Three-dimensional range shifts in biodiversity driven by recent global warming

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Running title: Three-dimensional range shifts

Keywords: climatic debt, community temperature index, climate change, linear mixed-effects model, benthic invertebrates

Type of article: Letters

Number of words in the abstract: 182

Number of words in the main text: 2570

Number of references: 52

Number of figures, tables and text boxes: 5

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.1034v2 | CC BY 4.0 Open Access | rec: 24 Aug 2017, publ: 24 Aug 2017

Abstract

Studies investigating changes in community composition in response to recent global warming are mostly restricted to one-dimensional (e.g. elevational or latitudinal) gradients, whereas species movements are in reality three dimensional (i.e. elevational, latitudinal and longitudinal). Based on 3,245 benthic invertebrate samples from Central European streams over large elevational, latitudinal and longitudinal gradients during the period from 1986 to 2009, we developed an advanced community temperature index (CTI). This CTI enables the analysis of three-dimensional community range shifts not only in freshwater but also in marine and terrestrial environments. Overall, in contrast to terrestrial communities, benthic invertebrate communities have been able to keep up with recent global warming. However, their ability to track temperature shifts differed grossly between the three spatial dimensions, with the strongest response to elevation. Nevertheless, the price these communities had to pay was high, as total benthic invertebrate abundance and richness in cold-dwelling species have already declined by 21% and 52.5%, respectively. Our approach emphasizes the complex reaction of aquatic communities towards increasing temperatures, allowing a more complete picture of the subtle community shifts in response to global warming.

Introduction

An increasing number of studies on the effects of future global warming on biodiversity have predicted substantial losses at both the species [1-3] and genetic levels [4]. In fact, global warming has already accelerated over the past three decades [5], and a number of studies have shown that this warming has already triggered community changes in a wide range of taxonomic groups [6-12]. A promising framework to measure such community changes in response to global warming is the community temperature index (CTI) [13]. Originally proposed by Devictor *et al.* [13], the CTI is the average temperature preference of all species within a given community, weighted by their abundance, thus reflecting the balance between cold- and warm-dwelling species. As the CTI is a measure of average temperatures, it can reflect temporal and spatial differences. These differences give an estimate of the distance a community must shift during a given time interval to keep up with global warming. Subsequent shifting velocities can then be compared with the velocity of isotherm movements driven by global warming, identifying any climatic debt or mismatches between the two velocity measures, such as communities lagging behind the ongoing temperature shifts [10].

Previous CTI studies, as well as most of the other studies on community changes in response to global warming, have had a one-dimensional focus that discounted the fact that most organisms live and move in a three-dimensional space. For instance, based on a latitudinal gradient across Europe, Devictor *et al.* [10] detected a climatic debt in birds and butterflies of 212 and 135 km between 1990 and 2008, respectively. These climatic debts may be either under- or overestimated if other potentially synergistic or antagonistic spatial dimensions (i.e. elevation and longitude) are not considered. In particular, in non-lowland areas moving uphill is the shortest way for a certain species to track its climatic niche as the distance between isotherms in elevation are much shorter than in latitude.

Elevational range shifts may be especially important for riverine benthic invertebrates because rivers and their inherent community composition follow a natural elevational gradient from source to mouth and riverine organisms have higher dispersal capacities within compared to between river networks [14]. Thus, benthic invertebrates might use their river as a ’highway’ to higher elevations to keep up with global warming. However, despite the clear importance of the river network in structuring riverine communities [15], this issue has been largely overlooked to date.

Previous CTI studies on taxonomic groups not incurring a climatic debt, assumed that organisms would keep up with temperature change and be unaffected by global warming [6]. However, the community-level effects of global warming must be clearly distinguished from the underlying effects on the species forming such communities, because an increase in CTI may manifest out of a) simultaneous decreases in cold-dwelling species and increases in warm-dwelling species, b) decreases in cold-dwelling species only, or c) increases in warm-dwelling species only. These three alternative mechanisms for increasing CTI values differ fundamentally in their effects on species diversity. Under a), the species diversity remains unaffected by changes in the CTI, whereas under the alternatives b) and c), losses or gains in species diversity, respectively, will occur. Thus, even if a community can keep up with global warming according to the CTI, severe changes in species diversity cannot be ruled out, which is another important issue that has been unaccounted for in the current CTI approach.

By means of linear mixed-effects model (LMEM), we developed an improved three-dimensional CTI approach that can analyze each dimension independently. We tested our approach using a comprehensive dataset of 3,245 benthic invertebrate samples from Central European low mountain streams taken between 1986 and 2009 and comprising approximately 4.5 million specimens (Supplementary Fig. S1). As a result of the 'highway' effect, we expected a shift in benthic invertebrate communities commensurate with global warming, indicating no climatic debt. Instead of a poleward shift that was highlighted in terrestrial studies, we expected the increase in the CTI should be mainly driven by elevational shifts in communities and only marginally by latitudinal or longitudinal shifts. We further expected that the anticipated increase in the CTI would be caused by an imbalanced loss of cold-dwelling species outweighing the gains of warm-dwelling species, leading to the loss of species diversity.

Results

Community temperature index.

Between 1986 and 2009, both the CTI and annual mean air temperature increased significantly (LMEM: $2.09 \pm 0.93 \times 10^{-2}$ °C yr^{-1}, $t = 2.24$, $P = 0.0274$, Fig. 1a and $3.31 \pm 0.20 \times 10^{-2}$ °C yr^{-1}, $t = 16.39$, $P < 0.0001$, Fig. 1b, respectively). With our three-dimensional approach, elevation was the most important variable covering 68.6% of the explained variability in the CTI, whereas longitude and latitude had low explanative power (4.5% and 2.3%, respectively; Table 1). The elevational velocity of the CTI was 4.86 ± 2.16 m yr^{-1}, which was not significantly different from the required velocity of the uphill isotherm shifts of 5.84 ± 0.36 m yr^{-1} (Table 2; Fig. 1a–d). For the marginally important latitudinal and longitudinal velocity components, required and observed values differed. Benthic invertebrate communities simultaneously shifted northward with a higher velocity (25.03 ± 11.15 km yr^{-1}) than required (7.83 ± 0.48 km yr^{-1}) and westwards by 10.18 ± 4.54 km yr^{-1}, while

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isotherms shifted eastwards with a velocity of 17.14 ± 1.05 km yr^{-1} (Table 2, Fig. 1a, b, e–h; Supplementary Table S1).

The difference between observed and required shifting velocities could be tested for all three spatial dimensions in the LMEM, while only one dimension could be tested when using the original one-dimensional CTI approach, based on the single linear regression model (SLRM) (Table 2). In fact, accounting for all three spatial shifting components simultaneously could substantially alter both the required and observed shifting velocities, compared to SLRM. For the most relevant component, elevation, the required and observed shifting velocities approximately halved in the LMEM compared to SLRM (Table 2; Supplementary Fig. S2). The use of presence/absence or abundance data to calculate shifting velocities produced similar results in both one- and three-dimensional models (Table 2; Fig. 1; Supplementary Table S1; Fig. S2, S3).

Biodiversity loss.

From 1986 to 2009, the abundance of benthic invertebrates decreased by 21% (Fig. 2a). This loss was mainly driven by a decline in abundance of cold-dwelling species (slope ± SE = -0.60 ± 0.23, $F_{1,22} = 6.60$, $P = 0.0175$) and that is only partly mitigated by the concurrent increase in warm-dwelling species (slope ± SE = 0.05 ± 0.02, $F_{1,22} = 10.46$, $P = 0.0038$), which contribute less than 5% to the total benthic invertebrate abundance (Fig. 2c). In contrast, the overall species richness has remained relatively constant over the same period (Fig. 2b). The number of cold-dwelling species decreased by 52.5% during our study period ($F_{1,22} = 10.03$, $P = 0.0045$), however this loss was compensated for by a 39.6% increase in medium- to warm-dwelling species ($F_{1,22} = 5.67$, $P = 0.0264$; Fig. 2d).

Discussion

We examined the shifts in benthic invertebrate communities in Central European low mountain streams in relation to elevation, latitude and longitude, using a modified CTI approach incorporating the three spatial dimensions simultaneously. In contrast to recent terrestrial studies, we found that Central European benthic invertebrate communities are largely tracking temperature shifts. Our results clearly showed that the uphill movement of benthic invertebrates is by far the most important spatial dimension in terms of the response of these communities to global warming. Given there was no significant difference between the observed and required shifting velocities in this dimension, our results indicate that benthic invertebrates have so far kept up with global warming, as the flow direction of rivers can be in any cardinal direction. This specific spatial configuration of riverine ecosystems (dendritic networks) is likely a key reason why riverine benthic invertebrates have been able to keep up with ongoing global warming. The ‘highway’ effect of river networks explains why elevation is more than ten times more important than longitude and latitude in explaining the variation in the CTI. Uphill movement is also a common response of various organism groups to global warming [6,11,12]. Fragmentation of streams by barriers apparently did not impede compensatory movements of benthic invertebrates, as has already been shown in another context [16].

While the two other velocity components, latitude and longitude, were only of marginal importance, their responses to global warming seem to be counterintuitive. Beside the previously mentioned fact that the within-stream movement of benthic invertebrates is the most natural mode of dispersal and independent of latitudinal and longitudinal direction, there are two further explanations for such velocity mismatches. First, as the required shifting velocity is inversely related to the slope of the temperature gradient along each spatial component, small mismatches between observed temperature changes and CTI changes will result in relatively large mismatches in observed and required shifting velocities. This is particularly evident if the spatial temperature gradient associated with one spatial dimension is weak, as was the case for longitudinal and latitudinal temperature gradients in this study. Second, species not only respond to changes in temperature, but also to other environmental variables associated with global warming. Therefore, mismatches between the required and observed shifting velocities in relation to temperature can manifest with associated mismatches in the vectors of temperature and environmental change. For instance, global warming can alter precipitation, leading to alterations in stream discharge regimes [17], which is a key structuring agent of benthic invertebrate communities [18]. The shifting directions of precipitation and temperature isoclines associated with ongoing global warming are not necessarily identical. Instead, diverging shifts may cause spatial (and also temporal) mismatches of suitable living conditions for species [19,20]. Hence, our study contributes to the growing awareness that focusing on one-dimensional shifts of individual aspects of global warming is insufficient to explain recent changes in species ranges [21].

One of the clear strengths of the CTI approach is its ability to track subtle changes in species distribution shifts, compared to examining species range boundaries [13]. However, the markedly different methods in which the benthic invertebrate communities track warming temperatures in elevation, latitude and longitude emphasize that all three spatial dimensions must be considered simultaneously to understand the changes. This is supported by a direct comparison of our three-dimensional model with the previous one-dimensional CTI approach. This demonstrated that the simultaneous consideration of all three spatial dimensions is necessary to track community shifts especially among landscapes in which elevation co-varies with one of the other spatial components. In our study area, for example, higher elevations predominantly occur in the south; therefore, species moving northwards simultaneously experience a negative latitudinal temperature gradient and counteracting positive temperature gradient by moving downhill. Thus, they have to move even further north to track isotherm shifts. Our three-dimensional model accounts for this covariation and considers the net velocities for each of the three dimensions.

In addition to the strong differences resulting from the compensational effects of three-dimensional movements, velocities of ca. 11.8 m y^{-1} in elevation, as calculated by the SLRM appear extremely high; higher, in fact, than those of most other taxonomic groups examined (Fig. 3). The 4.9 m y^{-1} calculated with our LMEM (Fig. 3) fits much better within the existing average range of 4.5 to 6.8 m y^{-1} in other fauna [6,11,12,22-25]. This may be an indication that the CTI values based on single models tend to overestimate shifting velocities.

The current ability of benthic invertebrate communities to track their temperature niche uphill cannot be projected into the future indefinitely as all rivers have a natural endpoint at their source. Therefore, future global warming will inevitably lead to the so-called summit trap effect [26-28], resulting in abrupt and dramatic losses in freshwater biodiversity. Of course, this will depend strongly on the dispersal mode and ability of freshwater organisms, with strong terrestrial dispersers likely to be less affected than those without an aerial dispersal stage. In contrast, the dispersal of most terrestrial species is less restricted by the spatial configuration of their ecosystems, so they have the potential to move in all directions to track suitable habitats [29]. However, the sensitivity of species towards 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 longer distances to track warming temperatures than species living in areas with wide temperature gradients at small spatial scales (e.g. mountains) [7]. Thus, the chance of surviving future global warming not only depends on the species' adaptation potential and dispersal capacity but also on the topographical configuration of their ranges.

Although the CTI of benthic invertebrate communities currently appears in equilibrium with global warming, we detected significant losses of cold-dwelling species and in both overall abundance and richness. From a CTI perspective, this is compensated by a gain in abundance of warm-dwellers and by a gain in richness of medium-to-warm dwellers. Yet, from a conservation perspective, these observed changes in biodiversity are of utmost importance. In response to global warming, the requirements of low temperature habitats drive organisms toward higher elevations or latitudes [6,11,27]. However, significant shifts in geographical ranges are difficult for many riverine cold-dwelling species. The dispersal capacity of riverine insects vary widely, but are often considerably weaker than terrestrial insects [30], suggesting that losses of riverine organisms, particularly cold-dwellers, are likely higher than those of terrestrial species [31,32]. Many of the cold-dwelling species in Europe are endemic freshwater insects [33,34], and their losses can lead to an extinction of the entire species.

On a local scale, losses of cold-dwelling species could be compensated for by the immigration of warm-dwelling species, which would produce no change in α-diversity. However, due to high rates of recruitment, community compositions are likely to change dramatically [2,12]. While such warm-dwelling species are typically species that are already widespread, this replacement of local endemics will reduce biodiversity at larger spatial scales through a reduction of β-diversity (i.e. species turnover), leading to a homogenization of communities [35-37]. At the continental scale, extinctions of cold-dwelling species can only be compensated for by introducing species (i.e. alien species) or by speciation, which usually only occurs at much larger time scales, leading eventually to an overall loss in biodiversity [38,39]. Overall, the observed ongoing losses in benthic invertebrate abundances may be an early indicator that benthic invertebrates have already reached their upper elevational limit, which will subsequently lead to a significant decrease in riverine biodiversity and a climatic debt.

By investigating a comprehensive, long-term dataset of Central European stream benthic invertebrates we demonstrated that species´ response to recent global warming differs grossly in the three spatial dimensions, emphasizing the complex reaction patterns towards increasing temperatures. According to our advanced CTI approach, stream benthic invertebrates are among the very few organism groups that are so far able to keep up with global warming. This reflects the dendritic network structure of riverine ecosystems promoting efficient uphill movement along the river network. Yet, to fully grasp the ecological implication of changes in CTI, changes in biodiversity patterns over time need to also be considered. By examining cold- and warm-dwelling species independent of CTI, we demonstrate clear differences in the response of different organisms to global warming, otherwise overlooked by the CTI approach. Our approach has, therefore, led to a more complete picture of a community's true shift in response to global warming and can also be applied in marine or terrestrial ecosystems.

Methods

Data collection.

A collection of 14,271 benthic invertebrate samples was obtained from standardized field surveys in Austria, Czech Republic, Germany and Luxembourg for the period 1986–2009 that covered 595 km in latitude, 811 km in longitude, and 1,123 m in elevation. Two sampling methods were used in those survey programs. Within the pre-2000 method (a semi-quantitative sampling method), all major habitats were sampled with each one was collected approximately three minutes [40], whereas post-2000, multiple habitat samples were taken using a handnet with a 25 cm × 25 cm opening, resulting in 1.25 m^2 of river bed being sampled [41,42]. Both methods were semi-quantitative and all of the analyses in this study were repeated for abundance data (namely number of individuals per sample) and presence/absence data. Moreover, to account for the change in sampling methodology, the sampling method was included as a covariable in the analysis.

Five filter criteria were applied to the entire survey database to filter out low quality data with human disturbance and to homogenize data: First, only samples of small low mountain streams in Central European highlands were selected to eliminate potential effects of different stream types. Second, all taxa were identified to the level proposed by the EU Water Framework Directive "Operational Taxalist" to ensure comparable taxonomic resolution [43]. Third, samples were considered only if they were collected from March to May to avoid the confounding effects of seasonality [44]. Fourth, to exclude samples from heavily deteriorated sites with very few taxa, samples with species richness and abundance in the lower 10th percentile of all of the samples were excluded from the analysis (species richness: pre-2000 method < 9; post-2000 method < 16; abundance: pre-2000 method < 112 ind. m^{-2}; post-2000 method < 180 ind. m^{-2}). Such samples are not suitable when examining the effects of global warming due to the low species richness and abundance potentially reflecting heavy human disturbance. Fifth, we ensured that a minimum number of ten sites had to be available for each sampling year. After application of the five criteria, 672 species and 3,245 samples remained (Supplementary Fig. S1) at elevations between 25 and 1,148 m a.s.l., and with catchment areas between 0.01 and 524 km^2.

Elevation and catchment area were extracted for each sampling location from digital elevation maps (U.S. National Aeronautics and Space Administration, https://wist.echo.nasa.gov, resolution: 30 m). To estimate the shifting velocity of the isotherms, we obtained the annual mean air temperatures for the period 1985–2008 from the following research projects: "Tools for Sustainable Economy Models" (Austria; http://www.landnutzung.at); Czech Hydrometeorological Institute (http://www.chmi.cz); the German Weather Service (http://www.dwd.de); and Portal Statistics of Luxembourg (http://www.statistiques.public.lu). To account for the cumulative effect of temperature on the life history of the taxa, the reference period for air temperature data was one year prior to the sampling period of benthic invertebrates [18,45,46].

Three-dimensional CTI and species diversity.

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We calculated the CTI according to the method of Devictor *et al.* [13] as the average of the individual species temperature indices (STI) weighted by the abundance of the individual species in a community. All of the analyses were also repeated without weighting (i.e. based only on the presence/absence of the species).

As studies published so far using the CTI have been restricted to terrestrial species only, the temperature envelopes of these species were calculated using air temperatures. This approach is also applied in most freshwater studies using species distribution models (SDM) [1,2] because appropriate water temperature data are still lacking. However, although there are clear links between air and water temperatures [47], there are also clear inconsistencies; for example, in contrast to air temperatures, water temperatures cannot drop below zero in running waters. Therefore, rather than calculate the STI based on species air temperature ranges, we calculated STIs based on the species´ stream zonation index [33], which reflects the inherent differences in water temperature along a longitudinal gradient from the source to mouth [33].

Seven stream zones were considered from the river source to mouth: 1) eucrenal, spring region; 2) hypocrenal, spring brook; 3) epirhithral, upper-trout region; 4) metarhithral, lower-trout region; 5) hyporhithral, grayling region; 6) epipotamal, barbel region; and 7) metapotamal, bream region [48]. In Europe, the occurrence probability for most taxa in each of the stream zones has already been compiled and summarized into a species-specific stream zonation index [49]. A 10-point assignment system produced the zone preference value for each taxon (one taxon can occupy several zones). A further advantage of the zonation index is that this index already reflects the entire distribution range of a species and that it is independent of elevation and latitude. Hence, the use of the zonation index avoids the recurring criticism that in many studies, temperature niches of species are estimated from distribution data that did not cover the entire distribution area. The zonation preference value can be translated to water temperature by using the mean annual amplitudes for each zone: (zone 1) 2 °C, 2) 5 °C, 3) 9 °C, 4) 13 °C, 5) 18 °C, 6) 20 °C and 7) 22 °C [48,50]. The STI of a given species is then calculated based on the average temperature conditions over the stream zones in which it is found. The STI of benthic invertebrate species may not be the actual temperature; however, the species can be ordered along a temperature gradient and their relative temperature values can be estimated through this approach. Nevertheless, there are technical issues in the estimation of CTI-type values. For instance, Rodríguez-Sánchez *et al.* (2012) [51] argued that microclimatic variation is not captured by the coarse resolution of temperature database, where differences of several degrees in temperature may exist at the same grid. More fundamentally, STI estimates based on species' current distributions may be biased indicators of their thermal tolerances. In our study, one of advantages of STI-approach based on the species' stream zonation index is that this approach covers the entire distribution range of the benthic invertebrates used in our study region.

The CTI reflected the relative composition of cold- versus warm-dwelling species in local communities. This composition is calculated for a given sampling site as the average STI weighted by the species abundance (CTI-Abundance) and presence/absence (CTI-Presence/absence) [13].

Statistical methods.

To deal with the problem of spatial auto-correlation within our database, we applied a linear mixed-effects model (LMEM) to examine the CTI (CTI-Abundance and CTI-Presence/absence) variation in three dimensions (elevation, latitude and longitude) and over time. Six abiotic variables were selected for the LMEMs, among elevation, latitude, longitude and sampling year of each sample were used as continuous independent variables; additionally, we included catchment area and sampling method (pre-2000 method = 1 and post-2000 method = 2) in the models to control for confounding factors. Within the LMEMs of CTI, variables with the fixed effects were elevation, latitude, longitude, sampling year and catchment area, whereas sampling method and geographic coordinate were treated as the variables with random effects.

The slope (or regression coefficient) of each explanatory variable allows for the expression of the rate of change in the CTI metrics that is dependent on the temporal (time, °C yr^{-1}) and spatial (elevation: °C m^{-1}; latitude and longitude: °C km^{-1}) trends. The ratio between the temporal and spatial trends in the CTI (elevation: °C yr^{-1} / °C m^{-1} = m yr^{-1}; latitude and longitude: °C yr^{-1} / °C km^{-1} = km yr^{-1}) can be used to show the real (or observed) spatial shifting velocity of the CTI in response to global warming [10]. Estimating all of the regression coefficients simultaneously in one model has the advantage of accounting for moderate co-variation in gradients so that the resulting velocities are independent of local topographical settings.

The 'required shifting velocity' (or mean air temperature; i.e. concurrent movement of temperature isotherms based on the annual mean air temperature) can be estimated using the ratio between the temporal and spatial slopes of mean air temperature. We only selected the sampling year and three spatial variables in the LMEMs of temperature because changes in air temperature were not related to the catchment area and sampling method. Within the LMEMs of temperature, variables with the fixed effects were elevation, latitude, longitude and sampling year, whereas geographic coordinate was treated as the variable with random effects. The comparison between the observed shifting velocity of the CTI and required shifting velocity of air temperature provided an estimate of the lag (i.e. climatic debt) between the shift in air temperature and response of the benthic invertebrate communities [10].

Taking the elevational shifting velocity as an example, the temporal CTI and annual mean air temperature were $2.09 \pm 0.93 \times 10^{-2}$ °C yr^{-1} (Fig. 1a; Supplementary Table S1) and $3.31 \pm 0.20 \times 10^{-2}$ °C yr^{-1} (Fig. 1b; Supplementary Table S1), respectively. The elevational gradients of CTI and temperature were equivalent to $4.31 \pm 0.19 \times 10^{-3}$ °C m^{-1} (Fig. 1c; Supplementary Table S1) and $5.67 \pm 0.06 \times 10^{-3}$ °C m^{-1} (Fig. 1d; Supplementary Table S1), respectively. Therefore, the velocity of the elevational (uphill) shifts in the CTI and isotherm could be calculated as the ratio between the temporal and spatial trends, and they were 4.86 ± 2.16 m yr^{-1} ($2.09 \times 10^{-2} / 4.31 \times 10^{-3}$) and 5.84 ± 0.36 m yr^{-1} ($3.31 \times 10^{-2} / 5.67 \times 10^{-3}$), respectively.

We used partial residual plots to show the temporal and spatial gradients of the CTI metrics and temperatures, which were estimated by the LMEM. These plots allowed for a direct comparison of the slope of the regression lines between the CTI metrics and mean air temperatures (or required velocity) given that the other independent variables were also included in the model. To compare the importance of simultaneously considering the three spatial dimensions with previously used one-dimensional CTI approaches, we also compared one-dimensional SLRMs for each of the regression coefficients used in the LMEM (i.e. elevation, latitude and longitude), individually.

We examined multicollinearity in the final models using the Variance Inflation Factor (VIF; Supplementary Table S1; all values < 5). We assessed the differences between the observed and required shifting velocities using the Wilcoxon test in R, with 9,999 random bootstraps. These analyses were repeated ten times, and the final *P* value was the median of these repeats. The climatic debt can be determined only if there is significant difference between the observed and required shifting velocities. In addition, we analyzed the relative importance of the six explanatory variables using the *relaimpo* package in R [52]. Four bootstrapping algorithms (LMG [Lindeman, Merenda and Gold], last, first and pratt) were considered for the final relative importance analyses.

To test changes in the community composition, we allocated all of the taxa to four thermal condition groups. We arranged all of the taxa in ascending order according to the STI. The taxa in the 1st quartile (Q1) were defined as cold-dwelling species, and the taxa in the 4th quartile (Q4) were defined as warm-dwelling species. Taxa in the 2nd (Q2) and 3rd quartiles (Q3) were defined as medium-to-cold- and medium-to-warm-dwelling species, respectively. We examined the trends of both relative abundance and species richness for each of the four thermal groups in responses to global warming using single linear regressions.

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Acknowledgments

The authors wish to thank Bob O´Hara for providing statistical advice, all contributors to the freshwaterecology.info database and the state authorities for providing most of the benthic invertebrate data. This study was supported by Umweltbundesamt (UFOPLAN 3710 24 207) and the research funding program “LOEWE - Landes-Offensive zur Entwicklung Wissenschaftlich-oekonomischer Exzellenz” of Hesse’s Ministry of Higher Education, Research and the Arts.

Author contributions

PH, FL and SS developed the basic idea and concept of the manuscript. FL collected data and analysed output data. PH, FL and SS wrote the first draft of the manuscript, AS, AWL and JDT contributed substantially to revisions.

Competing financial interests

The authors declare no competing financial interests.

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Table 1. The relative importance of environmental variables for the community temperature index (CTI). Four bootstrapping algorithms (LMG [Lindeman, Merenda and Gold], last, first and pratt) are used to calculate the relative importance of abiotic variables. The three most important variables are ordered in **a**, **b** and **c**. Area = Catchment area.

Variable	Algorithm	Elevation (%)	Latitude (%)	Longitude (%)	Year (%)	Area (%)	Method (%)	Explained variation (%)
CTI-Abundance	LMG	64.1 **a**	4.6	4.8	7.4	11.5 **b**	7.6 **c**	28.1
	Last	77.5 **a**	2.4	10.0 **b**	1.0	9.0 **c**	0.1	
	First	51.5 **a**	7.9	0.6	14.3 **c**	10.6	15.1 **b**	
	Pratt	81.3 **a**	–5.7	2.7	8.7 **c**	10.6 **b**	2.5	
CTI-Presence/absence	LMG	61.6 **a**	4.2	2.3	7.2	17.2 **b**	7.6 **c**	32.5
	Last	73.6 **a**	5.3 **c**	4.9	0.9	15.2 **b**	0.2	
	First	50.5 **a**	5.2	0.1	13.9	15.2 **b**	15.0 **c**	
	Pratt	77.9 **a**	–6.9	0.7	7.9 **c**	16.4 **b**	4.0	

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Table 2. Summary of shifting velocities of benthic invertebrates in three dimensions. Wilcoxon tests were used to assess differences between the observed and required shifting velocities. NS refers to non-significance.

Data category	Variable	Single linear regression model			Linear mixed-effects model		
		Required	Observed	*P*	Required	Observed	*P*
Abundance	Elevation (m yr^{-1})	–12.14 (± 3.76)	–11.76 (± 3.51)	0.5627	–5.84 (± 0.36)	–4.86 (± 2.16)	0.2356
	Latitude (km yr^{-1})	NS	19.59 (± 5.85)	–	–7.83 (± 0.48)	–25.03 (± 11.15)	0.0036
	Longitude (km yr^{-1})	–18.59 (± 5.75)	NS	–	–17.14 (± 1.05)	10.18 (± 4.54)	<0.0001
Presence/absence	Elevation (m yr^{-1})	–12.14 (± 3.76)	–11.57 (± 3.48)	0.5855	–5.84 (± 0.36)	–4.56 (± 1.99)	0.1331
	Latitude (km yr^{-1})	NS	23.14 (± 6.95)	–	–7.83 (± 0.48)	–13.57 (± 5.92)	0.0687
	Longitude (km yr^{-1})	–18.59 (± 5.75)	NS	–	–17.14 (± 1.05)	12.53 (± 5.47)	<0.0001

Figure legends

Figure 1. Partial residual plots of the CTI (community temperature index) for benthic invertebrates and mean temperatures by using the linear mixed-effects models in the low mountain rivers in Central Europe. Instead of original values, partial residuals obtained by the linear mixed-effects models are used to make plots. The residual CTI is based on abundance data. The temporal trends of (a) the CTI for benthic invertebrates from 1986 to 2009 and (b) mean temperatures from 1985 to 2008; (c) spatial trends of the CTI and (d) mean temperatures from low to high elevation; (e, f) from south to north; and (g, h) from west to east. The results of significance tests are in Supplementary Table S1.

Figure 2. Temporal trends of (a) abundance, (b) species richness and (c, d) their proportions among four thermal condition groups in the low mountain rivers in Central Europe from 1986 to 2009. ** $P < 0.01$ and * $P < 0.05$.

Figure 3. Observed elevational shifting velocity of flora and fauna communities in response to global warming. The values of benthic invertebrates are from the current study using the linear mixed-effects models, and the remaining values are from literature. The complete literature list is available in Supplementary Appendix S1. The error bar refers to standard deviation. The number above the error bar refers to the number of studies on which the calculation is based.

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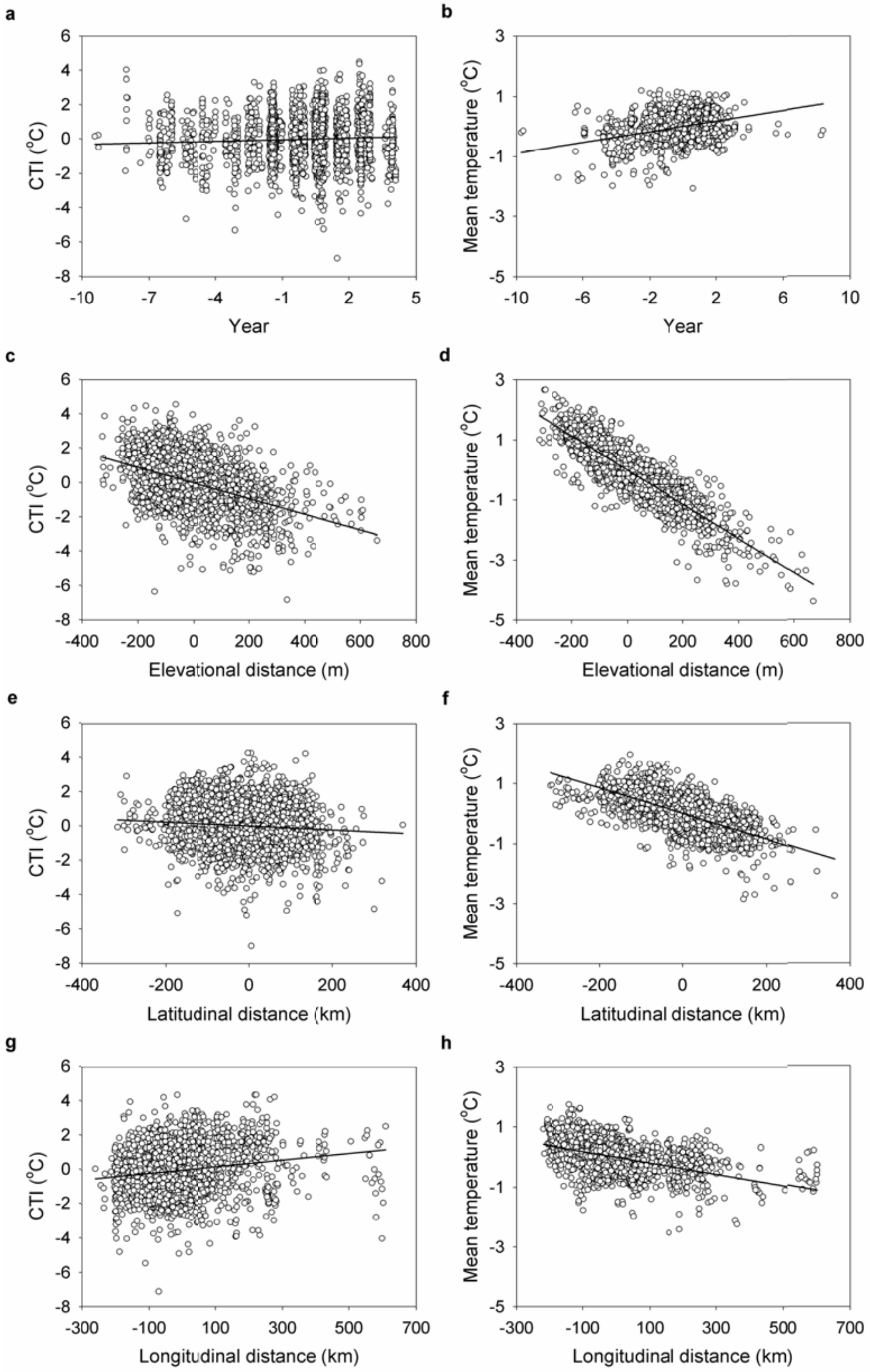

Figure 1.

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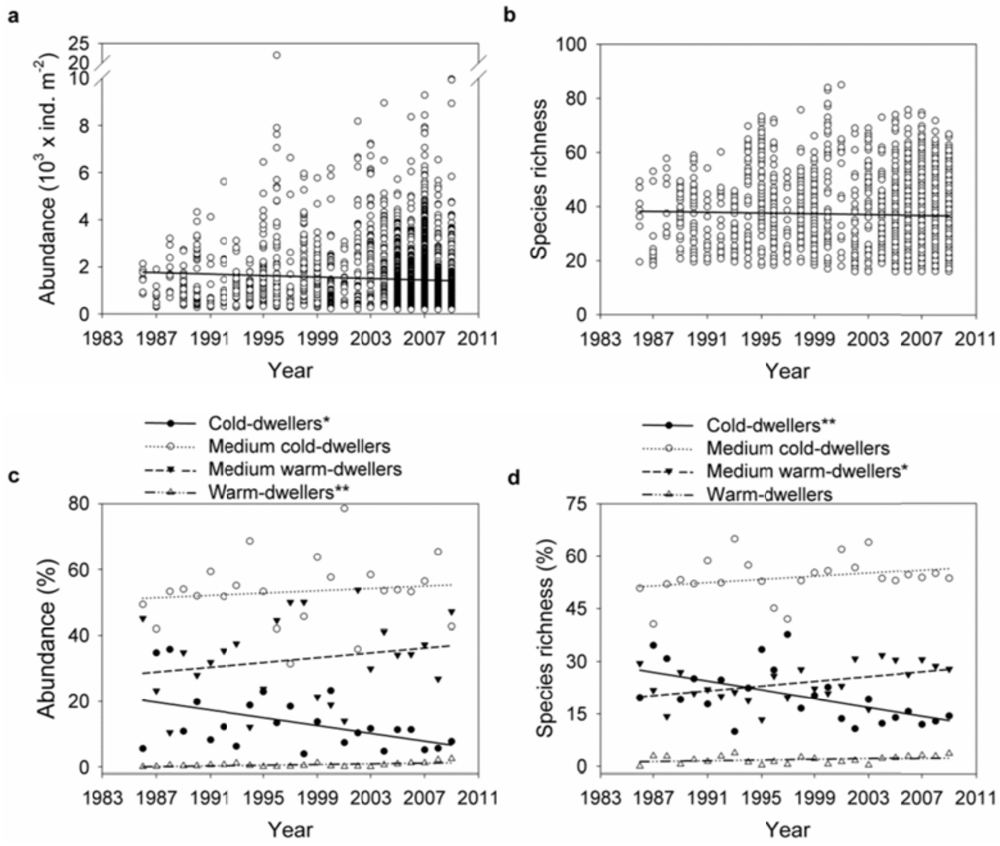
a
b
c
d
Abundance (10^3 x ind. m^{-2})
Species richness
Abundance (%)
Species richness (%)
Year
1983 1987 1991 1995 1999 2003 2007 2011
Cold-dwellers*
Medium cold-dwellers
Medium warm-dwellers
Warm-dwellers**
Cold-dwellers**
Medium cold-dwellers
Medium warm-dwellers*
Warm-dwellers

Figure 2.

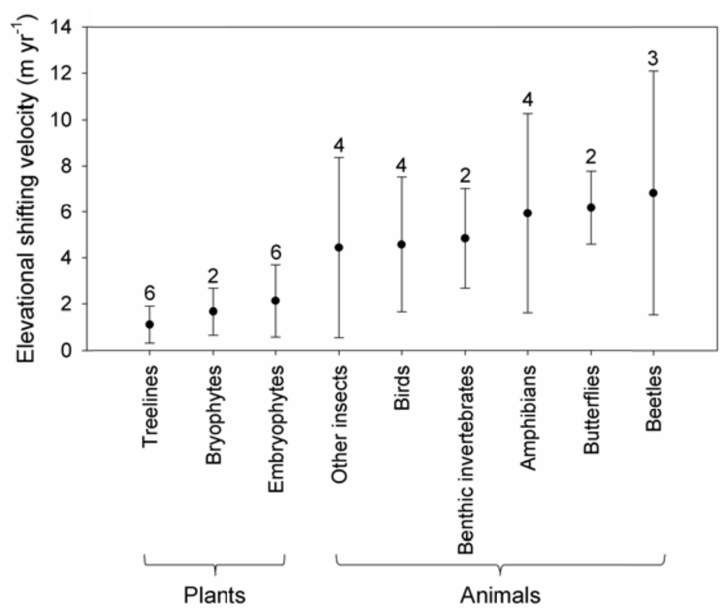
Elevational shifting velocity (m yr^{-1})
14
12
10
8
6
4
2
0
6
2
6
4
4
2
4
2
3
Treelines
Bryophytes
Embryophytes
Other insects
Birds
Benthic invertebrates
Amphibians
Butterflies
Beetles
Plants
Animals

Figure 3.