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Spatial and temporal effects of heat waves on the diversity of European stream invertebrate communities

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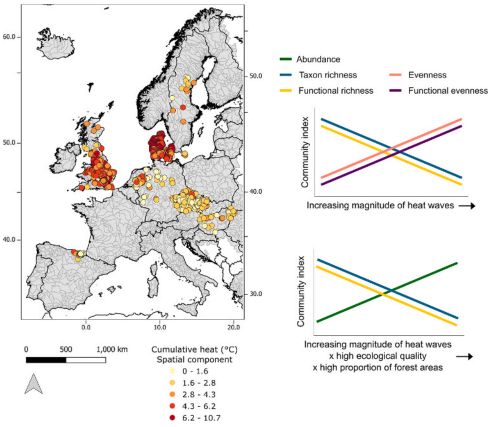
HIGHLIGHTS

- The magnitude of heat waves is increasing with climate change.
- Taxon and functional richness decreased with increasing magnitude of heat waves.
- Heat waves affected more streams with high ecological quality or in forested areas.
- High quality streams or in forested areas harbor more taxa vulnerable to heat waves.

GRAPHICAL ABSTRACT



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ABSTRACT

The frequency and magnitude of extreme events, such as heat waves, are predicted to increase with climate change. However, assessments of the response of biological communities to heat waves are often inconclusive. We aimed to assess the responses in abundance, taxonomic and functional diversity indices of stream invertebrate communities to heat waves using long-term monitoring data collected across Europe. We quantified the heat waves' magnitude, analyzed the spatial (i.e., long-term mean) and temporal (anomaly around the long-term mean) components of variation in the magnitude of heat waves, and their interaction with anthropogenic stressors (ecological quality and land cover). For the spatial component of variation, we found a negative association of the community indices to the increasing magnitude of heat waves. Sites undergoing heat waves of higher magnitude showed fewer species and lower trait diversity compared with sites experiencing lower magnitude heat waves. However, we could not detect an immediate temporal response of the communities to heat waves (i.e., the temporal component). Furthermore, we found that the effects of heat waves interacted with the ecological quality of the streams and their surrounding land cover. Diversity declined with increasing heat

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waves' magnitude in streams with higher ecological quality or surrounded by forest, which may be due to a higher proportion of sensitive species in the community. Heat waves' impacts on diversity were also exacerbated by increasing urban cover. The interaction between heat waves' magnitude and anthropogenic stressors suggests that the effects of extreme events can compromise the recovery of communities. Further, the predicted increase in heat waves will likely have long-term effects on stream invertebrate communities that are currently undetected.

1. Introduction

The frequency and magnitude of extreme weather events have already increased and are predicted to further increase with ongoing climate change (Seneviratne et al., 2021; IPCC, 2023). However, the ecological consequences of such events are not yet fully understood. An emerging conclusion from studies so far (e.g., special issues in Journal of Ecology; Smith, 2011a, 2011b; Freshwater Biology; Ledger and Milner, 2015a, 2015b; Philosophical Transactions of the Royal Society B; van de Pol et al., 2017) is that the ecological consequences are highly variable: some species' populations might benefit from them, while some others are severely affected, and responses at the community level are often inconclusive. Extreme weather events are, by definition, rare or unusual in terms of probability (e.g., < 5 % frequency of occurrence) based on the historical climate record or based on species- or system-specific critical thresholds (e.g., specific temperature threshold; Ledger and Milner, 2015a, 2015b; Smith, 2011a, 2011b). This limits our understanding because local, opportunistic (an extreme event occurred during a long-term study), or experimental studies usually focus on single or few species (Chessman, 2015; Maxwell et al., 2019; Mouthon and Daufresne, 2015; Ross et al., 2022). Meanwhile, the effects of extreme events on communities might either escalate through the food web and other species interactions or be mitigated by compensatory mechanisms (Neilson et al., 2020; Ross et al., 2022; Supp and Morgan Ernst, 2014; Thompson et al., 2013), implying that generalities about the effects of extreme events at the community level are still debated.

Heat waves are among the extreme weather events projected to increase due to climate change (Meehl and Tebaldi, 2004), with freshwater ecosystems being particularly vulnerable to them (Graham et al., 2024; Ledger and Milner, 2015a, 2015b; Tassone et al., 2023; Woolway et al., 2021). Heat waves are highly significant for freshwater ecosystems because most freshwater species are ectotherms and sensitive to large increases in temperature (Bonacina et al., 2023). At local scales, temperature affects metabolic rates, population growth, and species interactions (Bonacina et al., 2023; Woodward et al., 2016). At broad geographical scales, temperature is a climatic driver that influences species' distributional ranges by defining the conditions within which a species can persist (Addo-Bediako et al., 2000). Ecological impacts of large temperature increases might include compositional changes due to high mortality of sensitive species, the introduction of invasive species, or dispersal of some species to avoid unfavorable conditions or move towards more suitable areas during range shifting (Gu et al., 2023; Jourdan et al., 2018; Mouthon and Daufresne, 2015; Polazzo et al., 2022). Furthermore, it has been suggested that pulses or discrete extreme events such as heat waves and increased fluctuations in temperature might strongly affect communities, unlike moderate effects of long-term increasing trends in mean temperatures (i.e., press disturbances Sabater et al., 2022; Thompson et al., 2013; Vasseur et al., 2014). However, most studies on freshwater ecosystems have been focused on temperature trend effects, i.e., warming (e.g., Haase et al., 2019, 2023; T. Sinclair et al., 2024), or are focused on heat waves but are rather local (e.g., Dietrich et al., 2023; Harris, 2020; but see Jourdan et al., 2018; Mouthon and Daufresne, 2015; Neilson et al., 2020), while large-scale studies that might bring up general conclusions about the effects of heat waves on freshwater ecosystems are lacking.

The capacity of freshwater ecosystems to cope with heat waves depends on the community structure and composition of functional traits (Mouillot et al., 2013). Species' responses might be positive, neutral, or negative to high temperatures (Gu et al., 2023; Maxwell et al., 2019; Neilson et al., 2020; Polazzo et al., 2022), depending on a range of functional traits, including thermal limits, dispersal capacity, resistance forms, duration of the life cycle, or reproductive strategy (Bonacina et al., 2023). In turn, responses at the community level will depend on the collective diversity of these responses (Ross et al., 2022) and how species interactions maintain —or not— the community's taxonomic and functional structure (Boucek and Rehage, 2014; Harris, 2020; Supp and Morgan Ernst, 2014). Moreover, the capacity to resist or recover from heat waves depends on other stressors that simultaneously affect freshwater ecosystems, such as declines in diversity and changes in composition due to land-use intensification, contaminants, or flow alterations (Maxwell et al., 2019; T. Sinclair et al., 2024; Uhler et al., 2021). So far, several studies indicate that heat waves typically lead to reduced population sizes and diversity (Dietrich et al., 2023; Maxwell et al., 2019; Palmer et al., 2017; Sabater et al., 2022; Supp and Morgan Ernst, 2014). Moreover, previous studies have found decreases in abundance and richness driven by interactions between climate and change in land cover (Outhwaite et al., 2022; Uhler et al., 2021), further emphasizing the need to assess the interacting effects of heat waves with other anthropogenic stressors. A mechanistic understanding of how heat waves affect communities' composition and functional structure and interact with other stressors is an important prerequisite to predicting if ecosystem processes, functions, and services will be disrupted by these extreme events (Oliver et al., 2015).

In this study, we aimed to assess the responses in abundance, taxonomic, and functional diversity (i.e., community indices) of stream invertebrate communities to heat waves across Europe. We used a probabilistic approach to define heat waves (Seneviratne et al., 2021) based on ambient maximum daily temperature and an extensive dataset of 910 time series of stream communities from eight European countries, which allowed us to evaluate communities' responses across multiple sites and years to heat waves of varying magnitudes. Moreover, given climate is a spatio-temporally varying variable, we also disentangled the spatial and temporal relationships between the temperature and the community indices (Blüthgen et al., 2022), following recent studies that indicated differing responses, at least when assessing mean temperature effects (Bradter et al., 2022). High-magnitude heat waves likely result in reductions in the populations of sensitive species and traits (Biswas and Mallik, 2011; Mouillot et al., 2013). Consequently, we hypothesized (H1) a decrease in abundance, taxonomic, and functional diversity with the increasing magnitude of heat waves. We also hypothesized (H2) a stronger effect of the spatial component of heat waves because maximum temperatures likely vary more spatially than temporally and because lags in the communities' responses might hinder the immediate effect of the temporal component. Furthermore, we analyzed the effects of heat waves on communities with varying levels of anthropogenic impact, assessed through the ecological quality ratio (EQR) from the European Union Water Framework Directive (EC, 2000) and the proportion of forested, agricultural, and urban land cover surrounding the streams. Declines in ecological quality and increases in urbanization (i.e., agricultural and urban areas) are reflected by declines in diversity (Outhwaite et al., 2022; J.S. Sinclair et al., 2024); therefore, the effects of ecological quality and land cover are likely to interact with those of heat waves reducing stream diversity. Consequently, we hypothesized (H3) a synergistic interaction between (a) low ecological quality and high magnitudes of heat waves due to action of multiple stressors, and (b) high proportion of agricultural and urban areas and high magnitudes of heat waves leading to the lowest levels of invertebrate diversity.

2. Materials and methods

2.1. Biological data

We analyzed the responses of stream communities to heat waves across temporal and spatial scales. For this, we used a subset of the time series of stream invertebrate communities from Haase et al. (2023), complemented with data from the Czech Republic from J.S. Sinclair et al. (2024). For most of the sampled streams, only spring (sampling between March and May) samples were available. In addition, selecting only spring samples allowed us to exclude for the effects of seasonal variation in invertebrate communities. Our final dataset consists of 11,290 observations from 910 sites across eight European countries: Spain, Hungary, Czech Republic, Germany, Netherlands, Denmark, UK, and Sweden. The dataset comprises between 13 and 310 sites per country and overall spans 30 years, from 1992 to 2021. Individual sites have between 5 and 28 sampling years (median = 11 years). Sampling methods and taxonomic resolution (identification level) are consistent within time series (intra-site), but may not be among countries. The taxonomic resolution is mixed between species, genus, and family; sensitivity analyses previously performed on the data showed that differences in the taxonomic resolution among time series have little effect on the models' outputs (Haase et al., 2023). In total, we analyzed 849 taxa, from 194 families and 31 groups (mostly orders). Across countries, insects from Coleoptera, Trichoptera, and Diptera represented the highest number of taxa and families (431 taxa and 70 families), while 15 groups were represented by only one taxon (Table S1). Between 152 and 318 taxa were registered in each country across sampling years. Most data were collected by kick-sampling and represent, as far as possible, community-level sampling of all invertebrates. Abundance data were recorded for each sampled taxon.

From our dataset of 11,290 observations, the ecological quality ratio (EQR) was available only for 8031 observations corresponding to 655 sites across eight countries. The EQR is a similarity index that provides a measure of ecological quality by comparing biological communities and multi-metric indices to a reference community, not impacted by human activities such as hydromorphological alterations, physico-chemical degradation, and biological elements, obtained by modeled or collected data. The EQR ranges from 0 to 1, with 1 representing type-specific reference conditions and 0 bad ecological status. The purpose of the EQR is to provide a numerical scale meant for the biological assessment and ecological status of water bodies required by the EU Water Framework Directive (WFD, 2000) ensuring comparability among freshwater ecosystems under different pressures and anthropogenic impacts; therefore, it provides a standard metric that allows us to compare the ecological status of streams under different anthropogenic pressures.

2.2. Community indices

Changes in the communities can be assessed with abundance, taxonomic, and functional diversity indices (Table 1). Changes in these community indices reflect changes in the presence and the abundance distribution of species and traits in the community; therefore, they provide a metric indicating which properties of the community change after a disturbance such as a heat wave. For example, the number of species or traits could change, or the dominance of certain species or traits. We calculated total abundance, and taxonomic and functional diversity for each site and for every sampling year. To compute total abundance, we first standardized values at each site using the Hellinger transformation to ensure that values from different providers are comparable and to deal with data containing many zeros (Legendre and Gallagher, 2001). Taxon richness and evenness were computed using the "vegan" package (Oksanen et al., 2022).

Table 1
Definition of community indices and extreme events-related terms used in this study.

Term	Definition	Rationale
Abundance	The Hellinger-transformed total number of individuals in a community Continuous variable with positive values	A basic metric reflecting changes in the number of individuals
Taxon richness	Total number of distinctive taxa in a community Discrete variable with positive values	Its change reflects changes in the number of taxa in the community
Evenness	Pielou's evenness, the ratio of Shannon diversity index to the logarithm of taxon richness Continuous variable with values between 0 and 1	Its change reflects changes in the distribution of common and rare taxa in the community
CTI	Community temperature index. The abundance-weighted average of the taxon-specific temperature preferences of each taxon in the sample (Haase et al., 2019) Continuous variable with positive values	Its change measures changes in the mean temperature preferences of the community
Functional richness	The volume of multidimensional space occupied by the traits of all species in a community within functional space (Mouillot et al., 2013) Continuous variable with values between 0 and 1	Its change reflects changes in trait composition and the functional space
Functional evenness	The regularity of the distribution and relative abundance of species in functional space for a given community (Mouillot et al., 2013) Continuous variable with values between 0 and 1	Its change measures changes in the regularity of abundance distributions in the functional space
Q 0.9	0.9 quantile. The threshold indicating where 90 % of the annual data is below its value and 10 % is above it.	It provides a probabilistic definition of extremeness
Extreme temperature event/day	A day with maximum temperatures exceeding the Q 0.9 threshold (Seneviratne et al., 2021)	It provides a probabilistic definition of extremeness
Heat wave	At least three consecutive days registering extreme temperatures (Perkins-Kirkpatrick and Lewis, 2020)	The main focus of this study
Cumulative heat	The exceedance heat produced by a heat wave. It is the sum of the differences between values of days with extreme temperatures and the annual Q 0.9 value across heat wave days (Perkins-Kirkpatrick and Lewis, 2020). Used as the magnitude of heat waves in this study	It provides a magnitude for the excess heat exposure over consecutive days
Spatial component of the cumulative heat	The average cumulative heat of each site across years	It quantifies the spatial variation of mean cumulative heat
Temporal component of the cumulative heat	The difference between the annual cumulative heat of each site and the average across years (the spatial component)	It quantifies the temporal anomalies of cumulative heat after accounting for the mean spatial variation

Functional indices were computed using trait information from freshwaterecology.info (Schmidt-Kloiber and Hering, 2015) at the species level when available or at a higher taxonomic level otherwise (see below). We selected six traits with 25 modalities related to the responses of invertebrates to disturbance (Table S2): body size, life cycle duration, number of reproductive cycles per year, dispersal strategy, aquatic stages, and resistance forms following Tachet et al. (2010). We expected these life-history traits would affect species' response to heat waves given that higher temperatures accelerate metabolic rates, reducing body size and the life cycle duration, and allowing for a higher number of reproductive cycles per year (Bonacina et al., 2023). Species with active dispersal strategies, fewer aquatic stages, or resistance forms might resist disturbances more effectively by dispersing to suitable environments or enduring the disturbance in their resistance forms or terrestrial phases (Bonacina et al., 2023; Van Looy et al., 2019).

Trait coverage varied between 50 and 60 % at the provided taxonomic level (species and genera); when information at the species or genus level was not available, we replaced missing values using average trait values of a higher taxonomic level, e.g. information of all species in the taxon list of the same genus, or all genera of the same family, to reach a final coverage of 91 to 95 % of taxa with trait information. The taxa that remained without trait information after this process were removed from subsequent trait analysis. We assumed that the use of mixed-level trait information is a reliable approach to dealing with missing values, as it has been shown that aggregating trait values to higher taxonomic levels shows similar results to the species-level trait analyses (Kunz et al., 2022) and closely related taxa have similar traits, especially for freshwater macroinvertebrates (Burns and Strauss, 2011; Mayfield and Levine, 2010).

To calculate functional indices, we first scaled trait values between 0 and 1 to account for differences in the coding system in freshwaterecology.info (e.g., fuzzy coding, ten-point assignment, single assignment), so that each taxon was assigned an affinity score for each modality (i.e., a proportion). Then, we used the trait proportions and weighted the matrix to obtain an even distribution of traits with different numbers of modalities using the function *gawdis* from the "gawdis" package (Bello et al., 2021). The weighted matrix was used to compute a dissimilarity matrix based on Gower's distances using the *gowdis* function from the "vegan" package, which is suitable for heterogeneous data types. Using the dissimilarity matrix and the abundance matrix, we computed functional richness and functional evenness with *dbFD* function from the "FD" package (Laliberté et al., 2014).

We also computed the community temperature index (CTI) following Haase et al. (2019). The community temperature index is the abundance-weighted average of taxon-specific temperature preferences of the community. The taxon-specific temperature preferences were based on the stream zonation preference trait extracted from freshwaterecology.info (Schmidt-Kloiber and Hering, 2015), which reflects the differences in typical temperatures experienced by species living in different sections of a river. We assigned temperature values to the stream zone modalities, from the lowest in the spring zone (2 °C, eucrenal) to the highest in the bream region (22 °C, metapotamal), to calculate taxon-specific preferences (Haase et al., 2019; Moog, 2002), and then calculated a weighted mean for each community using transformed abundances. The CTI has been compared to indices based on water temperature (e.g., KLIWA) showing a high correlation between the two indices (Sundermann et al., 2022) and supporting its use as a proxy of the community temperature preference. However, direct measurements of physiological tolerance could help understand variation within and among species in sensitivities to extreme events.

2.3. Temperature and land cover data

We used air temperature as a proxy of stream temperature. Air temperature is generally strongly related to water temperature, especially for stream ecosystems (Arora et al., 2016; Morrill et al., 2005; Toffolon and Piccolroaz, 2015; Zhu et al., 2024), and it is available at a better spatial and temporal resolution for all our sampling sites. Moreover, even when the relationship between air and water temperature is not linear due to shade or runoff, increases in air temperature consistently result in increases in water temperature (Graham et al., 2024; Van Vliet et al., 2023). Temperature data was obtained as the daily maximum temperature from the E-OBS dataset (EU-FP6 project UERRA, https://www.uerra.eu) and the Copernicus Climate Change Service (https://surfobs.climate.copernicus.eu/surfobs.php; Cornes et al., 2018) with a resolution of 0.1°. This dataset is based on surface in-situ observations owned and operated by National Meteorological Services and others for climate monitoring across Europe. Details on the calculations, gridding method, and ensemble generation can be found in Cornes et al. (2018). We extracted daily values from 1991 to 2021 using the geographical coordinates of the sampling sites.

We obtained land cover data from the Copernicus Climate Change Service, Climate Data Store (2019) database with a horizontal resolution of 300 m (CDR and ICDR Sentinel-3 satellite with 21 bands between 400 and 1020 nm). We extracted yearly values of the proportion of land cover of the upstream areas of the sampling sites from 1991 to 2021 for three main types of land cover: forested areas, including tree cover and mosaic trees and shrubs, agricultural areas, including croplands and mosaic croplands, and urban areas. Upstream areas were defined using the hydrological model Hydrography90m with a spatial resolution of 90 m (Amatulli et al., 2022).

2.4. Heatwaves

We focused on the effects of heat waves in summer preceding the sampling date and the lagged effects reflected in the communities' survival and reproduction in the following spring season. To define an event of extremely high temperature (Table 1, Fig. 1), we used the 0.9 quantile values of maximum daily temperatures in the summer months (June to August) of the previous year at each sampling site as a threshold (Seneviratne et al., 2021). At least three consecutive days with extremely high temperatures defined a heat wave. The magnitude of the heat wave was quantified as the cumulative excess heat, this is, the sum across heat wave days of the differences between values of extreme temperature days and the annual 0.9 quantile (Perkins-Kirkpatrick and Lewis, 2020). By using the cumulative heat, we focused on the excess heat exposure over consecutive days, rather than the absolute temperature values, since it is the exceedance of a threshold, and not the temperature experienced, that results in adverse effects (Perkins-Kirkpatrick and Lewis, 2020). To assess if the responses to the magnitude of heat waves vary along spatial or temporal gradients, we further disentangled the temporal and spatial components of the cumulative heat variable (Blüthgen et al., 2022; Bradter et al., 2022). For this, the spatial component was calculated as the average cumulative heat of each site across sampling years, and the temporal component was calculated by subtracting the value of each year from that average, i.e., the temporal anomaly around the long-term mean.

2.5. Statistical analysis

To estimate the effects of heat waves on stream communities, we tested the cumulative heat, and its temporal and spatial components, as predictors of the community indices. The response variables, i.e., community indices, were fitted to the corresponding distribution according to the data characteristics. Abundance and CTI were fitted as gamma distributions (for continuous variables, positive values without upper limit), taxon richness was fitted as Poisson distribution (counts), and evenness, functional richness, and functional evenness were fitted as beta distributions (values bounded between 0 and 1).

We focused on assessing the evidence for a linear response of the community indices with an increasing magnitude of heat waves of the previous summer, since graphical exploration did not suggest any non-linearity. Therefore, we included cumulative heat as a linear fixed effect (Model 1). We also included a non-linear long-term trend of the community indices (i.e., a smoothed term for 'year' with $k = 9$, syntax s

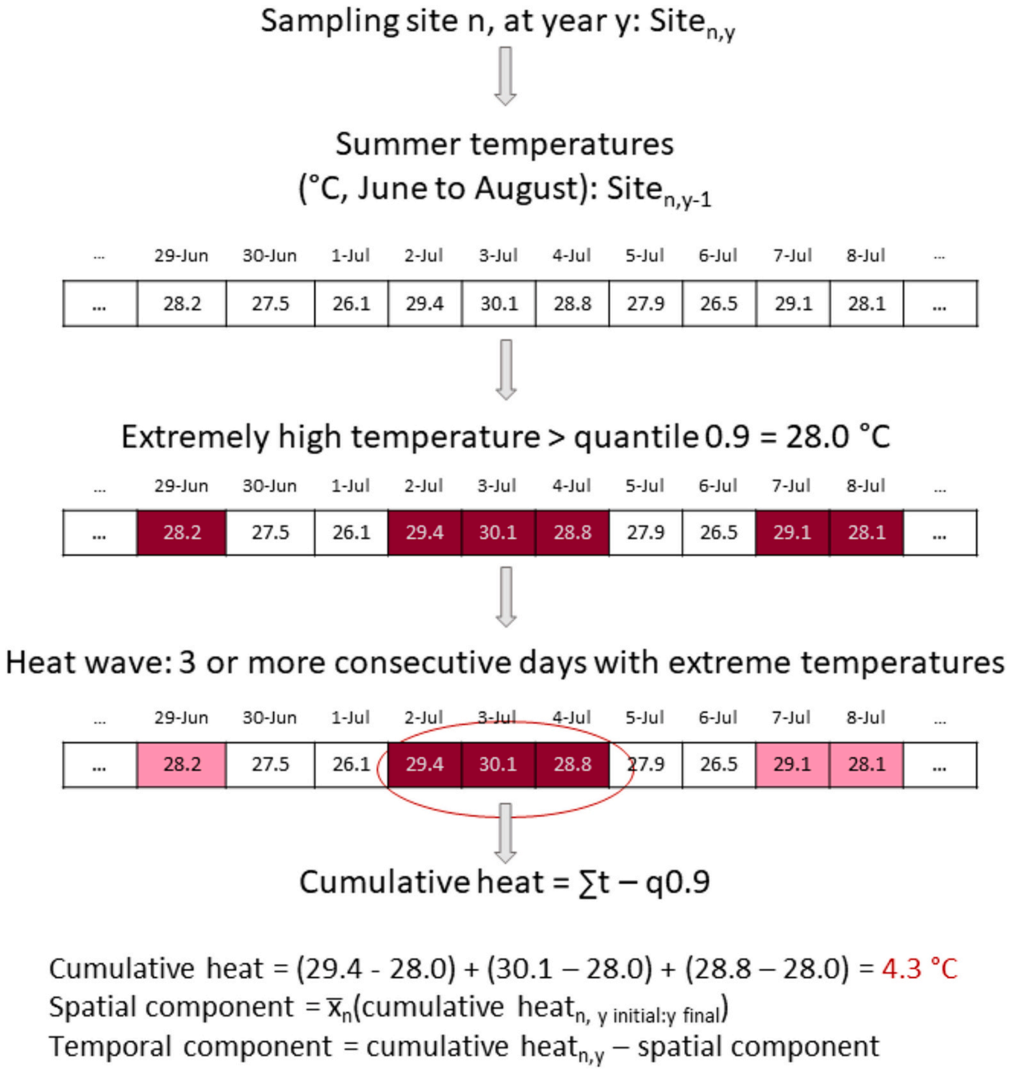

Fig. 1. Scheme exemplifying the methodology used to detect heat waves.

() in the models; Fewster et al., 2000) to separate the heat wave effects from long-term community trends driven by variables not included in our analyses, which previous analyses indicate have changed through time due to historic declines and more recent signs of recovery (Haase et al., 2023). We included random effects (intercepts) for site, sampling month, and country (syntax bs = "re" in the models) to account for other mean differences in the community indices that may be due to unmodeled covariates, including site characteristics, species' phenologies, and differences in sampling season, methods, and units. The form of Model 1 was gam(community index ~ s(year) + cumulative heat + s(site, bs = "re") + s(month, bs = "re") + s(country, bs = "re") with 'community index' being abundance and each taxonomic and functional index described in Section 2.2. We ran a second series of models that decomposed the cumulative heat variable into its spatial and temporal components, which were both included as linear fixed effects instead of the original cumulative heat variable (Model 2). The form of Model 2 was gam(community index ~ s(year) + spatial component + temporal component + s(site, bs = "re") + s(month, bs = "re") + s(country, bs = "re").

From Model 2, we identified that the spatial component of variation was the only one showing significant effects on communities. Therefore, we tested our third hypothesis, i.e., synergistic effects of EQR and land cover with heat waves on communities, using only the spatial component of the cumulative heat. To directly relate predictors to the spatial component, we further calculated EQR and land cover values as spatial variables, i.e., static on time, using the mean values over years for each site. We used the subset of observations with EQR values (71.1 % of observations) and ran models with the spatial component of cumulative heat, EQR, and their interaction as linear fixed effects, a non-linear effect of time, and site, month, and country as random factors (Model 3). The form of Model 3 was gam(community index ~ s(year) + spatial component + EQR + spatial component:EQR + s(site, bs = "re") + s(month, bs = "re") + s(country, bs = "re"). Lastly, we ran separate models for the interaction of the spatial component with the proportion of three types of land cover, i.e., forested, agricultural, and urban areas (Model 4). The form of Model 4 was gam(community index ~ s(year) + spatial component + land cover proportion + spatial component:land cover proportion + s(site, bs = "re") + s(month, bs = "re") + s(country, bs = "re"). With models 3 and 4, we aimed to answer if the patterns of the diversity indices with increasing magnitude of heat waves intensified in sites with lower ecological quality or higher proportion of agricultural and urban areas.

All models were visually validated by checking the residual variation. To check for spatial autocorrelation, we ran a Moran's I Test using the function *moran.randtest* from the "adespatial" package (Dray et al., 2012) on the models' residuals and did not find significant autocorrelations. To check for collinearity, we calculated the variance inflation factor VIF for the parametric terms of the models using the function *vif*.

gam from the “mgcv.helper” package. All VIF values were < 5, suggesting low to moderate collinearity. In addition, we visually examined the relationship between the spatial component of cumulative heat, EQR, and the land cover variables (Fig. S1) and detected no evident patterns. We present the model results as partial effects of the response variables, this is, the results are centered around 0 representing the overall mean effect of the response variable and scaled in standard deviation units. Positive values indicate where the predictors increase the response above the average value, and negative values indicate where the predictors reduce the response below the average value. Partial effects allow for comparison between indices in different scales. We ran all models using the “mgcv” package (Wood, 2017) in R 4.3.2–4.

3. Results

3.1. Cumulative heat and temperature variation

Maximum temperatures across countries and years reached up to 38.4 °C, and temperature thresholds varied between 17.2 °C in the UK and 35.6 °C in Spain (Fig. 2, Table S2). Spain and Hungary showed the highest maximum temperatures across years and consequently, the highest thresholds. Sweden, Denmark, and the UK showed the lowest temperatures and thresholds across years (Fig. 2a). The cumulative heat was similar among countries, with most of the values ranging between 3.3 and 16.1 °C, but as high as 35.3 °C accumulated over one summer (Fig. 2b). The spatial component of heat varied markedly, with the highest values in northern countries, e.g. Denmark and the UK, and the lowest in Hungary, Czech Republic, and Germany (Fig. 2c, a). Similar to total cumulative heat, the temporal component did not markedly vary among countries (Fig. 2d) but varied over years in most countries, except for Germany and Sweden where it showed low variation (Fig. 3b). Overall, there was more spatial variation in the cumulative heat than temporal variation among the countries, indicating long-term persistent differences in cumulative heat (Fig. 2c vs d).

The cumulative heat and its spatial and temporal components showed a low correlation to the maximum temperature (Pearson r range from −0.5 to 0.1, Fig. 3c). Accounting for all sites, the spatial component showed a moderate negative correlation to maximum temperature ($r = -0.5$), meaning that colder sites, e.g., sites in Denmark or the UK, showed the highest heat wave magnitudes. On the contrary, the temporal component showed a positive, albeit very weak, correlation with the maximum temperature ($r = 0.1$).

3.2. Community responses to heat waves

Models explained 33 to 67 % of the variation of community indices (Table 2), with significant variation between sites, months, and countries. The cumulative heat and its temporal component did not show a significant effect on the community indices, except for the functional evenness that increased with increasing cumulative heat (Fig. 4). Differently, the spatial component showed significant effects on taxon richness, evenness, functional richness, and functional evenness. This means that an association with heat waves was indicated by comparing mean differences among sites. By contrast, we could not detect an effect of heat waves when comparing differences in the community indices among years, i.e., the indices did not systematically change at a site according to the magnitude of heat waves in the preceding year. Both taxon and functional richness were lower at sites with heat waves of higher mean magnitude (decrease of 2.11 and 1.60 % per 1 °C, respectively). Evenness and functional evenness were higher at sites with heat waves of higher mean magnitude (increase of 2.43 and 2.14 % per 1 °C, respectively). Overall, our results suggest that sites affected by heat waves of higher magnitude have fewer species and a lower diversity of traits, but an even distribution of species and traits.

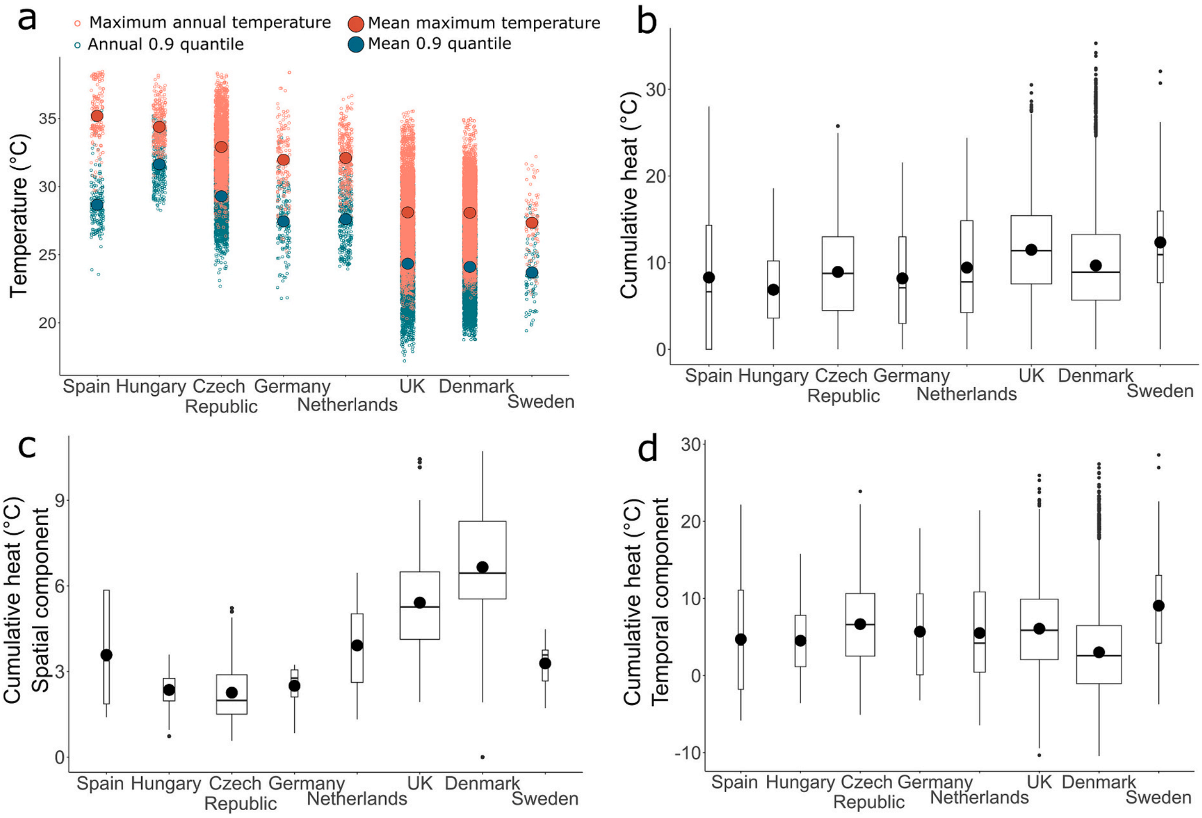

Fig. 2. (a) Maximum annual temperature (red symbols) and annual extreme temperature thresholds (green symbols) by country. (b) Cumulative heat variation, and its (c) spatial and (d) temporal components, by country. (a–d) Large circles are mean values. (b–d) The width of the boxes represents the number of samples.

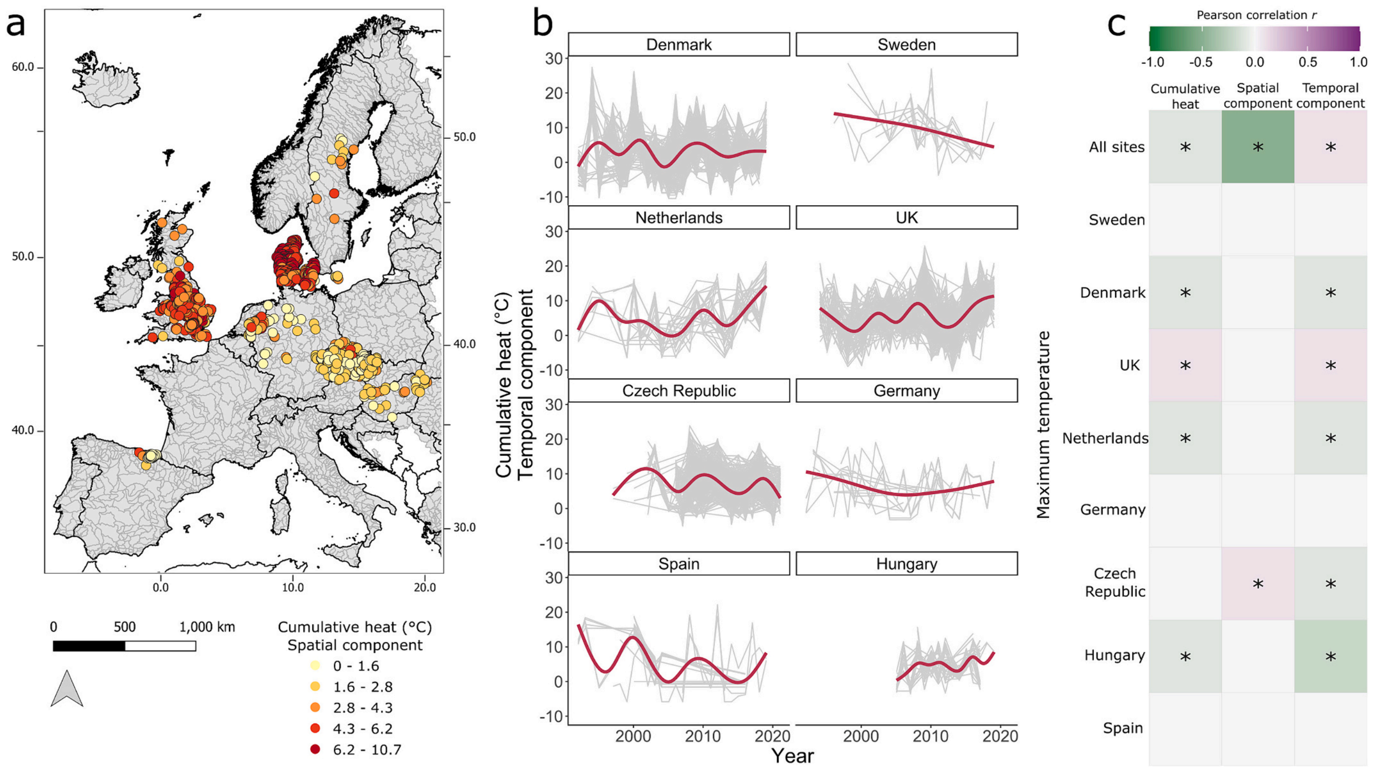

Fig. 3. (a) Spatial component of the cumulative heat at sampling sites. Gray lines show the river network. (b) Temporal component of the cumulative heat over time (x-axis) at sampling sites (gray lines) and overall pattern per country (red lines). (c) Correlation between maximum temperature (vertical axis) and cumulative heat, its spatial and temporal components at all sites and per country. Asterisks indicate significant correlations.

Table 2
Models' coefficients for community indices as a response to cumulative heat, and its spatial and temporal components. Significant terms are shown in bold and their significance is indicated with asterisks (*<0.05, **<0.01, ***<0.001).

Index		Parametric coefficient	Estimate	Standard error	t value	Adjusted r^2 (%)
Abundance	Model 1	Cumulative heat	8.5E−06	8.1E−05	0.11	61.0
	Model 2	Spatial component	9.2E−04	1.4E−03	0.67	61.0
		Temporal component	6.6E−06	8.1E−05	0.08	
Taxon richness	Model 1	Cumulative heat	−1.2E−04	3.7E−04	−0.33	66.8
	Model 2	**Spatial component**	**−2.1E−02**	**7.1E−03**	**−2.97****	66.8
		Temporal component	−2.9E−05	3.7E−04	−0.08	
Evenness	Model 1	Cumulative heat	−3.9E−04	7.1E−04	−0.55	53.9
	Model 2	**Spatial component**	**2.4E−02**	**9.0E−03**	**2.69****	54.2
		Temporal component	−3.2E−04	7.2E−04	−0.44	
CTI	Model 1	Cumulative heat	−9.2E−06	7.6E−06	−1.21	50.7
	Model 2	Spatial component	9.1E−05	9.5E−05	0.95	50.7
		Temporal component	−9.6E−06	7.6E−06	−1.26	
Functional richness	Model 1	Cumulative heat	−2.6E−04	6.3E−04	−0.42	53.7
	Model 2	**Spatial component**	**−1.6E−02**	**7.4E−03**	**−2.16***	53.7
		Temporal component	−1.9E−04	6.3E−04	−0.31	
Functional evenness	Model 1	**Cumulative heat**	**1.3E−03**	**4.9E−04**	**2.74****	33.3
	Model 2	**Spatial component**	**2.1E−02**	**4.0E−03**	**5.30*****	33.2
		Temporal component	**1.2E−03**	**4.9E−04**	**2.39***	

3.3. Interactions of heat waves with ecological quality and land cover

The models including the spatial component of cumulative heat and EQR were significant for abundance, and taxon and functional richness (Fig. 5, Table 3). In low quality sites, usually located in warmer and southern countries like Spain and the Netherlands (Fig. S2), abundance decreased and functional richness increased with heat waves (Fig. 5a, e). By contrast, in high quality sites, usually in colder and northern countries like Sweden and the UK (Fig. S2), abundance increased and taxon and functional richness decreased with heat waves (Fig. 5a, b, e).

Interactions with land cover types were also significant for abundance and taxon and functional richness (Fig. 5, Table 3). In sites with a high proportion of forest cover, abundance increased but taxon richness, evenness, and functional richness decreased with heat waves, similarly to the responses to high EQR values. However, in sites with high proportion of urban cover, taxon and functional richness also decreased with heat waves. Nonetheless, these results should be analyzed carefully because urban cover were generally very low for most sites, expect for those in the Czech Republic that showed high proportion of urbanization. CTI and functional evenness did not show any patterns with the interactions between EQR, land cover, and the magnitude of heat waves.

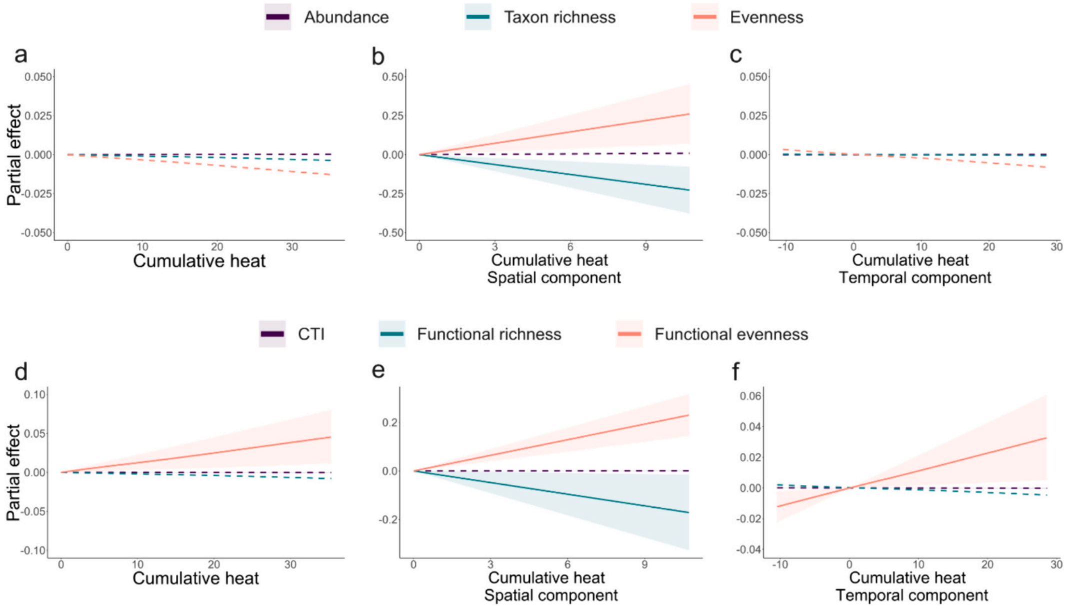

Fig. 4. Partial effect of community indices by cumulative heat (left panels), and its spatial (middle panels) and temporal components (right panels). a–c: abundance, taxon richness and evenness, d–f: CTI, functional richness, and functional evenness. Continuous lines represent significant effects and dotted lines represent no significant effects.

4. Discussion

We found that communities were overall negatively associated with heat waves, by reducing taxon and functional richness; however, heat waves' impacts varied with environmental conditions, such as land cover and streams' ecological quality. Moreover, we showed that heat waves have contrasting responses from the long-term trends of increasing taxon and functional richness identified for these same stream communities, which has likely been aided by improvements in water quality (Haase et al., 2023). This suggests that the recovery of European stream communities might be hindered by the effects of heat waves on community structure. Decreases in taxon and functional richness likely reflect the removal of sensitive species with traits that are poorly adapted to resist or recover from abrupt temperature increases (Mouillot et al., 2013). Previous studies suggested that the effects of heat waves or other extreme events on populations, although mostly negative, are weakly correlated to the community structure and functioning (Palmer et al., 2017; Sabater et al., 2022; Supp and Morgan Ernst, 2014) because communities have compensatory mechanisms, such as density-dependent dynamics, functional redundancy, and species replacement (Neilson et al., 2020; Supp and Morgan Ernst, 2014; Van Looy et al., 2019; Woodward et al., 2016). However, our results suggest that the increasing magnitude of heat waves overcame the compensatory mechanisms and modified the community composition and structure. By disrupting its structure and functioning, communities might not recover from further disturbances (Maxwell et al., 2019), stressing the vulnerability of communities undergoing heat waves of increasing magnitude.

Responses of the community indices were only significant to the spatial component of cumulative heat, but not to the temporal component. This may suggest that heat waves likely have a long-term effect on the communities not detectable in the short term. A lack of significance to the temporal component might be due to lags in the responses to heat waves occurring in the preceding year, probably related to the species life cycles (Leigh et al., 2015). Species with longer aquatic phases for larval development might show longer and more complex lags than faster developing species. This means that linking annual heatwaves to subsequent population responses could require a more complex analysis than we conducted. The spatial component more likely represents long-term responses in sites consistently undergoing heat waves. The detected effects of spatial variation could be influenced by other spatially co-varying factors; however, we found only weak correlations between the spatial component and the maximum temperature of the sites. Although the temporal component offers a stronger test of a causal relationship, by verifying whether a preceding heatwave has a detectable impact on the community in the following year, spatial analysis, or the combination of spatial and temporal components, offers a powerful approach to detecting and attributing changes in communities (Banet and Trexler, 2013), particularly given that time series tend to be more limited than spatial data. Moreover, the higher number of sites versus the more limited number of years in our analysis might contribute to the statistical power of the spatial over the temporal component (Blüthgen et al., 2022). We found that spatial variables were strong predictors of the community structure, which has been observed in communities with high connectivity (Banet and Trexler, 2013), but further research is needed to verify the possible causal pathways through which heat waves affect communities, including the short-term direct pathways (e.g., physiological impacts of extreme temperature) and the potentially longer-term indirect pathways (e.g., impacts mediated by changes in water discharge or stream habitat).

Communities undergoing heat waves of higher magnitude were primarily in colder countries, e.g., Denmark and the UK, stressing their vulnerability to climate change. Significant decreases in taxon and functional richness in colder countries could reflect the poor adaptation of typically cold-tolerant species to abrupt temperature increases (Addo-Bediako et al., 2000). However, the absolute temperature values were higher in southern countries, such as Spain, which could also have affected communities. Increasing temperatures are worrying for these southern countries since temperatures are already closer to species' physiological thermal limits and further severe increases in temperature are predicted (Meehl and Tebaldi, 2004; Müller et al., 2023; Newbold et al., 2020). When approaching their thermal limits, organisms show signs of stress and might display behavioral and physiological responses, such as dispersal to avoid unfavorable conditions, alterations in sex ratios, or mortality once such limits are exceeded, with important consequences in demographic dynamics and fitness (Bonacina et al., 2023; Leigh et al., 2015). In addition, we cannot rule out that shifts in phenology affected the sampled communities. For instance, summer heat waves might affect emergence times during the following spring.

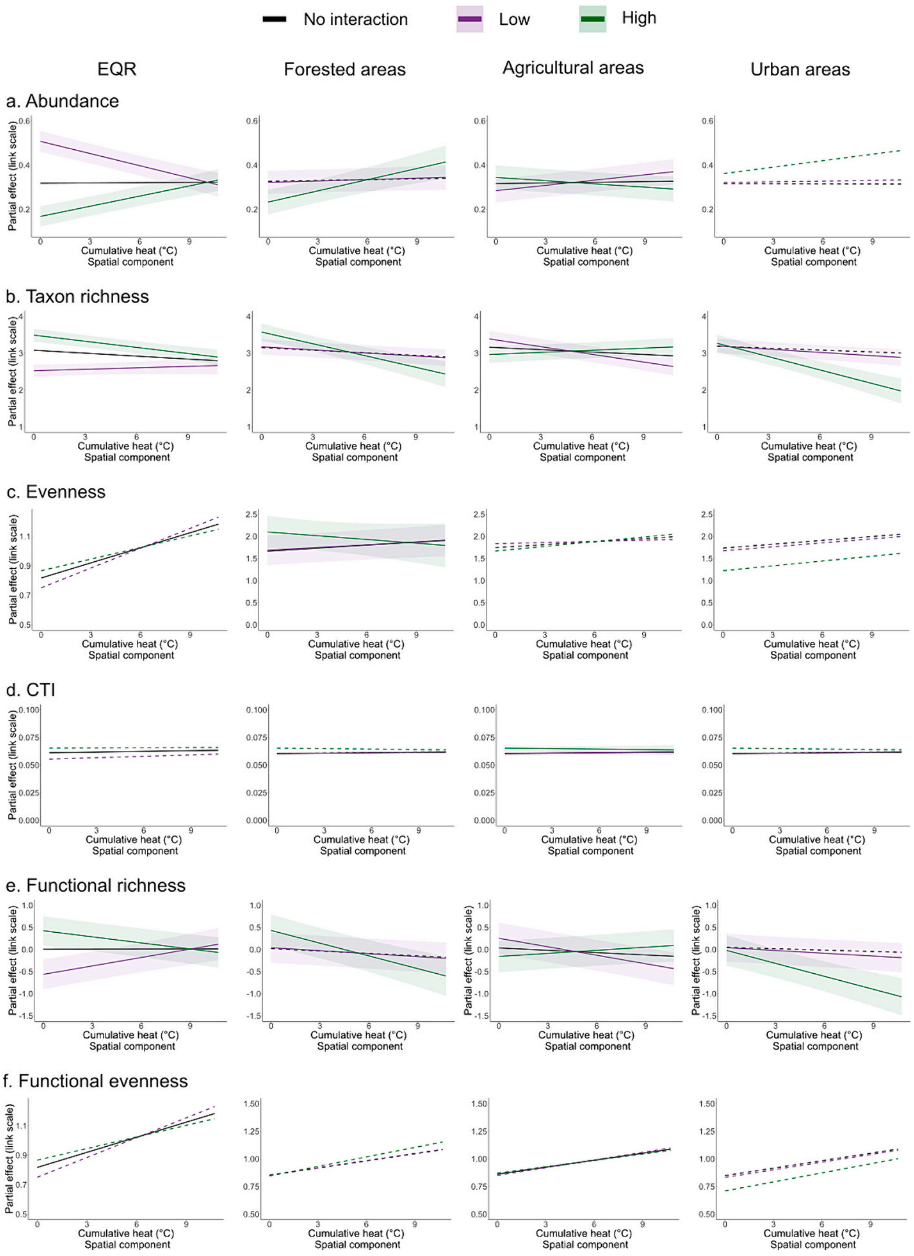

Fig. 5. Partial effect of community indices by the spatial component of cumulative heat and its interaction with the EQR and land cover types. Black lines show the effect of the spatial component without the interaction. Purple lines represent the interactive effect of the spatial component with high EQR values (high ecological quality) or high proportion of land cover (80 % cover of upstream areas), and green lines represent the interactive effect of the spatial component with low EQR values (low ecological quality) or low proportion of land cover (20 % cover of upstream area).

Large-scale, observational studies can help to focus research on particularly vulnerable regions (Maxwell et al., 2019), while at the same time, they provide general insights about the effects of extreme events on communities.

The responses of the community indices to heat waves were influenced by stream ecological quality and land cover, suggesting potential interactions between stream recovery from habitat degradation and climate change. In high-quality sites, abundance increased but taxon and functional richness decreased with heat waves, probably due to a combination of increases in abundance of warm-tolerant species that could benefit from heat waves (Gu et al., 2023), but losses of more sensitive and rare species (Haase et al., 2023). Furthermore, the steep decrease of taxon and functional richness in high-quality sites match our results indicating strong responses to heat waves in colder countries that also showed higher EQR values. By contrast, increases in functional richness in low-quality sites with increasing magnitude of heat waves might be due to species with tolerance-related traits, e.g., species with small body sizes, rapid life cycles, or resistance structures (Bonacina et al., 2023; Chessman, 2015; Nelson et al., 2021). The interacting effects of heat waves and the ecological quality of streams, by benefiting tolerant species and filtering sensitive species, suggest that extreme events exacerbate the declines in diversity due to anthropogenic factors on invertebrate communities.

Taxon and functional richness in forested and urban areas decreased with increasing magnitude of heat waves, which suggest complex interactions of climate and land cover variables in the community responses. A decrease of diversity in urban areas supports our expectation of synergistic effects between the magnitude of heat waves and high urbanization, and agrees with previous studies showing strongest decreases of insect diversity to warming in urban or agricultural areas

Table 3

Model coefficients for community indices responses to the spatial component of cumulative heat, EQR, land use types, and their interactions. Significant terms are shown in bold and their significance is indicated with asterisks (*<0.05, **<0.01, ***<0.001).

Response variable		Cumulative heat - Spatial component	Spatial variable	Interaction	Adjusted r^2 (%)
Abundance	EQR	__−0.023***__	__−0.425***__	__0.042***__	60.6
	Forested areas	−0.002	__−0.126***__	__0.015***__	61.0
	Agricultural areas	__0.011***__	__0.093***__	__−0.019***__	61.0
	Urban areas	0.000	__0.093***__	−0.001	60.9
Taxon richness	EQR	__0.036*__	__1.610***__	__−0.114***__	69.3
	Forested areas	−0.002	__0.666***__	__−0.131***__	66.7
	Agricultural areas	__−0.099***__	__−0.704***__	__0.149***__	66.7
	Urban areas	0.001	0.119	__−0.152***__	66.7
Evenness	EQR	__0.176***__	__2.089***__	__−0.260***__	46.0
	Forested areas	__0.037***__	__0.687***__	__−0.081*__	53.8
	Agricultural areas	0.001	__−0.278*__	0.042	53.8
	Urban areas	__0.028**__	__−0.750***__	0.011	53.8
CTI	EQR	__0.001*__	__0.017***__	−0.001	55.0
	Forested areas	__0.000*__	__0.008***__	0.000	50.6
	Agricultural areas	__−0.001***__	__−0.008***__	__0.001***__	50.6
	Urban areas	__0.000*__	__−0.006***__	−0.001	50.6
Functional richness	EQR	__0.100***__	__1.644***__	__−0.182***__	52.4
	Forested areas	−0.093	__0.649***__	__−0.123***__	53.7
	Agricultural areas	__−0.093***__	__−0.686***__	__0.145***__	53.7
	Urban areas	0.005	−0.102	__−0.128***__	53.7
Functional evenness	EQR	__0.051***__	__0.193*__	−0.031	34.7
	Forested areas	__0.020***__	−0.011	0.011	33.1
	Agricultural areas	__0.025***__	0.035	−0.007	33.1
	Urban areas	__0.022***__	__−0.204***__	0.007	33.0

(Outhwaite et al., 2022; Uhler et al., 2021). On the contrary, diversity declines in forested areas are opposite to our expectations. Forested areas might buffer increasing temperatures by shading effects; consequently, species inhabiting such streams are adapted to these buffered temperatures during summer, resulting in communities harboring more sensitive species and explaining why these communities were highly sensitive to heat waves. Our results suggest that communities composed of sensitive species, as in high quality streams or in forested areas, are especially vulnerable to extreme events.

Our study focused on the effects of heat waves on stream communities; however, other extreme events are also predicted to increase in magnitude and frequency with potential consequences for communities and ecosystems (Seneviratne et al., 2021). For example, we did not investigate extreme fluctuations in water flow, like droughts or floods, that possibly occurred during the study years and that might have as well affected communities. Extreme events affecting water flow are likely to have strong effects on stream communities (Sabater et al., 2022), and even more pronounced effects when they co-occur with other threatening processes or when they occur before the community has completely recovered from a previous event (Maxwell et al., 2019; Ross et al., 2022). Although our models accounted for the effects of long-term community trends, we did not explicitly include the interaction of heat waves with press disturbances, such as warming, which was previously assessed for these communities (Haase et al., 2023). Warming increased the number of species in the communities, suggesting an opposite —antagonistic— direction as heat waves. When warming has not reach critical levels, it might help communities recover faster after an extreme event because higher temperatures positively affect growth and development rates (Nelson et al., 2021; Vasseur et al., 2014). However, increasing warming over time can lead to high mortality rates due to habitat reduction, exceedance of thermal limits, or higher exposure to predators and pathogens (Bonacina et al., 2023; Haase et al., 2023; Maxwell et al., 2019; Sabater et al., 2022; but see Mieszkowska et al., 2021). Understanding the factors driving biodiversity short- and long-term responses to extreme events will increase our ability to predict the future behavior of ecosystems and mitigate their effects (Solow, 2017).

5. Conclusions

Extreme events are a growing concern under on-going climate change, and the assessment of community responses to these events becomes paramount for biodiversity conservation. This study advanced our understanding of how heat waves affect communities at large spatio-temporal scales. Our observations of declines in diversity of communities in colder countries, streams with high ecological quality, and forested areas indicate regions and conditions where sensitive communities require increased conservation efforts. It is also clear from our results that there are more factors to disentangle. For example, the lack of significance in the temporal component of heat waves is likely related to the complex life cycles of invertebrates that produces lagged responses to disturbance, highlighting the relevance of the timing of extreme events for communities (e.g., Dietrich et al., 2023). The interactions between heat waves, ecological quality, and land cover highlight the complexity of environmental change affecting biological communities. Interactions of heat waves with other climate extremes and long-term trends will also impact communities in ways that are to be investigated. Lastly, changes in composition and declines in diversity due to extreme events have implications for ecosystems functioning through shifts in productivity, decomposition rates, phenology, and food web structure (Thompson et al., 2013; Woodward et al., 2016, 2010), and evolutionary consequences, such as shifts in genotypic frequencies of populations and extinctions (Parmesan, 2006; Pau et al., 2011). We encourage future studies to assess the impacts on ecosystem functioning and evolutionary consequences of extreme events in freshwater ecosystems.

CRediT authorship contribution statement

Daniela Cortés-Guzmán: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Diana E. Bowler:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Peter Haase:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

The data and code that supports the findings of this study are available in GitHub (DanielaCortesGuzman/Effects-of-heat-waves-on-invertebrates).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.176229.

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