

Macroinvertebrate Diversity and Rarity in Non-Glacial Alpine Streams

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**Running Head:** Biodiversity in Alpine Streams

## Abstract

Alpine landscapes are being transformed through the rapid recession of glaciers, resulting in the development of numerous non-glacial headwater streams inhabited by a diverse assemblage of macroinvertebrates. We examined spatial patterns in biodiversity and rarity of macroinvertebrates in 41 non-glacial streams from five glacierized catchments in the Swiss Alps undergoing rapid glacial recession over the last decades. Water physico-chemistry and food resources (periphyton, benthic organic matter) varied widely among streams within each catchment, while no significant differences occurred among catchments. Variability in community composition was similar among streams within each catchment but differed among catchments, reflecting differences in catchment-scale species pools due to biogeographical context and season. Overall, 101 taxa from ca 33,000 individuals collected were identified in the streams with 7 to 33 taxa found in individual streams. Some 64% of the taxa comprised less than 5% of the total abundances at the streams (rare in abundance) with 78% of the taxa being represented by less than 5% of the most common taxon (*Baetis* sp.), whereas 47% of the taxa were found in less than 10% of the streams (rare in distribution). No taxon was found at all sites (maximum presence at 85% of the sites), while 15% of the taxa were found at 50% of the sites or more. However, analyzing the rank-abundance distribution showed that rarity was less prevalent than previously shown in other ecosystems. The results indicated that community assembly of alpine headwater streams is a complex interaction between environmental properties (habitat filtering), habitat stability coupled with dispersal (source sink dynamics), and time since deglaciation (island biogeography). Integrating these processes is essential towards understanding ongoing colonization events in headwater streams of alpine catchments as glaciers continue to recede.

**Key words:** aquatic macroinvertebrates, dispersal, stream headwaters, species abundance distribution, community ecology, rarity

## Introduction

Globally, alpine landscapes are undergoing major transformations in response to rapid glacial recession and altered precipitation patterns due to environmental change (IPCC 2014). Alpine catchments encompass a diversity of stream types, comprising strictly pro-glacial (kryal), groundwater-fed (krenal), and precipitation-fed (rhithral) streams (Milner and Petts 1994; Ward 1994), as well as streams with combinations of those water sources (Brown et al. 2009). In addition, streams differ in their water availability throughout the course of the year, including permanent streams but also intermittent/ephemeral streams (Robinson and Matthaei 2007; Brown et al. 2009; Robinson et al. 2015). Many alpine streams lengthen as glaciers retreat, glacial-fed streams in particular (Finn et al. 2010; Robinson et al. 2014), and new tributary streams and even proglacial lakes can develop (Milner et al. 2009).

Although a relatively recent research area (essentially beginning in the late 1990s), most stream research in alpine catchments has focused on glacial streams (see Milner et al. 2001; Jacobsen et al. 2012) with only a handful of studies examining other stream types (e.g., Fureder et al. 2001; Hieber et al. 2005; Cauvy-Fraunie 2014; Robinson et al. 2015). Stream intermittency can impose limitations on stream biodiversity (Datry et al. 2014), but permanent non-glacial (kreno-rhithral) streams likely enhance the overall biodiversity of alpine catchments by providing more optimal environmental conditions for aquatic insects than glacial and intermittent streams (Fureder et al. 2001; Hieber et al. 2005; Clitherow et al. 2013). Presently, there is major concern that changes in the eco-hydrology of glacial streams from climate change threaten the

biodiversity of alpine catchments via the loss of alpine specialists (Balint et al. 2011; Jacobsen et al. 2012; Finn et al. 2013; Cauvy-Fraunie et al. 2016).

The dendritic structure of streams across landscapes often influences spatial biodiversity patterns (Campbell Grant et al. 2007; Altermatt et al. 2013; Tonkin et al. 2018). This effect should be pronounced in alpine catchments in which mainstem channels are typically glacial-fed and therefore harsh environments due to unstable channels and cold temperatures (Fureder 1999; Milner et al. 2001). These environmental factors constrain species distribution and abundance (Clitherow et al. 2013; Cauvy-Fraunie 2014). In fact, species endemism is common in alpine streams (Ward 1994; Robinson et al. 2010) and dispersal likely limited between stream types (i.e., following source sink dynamics) (Finn et al. 2013; Cauvy-Fraunie et al. 2015). Further, immigration is fed mostly from downstream sources, with species ranges moving upstream as glaciers recede (Finn et al. 2010; Robinson et al. 2014). In this context, permanent tributaries may act as stepping stones and continuous sources of immigrants for the colonization of other non-glacial streams in alpine landscapes (Shama et al. 2011), and in particular streams emerging during ongoing and rapid glacial recession. These newly colonized streams in turn may impose strong environmental sorting mechanisms in the beginning that select for adapted specialist species. This dynamic interplay has its roots in island biogeography theory (i.e., immigration and extinction processes; MacArthur and Wilson 1967) placed within a habitat template framework (sensu Southwood 1977, 1988).

Rarity is a common feature in the distribution and abundance of organisms in ecosystems (Brown 1984; Gaston 1994; Brown et al. 1996; Magurran and Henderson 2003). Rabinowitz (1981) described seven forms of rarity that are related to restricted geographic distribution, narrow habitat distribution, and low local population abundance. Gaston and Fuller (2007) noted

that the presence of a few common species is a further type of rarity in community assembly, and likely important in structuring biodiversity patterns among alpine streams (e.g., Clitherow et al. 2013). Indeed, rarity is often equated with the relationship between geographic range size and dispersal (Lester et al. 2007). The high spatio-temporal heterogeneity in the habitat template of alpine streams (e.g., Tockner et al. 1997) suggests that rarity may be an important component in community assembly.

The contribution of rarity in the biodiversity of alpine streams has yet to be determined, although food webs of glacial streams appear simple and dominated by a few common species (Clitherow et al. 2013). Other studies have documented the presence of rare taxa in streams with rarity ranging from ca. 37 to 75% of macroinvertebrate community composition (Resh et al. 2005; Arscott et al. 2006; Robinson et al. 2016). Further, how different stream types may interact regionally in species distribution is still unclear. Rarity may act as a spatially shifting mosaic of taxa presence in close vicinity to receding glaciers through a complex interplay of mass effects and habitat filtering related to distance to the receding glacier (sensu Cottenie 2005). Newly appearing streams next to the receding glacier may quickly be colonized by specialist species but later harbor mostly generalist species since disturbance favors generalist species (Büchi and Vuilleumier 2014). Work in arctic regions showed that less stable snowmelt-fed streams may lose specialist species (Docherty et al. 2018) and extreme hydrological events and flow variability impose strong effects on community assembly, favoring generalist species (Sarremejane et al. 2018).

The primary objective of this study was to examine the biodiversity and rarity of macroinvertebrates in tributary streams in alpine catchments undergoing rapid glacial recession. Study streams lacked a glacial influence (i.e., kreno-rhithral) and had permanent flow, thus

providing more optimal environmental conditions for aquatic macroinvertebrates than so-called harsh pro-glacial and intermittent streams (Ward 1994). We hypothesized that (1) tributary streams show a large variation in environmental conditions with comparable variability within and between catchments, and house a diverse macroinvertebrate community, even though having low primary production and allochthonous inputs. (2) These environmental differences in physico-chemical variables and productivity will drive observed community differences. Unlike previous studies, we expected to find a deficiency of rare species in the study streams due to prevalent benign conditions (e.g., water temperature) in comparison to nearby glacial-fed streams and in combination with seasonal changes (Mykrä and Heino 2017). We further hypothesized that (3) the rank abundance distributions in these streams fit a log-normal distribution, with no excess of rare species. However, (4) the fraction of rare species was expected to be higher in younger streams closer to the retreating glacier due to the advantage of specialized species in colonizing these developing habitats, later to be replaced by generalist species (Sgarbi and Melo 2018).

## **Methods**

### **Study sites**

We selected five alpine catchments in Switzerland (Fig. 1) that contribute to three major drainage basins in Europe: Rhine River flowing to the North Sea, Rhone River flowing to the Mediterranean Sea, and the Inn/Danube River flowing to the Black Sea. The glaciers in each catchment have receded dramatically in the last decades; e.g., the Roseg glacier receded over 4 km from 1855 to 2011 and the Morteratsch glacier receded over 2.4 km from 1878 to 2011 (Burga 1999). In the last 50 years, Stein glacier receded 503 m, Lang glacier 572 m, Morteratsch 986 m, and Roseg receded 2663 m (data generated from Gletscherberichte 1881-2009). Glacial

recession has resulted in the emergence and lengthening of new stream channels and the presence of pro-glacial lakes (Finn et al. 2010; Robinson et al. 2014).

Study streams in each catchment were first and second order headwater streams situated between 1798 and 2494 m above sea level (a.s.l.) (Table 1) with permanent flow and surrounded by sparse riparian vegetation and alpine pastures with small shrubs (mostly *Salix* and *Alnus* spp.). The number of streams sampled in each catchment ranged from 5 (Mortersatsch) to 8-10 (other catchments) (Fig. 1), totaling 41 tributaries. Sampling took place from mid-June to early September 2012. The water source for each stream was groundwater and precipitation (rain and snow-melt fed)(krenal/rhithral streams); and importantly, no stream was fed by glacial meltwater (kryal streams) since there were no glaciers upstream potentially feeding into the sampled streams (also see Fig. 1). All streams flowed into the main glacial-fed channel draining each catchment and no stream was directly flow-connected to another study stream, meaning that aquatic organisms dispersing between them must cross the main glacial-fed channel. Representative 30-50 m reaches were sampled upstream of any physical influence of the confluence with the glacial main channel; i.e., at least 100 m or more upstream of the confluence depending on access to a stream. Each site location was recorded with a Garmin eTrex Vista GPS device. Time since deglaciation was calculated with glacial recession data from the Gletscherberichte (1881-2009). The time since deglaciation is a rough estimate since it is the direct distance from the glacial snout compared to receding data and it assumes constant glacial recession.

## **Field and laboratory protocols**

At each site, we collected a 0.5 liter water sample for chemical analysis in the laboratory. In the laboratory, water samples were analyzed for dissolved organic carbon (dorc), ortho-phosphate (opho), dissolved phosphorus (dpho), total phosphorus (tpho), dissolved nitrogen (dnit), nitrate (nitr), chloride (chlo), silicate (sili), sulfate (sulf), sodium (sodi), potassium (pota), calcium (calc) and magnesium (magn) following methods detailed in Tockner et al. (1997). Most values for dissolved nitrogen, nitrate, chloride, dissolved phosphorus, sodium, potassium, calcium and magnesium were below detection limits of the analytical procedures and not included in additional analyses. Spot recordings of temperature (temp), electrical conductivity (cond) (WTW, Germany) and turbidity (turb) (Cosmos, Switzerland) were made with field portable meters at each site. Discharge (disc) of each stream at the time of sampling was estimated using width, depth and velocity (MiniAir 2, Schiltknecht AG, Gossau, Switzerland) measures averaged across 20 transects (Allan and Castillo 2009).

Periphyton biomass as a measure of food resource availability was determined quantitatively for each stream by collecting three randomly selected stones (b-axis: mean = 6.3 cm, SD = 1.4) and storing at -20°C for subsequent processing in the laboratory. Periphyton was removed from the surface of each stone with a metal bristle brush and a 5-10 ml aliquot filtered through a combusted GF/F Whatman<sup>TM</sup> filter. The filtered material was dried at 60°C, weighed, ashed at 500°C for 4 hours, and reweighed for determination of ash-free dry mass (AFDM). Each AFDM value was standardized to the surface of the corresponding stone ( $a\text{-axis} \times b\text{-axis} \times \pi/4$ ) (after Uehlinger 1991). Benthic organic matter (BOM), also as a measure of food resource availability, was collected at three randomly selected locations in each stream. The collection area (15x15 cm) was disturbed to a depth of 10 cm and the suspended material collected in a net (mesh size = 250  $\mu$ m) placed directly downstream. Samples were stored frozen (-20°C) and



analyzed later in the laboratory. After removing macroinvertebrates, the ash-free dry mass of each sample was determined as for periphyton.

We used a circular kicknet (mesh size = 250  $\mu$ m, diameter = 20 cm) for the qualitative sampling of macroinvertebrates in each stream. Sampling was conducted for 5 minutes along the study reach in each stream, sampling in a corresponding ratio of fast- to slow-flowing areas to ensure coverage of the most common habitat types in each stream. The streambed was disturbed manually, turning single stones and digging in the stream bottom to collect as many taxa as possible inhabiting each stream. Macroinvertebrate samples were preserved with 70% ethanol for later processing in the laboratory. In the laboratory, each sample was presorted, separating all clearly visible individuals from the coarse organic matter such as leaf litter and branches.

Depending on the density of the most frequent taxon, a fraction of the sample was sorted using a stereomicroscope. Individuals were handpicked from subsamples until a threshold of 50 individuals from the most frequent taxon was reached. All specimens were identified with a Leica M205C or Olympus SZH-ILLB dissecting stereomicroscope and counted. For analysis, individuals from the subsamples were up-scaled by the fraction and added to the total numbers.

Species keys used for identification were *Invertébrés d'eau douce* (Tachet et al. 2010), *Ephemeroptera (Fauna Helvetica; 9)* (Studemann et al. 1992), *Die Steinfliegen der Schweiz (Fauna Helvetica; 27)* (Lubini et al. 2012), *Atlas of Central European Trichoptera Larvae* (Waringer and Graf 2011), and *Bestimmung wirbelloser Tiere* (Bährmann 2011). Chironomids (larvae) were identified to species/genus and species groups (Wiederholm 1983, 1986; Serra-Tosio 1989; Langton 1991; Schmid 1993; Saether 1995; Brooks et al. 2007; Lencioni et al. 2007; Ilyashuk et al. 2010). A large majority of the chironomid material was mounted (microscopic slides) in Euparal and all the collection material (slides and alcohol samples) deposited in the

Museum of Zoology in Lausanne (Switzerland) for archiving. Simuliidae were classified as either *Simulium* or *Prosimulium* spp. based on the coloration of antenna and the form of the frontoclypeus (Tachet et al. 2010). We identified the Plecoptera and Ephemeroptera to genus and Trichoptera to species, thereby allowing a tentative comparison with the official Swiss biodiversity monitoring data (IBCH method; Stucki 2010). All identified individuals, except chironomids, were stored in 70% ethanol as a reference collection at Eawag, Duebendorf, Switzerland.

## Data analysis

All raw data are available in the Supplement Data S1. The environmental variables were tested for a normal distribution using a Shapiro-Wilk test. Except for temperature and silicate that met normality assumptions, variables were  $\ln(x)$  or  $\ln(x+1)$  transformed (Zar 1984). Following transformation, all variables meeting the assumptions of a normal distribution (temperature, silicate, elevation, conductivity, discharge, AFDM, BOM) were tested for significant differences among catchments using ANOVA and MANOVA using the Pillai–Bartlett statistic. Those variables not meeting a normal distribution (DOM, sulfate, ortho-phosphorus, total phosphorus) were excluded from further analysis. Environmental data also were analyzed using principal components analysis (PCA) to illustrate any basin or stream differences (Legendre and Legendre, 2012) using the function *princomp* in R.

Macroinvertebrate diversity was assessed using abundance data (individuals per 5-min kick sample) and taxon richness (as morphospecies). We calculated Simpson's Index (1- $D$ ) as  $D = \sum \frac{n_i(n_i-1)}{N(N-1)}$ , where  $n_i$  is the number of individuals of the  $i^{\text{th}}$  taxon and  $N$  the total number of individuals within the sample, and the Shannon-Weaver Index ( $H'$ ) as  $H' = -\sum p_i * \ln p_i$ , where

$p_i = n_i / N$  (Jost 2007) using the function *diversity* from package *vegan* (Oksanen et al. 2018).

These indices were calculated for each site and represent the classical  $\alpha$ -diversity (after Whittaker 1956). Taxa turnover between sites and catchments was assessed using  $\beta$ w-diversity calculated as  $\beta_w = \frac{\gamma - \alpha}{\alpha} = \frac{\gamma}{\alpha} - 1$  and is analogous to  $\delta$ -diversity, where  $\gamma - \alpha = \beta_A$  or the absolute taxa turnover (Whittaker 1972; Koleff et al. 2003). Taxon accumulation curves were generated using the function *specaccum* from package *vegan*, adding sites randomly and doing 100 permutations. Rank-abundance distributions were directly accessible from ordered raw abundance data (after Kendall 1938). Rarity was calculated using a threshold value of 5% for abundance rarity, defining species as being rare if represented by less than 5% of the total number of sampled individuals or if represented by less than 5% of the individuals of the most common taxon. Additionally, we defined taxa as being rare at sites if they were found in less than 10% of the sampled sites (4 sites or less).

Distance matrices for the community data were calculated from absolute numbers using the Bray-Curtis index (Bray and Curtis 1957) using the function *vegdist* from package *vegan*. We performed a nonmetric dimensional scaling analysis (NMDS) to examine for community differences among catchments. The number of dimensions was chosen such that the stress values were below 0.05. To statistically check for differences between communities present among catchments, we used an analysis of similarity (ANOSIM) (Anderson 2001) using the function *adonis* from package *vegan*. To assess the potential influence of environmental variables on community composition, we performed a distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999) using the function *dbrda* from package *vegan*. Since two measures were missing, we only considered 39 sites and temperature, silicate, elevation, conductivity, discharge, AFDM, and BOM as explanatory environmental variables.

To assess differences in  $\beta$ -diversity, we performed a multivariate test of homogeneity of dispersions (PERMDISP; Anderson 2006) using the function *betadisper* from package *vegan*. We assessed statistical significance of the result using a permutation test with 999 runs. To compare the observed rank-abundance distribution to theoretical log-normal and log-series distributions, we generated the expected distributions using 999 simulated draws from these distributions either providing the observed mean and standard deviation (for log-normal, *rlnorm*) or Fisher's alpha (Fisher et al. 1943), derived with the function *fisherfit* from package *vegan* (for log-series *rls* from package *sads*). To statistically assess, if our abundance data fit a log-normal distribution we performed a Shapiro-Wilk test of the log-transformed data.

To test if distance to the glacier had an influence on the fraction of rare species at single sites, we ran a generalized linear model with log-transformed distance to glacier snout assuming a quasi-binomial response. Since assuming a quasi-binomial response is only an approximation, we ran a Beta regression assuming a beta-distributed response with the function *betareg* from package *betareg* (Cribari-Neto and Zeileis 2010). Package versions were ver 2.4-6 for *vegan* (Oksanen et al. 2018) and ver 3.1-0 for *betareg* (Cribari-Neto and Zeileis 2010). All statistical analyses were performed using R 3.4.4 (R Core Team, 2018) and R Studio ver. 1.1.442 (© 2009-2018, R Studio, Inc.). The whole R script used for analysis is available in the Supplement Data S2.

## Results

### Environmental characteristics of streams

All streams had clear water at the time of sampling with turbidity <10 NTU (Table 1). Mean site elevation was 2080 m a.s.l. (SD 154 m a.s.l.) with the lowest stream at 1798 m a.s.l. (Lang) and the highest (2495 m a.s.l.) at Jöri (Table 1). The mean discharge of streams was

generally low, ranging from 0.08 (Stein) to 0.33 (Morteratsch)  $\text{m}^3 \text{s}^{-1}$ , although varying considerably among streams ( $\text{CV} = 166\%$ ). Mean conductivity was low at  $45.5 \mu\text{S cm}^{-1}$  (SD  $24.7 \mu\text{S cm}^{-1}$ ), ranging from 21.1 (Morteratsch) to  $63.4 \mu\text{S cm}^{-1}$  (Lang). Mean stream temperature was  $8.2^\circ\text{C}$  (SD  $3.5^\circ\text{C}$ ) and mean silicate concentration was  $4.94 \text{ mg L}^{-1}$  (SD  $1.85 \text{ mg L}^{-1}$ ). Mean BOM was  $0.42 \text{ g AFDM}$  (SD  $0.41 \text{ g}$ ) among catchments. Mean periphyton biomass (AFDM) was  $34.3 \text{ g m}^{-2}$  (SD  $24.5 \text{ g m}^{-2}$ ). All values are summarized in Table 1.

Significant differences were found among catchments for temperature, silicate, and elevation (ANOVA,  $F_{4,36} = 4.18; 4.07; 5.45$ , all  $p < 0.01$ ). The other variables (conductivity, discharge, AFDM, BOM) were not significantly different among catchments (ANOVA,  $p > 0.05$ ). MANOVA confirmed the overall environmental differentiation among catchments (approx.  $F_{4,34} = 3.11$ ,  $p < 0.001$ ). A PCA-ordination containing all environmental variables showed these subtle differences of stream environmental properties among the different catchments (Supp. Fig. S1).

## **Biodiversity patterns**

Overall, 101 aquatic taxa representing 12 taxonomic orders were identified from the 33,150 collected individuals from the 41 streams. Average taxa richness per site was 21.8 (SD 7.1), with a minimum of 7 taxa (Lang) and maximum of 33 taxa (Lang). The number of sites occupied per taxon ranged from 1 (*Amphinemura* sp.) to 35 (*Baetis* sp.) (mean 8.9, SD 8.9). Abundance within streams ranged from 18 to 2539 (both in Lang) individuals per kick sample (mean 808.5, SD 667.2) (Table 2). The mean number of individuals per species was 328.2 (SD 764.9), and ranged from 1 (e.g. Hydrophilidae) to 5643 (*Baetis* sp.). The taxon accumulation

curve showed that there were a few more species to be expected if our sampling was continued (Supp. Fig. S2).

The number of taxa and abundance of individuals did not differ significantly between catchments (ANOVA,  $F_{4,36} = 1.66$  and  $0.051$ ,  $p = 0.18$  and  $0.99$ , respectively). Mean catchment values for Shannon's  $H'$  ranged from  $1.88$  (Roseg) to  $2.35$  (Jöri), and for the Simpson's index from  $0.72$  (Roseg) to  $0.85$  (Jöri). Mean catchment  $\beta_w$ -diversity (beta diversity) ranged from  $0.43$  (Jöri) to  $0.60$  (Lang) and ranged from  $0.22$  to  $0.88$  among streams within a catchment. Mean catchment  $\beta_a$  (absolute taxa turnover) ranged from  $10.4$  (Morteratsch) to  $12.6$  (Jöri) (Table 2). Shannon's  $H'$  and Simpson's index ( $1-D$ ) were not significantly different among catchments (ANOVA,  $F_{4,36} = 1.22$  and  $0.73$ ,  $p = 0.32$  and  $0.58$ , respectively).

Most individuals were Diptera and EPT taxa (Ephemeroptera/Plecoptera/Trichoptera). Around 95% of the identified individuals were represented by the 36 most abundant taxa, indicating that the other 65 taxa (64%) were rare in abundance. Some 47 taxa (47%) would be considered rare when defining rarity as those taxa occurring only at a few sites (present at <10% of the sites; i.e., present at 4 sites or fewer). Twenty taxa occurred only at one site, whereas a different set of 15 taxa were found at 50% of the sites or more. No taxon was found at all sites (maximum number sites for presence was 35 (85%) for *Baetis alpinus* (Ephemeroptera) and *Pediciini* (Diptera).

A nonmetric multidimensional scaling (NMDS) with 8 dimensions and Hellinger transformed community data separately grouped streams among catchments (Fig. 2). The catchments of Morteratsch, Roseg and Lang overlapped along axis 1 and 2. These results were confirmed by the analysis of similarity (ANOSIM), showing subtle but significant differences

among catchments based on Bray-Curtis community dissimilarity ( $R = 0.33$ ,  $p < 0.001$ ; Supp. Fig. S3).

The distance-based redundancy analysis using Hellinger-transformed community data and the environmental data showed that there was a significant effect of environmental variables on community dissimilarity (permutation test,  $F_{7,31} = 1.52$ ,  $p = 0.003$ ; Fig. 3). A permutation test adding terms sequentially showed that these differences were explained mostly by differences in temperature and elevation.

The PERMDISP analysis (Supp. Fig. 4) to assess community divergence showed that there was no significant difference in  $\beta$ -diversity between catchments (permutation test,  $F_{4,34} = 1.38$ ,  $p = 0.26$ ). This result suggests that community variance ( $\beta$ -diversity) within catchments is comparable to between catchment variance. Only the comparison between Jöri and Lang revealed a significant community divergence (permutation test,  $F_{4,34} = 1.38$ , observed  $p = 0.046$ ).

The comparison of observed rank-abundance distribution to the theoretically expected log-normal or log-series distributions showed that our community data were log-normal distributed (Fig. 4). This result indicates that there were less rare species than previously shown in many ecosystems (Magurran and Henderson 2003). However, the Shapiro-Wilk test on the log-scale showed that the abundance data did not exactly fulfill the assumptions of log-normal ( $W = 0.969$ ,  $p = 0.019$ ). Checking the histogram of log-transformed abundance data (Supp. Fig. S5) showed that there was an excess of single findings and a slight excess of very common species, which also is visible in the log-normal QQ-plot (Supp. Fig. S6).

The time (in years) since study streams emerged from beneath retreating glaciers was highly correlated with the actual spatial distance to the glacial snout (Spearman's  $\rho = 0.92$ ;  $p < 0.0001$ ) and so distance can be used as a surrogate for stream age. A quasi-binomial GLM

confirmed our assumption that the fraction of rare species decreased with increasing distance of the sampling site from the glacier ( $p < 0.001$ ; Fig. 6). Beta regression supported this result, showing a highly significant response ( $z = 4.18$ ,  $p < 0.001$ ), even though the Pseudo  $R^2$  was only 0.374 (Fig. 5).

## Discussion

Globally, alpine landscapes are being transformed at unprecedented rates concomitantly with rapid glacial recession. How this rapid environmental transformation influences the distribution and abundance of aquatic macroinvertebrates is a key question regarding future trajectories in biodiversity within these landscapes (e.g., Leys et al. 2016). Current thinking infers a biodiversity crisis with major reductions in beta diversity (Jacobsen et al. 2012; Finn et al. 2013), reflecting losses in cryptic species and genetic diversity of macroinvertebrates in general (Balint et al. 2011; but see Isaak et al. 2016). The dendritic nature of stream networks strongly affects the dispersal of aquatic organisms across the landscape (Altermatt et al. 2013; Wilson and McTammany 2016), especially in alpine landscapes in which the harshness of glacial mainstem channels limits dispersal of truly aquatic species among tributary streams (see Cauvy-Fraunie et al. 2015). This critical constraint on macroinvertebrate dispersal in glacierized catchments infers the important role of rarity in biodiversity patterns within and among non-glacial tributary streams (sensu Kunin and Gaston 1993). Our results document that rarity is less prevalent than in other ecosystems and hence generalist species likely play an important role in the ecology of non-glacial alpine streams and in the overall biodiversity of glaciated alpine catchments.

As expected, rarity contributed to the  $\alpha$ -diversity within the sampled streams, contributing upwards of 90% to the overall biodiversity within individual streams. In terms of



abundance, 65 of 101 identified taxa represented < 5% of the total abundance when all streams were considered. Indeed, no taxon was found at all sites (maximum presence was 35 of 41 sites), whereas 47 taxa were found at <10% of the sites. This pattern of diversity fits general theory in which a strong correlation exists between abundance and occupancy (after Gaston et al. 2000) and also fits abundance patterns of diatoms (Robinson et al. 2010) and bacteria (Besemer et al. 2013) in alpine headwaters. Chironomidae dominated most stream assemblages in terms of abundance (see Robinson et al. 2010; Robinson et al. 2016), and are usually the first to colonize newly developed proglacial streams (Finn et al. 2010; Robinson et al. 2014). Lencioni et al. (2011) found 67% of the chironomids identified in their study were rare, thus showing a similar pattern as this study in terms of overall rarity. Typically, a few common species (i.e., rarity in commonness) maintain ecosystem function (Smith and Knapp 2003; but see Leitao et al. 2016 for an alternate view), whereas the commonness of rare species (in terms of abundance) increases the invasibility of ecosystems (Lyons and Schwartz 2001). In this respect, the expected threat to biodiversity through the loss of rare species, and endemic specialists in particular, may enhance invasion of these systems by other species (e.g., those expanding their upstream distribution with glacial recession, see Finn et al. 2010). How these new species influence future trends in ecosystem function, e.g. functional diversity or redundancy (see Leitao et al. 2016; Logares et al. 2016), has yet to be determined.

Many of the taxa involved were aquatic insects and had a flying adult stage in the life cycle, thus allowing overland dispersal between streams. Cauvy-Fraunie et al. (2015) found that dispersal in glaciated catchments was restricted by the harsh environmental conditions of glacial mainstem channels into which non-glacial streams flow, thus restricting active dispersal among alpine streams to primarily aquatic insects with a flying adult stage (also see Thompson and

Townsend 2006 for similar ideas regarding species traits and dispersal limitations). This dispersal pattern follows that described by stepping stone models and source sink dynamics (Finn et al. 2014; Finn et al. 2016). Non-glacial streams likely are colonized first by migrants from adjacent or nearby non-glacial streams as stepping stones (Shama et al. 2011). Likewise, immigrants attempting to colonize the environmentally harsh glacial mainstem or nearby temporary alpine streams probably fail to maintain adequate populations and the channel/streams can thus act as a sink for these organisms (e.g. Tonkin et al. 2016a,b). For instance, Shama et al. (2011) documented strong bottleneck effects in the spatial genetic structure of a caddisfly between permanent and temporary alpine streams. Leys et al. (2016) also showed distribution differences between cryptic species of the alpine mayfly *Baetis alpinus*, the most common taxon (abundance and distribution) in the current study.

Despite subtle differences in stream environmental conditions that reflected regional differences in geology, e.g. between Stein catchment and the other catchments, this was not reflected directly in community composition. Consequently, the mean beta ( $\beta_w$ ) diversity was similar among catchments, although varying substantially among streams within a catchment, suggesting similar community assembly processes were operating within the different catchments (see Tonkin et al. 2016b regarding mass effects vs. species sorting processes in river networks). Due to the sampling campaign being conducted in a single season, temporal variation could not be studied and future studies are needed to understand this aspect, potentially being pronounced in non-glacial tributaries.

Future environmental trajectories predict the continuing loss of glaciers in many alpine catchments worldwide (IPCC 2014) with a concomitant reduction in glacial influence on the ecohydrology of river networks (Huss et al. 2008; Sorg et al. 2012). Furthermore, the projected

degree of climate change is expected to be greater at higher altitudes due in part to a proportionately larger decrease in snow cover (IPCC 2014). A recent global study by Ohmura (2012) based on observations from the last 50 to 125 years found enhanced warming with elevation in about two-thirds of the mountain regions examined. Additionally, various studies have documented a high degree of stream intermittency due to seasonal expansion and contraction cycles in the hydrology of alpine landscapes (Malard et al. 2006; Robinson and Matthaei 2007; Robinson et al. 2015) with the degree of intermittency likely to increase in the future (Robinson et al. 2003; Datry et al. 2014). The reduction in glacial influence will likely enhance the dispersal potential of macroinvertebrates among alpine streams by allowing more species to disperse via mainstem channels (*sensu* Cauvy-Fraunie et al. 2015) but also provide more optimal environmental conditions for immigrants from downstream to colonize permanent alpine streams (Finn et al. 2010; Cauvy-Fraunie et al. 2016). The more favourable and connected tributary habitats may even enhance biological invasion by non-native species.

The observed pattern of abundance seems to imply that there is a surplus of generalist species, with less rare species than would be expected in comparison to other ecosystems. The effects of this interplay (habitat homogenization and intermittency versus dispersal and colonization) on alpine stream biodiversity is unknown but suggests that both generalist and specialist species will still be important as some species are lost while others redistribute through dispersal and immigration (*sensu* MacArthur and Wilson 1967). Species presence and absence among streams will be a function of local habitat conditions (*sensu* Southwood 1977, 1988) with a few common taxa (some rare taxa as well becoming common) dominating community assemblages and ecosystem functioning (after Gaston and Fuller 2007). Lastly, only a small fraction of rare species will potentially change their status at a given site over time (Magurran

and Henderson 2003; Sgarbi and Melo 2018). Regardless, regional species pools will likely decrease with loss of endemic, alpine and glacier stream specialists (Jacobsen et al. 2012) along with the loss in cryptic species and overall genetic diversity (Balint et al. 2011; Pauls et al. 2013; Finn et al. 2014). As suggested by Lennon et al. (2004) for birds, patterns of richness may be explained better through the spatial distribution of the few common species in the ecosystem and their response to environmental change on stream structure and function.

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679 TABLE 1. Environmental characteristics of the study streams in each catchment. Data summarized as means, standard deviations (SD),  
680 and coefficients of variation (CV). Number in parentheses is the number of tributaries sampled in each catchment (see Figure 1).  
681 DOM = dissolved organic matter, BOM = benthic organic matter. Asterisks (\*) indicate streams significantly differed among  
682 catchments (ANOVA,  $p < 0.05$ ). Note: Abbreviations of measured variables in parentheses

Catchment		Elevation* (elev)	Conductivity (cond)	Temperature* (temp)	Turbidity	DOM	Sulfate (sulf)	Silicate* (sili)	Ortho- phosphate* (opho)	Total P (tpho)	Discharge (disc)	Periphyton	BOM (bom)
		(m a.s.l.)	( $\mu\text{Scm}^{-1}$ )	( $^{\circ}\text{C}$ )	(NTU)	( $\text{mg l}^{-1}$ )	( $\text{mg l}^{-1}$ )	( $\text{mg l}^{-1}$ )	( $\mu\text{g l}^{-1}$ )	( $\mu\text{g l}^{-1}$ )	( $\text{m}^3\text{s}^{-1}$ )	(AFDM $\text{gm}^{-2}$ )	(AFDM $\text{g/sample}$ )
Total	Mean	2074	44	8.0	5.4	0.52	9.5	4.9	1.4	4.8	0.20	35.0	0.42
	SD	150	24	3.5	8.3	0.41	10.1	1.8	0.9	3.5	0.32	25.3	0.39
Lang (9)	Mean	1972	63	5.4	6.8	0.82	15.1	5.9	2.4	6.9	0.08	33.3	0.63
	SD	123	35	3.2	9.7	0.76	12.4	1.4	1.3	5.5	0.10	16.4	0.58
Jöri (9)	Mean	2222	53	7.8	6.9	0.44	19.7	5.2	1.3	2.9	0.26	21.1	0.44
	SD	219	18	1.6	10.2	0.19	10.4	1.0	0.9	2.1	0.42	15.9	0.30
Morteratsch (5)	Mean	2026	21	9.3	NA	0.51	2.5	4.0	0.9	2.7	0.33	35.3	0.54
	SD	42	8	1.7	NA	0.27	0	0.5	0.6	2.6	0.27	12.4	0.49
Roseg (10)	Mean	2090	44	7.6	NA	0.46	4.3	5.3	1.4	6.2	0.10	45.5	0.34
	SD	76	19	3.1	NA	0.26	2.6	2.8	0.3	2.4	0.08	37.2	0.38
Stein (8)	Mean	2064	35	11.8	2.2	0.35	2.8	3.7	0.9	5.7	0.08	38.9	0.22
	SD	107	14	3.9	2.1	0.19	0.9	1.5	0.5	1.6	0.12	28.5	0.16

683

684 TABLE 2. Summary of the number of individuals, taxa richness, Shannon's Index ( $H'$ ),  
685 Simpson's Index ( $1-D$ ), Whittaker's  $\beta_w$  (beta diversity) and Lande's  $\beta_a$  (absolute species  
686 turnover) for each catchment (number of streams sampled in each catchment in  
687 parentheses).

688

Catchment		Individuals	Taxa richness	Shannon's $H'$	Simpson's $1-D$	Whittaker's $\beta_w$	Lande's $\beta_a$
Lang (9)	Mean	879.8	22.7	2.02	0.76	0.60	12.6
	SD	768.3	11.1	0.69	0.21	0.19	3.1
	Range	18-2539	7-33	0.63-2.75	0.24-0.91	0.30-0.88	4-17
Jöri (9)	Mean	774.6	26.3	2.35	0.85	0.43	11.3
	SD	512.4	3.0	0.22	0.06	0.09	2.5
	Range	288-1666	21-30	2.05-2.58	0.73-0.89	0.22-0.64	6-18
Morteratsch (5)	Mean	860.4	18.2	1.98	0.78	0.58	10.6
	SD	987.8	8.1	0.28	0.08	0.11	3.8
	Range	70-2501	11-32	1.56-2.25	0.66-0.87	0.42-0.72	6-16
Roseg (10)	Mean	797.9	19.5	1.88	0.72	0.54	10.4
	SD	694.3	5.1	0.68	0.24	0.12	2.3
	Range	198-2376	7-24	0.32-2.61	0.11-0.91	0.28-0.78	6-18
Stein (8)	Mean	747.6	21.0	1.93	0.77	0.49	10.4
	SD	614.2	4.6	0.26	0.07	0.10	2.7
	Range	322-2234	14-29	1.48-2.25	0.65-0.86	0.28-0.69	5-16

## Figure Legends

Figure 1. Maps of the glacial catchments (L, M, R, S, J) and the corresponding stream network and lakes (dark blue). Glaciers (grey) and flow directions (red arrows) together with all sampling sites (red dots) are shown. All catchment maps show the same scaling and are northwards oriented. Note: Glacial snout positions are drawn for the year 2008 since no newer data were available, thus sites S1, S2 and S4 are ice covered in the figure but were accessible in 2012.

Figure 2. Nonmetric multidimensional scaling (NMDS) of the community data reveals subtle differences between catchments in taxa composition. The adjacent Morteratsch and Roseg catchments show very similar communities, whereas the other catchments differ from each other.

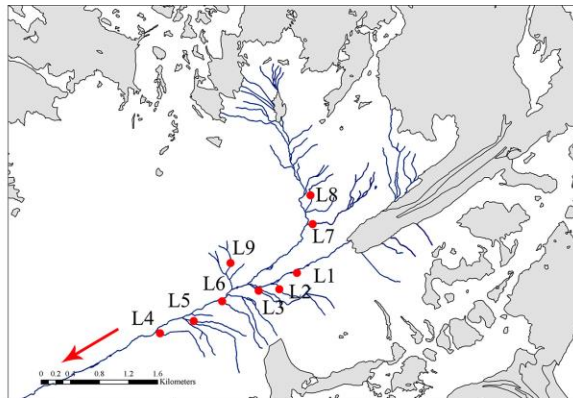
Figure 3. The distance-based redundancy analysis (dbRDA) shows a significant impact of the environmental variables on the community dissimilarity, clustering them mainly along the temperature and elevation gradient. Spatially close communities cluster only partially in the dbRDA, supporting the importance of environment on community composition.

Figure 4. Comparing the observed rank-abundance data (black dots) with simulated log-normal (red line) or log-series (blue line) distributions showed that the data were almost perfectly log-normal distributed, indicating less rare species than expected. However, there was still an excess of single findings and a slight excess of very common species.

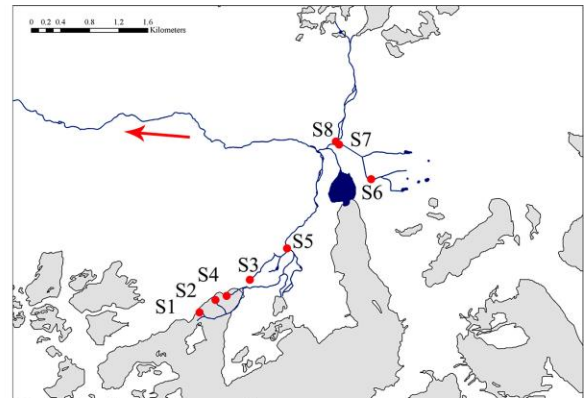
Figure 5. Distance to the glacier (as a surrogate for stream age) explains the fraction of rare species occurring at single sites. The red line shows a quasi-binomial GLM, with 95%

712 confidence intervals shown as shading. A Beta regression (blue dotted line) showed almost  
713 exactly the same highly significant pattern ( $R^2 = 0.374$ ). Different sites are colored according to  
714 the catchment of origin.

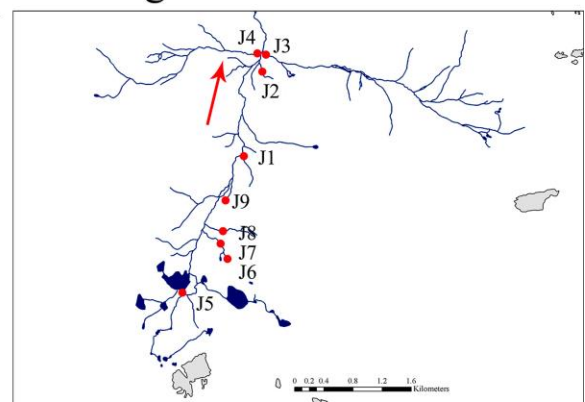
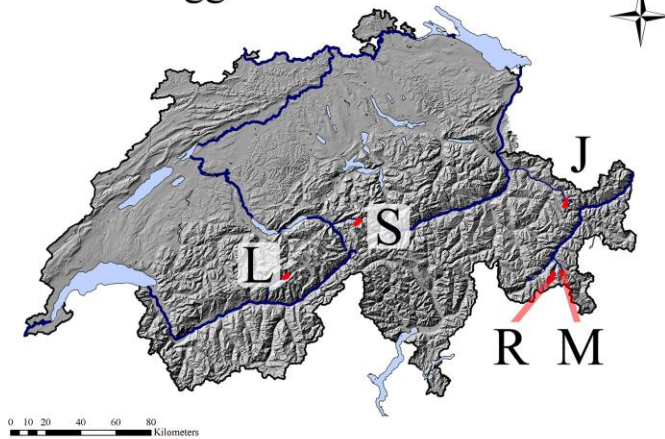




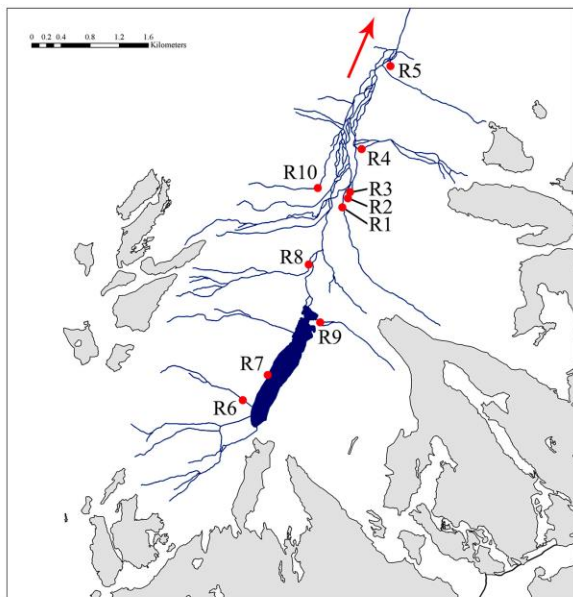
L: Langgletscher



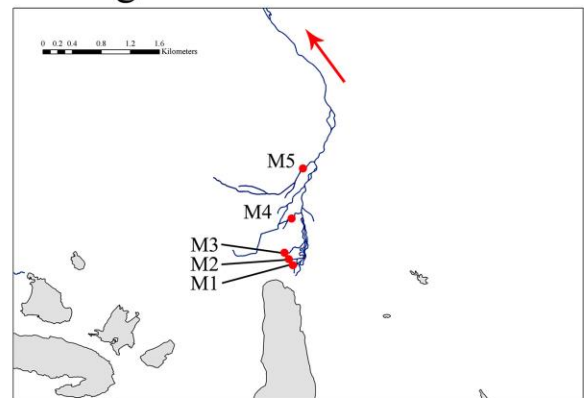
S: Steingletscher



J: Jörigletscher



R: Roseggletscher



M: Morteratschgletscher



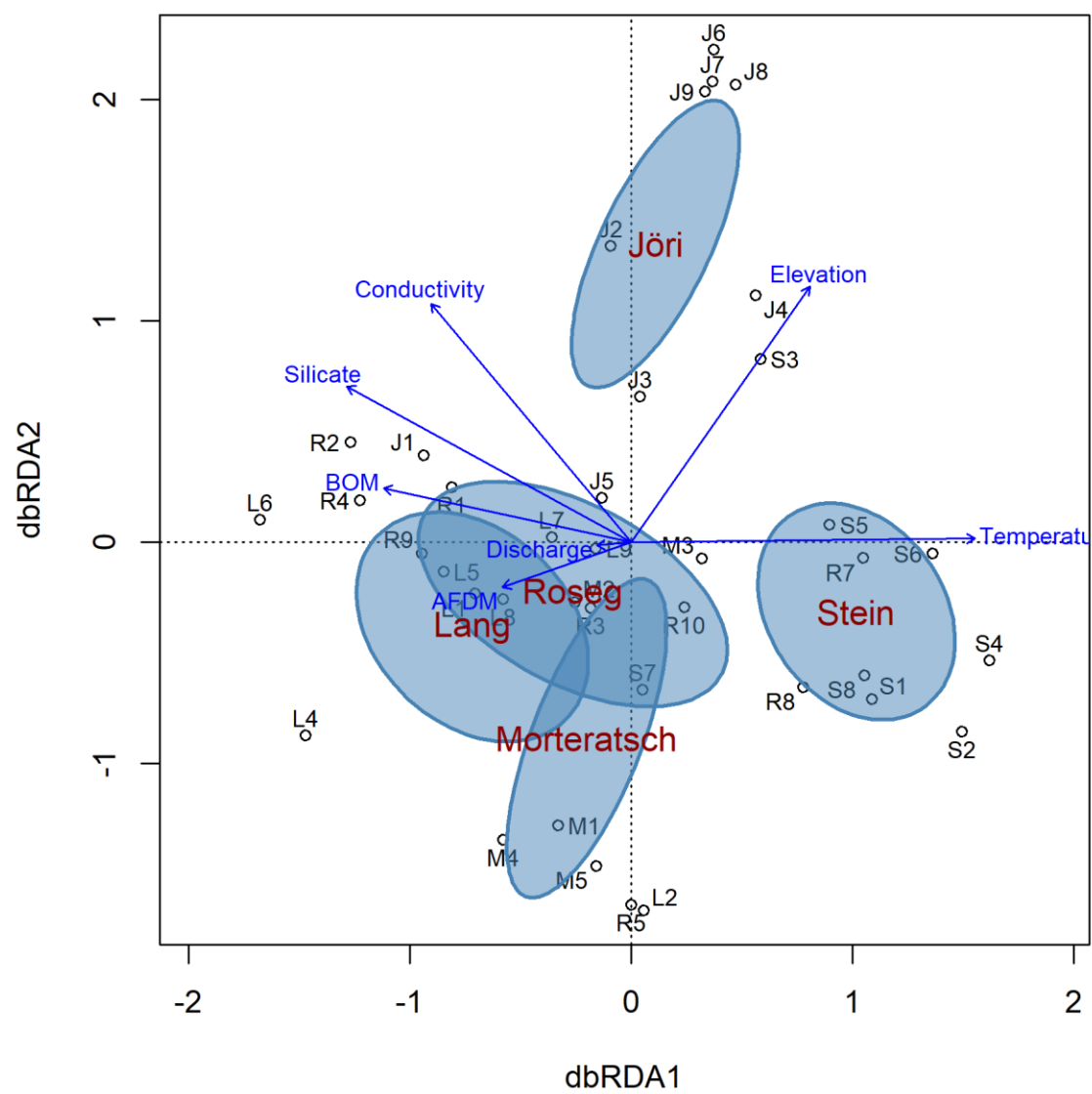
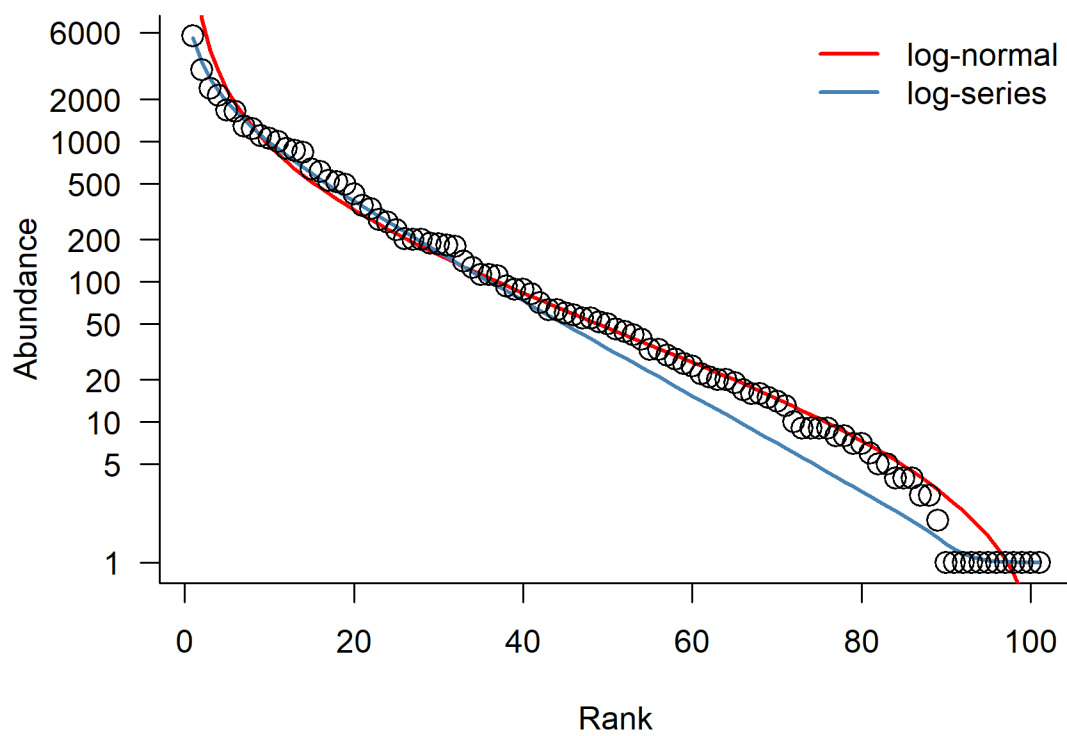


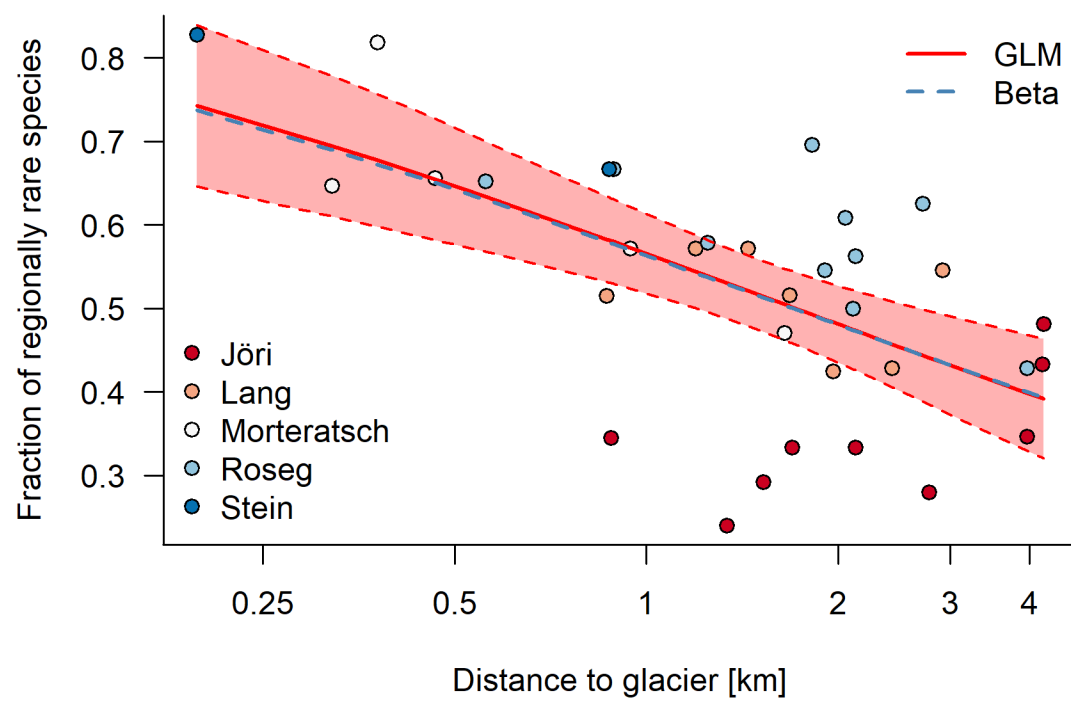
Figure 3



722

723 Figure 4

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726 Figure 5

Figure S1. Summary plot of the principal components analysis (PCA) completed using environmental measures collected for the study. Measures used in the PCA included elevation, electrical conductivity, temperature, silicate, discharge and benthic organic matter (BOM).

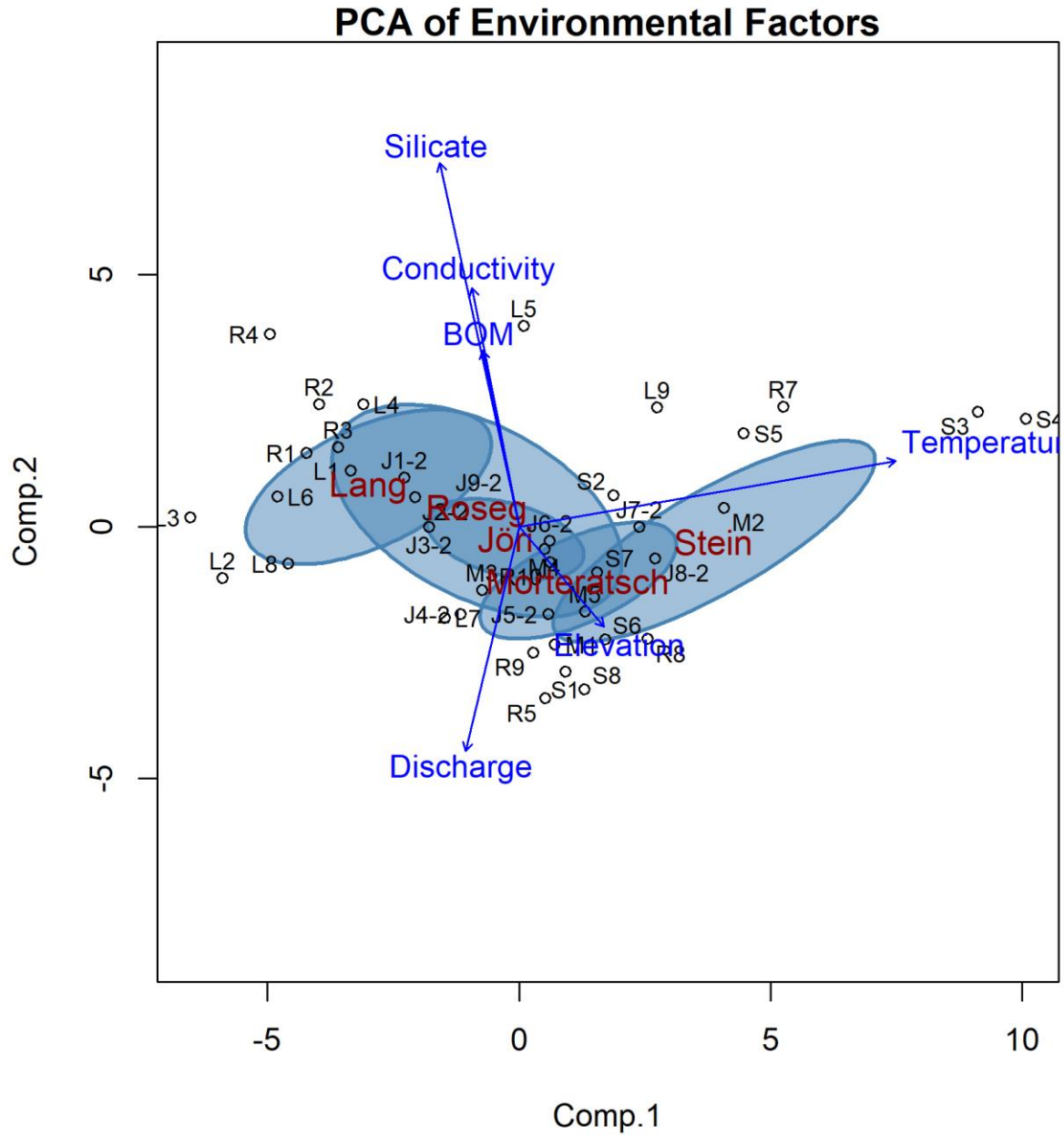
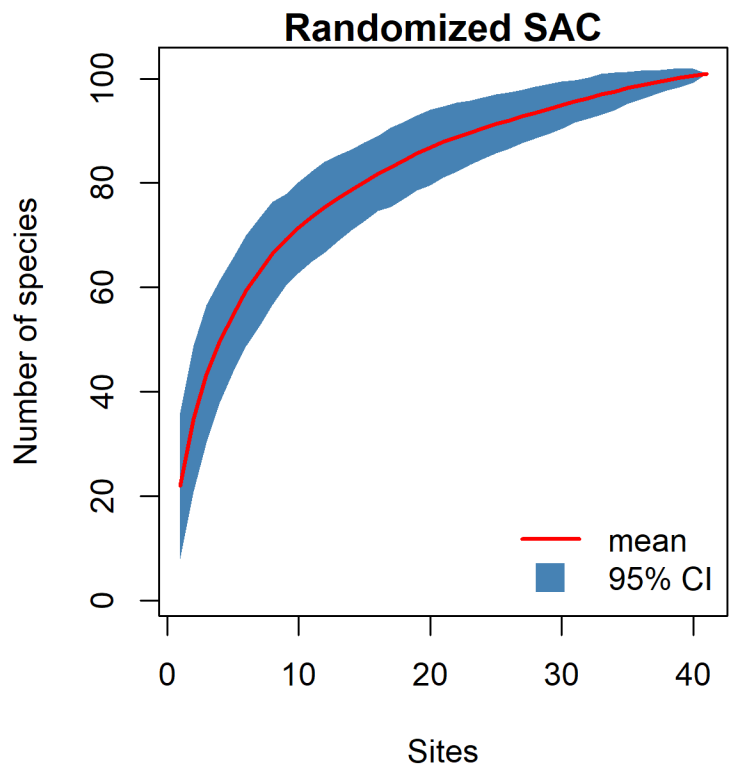
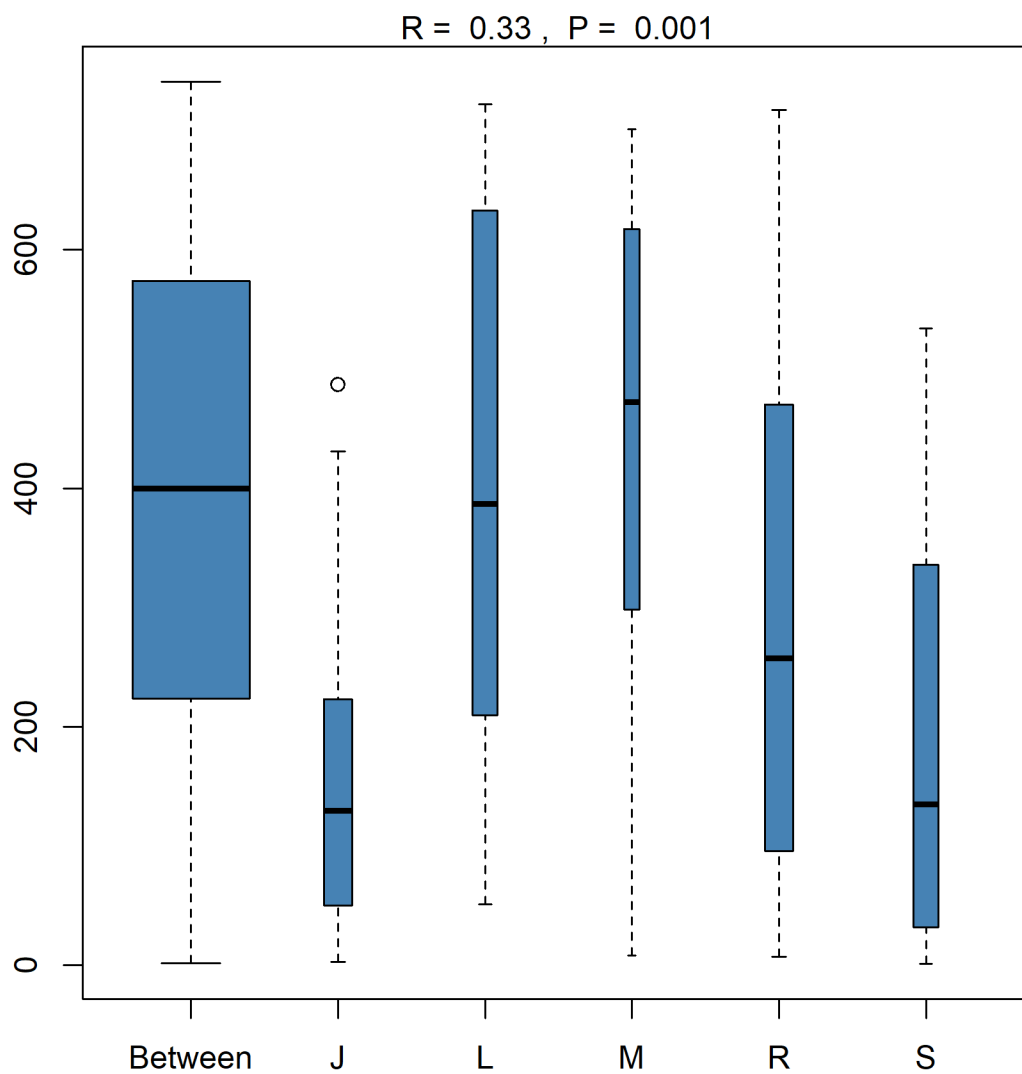


Figure S2. Taxon accumulation curve created by adding sites randomly and doing 100 permutations.

Richness saturation was not reached using 41 sites, but only few more species would be expected.



736 Figure S3. ANOSIM showing subtle but significant differences among catchments based on the Bray-  
737 Curtis community dissimilarity. However, differences within and between sites fall into the same range.  
738 Width of the bars show the differences in number of comparisons.

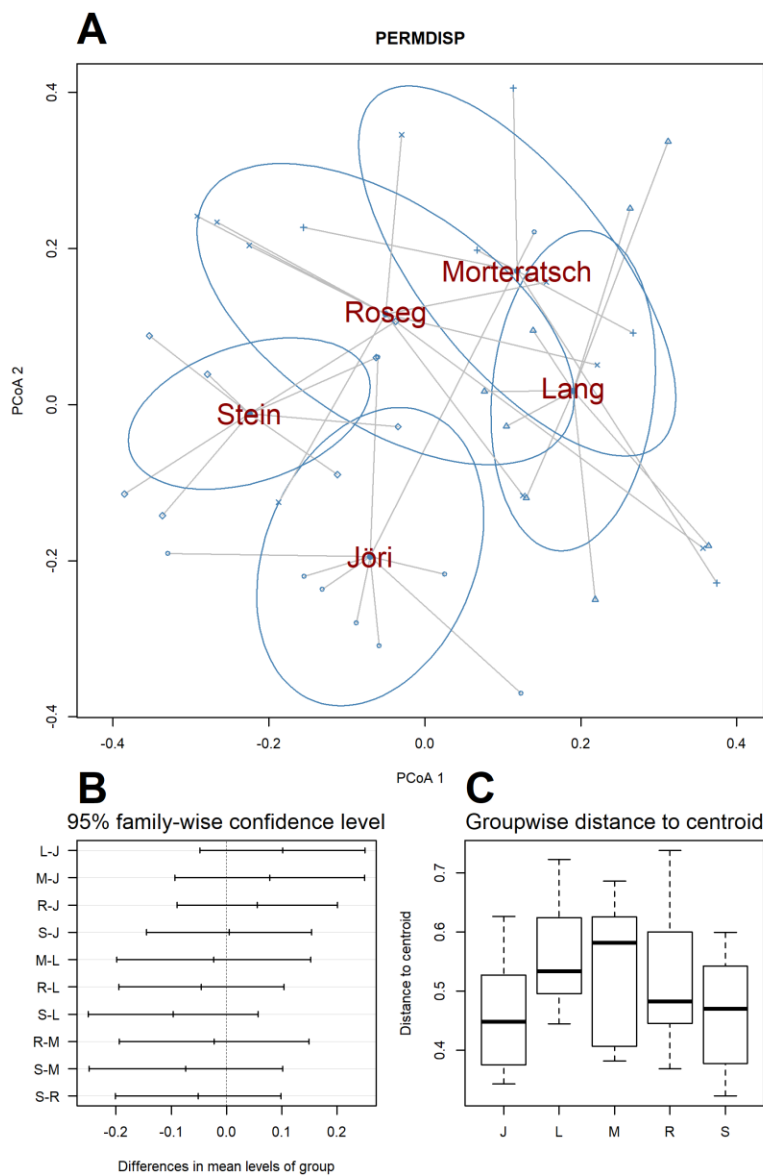


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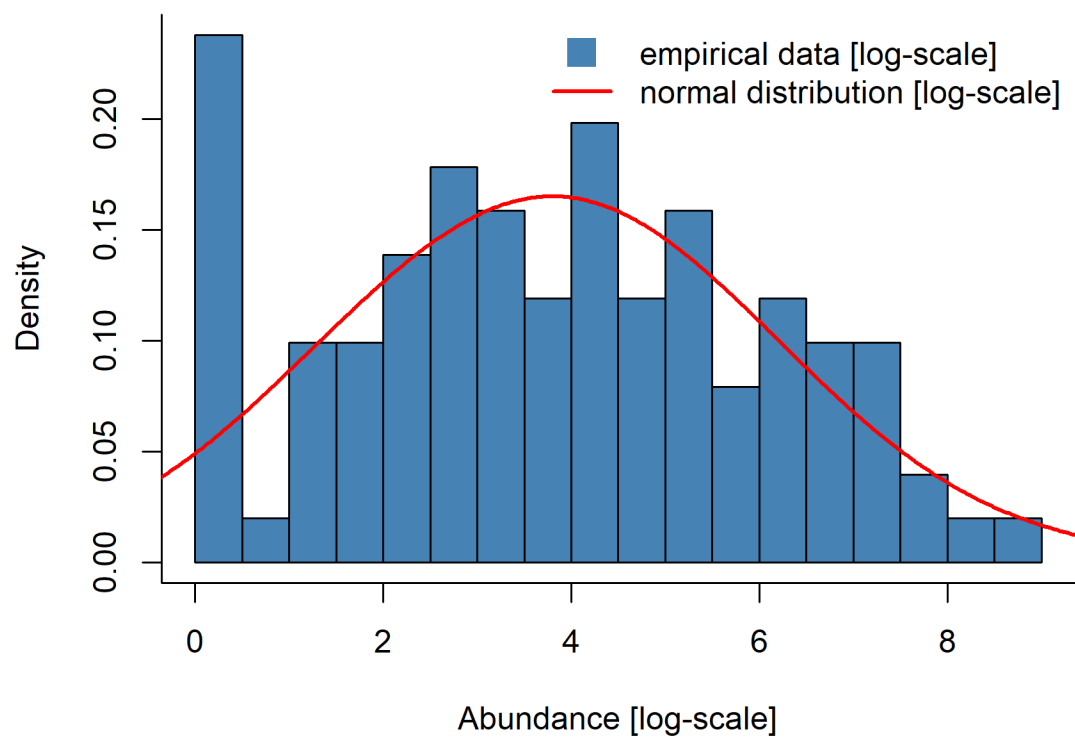
740



Figure S4. PERMDISP revealed no significant difference in  $\beta$ -diversity among catchments, suggesting differences within catchments are comparable to among catchment differences in community composition. A) Plotting PCoA 1 and 2 shows overlaps of the 95% confidence hulls around the centroids of individual catchments. B) This is supported by Tukey's Honest Significant Differences (Tukey's HSD) between all pairs of combinations. C) The mean distance of sites to the catchment centroid was comparable among all catchments.



749 Figure S5. Histogram of observed abundances, with the log-normal distribution overlaid, depicting the  
750 excess of single findings to the very left and a slight excess of common species at the right tail of the  
751 distribution.



752

Figure S6. QQ-plot of observed abundances against theoretically expected values from the log-normal distribution where the excess of single findings at the lower left end and a slight excess of common species at the upper right end become apparent.

