-1721.https://doi.org/10.1046/j.1365-2427.2001.00853.x

Clarke KR, Gorley RN (2006) PRIMER version 6: User Manual/Tutorial. PRIMER-E, Plymouth. p 192 .

Costa SS, Melo AS (2008) Beta diversity in stream macroinvertebrate assemblages: among-site and among-microhabitat components. Hydrobiology 598: 131-13. https://doi.org/10.1007/s10750-007-9145-7

Cranston PS, Krosch M (2011) Barbadocladius Cranston & Krosch, a new genus of Orthocladiinae (Diptera: Chironomidae) from South America. Neotropical Entomology 40: 560-567. http://doi.org/10.1590/S1519-566X2011000500007

Dominguez E, Fernández HR (2009) Southamerican benthonic macroinvertebrates. Systematics and biology. Miguel Lillo Foundation, Tucumán, Argentina. p. 654 (In Spanish)

Feld CK, Hering D (2007) Community structure or function: Effects of environmental stress on benthic macroinvertebrates at different spatial scales. Freshwater Biology 52: 1380-1399. https://doi.org/10.1111/j.1365-2427.2007.01749.x

Finn DS, Poff, NL (2005) Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. Freshwater Biology 50: 243-261. https://doi.org/10.1111/j.1365-2427.2004.01320.x

Füreder L (1999) High alpine streams: cold habitats for insect larvae. In: Margesin R, Schinner F (eds.), Cold-adapted organisms. Ecology, Physiology, Enzymology and Molecular Biology Springer Verlag. Berlin, Germany. pp 181-196.

Füreder L (2007) Life at the edge: habitat condition and bottom fauna of Alpine Running Waters. International Review of Hydrobiology 92 (4-5): 491-513. https://doi.org/10.1002/iroh. 200610987

Füreder L, Wallinger M, Burger R (2005) Longitudinal and seasonal pattern of insect emergence in alpine streams. Aquatic Ecology 39: 67-78. https://doi.org/10.1002/ece3.4968

Haghkerdar JM, Mc Lachlan JR, Ireland A, et al. (2019) Repeat disturbances have cumulative impacts on stream communities. Ecological Evolution 9: 2898-2906. https://doi.org/10.1002/ece3.4968

Hawkins CP, Hogue JN, Decker LM, et al. (1997) Channel morphology, water temperature, and assemblage structure of stream insects. Journal of North American Benthological Society 16(4): 728-749. https://doi.org/ 10.2307/1468167

Heino J, Louhi P, Muotka T (2004) Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. Freshwater Biology 49: 1230-1239. https://doi.org/10.1111/j.1365-2427.2004.01259.x

Jacobsen D (2004) Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. Freshwater Biology 49: 1293-1305. https://doi.org/10.1111/j.1365-2427.2004.01274.x

Jacobsen D, Encalada A (1998) The macroinvertebrate fauna of Ecuadorian highland streams in the wet and dry season. Archive für Hydrobiology 142: 53-70. https://doi.org/10.1127/archiv-hydrobiol/142/1998/53

Jacobsen D, Milner AM, Brown L, et al. (2012) Biodiversity under threat in glacier-fed river systems. Natural Climatic Change 2: 361-364.https://doi.org/10.1038/nclimate1435

Laursen SK, Hamerlik L, Moltesen K, et al. (2015) Diversity and composition of macroinvertebrate assemblages in high-altitude Tibetan streams. Inland Waters 5: 263-274. https://doi.org/10.5268/IW-5.3.818

Maiolini B, Lencioni V (2001) Longitudinal distribution of macroinvertebrate assemblages in a glacially influenced stream system in the Italian Alps. Freshwater Biology 46: 1625-1639. https://doi.org/10.1046/j.1365-2427.2001.00849.x

Meade J, Van Der Wal J, Storlie C, et al. (2018) Substantial reduction in thermo-suitable microhabitat for a rainforest marsupial under climate change. Biology Letters 14 (12): 20180189. https://doi.org/10.1098/rsbl.2018.0189

Mérigoux S, Dolédec S (2004) Hydraulic requirements of stream communities: a case study on invertebrates. Freshwater Biology 49: 600-613. https://doi.org/10.1111/j.1365-2427.2004.01214.x

Milner VS, Willby NJ, Gilvear DJ, et al. (2015) Linkages between reach-scale physical habitat and invertebrate assemblages in upland streams. Marine and Freshwater Research 66: 438-448. https://doi.org/10.1071/MF14008

Milner AM (2016) The Milner and Petts (1994) conceptual model of community structure within glacier-fed rivers: 20 years on. In: Gilvear DJ et al. (eds.), River science: Research and management for the 21st Century, First Edition, Chapter 8. John Wiley and Sons, Ltd. USA-UK.

Miserendino ML, Pizzolón LA (2000) Macroinvertebrates of a fluvial system in Patagonia: altitudinal zonation and functional structure. Archive für Hydrobiology 150: 55-83. https://doi.org/10.1127/archiv-hydrobiol/150/2000/55

Miserendino ML, Pizzolón LA (2003) Distribution of macroinvertebrate assemblages in the Azul-Quemquemtreu river basin, Patagonia, Argentina. New Zealand Journal of Marine and Freshwater Research 37: 525-539. https://doi.org/10.1080/00288330.2003.9517187

Miserendino ML, Pizzolón LA (2004) Interactive effects of basin features and land use change on macroinvertebrate communities of headwater streams in the Patagonian Andes. River Research Applied 20: 967-82. https://doi.org/10.1002/rra.798

Miserendino ML, Archangelsky M, Brand C, et al. (2012). Environmental changes and macroinvertebrate responses in Patagonian streams (Argentina) to ashfall from the Chaitén Volcano. Science Total Environment 424: 202-212. https://doi.org/10.1016/j.scitotenv.2012.02.054

Nautiyal P, Mishra AS, Semwal VP (2015) Spatial Distribution of Benthic Macroinvertebrate Fauna in Mountain Streams of Uttarakhand, India. In: Rawat M, et al. (eds.), Aquatic Ecosystem: Biodiversity, Ecology and Conservation. Springer, New Delhi. pp 31-51.

Niedrist GF, Füreder L (2016) Towards a definition of environmental niches in alpine streams by employing chironomid species preferences. Hydrobiology 781: 143-160. https://doi.org/10.1007/s10750-016-2836

Paggi AC (2009) Diptera Chironomidae. In: Domínguez E, Fernández HR (eds.), Macroinvertebrados bentónicos sudamericanos. Sistemática y biología. Fundación Miguel Lillo, Tucumán, Argentina. pp. 383-409. (In Spanish)

Poff NL (1997) Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16: 391-409.https://doi.org/10.2307/1468026

Poff NL, Ward JV (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805-1818. https://doi.org/10.1139/f89-228

Prat N, Riradevall M, Acosta R, et al. (2011) Identification guide for larvae of Chironomidae (Diptera) of the high Andean rivers of Perú and Ecuador. Available online at: http//www.riosandes.ub.edu (Accessed August 2017) (In Spanish).

Prat N, González-Trujillo JD, Ospina-Torres R (2014) Determination key of chironomid pupal exuviae (Diptera, Chironomidae) in tropical high Andean rivers. Revista de Biologia Tropical 62: 1385-1406. (In Spanish).

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at: http://www.R-project.org/ (Accessed on August 2017).

Richards C, Haro RJ, Johnson LB, et al. (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshwater Biology 37: 219-230. https://doi.org/10.1046/j.1365-2427.1997.d01-540.x

Robinson CT, Thompson C, Lods-Crozet B, et al. (2016) Chironomidae diversity in high elevation streams in the Swiss Alps. Fundamental and Applied Limnology 188: 201-213. https://doi.org/10.1127/fal/2016/0891

Robinson CT, Burgherr B, Malard F, et al. (2003) Synthesis and perspectives. In: Ward JV, Uehlinger U (eds.), Ecology of a Glacial Flood Plain. Kluwer Academic Publishers. The Netherlands. pp 259-272.

Scheibler EE (2007) Macroinvertebrados bentónicos como indicadores de calidad del agua en la cuenca del Río Mendoza (Argentina). PhD thesis, Universidad Nacional de la Plata, Buenos Aires, Argentina. (In Spanish)

Scheibler EE, Debandi GO (2008) Spatial and temporal patterns in the aquatic insect community of a high-altitude Andean stream (Mendoza, Argentina). Aquatic Insects 30:145-161. https://doi.org/10.1080/01650420701880974

Scheibler EE, Claps MC, Roig Juñent SA (2014a) Temporal and altitudinal variations in benthic macroinvertebrate assemblages in an Andean river basin of Argentina. Journal of Limnology 73: 76-92. https://doi.org/10.4081/jlimnol.2014.789

Scheibler EE, Roig Juñent SA, Claps MC (2014b) Chironomid (Insecta: Diptera) assemblages along an Andean altitudinal gradient. Aquatic Biology 20: 169-184. https://doi.org/10.3354/ab00554

Servicio Meteorológico Nacional (2017). Ministry of Agriculture, Livestock and Fisheries. Argentine Republic. Climatic Report. 1961-1990. Available online at: http://test.smn.gov.ar/caracterización-del-clima (Access on August 2017) (In Spanish)

Studholme AM, Hipo León LF, Ríos Rivera AC, et al. (2014) Altitudinal and temporal variability of four macroinvertebrate communities in Andean streams, Sangay National Park, Ecuador. Entomotrop 29: 149-158.

Trombotto D (1991) Investigations of periglacial forms and periglacial sediments at 'Lagunita del Plata', Mendoza, Argentinien. In Heidelberger Geographische Arbeiten. Heft 90. Germany. p 171. (In German)

Uieda VS, Iwai MLB, Ono ER, et al. (2017) How seasonality and anthropogenic impacts can modulate the structure of aquatic benthic invertebrate assemblages. Community Ecology 18: 47-55. https://doi.org/10.1556/168.2017.18.1.6

Ward JV (1994) Ecology of alpine streams. Freshwater Biology 32: 277-294. https://doi.org/10.1111/j.1365-2427.1994.tb01126.x

Wellnitz T, Poff NL, Cosyleon G et al. (2001) Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects. Landscape Ecology 16: 111-120. https://doi.org/10.1023/A:1011114414898

Woodward G, Bonada N, Brown LE, et al. (2016) The effects of climatic fluctuations and extreme events on running water ecosystems. Philosophical Transactions of the Royal Society of London. Series B, Biological Science 371: 20150274. https://doi.org/10.1098/rstb.2015.0274