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Effects of changing climate on European stream invertebrate communities: A long-term data analysis

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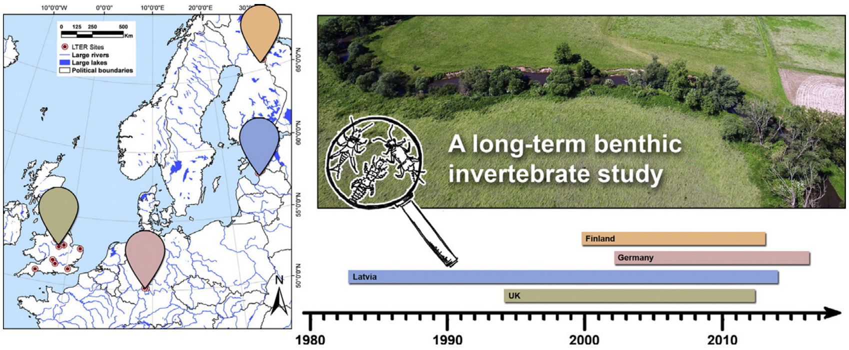
HIGHLIGHTS

- We examined the effects of climate change on benthic invertebrate communities.
- Stronger effects of previous year climatic conditions than gradual changes over time
- No changes in overall abundance and number of taxa, but taxon-specific changes
- Stronger impact of temperature on sensitive taxa in agricultural regions
- Changing climatic conditions associated with changes in feeding group composition

GRAPHICAL ABSTRACT



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ABSTRACT

Long-term observations on riverine benthic invertebrate communities enable assessments of the potential impacts of global change on stream ecosystems. Besides increasing average temperatures, many studies predict greater temperature extremes and intense precipitation events as a consequence of climate change. In this study we examined long-term observation data (10–32 years) of 26 streams and rivers from four ecoregions in the European Long-Term Ecological Research (LTER) network, to investigate invertebrate community responses to changing climatic conditions. We used functional trait and multi-taxonomic analyses and combined examinations of general long-term changes in communities with detailed analyses of the impact of different climatic drivers (i.e., various temperature and precipitation variables) by focusing on the response of communities to climatic conditions of the previous year. Taxa and ecoregions differed substantially in their response to climate

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Disturbances
Extreme events
Freshwater macroinvertebrates
Global change
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change conditions. We did not observe any trend of changes in total taxonomic richness or overall abundance over time or with increasing temperatures, which reflects a compensatory turnover in the composition of communities; sensitive Plecoptera decreased in response to warmer years and Ephemeroptera increased in northern regions. Invasive species increased with an increasing number of extreme days which also caused an apparent upstream community movement. The observed changes in functional feeding group diversity indicate that climate change may be associated with changes in trophic interactions within aquatic food webs. These findings highlight the vulnerability of riverine ecosystems to climate change and emphasize the need to further explore the interactive effects of climate change variables with other local stressors to develop appropriate conservation measures.

1. Introduction

Ongoing global climate change is regionally specific, but generally characterized by increasing global mean temperature and changing precipitation patterns, coupled with an increasing frequency of extreme temperature and precipitation events (Coumou and Rahmstorf, 2012; IPCC, 2014). While increasing temperatures may have long-term effects on riverine ecosystems, an increasing frequency of extreme weather events may have more immediate consequences for such ecosystems (Leigh et al., 2015). For example, a change in timing and a higher frequency of floods and droughts is changing the flow regime of rivers significantly (Blöschl et al., 2017; Daufresne et al., 2007; Feyen and Dankers, 2009; Hirabayashi et al., 2013) leading to severe consequences on the structure of riverine and riparian ecosystems (Bunn and Arthington, 2002; Lytle et al., 2017; Tonkin et al., 2017b; Woodward et al., 2016). Higher frequencies of extreme events may therefore have greater impacts on stream biota than steady changes in temperature and precipitation (Death, 2010; Lake, 2000; Mouthon and Daufresne, 2006).

Long-term biomonitoring is crucial to identify actual and potential trajectories of climate change effects on communities (Jackson and Fuereder, 2006; Parmesan and Yohe, 2003) and especially to disentangle the effect of steady changes and immediate response to recent climatic conditions and extreme events. A previous long-term study on stream invertebrate communities in the UK revealed that total abundance tended to decline over time in response to increasing winter temperatures (Durance and Ormerod, 2007). However, the authors found contrasting effects of rising temperature on communities depending on local conditions (Durance and Ormerod, 2007). Recent findings by Bowler et al. (2017) demonstrated that long-term shifts in aquatic communities due to climate change were less predictable than in terrestrial communities, indicating that complex interactions in the riverine multiple stressor context may explain different responses of freshwater communities. Similar observations were made in large rivers in France where a transition towards generalist and tolerant (often invasive) species was observed (Floury et al., 2013). This transition, however, was partially confounded by local improvement in water quality that explained the settlement of new pollution-sensitive taxa (Floury et al., 2013). To date, most studies on the ecological effects of climate change have focused on long-term changes in average conditions, while the implications of altered climate extremes remains poorly understood despite being key drivers of ecological change (Smith, 2011).

The mechanisms by which climate change affects invertebrate communities will depend on many factors including species traits (e.g. thermal preferences), and regional conditions (Easterling et al., 2000; Jähnig et al., 2017). For example, communities in mountainous regions with lower temperatures and/or higher flow velocity are more likely to experience loss of taxa and range reductions resulting from increasing temperatures and reduced flow (Buisson et al., 2008; Domisch et al., 2011; Poff et al., 2010; Sauer et al., 2011). Similarly, cold stenotherm taxa in the colder regions of Europe might be negatively affected by increasing temperatures as they lack northern refuges, while eurytherm taxa might benefit from changing thermal conditions and be able to expand their range (Hering et al., 2009; Jyväsjärvi et al., 2015). Climate change and extreme events may also influence the quality and quantity of feeding resources and thus specifically affect certain trophic guilds (functional feeding groups; FFGs). Changes in the trophic composition of invertebrate communities could adversely affect aquatic food webs and ecosystem functioning. To investigate the response at different levels of biological organization, a multi-taxa approach incorporating the ecological role of each taxa is essential (Woodward et al., 2010).

Here we combined taxonomic richness and species abundance metrics, sensitivity metrics (i.e., biomonitoring indices), and functional metrics (Feld and Hering, 2007; Hering et al., 2004) to analyze the community response to changing climate. Similar to previous studies we considered overall taxonomic richness and abundance (e.g., Durance and Ormerod, 2007; Floury et al., 2013; Hallmann et al., 2017; Vaughan and Ormerod, 2012). Furthermore, we investigated the response of changes in numbers and abundance of widespread freshwater insects (Ephemeroptera, Plecoptera and Trichoptera; EPT-taxa), that are known to be susceptible to a broad variety of stressors (Hering et al., 2004; Piggott et al., 2012). Foremost, sensitive groups like Plecoptera are expected to be vulnerable to warming temperatures, since they show frequent cold-adaptation and have very narrow environmental tolerances (Fochetti and de Figueroa, 2006; Pritchard et al., 1996; Tierno de Figueroa et al., 2010). Additionally, we analyzed classic sensitivity metrics like saprobic indices (Rolauffs et al., 2004; Zelinka and Marvan, 1961) and the ASPT (Average score per taxon, an index of the Biological Monitoring Working Party, see Armitage et al., 1983) that have traditionally been used in the European Union to assess the organic pollution of streams (Hering et al., 2004). These metrics are also expected to be affected by climate change, as increased temperatures can reduce oxygen concentrations in water (Verberk et al., 2016). Finally, we considered FFGs, as previous studies have suggested that climate change has the potential to modify their composition (e.g., by affecting detrital decomposition rates or algal consumption; Pyne and Poff, 2017). Detrital shredders and algal grazers were suggested to be disproportionately vulnerable to projected thermal warming and streamflow reductions (Pyne and Poff, 2017), probably because many of these taxa belong to cool-adapted taxa that may be close to their thermal maxima (Boyero et al., 2012). Additionally, invasive species might displace congeneric native species, without being functionally redundant (as shown for amphipods: Bacela-Spychalska and van der Velde, 2013; Jourdan et al., 2016). A change in FFGs could therefore induce a strong effect on energy flow dynamics of the stream detritus-based food web (Graça, 2001; Pyne and Poff, 2017), indicating the vulnerability to climate change also at a functional level.

In our study, we investigated the long-term responses of benthic invertebrate communities to climate change and examined the short-term responses of these communities to the climatic conditions (and extreme events) experienced over the year leading up to sampling. We used data from 26 sampling sites within the Long-Term Ecological Research (LTER) network (Haase et al., 2016; Mirtl et al., submitted) located in four European countries, where benthic invertebrates were surveyed annually for between 10 and 32 years. We used a set of 20 different metrics to cover responses at different levels of biological organization. We hypothesized that 1) antecedent climatic conditions and the occurrence of extreme events affect community metrics more than steady climatic changes over time. More specifically, we expected, that 2) overall taxonomic richness and abundance declined under climate change conditions (i.e., over time and with increasing temperatures). This decline should be most pronounced in changing numbers and abundance of sensitive EPT-taxa (Rahel and Olden, 2008; Tierno de Figueroa et al., 2010) and to a slight degree counterbalanced by an increase of invasive (often tolerant) species. Furthermore 3) sensitivity metrics would be negatively affected by higher mean temperatures and extreme precipitation events (Verberk et al., 2016); and 4) FFGs should be affected by increasing temperature and extreme events, with a reduction in shredders and grazers, as suggested by recent studies (e.g., Pyne and Poff, 2017).

2. Materials and methods

2.1. Sampling sites and data collection

Our survey included sampling sites at 26 perennial rivers located in Finland, Germany, UK and Latvia (Fig. 1, Table 1). Streams in Finland were located in conifer-dominated riparian forests, while the streams in Germany and the UK were mostly surrounded by agricultural land. The Latvian sample sites were situated in North Vidzenme Biosphere Reserve and partly surrounded by agricultural land. Sampling season varied across sites, but was consistent for each site through time. Sampling took place anually and typically across 10–32 years (mean ± SD: 15 ± 3.5 years, for details see Table 1). Benthic invertebrate abundance data was compiled from routine surface water survey data, which followed standardized multi-habitat sampling protocols (e.g., Haase et al., 2004; Mykra et al., 2006; Table 1) and taxonomic processing. Prior to analysis, all taxonomic levels were adjusted according to Haase et al. (2006a) to standardize the taxonomic level and enable consistency in the identification work of involved laboratories. For most taxa, the resolution was at the genus or species level, but selected families such as Chironomidae, Naididae, or Tubificidae were determined only to the sub-family or family level.

2.2. Calculation of community metrics

To characterize the benthic invertebrate assemblages, we used invertebrate abundance data and initially calculated 23 community metrics for each site and sampling event. Since some were strongly correlated with each other we finally selected 20 metrics. The final set of metrics is well suited to analyze the effect of environmental stressors at different levels of biological organization (e.g., Feld and Hering, 2007; Leps et al., 2015; for a full list of metrics see Table 2). All metrics were calculated using abundance data with the software ASTERICS, Version 4.04 (AQEM Consortium, 2013) based on the Water Framework Directive (WFD) compliant operational taxon list (Haase et al., 2006b).

Some metrics are not self-explanatory, thus we provide details in the following text. The index of biocoenotic region (IBCR) describes the

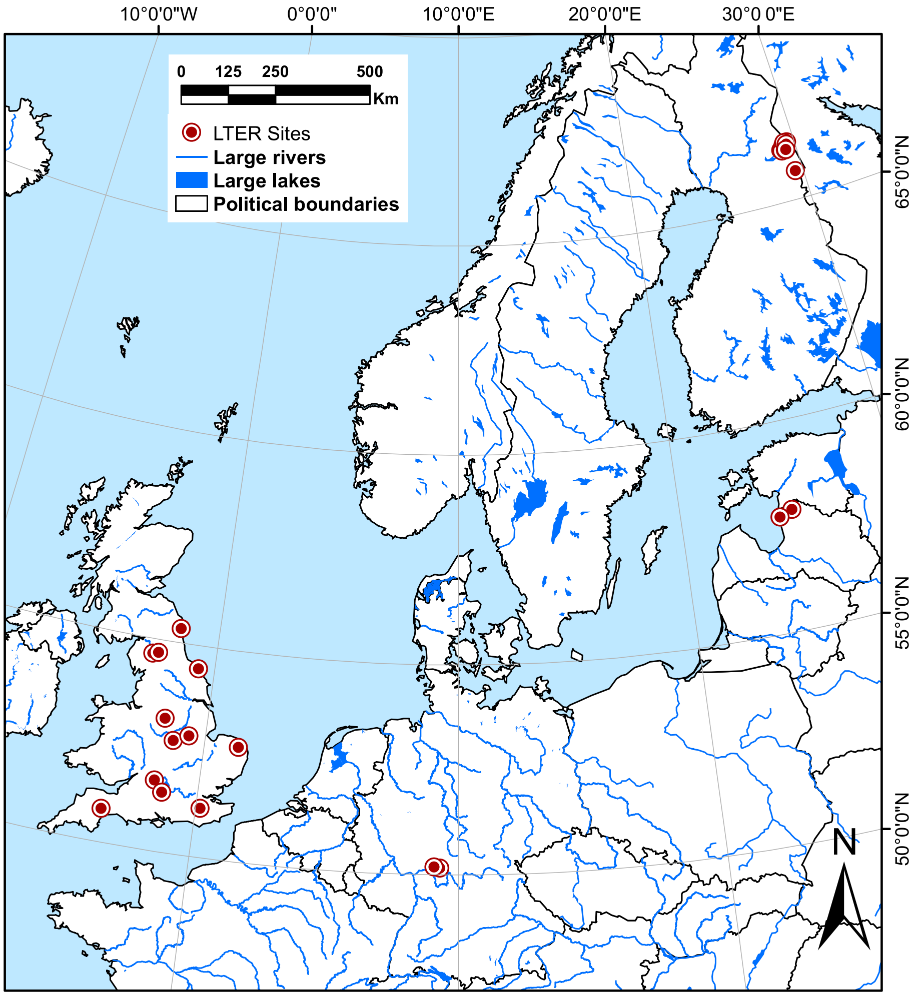

Fig. 1. Overview of sampling sites located in Finland, Germany, Latvia and the UK. All sites are part of the long-term ecological research (LTER) network and were sampled anually across 10–32 years.

Table 1
Overview of sampling sites used for estimating the impact of climate change on benthic invertebrate communities, with stream characteristics, ecoregion, site location, sampling method and sampling period considered in the analyses.

Country	Ecoregion (according to Illies et al., 1978)	Site name	Site code	Latitude	Longitude	Catchment size (km^2)	Altitude (m)	Sampling period	Sampling time	Sampling method	Flow pattern	Land use
Finland	Fenno-scandian shield	Hangaspuro	Fi_Ha	66.3358	29.3333	8.2	256	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Kantojoki	Fi_Ka	66.2270	29.1148	29.7	244	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Kotioja	Fi_Ko	66.3813	29.4667	11.0	247	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Matinjärvenpuro	Fi_Ma	66.3818	29.5758	4.0	247	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Pessaripuro	Fi_Pe	66.2030	29.1641	5.2	259	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Porontimajoki	Fi_Po	66.2083	29.3861	21.9	259	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Putaanoja	Fi_Pu	66.3792	29.4236	33.0	217	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Salmipuro	Fi_Sa	65.6699	29.5808	4.1	239	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Uopajanpuro	Fi_Uo	66.3380	29.5186	11.4	177	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Surface-water dominated	Conifer-dominated riparian forest
Finland	Fenno-scandian shield	Vansselijoki	Fi_Va	66.2155	29.4031	6.7	258	2000–2013	Autumn	Multi-habitat kick sampling (Mykra et al., 2006)	Ground-water dominated	Conifer-dominated riparian forest
Germany	Central highlands	Bieber	Ge_Bi	50.2005	9.2749	25	154	2001–2016	Spring	Multi-habitat kick sampling (Haase et al., 2004)	Ground- and surface-water	Agricultural dominated land
Germany	Central highlands	Kinzig	Ge_Ki	50.1950	9.1327	713	124	2002–2016	Summer	Multi-habitat kick sampling (Haase et al., 2004)	Ground- and surface-water	Agricultural dominated land
Latvia	Baltic province	Vecsalaca	La_Vs	57.7531	24.4095	3420	8	1983–2015	Summer	Standardized quantitative sampling (APHA-AWWA-WPCF, 1992)	Surface-water dominated	1/2 mixed and coniferous forest, 1/2 agricultural land
Latvia	Baltic province	Mazsalaca	La_Ma	57.8740	24.9965	2300	57	1996–2015	Summer	Standardized quantitative sampling (APHA-AWWA-WPCF, 1992)	Surface-water dominated	1/2 mixed and coniferous forest, 1/2 agricultural land
UK	Great Britain	Bradgate Brook	UK_BB	52.6834	−1.2284	4	75	1997–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Ground-water dominated	Agricultural dominated land
UK	Great Britain	River Bure	UK_Bu	52.7283	1.3560	330	12	1996–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Ground-water dominated	Agricultural dominated land
UK	Great Britain	Cringle Brook	UK_CB	52.8488	−0.6338	38	97	2002–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Ground-water dominated	Agricultural dominated land
UK	Great Britain	River Coln	UK_Col	51.6883	−1.7077	120	31	1999–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Ground-water dominated	Agricultural dominated land
UK	Great Britain	River Coquet	UK_Coq	55.3382	−1.6294	480	109	1995–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Surface-water dominated	Agricultural dominated land
UK	Great Britain	River Eden (Cumbria)	UK_EdC	54.6485	−2.6146	580	85	1998–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Surface-water dominated	Agricultural dominated land
UK	Great Britain	River Eden (Kent)	UK_EdK	51.1729	0.1738	180	11	1998–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Ground- and surface-water	Agricultural dominated land
UK	Great Britain	River Esk	UK_Es	54.4615	−0.6617	235	120	1999–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Surface-water dominated	Agricultural dominated land
UK	Great Britain	River Exe	UK_Ex	50.8041	−3.5114	600	27	2000–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Surface-water dominated	Agricultural dominated land
UK	Great Britain	River Lambourn	UK_Lam	51.4207	−1.3515	210	81	1998–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Ground-water dominated	Agricultural dominated land
UK	Great Britain	River Lathkill	UK_Lat	53.1777	−1.6716	310	142	1994–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Ground-water dominated	Agricultural dominated land
UK	Great Britain	Trout Beck	UK_TB	54.6945	−2.3800	12	6	1997–2012	Spring	Multi-habitat kick sampling (ECN, 1999)	Surface-water dominated	Moorland

Table 2
Calculated community metrics and whether they were considered in the statistical analysis. Percentage values were calculated based on the overall abundance of sampled invertebrates. For details see Hering et al. (2004).

Full names	Short name	Considered for final analysis?
Taxonomic richness	Taxa_richness	Yes
Number of families	Num_Fam	No (strong collinearity with taxa richness)
Number of EPT-taxa	Num_EPT	Yes
Simpson diversity index	Simpson	No (strong collinearity with Shannon diversity index)
Shannon diversity index	Shan	Yes
Evenness	Evenness	No (strong collinearity with Shannon diversity index)
Total abundance	TAbund	Yes
Ephemeroptera, Plecoptera and Trichoptera; percentage of abundance	EPT_perc%	Yes
Ephemeroptera; percentage of abundance	E%_perc	Yes
Plecoptera; percentage of abundance	P%_perc	Yes
Trichoptera; percentage of abundance	T%_perc	Yes
Percentage of invasive species	Neoz%	Yes
Saprobic index according to Zelinka & Marvan	SI_ZM	Yes
German saprobic index	GSI	Yes
Biological Monitoring Working Party	BMWP	Yes
Average score per taxon	ASPT	Yes
Index of biocoenotic region	IBCR	Yes
Percentage of active filter feeders	ActFilFeed%	Yes
Percentage of passive filter feeders	PasFilFeed%	Yes
Percentage of gatherers and collectors	GathCol%	Yes
Percentage of grazers and scrapers	GrazScra%	Yes
Percentage of predators	Pred%	Yes
Percentage of shredders	Shred%	Yes

characteristic position of each taxon across the (largely temperature-determined) stream gradient (from source to mouth) and is averaged across all taxa. The IBCR score range from 1 to 10, lower scores indicating preference for spring (crenal) sites, and higher scores indicating preference for brackish (score: 8, hypopotamal) and stagnant waters (score: 9–10; AQEM Consortium, 2013; Moog, 1995). The German saprobic index (GSI; Rolauffs et al., 2004) and the saprobic index developed by Zelinka and Marvan (1961) are commonly used to assess the organic pollution of streams via estimated oxygen demand of benthic invertebrate species (Hering et al., 2004). Scores range from 1 to 4 (GSI) and 0 to 4 (Zelinka and Marvan), respectively, with low values indicating lower tolerance of community to organic pollution. The Biological Monitoring Working Party (BMWP) score is derived from the known or perceived tolerances of all benthic invertebrate families to organic pollution; the higher the BMWP score, the better the water quality (Armitage et al., 1983). The Average Score Per Taxon (ASPT) is the BMWP score of the sample divided by the number of scoring families; scores range from 1 to 10, higher scores indicating greater intolerance of poor water quality (Armitage et al., 1983).

2.3. Climatic conditions and extreme events

In order to analyze the effect of antecedent climatic conditions and extreme weather events on invertebrate communities, we extracted daily maximum, minimum and mean air temperature, and precipitation, from the European Climate Assessment Dataset (0.25° resolution) for each site (Klein Tank et al., 2002). We used data from 1950 to 2016 to calculate monthly mean values for each site and to define the threshold for extreme events (Supplementary Fig. S1). So far, there is no consistent method to identify a threshold for the definition of an extreme event (see Stephenson, 2008). Here, we defined the threshold as the value that exceeded the monthly mean value by at least two standard deviations (e.g., Ewald et al., 2015; Fowler and Kilsby, 2003). That means we classified a day as extreme, if mean daily values exceeded the mean daily value of that month by at least two SDs. Calulation of 'extreme hot days' was based on daily maximum air temperature, for 'extreme cold days' we used daily minimum air temperature and for 'extreme precipitation' we used mean daily precipitation data. The daily resolution of our data enabled us to check how many days were above the threshold and can therefore be classified as extreme. We then counted the number of extreme days (hot or cold days and days with high precipitation) within a 12-month period prior to the month of sampling. Furthermore, we included 'mean temperature' and 'mean daily precipitation' during the 12 month period. We chose a 12-month period, since most aquatic species have an annual life cycle (e.g., 68% of all listed taxa in Tachet et al., 2000) and climatic conditions of the previous 12 months likely affected the survival of the previous generation (both in their larval and adult stage), which may affect the number of laid eggs and thus the new generation.

2.4. Statistical analysis

To simultaneously investigate the impact of time and climatic conditions on benthic invertebrate communities, we used multiple regression analyses. Metrics were used as dependent variables in separate linear mixed-effects models (LMM) using the *lmer* function of the lme4 package (Bates et al., 2012) in R 3.3.2 (R Development Core Team, 2016). Prior to statistical analyses we log-transformed total abundance data and logit-transformed all percentage metrics, according to Warton and Hui (2011). As explanatory variables we used antecedent climatic conditions and extreme events over the twelve months leading up to sampling. The explanatory variables were initially checked for collinearity using Spearman's rank correlation test (collinearity was assumed for $|\rho| \geq 0.7$; see Dormann et al., 2013). 'Year' was included as both a continuous covariate, to account for any climatic steady trends over time, and also as random factor, to account for variation among years. We considered regional responses of communities by including 'country' as a fixed factor in our LMMs (four levels: 'Finland', 'Germany', 'Latvia' and 'UK'). Full initial LMMs were built including all explanatory variables and their interactions with 'country'. We always included 'site' as random factor, to account for dependencies within sites. So the model structure was lmer ('response metric' ~ ('year' + 'antecedent mean temperature' + 'number of extreme hot days' + 'number of extreme cold days' + 'antecedent mean daily precipitation' + 'number of extreme precipitation days') ∗ Country + (1|Site) + (1|Year). Inspection of model residuals did not indicate major violations of model assumptions (i.e., normal error distribution and homoscedasticity) in any models, except for some issues associated with variables being bounded at 0 (see Supplementary Figs. S4 and S5). We reported on estimated effect sizes (i.e., the standardized regression coefficients from the LMMs) and visualized the impact of climatic variables in detail in case that climatic variables explained ≥10% of total variance.

3. Results

3.1. General climatic trends

Climatic trends for all sampling sites were provided in Supplementary Fig. S1. In summary, we observed that air temperatures across all sites have undergone pronounced increases since the 1970s. The number of extreme hot days also increased at all sites while the number of extreme cold days has decreased at all but one site. Mean daily precipitation and extreme precipitation days at the Finish and Latvian sites show relatively linear increase through time. At the German sites we observed a slight decrease in mean daily precipitation and extreme precipitation in recent years. At UK sites we observed relatively stable precipitation trends, with some sites showing slight increases in precipitation (e.g., site 'UK_Es') and others slight decreases (e.g., 'UK_CB'). Changes were less pronounced over the period of invertebrate sampling, however, we still observed increasing temperatures in Germany, Latvia and UK (see Supplementary Fig. S2). Mean daily precipitation increased in Finland and Latvia while it decreased in Germany and the UK. Across all sites, we found strong fluctuations between subsequent years, illustrating that years with high temperatures or many extreme days were still often followed by moderate years.

3.2. Drivers of change

Our multiple regression models revealed that, overall, of the explanatory variables included in the model, variance in the 20 community metrics was primarily explained by country (mean ± SD variance explained: 34.3% ± 22.7%), followed by antecedent climatic conditions (21.5% ± 17.2%) and local site effects (19.2% ± 15.4%; Fig. 2). Changes over time (as represented by the variable 'year') explained much less of variance (1.2% ± 1.1%; Fig. 2).

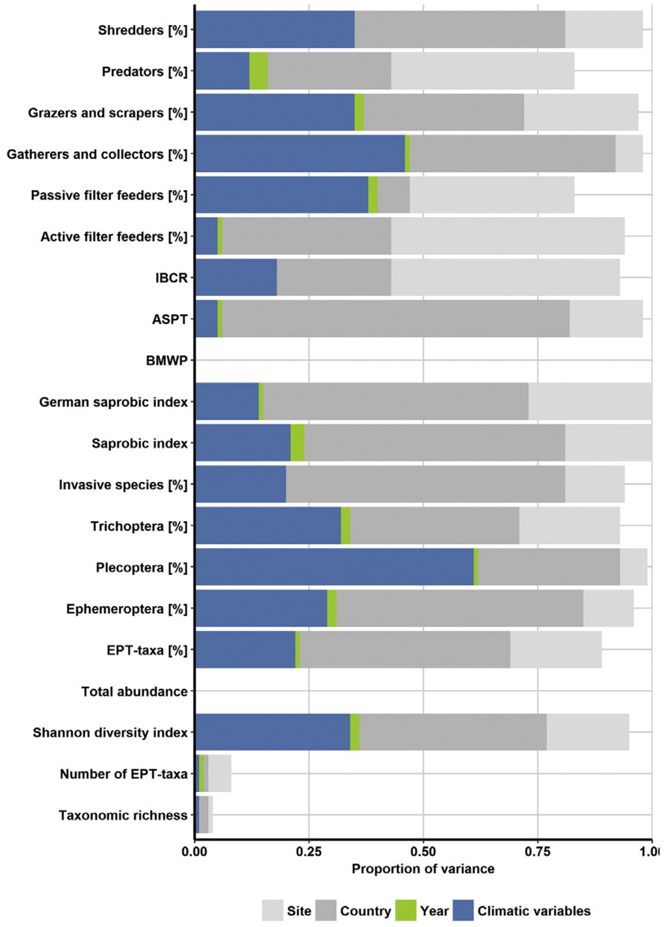

Fig. 2. Proportions of total variance explained by the antecedent climatic conditions (i.e., 'climatic variables', shown in blue), steady changes over time, represented by 'year' (effect includes both the trend and the random effect; shown in green), 'country' (shown in dark gray) and the random effect 'site' (shown in light gray) on 20 community metrics. The remaining part is the residual variance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Taxonomic richness and species abundance

We found pronounced differences among the taxonomic metrics. Overall taxonomic richness as well as overall abundance were not explained by our climatic variables (variance explained: ≤1% in both cases; Fig. 2). Furthermore, number of EPT-taxa was also only slightly affected by climatic variables (1% variance explained). However, pecentage of EPT-taxa (22% variance explained) and invasive species (20% variance explained) were affected by antecedent climatic conditions and extreme events. In particular, percentage of Plecoptera (61% variance explained) and to a lesser extent Ephemeroptera (29% variance explained) and Trichoptera (32% variance explained) showed responses to antecedent climatic conditions.

For those metrics where fixed effects explained > 10% of variance, we examined the impact of different climatic variables in detail and found pronounced regional differences. Shannon diversity index increased in Latvia in response to higher mean temperatures, while it decreased in Finland. The percentage of EPT-taxa was mostly affected by mean temperature, with a positive effect in Finland and Latvia and a negative effect in UK (Fig. 3). The percentage of Ephemeroptera showed a similar pattern, with a positive effect of temperature in Finland and Latvia and a negative effect in Germany. Plecoptera, however, decreased in Finland and the UK in response to higher mean temperatures. The percentage of Trichoptera was negatively impacted by increasing temperatures in Finland. Changes in the abundance of invasive species were only observed in the UK, as all other sites had almost no invasive species (mean ≤ 2.0% of total abundance). The percentage of invasive species was positively correlated with the number of extreme hot days and extreme precipitation days.

3.4. Sensitivity metrics

Saprobic indices were affected by antecedent climatic conditions. Climatic variables explained 21% of variance in the saprobic index, 14% of variance in German saprobic index and 5% of variance in ASPT (Fig. 2). Furthermore, climatic variables explained 18% of variance of the IBCR. When considered in detail we found that temperature, in particular, affected sensitivity metrics in different ways; while saprobic indices were positively affected with increasing temperatures in the UK (indicating loss of sensitive taxa), they were negatively affected in Finland (indicating higher numbers of sensitive taxa; Fig. 4). We also found region-specific responses of saprobic according to antecedent mean precipitation; increasing precipitation induced a shift towards less pollution sensitive species in Finland and a shift towards more sensitive species in UK. Changes in the IBCR were mostly explained by extreme precipitation days and extreme hot days. Extreme precipitation induced a decrease in IBCR (shift towards a more upstream like community) in Finland, while extreme hot days resulted in an increase of IBCR, indicating a shift towards a more downstream like community.

3.5. Functional feeding groups

Changes in functional feeding groups were mostly explained by site (mean variance explained across feeding groups ± SD: 29.2% ± 16.4%) and country effects (32.8% ± 14.5%; Fig. 2). However, antecedent climatic conditions explained 28.5% ± 16.2% of variance. When inspecting the climatic variables in detail we found regionally different responses; for example, mean precipitation affected passive filter feeders mostly in Finland, with a positive impact of mean precipitation and a negative impact of mean temperature (Fig. 5). We found a pronounced positive response of gatherers and collectors to increasing temperatures in Finland and the UK. Grazers and scrapers decreased in UK and Germany in response to warmer years, while they increased in Finland. Furthermore, shredders were negatively impacted by increasing temperatures and increased precipitation in Finland.

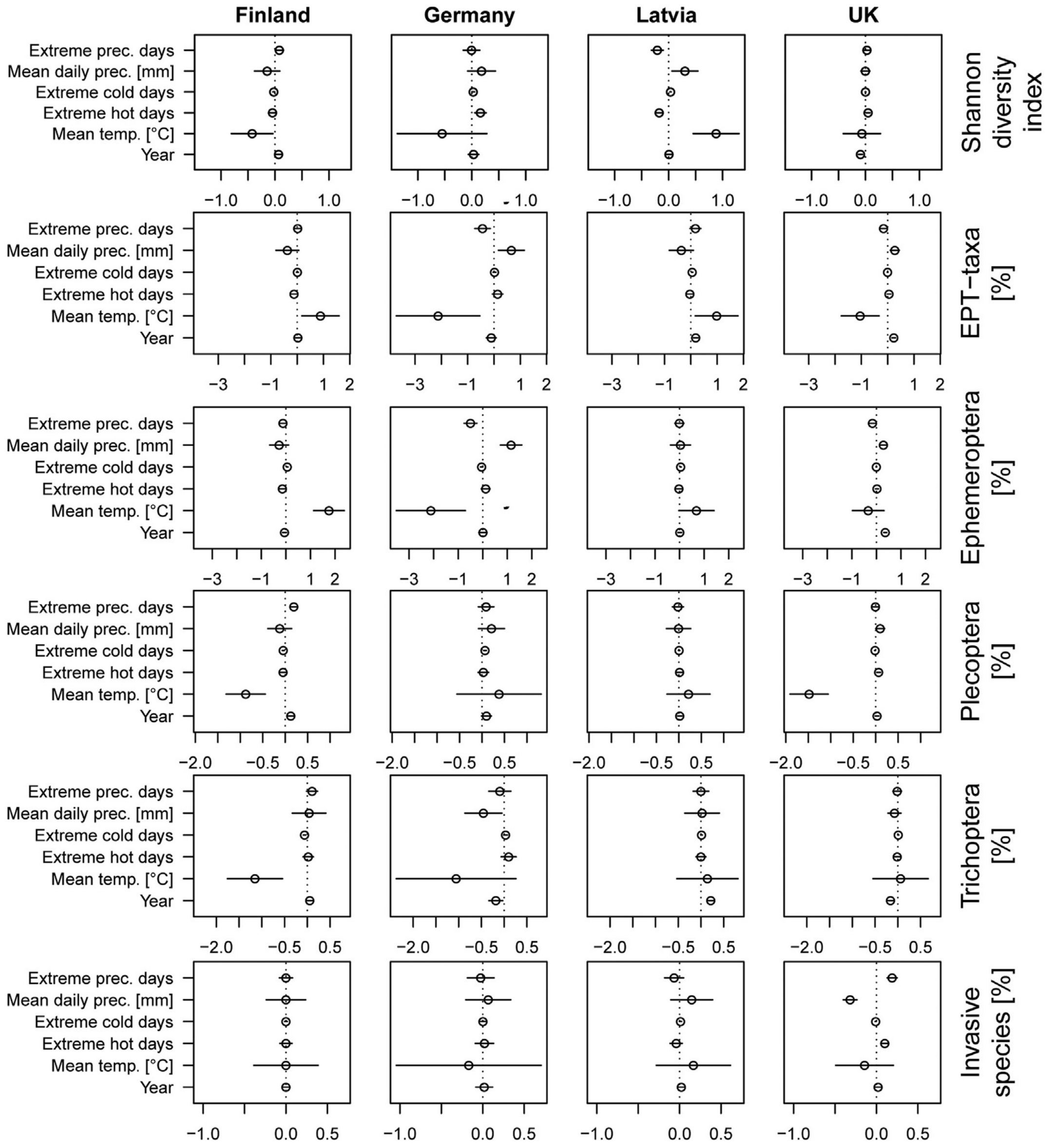

Fig. 3. Impacts of climatic drivers on Taxonomic richness and species abundance metrics. The estimated effects sizes show the relative magnitudes and standard deviation of climatic variables on Shannon diversity index, the percentage of EPT-taxa, Ephemeroptera, Plecoptera, Trichoptera and invasive species (i.e., their regression coefficients from the multiple regression models). The covariates have been standardized, so they represent the effects of changing the covariate by one standard deviation. Shown were response variables with ≥25% of their variance explained by climatic variables. For all effects see Supplementary Fig. S3 and Supplementary Tables S2–S10.

4. Discussion

4.1. Drivers of change

Our results highlight the importance of antecedent climatic conditions and the occurrence of extreme events on the structuring of riverine communities. We found that antecedent climatic variables were better predictors of community metrics than background long-term (climatic) changes, which likely reflects the direct effects that temperature and precipitation have on benthic invertebrate communities through regulation of local habitat conditions. Although local and regional conditions explained much of the variance in our dataset, the effects of antecedent climate were clear. Nevertheless, the importance of local and regional conditions was to be expected as sites were spread across multiple ecoregions with a broad range of abiotic conditions. For example, sites in the UK were exposed to much higher levels of anthropogenic stressors than those in Finland, suggesting a potential influence of multiple stressors (Ormerod et al., 2010; Sundermann et al., 2013; see below) beyond the climate-induced changes (e.g., Vaughan and Ormerod, 2014). We found different impact of antecedent climatic conditions, with strongest effect sizes of antecedent mean temperature, while precipitation mostly had a minor impact on community metrics. Responses to precipitation reflect catchment characteristics, and since most of our samplings sites were located in groundwater-dominated systems, they were buffered against flow variability. Therefore, the impact of high rainfall might be more pronounced in surface water dominated rivers than our results suggest.

4.2. Taxonomic richness and species abundance

The response of taxonomic metrics to climatic variables was highly variable. However, and contrary to our expectation, taxonomic richness and overall abundance were not affected by antecedent climatic conditions. This emphasized that taxonomic richness and overall abundance were not suited to track climate change effects in our dataset (contrary to other climate change studies; e.g., Durance and Ormerod, 2007; Hallmann et al., 2017). The loss of some invertebrate species may have been compensated by the appearance of others, indicating a

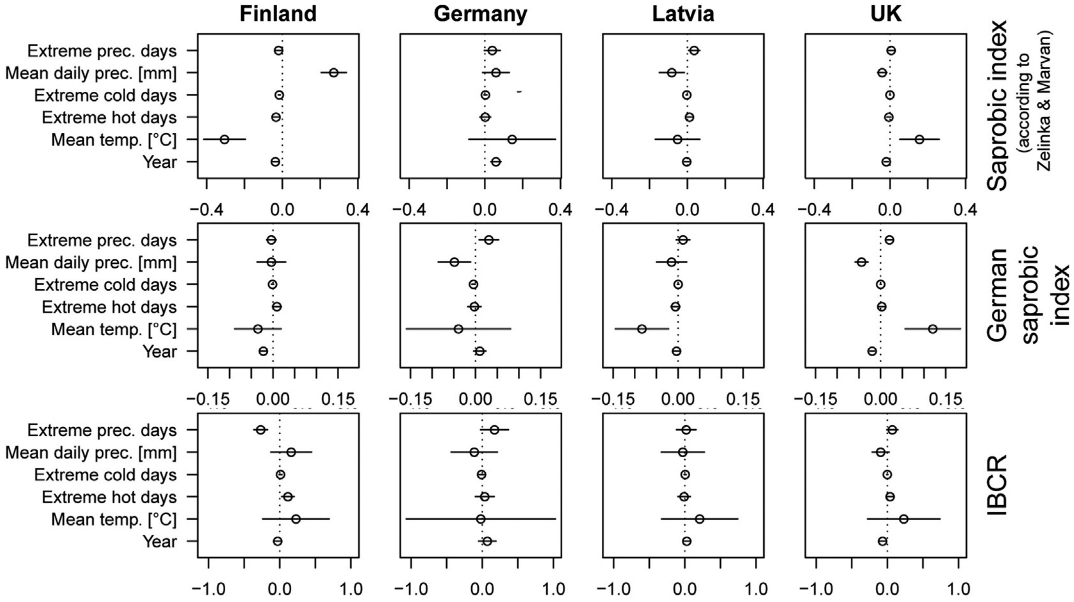

Fig. 4. Impacts of climatic drivers on sensitivity metrics. The estimated effects sizes show the relative magnitudes and standard deviation of climatic variables on saprobix index (Zelinka & Marvan), German saprobic index and IBCR (i.e., their regression coefficients from the multiple regression models). The covariates have been standardized, so they represent the effects of changing the covariate by one standard deviation. Shown were response variables with ≥25% of their variance explained by climatic variables. For all effects see Supplementary Fig. S3 and Supplementary Tables S11–S15.

species turnover with no change in overall taxonomic richness and species abundance. This assumption is supported by our other results, as relative abundances of taxonomic groups were strongly affected in different ways.

Our results provide evidence for regional different responses to climatic conditions between and within taxonomic groups. For example, EPT-taxa, which increased in northern regions (Finland and Latvia) and decreased in Germany and the UK. The congruence of this pattern with that of Ephemeroptera (but not Plecoptera and Trichoptera) suggests that these patterns were mostly driven by changes of Ephemeroptera abundance. Up to a certain limit, increasing temperature may have positive effects on the individual fitness of ectotherms as long as they do not exceed their physiological optima (Deutsch et al., 2008). Many Ephemeroptera are considered to be warm-adapted species which could potentially explain increased abundance of Ephemeroptera in colder regions, most probably also favored by improved overwinter survival (Musolin, 2007). In warmer regions like Germany, however, we recorded a decrease in the abundance of Ephemeroptera with increasing temperatures, probably because it exceeded the species physiological optima. Plecoptera were—more than any other metric in our dataset—affected by antecedent climatic conditions and showed a consistent decrease in relative abundance with increasing temperatures, confirming that Plecoptera were disproportionally vulnerable to increasing temperatures (Pritchard et al., 1996). Previous work has shown that Plectopera richness is better explained at the European scale by current climatic factors than other aquatic insects indicating their narrow temperature tolerances (Shah et al., 2015). This was also shown by Tierno de Figueroa et al. (2010), who suggested that 63% of the European Plecoptera should be considered as vulnerable, according to climate change predictions. By contrast, Trichoptera in northern parts of Europe were mainly considered as generalists, expected to be buffered against climate change impacts (Hering et al., 2009). However, our results differed considerably from those assumptions as we found a pronounced decrease of Trichoptera in Finland in response to warmer temperatures, while Trichoptera in Latvia and UK were not affected by temperature.

Invasive species were found to increased in relative abundance in the UK, which was linked to an increase in extreme events. This observation is congruent with previous studies on disturbances as a consequence of extreme events, which were recognized as driving factors for the spread of invasive species because they tend to have broader environmental tolerances than co-occurring native taxa (Daufresne et al., 2007; Diez et al., 2012; Dukes and Mooney, 1999; Früh et al., 2012). Altered frequency and timing of high-flow disturbance events in rivers, which are projected to occur with climate change (Blöschl et al., 2017), can severely affect riverine communities and their invasibility as organisms have life histories that key into specific components of the flow regime (Lytle et al., 2017; Tonkin et al., 2017b). Such alterations to climate and river flows may affect communities in more ways than can be detected using data collected once per year, which masks any community dynamics that occur at the intra-annual scale. In predictable seasonal climates, intra-annual turnover can allow more than one community to share the same location through temporal niche segregation (Tonkin et al., 2017a). While our approach did not address questions related to event timing and intra-annual community dynamics, this presents a fruitful avenue to explore in future studies on the effects of climate change on riverine communities.

4.3. Sensitivity metrics

The results of our analysis on sensitivity metrics met our expectations partially and revealed regional patterns of losses of pollution-sensitive taxa (increase in saprobic indices) with increasing temperatures. Higher water temperatures are likely to result in lower dissolved oxygen concentrations causing increased oxygen stress (Jones et al., 2013), and increasing temperatures are likely to be associated with reduced river flows, concentrating pollutants (Jones et al., 2013). Such observations have been made in the Rhône river, where changes in community structure towards more tolerant species were linked to varying oxygen and temperature conditions as well as extreme flood and heatwave events (Daufresne et al., 2007). However, we found this effect only for sites located in the UK, which were located in agricultural regions. Therefore, the effect of increasing temperatures might be strengthened due to multiple additional local stressors, including both point source and diffuse pollution (Allan, 2004; Kuemmerlen et al., 2015), nutrient-loads (Bouraoui et al., 2002), use of pesticides (Berger et al., 2017) or hydromorphological alteration (Elosegi et al., 2010). For example, riparian vegetation is often rare or absent in agricultural

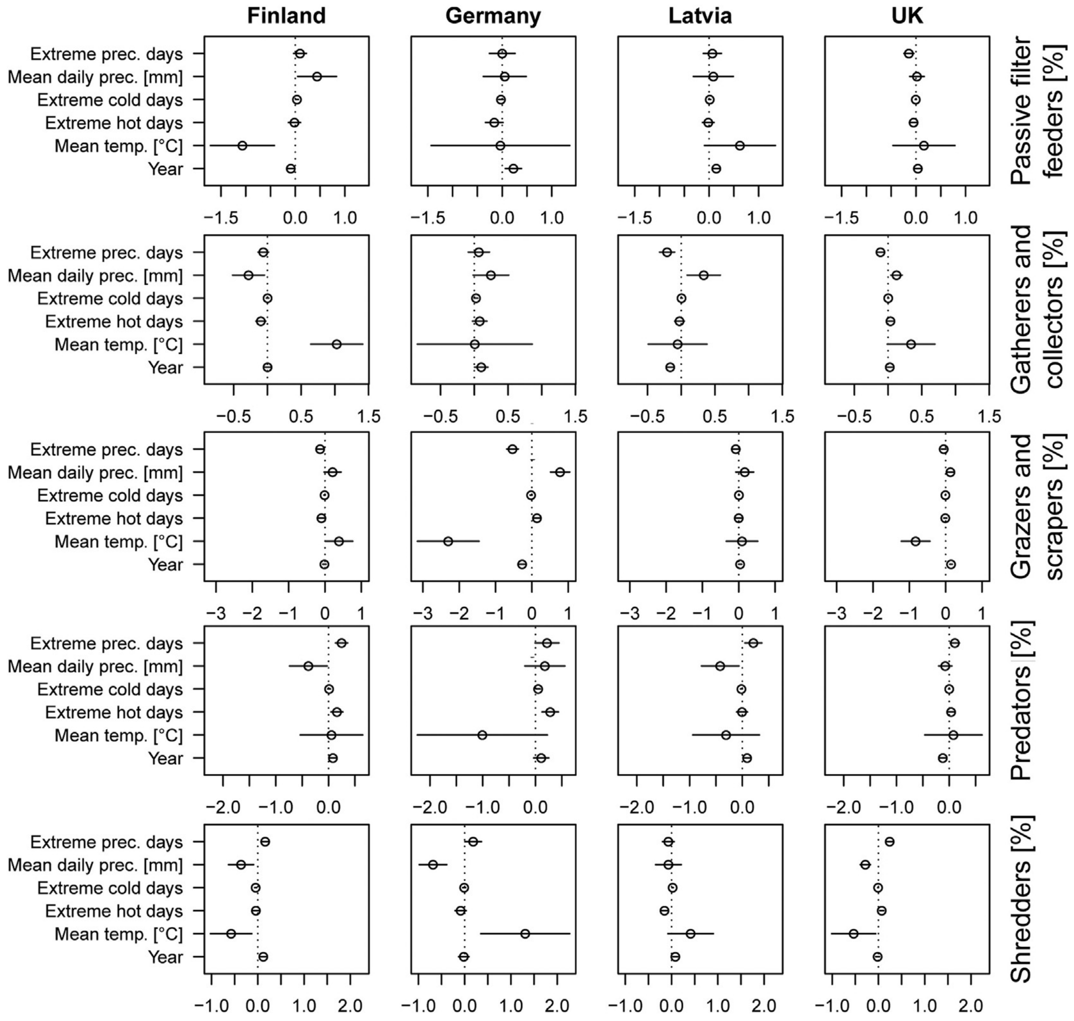

Fig. 5. Impacts of climatic drivers on functional feeding groups. The estimated effects sizes show the relative magnitudes and standard deviation of climatic variables on the percentage of passive filter feeders, gatherers and collectors, grazers and scrapers, predators, shredders (i.e., their regression coefficients from the multiple regression models). The covariates have been standardized, so they represent the effects of changing the covariate by one standard deviation. Shown were response variables with ≥25% of their variance explained by climatic variables. For all effects see Supplementary Fig. S3 and Supplementary Tables S16–S21.

used areas and there is growing recognition that community response to changing climatic conditions is intensified when riparian vegetation is removed (Capon et al., 2013; Davies, 2010; Thomson et al., 2012). Beside ecological benefits of riparian vegetation, like the provisioning of nutrients from litter fall, riparian vegetation provides shade to control water temperature and algal growth (Davies, 2010; Tabacchi et al., 1998). Riparian forests at Finish and Latvian sites, might have prevented the negative impact of temperature on sensitivity metrics and the above mentioned regional increase of Ephemeroptera abundance may have caused the decrease of saprobic indices, since Ephemeroptera are considered to be pollution sensitive and are therefore assigned to low saprobic classes.

Extreme precipitation events and extreme hot days accounted for a change in the IBCR. In Finland, we found that extreme precipitation events induced a shift towards a community more characteristic of upstream zones. On the other hand, extreme hot days resulted in an increase of IBCR, indicating a shift towards a more downstream like community. So far, those assumptions have mostly derived from statistical models (e.g., Domisch et al., 2011) while empirical evidence is scarce. This change towards a more downstream like community could be explained by an increase of richness/abundance of warm-dwelling taxa (typical of downstream river sections) and/or by a decrease of richness/abundance of cold-dwelling taxa (typical of upstream taxa river sections). A similar gradual disappearance of cold-dwelling taxa was also observed in a long-term study of the Rhône river (Daufresne et al., 2004).

4.4. Functional feeding groups

The composition of functional feeding groups was strongly impacted by local site-specific conditions. However, as anticipated by a recent climate change simulation study (Pyne and Poff, 2017), our results also provide empirical evidence that climatic variables affect the relative abundance of functional feedings groups. In theory, the negative impact of changing species composition on the functionality of the ecosystem could be diminished by an overlap of species function (i.e., functional redundancy; Rosenfeld, 2002). However, we found pronounced shifts in the composition of functional feeding groups and our results illustrated the importance of temperature and precipitation on the structuring of functional community composition. More specifically, our findings confirmed previous assumptions that grazers and scrapers were disproportionately vulnerable to higher temperatures (Pyne and Poff, 2017; Statzner and Beche, 2010). This effect, however, was regionally specific with a strong decrease in relative abundance in Germany and the UK. Grazers and scrapers are also reported to be vulnerable to reductions in stream flow (Statzner and Beche, 2010), which is expected to occur in low precipitation years (Filipe et al., 2013). Our results confirmed this assumption, as grazers and scrapers increased in relative abundance with increasing mean precipitation. Extreme precipitation events negatively affected gatherers and collectors, which tend to be negatively affected by high flow disturbance associated with exreme precipitation (Statzner and Beche, 2010). Predators increased with the frequency of extreme precipitation events, possibly due to their higher body mass and their possibility to withstand periods of high velocity (McMullen et al., 2017). Our findings on the vulnerability of certain functional groups confirm the results of Theodoropoulos et al. (2017), who investigated the consequences of rainfall-induced high flow event and found that gatherers and collectors strongly decreased in abundance while predators increased. In line with previous findings (e.g., Boyero et al., 2012; Pyne and Poff, 2017), we also found a negative impact of increasing temperatures and reduced precipitation on shredders (with regional differences in Germany and Latvia), which play a critical role in stream ecosystem function, as their shredding activity accelerates leaf fragmentation, produces fecal pellets, and transfers nutrients into secondary production, all of which are vital for maintaining diverse aquatic food webs (Dangles and Malmqvist, 2004; Graça, 2001; Wallace et al., 1997). Hence, a decline of shredder species could adversely affect ecosystem functioning and energy flow in freshwater ecosystems. Taken together, our findings highlighted the complex interactions of temperature and precipitation on functional composition of communities and raised concerns about the resilience of stream ecosystem function under projected climate change.

5. Conclusion

In conclusion, we found clear responses in riverine communities to climatic variables. As temperatures and the frequency of extreme events are both predicted to increase in response to global climate change during the second half of the 21st century (Beniston et al., 2007; IPCC, 2014), the results imply that sensitive taxa like Plecoptera could be seriously threatened. Our results unambiguously indicate that the composition of functional feeding groups is affected by changing climatic conditions, which cause functional changes at the ecosystem level. Future warming is one stressor among many in freshwater ecosystems (Ormerod et al., 2010) that shape species composition. Those stressors (e.g., habitat loss or increasing impact of invasive species) are often intensified by climate change (Rahel and Olden, 2008) and interact with increasing temperature and altered precipitation regimes. Therefore, the impact of climate change on riverine communities might even be higher than predicted by changing temperature and precipitation alone. Long-term monitoring provides the most suitable data for the empirical analysis of climate change effects on ecosystems and biodiversity. With the current network of LTER sites important insights have been gained, but more thorough and complex analyses will require improved monitoring methods (e.g., consistently monitoring a suite of essential biodiversity variables, see Haase et al., 2018; Schmeller et al., 2017) as well as more data and more monitoring sites. Such an approach helps to predict the future status of global biodiversity and to apply appropriate conservation measures that promote the conservation of biodiversity and the integrity of ecosystem processes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2017.11.242.

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