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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 located 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, small peak flow, and low flow (LF) events were defined based on discharge thresholds. Multivariate statistics showed that 14 hydrological indices were significantly related to the aquatic community. Further, the study revealed that (a) peak events produced stronger effects on communities than LF events, (b) the observed effects of LF events were weaker than those encountered in other latitudes, and (c) local benthic communities have more resilience than similar communities studied in other latitudes.

KEYWORDS

Andean streams, ecohydrology, ecological responses, hydrological indices, macroinvertebrates, mesohabitat

1 | INTRODUCTION

The influence of hydrological factors on benthic macroinvertebrate communities received increasing attention in the last decade (Belmar et al., 2012; Chang, Tsai, Tsai, & Herricks, 2008; 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 (Kennen, Riva-Murray, & Beaulieu, 2010; Poff et al., 1997; Rolls, Leigh, & Sheldon, 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 colonized 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 & Hildrew, 1993; Suren & 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 (Calapez, Elias, Almeida, & Feio, 2014; Leigh, 2013; Rolls et al., 2012). 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 (Robinson, 2012; Suren & Jowett, 2006). 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 (Mouthon & Daufresne, 2006; Wood & Armitage, 2004).

In tropical zones, the climate is characterized by marked seasonality between wet and dry periods (Flecker & Feifarek, 1994); however, these seasons are less pronounced in the south Andean region of Ecuador due to the strong effect of the Andes range (Buytaert, Celleri, Willems, Bièvre, & Wyseure, 2006; Nouvelot, Le Goulven, Alemán, & Pourrut, 1995). 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, amount of rainfall, and, therefore, the volume and frequency of water reaching the rivers (Bispo, Oliveira, Bini, & Sousa, 2006; Buytaert et al., 2006; Nouvelot et al., 1995).

Studies at medium altitude in the Andean region report a decrease in the density and species richness on the seasonal and annual timescales mainly due to an increase in shear stress (SS) during heavy floods in the rainy season (Jacobsen & Encalada, 1998; Mesa, 2012; Ríos-Touma, Encalada, & Prat Fornells, 2011). In the high Andes, only few of such studies have been carried out so far. For example, Moya, Gibon, Oberdorff, Rosales, and Domínguez (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 Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa richness. In other words, aquatic communities at these altitudes seem to be regulated not only by seasonal features but also by aspects such as (a) the susceptibility of taxa to disturbances, (b) the taxa ability to recolonize habitats, (c) the number of colonizing taxa, and (d) the number of life cycles of the colonizers.

The influence of hydrology on the natural dynamics of macroinvertebrate communities is very relevant for the conservation of the delicate high Andean ecosystems. Notwithstanding Ecuadorian regulations require environmental flow assessments for hydroelectricity projects, which normally are located at high elevations, these are normally carried out within the frame of simple consulting works; consequently, little of the information produced by these studies is linked to the aquatic habitat density and composition, with the exception of a few efforts such as Herrera and Burneo (2017). Generally, in those studies, 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 (LFs) on the aquatic community.

In temperate zones, recent studies have focused on defining discharge thresholds, for both flooding and drought events, that significantly affect aquatic communities in natural (Chang et al., 2008; Monk, Wood, Hannah, & Wilson, 2007; Suren & Jowett, 2006; Wood, Agnew, & Petts, 2000) and altered rivers (Armanini et al., 2014; Freeman, Bowen, Bovee, & Irwin, 2001; Macnaughton et al., 2015). The studies on altered ecosystems focus particularly on the effects on fish (i.e., Freeman et al., 2001; Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Macnaughton et al., 2015) and less on macroinvertebrates (Armanini et al., 2014; Miller, Judson, & Rosenfeld, 2014). However, in the tropical zones, most of the studies concentrate on the temporal variability of the aquatic communities as a function of the season in the year (Jacobsen & Encalada, 1998; Mesa, 2012; Ríos-Touma et al., 2011) without considering flood and drought discharge (i.e., hydrological) thresholds and their impact on aquatic communities. Exceptions hereon are the studies in altered rivers of Castro, Hughes, and Callisto (2013), Miserendino (2009), and Herrera and Burneo (2017) that examined the response of macroinvertebrates and Lima et al. (2018) and García, Jorde, Habit, Caamaño, and Parra (2011) of fish.

In contrast to previous works, 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 (characterized 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, Martínez-Capel, & Hampel, 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, Hoffmann, and Pusch (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 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: (a) which hydrological indices related to LPF, SPF, and LF events are fundamental to explain the changes in the community's structure and composition? and (b) what are the changes one can observe in the community as a result of the referred hydrological events?

2 | MATERIALS AND METHODS

2.1 | Study area

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 (9,662,500 m N, 9,658,750 m S, 694,630 m W, and 698,010 m E; UTM coordinate system, Zone 17S, geoid PSAD56) at approximately 3,600 m a.s.l. (Figure 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 nonintensive farming activities (Hampel, Cocha, & Vimos, 2010; Studholme, Hampel, Finn, & Vázquez, 2017). The topography of the study site is characterized by slopes ranging between 0.14 and 0.24 m m^{-1} (Mosquera, Lazo, Célleri, Wilcox, & Crespo, 2015).

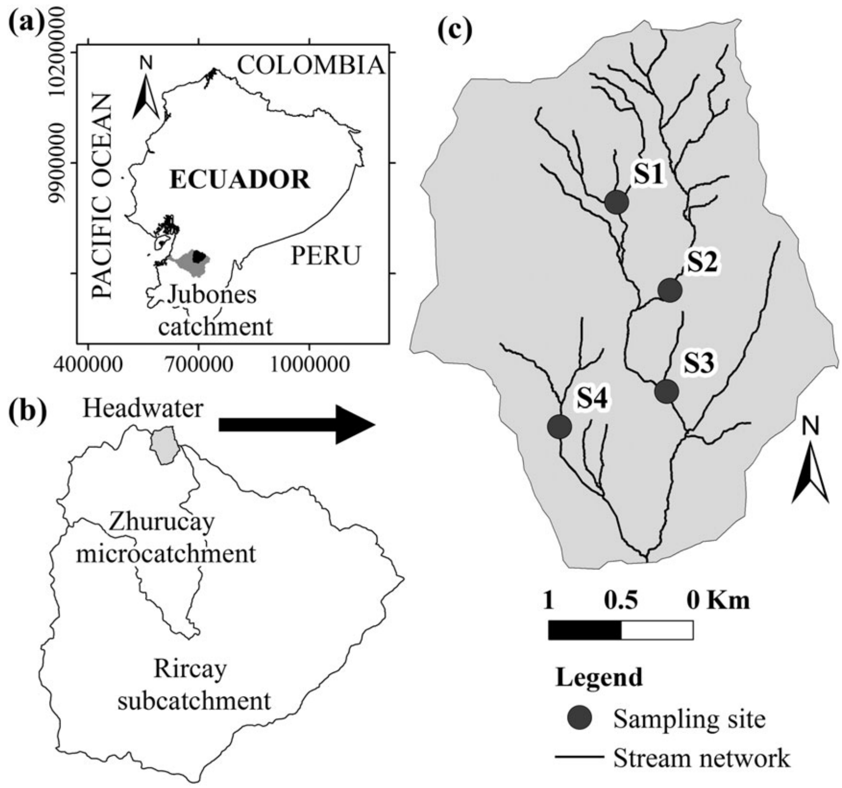

FIGURE 1 Location of (a) the Jubones river catchment in Ecuador and the Rircay river subcatchment; (b) the study site (Zhurucay microcatchment headwater), located inside the Rircay river subcatchment; and (c) the four sampling points in the study site

Climate in the region is characterized 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 monthly average in the period: 66 mm), whereas the rainy season stretches from October to May (maximum monthly average in the period: 113.7 mm). February was the month with the highest interannual fluctuation in precipitation, with a maximum monthly value of 257 mm and a minimum monthly value of 40.2 mm. The average daily air temperature throughout the whole study period was 5.9°C, and the relative humidity ranged between 82% and 91% (Padrón, 2013). The seasonal variation of air temperature is very low (i.e., minimum daily average of 4.8°C in July of 2011; maximum daily average of 6.7°C in November of 2011), whereas within-day 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. These hydraulic variables were recorded when the average discharge fluctuated between 33.9 and 352.1 L s^{-1}. The four studied streams are characterized by a large substrate heterogeneity dominated by angular rocks, consisting of blocks (concentration of about 18%; size bigger than 250 mm), cobbles (concentration higher than 33%; size between 60 and 250 mm), and pebbles (concentration of about 23%; size between 20 and 60 mm) in a matrix of gravel (concentration of about 24%; size between 0.2 and 20 mm), sand (concentration of about 1.5%; size between 0.006 and 0.2 mm), and silt (concentration of about 0.5%; size smaller than 0.006 mm). The average stream channel width is in the order of 1 m; the minimum and maximum recorded widths are, respectively, 0.15 and 1.63 m. The channel gradient varies between 0.01 and 0.43 m m^{-1}, with an average value of 0.095 m m^{-1}, in the sampled branches of the stream network of the study microcatchment. Additional hydrological and hydraulic characteristics of the studied stream reaches are presented in Appendix A.

2.2 | Sampling methods

In each of the four selected streams, 50-m-long reaches were sampled in the period between December 2011 and October 2013. Although bankfull width was not identified in these high mountain rivers, 50 m means 31 times the maximum recorded width; thus, each of the reaches included all types of mesohabitats and was considered representative of the river habitat sequence. Five cross sections were established in each of the reaches. A total of 19 sampling campaigns were carried out. A wide variety of hydrological conditions (wet and dry) was recorded in this period.

2.2.1 | Sampling of abiotic data

In each sampling campaign, hydraulic measurements were taken at the biological sampling points located at the centre of each of the five cross sections. There 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, Oglęcki, Radecki-Pawlik, Skalski, & Zawiejska, 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, Maidment, & Mays, 1988), a process that was validated using the data recorded by the propeller flow meter. These subdaily 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 × 25 cm^2 reference quadrants.

2.2.2 | 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), located near the centre of each cross section, vigorously stirring by hand the substrate. The collected sample was placed in a plastic bottle, preserved in a solution of 4% formaldehyde (Durance & Ormerod, 2010; Rîşnoveanu, Chriac, & Moldoveanu, 2017; Urbanic, 2013), 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 noninsect 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 (Acosta & Prat, 2010; Domínguez, Fernández, & Lillo, 2009).

2.3 | Hydrological and biological data processing

The daily discharge values were transformed into daily values of volume per catchment area (mm) to derive a single comparative scale of the discharges (Q_{S1}, Q_{S2}, Q_{S3}, and Q_{S4}) monitored at the four studied streams (Chow et al., 1988). Then, the arithmetic mean (Q_{aver}) of the transformed daily discharges was calculated from 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 Q_{S1}, Q_{S2}, Q_{S3}, and Q_{S4} by means of three complementary procedures. These procedures, applied at each of the monitored streams, were (a) evaluation of the correlations between the magnitudes of Q_{aver} and Q_{S1}, Q_{S2}, Q_{S3}, and Q_{S4}; (b) calculation on a daily basis of the coefficient of variation (CV) using the discharge of the four streams in a given day of interest. In this way, the average of the entire time series of daily CV (CV_{aver}) constitutes an index of similarity among the time series of Q_{S1}, Q_{S2}, Q_{S3}, and Q_{S4}; and (c) comparison of the evolution and magnitude of the duration curves of the average daily discharges of the four monitored streams (Q_{S1}, Q_{S2}, Q_{S3}, and Q_{S4}).

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 timescale of the daily discharge values. In line herewith, no indices of LF 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 1-year period prior to every sampling date. Thus, for Q_{aver} and considering exceedance percentiles, LPFs were defined as (see Figure 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 SPFs; and values equal or lower than the percentile 75% (Q_{75} = 8 mm) were considered LFs. Two or more consecutive 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 peak flow event (for instance, LPF 5 and LPF 7 in Figure 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 peak event. This consideration was based on the fact that (Flecker & Feifarek, 1994) a period shorter than 20 days is not enough for observing a complete recovery of the aquatic communities.

On the other hand, an LF event was defined if the discharge was lower than or equal to Q_{75} (Yulianti & Burn, 1998) during a period of at least 7 days. The extent of this event lasted until a water pulse greater than Q_{10} (45 mm) occurred. The Q_{10} threshold was defined in this

TABLE 1 Description of the hydrological indices calculated from the mean daily discharges (Q_{aver})

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 of large peak flow pulses observed throughout a 1-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 (in order of magnitude, where 1 is the largest of the three)
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

Note. 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.

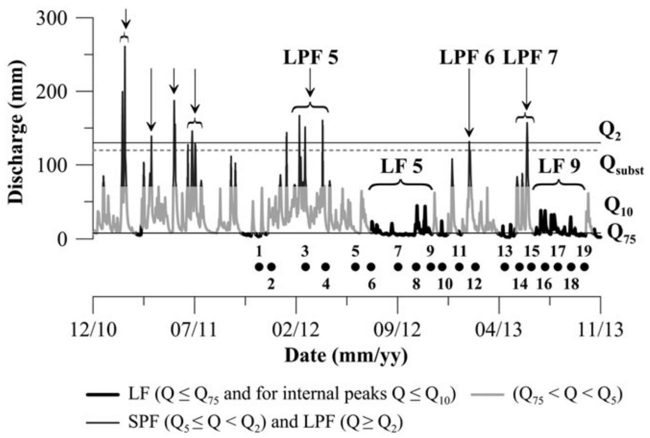

FIGURE 2 Average daily discharge (Q_{aver}) hydrograph and time evolution of the sampling campaigns (identified by means of dots); large peak flow (LPF) events ($Q \geq Q_2$; identified through vertical arrows) and low flow (LF) events ($Q \leq Q_{75}$ and for internal pulses $Q \leq Q_{10}$; identified 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. SPF: small peak flow

study after 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 (Figure 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 aforementioned discharge thresholds, namely, (a) an extreme value (hydrological) analysis (EVA) and (b) 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, 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 generalized (extreme value) Pareto distribution (Pickands, 1975; Vázquez, Beven, & Feyen, 2009). Hence, the peak discharge data fitting was performed using the peak over threshold methodology. To this end, a series of daily extreme values was generated using the partial duration time series methodology (Vázquez & Feyen, 2003; Vázquez, Willems, & Feyen, 2008). This partial duration time series analysis was carried out with the aid of specific task subroutines that were previously (Vázquez & Feyen, 2003; Vázquez et al., 2008) programmed with the FORTRAN and PERL (Practical Extraction and Report Language) programming languages.

Because substrate movement is an important factor influencing the composition and structure of communities (Milhous & 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 (1998); further, these values were averaged into a single one that was finally compared with 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 the shear stress (SS) required by the substrate to start moving. Given the aforementioned physical characteristics of the substrates of the riverbed in the study sites, the dimensionless value of SS that is required in the Milhous equation was kept constant and equal to 0.050 (Milhous & Bradley, 1986; Olsen, Hayes, Booker, & Barter, 2014).

With regard to the biological data, rare taxonomic groups (having a relative abundance lower than 0.01%, with respect to the total number of individuals; Kennen et al., 2010) were removed from the analysis. 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 relative abundances, EPT taxa richness, and the noninsect taxa richness were calculated. Thus, the samples were grouped according to the type of mesohabitat, defined on the basis of Fr 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 & Jowett, 2006) for further analysis.

2.4 | Statistical analysis

To answer the first question of the study, concerning which hydrological indices are determinant for 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 & 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 (standardized regression) coefficient, measuring how strongly each predictor influences the dependent variable, was calculated. The beta coefficients have a t value and significance of the t value (the p value) associated with them. If the t value is significant, then the beta coefficient 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 beta coefficients were always at least 0.25 (i.e., subjectively, this absolute value was adopted herein as a minimum beta coefficient 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; IBM/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 LPF and SPF 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 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 permutational multivariate analysis of variance (PERMANOVA) test based on the Bray–Curtis similarity analysis (Anderson, 2001; Suren & Jowett, 2006) using the PAST software (version 3.08; Øyvind Hammer, Natural History Museum, University of Oslo).

3 | 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 Appendix B. The Orthocladiinae subfamily was the 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 separately 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 (Figure 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} and 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 of the four study streams (microcatchments), all of the collected samples were grouped to proceed with the statistical analysis.

The EVA showed that the time series of daily peaks optimally fitted an exponential distribution (a particular case of a generalized Pareto distribution) 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, 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, implying that the events defined herein as LPF can have a significant effect on the community metrics and taxa due to the associated implicit mobilization of the benthic substrate.

3.1 | Key hydrological indices

Fourteen hydrological indices were identified by the multiple regression analyses as being influential on the following aspects: (a) community metrics and (b) the relative abundance of the 10 most abundant taxa. From these 14 indices, seven were influential in the pool mesohabitats, eight in the run mesohabitats, and seven in the riffle mesohabitats (Appendix C). That is, some of these hydrological indices were important in more than one of the study mesohabitats types.

In the pool mesohabitats, the multiple regression analyses on the LPF variables revealed that with absolute values higher than 0.33 of the beta coefficient (i.e., standardized slope of the regression), negative correlations were obtained between MAXDAYQ(7) and density, and FH(1) and total taxa richness and EPT taxa richness (Appendix C). In addition, also with a beta coefficient absolute value of 0.33, the LF index FL(3) was negatively correlated with EPT taxa richness. In taxonomic terms, two dominant noninsect taxa were recorded (Appendix D), namely, the *Helobdella* genus (42.6%) and the Lymnaeidae family (15.9%). With beta coefficient absolute values higher than 0.25, FH(4) and MAXDAYQ(60) were negatively correlated with Lymnaeidae, one of the dominant taxa. With similar beta coefficient absolute values, the LF index QMIN(1) was positively correlated with Hydrachnidia and *Heterelmis* (Appendix D).

In the run mesohabitats, the multiple regression analyses on the LPF variables indicated that, with beta coefficient absolute values above 0.40, negative correlations were recorded between MAXDAYQ(7) and density, FH(2) and total taxa richness, and FH(3) and noninsect richness and diversity. With beta coefficient 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 (Appendix C). In taxonomic terms, *Girardia* was the main dominant taxa, representing 27.8% of the community, followed by the Chironominae with 6.1% (Appendix D). With beta coefficient absolute values over 0.40, the LPF index FH(3) was negatively correlated with the relative density of Chironominae (Appendix D).

The analyses on the high flow variables in riffle mesohabitats showed some correlations with beta coefficient absolute values higher than 0.30, specifically negative correlations between FH(2) and the total taxa richness, FH(4) and noninsect richness, and COMAXDAY and diversity. Furthermore, concerning LFs, QMIN(1) showed a negative correlation with density (Appendix C). In taxonomic terms, *Hyalella* was the dominant taxon in riffles, representing 10.1% of the community, followed by *Metrichia* with 9.8% (Appendix D). With beta coefficient absolute values exceeding 0.25, the high flow index FL(1) was negatively correlated with the relative abundance of *Metrichia* (Appendix 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 (Appendix C). In this context, the density, the EPT and the noninsect relative abundances, the different metrics of richness (total, noninsect, 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 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).

3.2 | Effect of peak and LF 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 time period. The general trend in density (Figure 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 (Figure 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

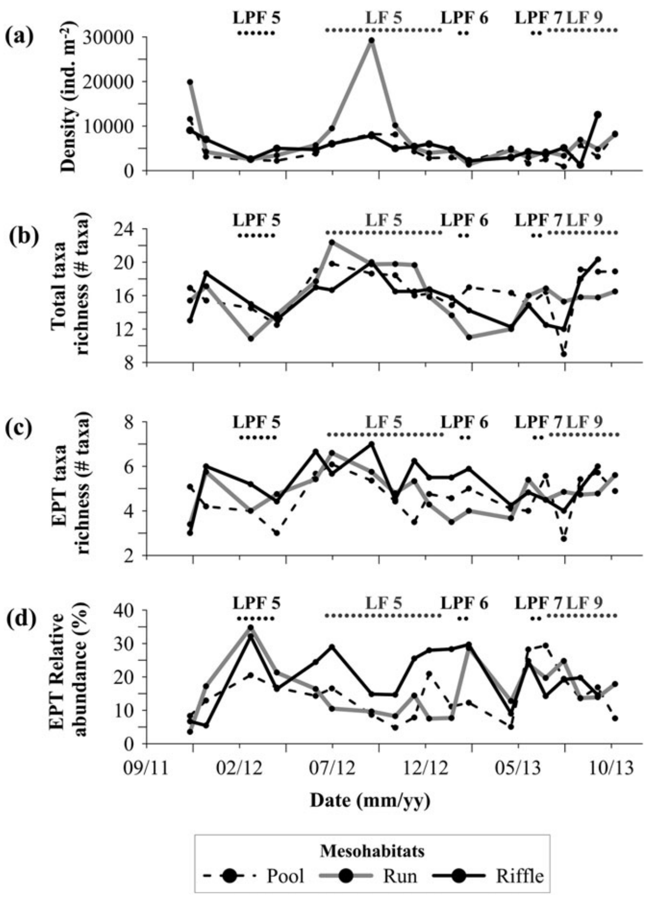

FIGURE 3 Temporal variation of the average community metrics as a function of the mesohabitat type, namely, (a) density (ind. m^{-2}), (b) total taxa richness (# total), (c) Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa richness (# total), and (d) EPT relative abundance (%). The text located over the horizontal dotty lines indicate the periods of large peak flows (LPF) and low flows (LF) depicted in Figure 2

(Figure 3c), as this metric fluctuated significantly throughout the period of analysis. Furthermore, it was observed that the EPT relative abundance (Figure 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 Figure 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 with 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 with 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 an 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 an SPF (Figure 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 SPFs were recorded in the studied period, some events, smaller in terms of magnitude than SPFs, were also studied. Specifically, three events were analysed, respectively, by the following preceding and proceeding campaigns: 1 and 2, 5 and 6, and 9 and 10 (Figure 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 events.

With regard to community metrics, large events with values of 160.4 mm (LPF 5) led to a significant decrease in the density in the three mesohabitats types (Table 2). 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 negative effect also 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, LPF 7 produced an increase in the relative abundance of Hydrachnidia, whereas 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, that is, first, 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 the longest duration of LF (Figure 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

TABLE 2 Effects of large peak flows and small peak flows on community metrics and relative abundance of taxa as a function of the type of mesohabitats according to the statistical test Permutational multivariate analysis of variance (PERMANOVA)

Mesohabitat type	Event characteristics	Community metric/taxa	X̄	*SD*	*F*	*p*
Pool	LPF 5 (160.4 mm)	Density	−3,972	1,609	5.49	0.040
	F_r = 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
	F_r = 1.04; SS = 132.3	Hydrachnidia	4.2	2.74	7.86	0.022
	SPF (108.0 mm)	Oligochaeta	−1.2	0.42	8.02	0.030
	F_r = 0.72; SS = 90.9					
Run	LPF 5 (160.4 mm)	Density	−6,602	3,260	7.93	0.000
	F_r = 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[a]	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
	F_r = 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
	F_r = 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
	F_r = 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
	F_r = 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
	F_r = 3.69; SS = 1,865.4	*Contulma*	6.4	6.81	2.46	0.031

Note. The values of the average (X̄), 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. EPT: Ephemeroptera, Plecoptera, and Trichoptera; LPF: large peak flow; PFs: peak flows; SPFs: small peak flows.

[a]Taxonomic groups belonging to the EPT orders.

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 3); the opposite effect was observed for evenness and diversity. When the period was longer, that is, 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 in 12.7%. With LFs, the EPT taxa richness exhibited a negative tendency after 10 days, which remained 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%

TABLE 3 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

Mesohabitat type	*n*	Community metric/taxa	X̄	*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*[a]	−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

Note. The values of the average (X̄), 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 $p \leq 0.05$. EPT: Ephemeroptera, Plecoptera, and Trichoptera.

[a]Taxonomic groups belonging to the EPT orders.

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 an LF period of 115 days. No significant trends were noticed in the riffle mesohabitats.

4 | DISCUSSION

4.1 | Key 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 (Belmar et al., 2012; Greenwood & Booker, 2015; Wood et al., 2000). According to Greenwood and Booker (2015), previous flow conditions directly affect the diversity, abundance, and composition of aquatic communities. In this context, at the high Andean region above 3,500 m a.s.l., this study aimed at both relating hydrological indices to the effect of flow on aquatic communities and assessing the influence of antecedent peak events on those communities. 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 and negative, which can be related with an increase in the drag by the flow (Figure 4). The rise in shear forces is likely to have influenced certain benthic taxa (Ríos-Touma et al., 2011; Rocha, Medeiros, & Andrade, 2012), mainly of the noninsect class (e.g., Lymnaeidae and Girardia; Ríos-Touma, Prat, & Encalada, 2012), which do not have body features to cope with the increase in SS associated with high flow conditions (Tomanová & Usseglio-Polatera, 2007). For instance, Lymnaeidae lacks supporting structures (i.e., legs, hooks, and suction cups), resulting in the incapability of individuals to cope with flooding (Lam & Calow, 1988; Ríos-Touma et al., 2012).

In the run and pool mesohabitats, LPF events lead to an increase in drag producing a decrease in the total taxa richness (i.e., several taxa abandoned these habitats). The latter has been observed in similar studies carried out at mountainous regions (Angradi, 1997) as well as in lower and flatter areas (Sueyoshi, Nakano, & Nakamura, 2014). In this study region, situated at an altitude over 3,500 m a.s.l. and having significant slopes (Mosquera et al., 2015), only run, riffle, and pool mesohabitats are present. No other mesohabitats types were found, such as abandoned pool, side channel, inundation area, usually existing at flatter (and lower) regions, or leaf pack and organic debris packs at mountainous regions (Angradi, 1997) that may serve as refuge for the taxa that are leaving run, riffle, and pool mesohabitats upon peak flow events (Sueyoshi et al., 2014). In the current study region, these taxa are likely washed away by the increasing current.

The above discussion does not account for the time variability and is based solely on the analysis of the density and total taxa richness. When the rest of the metrics and the time variability are included in the analysis, then the results suggest 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 was least affected (pool) in time by the antecedent peak flow conditions and which one was the most affected (riffle; Appendix C). As shown in Figure 4, the pool mesohabitats are the gentlest environment for the aquatic communities under peak events.

With respect to the change of taxa in the pool mesohabitats, it was observed an important increase in the relative abundance of *Helobdella* (Appendix D), explained by the hydrological index COMAXDAY that is referring to the CV of the maximum discharge observed in periods of n = 7, 15, 30, and 90 days before the sampling date, and *Hyalella*, explained by the hydrological index MAXDAYQ(7) that is referring to the maximum discharge observed in a period of n = 7 days before the sampling date. Nevertheless, it should be noticed that these maximum discharges, accounted for by COMAXDAY and MAXDAYQ, do not necessarily match LPFs. Hereafter, the above conclusion on the fact that LPFs decreased total taxa richness and density in pool mesohabitats does not contradict these findings of the analysis on the antecedent peak flow conditions. The latter is emphasized by the fact that the individual contribution of *Helobdella* and *Hyalella* as predictors in the multiple regression is relatively low. Both *Helobdella* (Stubbington & Wood, 2013) and *Hyalella* (McElravy & Resh, 1991) have the capacity of hiding in the substrate, which makes them less sensitive to higher drag forces, although not enough to resist the effects of LPF events in the study streams.

In the run mesohabitats, the genus *Girardia*, the second dominant group, was negatively affected by peak events occurring 30 days before the sampling date. A similar trend was observed at the Chattahoochee River in the southern Appalachian Mountains, where noninsect macroinvertebrates such as flatworms (Tricladida) were washed away during high flow events (Holt, Pfitzer, Scalley, Caldwell, & Batzer, 2015). Tomanová and Usseglio-Polatera (2007) report that the order Tricladida, to which the genus *Giardia* belongs, possesses low ability to adhere to the bottom materials of the streams despite

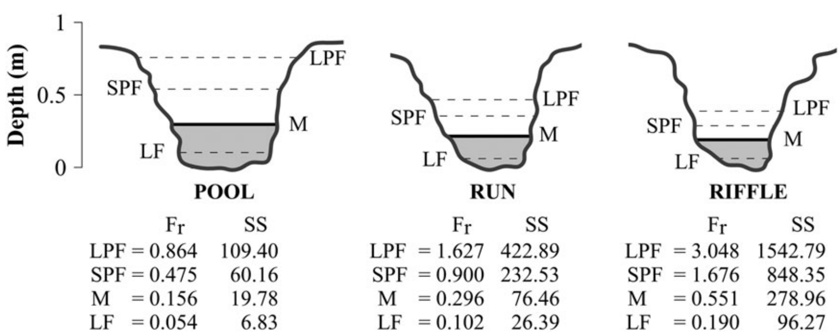

FIGURE 4 Typical cross sections observed in pool, run, and riffle mesohabitats, showing levels of water surface under different discharge conditions, namely, large peak flow (LPF), small peak flow (SPF), low flow (LF), and median (M, observed in the period from 2011 to 2013). Froude number (F_r) and shear stress (SS; N m^{-2}) values are given for these discharge conditions as a function of the type of mesohabitat

their flattened shape, suggesting why the genus *Girardia* does not resist significant discharges. On the other hand, *Metrichia*, owing to its body conditions (characteristics of the case), has the potential of adhering to the surrounding substrate (Barbero, Oberto, & Gualdoni, 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 (Appendix 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. A similar result was recorded at the low-elevation Itchen River, where drought eradicated small caddisflies (Glossosomatidae and Hydroptilidae; Aspin et al., 2018). Most likely the decrease in drag, associated with LF, makes that other organisms different from this taxon (i.e., *Hyalella* and Chironominae) gradually enter and recolonize these mesohabitats (Townsend & Hildrew, 1976), decreasing the relative abundance of *Metrichia*.

4.2 | Effect of hydrological events on aquatic communities

In aquatic ecology, the drag force associated to LPFs is known as being catastrophic (Melo & Froehlich, 2004; Snyder & 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, Galloway, & Flannagan, 1992). In the same context, Q_2 is approximately four times greater than Q_{25} (29.3 mm), generally used in other latitudes for defining LPF events in studies about the effects of peak events on fish communities (Knight, Murphy, Wolfe, Saylor, & Wales, 2014).

In this study, it was recorded large peak events with different duration, that is (Figure 2), (a) shorter duration large peaks, such as LPF 6, and (b) longer duration large peak events, such as LPF 5 and LPF 7. Density decreased more than 60%, and EPT relative abundance increased more than 15% in the three types of mesohabitats affected by either shorter or longer duration LPFs. Similar effects, although with different proportions of density decrement and EPT relative abundance increment from what is here reported, have been observed in several studies (Suren & 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 increment of evenness in the pool mesohabitats.

The comparison of the metrics calculated before and after peak events confirmed what was concluded by analysing the relationship between hydrological indices and community metrics and taxa. That is, less adapted aquatic taxa are more easily affected by peak events and their associated drag forces (Blanckaert, Garcia, Ricardo, Chen, & Pusch, 2012; Bonada, Rieradevall, & Prat, 2007; Lamouroux, Dolédec, & Gayraud, 2004; Poff et al., 1997). For instance, in the mesohabitats run and riffle, a decrease in the proportions of *Girardia* and Chironominae after peak flows was observed because 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). This finding is in contrast to what was noticed at the lower Himalayan streams during the monsoon, where chironomids were one of the dominating taxa due to their *r*-selected life history, which helps to persist harsh discharge regimes (Brewin, Buckton, & Ormerod, 2000). The decrease of the number of individuals of *Girardia* and Chironominae in the present study resulted in the increase of the relative abundance of *Metrichia* in the run mesohabitats because its relatively small size and its preference to be attached to thick substrates (Barbero et al., 2013; Brooks, Haeusler, Reinfelds, & Williams, 2005) helped *Metrichia* to resist better the drag of flooding. Thus, in the run mesohabitats, because most individuals of *Metrichia* resisted flooding events and remained in place, it is likely that their associated recolonization took place at a faster pace in comparison with organisms that were dragged away by flooding and started arriving back by the drift once flooding was over. It has to be noticed, however, that under LF conditions, *Metrichia* is less abundant and competitively inferior to other organisms with biological characteristics that are more adapted to these LF conditions (Gibbins, Dilks, Malcolm, Soulsby, & Juggins, 2001).

Further, LPF 6 had positive effects on Oligochaeta ratios, whereas 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 that likely led to a loss of the interstitial zone of the reach (Bruno, Maiolini, Carolli, & Silveri, 2010) and in turn to the sustained decline of the relative abundance of Oligochaeta. Similar strong reduction in the abundance of Oligochaeta was observed in the low-elevation Lules River after high flow periods (Mesa, 2010). In contrast, LPF 6 was a bit larger but 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 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), because head or small streams are reduced to small intermittent pools, being the only refuge for the aquatic biota at summer time (Dekar & Magoulick, 2007). This fact contrasts with the high Andean head streams that 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 total taxa richness. On the contrary, some studies conducted in temperate zones (Datry, 2012; Suren & Jowett, 2006) during long periods of low discharges report a decrease in richness in riffle mesohabitats. In addition, a decrease of the proportions of EPT relative abundance and taxa richness was observed, which may be due to the sensitivity of the EPT to the decrease in discharge, as observed by Dewson, James, and Death (2007) in riffle mesohabitats of several New Zealand rivers. Ledger, Edwards, Brown, Milner, and Woodward (2011) state that 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; this factor however was not observed in the current study (Table 3).

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, Benbow, and Burky (2002) who, for riffle mesohabitats in the Iao river (Hawaii), 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, characterized 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).

5 | 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. LPF events were defined on the basis of the Q_2 percentile, which is a much stronger discharge threshold than the ones commonly used elsewhere to define peak events. This threshold seems adequate because the aquatic communities in high Andean streams are likely to have more resilience to peak flow variations and conditions than similar communities that live in streams at different latitudes and elevations.

In this study region, LPFs can be of either shorter or longer duration. Either of these LPFs dragged away organisms from all of the different mesohabitat types. These dragged organisms were possibly washed away through the main current because in the study region, there are no other types of mesohabitats present, that is, abandoned pool, side channel, and inundation area, usually existing at flatter (and lower) regions, which could serve as their temporary refuge during peak flow 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 have 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 results suggested that antecedent peak events are an important factor in evaluating the aquatic community composition at that particular date. Further, this study pointed out which type of mesohabitats was least affected (pool) by antecedent peak flow conditions and which one was more affected (riffle). Moreover, this study indicated that pool mesohabitats were the gentlest environment for the aquatic communities under different hydraulic regimes (i.e., LFs, mean flows, and peak flows), although they did not act as a permanent refuge for the dragged taxa.

This study showed that peak flow events had stronger effects on the communities than LFs and the latter flows had less effect on the communities than similar ones observed at high mountains in temperate regions. In other latitudes, streams tend to be intermittent under long LF periods, which is not the case in high Andean streams because of the nature of the surrounding soils. Further, under LF events, pools are important because different taxa can find suitable habitat, whereas run mesohabitats are strongly impacted by the reduction of their area.

Finally, the results herein depicted indicate the importance of further research concerning the community dynamics related to stream flow, before facing further studies on the relations between specific taxa and their microhabitats and before other conservational studies and environmental flows assessments take place in the Southern Andes of Ecuador.

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APPENDIX A

MAIN PHYSICAL CHARACTERISTICS OF THE FOUR STUDIED STREAMS (S1, S2, S3, AND S4)

	Stream identifier			
Physical characteristic	**S1**	**S2**	**S3**	**S4**
Contributing area surface (km^2)	0.38	1.40	3.28	1.65
Average discharge (L s^{-1})	10.6	38.7	92.5	23.6
Minimum discharge (L s^{-1})	1.03	1.64	3.73	0.94
Maximum discharge (L s^{-1})	112.7	439.5	1,035.5	543.6
Average velocity (m s^{-1})	0.34	0.32	0.41	0.21
Maximum velocity (m s^{-1})	1.25	1.51	1.22	0.84
Average depth (cm)	10.8	18.2	19.7	14.2
Maximum depth (cm)	25.0	44.0	42.0	49.0
Average Froude number (F_r) (--)	0.37	0.25	0.30	0.19
Maximum F_r	1.35	0.96	0.96	0.65
Average shear stress (SS) (N m^{-2})	144.7	80.9	117.4	51.5
Maximum SS (N m^{-2})	1,428.0	762.1	641.6	342.2

APPENDIX B

PRESENCE OF TAXA AS A FUNCTION OF THE STUDIED MESOHABITATS AND STREAMS (S1, S2, S3, AND S4)

		Mesohabitat type											
		Pool				Run				Riffle			
Group	Taxa	S1	S2	S3	S4	S1	S2	S3	S4	S1	S2	S3	S4
Coleoptera	*Austrelmis*			X		X	X	X		X	X	X	
	Austrolimnius	X	X	X	X	X	X	X	X	X	X	X	X
	Heterelmis	X	X	X	X	X	X	X	X	X	X	X	X
	Hexanchorus	X	X	X	X		X	X	X	X	X	X	
	Palpomyia		X	X	X	X	X	X	X	X	X	X	X
Diptera	Chironominae	X	X	X	X	X	X	X	X	X	X	X	X
	Orthocladiinae					X	X	X	X	X	X	X	X
	Podonominae			X			X	X	X	X	X	X	X
	Tanypodinae				X	X	X	X	X	X	X	X	X
	Neoplasta		X		X	X	X	X	X	X	X	X	X
	Hexatoma	X	X	X	X	X	X	X	X	X	X	X	X
	Limonia				X	X	X	X	X	X	X	X	
	Pericoma				X		X	X	X			X	X
	Psychoda	X	X	X	X	X	X	X	X	X		X	X
	Gygantodax				X	X	X	X	X	X	X	X	X
Ephemeroptera	*Andesiops*				X			X	X	X	X		X
	Ecuaphlebia					X	X	X	X	X	X	X	X
Plecoptera	*Claudioperla*	X	X	X	X		X	X	X	X	X	X	X
	Anacroneuria				X	X	X		X	X			X
Trichoptera	*Contulma*	X	X		X	X	X	X	X	X	X	X	X
	Phylloicus	X	X		X	X	X	X	X	X			X
	Mortoniella							X	X				X
	Helicopsyche				X	X	X	X	X	X	X	X	X
	Atopsyche					X	X	X	X	X	X	X	X
	Smicridea	X	X	X	X	X		X	X	X	X		X
	Metrichia	X	X	X	X	X	X	X	X	X	X	X	X
	Ochrotrichia	X	X	X	X		X	X	X		X	X	X
	Atanatolica				X	X	X	X		X	X	X	
	Nectopsyche				X	X	X	X	X	X	X	X	X
	Xiphocentronidae				X	X	X	X	X	X	X	X	X
Acariformes	Hydrachnidia	X	X	X	X	X	X	X	X	X	X	X	X
Amphipoda	*Hyalella*	X	X	X	X	X	X	X	X	X	X	X	X
Gasteropoda	Lymnaeidae	X	X	X	X		X	X	X	X	X	X	
Hirudinea	*Helobdella*	X	X	X	X	X	X	X	X	X	X	X	X
Nematomorpha	Gordioidea		X	X	X	X	X	X	X	X	X	X	
Annelida	Oligochaeta	X	X	X	X	X	X	X	X	X	X	X	X
Tricladida	*Girardia*				X	X	X	X	X	X	X	X	X
Veneroidea	Sphaeriidae	X				X	X	X	X	X	X	X	X

APPENDIX C

BETA COEFFICIENTS 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

MT	Dependent variable	Adjust. R^2	Independent variable	No standardized reg. coeff. *B*	Stand. err.	Standardized reg. coeff. *β*	*t*	*p*
Pool	Density	0.158	MAXDAYQ(7)	−1,512.6	289.9	−0.405	−5.22	0.000
	EPT rel. abund.	0.060	MINDAYQ(30)	6.0	2.8	0.178	2.13	0.035
			COMAXDAY	−16.3	7.9	−0.172	−2.06	0.042
	Total taxa richness	0.115	FH(1)	−3.8	0.9	−0.396	−4.50	0.000
			FL(3)	−1.5	0.7	−0.177	−2.01	0.046
	EPT taxa richness	0.159	FH(1)	−1.8	0.4	−0.420	−4.85	0.000
			FL(3)	−1.2	0.3	−0.332	−3.83	0.000
			QMAX(1)	5.1	2.2	0.181	2.31	0.022
	Noninsect richness	0.051	FH(1)	−0.7	0.3	−0.240	−2.92	0.004
	Evenness	0.096	MAXDAYQ(15)	0.1	0.0	0.323	3.43	0.001
Run	Density	0.228	MAXDAYQ(7)	−3,895.2	1,013.0	−0.496	−3.85	0.000
			QMIN(1)	3,750.9	1,267.7	0.454	2.96	0.004
			FL(1)	5,737.1	1,820.1	0.306	3.15	0.002
			FH(2)	−3,152.9	1,545.7	−0.211	−2.04	0.043
	Noninsect rel. abund.	0.047	FH(1)	−8.7	3.1	−0.231	−2.82	0.006
	Total taxa richness	0.203	FH(2)	−3.9	0.7	−0.441	−5.76	0.000
			QMAX(1)	18.1	5.3	0.259	3.38	0.001
	Noninsect richness	0.270	FH(3)	−1.2	0.2	−0.589	−7.08	0.000
			FL(1)	−0.5	0.2	−0.191	−2.30	0.023
			QMAX(1)	3.4	1.3	0.190	2.62	0.010
	Evenness	0.111	COMINDAY	0.2	0.1	0.342	4.33	0.000
	Diversity	0.141	COMINDAY	0.9	0.2	0.561	4.89	0.000
			FH(3)	−0.3	0.1	−0.441	−4.31	0.000
			QMAX(1)	1.9	0.6	0.333	3.32	0.001
Riffle	Density	0.130	QMIN(1)	−1,351.2	386.0	−0.377	−3.50	0.001
	EPT rel. abund.	0.070	FL(1)	−13.9	5.4	−0.287	−2.58	0.012
	Noninsect rel. abund.	0.041	QMAX(1)	−51.9	25.4	−0.231	−2.04	0.045
	Total taxa richness	0.111	FH(2)	−2.8	0.9	−0.364	−3.07	0.003
			FHA	7.9	3.1	0.298	2.52	0.014
	Noninsect richness	0.106	FH(4)	−0.9	0.3	−0.301	−2.66	0.010
			COMAXDAY	−2.0	0.8	−0.290	−2.56	0.012
	Diversity	0.118	COMAXDAY	−1.6	0.7	−0.377	−2.44	0.020

Note. 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 $p \leq 0.05$. MT: mesohabitat type; adjust.: adjusted; *B*: no standardized regression coefficient; stand. err.: standard error of no standardized regression coefficient; *t*: *t* statistics; rel. abund. (%): relative abundance; reg. coeff.: regression coefficient; EPT: Ephemeroptera, Plecoptera, and Trichoptera.

APPENDIX D

BETA COEFFICIENTS 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

					No standardized reg. coeff.		Standardized reg. coeff.		
MT	Dependent variable	Mean rel. abund. (%)	Adjust. R^2	Independent variable	*B*	Stand. err.	*β*	*t*	*p*
POOL	*Helobdella*	42.6	0.044	COMAXDAY	30.4	11.1	0.226	2.73	0.01
	Hyalella	12.0	0.033	MAXDAYQ(7)	2.8	1.2	0.200	2.41	0.02
	Hydrachnidia	6.8	0.055	QMIN(1)	2.8	0.9	0.248	3.01	0.00
	Heterelmis	5.9	0.111	QMIN(1)	3.2	0.9	0.293	3.67	0.00
				QMAX(1)	−19.4	8.4	−0.185	−2.32	0.02
	Metrichia[a]	3.9	0.038	FH(4)	4.0	1.6	0.212	2.56	0.01
	Psychoda	2.7	0.040	COMAXDAY	5.2	2.0	0.217	2.62	0.01
	Claudioperla[a]	1.1	0.066	MINDAYQ(60)	1.2	0.4	0.270	3.31	0.00
	Lymnaeidae	15.9	0.161	MAXDAYQ(60)	−7.3	2.4	−0.255	−3.07	0.00
				FH(4)	−11.4	3.8	−0.250	−3.01	0.00
	Smicridea[a]	1.4	0.025	FL(1)	−1.1	0.5	−0.179	−2.15	0.03
RUN	*Metrichia*[a]	3.9	0.060	FH(1)	4.5	1.4	0.257	3.16	0.00
	Hydrachnidia	3.0	0.060	MINDAYQ(30)	1.6	0.5	0.259	3.18	0.00
	Helicopsyche[a]	2.3	0.089	MAXDAYQ(7)	1.8	0.5	0.308	3.85	0.00
	Ecuaphlebia[a]	2.1	0.028	MINDAYQ(60)	2.0	0.9	0.187	2.26	0.03
	Girardia	27.8	0.108	FH(1)	−10.7	2.9	−0.290	−3.66	0.00
				QMAX(1)	−50.6	22.4	−0.180	−2.26	0.03
	Chironominae	6.1	0.215	FH(3)	−7.7	1.3	−0.453	−6.03	0.00
				COMAXDAY	−1.8	0.6	−0.217	−2.89	0.00
	Austrolimnius	2.7	0.043	FL(1)	−2.1	0.8	−0.223	−2.72	0.01
RIFFLE	*Austrolimnius*	2.2	0.054	COMINDAY	3.3	1.4	0.257	2.29	0.02
	Hyalella	10.1	0.041	FH(2)	−6.1	3.0	−0.232	−2.05	0.04
	Metrichia[a]	9.8	0.057	FL(1)	−10.0	4.2	−0.264	−2.36	0.02
	Chironominae	2.8	0.076	FH(4)	−4.4	1.6	−0.298	−2.68	0.01

Note. 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 $p \leq 0.05$. MT: mesohabitat type; adjust.: adjusted; *B*: no standardized regression coefficient; stand. err.: standard error of no standardized regression coefficient; *t*: *t* statistics; rel. abund. (%): relative abundance; reg. coeff.: regression coefficient; EPT: Ephemeroptera, Plecoptera, and Trichoptera.

[a]Taxonomic groups belonging to the EPT orders.