Macroinvertebrates community structure in a highly glacial catchment

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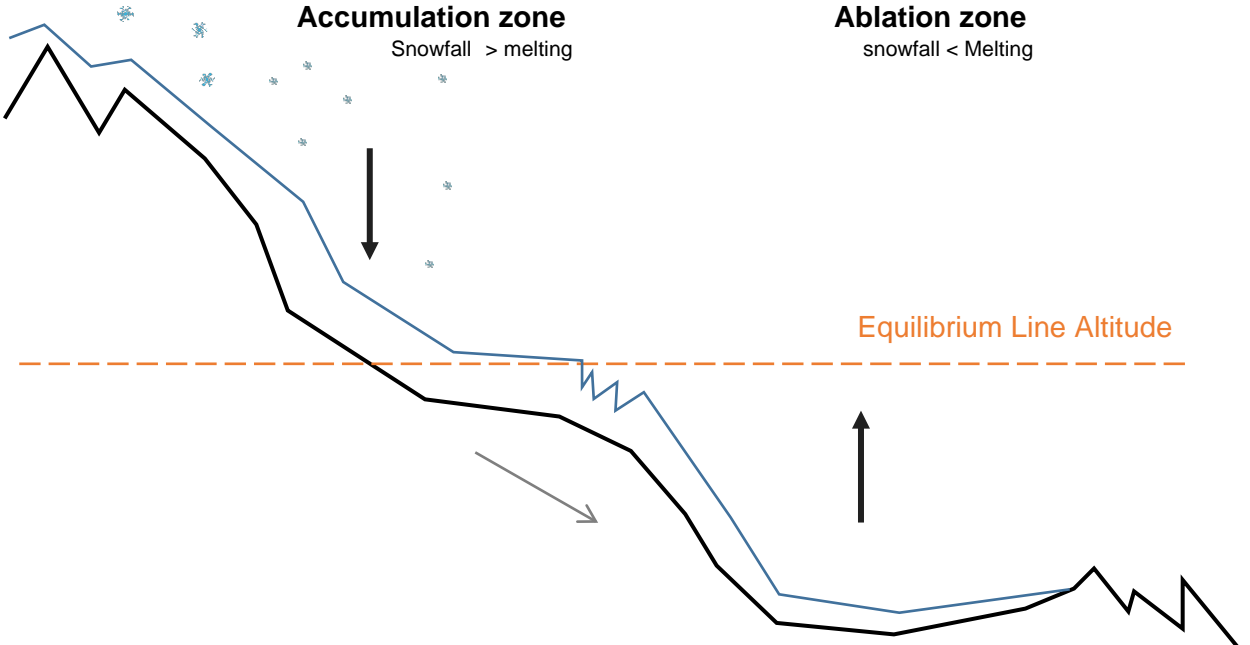

Figure 2. Illustration of the zones of a glacier. The bedrock is represented by the black line and the glacier outline by the blue line. Grey arrows give the flow direction. Adapted from Cuffey (2010).

1. INTRODUCTION

Over the last century, air temperature has significantly increased due to climate change. Warming temperatures combined with a modification of precipitation, has led to an overall shrinkage of glacier cover (Gobiet *et al.*, 2014; Vincent *et al.*, 2017). Glaciers are distributed worldwide (Fig. 1) and cover a surface of approximately 726,000km² which represent 0.5% of the Earth's land surface (IPCC AR5 Working Group 1, chapter 4). The formation of glacier depends on climatic conditions, mainly temperature and precipitation, as well as topographic characteristics (Cuffey, 2010). One notably consequences of the climate change is the increasing elevation of the Equilibrium Line Altitude (ELA; Rabatel *et al.*, 2005), which define the point where the snowmelt becomes higher than its accumulation (Fig. 2). Most mountain glaciers are therefore strongly negatively impacted by the climate change (Gardner *et al.*, 2013). This is especially true in the Alps, where the overall glacier coverage decreased from 340km² in the mid-1980s and to approximately 275 km² by the late 2000s, a loss of more than 20% in only 20 years (Gardent *et al.*, 2014; Rabatel *et al.*, 2016; Vincent *et al.*, 2017). Alpine ecosystems, widely distributed throughout both hemispheres, are particularly sensitive to environmental changes due to the combined effects of mountaintop insularity and longitudinal shifts of environmental conditions, decreasing areas of suitable habitat (Walther *et al.*,2005; Galbreath *et al.*, 2009). Climate change is substantially shrinking glacier which is expected to modify the hydrological characteristics in the existing streams (Milner *et al.*, 2009; Jacobsen *et al.*, 2014).

Alpine aquatic ecosystems are dendritic network consisting of headwaters connected to multiple channels (Altermatt, 2013a). They share common features such as steep gradients, high velocity, and high dissolved oxygen concentration. However, they can differ from each other depending on their water sources: groundwater, glacial meltwater, and snowmelt (Milner & Petts, 1994; Brown *et al.*, 2003). Usually, glacially dominated rivers are characterized by a set of environmental conditions, including cold water (maximum of 4°C), low conductivity (below 50 µs.cm^{-1}) due to the weak ionic concentration, high turbidity (exceeding 30 NTU), and usually low channel stability, partially due to the strong daily and seasonally discharge fluctuations associated with glacier run-off (Milner & Petts, 1994; Füreder, 1999). The turbidity is mostly due to suspended particles, so-called glacial flour or glacial milk, resulting from subglacial erosion of the bedrock and delivered to recipient aquatic ecosystems by runoff (Clarke, 2005). Snowmelt dominated rivers are typically more stable, with a higher temperature from 5 to 10°C (Ward, 1994). Usually, they transport little sediment but may have elevated turbidity during high flows. Finally, groundwater streams have a water temperature close to the mean air temperature, a much greater conductivity, and do not exhibit marked flow fluctuations (Ward, 1994; Füreder, 1999). Groundwater transits through the bedrocks and captures minerals, increasing the conductivity. All these environmental conditions vary spatially from streams to the catchment scale creating a very high spatial heterogeneity with different environmental conditions (Heino *et al.*, 2015a). This heterogeneous environment acts like as metaphorical 'sieve' or 'filter', where only certain species are able to establish and persist, excluding all others (Nobel & Slatyer, 1977; Bazzaz, 1991). Modification of glacial contributions to river sources will change the meltwater contribution to water flow, resulting in the alteration of hydrological parameters (turbidity, conductivity, temperature, channel stability) which will significantly impact the aquatic community structure (Milner *et al.*, 2009; Slemmons *et al.* 2013). Therefore, alpine rivers are suitable locations to assess the impacts of climate change. Understanding how climate

change, especially, the associated environmental changes, such as warming temperature and increase in glacier run-off, impacts aquatic biodiversity in such streams represents a future research challenge. Despite advances in research over the past decade in this field (e.g. Jacobsen *et al.*, 2012; Hotaling *et al.*, 2017), little has yet been done at the catchment scale, particularly in the southern Alps.

Macroinvertebrates are widely distributed in all types of freshwater bodies and their larvae represent suitable model species as they have a relatively low mobility, a generally high abundance, a high species diversity, and can spend up to one year in a particular stream (Lancaster & Downes, 2013). They play a key role in aquatic food webs by producing and structuring the matter, energy and information fluxes, as well as being a food resource for predators, in aquatic ecosystems (Wallace & Webster, 1996; Allan & Castillo, 2007). Thus, changes in community structure could alter the food webs, which may influence the stability of the existing aquatic ecosystems. Additionally, previous studies have shown that variation between macroinvertebrate communities is thought to be typically driven by an environmental filtering mechanism, the species sorting (Cottenie, 2005). Species abundances and richness can be tied to the abundance of available resources at a specific environment and the ability of a species to take advantage of a particular habitat (Székey & Langenheder, 2013). Spatial processes (e.g. ability of dispersal) can also potentially affect local community composition (Altermatt et al., 2013b, Heino et al., 2015a), where low dispersers will be restricted to a small area, while high dispersers will be able to establish in farther environment (Padial *et al.*, 2014; Beishner *et al.*, 2006). One might expect species sorting to increase with increasing environmental gradient and heterogeneity (Jackson *et al.*, 2001; Grönroos *et al.*, 2013) and spatial factors to gain importance with increasing spatial extent of the region studied (Cottenie, 2005; Heino, 2011). Therefore, macroinvertebrates diversity and community structure are considered valuable bio indicators to assess streams health and understand how environmental changes influence community structure.

Taxonomic richness and diversity are usually lower in harsh (e.g. cold) than in more benign habitats (Currie *et al.*, 2004; Jacobsen & Dangles, 2012). A conceptual model of the longitudinal pattern taxa richness and diversity of macroinvertebrates has been described in many glaciers fed rivers (Milner *et al.*, 2001, Castella *et al.*, 2001). This model predicts an increase in richness and diversity with increasing temperature and channel stability (Milner *et al.*, 2001), as well as distance from the glacier margin (Lods-Crozet *et al.*, 2001a; Jacobsen *et al.*, 2014). The Diamesinae family is usually found close to the glacial margin where maximum water temperature is < 2°C and river channel stability is low. In aquatic bodies with higher stability and maximum temperature is < 4°C, Orhtocladiinae, Oligochaeta and Tipulidae are common groups. Further downstream, as channel stability and temperature increases, Ephemeroptera, Plecoptera and Trichoptera become more dominant (Fig.3). Brown *et al.* (2007), as well as Cauvy-Fraunié *et al.* (2015), found that taxonomic richness and total abundance were strongly influenced by meltwater contribution to water flow. Additionally, environmental parameters such as water turbidity, glacial influence, or conductivity have also found to be structuring the communities (Milner *et al.*, 2009; Jacobsen & Dangles, 2012).

Here, we examined the benthic macroinvertebrate spatial distribution in a highly glacierized catchment, in the Alps. For this, we (1) described the environmental conditions of the different types of alpine streams, (2) examined the aquatic-invertebrate community structure, and (3) investigated the main drivers structuring the macroinvertebrate community. We analyzed the impact of various environmental factors and the spatial configuration to study the macroinvertebrate community structure, based on diversity parameters and using

Figure 3. Conceptual model describing the likely distribution of macroinvertebrates along an upstream-downstream from the glacier margin with increasing temperature and channel stability during the mid-season for European glacier-fed rivers (Milner *et al.*, 2001).
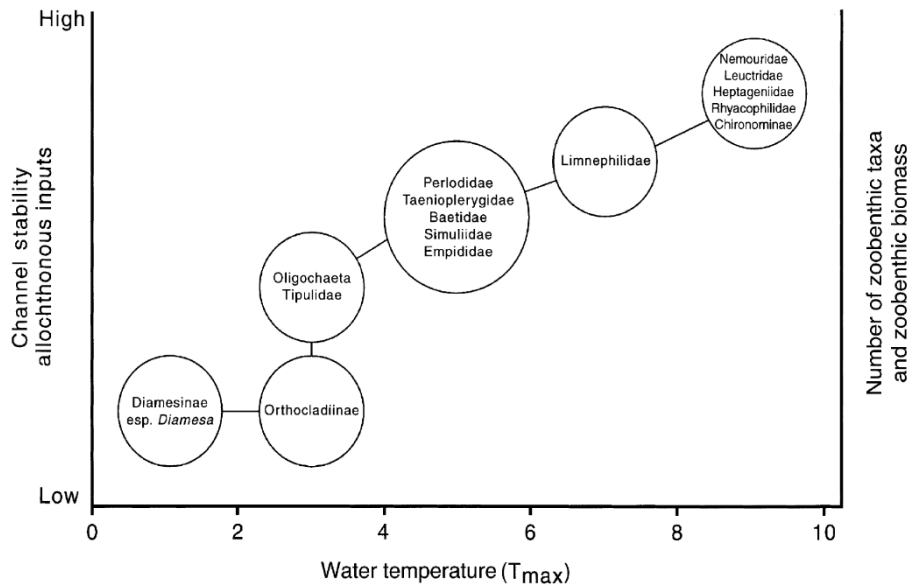
Figure 4. Study site. (a) Map of France: the department of the study site, Haute-Savoie (74), is highlighted in dark grey. (b) Haute-Savoie department enlarged: administrative district of the study site, Chamonix-Mont blanc, is highlighted in dark grey. (c) Map of the study watershed: sites are represented by red circles, numbers are IDs of each site, and each catchment basin is represented by polygons (grey dash lines). Major streams are represented with black lines and were obtained from the hydrological data of BD TOPO (ING 2018) from 2018. The glaciers outlines were obtained from Rabatel, A. (2018 – personal call).
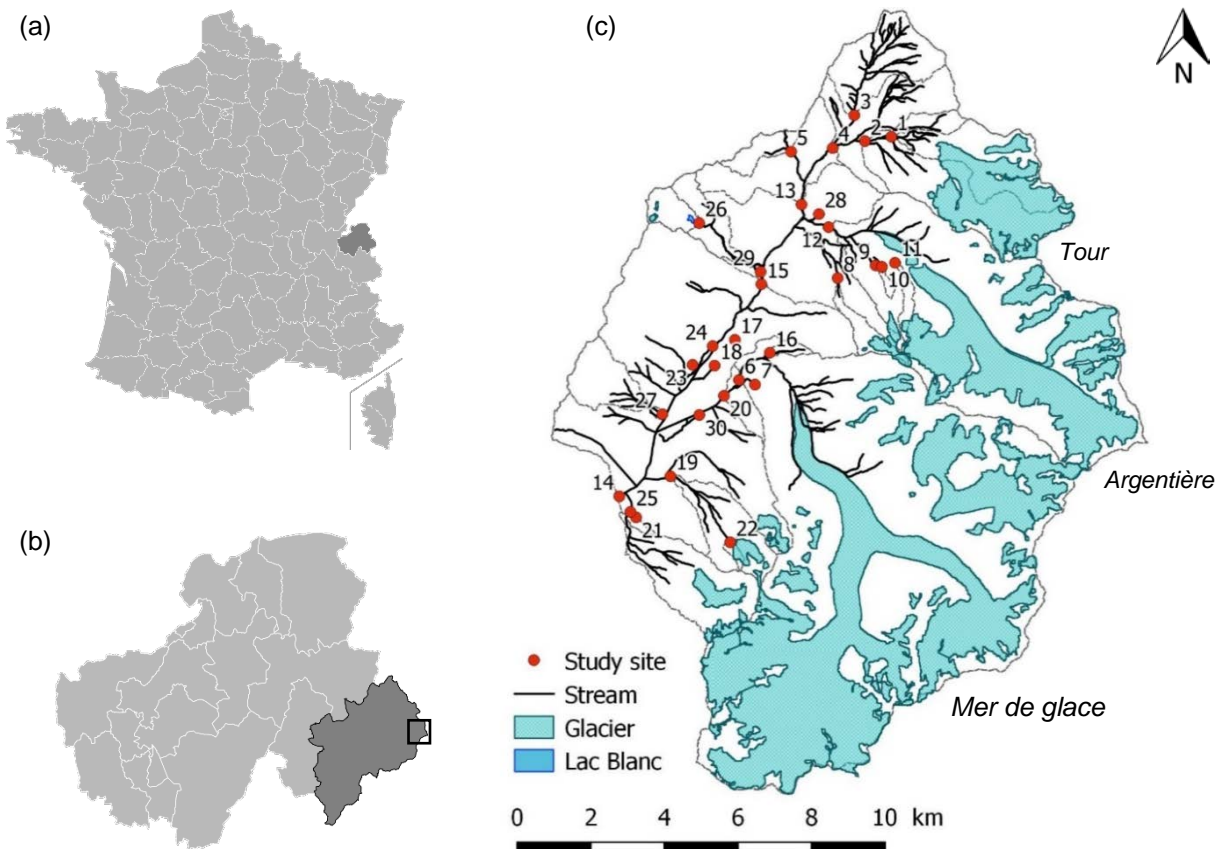
multivariate analysis and distance decay relationships (DDRs). Based on previous study, we hypothesized that higher turbidity, water discharge, but lower conductivity and temperature in glacier-fed rivers would be observed compared to non-glacial rivers (Brown *et al.*, 2003; Milner & Pretts, 1994). We expected a decrease of taxonomic richness and individuals' abundance with increasing glacial influence (Castella *et al.*, 2001; Jacobsen & Dangles, 2011), and a similar macroinvertebrate distribution as the conceptual model proposed by Milner et al. (2001; Fig. 3). Finally, we predicted an increase in community dissimilarity with increasing environmental heterogeneity and spatial variable (Cauvy *et al.*, 2015; Canedo *et al.*, 2015; Slemmons *et al.*, 2013). This study was part of an interdisciplinary project that aims to use chemical tracers and both microbial and invertebrate community variability to identify the source/origin of water.

2. MATERIALS AND METHODS

2.1. Study area and study sites

The study was conducted at the end of summer 2017, in the catchment of the river 'Arve', located in the Mont Blanc massif, French Alps. The study watershed, around 200km², included three large glaciers: the glacier "Mer de glace" (45° 54′ N, 6° 56′ E), "Argentière" (45° 55′ N, 6° 57′ E) and "Tour" (45° 59′ N, 6° 59′ E). The glacier « Mer de glace » is the largest glacier in the French Alps with an area of about 30km², from 4300 m to 1500 m. The glacier "Argentière" has an area of about 12 km². It extends from a maximum elevation of 3400 m to 1600 m at the glacier snout. The glacier "Tour" has an area of about 8 km² and extends from 3400 m to 2150 m. For all glaciers, a notably decrease in the total mass balance has been recorded with a decrease of 0.73 m w.e a^{-1}, 0.84 m w.e a^{-1} and 2.68 m w.e a^{-1} for the glacier "Tour", "Argentière", and "Mer de Glace" (including all its tributaries) respectively in the last 20 years (Viani *et al.*, 2018; Rabatel *et al.*, 2016). Other smaller glaciers contributed in the overall glacial cover catchment with the snout at a higher altitude. The study was conducted in 30 stream sites (Fig. 4 & Supplemental Figure S1), located in five different stream types according to the supposed water source (Table 1).

2.2. Environmental and hydrological parameters

At each site, hydrological (discharge) and chemical data (water temperature, electrical conductivity, pH, concentration in oxygen, and suspended solids sediments) were measured on the day of macroinvertebrates sampling (Table S1). Discharge (FLOW) was measured using the velocity-area methods (Herschy, 2009) with a flow meter (Marsh McBriney Flo-Mate 2000) or by using the bucket method. Turbidity (SSP), conductivity (COND), pH (PH), water temperature (TEMP) and dissolved oxygen (OXY) were recorded with an appropriate probe (HQ40D multiple measurement). Altitude (ALT) was given by the GPS.

'Geographical distances', the shortest straight line distance between two sites (Euclidean), were calculated among all pair of sites in ArcGis 10.15 using the *Analysis > Proximity > Point distance tools*. The 'stream network distances', the distance between two sites following the stream channel, were calculated after creating the stream network using *Network analyst tool*, then computed with *Network analyst > Make OD cost Matrix* and *Add location tools*. 'Environmental dissimilarity' was calculated as the difference between the multivariate centroids of each pair of sites on the first axis of the PCA based on their environmental characteristics (see below).

Table 1. Summary of the categories of streams used in our study. The sites in category A were defined as 'Sources' by the National institute of forest and geographic information (IGN map 2018). Other categories were chosen based upon the percentage of glacial cover catchment in the watershed.

Category	Water source	Number of study sites
A	Groundwater dominant (no glacial influence)	9
B	Snowmelt and rain fed (no glacial influence)	5
C	mix influence (GGC < 20%)	6
D	Medium glacial influence (40 < GGC < 20%)	5
E	High glacial influence (GGC > 40 %)	5

Excepted for sources in the valley botton, the watershed of each site was delimited based on a digital elevation model at 5 meters accuracy (DEM) using the package *Tools box > GRASS > Raster > r.watershed*, then computed with the package *r.water.outlet* (QGis 2.18.15 with GRASS 7.2.2). Glacial influence was estimated with the percentage of glacier cover in the catchment (1):

$$\%GCC = \frac{\text{glacier area}}{\text{watershed area}} \tag{1}$$

where '*watershed area*' the extension of each watershed for each study site. GCC varies from the lowest 0, no influence, to the highest 57% (Site 2).

2.3.   Macroinvertebrates sampling

At each site, five aquatic invertebrate samples were collected using a 0.05m² Surber (250µm mesh) along a 25 meters transect. All samples (150) were preserved in a 96% ethanol solution. Macroinvertebrate were rinsed through 2 mm, 500 µm, and 250 µm sieves, counted and sorted under a light microscope (10x magnification; Supplemental Figure S2). When very abundant, the taxa were subsampled. The sample was pour into a box divided in 5 x 5 cm squares, then the taxa counted in 5 cases were multiply by 5 in order to approximate their abundance. Because of the uncertainty of identification of small individual (< 500 µm) only the 2 mm and 500 µm fractions were used. High sensitive taxa to environmental changes, such as Ephemeroptera, Plecoptera, and Trichoptera (EPT) were identified to genus level, and species level when possible. Several taxa could not be identified to species, because of their small size and/or absence of larval description in this alpine region. In that case, the most frequent genus level of the same family in the sample was assigned to the non-identified individuals. Other taxa were confidently identified to order or family level. Identification keys are detailed by Tachet *et al.* (2010), Eiseler (2005), Lubini *et al.* (2012), and Waringer and Graf (2011).

2.4.   Data analysis

Environment characteristics

Pearson correlation test was applied to the environmental parameters. Principal component analysis (PCA) was used to identify the primary gradient of environmental variables. The environmental differences between the categories were assessed using the non-parametric Kruskal-Wallis test, as no homoscedasticity was found. When significant (p < 0.05), we used Dunn test to see the difference between each pair of categories. Environmental data were log(x) to remove the influence of differing scales of measurement.

Macroinvertebrates

To characterize the macroinvertebrate communities, we calculated, at each site, four ecological indices: 1) taxonomic richness (defined as the number of taxa sampled in each stream sites, S), 2) total abundance (defined as the total number of individuals), 3) Shannon diversity (2.1, describing the diversity with both relative abundance and evenness, H, Shannon and Weaver, 1949) and 4) Specie's evenness (2.2, describing homogeneous the community is, J, Pielou, 1975) index:

$$H = -\sum_{i=1}^{R} p_i \ln(p_i) \tag{2.1} \qquad\qquad J = \frac{H}{log(S)} \tag{2.2}$$

where p_i is the proportion of individuals belonging to the ith species.

Total abundance and relative abundance for EPT genera and Diptera were also calculated, given their distribution in most sites. The total abundance and taxa abundance were log(1+x) transformed prior to all analyses in order to avoid excessive weight of numerically dominant species (Clarke & Warwick, 2001). Results of the different indices are presented in supplementary information Table S2. The differences of ecological indices between categories were assessed using the non-parametric Kruskal-Wallis test. When significant ($p < 0.05$), we used Dunn test to determine the difference between each pair of categories. In addition, the abundance of taxa between categories was compared using the analysis of similarity (ANOSIM). ANOSIM is a non-parametric analogue for analyzing variance and testing multivariate differences between groups (Clarke,1993) based on Bray-Curtis distance and rank dissimilarity. The pairwise difference was calculated using the function *pairwise.adonis()*. The Similarity Percentage Analysis (SIMPER; Clarke, 1993; Clarke & Warwick, 2001) was used to determine the contribution of each macroinvertebrate taxa to the dissimilarity among groups.

Invertebrate-habitat relationship

Community dissimilarity, β-diversity, was measured using Bray-Curtis, d_{BC} (3.1, based on abundance) and Sorenson, d_{Sor} (3.2, based on presence-absence data) dissimilarity index.

$$BC_{ij} = 1 - \frac{2C_{ij}}{S_i + S_j} \qquad (3.1) \qquad\qquad d_{Sor} = \frac{2a}{2a + b + c} \qquad (3.2)$$

where S_i is the total number of specimens counted on site i, S_j the total number of specimens counted on site j, and C_{ij} is the sum of only the lesser counts for each species found in both sites. And where b and c are the cardinalities of the two sets and a is the number of species common to both sets. Furthermore, for each pairwise dissimilarity index we partitioned these dissimilarities into two components: nestedness and turnover. Nestedness reflects the loss of species (i.e. the poorest assemblage is a strict subset of the richest assemblage), whereas spatial turnover reflects the replacement of some species (Baselga, 2010). Bray-Curtis and Sorensen dissimilarity, as well as both nestedness and turnover, were analyzed versus environmental dissimilarity with decay distance relationships (DDRs). Mantel test was used to see if one of the distance had an influence on the community structure.

The possible relationship between community structure and environmental factors was examined by redundancy analysis (RDA), using the Hellinger-transformed abundance (Legendre and Gallagher, 2001). This method was chosen because we suggested the majority of species exhibited linear responses. When the global test was significant ($p < 0.05$), a stepwise selection procedure and Monte Carlo permutation test (1000 permutations) was performed to determine which variables were statistically significant in structuring macroinvertebrate community structure (Blanchet *et al.*, 2008). A forward selection was also performed on the four biodiversity indices. One site was not part of the analysis as it didn't have any taxa (Site 22). All statistical analyses were conducted using R software (R Development Core Team 2013, v3.3.4).
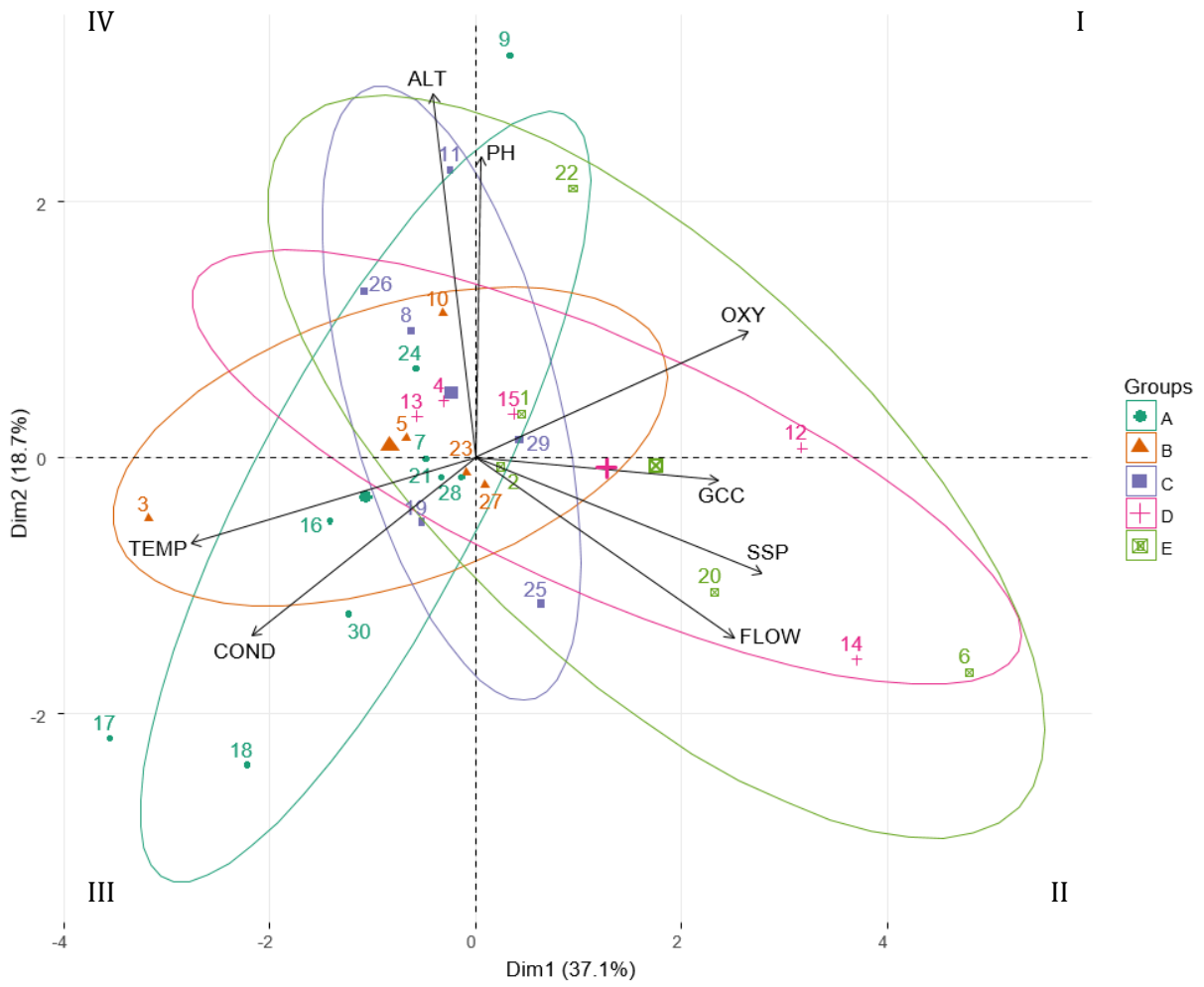
Figure 5. PCA biplots of the environmental data and sites. Sites were colored according their glacial influence.

3. RESULTS

3.1. *Environmental variables*

Our PCA analyses showed that the first three axes accounted for 68.7% (37.1%, 18.7%, and 12.9% respectively) of the variance among sites (Fig. 5). The environmental variables SSP, TEMP, OXY, FLOW, and GCC, mostly contributed to the first axis, while the second axis was represented by the variable ALT and PH. The third axis was mostly represented by GCC, PH, and COND. We noticed that sites 12, 20, 14, and 6, were located in the quadrant I-II, where SSP, FLOW and GCC values were the highest. At the opposite, sites 3, 16, 17, 18, and 30, were located in quadrant III-IV of the first axis. Among the 8 environmental variables, TEMP was significantly negatively correlated with OXY (r = -0.64***), SSP was significantly positively correlated with GCC (r = 0.58***, Supplemental Figure S3). Kruskal-wallis test revealed a significant difference between the parameters FLOW, COND, GCC, and SSP between the 5 categories (df = 4; $\mathcal{X}^2_{FLOW}$ = 16.7, p < 0.02; $\mathcal{X}^2_{COND}$ = 13.4, p < 0.01; $\mathcal{X}^2_{GCC}$ = 28.5, p < 0.001; $\mathcal{X}^2_{SSP}$ = 19.1, p < 0.001). We observed a tendency of decrease COND and increase SSP, FLOW, and GCC, from groundwater dominant stream (A) to glacier-fed streams (E). Other parameters did not show any significant differences (Supplemental Figure S4)

3.2. *Macroinvertebrate community structure*

From the 30 study sites, a total of 26,649 individuals were sorted out, identified, and classified into 6 different phyla: Arthropoda (74.2%), Plathelmintha (10.2%), Annelida (9.4%), and Cnidaria, Mollusca, and Nemathelmintha (6.2%). In total, 100 macroinvertebrate taxa were identified. The order Diptera was the most diverse (36 taxa) and abundant (11,787 individuals; 44%) group in our study. Among Diptera, Chironomidae family was the dominant group, with 10,689 individuals (40%), mostly divided into 3 sub-groups, Orthocladiinae (84%), Diamesinae (6.5%), and Chironominae (5.3%). The EPT genera accounted for 41 taxa (41%) and 6,326 individuals (23.7%) and was the second more dominant group. Non-insect taxa such as Oligocheta, Nematoda, and the turbellarian *Crenobia alpina*, were also predominant groups. Taxonomic richness ranged from 2 in site 6 to a maximum of 42 taxa in site 7. At only one site, no organisms were found (site 22). Total abundance per site ranged from 5 individuals in site 6 to 3461 in site 17. EPT genera abundance was the lowest in both sites 6 and 26 and the highest in site 18. Additionally, the Diptera abundance was the lowest in site 6 and the highest in site 9.

Taxonomic richness significantly varied among the groups of water source (Kruskal-Wallis; $\mathcal{X}^2$ = 15.806, df = 4, p < 0.01), as well as the total abundance ($\mathcal{X}^2$ = 18.547, df = 4, p < 0.001). Among the groups of water source, E and D significantly differed from A, B, and C (Fig. 6a & 6b). Neither of the Shannon index nor evenness were significant ($\mathcal{X}^2$ = 8.252, df = 4, p > 0.05; $\mathcal{X}^2$ = 4.879, df = 4, p > 0.05; Fig. 6c & 6d). The total abundance of EPT genera ($\mathcal{X}^2$ =10.011, df = 4, p < 0.05), and the total abundance of Diptera ($\mathcal{X}^2$ = 15.124, df = 4, p < 0.01) were significantly different. The relative abundance of EPT genera ($\mathcal{X}^2$ = 2.196, df = 4, p > 0.05) and Diptera ($\mathcal{X}^2$ = 2.448, df = 4, p > 0.05) did not significantly changed along the glacial gradient. When the EPT genera were fractioned into E, P, and T, their relative abundant changed with the glacial influence. Trichoptera did not significantly change ($\mathcal{X}^2$ = 9.113, df = 4, p > 0.05), Plecoptera significantly decreased ($\mathcal{X}^2$ = 15.238, df = 4, p < 0.01), and Ephemeroptera significantly increased ($\mathcal{X}^2$ = 13.271, df = 4, p < 0.01) from category A to E.
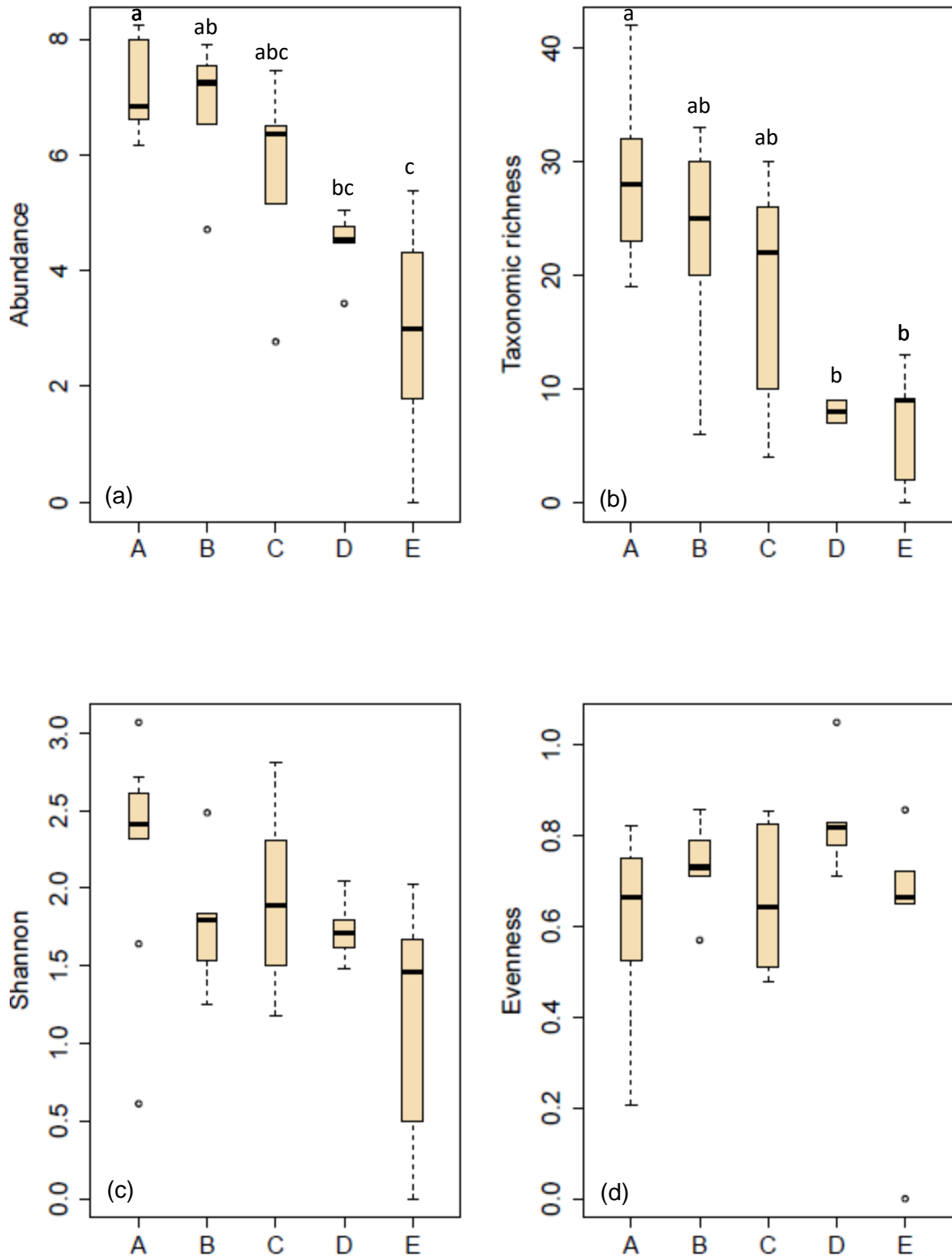
Figure 6. Boxplots of the diversity indices, (a) abundance, (b) taxonomic richness, (c) Shannon and (d) evenness, of macroinvertebrate communities in the five types of streams.

A significant difference in taxa composition was shown between the 5 groups of streams (R = 0.448, p = 0.001). The pairwise (ANOSIM) analysis revealed a significant difference between all pair of sites, excepted for the 'B' vs 'A' and 'C', and 'E' vs 'C' and 'D' (Supplemental Table S3). Most of the sites with different sources had an average dissimilarity of more than 60% excepted for 'high' vs 'medium' and 'mix' vs 'source'. The taxa that contributed most to dissimilarity among groups were *Baetis*, *Othocladiinae*, *Crenobia alpina*, *Oligocheta*, *Nematoda*, *Dicranota*, and *Diamesinae*.

3.3. Macroinvertebrate community structure in relation to environmental and spatial variables

Contribution of the spatial processes and environmental filtering

Neither the geographical distance (GD) nor stream network distance (SN) had a significant influence on the beta-diversity in our study area (Mantel test; r_{GD} = 0.03, p-value > 0.05; r_{SN} = 0.15, p-value > 0.05; Fig. 7a & 7b). Environmental dissimilarity had a significant influence on the community structure likeliness (r_{dBC} = 0.37, p-value < 0.001; r_{dSor} = 0.4, p-value < 0.001). We observed a higher beta-diversity, from both Bray-Curtis and Sorensen, with increasing environmental dissimilarity (Fig. 7c & 7d). We also observed that the turnover component of both Bray-Curtis and Sorensen indices significantly increased with increasing environmental dissimilarity (r_{tBC} = 0.25, p-value < 0.01; r_{tSor} = 0.36, p-value < 0.001; Fig. 7e & 7f), while no significant trend was observed for the nestedness component (r_{nBC} = 0.06, p-value > 0.05; r_{nSor} = 0.05, p-value > 0.05; Fig. 7e & 7f).

Macroinvertebrate community structure in relation to environmental variables

The RDA showed that all eight explanatory variables explained 30.2% of the total variability of macroinvertebrate community structure. RDA1 and RDA2 accounted for 11.2% and 7.2%. The first axis was represented by the environmental parameter GCC while the second axis was mostly represented by both ALT and SSP. RDA axes 1 and 2 separated the sites into roughly five groups: the sites with a high GCC and SSP on the upper left (IV quadrant), high GCC but lower SSP and ALT (III quadrant), and three groups with low or no glacial influence separated by ALT (I-II quadrant; Fig. 8). Forward selection identified that OXY, SSP, ALT, and GCC were the four parameters that contributed the most at shaping the communities (r_{OXY} = 0.27*, r_{SSP} = 0.23*, r_{ALT} = 0.20*, r_{GCC} = 0.15**). The taxa best associated with the GCC were *Diamesinae* and *Baetis*, while *Crenobia alpina* was the found only where no glacial influence was found. Additionally, GCC was the parameter which influenced the most taxonomic richness and abundance (r = 0.42*** and r = 0.5*** respectively), FLOW also influenced the abundance (r = 0.09*), while ALT influenced the taxonomic richness (0.09*). Both Shannon and evenness were influenced by ALT (r = 0.17* and r = 0.18* respectively), SSP also influenced Shannon (r = 0.18**).
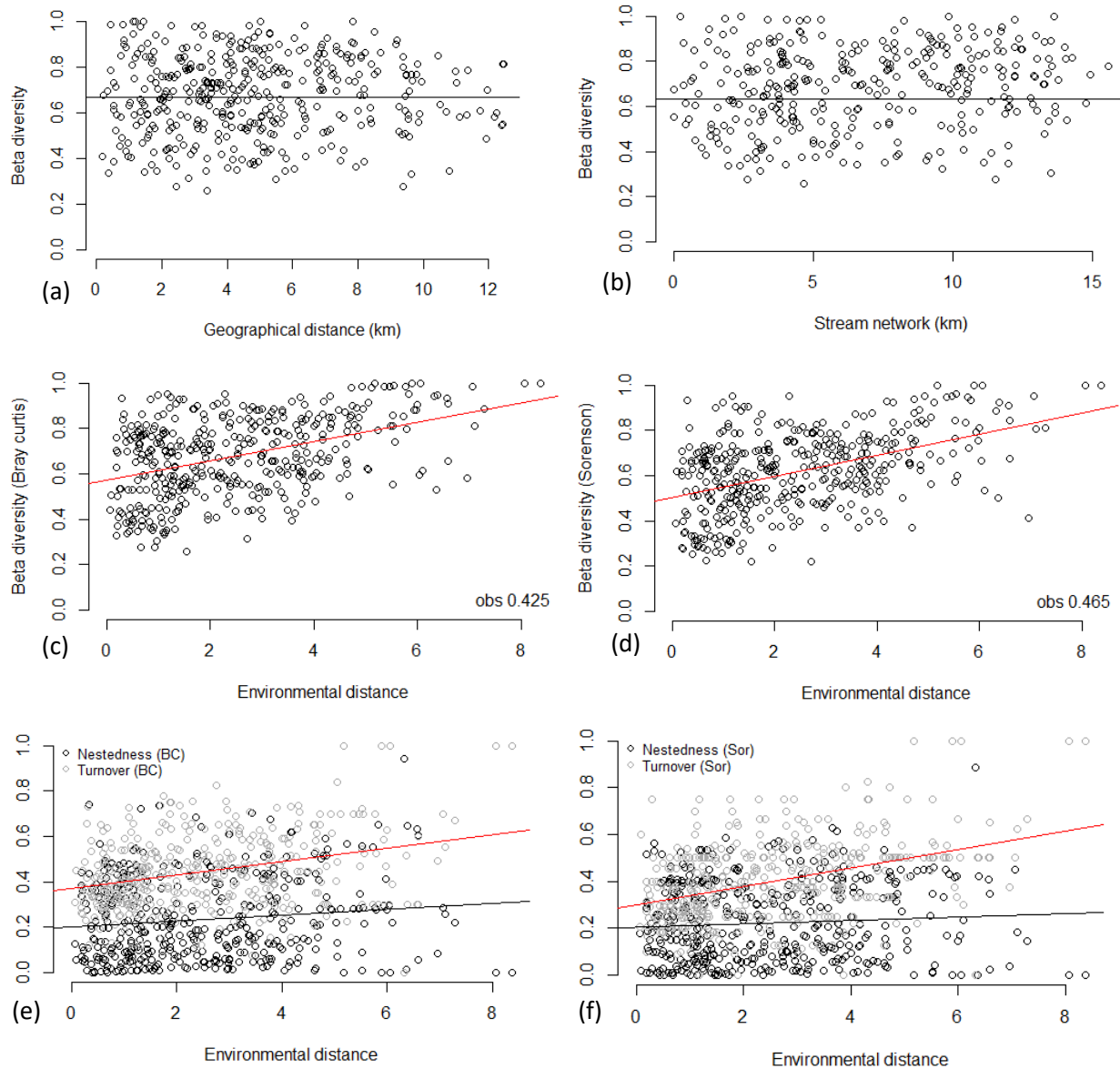
Figure 7. Scatter plot of the beta-diversity vs. (a) both geographical and (b) stream network distance. Scatter plot of the beta-diversity calculated from (c) Bray-Curtis and (d) Sorensen methods vs. environmental distance. Scatter plot of the nestedness (open black dots) and turnover (open grey dots), from both (e) Bray-Curtis and (f) Sorensen methods vs. environmental distance. Lines correspond to the prediction of the linear regression models; the red color indicates a significance.

4. DISCUSSION

Our study aimed to examine the benthic macroinvertebrate spatial distribution in a highly glacierized catchment. Our results showed that environmental filtering alone explained the macroinvertebrate community structure. Overall, the glacial cover catchment was the most responsible for structuring the communities, and abundance and taxonomic richness decreased as the glacial influence increased.

Environment characteristics of the different categories of streams

As expected, our results showed a significant difference of turbidity, discharge, and conductivity, among the five stream types. However, we observed no significant difference in the mean temperature, while we were expecting a lower temperature, and higher mean of dissolved oxygen for the glacier-fed rivers (Milner & Petts, 1994). Indeed, previous studies showed that water temperature in highly glacial-influenced streams do not exceed 2°C even in summer, while temperature punctually measured in our stream sites never reached temperature below 4°C, even for the closest sites to the glacier. Firstly, some of our glacier-fed study site had a low discharge, and were relatively farther from the glacier margin, that led to a warmer water temperature (Malard *et al.*, 2003), and lower oxygen, as both variables were strongly correlated. Conversely, some rivers with no apparent glacial influence exhibit a very low temperature, which reduce the disparity between our categories. On the other hand, as expected for glacier-fed streams, the discharge demonstrated significant higher values than streams with mix and no glacial influences. The melted water contains a high level of sediment coming from the bedrocks, the glacial flour, that is dragged into the river and contributes to its turbidity, which was consistent with the high value of turbidity found in our glacier-fed streams. However, we observed a surprisingly low discharge and turbidity in the site where the glacial influence was high. This can be explained by the existence of a water drainage installed directly at the glacier snout of Tour; the water is taken away as it melts, leading to a lower contribution to the mainstream flow. Finally, the conductivity was significantly higher in streams with glacial influence than groundwater-influenced, which supports the idea streams with water contribution from either glacier and snowmelt water. However, some groundwater sites in our study revealed very low conductivity (< 20 NTU). This result suggested that, although some streams do not show an apparent connection with the glacier, they can actually be the resurgence of rapid water transfer from the glacier and snowmelt infiltration. Thus the glacial index used in our study in order to separate our categories appears adequate, yet, it should be carefully used as exceptions exist. In particular, we showed that water temperature and discharge parameters used to assess the type of stream, should also be treated cautiously, as anthropogenic changes may influence them (Brown *et al.*, 2015; Webb *et al.*, 2008). Additionally, the glacial cover catchment was not successful in discriminate the glacial torrent from the smaller glacial rivers. In order to acutely separate the alpine rivers, both glacial index and other environmental parameters should be considered all together.

Benthic macroinvertebrate assemblages

The structure of macroinvertebrate communities showed significant dissimilarities between each pair of stream categories. No difference was found for the Shannon and Pielou's diversity indices, meaning that each study sites had a relatively equal numbers of individuals belong to each species. As expected (Milner and Petts, 1994), taxonomic richness and abundance increased progressively downstream from the glacial snout. These results were similar to previous studies where glacier-fed streams demonstrated a lower abundance and
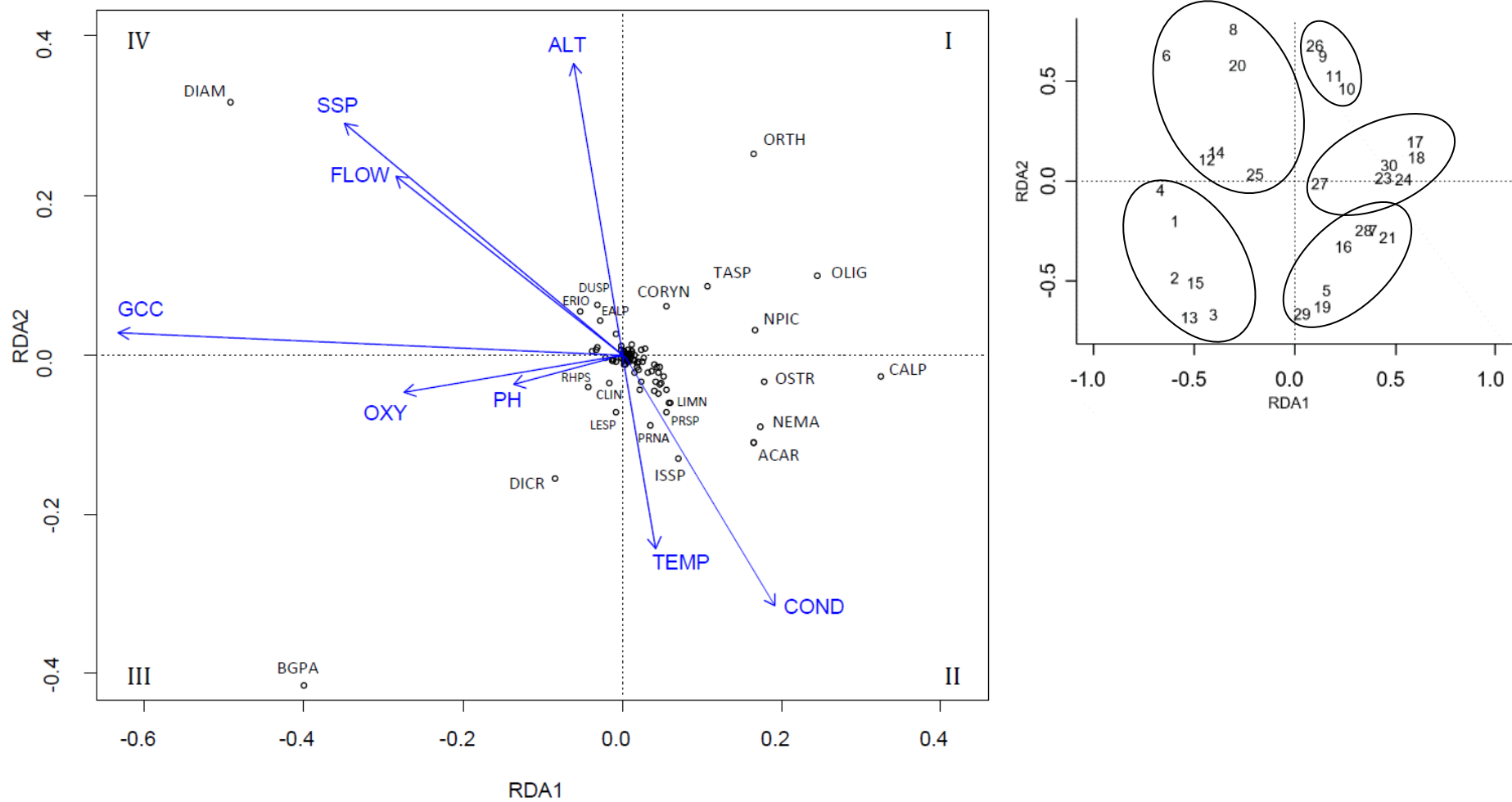
Figure 8. RDA of the Hellinger-transformed taxa abundance data constrained by all the environmental parameters. For a better visualization the sites are shown separately. Taxa shown are: Diamesinae (DIAM), Orthocladiinae (ORTH), Oligocheta (OLIG), Nematoda (NEMA), Eriopterini (ERIO), Dugesia (DUSP), Corynoneura (CORY), Crenobia alpina (CALP), Acarina (ACAR), Dicranota (DICR), Baetis gp. alpinus (BGPA), Nemurella picteti (NPIC), Isoperla (ISSP), Tanytarsini (TASP), *Limnephilidae* (LIMN), *Protonemura* (PRSP), *Protonemura nimborella* (PRNA), *Clinocerinae* (CLIN), *Rhithrogena* (RHPS), *Epeorus alpicola* (EALP), and *Leuctra* (LESP).

diversity (Castella *et al.*, 2001; Maiolini and Lencioni, 2001). Furthermore, the relative abundances of Diptera and EPT genera in the study sites did not changed along the glacial gradient, while we were expecting a higher proportion of EPT and lower proportion of Diptera farther from the glacier and *vice versa*. The proportion of EPT was not significant due to the high proportion of Ephemeroptera distributed widely across our study sites.

The longitudinal succession of taxa predicted by the model of Milner & Petts (1994) was basically supported by the present results with some exceptions. Differences among assemblages were mostly due to the total and relative abundances of taxa than occurrence of certain taxon. In general, we observed that Chironomidae was the predominant constituent of the macroinvertebrate assemblage in our study, as reported for many glacier-fed streams in Europe (Castella *et al.*, 2001; Ilg *et al.*, 2006; Steffan, 1971), and America (Elgmork and Saether, 1970; Cauvy-Frauniế *et al.*, 2015). Larvae of the family Diamesinae and Baetidae, particularly *Baetis alpinus,* were dominant in glacial streams. Although considered cold-stenotherm organisms (Oliver, 1971), some Diamesinae individuals occurred at warner temperature, further from the glacier (Lods-Crozet *et al.*, 2001b). Although, *Baetis alpinus* was present at high glacial influence, its abundance significantly increased with increasing distance from the glacier margin. Diptera such as Orthocladiinae, Tanytarsini, and Dicranota were broadly distributed among all sites, but their abundance increased as the abundance of Diamesinae decreased.

Environment filtering vs spatial variables

Multiple studies illustrated that both environmental and spatial parameters influenced the macroinvertebrate communities in both glacial and non-glacial stream network (Sarremejane *et al.*, 2017; Göthe *et al.*, 2013; Tonkin *et al.*, 2016). Other findings support evidence for local environmental factors having a greater impact on macroinvertebrate community structure, especially depending on the region scale, and dispersal abilities (Mykrä *et al.*, 2007; Canedo *et al.*, 2015; Heino et al., 2015b). In our study, we found that spatial variables, i.e. geographical and network distances, did not affect community dissimilarity. This result was similar to the study performed by Canedo *et al.* (2015) who examined invertebrate community distribution on a comparable spatial scale, in a highly heterogeneous watershed. Note that all studies were based on the dispersal ability of the macroinvertebrate which was not analyzed here. Therefore, it would be worth examining the geographical and watercourse distance using dispersal modes. Furthermore, our watershed exhibited a particularly high spatial heterogeneity on environmental conditions, linked to the variability in water source, streams size, altitude, and its human activities, so environmental dissimilarity could have overcome the potential effect of spatial variation. While glaciers are usually found at a relatively high altitude in the Alps, the three valley glaciers present in our study catchment, 'Tour', 'Mer de Glace' and 'Argentière', still flow down the valley until 1500 m at the lowest. This led to having both glacial torrent and groundwater-fed streams in the valley, at same altitude, and extremely close from each other. Thus, very different communities were found at very low distances. Therefore, in our specific case, a particularly highly glacierized catchment (GCC > 30%), the hypothesis stating that "everything is related to everything else, but near things are more related than distant things" (Tobler, 1970) was not verified. On the contrary, our result showed that differences in environmental conditions significantly explained the community dissimilarity among stream sites, based on both abundance and presence-absence. In our study, we found that the community dissimilarity was mostly due to the turnover component, meaning that the dissimilarity was due to change in and/or addition of species (versus subset of species – nestedness). For example, taxa such as *Nemurella picteti*, a Plecoptera, was only

found in groundwater-fed streams. We also observed an increase in taxonomic richness which is consistent with our turnover component.

Community structure and environment filtering

Temperature is usually a key factor structuring the macroinvertebrate composition (Ward & Stanford, 1982; Rossaro, 1991). It also is one of the most apparent abiotic variables related to changes along altitudinal gradients (Ward, 1985; Jacobsen *et al.*, 1997)*.* The influence of the temperature was not observed here, but as explained earlier, temperature between the categories of streams did not differ for various reasons. Therefore, the usual effect of temperature on macroinvertebrate communities could have been override by other environmental parameters. Overall, among all environmental parameters examined in this study, the glacial cover catchment, was the main factor driving macroinvertebrate community structure, followed by the water flow and altitude. Both total abundance and taxonomic richness decreased with increasing glacial influence, a pattern commonly observed in glacial study (Khamis *et al.*, 2016; Cauvy-Fraunié *et al.*, 2014; Jacobsen *et al.*, 2012; Brown *et al.*, 2007). The glacial influence often leads to harsh environmental conditions with high level of turbidity, high fluctuation in water discharge, low temperatures and conductivity. High discharge negatively impacts the stability of the stream, especially during high snowmelt season, sweeping away the substrate and making the establishment of life very difficult. Furthermore, the high turbidity and low temperature limited benthic primary production (Cordone & Kelley, 1961; Henley *et al.*, 2000). For that reason, only specialized species with adaptive traits survived and dominate in this harsh environment, such as *Diamesinae*. This was confirmed with the fact that turbidity significantly influenced the Shannon index. Finally, when looking at the sites within our categories in contrast with the assemblage of sites based on relative proportion of macroinvertebrate species, we can see that they are slightly different. For instance, one of our site define as mix influence actually showed a typical glacier-fed macroinvertebrate community. Hence, in order to reliably identify the contribution of water source, it is necessary to take both environmental parameters and bio indicators into account.

CONCLUSION

Our results demonstrated the importance of the glacial influence in structuring the spatial distribution of macroinvertebrate community in an alpine catchment. Under the ongoing climate change, glacier shrinkage is accelerating, leading to a change in the relative contribution of meltwater to stream flow, and consequently on macroinvertebrate communities. These changes may at first increase the environmental heterogeneity but will undoubtedly lead to a homogenization of both environment and taxonomic richness (Hotaling *et al.*, 2017; Cauvy-Fraunié *et al.*, 2015). Not only macroinvertebrate will be impacted, other studies already showed the possible effect of climate change on other communities, such as fishes or seaweeds (Milner et al., 2017; Pörtner *et al.*, 2010; Harley *et al.*, 2012). As the role of macroinvertebrate communities within alpine rivers is still an ongoing evaluation, the disappearance of species related to glacier could crucially alter the ecosystem functioning. Since it may be impossible to prevent the undesirable loss of such species, our results provide further support for the need of better strategic conservation approaches, including taking measure to reduce greenhouse gas emissions.

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6. SUPPLEMENTARY INFORMATIONS

Figure S1. Example of study site sampled. (A) Argentière 12, (B) Mer de Glace 20, (C) Arve 14, (D) Praz 18, (E) Blait 19, and (F) Tour 1. Pictures taken from the field work season 2017 ©Sophie Cauvy.

High glacial influence streams with a high concentration of suspended sediment from the glacial flour

Groundwater and mix water source influence streams
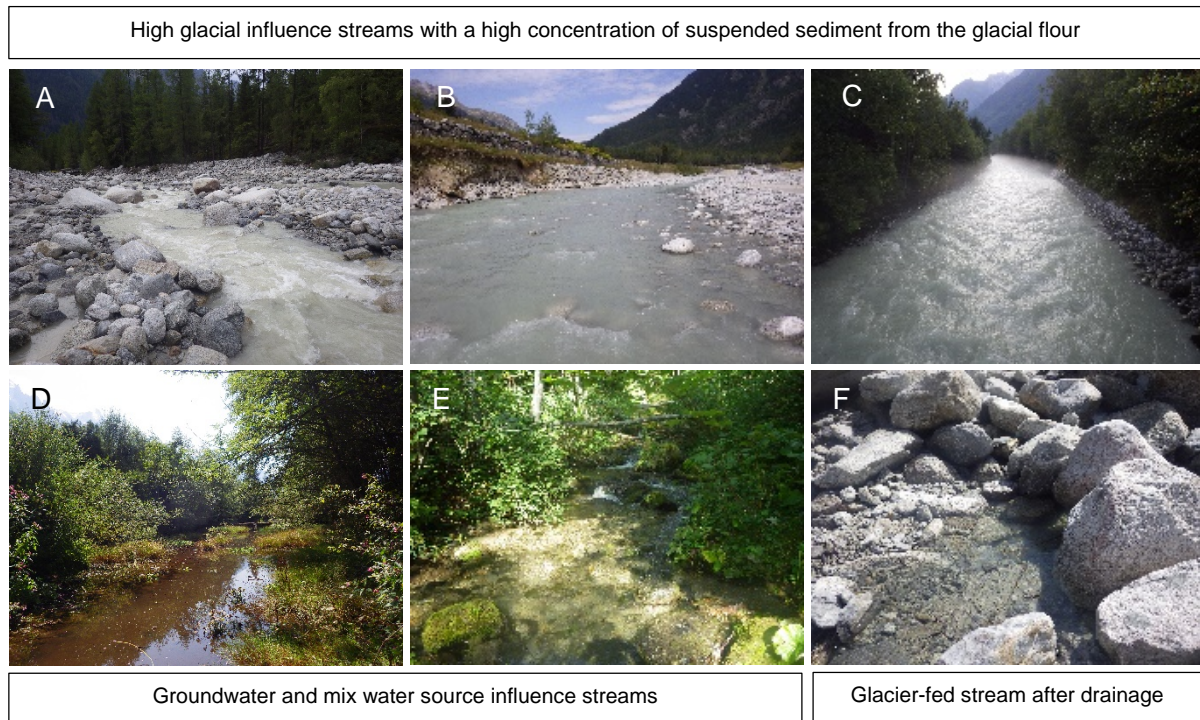
Glacier-fed stream after drainage

Figure S2. Example of taxa collected in our study site. (A) *Baetis*, (B) *Diamesinae*, (C) *Isoperla*, (D) *Creniobia alpina*, (E) *Drusinae*, and (F) *Hydracarina*. Pictures taken from http://www.perla.developpement-durable.gouv.fr/.

Table S1. Environmental data with the altitude (ALT), temperature (TEMP), potential hydrogen (PH), conductivity (COND), turbidity (SSP), dissolved oxygen (OXY), water discharge (FLOW), and glacial cover catchement (GCC). Sources refer to Table 1.

ID	Sources	ALT	TEMP (ºC)	PH	COND (µs.cm^{-1})	SSP (NTU)	OXY (mg.L^{-1})	FLOW (L.s^{-1})	GCC (%)
7	A	1199	8.7	8.08	161.7	0.1	10.15	0.9	0
9	A	2037	5.0	8.94	18.6	2.2	10.42	10.0	0
16	A	1424	8.0	8.11	609.0	5.0	10.25	7.5	0
17	A	1112	14.0	7.82	365.0	2.6	1.75	2.0	0
18	A	1084	11.0	7.27	306.0	0.5	5.29	10.0	0
21	A	1118	9.0	8.00	133.5	0.2	10.65	7.0	0
24	A	1087	10.4	8.62	67.9	0.0	9.62	80.0	0
28	A	1275	7.6	7.78	118.3	2.1	10.59	1.0	0
30	A	1099	12.7	7.55	106.2	1.4	8.71	0.5	0
5	B	1418	10.7	7.91	46.6	1.2	9.52	53.0	0
23	B	1110	8.5	7.93	66.2	8.5	10.69	15.0	0
27	B	1062	7.1	7.90	98.6	7.0	10.88	70.0	0
3	B	1507	18.0	8.40	517.0	3.5	7.90	20.5	0
10	B	2072	7.6	7.75	14.7	1.4	9.28	7.0	0
29	C	1203	5.9	7.87	56.2	5.9	11.14	100.0	1.32
8	C	1970	10.8	7.92	15.5	44.2	9.10	55.0	3.25
26	C	2348	12.0	7.79	15.2	8.2	8.53	80.0	3.42
11	C	2065	9.2	8.56	17.6	8.5	9.48	266.0	10.57
19	C	1089	12.0	7.87	47.2	6.0	9.73	50.0	11.67
25	C	1075	10.7	7.54	29.4	152.0	10.90	2000.0	16.50
13	D	1261	12.0	8.56	232.0	46.0	9.68	500.0	24.64
15	D	1193	8.7	8.31	120.0	17.0	10.57	680.0	27.87
14	D	1025	4.5	7.93	34.7	162.0	11.81	18000.0	30.48
4	D	1387	12.4	8.23	8.2	3.8	9.01	276.0	30.60
12	D	1304	5.1	8.18	16.3	635.0	11.43	200.0	41.79
22	E	2392	7.1	8.14	7.6	106.0	9.70	4.0	43.62
20	E	1082	10.0	7.98	19.4	405.0	10.64	5000.0	48.56
6	E	1098	3.4	7.78	13.5	600.0	11.79	12000.0	49.16
1	E	1658	9.9	7.82	13.4	12.0	9.15	9.0	53.30
2	E	1497	11.5	7.80	30.4	3.0	9.04	27.2	57.70

Table S2. Biodiversity index table

| Site	Taxonomic richness	Diversity	Species evenness	Total abundance	EPT proportion	Diptera proportion
7	42	3.069	0.932	931	0,48	0,25
9	19	0.612	0.246	3735	0,01	0,94
16	28	2.712	0.909	874	0,39	0,30
17	23	1.642	0.749	3461	0,22	0,18
18	37	2.319	0.855	2916	0,39	0,15
21	32	2.608	0.885	748	0,34	0,27
24	21	2.385	0.867	481	0,32	0,31
28	32	2.486	0.876	1475	0,29	0,25
30	27	2.413	0.839	717	0,11	0,26
5	30	2.487	0.807	682	0,66	0,17
23	20	1.795	0.742	1870	0,02	0,27
27	33	1.252	0.504	2690	0,22	0,74
3	6	1.536	0.729	110	0,90	0,10
10	25	1.833	0.737	1401	0,05	0,58
29	26	2.306	0.819	640	0,74	0,07
8	4	1.182	0.705	15	0,07	0,93
26	10	1.556	0.726	667	0,00	0,92
11	23	1.504	0.631	1750	0,05	0,70
19	30	2.809	0.894	523	0,51	0,10
25	21	2.227	0.788	170	0,36	0,61
13	8	1.481	0.692	152	0,71	0,29
15	9	1.797	0.796	91	0,56	0,44
14	7	2.043	0.885	30	0,30	0,63
4	9	1.712	0.744	116	0,40	0,58
12	7	1.617	0.763	88	0,36	0,61
20	9	2.024	0.877	19	0,11	0,74
6	2	0.500	0.400	5	0,20	0,80
1	9	1.462	0.663	74	0,69	0,31
2	13	1.670	0.717	217	0,81	0,19
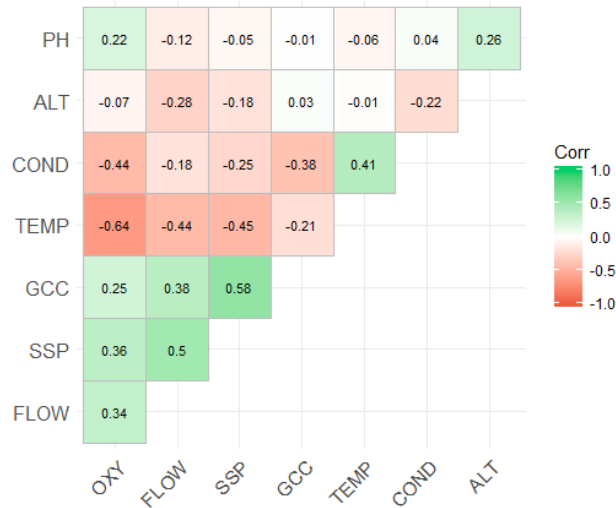
Figure S3. Pearson's correlation coefficient (r) between 8 explanatory environmental variables.
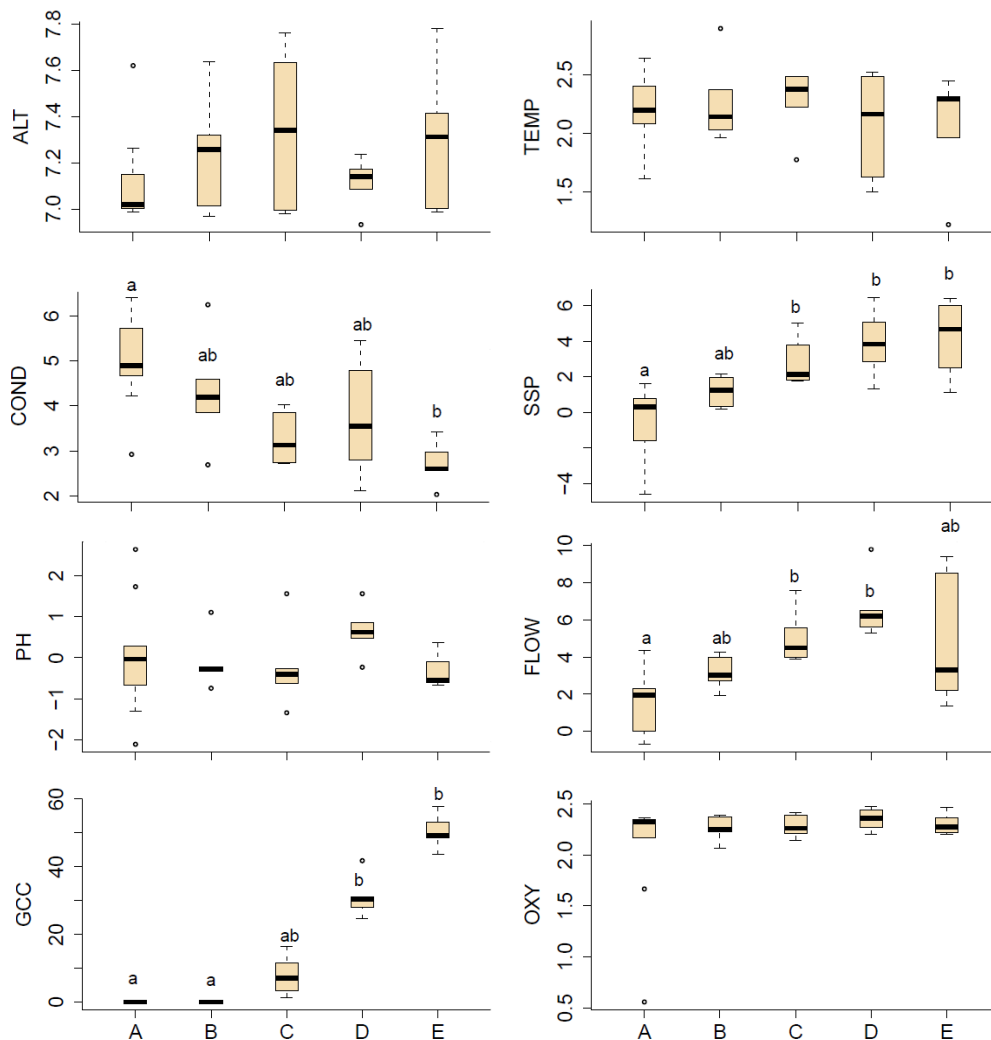

Figure S4. Boxplot of the environmental parameters among the five categories of water sources. Different letters indicate a significant difference.

Table S3. Results of the similarity percentage (SIMPER) analysis among the 5 categories and the analysis of similarity (ANOSIM) of variance. Only the first 5 taxa are presented.

High vs medium (Global test. R = 0.2. p-value = 0.077)   Average dissimilarity = 0.554

Taxa	Average abundance High / Medium		Cumulative contribution (%)
BGPA	2.48	3.44	16.9
DICR	0.173	2.08	31.6
RHSP	0.448	1.61	41
ORTH	1.41	2.05	49.3
DIAM	2.45	2.48	55.8

High vs low (Global test. R = 0.21. p-value = 0.117)   Average dissimilarity = 0.718

Taxa	Average abundance High / Low		Contribution (%)
ORTH	1.41	4.05	8.66
BGPA	2.48	2.96	16.7
CALP	0	2.72	22.9
TASP	0	2.20	28.8
OLIG	0.17	2.21	34.1

High vs mix (Global test. R = 0.563. p-value = 0.038)   Average dissimilarity = 0.796

Taxa	Average abundance High / Mix		Contribution (%)
ORTH	1.41	4.72	6.53
BGPA	2.48	4.26	12.8
OLIG	0.17	3.49	18.8
DIAM	2.45	0.94	23.9
DICR	0.17	2.17	28.9

High vs source (Global test. R = 0.938. p-value = 0.003)   Average dissimilarity = 0.852

Taxa	Average abundance High / Source		Contribution (%)
CALP	0	4.53	7.4
ORTH	1.41	5.58	14.3
OLIG	0.17	4.08	20.4
NEMA	0	3.30	25.6
ACAR	0.17	3.52	30.6

Medium vs low (Global test. R = 0.44. p-value = 0.019)   Average dissimilarity = 0.677

Taxa	Average abundance Medium / Low		Contribution (%)
BGPA	3.44	2.96	8
ORTH	2.05	4.05	14.2
CALP	0	2.72	20.3
TASP	0	2.20	26.1
DICR	2.08	0.95	31.7

Medium vs mix (Global test. R = 0.556. p-value = 0.044)   Average dissimilarity = 0.697

Taxa	Average abundance Medium / Mix		Contribution (%)
OLIG	0.22	3.49	6.39
ORTH	2.05	4.72	12.2
DIAM	2.48	0.94	17.6
SIMU	0.22	2.98	22.9
CALP	0	2.96	28.3

Medium vs source (Global test. R = 0.995. p-value = 0.001)   Average dissimilarity = 0.788

Taxa	Average abundance Medium / Source		Contribution (%)
CALP	0	4.53	7.6
OLIG	0.22	4.08	13.7
ORTH	2.05	5.58	19.6
NEMA	0.14	3.30	24.7
ACAR	0.28	3.52	29.6

Low vs mix (Global test. R = 0 p-value = 0.819)   Average dissimilarity = 0.59

Taxa	Average abundance Low / Mix		Contribution (%)
BGPA	2.96	4.26	5.7
OLIG	2.21	3.49	11
ORTH	4.05	4.72	15.8
DIAM	2.30	0.94	20.6
NEMA	0.91	2.72	24.9

Low vs source (Global test. R = 0.283. p-value = 0.014)   Average dissimilarity = 0.612

Taxa	Average abundance Low / Source		Contribution (%)
CALP	2.72	4.53	4.5
NEMA	0.91	3.30	8.9
ACAR	0.83	3.52	13.3
OLIG	2.21	4.08	17.5
OSTR	0.67	2.64	21.6

Mix vs source (Global test. R = 0.07. p-value = 0.297)   Average dissimilarity = 0.538

Taxa	Average abundance Mix / Source		Contribution (%)
OLIG	3.49	4.08	4.3
OSTR	0.50	2.64	8.4
ORTH	4.72	5.58	12.2
CALP	2.96	4.53	16
NEMA	2.72	3.30	19.7

Structure des communautés de macroinvertébrés dans un bassin versant sous forte influence glaciaire

Les écosystèmes alpins font partie des habitats les plus impactés par le changement climatique. Les rivières alpines, formant un réseau dendritique dense, ont des caractéristiques hydrauliques et environnementales spécifiques causés par la différence des apports en eaux : souterraines, pluie, fonte de neige et de glaciers. Ces habitats très hétérogènes présentent une vaste variabilité spatiale et richesse spécifique d'invertébrés aquatiques. Comprendre comment le changement climatique, notamment l'augmentation des températures et l'augmentation de la fonte des glaciers, impacte la biodiversité aquatique dans ces cours d'eau représente un futur défi pour la recherche. Dans cette étude, nous avons déterminés les facteurs majoritairement responsables de la structuration des communautés d'invertébrés dans un bassin versant sous forte influence glaciaire. Notre étude, basée sur l'analyse de 30 sites à travers de le bassin versant de l'Arve, dans les Alpes, a révélé une forte influence du recouvrement glacier sur la structure des communautés. Étonnement, la température, pourtant qualifié comme étant un facteur clé, n'a pas révélé d'influence significative. Nos résultats supportent l'idée que le filtre environnemental, plus que la variabilité spatiale, était le paramètre influençant le plus la structure des communautés à l'échelle du bassin versant. Le rôle des assemblages de macroinvertébrés dans les rivières alpines reste encore peu connu et pourrait crucialement altérer le fonctionnement des écosystèmes.

Mots-clés : faune benthic, filtres environnementaux, variation spatial, recouvrement glacier, changements climatique

Macroinvertebrates community structure in a highly glacial catchment

Alpine ecosystems are among the most affected habitats globally by climate change. Alpine rivers, shaped into dendritic networks, have specific hydrological and environmental conditions due do their different water contribution sources: groundwater, rainfall, snowmelt, and glacial meltwater. They are very heterogeneous environment which possess a large spatial variability and diversity of aquatic macroinvertebrates. Understanding how climate change, especially, the associated environmental changes, such as warming temperature and increase in glacier run-off, impacts aquatic biodiversity in such streams represents a future research challenge. Here, we aim to determine major factors responsible for shaping community structure of benthic macroinvertebrate in a highly glacierized watershed. Based on an analysis of 30 sites across the watershed of Arve, in the French Alps, we found that the glacial cover catchment played an important role in determining community structure. Surprisingly, temperature did not show a significant impact whereas it usually a key factor structuring the macroinvertebrate composition. Our results supported the idea that environmental filtering, more than spatial variability, was the dominant parameter shaping our macroinvertebrate communities at the basin level. As the role of macroinvertebrate communities within alpine rivers is still an ongoing evaluation, the disappearance of species related to glacier could crucially alter the ecosystem functioning.

Keywords: benthic fauna, environmental filtering, spatial variation, glacial cover catchment, climate change