Moderate warming over the past 25 years has already reorganized stream invertebrate communities

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HIGHLIGHTS

- We studied stream invertebrate communities over 25 years in central Europe.
- Temperature increased by 0.5 °C. Total abundance and richness increased.
- Cold-adapted species declined while warmer-adapted species increased.
- Community temperature index increased at a similar pace as physical temperature.
- Results raise conservation concerns in view of the stronger future warming.

GRAPHICAL ABSTRACT
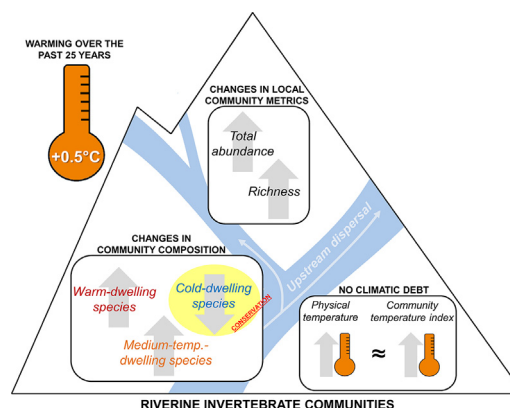
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ABSTRACT

Climate warming often results in species range shifts, biodiversity loss and accumulated climatic debts of biota (i.e. slower changes in biota than in temperature). Here, we analyzed the changes in community composition and temperature signature of stream invertebrate communities over 25 years (1990–2014), based on a large set of samples (n = 3782) over large elevation, latitudinal and longitudinal gradients in central Europe. Although warming was moderate (average 0.5 °C), we found a strong reorganization of stream invertebrate communities. Total abundance (+35.9%) and richness (+39.2%) significantly increased. The share of abundance (TA) and taxonomic richness (TR) of warm-dwelling taxa (TA: +73.2%; TR: +60.2%) and medium-temperature-dwelling taxa (TA: +0.4%; TR: +5.8%) increased too, while cold-dwelling taxa declined (TA: −61.5%; TR: −47.3%). The community temperature index, representing the temperature signature of stream invertebrate communities, increased at a similar pace to physical temperature, indicating a thermophilization of the communities and, for the first time, no climatic debt. The strongest changes occurred along the altitudinal gradient, suggesting that stream

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Community composition
Community temperature index
Thermophilization

invertebrates use the spatial configuration of river networks to track their temperature niche uphill. Yet, this may soon come to an end due to the summit trap effect. Our results indicate an ongoing process of replacement of cold-adapted species by thermophilic species at only 0.5 °C warming, which is particularly alarming in the light of the more drastic climate warming projected for coming decades.

1. Introduction

Global warming has accelerated over the past three decades (IPCC, 2013), and it has already triggered community changes in several taxonomic groups (Parmesan, 2006; Pecl et al., 2017) and species range shifts towards the poles and higher elevations (Comte and Grenouillet, 2013; Lenoir and Svenning, 2015; Parmesan, 2006). Locally, species range shifts appear as a "thermophilization" of the community (De Frenne et al., 2013). This consists of a decline or local extinctions of cold-dwelling species, for which the conditions have become unfavorable, and increased abundance or local immigration of warm-dwelling and eurytherm species, which are better adapted to the new conditions (Lenoir and Svenning, 2015).

Increasing water temperatures over recent decades have been reported for several rivers worldwide (Arora et al., 2016; Isaak et al., 2012). However, range shifts of freshwater species have been rarely studied compared to terrestrial species (Heino et al., 2009), with studies being limited to fish (Comte and Grenouillet, 2013) and two invertebrate orders: Odonata, and Heteroptera (Hickling et al., 2006). Warming-induced range shifts for several stream invertebrate species have only been inferred from modelled projections (Domisch et al., 2011) or observations at restricted geographical areas (Daufresne et al., 2004). Empirical evidence for a thermophilization of stream invertebrate communities at large geographical scales is still lacking. Elevational range shifts may be especially important for stream invertebrates because streams and their resident communities follow a natural elevation gradient from source to mouth and stream organisms have higher dispersal capacities within compared to between river networks (Hughes, 2007). Thus, benthic invertebrates might use streams as a "highway" to higher elevations (i.e. lower water temperatures) to keep up with warming. This may be particularly important for mountainous areas where strong elevation, and therefore climatic, gradients occur at short distances. However, despite the clear importance of the stream network in structuring stream communities (Tonkin et al., 2018), the role of elevation compared to the other spatial dimensions has been largely overlooked to date.

We analyzed changes in stream benthic invertebrate communities over a period of 25 years (1990–2014) in central Europe (Fig. 1), where we registered a warming of 0.5 °C (0.020 ± 0.001 °C yr^{-1}, mean $\pm$ S.E.; Table S1). We used a large dataset encompassing 3782 samples. We investigated how total abundance, taxonomic richness and community composition (i.e. proportion of taxa that are cold-, medium-, and warm-tolerant) changed over the 25-year period. We hypothesized a stronger loss of cold-dwelling taxa and a weaker gain of warm-dwelling taxa, leading to a decline in total abundance and richness, which would parallel the decline that has been already documented for several invertebrate groups (Conrad et al., 2006; Goulson et al., 2008; Hallmann et al., 2017; Thomas, 2016). To gather insights on the rate and spatial patterns of community changes, we computed two community temperature indices (CTI; Devictor et al., 2008) for each sample: CTI_{ab} (abundance-based CTI), as weighted average ($\pm$ SD) of the taxon-specific temperature preferences of each taxon in the sample, weighted by its abundance; CTI_{pa} (presence/absence-based CTI), as simple average ($\pm$SD) of the taxon-specific temperature preferences. We investigated how the CTI values changed along the temporal and spatial gradients. We expected CTI_{ab} to be more sensitive to increasing temperatures than CTI_{pa} because it reflects not only species turnover

but also changes in species abundance. Since the configuration of river networks could facilitate the upstream dispersal of benthic invertebrates, we expected stronger changes along the elevation gradient and a rate of increase in CTI in the same magnitude as the rate of increase in temperature, indicating a thermophilization of the communities and no climatic debt of biota.

2. Materials and methods

2.1. Climatic data

We analyzed the temporal and spatial climatic patterns as a baseline for our biotic analyses. For that we gathered historical data series of air temperature measurements from the following databases: Deutsche Wetterdienst (https://www.dwd.de) for Germany, Agrimeteo.lu (http://www.am.rlp.de) for Luxemburg, Czech Hydrometeorological Institute (http://portal.chmi.cz) for Czech Republic and HISTALP (Historical instrumental climatological surface time series of the greater alpine region, http://www.zamg.ac.at) for Austria. We extracted the monthly mean temperature data from the weather stations that satisfied the following requirements: (1) operating between the years 1990 and 2014, which is the time span covered by biological sampling, and (2) located within the latitudinal, longitudinal and altitudinal window of the biological data. In total, 239 weather stations were kept for the analysis, spanning the whole temporal, latitudinal, longitudinal and altitudinal gradients of the study area. For each station and year we computed the average annual mean temperature (239 stations × 25 years). We used air temperature instead of water temperature data because of their better temporal and spatial resolution in the study area, as only very few and spatially biased time series of water temperature are available for the study area. Despite local-scale discrepancies, air temperature is generally strongly correlated to stream temperature (Arora et al., 2016), and thus can be used as proxy for water temperature.
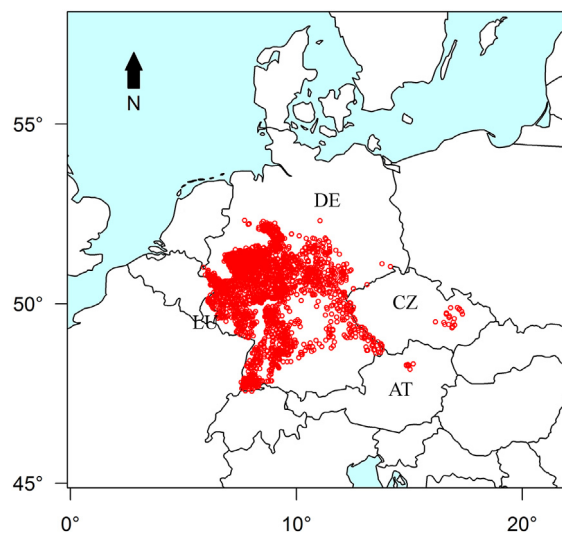

Fig. 1. Study area. The sampling sites are marked as red circles. DE: Germany, LU: Luxemburg, CZ: Czech Republic, and AT: Austria. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Biotic data

A collection of 12,375 stream benthic invertebrate samples was obtained from standardized field surveys in Austria, Czech Republic, Germany and Luxembourg for the period 1990–2014 (Fig. 1). Two sampling methods (hereby "old" and "new" methods) were used in those survey programs. Before year 2000 (i.e. "old" method), all habitats occurring at a site were sampled for approximately three minutes (Braukmann, 2000) and the resulting material was pooled into a bulk sample. From year 2000 (i.e. "new" method), 20 subsamples corresponding to a total of 1.25 m^2 of stream bed were collected at each site and pooled into a bulk sample, with subsamples distributed among the major habitats proportionally to their coverage within the site (Haase et al., 2004). To account for the change in sampling methodology, we included the sampling method (old/new) as a covariate in all statistical analyses. We also re-ran all analysis separately for the two time periods ("old": 1990–1999, "new": 2000–2014); results are shown in Table S2 and discussed in the Discussion section.

Our initial dataset comprised a large variety of samples and stream sites, covering different stream types, altitudes, geomorphological settings and anthropogenic stressors. Therefore, we applied six filter criteria to filter out low quality data and to homogenize the dataset. This ensured that the final dataset would include comparable stream sites throughout the whole study period. First, all taxa were identified to the level proposed by the EU Water Framework Directive "Operational Taxalist" (mostly to species and genus levels, subfamily or family levels for Chironomidae and Oligochaeta) to ensure comparable taxonomic resolution (Haase et al., 2006). Second, we removed taxa that were only sampled once during the whole study period to avoid the confounding effects of taxa that were not established in the study area. Third, only samples from small low mountain streams in Central European highlands were selected to eliminate potential effects of different stream types. Fourth, samples were only considered if they were collected from March to May to avoid the confounding effects of seasonality (Sundermann et al., 2008). Fifth, samples with species richness in the lower 10th percentile of all of the samples were excluded from the analysis (old method <12 taxa per sample; new method <21 taxa per sample). Such samples are not suitable for examining the effects of global warming due to the low species richness, potentially reflecting heavy human disturbance. Sixth, we ensured that a minimum number of ten sites had to be available for each sampling year. After the application of the six criteria, 3782 samples remained. The selected sites were located at elevations between 37 and 1148 m a.s.l., latitude between 47.56 ° and 52.91 ° and longitude between 6.09 ° and 17.36 °. The selected samples comprised 5.6 million individuals belonging to 588 taxa. The vast majority of sites were sampled once, while a small fraction (14%) of sites were sampled two to four times, at time intervals between one and four years.

2.3. Taxon-specific temperature preferences

We inferred the temperature preferences of the invertebrate taxa using the stream-zonation approach, which reflects the abiotic and biotic changes along the longitudinal stream gradient from source to mouth (Illies and Botosaneanu, 1963). According to this approach, streams and rivers are divided into seven zones (eucrenal, hypocrenal, epirhithral, metarhithral, hyporhithral, epipotamal and metapotamal) that are defined based on abiotic features, such as flow velocity, mean annual temperature amplitude, and mean and maximum summer water temperatures (Illies and Botosaneanu, 1963). The sequence of zones from upstream to downstream reflects the longitudinal succession of fish and invertebrate distributions (Illies and Botosaneanu, 1963; Moog, 2002). For central European systems, mean temperature values are associated to each stream zone (eucrenal: 2 °C, hypocrenal: 5 °C, epirhithral: 9 °C, metarhithral: 13 °C, hyporhithral: 18 °C, epipotamal: 20 °C and metapotamal: 22 °C, Illies and Botosaneanu,

1963; Moog and Wimmer, 1992; Moog, 2002). The occurrence probability for most European invertebrate taxa in each of the stream zones is summarized into a species-specific stream zonation index, which uses a 10-point assignment system of the distribution of each species across the different stream zones (Schmidt-Kloiber and Hering, 2015). The species zonation index was available for 60% of all taxa in our samples, representing 72% of the total abundance. For each taxon, we computed the taxon-specific temperature preference as the average (mean ± SD) of the temperature associated to the stream zones occupied by that taxon, weighted by the affinity of the taxon for each stream zone.

2.4. Community temperature index

Based on the taxon-specific temperature preferences, we computed two community temperature indices (CTI$_{ab}$ and CTI$_{pa}$) for each sample, representing the temperature signature of the invertebrate communities (Devictor et al., 2008). We computed CTI$_{ab}$ as the weighted average (±SD) of the taxon-specific temperature preferences of each taxon in the sample, weighted by its abundance. We computed CTI$_{pa}$ as the simple average (±SD) of the taxon-specific temperature preferences of each taxon in the sample (presence/absence data).

2.5. Validation of the zonation approach

To validate the zonation approach we analyzed real water temperature preferences from a subset of the studied taxa. Temperature preference data based on water temperature measurements (Halle et al., 2016) were available for 43% of the sampled taxa, covering 43% of total abundances. For this subset, we computed two analogous CTI indexes (CTI$_{T-ab}$ and CTI$_{T-pa}$) using the same approach described above, but based on real water temperatures. We then compared the CTI indices obtained using the zonation approach (CTI$_{ab}$ and CTI$_{pa}$) and the actual water temperature approach (CTI$_{T-ab}$ and CTI$_{T-pa}$) using Pearson's correlations. As the values were strongly correlated (CTI$_{T-ab}$ and CTI$_{ab}$: Pearson's product-moment correlation $r = 0.76$, $t = 72.93$, $df = 3781$, $p < 0.001$; CTI$_{T-pa}$ and CTI$_{pa}$: $r = 0.83$, $t = 91.58$, $df = 3781$, $p < 0.001$), we conclude that the zonation approach can reliably be used to infer temperature preferences in the study area. As actual temperature preferences were available for fewer species (i.e. 43% of total abundances) than zonation preferences (i.e. 72% of total abundances), we used the latter approach for our further analyses to fully exploit the available community dataset.

2.6. Changes in total abundance, taxonomic richness and community composition

We tested whether total abundances and taxonomic richness changed during the study period by running generalized linear mixed models (GLMM) using the function "glmer" in the R package "lme4", with Poisson distribution to fit count data (Bates et al., 2015). The models included total abundances or taxonomic richness as the dependent variable and temporal and spatial variables (year, elevation, latitude, and longitude) as fixed factors. Moreover, we included two additional fixed factors to account for their possible confounding effect: (log-transformed) catchment area and sampling method (old or new). Two random factors were included in the models: site, to account for repeated measurements, and observation (i.e. vector from 1 to the total number of observations), to account for over-dispersion (Elston et al., 2001). All predictors had variance inflation factors lower than four, indicating that they were not collinear (function "vif" in the R package "car"; Fox and Sanford, 2011).

To test for changes in community composition, we allocated all taxa to three thermal condition groups. We arranged the taxa in ascending order according to their taxon-specific temperature preferences and used the 0.33 and 0.66 quantiles (i.e. 12.02 °C and 18.74 °C) to classify the taxa into cold-, medium- and warm-dwelling taxa. For each sample,

we computed the proportion of abundances and richness of the taxa belonging to each thermal condition group and analyzed how those proportions changed through time. As the dependent variables were proportions, we used binomial models for proportional data (i.e. with weights for the total abundance or total number of taxa; Zuur et al., 2009). We included the same set of fixed and random factors as for the models described above. This analysis was run with the function "glmer" in the R package "lme4" (Bates et al., 2015).

2.7. Temporal and spatial patterns of CTI and mean air temperatures

We ran linear mixed effect models (LME) to estimate the temporal and spatial patterns of CTI_{ab}, CTI_{pa}, and annual mean air temperatures. For that, we used the function "lme" in the R package "nlme" (Pinheiro et al., 2017). The models included year, latitude, longitude and elevation as fixed effects. Sampling site (for biotic data) and weather station (for climatic data) were included as random factors to account for repeated measures. Moreover, to account for possible confounding factors, we included (log-transformed) catchment area and sampling method (old or new) as additional fixed factors in the models for CTI_{ab} and CTI_{pa}. In contrast to previous CTI studies (Devictor et al., 2008), we also included CTI_{ab} and CTI_{pa} variances as weighting factors (higher weight to values with lower variance) to account for the uncertainty associated to the computation of CTI_{ab} and CTI_{pa}.

3. Results

Contrary to our expectations, total abundance and total taxonomic richness have increased on average by 1.4% and 1.6% per year (GLMM: $p < 0.001$; Table S3), corresponding to a 35.9% and 39.2% increase over the 25-year period, respectively. In parallel to such increases, we recorded a substantial reorganization of stream invertebrate communities, consisting of increases in the share of warm-dwelling taxa (relative abundance: +73.2%; relative number of taxa: +60.2%; GLMM: $p < 0.001$) and of medium-temperature-dwelling taxa (relative abundance: +0.4%, $p = 0.645$; relative number of taxa: +5.8%; $p < 0.001$), and significant decreases in cold-dwelling taxa (relative abundance: −61.5%; number of taxa: −47.3%; $p < 0.001$) during the study period (Fig. 2; Table S4).

The reported shift towards warm-dwelling species is an indication that stream benthic invertebrate communities are changing in response to climate warming. To gather insights on the rate and spatial patterns of such community changes, we analyzed the temperature signature of the communities. Our results indicate that the thermophilization of stream invertebrate communities is occurring at a similar pace as the temperature increase (Fig. 3b–c; Fig. S1 and Table S1). Indeed, CTI values computed on species abundances (CTI_{ab}) increased by $0.022 \pm 0.007\,°C\,yr^{-1}$ (linear mixed effect models, LME: $p < 0.001$), corresponding to a total increase of 0.54 °C over the 25-year period, and CTI values computed on presence/absence data (CTI_{pa}) increased by 0.015 ± 0.005 °C yr^{-1} (LME: $p < 0.001$), corresponding to a total increase of 0.28 °C over the 25-year period. The rates of change (slopes) of physical temperature, CTI_{ab} and CTI_{pa} did not differ statistically, as shown by the lack of overlap of the 95% confidence intervals (Fig. 3d). Our analysis also showed that the strongest spatial changes in temperature and CTI values occurred along the elevation gradient (Fig. 4; Table S1).

4. Discussion

Our results showed that the warming of 0.5 °C over the past 25 years was associated to profound changes in stream invertebrate communities in central Europe. Contrary to our expectations, total abundance (+35.9%) and richness (+39.2%) significantly increased over the 25-year period. Such increases in abundance and taxonomic richness seem to contradict studies showing ongoing trends of declining biodiversity (Dirzo et al., 2014). In this respect, the 76% decline in airborne insect biomass over 27 years in German nature reserves (Hallmann et al., 2017) is particularly notable, as well as the severe decline in the distributions of several butterfly (Thomas, 2016), moth (Conrad et al., 2006) and bumble bee species (Goulson et al., 2008) across Europe. Rather, our results parallel the recorded increases in invertebrate richness in English, Welsh and French streams, which was associated with improvements in water quality (Van Looy et al., 2016; Vaughan and Ormerod, 2012), and the increase in plant species in mountain areas, which resulted from a faster invasion of species from lower elevations than the local extinction of resident species (Steinbauer et al., 2018). Although we cannot exclude a change in water quality in the study area, our analysis of the composition of stream invertebrate communities (i.e. decline
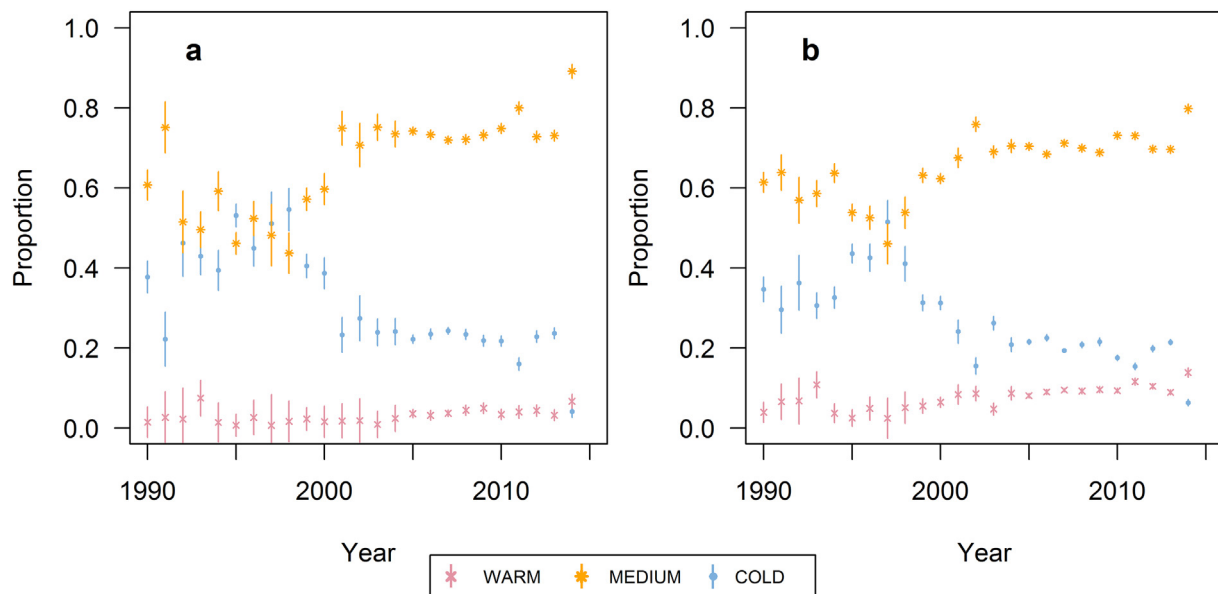

Fig. 2. Changes in invertebrate community composition during the study period (mean ± S.E.). a: Abundance, b: Taxonomic richness. Different colors represent different components of the invertebrate communities, pink: warm-dwelling taxa, orange: medium-temperature-dwelling taxa and blue: cold-dwelling taxa. All trends (increasing for medium-temperature and warm-dwelling taxa, decreasing for cold-dwelling taxa) are statistically significant (GLMM: $p < 0.001$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
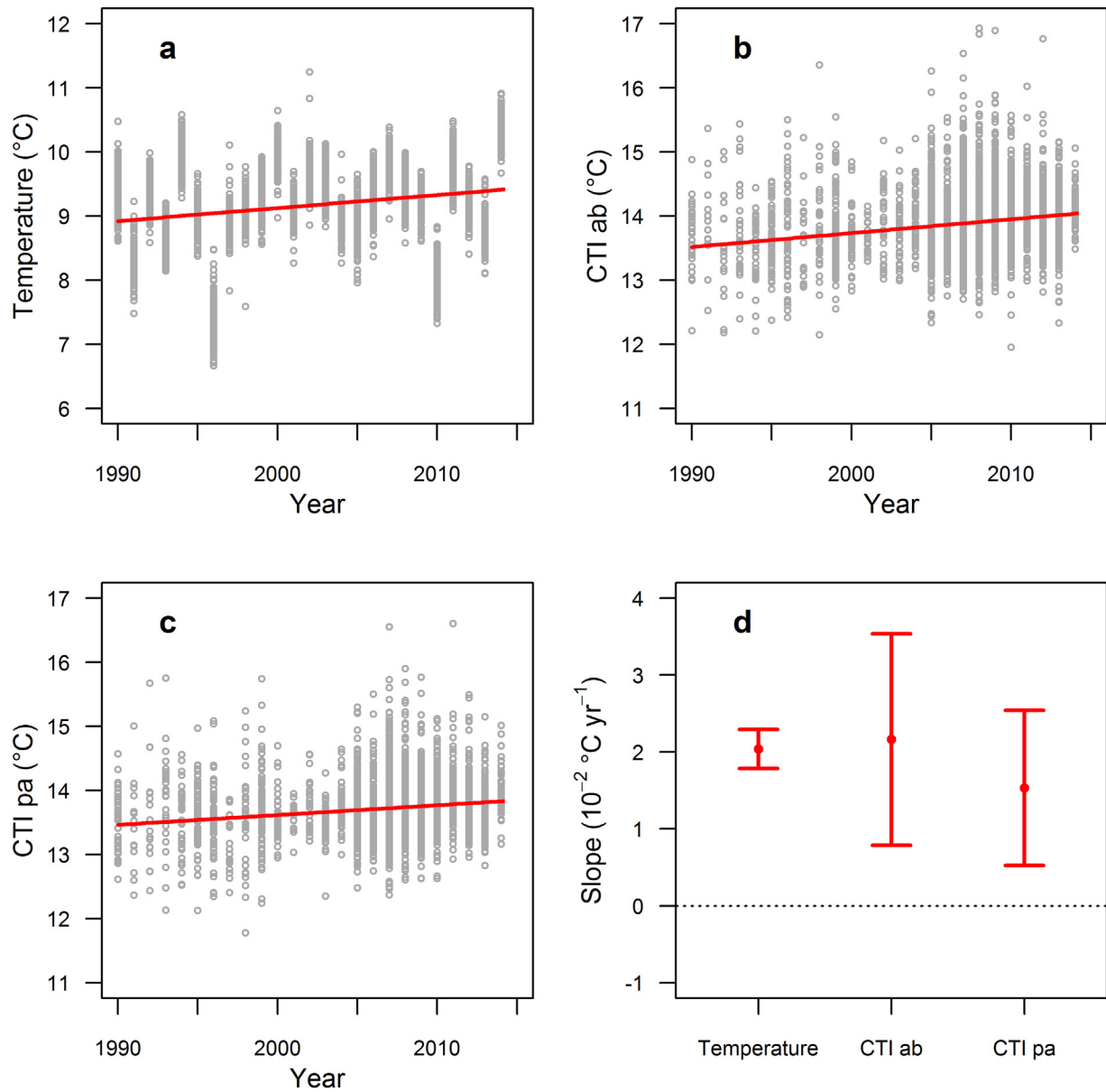
Fig. 3. Changes in mean annual temperature, CTI_{ab} and CTI_{pa} during the study period. a–c: conditional plots obtained by holding all other covariates constant to their median values in the linear mixed models; d: slopes ($\pm$95% CI) of the relationships between the response variables (mean annual temperature, CTI_{ab} and CTI_{pa}) and time, resulting from the linear mixed models. All slopes were significantly different from zero ($p < 0.05$), but they were not different from each other.

of cold-dwelling species and increase in species adapted to higher temperatures) suggests a similar underlying process as the one found by Steinbauer et al. (2018). As shifts in relative abundances are regarded as early warning signals of upcoming local extinctions (Steinbauer et al., 2018), the current state of increasing taxonomic richness has to be considered as a transient condition that could eventually result in the local extinction of cold-dwelling species and a consequent dominance of generalist species adapted to higher temperatures (Steinbauer et al., 2018). The increase in abundance and richness of benthic invertebrate communities in response to recent climate warming might be related to our focus on small low mountain streams (average catchment size 34.4 $\pm$ 43.8 km^2), which are characterized by low water temperatures, low proportions of warm-adapted species and low productivity. Slight increases in temperature in these streams may increase primary productivity and provide additional food resources and niche space for invaders, enabling a higher abundance and richness of consumer species (Woodward et al., 2010).

According to our hypotheses, our results showed that the thermophilization of stream invertebrate communities is occurring at a similar pace as the temperature increase. This is in contrast with what has been observed for several other biotic groups, for which a climatic debt was documented, such as birds (facing a warming of 0.068 °C yr^{-1}; Devictor et al., 2008), fishes (warming: 0.024 °C yr^{-1}; Comte and Grenouillet, 2013) and plants (warming: 0.025 °C yr^{-1}; Bertrand et al., 2011). The onset and magnitude of the climatic debt depends on several inflating factors, including species tolerances, evolutionary adaptation, phenotypic plasticity, and mitigating factors, such as dispersal abilities, landscape structure and topography (Bertrand et al., 2016). We did not analyze potential mechanisms of within-species adaptations or resistance to warming. However, the lack of a climatic debt and the changes in community composition that we recorded indicate that these mechanisms have limited impacts on stream invertebrate populations and do not prevent the loss of cold-adapted species (Parmesan, 2006). Nevertheless, our results suggest that the lack of a climatic debt
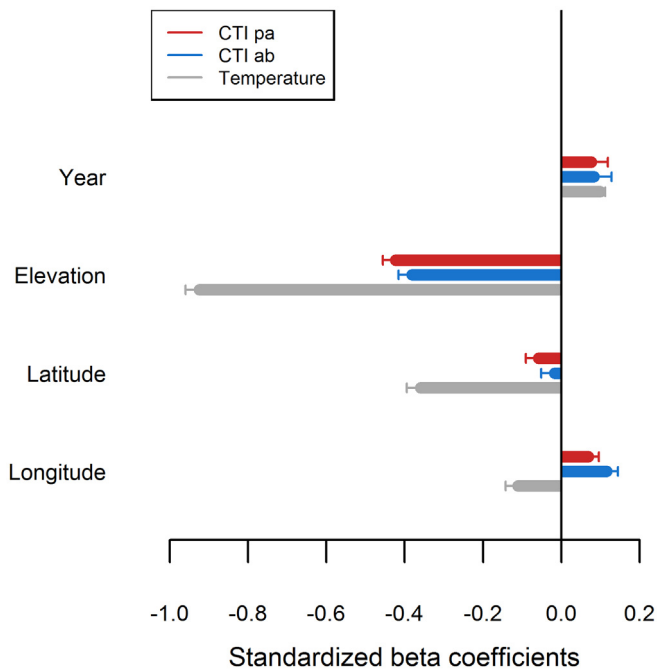
Fig. 4. Effect sizes of the temporal and spatial gradients on mean annual temperature and on the two community temperature indices (CTI_{ab} and CTI_{pa}). Effect sizes are expressed as standardized beta coefficients (±95% C.I.) resulting from linear mixed models.

for stream invertebrates may be due to the structure of the river networks. The vulnerability of species to global warming is inversely related to the slope of the temperature gradient within their range, with species living in areas with low temperature gradients (e.g. lowlands) having to move (disperse) longer distances to track increasing temperatures compared to species living in areas with strong temperature gradients at small spatial scales (e.g. mountains; Bertrand et al., 2016).

As expected, our analysis showed that the elevation gradient was by far the most important spatial dimension in terms of temperature and CTI gradients. This finding and the fact that the most common dispersal route of stream invertebrates is along the river network (Hughes, 2007) suggest that stream invertebrates use streams as a "highway" to track the shift in their optimal temperature ranges uphill. The current ability of stream invertebrate communities to track their temperature niche uphill cannot be projected infinitely into the future, as all streams have a natural endpoint at their source. Therefore, future global warming will inevitably lead to the so-called summit trap effect (Sauer et al., 2011), eventually resulting in abrupt and dramatic losses of cold-dwelling species. The potential of adaptive latitudinal or longitudinal range shifts to offset range losses seems to be limited in freshwater taxa (Bush and Hoskins, 2017). However, species vulnerability will depend strongly on their dispersal mode and ability (Tonkin et al., 2018), with strong aerial dispersers likely to be less affected than those restricted to aquatic dispersal only (Bush and Hoskins, 2017).

As all observational studies, this work has potential weaknesses. First, we are aware that several variables, other than the ones analyzed in this study, also influence stream invertebrate community composition. We are confident that our data filtering criteria (see Section 2.2) allowed selecting a rather comparable set of sites (low mountain streams without strong anthropogenic pressures), but we cannot exclude that other abiotic or biotic changes in the study area, such as changes in water quality or land use, could have affected the studied communities. Unfortunately, the lack of detailed local variables is a common issue in macroecological studies (see e.g. Bowler et al., 2017; Devictor et al., 2012; Dornelas et al., 2014), as a result of a trade-off between large temporal and/or spatial extent and detailed local information. In this respect, site-based collections of long-term biotic and

abiotic data should be encouraged, but unfortunately such datasets are still spatially and temporally limited (Haase et al., 2018; Mirtl et al., 2018). Second, as mentioned above, the sampling method changed during the study period and there is the risk that this change could have an influence on our results. To account for this, we included the sampling method as a covariate in all statistical analyses and we also re-ran all analyses for the two time periods separately. The trends in the two time periods resulted similar to the trends for the whole period for total abundance and richness, and for the two CTI metrics, thus confirming our main results (Table S2). Only the analysis of community composition showed discordant trends between the two periods, which we cannot exclude being dependent on the method (Table S2). However, the trends that we found for the most recent (and longest) period (2000–2014) were concordant with the general overall trends (i.e. decline of taxa adapted to low temperatures and increase in taxa adapted to medium and high temperatures), which, once again, confirms our results.

5. Conclusion

Taken together, our results indicate that stream invertebrates are among the very few organism groups that have so far been able to keep up with temperature increase, as their communities have reorganized themselves to adapt to the changing conditions. This confirms the lack of common response patterns to climate warming among different biota (Bowler et al., 2017) and calls for caution when generalizing climate change effects on biodiversity. Yet, the expense of this community reorganization is high and of utmost importance from a conservation perspective, as the observed loss in cold-dwelling species will eventually lead to a decline of biodiversity at larger spatial scales (Daufresne et al., 2004; Steinbauer et al., 2018). The observed extent of reorganization of community composition in response to 0.5 °C warming is especially alarming in view of the far stronger projected climate warming for future decades (IPCC, 2013). Therefore, studies addressing the biotic responses to climate warming should investigate the changes in community composition, besides total abundance or biomass or synthetic indexes (e.g. CTI), to better understand the degree and trajectory of change (Larsen et al., 2018).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.12.234.

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