Taxonomic and functional reorganization in Central European stream macroinvertebrate communities over 25 years

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HIGHLIGHTS

- River macroinvertebrates undergo a taxonomic and functional reorganization.
- Climate warming has led to a thermophilization of river macroinvertebrates.
- Thermophilic taxa displayed more diverse ecological traits than cold-adapted taxa.
- Thermophilic taxa contributed to increase the functional diversity.
- At the same time, communities converge towards similar taxonomic composition.

GRAPHICAL ABSTRACT
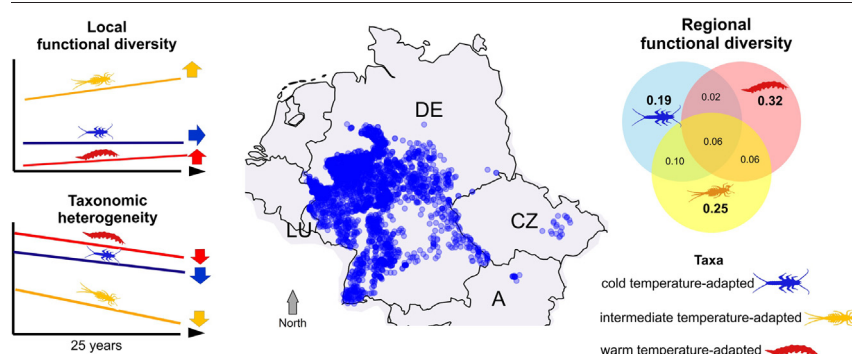
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ABSTRACT

Climate warming can lead to a replacement of species that favour cold temperatures by species that favour warm temperatures. However, the implications of such thermic shifts for the functioning of ecosystems remain poorly understood. Here, we used stream macroinvertebrate biological and ecological traits to quantify the relative contribution of cold, intermediate and warm temperature-adapted taxa to changes in community functional diversity (FD) using a dataset of 3781 samples collected in Central Europe over 25 years, from 1990 to 2014.

Our analyses indicated that functional diversity of stream macroinvertebrate communities increased over the study period. This gain was driven by a net 39 % increase in the richness of taxa that favour intermediate temperatures, which comprise the highest share in the community, and to a 97 % increase in the richness of taxa that favour warm temperatures. These warm temperature-adapted taxa displayed a distinct and more diverse suite of functional traits compared to the cold temperature-adapted group and thus contributed disproportionately to local FD on a per-taxon basis. At the same time, taxonomic beta-diversity declined significantly within each thermal group, in association with increasing local taxon richness.

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This study shows that over recent decades, small low-mountain streams in Central Europe have experienced a process of thermophilization and increasing functional diversity at local scales. However, a progressive homogenisation occurred at the regional scale, with communities converging towards similar taxonomic composition. As the reported increase in local functional diversity can be attributed mostly to the intermediate temperature-adapted taxa and a few expanding warm temperature-adapted taxa, these patterns could mask more subtle loss of sensitive cold temperature-adapted taxa with irreplaceable functional traits. In light of increasing climate warming, preservation of cold habitat refuges, should be considered a priority in river conservation.

1. Introduction

Global climate warming over recent decades (IPCC, 2013) has caused shifts in the geographic distribution of species across different ecosystems and taxonomic groups (Parmesan, 2006; Comte and Grenouillet, 2013; Lenoir and Svenning, 2015; Pecl et al., 2017). One consequence is that many natural communities are undergoing a process of "thermophilization", whereby species that favour warm temperature and species with wide temperature tolerances (i.e., eurytherm) replace those requiring colder conditions (De Frenne et al., 2013; Lenoir and Svenning, 2015; Haase et al., 2019).

Riverine ecosystems are particularly sensitive to global warming for a number of reasons (Durance and Ormerod, 2007; Isaak et al., 2012; Arora et al., 2016). Streams and rivers are dominated by ectothermic organisms, whose metabolic rates and fitness are influenced by the direct effect of water temperature, and by indirect effects such as changes in dissolved oxygen (Verberk et al., 2016). Moreover, the dendritic structure of river networks constrains dispersal pathways of aquatic organisms, limiting connectivity among habitats, and the potential to shift ranges (e.g. Peterson et al., 2013; Tonkin et al., 2018; Larsen et al., 2021). Evidence of climate-induced ecological changes in riverine systems is growing (Tonkin, 2022). For instance, the distribution of stream fish species across France over three decades have systematically shifted towards upstream reaches and higher elevation, consistent with geographic variation in climate change velocity (Comte and Grenouillet, 2013). In New Zealand, stream macroinvertebrate communities have experienced considerable range shifts and community reorganization over the past 25 years, including contrasting taxonomic and functional change (Mouton et al., 2020, 2022). Warming-induced longitudinal and altitudinal shifts have also been observed in Odonata and Heteroptera (Hickling et al., 2006), in line with modelled projections for many macroinvertebrate species (Domisch et al., 2011). However, the response of riverine biodiversity at specific locations to directional changes in temperature is not consistent. Both declines (Domisch et al., 2011; Mouton et al., 2020) and increases (Buisson et al., 2008; Vaughan and Ormerod, 2014; Lorenz, 2021; Pilotto et al., 2020) in taxonomic diversity have been observed. The interpretation of biodiversity trends requires approaches that go beyond the quantification of local species richness to include measures able to reflect the outcome of systematic compositional changes and allow the comparison among river basins and across geographic borders (Hillebrand et al., 2018; Larsen et al., 2018; Manfrin et al., 2019).

The consequences of thermophilization on the functional composition of communities have so far received little attention. Environmental filtering by increased water temperature would favour taxa with behavioural, anatomical and physiological adaptations to cope with such conditions. For example, warming favours flexible life cycles and multivoltinism, whereas it negatively affects shredders (Tomczyk et al., 2022) and grazers-scrapers (Jourdan et al., 2018). In turn, the association across response traits (sensu Gutiérrez-Cánovas et al., 2019) within species implies that any environmental filter selecting for a specific trait could indirectly affect the diversity and distribution of multiple traits in the community with implications for the overall functioning of ecosystems (Poff, 1997; Lamouroux et al., 2002; Gutiérrez-Cánovas et al., 2019). The degree to which taxonomic diversity reflects functional diversity (FD) in communities depends on the level of overlap in the distribution of functional traits across species (Cadotte, 2017). For this reason, increased taxonomic diversity may not always correspond to higher or more diverse ecosystem functions and vice versa (Baker et al., 2021). Measuring the functional diversity of communities thus provides a better proxy of ecosystem functions than simple taxonomic measures (Petchey and Gaston, 2002; Ernst et al., 2006; Cadotte et al., 2011; Cadotte, 2017). Moreover, analyses of functional diversity at different spatial scales would allow differentiating between local adaptations and regional processes of, for instance, functional homogenisation (Arellano and Halffter, 2003; Socolar et al., 2016).

Previous studies showed a thermophilization of communities in low-mountain Central European rivers over 25 years, associated with an increase in abundance and taxon richness of warm and intermediate temperature-adapted taxa (Haase et al., 2019), paralleled by a decline in niche specialization and trait β-diversity (Pilotto et al., 2022). However, the mechanistic links between macroinvertebrate compositional reorganization and changes in functional responses, following changes in environmental conditions, remain unresolved (but see e.g. Mouton et al., 2020).

In this study, we examined the contribution of macroinvertebrate taxa that favour cold, intermediate and warm temperature (hereafter referred to as "cold", "intermediate" and "warm" taxa) to functional diversity, to understand how progressive thermophilization and compositional reorganization (Haase et al., 2019) have altered the patterns of functional diversity of Central European streams. We tested a set of three competing hypotheses. Hypothesis 1: if the newly colonising warm taxa were highly functionally redundant among each other, they would not contribute to increase FD. Rather, the raise of such taxa and the loss of cold taxa would result in declines of FD. This would be the case if warm taxa share common traits that make them successful colonisers during climate warming (e.g. good dispersers, rapid reproducers, feeding generalists), as already found for invasive macroinvertebrate species (Früh et al., 2012a,b). Hypothesis 2: if the newly colonising warm taxa provided novel or unique combination of traits, they would contribute positively to FD. This would be the case if warm taxa reflected a separate eco-evolutionary history of exposure to environmental filters (Poff, 1997) among each other and compared to resident cold taxa. It is in fact possible that the rather unique set of traits of these thermophilic taxa evolved under different environmental settings than low mountain streams, and were thus less redundant compared to the other, locally adapted thermal groups. Under this scenario, the increase in warm taxa would thus result in increases in FD if the rest of the community (intermediate and cold taxa) remains constant. Hypothesis 3: if the functional role of taxa was independent from their thermal adaptations, changes in functional diversity would be directly proportional to changes in species richness.

To test these hypotheses, we used 3781 quantitative macroinvertebrate samples from Central European rivers (Fig. S1), which have experienced 0.5 °C of warming, over a period of 25 years (1990–2014) and an increase (>60 %) in the share of taxa adapted to warm and intermediate temperatures (see Haase et al., 2019). We specifically examined temporal trends in taxon richness, taxonomic heterogeneity (as multivariate distance from group median and a measure of beta-diversity), and FD. We use the term "functional diversity" in the sense of Schmera et al. (2017). Accordingly, we used functional traits that reflect responses to environmental changes within the community and provide a direct link to ecosystem function (Violle et al., 2007; Mouillot et al., 2013; Schmera et al., 2017; Gutiérrez-Cánovas et al., 2019; McLean et al., 2019). Moreover, we quantified the relative contribution (on a per-taxon basis) of taxa adapted to cold,

intermediate and warm temperature to the observed community FD. Functional diversity was quantified at both local (stream reach) and regional (Central Europe) scales, to identify local adaptations, and possible homogenisation processes. To specifically estimate the degree of functional overlap associated with the three thermal groups, we also measured the functional uniqueness (i.e., trait overlap) for each of the taxa belonging to cold, intermediate or warm temperature-adapted group.

2. Materials and methods

2.1. Macroinvertebrate dataset

We used the same dataset and filtering procedure as described by Haase et al. (2019) and Pilotto et al. (2022). Briefly, macroinvertebrate samples (n = 12,375) were collected between 1990 and 2014 in Austria, Czech Republic, Germany and Luxembourg (Fig. S1). The sampling procedure was standardised across sites, but the sampling protocol changed in 2000. Before 2000, all habitat types occurring at a site were sampled for approximately 3 min (Braukmann, 2000) and the resulting material was pooled into a bulk sample. From 2000 onwards, following the EU Water Framework Directive (WFD), a standard multi-habitat sampling approach was adopted (Haase et al., 2004). Twenty subsamples were collected from the major habitats proportionally to their extent in the site and then pooled together (total sampled area: 1.25 m^2) (Haase et al., 2004). Change in sampling methodology was accounted for in the statistical analyses (detailed below, see Haase et al., 2019 for a similar approach). Taxonomic identification level followed the "operational taxalist" (mostly to species and genus levels, subfamily or family levels for Chironomidae and Oligochaeta) (Haase et al., 2006).

The initial dataset was filtered to 3781 observations to assure data comparability and quality. We only considered: samples from small low-mountain streams (stream types 5, 5.1 and 9 according to Pottgiesser and Sommerhäuser, 2008) to limit stream variability in the data set; samples that were collected from March to May to minimize the effects of seasonality (Sundermann et al., 2008); taxa that were observed more than once; samples with taxon richness values above the lower 10th percentile of all samples, to remove species-poor sites likely influenced by heavy local habitat modification (Haase et al., 2019). The resulting dataset had a minimum number of ten sampling sites for each sampling year, the majority of sites were sampled only once over the study period, while a small fraction (14 %) of sites were sampled two to four times, at time intervals between one and four years (Haase et al., 2019). The final dataset included 5.6 million individuals belonging to 589 taxa. Sample elevation spanned between 37 and 1148 m a.s.l., latitude between 47.56° and 52.91° and longitude between 6.09° and 17.36°.

2.2. Classification of cold intermediate and warm taxa

Following Haase et al. (2019), we characterized the temperature niche of species based on the well-established species river zonation approach (Illies and Botosaneanu, 1963). For each taxon, we computed the taxon-specific temperature preference as the average (mean ± SD) of the temperature associated with the stream zones occupied by that taxon (Illies and Botosaneanu, 1963; Moog and Wimmer, 1992; Moog, 2002), weighted by the affinity of the taxon for each stream zone (as reported by Schmidt-Kloiber and Hering, 2015). We arranged the taxa in ascending order according to their taxon-specific temperature preferences. We then used the 0.33 and 0.66 quantiles (i.e. 12.02 °C and 18.74 °C) to classify the taxa into cold, intermediate and warm. Taxa whose affinity for the stream zone was not available were removed from the analysis (40 % of all taxa in the dataset).

2.3. Taxon richness and heterogeneity

For each sample we computed the number of taxa belonging to each thermal group (taxon richness). For each thermal group, as a measure of compositional (beta) diversity, we also assessed taxonomic heterogeneity within each year as the average multivariate distance to group median (Anderson et al., 2006). Taxonomic heterogeneity was calculated using the function betadisper from the package vegan (Oksanen et al., 2013) in R (R Core Team, 2019).

2.4. Functional traits

To characterize the functional diversity of the stream macroinvertebrate samples, the trait composition was defined using 49 categories of 8 biological traits and 7 categories of one ecological trait obtained from published macroinvertebrate trait databases (www.freshwaterecology.info; Schmidt-Kloiber and Hering, 2015; Tachet et al., 2010) (see Table S1). The biological traits described feeding type (10 categories; Schmidt-Kloiber and Hering, 2015), locomotion type (6 categories, Schmidt-Kloiber and Hering, 2015), microhabitat preference (9 categories, Tachet et al., 2010), maximal potential size (7 categories, Tachet et al., 2010), dispersal (4 categories, Tachet et al., 2010), life cycle duration (2 categories, Tachet et al., 2010), potential number of cycles per year (3 categories, Tachet et al., 2010) and reproduction (8 categories, Tachet et al., 2010). The ecological trait describes the current preference (7 categories; Schmidt-Kloiber and Hering, 2015) (see Table S1). The 56 categories of functional traits were chosen as considered responsive to global warming, and to cover major ecological differences between species. All selected trait categories provided information for the majority of the taxa (feeding type: 99.1 %; locomotion: 79.8 %; microhabitat preference: 96.1 %; maximal potential size: 89.1 %; dispersal: 88.8 %; life cycle duration: 87.9 %; potential number of cycles per year: 88.5 %; reproduction: 88.5 %; current preferences: 99.4 %). When available, trait information was obtained at the species level. If not available for the species level, trait information available at genus level was used (except for Chironomidae and Oligochaeta where subfamily or family information was used), assuming a sufficient degree of accuracy. Traits were reported as fuzzy-codes, representing the affinity of each taxon to each trait category, thus accounting for intra-genus and intra-family variation (Chevenet et al., 1994; Dolédec et al., 2006). We standardised the affinity scores within each trait between 0 and 1, using the function "prep.fuzzy.var" from package ade4 (Dray and Dufour, 2007) for R.

2.5. Functional diversity

To test our hypotheses, we quantified the contribution of different thermal groups to the functional diversity (FD) of the community. Therefore, we applied a method that allows to simultaneously compute the FD of a certain community and the contribution of each taxon (or groups of taxa) in the community to the total FD. We calculated FD as the Faith Index (Faith, 1992) for unweighted samples (i.e., incidence data), using the package "picante" (Kembel et al., 2010) for R. The species-by-trait matrix was converted into a functional distance matrix using a fuzzy-coding-adapted Gower's index (Pavoine et al., 2009; Gutiérrez-Cánovas et al., 2019) and this was clustered to produce a dendrogram describing the functional relationships between taxa (Petchey and Gaston, 2002; Petchey et al., 2007). Individual branch lengths were standardised to the total branch length of the dendrogram, (i.e. a hypothetical community of all 332 taxa with the maximum functional diversity has a value of 1, a community consisting of only one species has a functional diversity value of 0). The functional diversity of a community is then the total length of the branches required to connect all taxa in the assemblage (Faith, 1992; Petchey and Gaston, 2006), and the length of each individual branch is the contribution of a specific taxon. We calculated FD at local and regional scales. Local FD was calculated for each observation (with no spatial and temporal aggregation) considering the entire community as well as the subsets of cold, intermediate and warm taxa. Regional FD was assessed at the regional scale (across all sites), separately for each thermal group. In order to estimate the functional diversity associated with the entire pool of taxa observed, Regional FD was calculated by aggregating all observations (over sites and time).

2.6. Data analysis

2.6.1. Taxon richness, local FD and taxonomic heterogeneity

To analyse differences in taxon richness, local FD and taxonomic heterogeneity between the three macroinvertebrate thermal groups, we used a non-parametric Kruskal-Wallis variance test. In the case of a significant result, a pairwise Wilcox test was used as post-hoc analysis with a Bonferroni correction of the p-values to account for multiple comparisons and control for false positives (Haynes, 2013).

To analyse trends in taxon richness, local FD and taxonomic heterogeneity over the study period (from 1990 until 2014), we used linear mixed effect models using the package "nlme" (Pinheiro et al., 2022) for R. Four linear mixed effect models analysed trends in richness, local FD and taxonomic heterogeneity for i) the entire community (i.e., total), and for the subsets of ii) cold, iii) intermediate and iv) warm taxa. Year of sampling was included as a fixed factor as well as elevation, catchment size, latitude, longitude, and sampling method (see above) to account for spatial and methodological variability. The sampling site was included in all local FD models as a random factor to account for repeated observations in time within each site.

To test whether temporal changes in local FD did not derive solely from the observed increases in taxon richness, we calculated the standardised effect size of local FD (SES local FD) by computing local FD for randomized communities. For each sample, the observed community structure was maintained (i.e., richness and abundances), and the null distribution of local FD values (null local FD) was calculated 999 times by shuffling taxa names at the tip of the functional dendrogram (function tipShuffle from the picante package). Finally, the SES local FD was calculated as:

$$\text{SES local FD} = [\text{observed local FD} - \text{mean (null local FD)}]/\text{sd (null local FD)}$$

SES local FD thus represents the deviation of local FD values from what would be expected given the observed taxon richness.

2.6.2. Per-taxon contribution of cold, intermediate and warm temperature-adapted groups to the local FD

A linear mixed effect model was used to assess the contribution of each individual taxon of the cold, intermediate and warm temperature-adapted groups to the local FD. The model included local FD as a dependent variable and the number of cold, intermediate and warm taxa as fixed factors. Sampling site was included in the model as a random factor to account for repeated observations within each site. As we were interested in assessing whether taxa's contribution to community FD depended on their thermal preference, we also analysed graphically, for each thermal group, the null distribution of local FD values expected for taxon richness ranging from one to 50 taxa. The null local FD distribution was obtained by shuffling (999 permutations) the names of taxa at the tip of the functional dendrogram, separately for each thermal group. This procedure allowed appraising the influence of taxa thermal preference on community local FD accounting for its inherent relationship with taxon richness.

2.6.3. Factor selection and model validation

In all models, factors were backward-selected using likelihood ratio tests against reduced models (Zuur et al., 2009c). The final model validation was conducted using residuals versus fitted value plots (Zuur et al., 2009c) and qq-plots (Wilk and Gnanadesikan, 1968). When necessary, dependent and independent variables were log-transformed to meet variance homogeneity assumptions (Zuur et al., 2009a,b) and temporal autocorrelation was assessed and, where required, corrected using a correlation structure (corARMA function in nlme R package) (Zuur et al., 2009d). To determine the best correction approach, residuals in multiple linear mixed effect models with different autocorrelation structure were tested using an Akaike Information Criterion assessment (Zuur et al., 2009d). The variance explained by the fix factors was calculated for each mixed effect model as marginal (R^2m) (Nakagawa and Schielzeth, 2013) using the MuMln package (Barton, 2016) for R.

2.6.4. Trait composition and functional uniqueness

We tested the difference in multivariate trait composition among thermal taxa groups using a one-way Permutational Multivariate Analysis of Variance (perMANOVA) using the function "adonis2" in the package vegan (Oksanen et al., 2013) for R. In case of factor significance, a perMANOVA analysis was performed between each pair of thermal groups as a post-hoc test.

Functional uniqueness was assessed following the concept of functional rarity (Violle et al., 2017). A taxon can be classified in terms of its functional rarity based on how similar its traits are to those of the co-occurring taxa in the community (Pavoine et al., 2005). Using the package "funrar" (Grenié et al., 2017) for R, functional distance, calculated using a fuzzy-coding-adapted Gower's index, and presence-absence taxa composition matrices were used to assess uniqueness as the functional distance of a taxon to its nearest neighbour in a set of assemblages. In our study, we assessed uniqueness at the regional scale for the entire study period as a measure of functional trait uniqueness of each taxon with respect to the whole set of taxa. Uniqueness values ranged from 0 to 1: a value of zero indicates functional overlap of a taxon compared to the regional pool of taxa, while a value of 1 indicated complete functional uniqueness (Grenié et al., 2017; Violle et al., 2017).

To analyse overall differences in uniqueness between cold, intermediate and warm taxa we used a non-parametric Kruskal-Wallis variance test. In the case of a significant result, a pairwise Wilcox test was used as post-hoc analysis with a Bonferroni correction of the p-values to account for multiple comparisons and control for false positives.

3. Results

3.1. Taxon richness, local FD and taxonomic heterogeneity

On average, local communities comprised approximately 39 taxa. Intermediate taxa dominated local communities (16.0 ± 6.0 SD) with few cold taxa (5.2 ± 4.1 SD) and fewer warm taxa (2.1 ± 2.0 SD) (Kruskal-Wallis $\chi^2 = 7253.8$, $p < 0.001$). Differences in richness at the local scale were also reflected in differences in local FD, with intermediate species showing the highest local FD value (0.10 ± 0.03 SD), followed by cold taxa (0.03 ± 0.02 SD) and warm taxa (0.01 ± 0.01 SD) ($\chi^2 = 7405.8$, p < 0.001). Warm taxa exhibited the highest value of taxonomic heterogeneity averaged across the study period (0.65 ± 0.07 SD), followed by cold (0.61 ± 0.11 SD) and intermediate taxa (0.56 ± 0.09 SD) ($\chi^2 = 1413.2$, p < 0.001).

3.2. Temporal patterns of taxon richness, local FD and taxonomic heterogeneity

From 1990 to 2014 the estimated average local taxon richness increased from 1.1 (± 0.12 SE) to 2.9 (± 0.06 SE) taxa for warm taxa and from 12.8 (± 0.55 SE) to 18.9 (± 0.22 SE) for intermediate taxa. Taxon richness of cold taxa was of ca. 5 taxa and did not change over time (Fig. 1a, Tables 1, S2). Overall, this resulted in an estimated 38 % increase in community taxon richness, from 30.4 (± 1.18 SE) to 44.2 (± 0.46 SE). For cold taxa, intermediate taxa and the overall community, taxon richness increased with elevation whereas fewer warm taxa were found with increasing elevation (Tables 1, S2). A positive relationship between taxon richness and catchment size was visible at the community level and for intermediate and warm taxa (Tables 1, S2), while in cold taxa, a higher taxon richness was found in small catchments (Tables 1, S2).

Estimated local FD of macroinvertebrate communities increased overall by ca. 36 % over the study period (Fig. 1b, Tables 1, S2). This trend was not solely due to the increase in taxon richness, as shown by the steady rise in standardised effect sizes (SES) of local FD (from null model analysis) values over time (Fig. S2). In other words, values of local FD show an increasing temporal trend independently from the observed richness. Warm- and intermediate taxa were responsible for the increase in local FD. The local FD of warm taxa increased ca. 261 % over the 25-year period ranging from 0.001 (± 0.001 SE) in 1990 to 0.014 (± 0.0004 SE) in 2014 (Fig. 1b, Tables 1, S2) with an estimated mean annual increase of 10.9 %.
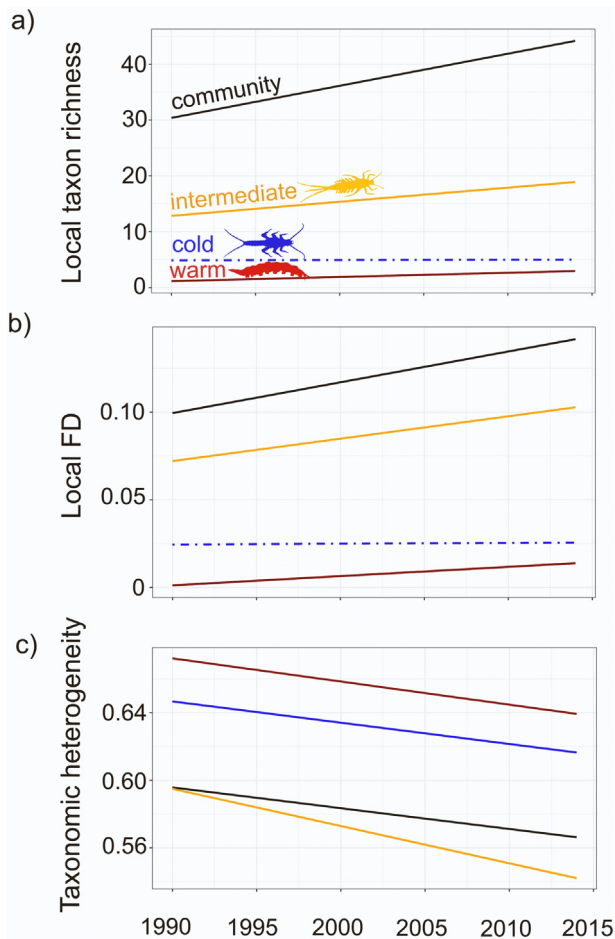
Fig. 1. Local taxon richness (a), local functional diversity (FD) (b) and taxonomic heterogeneity as multivariate distance from group median (c) are shown as trend estimates (1990–2014) obtained using linear mixed effect models. Trend estimates were obtained for the entire set of taxa (community), and for cold, intermediate and warm taxa. Significant trends (LME significance < 0.05) are shown as solid lines.

In intermediate taxa, the estimated local FD increased by ca. 36 % over 25 years from 0.07 ($\pm$0.003 SE) in 1990 to 0.10 ($\pm$0.001 SE) in 2014, with an estimated annual increase of 1.5 % (Fig. 1b, Tables 1, S2). No change in local FD over 25 years was found in cold taxa (Fig. 1b, Tables 1, S2). For intermediate and cold taxa, as well as for the overall community, local FD significantly increased with elevation; while local FD decreased with elevation for warm taxa (Tables 1, S2). Local FD increased with catchment size at the community level and for intermediate and warm taxa (Tables 1, S2), while it was higher within small catchments for cold taxa (Tables 1, S2). Null model analysis revealed that temporal trends in SES of local FD were contingent on stream catchment size. In particular, streams draining larger catchments tended to lose functional diversity with time, whereas streams within smaller catchments displayed increasing SES local FD values (Fig. S4).

Estimated taxonomic heterogeneity across the entire studied region decreased by 5 % over the study period, which was consistent across all thermal groups (cold: minus 5 %; intermediate: minus 9 %; warm: minus 5 %; Fig. 1c, Tables 1, S2). Taxonomic heterogeneity increased at lower elevations and in streams within smaller catchments for intermediate and warm taxa; on the other hand, a positive relationship was found between the taxonomic heterogeneity of cold taxa and both elevation and catchment size.

We found inconsistent longitudinal and latitudinal gradients for taxon richness, taxonomic heterogeneity and local FD in the different thermal groups. We found a positive correlation of taxon richness, local FD and

Table 1

Statistics for the significant (after backward selection) factors for local taxon richness, local functional diversity (FD) and taxonomic heterogeneity assessed with linear mixed effect models (LMEs) for the whole community, and for cold, intermediate and warm taxa. Factor estimates, standard errors (se), and significance (*** = $p \leq 0.001$, ** = $0.001 \leq p \leq 0.01$, * = $0.01 \leq p \leq 0.05$, · = $0.05 \leq p \leq 0.07$) are reported.

LMEs	Factors	Estimate	se	p-Value
Local taxon richness				
Community	Year	5.74E-01	6.53E-02	***
	Lat (km)	1.54E-02	2.12E-03	***
	Long (km)	−2.24E-02	1.63E-03	***
	Elevation (m)	2.93E-02	1.44E-03	***
	log(Catchment area) (km^2)	1.40E+00	1.71E-01	***
	Sampling (Old vs New)	−5.59E+00	9.76E-01	***
Cold	Lat (km)	2.02E-03	6.57E-04	**
	Long (km)	−6.26E-03	5.21E-04	***
	Elevation (m)	1.42E-02	4.61E-04	***
	log(Catchment area) (km^2)	−6.24E-01	5.48E-02	***
	Sampling (Old vs New)	−1.07E+00	2.09E-01	***
Intermediate	Year	2.53E-01	3.06E-02	***
	Lat (km)	5.00E-03	1.01E-03	***
	Long (km)	−1.27E-02	7.80E-04	***
	Elevation (m)	7.20E-03	6.90E-04	***
	log(Catchment area) (km^2)	1.59E+00	8.17E-02	***
	Sampling (Old vs New)	−2.19E+00	4.58E-01	***
Warm	Year	7.53E-02	6.89E-03	***
	Elevation (m)	−5.50E-04	2.18E-04	*
	log(Catchment area) (km^2)	5.36E-01	2.82E-02	***
Local FD				
Community	Year	1.76E-03	2.13E-04	***
	Lat (km)	3.10E-05	7.00E-06	***
	Long (km)	−9.50E-05	5.40E-06	***
	Elevation (m)	9.20E-05	4.80E-06	***
	log(Catchment area) (km^2)	7.16E-03	5.70E-04	***
	Sampling (Old vs New)	−1.46E-02	3.20E-03	***
Cold	Lat (km)	8.88E-06	3.75E-06	*
	Long (km)	−3.65E-05	2.97E-06	***
	Elevation (m)	7.72E-05	2.63E-06	***
	log(Catchment area) (km^2)	−3.59E-03	3.12E-04	***
	Sampling (Old vs New)	−6.38E-03	1.19E-03	***
Intermediate	Year	1.28E-03	1.57E-04	***
	Lat (km)	2.39E-05	5.17E-06	***
	Long (km)	−6.71E-05	3.98E-06	***
	Elevation (m)	3.10E-05	3.53E-06	***
	log(Catchment area) (km^2)	7.68E-03	4.19E-04	***
	Sampling (Old vs New)	−1.35E-02	2.35E-03	***
Warm	Year	5.27E-04	6.30E-05	***
	Elevation (m)	−3.20E-06	1.29E-06	*
	log(Catchment area) (km^2)	2.77E-03	1.67E-04	***
	Sampling (Old vs New)	2.92E-03	9.68E-03	**
Taxonomic heterogeneity				
Community	Year	−1.23E-03	3.15E-04	***
	Lat (km)	5.11E-05	1.39E-05	***
	Long (km)	4.56E-05	1.14E-05	***
Cold	Year	−1.26E-03	6.52E-04	.
	Lat (km)	1.82E-04	2.10E-05	***
	Long (km)	1.23E-04	1.63E-05	***
	Elevation (m)	9.88E-05	1.42E-05	***
	log(Catchment area) (km^2)	1.20E-02	1.70E-03	***
	Sampling (Old vs New)	−4.79E-02	9.64E-03	***
Intermediate	Year	−2.20E-03	3.33E-04	***
	Long (km)	5.50E-05	1.33E-05	***
	Elevation (m)	−5.00E-05	1.06E-05	***
	log(Catchment area) (km^2)	−3.22E-03	1.36E-03	*
Warm	Year	−1.37E-03	5.29E-04	**
	Lat (km)	−6.50E-05	1.74E-05	***
	Long (km)	3.60E-05	1.32E-05	**
	Elevation (m)	−6.00E-05	1.28E-05	***
	log(Catchment area) (km^2)	−6.61E-03	1.44E-03	***
	Sampling (Old vs New)	−3.28E-02	8.58E-03	***

taxonomic heterogeneity with a south-north gradient except for local FD in warm taxa which showed a negative correlation with the increasing latitude. We also identified a negative correlation in taxon richness and local

FD with the longitudinal west-east gradient in contrast to the taxonomic heterogeneity in which a positive correlation was found in each thermal group. The change in sampling methodology in 2000 increased all the metric values (Tables 1, S2), except for local FD in warm taxa for which a decrease was observed.
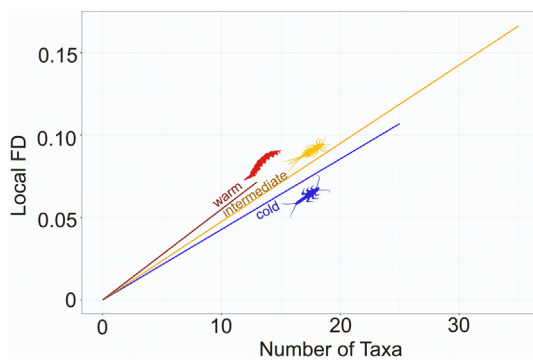
3.3. Per-taxon contribution to local functional diversity, regional functional diversity and functional uniqueness

The three thermal groups of taxa significantly differed in their trait composition (perMANOVA: $F = 3.09$, $p < 0.001$, all pairwise post-hoc tests < 0.05). On a per-taxon basis, taxa adapted to warm and intermediate temperatures contributed most to the local FD (Fig. 2, Table 2) and regional functional diversity (regional FD) across the entire study region (Fig. 3a). Their contribution to the regional functional diversity increased through time, especially from 2002 (Fig. 3b). Also, warm and intermediate taxa possessed a higher functional uniqueness (i.e., a less redundant suite of traits) compared to the cold taxa (Kruskal-Wallis $\chi^2 = 16.88$, p < 0.001) (Fig. 3c). Every additional warm and intermediate taxon increased the local FD by ca. 4 % (Fig. 2, Table 2). On the other hand, each cold taxon contributed to increasing the local FD by only 2.9 % (Fig. 2, Table 2). The null distribution of local FD values expected for communities with richness ranging 1–50 taxa, shows that for each level of taxon richness, communities of warm and intermediate taxa would generally display higher local FD than communities of cold taxa (Fig. S3). This null-model approach supports the notion that the contribution of warm taxa to community local FD is, on average, higher than the other thermal groups, independently of the number of taxa.

4. Discussion

Our analyses showed that the progressive thermophilization of Central European low-mountain streams led to a ca. 36 % increase in macroinvertebrate functional diversity over 25 years, from 1990 to 2014. Species adapted to warm and intermediate temperatures contributed the most to the increase in functional diversity at both local and regional scale. Our results support the hypothesis that the newly colonising warm and intermediate taxa provide novel or unique combination of traits contributing positively to community functional diversity. At the same time, the increasing functional diversity at the local scale was associated with a progressive taxonomic homogenisation at the regional scale. This is a finding that has been mirrored in New Zealand stream communities over the same period (Mouton et al., 2020).

We found increases in local taxon richness for warm and intermediate taxa. In the study area, only 25 % of the warm taxa were observed before 1995 and only 50 % before 2005 (see Fig. S5). Conversely, richness of cold taxa remained stable through time. Although Bruno et al. (2019) and Floury et al. (2013) found increases in warm taxa and declines in cold

Table 2

Per-taxon contribution of warm, intermediate and cold taxa to the local functional diversity (FD) analysed with linear mixed effect models (LMEs). Factor estimates, standard errors (se), degrees of freedom (df), *t*-statistic, significance (p) and marginal R^2 (R^2m) are given.

LMEs	R^2m	Factors	Estimate	se	df	*t*-Value	p-Value
Local FD	0.96	Intercept	1.38E-02	4.18E-04	3283	32.94	<0.001
		N° taxa warm	5.51E-03	7.88E-05	494	69.89	<0.001
		N° taxa cold	4.28E-03	3.68E-05	494	116.30	<0.001
		N° taxa intermediate	4.75E-03	2.65E-05	494	178.78	<0.001
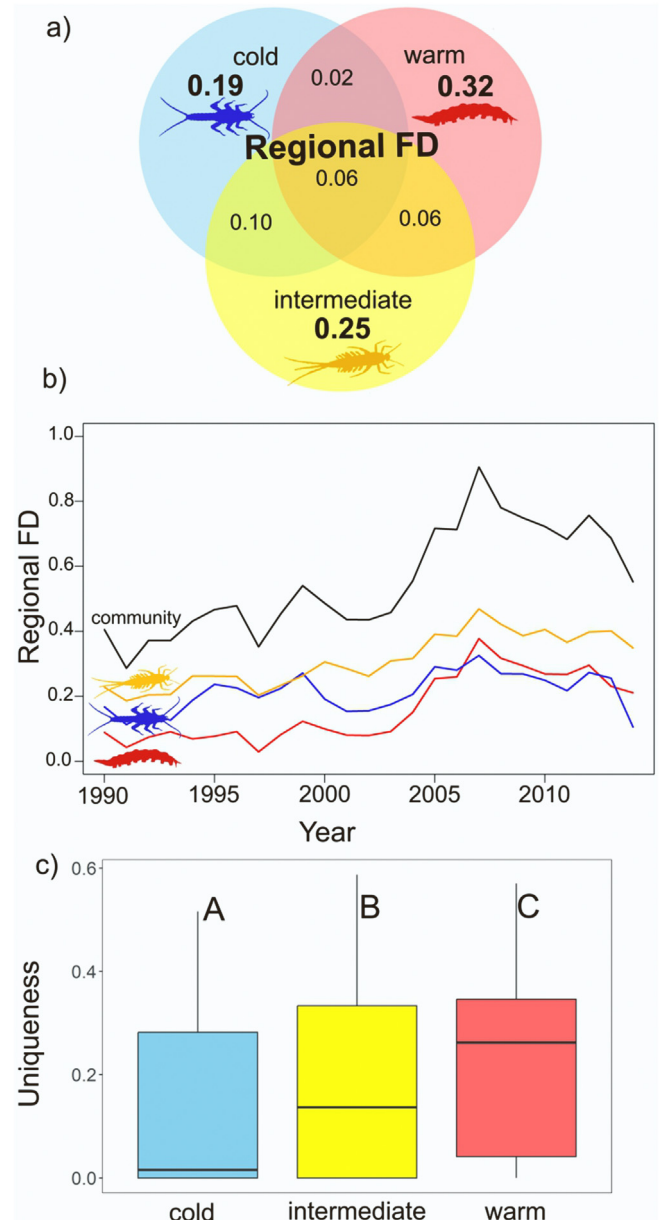
Fig. 3. Regional functional diversity (FD) calculated on the dataset aggregated over years and sites (panel a) and across time (panel b) for cold (blue), intermediate (yellow) and warm (red) temperature-adapted taxa. Functional uniqueness value (panel c) for the aggregated dataset expressed as taxa uniqueness with respect to the whole community, and reported for cold, intermediate and warm taxa. Uniqueness values for taxa belonging to each thermal group are shown as boxplots (with median and quartiles). Differences in Uniqueness among groups were tested with Kruskal-Wallis test; Significant (p < 0.001) post-hoc Wilcox pairwise comparisons are indicated with different letters (i.e., A, B, C).


Fig. 2. Model estimates of local functional diversity (FD) in relation to the local richness of cold, intermediate and warm taxa. All regression lines results were significant at $p < 0.05$. Line slope represents the per-taxon contribution to the local FD for each thermal group (see slope coefficients in Table 2).

thermal specialists, similar patterns have also been found in Swiss streams, with increases in warm taxa (and pesticide-tolerant taxa), and stable trends for cold taxa (Gebert et al., 2022). Despite being in apparent contrast with the well documented decline in biodiversity across Europe (e.g., Dirzo et al., 2014; Hallmann et al., 2017), these results align with several studies reporting increases in freshwater macroinvertebrate diversity over recent decades (Vaughan and Ormerod, 2012; Van Looy et al., 2016; Baranov et al., 2020; Pilotto et al., 2020; Baker et al., 2021). These patterns of increasing richness and diversity have been associated with improved water quality (Vaughan and Ormerod, 2012; Baker et al., 2021). While improvement in the water quality of the studied low-mountain streams may have been partly responsible for the observed gain in richness, this trend was solely driven by a net increase in the occurrence of generalist thermophilic taxa, as also shown for Swiss rivers (Gebert et al., 2022), and under experimental settings (Nelson et al., 2017).

The thermophilic warm-adapted taxa displayed a rather distinct and diverse suite of traits (i.e., higher functional uniqueness) compared to the cold-adapted taxa. Thus, when thermophilic taxa colonise cold low-mountain streams, they introduce new traits to the communities because they evolved under different environmental conditions than the typical communities of those streams. Conversely, since cold taxa displayed relatively lower functional uniqueness compared to the warm, the loss of one or a few such taxa may not immediately impact the community functional diversity. In addition, functional diversity (even after correction for the observed taxon richness) increased particularly in streams within smaller catchments (see Fig. S4). This finding further supports the notion that thermophilic taxa may be progressively colonising smaller upstream sites, as temperatures become warmer. Increases in functional diversity are considered as a positive indication of resilient communities (Van Looy et al., 2019), but increasing functional diversity can also be a transient process, in the light of a progressive climate warming for the coming decades (IPCC, 2021). Despite many macroinvertebrate taxa being capable of finding new suitable habitats further up the river network (Tonkin et al., 2018) all potential niches and mountain refugia (Brighenti et al., 2021) will eventually be occupied as the river network has a limited summit point (Sauer et al., 2011). This scenario might lead to new competitive interactions between stenothermal and eurythermal taxa (Haase et al., 2019) with generalist, good dispersers and high fecundity taxa (Sarremejane et al., 2020) likely being favoured (Milner et al., 2009). Our perMANOVA results show that cold-adapted taxa have a different suite of traits compared to the other two groups of taxa. This means that the eventual displacement of cold-specialist taxa (as shown by Bruno et al., 2019 and Floury et al., 2013) would lead to a loss of irreplaceable traits. In light of increasing climate warming, the preservation of cold habitat refuges, should be considered a priority in river conservation.

The apparent reorganization of communities, and the upstream colonisation by warm taxa is also likely to lead to regional homogenisation as found in our study. The increasing diversity at local scales was associated with a progressive taxonomic homogenisation at regional scales. While the increase in taxonomic homogenisation may be an inevitable consequence of increasing taxonomic alpha diversity across the study area, it was also paralleled by declining trait beta diversity and declining community specialization, as found by a previous work (Pilotto et al., 2022). Such homogenisation of freshwater habitats by colonisation of generalist taxa at the expense of specialist taxa is an on-going process of global concern (e.g. Olden et al., 2004; Olden and Rooney, 2006; Villéger et al., 2014).

Our study is based on a metric of functional diversity that is computed on presence/absence data (Petchey and Gaston, 2002; Petchey et al., 2007). We used this method because it allows a direct computation of the contribution of each taxon and taxa group (in our case thermal groups) to functional diversity, which was the main goal of this work. Compared with abundance-based methods, presence/absence data could amplify the effects of rare taxa in the communities. To minimize this risk, as described in the Materials and methods section, we excluded rare taxa (i.e. taxa that were sampled only once) before running the analysis. Using presence/

absence data could also mask nuanced changes. For example, if the abundance of cold-adapted taxa declines with time, presence/absence data would not track changes in functional diversity until those taxa become locally extinct. Also, the metric used here to calculate functional diversity has been shown to be dependent on taxon richness (Petchey and Gaston, 2002). Null modelling, however, revealed that the contribution to community functional diversity was on average higher for warm and intermediate taxa than for cold taxa (see Fig. S3), independently from increasing taxon richness (see Fig. S3). These findings are in line with the functional uniqueness analysis and suggest that warm taxa display a rather unique set of traits, which result in an overall increase in community functional diversity with climatic warming. Further, the deviation of functional diversity from what is expected, given the observed taxon richness, also increases through time (see Fig. S2). This indicates that even after controlling for increases in richness, the rising trend in functional diversity remains evident.

The lack of detailed local-scale environmental data prevented their inclusion in the analysis, and we could not use long time series from the same site because most sites were sampled just once. Unfortunately, site-specific collections of long-term biotic and abiotic data are still limited (see e.g., Durden et al., 2017; Mirtl et al., 2018). We are confident that our criteria of data filtering allowed limiting the variability across the studied locations (low mountain streams without strong direct anthropogenic pressures). However, we cannot exclude that local environmental conditions, biotic interactions or land use changes could have influenced the invertebrate communities in the studied systems. For example, our results showed that the trend in functional diversity with time was dependent on catchment size with stronger declines in larger catchments. This might suggest stronger declines in functional diversity in locations with stronger anthropogenic impacts as larger catchments are generally located at lower elevations, and thus they might experience greater anthropogenic impacts than small catchments. In addition, our analyses are based on only 60 % of the taxa that were present in the total data set. This is because only for these taxa information on the longitudinal distribution along the stream zonation was available. This information was necessary for the grouping into the three temperature classes. We recognize that this sub-setting may also influence the obtained results, and that the classification of species according to inferred temperature preferences may not fully represent those affinities over the study period. We also recognize the potential confounding influence of the two different methods used to sample macroinvertebrates, even though our models did not show large effects on the results. In any case, our study could track long-term and large-scale changes in stream invertebrate communities, while drivers of local changes over time remain to be resolved.

In conclusion, we found that different (thermal) groups of taxa showed different trends over 25 years, and they contributed differently to community functional diversity. Our findings indicate that the functional aspects of communities are changing in parallel with taxonomic change, and adjusting to the novel climatic conditions. At the same time, we urge caution when interpreting the apparent increases in functional diversity, as the ongoing community taxonomic and functional reorganization of macroinvertebrates could eventually lead to a loss of stenothermic taxa and a not replaceable set of functions resulting in a general loss in taxonomic and functional diversity at larger scales (Daufresne et al., 2004; Steinbauer et al., 2018; Haase et al., 2019). Analysis of functional diversity is used as proxy of ecosystem functions, community stability and resilience. However, in this study we show that the local increase in functional diversity is taxa-dependent and associated with an overall regional homogenisation.

CRediT authorship contribution statement

Alessandro Manfrin: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Francesca Pilotto:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Stefano Larsen:** Formal analysis, Writing – original draft, Writing – review & editing. **Jonathan D. Tonkin:** Writing – original draft, Writing – review & editing. **Armin W. Lorenz:** Data curation, Writing – review &

editing. **Peter Haase:** Conceptualization, Writing – review & editing. **Stefan Stoll:** Conceptualization, Writing – review & editing, Supervision.

Data availability

Data will be made available on request.

Declaration of competing interest

This manuscript has not been submitted to, nor is under review at, another journal or other publishing venue. The authors have no affiliation with any organization with a direct or indirect financial interest in the subject matter discussed in the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.164278.

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