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Declining glacier cover drives changes in aquatic macroinvertebrate biodiversity in the Cordillera Blanca, Perú

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Abstract

Ongoing climate change threatens the biodiversity of glacier-fed river ecosystems worldwide through shifts in water availability and timing, temperature, chemistry and channel stability. However, tropical glacier-fed rivers have received little attention compared to those in temperate and Arctic biomes, despite their unique biodiversity potentially responding differently due to additional stress from higher altitude locations thus lower oxygen availability, diurnal freeze-thaw cycles and annual monsoon rainfall disturbances. This study quantified aquatic biodiversity responses to decreasing glacier cover in the Cordillera Blanca range of the Peruvian Andes. 10 rivers were studied along a gradient of decreasing glacier cover in the in Parón, Huaytapallana and Llanganuco basins, with a specific focus on macroinvertebrates and physicochemical parameters in both the dry and wet seasons. We found higher temperatures, more stable and lower turbidity rivers as glacier cover decreased, which were related significantly to higher local diversity and lower β diversity. Analysis of Similarity revealed significant differences in the macroinvertebrate community among rivers with high, medium or low glacier cover, illustrating turnover from specialists to generalists as glacial influence decreased. Redundancy Analysis demonstrated that there were more species found to prefer stable beds and water temperatures in medium and low GCC rivers. However, certain taxa in groups such as *Paraheptagyia*, Orthocladiinae, *Anomalocosmoecus* and *Limonia* may be adapted to high glacial influence habitats and at risk of glacier retreat. Although species composition was different to other biomes, the Cordillera Blanca rivers showed similar benthic macroinvertebrate biodiversity responses to glacier retreat, supporting the hypothesis that climate change will have predictable effects on aquatic biodiversity in mountain ranges worldwide.

Keywords: Glacier Cover Gradient; benthic macroinvertebrates; biodiversity; Cordillera Blanca

Introduction

Increasing air temperature and precipitation variations are driving rapid reductions in the size and thickness of mountain glaciers worldwide (Hock et al., 2019). Glaciers of the Andes in South America are retreating particularly quickly (Dussaillant et al., 2019), with some studies reporting almost 30% of glacier cover lost between 2000-2016 in Peru alone (Seehaus et al., 2019). In basins with large glaciers, initially higher meltwater discharge decreases after ice cover reaches a critical transition point (Gobiet et al., 2014; Seehaus et al., 2019). Ice loss further leads to changes in the physicochemical characteristics of rivers including increasing water temperature, channel stability, dissolved loads and reduced suspended sediment, in turn influencing communities of biological organisms across all trophic levels (Brown et al., 2007; Milner et al., 2009; Fell et al., 2017). Under low glacial meltwater contribution scenarios, aquatic benthic communities become more homogenous, with the dominance of competing species and reduced abundance or extinction of species adapted to harsh, cold environmental conditions (Cauvy-Fraunié et al., 2015; Elser et al., 2020). Therefore, glacier retreat is anticipated to drive changes in alpha diversity (due to generalist species colonization), beta diversity (due to species turnover and extinction) and gamma diversity (due to species decline at the regional level; Brown et al., 2007; Quenta et al., 2016; Fell et al., 2018).

Benthic community structure and responses to glacier retreat have been well-studied in temperate and Arctic/sub-Arctic biomes (Brown et al., 2018; Dussaillant et al., 2019; Wilkes et al., 2023). However, the high altitude location of tropical-zone glacier-fed rivers generates additional environmental stress for aquatic fauna related to low oxygen saturation due to reduced atmospheric pressure (Acosta & Prat, 2010; Jacobsen et al., 2010) and high solar radiation (Loayza-Muro et al., 2013). Furthermore, tropical glacier-fed rivers present more extreme daily flow events that could lead to differences in aquatic biodiversity, especially among specialized taxa (Cauvy-Fraunié et al., 2013; Jacobsen, Cauvy-Fraunie, et al., 2014). Much of our understanding of tropical glacier-fed river ecosystems has developed from detailed studies in Ecuador (Crespo-Pérez et al., 2020; Espinosa et al., 2020) with only a handful of studies from other countries focusing either on specific invertebrate groups or small numbers of glacier-fed rivers (Acosta & Prat, 2010; Musonge et al., 2020). Therefore, further studies of tropical glacier-fed rivers are vital to enable the development of generalized versus location-specific ecological understanding of climate change effects on mountain river ecosystems.

Glacier-fed rivers are one of the harshest ecosystems for aquatic life (Kuhn et al., 2011) because of intense ultraviolet (UV) radiation at high altitude, low water temperature, and minimal concentrations of nutrients and ions (Brighenti et al., 2019). Additionally, diurnal and seasonal flow variations lead to highly variable concentrations of fine suspended sediment and regular channel-shifting disturbances (Milner et al., 2001;

Brown et al., 2003). These extreme conditions generate the principal environment filters to benthic macroinvertebrates communities in glacial rivers, where specialised species can be found (clingers with small, flattened bodies and short life cycle; Snook & Milner, 2002; Ilg & Castella, 2006; Milner et al., 2009; Brown & Milner, 2012). At the basin scale, glacier influence decreases as glacier mass is lost, or downriver distance increases and water contributions increase from snow-melt, rainfall and groundwater, leading to improved habitat conditions for generalist taxa (Brown et al., 2007; Jacobsen et al., 2010; Jacobsen, Andino, et al., 2014) and increased community richness and diversity (Brown et al., 2003; Jacobsen et al., 2012). Additionally, topographic barriers to dispersal are also considered to play key roles influencing community structure in mountain rivers (Brown et al., 2018).

Increases in invertebrate taxonomic richness have been noted as glacier cover in a catchment (GCC) decreases, although relationships are typically unimodal with peak diversity in rivers with low (5-30%) GCC, then a reduction as glaciers are lost completely (Jacobsen et al., 2012; Khamis et al., 2016). These richness dynamics occur with species compositional turnover, representing a trade-off between stronger abiotic (environmental harshness) stresses in high glacial systems versus more biotic stress in low/zero glacier rivers (Khamis et al., 2016). In temperate zone systems such as Wolf Point Creek, Alaska, the number of taxa increased from 5 to 24 when the GCC reduced from 70 to 0%, with the appearance of taxa Baetidae (<60% GCC) and Coleoptera (0% GCC) as glacial retreat proceeded. However, invertebrate communities in South American tropical rivers fed by glaciers are characterized by the replacement of the Chironomidae Diamesinae by Podonominae, leading to different taxonomic patterns to north-temperate glacier-fed rivers (Jacobsen et al., 2010). As a consequence, detailed studies are needed across a range of tropical river systems to understand fully the mechanisms for biodiversity changes as glaciers are lost.

In this study we analysed the response of benthic macroinvertebrates in rivers of the Cordillera Blanca, Peru, to declining glacier cover. This region is particularly important because: (1) it is the most glaciated mountain range in Peru and comprises almost a quarter of all tropical glaciers (Vuille et al., 2008), (2) these glaciers have retreated rapidly during recent decades (Silverio & Jaquet, 2017; Seehaus et al., 2019), and (3) due to its high vulnerability to ongoing climate change (Zemp et al., 2015), glacial retreat is anticipated to have a significant impact on water supply for biodiversity as well as agriculture, hydropower generation, and human consumption (Gobiet et al., 2014). The following hypotheses were tested: (1) the environmental conditions of glacial rivers become less harsh/adverse as the GCC decreases, leading to a higher α diversity; but β diversity reduction, (2) GCC decreases would shift benthic macroinvertebrates community composition, replacing specialists with generalists, and (3) water temperature, channel stability and turbidity determine the local composition of benthic macroinvertebrate communities.

Materials and methods

Study area

The study was carried out in 10 rivers (basins) belonging to the Parón (P1, P2), Huaytapallana (P3, P4) and Llanganuco (P5, P6, P7, P8, P9, P10) valleys (3701 to 4218 m a.s.l.) on the western flank of the Huandoy and Huascarán mountains in the Peruvian Cordillera Blanca (Fig. 1). Glacier-fed rivers were selected spanning GCC from 0-66%. Glaciers were found in basins between 4365 and 6673 m a.s.l. with a predominant orientation towards west and north (56%) followed by southeast and southwest (31%). In the last decade, glaciers have retreated rapidly; from 1962 to 2019, glacier cover in the study area has reduced by 30.6% (7.48 km^2). Remaining small ice patches are now considered to be in a transition phase to compete loss, making these river ecosystems particularly sensitive to further glacial retreat.

The intrusive geology of the Miocene granodiorite batholith (Siame et al., 2006) has generated a variety of Quaternary landforms. These include slope glaciers (fed by hanging ice masses), debris-covered glacial tongues, colluvial deposits, glacially polished surfaces, scree slopes, moraine deposits (dam pedestal, glacially disconnected plinth and veil type) and active and inactive glacial sediment cones, all located on slopes with steep topography (Iturrizaga, 2018). Due to the scarce hydrogeological information on the catchments, the traditional classification of rivers in glacial catchments (kryal, rhithral and krenal; Brown et al., 2003) was not possible and therefore this study considered GCC as the key indicator of glacial influence.

All collection sites were characterized by riparian vegetation typical of the Puna ecosystem. In low GCC sites (P8, P9) diverse and dense vegetation composed of trees (Quenual), grasses (Ichu), shrubs and bushes were found while at high GCC sites (P3, P7, P10) grasses and bushes were dominant. Climate is characterized by pronounced seasonality of precipitation: dry during the austral winter (May to September) and wet during the austral summer (October to April; Seehaus et al., 2019) when the Intertropical Convergence Zone (ITCZ) is in the southern position. Between 70-80% of precipitation occurs in the wet season and comes from the Amazon forest, while in the dry season runoff comes from glacial melt (Kaser & Georges, 1997) and groundwater input. Rivers were therefore sampled in both the wet and dry seasons to assess the extent to which hydroclimate modifies the influence of glacier influence on aquatic biodiversity. The average annual rainfall recorded in Parón is 770 mm (Vuille et al., 2008). The degree of seasonality of temperature is low with records at Artesoncocha Lagoon (~7 km from the study area) showing a variation between 1 and 12 ºC of mean annual temperature (Lizaga et al., 2019).

Glacier Cover and Geographical variables

Glacier outlines were determined using Sentinel-2 images with 10 m spatial resolution acquired in 2019 (August 17 and September 16), free of clouds and with little temporary snow. The contour delimitation was performed using the Normalised Differential Snow Index (NDSI) at bands 3 (green) and 11 (SWIR) with a threshold of 0.4. Debris-covered glaciers were manually delimited from visual interpretation of Sentinel-2 (432 bands) and Google Earth images. An Alos-Palsar digital elevation model (DEM; 12.5 m) was used to delimit the basin area (BA). The GCC was determined from the ratio between the glacier cover area and the drainage area of each basin. This gradient was classified into high (GCC≥40%), medium (10≤GCC <40%) and low/null (GCC<10%; Fig. 1). DEM and satellite images were also used to calculate slopes (SLP) in collections sites and distance from glacier (DG).

Physicochemical environmental variables

Samples were collected from October 14 to 30, 2019 (post dry season) and from March 07 to 16, 2020 (post wet season). In each river, water temperature, electrical conductivity (EC), pH and dissolved oxygen (DO) were measured using a Multi 3630 multiparameter probe (accuracy: 0.5% for conductivity and DO, 0.004 for pH and ±0.2°C). 10 ml of unfiltered water samples were collected for turbidity analysis using an Oakton T-100 sensor. Moreover, 50 ml of filtered water (0.45 μm cellulose filter paper) was collected to analyze organic and inorganic dissolved carbon (Analytik Jena Multi NC2100 micro elemental analyzer), phosphorus and total nitrogen (automatic wet chemistry analyzer), anions (HPLC-IC - Dionex ICS3000 high performance liquid chromatography) and metal ions (inductively coupled plasma optical emission spectroscopy). Channel stability was estimated with the Pfankuch index bottom component (Pfankuch, 1975) in which higher values equate to lower stability, considering substrate angularity, rock brightness, sediment particle size/compaction, scouring/deposition, percentage of stable channel and aquatic vegetation (mosses and algae).

Benthic macroinvertebrates

In a 15 m section of the ten rivers, six Surber samples (0.09 m^2; 250 μm mesh net) were collected from randomly selected patches, in both rainy and dry season (total N = 120). Sampling covered gravel and pebble substrates from riffles, pools and bankside habitats. Organisms were preserved with 96% ethanol, then sorted with a 250 μm sieve and an AmScope Sm-1ts-144s-m stereoscope (x10 magnification) before storage in 80% ethanol. Identification focused on larvae and pupae, except for Coleoptera, where aquatic adults were included. EPT and most of the Diptera taxa were identified to family/genus following Domınguez & Fernández (2009). Chironomidae were identified to subfamily and in the case of Diamesinae and Podonominae to genus level (x40 magnification) using Prat et al. (2011).

Data analysis

For each river, four Alpha biodiversity indices (Taxonomic Richness, Shannon-H, Fisher Alpha and Rarefied Richness with N_{inv} =111, and density) were determined in PAST v.4.03 (Dasgupta, 2013). β-diversity analysis used total dissimilarity (Sørensen index) and its components turnover (Simpson index) and nestedness (Nestedness index), using the *betapart* package in R (Baselga, 2010). Within-site β-diversity was calculated from the abundance of macroinvertebrates identified in the 6 replicate samples from individual rivers and between-site β-diversity was determined based on total abundances from summed replicates to determine a singular macroinvertebrates abundance value for each river.

Relationship between GCC and environmental variables (the average of two seasons) were examined using Pearson correlation ($p<0.05$). Before linear tests, non-normally distributed variables (Kolmogorov-Smirnov test) were transformed (*logx*+1). Relationships between GCC and biodiversity metrics were examined using generalized additive models (GAM) or generalized linear models (GLM) both with Gaussian distributions in the *mgcv* package in R (Wood, 2011), for both the dry and wet seasons separately. Moreover, relationships between physicochemical variables and each biodiversity index were established with multiple prediction GLM models. Akaike's information criterion (AIC) values were used for model selection in all cases.

Differences in macroinvertebrates taxonomic composition between the three GCC categories (low/none=0-10%, medium=10-40%, high=>40%) were examined using Analysis of Similarity (ANOSIM), then to identify macroinvertebrate taxa responsible for turnover we used Similarity Percentage (SIMPER). Both analyses were carried out in PAST v.4.03. Thereafter, GAM or GLM models were employed to examine associations between the most representative taxa and GCC.

An initial detrended correspondence analysis (DCA) showed a gradient length less than 3 (not a heterogeneous community). Therefore, redundancy analysis (RDA) was used in R to test the association between physicochemical variables and river macroinvertebrate communities (Lepš & Šmilauer, 2003). Less frequent (≤20%) taxa were excluded from the analysis which was based on a Hellinger transformed community matrix. Significance of canonical axes and environmental parameters was evaluated by Monte Carlo multiple permutation tests ($p<0.05$, Perm=5000).

Results

Benthic macroinvertebrate composition

11,005 individuals of the classes Insecta (92.61%), Oligochaeta (6.41%), Hirudinea (0.85%) and Gastropoda (0.08%) were collected. 41 taxa were identified, of which 34 were the most abundant, belonging to the order Diptera (25, 12 Chironomidae), Trichoptera (3), Coleoptera (3), Ephemeroptera (2) and Plecoptera (1). The most representative taxa in both sampling seasons were the mayfly Baetidae *Andesiops* sp. (16.85%), the caddisfly Limnephilidae *Anomalocosmoecus* sp. (16.62%) and the blackfly Simuliidae *Gigantodax* sp. (13.16%). Chironomids were dominated by Diamesinae *Paraheptagyia* sp. (7.41%) and Orthocladiinae sp. 1. (7.11%). Four taxa were cosmopolitan across all sampling sites: *Anomalocosmoecus* sp. (both seasons), *Gigantodax* sp. (both seasons), Orthocladiinae sp. 1. (wet season) and the biting midge Ceratopogoninae sp. (wet season). Some of the less abundant species, such as the mayfly *Meridialaris* sp., the stonefly *Claudioperla* sp. and the caddisfly *Apsytopsyche* sp. were exclusive to sites of low/moderate glacial influence in both seasons.

Relationship between decreasing GCC, environmental variables and biodiversity

GCC was positively correlated with turbidity, DO, PI, drainage area and altitude, and negatively correlated with water temperature, Na, Si and distance from glacier. Nutrients and dissolved organic and inorganic carbon showed no relationship with GCC (Supplementary Table 1). Water temperature was negatively correlated with altitude, drainage area and distance from glacier.

Richness and diversity indices increased significantly as GCC decreased in both dry and wet seasons (Fig. 2). In dry season taxonomic and rarefied richness, and Shannon H, peaking at moderate GCC values. The adjusted GAM curves for density were statistically significant in the wet season, with reduced glacier influence leading to lower macroinvertebrate abundance, particularly at moderate GCC levels, but rebounding under low GCC conditions. In both seasons, an increase in the total dissimilarity of within-site β-diversity was observed as GCC decreased (Fig. 3). Turnover (Simpson index) showed the same trend in the dry season. For between-site β-diversity, total dissimilarity and turnover in both seasons, and Nestedness in the wet season, were greatest among sites with large differences in GCC.

Water temperature was the strongest predictor in 3 of 4 GLM models (Specific Richness, Rarefied Richness and Fisher Alpha), followed by Pfankuch (Specific Richness) and Dissolved Organic Carbon (Specific Richness and Shannon H; Table 1).

Community composition response to decreasing glacier cover

ANOSIM revealed differences between communities belonging to the three GCC categories (R=0.46, P<0.001). The low GCC category showed differences with the medium GCC (R= 0.86, P<0.001, 67.22% dissimilarity) and the high GCC (R= 0.47, p<0.01, 81.4% dissimilarity). There were also differences between medium and high GCC (R= 0.32, P<0.01, 69.1% dissimilarity). According to the SIMPER analysis, ten taxa that generated the greatest contribution to the differentiation of the GCC categories accounted for a cumulative contribution > 77% (Table 2). *Anomalocosmoecus* sp. (both seasons), *Limonia* sp. (both seasons), *Paraheptagyia* sp. (wet season). and Orthocladiinae sp. 1. (wet season) decreased significantly (p<0.05) with decreasing GCC, whereas the abundance of the beetles Scirtidae sp. (wet season) and *Austrelmis* sp. (wet season); as well as Oligochaeta sp. (dry season) increased (Fig. 4).

Environmental variables influencing macroinvertebrate communities

RDA revealed that turbidity (F=3.24, P=0.012), water temperature (F=2.60, P=0.023) and the Pfankuch Index (F=2.24, P=0.049) were associated significantly with assemblages of macroinvertebrate taxa. Axes 1 and 2 explained 43.76% of the total species variance and 59.06% of cumulative variance of the species-physicochemical parameters relation. Most taxa were placed at low axis 1 values (low and medium GCC rivers) which had higher water temperatures and more stable channels (Fig. 5).

Discussion

Tropical glaciers are particularly susceptible to the effects of climate change due to continuous melting throughout the year (Rabatel et al., 2013). Therefore, spatio-temporal shifts of environmental conditions and the structure and functioning of aquatic ecosystems are to be expected as meltwater rivers adjust to glacier retreat. Due to the logistical difficulty of collecting long-term data in high mountain river catchments, we identified a GCC gradient (0-66.2 %), changing time for space. This method has been shown to be robust in a wide array of glacial basins to analyse trends and patterns of biodiversity response (Füreder, 2007; Füreder & Niedrist, 2020; Jacobsen et al., 2012; Milner et al., 2009; Robinson et al., 2001) including tropical glaciers in Bolivia (Quenta et al., 2016). Results have been demonstrated to be similar to those found in place where temporal studies have been carried out, supporting the predictive potential of these chronosequences for understanding hydroecological responses (Brown et al., 2018). In this regard, our results provide the first model of likely responses of benthic biodiversity and river environmental factors to the imminent disappearance of glaciers in the Cordillera Blanca.

Relationship between decreasing GCC, environmental variables and biodiversity

Supporting hypothesis 1, environmental conditions in Peruvian glacial rivers became more favourable as GCC decreased, most notably for water temperature, channel stability and turbidity. The results accord with the general models of glacier-fed river ecosystems proposed by Fell et al. (2017) which suggested that as glacier area decreases, it has less influence on downriver physicochemical conditions, due mainly to reducing meltwater contribution and mixing with other water sources. Improving environmental conditions, with water temperature and channel stability as the best significant drivers, led to higher local biodiversity as a GCC decreased, consistent with findings from temperate and Arctic zone systems spanning Europe, N. America and New Zealand (Jacobsen et al., 2012; Brown et al., 2018).

Decreasing GCC (lower differences between sites) led to reduced β diversity (total dissimilarity). This means that as glaciers retreat, rivers in the Cordillera Blanca with a high glacial influence and where adapted species live, may become more favourable for generalist species (Jacobsen et al., 2012), resulting in biological homogenization and a potential loss of regional diversity (Milner et al., 2009; Brighenti et al., 2019; Elser et al., 2020). However, the additional physiological stress caused by lower oxygen availability and higher UV radiation in high-elevation rivers in the Cordillera Blanca could be a constraint for generalist colonisation processes in glacially uncovered areas, and should be the focus of future studies (Jacobsen, 2008; Loayza-Muro et al., 2013; Birrell et al., 2020) We found that beta diversity (total dissimilarity) within sites tended to increase with decreasing glacial influence. These responses contrasted with those reported for diatom communities in Austria (Fell et al., 2018), but were similar (although stronger) than those reported for invertebrates by Khamis et al. (2016) in the French Pyrénées, although the latter study quantified glacier influence based on meltwater contributions from a chemical hydrograph separation method. Nevertheless, between-site analyses illustrated that significant reductions in glacier cover will drive beta diversity reductions in Peruvian mountain rivers, findings that are supported from several previous studies in other parts of the world (Brown et al., 2007; Milner et al., 2009; Khamis et al., 2016; Fell et al., 2018).

We found slight differences in the biodiversity response in the two sampling seasons. In the dry season we found the typical unimodal biological response similar to other studies (e.g. Jacobsen et al., 2012; Khamis et al., 2016; Brown et al., 2018), in which the total stress (biotic + abiotic) is lower at medium glacier influence (~20-25% GCC) compared to the extremes of the GCC (Khamis et al., 2016). However, in the wet season, biodiversity peaked in low glacier influence sites. Possible explanations are associated with more stable water source dynamics and increased temperature in low GCC sites fed predominantly from groundwaters at medium and low glacier-influenced sites during this period (Milner & Petts, 1994). However further detailed hydrological tracer research is needed to understand these differences fully. An unusual finding in the seasonal analysis of beta-diversity components between sites was the slight tendency for nestedness to increase in the wet season as differences in glacier cover increased, suggesting that wet season conditions improve conditions for generalist taxa either by enhancing watercourse dispersal, or that some specialists are found only at certain sites during the drier parts of the year.

Community composition response to decreasing glacier cover

Macroinvertebrate community composition changed as GCC decreases, with community differences among all GCC categories. In areas of high glacier influence (P10, T=2°C) were dominated by *Anomalocosmoecus* sp., *Limonia* sp., Diamesinae *Paraheptagyia* sp. and Orthocladiinae sp. 1., which contrasts with the biodiversity of rivers in European glacier-fed rivers, where the genus *Diamesa* usually dominates. According to Seather & Spies (2004) this taxon does not occur in Neotropical regions, as further noted by studies in Ecuador (Jacobsen et al., 2010; Kuhn et al., 2011). Likewise, Limnephilidae and Tipulidae are commonly found in sites of lower glacial influence (GCC<50% and GCC<40%, respectively) in temperate zones (Milner et al., 2009). The decrease in abundance at lower glacial influence of *Anomalocosmoecus* sp. and *Limonia* sp., and the similarity of the conditions found in this study to glacial rivers in the European Alps, suggest a possible adaptation and preference to the cold and conditions of near-glacial environments, where they may be as abundant as chironomids (Robinson et al., 2001). Similar findings have already been observed in Swiss glaciers where rivers with temperatures no higher than 4°C, Diamesinae and Orthocladiinae were found associated with other Diptera, as well as Ephemeroptera, Plecoptera and Trichoptera (Lods-Crozet et al., 2001).

At the site of highest glacier influence, Diamesinae *Paraheptagyia* sp. was prominent but showed reduced abundance at lower glacier cover sites, consistent with temperate glacier-fed river patterns for other Diamesinae that are adapted to cold, unstable rivers (Milner et al., 2009). This specialization aligns with reports in Patagonia (Miserendino et al., 2018), but contrasted with a study at the Antisana glacier (Ecuador), which the Podonominae were more abundant (Jacobsen, Cauvy-Fraunie, et al., 2014; Cauvy-Fraunié et al., 2015; Espinosa et al., 2020). The results also differ from those in the Cañete Basin (Peru), where the Podonominae *Podomopsis* and *Podomonus*, plus the Orthocladiinae *Limnophyes* were more abundant in the most glacial sites (Acosta & Prat, 2010). Despite varied cold-zone aquatic communities among hydrographic regions of Perú and the subtropical Andes, common traits such as substrate attachment adaptations, their short and often multivoltine life cycles, facilitate rapid colonization after extreme discharge or fine sediment events (Martyniuk et al., 2019; Crespo-Pérez et al., 2020).

In the wet season when glacial melt is higher, the abundance of *Anomalocosmoecus* sp., *Paraheptagyia* sp., Orthocladiinae sp.1., and *Limonia* sp. showed a more marked tendency to increase in sites of greater glacial influence compared to the dry season. The persistence of these taxa near the glacier even in the wet season when currents are more turbulent with unstable bottoms and high temporal flow fluctuations, may indicate life cycle timings of some cohorts to capitalise on these conditions, plus the ability of taxa to move between patches and capitalise on refugia (Ríos-Touma et al., 2011). In the rivers studied, deposits derived from alluvial events generate flow and protection patches for both algae and macroinvertebrates. River bed area is also much greater in the wet season, generating more potential refugia sites and microhabitats. Our findings shows that despite differences in Peruvian species compared to glacier-fed rivers in other parts of the world, mechanisms of adaptation (resilience and resistance) to the disturbances caused by glacial dynamics are similar among invertebrate assemblages throughout the world most likely due to convergent trait profiles (Füreder, 2007; Khamis et al., 2016; Brown et al., 2018).

With decreasing glacial influence, Coleoptera abundance increased. The highest abundance of Scirtidae sp. and *Austrelmis* sp. was observed in sites with moderate and low glacial influence respectively, which contrasted with typical observations in temperate glaciers where these taxa usually do not occur in glacier-fed rivers. Both beetles are common in Andean rivers, and have previously been reported in low-altitude sites near the Antisana glacier (Cauvy-Fraunié et al., 2014; Espinosa et al., 2020), Tambillos river in the Cordillera Frontal, Argentina (Scheibler et al., 2020), other Cordillera Blanca valleys (Livingston-Burgess, 2015) and the Cordillera Negra (a glacier-free mountain range parallel to the Cordillera Blanca; Loayza-Muro et al., 2010). These findings imply some notable differences in species adaptation to glacier loss in the Andes compared to glacier-fed systems on other continents.

Environmental variables influencing macroinvertebrate communities

Supporting hypothesis 3, we found that water temperature, channel stability and turbidity were the main drivers of local macroinvertebrate composition. Water temperature in particular affects macroinvertebrate community structure by controlling individual growth rates and lifespan (Brown et al., 2003; Elser et al., 2020). On the other hand, channel instability is associated with fast-flowing, sediment-laden water with significant temporal variability, creating an inhospitable environment with frequent sediment scouring and deposition inhibiting colonization of certain taxa (Milner & Petts, 1994; Cauvy-Fraunié, 2014). Although turbidity was not as high in comparison to other studies (e.g. Antisana glacier) it was still found to be significantly associated with aquatic fauna. This variable affects biota through abrasion, and impedes light transmission through the water column leading to primary production reduction (Cauvy-Fraunié, 2014). RDA results confirmed the patterns found in the correlations of physicochemical variables with GCC and individual species. *Anomalocosmoecus* sp., *Paraheptagyia* sp. and *Limonia* sp. displayed higher abundances in rivers with lower stability, water temperature and higher turbidity, whereas Scirtidae sp., *Austrelmis* sp. and Oligochaeta sp. preferred stable and warm rivers that were characteristic of sites with medium and low glacier influence. Likewise, zones of intermediate temperature and channel stability harboured the greatest number of taxa where *Andesiops* sp. predominated. The results evidenced a turnover of taxa promoted by the gradation of environmental conditions driven by changes in the GCC as is seen commonly in glacier-fed rivers worldwide (Jacobsen et al., 2012).

Conclusion

This study has demonstrated the influence of changing glacier cover on the biodiversity of river macroinvertebrate communities in the Cordillera Blanca, with findings suggesting that the ongoing retreat and imminent disappearance of glaciers due to climate change will have significant ecological effects, similar to other parts of the world. Although local biodiversity increased as GCC decreases, species adapted to cold and unstable conditions can be expected to be lost, reducing β and regional diversity. One of the major concerns that temperate and tropical glacier studies have highlighted is the potential extinction of specialist and endemic species from glacial environments. Our results provide the first evidence in support of this hypothesis, which is a significant step forward in understanding the impact of climate change on biodiversity in Peruvian glaciers.

Glaciers in the Cordillera Blanca region have a vital function in supporting river flow during dry periods, ensuring the persistence of mountain ecosystems (Polk, 2016) and associated services provided to society (Carey et al., 2017). Therefore, ongoing monitoring and research are important to understand the response of aquatic communities and their functional roles in maintaining services such as clean water provision. In particular, future studies need to extend the spatial scale of assessments to other valleys and ranges to quantify the importance of other environmental factors such as geology and wetland influence in tropical mountains (Loayza-Muro et al., 2010; Livingston-Burgess, 2015). Given the evidence for rapid rates of glacier retreat in the Andes and strong hydrological and ecological responses as demonstrated in this study, responsible institutions need to quickly develop a more complete knowledge base to inform policies for the conservation of biodiversity (Quenta-Herrera et al., 2022) across the Andes.

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Table 1. GLM summary statistics for the relationship between environmental variables and biological parameters. Only variables include in the final model are shown

	Specific Richness		**Rarefied Richness**		**Shannon H**		**Fisher Alpha**	
	Est. Coef.	p-value	Est. Coef.	p-value	Est. Coef.	p-value	Est. Coef.	p-value
Water temperature	0.057119	**0.0232** *	0.04682	**0.0372** *			0.17678	**0.0245** *
pH	0.54401	0.1057						
PI	-0.008417	**0.0497** *					-0.02231	0.150
DOC	-0.075162	**0.0286** *			-0.10534	**0.00572** **		
DIC					-0.31843	**0.02057** *		
SI	-0.138999	0.1323						
F					1.39677	**0.01153** *		
Cl					-0.89979	0.15375		
% Deviance Explained	50.73		93.91		51.18		41.52	
p-value	**$< 2.2e^{-16}$** ***		**$< 2.2e^{-16}$** ***		**0.003406** **		**0.002389** **	

* p < 0.05, ** p < 0.01 and ***p<0.001

Table 2. SIMPER and ANOSIM analysis of dissimilarities in macroinvertebrates composition among GCC categories. Only the 10 taxas most contributing to dissimilarity are shown

	ANOSIM		SIMPER			
GCC category	R	*p*	Overall average dissimilarity	Taxa	Contribution (%)	Cumulative contribution (%)
Low vs Medium	0.86	0.002	67.2	Oligochaeta sp.	25.31	25.31
				Andesiops sp.	19.84	45.15
				Ceratopogoninae sp.	12.09	57.24
				Gigantodax sp.	10.79	68.03
				Scirtidae sp.	5.907	73.93
				Austrelmis sp.	4.25	78.18
Medium vs High	0.32	0.003	69.1	*Andesiops* sp.	16.89	16.89
				Anomalocosmoecus sp.	15.46	32.35
				Gigantodax sp.	10.68	43.03
				Limonia sp.	8.475	51.5
				Scirtidae sp.	8.319	59.82
				Orthocladiinae sp.1.	7.43	67.25
				Paraheptagyia sp.	6.385	73.64
				Austrelmis sp.	4.017	77.65
Low vs High	0.47	0.002	81.4	*Oligochetas* sp.	21.93	21.93
				Anomalocosmoecus sp.	13.79	35.72
				Ceratopogoninae sp.	10.77	46.49
				Andesiops sp.	8.646	55.14
				Gigantodax sp.	7.497	62.64
				Limonia sp.	7.125	69.76
				Orthocladiinae sp.1.	6.336	76.1
				Paraheptagyia sp.	5.661	81.76

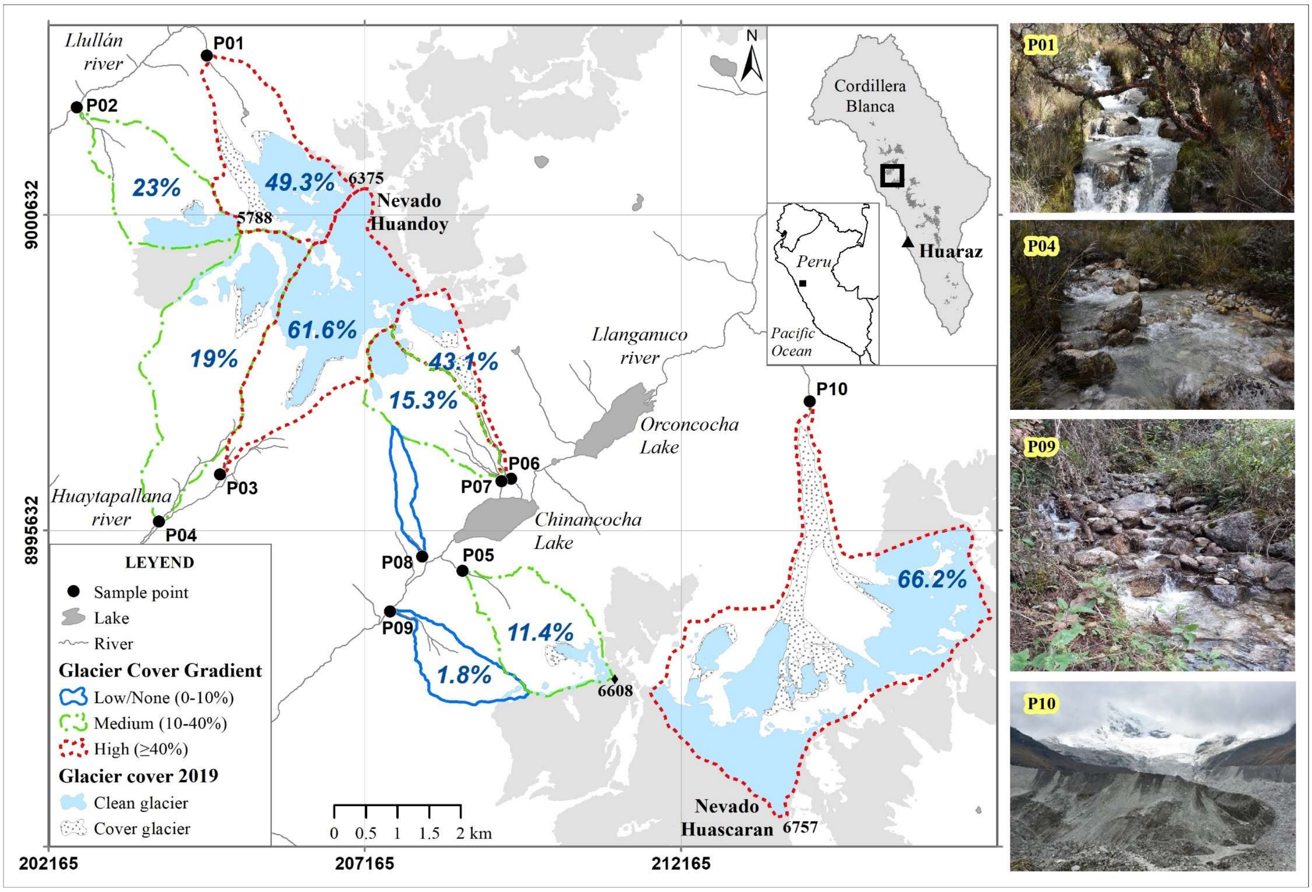

Fig. 1 Sampling sites across the gradient of catchment glacier cover in Llanganuco, Parón and Huaytapallana basins

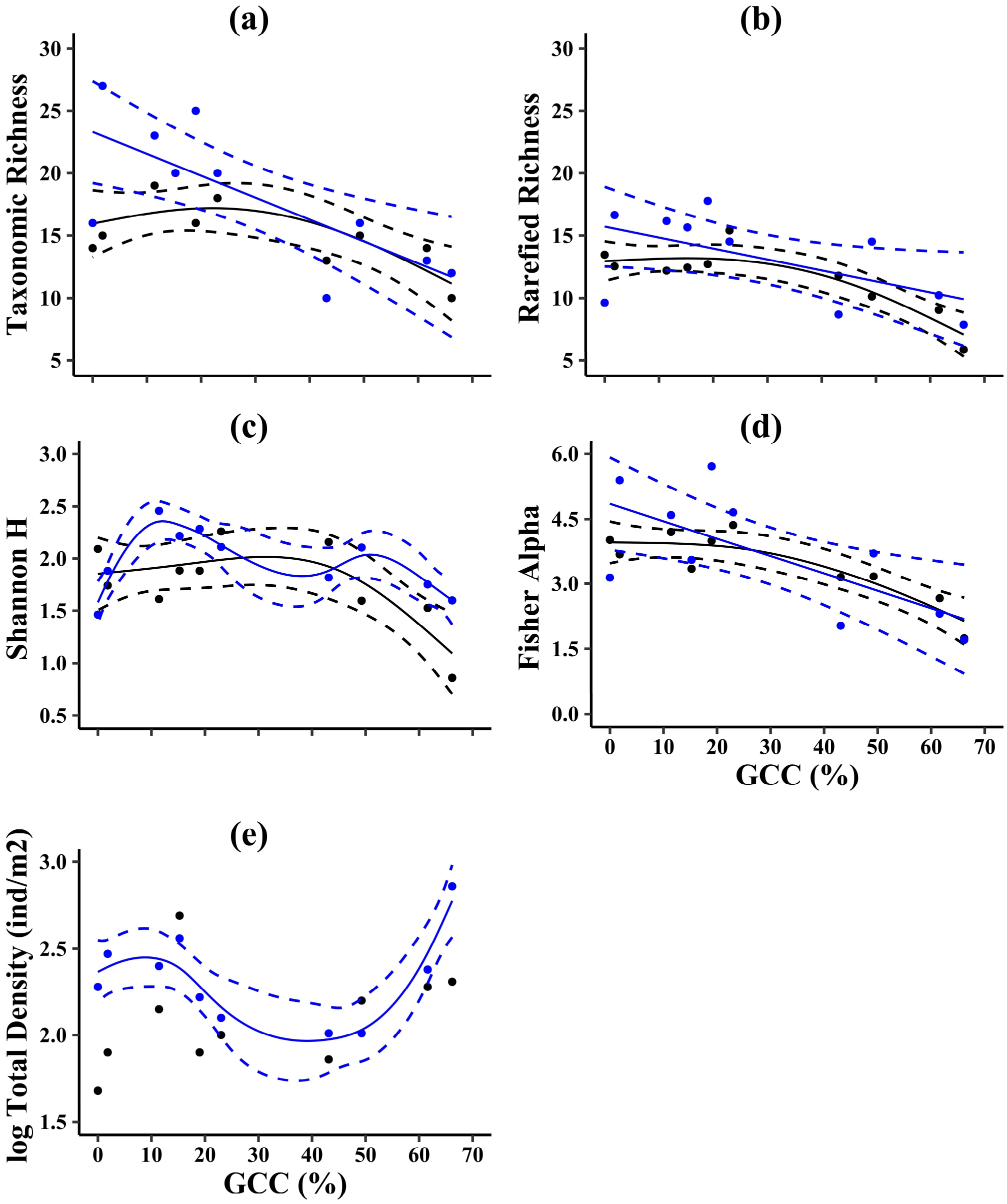

Fig. 2. Relationships between GCC and biodiversity indices: (a) Taxonomic Richness, (b) Rarefied Richness, (c) Shannon H, (d) Fisher Alpha, (e) Total Density. The colour of lines represents dry (black) and wet (blue) seasons. Lines represent of best fit represent in GAM models except (a), (b) and (d) in wet season, which represent GLM models. Dashed lines represent 95% confidence intervals.

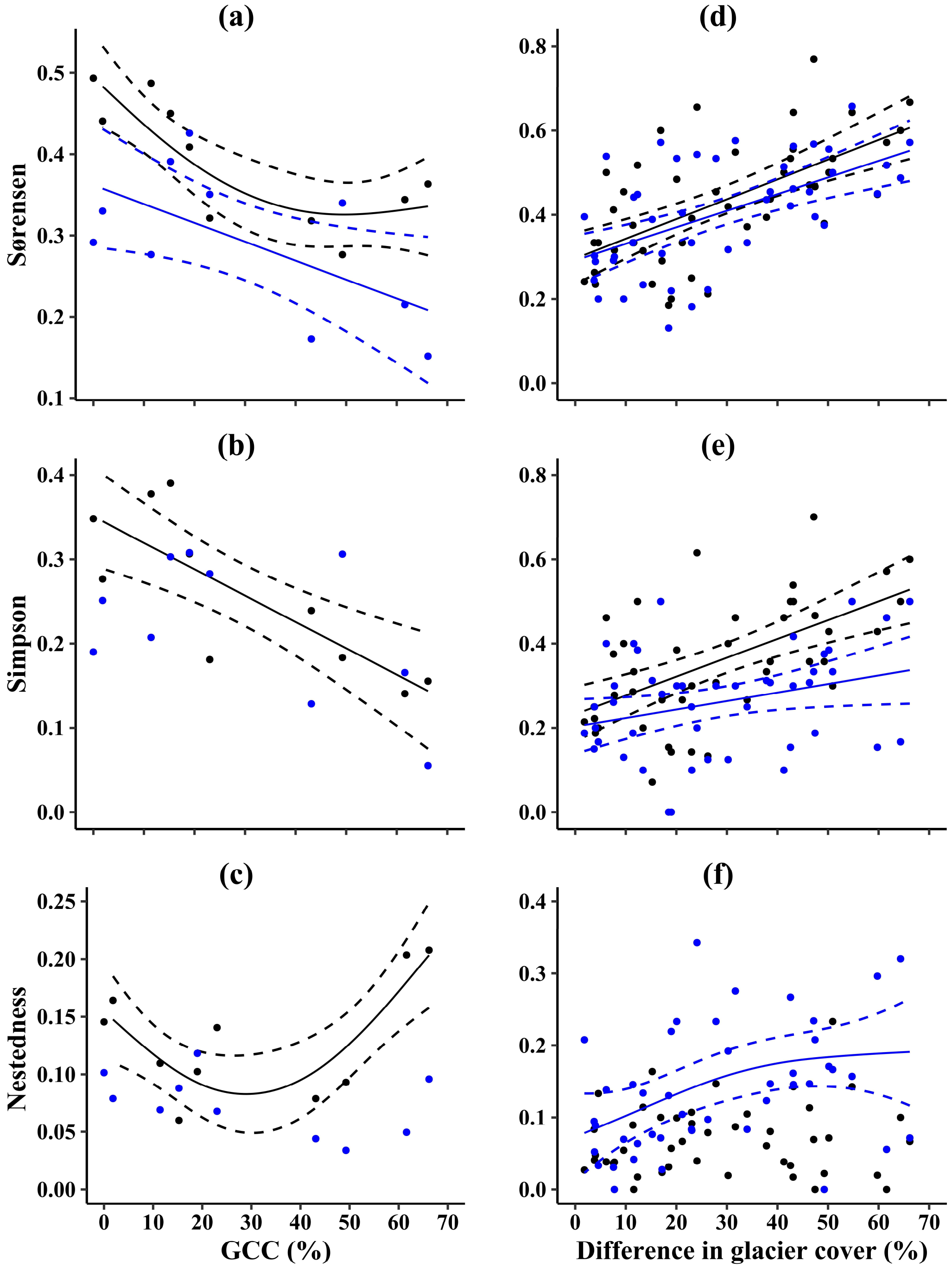

Fig. 3. Relationships between GCC and both within-site β diversity, (a-c), and between-site β diversity, (d-f). Components of β diversity include total dissimilarity (Sørensen index), turnover (Simpson index) and nestedness (Nestedness index). The colour of lines represents dry (black) and wet (blue) seasons. Lines represent of best fit represent in GLM models except (a) and (c) in dry season, and (f) in wet season, which represent GAM models. Dashed lines represent 95% confidence intervals.

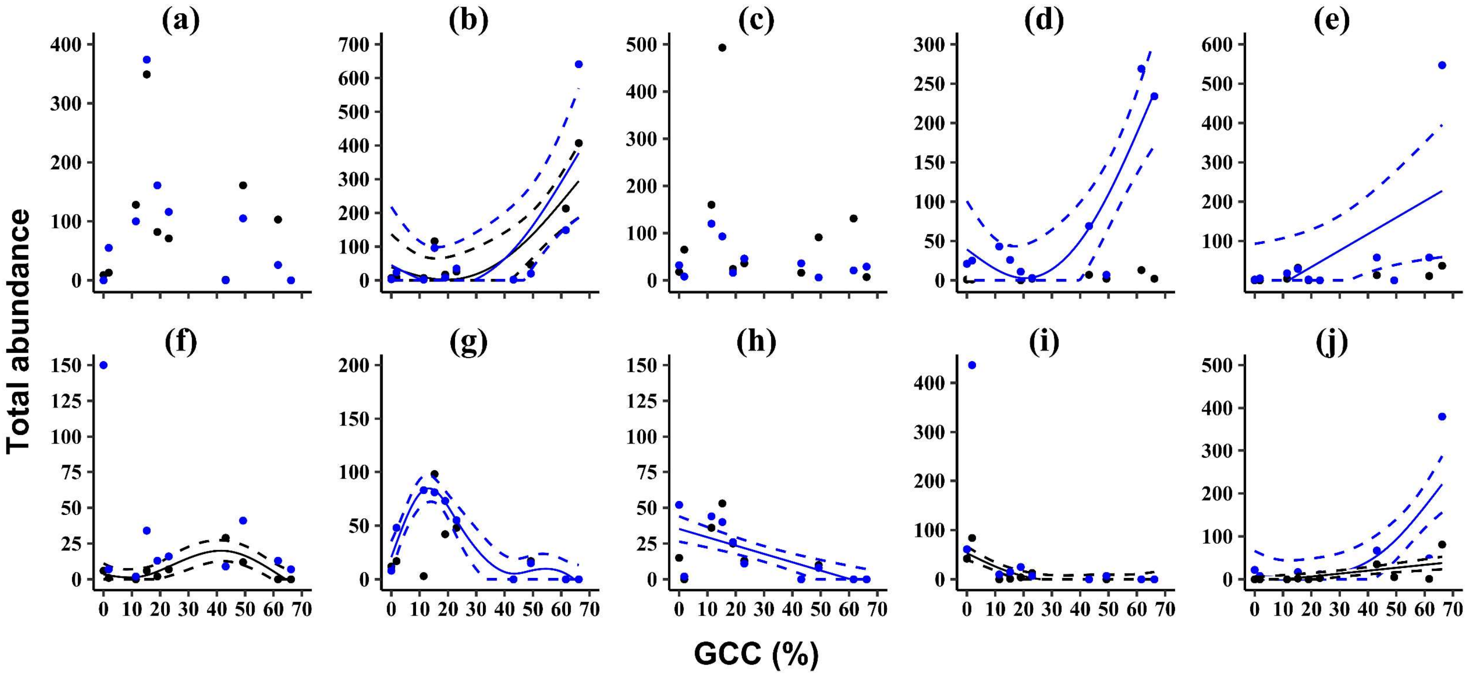

Fig. 4. Relationships between GCC and mean abundance of selected taxa: (a) *Andesiops* sp. (b) *Anomalocosmoecus* sp. (c) *Gigantodax* sp. (d) Orthocladiinae sp. 1. (e) *Paraheptagyia* sp. (f) Ceratopogoninae sp. (g) Scirtidae sp. (h) *Austrelmis* sp. (i) Oligochaeta sp. and (j) *Limonia* sp. The colour of lines represents dry (black) and wet (blue) seasons. Lines represent of best fit represent in GAM models except (e) and (h) in wet season, and (j) in dry season, which represent GLM models. Dashed lines represent 95% confidence intervals.

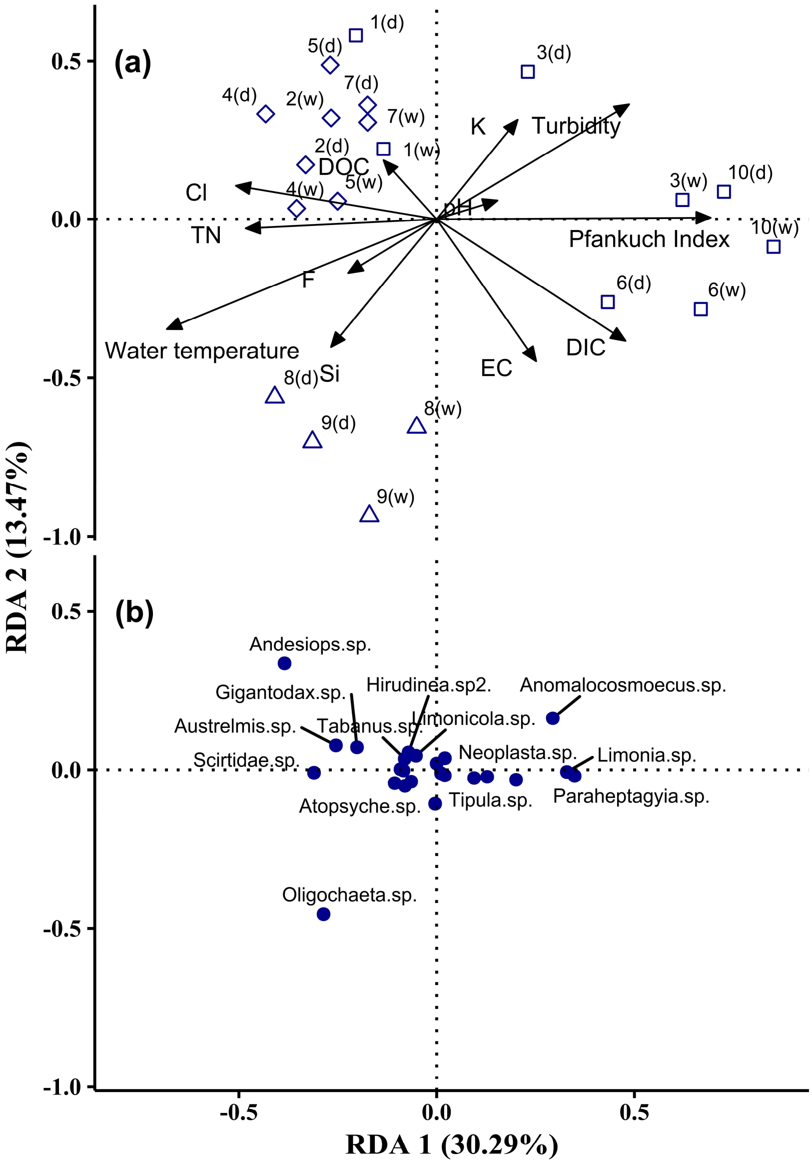

Fig. 5. Redundancy Analysis (RDA) ordination diagrams of (a) environmental variables and sites, and; (b) macroinvertebrate taxa. DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; EC, electrical conductivity; TN, total nitrogen. Numbers correspond to sites labelled in Figure 1; Letters in parentheses represent sample season; d: dry; w: wet. Shapes represent GCC categories (Low: △, Medium: ◇, High: □).