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Diversity patterns of aquatic macroinvertebrates across stream types and glacial influence in a tropical high-Andean catchment

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Certifico que la tesis de la maestría en Biología de la Conservación del candidato Rodrigo Eduardo Espinosa Barrera ha sido concluida de conformidad con las normas establecidas; por lo tanto, puede ser presentada para la calificación correspondiente.

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1. RESUMEN

La biodiversidad y la composición de las comunidades de los macroinvertebrados acuáticos de los altos-Andes fueron analizadas en 51 sitios de estudio que incluyen una variedad de riachuelos que fueron agrupados de acuerdo a sus orígenes y al porcentaje de la cobertura de glaciar en la cuenca. Para describir los patrones de la diversidad y distribución de los macroinvertebrados y para identificar taxa comunes, raros y exclusivos a lo largo de este gradiente de origen del río, se realizaron correlaciones bivariadas, modelos lineales generales, análisis del porcentaje de similitudes y análisis de correspondencias canónicas. Parámetros relacionados con la densidad y diversidad tuvieron una relación negativa con la altitud, así como otros factores ambientales como la temperatura y conductividad. Análisis múltiples de regresión indicaron que la altitud, la materia orgánica, el ancho promedio, la temperatura promedio, el pH y la turbidez fueron las principales variables en predecir los patrones de la composición de la biodiversidad a lo largo de estos diferentes tipos de ríos. Los ríos kryal (1, 2 & 3) contribuyeron con la mayoría de taxa exclusivos y raros, los tipos de ríos kryal 3 y rithral tuvieron la mayor biodiversidad en términos de alpha y beta diversidad. El análisis de porcentaje de similitudes mostró que *Hyalella* sp., *Andesiops* sp. y *Anomalocosmoecus* sp. tuvieron la mayor contribución a la diferencia significativa de las comunidades. La velocidad del agua, la altitud, la profundidad del río, la cobertura de glaciar en la cuenca, la turbidez, la distancia al glaciar, la conductividad y la temperatura fueron los factores más influyentes en el moldeamiento de las comunidades, siendo Podonominae Tipo 4, Staphylinidae y Podonominae Tipo 1 más comunes en los sitios altos de glaciar, y Corixidae y Ephydridae estuvieron solamente presentes en los ríos sin influencia de glaciar (krenal y rithral). En términos de conservación de la biodiversidad, este estudio confirma que existe una necesidad urgente de incrementar el conocimiento de la biodiversidad de los ríos alto-Andinos del mundo, y en especial los ríos tropicales, para así tener un mejor entendimiento de la biodiversidad regional de este ecosistema de agua dulce vulnerable al cambio climático.

Palabras clave: análisis de porcentaje de similitudes, análisis de correspondencias canónicas, biodiversidad, conservación, modelos lineales generales, krenal, kryal, rithral.

2. ABSTRACT

The biodiversity and community composition of high-Andes aquatic macroinvertebrate was analyzed in 51 stream study sites which include a variety of streams that were grouped according to their origins and to the percentage of glacier coverage in the catchment. To describe the macroinvertebrate diversity and distribution patterns and to identify common, rare and exclusive taxa along this stream origin gradient, bivariate correlations, generalized linear models, similarity percentage analyses and canonical correspondence analyses were performed. Density and diversity related parameters had a negative relation to altitude, as well as other environmental parameters such as temperature and conductivity. Multiple regression analyses showed that altitude, organic matter, mean width, mean temperature, pH and turbidity were the main variables in predicting biodiversity composition patterns across this different stream types. Kryal stream types (1, 2 & 3) contributed with the majority of exclusive and rare taxa, kryal 3 and rithral stream types had the greatest biodiversity in terms of alpha and beta diversity. Similarity percentage analysis showed that *Hyalella* sp., *Andesiops* sp. and *Anomalocosmoecus* sp. had the major contribution to the significant difference in their communities. Water velocity, altitude, water depth, glacier coverage in catchment, turbidity, distance from glacier, conductivity and temperature were the most influential factors in molding the species presence in these streams, being Podonominae Type 4, Staphylinidae and Podonominae Type 1 more common in the highest glacier sites and Corixidae and Ephydridae being present in streams with no glacier influence (krenal and rithral). In terms of biodiversity conservation, this study confirms that there is an urgent need in increasing the knowledge of high-Andean stream biodiversity of the world with special emphasis in the tropics in order to have a better understanding of the regional biodiversity of this highly vulnerable freshwater ecosystem to climate change.

Keywords: biodiversity, canonical correspondence analyses, conservation, generalized linear models, krenal, kryal, rithral, similarity percentage analyses.

3. INTRODUCTION

Community ecology aims at explaining the patterns of distribution, abundance and interaction of species (Leibold et al. 2004). A “Metacommunity” is defined as a set of local communities that are linked by dispersal of multiple potentially interacting species (Gilpin 1991; Wilson 1992). If species co-occur less than expected by chance, why should they do so? This question has been at the heart of community ecology in the last few decades, and several not mutually exclusive answers to the question have been proposed (Heino & Grönroos 2013). A number of reasons suggest why environmental heterogeneity across a set of sites should affect species segregation at the same scale in a metacommunity (i.e., a set of local communities connected by dispersal; Leibold et al. 2004). First, potentially competing species may be segregated among localities but co-occur in a metacommunity if they are forced to live in different environmental conditions due to competitive exclusion in suboptimal environments (Chase & Leibold 2003; Tokeshi 2009). Second, environmental heterogeneity across sites may be important for species co-occurrence even in the absence of strong competitive interactions. This is because increasing environmental heterogeneity should lead to increased species richness (Huston 1994; Rosenzweig 1995) and/or increasingly segregated distributions of species across sites (Bradley & Bradley 1985; Ellwood et al. 2009). Increasing variations in habitat conditions should lead to stronger species sorting and, thereby, increasing variation in community composition across sites (Heino & Mykrä 2008; Brown & Swan 2010).

Regional diversity, γ-diversity, can be partitioned in two components: α-diversity, i.e. diversity of species within sites which can be measured as species richness or with diversity indices (e.g. Fisher’s alpha, Shannon-Wiener, etc.); and β-diversity, i.e. species turnover calculated as the community dissimilarity among sites (Costa & Melo 2008). The community assembly, longitudinal patterns, and the relationships between environmental variables and natural communities are expected to be similar in streams that are located nearby (Finn et al. 2013). Understanding beta diversity is crucial for ecology, biogeography and evolution, as it could help to reveal the processes that mold biotic communities and to design areas for nature conservation (Condit et al. 2002; McKnight et al. 2007; Soininen et al. 2007; Anderson et al. 2011). Beta diversity provides a link between local (α) and regional (γ) diversity (Whittaker 1960; Whittaker 1972; Vellend 2010; Anderson et al. 2011) thereby allowing a better analysis of natural community dynamics than single species richness measures (Wang et al. 2012).

In streams with extreme environments (i.e. low temperature, high instability, isolation) like glacier-fed streams, in particular near the glacier, strong niche selection is expected to filter species from a regional *pool*, therefore producing similar communities with a more predictable composition than those in less extreme habitats located far away from the glacier snout (Leibold et al. 2004; Chase 2007). This is because harsh environmental conditions deterministically filter non-tolerant species from the regional *pool* (Chase 2007). Previous studies of streams under glacier influence found that local richness decrease with increasing glacial influence (Milner & Petts 1994; Milner et al. 2001; Jacobsen et al. 2010; Jacobsen et al. 2012). Nevertheless, (Espinosa et al. 2010; Jacobsen & Dangles 2012; Cauvy-Fraunié et al. 2014) found local richness peaked at intermediate levels of glacier influence due to higher species turnover rates throughout this gradient. The low taxonomic and functional richness of the aquatic fauna in catchments near glaciers in the Alps, Andes and the Artic (Milner et al. 2001; Ilg & Castella 2006;

Milner et al. 2008; Milner et al. 2009; Jacobsen et al. 2010), is thought to be limited in particular by low temperatures, hydrologic instability, and streambed disturbance (Milner et al. 2001). Improving our knowledge about mechanisms structuring those communities could help us to estimate the degree on which the biodiversity of a particular region is being affected by human and climatic alterations.

In this study, we examined the effect of environmental instream conditions on benthic macroinvertebrates in 51 stream sites in the tropical Andes. Our aims were to explore the local (α), among sites (β) and regional (γ) diversity of streams with different types of origins. Our main objectives were: (1) to describe macroinvertebrate diversity and spatial distribution patterns in relation to environmental variables and stream origin, and (2) to identify common, rare and exclusive taxa along a stream origin gradient. We hypothesized that glacier-fed and non-glacier fed streams shelter rare and probably endemic taxa that contribute to regional diversity of high-Andean tropical streams and that the continued shrinkage and a probable future loss of glacier contribution of glaciers will extinguish these endemic rare taxa.

4. MATERIALS AND METHODS

4.1. Study area

The study was conducted at 51 sites located in the Ecological Reserve of Antisana in the eastern cordillera of the Equatorial Andes (0°28’S, 78°09’W, 5760 m a.s.l.), *c.* 50 km south of the equator line. All sites were tributaries of the Río Antisana, headwater of the Napo River, a main tributary of the upper Amazon River. The ablation zone extends from *c.* 5150 m to the glacier snouts at 4730–4850 m a.s.l. Antisana is a Quaternary stratovolcano, with an estimated age of about 800 000 year, located on a basement of Mesozoic to Quaternary volcano-sedimentary and metamorphic rocks (Bourdon et al. 2002); the last eruption was in 1801 and it is currently dormant (Hall et al. 2008). Air temperature, humidity and radiation do not vary systematically during the year, while precipitation, cloud cover and wind speed show more seasonal variability in the study region (Cadier et al. 2007). The annual precipitation is about 800 mm, of which much falls as snow and hail (Maisincho et al. 2007). Mean annual air temperature varies from about 3.7 °C at the lowest site to 1.3 °C at the upper site (Cáceres et al. 2005). The ‘Crespo’ glacier (G12) which covers an area of 1.7 km^2, and with an ablation zone extending from 5150 to 4730 m a.s.l. has a retreat rate of 10-20 m per year (Vuille et al. 2008; Jacobsen et al. 2010), and glacier 15 has undergone a massive retreat event (up to 75%) from 1956 to 1998 (Francou et al. 2000), glacier 14 has not been studied since there is not field monitoring stations installed.

All kryal streams originated at three glaciers on Mt. Antisana. Stream sites were first divided into three main groups, depending on their origin: kryal (glacier-fed), krenal (comprising streams that originate from water springs), and rithral (corresponding to streams formed from precipitation, snowmelt and water accumulation on the drainage basins of the catchments) according to Brown et al. 2003. To our knowledge, this is the first study to investigate the contribution of krenal and rithral streams to general diversity patterns in glaciarized catchments. Then, on all the kryal streams, we applied a sub-classification depending on the percentage of glacier coverage in the catchment (GCC) (Cauvy-Fraunie et al. 2013). The three western glacier snouts that gave origin to all the kryal (glacier-fed) streams were (Fig. 1): glacier snout G12 (originating from glacier 12, also called Crespo, with an extension of 1.7 km²); glacier snout G14 (originating from glacier 14, extension of 0.65 km²) and glacier snout G15 (originating from glacier 15, extension of 0.46 km²). In the present study, all kryal sites were divided in three sub-groups depending on the percentage of glacier cover in the catchment, in that sense we had: kryal 1 streams with 6 sites that were located between 4520-4835 m a.s.l. and had a mean of 68.35 % of GCC; kryal 2 streams with 5 sites between 4109-4332 m a.s.l. and a mean of 23.35 % of GCC; and, kryal 3 streams with 16 sites located between 3930-4246 m a.s.l. and a mean of 7.86 % of GCC. The 5 krenal sites were located between 4006-4124 m a.s.l. Finally, the 19 rithral sites were located between 3917-4368 m a.s.l. (Fig. 1, Appendix 1).

4.2. Environmental variables

At each site, we measured water temperature (°C), conductivity (at 25 °C), and pH using a WTW portable meters and turbidity using a Eutech TN-100 Turbidimeter. Current velocity was measured 2-3 times at each sampling site by means of dilution gauging (Herschy 1997). A bucket with a known amount of dissolved salt (volume and conductivity) was added at the upstream end of the 15 – 25 m stream reach and we measured conductivity every 5 or 10 seconds at the downstream end of the reach. Mean current velocity was calculated as the time elapsed for half of the salt to pass the stream reach divided by the length of the reach. Stream slope at each site was measured using transparent plastic tube carrying flowing water from the upstream to the downstream end of the reach. The slope was calculated as the difference between the water level inside the tube when raised until flow stopped and that of the surface of the stream water at the downstream end, divided by the distance between the upstream and downstream end of the tube (ca. 25 m). To quantify the physical stability of the stream, a score system (15–60, with 60 as the most unstable) based on the channel bottom component of the Pfankuch index (Pfankuch 1975) was applied once to each of the 20- to 30-m reaches where invertebrate samples were collected (Appendix 2).

Five cross-sectional transects were selected in a representative reach of each study site in order to include all the possible habitats of the stream. We measured the total width of each transect and made ten depth measurements and ten classifications of the benthic stream mineral substrates which were grouped according to grain size: silt (0.004-0.062mm), sand (0.063-2mm), gravel (2-16mm), pebble (16-64mm), cobble (64-256mm), boulder (>256mm) following the Wentworth Scale (Giller & Malmqvist 1998); we also classified the substrate in algae, macrophytes and moss.

To estimate food resources available for macroinvertebrates, we quantified chlorophyll *a* concentration/biomass of sampled stones and collected the benthic detritus obtained in Surber samples. At each site, nine pebbles were collected at random (but avoiding those with filamentous algae), placed in three containers (three in each) and covered with 96% ethanol for 1–3 days in the dark until further processing in the laboratory. Later, the containers were given a 10-min ultrasonic bath to increase the extraction efficiency. After settlement for a few hours, a sample was transferred to a spectrophotometer and absorption measured at 665 and 750 nm. Stone surface area was estimated using the formula: $A = ((LW) + (LH) + (WH)) \cdot 1.15$ where L is length, W is width and H is height of the stones and 1.15 is a fixed factor to correct for the irregular shape of the stones (Graham et al. 1988). Chlorophyll *a* was calculated using the following formula: Chlorophyll *a* (mg m^{-2}) = $Abs_{(665–750)} \cdot V$ ml $\cdot$ 10 000 cm^{2} m^{-2} ⁄ 83.4 ml mg^{-1} $\cdot$ A cm^{2}, where V is the volume of ethanol used, 83.4 is the absorption coefficient for chlorophyll a in 96% ethanol and A is the summarized area of the stones (Københavns 1989).

Benthic detritus was quantified by collecting all material (inorganic and organic) present in the Surber samples after sorting of the animals. This material was dried at 80 °C for c. 24 h, weighed and the mass loss upon combustion at 550 °C taken as the amount of ash-free dry mass of organic material >200 µm in the sample.

4.3. Macrobenthos sampling

Macroinvertebrate sampling was carried out once at each site between May and October 2009 (i.e. during the dry season). In a previous study, Jacobsen et al. (2014a) did not find seasonal or periodical patterns in the variability of faunal metrics, even though the discharge of the stream showed signs of seasonality and periodicity. Therefore, sampling season is not expected to alter our results. At each site, five quantitative Surber samples (500 cm^{2}; mesh size 200 µm) were collected randomly from pebble–cobble substratum in riffle ⁄ run habitats. All samples were collected during daytime and preserved in the field in 70% ethanol. In the laboratory, samples were rinsed through a 200-µm sieve and sorted without the use of magnification. Subsampling was applied when the amount of material exceeded 250 ml of a plastic vial. Invertebrates were identified to morphospecies, genus or (sub) family according to North and South American macroinvertebrate keys (Pérez 1988; Merritt & Cummins 1996; Domínguez 2006; Domínguez et al. 2009).

4.4. Data treatment

The alpha diversity is usually expressed as the species richness of a confined ecosystem; number of taxa is a simple measure of biodiversity, but it can be strongly influenced by sample size (Vie 2010). The Shannon Wiener diversity index is based on species number and abundance and provides more information about the community structure, also including evenness, than a simple measure of species number (Magurran 2004). Fisher's alpha diversity index is used to compare different communities varying in the number of individuals (*N*), Fisher's alpha is only independent on sample size when the number of individuals in the sample exceeds 1000 (Fisher et al. 1943). In this study, species rarefaction was used to correct for sample size estimating taxa number at each locality. Species rarefaction based on all samples is not possible because the selected samples must come from the same habitat or community to fit the model (Gotelli y Colwell 2001). Shannon-Wiener diversity index, Fisher's alpha and Rarefaction were all calculated using the software 'Species Diversity and Richness' version 3.02, ©Pisces Conservation Ltd. (Lymington, UK).

Different sub-classifications were made especially distinguishing the chironomids from the rest (Individuals per square meter, individuals per square meter of macroinvertebrate taxa without chironomids and the percentage of chironomids). This additional subdivision of Chironomidae was made because this group has shown to be very important in species richness and abundance in these high-Andean streams (Jacobsen et al. 2010).

Relationships between variables were tested with Pearson product moment correlation analyses performed in ©Excel version 2010. The most important environmental variables defining the fauna parameters were determined through linear regression analysis (Ordinary Least Squares) using 13 environmental predictor variables. The best fit models were chosen based on the lowest Akaike's Information Criterion (AICc) value. AIC is a measure of the goodness of fit of an estimated statistical model. It is grounded in the concept of entropy, giving a relative measure of the information lost when a given model is used to describe reality. It is used to describe the tradeoff between bias and variance in model construction, balancing the precision vs. complexity of the model (Vie 2010). We used the corrected form of the AIC (AICc), which takes sample size into account, increasing the relative penalty for model complexity with small data sets. Since AICc values cannot be compared across models fitting different response variables, the adjusted r^2 (adj. r^2) value is given as an estimate of the accuracy of the model. In general the models selected based on the lowest AICc values include less environmental parameters fitting the variation in fauna than the models based on the highest adj. r^2 values. The adj. r^2 value is a modification of r^2, but adjusted according to the number of explanatory terms in the model. Unlike r^2, the adj. r^2 increases only if the new term improves the model more than would be expected by chance (Vie 2010). Linear multiple regression analysis was performed in SAM (Spatial Analysis in Macroecology) version 4.0, http://www.ecoevol.ufg.br/sam/

In order to have an estimation of the abundance of rare taxa found in the different types of streams, we plotted as histogram the number of taxa against the number of individuals, and against the number of localities that were found of these taxa. Taxa commonness and exclusiveness was assessed using a table where we placed all macroinvertebrate taxa of our different types of streams studied (kryal 1, 2 & 3, krenal and rithral) and then we searched for: (1) exclusive (unique) taxa per group, (2) total exclusive taxa at glacial- and (3) no glacial-fed streams, (4) glacier-fed common taxa, and (5) no glacier-fed common taxa as well as (6) total (shared) common taxa among all streams.

Differences in composition of macroinvertebrate communities among sites differing in altitude were further tested using an analysis of similarities (ANOSIM) that is widely used for testing hypotheses about spatial differences in plant and animal assemblages (Chapman & Underwood 1999). The ANOSIM tested the null hypothesis that within-site similarity was equal to between-site similarity. ANOSIM generates a statistical parameter R which is indicative of the degree of separation between groups: a score of 1 indicates complete separation, and a score of 0 indicates no separation (Gucht et al. 2005). Monte-Carlo randomization of the group labels was used to generate null distributions in order to test the hypothesis that within-group similarities are higher than would be expected by chance. To determine which macroinvertebrate taxa were most responsible for differentiating sites with different altitudes we performed a SIMPER analysis on density log-transformed data for all macroinvertebrate taxa. To evaluate which environmental parameters influenced the community composition of the aquatic macroinvertebrates a Canonical Correspondence Analysis (CCA) was performed. The broad aim of the CCA is to derive variates that 'explain' the species distributions as well as possible, while at the same time being a linear combination of the given environmental variables (Hill 1991). These procedures were performed using the freeware software PAST (PAleontological STatistics, version 2.17c).

Beta diversity was calculated as true beta diversity ($\beta = \gamma/\alpha$), absolute species turnover ($\beta = \gamma - \alpha$), Whittaker's species turnover ($\beta W = (\gamma - \alpha)/\alpha = \gamma/\alpha - 1$) and proportional species turnover ($\beta P = (\gamma - \alpha)/\gamma = 1 - \alpha/\gamma$), where γ diversity is the total species diversity of a landscape, and α diversity is the mean species diversity per habitat. Beta diversity quantifies how many subunits there would be if the total species diversity of the dataset and the mean species diversity per subunit remained the same, but the subunits shared no species (Tuomisto 2010a, b).

The gamma diversity for each of the three landscapes, measured as the cumulative number of species captured, was calculated using the following index proposed by (Ricklefs & Schluter 1993): $\gamma = \alpha \times isd \times sd$ where: α = the mean number of species per site in a landscape unit, isd = the inverse of the species dimension; that is, 1/the mean number of communities or locations occupied by a species, sd = sample dimension or total number of sites sampled. Gamma diversity can be obtained from the general species list for each landscape. However, the use of the equation above gives us an idea of which component of gamma diversity is the most important in each landscape, whether it is the mean alpha diversity, landscape heterogeneity or the number of communities occupied by species (Arellano & Halffter 2003).

To estimate the degree of dissimilarity in the species composition of the landscapes, we calculated complementarity between pairs of landscapes (Colwell & Coddington 1994).

The complementarity for landscapes A and B is expressed as: $C_{AB} = U_{AB} / S_{AB}$, where U_{AB} is the sum of the species unique to each of the two landscapes, calculated as: $U_{AB} = a + b - 2c$, with: a is the number of species of landscape A, b is the number of species of landscape B, c is the number of species common to landscapes A and B. S_{AB} is the total species richness of both landscapes combined, as follows: $S_{AB} = a + b – c$

5. RESULTS

A total of 90 589 specimens belonging to 15 macroinvertebrate Orders and 135 taxa were captured from the 51 sampled sites. Of these, 44 taxa belonged to Diptera (23 of which are from the family Chironomidae), 38 to Acari, 13 to Trichoptera and 10 to Coleoptera, 6 to Lepidoptera, 5 to Hemiptera, 4 to Haplotaxida and Glossiphoniiformes, 3 to Gordioidea, 2 to Amphipoda and 1 to Tricladida, Basommatophora, Veneroida, Plecoptera and Ephemeroptera.

5.1. Diversity and environmental patterns

The aquatic macroinvertebrates density decreased (individuals per square meter) with increasing altitude (Fig. 2a, Table 1). We found that the three diversity metrics Fisher's alpha, taxon richness and rarefied richness (Fig. 2b-d) significantly (P < 0.01) decreased with increasing altitude, while we found no significant relationship between Shannon-Wiener diversity index and altitude (Table 1). Twelve out of fifteen environmental parameters were significantly correlated with altitude (Table 2).

Mean conductivity (µS/cm) decreased with increased GCC percentage, and also showed to have significant correlations with other 8 variables (altitude, chlo 'a', organic matter, mean width, mean depth, mean temperature, turbidity and distance from glacier). Seven variables (turbidity, conductivity, altitude, organic matter, mean depth, water temperature and distance from glacier) correlated significantly with the percentage of GCC. Turbidity (NTU) also showed to have a significant (P < 0.01) correlation with other six environmental variables (Table 2).

Multiple regression analysis showed that organic matter (g/m^2) and altitude (m a.s.l.) were the best variables predicting the number of taxa (S) in all 51 sampled sites

(Table 3). In the case of the rarefied richness, the main variables explaining this response parameter were organic matter (g/m²) and mean width (cm) (Table 3). Mean width (cm), altitude (m a.s.l.) and pH were the main variables in explaining the Shannon-Wiener diversity index, while altitude and organic matter explained Fisher's alpha diversity index (Table 3).

The combination of altitude, organic matter, mean temperature, pH and turbidity seemed to be the main drivers of density related parameters, such as the total density in all the 51 study sites, the density of chironomids and the total density of macroinvertebrates without the presence of Chironomidae (Table 4). When we only took Chironomidae density into account, altitude, pH and mean water temperature (°C) were the main parameters explaining this response variable (Table 4). The main variables explaining percentage of chironomids were mean temperature and pH. Finally, organic matter and the turbidity of the streams were the main variables explaining macroinvertebrate density excluding Chironomidae (Table 4).

5.2. Taxa distribution patterns among stream types

Kryal stream types (1, 2 & 3) had an important proportion of rare taxa (kryal 1: 6; kryal 2: 11 & kryal 3: 23 singletons) compared to krenal and rithral stream types, where non-rare taxa highly contributed to the number of individuals collected (Fig. 3). In all five stream types, just one locality was much more taxon rich than the rest (Fig. 4). A total of 48 exclusive taxa were found, being kryal 3 and rithral the stream types that contributed the most (18 & 19 taxa respectively). We also found that only 13 taxa were common to all stream types (e.g. *Atopsyche* sp.1, *Cailloma* sp.1, *Chelifera* sp.2, Diamesinae Type 1, etc.). In contrast, kryal streams had 23 unique or exclusive taxa, while krenal and rithral streams had a total of 25 unique taxa. Dytiscidae sp.1 and Staphylinidae sp.1 are the only taxa found on the kryal 1 streams; Chironominae Type 4, Staphylinidae sp.2 and *Tipula* sp. are unique taxa from kryal 2 streams, and 18 unique taxa are found in kryal 3 streams (e.g. *Blepharicera* sp.3, *Cailloma* sp.3, Chironominae Type 1 and 3, etc). Krenal streams had Ephydridae, *Haliplus* sp., Hydracarina Type 28, Muscidae sp.5 and 6, Naididae sp.3 as unique taxa and the rithral streams had 19 unique taxa, for example: *Atopsyche* sp.2, Corixidae Type 2, Curculionidae sp.2, *Helichopsychidae* sp., etc. (Appendix 3). Kryal 3 stream type, had the highest mean taxon richness (33) compared to all stream types (kryal 1: 9; kryal 2: 17; krenal: 28 & rithral: 29) (Fig. 5).

Mean alpha diversity for each type of stream was 9, 17, 33, 28 and 29 for kryal 1, 2, 3, krenal and rithral streams respectively; beta diversity varied across the stream types being kryal 3 (2.94) and rithral (3.34) the streams with the highest values. These two streams also had the greatest percentage of species (75 %) shared with each other. Kryal 1 streams had a low percentage (18 and 20 %) of shared with the rest of streams. In terms of complementarity (degree of dissimilarity in species composition), rithral and kryal 3 streams were the least complementary while kryal 3 had the most taxa composition complementarity with kryal 1 stream type (Table 5).

5.3. Community composition patterns

The Similarity Percentage analysis (SIMPER) of all the five stream types pooled showed that *Hyalella* sp., *Andesiops* sp. and *Anomalocosmoecus* sp. had the major contribution (> 1.6 of contribution) to the significant difference (ANOSIM: R = 0.4525, $p = 0.001$) in their communities and an overall average dissimilarity of 55.4 % (Table 6). Kryal 1 streams differed from Kryal 3 and rithral streams significantly ($p < 0.001$), with *Hyalella* sp., *Andesiops* sp. and *Neoelmis* sp.1 as the major contributors between kryal 1 vs. kryal 3 (> 3.2), and an overall average dissimilarity of 76.8 %; while mainly *Hyalella* sp., *Andesiops* sp., Lumbriculidae and Orthocladiinae accounted for the difference between kryal 1 vs. rithral (> 3.4) with an overall average dissimilarity of 79.1 %. Kryal 2 streams differed significantly from kryal 3 and rithral streams (p = 0.004; p = 0.008 respectively) with *Hyalella* sp. and *Anomalocosmoecus* sp. as the major contributors between kryal 2 vs. kryal 3 (>2.3) and an overall average dissimilarity of 53.6 %; while the difference between kryal 2 vs. rithral was mainly due to *Hyalella* sp. and *Anomalocosmoecus* sp. (>2.4), with an overall average dissimilarity of 58.2 %. Finally, there were no significant differences in community assemblages between kryal 3, krenal y rithral stream types (p > 0.05) (Appendix 4).

Canonical axis 1 (32%) and axis 2 (21.8%) explained a significant amount of the variance in the macroinvertebrate-environment interaction. Axis 1 was defined by altitude (m. asl) conductivity (µS/cm) and temperature (°C), axis 2 by Pfankuch index and distance from glacier (m). The eigenvalues of axis 1 and axis 2 were 0.17 and 0.12, respectively. On the basis of environmental vector lengths, water velocity, altitude, water depth, GCC, turbidity, distance from glacier, conductivity and temperature, in descending order, were found to be the most important environmental factors (Fig. 6). Altitude and GCC as the most influential factors for all the kryal streams (1, 2 and 3), had a great effect on the presence of Podonominae Type 4, Staphylinidae and Podonominae Type 1 which were common at higher altitudes and streams with the highest influence of the glacier. Slope, water temperature, water depth and conductivity showed an opposite relation to altitude. Current velocity explained the presence of taxa as *Synclita* sp., *Mortoniella* sp. *and*

Blepharicera sp. which are high flow adapted taxa. Turbidity and GCC seemed to affect positively the presence of Podonominae Type 3, on which temperature, conductivity and organic matter had the opposite relation. The families Corixidae and Ephydridae seem to be more adapted to streams with no glacial influence (rithral and krenal) (Fig. 6).

6. DISCUSSION

Previous studies from the Antisana area have focused on longitudinal patterns (Jacobsen et al. 2010), environmental drivers (Vie 2010), spatial variability (Kuhn et al. 2011), decomposition rates (Fugère et al. 2012), glacial pulse effects (Cauvy-Fraunié et al. 2013) and temporal variability of stream macroinvertebrates in glacier-fed streams (Jacobsen et al. 2014a). The novelty in this study is the large number of study sites and the inclusion of streams that have no glacial influence (e.g., krenal and rithral streams). This study examined how patterns in biodiversity (α, β and γ) varied along environmental gradients (i.e. altitude, temperature, etc.) and among different stream types (i.e. kryal, krenal and rithral) at the catchment scale showing that intermediate disturbed streams such as kryal 3 stream type contributed the most to the local and regional diversity of all the studied streams. Furthermore, it is worth noting that there are no previous studies with this type of biodiversity analysis in tropical glacier-fed and high-altitude streams around the globe.

6.1. Stream classification

Classification systems are used to organize entities into sets on the basis of their similarities or relationships. The main purpose of classifying is to minimize variation by recognizing definable groups with similarities, and increase one's knowledge about a member of such a group by observing the patterns characteristic of the group in general. Often, environmental classifications are based on measurable attributes of physical structure or pattern (Rosgen, 1996). Despite the different ways of stream classification, here we chose to classify our streams depending on the type of origins (kryal, krenal and rithral), and we also made an additional sub-classification of all the kryal streams depending on the degree of the percentage of glacier coverage in the catchment (GCC) in order to have a better clustering of our macroinvertebrates communities according to the stream type.

6.2. General environmental and diversity patterns

In general, as we move up, the altitudinal gradient, temperature and oxygen tend to decrease (Jacobsen et al. 2003; Jacobsen 2008; Jacobsen & Marín 2008). In this study, water conductivity and water depth tended to decrease with increasing altitude, while water turbidity tended to increase with altitude and to go closer to the glacier snout.

With this study we confirm the clear longitudinal patterns of faunal metrics along an altitudinal gradient reported in previous studies from the REA (Jacobsen et al. 2010; Kuhn et al. 2011). These correspond to a worldwide general pattern of glacier fed streams around the globe (Jacobsen & Dangles 2012), and the general conceptual model from temperate glacial streams (Milner et al. 2001). Alpha diversity parameters (Fisher's alpha, taxa richness and rarefied richness), total density (individuals per square meter) and the density of Chironomidae (Diptera) all decreased with increasing altitude, and showed a negative relationship with turbidity; the relative contribution of this dipteran family (%) showed a negative relationship with temperature (Table 1). Glacial shrinkage would lead to an initial increase in meltwater run-off for a few years to decades, followed by a decrease in run-off over the longer term after a critical tipping point of glacial mass has been reached (Jansson, Hock & Schneider 2003; Barnett, Adam & Lettenmaier 2005; Huss et al. 2008; Baraer et al. 2012). In conjunction with these run-off changes, several other key environmental characteristics are expected to change (e.g. discharge, conductivity, temperature, turbidity) (Jacobsen et al. 2014b), which would lead to a change in the community composition over the following years of this glacier shrinkage, probably with the gain of new taxa from downstream to upper sites or with the loss of specific taxa adapted to live in these extreme environmental conditions.

6.3. *Taxon commonness and rarity patterns*

Understanding how biodiversity patterns emerge from the distributions of rare and common species is a key concern of conservation biology (Murray et al. 2002; Storch & Šizling 2002; Lennon et al. 2004; Pearman & Weber 2007). We found that kryal streams (1, 2 & 3) had an important contribution of rare (singletons) taxa to local and regional biodiversity in the REA compared to non-glacial streams. In addition, just one locality (Kryal 3) was proved to contribute the most (33) to total taxon richness (Fig. 5).

True Beta diversity was greatest on kryal 3 and rithral streams (2.94 and 3.34 respectively). This same pattern could be found on absolute, Whittaker's and proportional species turnover. All these values were obtained from gamma diversity (overall region diversity) and alpha diversity (overall local diversity) components of all beta diversities formulas (Table 5). Gamma diversity is the total species diversity in the dataset and alpha diversity the mean species diversity per subunit. Beta diversity quantifies how many subunits there would be if the total species diversity of the dataset and the mean species diversity per subunit remained the same, but the subunits shared no species (Tuomisto 2010a, b). Kryal 3 and rithral streams had the highest values of alpha and gamma components; and, kryal 3 being the most diverse in a local (alpha diversity) sense (Table 5). As described previously by Jacobsen et al. (2012), a potential mechanism behind this peak in local richness can be predicted from the intermediate disturbance hypothesis (Connell 1978): turbid glacier-fed rivers, with low water temperature and solute concentrations and varying hydrological regimes restrict the fauna to a few specialized species, but farther downstream, mixing with warmer, clearer water (that is, snow melt, rain and/or groundwater-fed) creates intermediate disturbance that maximizes diversity because superior competitors cannot dominate and co-exist with opportunistic species.

6.4. Biodiversity, endemicity and future conservation efforts

Loss of biodiversity is proceeding faster in freshwater than in any other major biome (Dudgeon et al. 2006, Strayer and Dudgeon 2010, Geist 2011). Many studies in biological conservation have examined concordance in taxon richness patterns between different taxonomic levels, and concluded that variability in species richness is often strongly correlated to that of higher taxon richness (e.g. Gaston & Williams 1993; Balmford et al. 2000). Bowman and Bailey (1997) found that species- and genus-level resemblance matrices showed high correlations to family-, order- and even class-level matrices in freshwater macroinvertebrates. Therefore, the level of identification in this study would not be an issue of the general species richness and conservation patterns, although, the state-of-the-art molecular tools would be of great interest in future studies that will require the identification of native and endemic species of these highly vulnerable Andean ecosystems.

The stream types with the highest gamma diversity were those with the lowest percentage of GCC, with 97% of all the taxa found for the whole study area. This suggests that streams that are a mixture of the different water sources (glacial, ground water, rain & snowmelt) comprise the highest macroinvertebrate aquatic diversity of the region. This information helps to improve our understanding of the underlying processes that generate aquatic biodiversity patterns, and is useful and important for successful environmental management and species conservation endeavors (Stendera & Johnson 2005). Any credible plan for biodiversity conservation must maintain beta diversity (and the processes that shape it) across the full range of taxa and spatial scales (Barton et al. 2013). Alpine aquatic species are important to regional biodiversity in mountain ecosystems (Pounds et al. 1999; Hauer et al. 2007; Brown et al. 2009). For example, it is expected that when the glaciers in the Parc National des Pyrénées are lost, much of the unique genetic and taxonomic diversity will also be lost; but systems like this can serve as beacons (Finn et al. 2013). In some cases, however, reduced meltwater from snow and ice masses may favor a more diverse suite of species adapted to warmer temperature regimes (Ward 1994), resulting in increased local (alpha) diversity (Brown et al. 2007).

Mountaintop aquatic invertebrates which exhibit severe climate-related range-restrictions are ideal early-warning indicators of thermal and hydrological modification that may be associated with climate warming in mountain ecosystems (Muhlfeld et al. 2011). Because there is relatively little knowledge about mountaintop invertebrates, yet they are increasingly threatened by climate change, more research and monitoring is urgently needed to avoid extinctions and to predict effects of extirpation on ecosystem integrity and function worldwide (Muhlfeld et al. 2011). This is especially the case for tropical glacier mountaintop aquatic invertebrates. In the REA, previous studies have found one or two endemic species of this region. There is an urgent need to extend the spatial range of research for glacier-fed streams in order to discover new endemic species, ecological insights and key functional roles of these highly unknown appreciable tropical ecosystems, and the potential threats to biodiversity demonstrated by these studies, indicate that strategic conservation should take a holistic approach that includes both invertebrate and vertebrate aquatic species (Jacobsen et al. 2012).

Finally, we would like to note that the regional biodiversity we focused on in this study was from a catchment scale that only comprises the streams that are part of the upper catchment of the Antisana river, this is important to mention because there is a special need to study more glacier-fed, high-Andean tropical streams in order to generalize or discard the existing patterns we found on this study. Glacier-fed stream macroinvertebrate taxa proved to have a great potential in being early indicators of climate change (Khamis et al. 2014), since glacial influence has been found to act as an environmental filter to colonization (Brown and Milner 2012). The genetic and functional diversity that is expected to be lost with drastically reduced glacier influence reveals an imperative need to extend the scale of these studies and to include molecular tools. As shown by a recent study by Finn et al. (2014) in the Alpine Pyrenees, incorporating such information would give more insights about the historical evolution of these highly specialized stream macroinvertebrates.

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8. FIGURES

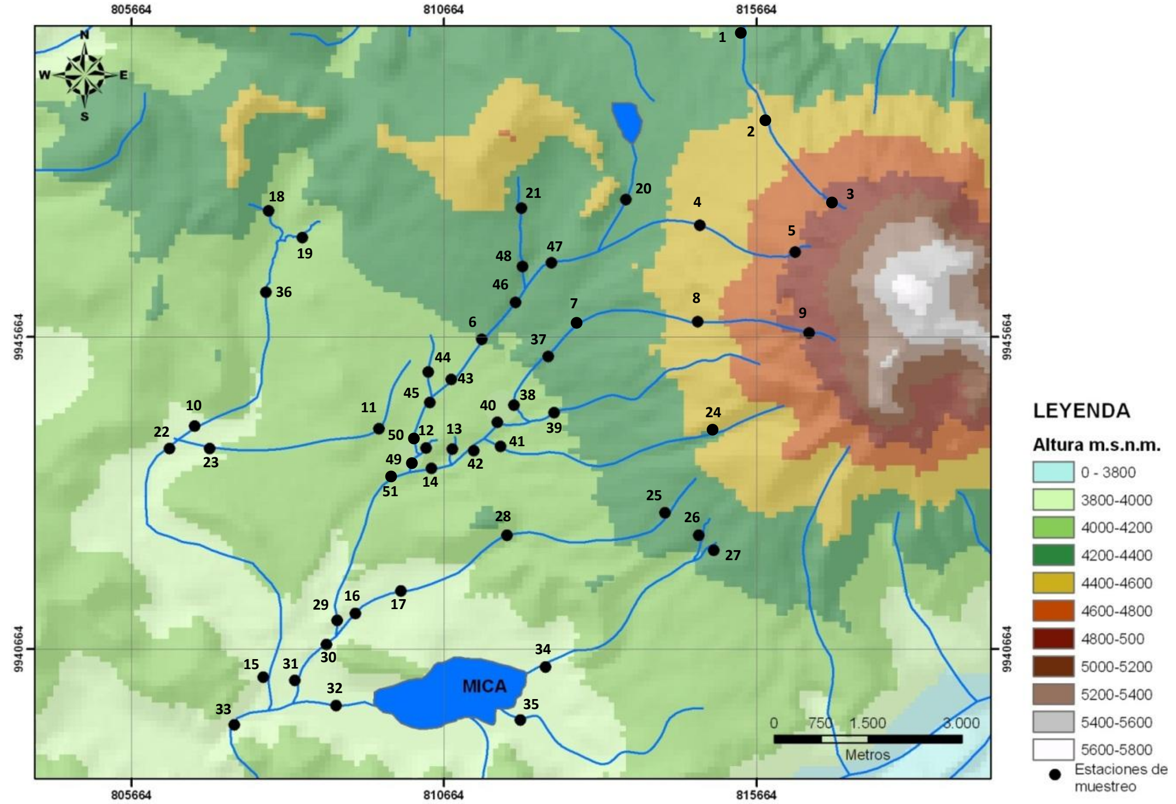

Figure 1. Topographic map of the study area with 51 study sites.

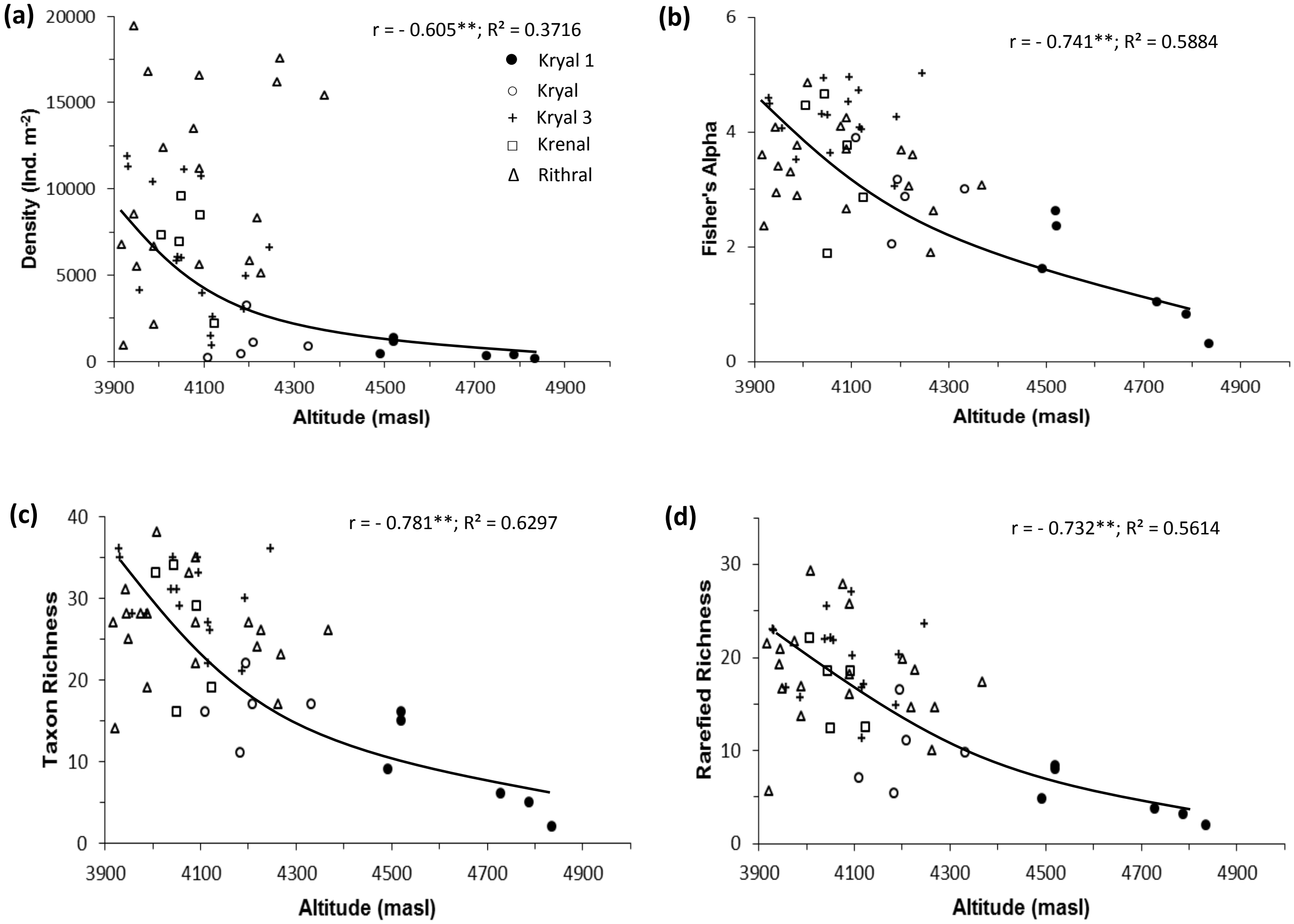

Figure 2. Scatter plots of the relationships between significant taxa derived variables (Pearson Correlation) and altitude for the 51 study sites. (a) Density (Ind/m²); (b) Fisher's alpha; (c) Taxon richness ; (d) Rarefied richness. R = linear tendency coefficient; r² = correlation coefficient; * significant correlation at 0.05; ** significant correlation at 0.01.

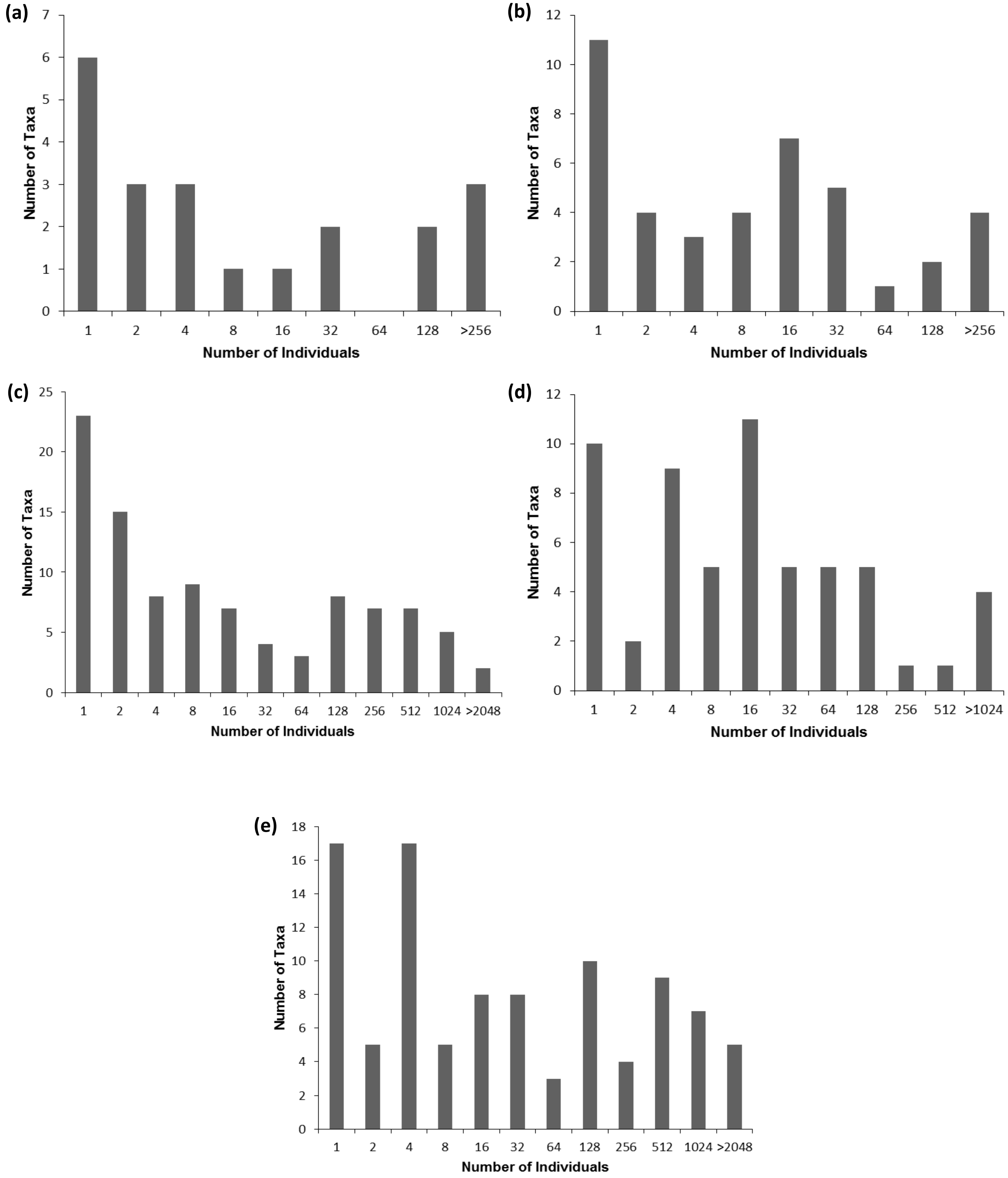

Figure 3. Histograms of the number of taxa and the number of individuals where found at (a) Kryal 1; (b) Kryal 2; (c) Kryal 3; (d) Krenal and (e) Rithral.

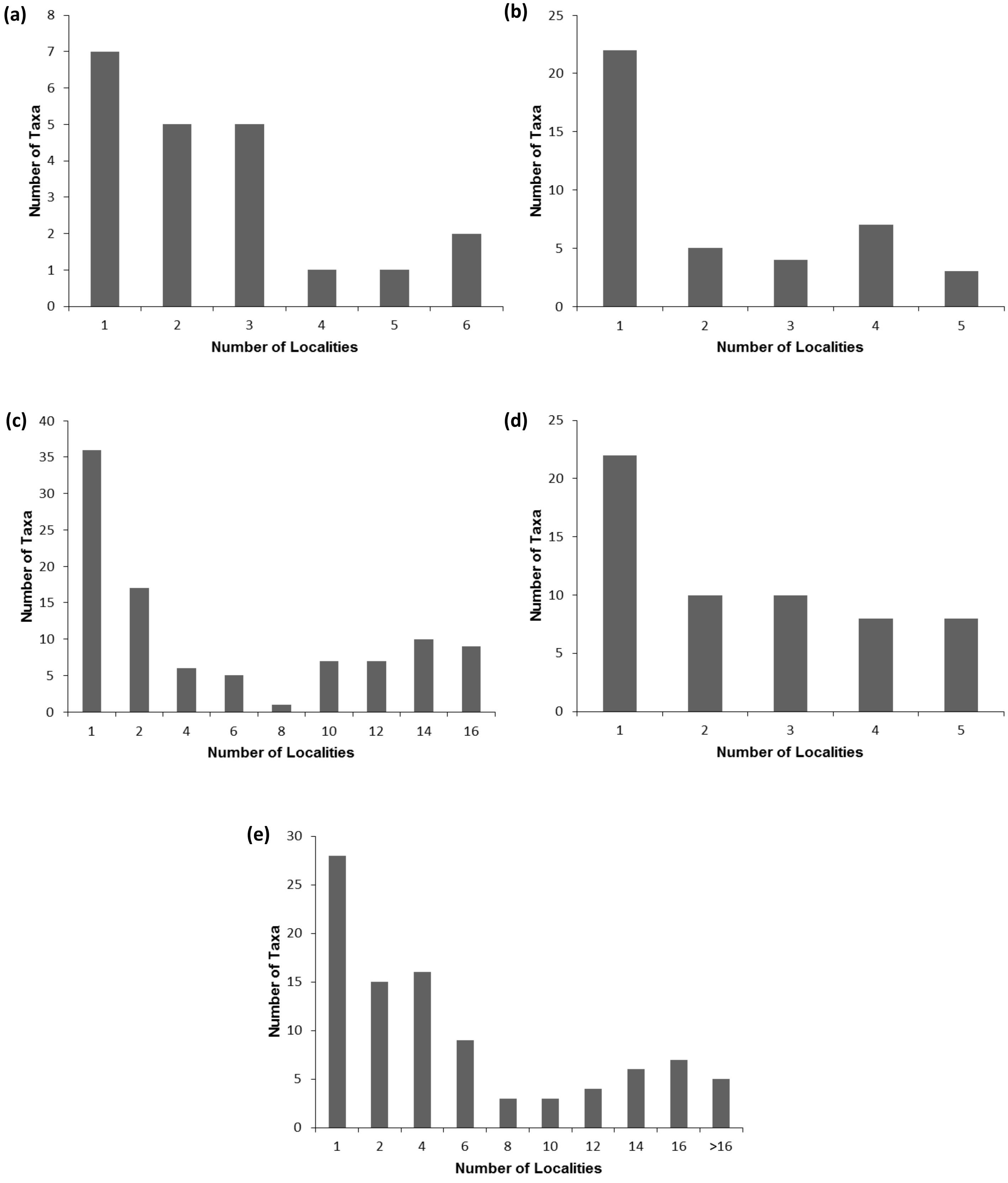

Figure 4. Histograms of the number of taxa and the number of localities where found at (a) Kryal 1; (b) Kryal 2; (c) Kryal 3; (d) Krenal and (e) Rithral.

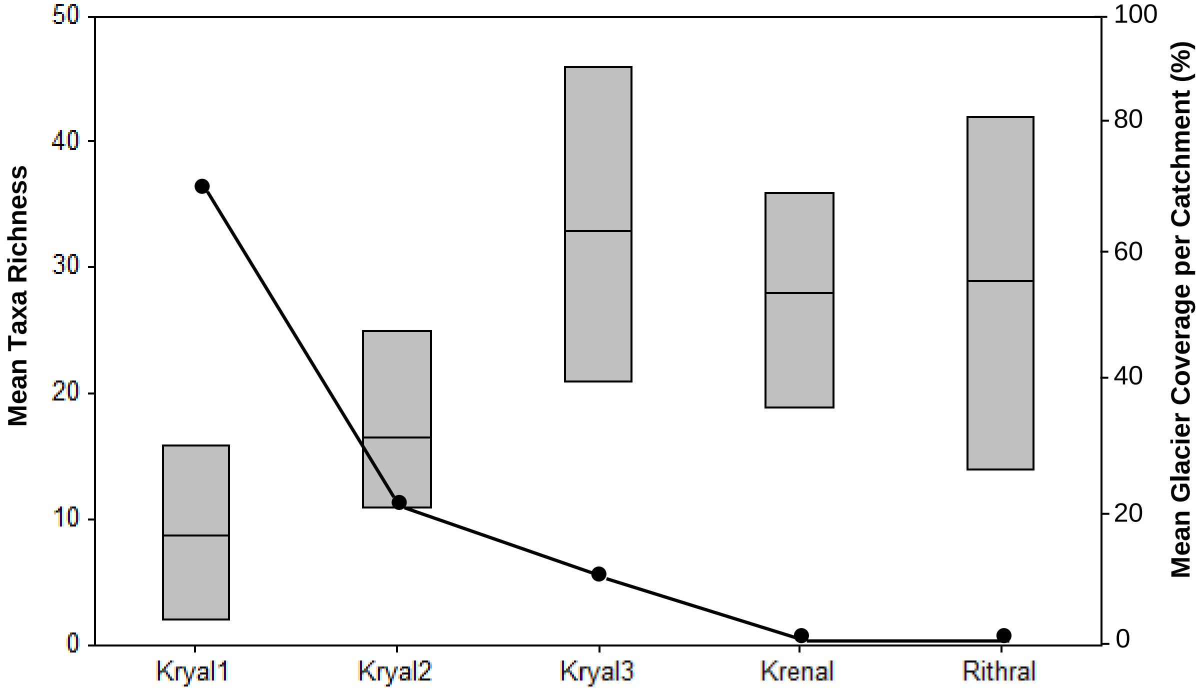

Figure 5. Bar plots of the mean taxa richness (maximun, minimun value) of each type of stream and the mean percentage of GCC.

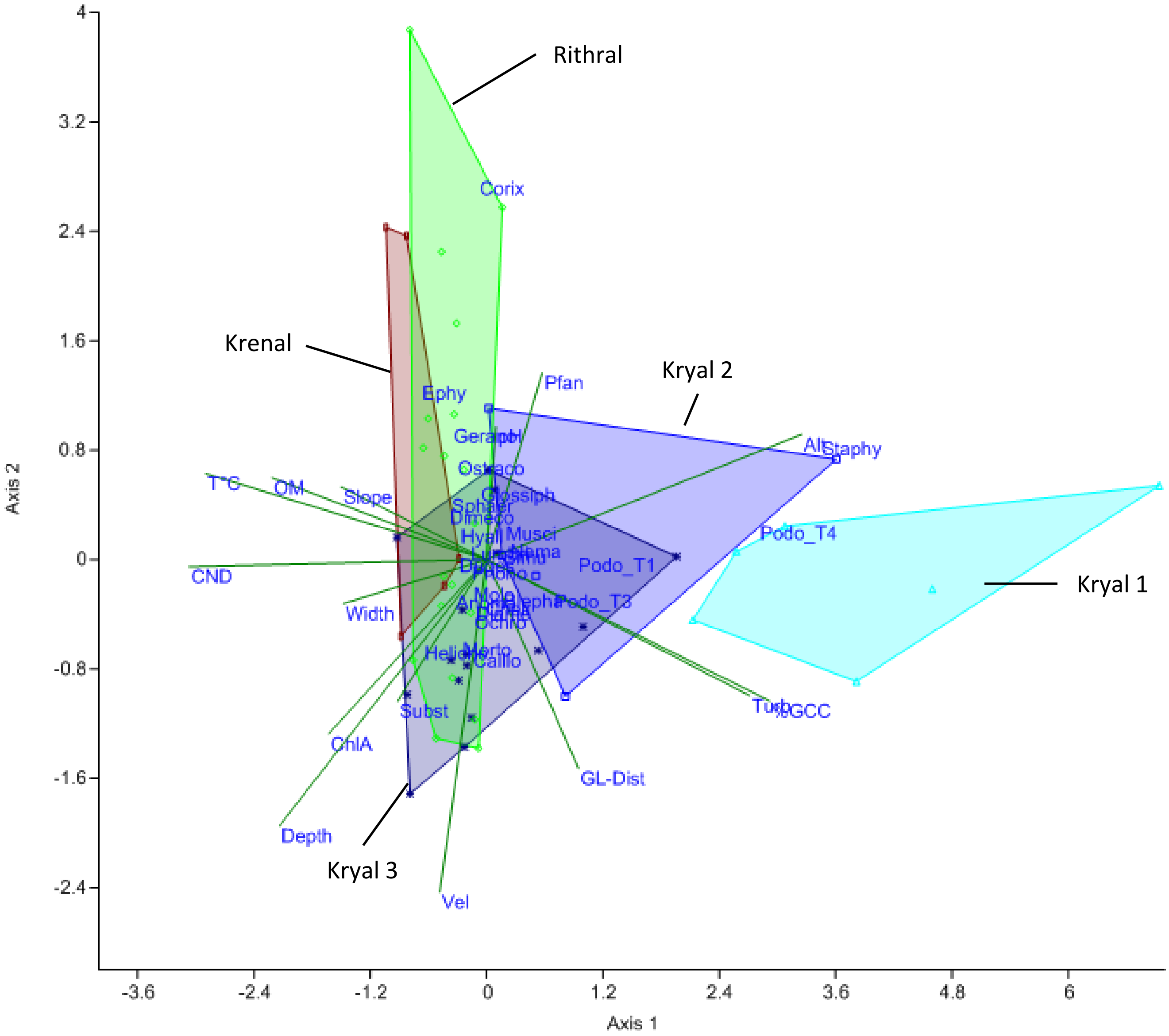

Figure 6. Canonical Correspondence Analysis (CCA) of the biotic and abiotic variables and the benthic invertebrate communities sampled in 51 study sites, grouped by the stream type. Each point represents the benthic invertebrate assemblage of 5 pooled Surber samples from each of the 51 study sites. Macroinvertebrate densities (Ind/m2) were Log (x + 1) transformed.

9. TABLES

Table 1. Pearson correlation coefficients between macroinvertebrate diversity and composition variables. * $P < 0.05$ and ** $P < 0.01$. Bonferroni correction not applied.

	Richness (S)	Rarefied Richness	Shannon (H)	Fisher's alpha	Fauna (Individuals/m²)	Chironomids Only (Individuals/m²)	Chironomids (%)	Without Chironomids (Individuals/m²)
Altitude (m.asl)	**-0.781****	**-0.732****	-0.276	**-0.741****	**-0.605****	**-0.391****	0.119	**-0.694****
Chlo a (mg/m²)	**0.446****	**0.409****	0.109	**0.446****	**0.293***	**0.278***	0.096	**0.302***
Organic Matter (g/m²)	**0.574****	**0.600****	**0.353***	**0.497****	**0.561****	**0.302***	-0.216	**0.642****
Mean Width (cm)	0.168	0.112	**-0.300***	0.106	0.211	0.227	0.115	0.156
Mean Depth (cm)	**0.511****	**0.517****	**0.289***	**0.516****	**0.334***	**0.317***	0.103	**0.384****
Mean Velocity (m/s)	0.209	0.243	0.258	**0.281***	0.033	0.103	0.129	0.044
Mean Temperature (°C)	**0.604****	**0.540****	**0.389****	**0.602****	**0.426****	0.048	**-0.471****	**0.687****
Mean Conductivity (µS/cm)	**0.686****	**0.670****	0.115	**0.578****	**0.683****	**0.452****	-0.111	**0.678****
pH	-0.070	-0.066	0.241	0.004	-0.208	**-0.283***	-0.223	0.025
Turbidity (NTU)	**-0.568****	**-0.606****	-0.148	**-0.400****	**-0.716****	**-0.462****	0.141	**-0.704****
Slope (cm/m)	**0.325***	**0.314***	0.108	**0.311***	**0.291***	0.014	**-0.347***	**0.313***
Substrate Types	0.239	0.227	0.187	0.276	0.075	0.017	-0.071	0.202
Pfankuch Index	-0.236	-0.195	-0.173	**-0.324***	-0.027	0.021	0.072	-0.023
% GCC	**-0.570****	**-0.590****	-0.074	**-0.393****	**-0.733****	**-0.435****	0.208	**-0.734****
Distance from Glacier (m)	-0.034	-0.090	0.165	0.148	**-0.369****	-0.239	0.067	**-0.279***

Table 2. Pearson correlation coefficients between the environmental variables.* $P < 0.05$ and ** $P < 0.01$. Bonferroni correction not applied.

	Altitude (m.asl)	Chlo a (mg/m²)	Organic Matter (g/m²)	Mean Width (cm)	Mean Depth (cm)	Mean Velocity (m/s)	Mean Temperature (°C)	Mean Conductivity (µS/cm)	pH	Turbidity (NTU)	Slope (cm/m)	Substrate Types	Pfankuch Index	% GCC	Distance from Glacier (m)
Altitude (m.asl)	1														
Chlo a (mg/m²)	**-0.558****	1													
Organic Matter (g/m²)	**-0.313***	0.048	1												
Mean Width (cm)	**-0.464****	0.232	-0.010	1											
Mean Depth (cm)	**-0.703****	**0.334***	0.154	**0.432****	1										
Mean Velocity (m/s)	**-0.299***	0.262	0.009	0.186	**0.529****	1									
Mean Temperature (°C)	**-0.618****	0.244	**0.324***	0.145	**0.242***	-0.061	1								
Mean Conductivity (µS/cm)	**-0.819****	**0.419****	**0.405****	**0.417****	**0.603****	0.135	**0.507****	1							
pH	0.175	-0.091	0.092	-0.072	0.063	0.187	-0.154	-0.105	1						
Turbidity (NTU)	**0.557****	-0.250	**-0.549****	-0.172	**-0.314***	0.102	**-0.389****	**-0.790****	-0.036	1					
Slope (cm/m)	-0.140	0.106	**0.449****	-0.219	-0.209	-0.153	**0.270***	0.095	-0.160	-0.145	1				
Substrate Types	**-0.287***	**0.489****	0.096	-0.032	0.204	0.171	0.131	0.067	0.095	-0.008	**0.238***	1			
Pfankuch Index	0.158	-0.232	0.009	0.196	-0.010	-0.190	-0.082	0.071	0.180	-0.188	**-0.366****	**-0.296***	1		
% GCC	**0.629****	-0.223	**-0.497****	-0.197	**-0.301***	0.179	**-0.528****	**-0.820****	0.168	**0.904****	-0.201	-0.049	-0.191	1	
Distance from Glacier (m)	0.128	0.065	-0.232	-0.015	0.105	**0.424****	-0.120	**-0.438****	0.203	**0.658****	0.042	0.122	**-0.384****	**0.761****	1

Table 3. The best fit model results from multiple linear regression analysis on the taxa diversity data. Only showing the environmental variables included in the models.

	Richness (S)			Rarefied Richness			Shannon H			Fisher Alpha		
	coeff	std. coeff.	p value	coeff	std. coeff.	p value	coeff	std. coeff.	p value	coeff	std. coeff.	p value
Altitude (m.asl)	-0.016	-0.392	**0.018**	-0.011	-0.361	0.032	-0.001	-0.583	**0.005**	-0.003	-0.682	**<0.001**
Chlo a (mg/m²)	0.024	0.107	0.288	0.028	0.158	0.134	-0.002	-0.167	0.171			
Organic Matter (g/m²)	0.359	0.295	**0.004**	0.314	0.332	**0.002**				0.030	0.196	**0.045**
Mean Width (cm)	-0.008	-0.104	0.330	-0.012	-0.214	**0.040**	-0.002	-0.452	**<0.001**	<0.001	-0.109	0.348
Mean Depth (cm)												
Mean Velocity (m/s)	8.772	0.165	0.088	8.964	0.217	0.029	0.455	0.159	0.184			
Mean Temperature (°C)							0.040	0.201	0.144	0.060	0.128	0.260
Mean Conductivity (µS/cm)							-0.001	-0.218	0.179	-0.001	-0.103	0.502
pH							0.098	0.325	**0.005**	0.121	0.171	0.074
Turbidity (NTU)	-0.011	-0.255	0.086	-0.008	-0.236	0.125						
Slope (cm/m)												
Substrate Types							-0.008	-0.036	0.753			
Pfankuch Index	-0.125	-0.103	0.279							-0.033	-0.214	0.058
Adjusted r² value			0.649			0.622			0.506			0.606
Constant			0.002			0.009			0.004			<0.001
p-value			<0.001			<0.001			<0.001			<0.001

Table 4. The best fit model results from multiple linear regression analysis on the total density and the quantitative Chironomidae family data. Only showing the environmental variables included in the models.

	Fauna (Individuals/m²)			Chironomids Only (Individuals/m²)			Chironomids (%)			Without Chironomids (Individuals/m²)		
	coeff	std. coeff.	p value	coeff	std. coeff.	p value	coeff	std. coeff.	p value	coeff	std. coeff.	p value
Altitude (masl)	-2.305	-0.070	0.702	-11.859	-0.436	**<0.001**				7.724	0.453	0.019
Chlo a (mg/m²)										15.666	0.165	0.195
Organic Matter (g/m²)	219.793	0.222	0.084							197.851	0.385	**0.003**
Mean Width (cm)							0.039	0.160	0.119			
Mean Depth (cm)												
Mean Velocity (m/s)												
Mean Temperature (°C)	-368.842	-0.122	0.384	-885.18	-0.353	**0.007**	-7.201	-0.577	**<0.001**	510.564	0.326	0.018
Mean Conductivity (µS/cm)												
pH	-2153.07	-0.473	**<0.001**	-2273	-0.601	**<0.001**	-7.745	-0.411	**<0.001**	329.41	0.139	0.22
Turbidity (NTU)	-11.72	-0.341	**0.074**				0.023	0.162	0.166	-8.574	-0.48	**0.008**
Slope (cm/m)				12.123	0.149	0.161						
Substrate Types										-226.3	-0.127	0.2900
Pfankuch Index										83.847	0.164	0.156
Adjusted r² value			0.36			0.493			0.518			0.463
Constant			0.187			<0.001			<0.001			0.011
p-value			<0.001			<0.001			<0.001			<0.001

Table 5. Alpha, Beta and Gamma diversity of the benthic invertebrate communities of the five study stream types. Percentage of shared species and complementarity.

	Stream Type				
Indicators of Diversity	Kryal1	Kryal2	Kryal3	Krenal	Rithral
Alpha Diversity (α)	9	17	33	28	29
Beta diversity ($\beta = \gamma/\alpha$)[1]	2.33	2.35	2.94	2.04	3.34
Beta diversity ($\beta_A = \gamma - \alpha$)[2]	12	23	64	29	68
Beta diversity ($\beta_W = (\gamma - \alpha)/\alpha = \gamma/\alpha - 1$)[3]	1.33	1.35	1.94	1.04	2.34
Beta diversity ($\beta P = (\gamma - \alpha)/\gamma = 1 - \alpha/\gamma$)[4]	0.57	0.58	0.66	0.51	0.70
Gamma Diversity (γ)	21	40	97	57	97
% taxa shared					
with the kryal 1 streams	-				
with the kryal 2 streams	18	-			
with the kryal 3 streams	20	38	-		
with the krenal streams	18	31	51	-	
with the rithral streams	18	35	75	52	-
% of complementarity					
with the kryal 1 streams	-				
with the kryal 2 streams	0.6	-			
with the kryal 3 streams	0.8	0.6	-		
with the krenal streams	0.7	0.5	0.4	-	
with the rithral streams	0.8	0.6	0.2	0.4	-

[1] True beta diversity

[2] Absolute species turnover

[3] Whittaker's species turnover

[4] Proportional species turnover

Table 6. SIMPER and ANOSIM of the dissimilarity in benthic invertebrate community composition between the pooled group and the three study stream types. Only the 15 taxa that contributed the most (>1.45) to the dissimilarity are showed.

All Groups Pooled

Taxon	**Contribution**	**Cumulative %**	**Overall Average Dissimilarity**	**ANOSIM**	
				R	**P**
Hyalella sp.	2.68	4.837	55.41	0.4525	0.001
Andesiops sp.	2.355	9.087			
Anomalocosmoecus sp.	2.062	12.81			
Alluaudomyia sp.	1.914	16.26			
Orthocladinae	1.876	19.65			
Planariidae	1.83	22.95			
Neoelmis sp.1 (Larvae)	1.829	26.25			
Lumbriculidae	1.828	29.55			
Podonominae Type 1	1.693	32.60			
Simulium sp.	1.662	35.60			
Hydracarina (TOTAL)	1.627	38.54			
Podonominae Type 3	1.598	41.42			
Chironominae	1.536	44.19			
Ostracoda	1.531	46.95			
Chelifera sp.	1.469	49.61			

10. APPENDICES

Appendix 1. Stream sites summary at the 51 study sites in the REA.

Stream Type	**Number of streams per type**	**Stream Order**	**Mean Altitude (min-max)**	**Mean Glacier Coverage in Catchment (min-max)**	**Mean Distance from Glacier (min-max)**	**Mean Abundance (min-max)**	**Mean Taxa Richness (min-max)**
Kryal1	6	1	4648 (4520-4835)	68.35 (39.38-93.24)	927.42 (15-1847.38)	638.66 (176-1360)	9 (2-16)
Kryal2	5	1, 2	4206 (4109-4332)	23.35 (16.95-27.42)	5573.12 (3714.79-7189.49)	1168.8 (232-3236)	17 (11-25)
Kryal3	16	1, 2, 3	4072.4 (3930-4246)	7.86 (1.03-18.49)	9047.93 (3900-15183.38)	6305 (904-11876)	33 (21-46)
Krenal	5	1	4063.4 (4006-4124)	0	0	6909 (2220-9600)	28 (19-36)
Rithral	19	1, 2, 3	4080.4 (3917-4368)	0	0	11433.89 (928-42256)	29 (14-42)

Appendix 2. Environmental characteristics of the 51 streams types.

Number in map	Stream Type	Chlo '*a*' (mg/m^2)	CPOM (g/m^2)	Velocity (m/s)	pH	Conductivity (µS/cm)	Temperature (° C)	Turbidity (NTU)	Slope (cm/m)	Width (cm)	Depth (cm)	Substrate Types	Pfankuch	% GCC
2	Kryal 1	11.98	2.65	0.11	6.87	8.98	10.60	325.00	9.70	59.00	6.00	8	39	39.38
3	Kryal 1	0.47	1.60	0.24	7.59	4.08	6.07	1000.00	11.70	67.00	5.00	6	41	72.34
4	Kryal 1	20.36	4.91	0.24	6.97	13.70	5.18	511.00	10.80	133.00	10.00	6	32	64.61
5	Kryal 1	1.84	1.85	0.25	6.41	14.20	1.58	237.00	24.00	72.00	6.00	5	29	84.28
8	Kryal 1	11.27	12.52	0.38	6.63	11.05	4.88	774.00	8.70	204.00	13.00	6	39	56.26
9	Kryal 1	1.48	1.74	0.22	7.85	5.15	2.65	543.00	1.40	39.00	3.00	5	39	93.24
1	Kryal 2	8.10	2.27	0.13	6.87	21.96	8.92	290.00	7.30	63.00	10.00	6	43	22.32
7	Kryal 2	3.69	9.65	0.21	6.66	13.90	8.60	414.00	9.00	158.00	19.00	10	36	27.42
37	Kryal 2	36.39	1.72	0.26	7.90	7.65	9.57	282.00	62.50	199.04	6.79	10	23	26.89
38	Kryal 2	22.94	6.03	0.20	7.74	19.37	10.53	284.00	94.00	66.00	8.24	7	23	23.16
47	Kryal 2	23.93	9.09	0.53	7.60	16.72	8.48	133.00	140.00	65.64	10.35	9	25	16.95
6	Kryal 3	6.03	4.41	0.19	7.60	53.60	8.10	58.00	2.20	133.00	18.00	8	31	11.28
14	Kryal 3	34.04	4.80	0.58	8.14	143.60	10.11	202.00	2.30	146.00	33.00	6	23	8.62
24	Kryal 3	1.61	15.47	0.46	7.36	45.10	10.75	75.30	120.00	50.60	18.47	5	29	2.67
29	Kryal 3	41.06	3.56	0.57	8.39	129.50	9.90	66.60	60.00	259.00	27.15	11	30	7.35
30	Kryal 3	22.19	16.27	0.59	7.56	163.20	6.80	24.40	30.00	408.00	30.32	7	34	6.07
31	Kryal 3	139.55	9.68	0.21	7.30	180.60	7.57	21.00	55.00	344.00	13.74	5	28	6.06
33	Kryal 3	102.65	3.91	0.37	6.72	221.10	9.33	19.60	53.00	462.00	37.80	8	25	2.72
40	Kryal 3	16.23	14.75	0.25	7.72	141.28	11.96	111.00	125.00	82.04	18.57	9	23	18.49
41	Kryal 3	26.70	16.03	0.37	7.59	106.93	9.28	7.00	77.00	80.20	24.47	8	38	1.03
42	Kryal 3	22.94	13.73	0.44	7.66	112.65	10.52	44.00	50.00	115.00	29.20	6	23	9.55
43	Kryal 3	21.20	28.46	0.24	7.23	42.51	9.78	92.00	66.00	74.60	19.13	8	26	10.71
45	Kryal 3	81.49	7.31	0.32	7.09	126.06	9.94	32.00	75.00	76.00	20.06	10	25	7.47
46	Kryal 3	24.92	5.50	0.15	7.67	21.98	9.12	131.00	102.50	91.44	15.17	13	24	11.30
49	Kryal 3	34.64	6.10	0.53	7.45	106.49	8.37	17.00	60.50	98.20	31.52	9	30	7.26
50	Kryal 3	187.72	6.29	0.40	7.90	99.14	9.03	62.00	127.50	58.20	18.72	8	34	7.30
51	Kryal 3	23.31	27.00	0.69	7.66	62.50	7.90	60.00	107.50	176.00	37.23	9	37	7.84

Appendix 2. *Continued.*

Number in map	Stream Type	Chlo '*a*' (mg/m²)	CPOM (g/m²)	Velocity (m/s)	pH	Conductivity (µS/cm)	Temperature (° C)	Turbidity (NTU)	Slope (cm/m)	Width (cm)	Depth (cm)	Substrate Types	Pfankuch	% GCC
11	Krenal	68.70	16.17	0.10	7.92	234.00	10.60	1.22	1.70	531.00	19.00	6	49	0
12	Krenal	90.28	11.61	0.28	6.93	137.21	7.50	1.01	6.80	356.00	32.00	8	37	0
13	Krenal	72.94	7.30	0.31	7.79	121.91	8.34	1.75	9.60	56.00	18.00	7	34	0
23	Krenal	23.31	12.45	0.42	7.74	230.00	10.65	4.60	17.50	212.00	14.72	8	30	0
39	Krenal	32.93	10.46	0.18	7.63	246.19	12.64	5.00	107.00	93.96	12.29	7	41	0
10	Rithral	11.34	4.70	0.31	7.43	172.85	8.35	4.97	1.50	60.00	56.00	5	32	0
15	Rithral	43.33	5.04	0.61	8.50	264.70	11.25	9.25	3.20	181.00	19.00	9	32	0
16	Rithral	66.80	6.97	0.42	7.91	255.33	10.37	6.37	4.10	228.00	43.00	7	42	0
17	Rithral	NA	7.47	0.17	7.75	304.50	9.51	6.76	4.00	223.00	66.00	6	50	0
18	Rithral	42.24	21.11	0.18	7.33	121.00	7.80	9.09	125.00	57.00	18.36	11	28	0
19	Rithral	72.20	12.40	0.10	7.33	146.50	9.20	4.19	132.00	68.60	8.53	11	27	0
20	Rithral	37.11	23.55	0.13	7.70	85.65	10.45	4.31	46.00	48.80	5.51	8	29	0
21	Rithral	NA	22.08	0.18	8.44	84.75	7.85	5.92	39.20	80.40	6.80	6	35	0
22	Rithral	22.28	13.66	0.33	6.51	201.00	11.15	4.71	22.00	111.00	26.00	8	27	0
25	Rithral	NA	11.53	0.00	7.49	94.10	14.75	5.20	170.00	194.00	4.28	2	46	0
26	Rithral	1.81	18.64	0.07	7.23	79.40	9.45	20.50	270.00	140.00	8.64	11	31	0
27	Rithral	1.51	14.80	0.05	6.60	100.40	9.35	7.32	262.00	101.00	13.07	5	30	0
28	Rithral	19.75	26.54	0.45	8.08	270.00	8.10	3.17	115.00	195.00	23.37	8	36	0
32	Rithral	112.87	2.05	0.17	5.74	352.00	9.00	97.00	14.00	504.00	24.73	9	44	0
34	Rithral	35.41	10.22	0.21	0.00	183.20	14.80	30.00	71.00	148.33	9.02	6	32	0
35	Rithral	37.91	4.23	0.12	0.00	128.80	9.50	33.30	163.00	136.67	17.65	7	21	0
36	Rithral	94.43	12.30	0.21	7.21	124.40	8.05	8.49	107.00	96.40	19.66	10	39	0
44	Rithral	62.34	16.31	0.21	6.87	175.61	10.17	10.00	118.50	70.60	13.06	9	40	0
48	Rithral	37.82	20.20	0.06	8.18	72.43	8.25	4.00	310.00	55.54	7.01	9	33	0

Appendix 3. Common and unique taxa found at each type of streams. (Bold indicates taxa found in every stream type).

Taxon	Kryal1	Kryal2	Kryal3	Krenal	Rithral	Total
Alluaudomyia sp.						
Andesiops sp.						
Anomalocosmoecus sp.						
***Atopsyche* sp.1**						
Atopsyche sp.2					X	
Blepharicera sp.1						
Blepharicera sp.2						
Blepharicera sp.3			X			
***Cailloma* sp.1**						
Cailloma sp.*2*						
Cailloma sp.*3*			X			
Ceratopogonidae indet.						
***Chelifera* sp.2**						
Chironomidae indet.						
Chironominae						
Chironominae Type 1			X			
Chironominae Type 3			X			
Chironominae Type 4		X				
Claudioperla sp.						
Contulma sp.						
Corixidae Type 2					X	
Crambidae						
Curculionidae sp.1						
Curculionidae sp.2					X	
Diamesinae Type 1						
Diamesinae Type 2						
Dimecoenia sp.						
Dolichopodidae sp.			X			
Dytiscidae sp.	X					
Ephydridae sp.				X		
Geranomyia sp.						
Haliplus sp.				X		
Helichopsychidae sp.					X	
***Hemerodromia sp.*1**						
Hyallela sp.						
Hydracarina sp.1						
Hydracarina sp.2						
Hydracarina sp.3						

Appendix 3. *Continued.*

Taxon	Kryal1	Kryal2	Kryal3	Krenal	Rithral	Total
Hydracarina sp.4					X	
Hydracarina sp.5						
Hydracarina sp.6						
Hydracarina sp.7						
Hydracarina sp.8						
Hydracarina sp.9						
Hydracarina sp.10						
Hydracarina sp.11						
Hydracarina sp.12						
Hydracarina sp.13						
Hydracarina sp.14						
Hydracarina sp.15						
Hydracarina sp.16						
Hydracarina sp.17					X	
Hydracarina sp.18						
Hydracarina sp.19					X	
Hydracarina sp.20						
Hydracarina sp.21			X			
Hydracarina sp.22			X			
Hydracarina sp.23						
Hydracarina sp.24					X	
Hydracarina sp.25					X	
Hydracarina sp.26						
Hydracarina sp.27					X	
Hydracarina sp.28				X		
Hydracarina sp.29						
Hydracarina sp.30						
Hydracarina sp.31					X	
Hydracarina sp.32						
Hydracarina sp.33			X			
Hydracarina sp.34			X			
Hydracarina sp.35			X			
Hydracarina sp.36			X			
Hydracarina sp.37					X	
Hydracarina sp.38					X	
Hydracarina sp.39					X	
Hydroscaphidae cf.						
Glossiphoniidae sp.1						
Glossiphoniidae sp.2						

Appendix 3. *Continued.*

Taxon	Kryal1	Kryal2	Kryal3	Krenal	Rithral	Total
Glossiphoniidae sp.3						
Glossiphoniidae sp.4					X	
Leucotabanus sp.					X	
Limoniidae indet.					X	
Lumbriculidae						
Lymnaeidae						
Mayatrichia sp.			X			
***Molophilus* sp.1**						
Molophilus sp.2						
Mortoniella sp.						
Muscidae sp.1						
Muscidae sp.2						
Muscidae sp.3						
Muscidae sp.4						
Muscidae sp.5				X		
Muscidae sp.6				X		
Muscidae sp.7			X			
Naididae sp.1						
Naididae sp.2						
Naididae sp.3				X		
Nectopsyche sp.						
Nematoda						
Neoelmis (L) sp.1						
Neoelmis (L) sp.2						
Neoelmis (A)sp.1						
Neoelmis (A) sp.2						
Neotrichia sp.1						
Neotrichia sp.2						
Nepticulidae						
Nonagria sp.1			X			
Nonagria sp.2			X			
Ochrotrichia sp.						
Orthocladinae						
Ostracoda						
Planariidae						
Podonominae Type 1						
Podonominae Type 2						
Podonominae Type 3						
Podonominae Type 4						

Appendix 3. *Continued.*

Taxon	Kryal1	Kryal2	Kryal3	Krenal	Rithral	Total
Prionocyphon sp1						
Prionocyphon sp2						
Prionocyphon sp3			X			
Schoenobiinae			X			
***Simulium* sp.1**						
Sphaeriidae						
Staphylinidae sp. 1	X					
Staphylinidae sp. 2		X				
Stilobezzia sp.1						
Stridulivelia sp.					X	
Synclita sp.1						
Tanypodinae						
Tanypodinae type 1			X			
Tipula sp.		X				
Trichocorixa sp.					X	
Total Unique Taxa per Group	2	3	18	6	19	**48**
Total Kryal Unique Taxa						**23**
Total No Kryal Unique Taxa						**25**
Total Kryal Common Taxa						**18**
Total No Kryal Common Taxa						**16**
Total Common Taxa						**13**

Appendix 4. Pairwise SIMPER and ANOSIM of the dissimilarity in the benthic invertebrate community composition between the five study stream types. Only 5 taxa are showed.

Taxon	**Contribution**	**Cumulative %**	**Overall Average Dissimilarity**	**ANOSIM**	
				R	**p**
Kry1 vs. Kry2					
Andesiops sp.	6.423	9.172	70.03	0.6347	0.019
Podonominae Type 1	4.529	15.64			
Neoelmis sp.1 (Larvae)	4.393	21.91			
Alluaudomyia sp.	4.228	27.95			
Simulium sp.	4.143	33.87			
Kry1 vs. Kry3					
Andesiops sp.	5.286	6.885	76.78	0.977	0.001
Hyalella sp.	3.53	11.48			
Neoelmis sp.1 (Larvae)	3.266	15.74			
Alluaudomyia sp.	3.086	19.76			
Orthocladinae	3	23.66			
Kry1 vs. Krn					
Hyalella sp.	6.603	8.178	80.73	0.928	0.023
Andesiops sp.	5.739	15.29			
Planariidae	4.476	20.83			
Lumbriculidae	4.039	25.83			
Anomalocosmoecus sp.	3.458	30.12			
Kry1 vs. Rth					
Hyalella sp.	5.461	6.901	79.14	0.9554	0.001
Andesiops sp.	4.751	12.9			
Lumbriculidae	3.493	17.32			
Orthocladinae	3.442	21.67			
Hydracarina (TOTAL)	3.294	25.83			
Kry2 vs. Kry3					
Hyalella sp.	2.549	4.752	53.64	0.7023	0.004
Anomalocosmoecus sp.	2.385	9.197			
Orthocladinae	2.088	13.09			
Planariidae	2.045	16.9			
Mortoniella sp.	2.021	20.67			

Appendix 4. *Continued.*

Taxon	**Contribution**	**Cumulative %**	**Overall Average Dissimilarity**	**ANOSIM**	
				R	**p**
Kry2 vs. Krn					
Hyalella sp.	4.9	8.091	60.55	0.656	0.083
Planariidae	3.303	13.55			
Anomalocosmoecus sp.	2.859	18.27			
Orthocladinae	2.376	22.19			
Simulium sp.	2.309	26.01			
Kry2 vs. Rth					
Hyalella sp.	3.979	6.835	58.21	0.6421	0.008
Anomalocosmoecus sp.	2.476	11.09			
Hydracarina (TOTAL)	2.438	15.28			
Orthocladinae	2.358	19.33			
Planariidae	2.281	23.24			
Kry3 vs. Krn					
Alluaudomyia sp.	1.854	4.205	44.09	0.3879	0.201
Anomalocosmoecus sp.	1.65	7.947			
Simulium sp.	1.586	11.54			
Hyalella sp.	1.565	15.09			
Mortoniella sp.	1.492	18.48			
Kry3 vs. Rth					
Alluaudomyia sp.	1.486	3.593	41.35	0.05817	0.643
Anomalocosmoecus sp.	1.469	7.146			
Mortoniella sp.	1.394	10.52			
Hyalella sp.	1.356	13.8			
Ostracoda	1.313	16.97			
Krn vs. Rth					
Simulium sp.	1.912	4.284	44.64	0.1201	1
Anomalocosmoecus sp.	1.757	8.221			
Alluaudomyia sp.	1.532	11.65			
Tanypodinae	1.509	15.03			
Ostracoda	1.505	18.4			