Biotic diversity of benthic macroinvertebrates at contrasting glacier-fed systems in Patagonia Mountains: The role of environmental heterogeneity facing global warming

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HIGHLIGHTS

- Research on environment and macroin-vertebrates at retreating glacier-fed systems
- Sensible and highly endemic macroin-vertebrate species dominated glacier-fed streams.
- Longitudinal zonation of macroinverte-brates partially fitted to temperate arctic systems model.
- Benthos assemblage's predictors associated to forest, wetlands, groundwater, and stream/lake sequences
- Changes in local (alfa) and regional (gamma) macroinvertebrate diversity are expected.

GRAPHICAL ABSTRACT
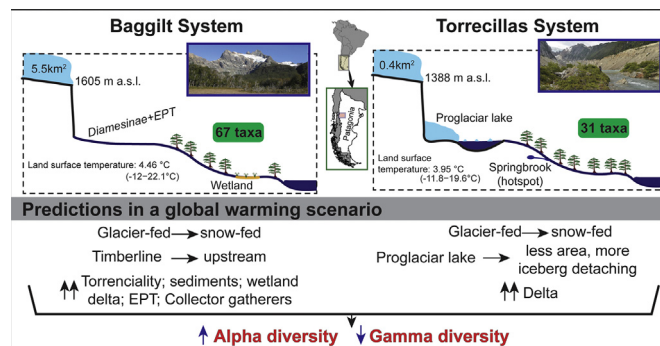
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ABSTRACT

Patagonia is by far the largest glacierized area in South America. However, little is known about ecology, function-ing and biodiversity of glacier-fed streams facing global warming. We investigated changes in environmental fea-tures and macroinvertebrate communities along a longitudinal gradient of glacier influence of two Patagonian systems that differ in glacier cover magnitude and the spatial sequence of lotic and lentic phases. Both glaciers, Torrecillas (~5.5 km², Torrecillas system) and Cónico (~0.44 km², Baggilt system), are retreating. Longitudinal distribution of benthic invertebrates partially fitted to predictions for glacierized temperate systems, with Diamesinae spp. dominating at closest sites to the Cónico, and Orthocladiinae increasing downstream, but pat-terns were unclear at Torrecillas. Generalized Linear Model identified chlorophyll *a* and conductivity as having significant effect on richness and density respectively at Torrecillas; detritus biomass and gravel influenced spe-cies richness, and boulder percentage and water temperature affected density, at Baggilt. Canonical Correspon-dence Analyses integrating benthic biota and environmental variables revealed that a higher environmental heterogeneity at Baggilt, related with spatial dimension (unshaded/shaded reaches, wetland reaches), local re-sources (detritus, bryophytes) and temperature, probably explained the unexpected high richness in benthic as-semblages (67 taxa). Environmental conditions imposed by the lake outlet (proglacial) at Torrecillas resulted in a less diverse community (31 taxa). Finally our results suggest that these isolated, small glacier-fed streams typical of the Patagonian landscape appear highly vulnerable to global warming. Endemic elements could disappear at upper segments being replaced by other species common at rhithral environments, which might increase local

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diversity (alfa diversity) but decrease regional diversity (gamma diversity). From an ecosystem perspective stream functioning can result altered. Glacier retreating or disappearing threatens major ecosystem services for Patagonian inhabitants such as water supply, hydrological regulation, recreation and tourism.

1. Introduction

High latitude and altitude freshwater ecosystems in remote areas are receiving special attention since they are rapidly responding to anticipated global temperature rise (Robinson et al., 2001; Cauvy-Fraunié et al., 2015). Glacier-melt dominated systems are one of the most vulnerable environments to global warming (Jacobsen et al., 2012). Over the last century glacier mass-balances have shown consistent decreases in most regions of the world, and retreat has accelerated at several locations (Brittain and Milner, 2001; Füreder et al., 2001). Negative glacier mass-balance determines major changes in water sourcing of alpine streams, frequently with an important reduction of glacier and snowmelt (Barnett et al., 2005), as well as greater groundwater contributions and shifts in the proglacial riverscape dynamics (Brown et al., 2006). These alterations in the functioning and integrity of glacier-fed systems are threatening aquatic biodiversity (Jacobsen et al., 2012). Besides, downstream aquatic ecosystems are highly interactive with processes taking place at headwaters. For this reason, several ecosystem services provided by glacier-fed environments that sustain socio-economic activities could be damaged (e.g. water quality and quantity, hydrological regulation, etc.) (Hieber et al., 2002).

It has been predicted that freshwater biodiversity in glacierized catchments will decline significantly with the shrinkage and disappearance of glaciers. Specific species assemblages are harbored in these environments, with highly endemic and specialized components in the benthic invertebrate community (Brown et al., 2007; Muhlfeld et al., 2011; Khamis et al., 2014; Sandin et al., 2014). At glacier-fed streams substratum instability, suspended solid concentration, and channel width/depth ratio typically decrease downstream from the glacier, which results in increased macroinvertebrate and algal taxonomic richness and abundance, reflecting a reduction in habitat harshness (Clitherow et al., 2013). In a climate change scenario, benthic species are seriously at risk because they are deterministically influenced by meltwater from glaciers and snowpacks, and there are limited options for dispersal due to a low biogeographical connectivity. Glacier runoff acts as an aquatic dispersal barrier, isolating species in headwater streams, and preventing specialized taxa to colonize throughout the entire stream network (Cauvy-Fraunié et al., 2015).

Altered water temperature and thermal regimen can have serious effects on cold stenothermic species in these areas, since their growth, metabolism, reproduction, emergence and distribution is determined by temperature (Milner et al., 2001a). There are several examples of Plecoptera, Ephemeroptera, Trichoptera (Muhlfeld et al., 2011; Sandin et al., 2014), and Chironomidae species (Robinson et al., 2007; Niedrist and Füreder, 2016) being strongly affected. Extinction trends of some endemic alpine aquatic species have been modeled under scenarios of future climate and hydrological change (Brown et al., 2007).

As has been proposed for artic and alpine glaciered fed systems, the increase in channel stability and maximum stream temperature (T max) with distance from the glacier, are thought to be the main factors affecting the biota along streams (Milner and Petts, 1994; Milner et al., 2001a). In this sense, larvae of the genus *Diamesa* appear as typical sole inhabitants when T max <2 °C, and associated with Orthocladiinae and Simuliidae when T max >2 < 4 °C, and above 4 °C, stoneflies, mayflies (*Baetis*), limnephilid caddisflies and dipterans such as Empididae and Tipulidae can potentially colonize (Milner et al., 2001a, 2001b). Just a few studies in South America (Neotropical region) examining the longitudinal zonation and testing proposed patterns at glaciered systems have been conducted (Kuhn et al., 2011; Jacobsen et al.,

2010). In view of the important zoogeographical differences characterized by an endemic fauna and the absence of common taxa with the Holarctic region (e.g. *Baetis*, *Nemouridae*, *Chloroperlidae*), some variation in the longitudinal distribution pattern can be expected.

The Patagonian Andes contain over 20,000 km² of glaciers, and by far is the largest glacierized area in South America. Significant glacier and hydroclimatic changes in northwestern Patagonia have been documented in a recent work by Masiokas et al. (2008). The pattern of drastic and widespread glacier recession was related with a strong negative trend in the regional runoff record and with a significant warming according to data series (1912–2002) being particularly marked in the last decade of the twentieth century. This has resulted in recession of ice margins, thinning of the ice cover, raising elevation of the regional snow line and reduction of Andean areas under permafrost conditions (Delgado et al., 2002; Rabassa, 2010).

Research conducted at mountainous freshwater systems in Patagonia examined environmental features, aquatic communities and ecological functioning of pristine streams and rivers (Oyanedel et al., 2008; Miserendino et al., 2011; Tagliaferro et al., 2013). Nevertheless, most emphasis has been placed on rhithral or seasonal snowmelt-dominated systems (Miserendino, 2001; Miserendino and Pizzolon, 2000, 2004; Miserendino et al., 2012) than on glacier-fed streams (Valdovinos et al., 2010; Tagliaferro and Pascual, 2016). New approaches on lentic environments in the area revealed that higher turbidity levels derived of glacier melting is interfering in foraging performance of some invertebrate and vertebrate species (Jönsson et al., 2011) and altering zooplankton distributions (Laspoumaderes et al., 2013). Therefore there are no comprehensive studies focused in glacier-fed systems specially those having streams, proglacial lakes, and wetlands in the network. The achievement in the filling of these knowledge gaps, in one of the most important glacierized landscapes in South America, is critical to maintain the biodiversity and hydrological functions that they provide. These systems are involved in socio-economic activities of sustainability (water supply, hydroelectric power generation, agriculture, and tourism).

In this paper we investigated the environmental background including geomorphological features, nutrients, particulate organic matter, chlorophyll, and benthic communities of two contrasting glacier-fed systems: Torrecillas and Baggilt (Patagonia, Argentina), which differ in glacier cover magnitude and the spatial sequence of lotic and lentic phases. The incidence of the existence of a proglacial lake at Torrecillas and of wetlands at Baggilt is also examined. We hypothesized that biological diversity will strongly depend on the spatial heterogeneity of each system, and this will affect the biological richness and complexity of environmental and species relationships. Some predictions of how the associated biota can evolve in current scenarios of global warming, analyzing main environmental filters, are proposed. We also test for the first time in Patagonia the conceptual model of the ecology and longitudinal distribution of macroinvertebrate communities in glacier-fed streams proposed for temperate-arctic systems (Milner et al., 2001a; Jacobsen et al., 2010).

2. Methodology

2.1. Study area description and glaciological background

The study was conducted at two retreating glacier systems belonging to the Futaleufú Basin: the Torrecillas and Baggilt, which are fed by the Torrecillas and Cónico glaciers, respectively (Table 1). From a glaciological point of view the Torrecillas can be described as a regenerated,

Table 1
Characteristics of two glacier systems (lentic and lotic phases) including some predicted changes facing global warming.

	Torrecillas system	Baggilt system
Glacier name	Torrecillas glacier	Cónico glacier
Glacier type	Complex: a) a small icecap glacier (primary glacier) that produces avalanches that feed and originates a b) regenerated glacier (secondary glacier in contact with El Antiguo Lake).	Single: Cirque glacier. Glacier retreating by ablation and ice detaching from the glacier snout (avalanches).
Lake	Proglacial: rocky bottom, turbid by meltwater production, low water temperature, seasonal presence of icebergs, with direct influence from the hillsides (landslides). Hydrothermal alteration at headwaters eventually with leaching of metals (Fe, Cu, Pb, Zn) and sulfurs (possible acidification).	Not glacial: (3.5 km from the glacier snout). Sedimentary clogging/filling evident. Bottom sediments mixed (rocky, sand, mud). Little or null influence of landslides from their margins.
Fluvial watercourses	Single stream draining from the proglacial lake. Subjected to alluvial floods related with glacier stabilization from the regenerated glacier during the last three centuries.	Mainly a glacier-fed stream, draining into a wetland area (3.5 km downstream from the Cónico Glacier snout), ending into the Baggilt Lake forming a delta.
Probably future scenarios	Dramatic glacier retreating and reduction of primary glacier. Unpredictable trend of the regenerated glacier: a) Possible advance with a reduction of the lake area. b) Higher iceberg detaching. Increase of stream discharge, higher erosion in the upper reaches, and higher sedimentation and inundations in the lower section (delta). Disappearance of the glacier mass modifying hydrological regime (torrential, marked flow peaks).	Disappearance of the glacier mass modifying the hydrological regime in the basin (torrential, lower buffering with marked peak flows, higher waterlogging in the middle lower basin). Possible acceleration in the delta development. Important changes in the phreatic level at the wetland. (Greater unpredictability of drying and pronounced flooding). Possible expansion of the forest.

relatively young glacier (Holocene), which is continuously fed by ice avalanches proceeding from the southwest walls from a major Glacier, relict of Pleistocene mountain ice sheet. Cónico glacier, is a cirque glacier, a relict too of the mountain ice sheet that covered the Patagonian Cordillera during the Last Glaciation Maximum (24–18 thousand years b.p.). In this glacier the glaciofluvial flow is transported by two small tributaries that join in the main Baggilt stream. Above the stream outflow, there are two important wetlands.

Due to the generalized global warming and as expressed in the raised elevation of the regional snow line, both glaciers are retreating at present time (Masiokas et al., 2008; Rabassa, 2010). The studied systems have a different sequence between lotic and lentic compartments (Fig.1). El Antiguo Lake (a proglacial lake) and Torrecillas Stream drain into the Menéndez Lake, in the Patagonian mountain range (Los Alerces National Park) (Table 1). The system is fed by the Torrecillas glacier (~5.5 km^2, max: 2206, min: 1388 m a.s.l.), an alpine type glacier (~Equilibrium Line 1805 m a.s.l.), which generates 350 m below a debris flow of 1 km extent. This is a reservoir of melting water and of sediments (till). The El Antiguo Lake (0.27 km^2, 750 m a.s.l.) is connected with Menéndez Lake through a high gradient small tributary (1.83 km), the Torrecillas Stream.

The Cónico glacier (S-SE) (~0.44 km^2, max: 1950, min: 1605 m a.s.l), shows the Equilibrium Line at ~1735 m a.s.l. and feeds a small tributary (4.41 km). The stream crosses a wetland (0.16 km^2) and drains into Baggilt Lake (0.79 km^2, 1072 m a.s.l.) through a small delta (Table 1).

Most of Patagonia is dominated by air masses coming from the Pacific Ocean (westerlies) and the Andes play a crucial role in determining the climate. The north-south distribution of the mountains imposes an important barrier for humid air masses; most of the water falling on the Chilean side (West) (Paruelo et al., 1998). For this reason most of the precipitation in the Argentinean side occurs in the cordillera. This cold temperate pattern and high precipitation ranges define the Andean-Humid biozone (3000–800 mm West–East decreasing gradient, mean annual temperate range 11–6 °C) (del Valle et al., 1998). From a phytogeographical perspective, both basins are placed in the Sub-Antarctic forest.

At Torrecillas, the forest is dominated by *Nothofagus pumilio* ("lenga") and *N. dombeyi* ("coihue") and other typical species from the Valdivian rainforest such as *Fitzroya cupressoides* ("alerce"), *Drimys winteri* ("canelo"), *Weinmannia trichosperma* ("tineo") and *Hydrangea serratifolia* ("pahueldin"). The shrub and herbaceous strata are well constituted and rich in species. The lake shore at El Antiguo shows sparse vegetation, with only some young specimens of *N. dombeyi*, some herbaceous, bryophytes and lichens.

Both *N. dombeyi* and *N. pumilio* co-dominate at Baggilt basin, the area displays less humidity and there are no Valdivian elements present. However, at the forested section of the stream the coverage of the forest, shrub and herbaceous strata is complete (100%). The wetland displays a high richness of emergent macrophytes, with high coverage of Poacea, Juncaceae and Cyperaceae.

2.2. Site selection and design

To study the longitudinal glacial influence at streams, the objective was to cover most possible changes (elevation, slope and discontinuities) in a small distance either from the glacier or from the proglacial lake. At Torrecillas glacier system, six sampling points were placed along a 1 km stretch, between 758 and 560 m a.s.l., in the glacier-fed stream. Site T1 was adjacent to the lake outflow, followed by T2 and T3. Site T4 was located in a densely canopied site, whereas T5 and T6 were open-canopied sites. At Baggilt stream, eight sites were selected along 2.28 km and between 1266 and 1071 m a.s.l., three of them placed upstream the timberline (B1, B2 and B3). The remaining sites were selected on reaches once the stream run into the forest, three sites (B4, B5 and B6) upstream, and two sites (B7 and B8) downstream along the wetland area (Fig. 1).

As occurs with typical high-altitude areas, some of the places are of low accessibility. For this reason the survey was limited to summer months and the effort concentrated in gathering all possible environmental background, and in studying the biological communities. Both basins were visited twice between February and April of 2015, and the first three sites at Baggilt (B1–B3) were visited only once (March 2017).

2.3. Environmental characterization

Geographical variables (altitude, catchment extension, and distance from glacier), and other hydrological, chemical and biological features were acquired (Google Earth Software). Pattern of air surface temperature (night and day) at both sampling areas was obtained from MODIS using the global Land Surface Temperature (LST) tool.

At each tributary and at each one of the 14 study sites, three transects were laid across the stream and used to record width and depth. Average depth (cm) was estimated from five measurements along a transect across the channel with a calibrated stick, wet width (m) of
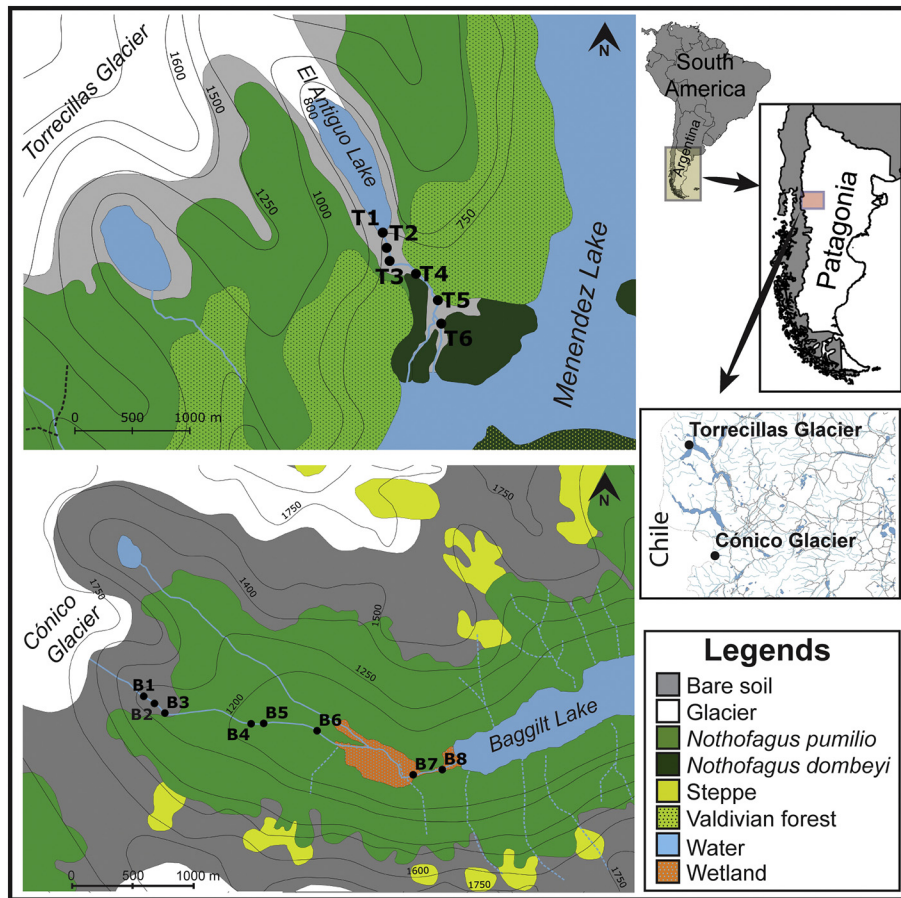
Fig. 1. Location of sampling sites on Baggilt and Torrecillas glacier-fed streams. Patagonia, Argentina.

the channel was also determined. Current speed (m s^{-1}) was measured in mid-channel on three occasions by timing a float (average of three trials) as it moved over a distance of 10 m (Gordon et al., 2004). Discharge (m^3 s^{-1}) was obtained by combining depth, wet width and current velocity as in Gordon et al. (2004). Substrate size composition was estimated as percentage of boulder, cobble, gravel, pebble, and sand in the reach, using a 1 m^2 grid. Channel stability was assessed using the Pfankuch Index (Pfankuch, 1975; Collier, 1992), which scores fifteen attributes or variables from upper (landform slope, mass wasting or slope, debris jam potential, vegetative bank protection), lower banks (channel capacity, bank rock content, obstruction, etc.) and bottom (rock angularity, bed-surface brightness, particle packing, percentage of stable materials, scouring, and aquatic vegetation). Scores were added to provide an overall index of channel stability with a potential range of 38–169 (high scores representing unstable channels at the reach scale).

At each occasion and in the mid channel section of the reach, water temperature, specific conductance, pH, turbidity and dissolved oxygen were measured with a Hach SensION 156 multiparameter probe. Total suspended solids (TSS) were assessed gravimetrically from separate water samples (plastic bottles 2000 ml). Suspended particles were measured by filtering through pre-dried and pre-weighed 47-mm GF filters. Differences between the final and initial weights of dried filters (105 °C for 4 h) were obtained. For nutrient analyses water samples were collected below the water surface, kept at 4 °C and transported to the laboratory for analysis. Nitrate plus nitrite nitrogen (NO$_3$ + NO$_2$), ammonia (NH$_4$) and soluble reactive phosphate (SRP) were analyzed using standard methods (APHA, 1999). The major dissolved cations, calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na$^+$), and potassium (K$^+$), were quantified by titration and spectrophotometry (APHA, 1999) at the Dirección de Salud Ambiental (Chubut Province), this was carried out during February (2015).

Pigment analysis was performed in order to estimate algal biomass. Stream samples were taken from rock surface, each sample consisted of scraping an area (20 cm^2) on the exposed surface of three randomly selected rocks. The content was preserved in water from the site and cooled while transported in dark containers to the laboratory, where they were filtered on GF/FF filters. All samples were frozen until analysis. Chlorophyll *a* was extracted from filters in 90% acetone, and measured spectrophotometrically with correction by phaeopigments, according to standard methods (APHA, 1999; Wetzel and Likens, 1991).

Detritus obtained from benthic samples was divided into fine (250–1000 μm) and coarse (1000 μm) particulate fractions (FPOM and CPOM, respectively). The CPOM fraction was subdivided into following items: wood, leaves (mainly entire leaves), macrophytes, bryophytes and others (fragments of leaves, grass, seeds, roots, buds, etc.). All fractions were dried (105 °C for 4 h or until constant weight) and then weighed on an electronic balance (Ohaus-Pioneer) to ±0.0001 g (Miserendino and Masi, 2010).

2.4. Macroinvertebrate sampling

At each site, four benthic macroinvertebrate samples (replicates) were collected from run/riffles along a 5 to 10 m long stretch with a Surber sampler (frame area 0.09 m^2, 250 μm mesh). This protocol was adjusted based on previous studies conducted in similar small streams in the area (Miserendino et al., 2011). Samples were kept separated for quantitative analysis, fixed in a 4% formaldehyde solution and in the laboratory were washed, sieved, sorted, and identified using a stereo microscope. All individuals were picked from the samples and stored in 70% ethyl alcohol. Species were identified using available keys (Domínguez and Fernández, 2009). Functional feeding groups (FFGs) were assigned using available references, knowledge of feeding modes

(mouthpart morphology and behavior), and analysis of gut contents (Merrit and Cummins, 1996).

2.5. Fish inventory

A survey of the fish community was carried out in order to know the presence of fish species at both systems (Torrecillas: T6; Baggilt: B3, B4 and B5). Sampling was limited to the accessible area for this community, thus the presence of a fall was considered as an upstream barrier for individuals. Survey was carried out by electro-fishing with a battery powered backpack machine (output 300 W) set at 300 V and a hand net. Reaches assessed were 100 m long; three passes were made at each site in all months by the same operator (Di Prinzio et al., 2009).

2.6. Data analysis and statistical approach

Differences in physicochemical parameters and attributes of macroinvertebrate communities between glacier-fed systems or among particular sites were tested using non parametric ANOVA test (Kruskal-Wallis). The interpretation of this test is basically identical to that of the parametric one-way ANOVA, except that it is based on ranks rather than on means (Sokal and Rohlf, 1995). For pair-wise comparisons we performed Mann-Whitney *U* test which is a nonparametric alternative to the *t*-test for independent samples.

We calculated a set of macroinvertebrate community descriptors for each site and sampling date, including richness measures: taxa richness, total density, and diversity (H′ Shannon Wiener index). Moreover, macroinvertebrate richness of both streams was rarefied to the number of individuals in the sample with the fewest animals to allow comparison between samples with different densities of individuals (Gotelli and Colwell, 2001). Rarefied richness was calculated using "rarefy" function, available in the "vegan" package (Oksanen et al., 2017) and using the statistical software R version 3.2.3. We examined the longitudinal patterns of biological measures considering the distance from the glacier at each system. Dispersion models were employed with species richness, rarefied richness, density and H′ as dependent variables to analyze their relationships with water temperature, food resources and spatial heterogeneity given by explaining variables as biomass of total benthic detritus and specific fractions (FPOM, leaves, wood, CPOM), chlorophyll *a*, and bryophytes. The significance of this relationships were assessed using single regression models based on mean values of dependent variables ($p < 0.05$). Prior pattern examination, all predictor (i.e., independent) and response (i.e., dependent) variables were tested for normality with the Komolgorov– Smirnov (KS) test and transformed, when necessary.

Generalized Linear Models (GLM) were also applied, models that included all the environmental variables as fixed effects were tested. The richness and density from both systems were the response variables in four separate linear model analysis. The response variables were modeled assuming a Poisson distribution of errors, and applying the log function as link between the response variable and the linear predictor. Overdispersion was compensated by refitting the density model (Baggilt system), using a quasi-Poisson distribution rather than Poisson errors (Zuur et al., 2009). Models were evaluated with an automatic forward stepwise selection procedure. To supplement parameter evidence of important effects, the model parameters were bootstrapped, and confidence intervals limits (CL) were calculated. Explanatory variables with CL excluding zero were retained in the final model. To avoid collinearity between explanatory variables, only terms with variance inflation factors ≤ 4 were allowed. The percentage of explained deviance by each model was calculated. Statistical analyses were performed using R software, Version 3.2.3 (R Core Team, 2016), boot (Canty and Ripley, 2014), and car (Fox and Weisberg, 2011) packages.

Spatial patterns of some groups expected in glacier-fed systems were also examined, and then special attention was dedicated to Chironomidae and the relative contribution of the subfamilies regarding the distance from the glacier. To compare community composition and relative abundance of macroinvertebrates between systems, a Non Metric Multidimensional Scaling approach was applied. In the procedure, a correlation matrix was performed on log $(x + 1)$ density data per site and then used to run the NMDS, were two dimension were extracted and plotted. Both NMDS1 and NMDS2 were correlated (Pearson correlation) with environmental variables (Bonferroni adjustment) in order to know main stressors explaining differences in community structure.

At each glacier-fed system, and to assess relationships between macroinvertebrate species and environmental variables, two separated Canonical Correspondence Analysis (CCA) were run using CANOCO (ter Braak and Smilauer, 1999). CCA was chosen because previous inspection of the data revealed a unimodal mode rather than a linear response in the species data (ter Braak and Smilauer, 1998). All environmental variables included in Tables 2, 3 and 4 were used, initially, to evaluate the response of community descriptors and sites to environmental gradients. Variables (except pH and chlorophyll *a*) were transformed (log $(x + 1)$) prior to analysis. Variables that were strongly intercorrelated with others (those with an inflation factor > 10) in the initial analysis, were removed and a further analysis was carried out with the remaining environmental variables. A Monte Carlo permutation test (9999 permutations) was used to verify the significance of the models (ter Braak and Smilauer, 1998).

3. Results

3.1. Environmental gradients at Torrecillas and Baggilt glacier-fed systems

Main environmental features clearly displayed the harsh nature of glacier-fed streams, as is shown in slope gradients, low water temperature, and substrate stability (Table 2). All sites had low ionic content, low water conductivity, and were poor in nutrients. The physical and chemical measures reflected some differences between both glacier-fed systems, which were related to elevation and geographical location of the basins. Differences observed in water temperature were related with warmer air masses at Baggilt (Fig. 2) which according to surface temperature patterns are probably higher at this area.

In general, TSS contents at Torrecillas were lower, and conductivity higher than at Baggilt stream. A significant decreasing trend of TSS with distance from the glacier was observed ($r^2 = 0.24$, $p < 0.05$, $n = 25$), maximum values were recorded at closest sites at Cónico glacier G. (B3: 269.07 mg l^{-1}), probably related with higher meltwater contribution at the time of sampling (near midday). Moreover, stability Pfankuch significantly increased with distance from the glacier ($r^2 = 0.23$, $n = 14$).

All sites showed well oxygenated waters (all sites >10.4 mg l^{-1}), at site T4 saturation value showed a light depletion. Additionally, nutrient and ion composition, mostly NO_3-NO_2 (between 8 and 13 times higher than values recorded at other sites), and also Ca^{2+} and Mg^{2+} values suggested groundwater contribution at this site (Table 3).

3.2. Particulate organic matter, bryophytes, chlorophyll a

Except for the first three sites located above the timberline at Baggilt (B1, B2 and B3), most sites displayed a good contribution to benthic detritus which ranged from 10.73 (at T1) to 81.50 g DM m^2 (at T4) at Torrecillas stream, and from 16.91 (at B7) to 27.61 (at B8) at Baggilt Stream (Table 2). A detailed analysis of detrital fractions showed that the contribution of fragmented material (CPOM) and wood raised >50% at most sites at Torrecillas. Nevertheless benthic samples were largely dominated by bryophytes during February (>68.8% all Torrecillas sites, except T4) (Kruskal Wallis $p < 0.05$). Similarly, at Baggilt sites coarse detrital items were well represented (wood: 4 to 40% and CPOM: 11 to 35%), but bryophytes contributed with 40 to 70% in benthic samples at shaded sites (B4, B5 and B6) (Table 4).

Table 2
Geomorphological descriptors and habitat features of studied glacier-fed streams: data at Torrecillas ($n = 6$) and Baggilt tributaries ($n = 8$) sampled during February and April of 2015. Data at B1, B2 and B3 sites correspond to one visit (March 2017). - not available.

Sites	Altitude (m a.s.l.)	Distance from glacier (km)	Slope (%)	Pfankuch bed index	Depth (cm)	Width (m) Min–max	Mean current velocity (m s^{-1})	Discharge (m^3 s^{-1})	Benthic detritus (g DM m^{-2})	Benthic algae (μg Chl cm^{-2})
Torrecillas S.										
T1	758	2.62	6.01	72	35.0	5.9–6	1.2	2.65	10.73	0.05
T2	735	2.83	18.30	75	17.4	5.5–10	0.50	0.54	34.18	0.23
T3	656	2.97	18.30	66	24.7	5.3–10	0.45	0.74	16.06	0.14
T4	636	3.12	6	59	17.1	0.5–1.9	0.37	0.11	81.59	–
T5	555	3.14	6.01	66	16.4	0.8–4.2	0.49	0.11	25.20	0.24
T6	560	3.64	6.01	67	16.6	0.6–7.1	0.45	0.20	55.40	0.14
Baggilt S.										
B1	1266	0.68	22.55	54	16	1.4	0.90	0.20	2.22	0.04
B2	1241	0.83	18.30	54	16.66	1.58	0.47	0.13	0.33	0.02
B3	1227	0.97	10.05	59	14.11	2.64	1.13	0.42	0.11	0.02
B4	1143	1.26	12.09	59	21.8	3.5–4	0.64	0.55	23.80	0.17
B5	1137	1.37	16.21	66	19.3	4–7	0.53	0.53	29.29	0.09
B6	1110	1.84	4.00	67	14.9	4–5	1.02	0.68	44.57	0.10
B7	1084	2.7	0	80	25.8	5.9–8	0.34	0.62	16.91	0.90
B8	1071	2.96	6.01	91	14.2	15–15.2	0.49	1.02	27.61	1.08

As expected, algal biomass (chlorophyll *a*) was very low at both glacier-fed systems and ranged between 0.02 and 1.08 μg cm^{-2} (B1 and B8 respectively) at Baggilt stream, and between 0.05 and 0.24 μg cm^{-2} (T1 to T5 respectively) at Torrecillas (Table 2). Absence of rocky substrates at T4 prevented chlorophyll *a* extraction.

3.3. Longitudinal patterns of macroinvertebrates at glaciered systems

Patterns observed in density, species richness, rarefied richness, and diversity between Baggilt and Torrecillas streams are presented in Fig. 3. Total richness and density values were markedly higher at Baggilt than at Torrecillas, and similar trends were highlighted by rarefied curves. Overall species richness more than doubled between sites at Baggilt and Torrecillas (64/31 taxa). At Baggilt, sites closest to the glacier snout (B1, B2, and B3) were extremely poor in richness and density but not in diversity. Values increased markedly (70% in richness and 90% in density) at the shaded forest sites (B4, B5). Species that appeared immediately below open forest sites belong to the EPT group, and were mainly shredders (*Udamocercia arumifera*, *Neopentura semifusca*, *Senzilloides panguipulli*, *Klapoteryx kuscheli*) and grazers/scrapers (*Metamonius anceps*, *Andesiops torrens*, *A. peruvianus*, *Metrichia neotropicalis* and *Austrocentrus valgiformis*) (Appendix A). Additionally, collector-gatherers (mostly Chironomidae species) enriched assemblages at shaded places. A decreasing pattern in species richness and diversity was observed starting at B6; composition at upstream and downstream the wetland differed. For example *Notoperla* sp., *M. anceps*, were no longer recorded downstream the wetland area whereas other taxa such as *Nais communis* and Tabanidae sp. were only recorded at B7 and B8. Density decreased from B4 towards B7 and increased again at B8.

At Torrecillas stream only diversity seemed to increase with distance from the glacier. In terms of taxa richness and density, site T4 (with ground water contribution) displayed a peak. Species assemblage at T4 was dominated by *Myotrichia murina*, *Gigantodax* sp., *Smicridea* sp. and *Aubertoperla illiesi* (Appendix A). The site also exhibited a high contribution to detritus, and was stable regarding water temperature (low thermal range) (Table 2). Mean taxon richness in the remaining sites was always ≤6 taxa.

The relative contribution of Chironomidae subfamilies at Baggilt, showed a consistent pattern as was expected for glaciered systems; Diamesinae relative contribution was higher at sites closer to the glacier, whereas Orthocladiinae increased downstream (Fig. 4). Other taxa were also important at the first three sites: *Edwardsina* sp. (Blephariceridae), *Notoperla* sp. (Plecoptera), and *Pedrowygomyia* sp. (Simuliidae). This pattern was not observed at Torrecillas, since Orthocladiinae contributed with more of 50% at T1, T2 and T6. Podonomidae barely reached 5% at T1 and T6, and Diamesinae were not recorded.

Table 3
Physicochemical features of studied glacier-fed streams: Torrecillas ($n = 6$) and Baggilt ($n = 8$) tributaries sampled during February and April of 2015 (data are mean values, water temperature and TSS is range, and cations one record). Data at B1, B2 and B3 sites correspond to one visit (March 2017), −: not available.

	Water temperature (°C)	Conductivity (μS cm^{-1})	Dissolved oxygen (mg l^{-1})	% oxygen saturation	pH	TSS (mg l^{-1})	NO$_3$-NO$_2$ (μg l^{-1})	NH$_4$ (μg l^{-1})	SRP (μg l^{-1})	Na$^+$ (mg l^{-1})	K$^+$ (mg l^{-1})	Mg^{2+} (mg l^{-1})	Ca^{2+} (mg l^{-1})
Torrecillas stream													
T1	3.6–8.1	21.9	12.3	103.4	6	0–3	40.0	7.2	4.3	<1	<1	1	5
T2	3.4–6.6	19.1	12.2	99.5	5.9	0–0.4	28.1	13.1	4.3	<1	<1	1	5
T3	3.7–7.4	21.7	12.7	101.9	5.6	0.2–0.8	25.9	13.9	1.4	<1	<1	<1	5
T4	5.3–5.9	36.4	10.6	86.9	6.6	0	340.7	5.9	9.5	1	<1	5	8
T5	4.4–8	20.1	12.1	98.5	6.2	0–0.2	36.2	13.7	5.2	<1	<1	1	4
T6	4.3–8.6	22.5	12.7	101.4	6.4	0.0.4	41.0	13.3	12.8	<1	<1	<1	5
Baggilt stream													
B1	8.1	7.4	10.7	96.4	8.5	37.9	0	2	0	–	–	–	–
B2	9.4	7.1	10.4	96	8.5	59.6	0	7.3	0	–	–	–	–
B3	9.4	6.9	10.4	96.7	8.5	269.1	0	11.9	3.7	–	–	–	–
B4	5.6–7.5	9.8	11.4	95	7.7	9.2–12	61.6	5.6	6.6	<1	<1	<0.4	<0.4
B5	6.7–8.7	10.6	11.1	98.4	6.7	11.4–8.2	35.1	6.3	2.8	<1	<1	<0.4	<0.4
B6	7.1–10.1	10.7	10.9	98.8	7.2	9.2–10	23.2	7.5	6.6	<1	<1	<0.4	<0.4
B7	8.5–11.2	17.3	10.9	101.6	7.6	0–2.8	23.8	11.6	2.4	<1	<1	<0.4	<0.4
B8	8.14–9	16.5	16.6	144.5	7.4	1.4–10.5	17.8	16.7	41.3	<1	<1	<0.4	<0.4

Table 4
Biomass of detrital fractions and bryophytes at sampling sites Torrecillas and Baggilt glacier fed streams, data are mean values (February and April of 2015). Data at B1, B2 and B3 sites correspond to one visit (March 2017).

Sites	Bryophytes	Leaves	Wood	CPOM	FPOM
	g DM m^{-2}	g DM m^{-2}	g DM m^{-2}	g DM m^{-2}	g DM m^{-2}
Torrecillas stream					
T1	10.18	2.58	0.25	2.45	5.45
T2	66.91	0.97	3.42	23.34	6.45
T3	21.07	1.99	0.73	9.31	4.03
T4	41.94	5.62	39.88	27.07	9.02
T5	103.5	1.12	4.71	10.54	8.84
T6	65.07	3.07	3.40	38.59	10.34
Baggilt stream					
B1	1.46	0	0	0.71	0
B2	0	0	0	0.28	0
B3	0	0	0.02	0.15	0
B4	39.39	2.07	3.99	10.62	7.11
B5	30.92	2.22	2.34	14.90	9.83
B6	57.62	3.44	6.87	11.32	22.94
B7	1.83	0.57	3.17	5.72	7.44
B8	0.15	0.16	10.90	9.81	6.74

Bivariate dispersion plots highlighted some relationships between structural community attributes and environmental features (Fig. 5). At Baggilt, benthic detritus biomass appeared as a good predictor of density, richness and rarefied richness, whereas at Torrecillas a good fitness was obtained for H diversity and benthic detritus. Bryophyte biomass was important at Baggilt, resulting in more complex invertebrate assemblages. Additionally, in GLM approaches, model parameter estimated and confidence intervals indicated for Torrecillas system a negative effect of chlorophyll a on richness, and a positive effect of conductivity on density. Higher conductivity probably resulted in less stressing conditions for organisms (e.g. osmoregulation). At Torrecillas the capture of conductivity as density predictor was probably related with site T4 conditions, which also showed nutrients supply from groundwater (Table 3). At Baggilt system, model parameters showed a positive effect of CPOM and gravel substrates on richness, and a negative one of boulder substrates and water temperature on density (Table 5).

As expected, the non-native fish species *Oncorhynchus mykiss* was found only at the Baggilt system in very low numbers (<0.1 ind m^{-2}), upstream and downstream the wetland location. Fish were not recorded at Torrecillas stream.
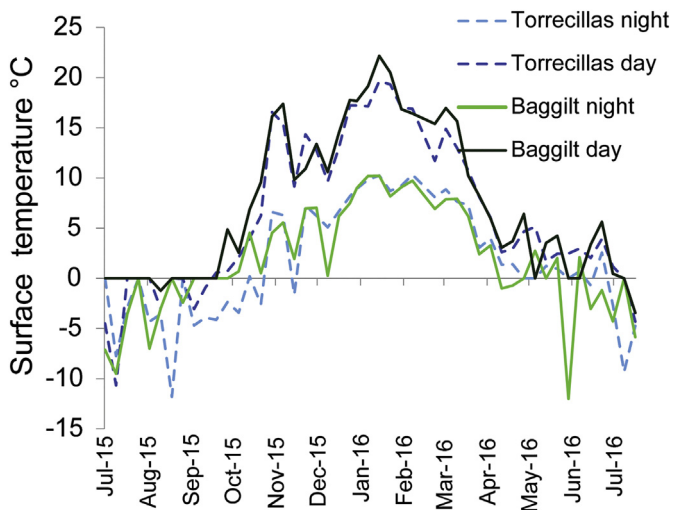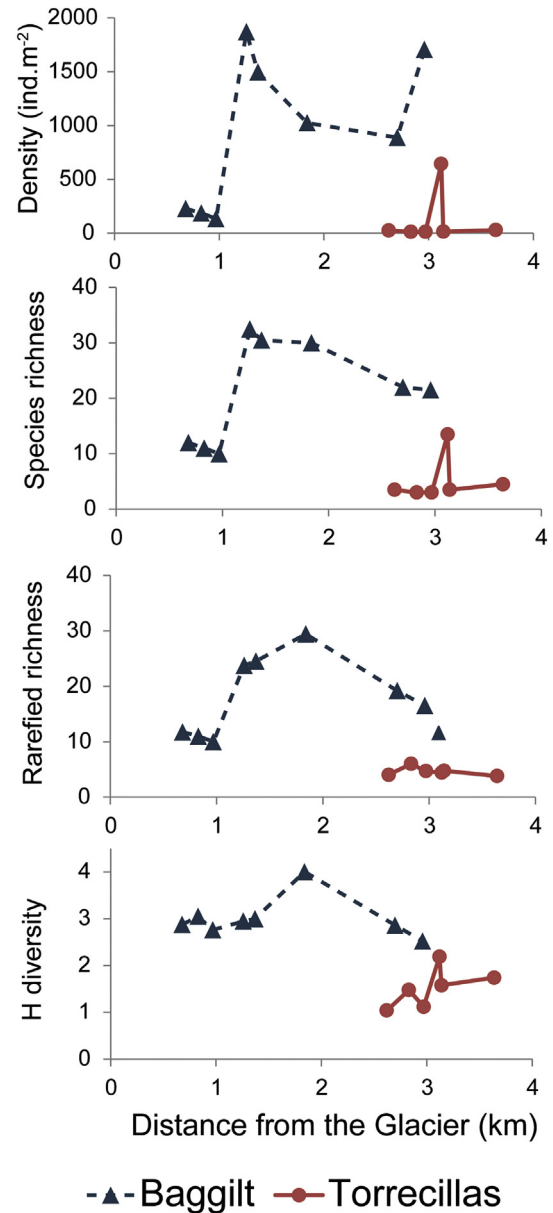

Fig. 3. Longitudinal patterns of density of individuals, species richness, rarefied richness, and Shannon-Wiener diversity index of macroinvertebrate assemblages at studied glacier-fed streams: Torrecillas and Baggilt (Patagonia, Argentina).

3.4. Macroinvertebrates commonalities at studied glaciered systems

Altogether 76 taxa were collected in the study, but only 21 taxa (most endemic) were present at both systems, examples of that were: *Aubertoperla illiesi* and *Udamocercia arumifera* (Plecoptera), *Meridialaris chiloeensis* (Ephemeroptera), *Cailloma pumida*, *Rheochorema robustum* and *Austocentrus valgiformis* (Trichoptera). Among Chironomidae, seven taxa (*Ablabesmyia* sp., *Pentaneura* sp., *Parapsectrocladius* sp., *Paratrichocladius* sp., *Parametriocnemus* sp., *Parochlus* sp. and *Podonomus* sp.) were also present at both streams. Nevertheless, the studied glacier-fed systems supported very different macroinvertebrate assemblages because >73% of the taxa were not commonalities. This was clearly shown in the unconstrained ordination by NMDS in which a significant (stress 0.17) distinction between Torrecillas and Baggilt sites is seen (Fig. 6A). Separation along NMDS 1 showed strong differences among faunal composition between systems, NMDS 2 displayed different groups from those located at open (B1, B2 and B3) and shaded
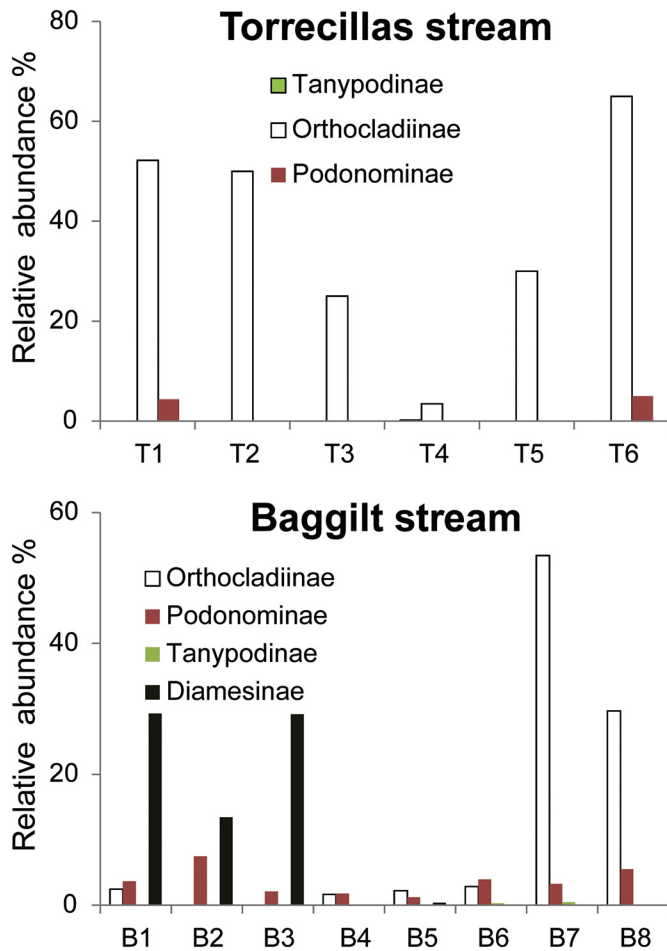

Fig. 2. Dairy land surface temperature (2015–2016) at study areas (night and day).

Fig. 4. Relative contribution of Chironomidae families in the longitudinal dimension at the studied glacier-fed streams: Torrecillas and Baggilt (Patagonia, Argentina).

sites at Baggilt, moreover those upstream and downstream the wetland appeared as recognizable groups.

3.5. Species environmental relationship at glacier-fed system

The most significant variables (Pearson correlation with Bonferroni correction $p < 0.05$) explaining the site arrangement regarding species abundance at NMDS were elevation, pH and TSS (r Pearson: 0.89, 0.66 and 0.79 respectively), which increased towards the positive side of the axis. NMDS1 displayed negative correlation with conductivity and distance from the glacier (r Pearson, −0.64 and −0.76 respectively). Species richness also showed a strong and positive association with NMDS1 (r Pearson: 0.91), highlighting major differences between systems. Regarding NMDS2, stability (Pfankuch index) and wet width were the most significant variables affecting macroinvertebrate structure (Fig. 6 A).

Results of CCA at Baggilt for benthic macroinvertebrates had eigenvalues of 0.44 and 0.29 for the first two axes and explained 57.6% of species-environment relationships (Monte Carlo test: CCA1 $p < 0.0032$, all axes $p < 0.0001$). The CCA triplot of macroinvertebrates, sites, and environmental data showed a clear distinction among sites closest to the glacier (upper left quadrant), sites upstream (lower left quadrant) and downstream the wetland (positive side of CCA1). The main natural environmental gradient was defined by distance from the glacier, chlorophyll a, and TSS content (CCA1), and species were distributed accordingly along this axis. Diamesinae sp. 1 and sp. 2 were very abundant at turbid reaches, closest to the glacier, and were positioned on the upper left

quadrant. *Polycentropus* sp., *Paratrichocladius* sp., *Nais communis*, *Pentaneura* sp. more abundant at the more distant sites (B7 and B8), were placed on the positive end of CCA1. Variables more strongly related to CCA2 were bryophyte biomass, CPOM and NO₃, where sites B4, B5 and B6 were grouped. The shredders *Senzilloides panguipulli* and *Neopentura semifusca*, and the scrapers *Contacyphon* sp. and *Austrocentrus valgiformis* peaked at these sites (Fig. 6 B).

The results of the CCA analysis at Torrecillas (eigenvalues CCA1: 0.85 and CCA2: 0.45) where sites and also species were distinguished by 6 significant variables: water temperature, NO₃, chlorophyll a (CCA1), distance from the glacier, elevation, and bryophyte biomass (CCA2) separated site T4 from the rest (Fig. 6C). *Parochlus*, *Parapsetrocladius* sp., and *Cailloma pumida* (T1 and T2) were positioned on the lower right quadrant; *Podonomus* sp., *Cura* sp., and *Molophilus* sp., more frequent at lower sites (T5, T6), were placed on the positive side of CCA2. As explained before, a more rich assemblage of invertebrates (lower left quadrant) was found at T4, and this was clearly highlighted in the ordination procedure.

4. Discussion

4.1. Do Patagonian fed-glacier systems fit the temperate model?

Temperate artic and alpine glacier-fed streams are characterized by very low water temperature (Max. $T < 2$ °C to <4) (Brittain and Milner, 2001), but none of the two studied systems fit properly to that pattern, even at those sites very close to the glacier such as the Cónico (Baggilt S., B1: 680 m) water temperature reached 8.1 °C. On the other hand, turbidity and stability of the substrates, which are other relevant features defining the harsh nature of these environments, displayed the predicted trend according to the conceptual model (Milner and Petts, 1994) with total suspended solids decreasing and substrate stability increasing with distance from the glacier (Milner et al., 2001a). At Baggilt, the general pattern reflected by benthic fauna in terms of richness and density was also consistent with what was expected, and assemblages at the first three sites displayed lower richness (50 to 70% less) than what has been reported at snowmelt-dominated headwater streams at Patagonia (Miserendino and Pizzolon, 2000; Miserendino et al., 2011). At Torrecillas, however, the pattern was unclear because the lake outflow probably imposed different environmental conditions on the stream. Discontinuities produced by lake outlets in the downstream gradient were included in the conceptual model originally proposed (Brittain and Milner, 2001) since lakes can act as thermal and hydrological regulators. Lake outlets at kryal streams harbor a distinctive biota, and can result less harsh for organisms because the presence of a proglaciar lake can attenuate the glacier effects (Hieber et al., 2002). Our data do not confirm this tendency; in fact, macroinvertebrate communities at Torrecillas were extremely poor in terms of richness and density compared with those at Baggilt. Similarly, Perić and Robinson (2015), observed significantly lower benthic macroinvertebrate richness and density in a glacier lake outlet stream than at a proglacier alpine stream. Apparently, the lake acted by ameliorating physical and chemical conditions, but diminished the content of suspended organic matter for filter feeders survival. Torrecillas system was probably less turbid but colder than Baggilt, and water temperature could act as a significant environmental filter for invertebrate species.

At Torrecillas stream some Staphylinidae, Hydrobiosidae (*Cailloma pumida*), and Orthocladiinae (*Paratrichocladius* sp., *Parapsetrocladius* sp. and *Parametriocnemus* sp.) occurred, similar to what has been recorded at other glaciered Andean systems (Miserendino, 2001; Kuhn et al., 2011; Tagliaferro et al., 2013). Site T4, however, likely with groundwater contribution, displayed an unexpected high richness in which shredders (*Udamocercia arumifera*, *Myotrichia murina* and *Austrocosmoecus hirsutus*) as well as collector-filterers (*Smicridea* sp. and *Gigantodax* sp.) dominated the assemblage. Here, a greater environmental heterogeneity, given by the vicinity of a dense forest provided a
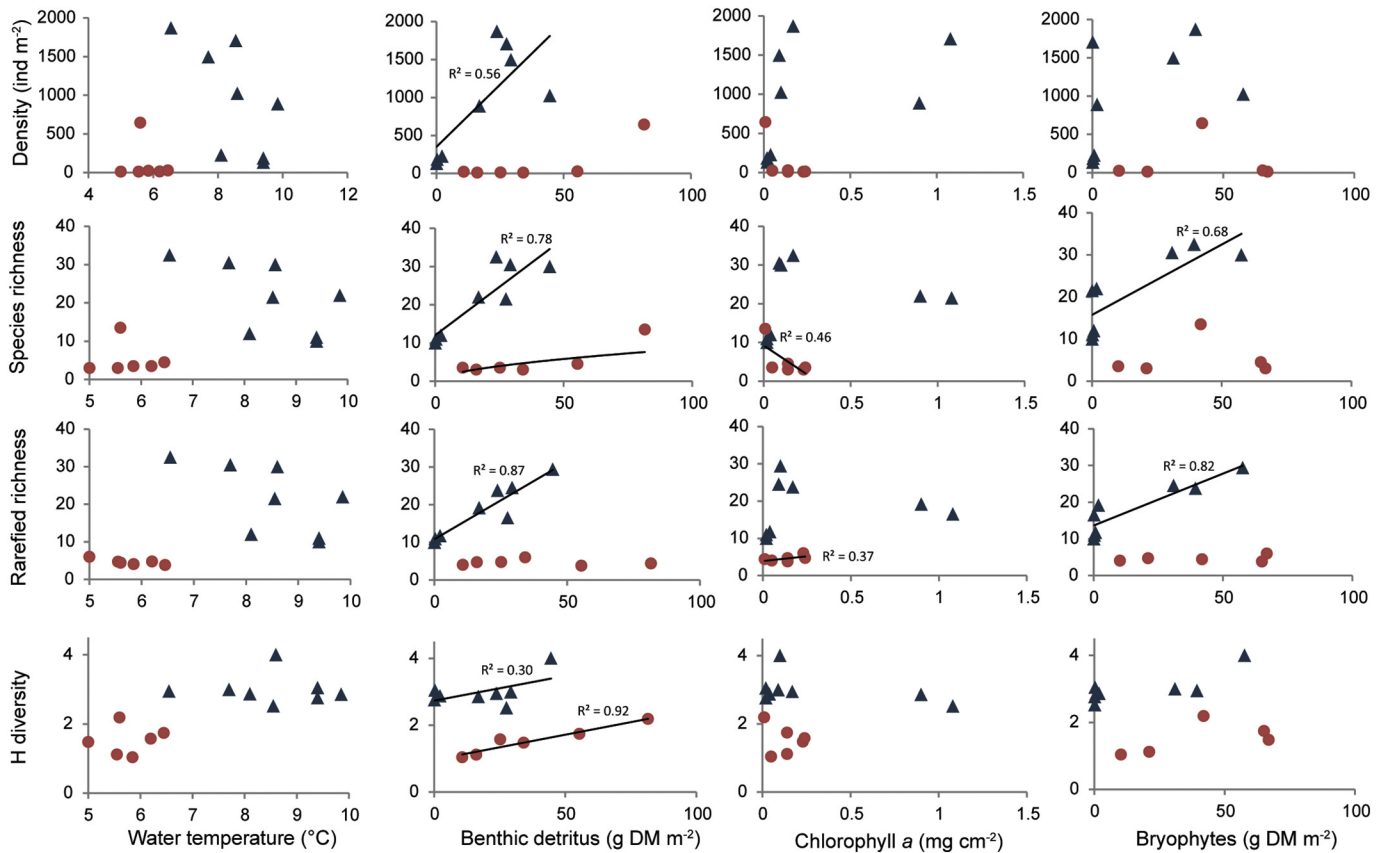
Fig. 5. Relationships of main macroinvertebrate metrics (density of individuals, species richness, rarefied richness, and Shannon-Wiener diversity index) at Torrecillas (triangles) and Baggilt (circles) glacier-fed streams and water temperature, benthic detritus, chlorophyll *a*, and bryophytes biomass.

major offer of detrital food and better habitat conditions. As found by Niedrist and Füreder (2016), the availability of broad food sources such as diatoms, periphyton and detritus, had an important role in structuring community at groundwater fed alpine streams. Nevertheless, macroinvertebrate taxa richness at most Torrecillas sites was very low, and comparable to that reported for glacier-fed streams in other regions (Robinson et al., 2001; Ilg and Castella, 2006).

Macroinvertebrate composition on the longitudinal dimension was quite consistent with those described for other temperate Southern Hemisphere environments such as New Zealand glacier-fed streams (Milner et al., 2001b). Among Chironomidae, the subfamilies Diamesinae, Podonominae and Orthocladiinae were present at sites

closer to the glaciers. As occurred in other South American glacier-fed systems (Jacobsen et al., 2010; Kuhn et al., 2011), some departures observed in faunal distribution undoubtedly responded to zoogeographical differences, for example Gripoterygidae (*Aubertoperla illiesi*, *Chilenoperla* sp. and *Notoperla* sp.) and Blephariceridae (*Edwardsina* sp.) showed a good contribution at the first sites at Baggilt. *Meridialaris chiloeensis* (Leptophlebiidae) was able to colonize the first reaches too, as apparently does *Deleatidium* (Leptophlebiidae) at New Zealand similar stream types (Winterbourn et al., 2008).

Benthic assemblages at the first three sites at Baggilt, were entirely composed by flying insect taxa, this might indicate that downstream forested reaches probably acted as sources for colonizers through flight

Table 5
Generalized linear models results for Torrecillas (*n* = 6) and Baggilt systems (*n* = 8) explaining the effect of environmental variables on richness and density. Explanatory variables, parameter estimates (β) (±standard error), and confidence intervals (CL) are shown.

System	Model	Explanatory variables	β ± SE	z value	*p* value	CL: lower	CL: upper
Torrecillas	Richness	Intercept	2.2 ± 0.3	8.3	2e − 16	2	2.3
		Chlorophyll	−5.7 ± 2.2	−2.6	0.009	−7.3	−3.8
	Density	Intercept	−2.2 ± 0.3	−8.3	2e − 16	−3.4	2.4
		Conductivity	0.2 ± 0.008	31.4	2e − 16	0.006	0.3
Baggilt	Richness	Intercept	2.4 ± 0.2	14.8	2e − 16	2.3	2.5
		CPOM	0.7 ± 0.2	3.9	0.0001	0.4	0.9
		Gravel	0.02 ± 0.01	1.8	0.08	0.0001	0.03

System	Model	Explanatory variables	β ± SE	t value	*p* value	CL: lower	CL: upper
Baggilt	Density	Intercept	10.5 ± 0.8	13.9	3.4e − 05	7.1	17.7
		Boulder	−0.03 ± 0.006	−5	0.004	−0.04	−0.01
		W. Temp.	−0.4 ± 0.09	−4	0.01	−0.5	−0.08

Explanatory variables with CL including zero were excluded from the final model. Percentage of explained deviance by each model: 94% (Torrecillas: Richness), and 99% (Torrecillas: Density), 97% (Baggilt: Richness), 90% (Baggilt: Density).
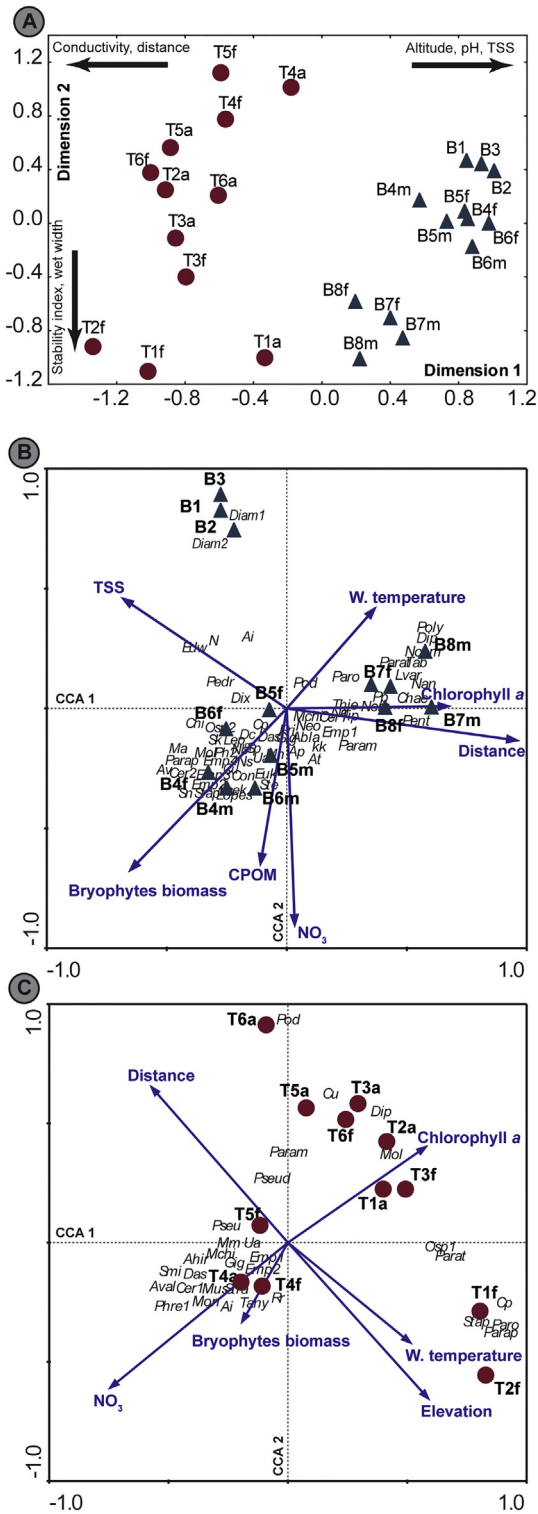
Fig. 6. a) Non Metric Multidimensional Scaling (NMDS) ordination of log (x + 1) transformed community data (stress = 0.17) of the two glacier-fed systems Torrecillas (n = 12) and Baggilt (n = 13), Patagonia, Argentina. b and c) Triplots (sites, macroinvertebrate species and environmental variables) based on Canonical Correspondence Analysis at Baggilt (triangles) and Torrecillas (circles) glacier-fed streams. Code of species in Appendix A.

dispersal mechanisms. Only Diamesinae spp., appeared more confined to the upland sites, where glacier meltwater is pronounced, displaying their ability to better survive at more turbid reaches.

4.2. Benthic detritus, chlorophyll a and bryophytes

As expected for turbid streams, and even considering that data were taken in summer (major sunlight exposition), epilithic algal biomass was very low (Torrecillas <0.24 and Baggilt <1.08 μg Chl cm^{-2}). Values were consistent with those reported for other glaciered systems from Europe (Niedrist and Füreder, 2016), New Zealand (Milner et al., 2001b), and South America (Jacobsen et al., 2010). Regarding detritus availability, and with the exception of the first three sites, a good contribution of allochthonous particulate organic matter occurred at most sites in Baggilt, being quite similar to what was observed on rhithral or seasonal snowmelt-dominated systems in Patagonia (Miserendino et al., 2011; Brand et al., 2012). Bryophyte biomass was markedly high at most visited sites, and values were equivalent to those found at undisturbed low order snow-fed mountain streams (Masi and Miserendino, 2009).

4.3. Spatial heterogeneity at glacier-fed streams: wetlands, groundwater and forest

In the longitudinal dimension of the studied systems, spatial complexity increased with the presence of wetlands, groundwater or a close and dense forest. All these features increased habitat offer and were of great value to explain macroinvertebrate structure and the observed shifts in composition and species richness as well. In alpine systems and in terms of hydrological stores, the main sources of runoff are glaciers and snowpacks (meltwater), but also alluvial or regional aquifers (groundwater). Consequently distinct benthic macroinvertebrate assemblages exist depending on stream being originated from snow, glaciers and groundwater (Brown et al., 2006). High elevation wetlands appear as significant components of the Patagonian mountain landscape, but there is a paucity of ecological and biological knowledge regarding these natural aquatic reservoirs (Mazzoni and Rabassa, 2013; Epele and Miserendino, 2015). These environments would act not only as water reservoirs, but also providing hydrological stability facing floods, offering new habitats, refuges and food, and even ameliorating turbidity conditions derived from glacier melting. As was observed in the ordination (NMDS), sites located up and downstream the wetland at Baggilt were clearly separated. Compositional changes at these sites responded to a decreasing trend in TSS content, and to an increase in water temperature and chlorophyll a (CCA) where benthic assemblages were enriched with species of collector-gatherers (*Thienemaniella* sp., *Paratrichocladius* sp., *Pelurgoperla personata* and Naidinae sp.) and grazers (*Nousia delicata*, *Andesiops peruvianus* and *A. torrens*). As in other alpine landscapes (Oertli et al., 2008; Jacobsen et al., 2012), our data confirm that wetlands at Patagonian glaciered fed system constitute important environmental filters. At a landscape scale and at a basin scale, some aspects of relevance to be considered are presence, extension and hydrological features of the wetlands, especially concerning conservation issues (Erwin, 2009). According to Khamis et al. (2014) the role of wetlands facing global warming is that they can enhance resilience during extreme events or enable migration upstream or downstream to more suitable climates.

4.4. Climate change and environmental shifts in Patagonian glacier-fed streams

As recognized by Masiokas et al. (2008) glaciers between 39°S and 43°S in Patagonia displayed a strong recession over the past century, and predictions are that this trend will probably continue well into the 21st century. In this context, we propose some potential future scenarios linked with global warming for lentic and lotic sections at our studied system after glaciers retrieve or disappear (Table 1). Higher torrentiality and increases in discharge peaks can be expected at both glacier-fed streams, but this process will be probably faster in the Cónico in which changes in the phreatic level at the wetland, increases in the

delta development and even a forest expansion can occur. As stated by Milner et al. (2001a, 2001b), upstream colonization of stoneflies, may-flies, limnephilid caddisflies and other dipterans such as Empididae and Tipulidae can be expected when water temperature exceeds 4 °C. Our data at Baggilt suggests that this system is rapidly changing; the kryal zone is apparently disappearing due to accelerated retreating and melting of the Cónico glacier. A shift from a species poor community dominated by Diamesinae spp. to a more diverse community with spe-cies of EPT group is apparently occurring. Absence of macroinvertebrate data prior to our study prevents a confirmation. However, this trend has been modeled for stream systems fed by small glaciers (Khamis et al., 2014), in which glacier size and rapid meltwater productions play a cru-cial role in adaptation process of key species. Concerning diversity re-sponses facing global warming, at a reach scale (alpha diversity) will probably increase by the arrival of new favored taxa, while at a regional scale (gamma diversity) this might decrease. Specialist taxa such as Diamesinae might disappear (Brown et al., 2007; Jacobsen et al., 2012; Khamis et al., 2014), because suitable areas for colonization are missing once the glacier recedes. In this scenario, the presence of wetlands will add environmental heterogeneity (Oertli et al., 2008) having remark-able effects in faunal configuration, although some unpredictability on flow and drought is expectable.

At the Torrecillas another scenario can be expected, here we demon-strated that a small deviation from the main watercourse with ground-water contribution supported a richer assemblage, increasing substantially the local diversity. But certainly the hydrological and sed-imentological changes predicted can favor the invasion of invertebrate species adapted to the new conditions (e.g., deposit feeders).

5. Conclusion

Patagonia is by far the most glacierized area in South America, where numerous alpine streams are important providers of ecosystem ser-vices. The consequences of global warming on glacier-fed environments can be considerable on this ecoregion. Our comparative study at two currently retreating glaciers, revealed important aspects not only re-garding dynamics and functioning, but also about the composition and longitudinal patterns of aquatic macroinvertebrate communities. Al-though some species such as Diamesinae responded as predicted in the conceptual model for temperate glacier-fed system, other aspects besides zoogeographical ones are relevant in Patagonia kryal systems. Communities are governed by an environmental complexity generated by: lake outlet position, wetland presence, groundwater contribution, and forest vicinity, which in turn can control other interactive features such as water temperature, flood, habitat condition, food supply, and turbidity. Glacial melting appears as rapidly occurring in the smaller gla-cier (Cónico), in which apparently the predicted sequence is a shift in composition of species adapted to a glacier melt to a snowmelt fed sys-tem. Instead, at Torrecillas stream (4 km long) prevailed the imposed hydrological and thermal conditions from the El Antiguo proglacial lake.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2017.11.320.

References

APHA, 1999. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, Hanover, MD, USA.

Barnett, T.P., Adam, J.C., Lettenmaier, D.P., 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303–309. https://doi.org/10.1038/nature04141.

ter Braak, C.J.F., Smilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4). Microcom-puter power, Ithaca, NY, USA (352 pp.).

ter Braak, C.J.F., Smilauer, P., 1999. CANOCO for Windows (Version 4.02) a FORTRAN Pro-gram for Canonical Community Ordination. Centre for Biometry (Wageningen, The Netherlands).

Brand, C., Miserendino, M.L., Epele, L.B., 2012. Spatial and temporal pattern of caddisfly distribution at a mesohabitat scale in two Patagonian mountain streams subjected to pastoral use. Int. Rev. Hydrobiol. 97:83–99. https://doi.org/10.1002/iroh.201111368.

Brittain, J.E., Milner, A.M., 2001. Ecology of glacier-fed rivers: current status and concepts. Freshw. Biol. 46 (12):1571–1578. https://doi.org/10.1046/j.1365-2427.2001.00845.x.

Brown, L.E., Milner, A.M., Hannah, D.M., 2006. Stability and persistence of alpine stream macroinvertebrate communities and the role of physicochemical habitat variables. Hydrobiologia 560:159–173. https://doi.org/10.1007/s10750-005-1260-8.

Brown, L.E., Hannah, D.M., Milner, A.M., 2007. Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. Glob. Chang. Biol. 13:958–966. https://doi.org/10.1111/j.1365-2486.2007.01341.x.

Canty, A., Ripley, B., 2014. Bootstrap R (S-Plus) Functions. R Package Version. 1 pp. 3–13.

Cauvy-Fraunié, S., Espinosa, R., Andino, P., Jacobsen, D., Dangles, O., 2015. Invertebrate metacommunity structure and dynamics in an Andean glacial stream network facing climate change. PLoS One 10. https://doi.org/10.1371/journal.pone.0136793.

Clitherow, L.R., Carrivick, J.L., Brown, L.E., 2013. Food web structure in a harsh glacier-fed river. PLoS One 8. https://doi.org/10.1371/journal.pone.0060899.

Collier, K., 1992. Assessing river stability: use of the Pfankuch method. Science and Re-search Internal Report No. 131. Department of Conservation, New Zealand (17 pp.).

Delgado, S., Masiokas, M., Villalba, R., Trombotto, D., Ripalta, A., Hernández, J., Calí, S., 2002. Evidencias históricas y dendrocronológicas de las variaciones climáticas en la Patagonia durante los últimos 1000 años (Patagon-1000). Dendrocronología 47–51.

Di Prinzio, C.Y., Casaux, R.J., Miserendino, M.L., 2009. Effects of land use on fish assem-blages in Patagonian low order streams. Ann. Limnol. Int. J. Limnol. 45:267–277. https://doi.org/10.1051/limn/2009030.

Domínguez, E., Fernández, H.R., 2009. Macroinvertebrados bentónicos sudamericanos sistemática y biología. Fundación Miguel Lillo, Tucumán (656 p.).

Epele, L.B., Miserendino, M.L., 2015. Environmental quality and aquatic invertebrate met-rics relationships at Patagonian wetlands subjected to livestock grazing pressures. PLoS One 10:1–19. https://doi.org/10.1371/journal.pone.0137873.

Erwin, K.L., 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. Wetl. Ecol. Manag. 17:71–84. https://doi.org/10.1007/s11273-008-9119-1.

Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression. Second edition. Sage, Thousand Oaks CA (Available from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion).

Füreder, L., Schütz, C., Wallinger, M., Burger, R., 2001. Physico-chemistry and aquatic in-sects of a glacier-fed and a spring-fed alpine stream. Freshw. Biol. 46 (12): 1673–1690. https://doi.org/10.1046/j.1365-2427.2001.00862.x.

Gordon, N.D., McMahon, T.A., Finlayson, B.L., Gippel, C.J., Nathan, R.J., 2004. Stream Hy-drology: An Introduction for Ecologists. John Wiley & Sons, England.

Gotelli, N.J., Colwell, R.K., 2001. Quantifyinf biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4:379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x.

Hieber, M., Robinson, C.T., Uehlinger, U., Ward, J.V., 2002. Are alpine lake outlets less harsh than other alpine streams? Archiv. Hydrobiol. 154 (2):199–223. https://doi.org/10.1127/archiv-hydrobiol/154/2002/199.

Ilg, C., Castella, E., 2006. Patterns of macroinvertebrate traits along three glacial stream con-tinuums. Freshw. Biol. 51:840–853. https://doi.org/10.1111/j.1365-2427.2006.01533.x.

Jacobsen, D., Dangles, O., Andino, P., Espinosa, R., Hamerlík, L., Cadier, E., 2010. Longitudinal zonation of macroinvertebrates in an Ecuadorian glacier-fed stream: do tropical glacial systems fit the temperate model? Freshw. Biol. 55:1234–1248. https://doi.org/10.1111/j.1365-2427.2009.02348.x.

Jacobsen, D., Milner, A.M., Brown, L.E., Dangles, O., 2012. Biodiversity under threat in glacier-fed river systems. Nat. Clim. Chang. 2:361–364. https://doi.org/10.1038/nclimate1435.

Jönsson, M., Ranaker, L., Nicolle, A., Ljungberg, P., Fagerberg, T., Hylander, S., Jephson, T., Lebret, K., von Einem, J., Hansson, L.A., Nilsson, P.A., Balseiro, E., Modenutti, B., 2011. Glacial clay affects foraging performance in a Patagonian fish and cladoceran. Hydrobiologia 663:101–108. https://doi.org/10.1007/s10750-010-0557-4.

Khamis, K., Hannah, D.M., Clarvis, M.H., Brown, L.E., Castella, E., Milner, A.M., 2014. Alpine aquatic ecosystem conservation policy in a changing climate. Environ. Sci. Pol. 43: 39–55. https://doi.org/10.1016/j.envsci.2013.10.004.

Kuhn, J., Andino, P., Calvez, R., Espinosa, R., Hamerlík, L., Vie, S., Dangles, O., Jacobsen, D., 2011. Spatial variability in macroinvertebrate assemblages along and among neighbouring equatorial glacier-fed streams. Freshw. Biol. 56:2226–2244. https://doi.org/10.1111/j.1365-2427.2011.02648.x.

Laspoumaderes, C., Modenutti, B., Souza, M.S., Bastidas Navarro, M., Cuassolo, F., Balseiro, E., 2013. Glacier melting and stoichiometric implications for lake community struc-ture: zooplankton species distributions across a natural light gradient. Glob. Chang. Biol. 19:316–326. https://doi.org/10.1111/gcb.12040.

Masi, C.I., Miserendino, M.L., 2009. Usos de la tierra y distribución de la materia orgánica particulada béntica en ríos de montaña (Patagonia, Argentina). Ecol. Austral 19, 185–196.

Masiokas, M.H., Villalba, R., Luckman, B.H., Lascano, M.E., Delgado, S., Stepanek, P., 2008. 20th-Century glacier recession and regional hydroclimatic changes in northwestern Patagonia. Glob. Planet. Chang. 60:85–100. https://doi.org/10.1016/j.gloplacha.2006.07.031.

Mazzoni, E., Rabassa, J., 2013. Types and internal hydro-geomorphologic variability of mallines (wet-meadows) of Patagonia: emphasis on volcanic plateaus. J. S. Am. Earth Sci. 46:170–182. https://doi.org/10.1016/j.jsames.2011.08.004.

Merrit, R.W., Cummins, K.W., 1996. An Introduction to the Aquatic Insects of North America. Kendall-Hunt, Dubuque, IA.

Milner, A.M., Petts, G., 1994. Glacial rivers: physical habitat and ecology. Freshw. Biol. 32: 295–307. https://doi.org/10.1111/j.1365-2427.1994.tb01127.x.

Milner, A.M., Britain, J., Castella, E., Petts, G., 2001a. Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. Freshw. Biol. 46 (12). https://doi.org/10.1046/j.1365-2427.2001.00861.x.

Milner, A.M., Taylor, R.C., Winterbourn, M.J., 2001b. Longitudinal distribution of macroinvertebrates in two glacier-fed New Zealand rivers. Freshw. Biol. 46:1765–1775. https://doi.org/10.1046/j.1365-2427.2001.00856.x.

Miserendino, M.L., 2001. Macroinvertebrate assemblages in Andean Patagonian rivers and streams: environmental relationships. Hydrobiologia 444:147–158. https://doi.org/10.1023/A:1017519216789.

Miserendino, M.L., Masi, C.I., 2010. The effects of land use on environmental features and functional organization of macroinvertebrate communities in Patagonian low order streams. Ecol. Indic. 10:311–319. https://doi.org/10.1016/j.ecolind.2009.06.008.

Miserendino, M.L., Pizzolon, L. a, 2000. Macroinvertebrates of a fluvial system in Patagonia: altitudinal zonation and functional structure. Arch. Fur Hydrobiol. https://doi.org/10.1127/archiv-hydrobiol/150/2000/55.

Miserendino, M.L., Pizzolon, L.A., 2004. Interactive effects of basin features and land-use change on macroinvertebrate communities of headwater streams in the Patagonian Andes. River Res. Appl. 20:967–983. https://doi.org/10.1002/rra.798.

Miserendino, M.L., Casaux, R., Archangelsky, M., Di Prinzio, C.Y., Brand, C., Kutschker, A.M., 2011. Assessing land-use effects on water quality, in-stream habitat, riparian ecosystems and biodiversity in Patagonian northwest streams. Sci. Total Environ. 409: 612–624. https://doi.org/10.1016/j.scitotenv.2010.10.034.

Miserendino, M.L., Archangelsky, M., Brand, C., Epele, L.B., 2012. Environmental changes and macroinvertebrate responses in Patagonian streams (Argentina) to ashfall from the Chaitén volcano (May 2008). Sci. Total Environ. 424:202–212. https://doi.org/10.1016/j.scitotenv.2012.02.054.

Muhlfeld, C.C., Giersch, J.J., Hauer, F.R., Pederson, G.T., Luikart, G., Peterson, D.P., Downs, C.C., Fagre, D.B., 2011. Climate change links fate of glaciers and an endemic alpine invertebrate. Clim. Chang. 106:337–345. https://doi.org/10.1007/s10584-011-0057-1.

Niedrist, G.H., Füreder, L., 2016. Towards a definition of environmental niches in alpine streams by employing chironomid species preferences. Hydrobiologia:1–18 https://doi.org/10.1007/s10750-016-2836-1.

Oertli, B., Indermuehle, N., Angélibert, S., Hinden, H., Stoll, A., 2008. Macroinvertebrate assemblages in 25 high alpine ponds of the Swiss National Park (Cirque of Macun) and relation to environmental variables. Hydrobiologia 597:29–41. https://doi.org/10.1007/s10750-007-9218-7.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. Vegan: Community Ecology Package R Package Version 2.4-3.

Oyanedel, A., Valdovinos, C., Azocar, M., Moya, C., Mancilla, G., Pedreros, P., Figueroa, R., 2008. Patrones De Distribucion Espacial De Los Macroinvertebrados Bentonicos De La Cuenca Del Rio Aysen (Patagonia Chilena). Gayana (Concepción) 72:241–257. https://doi.org/10.4067/S0717-65382008000200011.

Paruelo, J.M., Jobbagy, E.G., Sala, O.E., 1998. Biozones of Patagonia (Argentina). Ecol. Austral 8, 145–153.

Perić, M.S., Robinson, C.T., 2015. Spatio-temporal shifts of macroinvertebrate drift and benthos in headwaters of a retreating glacier. Hydrobiologia 751:25–41. https://doi.org/10.1007/s10750-014-2149-1.

Pfankuch, D., 1975. Stream Reach Inventory and Channel Stability Evaluation. USDA Forest Service, R1-75-002. Government Printing Office, Washington, DC.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (Available from http://www.R-project.org/).

Rabassa, J., 2010. El cambio climático global en la Patagonia desde el viaje de Charles Darwin hasta nuestros días. Rev. la Asoc. Geológica Argentina 67, 139–156.

Robinson, C.T., Uehlinger, U., Hieber, M., 2001. Spatio-temporal variation in macroinvertebrate assemblages of glacier streams in the Swiss alps. Freshw. Biol. 46, 1663–1672.

Robinson, C.T., Hieber, M., Wenzelides, V., Lods-Crozet, B., 2007. Macroinvertebrate assemblages of a high elevation stream/lake network with an emphasis on the Chironomidae. Fundam. Appl. Limnol. 169:25–36. https://doi.org/10.1127/1863-9135/2007/0169-0025.

Sandin, L., Schmidt-Kloiber, A., Svenning, J.C., Jeppesen, E., Friberg, N., 2014. A trait-based approach to assess climate change sensitivity of freshwater invertebrates across Swedish ecoregions. Curr. Zool. 60, 221–232.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. 3rd edition. W.H. Freeman and Company, New York (859 pp.).

Tagliaferro, M., Pascual, M., 2016. First spatio-temporal study of macroinvertebrates in the Santa Cruz River: a large glacial river about to be dammed without a comprehensive pre-impoundment study. Hydrobiologia:1–15 https://doi.org/10.1007/s10750-016-2850-3.

Tagliaferro, M., Miserendino, M.L., Liberoff, A., Quiroga, A., Pascual, M., 2013. Dams in the last large free-flowing rivers of Patagonia, the Santa Cruz River, environmental features, and macroinvertebrate community. Limnologica 43:500–509. https://doi.org/10.1016/j.limno.2013.04.002.

Valdovinos, C., Kiessling, A., Mardones, M., Moya, C., Oyanedel, A., Salvo, J., Olmos, V., Parra, Ó., 2010. Distribución de macroinvertebrados (Plecoptera y Aeglidae) en ecosistemas fluviales de la Patagonia Chilena: muestran señales biológicas de la evolución geomorfológica postglacial? Rev. Chil. Hist. Nat. 83:267–287. https://doi.org/10.4067/S0716-078X2010000200008.

del Valle, H.F., Elissalde, N.O., Gagliardini, D.A., Milovich, J., 1998. Status of desertification in the Patagonian region: assessment and mapping from satellite imagery. Arid L. Res. Manag. 12:95–121. https://doi.org/10.1080/15324989809381502.

Wetzel, R.G., Likens, G.E., 1991. Limnological Analysis. 2nd edition. Springer-Verlang, New York.

Winterbourn, M.J., Cadbury, S., Ilg, C., Milner, A.M., 2008. Mayfly production in a New Zealand glacial stream and the potential effect of climate change. Hydrobiologia 603:211–219. https://doi.org/10.1007/s10750-007-9273-0.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.