WILEY

Real-time warming of alpine streams: (re)defining invertebrates' temperature preferences

Georg H. Niedrist [ORCID] | Leopold Füreder

River and Conservation Research, Department of Ecology, University of Innsbruck, Innsbruck, Austria

Correspondence
Georg H. Niedrist, River and Conservation Research, Department of Ecology, University of Innsbruck, Technikerstr. 25, 6020 Innsbruck, Austria.
Email: georg.niedrist@uibk.ac.at

Abstract

The accelerating climate crisis intensifies environmental changes in high-altitude ecosystems worldwide, with rising air temperature among the main stressors. While past research in alpine streams has primarily focused on how retreating glaciers might affect the ecology of glacier-fed streams on the long run, observations of real-time alterations of water temperature in such pristine environments are rare. Using long-term measurements of water temperature (2010–2017) together with datasets on benthic invertebrate communities from 18 glacial and nonglacial alpine and subalpine streams in the European Alps, we illustrate significant ecological relationships of water temperature regimes and the identity of benthic communities and forecast changes thereof due to considerable warming of stream water. Besides reporting multiannual warming of all observed streams during summer with a mean rate of 2.5 (±0.6)°C decade^{-1}, this work redefines temperature optima and ranges using robust regression modelling and thereby identifies potential winners and losers among the invertebrate species. We conclude that the various invertebrate taxa in alpine stream networks will respond differently to thermal alterations and that the herein modelled temperature ranges of invertebrates is an essential step towards the understanding of future shifts in species distributions and success.

KEYWORDS
alpine streams, autecology, Chironomidae, cold-tolerant, Diamesinae, stream invertebrates, warming, water temperature

1 | INTRODUCTION

Freshwater stream habitats at high altitude are strongly influenced by their water source contribution (via melting snow or ice or via springs), but also by local environmental stressors that influence their properties along the longitudinal progression of the rivers. Among others, the water temperature is the most critical factor influencing biota and structuring benthic communities in mountain streams (e.g. Milner, Brittain, Castella, & Petts, 2001; Rott, Cantonati, Füreder, & Pfister, 2006). As the atmospheric temperature continues to rise globally (IPCC, 2018), not only stream sources will change considerably, for example through rapid glacier-retreat(Zemp et al., 2015), but also water temperature will adjust to local environmental conditions, such as local air temperature (van Vliet, Ludwig, Zwolsman, Weedon, & Kabat, 2011). Stream temperatures are rising globally as a consequence of atmospheric warming and other thermal pollutions (Kaushal et al., 2010; Lepori, Pozzoni, & Pera, 2015; Ormerod, 2009), and also temperature regimes of mountain waters are were observed to closely track local air temperatures (Caissie, 2006; Niedrist, Psenner, & Sommaruga, 2018). Since water temperature is crucial not only for the

distribution of species in alpine streams, but also for the performance and physiological processes of these species (Füreder & Niedrist, 2020; Niedrist & Füreder, 2018; Schütz & Füreder, 2019), it can be expected that the recorded intensification of atmospheric change in recent and coming years and especially during summer (Christidis, Jones, & Stott, 2014; Hock et al., 2019; Meehl & Tebaldi, 2004) leads to considerable alterations of structural and functional assets of alpine stream ecosystems (Füreder & Niedrist, 2020).

The sensitivity of aquatic invertebrates to key-environmental conditions determines their spatial and stream-type specific distribution and relative abundance in different environments (Bêche & Resh, 2007). The definition into classes (e.g. warm- or cold-tolerant species) generally allows to identify resistant groups to environmental change and provides the basis for scenario modelling (e.g. identify community changes due to anticipated warming). The sensitivity of taxa is usually characterized by its optimal level together with the tolerance range, which allows discriminating between taxa with wide or narrow ranges (e.g. eurytherm or stenotherm). Such autecological characteristics are usually collected in and retrieved via specific databases (such as Schmidt-Kloiber & Hering, 2015). Generally, warming of stream water is supposed to alter the invertebrate community composition (Durance & Ormerod, 2007; Hering et al., 2009; Ward, 1992), and the effect of different temperature regimes on the communities in alpine rivers has been confirmed (Füreder, 1999; Lods-Crozet et al., 2001; Niedrist & Füreder, 2016). Increasing water temperatures in mountain streams are found (a) to force species with limited distribution to upstream migration (Giersch et al., 2015; Sheldon, 2012), where environmental conditions fit their eco-physiological requirements, (b) to facilitate the immigration of warmer-water predators into mountain stream habitats with all its ecological consequences (Khamis, Brown, Hannah, & Milner, 2015), or at worst, (c) to potentially transform river sections into inhospitable habitats for cold-water fish (Eaton & Scheller, 1996; Hari, Livingstone, Siber, Burkhardt-Holm, & Guttinger, 2006). Hence, the understanding of temperature optima and limits of key species in alpine streams is of high importance to anticipate consequences of climate change on the integrity of these headwater stream ecosystems.

Here, we analyzed multiyear water temperature records from distinct stream types in the European Alps and linked them to local air temperature patterns. Further, we assessed the benthic invertebrate communities in diverse alpine and subalpine stream habitats and (re) defined the water temperature preferences (optima and limits) of key species in these ecosystems. The objective of this study was thus to improve the understanding of how vulnerable species are to impacts of climate change, which is the essential basis to forecast multispecies shifts during the warming of mountain waters.

By studying the temperature regime and change together with the benthic invertebrate communities in stream types with differing water source contribution at different altitudes in the European Alps, (a) we quantify the changes in local air and water temperatures in recent years to compare them with known rates from mountain regions, (b) we determine the influence of distinct water temperature regimes on the long-term development of different invertebrate communities and (c) we (re)define existing temperature limits of key-invertebrate species in alpine streams, which will help to identify potential winners and losers among the invertebrate species in these Central European headwaters.

2 | METHODS

2.1 | Study area

The Hohe Tauern National Park is in central Austria with a latitudinal extension of 100 km, which corresponds to >11% the length of the alpine arc and where pristine catchments with limited direct anthropogenic influences (such as pollution or hydromorphological alterations) allow conclusions about environmental situations and changes. Within this park, 18 remote stream reaches in 4 glaciated catchments, which represent the most common stream types in this park (kryal, krenal, glacio-rhithral) were monitored since 2009 (Figure 1). These sites differ in water sources, stream length, altitude (between 1,354 and 2,216 m a.s.l.) and form a gradient of environmental harshness (Niedrist, Cantonati, & Füreder, 2018), where the water temperature is considered to be the main stressor for invertebrate occurrence. The study streams' catchment areas (upslope areas) range from 0.31 to 33.62 km^2, and the distances to the source (glacier or spring) are between 28 and 6,448 m (Table 1).

Temperature records of water and air range from 2010 to 2017/2018, while the benthic invertebrate communities were surveyed in the summer of 2015 (July).

2.2 | Air and water temperature

Air temperature data were obtained from weather stations distributed throughout the study region, located at low (950 and 1,005 m a.s.l.) and high (3,105 m a.s.l.) elevations and at distances between 6.5 and 23 km from studied streams (monthly mean air temperature from the HISTALP database [Auer et al., 2007]), and close to 4 of the 18 stream sites in catchment B at 1690 m a.s.l. (daily mean air temperature from the *Tiroler Hydrographischer Dienst*, 'AIR X' in Figure 1). While HISTALP datasets ranged from 2000 until 2019, the latter dataset started in 2012.

Water temperature was monitored continuously with digital loggers (Tidbit; Onset, Bourne, Massachusetts) throughout the years with intervals of 30 min. We averaged these values to daily mean water temperatures, and extracted daily summer water temperature data for each year (all daily mean temperatures between July and August from 2010 until 2017).

2.3 | Benthic invertebrate communities

At each stream in July 2015, we took six samples of aquatic invertebrates with a Surber sampler (0.09 m^2, 100-μm mesh size) by sampling
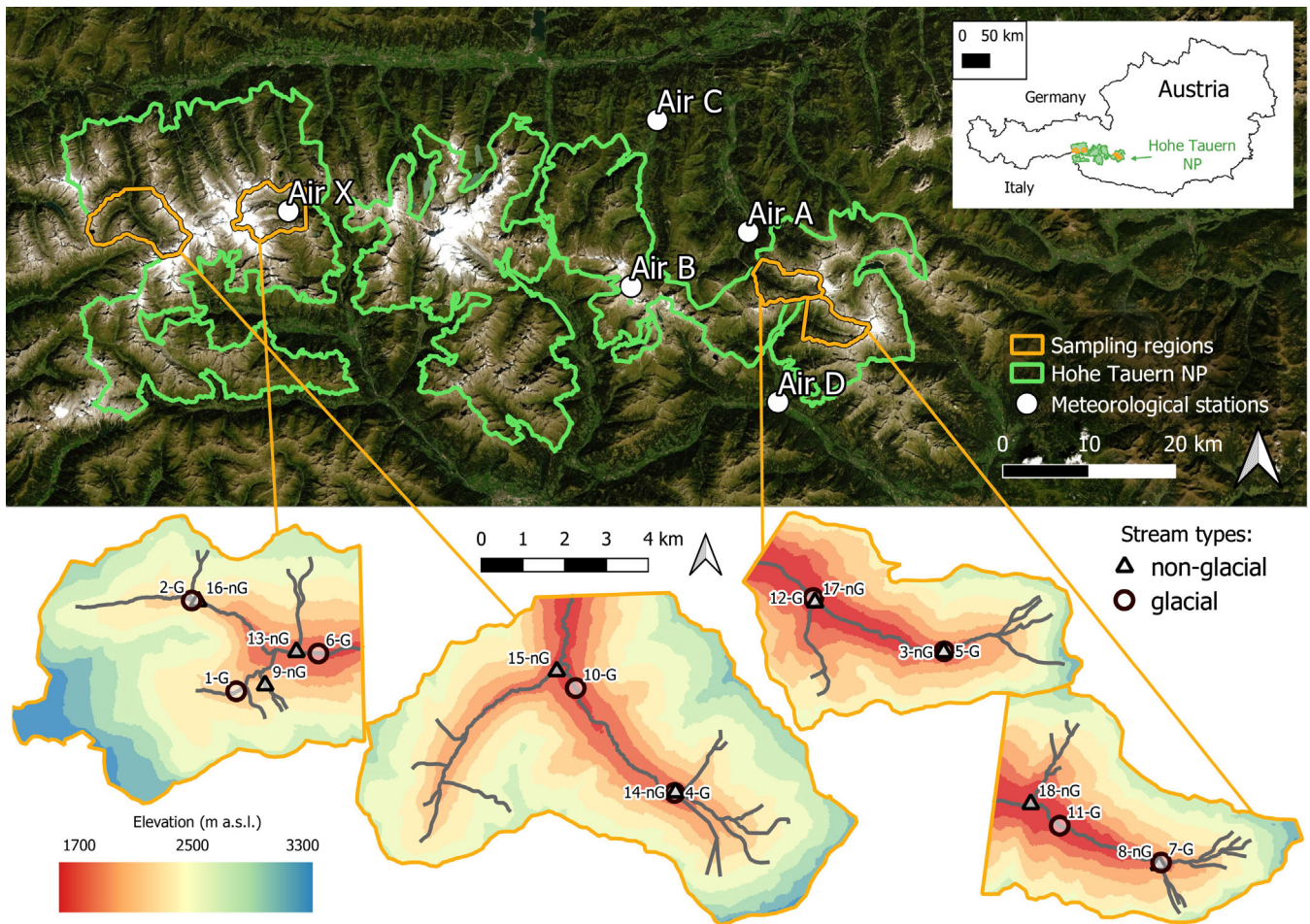
FIGURE 1 Map of the Austrian Alps and the sampled Glacial (G) and nonglacial (nG) stream sections in glaciated and nonglaciated catchments within the Hohe Tauern national park der

the same microhabitats mesolithal (cobbles, n = 2), macrolithal (coarse cobbles, n = 2) and megalithal (boulders, n = 2), which represent the main substrates and microhabitats in all streams (=108 individual samples). The invertebrates (mostly insect larvae, see Table S1) were preserved in 75% ethanol and later identified to the highest possible resolution using available keys (Bauernfeind & Humpesch, 2001; Rossaro & Lencioni, 2015; Schmid, 1993; Zwick, 2004).

2.4 | Data analysis

We considered air temperature data from July and August as summer air temperature. This was extracted as daily mean or monthly means from the years 2010 until 2018. From the year-round records of water temperature, we extracted the data from July and August as summer water temperature (WT_{Summer}). Differences in the overall mean and change (slope) of WT_{Summer} during 2010 and 2017 between stream types (glacial vs. nonglacial) were examined using estimation statistics rather than null hypothesis tests (Halsey, 2019; Ho, Tumkaya, Aryal, Choi, & Claridge-Chang, 2019), presenting all data points, group means and standard deviations and effect sizes with

95% confidence intervals computed from 5,000 bootstrapped samples (nonparametric bootstrap resampling). The corresponding Cumming estimation plots, which illustrate differences as effect sizes were produced using the "*dabestr*" package in R v.3.5.1. (R Core Team, 2018).

We applied nonmetric multidimensional scaling (NMS) of invertebrate communities at each stream site to visualize the qualitative differences between sites and stream types. For this, all six samples per stream were pooled. Variations in community composition as a function of glacier cover in the catchment (%) and stream water temperatures were tested by applying a two-way PERMANOVA (using *Adonis* function from "*vegan*" package in R, Oksanen et al., 2017) with 999 permutations on the Bray-Curtis similarities of averaged total invertebrate communities. The weighing of the variable importance was done based on the partial R^2 and the p-value. The significant environmental vectors (p < .05) were fitted onto the ordination space using *envfit* function from the "*vegan*" package (Oksanen et al., 2017). The relationship between WT_{Summer} and taxa richness in the streams was tested and described using a simple linear model together with an *F*-test and each stream reach as one data point, while deviations per site were also illustrated. We used weighted averaging regression models for optima and tolerance quantifications (using the functions of the "*analogue*" package,

TABLE 1 Names and abbreviations (used in Figure 1) of study streams with the description and summary of decisive environmental characteristics: dominant water source (water source), distance of the sampling site to the source, catchment area (upslope area from sampled reach), altitude, glacier cover in that catchment (as % of catchment area, GCC) and averaged daily mean water temperature during summer (WT$_{Summer}$) in the year 2015

# study stream	Water source	Map labels	Distance to source (m)	Altitude (m a.s.l.)	Catchment area (km^2)	GCC (%)	WT$_{Summer}$	Latitude	Longitude
1	Glacial	G-1	543	2,120	11.25	78.3	1.2	47.1141	12.4183
2	Glacial	G-2	1931	2,216	9.65	48.4	3.2	47.1334	12.4033
3	Nonglacial	nonG-3	28	1,775	0.54	0.0	4.5	47.0558	13.2070
4	Glacial	G-4	2,638	1,799	17.13	38.5	5.9	47.0975	12.2262
5	Glacial	G-5	2,675	1,773	8.79	10.7	6.2	47.0559	13.2071
6	Glacial	G-6	5,613	1,695	33.62	42.6	6.2	47.1229	12.4438
7	Glacial	G-7	2,473	1853	5.54	14.5	6.7	47.0107	13.2780
8	Nonglacial	nonG-8	1,141	1886	0.32	0.0	7.1	47.0102	13.2773
9	Nonglacial	nonG-9	190	2,132	0.45	0.0	7.3	47.1156	12.4273
10	Glacial	G-10	6,448	1,673	33.51	19.9	7.6	47.1193	12.1937
11	Glacial	G-11	5,215	1,530	14.8	5.5	7.7	47.0183	13.2453
12	Glacial	G-12	6,357	1,386	21.94	3.8	7.7	47.0669	13.1649
13	Nonglacial	nonG-13	2,105	1,711	1.04	0.0	7.9	47.1231	12.4368
14	Nonglacial	nonG-14	2,116	1,797	3.79	12.8	8.3	47.0976	12.2264
15	Nonglacial	nonG-15	5,305	1,682	17.13	2.4	8.5	47.1228	12.1875
16	Nonglacial	nonG-16	705	2,212	0.31	15.4	8.5	47.1333	12.4053
17	Nonglacial	nonG-17	2,247	1,400	4.46	0.0	8.6	47.0660	13.1655
18	Nonglacial	nonG-18	2,344	1,399	3.57	0.0	10.6	47.0229	13.2359

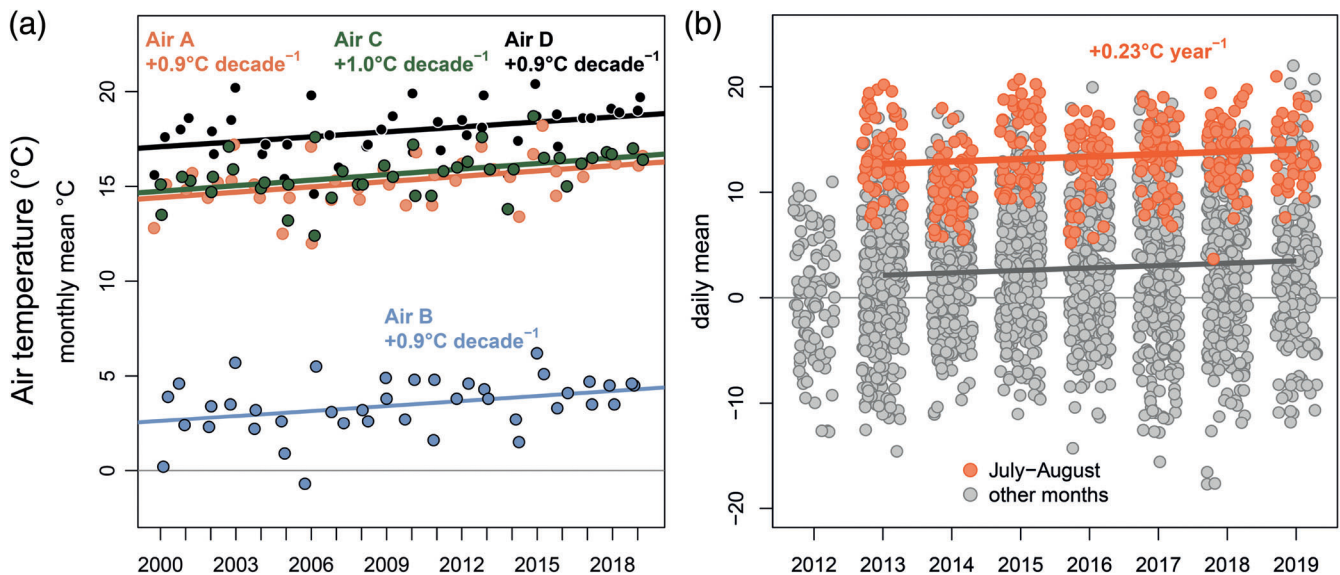*Note:* Latitude and longitude are based on the WGS 1984 reference system.

FIGURE 2 Monthly (a) and daily (b) air temperature patterns from weather stations in the study region (see Figure 1). The data sets range from 2000 to 2018 (a) and from 2013 to 2019 (b), panel A shows summer (July–August) temperature only

Simpson & Oksanen, 2019), based on the taxa matrix and the water temperature data per site. Such weighted averaged optima indicate the optimal temperature of a taxa, where it is expected to have its highest abundance, while tolerance indicates the ranges of the species occurrence (i.e. the ecological amplitude with respect to temperature, ter Braak & Looman, 1986). Modelled preferences are displayed via univariate forest plots from package *"metafor"* (Viechtbauer, 2010) for taxa that were found in more than 3% of all samples.

3 | RESULTS

3.1 | Air and water temperatures

Monthly mean air temperatures during summer (July–August) increased significantly in the low elevated sites from 2000 to 2019 with mean slopes between 0.9 and 1.0°C per decade ($p < .05$), at low and high elevated sites (Figure 2a). While low elevated sites had a higher temperature level (>10°C) than the high elevated site (Air B, Figure 2a), this latter site warmed at a similar rate (+0.9 ± 0.4°C, mean slope ± standard error) compared to the other sites. The daily averages of air temperature during summer increased even more with an average gradient of 0.23°C per year (Air X, Figure 2b).

Between 2010 and 2017, summer water temperature increased in all streams with rates between 0.19 and 0.32°C year^{-1} (80% confidence interval). The WT_{Summer} was significantly higher in nonglacial streams (mean difference in WT_{Summer} of 2.02°C, 95% CI = 0.3–4.4°C, Figure 3c) and significantly related to altitude ($F_{2, 15} = 7.0$, $R^2 = 0.48$, $p < .05$, altitude was significantly correlated with distance from the source). The identified slopes (WT_{Summer} ~ years), however, were not significantly different between stream types (glacial vs. nonglacial, Figure 3d) or related to altitude, or distance from the source ($p > .05$). Overall, from 2010 until 2017, the study streams warmed with a mean yearly rate of 0.25°C year^{-1} (95% CI 0.15–0.35°C, Figure 3a,b).

### 3.2 | Benthic invertebrates and water temperature regimes

The NMS ordination of the invertebrate community compositions converged on a two-dimensional solution (stress = 0.15) and the environmental variables were well and significantly fitted in this ordination space ($R^2 = 0.69$ for WT_{summer} and $R^2 = 0.52$ for *glaciation*, Figure 4). The communities from glacial and nonglacial streams overlapped partially in the ordination space, but the difference in community composition was significant when comparing both groups of streams (PERMANOVA, $p < .003$). The community composition was related to the prevailing summer water temperature and degree of glaciated catchment (PERMANOVA, $p = .007$). Differences in water temperature, however, explained more of the variation in community composition ($F_{1, 15} = 2.8$, $R^2 = 0.14$, $p = .004$) than the different levels of glaciation in the catchment area ($F_{1, 15} = 2.3$, $R^2 = 0.11$, $p = .009$).

Selected species of all key invertebrate families and orders were decisive for the distribution of the different community composition and are referred to as intrinsic taxa. While most chironomid species contributed to the separation of cold stream communities with high glacial cover in the catchment (e.g. *D. steinboecki*, *D. cinerella-zernyi*-gr. and *Diamesa latitarsis*-A,*D. latitarsis*-B [i.e. two morphotypes within the *D. latitarsis*-gr.]), warmer streams were indicated by increased occurrences of Ephemeroptera species typical of alpine streams (e.g. *Baetis alpinus* or *Rhitrogena loyolaea*) or Trichoptera (e.g. *Drusus discolor*). Among the Plecoptera taxa that contributed to the discrimination of sites, the identified taxa (*Leuctra* sp., *Protonemura auberti*, *P. brevistyla*, *P. nimborum* and *P. risi*) were mostly decisive for habitats with intermediate glacial influence and water temperatures.

Taxa richness in the streams was significantly related to WT_{Summer} ($F_{1, 16} = 5.14$, $p = .038$; Figure 5). While the density of invertebrates was not significantly related to WT_{Summer}, the relative abundance of chironomids significantly decreased with increasing water temperature ($F_{1, 16} = 10.37$, $p = .005$, $R^2 = .39$).

FIGURE 3 Summer water temperature (July and August) development in studied glacial (a) and nonglacial streams (b) from 2010 to 2017 with the overall level of summer water temperature (WT_{Summer}, C) and change over time (d) in both stream types. The individual slopes (a and b) are identified with the abbreviations of study sites presented in Figure 1. Cumming estimation plots illustrate the differences in the overall mean temperature (c) and of the overall slopes over time (d) between both stream types (i.e. glacial vs. nonglacial streams). The horizontal lines limit the effect sizes of stream type, the vertical bars limit the 95% confidence intervals of bootstrapped distributions of these (see Methods for details)
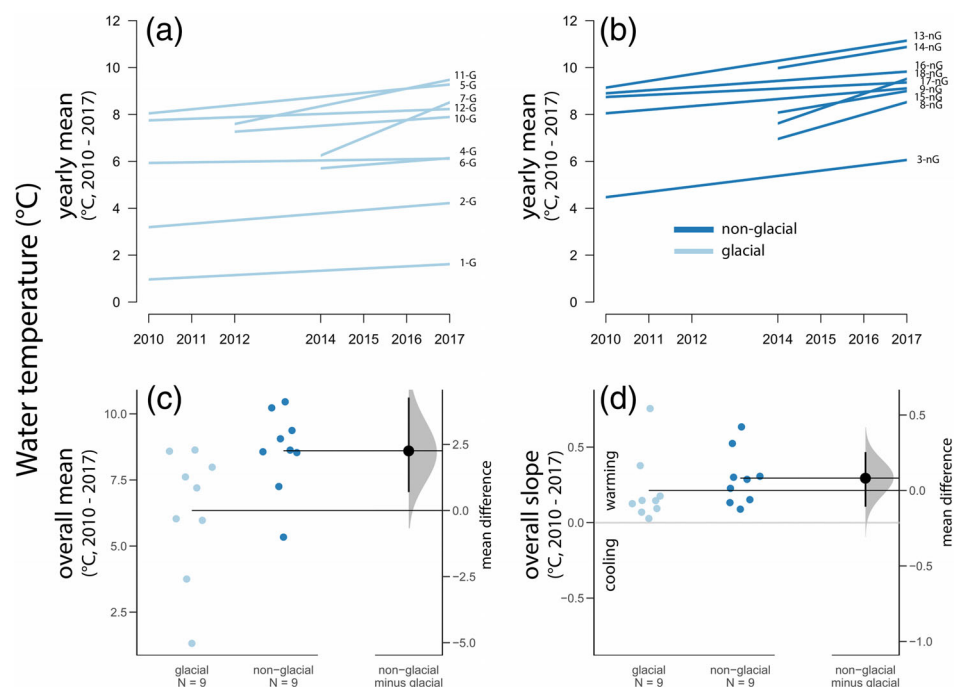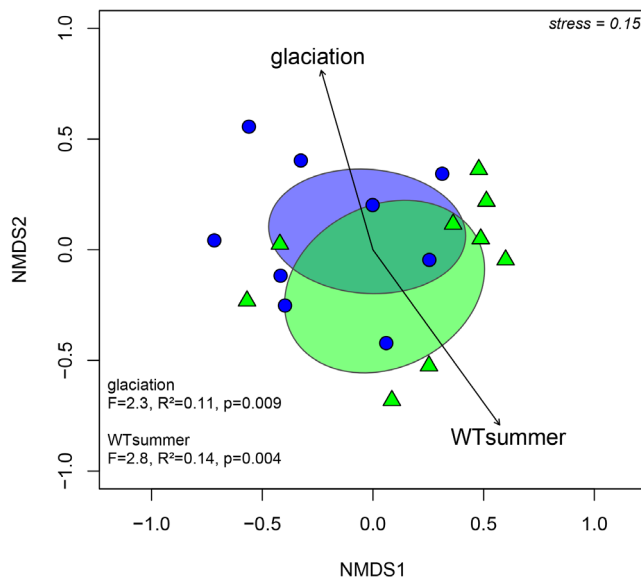
FIGURE 4 Nonmetric multidimensional scaling (NMS) plot showing differences in macroinvertebrate communities from the 18 study stream habitats together with fitted variables (function *envfit*, package *vegan*, Oksanen et al., 2017) and their explanatory power (R^2 and *p*-value from Adonis-test). The strongly significant factors ($p < .01$) are correlated with the ordination samples ($R^2 > 0.52$). Communities from glacial (circles) and nonglacial (triangles) stream types are grouped by ellipse hulls
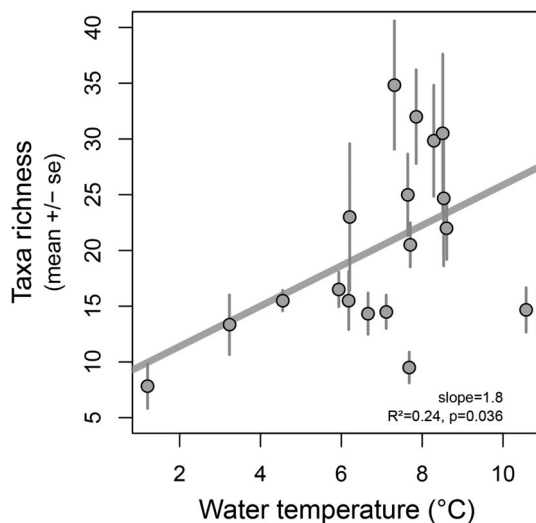

FIGURE 5 Relationship between mean invertebrate taxa richness and the summer water temperature (°C, July–August), *n* = 6. The bold grey line indicates the significant regression slope (+1.8 taxa/+1°C), horizontal grey lines quantify the standard error of the mean

3.3 | Thermal optima and tolerances of alpine stream invertebrates

The mean summer water temperature data per site used for optima and tolerance modelling ranged between 1.2 and 10.6°C (Figure 6c). Thus, the modelled optima did not exceed these minimum and

maximum values. *Diamesa* spp. (Diptera: Chironomidae) were among the taxa with lowest temperature optima ranging between 3.5 and 6.0°C (Figure 6a). Although the tolerance limits of many taxa overlap, no other taxa within the Chironomidae family, but also not of the Ephemeroptera, Plecoptera and Trichoptera order (Figure 6b), had a lower temperature optimum than these Diamesinae taxa.

While the chironomids showed a clear pattern of taxa with cold and warmer temperature optima (e.g. Diamesinae vs. Orthocladiinae), this was not evident in EPT orders (Figure 6b). Within the chironomid family, however, the identified amplitudes were mostly broad (especially for species groups) and only few chironomid taxa (all at species level) showed narrower tolerance ranges (e.g. *Thienemanniella clavicornis, Tvetenia calvescens, Paratrichocladius skirwithensis, Paratrichocladius nivalis*). In contrast to that, selected chironomid species such as *Orthocladius frigidus, O. rivicola, O. luteipes*, or *Pseudodiamesa branickii* exhibited broad ecological ranges for water temperature (Figure 6a).

4 | DISCUSSION

Stream water temperature varies considerably within alpine stream networks, also depending on the proximity to the water source (Brown, Hannah, & Milner, 2006). Compared to lowlands, water temperature is lower in high altitudes (Milner & Petts, 1994), where it is stable and very low during winter (Niedrist & Füreder, n.d.; Johnson, 1971) but can reach higher levels and variabilities during summer (e.g. Füreder, Schütz, Wallinger, & Burger, 2001). The highest daily mean water temperature in the studied streams was 16.4°C in a glacier-fed stream (site 11-G in Figure 1) at 1530 m a.s.l. and at 5 km distance from the source, while most streams had maximum daily temperatures around 12.0°C (95% CI 10.2–13.9°C). During the summer season, however, the mean daily temperatures – despite the great variance found between individual streams – differed considerably between distinct stream types (glacial vs. nonglacial), with glacier-fed streams being on average colder by 2°C (95% CI 0.3–4.4°C) due to the water source contribution by melting glacier-ice.

To show the potential effects of global and local rising air temperature on the temperature of alpine stream water, the slopes of air and stream temperature have been computed using linear regression over the study period data series from 2010 to 2017 (2010 to 2019 for air temperature), but using daily temperature data from summer months (July and August) only. This analysis revealed that summer water temperature has risen in all study streams and considerably at an average rate of 0.25°C per year (95% CI 0.15–0.35°C), but also that the warming rate does not differ between glacial and nonglacial streams (streams with and without glacial meltwater contribution). Although glacier-fed rivers have a unique seasonal temperature regime (Niedrist & Füreder, n.d.; Milner et al., 2001), the studied glacial streams warmed at similar rates as nonglacial streams, which finding confirms the recent report about the missing – but long suspected – summer cooling effect in glacial streams (Williamson, Entwistle, & Collins, 2019).

FIGURE 6 Summer water temperature optima (points) and tolerances (lines, 95% CI) of common invertebrate taxa belonging to the macroinvertebrate groups (a) Chironomidae (Diptera) and (b) Ephemeroptera, Plecoptera and Trichoptera. The columns on the right indicate the weighted mean and the limits of the 95%-confidence interval. The temperature lines (panel c) display the range between minimum and maximum daily mean water temperatures in all sampled streams during summers (2010–2017). cin_zer, cinerella/zernyi-group; COP, Cricotopus/Orthocladius/Paratrichocladius group; J, juvenile larvae; Gr. = group
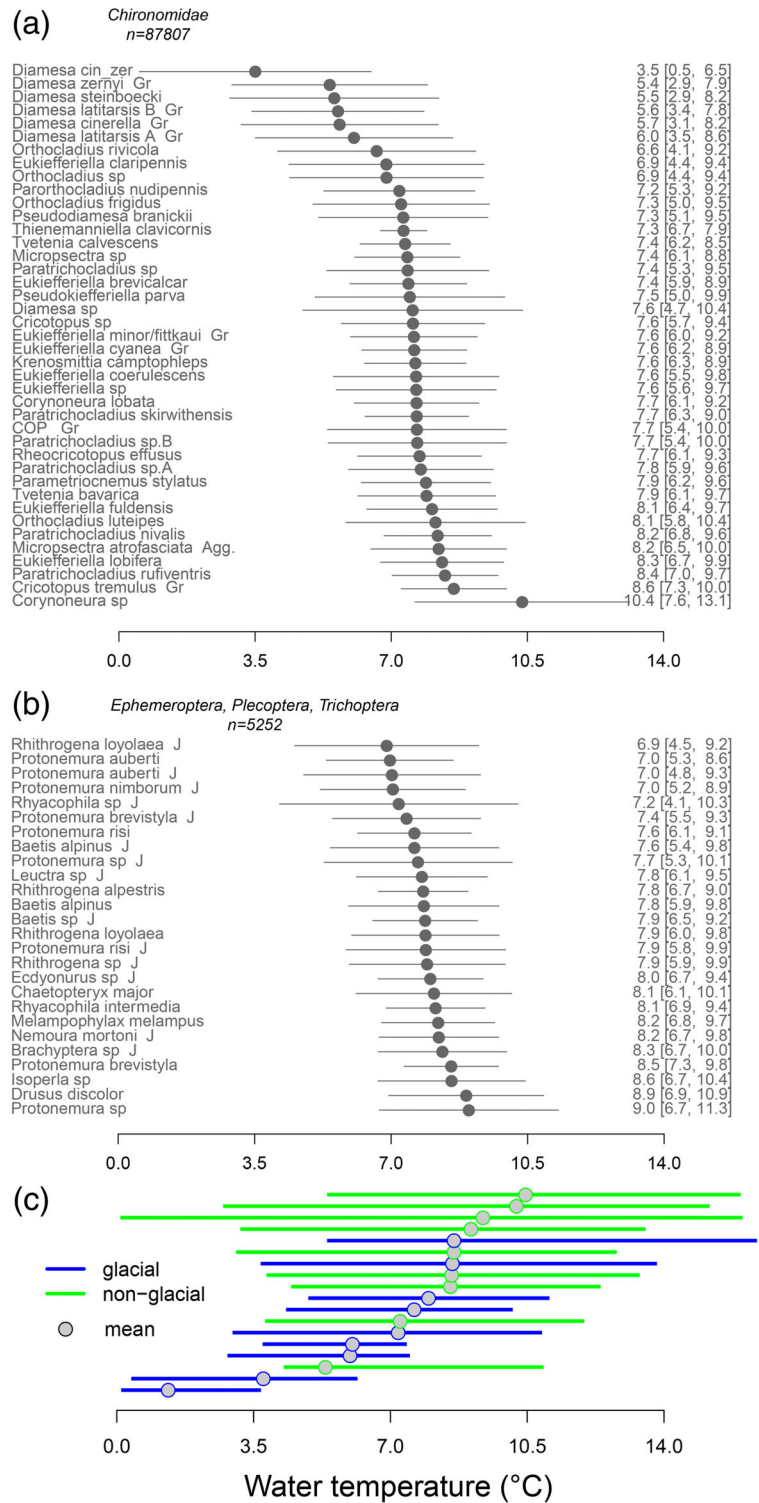
The averaged warming rate of studied streams during the last years (0.25°C per year, 80% CI 0.19–0.32°C) is considerably higher than that of local air temperature and the recently observed and modelled warming of Swiss streams in alpine settings (Michel, Brauchli, Lehning, Schaefli, & Huwald, 2020). This long-term survey over 40 years revealed an average slope of +0.33°C per decade for Swiss streams with diverse catchment topography, elevation and size. Although focusing on summer temperature only, our results imply that

the warming rate has risen considerably in the last years, which was also found in other streams (e.g. accelerated warming of northern German streams in recent years in comparison to previous decades, Arora, Tockner, & Venohr, 2016).

In addition to the observed fast warming of water temperatures, local air temperature during same summer months increased faster (+0.9–1.0°C per decade) than the global average (+0.2 ± 0.1°C per decade, Trenberth et al., 2007). Comparable to water temperature

patterns, the warming of air during summer accelerated considerably in recent decades and is known to be higher than the global average in many regions of the world (IPCC, 2018). It can thus be confirmed and concluded that near-surface air temperature in the European Alps are experiencing greater warming compared to other regions and the global average. Although this was previously covered by previous works (Gobiet et al., 2014; Hock et al., 2019), our study revealed that this fast warming of air temperature is also conveyed to other mountain ecosystems like mountain streams. This study thus demonstrates that the generally increasing warming rates expected for the near future around the world (IPCC, 2014) can already be observed in mountain regions (also found in Hock et al., 2019) also in aquatic environments, and thereby confirms these areas as suitable testing grounds for examining ecological consequences due to rapid warming of stream ecosystems, as once claimed by Brittain and Milner (2001).

4.1 | Temperature mediates invertebrate community structures

Differences in water temperature levels associated with stream type and the distance from the source drove differences in taxa richness and the community composition of invertebrates in the studied alpine and sub-alpine streams. Many studies have identified water temperature as a critical factor in the formation of distinct invertebrate communities in rivers, including glacial streams (Milner et al., 2001; Niedrist & Füreder, 2016; Scrine, Jochum, Ólafsson, & O'Gorman, 2017). While most of these studies have shown these relationships on family or subfamily level, our results support and extend this finding on a higher taxonomic level and consider streams with and without glacial influence. In contrast to the often-used proxy for environmental harshness or indicator of glacial influence, that is, the ratio of glacier cover to total catchment area (Brown, Hannah, & Milner, 2007; Brown & Milner, 2012; Fell, Carrivick, Kelly, Füreder, & Brown, 2018; Füreder & Niedrist, 2020; Rott et al., 2006), this study disentangled that the properties of biotic communities were more related to summer water temperatures than to catchment glaciation. We conclude that the temperature of stream water influences the stream biota more directly and depends on many local and small-scale conditions, such as slope, length, width, current velocity, and exposition of stream reaches (Williamson et al., 2019), which can be derived from a land-use proxy only to a limited extend. Thus, and although water temperature and glaciated catchment area correlated within the studied stream reaches, this work demonstrated that differences in immediate habitat characteristics, such as the temperature of the water itself, are more crucial for the invertebrate communities.

In addition to shifting invertebrate community composition through the exchange of certain taxa, taxa richness is expected to increase with rising summer water temperatures. As expected by previous works and underpinned by this study, warm-tolerant taxa will immigrate, while there will only be a small decline in the number of cold-tolerant taxa. The expected immigrants mainly belong to Ephemeroptera, Trichoptera and Plecoptera, based on their higher

optima and tolerances of water temperature. In general, our study confirms the common regularity, that warmer alpine streams are colonized by communities with higher taxa richness, and estimates that warming of 1°C in such cold habitats leads to an overall increasing richness by approximately two taxa. In contrast to the pure temperature preferences, however, studies using habitat modelling and vulnerability assessments showed that warming in the alpine region could be particularly devastating for representatives of Plecoptera due to the totality of species characteristics (Besacier Monbertrand et al., 2019; de Figueroa et al., 2010). Due to the current rapid change of habitat conditions (i.e. water temperature), however, current distribution patterns and space-for-time substitutions might not be able to fully grasp the expected change. For the final assessment of potential winners and losers due to climate change in alpine rivers, we therefore recommend considering not only the here presented temperature preferences for alpine stream invertebrates, but also other species traits (Schmidt-Kloiber & Hering, 2015), the modelling of their estimated niche extension (Besacier Monbertrand et al., 2019; Domisch, Jähnig, & Haase, 2011), species-specific potentials for dispersal (Schmidt-Kloiber & Hering, 2015), physiological capabilities (Hotaling, Shah, & Tronstad, 2020; Niedrist & Füreder, 2018), or reactions to other changes (e.g. such as glacier retreat, Cauvy-Frauniè & Dangles, 2019).

Different temperature regimes in alpine rivers contribute significantly to the occurrence and dominance of individual taxa groups, based on the optima and tolerances for certain temperature ranges. Cold mountain streams have been previously reported to be dominated by the chironomid subfamily Diamesinae (Füreder, 1999; Füreder et al., 2001; Lods-Crozetet al., 2001; Niedrist et al., 2017; Niedrist & Füreder, 2016), with occurrences of additional groups in warmer reaches (Milner et al., 2001). Our results support and extend this long-known pattern by defining modelled optimal temperature range and delineated tolerance ranges for a variety of invertebrate taxa. In particular, exclusively six Diamesinae taxa were found to have their temperature optima in cold temperature ranges (3.5–6.0 ° C), which autecological property corresponds to their general dominance in cold mountain streams and the highest frequency and abundance in the streams studied here. Further, the defined temperature optima of Diamesinae taxa coincide with the identified temperature preferences of the same genus in previous assessments in the Italian Alps (Marziali & Rossaro, 2013). Thus, Diamesinae (and especially the genus *Diamesa*) could be classified as taxa preferring cold temperatures. However, due to the design of this work as a field study, our results do not allow a distinction between the classification as cold-tolerant(i.e. surviving also in cold environments) and psychrophilic (i.e. preferring low temperatures). Knowing that some of the Diamesinae have evolved special strategies to survive harsh conditions (Füreder & Niedrist, 2020), including behavioural and physiological capabilities to tolerate and survive freezing (Lencioni, Jousson, Guella, & Bernabò, 2015) and growing under harsh conditions (Niedrist & Füreder, 2018), we assume that it is their cold-tolerance rather than their preference for cold temperature that gives them an edge over other invertebrates in harsh glacier-fed rivers. Regarding previously identified temperature preferences of invertebrate groups,

we can conclude that the identified optima of Diamesa, of Diamesinae, of other chironomid subfamilies and of other invertebrate orders in European alpine streams roughly correspond to the conceptualized progression of invertebrates in glacier-fed streams across Europe (Milner et al., 2001). This consensus confirms the importance of water temperature as a major mediator of invertebrate communities in alpine and subalpine streams and the analogous relationships between invertebrate occurrence and the abiotic conditions in these aquatic habitats.

Our results extend the general understanding of aquatic invertebrate autecology by complementing the conceptual model of Milner et al. (2001) with a higher taxonomic resolution and by improving the preference modelling in considering multiple study streams in a broader geographic distribution across the Central Alps than used for previous niche assessments (Niedrist & Füreder, 2016). In modelling requirement-based species preferences in relation to summer water temperature, which environmental condition is demonstrably related to the identity of the invertebrate communities and is expected to drastically increase in the coming years (Hock et al., 2019), this study does not only identify potential winners and losers within the communities but also provides highly needed information for improving available autecological datasets (e.g. Schmidt-Kloiber & Hering, 2015) of invertebrates in alpine and subalpine stream ecosystems in the Alps. Such data sets will be essential for forecasting ecological situations and trends in mountain streams.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author (River and Conservation Research group, University of Innsbruck) upon reasonable request.

ORCID

Georg H. Niedrist https://orcid.org/0000-0002-2852-4661

REFERENCES

Arora, R., Tockner, K., & Venohr, M. (2016). Changing river temperatures in northern Germany: Trends and drivers of change. *Hydrological Processes*, 30(17), 3084–3096. https://doi.org/10.1002/hyp.10849

Auer, I., Böhm, R., Jurkovic, A., Lipa, W., Orlik, A., Potzmann, R., ... Nieplova, E. (2007). HISTALP—Historical instrumental climatological surface time series of the greater alpine region. *International Journal of Climatology*, 27(1), 17–46. https://doi.org/10.1002/joc.1377

Bauernfeind, E., & Humpesch, U. H. (2001). *Die Eintagsfliegen Zentraleuropas (Insecta: Ephemeroptera): Bestimmung und Ökologie*. Wien: Verlag des Naturhistorischen Museums.

Bêche, L. A., & Resh, V. H. (2007). Biological traits of benthic macroinvertebrates in California mediterranean-climate streams: Long-term annual variability and trait diversity patterns. *Fundamental and Applied Limnology*, 169(1), 1–23. https://doi.org/10.1127/1863-9135/2007/0169-0001

Besacier Monbertrand, A.-L., Timoner, P., Rahman, K., Burlando, P., Fatichi, S., Gonseth, Y., ... Lehmann, A. (2019). Assessing the vulnerability of aquatic macroinvertebrates to climate warming in a mountainous watershed: Supplementing presence-only data with species traits. *Water*, 11(4), 636. https://doi.org/10.3390/w11040636

Brittain, J. E., & Milner, A. M. (2001). Ecology of glacier-fed rivers: Current status and concepts. *Freshwater Biology*, 46(12), 1571–1578. https://doi.org/10.1046/j.1365-2427.2001.00845.x

Brown, L. E., Hannah, D. M., & Milner, A. M. (2006). Hydroclimatological influences on water column and streambed thermal dynamics in an alpine river system. *Journal of Hydrology*, 325(1-4), 1–20. https://doi.org/10.1016/j.jhydrol.2005.09.025

Brown, L. E., Hannah, D. M., & Milner, A. M. (2007). Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology*, 13(5), 958–966. https://doi.org/10.1111/j.1365-2486.2007.01341.x

Brown, L. E., & Milner, A. M. (2012). Rapid loss of glacial ice reveals stream community assembly processes. *Global Change Biology*, 18(7), 2195–2204. https://doi.org/10.1111/j.1365-2486.2012.02675.x

Caissie, D. (2006). The thermal regime of rivers: A review. *Freshwater Biology*, 51(8), 1389–1406. https://doi.org/10.1111/j.1365-2427.2006.01597.x

Cauvy-Fraunié, S., & Dangles, O. (2019). A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology & Evolution*, 3(12), 1675–1685. https://doi.org/10.1038/s41559-019-1042-8

Christidis, N., Jones, G. S., & Stott, P. A. (2014). Dramatically increasing chance of extremely hot summers since the 2003 European heatwave. *Nature Climate Change*, 5(1), 46–50. https://doi.org/10.1038/nclimate2468

Core Team, R. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

de Figueroa, J. M. T., López-Rodríguez, M. J., Lorenz, A., Graf, W., Schmidt-Kloiber, A., & Hering, D. (2010). Vulnerable taxa of European Plecoptera (Insecta) in the context of climate change. *Biodiversity and Conservation*, 19(5), 1269–1277. https://doi.org/10.1007/s10531-009-9753-9

Domisch, S., Jähnig, S. C., & Haase, P. (2011). Climate-change winners and losers: Stream macroinvertebrates of a submontane region in Central Europe. *Freshwater Biology*, 56(10), 2009–2020. https://doi.org/10.1111/j.1365-2427.2011.02631.x

Durance, I., & Ormerod, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, 13(5), 942–957. https://doi.org/10.1111/j.1365-2486.2007.01340.x

Eaton, J. G., & Scheller, R. M. (1996). Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography*, 41(5), 1109–1115. https://doi.org/10.4319/lo.1996.41.5.1109

Fell Sarah C., Carrivick Jonathan L., Kelly Martyn G., Füreder Leopold, Brown Lee E. (2018). Declining glacier cover threatens the biodiversity of alpine river diatom assemblages. *Global Change Biology*, 24, (12), 5828–5840. http://dx.doi.org/10.1111/gcb.14454.

Füreder, L. (1999). High alpine streams: Cold habitats for insect larvae. In R. Margesin & F. Schinner(Eds.), *Cold-adapted organisms* (pp. 181–196). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-662-06285-2_10

Füreder, L., & Niedrist, G. H. (2020). Glacial stream ecology: Structural and functional assets. *Water*, 12(2), 376. https://doi.org/10.3390/w12020376

Füreder, L., Schütz, C., Wallinger, M., & Burger, R. (2001). Physico-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. *Freshwater Biology*, 46(12), 1673–1690. https://doi.org/10.1046/j.1365-2427.2001.00862.x

Giersch, J. J., Jordan, S., Luikart, G., Jones, L. A., Hauer, F. R., & Muhlfeld, C. C. (2015). Climate-induced range contraction of a rare alpine aquatic invertebrate. *Freshwater Science*, 34(1), 53–65. https://doi.org/10.1086/679490

Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., & Stoffel, M. (2014). 21st century climate change in the European Alps—A review. *Science of the Total Environment*, 493, 1138–1151.

Halsey, L. G. (2019). The reign of the *p* -value is over: What alternative analyses could we employ to fill the power vacuum? *Biology Letters*, 15(5), 20190174. https://doi.org/10.1098/rsbl.2019.0174

Hari, R. E., Livingstone, D. M., Siber, R., Burkhardt-Holm, P., & Guttinger, H. (2006). Consequences of climatic change for water temperature and brown trout populations in alpine rivers and streams. *Global Change Biology*, 12(1), 10–26. https://doi.org/10.1111/j.1365-2486.2005.001051.x

Hering, D., Schmidt-Kloiber, A., Murphy, J., Lücke, S., Zamora-Muñoz, C., López-Rodríguez, M. J., ... Graf, W. (2009). Potential impact of climate change on aquatic insects: A sensitivity analysis for European caddisflies (Trichoptera) based on distribution patterns and ecological preferences. *Aquatic Sciences*, 71(1), 3–14. https://doi.org/10.1007/s00027-009-9159-5

Ho, J., Tumkaya, T., Aryal, S., Choi, H., & Claridge-Chang, A. (2019). Moving beyond P values: Data analysis with estimation graphics. *Nature Methods*, 16(7), 565–566. https://doi.org/10.1038/s41592-019-0470-3

Hock, R., Rasul, G., Adler, C., Cáceres, B., Gruber, S., Hirabayashi, Y., ... Steltzer, H. (2019). High Mountain areas. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, ... N. M. Weyer(Eds.), *IPCC special report on the ocean and cryosphere in a changing climate* (p. 72). Geneva, Switzerland: IPCC.

Hotaling, S., Shah, A. A., & Tronstad, L. M. (2020). Mountain stoneflies may tolerate warming streams: Evidence from organismal physiology and gene expression. BioRxiv, 2019.12.16.878926. https://doi.org/10.1101/2019.12.16.878926

IPCC (2014). In T. F. Stocker, D. Qin, G. K. Plattner, M. Tignor, S. K. Allen, J. Boschung, et al. (Eds.), *Climate Change 2013—The Physical Science Basis*. Cambridge, United Kingdom and New York, NY: Cambridge University Press. https://doi.org/10.1017/CBO9781107415324

IPCC (2018). Summary for Policymakers. In V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P. R. Shukla, et al. (Eds.), *Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change* (p. 32). Geneva, Switzerland: IPCC. Retrieved from). https://report.ipcc.ch/sr15/pdf/sr15_spm_final.pdf

Johnson, F. A. (1971). Stream temperatures in an alpine area. *Journal of Hydrology*, 14(3-4), 322–336. https://doi.org/10.1016/0022-1694(71)90042-4

Kaushal, S. S., Likens, G. E., Jaworski, N. A., Pace, M. L., Sides, A. M., Seekell, D., ... Wingate, R. L. (2010). Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment*, 8(9), 461–466. https://doi.org/10.1890/090037

Khamis, K., Brown, L. E., Hannah, D. M., & Milner, A. M. (2015). Experimental evidence that predator range expansion modifies alpine stream community structure. *Freshwater Science*, 34(1), 66–80. https://doi.org/10.1086/679484

Lencioni, V., Jousson, O., Guella, G., & Bernabò, P. (2015). Cold adaptive potential of chironomids overwintering in a glacial stream. *Physiological Entomology*, 40(1), 43–53. https://doi.org/10.1111/phen.12084

Lepori, F., Pozzoni, M., & Pera, S. (2015). What drives warming trends in streams? A case study from the alpine foothills. *River Research and Applications*, 31(6), 663–675. https://doi.org/10.1002/rra.2763

Lods-Crozet, B., Castella, E., Cambin, D., Ilg, C., Knispel, S., & Mayor-Simeant, H. (2001). Macroinvertebrate community structure in relation to environmental variables in a Swiss glacial stream. *Freshwater Biology*, 46(12), 1641–1661. https://doi.org/10.1046/j.1365-2427.2001.00850.x

Lods-Crozet, B., Lencioni, V., Olafsson, J. S., Snook, D. L., Velle, G., Brittain, J. E., ... Rossaro, B. (2001). Chironomid (Diptera: Chironomidae) communities in six European glacier-fed streams. *Freshwater Biology*, 46(12), 1791–1809. https://doi.org/10.1046/j.1365-2427.2001.00859.x

Marziali, L., & Rossaro, B. (2013). Response of chironomid species (Diptera, Chironomidae) to water temperature: Effects on species distribution in specific habitats. *Journal of Entomological and Acarological Research*, 45(2), 14. https://doi.org/10.4081/jear.2013.e14

Meehl, G. A., & Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st century. *Science*, 305(5686), 994–997. https://doi.org/10.1126/science.1098704

Michel, A., Brauchli, T., Lehning, M., Schaefli, B., & Huwald, H. (2020). Stream temperature and discharge evolution in Switzerland over the last 50 years: Annual and seasonal behaviour. *Hydrology and Earth System Sciences*, 24(1), 115–142. https://doi.org/10.5194/hess-24-115-2020

Milner, A. M., Brittain, J. E., Castella, E., & Petts, G. E. (2001). Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: A synthesis. *Freshwater Biology*, 46(12), 1833–1847. https://doi.org/10.1046/j.1365-2427.2001.00861.x

Milner, A. M., & Petts, G. E. (1994). Glacial rivers: Physical habitat and ecology. *Freshwater Biology*, 32(2), 295–307. https://doi.org/10.1111/j.1365-2427.1994.tb01127.x

Niedrist, G. H., Alber, R., Rauch, H., Vorhauser, S., Kiebacher, T., Scotti, A., & Bottarin, R. (2017). Aquatic invertebrates along the progression of glacial and non-glacial streams in Matsch Valley (South Tyrol, Italy). *Gredleriana*, 17, 129–140.

Niedrist, G. H., Cantonati, M., & Füreder, L. (2018). Environmental harshness mediates the quality of periphyton and chironomid body mass in alpine streams. *Freshwater Science*, 37(3), 519–533. https://doi.org/10.1086/699480

Niedrist, G. H., & Füreder, L. (2016). Towards a definition of environmental niches in alpine streams by employing chironomid species preferences. *Hydrobiologia*, 781(1), 143–160. https://doi.org/10.1007/s10750-016-2836-1

Niedrist, G. H., & Füreder, L. (2018). When the going gets tough, the tough get going: The enigma of survival strategies in harsh glacial stream environments. *Freshwater Biology*, 63(10), 1260–1272. https://doi.org/10.1111/fwb.13131

Niedrist, G. H., & Füreder, L. (n.d.). Real-time warming of high-altitude streams and potential consequences within invertebrate communities.

Niedrist, G. H., Psenner, R., & Sommaruga, R. (2018). Climate warming increases vertical and seasonal water temperature differences and inter-annual variability in a mountain lake. *Climatic Change*, 151(3-4), 473–490. https://doi.org/10.1007/s10584-018-2328-6

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., ... Oksanen, M. J. (2017). Vegan: Community Ecology Package. p. 292. Retrieved from https://cran.r-project.org/package=vegan

Ormerod, S. J. (2009). Climate change, river conservation and the adaptation challenge. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19(6), 609–613. https://doi.org/10.1002/aqc.1062

Rossaro, B., & Lencioni, V. (2015). A key to larvae of species belonging to the genus Diamesa from Alps and Apennines (Italy). *European Journal of Environmental Sciences*, 5(1), 62–79. https://doi.org/10.14712/23361964.2015.79

Rott, E., Cantonati, M., Füreder, L., & Pfister, P. (2006). Benthic algae in high altitude streams of the Alps - a neglected component of the aquatic biota. *Hydrobiologia*, *562*(1), 195–216. https://doi.org/10.1007/s10750-005-1811-z

Schmid, P. E. (1993). A key to the larval Chironomidae and their instars from Austrian Danube region streams and rivers with particular reference to a numerical taxonomic approach. Part I. Diamesinae, Prodiamesinae and Orthocladiinae. *Wasser Und Abwasser Suppl*, *3*, 1–514.

Schmidt-Kloiber, A., & Hering, D. (2015). An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, *53*, 271–282. https://doi.org/10.1016/j.ecolind.2015.02.007

Schütz, S. A., & Füreder, L. (2019). Egg development and hatching success in alpine chironomids. *Freshwater Biology*, *64*(4), 685–696. https://doi.org/10.1111/fwb.13254

Scrine, J., Jochum, M., Ólafsson, J. S., & O'Gorman, E. J. (2017). Interactive effects of temperature and habitat complexity on freshwater communities. *Ecology and Evolution*, *7*(22), 9333–9346. https://doi.org/10.1002/ece3.3412

Sheldon, A. L. (2012). Possible climate-induced shift of stoneflies in a southern Appalachian catchment. *Freshwater Science*, *31*(3), 765–774. https://doi.org/10.1899/11-135.1

Simpson, G. L., & Oksanen, J. (2019). Analogue: Analogue matching and modern analogue technique transfer function models (R package version 0.17.3). Retrieved from https://cran.r-project.org/package=analogue

ter Braak, C. J. F., & Looman, C. W. N. (1986). Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio*, *65*(1), 3–11. https://doi.org/10.1007/BF00032121

Trenberth, K. E., Jones, P. D., Ambenje, P., Bojariu, R., Easterling, D., Tank, A. K., … Zhai, P. (2007). Observations: Surface and atmospheric climatic change. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, et al. (Eds.), *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change*. Cambridge, England and New York, NY: Cambridge University Press.

van Vliet, M. T. H., Ludwig, F., Zwolsman, J. J. G., Weedon, G. P., & Kabat, P. (2011). Global river temperatures and sensitivity to atmospheric warming and changes in river flow. *Water Resources Research*, *47*(2), W02544. https://doi.org/10.1029/2010WR009198

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Ward, J. V. (1992). *Aquatic insect ecology*. New York, NY: John Wiley & Sons.

Williamson, R. J., Entwistle, N. S., & Collins, D. N. (2019). Meltwater temperature in streams draining alpine glaciers. *Science of the Total Environment*, *658*, 777–786. https://doi.org/10.1016/j.scitotenv.2018.12.215

Zemp, M., Frey, H., Gärtner-Roer, I., Nussbaumer, S. U., Hoelzle, M., Paul, F., … Vincent, C. (2015). Historically unprecedented global glacier decline in the early 21st century. *Journal of Glaciology*, *61*(228), 745–762. https://doi.org/10.3189/2015JoG15J017

Zwick, P. (2004). Key to the west palaearctic genera of stoneflies (Plecoptera) in the larval stage. *Limnologica*, *34*(4), 315–348. https://doi.org/10.1016/S0075-9511(04)80004-5

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.