# Extreme climatic events alter the aquatic insect community in a pristine German stream

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## Abstract

As a result of ongoing climate change, extreme climatic events (ECEs) are expected to become more frequent and severe. The high biodiversity of riverine ecosystems is susceptible to ECEs, especially to water temperature (extreme heat and extreme cold) and discharge-related (flood and drought) events. Long time series are needed to unravel the effects of ECEs on ecological communities. Here, we used 20 years (1986–2005) of unusually high-resolution data from a pristine first-order stream in Germany. Daily recordings of species-level identified aquatic insect (Ephemeroptera, Plecoptera, Trichoptera: EPT) emergence, water temperature and discharge data were used to examine the effects of four types of ECEs (extreme heat, extreme cold, flood, and drought events) on insect abundance, common taxonomic diversity metrics, and selected traits after five different time lags (2 weeks, 1, 3, 6, and 12 months). Extreme heat events increased from $1.8 \pm 1.9$ SE events per year before 2000 to $5.3 \pm 1.9$ SE events per year after 2000. Water temperature-related ECEs restructured the EPT community in abundance, species richness, and traits (community temperature index: CTI, and dispersal capacity metric: DCM). The strongest effects on the EPT community were found when it was exposed to multiple ECEs and 1 and 3 months after an ECE. The changing frequencies and durations of ECEs, especially the increasing frequency of extreme heat events and the negative cumulative effects of ECEs, paint a worrisome picture for the future of EPT communities in headwater streams. High-resolution, long-term data across sites is needed to further disentangle the effects of different ECE stressors.

**Keywords** Freshwater · Extreme climatic events · Macroinvertebrate · Biodiversity · Community traits · Long term

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# 1 Introduction

Extreme climatic events (ECEs) are rare by definition, but they are expected to increase in both frequency and magnitude as a result of anthropogenic climate change (IPCC 2012, 2021). ECEs restructure ecological communities, through reducing local abundances of many species (Moi et al. 2020) while favoring a few more adapted species. However, most work on the ecological consequences of ECEs has examined their effects on single or few species, while community level impacts are less well understood (Filazzola et al. 2021; Harvey et al. 2020; Marquis et al. 2019; Polazzo et al. 2022). Consequently, few studies have been able to make general statements about the effects of ECEs on species and ecological communities, especially since this requires long time series to capture multiple events and lagging responses (Rastetter et al. 2021).

ECEs are easy to recognize in the field, but they are difficult to define (Stephenson et al. 2008). While there is no standard definition of ECEs across nor within scientific disciplines, several methods for classifying ECEs have been proposed, varying with event type, study system, and research question (Bailey and van de Pol 2016; Beniston & Stephenson 2004; McPhillips et al. 2018; M. D. Smith 2011). One method is to use either a fixed numeric or percent threshold and define ECEs as periods surpassing the threshold (McPhillips et al. 2018). While these thresholds have been criticized as being arbitrary (Bailey and van de Pol 2016), concerns can be mitigated by applying multiple thresholds. Other definitions take into account the effects of ECEs on ecological communities (McPhillips et al. 2018). However, these definitions are not useful for studies that aim to assess variation of ecological communities in response to ECEs.

River and stream ecosystems harbor high biodiversity and are particularly sensitive to ECEs related to hydrology (floods and droughts) or water temperature (extreme heat and extreme cold events) (Bêche & Resh 2007; Daufresne et al. 2007; Leigh et al. 2015; Smith et al. 2019). The effects of hydrological and water temperature ECEs on abundance and taxonomic diversity metrics are highly variable. Floods often reduce freshwater macroinvertebrate densities and diversity (Milner et al. 2018; A. J. Smith et al. 2019; Stamp et al. 2020; Theodoropoulos et al. 2017) and have been shown to favor eurytolerant and invasive taxa (Daufresne et al. 2007). Droughts can have strong filtering effects on community composition (Boulton & Lloyd 1992; Nelson et al. 2021), but their long-term effects are poorly characterized. The effects of heat extremes have been well investigated on terrestrial insects (Rocha et al. 2017; Soroye et al. 2020) but less so on aquatic insects (Hotaling et al. 2020; Leigh et al. 2015). Despite some studies on aquatic macroinvertebrates in glacier-fed streams and rivers (Jacobsen et al. 2014; Milner et al. 2017; Tian et al. 2022), studies on the effects of ECEs related to extreme cold water temperature events on the biodiversity of riverine aquatic macroinvertebrate communities are particularly scant.

ECEs are likely to reshape trait composition in addition to biodiversity composition. The presence and frequency of traits in ecological communities can determine ecosystem function, including decomposition, nutrient cycling, and water filtration. Further, traits are often sensitive to changing environmental conditions as a result of environmental filtering, thus trait composition reflects current and past conditions. Moreover, trait composition affects the resilience of an ecological community (Moi et al. 2020; Schülting et al. 2016). For example, heat waves are likely to favor species with higher water temperature preferences and restrict cold-dwelling species. A heat wave is expected to both result in a "thermophilization" of the community, and to have a larger effect on communities with an initially higher proportion of cold-adapted taxa. Extreme floods can select for species with

high dispersal capacities that can recolonize habitats faster (Bogan et al. 2015). Through altering community trait composition, ECEs may indirectly alter ecosystem functioning (Li et al. 2021).

The effects of ECEs on aquatic macroinvertebrate communities are expected to be both immediate, through direct mortality, and to follow time lags, as communities continually restructure in the aftermath of the ECE. However, the effects of ECEs on both ecological communities and their trait composition have rarely been examined across multiple time-points. Most aquatic insects have a reproduction cycle of a few weeks up to 1 year with a few longer exceptions (up to 5–7 years) (Buffagni et al. 2009, 2020; Graf et al. 2020a, b; Schmidt-Kloiber & Hering 2015). While the length of time needed to detect potential changes in both community and trait composition in response to ECEs is unclear, examining several time slices from a few weeks up to one year can help encompass the different reproductive cycles of most riverine insects. Further, ECEs can vary in their severity and duration, which presumably leads to differences in the extent of effects. Therefore, long-term studies with high sampling frequency and high taxonomic resolution are needed to understand the effects of ECEs on ecological communities.

In this study, we examined the effects of ECEs on an aquatic insect community (Ephemeroptera, Trichoptera, Plecoptera: EPT). We quantified the responses of emerging EPT abundance, taxonomic diversity and selected traits to four different ECEs (extreme heat, extreme cold, flood, and drought events). The use of a two decade-long time series with a daily resolution allowed us to examine responses to multiple occurring ECEs and to test for variation in community responses after five different lag times (2 weeks to 12 months) following ECEs. We predicted that (1) ECEs of longer duration will have stronger effects on aquatic insect abundance, taxonomic diversity and the three selected traits. Additionally, we predicted that (2) the extent of changes in aquatic insect abundance, taxonomic diversity, and the three selected traits would vary with the type of ECE (extreme heat, extreme cold, flood, and drought events). Specifically, we expect heat waves to result in a higher community temperature index by favoring heat-tolerant species. Conversely, we expect extreme cold events to lead to a lower community temperature index. We expect community current preference to increase after flood events as species with higher current preferences were expected to profit from floods. Conversely, we predicted droughts will lead to a lower community current preference. In addition, we expect longer and more frequent ECEs to result in a higher community dispersal capacity.

## 2 Methods

### 2.1 Site and aquatic insect sampling

Sampling was conducted at the Breitenbach stream (50°39′42N 9°37′26E), a small first-order stream underlain by Bunter Sandstone in Hesse, Germany. The data used in this study was collected as part of a long-term project at the Research Station Schlitz of the Max-Planck Institute for Limnology (Plön, Germany). More information on the study site as well as research questions and methods can be found in Wagner et al. (2011). From 1969 to 2010, emerging insects were captured in an emergence trap (i.e., a greenhouse placed over the stream). The greenhouse was placed in the middle section of the Breitenbach (base flow: width: approx. 1 m; depth: variable but commonly < 40 cm). The stream substrate was dominated by sand (0.5 mm) as well as gravel and pebble

(0.5–6.0 cm) (Wagner et al. 2011). Daily values for water temperature and discharge data were available from 1986 to 2005 only, thus we selected a homogeneous subset with daily resolution of all three main variables ranging from 1986 to 2005 (20 consecutive years) for our analyses. A tent within the greenhouse directed the emerging insects into a tray with a preservative from which they were collected daily. Emerged (adult) Ephemeroptera, Plecoptera, and Trichoptera (EPT) were identified to species level by taxonomists working at the Research Station Schlitz of the Max-Planck Institute for Limnology. Identification was supervised and if needed revised by renown taxonomists (such as Prof. Dr. Peter Zwick and Prof. Dr. Rüdiger Wagner). During our study period (1986–2005) neither the emergence trap nor the devices for sampling the insects and recording water temperature and discharge changed. Water temperature [°C] and discharge [L/s] were measured daily using an automatic measuring station with PT 100 sensors and recorded with one digit behind the comma (Wagner et al. 2011). Annual average water temperatures at the site ranged between 7.4 and 9.0 °C (January: −3.7 to 6.6 °C, July: 9.8 to 12.5 °C) during the studied period. Annual average discharge varied strongly from 4.8 to 42.0 l/s. The stream and entire catchment area are located in a nature reserve, which was established in 1993 (Wagner et al. 2011). There are no settlements in the mostly forested catchment area and during the period of limnological research the few meadows were used for making hay (Wagner et al. 2011). Overall, the Breitenbach stream is in relatively pristine condition, isolated from intense human land use change albeit susceptible to climate change and long-ranging pollution (Baranov et al. 2020).

## 2.2 Statistical analysis

### 2.2.1 Classification of ECEs

Daily discharge and water temperature values were used to identify and assess ECEs. While there is no universal definition of extreme climatic events (Broska et al. 2020), similarly to Ledger and Milner (2015) we chose a probability-based definition. We followed the IPCC approach (IPCC 2012) choosing the 5% and 95% percentile as threshold values. We applied these thresholds in two ways. First, we used an overall occurrence probability curve with values across all 20 years to classify ECEs over the whole study period. Second, to correct for possible long-term trends in discharge and water temperature, we used yearly probability curves to classify ECEs, as any values within each year that were extreme in comparison to the yearly values (as opposed to the values from all 20 years). For the classification using an overall 20-year probability, each day with a water temperature or discharge value in the top or bottom 5% of all values was classified as extreme, while for the classification using yearly probabilities, we used the top and bottom 5% of the values from individual years. We examined four types of ECEs: extreme heat and extreme cold events (respectively, top and bottom 5% of water temperature values), and floods and droughts (respectively, top and bottom 5% of discharge values). For each ECE, the duration was calculated using the start and end date of consecutive extreme days of the same type. ECEs of the same type separated by only one gap day were merged to one event. Duration and magnitude of ECEs were highly correlated (overall probability: Pearson's $\rho = 0.978$, yearly probabilities: Pearson's $\rho = 0.976$), therefore only duration was analyzed.

### 2.2.2 Aquatic insect biodiversity

We examined the effects of ECEs on abundance, taxonomic diversity, and community traits of EPT taxa. In particular, we tested the responses of abundance, species richness, Shannon-Index of diversity, and Shannon's evenness and three abundance-weighted community traits covering temperature preferences, current preferences, and dispersal capacities. All examinations were performed using EPT imagines as the emergence traps did not capture larvae. These particular traits were chosen as they were predicted to be strongly affected by ECEs. Changes in the community temperature index are expected for ECEs related to water temperature (extreme heat, extreme cold), while community current preference is expected to change for flow-related ECEs (flood, drought). In addition, the community dispersal capacity metric was examined as a measure of a community's capacity for recolonization.

Shifts in water temperature preferences were analyzed using the Community Temperature Index (CTI), which was calculated as an abundance-weighted average of the taxon-specific water temperature preferences of each taxon in the sample (Haase et al. 2019). Similarly, shifts in current preferences were analyzed using the Community Current Preference (CCP), calculated as an abundance-weighted average of the taxon-specific dummy-coded current preference (1 = limnobiont [preferring stagnant water] to 6 = rheobiont [preferring running water with higher current velocities]). Taxon-specific water temperature and current preferences were obtained from freshwaterecology.info and were available for 100% and 99% respectively of all species present (AQEM expert consortium 2002; Bauernfeind et al. 1995, 2002; Buffagni et al. 2009, 2020; Graf et al. 2008, 2009; Graf et al. 1995a, 2002b; Graf et al. 1995b, 2002b; Graf et al. 2020a, b; Schmedtje & Colling 1996; Schmidt-Kloiber & Hering 2015). For taxa identified only to genus level, we used the mean preference values of all species present within the genus.

We analyzed changes in dispersal capacity using the standardized community dispersal capacity metric (DCM), which was calculated as an abundance-weighted mean of the taxon-specific standardized dispersal capacity metrics (Li et al. 2016). Information on taxon-specific dispersal capacity was only available at the genus level, was obtained from the DISPERSE database and available for 98% of all taxa recorded at the study site (Sarremejane et al. 2020).

### 2.2.3 Studied lag time periods

We quantified responses to ECEs at several lag time periods. Since 83.1% of all taxa captured have a lifecycle not longer than 1 year (Buffagni et al. 2009, 2020; Graf et al. 2008, 2009; Graf et al. 2020a, b; Schmidt-Kloiber & Hering 2015), this was chosen as the longest lag period. Shorter lag lengths were included to identify the period when ECEs had the strongest effects. In total, we examined five lag periods following ECEs: 2 weeks, 1 month, 3 months, 6 months, and 12 months after the start date of the ECE. For each of these lag time periods, the response variables of the EPT community were calculated for a 15-day period covering 7 days before and 7 days after the date of the lag period (Fig. 1). To correct for possible trends over the years, EPT biodiversity responses were included in the models as ratio of present to past values, where past values were calculated as the average value that occurred during the same 15-day time period in the preceding 5 years. The 5-year average was chosen instead of the previous year's average to buffer against exceptional values occurring in just 1 year.
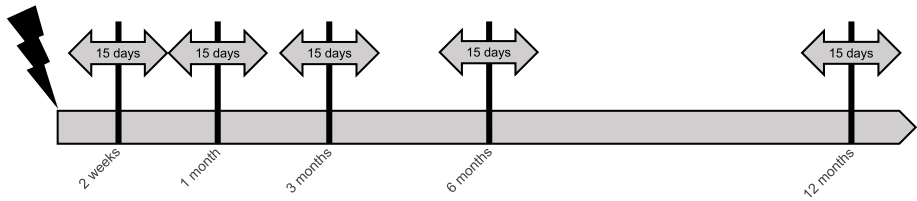
**Fig. 1** Schematic overview of the study design. Response variables were calculated for a 15-day period spanning 7 days before and 7 days after the date of the lag period (2 weeks, 1 month, 3 month, 6 months and 12 months after an ECE)

### 2.2.4 Model fitting

Since relationships were non-linear, we used generalized additive models (GAMs) (Hastie & Tibshirani 1986; Zuur et al. 2009) to test for relationships between ECEs and changes in biodiversity and traits of the aquatic insect community. For each unique combination of ECE type, response variable (abundance, richness, Shannon index, evenness, CTI, DCM, CCP), classification method and lag time period, we fitted one model. However, drought events classified by overall probability were not included as there were only 24 events and no meaningful GAM could be fitted. In total, we fitted 245 models (Table 1).

Despite the multiple tests we did not make any *p* value adjustments. Correction methods such as Bonferroni correction are quite conservative (Bender & Lange 2001; Narum 2006; Ranstam 2016) and may lead to results falsely classified as non-significant especially with large numbers of tests. Thus, we decided to take a similar approach to Bender and Lange (2001) and do without multiple test adjustments. As our data comes from a single study site, results should not be overly generalized, but rather are primarily descriptive.

Given our predictions, our primary fixed variables of interest were duration of the ECE and additional events. To quantify additional events, we counted the number of ECEs (of the same event type) occurring between an ECE and the lag time period. Year of the ECE was included to correct for temporal changes. To correct for the influence of past values of biodiversity and community characteristics, the average response variable for 1 year preceding the lag time period was included. Finally, in order to account for background responses to climate conditions, we included average water temperature during the lag time period, precedent minimum winter and maximum summer water temperature for water temperature related ECEs (extreme heat and extreme cold events), average discharge during the lag time period, and minimum and maximum discharge in the preceding year for discharge related ECEs (flood and drought events). Minimum winter water temperature refers to the lowest recorded value from December to February, while maximum summer water temperature refers to the highest recorded value from June to August. For each model, the selection of which explanatory variables to include was made using AICc

**Table 1** Models fitted for each ECE type and response variable. Twenty-one models (3 types of ECEs × 7 response variables) per cell were fitted for the overall probability and 28 models (4 types of ECEs × 7 response variables) for the yearly probabilities

| Lag time period | 2 weeks | 1 month | 3 months | 6 months | 12 months |
|---|---|---|---|---|---|
| Occurrence probability used to classify ECE | Overall | Overall | Overall | Overall | Overall |
| | Yearly | Yearly | Yearly | Yearly | Yearly |

(Burnham & Anderson 2002). More information on the parametrization can be found in the Supplementary Materials.

All analyses were performed in R version 4.0.4 (R Core Team 2021) using RStudio version 1.4.1106 (RStudio Team 2021) and packages mgcv (S. N. Wood 2017), nlme (Pinheiro et al. 2021), and MuMIn (Barton 2020). Additional packages were used for data preparation and plotting (Auguie 2017; Breheny & Burchett 2017; James & Hornik 2020; Kassambra 2020; Lüdecke 2018; McCreight et al. 2015; Oksanen et al. 2020; Schauberger & Walker 2020; Thoen 2020; van den Brand 2022; Wickham 2007, 2011, 2016, 2021; Wickham et al. 2021; Wickham & Bryan 2019; Wilke 2020; Yu 2019).

# 3 Results

The number of overall extreme heat events increased over the 20-year duration of our study from an average of $1.8 \pm 1.9$ SE events per year before 2000 to $5.3 \pm 1.9$ SE events from 2000 to 2005 (Fig. 2). Extreme cold events were common from 1986 to 1991 (mean $= 7.0 \pm 2.8$ SE events per year), then occurred seldomly from 1992 to 2002 (mean $= 2.5 \pm 1.4$ SE events per year) and again were common from 2003 to 2005 (average of $8.7 \pm 1.2$ SE events per year). The number of floods (mean $= 2.5 \pm 1.9$ SE events per year) and droughts (mean $= 1.2 \pm 1.4$ SE events per year) was less variable but tended to decrease (Fig. 2). Durations of the ECEs show similar patterns (Supplementary Material 1).

The number and duration of yearly ECEs did not vary over time (Supplementary Material 1).

ECE duration had a significant effect on the EPT community in 23 out of the 245 models. The EPT community was mainly affected by water temperature related ECEs as additional ECEs occurring between an ECE and the lag time period were significant in 15 (extreme cold events) and 11 (extreme heat events) models, but only 8 (droughts) and 2 (floods) discharge related ECE models. Responses varied significantly with year in 38.8% of all models. The EPT taxa showed the biggest response to water temperature during the lag time period (significant in 46 models) maximum preceding summer water temperature
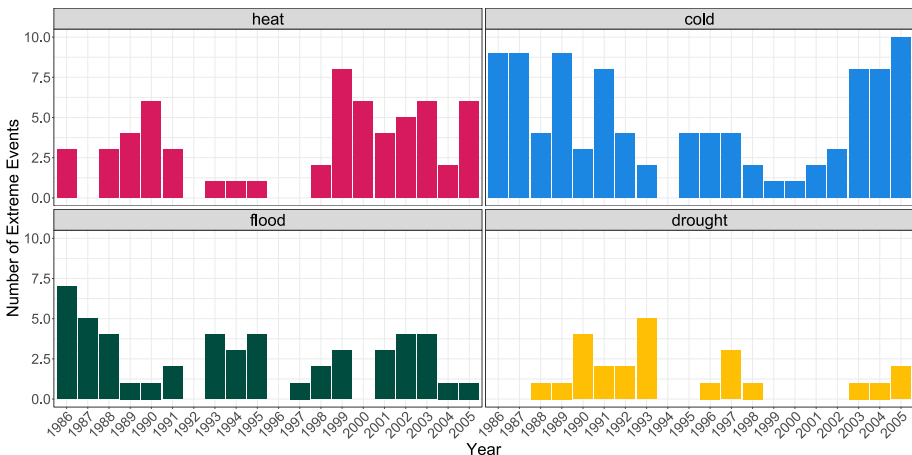


**Fig. 2** Number of overall ECEs per year

(significant in 44 models) and minimum preceding winter water temperature (significant in 40 models; Supplementary Material 3). The strongest and most numerous ECE effects were found 1 month and 3 months after the event (Figs. 3 and 4).

## 3.1 ECE duration

Longer durations of extreme heat events had a significant positive effect on EPT abundance and richness after 3 months, when the ECE was identified using an overall probability of occurrence across the 20-year study duration (Fig. 3). When yearly probabilities were used, longer duration of extreme heat events significantly increased richness after 6 months. Abundance increased after 6 months for extreme cold events (overall probability) and 3 months for flood events (yearly probabilities). Shannon index significantly decreased after 1 month for extreme heat events classified by an overall probability. Duration of extreme heat events lead to increased CTI values 1 month (yearly probabilities) and 3 months (overall probability) after the ECE (Fig. 3).

## 3.2 Additional ECEs

An increasing number of additional extreme heat events between initial extreme heat ECE and the lag time period led to a significant decrease of the Shannon index and an increase of evenness after 1 month and a decrease in abundance after 12 months (overall
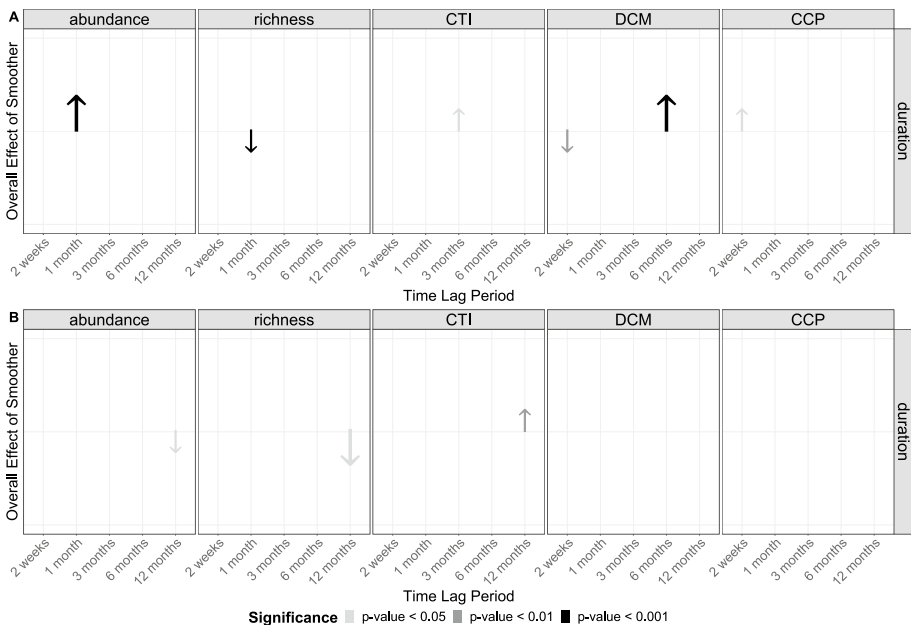


**Fig. 3** Graphical summary of the GAMs with ECE duration as explanatory variable for the different classification of ECEs (**A** overall probability, **B** yearly probabilities). Only significant and non-neutral effects are shown. Shannon index and evenness are not represented as there were no significant non-neutral effects. Upwards and downwards pointing arrows indicate increasing and decreasing values, respectively. Arrow size reflects the extent of effects. The detailed results can be found in the Supplementary Materials
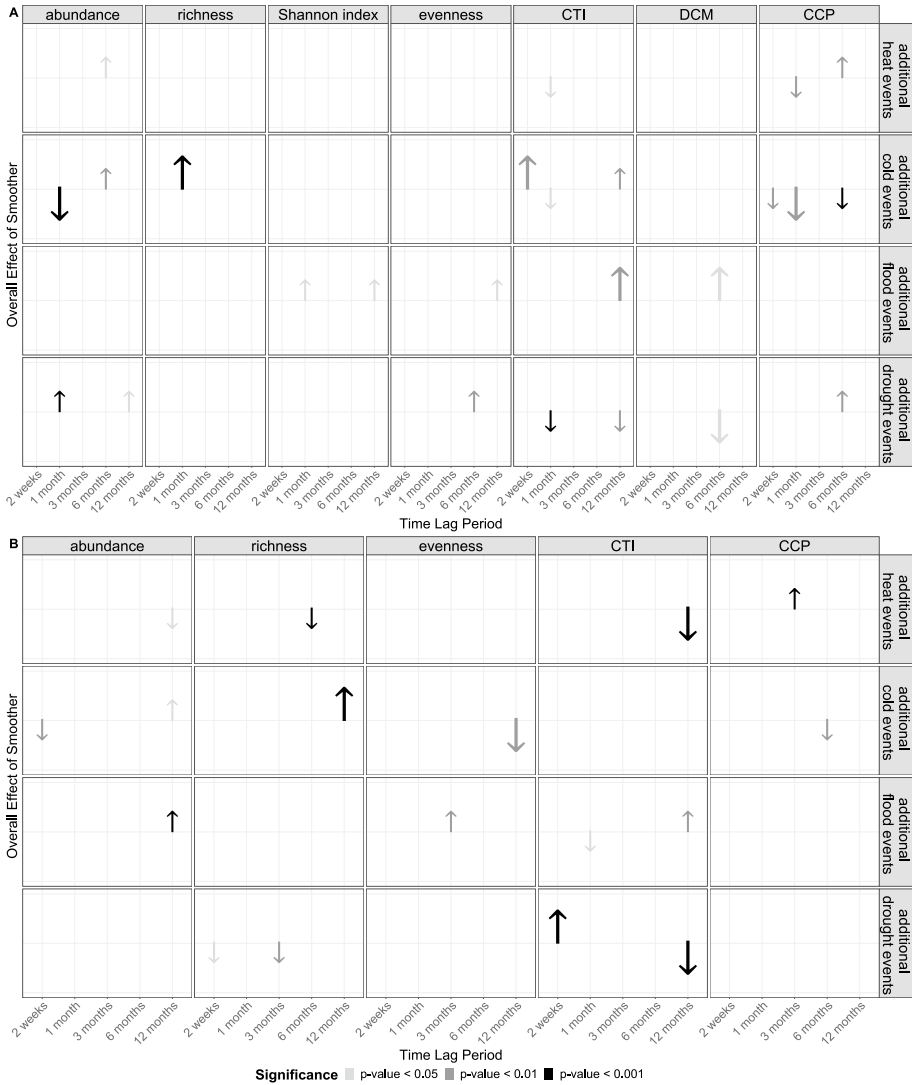
**Fig. 4** Graphical summary of the GAMs with additional ECE as explanatory variable for the different classification of ECEs (**A** overall probability, **B** yearly probabilities). Only significant and non-neutral effects are shown. Shannon index and DCM are not represented for ECEs classified by yearly probabilities as there were no significant non-neutral effects. Upwards and downwards pointing arrows indicate increasing and decreasing values, respectively. Arrow size reflects the extent of effects. The detailed results can be found in the Supplementary Materials

probability). CTI values increased significantly after 1 month with increasing numbers of extreme heat events, regardless of whether these events were classified using an overall or yearly probabilities. DCM values decreased after 3 and 6 months (yearly probabilities) (Fig. 4). Additional extreme cold events led to a significant increase in abundance after 1 month (overall probability). CTI values decreased significantly after 12 months (overall probability) (Figs. 3 and 4). Increasing numbers of additional flood or drought events had

no effects on the EPT community except for a significant but weak positive effect on EPT abundance after 3 months for flood events and an increase in richness 2 weeks for drought events (both classified by yearly probabilities) (Fig. 4).

The detailed model output can be found in the Supplementary Material 2 and 3.

## 4 Discussion

While longer duration ECEs did not have lasting, negative effects on aquatic insect (Ephemeroptera, Plecoptera, Trichoptera: EPT) biodiversity or traits contrary to our first prediction, they drove short-term increases in EPT abundance and species richness. This pattern indicates that some species became temporarily more abundant after longer duration ECEs. Such shifts are consistent with certain species taking advantage of ECEs, potentially benefitting from reduced competition, whereas other species decline (Feio et al. 2010; Leigh et al. 2015; Milner et al. 2018). While the EPT community is able to recover even from ECEs with long durations, its sensitivity to sudden relative change suggests that the occurrence of extreme climatic events and, even more importantly, their increasing occurrence, could alter EPT community composition and species population sizes.

While we did find varying effects depending on the type of ECE, we did not find all of the expected patterns of our second prediction. Effects of successive water temperature-related ECEs were found for EPT abundance and diversity. Additional extreme cold events lead to a short-term increase in abundance. As evenness was not affected, it is unlikely that extreme cold events favored a few species which became dominant, but rather suggests that hatching is delayed after extreme cold events, leading to more concentrated emergence 1 month after an extreme cold event. Previous studies found that the duration of the egg state and transition to larval stage is water temperature-dependent for two EPT species (Taylor et al. 1999: Megarcys signata; Uno & Stillman 2020: Ephemerella maculata) and species present at the Breitenbach are likely to similarly have temperature-dependent development. In the River Severn in the UK, EPT richness declined after a thermal discharge (Worthington et al. 2015). In our study, the effects of additional extreme heat events are more pervasive, as they led to short-term reductions in Shannon's diversity, increases in evenness, and a long-term decrease in abundance. As extreme heat events were the only type of ECE that increased in frequency, even their short-term effects but especially their long-term effects may strongly influence future aquatic insect communities.

Additional water temperature-related events resulted in the expected trait changes. Specifically, increasing numbers of additional extreme heat events led to an increase in CTI values, with the reverse true for increasing extreme cold events. Similarly, Haase et al. (2019) found a positive correlation between CTI and temperature increases. In the Breitenbach, extreme heat events favored species with lower dispersal capacities. While additional extreme heat waves only had short-term effects, additional extreme cold waves changed the EPT community in the following year towards a higher proportion of cold-adapted taxa. Increasing frequencies of extreme heat events and decreasing frequencies of extreme cold events are likely to result in a shift of the EPT community towards more heat-resistant species.

In contrast to previous work, we did not find negative effects of additional flow-related ECEs on EPT abundance, richness and diversity (Leigh et al. 2015; Milner et al. 2018; Stubbington et al. 2009; Theodoropoulos et al. 2017) or an effect on community traits (Bogan et al. 2015; Moi et al. 2020). Even when additional flow-related ECEs improved

model performance, their effects were minor or not significant. Our results suggest that the recurring ECEs in the Breitenbach have resulted in a community well-adapted to floods and droughts.

Effects of ECEs were delayed and not persisting within our lag intervals. All effects were present for a maximum of two consecutive lag time periods suggesting most responses were transient. The delayed response could be due to delayed hatching of eggs or could be the result of complex species interactions. However, it might also be an artifact of lag time period definition. As the calculation for the lag time period starts on the first day of the ECE, effects that are visible only after the ECE has passed, would not be visible in the earlier lag time periods of longer duration ECEs. Further, flow-related ECEs can be followed by quick recoveries (Death et al. 2015; A. J. Smith et al. 2019; Wood et al. 2000). We found similar patterns for water temperature-related events, with the EPT community generally recovering after a few months, suggesting that species either survive in refugia (e.g., in the interstitial below the stream bottom) or are able to quickly recolonize the Breitenbach stream from other habitats.

Certain discharge patterns (e.g., spring spates) have significant effects on some EPT species occurring in the Breitenbach (Wagner et al. 2011). Low-flow conditions favor a certain subset of species, while different species increase in abundance during high-flow conditions (Wagner et al. 2011). Using our classification method, extreme spring spates — which are common in the Breitenbach — are classified as ECE, but less extreme floods at unusual times of the year may be missed. Due to our focus on community changes and for reasons of model complexity, we did not examine the effects of seasonality in this study, but these effects may elucidate patterns when more data are available.

The frequency and duration of extreme climate events (ECEs) at the Breitenbach changed through time. In general, water temperature-related events were more common than flow-related ECEs. While flow-related ECEs occurred more rarely, they tended to last longer. Extreme heat events increased in frequency, but duration stayed rather constant. In contrast, duration of extreme cold events decreased. These trends are in support of the IPCC (2012) findings. In general, heavy precipitation events and ecological droughts (definition based on soil moisture) are increasingly common (IPCC 2021). In contrast, at the Breitenbach, floods and droughts tended to decrease in frequency over our study period.

## 4.1 Caveats

Our study was subject to a few constraints which limit our interpretation of the effects of ECEs on the EPT community. First, while the study is long-term and data are high resolution, the study includes only a single site. Second, a major challenge when attempting to disentangle the effects of many ECE types is sufficient data to capture system complexity. Models failed to converge when interaction terms or too many explanatory variables were included; thus driver interactions and seasonality of ECEs could not be evaluated.

## 5 Conclusion

Using this unique long-term sampling of EPT taxa and accompanying water temperature and discharge data across two decades, we detected sensitivity of biodiversity and community traits to extreme climatic events. We show that effects of ECEs on EPT communities are manifold with cumulative effects of ECEs having the largest impact. The relatively

pristine habitat quality of the site, absence of direct anthropogenic stressors, and particularly high resolution (daily sampling) of the 20-year time series provide a unique opportunity to study climate change effects on EPT communities. The changing frequencies and durations of ECEs, especially the increasing frequency of extreme heat events and the negative cumulative effects of ECEs, paint a worrisome picture for the future of EPT communities in headwater streams. Long-term experiments could help disentangle the effects of different ECE stressors and provide a possibility to study effects of certain combinations of ECEs (Ledger & Milner 2015). In addition, high-resolution, continuous long-term data from various locations, collected in parallel with abiotic data are indispensable to understand how climate change is restructuring Earth's biota.

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