

Chironomid (Diptera) distribution and diversity in Tibetan streams with different glacial influence

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Abstract. 1. We collected chironomid larvae and measured basic environmental variables in eight high mountain streams with different degrees of glacial influence in southern Tibet.

2. In total, 32 chironomid taxa were collected. The Orthoclaadiinae subfamily dominated both in taxon number and in abundance.

3. Both average taxon number and abundance were lower in glacier-fed streams compared with those of non-glacial origin. The total taxon number collected (γ diversity) was similar regardless of glacial influence. However, spot diversity (α diversity) was higher in non-glacial streams, while glacier-fed streams supported higher species turnover (β diversity).

4. Detrended correspondence analysis scattered the study sites along the first ordination axis, representing a combination of distance from glacier and channel stability. Two-way indicator analysis distinguished three groups of sites. Group 1 represented the sites closest to the glacier and were characterised by unstable channel conditions and low temperature with characteristic taxa *Diamesa* sp. 1, *Orthocladius* (*Eud.*) sp. and *Rheocricotopus* sp. Group 2 was made up of glacier-fed streams situated further from glaciers, with unstable channels and characterised by *Orthocladius* (*Euo.*) sp. Group 3 contained non-glacial streams as well as a glacier-fed stream further from the glacier margin. For these sites, stable channels and high conductivity were characteristic and *Cricotopus* (*C.*) sp., *Pseudosmittia* sp., *Polypedilum* sp., *Eukiefferiella* *gracei* group and *Pagastia* sp. 1 were the dominating taxa.

5. We propose a general distribution pattern of chironomids in the streams of glacial and non-glacial influence in Tibet, which is in accordance with the model proposed by Milner *et al.* (2001a) *Freshwater Biology*, **46**, 1833–1847.

Key words. Aquatic insects, Chironomidae, diversity measures, glacier-fed streams, non-glacial streams, Tibetan Plateau, Himalayas.

Introduction

Glacier-fed streams provide distinctive, high-altitude habitats with characteristic biota (Ward, 1994). Even though glacial streams usually have low biological diversity, their communities are highly specialised and adapted to the cold water and fluctuating current. With the current climatic trends, awareness for glaciers and subsequently glacier-fed streams has gained attention

worldwide. Patterns in biodiversity and community structure along the glacial gradient have been described from North America and Europe (Milner, 1994; Lods-Crozet *et al.*, 2001b), New Zealand (Milner *et al.*, 2001b), Greenland (Friberg *et al.*, 2001) and high-altitude South America (Jacobsen *et al.*, 2010). Although retreating glaciers may open new habitats and lengthen the stream gradient (Finn *et al.*, 2010), glacial streams will eventually lose their in-flow. In addition, more sporadic precipitation will markedly change the temporal and spatial patterns of the stream flow. Changes in stream flow and temperature are expected to reduce species turnover (β diversity) and diversity at a regional scale (γ diversity) (Brown *et al.*, 2007).

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Insects of the Chironomidae family are usually the dominant benthic dwellers of glacier-fed streams (Ward, 1994). The general distribution of biota in glacier-fed streams follows a similar pattern around the world: the communities closest to the glacier are rather poor (Milner *et al.*, 2001a), yet composed of species adapted to that specific environment. The subfamily Diamesinae (especially *Diamesa*) dominates the reaches where $T_{\max} < 2\text{ }^{\circ}\text{C}$, while the Orthoclaudiinae subfamily usually dominates where T_{\max} exceeds $2\text{ }^{\circ}\text{C}$ (Milner *et al.*, 2001a). With increasing distance from the glacier, temperature and channel stability increases, which is reflected in increased biological diversity and abundance (Lods-Crozet *et al.*, 2001b; Milner *et al.*, 2001a; Jacobsen *et al.*, 2010). While chironomid communities of glacier-fed streams of some zoogeographical regions, especially western Palaeartic, are well documented (e.g. Lods-Crozet *et al.*, 2001b), other areas are almost unknown.

High-altitude streams of some regions of the Himalayas, such as Nepal, are relatively well studied (Roback & Coffman, 1987; Rundle *et al.*, 1993; Ormerod *et al.*, 1994; Suren, 1994). And yet, the Tibetan part of the Himalayas, representing an ecologically interesting transition between the Palaeartic and Oriental region, has so far been overlooked. Streams in Tibet are some of the highest and least studied aquatic ecosystems in the world. They cover a wide area, contributing large quantities of glacial melt water, and many of them are still relatively pristine. Although the current atmospheric warming and glacial retreat in Tibet has probably affected the streams (Yao *et al.*, 2007), the effects are likely to intensify in the future. The possible consequences on ecological processes and aquatic biodiversity in Tibetan streams have yet to be evaluated. For example, we do not know which species, if any, might be lost when glaciers are reduced even further or have disappeared altogether.

During a Sino-Danish multidisciplinary Tibetan expedition, we took the opportunity to survey the aquatic macroinvertebrate fauna in streams on the Tibetan Plateau. The overall objective of this paper is (1) to describe the chironomid distribution pattern of the streams of the Tibetan Plateau, particularly in relation to glacial influence on stream flow and (2) to estimate the effect of glacial influence on the biodiversity in different scales (α , β and γ). Our hypothesis is that glacier-fed streams support taxa characteristic to that particular stream type, and therefore increase regional biodiversity of Tibetan streams.

Material and methods

Study area

Eight small streams (1–8 m in width) located at altitudes between 4990 and 4315 m in three areas of southern Tibet were surveyed during July 2009: the Karola glacier (sites 1 and 2), Jiacun (sites 3–6) and Nyanchentangla (sites 7 and 8) (Fig. 1). Five of the streams were glacier fed, but located at varying distances from the glaciers, and site 1 represented an outlet stream of a lake with glacial influence. The remaining three streams had no glacial influence. Spot measurements of water temperature, conductivity, pH, oxygen saturation, and water turbidity were taken in the field with portable meters. Current velocity, periphyton

biomass, and channel stability were visually estimated on the site and assigned to three categories. Current: moderate (approximately $0.1\text{--}0.3\text{ ms}^{-1}$), fast (approximately $0.3\text{--}0.6\text{ ms}^{-1}$) or strong (approximately $0.6\text{--}1.0\text{ ms}^{-1}$). Periphyton: none (no detached biofilm upon scraping of stones), moderate (stones with some algal dominated biofilm), or high (stones completely smothered in algal growth). Channel stability: unstable (wandering channel with lower banks consisting of loose pebble & cobble), fairly stable (part of the banks vegetated and other parts eroding), or stable (completely vegetated lower banks). Distance to feeding glaciers was measured using Google Earth. For stream characteristics see Table 1.

Benthos sampling

At each site, five quantitative Surber samples (500 cm^2 , mesh size of $200\text{ }\mu\text{m}$) were collected randomly from pebble-cobble substratum in riffle/run habitats. The material collected was placed into plastic bottles, labelled and preserved with 75% ethanol. In the laboratory, chironomid larvae were sorted, counted and mounted in Berlese fluid under a low-power stereomicroscope. Identification of larvae was made under high magnification ($400\times$) to the lowest possible level following Wiederholm (1983), Roback and Coffman (1987), and Makarchenko and Makarchenko (2000).

Statistical methods

Glacial influence of the glacier-fed streams, used for calculating correlations with number of taxa and abundance, was expressed tentatively as a reciprocal value of the log-transformed distance from the feeding glacier, where non-glacial streams had a 0 value of glacial influence. To test the significance of differences in taxa number and density of glacier-fed and non-glacial streams, *t*-test was performed. Site 1, representing an outlet stream, was excluded from this analysis. Spot diversity (α diversity) was defined as the mean number of taxa found at one locality. The regional taxon richness (γ diversity) was estimated as the total number of taxa in a collection of samples found in glacier-fed and non-glacial streams, respectively. Two measures of species turnover (β diversity) were used. Cody's β :

$$\beta_c = \frac{g(H) + l(H)}{2}$$

where $g(H)$ is the number of species gained and $l(H)$ the number lost moving along the transect (Wilson & Shmida, 1984) was calculated using the software package Species Richness and Distribution (Seaby & Henderson, 2004). The second measure was the proportion of the within-site diversity occurring in the regional species pool (γ/α). To test the significance of the observed level of the β diversity, diversity partition was conducted using PARTITION 3.0 (Veech & Crist, 2009). Individual-based randomization combined with balanced sampling design was used to calculate the expected values. Randomization level was set on 1000. The power of the individual-based randomization method was estimated by comparing the sampling distribution of the diversity

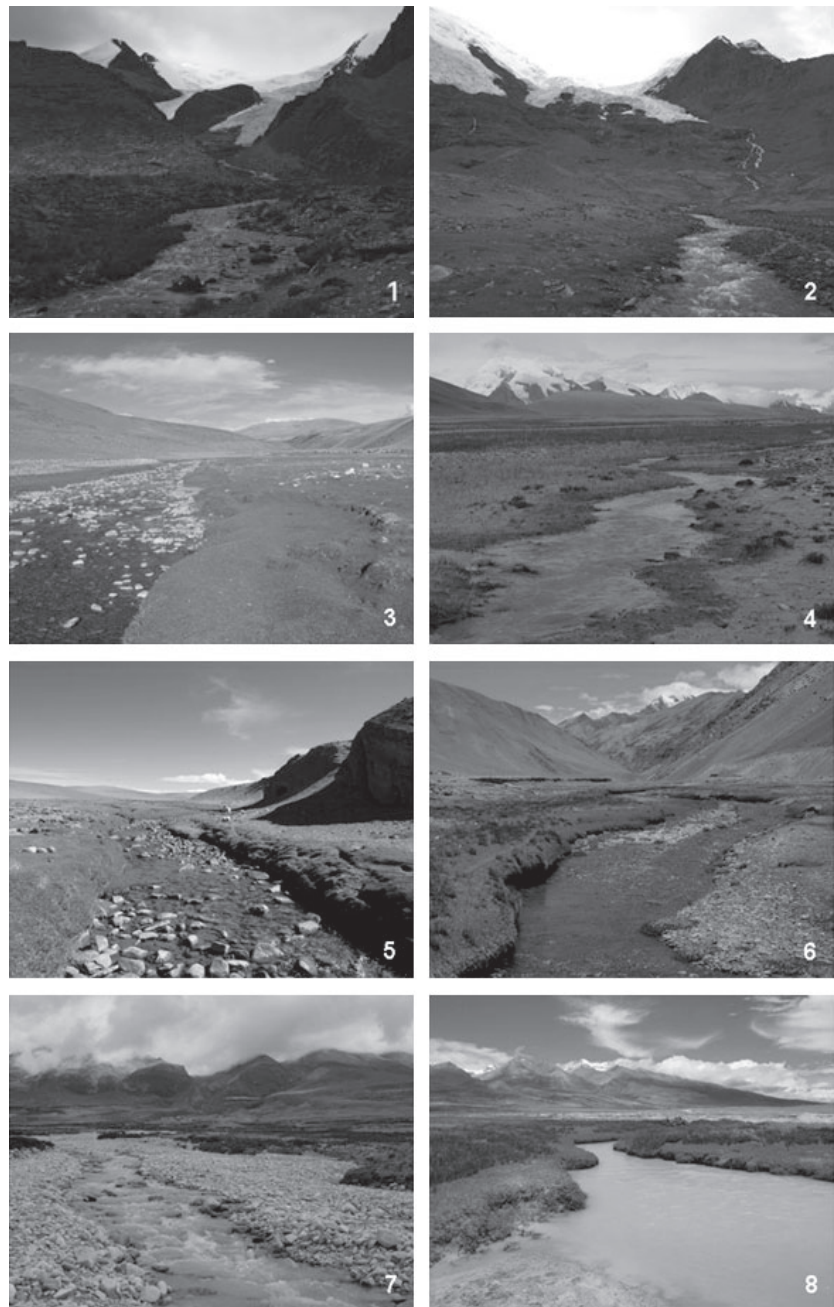


Fig. 1. View of the sampling sites. Sites 1, 2, 4, 7 and 8 represent glacier-fed streams; sites 3, 5 and 6 have no glacial influence (Photo D. Jacobsen).

component with its corresponding null distribution (J. A. Veech and T. O. Crist, unpubl. data).

Detrended correspondence analysis (DCA) was used to visualise the distribution of species data along a main environmental gradient using CANOCO 4.5 package (ter Braak & Šmilauer, 2002). Species abundance data (ind. m⁻²) were log₁₀ ($x + 1$) transformed prior to the analyses. Different stream types were distinguished based on two-way indicator species analysis (TWINSpan; Hill, 1979). The result was displayed in a DCA sample plot as groups distinguished by different symbols. Analysis of similarity

(ANOSIM, Clarke & Green, 1988) was performed to test the significance of the groups that had been defined according to TWINSpan. Similarity percentage analysis (SIMPER, Community Analysis Package Version 3.0, Pisces Conservation Ltd., Lymington, UK) was used to determine the contribution of each species to the observed similarity within each group. It allowed us to identify the species that are most important in creating the observed pattern of similarity. Both SIMPER and ANOSIM was performed using the Community Analysis Package 3.0 (Seaby & Henderson, 2004).

Table 1. Basic parameters of the sampling sites.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Alt	4840	4990	4865	4722	4748	4324	4379	4315
Coordinates	28 53' 48" 90 13' 31"	28 54' 06" 90 09' 50"	28 34' 53" 84 09' 08"	28 41' 06" 85 48' 55"	28 35' 30" 86 02' 44"	28 22' 32" 86 06' 02"	30 04' 00" 90 26' 28"	30 01' 52" 90 26' 02"
Conductivity	92	109	515	95	263	535	43	45
pH	7.47	7.1	8.08	7.74	8.17	7.09	7.85	7.19
Temperature	7.4	6.3	16.8	17.3	16.6	10.6	10.7	12.7
O ₂	100	100	109	123	104	116	115	102
Turbidity	12	2	1	137	1	1	43	120
Width, mean	8	4	4	0.9	3	3	4	1
Depth, mean	0.15	0.15	0.1	0.1	0.3	0.3	0.15	1
Current	Fast	Strong	Moderate	Fast	Moderate	Fast	Strong	Moderate
Periphyton	None	None	Moderate	High	High	High	None	None
Prevalent substratum	Pebble/cobble	Pebble	Cobble	Sand/gravel	Cobble	Pebble/cobble	Cobble	Sand/gravel
Glacial influence	Yes	Yes	No	Yes	No	No	Yes	Yes
Distance to glacier	2	1.5	—	30	—	—	6	11
Channel properties	Lake outlet	Straight	Sinuuous	Anastomizing	Straight	Meandering	Straight	Meandering
Channel stability	Fairly stable	Unstable	Stable	Unstable	Stable	Stable	Unstable	Stable

Results

Water temperature of the eight study sites varied from 6.3 to 17.3 °C and increased with distance from the feeding glacier in glacier-fed streams. Turbidity varied from 2 to 137 NTU in the glacial sites, but was very low (< 1 NTU) in all non-glacial sites. Conductivity was lower in glacial sites (43–109 µS cm⁻¹) than in non-glacial sites (263–535 µS cm⁻¹). pH did not show a correlation with the distance from the glacier or glacial origin and varied from 7.1 to 8.2. For more environmental parameters of the streams see Table 1.

We collected 32 taxa from three chironomid subfamilies (Appendix S1). The subfamily Orthoclaadiinae dominated both in number of taxa (20) and abundance (approximately 90% of all specimens). Diamesinae and Chironominae, with six taxa each, represented approximately 6% and 4% of the total abundance, respectively. Within the Chironominae, the Tanytarsini predominated with five taxa. Taxon number varied from 4 to 11

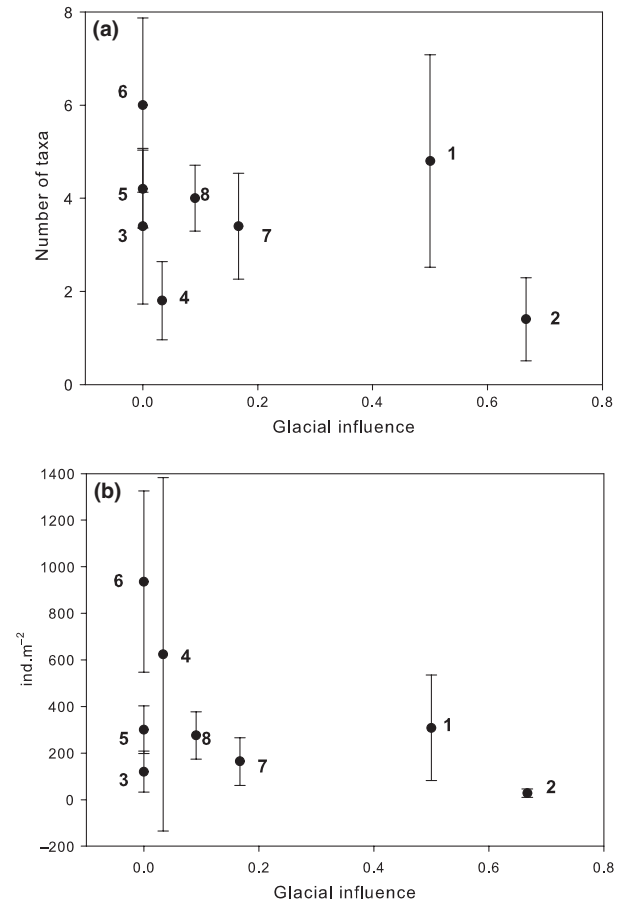


Fig. 2. Scatter plots of average number of taxa (a) and density (b) recorded in each site ordered along increasing glacial influence. Plots represent mean values, error bars represent standard deviations (SD). Numbers 1–8 refer to the sites. Glacial influence of the glacier-fed streams was expressed tentatively as a reciprocal value of the log-transformed distance from the feeding glacier; non-glacial streams had 0 value.

Table 2. Data on α , β and γ diversity of chironomids from streams of glacial and non-glacial origin. Two measures of β -diversity are presented: Cody's β and the proportion of the within-site diversity occurring in the regional species pool (γ / α). In glacial streams, the diversity measures were calculated both including (Incl. S1) and excluding (Excl. S1) the lake outlet stream site.

Diversity		α	β		γ
			Cody's β	γ / α	
Glacial streams	Incl. S1	7	15.5	3.57	25
	Excl. S1	6	13.5	3.33	20
Non-glacial streams		10	7.0	1.80	19

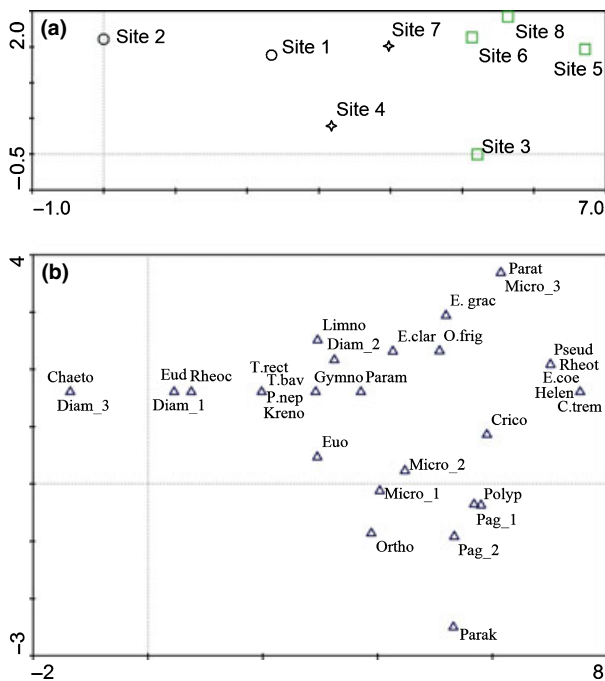


Fig. 3. Detrended correspondence analysis of sites (a) and chironomid taxa (b). Symbols represent different stream types, distinguished with TWINSpan: circles = Group 1 – glacier-fed streams close to the glacier; stars = Group 2 – glacier-fed streams far from the glacier; squares = Group 3 – non-glacial and glacier-fed streams with stable channel.

per site with 14 taxa collected from glacier-fed streams and seven taxa only from non-glacial streams (Fig. 2a). The average density was low, varying from 28 to 936 ind. m^{-2} (Fig. 2b). Both average taxon number and density was lower in glacier-fed streams compared with those of the non-glacial origin, but only the difference in taxa number was significant ($P < 0.033$). Neither taxon number nor abundance was correlated significantly with the degree of glacial influence.

Excluding the lake outlet (site 1), total richness (γ diversity) for the glacier-fed streams was 20 taxa and 19 taxa for non-gla-

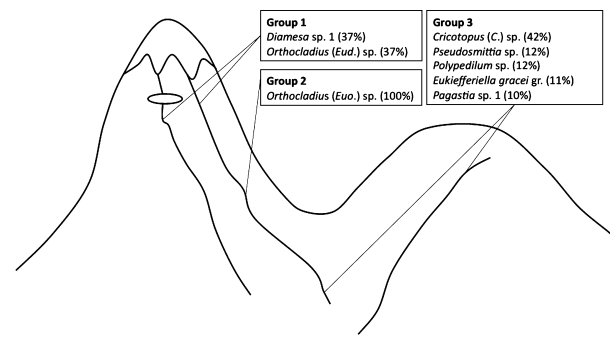


Fig. 4. Scheme of an idealised distribution pattern of the characteristic chironomid taxa. Numbers in parentheses after each taxa represent the share on the within-group similarity calculated by Similarity percentage analysis (SIMPER); taxa with $< 10\%$ distribution are not pictured.

cial streams. Average within-site (α) diversity was higher in non-glacial streams (10 taxa) than in glacial streams (six taxa). On the contrary, taxon turnover (Cody's β) was higher in the glacial streams (13.5) compared with streams without glacial influence (7.0). The observed proportion of within-site diversity occurring in the regional species pool (γ/α) represented 3.3 and 1.8 ($P < 0.001$) in glacier-fed and non-glacial streams, respectively. For overview of diversity measures, see Table 2.

The first two ordination axes of the DCA explained 33.7% variability of the taxon data (gradient lengths 6.7 SD, Fig. 3a,b). Generally, from left to right, both distance from glacier and channel stability increased. TWINSpan distinguished three groups of sites with similar communities and conditions. Group 1 (streams 2 and 1) is situated in the left part of the ordination diagram, representing the closest sites to the glacier having unstable channel conditions and low temperature (7.4 and 6.3 °C, respectively) as well as the highest altitude among all sites. The characteristic species for this group were *Diamesa* sp. 1, *Orthocladius* (*Eud.*) sp. and *Rheocricotopus* sp. (SIMPER, Fig. 4). Group 2 consists of glacier-fed streams being situated further from the glacier and showing unstable channel conditions (sites 4 and 7). The single taxon characteristic of this group was *Orthocladius* (*Euo.*) sp. Group 3 contained all the non-glacial streams (sites 3, 5 and 6) as well as a glacier-fed stream (site 8) located 11 km from the glacier margin. The common features of the group 3 streams were stable channel conditions and high conductivity (only in the non-glacial streams). For these streams, *Cricotopus* (*C.*) sp., *Pseudosmittia* sp., *Polypedilum* sp., *Eukiefferiella graciei* group and *Pagastia* sp. 1 were the most characteristic. According to ANOSIM, the chironomid assemblages of the three groups were not significantly different (however, both group 1 and 2 differed from group 3 on level $P = 0.06$).

Discussion

We expected that the Tibetan streams would follow the typical pattern of low community diversity closest to the glacier, while downstream, the biological community will increase in abun-

dance and species diversity. Indeed, there was an overall tendency of decreasing diversity and abundance of the chironomids with increasing glacial influence. Orthocladiinae dominated in all sites, most likely because metakryal habitats ($T_{\max} < 2\text{ }^{\circ}\text{C}$, sensu Steffan, 1971) were not included. However, as expected, with higher glacial influence, the proportion of Diamesinae (mostly *Diamesa*) increased. On the contrary, with decreasing glacial influence, Chironominae became more abundant at the expense of Orthocladiinae. A high proportion of *Diamesa* at relatively high water temperatures ($> 40\%$ of total abundance at $6.3\text{ }^{\circ}\text{C}$ in site 2) supports the findings of Lods-Crozet *et al.* (2001a) that populations of *Diamesa* can be maintained in warmer temperatures in unstable channels, where other chironomids are not abundant. However, in case of the glacial sites being located further from the glacier with unstable channels (sites 4 and 7), *Diamesa* (and other Diamesinae) were either not present or represented a negligible part of the community assembly. The most likely reason for its absence was the high water temperature, 10.7 and $17.3\text{ }^{\circ}\text{C}$. The optimal temperature calculated for European *Diamesa* was $6\text{--}7\text{ }^{\circ}\text{C}$ (Castella *et al.*, 2001), but in European glacier-fed streams, some species of the genus could maintain abundant populations even in warmer environments ($T_{\max} \leq 15\text{ }^{\circ}\text{C}$, Lods-Crozet *et al.*, 2001b).

Characterisation of the sites closest to the glacier (group 1) by *Orthocladius* (*Eud.*) sp. and *Orthocladius* (*Euo.*) sp. in the sites further down from the glacier with unstable channels (group 2, Fig. 4) was in accordance with the model of Milner *et al.* (2001a). The subgenus *Eudactylocladius* often dominates the fauna of thin water films in temperate regions. We assume that it is not the low temperature alone, but rather the combination of unstable channel and low temperature, typical for streams with high glacial influence, which provides optimal conditions for this taxon. Species of the *Euorthocladius* subgenus represents the dominant Orthocladiinae in glacier-fed streams, such as *Orthocladius* (*Euo.*) *frigidus* (which has recently been moved to the Mesorthocladius subgenus (Saether, 2005) and *O.* (*Euo.*) *rivicola* group in Europe (Milner *et al.*, 2001a) or *O.* (*Euo.*) *thienemanni* Kieffer in western Greenland (Friberg *et al.*, 2001). Generally, species of the genus *Orthocladius*, along with *Tvetenia* and *Eukiefferiella*, are able to colonise the reaches very close to the glacier terminus at mean temperature close to $0\text{ }^{\circ}\text{C}$ (Milner, 1994; Lods-Crozet *et al.*, 2001b; Lencioni & Rossaro, 2005) and in unstable channels. We recorded *Tvetenia bavarica* group only in a glacial site and *Eukiefferiella claripennis* and *E. gracei* groups occurred in both non-glacial and glacier-fed streams.

Group 3 contained all the non-glacial sites and the only glacial site with stable channel conditions. The characteristic taxa for these sites were *Cricotopus* (*C.*) sp., *Pseudosmittia* sp., *Polypedilum* sp., *Eukiefferiella gracei* group and *Pagastia* sp. 1. With the exception of *Pagastia*, all the taxa have been found in glacial streams in the Alps, Norway, Iceland or Svalbard (Lods-Crozet *et al.*, 2001b), but always far from the glacier or after a confluence with a non-glacial tributary (Maiolini & Lencioni, 2001). Even though the *Eukiefferiella gracei* group has not been collected in the studies mentioned, a number of *Eukiefferiella* species were well represented in subkryal, glacio-rhithral and kreno-rhithral Alpine streams (Lods-Crozet *et al.*, 2001b; Lencioni & Rossaro, 2005). The genus *Pagastia* was frequent in

the Tibetan non-glacial streams, but absent in the European streams, which is given by the Nearctic and eastern Palaearctic geographical distribution of the genus (Makarchenko & Makarchenko, 2000).

There was a significant difference in the taxon richness between the two glacier-fed streams situated closest to the glacier: site 1, representing a lake outlet, supported two-fold more taxa than site 2. This finding supports the role of lakes as modifiers of the conceptual model of species distribution by improving the physical conditions further downstream, allowing increased faunal diversity suggested by Milner and Petts (1994) and supported by others (e.g. Burgherr & Ward, 2000; Brittain *et al.*, 2001).

In contrary to our hypothesis, the total taxa number collected (γ diversity) in the Tibetan streams with and without glacial influence was similar. However, α diversity was higher in non-glacial streams, while glacier-fed streams supported higher β diversity (species turnover). This result supports the finding of Brown *et al.* (2007), who suggested that with future meltwater reductions, α diversity of streams fed by meltwater will increase, while β diversity will be reduced. The main reason for this is the decrease in habitat heterogeneity associated with spatiotemporal variability of water source, as contributions will become lower.

With reduced meltwater contributions, extinction of some oligo-stenothermal and endemic alpine aquatic species is expected (Rossaro *et al.*, 2006; Brown *et al.*, 2007), which leads to decreases in γ diversity. However, Finn *et al.* (2010) found no evidence for local extinction even in streams fed from a dramatically receding glacier. They observed a general upward movement of a biota: taxa specialised on pro-glacial conditions have colonised the upper extent of the newly formed section, while common species typical for lower altitude streams have colonised the lower section of the gradient. Complete loss of glaciers will, however, have a much stronger impact on the aquatic assemblages, imposing a real threat of extinction of the pro-glacial species.

To find the species most threatened by glacial retreat in Tibet, we focused on the sites located closest to the glacier margin. There were only two taxa collected in site 2 not occurring in other sites: *Diamesa* sp. 3 and *Chaetocladius* sp. The other taxa (*Diamesa* sp. 1, *Rheocricotopus* sp. and *Orthocladius* (*Eud.*) sp.) occurred also in site 1, representing a lake outlet with a more benign environment, and these are therefore not likely to be threatened by glacier retreat. Roback and Coffman (1987) collected larvae of the *Chaetocladius* genus both in streams with glacial and non-glacial origin distributed between altitudes 2480–3500 m, and it was not characteristic to glacier-fed streams only. Moreover, the *Chaetocladius* genus is frequent not only in kryal, but also in rhithral and krenal streams (Lencioni & Rossaro, 2005). To discover whether some species of the *Chaetocladius* genus could be restricted to glacier-fed streams, higher taxonomic resolution would be necessary. Based on the distribution of *Diamesa* sp. 3 in the streams studied, the ecological requirements and meltwater distribution optima of the genus (Brown *et al.*, 2007), this species seems to be the most threatened by glacier retreat. Unfortunately, because only larvae were captured, it was not possible to identify the species of the genera. To deter-

mine which species may go extinct with a complete disappearance of glaciers, more comprehensive knowledge of the community structure and distribution of the fauna at species-level in glacier-fed as well as in non-glacial streams is essential.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2011.00167.x:

Appendix S1. Average density (ind. m⁻²) of the chironomid taxa recorded.

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