Hydrological influences on aquatic communities at the mesohabitat scale in high Andean streams of southern Ecuador

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ABSTRACT

This study assessed the effects of hydrological events on aquatic communities at the mesohabitat scale (pool, run and riffle) in the high Andean region. Four headwater sites in the Zhurucay microcatchment (southern Ecuador), with elevations higher than 3,500 m, were selected and monitored considering in each site a 50-m-long reach, and within each reach five cross-sections. In each of these reaches 19 sampling campaigns were conducted in the period December 2011 – October 2013, collecting macroinvertebrates and physical characteristics. A total of 27 hydrological indices were calculated using the daily flow rate as input. Large Peak flow (LPF), Small Peak flow (SPF), and Low flow (LF) events were defined based on discharge thresholds. Multivariate statistics showed that 15 hydrological indices were significantly related to the aquatic community. Further, the study revealed that (i) peak events produced stronger effects on communities than LF events; (ii) the observed effects of LF events were weaker than those encountered in other latitudes; and (iii) local benthic communities have more resilience than similar communities studied in other latitudes.

Keywords: Ecohydrology, Andean streams, hydrological indices, mesohabitat, macroinvertebrates, ecological responses

INTRODUCTION

The influence of hydrological factors on benthic macroinvertebrate communities received increasing attention in the last decade (Chang *et al.*, 2008; Belmar *et al.*, 2012; Mesa, 2012). Several studies have shown that the prior hydrological flow conditions affect the temporality of habitats and the distribution of aquatic flora and fauna (Poff *et al.*, 1997; Kennen *et al.*, 2010; Rolls *et al.*, 2012). Further, it is known that changes caused by variations in discharge result in periodic interruptions in the stable conditions of the habitats used by species and that when stable flow conditions return, new habitats are created that are then colonised and repopulated by the biota (Lake, 2003). Commonly, the influence of hydrological variability is analysed using hydrological indices and the physical characteristics of the riverbed, which are then associated with the macroinvertebrate communities (Lancaster and Hildrew, 1993; Suren and Lambert, 2010).

In this regard, previous studies concentrated on temperate zones, where the increased discharges from floods (i.e., hydrological pulses) and the reductions from droughts are clearly differentiated (Rolls *et al.*, 2012; Leigh, 2013; Calapez *et al.*, 2014). For instance, Suren and Jowett (2006) described clear variations in the composition and structure of aquatic communities between samples taken before and after flood or drought events. Following flood events of varying magnitude, significant decreases in the density and species richness of aquatic communities have been observed (Suren and Jowett, 2006; Robinson, 2012). On the other hand, it has been noticed that the effect of droughts on benthic communities depends on the duration of such events. When the duration is long, the area available for macroinvertebrate communities decreases, causing a dramatic decline in the density and species richness (Wood and Armitage, 2004; Mouthon and Daufresne, 2006).

In tropical zones, the climate is characterised by marked seasonality between wet and dry periods (Flecker and Feifarek, 1994); however, these seasons are less pronounced in the south Andean region of Ecuador due to the strong effect of the Andes range (Nouvelot *et al.*, 1995; Buytaert *et al.*, 2006). This range influences the specific characteristics of every fluvial network (discharge, vegetation cover, slope and substrate type), the air mass transferences and the transition zones between ecosystems, which affect the frequency, intensity, and amount of rainfall and, therefore, the volume and frequency of water reaching the rivers (Nouvelot *et al.*, 1995; Bispo *et al.*, 2006; Buytaert *et al.*, 2006).

Studies at medium altitude in the Andean region report a decrease in the density and species richness on the seasonal and annual time scales mainly due to an increase in shear stress during heavy floods in the rainy season (Jacobsen and Encalada, 1998; Ríos-Touma *et al.*, 2011; Mesa, 2012). In the high Andes, only few of such studies have been carried out. For example, Moya *et al.* (2009) studied in Bolivian streams, at elevations higher than 3,000 m above sea level (a.s.l.), the effect of variations in streamflow on the density and species richness, although with a very

limited sampling period and seasonal variability. They concluded that seasonality is not a critical factor for the richness or density of macroinvertebrates in the riffles, except for the EPT taxa richness. With other words, aquatic communities at these altitudes seem not to be regulated only by seasonal features but also by aspects such as (i) the susceptibility of taxa to disturbances; (ii) the taxa ability to recolonise habitats; (iii) the number of colonising taxa; and (iv) the number of life cycles of the colonisers.

The influence of hydrology on the natural dynamics of macroinvertebrate communities is very relevant for the conservation of the delicate High-Andean ecosystems. In this context, Ecuadorian regulations require environmental flow assessments for hydroelectricity projects, which normally are located at high elevations and carried out within the frame of consulting works, little of this information is linked to the aquatic habitat density and composition, with the exception of a few efforts such as Herrera and Burneo (2017). In those studies, in general only a very limited set of hydrological indices are defined for estimating the monthly environmental flow but not for inspecting the effect of hydrological extreme events on the dynamics of the aquatic communities. Indeed, it is worth noticing that no one of the recently cited studies in tropical zones are considering hydrological indices to explore the effects of peaks and low flows on the aquatic community.

In temperate zones recent studies are focusing on defining discharge thresholds, both for flooding and drought events, that significantly affect aquatic communities in natural (Wood *et al.*, 2000; Suren and Jowett, 2006; Monk *et al.*, 2007; Chang *et al.*, 2008) and altered rivers (Freeman *et al.*, 2001; Armanini *et al.*, 2014; Macnaughton *et al.*, 2015). The studies on altered ecosystems focus particularly on the effects on fish (i.e., Freem *et al.*, 2001; Armstrong, 2003; Macnaughton *et al.*, 2017) and less on macroinvertebrates (Armanini *et al.*, 2014; Miller *et al.*, 2014) concentrate on the temporal variability of the aquatic communities as a function of the season in the year (Jacobsen and Encalada, 1998; Ríos⬜Touma *et al.*, 2011; Mesa, 2012) discharge (i.e. hydrological) thresholds and their impact on aquatic communities. Exceptions hereon are the studies in altered rivers of Castro *et al.* (2013), Miserendino (2009), Herrera and Burneo (2017) that macroinvertebrates, and Lima *et al.* (2018) and García *et al.* (2011) of fish.

In contrast to previous studies, this study assessed for the first time in an Andean microcatchment with an elevation higher than 3,500 m a.s.l. the effect of extreme hydrological events (characterised by both, suitable hydrological indices and flow thresholds) on community changes. The mesohabitat spatial scale was selected for this study, in line with a previous study on the same site (Vimos-Lojano *et al.*, 2017), which demonstrated that the distribution of aquatic communities is directly related to the physical characteristics of the habitat at this spatial scale. Further, as stated by Brunke *et al.* (2001) this scale provides a more appropriate approach to study the composition and structure of the community as a function of the fluctuation of flow in streams and rivers. Thus, the main objective of the research presented herein was to discern the effects of

the Large Peak flow (LPF), Small Peak flow (SPF) and Low flow (LF) events on the aquatic macroinvertebrate community in the headwaters of an Andean microcatchment with an elevation higher than 3,500 m a.s.l. Specifically, it was aimed at answering the following research questions: (i) which hydrological indices related to LPF, SPF and LF events are fundamental to explain the changes in the community's structure and composition?; and (ii) what are the changes one can observe in the community as a result of the referred hydrological events?.

MATERIALS AND METHODS

Study site

Four streams were selected in the headwater of the Zhurucay river microcatchment (7.5 km^2), belonging to the Jubones river catchment. The microcatchment is located in southern Ecuador (9662500 m N, 9658750 m S, 694630 m W and 698010 m E; UTM coordinate system, Zone 17S, geoid PSAD56) at approximately 3,600 m a.s.l. (Fig. 1). The dominant vegetation type is grassland (Tussock grass, 58.6%, *Calamagrostis intermedia,*) with few patches of Quinoa trees (17.5%; *Polylepis incana* Kunth and *Polylepis reticulata* Kunth) and sparse small shrubs. There is a low degree of human intervention, consisting mainly of non-intensive farming activities (Hampel *et al.*, 2010; Studholme *et al.*, 2017).

Climate in the region is characterised by the constant presence of fog and drizzle and annual (bimodal) rainfall average is approximately 1,289 mm. Six years of historical precipitation data were available, and the lowest rainfall occurred in the period June to September (minimum and maximum average of 65.97 mm and 113.73 mm respectively) while the rainy season stretches from October to May. February was the month with the highest inter-annual fluctuation in precipitation, with a maximum monthly value of 257 mm and a minimum value of 40.2 mm. The average daily temperature during the whole study period was 5.9°C and the relative humidity ranged between 82% and 91% (Padrón, 2013). The seasonal variation of temperature is very low (i.e. minimum daily average of 4.8 ° C in July of 2011, the maximum daily average of 6.7 ° C in November of 2011), while daily temperature fluctuation can exceed 15 ° C.

With respect to the hydraulic conditions, the maximum velocity recorded throughout the sampling period (December 2011 to October 2013) was 1.51 m s^{-1}, with an average of 0.31 ± 0.012 m s^{-1}. The highest Froude number (F_r) was 1.35, with an average of 0.27 ± 0.011. The maximum water depth was 0.49 m, with an average of 0.16 ± 0.004 m. The maximum stream channel width and slope were 1.61 m y 0.05 respectively. These hydraulic variables were recorded when the average discharge fluctuated between 33.9 l s^{-1} and 352.1 l s^{-1}. The four studied streams, are characterised by a large substrate heterogeneity dominated by angular rocks, consisting of dominant cobbles > 50% (between 60 and 250 mm) and pebbles about 25% (between 20 and 60 mm) in a matrix of gravel about 20% (between 0.2 and 20 mm) and sand about 5% (0.006 and 0.2 mm). Additional hydrological and hydraulic characteristics of the studied stream reaches are

presented in Annex A.

Sampling methods

50-m-long reaches in each of the four selected streams were sampled in the period between December 2011 and October 2013. Five cross-sections were established in each of the four 50-m-long reaches. A total of 19 sampling campaigns were carried out. A wide variety of hydrological conditions (wet and dry) was recorded in this period.

Sampling of abiotic data

In each sampling campaign, hydraulic measurements were taken at the biological sampling points located at the center of each of the five cross-sections. Were measured the water depth (m), width of the water surface (m) and average velocity (m s^{-1}) at 60% of the water depth from the water surface (Wyżga *et al.*, 2012) using a propeller flow meter (HydroMate CMC3, Sydney, Australia). Additionally, information regarding water levels was recorded at gauging stations located in each of the streams under study using the Mini-Diver DI1501 and Baro-Diver DI500 pressure sensors (Schlumberger Water Services, France) considering a measurement interval of 5 min. These water level data were converted to discharge data according to appropriate hydraulic equations for gauging weirs with known geometry and free spill (Chow *et al.*, 1988); a process that was validated using the data recorded by the propeller flow meter. These sub-daily discharges were averaged to daily values by means of a simple arithmetic averaging process. The substrate was visually classified using six groups that were defined based on the simplified classification of Elosegi (2009), considering 25 x 25 cm^2 reference quadrants.

Sampling of biotic data

Macroinvertebrate samples were collected each campaign using a modified Surber net (coverage area: 625 cm^2; 250-µm net mesh opening; sampling effort: 30 s) vigorously stirred by hand, located near the center of each cross-section and the substrate. The collected sample was placed in a plastic bottle, preserved in a solution of 4% formalin and transferred to the laboratory, where the organisms were separated and identified to the genus level with the use of a stereomicroscope (Olympus SZ-6145TR, Japan) and species identification keys. Nevertheless, some non-insect specimens were identified at a higher taxonomic level (i.e., Hydrachnidia, Gasteropoda, Oligochaeta, and Sphaeriidae), including organisms of the Chironomidae family and the larvae of the Xiphocentronidae family whose taxonomical identification is complex (Domínguez *et al.*, 2009; Acosta and Prat, 2010).

Hydrological and biological data processing

The daily discharge values were transformed into daily values of volume per unit catchment area (mm) to derive a single comparative scale of the discharges of the four studied streams (Chow *et al.*, 1988). Then, the arithmetic mean (Q_{aver}) of the transformed daily discharges were calculated (Q_{S1}, Q_{S2}, Q_{S3} and Q_{S4}) to obtain a single series of representative discharges and derive one single set of hydrological indices. For assessing the similarity (i.e. representativeness) of Q_{aver} regarding the magnitude and evolution of flow, a comparative analysis was made between Q_{aver} and the individual daily hydrographs of the studied streams by means of three complementary procedures. The procedures applied at each of the monitored streams consisted in: (i) evaluation of the correlations between the magnitudes of the discharges and Q_{aver}; (ii) calculation on a daily basis of the coefficient of variation (CV) using the discharge of the four streams in the same day of interest and the average of the entire timeseries of daily CV (CV_{aver}), which constitutes an index of similarity among the discharges of the four monitored streams; and (iii) comparison of the evolution and magnitude of the duration curves of the average daily discharges.

Accordingly, Q_{aver} was used in this study to calculate 27 hydrological indices (Table 1) for each sampling campaign, which were defined based on Monk *et al.* (2006) and Chang *et al.* (2008). No specific indices of the duration of peak flows were computed, because peak events had an average duration of 1 day equal to the time basis of the daily discharge values. In line herewith, no indices of low flow duration were determined but, instead, different LF durations were explicitly considered in the analysis (i.e., 10, 30, 60, 75, 90, 115, and 140 days). For the identification of hydrological peaks, relevant to the present study, thresholds were defined based on the analysis of the series of discharge events that occurred in the one-year period prior to every sampling date.

Thus, for Q_{aver} and considering exceedance percentiles, large peak flows (LPfs) were defined as (see Fig. 2) flows with a value higher than the percentile 2% ($Q_2 = 130$ mm); values between the percentile 5% ($Q_5 = 70$ mm) and Q_2 were considered small peak flows (SPFs); and values lower than the percentile 75% ($Q_{75} = 8$ mm) were considered low flows (LFs). Two or more peak flow pulses (LPFs and/or SPFs) were grouped together if the time lag between successive pulses was shorter than 20 days; this group of peak pulses was considered as a single (global) peak flow event (for instance, LPF 5 and LPF 7 in Fig. 2). For the calculations of the hydrological indices, the date of the last of these grouped peak pulses was adopted as the date of the global peak event. This consideration is based on the fact that a period shorter than 20 days is not enough for observing a complete recovery of the aquatic communities (Flecker and Feifarek, 1994).

On the contrary, a LF event was defined if the discharge was lower than or equal to Q_{75} (Yulianti and Burn, 1998) during a period of at least 7 days. The extent of this event lasted until a water pulse more than Q_{10} (45 mm) occurred. The Q_{10} threshold was defined in this study based on the comparison of the effects of different pulses on the community metrics recorded in

successive sampling campaigns (i.e., comparing campaigns 5 with 6, 6 with 7, 7 with 8, 8 with 9, 16 with 17, 17 with 18 and 18 with 19); in this context, water pulses with magnitudes lower than Q_{10} did not cause significant effects on the community metrics. Therefore, campaign 5 is not part of the LF event 5 (Fig. 2), despite being preceded by 7 days of discharges lower than Q_{75}, since immediately after it a pulse higher than Q_{10} was recorded.

Two tests were carried out to inspect on the congruency of the magnitude of the above defined discharge thresholds, namely (i) an extreme value (hydrological) analysis (EVA); and (ii) a comparison of the Q_2 threshold with the discharge threshold for substrate movement (Q_{subst}). In this context, the EVA was conducted to verify that the SPF and LPF events defined by Q_5 and Q_2 are part of the population of independent extreme flows at the studied streams, that is, are hydrologically independent. If that is the case, the peak discharge thresholds used in this study (i.e. Q_5 and Q_2) should be greater than, or at least equal to, the minimum peak threshold (Q_{Hydrol}) necessary to obtain an optimal fitting of the time series of daily peaks to a generalised (extreme value) Pareto distribution (GPD; Pickands, 1975; Vázquez *et al*., 2009). Hence, the peak discharge data fitting was performed using the peak over threshold (POT) methodology. To this end, a series of daily extreme values was generated using the partial duration time series (PDS) methodology (Vázquez and Feyen, 2003; Vázquez *et al.*, 2008). This PDS analysis was carried out with the aid of specific-task subroutines that were previously (Vázquez and Feyen, 2003; Vázquez *et al.*, 2008) programmed with the FORTRAN and PERL (Practical Extraction and Report Language) programming languages.

Since, substrate movement is an important factor influencing the composition and structure of communities (Milhous and Bradley, 1986), a second test on Q_2 was performed to check on whether it is likely to produce substrate movement. Thus, for each of the four studied streams, Q_{subst} was generated using the equation of Milhous (Milhous, 1998); further, these values were averaged into a single one that was finally compared to Q_2. The Milhous equation considers the relationship between the hydraulic radius (depending on the circulating flow), the slope and the physical properties of the riverbed, and the shear stress required by the substrate to start moving. Given the physical properties of the riverbed substrates in the study sites, shear stress was considered to be a dimensionless constant with a value of 0.050 (Milhous and Bradley, 1986; Olsen *et al.*, 2014).

With regard to the biological data, rare taxonomic groups (relative abundance less than 0.01% with regard to the total number of individuals; Kennen *et al.* (2010)) were removed. Several community metrics were calculated, such as individual density m^{-2} (density), total taxa richness, Pielou's evenness (evenness), and the Shannon-Wiener diversity index (diversity), using the PRIMER statistical software (Version 6; Ivybridge, UK).

In addition, the EPT (Ephemeroptera, Plecoptera and Trichoptera) relative abundances, EPT taxa richness, and the non-insect taxa richness were calculated. Thus, the samples were grouped according to the type of mesohabitat, defined on the basis of the Froude number (F_r), which is a function of the discharge and the hydraulic conditions of each sampling cross-section (Jowett, 1993). Hence, according to Jowett (1993) the different mesohabitats are pool ($F_r < 0.18$), run ($0.18 \leq F_r \leq 0.41$) or riffle ($F_r > 0.41$). Furthermore, the 10 most abundant taxa, representative of each mesohabitat, were chosen, and their relative abundances were calculated (Suren and Jowett, 2006) for further analysis.

Statistical analysis

To answer the first question of the study, concerning which hydrological indices related to LPF, SPF and LF events are determinant to explain the changes in the community's structure and composition at high-Andean streams, a multiple regression analysis in successive steps (Monk *et al.*, 2006; Suren and Jowett, 2006) was performed between the hydrological indices and the response variables (community metrics and relative abundances of taxa). For every predictor included in the regression analysis, the beta (standardised regression) coefficient (β), measuring how strongly each predictor influences the dependent variable, was calculated. The β have a t-value and significance of the t-value (the p-value) associated with this. If the t-value is significant, then the β is significantly different from zero and, as such, significantly predicts the dependable variable. Hereafter, in this study, the stronger predictors were always considered for the description of the results and the respective discussion; the absolute values of their associated β were always at least 0.25 (i.e., subjectively, this absolute value was adopted herein as a minimum β threshold). Prior to the multiple regression analysis, redundant hydrological indices from each mesohabitat type were discarded (considering the correlation analysis parameters Spearman rho > 0.7, $p \leq 0.05$) using the SPSS software (version 20; IMB/SPSS, Inc., Armonk, New York). A total of 20, 18, and 17 indices were included in the statistical analysis for the pool, run, and riffle mesohabitats, respectively.

Regarding the second research question, concerning what changes can be observed in the community as the result of peak (LPF and SPF) and LF events, the differences in community metrics and the relative abundance of the 10 most dominant taxa, before and after events, were analysed for each mesohabitat. In addition, in the case of LF events, changes occurring in the community metrics and relative abundances of taxa were analysed throughout the entire LF periods. Specifically, the biological variables were compared, in terms of time, between the first sampling campaign occurring in the LF period and the posterior campaigns that are included in the same LF period. These differences were statistically analysed by means of the PERMANOVA test based on the Bray-Curtis similarity analysis (Anderson, 2001; Suren and Jowett, 2006) using

the PAST software (version 3.08; Øyvind Hammer, Natural History Museum, University of Oslo).

RESULTS

A total of 361 biological samples were analysed between December of 2011 and October of 2013. The number of aquatic macroinvertebrate specimens identified was 106,996, belonging to 38 different taxonomic groups (with an average density of 5,604 ind. m^{-2}) as detailed in Annex B. The Orthocladiinae subfamily was the most dominant taxon, accounting for 31.3% of all individuals, followed by the *Girardia* genus with 24.0%, the Chironominae subfamily with 7.2%, and *Hyalella* with 7.1%. The other taxa did not exceed individually the 5.0% of all individuals. The most frequent taxa (present in over 80% of the samples) were Orthocladiinae, *Hyalella*, *Girardia*, Hydrachnidia, and *Austrolimnius*.

The recorded discharges at the four study sites exhibit significant correlations among them. In what follows Q_{Si} stands for the discharge observed in the i-th stream, with i = 1, 2, 3 and 4 (Fig. 1). Regarding the correlation between Q_{aver} and each of the monitored time series, the range of values of the Pearson correlation coefficient varied between 0.95 for Q_{S4} to 0.97 for Q_{S1}. Additionally, the current study suggested an acceptable similarity (i.e., low value of $CV_{aver} = 0.39$) of the magnitude and temporal variability of the daily discharge series. The analysis of the duration curves of the daily flows confirmed the latter. Given the similar hydrological behaviour were the collected samples grouped in the statistical analysis.

The EVA showed that the time series of daily peaks optimally fitted an exponential distribution (a particular case of a GPD) for peak values greater than or equal to $Q_{Hydrol} = 52.6$ mm. This hydrological threshold is lower than both $Q_2 = 130$ mm and $Q_5 = 70$ mm, implying that the LPF and SPF events defined in this study, based on Q_2 and Q_5, follow the extreme value exponential distribution and, as such, are part of the population of independent extreme flows in the studied streams; that is, are hydrologically independent. Further, the average (Q_{subst}) of the threshold values generated for each stream by the method that is based on the equation of substrate movement (Milhous, 1998) was 119.8 ± 6.6 mm. It is lower than Q_2, suggesting that the events defined herein as LPF had a significant effect on the community metrics and taxa due to the implicit mobilisation of the benthic substrate.

Key hydrological indices

A total of 15 hydrological indices were identified by the multiple regression analyses as being influential on the following aspects: (i) community metrics; and (ii) the relative abundance of the 10 most abundant taxa. Of both aspects, eight variables were influential in the pool mesohabitats, four in the run mesohabitats and six in the riffle mesohabitats (Table 2). Some of the hydrological indices were important in more than one of the mesohabitats.

In the pool mesohabitats, the multiple regression analyses on the LPF variables revealed that with absolute values higher than 0.33 of the β (i.e., standardised slope of the regression) negative correlations were obtained between MAXDAYQ(7) and density, and FH(1) and total taxa richness and ETP taxa richness (Table 2 and Annex C). On the other hand, also with a β absolute value of 0.33, the LF index FL(3) was negatively correlated with EPT taxa richness. In taxonomic terms, two dominant non-insect taxa were recorded (Annex D), namely, the *Helobdella* genus (42.6%) and the Lymnaeidae family (15.9%). With β absolute values higher than 0.25, the LPF indices FH(4) and MAXDAYQ(60) were negatively correlated with Lymnaeidae dominant taxa. With similar β absolute values the LF index QMIN(1) was positively correlated with Hydrachnidia and *Heterelmis* (Annex D).

In the run mesohabitats, the multiple regression analyses on the LPF variables indicated that, with β absolute values above 0.40, negative correlations were recorded between MAXDAYQ(7) and density, FH(2) and total taxa richness, and FH(3) and non-insect richness and diversity. With β absolute values higher than 0.30, some LF variables exhibited a positive correlation, namely, QMIN(1) and FL(1) with the density, and COMINDAY with evenness and diversity (Table 2 and Annex C). In taxonomic terms, *Girardia* was the main dominant taxa, representing 27.8% of the community, followed by the Chironominae with 6.1% (Annex D). With β absolute values over 0.4, the LPF variable FH(3) was negatively correlated with the relative density of Chironominae (Annex D).

The multiple regression analyses on the LPF variables in the riffle mesohabitats showed that with β absolute values higher than 0.30, negative correlations were obtained between FH(2) and the total taxa richness, FH(4) and non-insect richness, and COMAXDAY and diversity. Furthermore, the LF variable QMIN(1) showed a negative correlation with density (Table 2 and Annex C). In taxonomic terms, *Hyalella* is the most dominant taxon representing 10.1% of the community, followed by *Metrichia* (Tricoptera), with 9.8% (Annex D). With β absolute values exceeding 0.25, the LPF variable FL(1) was negatively correlated with the relative abundance of *Metrichia* (Annex D).

With regard to the analysis of antecedent peak flow conditions, some hydrological indices such as MAXDAYQ(7), COMAXDAY, FH(1) and FH(2), indicated the time-accumulated effects of past high flow events (i.e. antecedent conditions) on the community structure at a given sampling date (Table 2). In this context, the density, the EPT and the non-insect relative abundances and the different metrics of richness (total, non-insect and EPT) and the diversity exhibited changes owing to peaks occurring between 7 and 120 days prior to sampling dates. Specifically, in the pool mesohabitats the most important hydrological indices (MAXDAYQ(7) and FH(1)) showed an effect of past peak flows on the community between 7 and 30 days. In the run mesohabitats the effects of past peaks occurring longer ago from the sampling dates (up to 90

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days) were noticed through the indices MAXDAYQ(7), FH(1) FH(2) and FH(3). In the riffle mesohabitats the effects of past peaks happening even longer ago (up to 120 days) from the sampling dates were reflected by the indices COMAXDAY, FH(2) and FH(4).

Effect of peak and low flow events

Figure 3 shows the temporal variation of the community metrics as a function of the flow in the pool, run, and riffle mesohabitats throughout the study period. The general trend in density (Fig. 3a) was positive in the LF periods increasing up to approximately 30,000 ind. m^{-2} in the run mesohabitats; for the other mesohabitat types (pool and riffle) the density values were always less than 13,000 ind. m^{-2}. In terms of the total taxa richness (Fig. 3b), the results showed higher values in the three types of mesohabitats during LF events. However, this trend was not observed for the EPT taxa richness (Fig. 3c), as this metric fluctuated significantly throughout the period of analysis. Furthermore, it was observed that the EPT relative abundance (Fig. 3d) increased with flooding and decreased with LFs in the run and riffle mesohabitats; these differentiated trends were not that obvious in the pool mesohabitats.

To evaluate the effects of the different hydrological events on the community metrics and relative abundance of the 10 most abundant taxa, the sampling campaigns are numbered in Fig. 2 following a chronological order. With respect to the assessment of the effects of LPFs on the communities, the LF campaigns that are immediately posterior to these peak events are compared to the respective ones that are preceding them. Hereafter, the LF campaigns that are posterior to LPFs (i.e., for LPF 5, campaigns 3 and 4; for LPF 6, campaign 12; and for LPF 7, campaign 15) were compared to the preceding LF campaigns (i.e., for LPF 5, campaigns 1 and 2; for LPF 6, campaign 11; and for LPF 7, campaign 13, although this latter campaign, similarly to campaign 12, is not strictly a LF campaign, given that the duration of the respective LF event was shorter than 7 days). On the other hand, campaigns 10 and 11 preceding and proceeding a SPF (Fig. 2) were compared for evaluating whether the SPF in between had any effect on the communities. In the same context, campaigns 13 and 14 were as well compared. Although no other SPF were recorded in the studied period, some events, smaller in terms of magnitude than SPFs were also studied. Concretely, three events were analysed, respectively, by the following preceding and proceeding campaigns: 1 and 2, 5 and 6, and 9 and 10 (Fig. 2). The applied PERMANOVA analysis suggested no significant differences in community metrics among the respective campaigns (i.e., 1 and 2, 5 and 6, and 9 and 10) and, as such no significant effects of the inspected small events.

The LPF value of 160.4 mm (LPF 5) on community metrics led to a significant decrease in the density in the three studied mesohabitats (Table 3). However, the LPF of 131.7 mm (LPF 6) only had a negative effect on the density in the riffle mesohabitats. Positive effects of LPFs on

evenness were observed in the pool mesohabitats after LPF 5 and in the riffle mesohabitats after LPF 6. In addition, LPF 5 exerted a negative influence on the total taxa richness in the pool and run mesohabitats. A positive effect occurred in terms of the EPT relative abundance in the pool (after LPF 7), run (after LPF 5 and LPF 6) and riffle (after LPF 5) mesohabitats. In the pool and riffle mesohabitats produced LPF 7 an increase in the relative abundance of Hydrachnidia, while in the run mesohabitats LPF 5 produced an increase in the relative abundance of *Metrichia* (7.5%) and a decrease in the relative abundance of *Girardia* genus (-16.1%) and Chironominae subfamily (-9.2%). The relative abundance of Oligochaeta exhibited two different responses, i.e., firstly, an increase (7.9%) with a discharge of 131.7 mm day^{-1} and a decrease (-2.9%) with a higher discharge of 160.4 mm day^{-1}. In the riffle mesohabitats, after LPF 5, a sharp decline was observed in the proportion of the relative abundance of *Girardia* (-21.1%). Further, positive effects of LPF 7 on *Contulma* (6.4%) were observed.

The events of maximum duration of LF (Fig. 2) started in campaigns 6 (LF 5) and 16 (LF 9). To observe changes in the community during LF events, the samples from campaigns 6 and 16 were compared respectively with the samples from the posterior campaigns (i.e., for LF 5, campaigns 7, 8 and 9; and for LF 9, campaigns 17, 18 and 19). In the pool mesohabitats, a major density increase was observed in the first 90 days with LFs (Table 4); the opposite effect was observed for evenness and diversity. When the period was longer, i.e. 115 days, a further increase in the density was noticed. The total taxa richness was reduced (-3.5 taxa) in the first 10 days with LFs; however, the opposite trend was observed (11.8 taxa) after 30 days with LFs. After 30 days with LFs the relative abundance of EPT was reduced with 12.7%. With LFs, the EPT taxa richness exhibited a negative tendency after 10 days, which was maintained after 115 days. Regarding the taxa, the relative abundance of *Psychoda* genus decreased (-4.7%) over the first 30 days with LFs; however, this trend reversed after a longer LF event (115 days). In addition, a 5.2% decrease was observed in the relative abundance of Hydrachnidia over a period of 30 days. In the run mesohabitats, a negative effect was observed on the density after 75 and 115 days, and in the total taxa richness after 115 days. Furthermore, a significant increase in the relative abundance of the Orthocladiinae subfamily (8.6%) was observed over a LF period of 115 days. No significant trends were noticed in the riffle mesohabitats.

DISCUSSION

Use of hydrological indices

The use of hydrological indices to assess the effects of extreme flow conditions on the dynamics of aquatic communities increased in the last decade (Wood *et al.*, 2000; Belmar *et al.*, 2012; Greenwood and Booker, 2015). According to Greenwood and Booker (2015) affect flow conditions directly the diversity, abundance and composition of aquatic communities. In this context, this study aimed at examining the effect of river flow on aquatic communities in the high

Andean region above 3,500 m a.s.l., more in particular the influence of antecedent peak events. The multiple regression analysis showed that the impact of high discharge events (LPFs) on the density of macroinvertebrates in the pool and run mesohabitats is significant negative because of an increase in drag (Fig. 4). The rise in shear forces influence certain benthic taxa (Ríos-Touma et al., 2011; Rocha et al., 2012), mainly of the non-insect class (e.g. Lymneidae, *Girardia*) (Rios-Touma *et al.*, 2012), which do not have body features to cope with the increase in shear stress associated with high flow conditions (Tomanová and Usseglio-Polatera, 2007). For instance, Lymneidae lacks legs, supporting structures, to cope with flooding (Lam and Calow, 1988; Rios-Touma *et al.*, 2012).

In the run and riffle mesohabitats leads an increase in drag during flooding to a decrease in the diversity and total taxa richness. Sueyoshi *et al.* (2014) suggested that some of the taxa leaving other mesohabitats end up in pools, characterised by lower hydraulic stresses, given that connectivity between mesohabitats is warranted (Pringle, 2001). In this study area, situated at an altitude above 3,500 m a.s.l. and significant slopes, the multiple regression analysis does not indicate an increment in diversity in the pool mesohabitats; further, the total and the EPT richness, indirect measures of diversity, exhibit a decrement. This, notwithstanding, as depicted in Fig. 4, pool mesohabitats are the ones with the gentlest conditions, even during peak events. However, it has to be noticed that the pools in our study are smaller, steeper and less isolated than the ones studied for instance by Sueyoshi *et al.* (2014); as such, they can be affected more by high flow events.

The above discussion does not account for the time variability and is based solely on the analysis of the density and diversity metrics. When the rest of the metrics and the time variability are included in the analysis, then the current study suggests that, with regard to a sampling date, antecedent peak events have a very decisive influence on the aquatic community composition at that particular date. Further, the study points out which type of mesohabitats is least affected (pool) in time by the antecedent peak flow conditions and which one the most affected (riffle) (Table 2). As shown in Fig. 4 are the pool mesohabitats the gentlest environment for the aquatic communities under peak events; nevertheless they are not really a refuge for the dragged taxa. With respect to the change of taxa in the pool mesohabitats associated to peak events before the sampling date, an important increase of relative abundance of *Helobdella* and *Hyalella* (Annex D) was observed, notwithstanding their individual contribution as predictors in the multiple regression is relatively low. Both, *Helobdella* (Stubbington and Wood, 2013) and *Hyalella* (McElravy and Resh, 1991) have the capacity of hiding in the substrate, which makes them less sensitive to higher drag forces.

In the run mesohabitats was the genus *Girardia*, the second dominant group, negatively affected by peak events occurring 30 days before the sampling date. Tomanová and Usseglio-Polatera (2007) reports that the orden Planaria, to which the genus *Giardia* belongs, possesses

low ability to adhere to the bottom materials of the streams despite their flattened shape, explaining why the genus *Girardia* does not resist to significant discharges. At the other hand, *Metrichia*, owing to its body conditions (characteristics of the case), has the potential of adhering to the surrounding substrate (Barbero *et al.*, 2013), which enables this genus to resist the drag forces associated to peak events. In both, the run and riffle mesohabitats, the Chironominae shows a decrease of relative abundance with peak events occurring between 90 (run) and 120 (riffle) days before the sampling date (Annex D). Similar to *Girardia*, this taxon lacks the capacity to adapt to significant discharges. An important invertebrate in the riffle mesohabitats is the genus *Metrichia*, which is negatively correlated to the low discharge indices. Most likely the decrease in drag, associated with low flow, makes that other organisms different from this taxon (i.e., *Hyalella* and Chironominae) gradually enter and re-colonise these mesohabitats (Townsend and Hildrew, 1976), decreasing the relative abundance of *Metrichia*.

Effect of hydrological events on aquatic communities

In aquatic ecology the drag forces associated to LPFs are known as being catastrophic (Melo and Froehlich, 2004; Snyder and Johnson, 2006), producing serious repercussions on benthic biodiversity (Belmar *et al.*, 2012; Mesa, 2012) and even altering the hydromorphological conditions of a river (Belmar *et al.*, 2012; Mesa, 2012; Worrall *et al.*, 2014). In this study, the Q_2 (130 mm) discharge threshold that defines the LPF events is higher than the $Q_{subst} = 119.8$ mm (mean velocity $= 0.99$ m s^{-1}) for substrate movement, and likely affects certain aquatic communities owing to substrate movement as observed in other studies carried out at different latitudes (Cobb et al., 1992).

Lake (2000) describes two types of peak perturbations, i.e., (i) extreme events of high magnitude and of very short duration, known as pulses, that drastically reduces the density and species richness in the community; and (ii) continuous variation of the discharge and the presence of high peaks over time, known as ramps, that reduce the re-colonisation capacity of all taxa. In this study LPFs can be either type, namely LPF 6 in Fig. 2 can be considered as a pulse, whilst LPF 5 and LPF 7 may be regarded as being ramp events. Density decreased more than 60% and EPT relative abundance increased more than 15% in the three types of mesohabitats affected by either pulse or ramp type of peak event. Similar effects, although with different proportions of density decreased and EPT relative abundance increased from what is here reported, have been observed in several studies (Suren and Jowett, 2006; Worrall *et al.*, 2014). Moreover, LPF effects were evident through the decrease in total taxa richness and density in the mesohabitats pool and run, which resulted in the increase of evenness in the pool mesohabitats.

The comparison of the metrics calculated before and after peak events confirmed what was concluded analysing the relationship between hydrological indices and community metrics, in the sense that less adapted aquatic taxa are more easily affected by peak events and their associated

drag forces (Poff *et al.*, 1997; Lamouroux *et al.*, 2004; Bonada *et al.*, 2007; Blanckaert *et al.*, 2012). For instance, in the mesohabitats run and riffle a decrease in the proportions of *Girardia* and Chironominae after peak flows was observed, which indicates that the forms and structures of both pose little resistance to significant discharges, mainly due to their low ability to adhere to the bottom and bank material of streams (Tomanová, 2007). Hence, the negative effect on the abundances of *Girardia* and Chironominae possibly caused a significant increase in the proportion of individuals of the genus *Metrichia* in the run mesohabitats, favoured by their relatively small size and their preference to be attached to sites with thick substrates (Brooks *et al.*, 2005; Barbero *et al.*, 2013). Thus, in the run mesohabitat, it is likely that the organisms less adapted to the increase of discharge produced a faster re-colonisation of *Metrichia*, in comparison to organisms that arrived by the drift and which re-colonised with a slower rate (Townsend and Hildrew, 1976). In this regard, in stable environments, the genus *Metrichia* is less abundant and competitively inferior to other organisms with biological characteristics adapted more to low discharge conditions (Gibbins *et al.*, 2001).

Further, LPF 6 had positive effects on Oligochaeta ratios, whilst LPF 5 had negative ones, confirming that these are two different types of peak events. LPF 5 previously had several continuous disturbances of high discharges which led to a loss of the interstitial zone of the reach (Bruno *et al.*, 2010), and in turn to the sustained decline of the relative abundance of Oligochaeta. In contrast, LPF 6 was isolated in time, as well as the associated entrainment, allowing those organisms to settle down in the interstitial zone (Bruno *et al.*, 2010), to remain and increase their ratios in relation to other groups. On the other hand, the effects of discharges of the evaluated LF events were lower than in other latitudes (Leigh, 2013) where magnitude and duration may cause large changes in aquatic communities (Rolls *et al.*, 2012), since head or small streams are reduced to small intermittent pools, the only refuge for the aquatic biota at summer time (Dekar and Magoulick, 2007). This fact contrasts with the high Andean head streams, which maintain a permanent flow in the periods of low discharge due to the capacity of flow regulation of the surrounding soils, through absorption and retention (Crespo *et al.*, 2012).

The observed response in the pool mesohabitats after a long period with low discharges was an increase in both, the density and the total taxa richness. For density, a similar increase was reported by Bogan and Lytle (2011) at pool mesohabitats in a temperate river, while, on the contrary, for the total taxa richness a decrease was observed by García-Roger *et al.* (2011) at pool mesohabitats also in a temperate river. In addition, a decrease of the proportions of EPT relative abundance and taxa richness was observed in pools which may be due to the sensitivity of the EPT to the decrease in discharge, as observed by Dewson *et al.* (2007), although, in riffle mesohabitats of several New Zealand rivers. Another factor that might influence the decrease in the proportion of EPT is the increase and dominance of certain taxonomic groups, generally belonging to the order Diptera (*Psychoda*), owing to their tolerance to low discharge conditions

and to their short life cycles (Ledger *et al.*, 2011); a tendency not observed in the current study (Table 4). On the contrary, in the run mesohabitats, LF conditions decreased the density and total taxa richness. There was a significant loss of individuals with prolonged LF periods (greater than 75 days), almost to what was reported by McIntosh *et al.* (2002) who, for riffle mesohabitats in the Iao river (Hawai), observed a decline of the community (density and total taxa richness) for LF periods longer than 100 days. In the present study, reduction of water depth and discharge may have influenced the area of the available habitats in LF periods (Rolls *et al.*, 2012). Further, no response was observed on community metrics or taxonomic groups for low discharges in the riffle mesohabitats, suggesting that this type of events, characterised by low velocities, is of little importance to the aquatic communities in this type of mesohabitats. As already stated, the latter differs from the results found by McIntosh *et al.* (2002).

CONCLUSIONS

The presented research is unique in assessing the influence of hydrological events of different magnitude on aquatic communities in three different mesohabitats (i.e., pool, run and riffle) located above 3,500 m a.s.l. The observed peak events can be classified as pulses and ramps and were defined on the basis of the Q_2 percentile, which is a much stronger discharge threshold than the ones commonly used to define peak events elsewhere. The latter suggests that the aquatic communities in high Andean streams have more resilience to peak flow variations and conditions than similar communities that live in streams at different latitudes and elevations. Further, either pulses or ramps dragged away organisms, particularly, from the run and riffle mesohabitats. The majority of these organisms did not refuge in pool habitats, as it has been reported in temperate and flat zones, except for few taxa. It is likely to be the result of the fact that the pools in our study are smaller (i.e., horizontally and vertically), steeper and less isolated than the ones studied elsewhere; as such, they can be affected more by peak events.

Different analyses coincided in the general idea that the dominant taxa with the least adapted body characteristics are the most sensible to peak events. In this context, some taxa belonging to the EPT groups, that pose suitable traits, were the ones less affected by peak conditions. When all metrics and time variability of peak events occurring prior to the sampling date were considered, then the current study suggests that, with regard to a sampling date, antecedent peak events are an important factor in evaluating the aquatic community composition at that particular date. Further, the study points out which type of mesohabitats is least affected (pool) in time by antecedent peak flow conditions and which one is most affected (riffle). The latter implies that in the current study site the pool mesohabitats were the gentlest environment for the aquatic communities under peak events, although they did not act as a permanent refuge for the dragged taxa.

The study showed that peak flow events had stronger effects on the communities than low flows. Low flow events had less effects on the communities than the ones observed in temperate regions where streams tend to be intermittent under long low flow periods, which is not the case in high Andean streams because surrounding soil continuously provide water to the streams preventing stream intermittence. Further, in low flow events pools are important since different taxa can find suitable habitat whilst run mesohabitats are strongly impacted by the reduction of their area.

The current study may be considered as a first step towards future environmental flow assessments, a relevant task still to be done in South Andean regions under scientific considerations.

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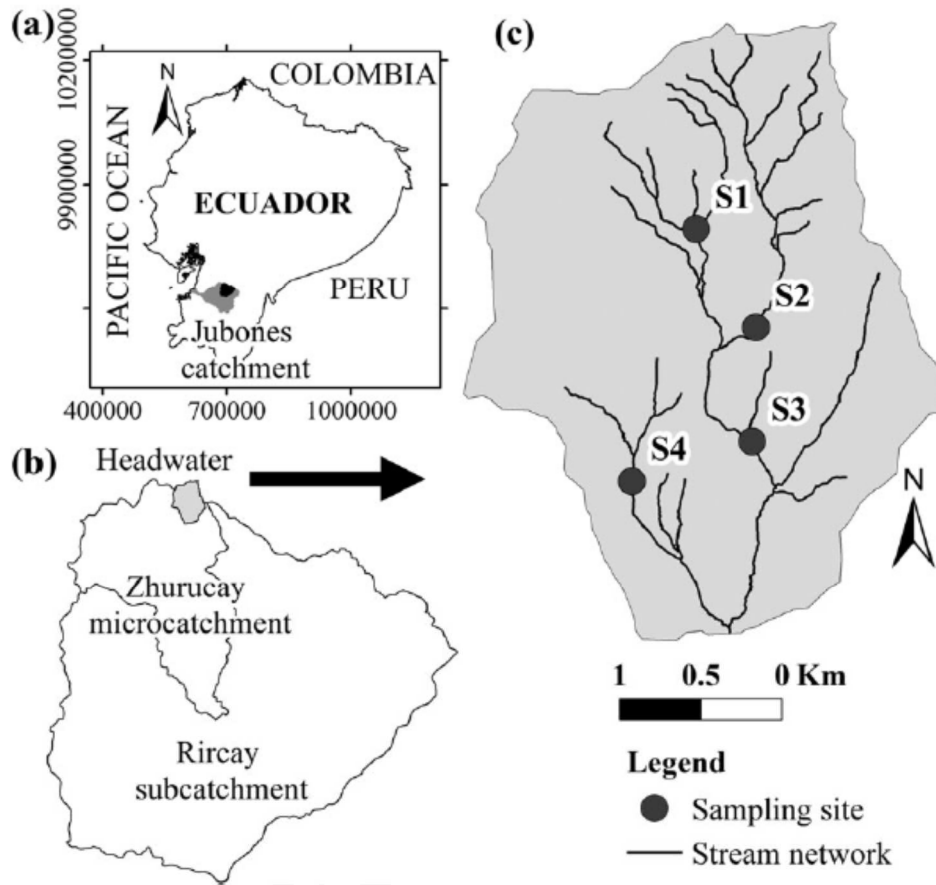
Figure 1. Location of (a) the Jubones river catchment in Ecuador and the Rircay river subcatchment; (b) the study site (Zhurucay microcatchment headwater), located inside the Rircay river subcatchment; and (c) the four sampling points in the study site.
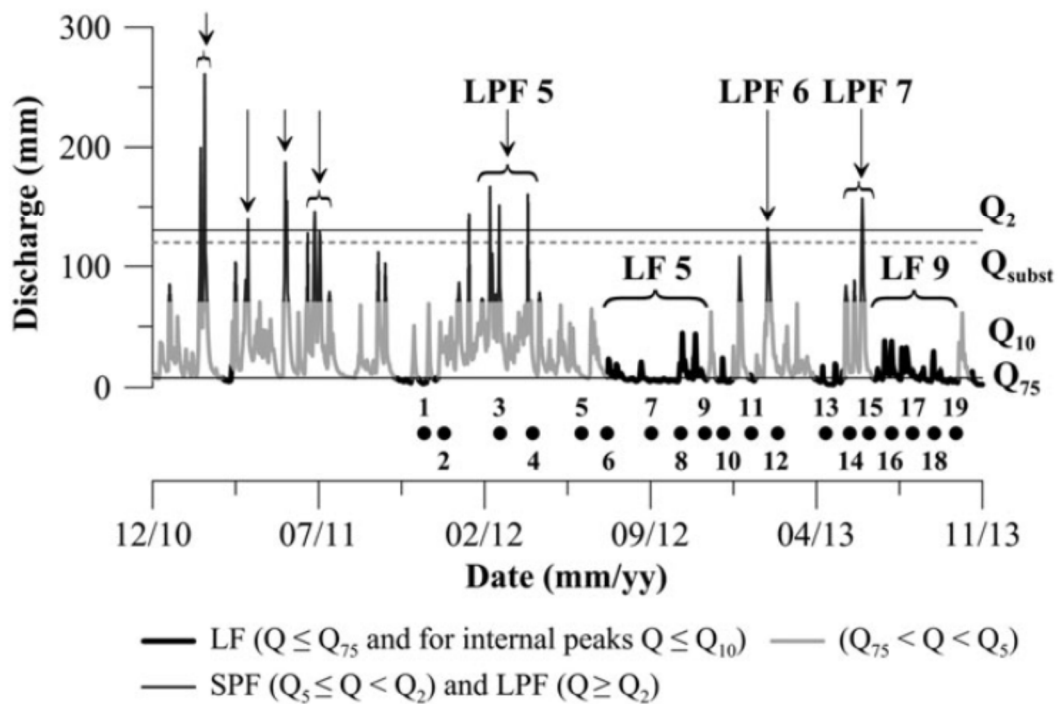
Figure 2. Average daily discharge (Q_{aver}) hydrograph and time evolution of the sampling campaigns (identified by means of dots); Large Peak flow (LPF) events ($Q \geq Q_2$; identified through vertical arrows); and Low flow (LF) events ($Q \leq Q_{75}$ and for internal pulses $Q \leq Q_{10}$; identified through a solid black line in the hydrograph). Q_{subst} (119.8 mm) is the flow threshold for movement of substrate. Q is the discharge. Discharge thresholds refer to exceedance percentiles.
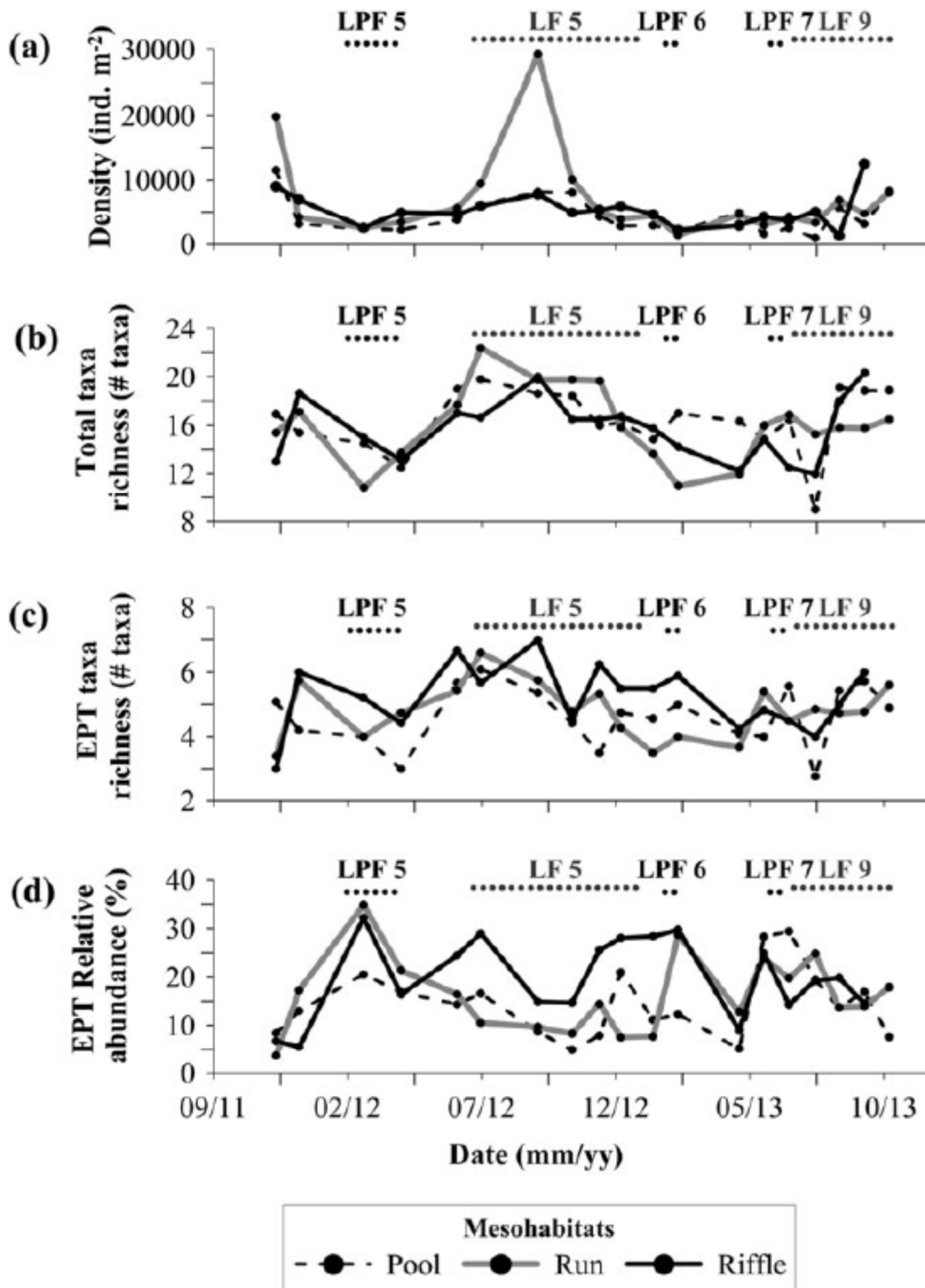
Figure 3. Temporal variation of the average community metrics as a function of the mesohabitat type, namely, (a) density (ind. m^{-2}); (b) total taxa richness (# total); (c) EPT taxa richness (# total); and (d) EPT relative abundance (%).
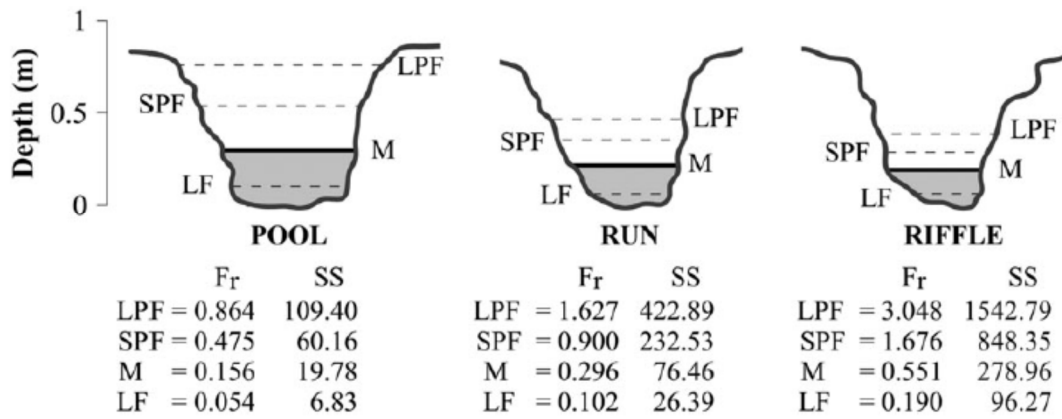
Figure 4. Typical cross-sections observed in pool, run, and riffle mesohabitats, showing levels of water surface under different discharge conditions, namely, Large Peak flow (LPF), Small Peak flow (SPF), Low flow (LF) and median (M, observed in the period from 2011 to 2013). Froude number (F_r), and shear stress (SS; N m^{-2}) values are given for these discharge conditions as a function of the type of mesohabitat.

Table 1. Description of the hydrological indices calculated from the mean daily discharges (Q_{aver}). N_i is the total number of values that a given hydrological index may adopt as a function of the number of days (n) used in its calculation.

| Index	N_i	Description
Qsample	1	Mean daily discharge recorded on the sampling date.
MAXDAYQ(n)	4	Maximum discharge observed in periods of n = 7, 15, 30 and 90 days before the sampling date.
COMAXDAY	1	Coefficient of variation of the four values of MAXDAYQ(n).
FHA	1	Number Large Peak flow pulses observed throughout a one-year period before each sampling campaign.
QMAX(k)	3	k-th Large Peak flow pulse occurring immediately before the sampling date, where k = 1, 2, and 3 reflect occurrence in chronological order.
COQMAX	1	Coefficient of variation of the three QMAX values.
FH(m)	5	Number of Large Peak flow and Small Peak flow pulses occurring in the five periods defined by m = 1, 2, 3, 4, and 5 months before the sampling date.
MINDAYQ(n)	4	Minimum discharge observed in periods of n = 7, 15, 30 and 90 days before the sampling date.
COMINDAY	1	Coefficient of variation of the four values of MINDAYQ(n).
QMIN	1	Low flow pulse occurring immediately before the sampling date.
FL(m)	5	Number of Low flow pulses occurring in the five periods defined by m = 1, 2, 3, 4, and 5 months before the sampling date.

Table 2. Beta coefficients (β) of the multiple regression analysis using the hydrological indices as independent variables and community metrics and relative abundance of the 10 most abundant taxa as dependent variables, as a function of the mesohabitats. The sample sizes were: N = 141 in the pool mesohabitats ([Po]); N = 144 in the run mesohabitats ([Ru]); and N = 76 in the riffle mesohabitats ([Ri]). The metrics and taxa that are listed have an associated significance probability $p \leq 0.05$. For the description of the hydrological indices refer to Table 1.

	MAXDAYQ(7)	MAXDAYQ(15)	MAXDAYQ(60)	COMAXDAY	FH(1)	FH(2)	FH(3)	FH(4)	FHA	QMAX(1)	MINDAYQ(30)	COMINDAY	FL(1)	FL(3)	QMIN(1)
METRICS															
Density	-0.405[Po]				-0.211[Ru]								0.306[Ru]		0.454[Ru]
	-0.496[Ru]														-0.377[Ri]
EPT Rel. Abund.				-0.172[Po]								0.178[Po]	-0.287[Ri]		
Non-insect Rel. Abund.					-0.231[Ru]	-0.441[Ru]					-0.231[Ri]				
Total taxa richness					-0.396[Po]	-0.364[Ri]				0.298[Ri]	0.259[Ru]			-0.177[Po]	
EPT taxa richness					-0.420[Po]						0.181[Po]			-0.332[Po]	
Non-insect richness				-0.290[Ri]	-0.240[Po]		-0.589[Ru]	-0.301[Ri]			0.190[Ru]		-0.191[Ru]		
Evenness		0.323[Po]										0.342[Ru]			
Diversity				-0.377[Ri]			-0.441[Ru]				0.333[Ru]	0.561[Ru]			
TAXA															
Chironominae				-0.217[Ru]			-0.453[Ru]	-0.298[Ri]							
Girardia					-0.290[Ru]						-0.180[Ru]				
Helobdella				0.226[Po]											
Hyalella	0.200[Po]					-0.232[Ri]									
Lymnaeidae		-0.255[Po]							-0.250[Po]						
*Metrichia**					0.257[Ru]				0.212[Po]				-0.264[Ri]		

* Taxonomic groups belonging to the EPT orders.

Table 3. Effects of Large Peak (LPFs) and Small Peak flows (SPFs) on community metrics and relative abundance of taxa as a function of the type of mesohabitats according to the statistical test PERMANOVA. The values of the average ($\bar{x}$), standard deviation (SD), and F statistic (F) of the metrics and taxa are listed with the associated significance probability $p \leq 0.05$. Froude number (F_r) and shear stress (SS, N m^{-2}) estimates for each mesohabitat type and peak flow event are also included.

Mesohabitat Type	Event characteristics	Community metric/taxa	$\bar{x}$	SD	F	P
POOL	LPF 5 (160.4 mm)	Density	-3,972	1609	5.49	0.040
	Fr = 1.07; SS = 135.0	Evenness	0.13	0.02	12.07	0.020
		Total taxa richness	-5.3	3.45	5.24	0.050
	LPF 7 (157.2 mm)	EPT Rel. Abund.	20.2	11.85	7.68	0.026
	Fr = 1.04; SS = 132.3	Hydrachnidia	4.2	2.74	7.86	0.022
	SPF (108.0 mm) Fr = 0.72; SS = 90.9	Oligochaeta	-1.2	0.42	8.02	0.030
RUN	LPF 5 (160.4 mm)	Density	-6,602	3,260	7.93	0.000
	Fr = 2.02; SS = 521.7	Total taxa richness	-5.6	2.04	11.84	0.000
		EPT Rel. Abund.	20.5	4.79	4.77	0.020
		Metrichia*	7.5	3.9	3.82	0.030
		Girardia	-16.1	5.91	6.53	0.010
		Chironominae	-9.2	3.71	16.69	0.000
		Oligochaeta	-2.9	1.85	4.21	0.020
	LPF 6 (131.7 mm)	EPT Rel. Abund.	15.1	3.34	8.03	0.020
	Fr = 1.66; SS = 428.4	Oligochaeta	7.9	4.73	2.74	0.050
	SPF (108.0 mm)	Evenness	-0.1	0.02	8.83	0.020
	Fr = 1.36; SS = 351.3	Diversity	-0.4	0.13	7.69	0.020
		Helobdella	-0.6	0.2	3.88	0.040
RIFFLE	LPF 5 (160.4 mm)	Density	-5,022	1,866	4.57	0.010
	Fr = 3.76; SS = 1,903.4	EPT Rel. Abund.	26.0	8.06	4.52	0.030
		Girardia	-21.1	11.32	4.33	0.040
	LPF 6 (131.7 mm)	Density	-2,560	583	6.63	0.010
	Fr = 3.09; SS = 1,562.8	Evenness	0.13	0.04	5.77	0.050
		Chironominae	-6.3	4.15	15.73	0.010
	LPF 7 (157. 2 mm)	Hydrachnidia	3.9	3.02	4.92	0.030
	Fr = 3.69; SS = 1,865.4	*Contulma*	6.4	6.81	2.46	0.031

* Taxonomic groups belonging to the EPT orders.

Table 4. Effects of duration (n, in days) of Low flow on community metrics and relative abundance of taxa as a function of the type of mesohabitat according to the statistical test PERMANOVA. The values of the average ($\bar{x}$), standard deviation (SD), and F statistic (F) of the metrics and, in the case of taxa, the differences in relative abundances between two compared campaigns, are listed with an associated significance probability $p \leq 0.05$.

Mesohabitat Type	n	Community metric/taxa	$\bar{x}$	SD	F	p
POOL	90	Density	3,515.4	749.2	5.10	0.030
	115		6,393.3	1,543.3	11.44	0.030
	60	Evenness	-0.1	0.04	6.95	0.020
	90		-0.2	0.06	17.52	0.030
	10	Total taxa richness	-3.5	1.12	6.12	0.020
	30		11.8	3.71	8.18	0.030
	90	Diversity	-0.4	0.09	8.74	0.010
	30	EPT Rel. Abund.	-12.7	2.78	15.96	0.030
	10	EPT taxa richness	-2.7	0.33	7.07	0.020
	115		-1.0	0.71	6.01	0.050
	30	Hydrachnidia	-5.2	5.85	4.50	0.030
	30	*Psychoda*	-4.7	6.74	4.35	0.030
	115		1.6	1.21	2.77	0.040
	75	*Claudioperla**	-1.3	0.51	3.87	0.030
RUN	75	Density	-21,997.8	11,671.41	9.42	0.030
	115		-7,403.3	3,228.87	14.37	0.000
	115	Total taxa richness	-2.8	1.19	7.75	0.030
	115	Orthocladiinae	8.6	6.49	5.27	0.030

* Taxonomic groups belonging to the EPT orders.

ANNEXES

Annex A. Main physical characteristics of the four studied streams (S1, S2, S3 and S4).

Annex B. Presence of taxa as a function of the studied mesohabitats and streams (S1, S2, S3 and S4).

Annex C. Beta coefficients (β) of the multiple regression analysis using the hydrological indices as independent variables and the community metrics as dependent variables, as a function of the mesohabitats. The sample sizes were: N = 141 in the pool mesohabitats; N = 144 in the run mesohabitats; and N = 76 in the riffle mesohabitats. The metrics that are listed have an associated significance probability $p \leq 0.05$.

Annex D. Beta coefficients (β) of the multiple regression analysis using the hydrological indices as independent variables and the relative abundance of the 10 most dominant macroinvertebrate taxa as dependent variables, as a function of the mesohabitats. The sample sizes were: N = 141 in the pool mesohabitats; N = 144 in the run mesohabitats; and N = 76 in the riffle mesohabitats. The taxa that are listed have an associated significance probability $p \leq 0.05$.