



Original Research Article

Community structure and functional feeding groups of macroinvertebrates in pristine Andean streams under different vegetation cover



Diego Vimos-Lojano^a, Henrietta Hampel^{a,b}, Raúl F. Vázquez^{a,c,*},
Francisco Martínez-Capel^d

^aLaboratorio de Ecología Acuática (LEA), Universidad de Cuenca, Av. 12 de Abril S/N, Cuenca, Ecuador

^bFacultad de Ciencias Químicas, Universidad de Cuenca, Av. 12 de Abril S/N, Cuenca, Ecuador

^cFacultad de Ingeniería, Universidad de Cuenca, Av. 12 de Abril S/N, Cuenca, Ecuador

^dResearch Institute for Integrated Management of Coastal Areas (IGIC), Universitat Politècnica de València, Grao de Gandía, Spain

ARTICLE INFO

Article history:

Received 13 December 2019

Revised 30 March 2020

Accepted 18 April 2020

Available online 15 May 2020

Key words:

Andean

Macroinvertebrates

Pristine vegetation cover

Functional feeding groups

ABSTRACT

As a function of the dominant vegetation cover, patterns of variation in the structure and composition of both, the aquatic macroinvertebrate communities and their functional feeding groups (FFG) were examined at pristine streams of two high Andean micro-catchments of southern Ecuador. Ten sampling segments were defined in the study streams surrounded by either Tussock grass (TG), Quinoa forest (QF) or high mountain forest (HMF). In each segment, environmental and biological samples were collected. Different statistical analyses were implemented for assessing possible relationships between biological and environmental variables. TG and QF streams were found to share many physical and biological characteristics. HMF ecosystems, which are characterised by greater total hardness, water velocity, temperature, pH and nitrite/nitrate concentrations exhibited low values of diversity, richness, relative abundance of non-insects, piercer and parasites. Further, high values of relative abundance of Plecoptera (predators) were observed in HMF, apparently due to higher water velocities and their resistance to these flow conditions. The composition of the macroinvertebrate community showed similarity in TG and QF. It was observed at the three study sites a dominance of organisms generally tolerant to lower availability of oxygen (Chironomidae and non-insect class) and, curiously, to higher concentrations of nutrients. It was found some taxa associated with the presence of organic matter in the sediment because they use allochthonous resources (*Phylloecus*).

© 2020 European Regional Centre for Ecohydrology of the Polish Academy of Sciences.
Published by Elsevier B.V. All rights reserved.

1. Introduction

The ecological and hydrological characteristics of lotic systems are strongly depending on surrounding vegetation cover (Wallace et al., 1997; Feyen and Vázquez, 2015). In this context, riparian vegetation are important

filters protecting rivers from adjacent disturbed areas (Miserendino et al., 2011; Fraaije et al., 2019). Further, riparian vegetation influences the dynamics of the quality and quantity of food available for certain invertebrates (Fierro et al., 2017; Fraaije et al., 2019), directly, through allochthonous contribution of leaves, soil and wood, affecting as such benthic composition (Sponseller et al., 2010; Iñiguez-Armijos et al., 2014). Indirectly, riparian vegetation influences these dynamics of food availability for

* Corresponding author.

E-mail address: raulfvazquez@yahoo.co.uk (R.F. Vázquez).

benthic communities through the processes of microbial decomposition that imply the modification of carbon and dissolved organic nutrients (Collins et al., 2016). In addition, density of vegetation canopy influences the amount of solar radiation that reaches the river, which determines primary production and, as such, impacts the development of macroinvertebrates (Bücker et al., 2010; Larson et al., 2019). However, the relationship between native vegetation cover and aquatic communities in small headwater rivers of high mountain areas in South America (Miserendino and Pizzolon, 2004; Giraldo et al., 2014) and, particularly, in Ecuador (Bücker et al., 2010; Vimos-Lojano et al., 2017), has been, so far, little studied.

At a global scale, species richness has a strong relation with elevation (Albert et al., 2011; Wang et al., 2011). Herein, Jacobsen (2004) and Madsen et al. (2015) found that the number of species of aquatic communities in the Andean region increased as elevation decreased. A contrasting pattern was however observed in some families of different groups of organisms such as diatoms (Wang et al., 2011), macroinvertebrates (Jacobsen, 2004) and fish (Albert et al., 2011).

Benthic macroinvertebrate communities perform much of their life cycle in lotic ecosystems and appear to be structured by landscape factors such as land use/catchment vegetation cover, surface geology and geographic basin factors (Ding et al., 2017). However, other studies (Statzner and Beche, 2010; Rezende et al., 2014; Vimos-Lojano et al., 2017) indicate that local scale variables, e.g. hydraulic flow, substrate types, water chemistry, riparian vegetation, etc., seem to play a more prominent role in the structuring of macroinvertebrate communities. Due to the sensibility of macroinvertebrates to local and regional factors, their role for assessing the environmental conditions of aquatic ecosystems has been for long recognised (Hodkinson and Jackson, 2005; Acosta et al., 2009).

Approximately 80% of the Earth's land surface is already modified by anthropic activities, resulting in progressively significant impacts on a wide range of ecosystem services at different scales (Naiman et al., 1995; Barnett et al., 2008). Thus, today pristine ecosystems, considered true "natural laboratories" for the detection of environmental changes (Hannah et al., 2007; Hampel et al., 2010), are really scarce globally. Hereafter, they would provide baseline information that could be used in comparative studies with regard to altered ecosystems (Hodkinson and Jackson, 2005; Bailey et al., 2014).

Some studies have been conducted to assess the effects of climate change on freshwater systems in the northern hemisphere (Piggott et al., 2015; Lund et al., 2016). However, in Ecuador the lack of long-term meteorological and biological data precludes this type of research with the consequent difficulty for an adequate and sustainable management of land and water resources, particularly in current times characterised by a booming of hydroelectricity generation and mining projects being developed in these ecosystems (Espinosa and Rivera, 2016).

The main objective of this research was examining the patterns of variation in the structure and composition of aquatic macroinvertebrate communities and their functional feeding groups (FFG) as a function of the charac-

teristics of their habitats (i.e., pristine headwater Andean streams). Thus, this research aimed at answering the following research questions: (i) is it possible to find variations in biological variables or FFG or the structure of communities, as a function of the native riparian vegetation?; (ii) is it possible to discern which environmental conditions are responsible for the patterns observed in the biological variables, FFG and macroinvertebrate communities?; and (iii) can certain taxa be associated with the dominant type of riparian vegetation?. The results of this study are likely to contribute to establish a baseline for future research about the impact of local and global anthropic changes on Andean ecosystems.

2. Materials and Methods

2.1. Study area

The first study site, the Zhurucay microcatchment (Fig. 1), belongs to the Jubones River basin, which has an approximate area of 4,354 km², its river has an approximate length of 124 km, and is divided into nine sub-basins (Vázquez, 2010; Mosquera et al., 2015). Further, the elevation of this basin varies between 4,120 m above the average sea level (a.s.l.), by the western cordillera, and the sea level, by the Pacific Ocean. The Zhurucay microcatchment has a drainage area of 7.97 km² and its altitudinal range varies between 3,200 and 3,900 m a.s.l. The main land cover (for year 2010) is (Studholme et al., 2017) grassland (tussock grass; 58.6%), cushion plants and grasses other than pajonal (19.4%), riparian *Polylepis* woodlots (particularly *P. incana* Kunth y *P. reticulata* Kunth; 17.7%), and introduced pine (4.3%). Land use consists of light pasture (non-cultivated land with non-intensive grazing in the order of two heads ha⁻¹) and agriculture (particularly cultivated grass and potato; Vázquez et al., 2010).

The second study site, the Pallcayacu microcatchment (Fig. 1), is located in the upper basin of the Paute river, which has a surface of about 6,439 km², its main river reach spans about 120 km from the Andean headwaters to the Amazon region, has an elevation range between 440 and 4,680 m a.s.l., and is divided into 18 sub-basins (Sotomayor et al., 2018). The Pallcayacu microcatchment has an approximate area of 19.2 km² and an elevation range varying between 2,520 and 3,620 m a.s.l. The main land uses in the region are agriculture, forestry and pasture. The main land cover (year 2011) in the Pallcayacu microcatchment is tropical montane forest (TMF; 58%), agricultural land (18%), tussock grass (15%), pasture other than tussock grass (4%), wetlands (3%), and other (2%).

These two microcatchments were selected to represent the range of environmental heterogeneity in the upper Jubones and Paute basins, respectively. Precipitation patterns vary across the study regions depending on their geographical position on the Andean range. In the Zhurucay microcatchment the rainy period on average is from January to May with heavier rains in January and February and more dry days between June and December (Vázquez, 2010; Studholme et al., 2017). In the Pallcayacu microcatchment the drier season spans from Novem-

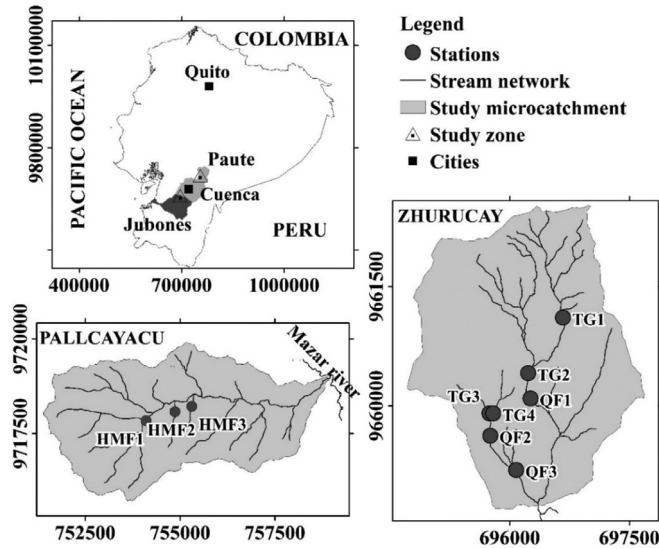


Fig. 1. Location of study areas, the Zhurucay microcatchment in the head of the Jubones River basin and the Pallcayacu microcatchment in the head of the Paute River basin, and distribution of the ten monitoring stream segments (TG = pajonal; QF = Quinua forest; HMF = high mountain forest). Coordinates system: WGS84 UTM Zone 17S.

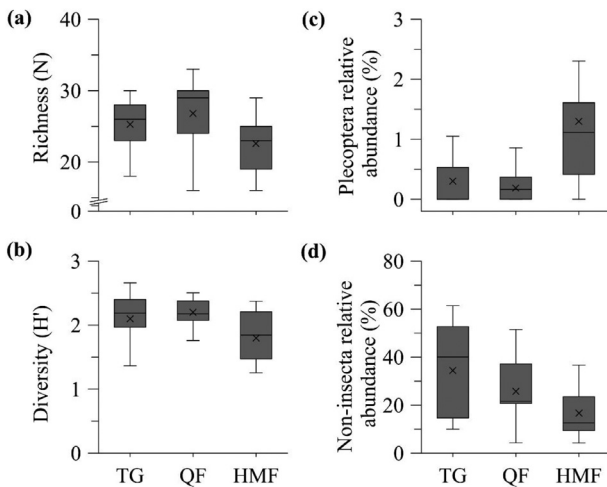


Fig. 2. Box plots of (a) richness; (b) the diversity; and the relative abundance of (c) plecoptera; and (d) non-insecta, as a function of vegetation cover (TG = pajonal; QF = Quinua forest; HMF = high mountain forest). Box plots elements are median (bold horizontal line), average ("X"), interquartile range (IQR, box), and range segments (up to 1.5 IQR). Number of averaged samples (6 replicates), N, are 20 (TG), 15 (QF) and 15 (HMF).

ber to February and the peak rainfall occurs in June/July (Studholme et al., 2017).

Three different riparian vegetation types were considered in this study, namely, "pajonal" (i.e., Tussock grass, TG), "Quinua" forest (QF) (i.e., *Polylepis* sp.), and High Montane Forest (HMF). In the TG locations, the dominant flora is *Calamagrostis intermedia*, whereas the QF locations are dominated by *Polylepis incana* Kunth and *P. reticulata* Kunth, concentrated in riparian banks. HMF locations host a high variety of species of trees and shrubs, such as, *Styloceras laurifolia* (Buxaceae), *Hedyosmum cum-balense* (Cloranthaceae), *Clusia multiflora* (Clusiaaceae), *Cy-*

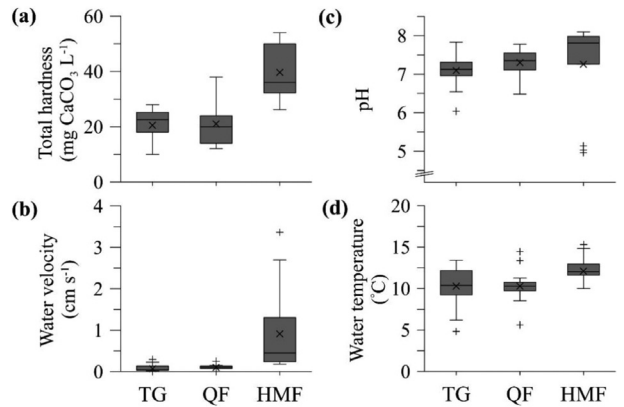


Fig. 3. Box plots of (a) total hardness; (b) water velocity; (c) pH; and (d) water temperature, as a function of vegetation cover (TG = pajonal; QF = Quinua forest; HMF = high mountain forest). Box plots elements are median (bold horizontal line), average ("X"), interquartile range (IQR, box), and range segments (up to 1.5 IQR). Outliers (data points greater than 1.5 IQR) are plotted with the symbol "+". Number of averaged samples (6 replicates), N, is 20 (TG), 15 (QF) and 15 (HMF).

atea sp. (Cyatheaceae), *Palicourea* sp. (Rubiaceae) and *Asteraceae* sp.

2.2. Monitoring environmental variables

Seven sampling stations (4 at TG and 3 at QF) were established within the Zhurucay microcatchment, whilst three stations at HMF were defined within the Pallcayacu microcatchment (Fig. 1). On average, TG stations were located at about 3,700 m a.s.l., QF stations at 3,640 m a.s.l. and HMF stations at 2,740 m a.s.l. In every station, a 50-m-long segment was defined for the monthly collection of biotic and abiotic samples throughout the period August-

December of 2017 that was chosen with the aim of avoiding as much as possible peak discharge events.

Physical-chemical variables were recorded *in situ* with the use of a multiple water quality sensor (U-50 series, <http://www.horiba.com>), including, water temperature (T; °C), electric conductivity (EC; $\mu\text{S cm}^{-1}$), total dissolved solids (TDS; g L^{-1}), turbidity (Turb; NTU), dissolved oxygen (DO; mg L^{-1}) and the redox potential (ORP; mV). In addition, surface water samples were collected and the following variables were analysed using standard methods (APHA, 2005): alkalinity ($\text{mg CaCO}_3 \text{ L}^{-1}$), total hardness (TH; $\text{mg CaCO}_3 \text{ L}^{-1}$) and nitrite/nitrate concentration (Nitri/Ni; $\mu\text{g N L}^{-1}$). Water depth (Depth; cm) was determined using a graduated rod. Water velocity (V; cm s^{-1}) was measured with a propeller-type flow-meter (Hydromate - CMC3). The stream discharge (Q) was calculated once per month, at each sampling station, by employing the velocity integration method (Boiten, 2008). The type of dominant substrate of the streambed at each sampling point was determined considering this simplified classification: bedrock, boulder, pebble, gravel, sand, silt, aquatic vegetation or the combination of these types, according to the guidelines provided by Eloseej (2009).

2.3. Biotic monitoring

At each of the 50-m-long stream segments, six macroinvertebrate samples (replicates) were collected using a Hess cylinder (diameter: 15.5 cm; mesh size: 250 microns). The six replicates were collected at the most representative habitats (run, riffle, pool). The samples were preserved in 10% formaldehyde solution and were washed at the laboratory using a 250 μm sieve. The macroinvertebrates were identified at the lowest possible taxonomic level using taxonomic keys of Domínguez *et al.* (2009). After removal of the organisms, the remaining sediment was used to measure the weight of organic matter (AFDW; g m^{-2}) according to Steinman *et al.* (2011).

For determining the chlorophyll *a* content (Chl_a; $\mu\text{g cm}^{-2}$), three stones were randomly collected from the streambed at each stream segment, monthly. The periphyton was extracted from the surface of the stones using a brush and the application of distilled water within a standard quadrant ($2 \times 2 \text{ cm}^2$). The resulting solution was filtered using a vacuum pump with Whatman GF/F filters (diameter: 47 mm; mesh size: 0.7 microns). The Chl_a was determined according to the spectrophotometric method described in Steinman *et al.* (2011).

2.4. Data analysis

The correlated environmental variables (Spearman's r value > 0.7) were discarded from the statistical analysis; hence, 4 were discarded out of the 16 physical-chemical variables. The density of the taxa for every one of the 50-m-long stream segments was defined by averaging the respective densities of the six replicates, avoiding as such the effects of microhabitats. This was done for all of the sampling campaigns and stream segments. These averaged densities were then transformed logarithmically (i.e., $\log(x + 1)$) and were further standardised by dividing

them by their mean value. The environmental variables with the exception of pH were logarithmically transformed (i.e., $\log(x)$ or $\log(x + 1)$), with the intention of increasing the homogeneity of their variances (Quinn and Keough, 2002).

The following biological variables (BV) were calculated: total taxa richness (richness; number of taxa), total density (density; ind. m^{-2}), Pielou's evenness (evenness; Quinn and Keough, 2002), Shannon-Wiener diversity index (diversity; Quinn and Keough, 2002), chlorophyll *a* content (Chl_a; $\mu\text{g cm}^{-2}$), the relative abundance of contamination-sensitive organisms (%Sen), and the relative abundance of the individuals belonging to the orders Ephemeroptera, Plecoptera and Trichoptera (%EPT; Ephemeroptera (%Ephe); Plecoptera (%Plec); Trichoptera (%Tric); and non-insects (%Non-insect). On the other hand, the following relative abundance of the main FFG were calculated (Tomanová, 2007) according to the principle of the Fuzzy code (Chevene *et al.*, 1994), using the following FFG: absorber (A), collector-gatherer (CG), shredder (SH), scraper (SC), filtering collector (CF), piercer (PI), predator (PR) and parasite (PA). Previously, species that had a relative abundance of less than the 5% of the total sample size were considered as rare and were, as such, eliminated from the data set to avoid a distortion effect on the statistical results.

Two tests were performed to inspect whether significant differences exist among biological variables and the FFG (BV&FFG) as a function of vegetation cover. Firstly, the Kruskal-Wallis-H test (K-W; Quinn and Keough, 2002) was used to define whether the variance of the ranks scores of the BV&FFG were significantly different as a function of the vegetation cover.

Secondly, in the case that the BV&FFG were significantly different, the Mann-Whitney-U post hoc test (M-W; Quinn and Keough, 2002) was performed for finding out the pairs of vegetation covers (i.e. TG vs. QF, TG vs. HMF, and QF vs. HMF) where the BV&FFG were significantly different. Type 1 error (i.e. rejecting the null hypothesis when it is true) was minimised by adjusting *p*-values with the Bonferroni correction (Quinn and Keough, 2002) and the K-W results were inspected through box charts.

Further, for the set of BV&FFG for which the K-W test found significant differences, a multiple linear regression model (Eq (1)) among these *n* BV&FFG (Y_j) and the *m* environmental variables (X_i) was developed using the forward step selection procedure (Quinn and Keough, 2002) in each vegetation type separately. This analysis was carried out to identify the plausible environmental variables that might be responsible for the differences of the BV&FFG:

$$Y_j = \beta_0 + \sum_{i=1}^{i=m} (\beta_i X_i) \quad (1)$$

where β_0 and β_i are the linear regression coefficients. For judging on the robustness of the statistical models of all of the studied BV&FFG, it was considered the adjusted R^2 value (R^2_{adj}) (Hieber *et al.*, 2005). The contribution of each independent (X_i) variable in the statistical model was identified by the value of the beta (β ; standardised regression) coefficient (Miles and Shevlin, 2001). Finally, the dif-

ferences among environmental variables, selected through the regression models, as a function of the predominant vegetation cover, were assessed through the application of the K-W test and the Mann-Whitney U post hoc tests with the Bonferroni correction. All of the above depicted statistical analyses were executed with the SPSS statistical software (version 20, IBM/SPSS, Inc., Armonk, New York).

For studying the relationship of aquatic communities with the environmental variables and with the dominant vegetation cover, the Detrended Correspondence Analysis (DCA) was applied, which suggested the use of a linear response model (Redundancy Analysis; Lepš and Šmilauer 2003). The forward automatic selection with Bonferroni correction was used to choose environmental variables that have a significant effect on the composition of the community (Šmilauer and Lepš, 2014). These statistical analyses were carried out with the help of the CANOCO software version 5 (Šmilauer and Lepš, 2014).

Finally, the compositions of the macroinvertebrate communities were compared as function of the predominant vegetation cover, through the Analysis of Similarity (ANOSIM) that uses the Bray-Curtis measure of similarity. Further, a global goodness of fit statistical value ($-1 \leq R \leq 1$) was obtained. R values close to 1 indicate that the majority of the most similar compositions of communities are within the same vegetation cover. This latter analysis was performed using the PRIMER software version 6 (Clarke and Gorley, 2006).

3. Results

3.1. Environmental characteristics of the sampling locations

Higher average values of T were observed in all of the sampling stations located in the HMF vegetation cover (Table 1); the highest recorded value was 12.6 °C (HFM3). It is the same case for Turb, EC, Q and Nitri/Ni, whose highest average values were observed at HMF1, i.e., 13.2 NTU (Turb), 99.6 $\mu\text{S cm}^{-1}$ (EC), 26.9 L s^{-1} (Q) and 72.4 $\mu\text{gN L}^{-1}$ (Nitri/Ni). Further, the highest average values of AFDW were (Table 1) 85.4 g m^{-2} (HMF1), 183.2 g m^{-2} (TG2) and 300.8 g m^{-2} (QF1). The highest average values of Chl_a were (Table 1) 0.49 $\mu\text{g cm}^{-2}$ (HMF3), 1.29 $\mu\text{g cm}^{-2}$ (TG4) and 2.06 $\mu\text{g cm}^{-2}$ (QF3).

3.2. Relationships among biological variables, aquatic communities and dominant vegetation cover

A total of 55 macroinvertebrate taxa belonging mostly to the insect class were collected at all sampling stations (Table 2). The number of taxa per sampling station ranged from 24 to 31 and the mean density ranged between 937 and 21,383 ind. m^{-2} .

The K-W test showed significant differences ($p < 0.05$) between richness and diversity as a function of the three vegetation covers (Annex A). The M-W test suggested that (Fig. 2a; Annex A) the average richness was significantly lower in HMF (23 taxa) in relation to QF (27 taxa). The K-W test suggested (Fig 2b; Annex A) a similar trend

for the average diversity, which was significantly lower in HMF (1.8) compared to TG (2.1) and QF (2.2). Further, the multiple regression analysis (Table 3), with richness as the dependent variable and $R^2_{\text{adj}} > 0.5$, selected Turb as the variable that is explaining the variation of richness in HMF. However non-significant differences were obtained for Turb as a function of the type of vegetation cover, after the Bonferroni correction. In addition, the multiple regression analysis suggested TH and pH as variables negatively influencing the diversity in QF and HMF and V positively influencing the diversity in HMF (Table 3). TH, V and pH exhibited (Fig. 3a,b,c; Annex B) significantly higher values in HMF than in TG and QF.

Furthermore, the K-W test indicated (Annex A) significant differences ($p < 0.05$) between the relative abundance of Plecoptera and non-insects. The M-W test (Annex A; Fig. 2c) suggested that the relative abundance of Plecoptera was significantly higher in HMF (1.3%) than at TG (0.3%) and QF (0.2%). In contrast, the relative abundance of non-insect (Annex A; Fig. 2d) was lower in HMF (16.3%) as compared to TG (34.4%). In this context, multiple regression analysis suggested (Table 3) that V had a positive influence on the relative abundance of Plecoptera at TG and HMF while T had negative influence at QF. The relative abundance of non-insect seemed to be determined negatively by pH at QF and HMF and positively by V at QF and by Turb at HMF (Annex B). Significantly higher values of T were observed (Fig. 3d; Annex B) at HMF than at TG and QF.

Upon the RDA, Fig. 4 illustrates some differences in the composition of the macroinvertebrates community as a function of the studied vegetation covers. This was corroborated by the ANOSIM test ($R = 0.64$; $p < 0.001$). The greatest community difference was observed among HMF and TG ($R = 0.93$; $p < 0.001$) and QF ($R = 0.81$, $p < 0.001$). The RDA suggested an overlap in terms of the composition of the community between the TG and QF ecosystems; similarly to ANOSIM where the low R value (0.26) suggest no composition differences despite of the p value (< 0.001).

Forward automatic selection on the explanatory variables revealed that V, Nitri/Ni, Turb and TH affected significantly the macroinvertebrate community (Fig. 4; Table 4). All of these environmental variables, except Turb, were significantly higher in HMF than in TG and QF (Annex B; Table 1). Further, the first ordering axis reflects a gradient related to these variables. *Leptohyphes*, *Mortionella*, *Anacroneuria*, *Simulium*, *Anchytarsus*, *Smicridea* are the typical taxa under these conditions in the HMF. The first and second axes explained respectively 24.1% and 6.1% of the variation of the community data set. Further, the second ordering axis indicated a gradient in relation to Depth and AFDW (Table 4). The taxa of Hydracarina, *Allaudomya*, Sphariidae, *Hyalella*, *Helobdella*, *Phylloecus* and *Heterelmis* seemed to be related to the higher AFDW. Depth was higher and seemed to be important in TG and QF, in particular for the taxa *Austrolimnius*, Tanypodinae, Limnidae, Chironominae and *Oxyethira*.

Table 1

Average values (5 sampling campaigns) and standard error (in parenthesis) of the environmental variables observed in the 10 monitoring stream segments located in the microcatchments of the rivers Zhurucay and Pallcayacu (Ecuador), as a function of the vegetation cover (TG = pajonal; QF = Quinoa forest; HMF = high mountain forest).

Environmental/physical variable	Sampling station									
	TG1	TG2	TG3	TG4	QF1	QF2	QF3	HMF1	HMF2	HMF3
Elevation (m a.s.l.)	3,729	3,697	3,656	3,657	3,677	3,630	3,590	2,994	2,988	2,979
Water temperature (T, °C)	10.5 (± 1.4)	11.0 (± 0.7)	9.8 (± 1.1)	10.3 (± 0.9)	11.5 (± 1.1)	9.3 (± 0.9)	10.1 (± 0.3)	12.1 (± 0.9)	12.1 (± 0.5)	12.6 (± 0.6)
Dissolved oxygen (DO, mg L ⁻¹)	8.9 (± 0.8)	8.5 (± 1)	9.7 (± 0.7)	8.9 (± 1.1)	9.4 (± 0.9)	9.8 (± 0.8)	9.5 (± 1.2)	9.5 (± 0.5)	10.1 (± 0.9)	8.8 (± 0.7)
Turbidity (Turb, NTU)	1.81 (± 0.5)	1.70 (± 0.3)	1.16 (± 0.2)	0.85 (± 0.3)	2.15 (± 0.8)	1.22 (± 0.3)	1.20 (± 0.3)	13.20 (± 10.3)	9.10 (± 2.3)	12.54 (± 7.7)
pH	7.00 (± 0.3)	6.90 (± 0.1)	7.10 (± 0.1)	7.40 (± 0.1)	7.00 (± 0.1)	7.30 (± 0.1)	7.50 (± 0.1)	7.30 (± 0.5)	7.30 (± 0.6)	7.30 (± 0.6)
Electrical conductivity (EC, µS cm ⁻¹)	63.2 (± 4.7)	55.8 (± 3.4)	51.2 (± 5.7)	41.0 (± 2.8)	55.0 (± 2.9)	52.0 (± 3.6)	48.6 (± 2.4)	99.6 (± 10.3)	76.8 (± 2.6)	91.6 (± 1.5)
Oxidation reduction potential (ORP, mV)	217 (± 16)	228 (± 21)	141 (± 29)	212 (± 28)	239 (± 33)	225 (± 29)	225 (± 27)	204 (± 8)	207 (± 11)	185 (± 16)
Total dissolved solids (TDS, g L ⁻¹)	0.042 (± 0.003)	0.035 (± 0.001)	0.029 (± 0.001)	0.026 (± 0.001)	0.036 (± 0.002)	0.033 (± 0.002)	0.032 (± 0.002)	0.064 (± 0.007)	0.05 (± 0.002)	0.059 (± 0.001)
Discharge (Q, L s ⁻¹)	1.00 (± 0.39)	9.53 (± 4.11)	0.96 (± 0.16)	0.52 (± 0.13)	5.73 (± 1.84)	1.97 (± 0.34)	4.58 (± 0.99)	26.89 (± 10.76)	9.49 (± 1.33)	18.55 (± 8.5)
Water depth (Depth, cm)	16.7 (± 0.5)	15.2 (± 3.7)	14.1 (± 1.0)	10.8 (± 1.0)	13.3 (± 0.6)	11.5 (± 0.9)	11.6 (± 1.5)	12.4 (± 3.4)	7.8 (± 1.2)	10.3 (± 3.1)
Water velocity (V, cm s ⁻¹)	8.8 (± 3.5)	19.5 (± 3.3)	3.4 (± 0.6)	30.0 (± 0.9)	12.9 (± 3.6)	7.7 (± 0.6)	11.8 (± 1.1)	71.8 (± 36.6)	106.3 (± 57.8)	96.7 (± 47.8)
Total hardness (TH, mg CaCO ₃ L ⁻¹)	23.3 (± 1.6)	23.8 (± 2.1)	16.6 (± 2.4)	18.5 (± 3)	25.2 (± 5)	18.8 (± 3.5)	19.2 (± 1.6)	42.6 (± 3.2)	36.0 (± 4.6)	40.0 (± 4.8)
Nitrite/nitrate (Nitri/Ni, µgN L ⁻¹)	44.6 (± 6.6)	13.6 (± 2.5)	21.4 (± 6.8)	12.0 (± 0.6)	27.9 (± 12.5)	25.2 (± 13.4)	13.8 (± 3.2)	72.4 (± 13.2)	67.3 (± 4.6)	54.2 (± 4.9)
Organic matter (AFDW, g m ⁻²)	67.5 (± 16.2)	183.2 (± 70.3)	61.0 (± 13.0)	63.6 (± 11.3)	300.8 (± 78.8)	153.6 (± 55.1)	62.6 (± 23.2)	85.4 (± 17.9)	82.7 (± 6.9)	85.0 (± 30.9)
Chlorophyll a (Chl _a ; µg cm ⁻²)	0.14 (± 0.14)	0.33 (± 0.16)	0.71 (± 0.46)	1.29 (± 0.59)	0.39 (± 0.2)	0.55 (± 0.23)	2.06 (± 1.16)	0.41 (± 0.15)	0.38 (± 0.12)	0.49 (± 0.16)

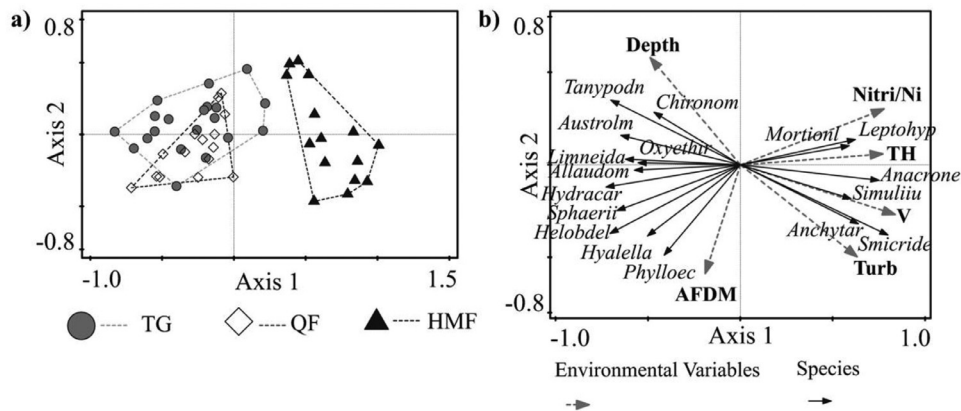


Fig. 4. Results of the Redundancy Analysis (RDA), including, (a) the spatial distribution of the samples given by the composition of the community as a function of the vegetation cover (TG = pajonal; QF = Quinoa forest; HMF = high mountain forest); and (b) the most influential environmental variables (dashed arrows): AFDW = ash free dry weight of organic matter, Nitri/Ni = nitrite/nitrate concentration, Depth = water depth, V = water velocity, Turb = turbidity and TH = total hardness; as well as, the 16 main taxa (discontinuous line arrows): *Allaudomyia* (*Allaudom*), *Anacroneuria* (*Anacrone*), *Anchytarsus* (*Anchytar*), *Austrolimnius* (*Austrolm*), *Chironominae* (*Chironom*), *Helobdella* (*Helobdel*), *Heterelmis* (*Heterelm*), *Hydracarina* (*Hydracar*), *Leptohyphes* (*Leptohyp*), *Limneidae* (*Limneida*), *Mortionella* (*Mortionil*), *Oxyethira* (*Oxyethir*), *Phylloecus* (*Phylloec*), *Simulium* (*Simuliu*), *Smicridea* (*Smicride*), *Sphaeriidae* (*Sphaerit*), *Tanypodinae* (*Tanypodn*).

3.3. Relationships among functional feeding groups (FFG) and dominant vegetation cover

With regard to FFG of macroinvertebrates, the K-W test identified four groups (scraper-SC, piercer-PI, predator-PR and parasite-PA) varying significantly among the different

types of vegetation covers (Annex A). The relative abundance of SC was higher and the relative abundance of PI was lower in HMF than in TG, without statistically differing from QF (Fig. 5a,b; Annex A). Multiple regression (Table 3) suggested that the SC were negatively related to the AFDW at QF, and positively to pH at HMF. PI were positively related

Table 2

Average number of individuals (\bar{X}) and their functional feeding groups (FFG) for each taxa found in the 10 sampling stream segments located in the micro-catchments of the rivers Zhurucay and Pallcayacu (Ecuador). TG = pajonal; QF = Quinoa forest; HMF = high mountain forest; A = absorber; CG = collector-gatherer; SH = shredder; SC = scraper; CF = filtering collector; PI = piercer; PR = predator; PA = parasite.

Order	Family	Taxa	TG	QF	HMF	FFG
Acariformes		Hydracarina	216.7	492.9	21.8	PI
Amphipoda	Hyalellidae	<i>Hyalella</i>	863.0	522.9	144.3	CG, SH
Coleoptera	Elmidae	<i>Austrelmis</i>	29.5	5.3	1.8	SH, CG
		<i>Austrolimnius</i>	126.5	226.1	18.8	SH, CG
		<i>Heterelmis</i>	218.2	243.8	72.3	SH, CG
		<i>Hexacylloepus</i>	0.5	0.6	12.4	SC
		<i>Hexanchorus</i>	31.8	4.8	-	SC
	Psephenidae	<i>Pheneps</i>	-	9.4	0.6	SC, CG
	Ptilodactylidae	<i>Anchytarsus</i>	-	-	19.6	SH, SC
	Scirtidae	<i>Cyphon</i>	4.9	7.7	6.0	SH, SC
Diptera	Athericidae	<i>Atherix</i>	-	-	4.7	PI, PR
	Cerapotonidae	<i>Allaudomyia</i>	179.3	433.9	67.2	PR, SC, SH
	Chironomidae	Chironominae	36.6	5.3	4.3	CG, SH, SC, PR
		Orthocladiinae	2010.3	3332.3	2745.2	CG, SH, SC, PR
		Podominae	3.6	13.5	-	CG, SH, SC, PR
		Tanytopodinae	372.8	192.5	78.3	CG, SH, SC, PR
		Tanytarsini	70.2	203.7	81.4	CG, SH, SC, PR
	Dixidae	<i>Dixella</i>	-	-	1.8	A, SH, SC, PR
	Dolichopodidae		0.5	-	4.7	PR, A, PI
	Empididae	<i>Neoplasta</i>	38.8	77.7	42.9	PR, PI
	Ephydriidae		-	0.6	0.6	A, CG, SH, PI
	Limoniidae	<i>Hexatoma</i>	2.7	10.0	131.3	PR, CG, SH
		<i>Orimarga</i>	3.5	6.5	1.2	PR
	Muscidae	<i>Lispe</i>	-	0.6	0.6	CG, SH, SC
	Psychodidae	<i>Pericoma</i>	102.9	721.3	152.5	CG, SH, SC
	Simuliidae	<i>Gygartodax</i>	0.5	0.6	0.6	SC, SH
		<i>Simulium</i>	19.1	48.8	202.5	SC, SH
	Tabanidae	<i>Tabanus</i>	4.0	-	-	PR
	Tipulidae	<i>Tipula</i>	1.4	2.9	6.5	PR, A, CG
Ephemeroptera	Baetidae	<i>Andesiops</i>	8.5	46.5	62.3	CG, SC, SH
		<i>Baetodes</i>	-	18.9	11.8	CG, SC
	Leptohyphidae	<i>Haplohyphes</i>	-	-	11.2	CG, SC, SH
		<i>Leptohyphes</i>	-	-	10.7	CG, SC, SH
	Leptophlebiidae	<i>Ecuaphlebia</i>	171.3	338.5	67.2	SC, CG, CF
Plecoptera	Grypopterygidae	<i>Claudioperla</i>	15.5	10.0	-	PR, SH, SC
	Perlidae	<i>Anacroncuria</i>	2.3	5.3	50.5	PR, CG, SH
Trichoptera	Calamoceratidae	<i>Phylloecus</i>	33.7	50.0	8.7	SH, CG
	Glossosomatidae	<i>Mortionella</i>	1.4	7.7	30.6	CG, SC
	Helicopsychidae	<i>Helicopsyche</i>	47.8	98.3	7.7	CG, SC
	Hydrobiosidae	<i>Cailloma</i>	0.5	-	-	PR, SH
	Leptoceridae	<i>Atopsyche</i>	8.1	34.8	13.1	SH, CG, SC
	Hydroptilidae	<i>Metrichia</i>	54.3	39.3	7.7	SC, PI
		<i>Neotrichia</i>	-	-	0.6	SH, CG, SC
		<i>Ochrotrichia</i>	72.7	8.9	5.9	SC, PI
		<i>Oxyethira</i>	26.5	7.1	-	SC, PI
	Hydrophychidae	<i>Smicridea</i>	-	0.6	55.9	CF, SH, PR
	Limnephilidae	<i>Contulma</i>	66.6	35.3	4.1	SC
	Xiphocentronidae		9.7	20.5	2.3	SC
Basommatophora	Lymnaeidae		60.8	22.9	-	CG
	Planorbidae		-	0.6	1.8	CG
Rhynchobdellida	Glossiphoniidae	<i>Helobdella</i>	26.1	103.5	0.6	PR
Gordioidea	Gordiidae		107.8	160.1	4.8	PA
Haplotaxida	Oligochaeta		438.1	1040.5	122.5	CG
Tricladida	Dugesidae	<i>Girardia</i>	90.9	58.9	211.9	PR, CG
Sphaeriida	Sphaeriidae		152.9	123.0	4.7	CF

lated to AFDW at QF and negatively related to the pH at HMF. Further, AFDW did not show significant differences as a function of the tree vegetation types (Annex B). The relative abundance of PR was higher (Fig. 5c; Annex A) in HMF than in TG and QF. In this respect, Depth and AFDW were selected by the multiple regression analysis (Table 3) as the environmental variables that negatively influenced this feeding group at TG and QF respectively. No significant

difference of Depth was observed in the three ecosystems (Annex B). Finally, the relative abundance of PA was significantly lower at HMF (Fig. 5d; Annex A) than at TG and QF; multiple regression (Table 3) suggested that this variable was defined positively by V and pH at TG and negatively by TH at HMF.

Table 3

Environmental variables that have significant effects on ^(a) biological variables (BV); and ^(b) the relative abundance of functional feeding groups (FFG) in the three sampled ecosystems (TG = pajonal; QF = Quinoa forest; HMF = high mountain forest), according to the multiple regression analysis. SE = standard Error; β = beta (standardised) coefficient, p = significance value.

BV ^(a) /FFG ^(b)	Vegetation cover	Environmental variable	R ² _{adj}	Unstandardised coefficients		β	t	p
				B	SE			
Richness ^(a)	HMF	Turbidity	0.54	-2.2	0.53	-0.76	-4.21	0.001
Diversity ^(a)	QF	Total hardness	0.43	-0.4	0.13	-0.68	-3.38	0.005
	HMF	Water velocity	0.69	0.2	0.07	0.57	3.38	0.006
%Plecoptera ^(a)	TG	pH		-0.1	0.06	-0.43	-2.52	0.029
		Water velocity	0.24	0.3	0.12	0.53	2.64	0.017
		Water temperature	0.24	-0.6	0.26	-0.55	-2.35	0.036
%Non-insect ^(a)	HMF	Water velocity	0.49	1.1	0.28	0.73	3.79	0.002
		pH	0.51	-29.2	7.81	-0.77	-3.74	0.003
		Water velocity		15.5	5.26	0.61	2.94	0.012
%Scrapper ^(b)	HMF	pH	0.52	-4.6	1.59	-0.54	-2.89	0.014
		Turbidity		3.4	1.40	0.45	2.39	0.034
		Organic matter	0.64	-3.0	0.59	-0.82	-5.12	0.000
%Piercer ^(b)	HMF	pH	0.45	1.3	0.36	0.70	3.53	0.004
		Organic matter	0.23	2.3	1.00	0.53	2.26	0.042
%Predator ^(b)	HMF	pH	0.31	-0.3	0.13	-0.60	-2.72	0.017
		Water depth	0.17	-4.4	1.99	-0.46	-2.20	0.041
%Parasite ^(b)	TG	Organic matter	0.23	-2.4	1.05	-0.53	-2.25	0.042
		Water velocity	0.64	1.3	0.34	0.57	3.88	0.001
HMF	HMF	pH		2.5	0.96	0.44	2.61	0.019
		Total hardness	0.25	-1.0	0.41	-0.55	-2.36	0.035

Table 4

Results of the Redundancy Analysis (RDA) and the selection of environmental variables that explain the composition of the community of aquatic macroinvertebrates as a function of the studied vegetation covers. Pseudo-F = the average of the eigenvalues of the unconstrained (residual) axes; p = significance value; p (adj) = significance value with Bonferroni correction.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4	
Eigenvalues	0.24	0.06	0.04	0.03	
Explained variation (cumulative)	24.1	30.2	34.4	37.1	
Pseudo-canonical correlation	0.92	0.82	0.72	0.65	
Explained fitted variation (cumulative)	60.4	75.5	86.0	92.9	
Environmental variable	Explained (%)	Contribution (%)	pseudo-F	p	p (adj)
Water velocity (V)	18.1	39.3	10.6	0.002	0.02
Nitrite/nitrate (Nitri/Ni)	6.7	14.5	4.2	0.002	0.02
Turbidity (Turb)	4.9	10.6	3.2	0.002	0.02
Total hardness (TH)	4.2	9.1	2.9	0.004	0.04
Water depth (Depth)	3.1	6.7	2.1	0.020	0.20
Organic matter (AFDW)	3.0	6.6	2.2	0.010	0.10

4. Discussion

The catchment scale spatial distribution of aquatic communities is largely due to the environmental conditions of the habitats, associated with the type of vegetation cover and the underlying geology (Fierro et al., 2017; Fraaije et al., 2019). However, factors that intervene in community control, exclusively in high-tropical-Andean aquatic ecosystems, are still relatively unknown (Bücker et al., 2010; Ríos-Touma et al., 2011; Vimos-Lojano et al., 2018). Hereafter, the current study focused on examining the catchment and local scale factors that could be relevant for the structure of the community and for the functional feeding groups of macroinvertebrates in two high mountain pristine micro-catchments.

4.1. Relationships among environmental characteristics and dominant vegetation cover

The predominance of Histosols, and TG vegetation in the Zhurucay microcatchment (Mosquera et al., 2015) apparently influenced the homogeneity of the physical-chemical characteristics of the water in the habitats of TG and QF, as compared to the respective characteristics in HMF. These physical-chemical characteristics (in TG and QF) resulted similar to those observed by Ríos-Touma et al. (2011) in the Piburja stream (páramo), located approximately at 315 km to the north of the current study site, at about 3,300 m a.s.l.

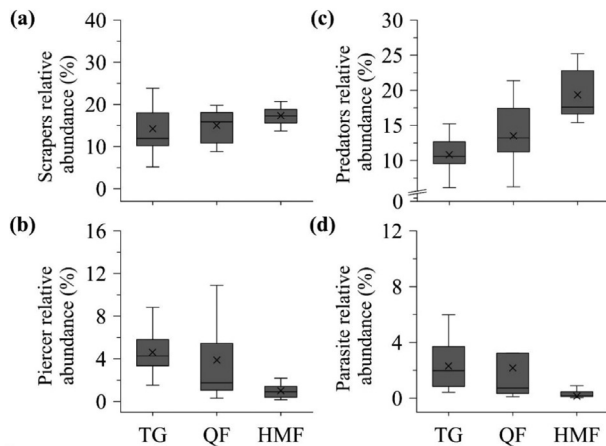


Fig. 5. Box plots of (a) scrapers; (b) piercer; (c) predators; and (d) parasite, as a function of vegetation cover (TG = pajonal; QF = Quinua forest; HMF = high mountain forest). Box plots elements are median (bold horizontal line), average ("X"), interquartile range (IQR, box), and range segments (up to 1.5 IQR). Number of averaged samples (6 replicates), N, are 20 (TG), 15 (QF) and 15 (HMF).

Low temperatures are very typical on high mountains (Kasangaki et al., 2008) and in general, temperature increases as elevation decreases (Jacobsen et al., 2003; 2004). T is among the most significant physical-chemical variables for macroinvertebrates in the high mountains (Miserendino et al., 2011). At the present study sites, higher T was observed at the lower HMF ecosystem. However, although this temperature variation was statistically significant, apparently did not represent an important factor for macroinvertebrate communities. Further, the effect that tree canopy has on rivers is normally the reduction of water temperature and primary productivity owing to the obstruction of the solar radiation (Bücker et al., 2010). However, this study revealed that, despite the significant canopy cover difference among arboreal (QF) and herbaceous (TG) ecosystems, T and primary productivity remained the same, suggesting as such that the type of vegetation cover is not very relevant for these variables at these high elevations, which differs from what has been observed at lower elevations (Bücker et al., 2010).

On the other hand, higher Turb and TDS is the result of increased Q and V, which was observed in the HMF ecosystem, likely as the result of (i) the greater cumulative rainfall in the Pallcayacu as compared to the Zhuruca microcatchment; and (ii) the approximately two-times-higher average slope of the Pallcayacu with respect to the Zhuruca microcatchment. Higher Nitri/Ni could be related to more intense rainfall and higher Q in rivers surrounded by agriculture or cattle raising (Monaghan and Smith, 2012); however, the sampling site at the Pallcayacu microcatchment was situated at a pristine environment. Hence, this could be attributed to the fact that the forest soil in high altitudes accumulate higher carbon (Marian et al., 2017) and nitrogen stores (Tashi et al., 2016), and are subjected to higher seepage rates; they have a greater potential for leaching of nitrate (Di and Cameron, 2002).

4.2. Relationships among biological variables, functional feeding groups (FFG), aquatic communities and dominant vegetation cover

The study revealed that V, Q, Turb, TH, pH, related to the type of vegetation cover (Bücker et al., 2010; Iñiguez-Armijos et al., 2014) and hydro-morphological characteristics of the catchment, directly affected the composition and structure of the benthic community and the FFG. In this context, change in pH affects aquatic life indirectly by modifying the dissolved oxygen level of the water, the photosynthesis of aquatic organisms (phytoplankton) and the sensitivity of these organisms to pollution (Ngodhe et al., 2014). Prommi and Payakka (2015) found direct correlation of richness and diversity to pH as many species favoured slightly alkaline pH in basic habitats. The present study also indicated that diversity, non-insects and several FFGs were sensitive even to the small changes in pH. Furthermore, the flow regime is a critical component in determining aquatic communities (Bunn and Arthington, 2002; Vimos-Lojano et al., 2018). This study suggested that the Pallcayacu microcatchment with higher V exhibited a decrease in the diversity of macroinvertebrates, resulting from the associated greater hydraulic stress. Apparently, organisms that are not adapted to strong velocities, such as those of the non-insect class, specifically the Oligochaeta (James et al., 2008), were significantly impacted unlike some taxa (i.e. *Anacroneuria*) of the order Plecoptera that are characterised by being relatively large and robust (Tamaris-Turizo et al., 2007), allowing them to be strongly attached to the substrate under higher velocity events (Tomanová and Tedesco, 2007). In this study, a greater number of *Anacroneuria* was found in the HMF streams, characterised by higher velocities, which matches the results of other studies on similar Andean streams (Sajamí et al., 2016). Another representative group in the HMF habitats was the genus *Simulium* (Ríos-Touma et al., 2011; Pavitra et al., 2019), the body structure of which is characterised by an anal ring with rows of hooks that may allow it adhering strongly to the substrate (Pavitra et al., 2019).

In general, many aquatic ecology studies relate TH, Turb, and Nitri/Ni with the impact of land use change on the macroinvertebrate community (Bücker et al., 2010; Miserendino et al., 2011). However, biotic variation in pristine areas is still poorly understood (Miserendino et al., 2011). Although the order Diptera and the non-insect class (Oligochaeta and *Hyalella*) are generally distinctive of pasture zones (James et al., 2008), these two groups were among the dominant taxa in the current pristine study sites, which matches the results of a previous study performed at pristine locations of New Zealand mountains (Olsen et al., 2001) and Andean streams (Scheibler et al., 2014). The elevation is likely to influence the dominance of Diptera and the non-insect class since it restricts the variability of the ecosystem to a certain number of taxa, mainly resistant to the availability of dissolved oxygen (Jacobsen et al., 2003) and the variability of Q (Mosquera et al., 2015). With regard to the order Diptera, the Chironomidae family, with a relative abundance of 47.7%, presents multivoltinism (Boothroyd, 1999) and a higher mobility in the adult state (Robinson et al., 2003), which may allow

it to prevail in these environments. The organisms of this family, mainly scrapers, are also abundant in neotropical streams situated in the lowlands of Costa Rica (Lorion and Kennedy, 2009). However, the availability of periphyton is low in the higher Andean streams so that the relative abundance of Chironomidae is likely to be more related to its plausible adaptation to the availability of food and hydraulic conditions (Vescovi-Rosa et al., 2011).

Furthermore, the entry of litter from riparian vegetation represents an important source of energy and nutrients for the macroinvertebrates, especially for the detritivores (shredders) that are very abundant in environments with an arboreal canopy (Graça, 2001). This study suggested that the amount of organic matter in the bed of streams was not significantly related to the presence of shredders as a function of the predominant vegetation cover. Among the factors that possibly explain this are the hydromorphological conditions such as V and the slope of the streams, which exert a pulling force that diminishes the availability of the organic matter (Ríos-Touma et al., 2009). Moreover, the low presence of shredders could be attributed to the leaf type of vegetation, tussock grass, *Polylepis* sp. and *Gynoxys* sp., which might be of little preference by these groups. It is reported that the characteristics of leaves can strongly influence the palatability of shredders (Reis et al., 2019). The genus *Phylloecus*, representative of shredders and mainly present in lower Andean rivers (< 1,300 m a.s.l.), characterised by smaller slopes than the ones of the streams herein studied (Encalada et al., 2010), however, in the current high mountain streams also exhibited an association with the available amount of organic matter. The presence of predators in the habitats with lower organic matter content could be related to the higher water velocity reigning in these habitats. Higher flows are likely to wash away the organic matter leaving the inorganic substrate, which do not affect considerably to predators due to their more robust body structure (Tamaris-Turizo et al., 2007).

5. Conclusions

The present study suggested that high Andean headwaters with QF and TG vegetation share many of the environmental characteristics. HMF differed both in environmental variables and macroinvertebrate communities from the other two sites. However, all of the three high Andean headwaters, because of their elevation, are restricted to a certain number of taxa mainly resistant to the lower availability of dissolved oxygen and variation of discharge. As for the spatial distribution of aquatic communities, the most influential variables were TH, Turb, V and Nitri/Ni, which were at the same time positively correlated to the HMF vegetation. In the same context, it was observed the influence of the chemical-hydromorphological characteristics (V, Turb, pH, TH) of the stream on some of the biological variables and functional groups. It was observed at the three study sites a dominance of organisms generally tolerant to lower availability of oxygen (Chironomidae and non-insect class) and, curiously, to higher concentrations of nutrients. In general, shredders are very abundant in environments with an arboreal canopy, however in this study

only some taxa of shredders (i.e., *Phylloecus*) were associated with the presence of organic matter in the sediment. Other taxa (predators of Plecoptera) are predominant in the high Andean ecosystems due to their resistance to flow conditions. It is worth noticing that no relevant differences were found between the QF and TG stream segments in terms of the important physical-chemical variables, as well as, the macroinvertebrate communities.

Finally, the sites selected for the current study still represent pristine ecosystems and, as such, could provide a baseline for comparison with relevant information from other impacted ecosystems and/or for future research that could concentrate, for instance, on examining the impact of local or regional anthropic changes, the more appropriate local definition of environmental flows, etc.

Conflict of Interest

The authors declare no conflict of interest.

Ethical Statement

The research was done according to ethical standards.

Acknowledgements

This work was supported by the Research Directorate of the Universidad de Cuenca (DIUC), Project “Bases científicas para la estima del caudal ecológico considerando distintas escalas de hábitat, integrando la eco-hidrología y la eco-hidráulica”. Preparation of the current manuscript took place in the framework of the ERASMUS+ project “Water Management and Climate Change in the Focus of International Master Courses (WATERMAS)” financed by the European “Education, Audiovisual and Culture Executive Agency (EACA)” [grant number 586345-EPP-1-2017-1-DE-EPPKA2-CBHE-JP]. This publication reflects only the authors’ views; thereby, neither the European Union nor EACA is liable for any use that may be made of the information contained herein. The authors would like to express their gratitude to the Non-Governmental Organisation (NGO) “Cordillera Tropical” that facilitated that field campaigns could take place at the Pallcayacu microcatchment.

Funding Body

This work was supported by the Research Directorate of the Universidad de Cuenca (DIUC), Project “Bases científicas para la estima del caudal ecológico considerando distintas escalas de hábitat, integrando la eco-hidrología y la eco-hidráulica”, and by the European “Education, Audiovisual and Culture Executive Agency (EACA)” [grant number 586345-EPP-1-2017-1-DE-EPPKA2-CBHE-JP], ERASMUS+ project “Water Management and Climate Change in the Focus of International Master Courses (WATERMAS)”.

References

- Acosta, R., Ríos-Touma, B.P., Rieradevall, M., Prat, N., 2009. Propuesta de un protocolo de evaluación de la calidad ecológica de ríos andinos (CERA) y su aplicación a dos cuencas en Ecuador y Perú. *Limnetica* 28 (1), 35–64.

- Albert, J.S., Petry, P., Reis, R.E., 2011. Major biogeographic and phylogenetic patterns. *Historical Biogeography of Neotropical Freshwater Fishes* 1, 21–57.
- APHA, A., 2005. *Standard Methods for Examination of Water and Wastewater*, 20th ed.. In: L.S., C., E., G.A., D., E.A. (Eds.). American Public Health Association, Washington, DC, p. 1220 Washington: American Public Health Association.
- Bailey, R.C., Linke, S., Yates, A.G., 2014. Bioassessment of freshwater ecosystems using the reference condition Approach: Comparing established and new methods with common data sets. *Freshwater Science* 33 (4), 1204–1211.
- Barnett, T.P., Pierce, D.W., Hidalgo, H.G., Bonfils, C., Santer, B.D., Das, T., Bala, G., Wood, A.W., Nozawa, T., Mirin, A.A., 2008. Human-Induced Changes in the Hydrology of the Western United States. *Science* 319, 1080–1083.
- Boiten, W., 2008. *Hydrometry: IHE Delft Lecture Note Series*. CRC Press, Netherlands, p. 256.
- Boothroyd, I., 1999. Life history of *Kaniwhaniwhanus chapmani* Boothroyd (Chironomidae: Orthocladiinae): population dynamics, emergence, and drift. *New Zealand Journal of Marine and Freshwater Research* 33 (3), 351–359.
- Bücker, A., Sondermann, M., Frede, H.-G., Breuer, L., 2010. The influence of land-use on macroinvertebrate communities in montane tropical streams—a case study from Ecuador. *Fundamental and Applied Limnology/Archiv für Hydrobiologie* 177 (4), 267–282.
- Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30, 492–507.
- Clarke, K., Gorley, R., 2006. *PRIMER v6, 2006: User Manual/Tutorial*. Plymouth Marine Laboratory, p. 190.
- Collins, S.M., Sparks, J.P., Thomas, S.A., Wheatley, S.A., Flecker, A.S., 2016. Increased light availability reduces the importance of bacterial carbon in headwater stream food webs. *Ecosystems* 19, 396–410.
- Chevone, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31 (3), 295–309.
- Di, H.J., Cameron, K.C., 2002. Nitrate leaching in temperate agroecosystems: sources, factors and mitigating strategies. *Nutrient Cycling in Agroecosystems* 64, 237–256.
- Ding, N., Yang, W., Zhou, Y., González-Bergonzoni, I., Zhang, J., Chen, K., Vidal, N., Jeppesen, E., Liu, Z., Wang, B., 2017. Different responses of functional traits and diversity of stream macroinvertebrates to environmental and spatial factors in the Xishuangbanna watershed of the upper Mekong River Basin, China. *Science of the Total Environment* 574, 288–299.
- Domínguez, E., Fernández, H.R., Lillo, F.M., 2009. Macroinvertebrados bentónicos sudamericanos: Sistemática y biología. *Fundación Miguel Lillo Tucumán, Tucumán, Argentina*, p. 656.
- Elosegui, A., 2009. La estructura física de los cauces fluviales. In: Elosegui, A., Sabater, S. (Eds.), *Conceptos y técnicas en ecología fluvial*. Fundación BBVA, Bilbao, España, pp. 71–84.
- Encalada, A.C., Calles, J., Ferreira, V., Canhoto, C.M., Graca, M.A., 2010. Riparian land use and the relationship between the benthos and litter decomposition in tropical montane streams. *Freshwater Biology* 55 (8), 1719–1733.
- Espinosa, J., Rivera, D., 2016. Variations in water resources availability at the Ecuadorian páramo due to land-use changes. *Environmental Earth Sciences* 75 (16), 1173.
- Feyen, J., Vázquez, R.F., 2015. Modeling hydrological consequences of climate and land use change—Progress and Challenges. *Maskana* 2 (2), 83–100.
- Fierro, P., Bertrán, C., Tapia, J., Hauenstein, E., Peña-Cortés, F., Vergara, C., Cerna, C., Vargas-Chacoff, L., 2017. Effects of local land-use on riparian vegetation, water quality, and the functional organization of macroinvertebrate assemblages. *Science of the Total Environment* 609, 724–734.
- Fraaije, R.G., Poupin, C., Verhoeven, J.T., Soons, M.B., 2019. Functional responses of aquatic and riparian vegetation to hydrogeomorphic restoration of channelized lowland streams and their valleys. *Journal of Applied Ecology* 56 (4), 1007–1018.
- Giraldo, L.P., Chará, J., del Carmen Zuñiga, M., Chará-Sema, A.M., Pedraza, G., 2014. Agricultural land use impacts on aquatic macroinvertebrates in small streams from La Vieja river (Valle del Cauca, Colombia). *Revista de Biología Tropical/International Journal of Tropical Biology and Conservation* 62, 203–219.
- Graca, M.A., 2001. The role of invertebrates on leaf litter decomposition in streams—a review. *International Review of Hydrobiology* 86 (4–5), 383–393.
- Hampel, H., Cocha, J., Vimos, D., 2010. Incorporation of aquatic ecology to the hydrological investigation of ecosystems in the high Andes. *Maskana* 1 (1), 91–100.
- Hannah, D.M., Brown, L.E., Milner, A.M., Gurnell, A.M., McGregor, G.R., Petts, G.E., Smith, B.P., Snook, D.L., 2007. Integrating climate-hydrology-ecology for alpine river systems. *Aquatic Conservation: Marine and Freshwater Ecosystems* 17 (6), 636–656.
- Hieber, M., Robinson, C.T., Uehlinger, U., Ward, J., 2005. A comparison of benthic macroinvertebrate assemblages among different types of alpine streams. *Freshwater Biology* 50 (12), 2087–2100.
- Hodkinson, I.D., Jackson, J.K., 2005. Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. *Environmental Management* 35, 649–666.
- Iñiguez-Armijos, C., Leiva, A., Frede, H.G., Hampel, H., Breuer, L., 2014. Deforestation and benthic indicators: how much vegetation cover is needed to sustain healthy Andean streams? *PLoS ONE* 9 (8), e105869.
- Jacobsen, D., 2004. Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology* 49 (10), 1293–1305.
- Jacobsen, D., Rostgaard, S., Váscquez, J.J., 2003. Are macroinvertebrates in high altitude streams affected by oxygen deficiency? *Freshwater Biology* 48 (11), 2025–2032.
- James, A., Dewson, Z., Death, R., 2008. The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications* 24 (1), 22–35.
- Kasangaki, A., Chapman, L., Balirwa, J., 2008. Land use and the ecology of benthic macroinvertebrate assemblages of high-altitude rainforest streams in Uganda. *Freshwater Biology* 53 (4), 681–697.
- Larson, D.M., Dodds, W.K., Veach, A.M., 2019. Removal of woody riparian vegetation substantially altered a stream ecosystem in an otherwise undisturbed grassland watershed. *Ecosystems* 22 (1), 64–76.
- Lepš, J., Šmilauer, P., 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge, United Kingdom, p. 269.
- Lorion, C., Kennedy, B., 2009. Relationships between deforestation, riparian forest buffers and benthic macroinvertebrates in neotropical headwater streams. *Freshwater Biology* 54 (1), 165–180.
- Lund, J.O., Wissinger, S.A., Peckarsky, B.L., 2016. Caddisfly behavioral responses to drying cues in temporary ponds: implications for effects of climate change. *Freshwater Science* 35 (2), 619–630.
- Madsen, P.B., Morabowen, A., Andino, P., Espinosa, R., Cauvy-Fraunié, S., Dangles, O., Jacobsen, D., 2015. Altitudinal distribution limits of aquatic macroinvertebrates: an experimental test in a tropical alpine stream. *Ecological Entomology* 40 (5), 629–638.
- Marian, F., Sandmann, D., Krashevskaya, V., Maraun, M., Scheu, S., 2017. Leaf and root litter decomposition is discontinued at high altitude tropical montane rainforests contributing to carbon sequestration. *Ecology and Evolution* 7 (16), 6432–6443.
- Miles, J., Shevlin, M., 2001. *Applying regression and correlation: A guide for students and researchers*. Sage, London, p. 262.
- 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. *Science of the Total Environment* 409 (3), 612–624.
- 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 Research and Applications* 20 (8), 967–983.
- Monaghan, R., Smith, L., 2012. Contaminant losses in overland flow from dairy farm laneways in southern New Zealand. *Agriculture, Ecosystems and Environment* 159, 170–175.
- Mosquera, G.M., Lazo, P.X., Celleri, R., Wilcox, B.P., Crespo, P., 2015. Runoff from tropical alpine grasslands increases with areal extent of wetlands. *Catena* 125, 120–128.
- Naiman, R., Magnuson, J.J., McKnight, D.M., Stanford, J., 1995. *The freshwater imperative. A research agenda*. Island Press, Washington, DC, p. 181.
- Ngodhe, S.O., Raburu, P.O., Achieng, A., 2014. The impact of water quality on species diversity and richness of macroinvertebrates in small water bodies in Lake Victoria Basin, Kenya. *Journal of Ecology and the Natural Environment* 6 (1), 32–41.
- Olsen, D., Townsend, C., Matthaei, C., 2001. Influence of reach geomorphology on hyporheic communities in a gravel-bed stream. *New Zealand Journal of Marine and Freshwater Research* 35 (1), 181–190.
- Pavitra, S.P., Low, V.L., Tan, T.K., Lim, Y.A.L., Ya'cob, Z., 2019. Temporal variation in diversity and community structure of preimaginal blackflies (Diptera: Simuliidae) in a tropical forest reserve in Malaysia. *Acta Tropica* 202, 105275.
- Piggott, J.J., Townsend, C.R., Matthaei, C.D., 2015. Climate warming and

- agricultural stressors interact to determine stream macroinvertebrate community dynamics. *Global Change Biology* 21 (5), 1887–1906.
- Prommi, T., Payakka, A., 2015. Aquatic insect biodiversity and water quality parameters of streams in Northern Thailand. *Sains Malaysiana* 44 (5), 707–717.
- Quinn, G.P., Keough, M.J., 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, p. 537.
- Reis, D.F., Machado, M.M.D., Coutinho, N.P., Rangel, J.V., Moretti, M.S., Morais, P.B., 2019. Feeding preference of the shredder *Phylloicus* sp. for plant leaves of *Chrysophyllum oliviforme* or *Miconia chartacea* after conditioning in streams from different biomes. *Brazilian Journal of Biology* 79 (1), 22–28.
- Rezende, R.S., Santos, A.M., Henke-Oliveira, C., Gonçalves Jr, J.F., 2014. Effects of spatial and environmental factors on benthic a macroinvertebrate community. *Zoologia (Curitiba)* 31 (5), 426–434.
- Ríos-Touma, B., Encalada, A., Prat Fornells, N., 2009. Leaf Litter Dynamics and Its Use by Invertebrates in a High-Altitude Tropical Andean Stream. *International Review Hydrobiology* 94 (4), 357–371.
- Ríos-Touma, B., Encalada, A.C., Prat, N., 2011. Macroinvertebrate Assemblages of an Andean High-Altitude Tropical Stream: The Importance of Season and Flow. *International Review of Hydrobiology* 96 (6), 667–685.
- Robinson, C.T., Uehlinger, U., Monaghan, M.T., 2003. Effects of a multi-year experimental flood regime on macroinvertebrates downstream of a reservoir. *Aquatic Sciences* 65, 210–222.
- Sajamí, J., Huamantínco, A., 2016. Distribución espacial de Ephemeroptera, Plecoptera, Trichoptera y Coleoptera (Insecta) en una quebrada de primer orden, bosque montano, Junín, Perú. *Revista Peruana de Biología* 23 (2), 95–102.
- Scheibler, E.E., Roig Juñent, S.A., Claps, M.C., 2014. Chironomid (Insecta: Diptera) assemblages along an Andean altitudinal gradient. *Aquatic Biology* 20 (2), 169–184.
- Šmilauer, P., Lepš, J., 2014. *Multivariate analysis of ecological data using CANOCO 5*. Cambridge University Press, Cambridge, p. 362.
- Sotomayor, G., Hampel, H., Vázquez, R.F., 2018. Water quality assessment with emphasis in parameter optimisation using pattern recognition methods and genetic algorithm. *Water Research* 130, 353–362.
- Sponseller, R.A., Grimm, N.B., Boulton, A.J., Sabo, J.L., 2010. Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream. *Global Change Biology* 16 (10), 2891–2900.
- Statzner, B., Beche, L.A., 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology* 55, 80–119.
- Steinman, A.D., Lamberti, G.A., Leavitt, P., 2011. Biomass and pigments of benthic algae. In: Hauer, F.R., Lamberti, G.A. (Eds.), *Methods in Stream Ecology*. Academic Press, Amsterdam, pp. 357–379.
- Studholme, A.M., Hampel, H., Finn, D.S., Vázquez, R., 2017. Secondary production of caddisflies reflects environmental heterogeneity among tropical Andean streams. *Hydrobiologia* 797, 231–246.
- Tamaris-Turizo, C.E., Turizo-Correa, R., Zúñiga, M., 2007. Distribución espacio-temporal y hábitos alimentarios de ninfas de *Anacroneria* (Insecta: Plecoptera: Perlidae) en el río Gaira (Sierra Nevada de Santa Marta, Colombia). *Caldasia* 29 (2), 375–385.
- Tashi, S., Singh, B., Keitel, C., Adams, M., 2016. Soil carbon and nitrogen stocks in forests along an altitudinal gradient in the eastern Himalayas and a meta-analysis of global data. *Global Change Biology* 22 (6), 2255–2268.
- Tomanová, S., 2007. *Functional aspect of macroinvertebrate communities in tropical and temperate running waters* PhD thesis (in czech). Masaryk University, Brno.
- Tomanová, S., Tedesco, P.A., 2007. Tamaño corporal, tolerancia ecológica y potencial de bioindicación de la calidad del agua de *Anacroneria* spp. (Plecoptera: Perlidae) en América del Sur. *Revista de Biología Tropical* 55 (1), 67–81.
- Vázquez, R.F., 2010. Modelación hidrológica de una microcuenca Altoandina ubicada en el Austro Ecuatoriano. *Maskana* 1 (1), 79–90.
- Vescovi-Rosa, B., Oliveira, V., Alves, R., 2011. Structure and spatial distribution of the Chironomidae community in mesohabitats in a first order stream at the Poço D'Anta Municipal Biological Reserve in Brazil. *Journal of Insect Science* 11 (36), 1–13.
- Vimos-Lojano, D., Martínez-Capel, F., Hampel, H., 2017. Riparian and microhabitat factors determine the structure of the EPT community in Andean headwater rivers of Ecuador. *Ecohydrology* 10 (8), e1894.
- Vimos-Lojano, D., Martínez-Capel, F., Hampel, H., Vázquez, R.F., 2018. Hydrological influences on aquatic communities at the mesohabitat scale in high Andean streams of southern Ecuador. *Ecohydrology* 12 (1), e2033.
- Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277 (5322), 102–104.
- Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X., Shen, J., 2011. Contrasting patterns in elevational diversity between microorganisms and macroorganisms. *Journal of Biogeography* 38 (3), 595–603.