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PRIMARY RESEARCH PAPER

Towards a definition of environmental niches in alpine streams by employing chironomid species preferences

Georg H. Niedrist · Leopold Füreder

Abstract Macroinvertebrates are widely used as indicators to detect and assess anthropogenic impacts on freshwater ecosystems. However, despite being considered useful in indicating effects of environmental change in alpine catchments, little is known about species preferences for local conditions in such environments. In exploring the occurrence of 59 taxa within the dipteran family Chironomidae in relation to key-environmental variables in alpine and sub-alpine streams, we showed that sediment load, water temperature, periphyton density, and fine particulate organic matter mostly explain assemblage structures. Two-way-cluster analyses identified stream-type specific assemblages, indicator value analysis defined indicator species for glacial and non-glacial streams, and weighted averaging regression models confined preferences for local environmental conditions by summing their optima and tolerance widths regarding environmental key factors. The definition of habitat requirements identified stenoecious taxa with preferences for high and low values of respective variables thus identified most suitable indicators for future studies. Our work reveals manifold preferences within the dominant benthic invertebrate family, underlines their enormous potential for monitoring purposes, and is a step forward in better understanding ecosystem properties and biodiversity. Fundamental requirements for these kinds of indicative traits, essential to understand cause–effect relationships in environmental change issues, are a robust taxonomy and a comprehensive set of physical and chemical data.

Keywords Alpine glacier-fed streams · Glacier retreat · Indicator · Autecology · Invertebrates · Sub-alpine

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Introduction

Organisms, which successfully inhabit extreme environments, are living in the ecological optimum for existence and reproduction (Begon et al., 1996). They tolerate harsh physical environmental conditions, grow at low temperatures, use limited food resources, and cope with predators and competing species (Wharton, 2002). According to the requirement-based concept by Grinnell (1917) and Hutchinson (1957), the term ecological niche was defined as a function

linking the fitness of individuals to their environment. One species' ecological niche is quantified as a multidimensional hypervolume (Blonder et al., 2014), where the individual dimensions are specific environmental conditions and resources that define the requirements of the present species to persist. Within this consideration, the ecological niche represents the suitable volume that permits positive population growth (Hutchinson, 1957; Hirzel & Le Lay, 2008). However, the characterisation of such niches in natural multi-species ecosystems is still debated (Soberón, 2007), although independent methods have been developed for different uses (Blonder et al., 2014).

Alpine stream networks are a mosaic of kryal (glacier-melt dominated), rhithral (rain/snowmelt dominated) and krenal (spring-fed, groundwater dominated) rivers (McGregor et al., 1995). Each source of stream generates characteristic conditions regarding physical (water temperature, discharge, substrate dynamics and suspended sediment load) and chemical water quality (Tockner et al., 1997; Füreder et al., 2001; Füreder, 2007), which are also responsible for the variety of environmental conditions further downstream (Brown et al., 2006a). This diverse abiotic character results in wide ecological gradients, suitable for a variety of benthic invertebrate species to coexist in alpine streams (Hutchinson, 1957; Levine & Hille Ris Lambers, 2009; Blonder et al., 2014). Larvae of the dipteran family Chironomidae typically dominate in streams at high altitude and latitude in terms of abundance and species number (Ward, 1994; Füreder, 1999; Füreder et al., 2001; Lods-Crozet et al., 2001a), and with the increasing harshness, they are often the only insects present (Füreder, 1999; Füreder et al., 2001; Lencioni & Rossaro, 2005). Considering specific adaptations and unique survival strategies (Danks, 1971; Danks & Oliver, 1972; Füreder, 1999; Bouchard et al., 2006), some species may be restricted to narrow environmental ranges concerning key environmental parameters (Lencioni & Rossaro, 2005). Hence, each type of stream (glacial, non-glacial) as well as reaches with low and high inputs of organic material (above and below the treeline) may therefore support a distinct assemblage of chironomid communities (Ward, 1994; Brown et al., 2006b). Many species may live close to their critical limits regarding not only the chemical and physical but also biological environment (Fjellheim et al., 2000). However, preferred ranges, the sensitivity to changes and the constancy of

preferences and occurrence are not known for most species.

The benthic biota is expected to possess a high potential to indicate long-term environmental changes not only due to their high abundance in alpine rivers, and adequate species richness, but also because of the observed sensitivity to environmental change (Ward, 1994; Füreder et al., 2001; Milner et al. 2001; Khamis et al., 2014). Several conceptual models (Milner & Petts, 1994; Milner et al., 2001), distribution and succession concepts (Füreder et al., 2001; Lods-Crozet et al., 2001a) and studies at species level (Lencioni & Rossaro, 2005) are available for alpine stream ecosystems as well as their key species. Attempting to quantify the effect of accelerated climate alterations (Beniston, 2005) and glacier retreat in alpine regions on benthic invertebrate communities living in glacially influenced streams (Jacobsen et al., 2012) has been a main research aim during the last decade (Brown et al., 2007). However, to date detailed autecological data (e.g., environmental preferences, trophic position, and functional role) are often lacking for invertebrates in alpine stream ecosystems, especially for the ubiquitous dipteran family, the Chironomidae. While most studies have shown relationships between habitat conditions and taxa richness, abundance and diversity, there is a lack of information demonstrating clear, species-specific habitat preferences, as well as niches and their boundaries.

To fill this research gap, we make the first approach to define fine-scale habitat requirements useful for a further niche-definition of chironomid assemblages and key-species in alpine stream habitats. We aim to identify the key environmental drivers that significantly shape the assemblages in order to define the potential species' ecological multidimensional hypervolume. To fulfil this purpose, we used wide gradients in various environmental conditions and in addition, we modelled multiple taxa-specific one-dimensional preferences. Furthermore, we combined them to characterise the multifactorial environmental preferences of the most abundant chironomid species. Based on the classification of the stream-type specific chironomid assemblages, along with the most representative taxa and their consistency of occurrence in the specific stream types in different watersheds, we aimed to identify the most suitable and useful organisms for ecological analysis and monitoring of environmental change.

Methods

Study area

The study area was located in the Austrian Central Eastern Alps, within the Hohe Tauern National park in the federal provinces of Salzburg and Carinthia (Fig. 1). In two glaciated catchments, the Anlauf and Seebach Valley (Fig. 1), we collected samples from four different river reaches (two non-glacial, two glacial) in each catchment of 20–30 m length above and below the treeline (Table 1). This sampling strategy was based on previous research conducted in the Hohe Tauern National park (Füreder & Amprosi, 2001; Füreder et al., 2002). The distance between the studied glacial-stream sites from the same valley were 3.5 and 2.52 km in Anlauf Valley and Seebach Valley, respectively. We used a paired study design which included replicate sites in the glacial and the spring-fed stream at a certain distance from the glacier in the alpine vegetation zone and further downstream within the montane vegetation zone. Vegetation coverage was scarcer in the Seebach valley at the lower sites, compared with the sites from the Anlauf Valley. Both catchments have the same geographic exposure and are in a natural hydromorphological condition and ecological status.

Sampling procedure

Benthic samples and reach-scale environmental variables were obtained on three occasions within the snow-free season (end of June, beginning of August and mid-September) in 2011. Our goal was to include a wide spectrum of environmental conditions, and as such, the selected streams were of glacial and non-
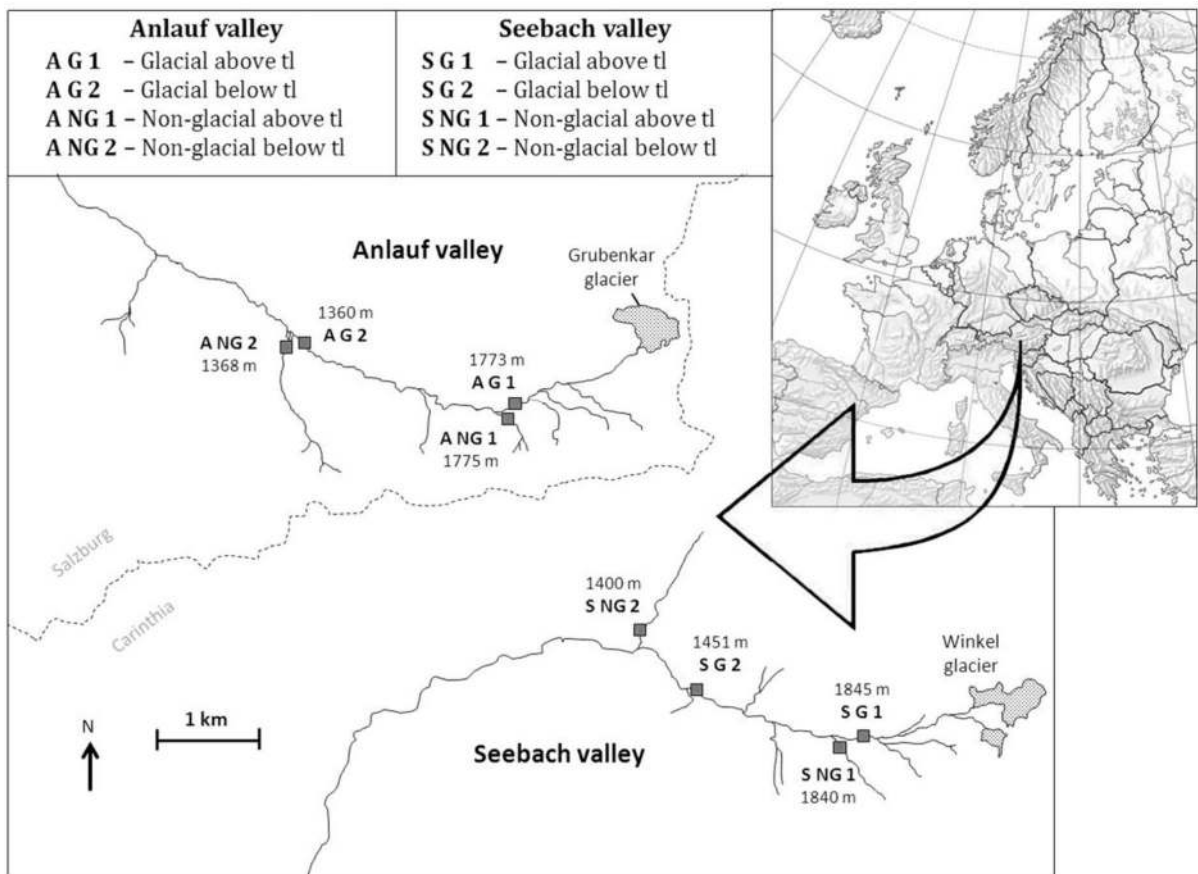

Fig. 1 Study area with the investigated catchments in the Anlauf valley and Seebach valley and the sampling sites in the glacial and non-glacial streams, above and below the treeline ('tl')

Table 1 Names, abbreviations, altitude and coordinates (WGS 84) of sampling sites in the Anlauf 'A' and Seebach 'S' valleys

Valley	Sampling site	Short name	Altitude (m)	Coordinates
Anlauf	Glacial above treeline	Glacial above tl—A	1773	47°03′21.3″N, 13°12′26″E
	Glacial below treeline	Glacial below tl—A	1360	47°03′20.6″N, 13°12′24.7″E
	Non-glacial above treeline	Non-glacial above tl—A	1775	47°04′00.9″N, 13°09′53.2″E
	Non-glacial below treeline	Non-glacial below tl—A	1368	47°03′57.5″N, 13°09′55.1″E
Seebach	Glacial above treeline	Glacial above tl—S	1845	47°00′38.5″N, 13°16′49.9″E
	Glacial below treeline	Glacial below tl—S	1451	47°01′05.7″N, 13°14′43.8″E
	Non-glacial above treeline	Non-glacial above tl—S	1840	47°00′35.5″N, 13°16′40.5″E
	Non-glacial below treeline	Non-glacial below tl—S	1400	47°01′23.2″N, 13°14′10.3″E

glacial origin and were sampled above and below the treeline.

The study was divided into three major stages: Firstly, we analysed the structure of chironomid communities in different stream types in one valley (Anlauf) including the analysis of seasonal effects to estimate the consistency of the structures. Secondly, we conducted an indicator value analysis, and for the test of suitability and appropriateness, we took samples from one substrate size. This was done based on the highest diversity (Shannon index), evenness and species numbers, and in addition, we compared them with the equivalent samples from the other valley (Seebachtal). Finally, we ordinated all the processed samples from the Anlauf and Seebach valleys together with the environmental data so as to identify the crucial environmental variables significantly related to community patterns. These variables, which demonstrate reach-scale dimensions of chironomids distribution in a multidimensional environment, were used to model the environmental optima and tolerance ranges for the most common chironomid species.

Physical and chemical characterisation

The temperature of the eight river reaches was recorded continuously with digital loggers (Onset TidbiT, MA, U.S.A.) throughout the snow-free season (records at 30 min intervals). This was summarised as maximum water temperature (highest daily mean) and the temperature variability (deviation of daily mean temperatures). The hydrological and the other physical and chemical parameters were assessed on each sampling date. With regard to the chemical analysis of the stream sites, electrical conductivity, pH and oxygen concentration were measured with a field multiprobe (WTW MultiLine® 3430, Weilheim, Germany). Water samples (2 l) were collected in acid-washed polyethylene bottles and analysed for the following chemical parameters: alkalinity, Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, SO_4^{2-}, NH_4^+, NO_3^-, dissolved nitrogen (DN), total and dissolved phosphorus (P_{tot}, P_{dis}), and dissolved organic carbon (DOC). Ion chromatography (Dionex 100/500 chromatograph) and Shimadzu TOC 5000 were used for the ionic and DOC analyses, respectively. Suspended inorganic and organic matter (mg/l) were assessed by filtering the water samples on pre-ashed Whatman GF/C-filters, dried and ashed in a muffle furnace at 450°C for 4 h according to Heiri et al. (2001). Discharge was measured by depth/velocity transects in each reach using a vane wheel probe (Höntzsch probe ZS25, Waiblingen, Germany). The inorganic sediment load (mg/s) of each reach per sampling date was modelled as the combination of 'suspended inorganic matter' and 'discharge'.

Biological assessment

All of the eight reaches were sampled on three occasions within the snow-free season. Within each studied reach and during each survey, six replicate Surber samples (mesh size 100 μm, area: 30 × 30 cm, 0.09 m^2) of aquatic invertebrates were collected (72 samples) and preserved in 75% ethanol. Stratified random sampling was performed, focussing on the three major substrate strata present in the riverbeds, i.e., megalithal (boulders, >40 cm grain size, 2 samples), macrolithal (coarse cobbles, 20–40 cm, 2 samples) and mesolithal (cobbles,

6.33–20 cm, 2 samples), whereas boulders were sampled on the surface only. For the suitability test, a comparison among the stream-type communities in both watersheds was carried out with a subset of all of the samples. In the laboratory, chironomids were identified to species or species-group level using available and accurate keys (Ferrarese & Rossaro, 1981; Horn, 1993; Rossaro, 1982). Total abundance was expressed as the number of individuals per m^2 for each reach on a given date. Two single samples from different sites were characterised as outliers due to their relative high number of early instar larvae, and therefore, they were not considered in the analyses. Periphyton chlorophyll a concentration was determined from three randomly collected stones in each reach and sampling period after filtering the scraped surface layer suspension onto a Whatman GF/C filter paper. Additionally, we filtered water to assess seston chlorophyll a concentration. Water chlorophyll a concentration was assessed the same way. Concentration was measured using a spectrophotometer (Hitachi U-2000) according to standard methods (Lorenzen, 1967). Contents of benthic coarse and fine particulate organic matter (BCPOM/BFPOM: items bigger/smaller than 1 mm) were determined by sieving, drying and ashing the residual sample content at 450°C for 4 h (Heiri et al., 2001).

Classification of chironomid assemblages

For the detection of stream-type specific chironomid community structures in the Anlauf Valley, a cluster analysis (Two-way cluster analysis, PC-ORD 5.01) was performed according to McCune & Mefford (2006) using samples from all three substrates. For this, the relative mean abundance data of chironomid species from each reach and date was used ($n = 6$). We excluded chironomid species with low abundances within the samples (<5%) to avoid unduly large influence of rare species on the analysis (ter Braak & Smilauer, 1998; Legendre & Legendre, 1998). A non-parametric permutational multivariate analysis of variance (non-parametric Manova, Anderson, 2005) was conducted to test for differences between the clustered assemblages using PAST software version 2.17c (Hammer et al., 2001). The seasonal effect on community structure was assessed by performing a redundancy analysis (gradient length of 3.0). Chironomid communities, taxa and factor date (June, August

and September) were ordinated including Monte Carlo permutation testing (9999 permutations).

In order to test for stream-type specific community structures in all of the stream reaches from both of the valleys, we conducted a second cluster analysis (Two-way cluster analysis) from Anlauf and Seebach Valley stream reaches ($n = 6$, grouped dates). We grouped these samples according to their faunal composition using *Sørensen's similarity coefficient* and *group average linkage*. For this, we used the relative mean abundance data of the chironomid taxa in the samples of each stream reach. The data were square rooted to reduce the analytical influence of dominant species (Kindt & Coe, 2005). Due to marginal seasonal differences in the Anlauf Valley assemblage structures (factor date accounted for only 8.6% of the total variation), samples from different months were grouped for each stream type in both valleys ('Glacial above treeline') in Anlauf ('A') and Seebach ('S') Valley, respectively ('Glacial above tl S'). To reveal the chironomid species that best characterised the group of sites, we conducted an indicator value analysis (*IndVal*; Dufrêne & Legendre, 1997) for grouped stream types showing similar community structures in both valleys. This method combines the abundance and the faithfulness of occurrence of a chironomid species in a particular stream reach (McCune et al., 2002). Indicator values emphasise the importance of different habitats for different species and identify the indicator species for each habitat, for example, a high and significant indicator value (%) of a species in a certain stream reach indicates its high frequency and abundance restricted to that habitat. Indicator values were calculated for each species and a Monte Carlo method was used to test the statistical significance (9999 permutations) using PC-ORD version 5 (McCune & Mefford, 2006).

Identification of environmental parameters crucial for chironomid community structures

The detection of analog community structures in both valleys (see Fig. 3) involved the inclusion of all the available samples from the Anlauf and Seebach Valleys for the identification of significant explanatory environmental variables. Chironomid communities, taxa and significant parameters were ordinated using a redundancy analysis, although we excluded chironomid species with low abundances within the

samples (<5%) and those two single samples with a high density of bryophytes to avoid a high proportions of juvenile larvae and thus low taxonomic resolution (two samples). Both, biotic and abiotic data were transformed to reduce skewed distributions (tested with Kolmogorov–Smirnov test, $P < 0.05$): environmental data shown in percentage (BFPOM, BCPOM) were square-root transformed (Legendre & Legendre, 1998; Li et al., 2012); the remaining environmental variables, with the exception of pH, and chironomid abundances were $(\ln(x + 1))$ transformed (Li et al., 2012). The automatically calculated gradient length of <3 standard deviations implied the use of a linear model such as a redundancy analysis (RDA) best fitting the data (Lepš & Šmilauer, 2003). Significant variables explaining the distribution of chironomid species in the sampled reaches were chosen by the forward selection method (Blanchet et al., 2008), and the significance of the RDA axes was determined by Monte Carlo permutation testing (9999 permutations) of the eigenvalues using CANOCO 5.0 software (Šmilauer & ter Braak, 2012). In this case, all of the biotic and abiotic environmental parameters (24) were included (see Annex 1—Supplemmentary Material).

Weighted averaging regression modelling

To quantify the relationships between the environmental variables showing the highest loads in the RDA (conductivity, fine particulate organic matter content (FPOM), maximum water temperature, temperature variability, chlorophyll *a* concentration, inorganic sediment load and periphyton chlorophyll *a* concentration) and the most abundant chironomid taxa, weighted averaging regression models (WARMs) were built using c2 version 1.7.4. (Juggins, 2007). The optimal values of the taxa were calculated as the mean of the selected environmental variables weighted by the abundance of the taxa at all sites according to ter Braak & Juggins (1993):

$$\text{Weighted average} = \frac{\sum_{i-1}^{n} x_i \times y_{ij}}{\sum_{i-1}^{n} y_{ij}}.$$

The weighted average shows the estimated species optimum, x_i is the environmental variable at site i, and y_{ij} stands for the abundance of species j in sample i. Additionally, tolerance values were calculated as the weighted standard deviation of the species abundance

in all of the samples according to ter Braak & Juggins (1993):

$$\text{Tolerance} = \sqrt{\frac{\sum_{i-1}^{n} (x_i - \text{weighted average})^2 \times y_{ij}}{\sum_{i-1}^{n} y_{ij}}}.$$

For the evaluation of the models' precision, the coefficients of determination (R^2) for the relationships between observed and generated environmental variables were compared. Errors were estimated using bootstrapping (9999 bootstrap cycles) integrated in the software C2 (Juggins, 2007). We performed the weighted averaging regression models using untransformed abundance and environmental data. Ecologically not worthwhile subzero tolerance ranges were truncated.

Results

Chironomid assemblage structure

More than 37,000 chironomids were sorted and identified from 84 samples. Chironomids (Diptera: Chironomidae) were the dominant insect family with 22,179 specimens and 59 taxa in the Anlauf valley (Annex 2—Supplementary Material), accounting for more than 60% of all collected individuals. Other major groups in these reaches were Ephemeroptera, Plecoptera and other dipteran families such as Simuliidae. The mean chironomid abundance ranged from 291 (Glacial above tl—Anlauf in September) to 7456 individuals per m^2 (non-glacial above tl—Anlauf in June). Generally, the mean abundance of the chironomidae, but also of all the other macroinvertebrates, was much lower in both glacier-fed (812 and 464 individuals m^{-2}) than in the non-glacial reaches (6170 and 4527 individuals m^{-2}). Both glacier-fed reaches had significantly less chironomids than the two non-glacial rivers (Kruskal–Wallis test, pooled samples with $n = 18$, $P < 0.001$). There were clear spatial distinctions in the chironomid densities according to the different river types; however, only marginal and non-significant seasonal differences were found with the highest densities in June for all the reaches. The subfamily Diamesinae dominated in reaches above the treeline (84.4% of all the chironomids in the glacial and 50.4% in the non-glacial reaches). On the other hand, the subfamily Orthocladiinae showed higher

relative abundances in reaches below the treeline (77.6% in the glacial and 98.4% in the non-glacial reaches). Generally, Orthocladiinae showed significantly higher abundances in the non-glacial streams when compared with the glacial streams ($P < 0.001$ for above and below the treeline).

Among the sampled substrates, mesolithal (6.33–20 cm) samples had the highest chironomid diversity in each stream type in the Anlauf Valley ranging from 3.1 (above the treeline) to 3.9 (below the treeline) in the glacial stream (Table 2). Additionally, in all of the reaches, we found the highest species number in mesolithal samples. The seasonal effect was small, explaining only 8.6% of the total variation.

River-type specific chironomid assemblages and indicator species

The chironomid communities in all of the stream reaches from the Anlauf valley sampled on the three different occasions clustered in four groups (Fig. 2): the PERMANOVA test found significant differences in the chironomid composition between these groups (F: 18.61; $P < 0.05$). While communities in the different glacial reaches were moderately dissimilar, those communities in the non-glacial streams at different altitudes hosted very different chironomid communities. Furthermore, well-separated communities were established in distinct stream types, but at the same altitudes. Communities from the same habitat differed only slightly seasonally and grouped together in significantly different groups (Fig. 2). The combination of Shannon-index, evenness and taxa number demonstrated that mesolithal substrate inhabits the most diverse, taxa rich and uniformly distributed chironomid communities in the studied streams

(Table 2). Thus, we chose samples from this substrate to compare community structures in both valleys. Communities in comparable stream types above the treeline in both catchments (glacial and non-glacial headwater sites) clustered in the same groups, whereas habitats below the treeline did not show any general community structures (Fig. 3).

The grouping of taxa revealed groups of chironomid taxa with main occurrences in one, two, or three stream reaches (Fig. 3). Taxa mainly occurring in alpine/subalpine glacier-fed -streams were *Diamesa steinboecki* (Goetghebuer)*, Diamesa latitarsis*-gr. I and II, *Diamesa* sp. Other taxa that uniformly appeared mainly in high non-glacial streams were *Pseudokiefferiella parva* (Edwards), *Diamesa cinerella/zernyi*-gr. and *Paratrichocladius rufiventris* (Meigen). The third cluster was characterised by various taxa occurring either in one, two or three different habitats. Moreover, in this cluster no uniform distributions were found in the same habitats from the different valleys.

The *IndVal* procedure revealed chironomid taxa that significantly characterised each of the clustered sites (Table 3). The group of alpine/subalpine stream habitats with glacial influence was best characterised by the taxa *D. steinboecki* and the *D. latitarsis*-gr. I, whereas indicative species for non-glacial stream habitats above the treeline were *P. parva*, *D. cinerella/zernyi*-gr. and *Orthocladius frigidus* (Zetterstedt). No general faunal patterns were found for the lower elevation stream habitat types; different chironomid taxa represented these habitats: *Tvetenia bavarica* (Goetghebuer), *Eukiefferiella brevicalcar* (Kieffer) and *Eukiefferiella fuldensis* (Lehmann) were found to be indicator species for low-altitude reaches (Table 3).

Table 2 Shannon diversity, (shannon-) evenness and taxa number of chironomid communities of the studied substrates (megalithal:> 40 cm diameter; macrolithal: 20–40 cm diameter; mesolithal: 6.33–20 cm diameter) in each of the 4 stream reaches in the Anlauf valley

Stream origin	Glacial stream						Non-glacial streams					
Location	Above tl			Below tl			Above tl			Below tl		
Sampled substrate (-lithal)	Macro-	Mega-	Meso-	Macro-	Mega-	Meso-	Macro-	Mega-	Meso-	Macro-	Mega-	Meso-
Shannon Index	3.0	2.4	**3.1**	3.8	2.9	**3.9**	3.0	**3.3**	**3.3**	2.7	2.4	**3.4**
Eveness	0.7	0.6	0.7	0.9	0.6	0.8	0.7	0.7	0.7	0.6	0.5	0.7
Number of taxa	**22**	20	**22**	20	**29**	28	24	**27**	**27**	23	26	**31**

'tl' stands for treeline, the highest values are shown in bold
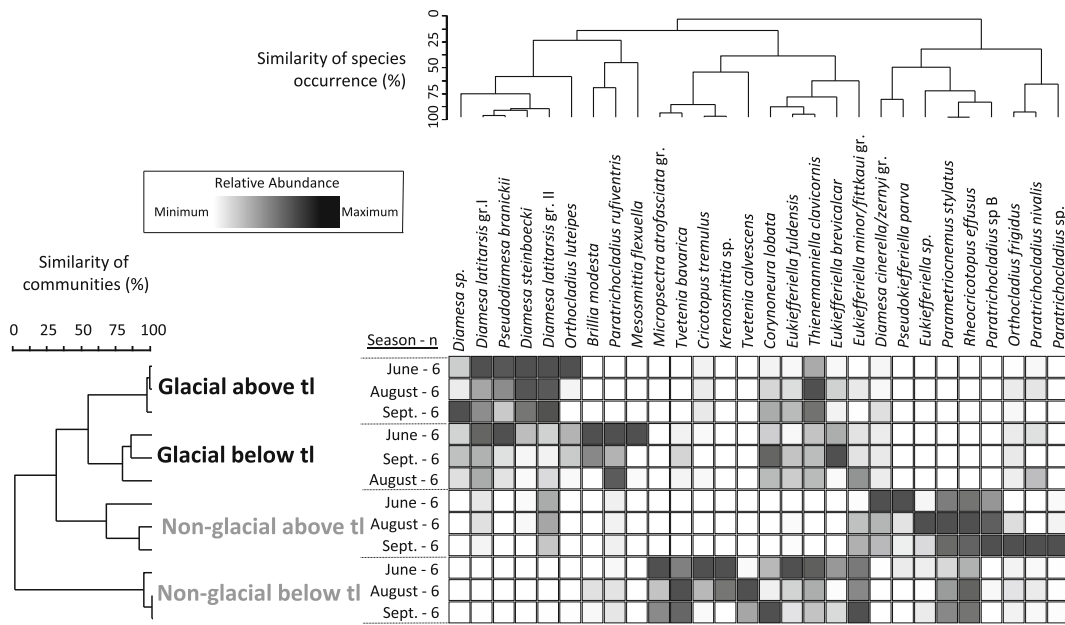
Fig. 2 Two-way cluster of (I) the most abundant chironomid taxa (*top*) and (II) stream-reach community structures (*left*) in glacial and non-glacial stream habitats above ('above tl') and below ('below tl') the treeline in the Anlauf Valley. Habitats were clustered according to their mean relative abundance of chironomid taxa, and taxa were clustered according to their relative mean abundance in different habitats ($n = 6$). The data matrix expresses the relative mean abundance of species in different habitats
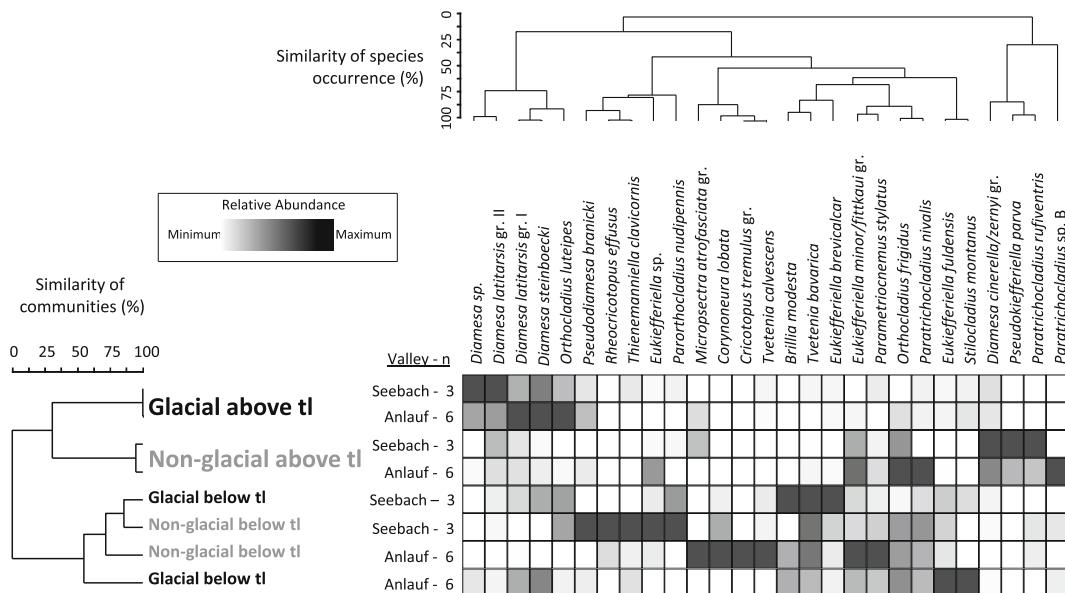
Fig. 3 Two-way cluster of (I) the most abundant chironomid taxa (*top*) and (II) the mean stream-reach community structures (*left*): In the Anlauf Valley ("Anlauf") and Seebach Valley ("Seebach"), the glacial and non-glacial stream habitats from the substrate mesolithal above ("above tl") and below ("below tl") the treeline were clustered according to their grouped mean relative abundance of chironomid taxa throughout the snow-free season (n Anlauf Valley = 6; n Seebach Valley = 3)

Table 3 Indicator values (*IndVal*, in percentage of perfect indication) of significant chironomid taxa (*P* < 0.05; 9,999 permutations) for significantly grouped assemblages identified by cluster analysis including habitats of both catchments (Fig. 3)

Stream type	Groups of habitats	Chironomid taxa	Indicator value (%)	*P* value
Glacial streams—above	Glacial above tl Anlauf	*Diamesa steinboecki*	69.7	0.033
	Glacial above tl Seebach	*Diamesa latitarsis*-gr. I	66.7	0.046
Non-glacial streams—above	Non-Glacial above tl Anlauf	*Pseudokiefferiella parva*	100	0.038
	Non-glacial above tl Seebach	*Diamesa cinerella/zernyi*-gr.	79.3	0.043
		Orthocladius frigidus	52.9	0.035
Glacial streams—below	Glacial below tl Anlauf	*Tvetenia bavarica*	88.3	0.013
	Glacial below tl Seebach	*Eukiefferiella brevicalcar*	80	0.046
Non-glacial streams—below	Non-glacial below tl Anlauf	*Eukiefferiella fuldensis*	80	0.012
	Non-glacial below tl Seebach			

'Above' and 'Below' denote the sampling sites above and below the treeline ('tl'), whereas 'glacial' and 'non-glacial' stand for glacial and non-glacial streams in both valleys Anlauf and Seebach valley

Relationship between chironomid communities and environmental variables

The redundancy analysis including all of the samples revealed a correlation among the samples, the selected local environmental characteristics, along with the distribution patterns of chironomid taxa (Fig. 4). All significant explanatory variables accounted for 48.6%

of the total variation. The first axis, explaining 27.54% of the total variance (*F*-ratio: 27.0; *P* < 0.001), was positively related to FPOM and water chlorophyll *a* content and negatively with conductivity. The second axis explained 10.63% of the total variance (*F*-ratio: 6.7; *P* < 0.001). This axis was positively related with periphyton chlorophyll *a* concentration, and negatively with temperature variability, maximum

Fig. 4 RDA of samples and chironomid taxa (*dots*) significantly explaining environmental features and chemical variables (*arrows*) in surveyed river reaches. Single samples are displayed with *circles* (glacier-fed reaches) and squares (non-glacial reaches) with reaches above (*empty*) and below (*filled*) the treeline. For taxa codes, see Annex 2—Supplementary Material
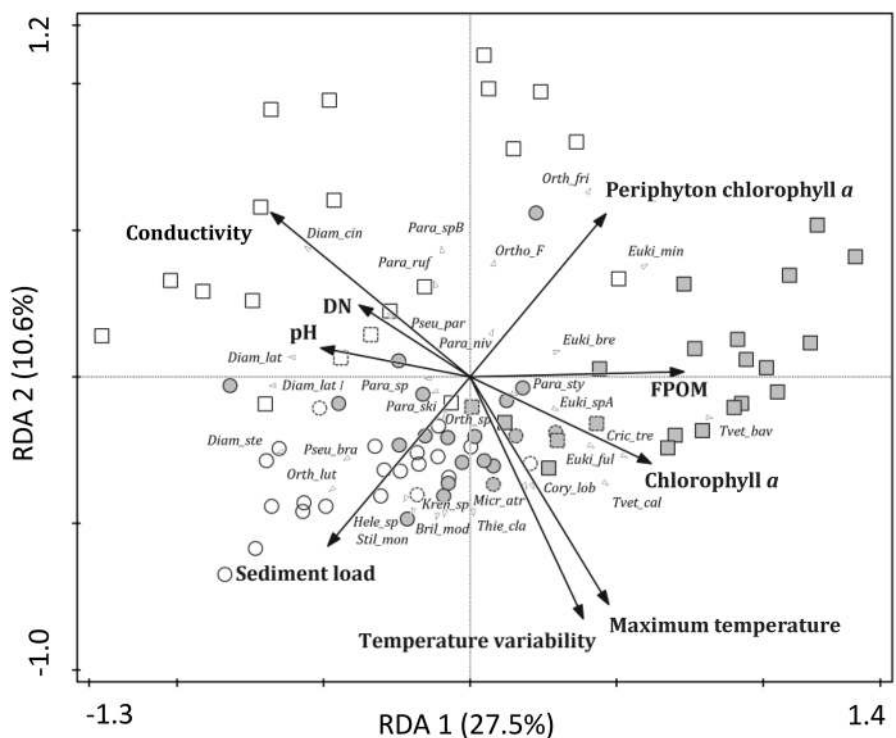
Table 4 Predictive power of weighted averaging regression models (WARM's) for environmental variables in alpine streams: coefficient of determination (R^2) and root-mean-square-error (RMSE) with and without bootstrapping (9999 cycles)

Variable	R^2	R^2_{boot}	RMSE	RMSE$_{boot}$
Conductivity	0.52	0.47	32.08	32.74
FPOM	0.54	0.48	3.91	3.99
Max. temperature	0.41	0.36	2.66	2.68
Temperature variability	0.44	0.39	2.43	2.42
Water Chl *a* conc.	0.37	0.33	0.21	0.21
Inorganic sediment load	0.30	0.23	23.49	23.17
Periphyton chl *a* conc.	0.30	0.22	8.28	7.83

Remarkable differences imply low accuracy of the model

Water Chl *a* conc. stands for the chlorophyll a concentration in the running water

Fig. 5 Modelled optima and tolerances of key-environmental ▶ variables for related chironomid species obtained by weighted averaging regression modelling with indication of species frequency in percentage of all of the samples: **a** maximum water temperature, **b** temperature variability, **c** inorganic sediment load, **d** conductivity, **e** chlorophyll a concentration 'Chl a concentration', **f** FPOM. *Dots* indicate optimal values, standard deviations show the tolerance ranges. Inferred sub-zero values were truncated
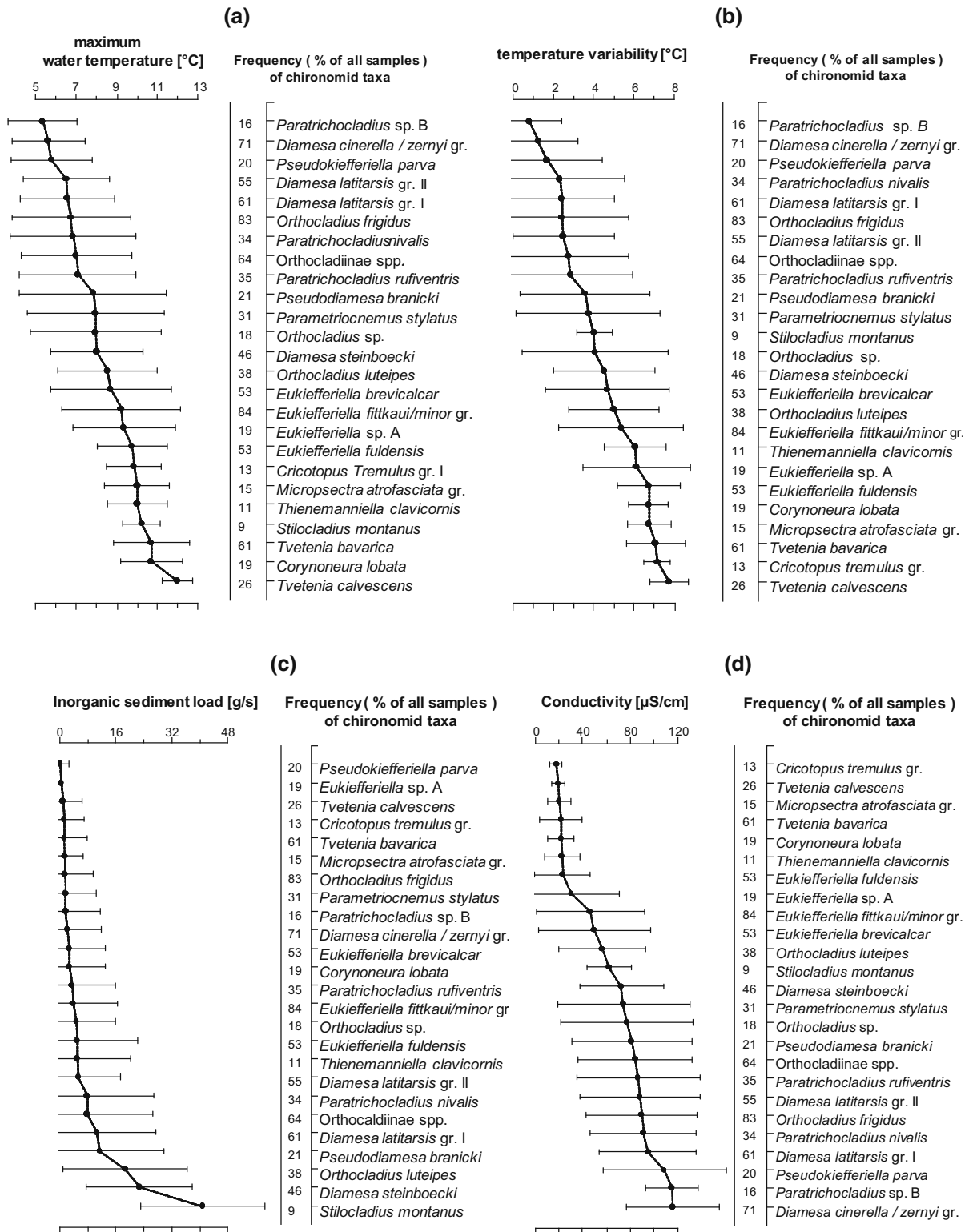
water temperature, and to a lesser extent with inorganic sediment load. The third axis, accounting for only 3.7% of the total variance, correlated positively with the dissolved nitrogen and negatively with the total phosphorus concentration. The chironomid communities had different structures of taxa when comparing sampling sites above and below the treeline, as well as glacial and non-glacial stream reaches of the same altitude. Most species of the subfamily Diamesinae (except *D. cinerella/zernyi–*gr.) prevailed in the higher altitude, cold and temperature-stable stream reaches with high inorganic sediment loads and low concentrations of organic matter. Other species (mainly members of Orthocladiinae and some Chironominae) dominated in reaches with higher and more dynamic temperature regimes as well as high primary production enriched with particulate organic material. The variable 'alkalinity' was correlated with 'conductivity' and was therefore excluded prior to the analysis.

Weighted averaging regression models

Conductivity, fine particulate organic matter content (FPOM), maximum water temperature, temperature variability, chlorophyll *a* concentration, inorganic sediment load, and periphyton chlorophyll *a* concentration were selected to evaluate the optimal requirements for selected chironomid taxa. These variables provided the highest explanatory power in the RDA.

Most regression coefficients (R^2) between the observed and inferred environmental variables were high and similar with and without the bootstrapping tests (Table 4); thus, the best environmental variables influencing the chironomid taxa were modelled reliably by the weighted averaging regression models. The selected taxa differed considerably in their environmental preferences. Whilst we detected a substantial number of generalists, we identified several specialists showing narrow preference ranges for the most important environmental variables. Here we focused on the most frequent taxa in all of the samples (Fig. 5): *T. bavarica* and *E. fuldensis* showed preferences for streams with low conductivity (10–50 µS/cm), whereas *D. latitarsis*-gr. I and II, *D. cinerella/zernyi*-gr., as well as *O. frigidus* occurred predominantly in streams with higher ionic contents (40–170 µS/cm). Taxa preferring low benthic FPOM content (0–4% of samples dry weight) were D. *steinboecki*, D. *latitarsis*-gr. I and II, and *D. cinerella/zernyi*-gr., and those living in streams with higher concentrations (until 16%) were *T. bavarica, E. fuldensis, Tvetenia calvescens* (Edwards) and *E. minor/fittkaui*-gr. The best and most frequent indicators for low maximum water temperatures (3.5–9°C) and low temperature variability (0–5°C) were *D. cinerella/zernyi*-gr., *D. latitarsis*-gr. I and II, whereas taxa related to high maximum water temperatures (8.5–12.5°C) and variability (5–9°C) were *E. fuldensis* and *T. bavarica*. With regard to inorganic sediment loads, most taxa showed optimal values around zero; however, *D. latitarsis*-gr. I, *Orthocladius luteipes* (Goetghebuer) and *D. steinboecki* showed their optima with 10, 18 and 23 g/s, respectively. The chironomid taxa did not show narrow tolerances for periphyton chlorophyll *a* content. Nevertheless, *D. steinboecki* and *O. luteipes* had preferences for lower concentrations (0–11 µg/cm^2), whereas the optimal periphyton density for frequent taxa like *E. fuldensis*, *E. brevicalcar* and *O.*

(a)

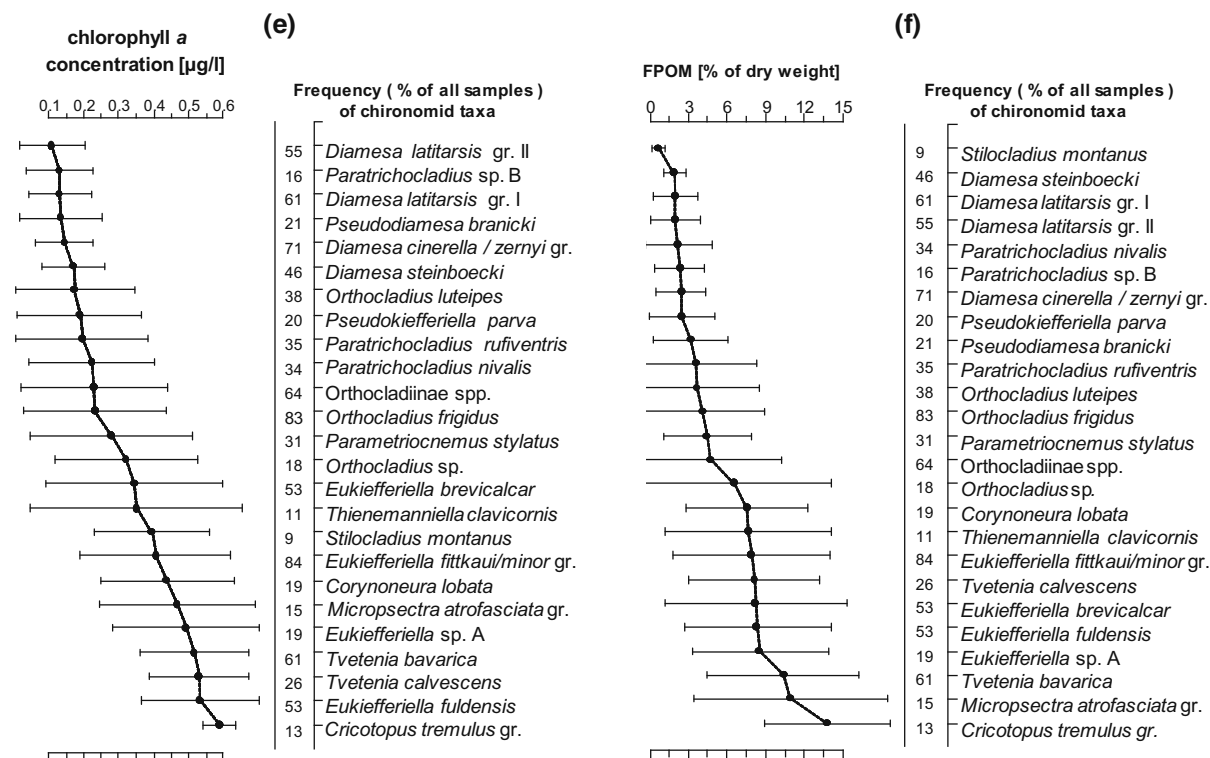maximum water temperature [°C]

Frequency (% of all samples) of chironomid taxa

Freq	Taxon
16	*Paratrichocladius* sp. B
71	*Diamesa cinerella / zernyi* gr.
20	*Pseudokiefferiella parva*
55	*Diamesa latitarsis* gr. II
61	*Diamesa latitarsis* gr. I
83	*Orthocladius frigidus*
34	*Paratrichocladius nivalis*
64	Orthocladiinae spp.
35	*Paratrichocladius rufiventris*
21	*Pseudodiamesa branicki*
31	*Parametriocnemus stylatus*
18	*Orthocladius* sp.
46	*Diamesa steinboecki*
38	*Orthocladius luteipes*
53	*Eukiefferiella brevicalcar*
84	*Eukiefferiella fittkaui/minor* gr.
19	*Eukiefferiella* sp. A
53	*Eukiefferiella fuldensis*
13	*Cricotopus Tremulus* gr. I
15	*Micropsectra atrofasciata* gr.
11	*Thienemanniella clavicornis*
9	*Stilocladius montanus*
61	*Tvetenia bavarica*
19	*Corynoneura lobata*
26	*Tvetenia calvescens*

(b)

temperature variability [°C]

Frequency (% of all samples) of chironomid taxa

Freq	Taxon
16	*Paratrichocladius* sp. *B*
71	*Diamesa cinerella / zernyi* gr.
20	*Pseudokiefferiella parva*
34	*Paratrichocladius nivalis*
61	*Diamesa latitarsis* gr. I
83	*Orthocladius frigidus*
55	*Diamesa latitarsis* gr. II
64	Orthocladiinae spp.
35	*Paratrichocladius rufiventris*
21	*Pseudodiamesa branicki*
31	*Parametriocnemus stylatus*
9	*Stilocladius montanus*
18	*Orthocladius* sp.
46	*Diamesa steinboecki*
53	*Eukiefferiella brevicalcar*
38	*Orthocladius luteipes*
84	*Eukiefferiella fittkaui/minor* gr.
11	*Thienemanniella clavicornis*
19	*Eukiefferiella* sp. A
53	*Eukiefferiella fuldensis*
19	*Corynoneura lobata*
15	*Micropsectra atrofasciata* gr.
61	*Tvetenia bavarica*
13	*Cricotopus tremulus* gr.
26	*Tvetenia calvescens*

(c)

Inorganic sediment load [g/s]

Frequency (% of all samples) of chironomid taxa

Freq	Taxon
20	*Pseudokiefferiella parva*
19	*Eukiefferiella* sp. A
26	*Tvetenia calvescens*
13	*Cricotopus tremulus* gr.
61	*Tvetenia bavarica*
15	*Micropsectra atrofasciata* gr.
83	*Orthocladius frigidus*
31	*Parametriocnemus stylatus*
16	*Paratrichocladius* sp. B
71	*Diamesa cinerella / zernyi* gr.
53	*Eukiefferiella brevicalcar*
19	*Corynoneura lobata*
35	*Paratrichocladius rufiventris*
84	*Eukiefferiella fittkaui/minor* gr
18	*Orthocladius* sp.
53	*Eukiefferiella fuldensis*
11	*Thienemanniella clavicornis*
55	*Diamesa latitarsis* gr. II
34	*Paratrichocladius nivalis*
64	Orthocaldiinae spp.
61	*Diamesa latitarsis* gr. I
21	*Pseudodiamesa branicki*
38	*Orthocladius luteipes*
46	*Diamesa steinboecki*
9	*Stilocladius montanus*

(d)

Conductivity [µS/cm]

Frequency (% of all samples) of chironomid taxa

Freq	Taxon
13	*Cricotopus tremulus* gr.
26	*Tvetenia calvescens*
15	*Micropsectra atrofasciata* gr.
61	*Tvetenia bavarica*
19	*Corynoneura lobata*
11	*Thienemanniella clavicornis*
53	*Eukiefferiella fuldensis*
19	*Eukiefferiella* sp. A
84	*Eukiefferiella fittkaui/minor* gr.
53	*Eukiefferiella brevicalcar*
38	*Orthocladius luteipes*
9	*Stilocladius montanus*
46	*Diamesa steinboecki*
31	*Parametriocnemus stylatus*
18	*Orthocladius* sp.
21	*Pseudodiamesa branicki*
64	Orthocladiinae spp.
35	*Paratrichocladius rufiventris*
55	*Diamesa latitarsis* gr. II
83	*Orthocladius frigidus*
34	*Paratrichocladius nivalis*
61	*Diamesa latitarsis* gr. I
20	*Pseudokiefferiella parva*
16	*Paratrichocladius* sp. B
71	*Diamesa cinerella / zernyi* gr.

(e)

chlorophyll *a* concentration [µg/l]

0,1   0,2   0,3   0,4   0,5   0,6

Frequency (% of all samples) of chironomid taxa

55	*Diamesa latitarsis* gr. II
16	*Paratrichocladius* sp. B
61	*Diamesa latitarsis* gr. I
21	*Pseudodiamesa branicki*
71	*Diamesa cinerella / zernyi* gr.
46	*Diamesa steinboecki*
38	*Orthocladius luteipes*
20	*Pseudokiefferiella parva*
35	*Paratrichocladius rufiventris*
34	*Paratrichocladius nivalis*
64	Orthocladiinae spp.
83	*Orthocladius frigidus*
31	*Parametriocnemus stylatus*
18	*Orthocladius* sp.
53	*Eukiefferiella brevicalcar*
11	*Thienemanniella clavicornis*
9	*Stilocladius montanus*
84	*Eukiefferiella fittkaui/minor* gr.
19	*Corynoneura lobata*
15	*Micropsectra atrofasciata* gr.
19	*Eukiefferiella* sp. A
61	*Tvetenia bavarica*
26	*Tvetenia calvescens*
53	*Eukiefferiella fuldensis*
13	*Cricotopus tremulus* gr.

(f)

FPOM [% of dry weight]

0   3   6   9   12   15

Frequency (% of all samples) of chironomid taxa

9	*Stilocladius montanus*
46	*Diamesa steinboecki*
61	*Diamesa latitarsis* gr. I
55	*Diamesa latitarsis* gr. II
34	*Paratrichocladius nivalis*
16	*Paratrichocladius* sp. B
71	*Diamesa cinerella / zernyi* gr.
20	*Pseudokiefferiella parva*
21	*Pseudodiamesa branicki*
35	*Paratrichocladius rufiventris*
38	*Orthocladius luteipes*
83	*Orthocladius frigidus*
31	*Parametriocnemus stylatus*
64	Orthocladiinae spp.
18	*Orthocladius* sp.
19	*Corynoneura lobata*
11	*Thienemanniella clavicornis*
84	*Eukiefferiella fittkaui/minor* gr.
26	*Tvetenia calvescens*
53	*Eukiefferiella brevicalcar*
53	*Eukiefferiella fuldensis*
19	*Eukiefferiella* sp. A
61	*Tvetenia bavarica*
15	*Micropsectra atrofasciata* gr.
13	*Cricotopus tremulus gr.*

Fig. 5 continued

frigidus varied between 15 and 16.5 µg/cm^2. Chlorophyll *a* concentrations in the running water were generally low. *D. latitarsis*-gr. II and I, *D. cinerella/ zernyi*-gr. and *D. steinboecki* are taxa tolerating concentrations until 0.25 µg/l, and on the other hand we found *T. bavarica, T. calvescens* and *E. fuldensis* living in productive streams with concentrations between 0.35 and 0.65 µg/l.

Discussion

Biodiversity in alpine areas is threatened by ever increasing land use and the effects of other human activities including rapid climate change. Even in relatively remote regions, e.g., high mountain protected areas, alpine stream ecosystems experience the consequences of climatic change including glacier retreat, altered water temperature, discharge dynamics as well as the availability of allochthonous and autochthonous organic matter (Braun et al., 2000; Zah & Uehlinger, 2001; Jansson et al., 2003; Knowles et al., 2006; Zemp et al., 2006). Research to determine the causal relationships between environmental characteristics and the distribution of aquatic organisms has resulted in several predictions of climate change effects on these unique ecosystems (Muhlfeld et al., 2011; Giersch et al., 2015). In this respect, understanding the spatial and temporal patterns, as well as the determinants of the structure of chironomid assemblages, which form the main components of the benthic invertebrate fauna (Füreder et al., 2001; Lods-Crozet et al., 2001a), are fundamental for the application of this ubiquitous dipteran family as indicators (Butler et al., 2012). For this purpose, we found it essential to define species-specific environmental requirements, to provide new insights into the range of species occurrence and their preferences.

This study has significantly enhanced the understanding of the relationship of reach-scale environmental conditions and macroinvertebrate assemblages across various alpine and sub-alpine stream types. It contributes, based on high-resolution data, novel definitions of environmental preferences of chironomid species, which explain the consistent stream-type specific occurrence of species and species-groups in

two watersheds in the Central European Alps. Along these lines, we undertook a redundancy analysis of chironomid species assemblages from different stream types in combination with a comprehensive set of fine-scale environmental parameters. We identified key environmental variables significantly influencing chironomid community structures and found that taxa-specific differences in modelled preferences for these environmental variables provoke the formation of stream-type specific chironomid assemblages in head-water streams with and without glacial influence. Taking into account all of the aforementioned, we are able to discuss the following:

Multifactorial effect of environmental stressors on chironomid assemblages and the characterisation of niche space of chironomidae in alpine and sub-alpine streams

The influence of environmental factors on alpine stream invertebrate communities was mainly studied in glacier-fed streams (e.g. Brittain & Milner, 2001; Milner et al., 2001). These studies identified maximum water temperature, Pfankuch-index and distance from the source as the main influences on community structures. Our results from all of the investigated stream types in both catchments indicated that additional environmental parameters contributed significantly to the structuring of chironomid communities. There is evidence that not only water temperature but also periphyton chlorophyll *a* content, and fine particulate organic material played an important role in shaping alpine stream invertebrate assemblages, as initially supposed by Milner et al. (2001). The availability of broad food sources (FPOM, algae) had a major effect on chironomid community structures, reinforcing the assumptions of Clitherow et al. (2013) that diatoms, periphyton and fine detritus form dominant food sources for invertebrates, especially in groundwater fed alpine streams (Zah & Uehlinger, 2001; Füreder et al., 2003). Besides these biotic variables, we identified sediment load and electrical conductivity to be related to chironomid assemblage patterns. Conductivity might not be a primal stressor for invertebrates but differs significantly between rhitral and kryal stream sites (Hieber et al., 2003) and is significantly related to invertebrate patterns in

recent studies (Mori et al., 2011; Brown et al., 2015). Although we did not quantify disturbance, we derived sediment load as a proxy for hydraulic stress, which integrates discharge and concentration of suspended solids. Both variables, conductivity and sediment load, integrate several hydrological and geochemical processes, allowing conclusions about glacial activity, streambed stability (Milner et al., 2001), or even disturbance. We are aware that other influences, which were not assessed in this study, might differ between years in most sites and consequently also trigger species occurrence and survival in these habitats. However, although the explanatory power is a bit lower compared to similar habitats with 52% (Lods-Crozet et al., 2001b), the identified environmental factors were significantly related to the structure of chironomid communities and explained most of their variation within our studied streams, thereby characterising most of the niche space of chironomidae in alpine and sub-alpine streams. This dependent relationship of species occurrence and prevailing environmental situation confirms the indicative potential of the chironomids as a tool for stream ecologists in alpine/subalpine zones. Furthermore, most of these factors will be altered due to climate change and anthropogenic impacts (Brown et al., 2015) and thus will be seen in chironomid assemblage structure. Our results extend the general understanding of chironomid autecology complementing the conceptual model of Milner et al. (2001) and expanding the findings of Lods-Crozet et al. (2001a) and Lencioni et al. (2012) with a high taxonomic resolution. For example, Diamesinae species and typically upstream Orthocladiinae were well separated from the other chironomid taxa by low temperatures, high conductivity and inorganic sediment load. In contrast, warmer habitats in the sub-alpine zone with high organic matter deposition as well as higher density of primary producers favoured the establishment of assemblages dominated by Orthocladiinae species like *T. bavarica*, *T. calvescens*, *E. fittkaui/minor*-gr. and *E. fuldensis*. This pattern of dominant species was not found in studies focussing on streams in the alpine region only (Lods-Crozet et al., 2001a, 2012). The difference is explainable by the coverage of a shorter gradient of different environmental conditions, when compared to this work.

Definition of stream-type specific assemblages in the alpine zone

In contrast to previous studies dealing with alpine stream environments (e.g. Füreder et al., 2001; Lods-Crozet et al., 2001a; Lencioni & Rossaro, 2005), our data from Central European Alps clearly document the dominance of chironomids in alpine and sub-alpine streams and identify the most dominant species for each type. Chironomid density was significantly higher in non-glacial sites than in glacial streams, a finding supported by previous studies (e.g. Füreder et al., 2001; Lencioni & Rossaro, 2005). Such patterns show that heterogeneous, but stable habitats favour high population densities, while dynamic environments are poorly populated (Staudacher & Füreder, 2007; Lencioni et al., 2011). Within these reaches, chironomid community structure changed marginally within the summer months, which is in disagreement with the recent findings of Brown et al. (2015). However, this difference might arise from the lower altitude and greater distance from the glacial margin of our sites, where conditions might be more stable.

Differences in key environmental variables like water temperature, sediment load, conductivity, FPOM and periphyton, chlorophyll *a* content led to the formation of significantly distinct and stream-type specific chironomid assemblages in the investigated watersheds. Cluster analyses revealed that chironomid communities were in general assembled and dominated by the same species in high elevation and extreme habitats of similar stream types in two different valleys separated by steep mountains (this has not been previously demonstrated). This distinction of stream-type specific assemblages with '*indicator taxa*' was very clear for upstream reaches above the treeline, whereas no strict stream-type specificity could be observed in the rhithral reaches below the treeline, and this was probably caused by the differences in the slope, vegetation coverage and streambed structure between both valleys. This pattern, underlining the importance of the heterogeneous nature of the highest-altitude headwaters for regional-scale biodiversity, was genetically shown by Finn et al. (2013) and now supported by structural ecological methods.

Our study identifies constantly dominant indicator taxa such as *D. steinboecki* and *D. latitarsis*-gr. I for glacial, and *P. parva*, *D. cinerella/zernyi*-gr., and *O.* *frigidus* for non-glacial headwater streams. This set of invertebrates dominating associated stream types will facilitate the design of studies focusing on functional alterations in alpine stream habitats such as development, feeding preferences or production. In addition to reports about dominating species along a glacier-fed stream (Lods-Crozet et al., 2001a), this is the first study providing indicator taxa constantly dominating in glacial or non-glacial alpine stream types within the most abundant and taxonomically most difficult freshwater invertebrate family.

Niche differentiation in a multi-species community

The observed patterns of chironomid occurrence confirmed a high stream type specificity of some taxa, which implies narrow preferences along certain small-scale environmental gradients. One of the longest unresolved problems in ecology, the critical role that niche differences have in stabilising species diversity and community dynamics has been addressed in several studies (Levine & HilleRisLambers, 2009; Vergnon et al., 2009). However, instead of comparing niche-based processes with neutral models (Vergnon et al., 2009), we provided modelled requirement-based species preferences in relation to key-environmental variables that mostly affect community structures. While other studies have used coarse indices to quantify glacial influence and selected indicator species for their changes (Khamis et al., 2014), we used reach-scale environmental variables to understand the local stressors provoking different community structures. Nevertheless, we identified similar patterns and indicator taxa.

We modelled the environmental stressors in the multidimensional environment defined by the variables that mostly affect the structure of chironomid communities. We were able to put narrower limits on environmental preferences for most of the abundant key taxa by conducting weighted averaging regression models and therefore obtaining optima and preference ranges along gradients of selected non-interacting habitat variables and abiotic environmental conditions. The combination of these modelled one-dimensional tolerances represents the main part of the species environmental niches. The models reveal a variety of preference types of the chironomid species for key environmental variables in the studied alpine

and sub-alpine streams and identify stenoecious and euryoecious taxa with preferences for both low and high environmental extremes. Among the most frequent chironomids, we identified stenoecious taxa preferring high and low values of respective variables; thus, these taxa are as indicators highly sensitive to environmental change.

Inorganic sediment load is influenced by substrate composition, its stability, the glacial extend and its melting rate. This factor is crucial for the formation of communities in glacier-fed headwaters, and it separates cold stenothermal Diamesinae species living in clear non-glacial streams (*D. cinerella/zernyi*-gr. and *P. parva*) from other Diamesinae tolerating high contents of fine rock fragments and turbid waters (*D. steinboecki*, *D. latitarsis*-gr. I and II). Thus, tolerating high sediment loads seems to be more crucial for survival in glacier-fed streams than withstanding cold water temperatures as suggested by other studies (Lods-Crozet et al., 2001a; Milner et al., 2001; Lencioni & Rossaro, 2005). The modelled optima may not directly reflect fundamental optima of Diamesinae species, as these species might also tolerate higher water temperatures and low sediment loads, or high concentration of suspended solids, but are competitively excluded from benign stream sites by other chironomid species as suggested by Castella et al. (2001). Still, our models illustrate the adaptation and environmental tolerance of this species group, being able to withstand harsh conditions, which we found to be their niche in alpine streams. Although we applied a different approach in contrast to other authors (Khamis et al., 2014), we congruently identified several species adapted to a high glacial influence (several *Diamesa* species). We are aware that the geographic scope of this study, which covered remote parts of the Eastern Alps, is relatively small compared to the geographic distribution of the chironomid species identified (e.g. *D. latitarsis* (Goetghebuer)*, O. frigidus*). However, the investigation of distinct stream types at different altitudes (from alpine glacial streams to non-glacial streams with high inputs of allochthonous material) allowed us to include data from a broad suite of environmental gradients. Additionally, we modelled unimodal and multifactorial species response curves which had not previously been computed for alpine stream invertebrates by weighted averaging regression models. This technique facilitates the coverage of a wide range of possible

environmental conditions where most alpine and sub-alpine chironomid species occur.

For the ordination, clustering and the modelling of optima and tolerance of communities and species, we partially included non-independent samples (e.g. different microhabitats in the same stream reach or the same stream reaches at different seasons), thus leading to an over-estimation of the statistical power of these analyses due to partial spatial and temporal autocorrelation. Nevertheless, these approaches permitted the estimation of the seasonal stability of the communities and facilitated the interpretation of the sample scale (e.g. FPOM, CPOM) and reach scale environmental preferences (e.g. temperature, sediment load) of the species within the studied streams.

The confirmation of the dependency of chironomid species on key environmental factors, the classification of species according to their preferences, as well as the demonstration of environmental niches (e.g., *D. cinerella/zernyi*-gr. in clear, 'high' conductive waters with low and stable temperatures or *D. steinboecki* in streams with high inorganic sediment loads, low primary production and FPOM content), enabled the creation of a new set of autecological information including environmental preferences and tolerance ranges of chironomid key species in alpine and sub-alpine stream ecosystems in the Central Alps. The most appropriate monitoring taxa can now be selected according to their width of environmental tolerance, relative abundances and frequencies.

In contrast to studies that related invertebrate structures and indicator taxa to altering environmental conditions in glacier-fed streams (Lods-Crozet et al., 2001a; Milner et al., 2001; Jacobsen et al., 2012; Khamis et al., 2014) and single non-glacial tributaries (Füreder et al., 2001), however, we described the typical communities and indicative chironomid species, along with identifying key environmental factors influencing these structures, and confined suitable environmental conditions of the most abundant species for both glacial and non-glacial streams. Nevertheless, we are aware of the presence of a temporal and spatial overlap of these preferences and niche mechanisms based on the organism's functional role. The functions performed by each chironomid taxa such as the different feeding strategies, specific food sources and processing in-stream products (Wallace & Webster, 1996; Füreder et al., 2003; Clitherow et al., 2013) may also lead to niche differentiation.

Glacier melt and anthropogenic influence have become increasingly apparent in alpine stream ecosystems (Füreder, 2012; Jacobsen et al., 2012), so too has the demand for reliable predictions of future alterations in such ecosystems. The findings of this study demonstrated the potential to deduce in-stream environmental conditions by the observation of community structure. The combination of identifying stream-type-specific communities and verifying their fidelity in occurrence in different watersheds, allowed modelled response curves for adequate indicator and monitoring species in alpine and sub-alpine streams. For that purpose, the definition of preferences for local environmental conditions (certain combination of species-specific optima and tolerance for different local environmental variables) was applied for alpine and sub-alpine invertebrates to identify not only the best-fitting indicators but also the species vulnerable to environmental change based on their ecological limitations (Beck, 2013). Autecological data of stream organisms together with hydrological prospects (Milner et al., 2009; Naz et al., 2014; Gan et al., 2015) is essential for forecasting future ecological situations and trends in alpine streams. Furthermore, the often-debated low accuracy of models projecting ecosystem change (Pearson & Dawson, 2003; Midgley et al., 2007; Brook et al., 2009) can definitely be improved using a robust taxonomy and a comprehensive and detailed set of physical and chemical data as presented in this study.

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