Article

Diversity and composition of macroinvertebrate assemblages in high-altitude Tibetan streams

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Abstract

Knowledge on the ecology of streams at extreme altitudes is relatively sparse. We conducted a preliminary survey of the macroinvertebrate fauna of Tibetan streams in June 2009 and August 2011 and compared streams with different water sources. We collected quantitative samples of macroinvertebrates and measured physicochemical variables at 16 sites (8 each sampling year) at altitudes ranging from 4315 to 5065 m a.s.l. and grouped the sites into 3 types according to origin: glacier-fed, rain-fed, and lake-outlets. We identified 38 taxa, with a mean of 8.9 taxa per site. Overall the benthic fauna was dominated by insects (71%), mainly Diptera (especially Chironomidae). Ephemeroptera, Plecoptera, and Trichoptera were found at nearly all sites but mostly in low numbers; however, the fauna was significantly different in the 2 sampling years, especially due to the proportions of Chironomidae (68% in June 2009 and 10% in August 2011) and Baetidae (6% vs. 35%, respectively). The 3 stream types had significantly different faunas. Rain-fed streams had the highest total taxon richness (γ-diversity), but glacier-fed streams had a slightly higher taxon turnover rate (β-diversity). Percent glacial cover in the catchment and water turbidity explained most of the variability in taxon richness. Although not particularly taxon rich compared to other high-altitude streams, the Tibetan stream fauna showed considerable spatial variability. The fast retreat of the glaciers and permanent snow fields in Tibet makes further studies on distribution patterns and driving forces for aquatic biodiversity urgent.

Key words: alpine streams, assemblage composition, benthic fauna, glacial influence, macroinvertebrates, seasonal variability, Tibet, water source

Introduction

Alpine streams are subject to a high degree of spatial variability in the abiotic environment, partly due to the variety of possible water sources (Smith et al. 2001). Groundwater may be relatively ion- and nutrient-rich, is usually clear, and adds stability in temperature, water flow, and channel morphology (Malard et al. 1999). Surface and subsurface runoff from rainfall and snow melt varies seasonally and is a key contributor of nutrients and organic carbon from the surroundings (Uehlinger et al. 2002). Glacier-fed streams are a harsh environment (Jacobsen and Dangles 2012); they are cold, usually nutrient poor and turbid, and physically unstable, with large fluctuations in water flow (Milner and Petts 1994). In the Holarctic, species of Diamesinae (Chironomidae) are usually the only ones occupying pro-glacial reaches immediately downstream from the glacier snout, but they cannot compete with the more wide-spread species found farther downstream (Ward 1994, Milner et al. 2001). Glacier-fed streams become more benign farther downstream as the atmosphere warms the water and the stream receives tributaries from other non-glacial catchments. The ameliorating conditions downstream gradually accommodate other chironomid groups such as Orthocladiinae and, eventually, species of Ephemeroptera,

Plecoptera, and Trichoptera (Milner and Petts 1994, Milner et al. 2001). Lakes may act as buffers against temperature and hydrological fluctuations and will typically alter the downstream faunal composition, giving rise to both higher taxon richness and densities of macroinvertebrates (Hieber et al. 2002, Maiolini et al. 2006).

In the extreme environment of glacier-fed streams, in particular near the glacier, a strong niche selection filters the species from the regional pool, leading to higher similarities and a more predictable community composition than in less extreme habitats located farther from glaciers and in non-glacial streams (Leibold et al. 2004, Chase 2007). Nevertheless, maximum β-diversity, both at the population–genetic (Finn et al. 2013) and community level (Jacobsen and Dangles 2012), was recently found in highly glaciated catchments. Glacier-fed streams thus seem to contribute to the aquatic environmental heterogeneity at the catchment level and therefore increase taxon turnover (β-diversity) and regional taxon richness (γ-diversity; Jacobsen et al. 2012). Although local diversity (α-diversity) will generally increase as a result of glacial shrinkage or disappearance, a reduction of both β- and γ-diversity at the population–genetic and community levels of biological organization is also expected (Jacobsen et al. 2012).

Most of what we know about macroinvertebrate communities in alpine streams comes from Europe (e.g., Füreder et al. 2001, Hieber et al. 2005) or North America (e.g., Ward 1986, Finn and Poff 2005), while studies from the Himalayas (Rundle et al. 1993, Suren 1994) and tropical Andes (e.g., Jacobsen 2003, Loayza-Muro et al. 2010) have provided additional insight into the organization of communities in very high-altitude (>3000 m a.s.l.) alpine streams. Although the Qinghai-Tibetan Plateau is the largest and highest plateau in the world and is surrounded by several biodiversity hot-spots (Favre et al. 2014), in terms of stream ecology and aquatic biodiversity, Tibet has virtually been a (large) white spot on the map (Jacobsen et al. 2013) until a few recent studies (Hamerlik and Jacobsen 2012, Murakami et al. 2012, Jiang et al. 2013) provided some insight into physicochemical parameters and biological communities of running waters.

Tibet is also highly affected by climate change and is currently experiencing one of the fastest increases in average temperatures outside the poles (Gautam et al. 2009). The region is witnessing a rapid change in natural vegetation, shift in crops and human land use (Wang et al. 2008), degradation of permafrost, shrinkage and/or disappearance of glaciers, and altered hydrological regime of rivers (Du et al. 2004, Yao et al. 2007). In light of this, studies on distribution patterns and driving factors of macroinvertebrate communities in Tibetan streams, in particular focusing on the effects of glacial sources, are important and timely.

Our 3 main objectives were therefore to (1) conduct a preliminary survey of the composition and diversity patterns of the macroinvertebrate fauna in Tibetan streams; (2) test for an effect of sampling time or season; (3) investigate the qualitative and quantitative differences in the fauna between streams with different water sources, comparing lake-outlets, rain-fed, and glacier-fed streams; and (4) analyze more specific relationships between the cover of glaciers in catchments and properties of the stream fauna.

Methods

Study area and site selection

Our study included 13 streams (14 sites) that are tributaries to the Brahmaputra (via Yalung and Dihang) and 2 streams within the River Salween basin (via River Nu). All sites were located 28°22′32″–31°01′05″N, 85°48′55″–92°21′10″E, covering a large part of southeastern Tibet. Altitudes of study sites ranged from 4315 to 5065 m a.s.l., all above the tree line. Field work was conducted on 2 occasions: half of the sites were sampled in June 2009 (sites 1–8) and the remaining in August 2011 (sites 9–16). We selected sites to cover differences in main water source and glacial influence, including 7 sites receiving varying amounts of meltwater from glaciers located upstream in the catchment, denoted "glacier-fed" (5 sampled in 2009 and 2 in 2011), and 7 sites without glaciers in the catchment and thus fed by subsurface and surface runoff of rainwater and snowmelt, denoted "rain-fed" (3 sampled in 2009 and 4 in 2011). In addition, 2 streams with a non-glacier–fed lake placed just upstream of the sampling sites, denoted "lake-outlets," were sampled in 2011. Two sites were located along the same stream and separated by a few hundred meters; one of these sites (1G) was sampled in 2009 and the other (11G) in 2011. These sites were located downstream of a pro-glacial lake, but we treat them here as glacier-fed. We had no way of estimating ground water contribution, but this likely contributed in varying degrees to the flow at all sites.

Several indices of glacial influence on the stream environment have been developed and used to investigate the effect of glacial meltwater contribution on aquatic biodiversity. These indices have been based on percentage of glacier cover in the catchment (Füreder 2007, Milner et al. 2009), glacier size and distance from the glacier terminus (Jacobsen and Dangles 2012), percentage of meltwater contribution (Milner et al. 2006, Brown et al. 2007), or physicochemical habitat variables (Ilg and Castella 2006). Because only spot measurements of such environmental data were available, however, we preferred to estimate glacial influence simply as the distance of stream sites from the

glacier terminus and as the percentage of glacier cover in the catchment, obtained using the software "Image J" based on topographic maps and satellite pictures in Google Earth.

Field measurements and sampling

At each site, we selected a representative reach spanning about 30 m. Coordinates and altitude were obtained with a GPS (Garmin eTrek 10). Conductivity, temperature, and dissolved oxygen were measured with a handheld multi-probe (YSI model 6000), and turbidity was measured using a Eutech-100 turbidity meter. The mean width and depth where calculated from a series of 3–5 transversal transects, while the current velocity was estimated and categorized as either moderate (~0.1–0.3 m s^{-1}), fast (~0.3–0.6 m s^{-1}), or strong (>0.6 m s^{-1}). The most abundant substrate types, stream channel stability, macrophyte cover, and periphyton biomass were estimated visually along each reach.

Macroinvertebrates were collected as 5 quantitative Surber samples (25 × 20 cm; mesh size 200 µm) obtained from representative riffle/run habitats and preserved in 70% ethanol. In the laboratory, samples were processed using a magnifying glass, without use of subsampling. Insects were identified to family or subfamily level using available identification keys (Edington and Hildrew 1981, Elliot et al. 1988, Wallace et al. 1990, Hynes 1993) but separated into different morpho-species. Non-insects were identified to higher taxonomic levels.

Data treatment

To compensate for varying sample sizes (i.e., number of individuals in samples), we used rarefied taxon number as a measure of taxon richness, estimating the number of taxa based on the sample with the lowest number of individuals, in this case 31. To measure the evenness of the macroinvertebrate assemblages we used Pilou's index (J′). For each stream group we calculated mean local diversity (α-diversity) as the mean number of taxa collected per site, total or regional diversity (γ-diversity) as the total number of taxa collected, and taxon turnover (β-diversity) as total divided by mean local diversity. A t-test on log-transformed data was used to test for differences between univariate fauna metrics and densities of specific families/taxa between sampling campaigns.

Analyses of similarities in the taxonomic composition among localities were based on Bray-Curtis (dis)similarity on log-transformed taxon data. These data were used to perform a nonmetric multidimensional scaling (NMDS) ordination to illustrate relative differences in assemblage composition. This ordination technique has no assumptions with repect to distributions and represents samples as points in low-dimensional space, such that the relative distances among points reflects the relative similarities of samples with respect to both abundance and composition (van der Gucht et al. 2005). The NMDS goodness-of-fit was estimated with a stress function (ranges from 0 to 1), with values close to 0 indicating a good fit. Our interest was not to perform cluster analyses of sites, but rather to test whether our 3 *a priori* defined groups of glacier-fed, rain-fed, and lake-outlets showed overall differences in assemblage composition. For this we used analysis of similarities (ANOSIM), which tests the null hypothesis that within-group similarity was equal to between-group similarity. ANOSIM generates a statistical parameter R, which indicates the degree of separation between groups; a score of 1 indicates complete separation, and a score of 0 indicates no separation (van der Gucht et al. 2005).

To elucidate taxonomic relationships among the 3 stream groups, we performed similarity percentage analysis (SIMPER). This analysis gives the contribution (in percentage) of each taxon to the observed similarity between groups or samples within groups and therefore identifies the most important taxa for creating the observed pattern of similarity. Univariate metrics were calculated and multivariate analyses were conducted with Primer-e (Clarke and PRIMER 2006).

To construct a simple predictive model for taxon richness, we used ordinary least squares (OLS) model selection, using the multiple regressions integrated in the SAM software (Rangel et al. 2010). All available explanatory variables were tested against taxon count, and the most parsimonious model was identified using the lowest corrected Akaike's Information Criterion (AICc).

Results

Stream site characteristics

Catchments sizes of the study sites varied from <6 km^2 to >400 km^2, with glacial cover varying from 0 to 78% of the catchment. Stream sites covered considerable physicochemical variability in all measured parameters (Appendix 1).

General patterns and temporal differences in macroinvertebrate assemblages

We collected 8014 individuals and 38 taxa (Appendix 2). At individual stream sites, the number of taxa varied from 3 to 13 (average 8.9 per site), and the number of individuals collected ranged from 31 to 2802 in the 5 Surber samples (~124–11 208 ind m^{-2}; Table 1). Rarefied taxon number (based on 31 individuals) ranged from 3.00 to 8.34, and the evenness index (J′) from 0.06 to 0.86 (Table 1).

Table 1. Univariate fauna metrics for 16 Tibetan stream sites. G denotes glacier-fed sites, R rain-fed sites, and L lake-outlets.

Stream Site	Sampled	Taxon Number	Individuals N m^{-2}	Richness Rarefaction	Evenness Pielou J'
1G	2009	10	3404	4.26	0.50
2G	2009	3	124	3.00	0.85
4G	2009	5	2532	1.42	0.06
7G	2009	7	824	5.13	0.53
8G	2009	10	1328	3.97	0.43
11G	2011	9	972	5.17	0.57
12G	2011	10	388	8.34	0.86
3R	2009	10	736	7.56	0.79
5R	2009	13	2232	7.01	0.63
6R	2009	11	11 208	4.65	0.49
14R	2011	9	1812	6.01	0.75
15R	2011	10	2184	5.41	0.68
16R	2011	8	528	5.26	0.48
9R	2011	11	1196	6.15	0.58
10L	2011	10	1112	4.15	0.33
13L	2011	10	1492	5.40	0.60
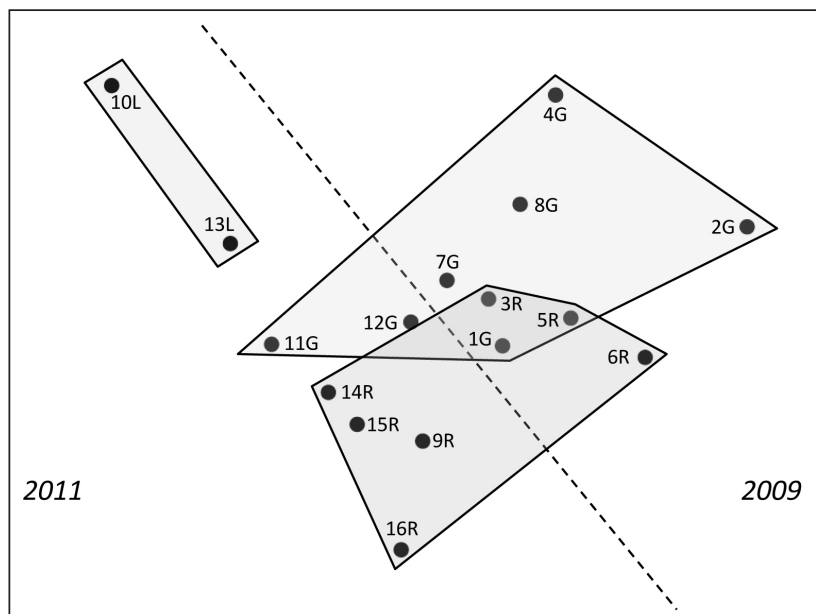
Fig. 1. NMDS ordination showing first and second axis based on Bray Curtis dissimilarities (Stress = 0.15) on macroinvertebrate samples (log transformed) from 16 Tibetan stream sites. The dashed line divides sampling years, and letters denote water source; (L) lake-outlets, (G) glacier-fed, (R) rain-fed.

There were large differences among sites in relative abundances of taxa (Appendix 2). Overall, the fauna was dominated by insect larvae, comprising 71% of all individuals. Diptera was the most abundant group, constituting on average 47% of all individuals and 55% of the insects at each site. Of these, the chironomids were the most numerous (39% of total and 46% of insects), and they were collected at all sites. The Orthocladiinae subfamily was the most dominant, and although Chironominae and Diamesinae were much less abundant, they distributed more evenly among the 16 sites. Oligocheates were found at 14 sites, occasionally in high numbers (average 9% of individuals). Ephemeroptera were represented by 3 families and accounted for 21% on average of the individuals at each site (26% of insects), mainly due to Baetidae, which occurred at 12 of the 16

sites. Plecoptera were more diverse (5 families identified) but less abundant (4% of individuals) and were found at 12 of the 16 sites. Trichoptera were also represented by 5 families but were even more scarce (found at only 7 sites) and low in numbers (3% of individuals on average).

Apart from these overall patterns, there was an overall significant difference ($P = 0.001$) between the 2 sampling years/seasons (Fig. 1). This temporal difference could be attributed mainly to significantly different relative proportions of Baetidae ($P < 0.01$) and Chironomidae ($P < 0.001$; Fig. 2). There were, however, no significant differences ($P > 0.05$) between sampling years in any of the 4 univariate fauna metrics measured (Table 1). There was a clear relationship between mean local abundance of taxa and the frequency of occurrence (number of sites where specific taxa were found; Fig. 3).
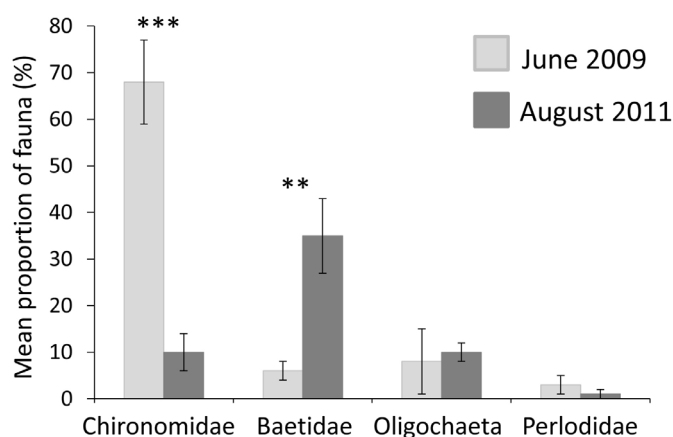
Fig. 2. Mean proportions of the taxa occurring at least at 4 of the 8 sites and with a mean proportion >1% in one of the sampling campaigns in 2009 and 2011. Significant differences in means are indicated as ** = $P < 0.01$, and *** = $P < 0.001$. Error bars denote SE.
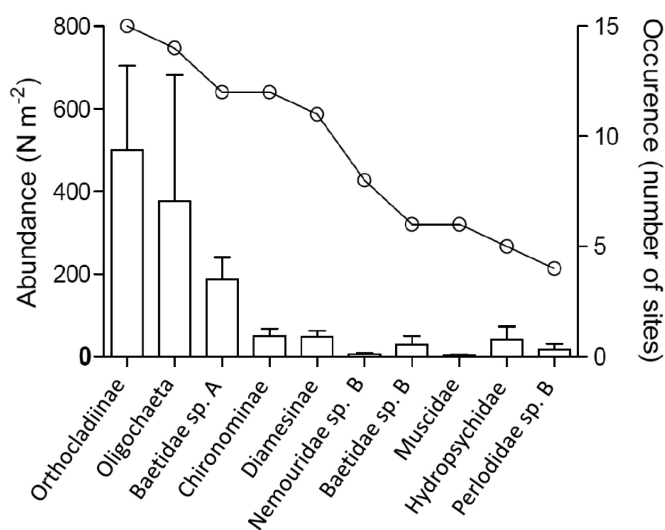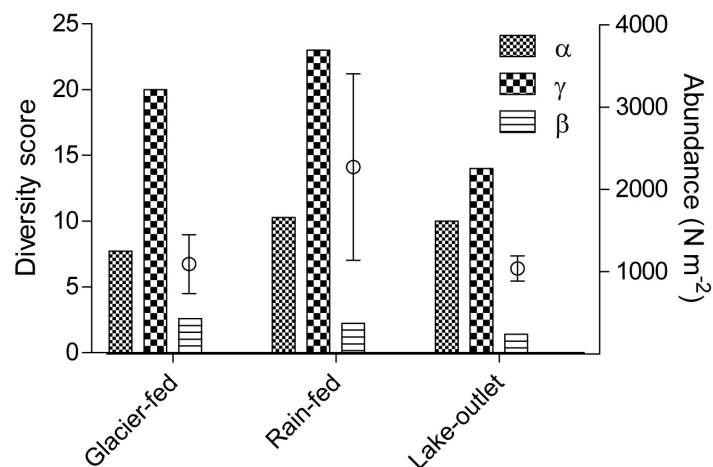

Fig. 3. Mean abundance of the 10 most common taxa (left y-axis, bars with SE) and the number of sites where they were observed (right y-axis, connected dots) in 16 Tibetan stream sites.

Stream types and macroinvertebrate assemblages

The macroinvertebrate assemblage composition differed significantly between our *a priori* defined stream groups; glacier-fed vs. rain-fed (P = 0.009, ANOSIM) and lake-outlet vs. either of the 2 (P = 0.028), even though glacier-fed and rain-fed streams had some overlap on the NMDS 2D projection (Fig. 1).

The SIMPER analysis showed that Orthocladiinae best characterized the glacier-fed stream fauna (Table 2). Baetidae and Chironominae were important groups in the classification of both glacier-fed and rain-fed streams. Diamesinae had more explicative power in the rain-fed streams than in the 2 other stream types. Oligochaetes were important in both rain-fed streams and lake-outlets. The best overall explicative taxa in lake-outlets were *Gammarus* sp., *Pisidium* sp., and *Radix peregra*. The number of Orthocladiinae and oligochaetes was the main difference between glacier-fed and rain-fed streams, while mainly the presence of *Gammarus* sp. and *Pisidium* sp. set the lake-outlets apart from the 2 other stream types (Table 3). No taxa were common in one stream type and absent from the other 2 types (i.e., no taxa seemed to be exclusive to a single stream type).

Mean local taxon richness (α-diversity) was slightly lower in glacier-fed streams than in rain-fed and lake-outlets (Fig. 4). Rain-fed streams had the highest regional richness (γ-diversity). Glacier-fed streams had a slightly higher β-diversity than the 2 other groups; note, however, that including only 2 true lake-outlets in the study likely led to an underestimated β-diversity and, particularly, γ-diversity for this stream group.

Table 2. SIMPER test results showing the most explanatory taxa for the differentiation of each stream type. 50% of the variation among the 3 types is explained by the given taxa.

| Characteristic taxa	Glacier-fed	Rain-fed	Lake outlet
Orthocladiinae	38.8		
Baetidae sp. A	19.1	18.6	
Chironominae	10.5	10.1	
Diamesinae	8.0	20.3	
Oligochaeta		21.4	16.0
Gammarus			33.4
Pisidium			25.3
Radix peregra			8.4

Environmental variables and macroinvertebrate assemblages

There was no correlation between altitude and any of the univariate fauna metrics or the assemblage composition (NMDS axis-1 or axis-2 coordinates; P > 0.05). Percentage glacial cover in the catchment (GC%) performed best of all available environmental variables (Appendix 1) to explain the variation in the univariate fauna metrics, but the effect was only significant for raw taxon numbers, and there was no tendency of a relationship to evenness (Fig. 5). It is noteworthy that both turbidity and conductivity were inversely related to GC% and inversely related to each other (Fig. 6).

A multiple regression of turbidity and GC% provided a significantly better predictor of taxon number than any single environmental variable (SP$_{est}$; Fig. 7). None of the remaining variables in Appendix 1 improved the model without increasing AICc or showing collinearity.

Fig. 4. Average abundances (right y-axis, squares) and α, β, and γ diversities (left y-axis, bars) of macroinvertebrates in 16 Tibetan stream sites of 3 types: glacier-fed, rain-fed, and lake-outlets. Error bars denote SE on abundances.

Table 3. SIMPER results of 50% of the taxa dissimilarities between the different stream types.

Taxon	Glacier-fed vs. rain-fed	Glacier-fed vs. lake outlet	Rain-fed vs. lake outlet
Orthocladiinae	10.6		
Oligochaeta	9.4		
Baetidae sp. A	7.8		
Elmidae	6.8		
Diamesinae	6.2		
Chironominae	6.2		
Simuiliidae	5.9		
Gammarus		16.5	
Pissidium		11.7	
Orthocladiinae		9.4	
Baetidae sp. A		8.7	
Gyraulus		5.8	
Gammarus			13.0
Pissidium			9.2
Diamesinae			7.7
Baetidae sp. A			7.1
Orthocladiinae			5.4
Elmidae			4.9
Chironominae			4.8
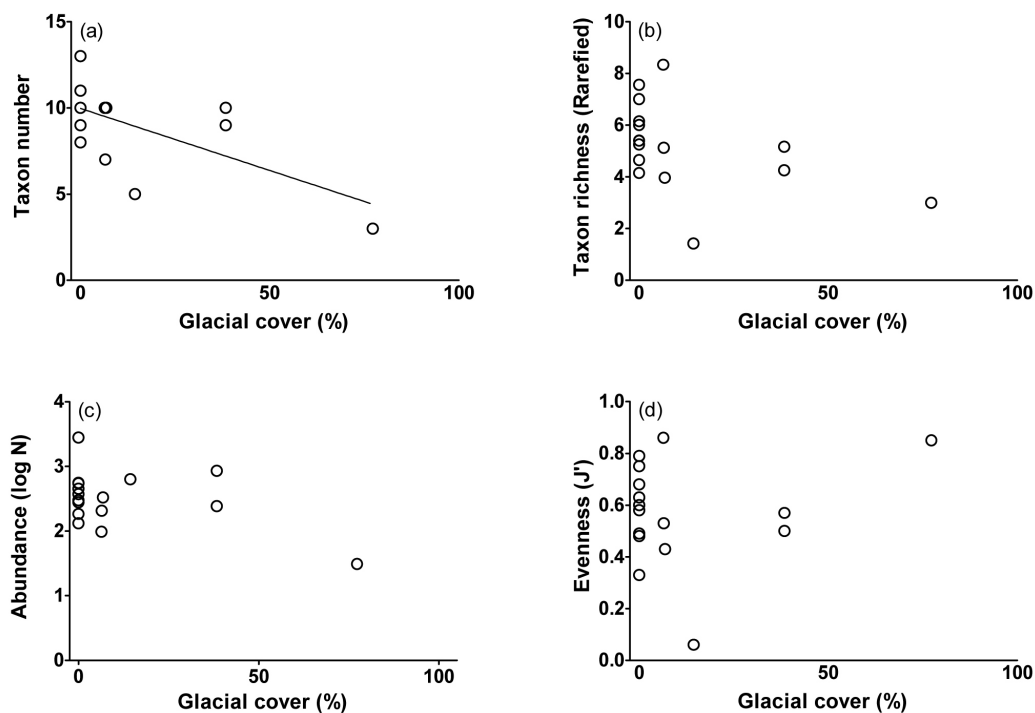
Fig. 5. (a) Taxon richness, (b) rarefied taxon number, (c) abundance (log transformed), and (d) evenness of benthic macroinvertebrates in 16 Tibetan stream sites as a function of percent glacier cover in the catchment. The linear regression line for taxon number: $R^2 = 0.415$; $P = 0.007$.
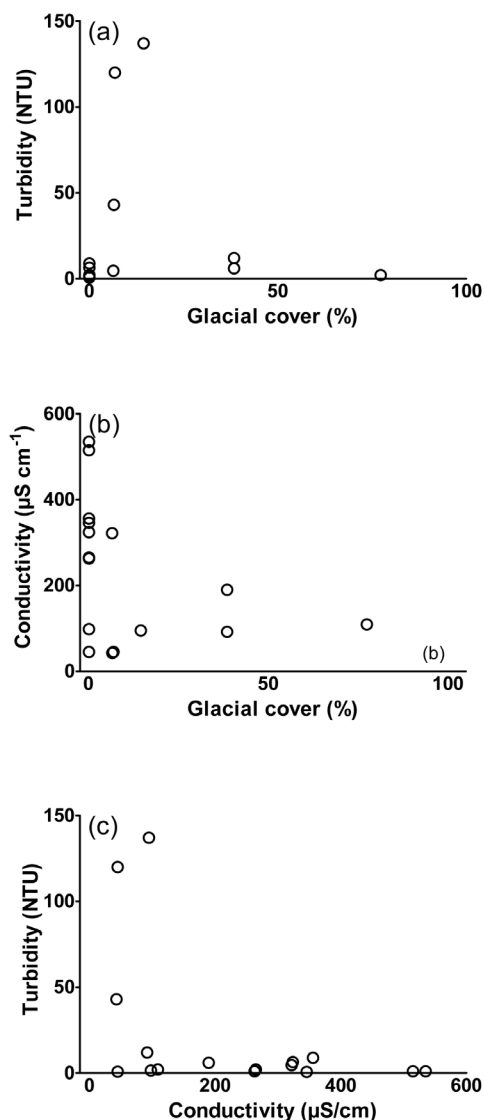
Fig. 6. Turbidity and conductivity in 16 Tibetan stream sites as a function of the percentage of glacier cover in the catchment.
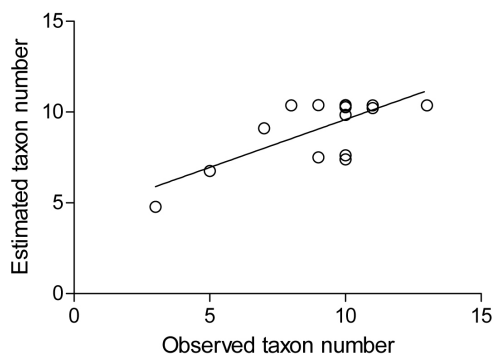
Fig. 7. Estimated taxon number as a function of observed taxon number calculated from a combination of glacial cover in the catchment (GC%) and turbidity (T): Taxaest = 10.391 − 0.072[GC %] − 0.019[T]. The linear regression: R² = 0.530; P = 0.001.

Discussion

General patterns and temporal differences in macroinvertebrate assemblages

The most widespread taxa were also the most locally abundant, a commonly observed distribution pattern of organisms in general (Brown 1984, Gaston 1996) as well as in high altitude streams (Jacobsen and Terneus 2001, Jacobsen and Marín 2008). Overall, the benthic macroinvertebrate fauna was dominated by insects, with the Chironomidae (specifically the Orthocladiinae subfamily) as the most abundant. Although we collected Ephemeroptera, Plecoptera, and Trichoptera taxa at most sites, these were found only in relatively small numbers compared to the chironomids; however, the composition of the fauna differed significantly between sampling campaigns, mainly due to relative proportions of some of the importance families: Chironomidae (68% in June 2009 and 10% in August 2011) and Baetidae (6% vs. 35%, respectively). Thus, our results agree with those obtained in 2 other recent studies on Tibetan streams, both with collections performed in August. Murakami et al. (2012) sampled 6 glacier-fed sites at 4700–5100 m a.s.l. and found ephemeropterans contributed 45% and chironomids 27% of total insect abundance. Jiang et al. (2013) sampled 7 sites at 3670 m a.s.l., where chironomids made up 22% of the total fauna while ephemeropterans and trichopterans contributed 32% and 29%, respectively. The much lower percentage of trichopterans found in our study (7% and 1% in the 2 sampling campaigns) is probably due to the considerably lower altitude of our sites.

As expected for streams at high altitudes (Jacobsen 2008), macroinvertebrate richness was low in the Tibetan streams. We found 32 different families or higher taxonomic groups, 8.2 per site. This finding is in accordance with the 2 recent studies from Tibetan streams with comparable taxonomic resolution; a mean of 9 taxa (2–14) were collected in the 6 glacier-fed streams (Murakami et al. 2012), and 20 total taxa were reported from the 7 slightly lower sites (Jiang et al. 2013). These values also correspond well with Nepalese Himalayan streams, where Brewin et al. (1995) reported a mean of 6 taxa per site for streams at 3800–4320 m a.s.l., while Suren (1994) found a mean of 16.7 taxa in streams at 4000–4250 m a.s.l., but in Suren (1994) the chironomids were identified to 15 different genera and subfamilies. Further, the mean taxonomic richness that we found in the present study is largely similar to a mean taxon richness (also mainly family) of 10.6 per site (only including Surber samples; excluding qualitative samples, as in the present study) reported from Andean streams 3800–4000 m a.s.l. on the Bolivian Altiplano (Jacobsen

and Marín 2008). In contrast, Andean streams 3900–4200 m a.s.l. in Ecuador, sampled with exactly the same method and effort as we used in Tibet, had an average family richness of 21.8 (Jacobsen et al. 2012). The Tibetan streams thus seem to follow the "norm" for macroinvertebrate richness of very high-altitude streams, while the environmentally heterogeneous conditions of the equatorial "páramo" of Ecuador seem to promote exceptionally high aquatic diversity.

Stream type and macroinvertebrate assemblages

Despite the large variability in glacial influence within the glacier-fed stream group, the 3 stream types formed significantly different groups based on their macroinvertebrate assemblages. Nevertheless, this result is in accordance with studies from the European Alps (Brown et al. 2003, Hieber et al. 2005) and the Ecuadorian Andes (Jacobsen 2008). In particular, the importance of lakes for downstream faunas, through their moderating effect on physical instability and environmental harshness of high-mountain streams, has previously been demonstrated (Hieber et al. 2002).

The lower mean local (α) and regional (γ) diversity but higher taxon turnover rate (β-diversity) in glacier-fed streams also largely confirms earlier studies (Hamerlik and Jacobsen 2012, Jacobsen et al. 2012, Jacobsen and Dangles 2012) and demonstrates how glacial runoff contributes to environmental heterogeneity in alpine catchments; however, macroinvertebrate assemblages in these temperate/subtropical streams are most likely subject to seasonal changes due to phenology as well as interannual variability. The overall significant effect of sampling year (2009 vs. 2011) and/or season (June vs. August) on assemblages, in concert with differing number of sites in each stream group in the 2 sampling campaigns, potentially flaws such comparisons. So, although there were no significant differences in any of the univariate fauna metrics between sampling years, these results should be interpreted with caution.

Glacier-fed streams were generally dominated by chironomids, especially Orthocladiinae. Only the site closest to the glacier snout (site 2G) as well as one of the more unstable glacier-fed streams (site 12G) showed a higher abundance of Diamesinae. Although Diamesinae is normally associated with pro-glacial stream reaches (Ward 1994, Milner et al. 2001), the presence of this subfamily better defined rain-fed streams in the SIMPER analysis, probably because most of our glacier-fed streams sites were located several kilometers from the glaciers. The lake-outlets were separated from the other stream types by the presence of *Gammarus* sp., *Radix* sp., and *Pisidium* sp. These groups are mainly shredders, scrapers, and filterers

respectively (Merritt and Cummins 1996), and their abundance indicates that the lakes included in this study act as sources of particulate carbon as food for downstream reaches (Hieber et al. 2002, Maiolini et al. 2006). In addition, lake-outlets also have higher hydrological stability (Hieber et al. 2002), allowing establishment of rooted macrophytes, which serve as habitat and food (indirectly as well as directly) for detritivores and herbivore shredders and scrapers (Jacobsen 2008). Macrophytes were abundant in the 2 non-glacial lake outlets but scarce in all other sites.

Glacial influence and macroinvertebrate assemblages

Glacial cover in the catchment had a uniform, negative effect on the number of both taxa and abundance of macroinvertebrates, a well-known pattern from a multitude of studies on longitudinal trends in invertebrate communities (e.g., Maiolini and Lencioni 2001, Robinson et al. 2001, Jacobsen et al. 2010). Nevertheless, recent studies have reported humped-shaped relationships between taxon richness and glacier cover in the catchment (Jacobsen et al. 2012, Cauvy-Fraunié et al. 2014). This pattern might also be the case in the Tibetan streams, but determination would have required a higher data density to be detected (i.e., a greater number of sites along the glacial gradient).

A better taxonomic identification of the chironomids conducted in 2009 as part of our survey (Hamerlik and Jacobsen 2012) revealed that *Diamesa* did become more common close to the glacier snout. A single species of *Diamesa* and a species of *Chaetocladius* genus were only found close to the glacier margins in that survey, suggesting that these species could be threatened by glacial retreat. In the present study, however, we could not identify any taxa that seemed to be restricted to glacier-fed streams, as has been shown in locations such as Montana, USA (Stagliano et al. 2007, Muhlfeld et al. 2011), the Pyrenées (Brown et al. 2007), and Ecuador (Espinosa et al. 2010), but this again may be related to our relatively coarse-level taxonomic resolution, particularly with respect to the chironomids, or long distances from the glaciers that characterize most of our samples sites. More research is needed to examine the endemic species in Tibetan glacier-fed streams to confirm this.

The multiple regression model accurately predicted the taxon number from a combination of glacial cover and turbidity. Turbidity tended to be negatively related to glacial cover in the catchment, and several of our streams close to glaciers were crystal clear. This finding is in contrast to most other studies reporting high mean levels of glacially derived suspended solids, and hence turbidity, in glacier-fed streams (e.g., Milner et al. 2001, Kuhn et al.

2011), and turbidity is even included in glaciality indices (Ilg and Castello 2006). Not only glacial flour contributes to turbidity, however; any type of erosion in the catchment, natural or from anthropogenic activities, will increase turbidity. The 2 sites with the highest turbidities (sites 4G and 8G) were located far from the glaciers, and elevated suspended sediment loads seemed to be derived from other than current glacial processes. There is ample evidence for the detrimental effect of fine suspended sediments on abundance and diversity of macroinvertebrates in connection with various land-use changes (Wood and Armitage 1997, Fossati et al. 2001, Wantzen 2006).

Conclusion

This preliminary survey has shown that although the Tibetan stream macroinvertebrate fauna is relatively taxon-poor, there is a considerable variety of stream types and benthic communities. We were only able to perform spot measurements of a few environmental variables; hence, our ability to identify regulating factors was relatively weak. In addition, fish such as stone loaches (*Triplophysa*) were widespread and locally abundant (Jacobsen et al. 2013), and their possible interaction with macroinvertebrates should be studied further. Because glacier-fed streams are a prominent contributor to the variability in aquatic habitats and biodiversity, the ongoing shrinkage of glaciers can be anticipated to have widespread effects on Tibetan running waters and their biological communities. To monitor and document these effects, more studies are needed on environmental driving factors and species distribution patterns, particularly focusing on the endemics of glacier-fed streams because these might serve as sentinels of climate changes.

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Supplementary Material

Supplementary Material is available for download via the Inland Waters website, https://www.fba.org.uk/journals/index.php/IW:

Appendix 1 and 2.