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# Long-term trends in stream benthic macroinvertebrate communities are driven by chemicals

Hong Hanh Nguyen<sup>1,2\*</sup>, Ellen A. R. Welti<sup>3</sup>, Phillip J. Haubrock<sup>2,4</sup> and Peter Haase<sup>1,2</sup>

## Abstract

**Background** Recent studies indicate a partial recovery of European stream macroinvertebrate diversity. However, the key determinants shaping the overall community trends are only partly explored, owing to insufficient long-term environmental data collected in parallel with community responses. We investigate long-term trends in stream macroinvertebrate communities (i.e., taxonomic and trait composition and metrics), and explore their relationships to diverse environmental drivers (i.e., land-use, runoff, water temperature, and in-stream chemicals). We use macroinvertebrate data collected annually in spring and summer between 2007 and 2021 at four sampling sites within the Rhine-Main-Observatory Long-Term Ecological Research site. These sampling sites encompass a gradient from less-disturbed to disturbed conditions.

**Results** Over time, shifts in taxonomic and trait composition and metrics indicated an improvement in environmental conditions. Long-term trends of biological trait metrics mirrored those for taxonomic metrics; for example, increases over time in taxonomic richness were paralleled by increases in functional richness and functional dispersion. Meanwhile, trends of ecological trait metrics were particularly driven by changes in environmental drivers. Land-use, water temperature, and runoff explained around 20% of the overall variance in long-term trends of macroinvertebrate communities. Water temperature and land-use played relatively equal roles in shaping taxonomic and trait composition and metric responses in spring, while water temperature emerged as the most influential driver in summer. However, when incorporating long-term chemical data as a more direct measurement of changes in land-use, the overall variance explained in macroinvertebrate community trends increased to c.a. 50% in both seasons.

**Conclusions** Examining more relevant driver variables beyond land-use and climate improves insights into why biodiversity exhibits long-term trends. We call for an increase in initiatives to link biodiversity monitoring with parallel sampling of relevant environmental drivers.

**Keywords** Temporal trends, Riverine, Macroinvertebrates, Traits, Multiple stressors, Runoff, Nutrients

\*Correspondence:

Hong Hanh Nguyen  
hanh.nguyen@senckenberg.de

Full list of author information is available at the end of the article



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## Background

Understanding long-term effects of multiple drivers on riverine communities requires comprehensive examination [33], with drivers generally co-occurring and interacting [32, 42, 48]. Macroinvertebrate communities are particularly sensitive to anthropogenic disturbance, rendering them efficient indicators of freshwater ecosystem health [38, 68]. Recent large-scale analyses have provided insights into freshwater macroinvertebrate community trends [24, 25, 68], but are often limited by insufficient long-term environmental driver data.

In addition to assessing long-term responses of macroinvertebrate communities to multiple drivers, the integration of taxonomic and trait approaches improves the mechanistic interpretation of these responses [7, 42, 48]. Identifying drivers of abundance, richness, diversity, and taxonomic composition are fundamental questions in community ecology (e.g., [30, 79]). Trait composition and trait metrics, such as functional richness, dispersal, and redundancy, complement taxonomic analyses, help identify why species respond to specific anthropogenic disturbances, and determine how shifts in taxonomic composition may affect ecosystem functioning [39, 56, 62, 73]. Changes in macroinvertebrate community taxonomic and trait metrics over time may exhibit similar responses or become decoupled. This variation often occurs, because the identity of species within a community may change, while the overall trait composition remains more stable due to different species sharing similar trait niches or occupying multiple niches [4, 6, 11, 67]. For example, an increase in total abundance, but decreases in functional richness and dispersal metrics, revealed strong post-drought responses of communities in the dry southeastern United States [11, 12]. In other cases, mixed non-monotonic trends in taxonomic and trait metrics may indicate a low disturbance intensity within a heterogeneous community, for example, due to species having variable sensitivity to pollution and distinct niches [42]. Communities with changes in taxonomic diversity over time that exceed changes in functional diversity are indicative of niche redundancy [7, 42]. An integrated taxonomic and trait approach provides insights into the causes and expected outcomes of ecological community change.

Long-term trends of macroinvertebrate communities are influenced by a wide array of anthropogenic drivers [18, 33, 46], that become significant stressors at higher intensities and in particular combinations [32, 54]. For instance, runoff and water temperature play fundamental roles in shaping river habitats, while precipitation and temperature extremes can severely limit populations and ecological function [19, 47, 62]. In addition, a combination of hydrological stress and physico-chemical

pollutants (such as nutrients, salinity, or micro-pollutants) may cause taxonomic and trait homogenization of macroinvertebrate communities over time [3, 37, 53].

A limited number of studies have considered how multiple drivers collectively influence temporal community responses (e.g., [42]). The lack of long-term studies is partly attributed to the scarcity and inconsistency of temporal records of drivers [5, 46], which are often not collected at corresponding times and sites as macroinvertebrate sampling. This is particularly true for in-stream physico-chemical variables, which often have poorer temporal coverage than ecological data [5], and are commonly substituted by land-use proxies [49, 52]. An alternative approach is to test the responses of macroinvertebrate communities to multiple drivers using 'space-for-time' approaches [31, 54]. While spatial experiments are needed to test hypothesized mechanisms of driver effects, they may differ from long-term responses and do not capture population dynamics that play out over generations [8, 32].

Responses of riverine macroinvertebrate communities to drivers may also vary seasonally [3, 69]. For example, in spring, the higher flow, colder temperatures, and abundance of organic matters from decaying plant leaves and detritus may support higher taxonomic richness and diversity of macroinvertebrate communities (e.g., [15]). In contrast, an increase in the total abundance and dominance of species adapted to low-flows, high temperature, and accumulated pollution conditions are often recorded in summer [3, 11, 37]. Climate change is altering seasonal patterns [75, 76], further highlighting the need for seasonal analyses within long-term investigations of ecological community responses to multiple drivers.

Here we investigate the role and relative importance of multiple drivers affecting long-term seasonal trends of riverine macroinvertebrate communities. We examine changes over a 15-year period (2007 to 2021) of freshwater macroinvertebrate communities collected twice a year (spring and summer) across two stream and two river sites in a Long-Term Ecological Research (LTER) site in central Germany to address two questions: (i) what are the long-term trends in taxonomic and trait composition and metrics and how do they vary between spring and summer seasons? and, (ii) What are the most influential drivers affecting these long-term trends in spring and summer seasons? We expect that: (H1) long-term trends in taxonomic composition of macroinvertebrate communities will vary significantly among spring and summer seasons due to different life cycles of species, while trait composition will remain more stable over time [14, 67]; (H2) taxonomic and trait metrics will exhibit stronger trends in summer driven by more extreme driver trends and intensities (higher temperatures, decreased runoff,

and accumulated pollutants; [50]); (H3) trends of in-stream pollutants will have stronger effects on macroinvertebrate community dynamics than trends in land-use and climate as they are a direct measure of the exposure to emissions of these communities in streams, that limit invertebrate fitness [e.g., 35, 57]. Using a comprehensive investigation of biodiversity, traits, seasons, and a suite of drivers, we aim to uncover how and why riverine macroinvertebrate communities are changing over time.

**Materials and methods**

**Study sites**

The study was conducted at four sampling sites within the Rhine-Main-Observatory (RMO; Table 1), which have continuous macroinvertebrate data available for spring and summer seasons over a 15-year period from 2007 to 2021. The RMO is referenced as a LTER site [26, 55] in central Germany (<https://deims.org/9f9ba137-342d-4813-ae58-a60911c3abc1>). The study includes Aubach and Bieber, two headwater streams, with upstream areas <50 km<sup>2</sup>, and attributed by clay sand soil. Meanwhile, KiO and KiW are two downstream river sites along the main stem of the Kinzig catchment, with total upstream areas ranging from around 700 to 900 km<sup>2</sup> and clay loam soil types. Three out of four study sites (Bieber, KiO and KiW) are experiencing various degrees of disturbance, ranging from bad to moderate, whereas Aubach is located in the ‘Spessartwiesen’ nature reserve in a less-disturbed area.

**Macroinvertebrate sampling**

Sampling of macroinvertebrate communities followed the standardized multi-habitat sampling protocol of the *European Water Framework Directive* (EU WFD), as described by [27]. At each sampling site, 20 subsamples of macroinvertebrates were collected from a 100 m stream section and preserved in 70% ethanol. Specimens were identified according to the operational taxon list

[27, 29], with 80% of taxa in our study identified to the species and genus levels. Macroinvertebrate data were consistently collected over time at each study site during two seasons: spring (March and April) and summer (June and July).

**Macroinvertebrate community responses**

Nine different metrics were estimated to account for diverse facets of macroinvertebrate community responses to multiple drivers over time. These included three taxonomic metrics: total abundance, richness, and Shannon’s diversity. Macroinvertebrate trait data were obtained from the websites [www.freshwaterecology.info](http://www.freshwaterecology.info) [72] and the *DISPERSE* database [70]. Three biological trait metrics are included to capture the changes in trait niche diversity [40, 66, 73, 77]: (1) functional richness ( $F_{Ric}$ ), a measure of trait diversity, (2) functional dispersion ( $F_{Dis}$ ), a measure of trait niche space, and (3) functional redundancy ( $F_{Red}$ ), a measure of niche overlap, with higher redundancy indicating the community and the ecological functions it provides are more robust to species loss. Three ecological trait metrics were examined to assess community tolerance to environmental drivers: (1) the Lotic-Invertebrate Index for Flow Evaluation (LIFE) index is used to measure the aquatic macroinvertebrate responses to changes in runoff [22], (2) the KLIWA index (Köppen–Geiger climate classification) measures the response of macroinvertebrates to water temperature [75], and (3) the Biological Monitoring Working Party (BMWP) reflects the responses of communities to water quality degradation [30].

The online tool *ASTERICS*—Perلودes (version 5.0.8) was used to calculate the three taxonomic metrics and the LIFE index [30]. Biological trait metrics were computed using the *dbFD* function of the *FD R* package [41] from a set of traits (Additional file 1: Table S1). The relevant traits were selected by eliminating traits that were not available for >30% of taxa, did not vary among study sites, and redundant traits (correlation >0.5) to avoid an overestimation or underestimation of ecological response patterns [17, 80]. The BMWP metric was calculated using the desktop version of *ASTERICS* (version 4.04; [2]), whereas the KLIWA index was calculated using the software *KLIWA-Index 1.1.1.1*. following the approach outlined in [75].

**Environmental drivers**

We examined three drivers at all study sites: land-use, runoff, and water temperature. First, land-use data were extracted based on the upstream catchment areas and the land-cover/-use maps. Using upstream catchment areas showed similar trends in land-use changes as using 1-km buffer areas, but they allow the capture of

**Table 1** Catchment attributes of four sites in the study area

No	Site characteristics (units)	Study sites			
		Aubach	Bieber	KiO	KiW
1	Catchment areas (km <sup>2</sup> )	40	28	745	905
2	Elevation (m above sea level)	247	197	121	117
3	Soil type <sup>a</sup>	Clay sands		Clay loams	
4	Stream type <sup>b</sup>	Type 5.1		Type 9.1	

<sup>a</sup> Soil classification based on the soil map of Germany (BÜK1000N V2.3), provided by the Federal Institute for Geosciences and Natural Resources (BGR)

<sup>b</sup> Stream types: Type 5.1: fine material, siliceous low mountain streams; Type 9.1: carbonate, fine-to-coarse-material middle mountain rivers [63]

both local and accumulated-from-upstream effects. We derived shapefiles of upstream catchment areas using the ‘Terrain analysis’ and ‘Calculate catchments from points’ functions in QGIS. Meanwhile, land-use information was aggregated from the two land-cover/-use shapefile maps: ‘Coordination of information on the environment’ (CORINE) [15] and the ‘Integrierte Verwaltungs- und Kontrollsystem’ (InVeKoS) [31]. The CORINE raster map, with a grid resolution of 100 m, provides information on 44 different land-use classes and is updated every 6 years. Meanwhile, the InVeKoS vector map is updated annually and incorporates a high-resolution crop database, including information on 203 land-use classes, such as arable land, agricultural land, grassland, and afforestation lands. The integration of these two maps resulted in a comprehensive annual land-use map featuring a detailed classification of 203 different land-uses, which were further grouped into broader categories of pasture, agriculture, urban, forest, and water classes. Second, the daily runoff data from 2006 to 2021 was collected at four gauging stations in close vicinity to our study sites: Hanau (KiW), Gelnhausen (KiO), Kassel (Bieber), and Frammersbach (Aubach). Finally, water temperature data were recorded in-situ bi-hourly at macroinvertebrate sampling sites over a 12-year period (2010–2021). Water temperature data for the preceding years (2007–2009) were estimated from corresponding air temperature records [21], which exhibited a high correlation between daily mean air and water temperatures at each study site (i.e.,  $R^2_{\text{Aubach}}=0.89$ ,  $R^2_{\text{Bieber}}=0.93$ ,  $R^2_{\text{KiO}}=0.84$ ,  $R^2_{\text{KiW}}=0.89$ ).

For a single site (slightly downstream of KiW), the Hessian Agency for Nature Conservation, Environment and Geology (HLNUG) ran a gauging station and provided bi-weekly to monthly values of physico-chemical variables. We examined 11 physico-chemical variables (including chloride, sulfate, potassium, magnesium, calcium, orthophosphate, total phosphorus, ammonium nitrogen, nitrate nitrogen, total nitrogen, and total organic carbon), which varied from 10 to 53 records per year. Data for other physico-chemical variables, such as micropollutants, was sparse during our study period and not included. The annual land-use index (LUI) was calculated based on the percentage of pasture, agriculture, and urban lands of upstream catchment areas [13]. Mean annual values of runoff, water temperature, and physico-chemical variables were calculated for the 12-month period prior to macroinvertebrate sampling dates to capture the duration of a full macroinvertebrate annual cycle.

### Statistical analyses

All statistical analyses were performed using R version 4.2.3 [65]. Taxonomic composition of macroinvertebrate

communities at study sites in spring and summer seasons were analyzed using Principal Component Analysis (PCA), performed using the *rda* function of the *vegan* R package [60]. Rare species that appeared only once during the whole study period were excluded, and taxon abundances were Hellinger transformed using the *decostand* function [44]. Trait composition of macroinvertebrate communities was calculated as community-weighted mean values of trait modalities and Hellinger-transformed taxa abundances [43], and results were visualized using the Multiple Factor Analysis (MFA; *FactoMineR* R package; [61]). To identify whether taxonomic and trait composition significantly changed over time, we implemented the permutational non-parametric multivariate analyses of variance (PERMANOVA; [1]) using the *adonis2* function in the *vegan* R package. We conducted separate analyses for communities at each site and during each season, examining community composition differences among the factor ‘year’. To analyze the significant trends over time in macroinvertebrate metrics, we used several approaches. First, we used Generalized Additive Models (GAMs; with restricted maximum likelihood, REML), calculated with the *mgcv* R package [81] to identify temporal trends of each metric. While ‘year’ was the main predictor, we accounted for spatial and temporal pseudoreplication effects by incorporating ‘site’ as a nested random effect and ‘year’ as random effect in the model structure [16, 64]. Second, we conducted PERMANOVAs to determine if the overall composition of all metrics at each site considered in our study significantly changed over time. We further employed a similar GAM model structure to assess nonlinear trends of main drivers (including land-use, runoff, and water temperature), mirroring the approach used for macroinvertebrate metrics to ensure consistency and comparability in analyzing temporal trends across driver and response variable groups. Meanwhile, changes over time in various physico-chemical variables in relation to changes in runoff at the single site KiW were assessed using a correlation test and plotted using the *MyMultipanel.ggp2* function provided in the built-in R package *HighstatLibV13.R* [82].

To identify influential drivers of long-term responses of macroinvertebrate community taxonomic and trait composition and metric responses at each study site over time, we applied a Variance Partitioning model using the *varpart* function from the *vegan* package [45]. For each driver, the *varpart* function reports the adjusted  $R^2$  value, which is corrected for the number of explanatory variables. In addition, the significance of each driver group was determined using the *anova.cca* function [60]. Before conducting Variance Partitioning models, a correlation test was employed to examine collinearity among drivers ( $|r|>0.7$ ; [20]). In addition, the variance inflation factor

(VIF) was used to check for multicollinearity ( $VIF < 5.0$ ; [83]). Results from both tests suggested that land-use, water temperature, and runoff at each study site and seasons were statistically independent, with maximum values of  $|r|=0.6$  and  $VIF=2.0$ . The same model structure was used to examine the single site KiW, except that in-stream physico-chemical variables were examined rather than their proxy of land-use. Other drivers with high collinearity were removed, and the retained drivers were chosen based on their ecological relevance. The results of variance partitioning analyses were plotted using radar charts prepared with the *ggadar* R package [10]. Finally, to investigate the effects of each driver on each metric at KiW, we calculated the slope and significance of effects ( $p$  value  $< 0.05$ ) of each driver based on the Generalized Least square (GLS) models using the *nlme* package in R [83]. The abundance metric was  $\log_{10}$  transformed to reduce heteroscedasticity and the 'year' effect was accounted for in GLS models using the autocorrelation method *corAR1*.

## Results

### Temporal trends of macroinvertebrate communities

#### Taxonomic and trait composition

The greatest distinction in community taxonomic composition was observed between stream (i.e., Aubach and Bieber) and river sites (KiO, and KiW) (Fig. 1a, b). The annual variability patterns in taxonomic composition were effectively represented by the first two PCA axes, which captured 42% and 48% variabilities in 180 and 151 species in springs and summers, respectively. Specifically, the taxonomic composition shifted from more sensitive species (such as *Protonemura* sp., *Sericostoma personatum*, and *Serratella ignita*) at the less-disturbed site Aubach, to more pollution-resistant species (such as *Gammarus* sp.) at the most disturbed sites of KiO and KiW (Additional file 10: Figure S1). Trait composition was also divergent between stream and river sites over time, with overall explained variance of more than 80% by the first two MFA axes in both seasons (Fig. 1c, d; Additional file 11: Figure S2). Communities in less-disturbed sites were characterized by species with grazer feeding types, aerial active dispersal modes, small body sizes, and univoltine life cycles, in contrast to communities in more disturbed sites were characterized by species with gatherer or active filter feeding types, primarily aquatic passive dispersal, larger body sizes, and polyvoltine life cycles.

Despite the consistent differences among sites over the 15-year period, taxonomic and trait composition of macroinvertebrate communities within each site also exhibited distinct temporal trends (Fig. 1). In springs, taxonomic composition changes were significant across

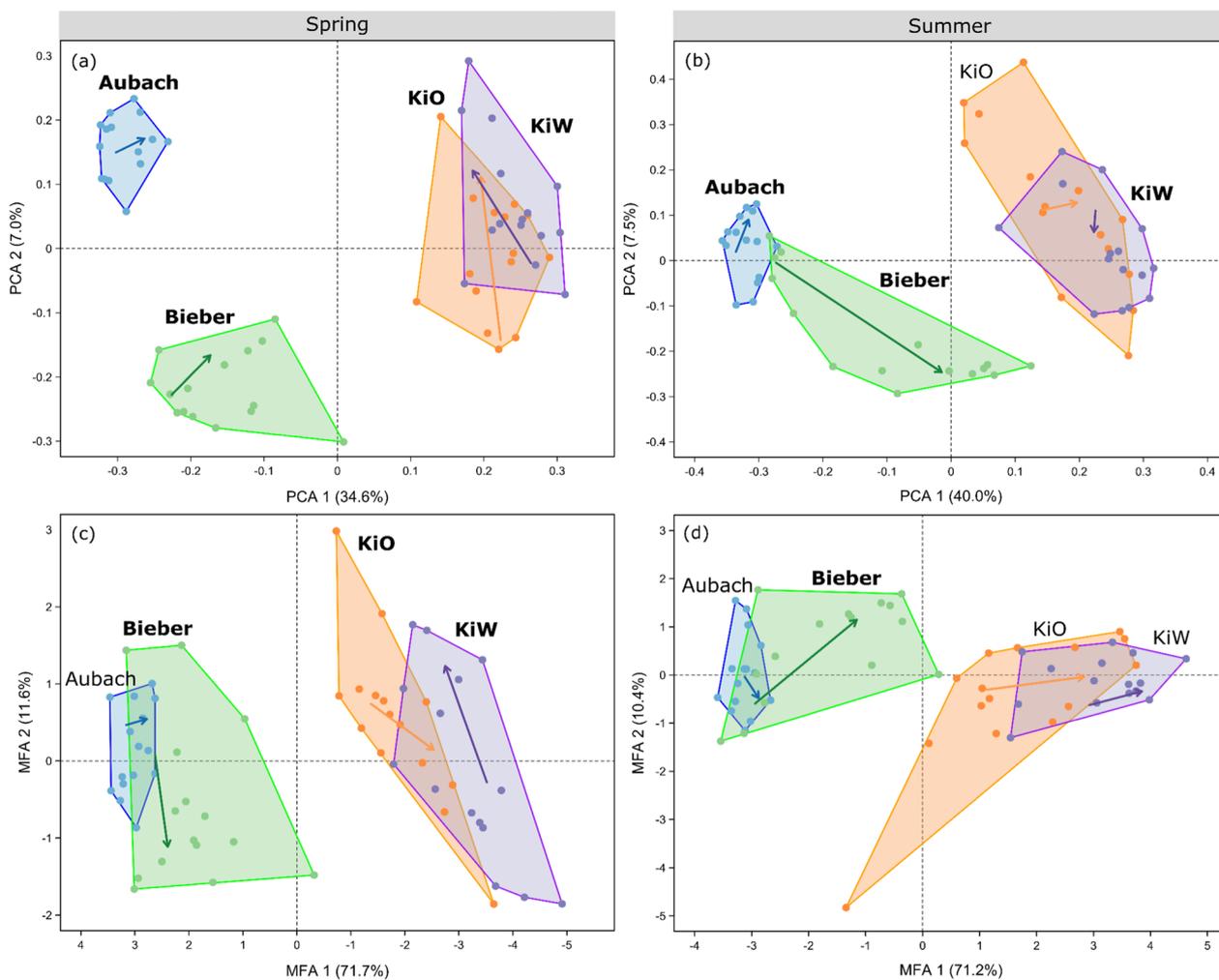
all study sites, and were more pronounced at the more disturbed ( $R^2_{\text{KiW}}=0.2$ ,  $R^2_{\text{KiO}}=0.2$ ) rather than at less-disturbed sites ( $R^2_{\text{Bieber}}=0.1$ ,  $R^2_{\text{Aubach}}=0.1$ ). In the summer season, the long-term trends of macroinvertebrate communities were most evident at Bieber ( $R^2=0.3$ ,  $p$  value  $< 0.001$ ) and KiW ( $R^2=0.3$ ,  $p$  value  $< 0.001$ ), which displayed a strong compositional shift of macroinvertebrate communities toward a dominance of Gammarids (e.g., *Gammarus pulex*, *Gammarus roeselii*) (PCA first axis; Fig. 1). Meanwhile, trait composition exhibited long-term shifts in spring at most study sites ( $R^2_{\text{Bieber}}=0.2$ ,  $R^2_{\text{KiO}}=0.2$ ,  $R^2_{\text{KiW}}=0.2$ ), while in summer the trait niches remained stable with the exception of trait shifts at Bieber ( $R^2_{\text{Bieber}}=0.4$ ; Fig. 1c, d).

#### Taxonomic and trait metrics

Total abundance significantly increased during summers at all sites, whereas in spring, a slight increase was observed at KiW (Fig. 2). In contrast to abundance, taxon richness was consistently higher during spring than summer seasons, particularly at KiW. Shannon diversity did not exhibit any changes over time across all study sites. Functional richness largely followed the patterns of taxon richness in spring, with the most significant increase over time at KiW. Functional dispersion and functional redundancy metrics showed contrasting trends at the two river sites of KiO and KiW, while no significant changes were observed at the two stream sites. KiO communities displayed a consistent increase in redundancy over time in both seasons with strong increases in summer redundancy paralleled by increases in taxonomic abundance over time. The LIFE index declined over time during summer seasons, particularly at the river sites KiO and KiW. In contrast, the KLIWA index showed neutral to increasing trends, with river sites exhibiting more significant increases over time compared to the stream sites in both seasons. The BMWP values displayed a linear increase at KiW over springs, and an increase at KiW, KiO, and Bieber over summers. Notably, there was a sharp increase in some taxonomic and trait metric trends in samples post 2010, i.e., total abundance, richness, functional richness, and the KLIWA index. In addition, macroinvertebrate communities exhibited the greatest temporal changes in summer (Additional file 3: Table S3).

#### Trends of drivers

Water temperature, land-use index (LUI), and runoff all varied from 2006 to 2020 (Additional file 4: Table S4, Additional file 5: Table S5, Additional file 12: Figure S3). Water temperature increased at all sites (Additional file 5: Table S5), with significant linear trends in both springs and summers at KiO. LUI values differed between less-disturbed and disturbed sites, with KiO



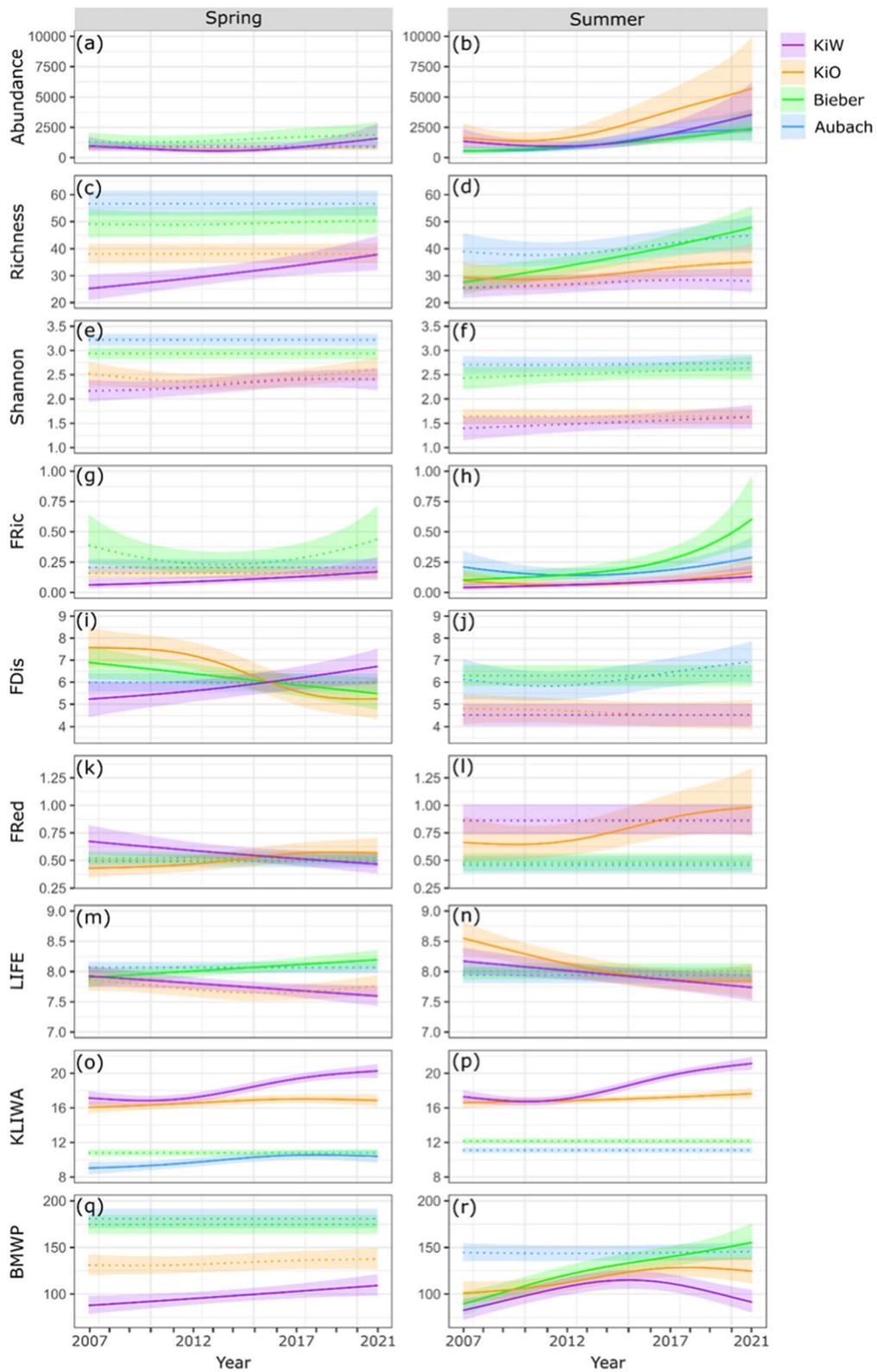
**Fig. 1** Taxonomic composition (**a, b**) and trait composition (**c, d**) in spring and summer seasons from 2007 to 2021. Dots represent the community composition of each year, with closer dots indicating more similar communities. Change directions in communities over time are described by arrows, connecting the mean values of dots from the first 3 years to the last 3 years within a site. The degree of community change over time at each site is represented by the size of the convex hull. Sites with significant changes over time in community composition ( $p < 0.05$ ) are marked in bold. Information of traits and species at study sites are shown in Additional file 1: Table S1, Additional file 10: Figure S1, Additional file 11: Figure S2

and KiW having higher LUI values due to high proportions of pasture, agricultural, and urban lands (> 55% of total upstream areas), compared to the two stream sites. Over time, the LUI varied significantly at three out of four sites (except at KiO), though the change magnitude was small (< 3%). Runoff followed slight

decreasing trends across study sites; however, a significant trend was only observed at Bieber (Additional file 4: Table S4, Additional file 12: Figure S3). Seasonally, runoff was lower and water temperature was higher in summer than in spring seasons across study sites from 2006 to 2020.

(See figure on next page.)

**Fig. 2** Annual trends of macroinvertebrate taxonomic and trait metrics at four study sites in springs (**a, c, e, g, i, k, m, o, q**) and summers (**b, d, f, h, j, l, n, p, r**) from 2007 to 2021 using Generalized Additive Models. Abundance—total abundance, Shannon diversity metric, FRic—Functional Richness, FDis—Functional Dispersion, FRed—Functional Redundancy, LIFE—Lotic-Invertebrate Index for Flow Evaluation, KLIWA—water temperature preference metric, BMWP—Biological Monitoring Working Party. Significant temporal changes of metric values at each study site are represented by solid lines



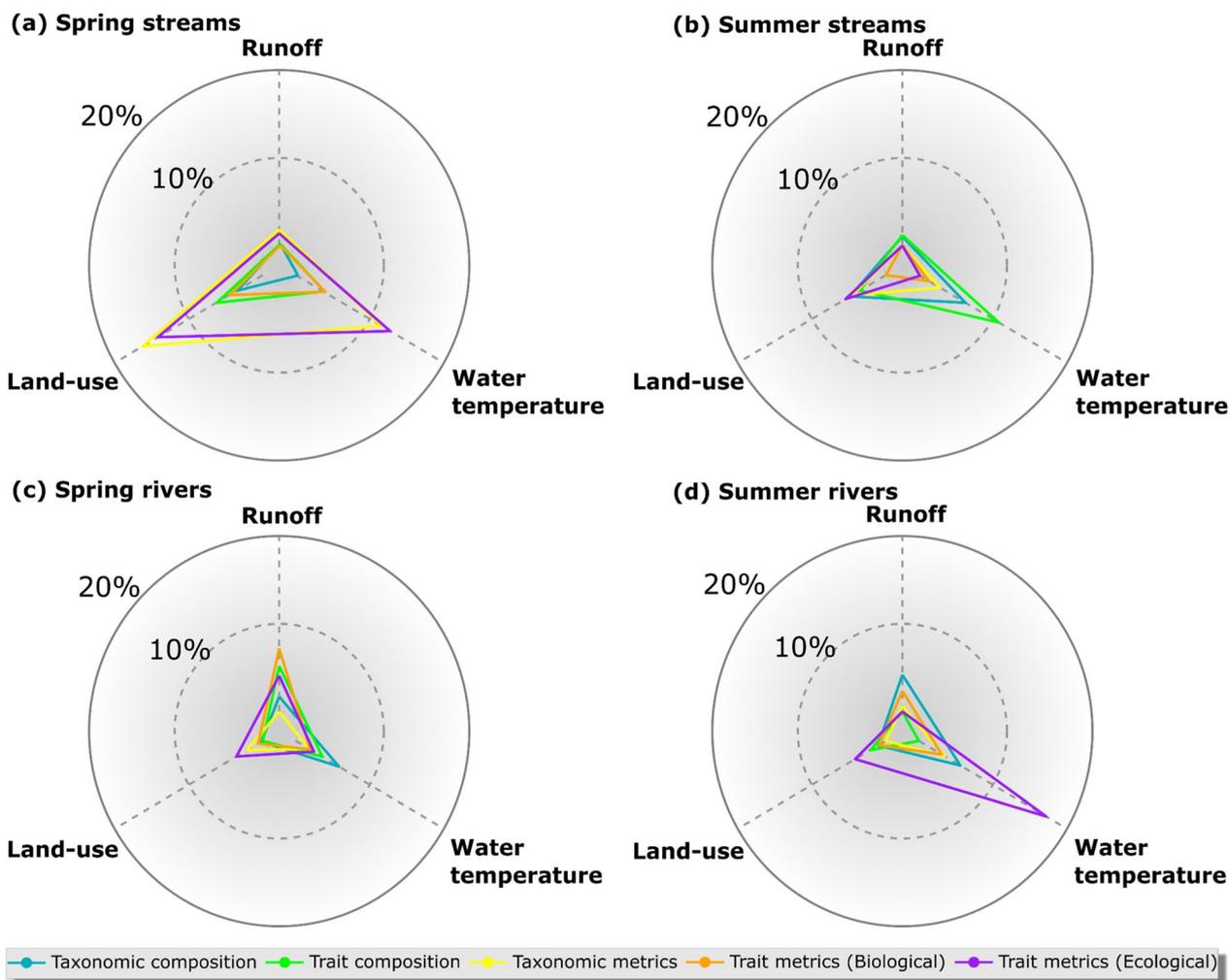
**Fig. 2** (See legend on previous page.)

The long-term data from KiW revealed contrasting trends in in-stream physico-chemical variables in relation to runoff (Additional file 6: Table S6, Additional file 13: Figure S4). Salinity (i.e., chloride and sulfate) and metals (including potassium, magnesium, and calcium) increased as runoff decreased. Orthophosphate (ortho-P) and total phosphorus (TP) concentrations increased weakly when runoff decreased ( $cor < 0.5$ ). In contrast, nitrate nitrogen ( $NO_3$ ) and total nitrogen (TN) concentrations increased with runoff. Finally, the correlations between runoff and total organic carbon (TOC) and ammonium nitrogen ( $NH_4-N$ ) were weak, suggesting only a slight decrease in these chemicals when runoff decreased. In total, we observed trends of increased salinity and metal concentrations, decreased nitrate and TOC

concentrations, and decreased rather than increased phosphorus concentrations (Additional file 6: Table S6). The long-term trends of physico-chemical variables were similar between spring and summer seasons.

**Drivers of macroinvertebrate community trends**

Water temperature was the most important driver affecting macroinvertebrate communities in all study sites, particularly in summer (Fig. 3; Additional file 7: Table S7). In spring, land-use also played a significant contributing role among multiple drivers in shaping long-term trends of macroinvertebrate communities. In contrast, runoff had reduced impacts on macroinvertebrate communities. Macroinvertebrate communities at Bieber in summer were particularly responsive to the cumulative effects



**Fig. 3** Variance partitioning analyses of effects of runoff, water temperature, and land-use on long-term trends of macroinvertebrate community taxonomic/trait composition and metrics at two stream (Aubach and Bieber) and two river (KiO and KiW) sites in spring and summer seasons from 2007 to 2021. Mean values of variance explained by each driver (adjusted  $R^2$ ) are shown in percentage. Details of variance partitioning results at each study site of each metric and season are shown in Additional file 7: Table S7

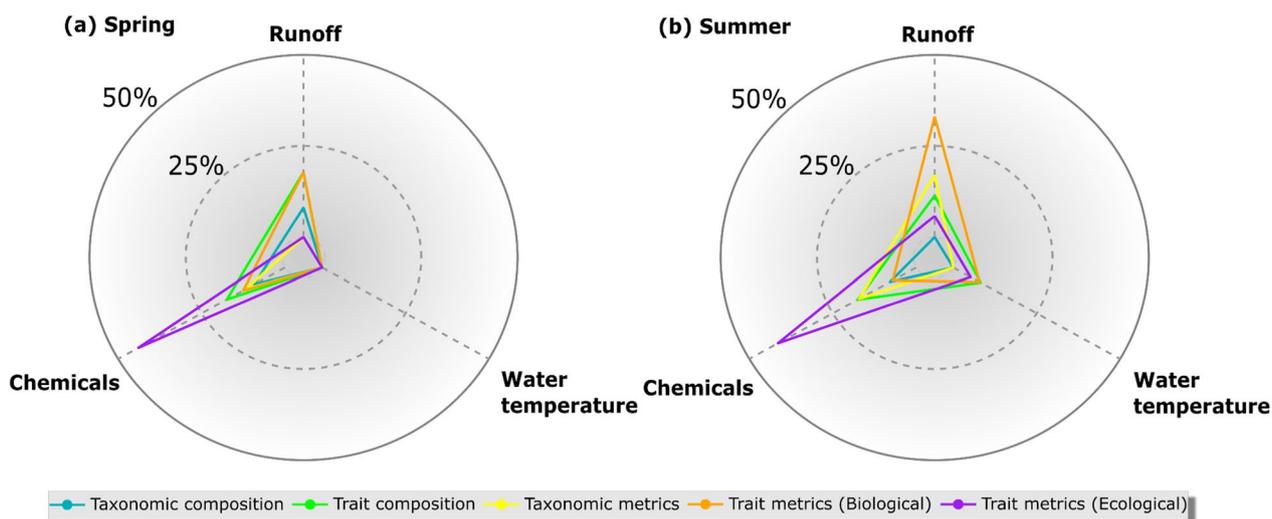
of changes in water temperature, land-use, and run-off (Additional file 7: Table S7), with changes in run-off suggesting this site experienced drier conditions over time (Additional file 11: Figure S2i, j). Water temperature and land-use had the strongest effects on ecological trait metrics, whereas none of the drivers had significant effects on temporal trends of biological trait metrics (Additional file 7: Table S7). Overall, the three drivers cumulatively explained a maximum proportion of 31% and 37% of the long-term variation in macroinvertebrate communities during the spring and summer seasons, respectively (Additional file 7: Table S7).

In-stream chemicals at KiW, including orthophosphate, total nitrogen, salinity, and total organic carbon, exerted stronger effects on long-term seasonal trends of most macroinvertebrate community taxonomic and trait composition and metrics when compared to the effects of runoff and water temperature (Fig. 4, Additional file 8: Table S8, Additional file 14: Figure S5). In-stream chemicals solely explained 7% to 44% (adjusted  $R^2$ s) of the variation in macroinvertebrate community trends, with higher variation explained for ecological trait metrics. Water temperature and runoff explained a maximum of 8% and 33%, respectively, in the variation over time of multiple macroinvertebrate community taxonomic and trait composition and metrics. The joint effects of runoff, water temperature, and physico-chemical variables explained 50% in spring and 62% in summer of the total variation in macroinvertebrate community trends at KiW. This exceeded the maximum combined effects of runoff and water temperature in

conjunction with land-use drivers at this site by approximately 40% (Additional file 7: Table S7, Additional file 8: Table S8). In-stream chemicals had the strongest effects on long-term seasonal changes of ecological trait metrics, followed by their impacts on taxonomic and trait composition (Fig. 4). Decreases of nutrients (represented by orthophosphate) in springs supported the increases in diversity of macroinvertebrate communities (reflected by the negative slope relations with total richness, Shannon diversity,  $F_{Ric}$ , and BMWP metrics; Additional file 9: Table S9).

### Discussion

In this study, we investigated the role of multiple drivers affecting seasonal long-term trends in stream macroinvertebrate communities during the spring and summer seasons from 2007 to 2021. We found trends for overall ecological improvement across all four study sites. Increases in water temperature were an important driver of macroinvertebrate community trends during summers. In springs, land-use and water temperature contributed equally in shaping various trends of taxonomic and trait composition and metrics. However, for our one site, where data were available on various in-stream pollutants, a decrease in nutrient pollution explained the most variation of all examined drivers on changes to the freshwater macroinvertebrate community. While efforts to improve Europe’s freshwater quality have resulted in successes in the past four decades [25, 68], our results suggest that continued improvements would benefit freshwater life.



**Fig. 4** Variance partitioning analyses of effects of runoff, water temperature, and other physico-chemical variables (including orthophosphate, total nitrogen, salinity, and total organic carbon) on long-term trends of macroinvertebrate taxonomic/trait composition and metrics at river site KiW in spring (a) and summer (b) seasons from 2008 to 2021. Values of variance explained by each driver (adjusted  $R^2$ ) are shown in percentage. Details of variance partitioning results of each metric and season are shown in Additional file 8: Table S8

### Trends of macroinvertebrate communities

The two stream sites and two river sites had distinct macroinvertebrate taxonomic and trait composition. Long-term trends in macroinvertebrate taxonomic composition were more pronounced compared to those in trait composition, particularly in summers, providing support for our first hypothesis. The long-term trends in taxonomic composition at all sites are paralleled by increases in sensitive species, indicating biodiversity recovery. These observations align with larger-scale European studies on compositional shifts in stream macroinvertebrates toward gradual recovery due to improvements in water quality [24, 25, 64]. Alternatively, increases in diversity across studied sites, regardless of anthropogenic disturbance levels, could also be an effect of climate warming [9, 24]. Our study took place in Germany, a country with a temperate climate where moderate increases in contemporary temperature at a given site may increase insect biomass [78]. The long-term decline in the number of Ephemeroptera and Plecoptera species, coupled with the increasing prevalence trends of Gammarid species (e.g., [6]) during summers, may represent species-specific responses to the prolonged seasonal low-flow periods [3, 37]. These changes may also be influenced by the emergence periods of these taxa groups (e.g., most Plecoptera emerge in spring and are, therefore, less frequently found in summer samples). In contrast to taxonomic composition, fewer site and season combinations exhibited significant variation over time in trait composition, which may indicate that (1) reductions in stress intensities are still insufficient, (2) trait compositional changes lag behind those in taxonomic composition [7, 42], or (3) the species gained first may bring in fewer additional traits [51]. Trends in taxonomic and trait metrics were stronger in summers than trends in taxonomic and trait composition, highlighting the need for integrated taxonomic and trait approaches to investigate the mechanistic responses of macroinvertebrate communities over time [42, 50]. An increase in taxonomic diversity metrics in spring was accompanied by a parallel increase in functional diversity metrics [67, 74], as shown at the most disturbed site KiW. The observed increases in the trait-based metric BMWP at this site in both seasons suggested that a decrease in organic pollution favored gains in taxa sensitive to pollution. In contrast, non-significant trends in taxonomic and trait composition at the disturbed KiO during the summer season, accompanied by collective increases in abundance, functional redundancy, the KLIWA index, and decreases in the LIFE index, suggest thermal and hydrological stress [3, 34]. At disturbed stream and river sites, continuous increases in

the KLIWA index and the BMWP index, were contrasted by decreases in the LIFE index. These trends may indicate complex community responses, encompassing a greater number of species adapting to warmer temperature, drier climates, and sensitivity to organic pollution, which may be attributed to climate warming in combination with the effects of other persistent drivers [23, 52]. Overall, the more significant trends in various taxonomic and trait metrics in summers rather than in springs, coupled with stable trends in Shannon's diversity, suggest differential seasonal long-term effects of multiple drivers on macroinvertebrate communities. Macroinvertebrate diversity metrics increased during warmer and drier summers, but the distribution of gained and lost species was relatively stable during springs [42, 50].

### Influential drivers of long-term trends of macroinvertebrate communities

Our results showed comparable importance of land-use and climate-related drivers (i.e., runoff and water temperature) in explaining the long-term responses of macroinvertebrate communities. However, long-term data at KiW indicated that pollutants were more important than land-use and climate-related drivers combined, supporting our third hypothesis that emphasizes the importance of incorporating chemical variables in long-term studies of multiple driver impacts on riverine ecosystems. This result aligns with findings from a previous shorter-term study in this area [58], confirming that disturbed downstream sites are significantly affected by accumulated pollutants causing a lesser improvement over time when compared to communities at less-disturbed upstream sites. However, it should be noted that pollutant data were only available for one site that was also particularly disturbed. Increases in some sensitive Ephemeroptera and Plecoptera species (such as *Serratella ignita* or *Protonemura* sp.) paralleled strong increases in water temperature. This may indicate that species previously limited to fast-flowing, colder headwaters are tolerating a broader range of warmer conditions at the study sites [28, 34]. Land-use may act as an important environmental filter for traits over time, as sites undergoing diverse land-use development patterns often support macroinvertebrate communities with distinct trait compositions [14, 38, 53, 54]. Reduced runoff enhanced taxonomic and trait diversity of macroinvertebrate communities, supporting previous studies (e.g., [35, 36]), but had negative effects on macroinvertebrate communities at streams experiencing intensified drying during summers (e.g., Bieber).

Previous studies [33, 46] reported extensive land-use changes as the primary driving stressor on macroinvertebrate communities, while our study revealed that changes in land-uses in recent decades might be a less influential than the emergent effects of in-stream pollutants. Decreases in nutrients, particularly phosphate concentrations, explained the consistent increases of macroinvertebrate diversity in springs, in contrast to the comparatively weaker influence of land-uses on riverine communities. This finding suggests that long-term river management plan efforts in reducing nutrient emissions across catchments in Germany have provided benefits to freshwater macroinvertebrate communities [59, 71]. Furthermore, stronger effects of in-stream pollutants on ecological traits compared to biological traits highlights the importance to consider wider trait responses of macroinvertebrate communities beyond functional traits. Changes in ecological trait metric trends in our study provide evidence of direct community responses to gradual shifts in habitat conditions (Additional file 8: Table S8).

### Conclusions

Our study highlights the importance of collecting high-resolution long-term chemical data alongside freshwater biodiversity sampling [25, 74]. Combining macroinvertebrate taxonomic and trait composition and metrics, we provide in depth insights into dynamic trends in riverine communities in response to trends of environmental drivers. Land-use, water temperature, and runoff helped explain seasonal trends in certain macroinvertebrate community components. However, when physico-chemical data were available, the most influential drivers of long-term seasonal community trends were in-stream chemicals.

While this finding is significant, it is important to acknowledge that this result stems from a single sampling site. The impact of drivers is likely to exhibit local variations along the river and among catchments with different water quality conditions, leading to divergent effects on macroinvertebrate communities. Thoroughly investigating long-term biodiversity trends of riverine macroinvertebrate communities necessitates consistent and comprehensive monitoring of environmental drivers, particularly concerning under-represented emerging pollutants (such as microplastics, heavy metals, and pharmaceutical substances). Establishing long-term bio-monitoring that integrates both biotic and abiotic data at identical locations and timepoints, is crucial to unravel the intricate dynamics and identify the overarching drivers that contribute to the significant patterns in macroinvertebrate populations. Such insights are vital and provide important elements for the effective long-term

conservation strategies and management of our valuable freshwater environments.

### Abbreviations

BMWP	Biological Monitoring Working Party
EU WFD	European Water Framework Directive
$F_{Dis}$	Functional dispersion
$F_{Red}$	Functional redundancy
$F_{Ric}$	Functional richness
GAMs	Generalized Additive Models
GLS	Generalized Least Square
HLNUG	Hessian Agency for Nature Conservation, Environment and Geology
KLIWA	Köppen–Geiger climate classification
LIFE	Lotic-Invertebrate Index for Flow Evaluation
LTER	Long-Term Ecological Research
LUI	Land-Use Index
MFA	Multiple factor analysis
NH <sub>4</sub> -N	Ammonium nitrogen
NO <sub>3</sub>	Nitrate nitrogen
Ortho-P	Orthophosphate
PCA	Principal Component Analysis
PERMANOVA	Permutational non-parametric multivariate analyses of variance
REML	Restricted Maximum Likelihood
RMO	Rhine-Main-Observatory
TN	Total nitrogen
TOC	Total organic carbon
TP	Total phosphorus

### Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12302-023-00820-6>.

**Additional file 1: Table S1.** Traits and trait modalities of macroinvertebrate communities at study sites.

**Additional file 2: Table S2.** Structures and results of Generalized Additive Models (GAMs) on changes of taxonomic and trait metrics over time at four study sites.

**Additional file 3: Table S3.** Metric correlations ( $R^2$ ) and p-values (in brackets) for overall temporal trends of macroinvertebrate communities based on all nine taxonomic and trait metrics at four study sites in spring and summer seasons from 2007 to 2021.

**Additional file 4: Table S4.** Structures and results of Generalized Additive Models (GAMs) on changes of land-use, runoff, and water temperature over time at four study sites.

**Additional file 5: Table S5.** Summary of mean (and relative change values, in %) of three main temporally-variable drivers at study sites from 2006 to 2020.

**Additional file 6: Table S6.** Summary of mean (and relative change values, in %) of physico-chemical variables at KiW in springs and summers from 2007 to 2020/2021.

**Additional file 7: Table S7.** Variance partitioning model at four study sites, examining effects of runoff (m<sup>3</sup>/s), water temperature (WT, °C), and land-use on macroinvertebrate taxonomic/trait composition and metrics in spring and summer seasons from 2007 to 2021.

**Additional file 8: Table S8.** Variance partitioning model at KiW of effects of runoff (m<sup>3</sup>/s), water temperature (WT, °C), and in-stream chemicals (mg/L) on macroinvertebrate taxonomic/trait composition and metrics in spring and summer seasons from 2007 to 2021.

**Additional file 9: Table S9.** Generalized Least square models defining impacts of single drivers on macroinvertebrate metrics at the KiW site from 2008 to 2021.

**Additional file 10: Figure S1.** Taxonomic composition in springs (a, b) and summers (c, d) from 2007 to 2021.

**Additional file 11: Figure S2.** Trait composition in springs (a, b) and summers (c, d) from 2007 to 2021.

**Additional file 12: Figure S3.** Annual trends of water temperature (°C), land-use index, and runoff (m<sup>3</sup>/s) at less-disturbed (Aubach and Bieber) and disturbed (KiO and KiW) sites in springs (a, c, e, g, i) and summers (b, d, f, h, j) from 2006 to 2020 using Generalized Additive Models.

**Additional file 13: Figure S4.** Relationship between mean monthly runoff and water temperature (°C) and eleven in-stream physico-chemical variables (mg/L) at KiW from 2007 to June, 2021.

**Additional file 14: Figure S5.** Annual trends of water quality variables (in mg/L) at KiW in springs and summers from 2007 to 2020 using Generalized Additive Models.

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### Author contributions

PH and HHN conceptualization of the study. HHN data analysis and original draft preparation. HHN, PJH, PH, and EARW visualization and interpretation. EARW editing. PH supervision. All authors read and approved the final manuscript.

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### Availability of data and materials

The data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

### Declarations

#### Ethics approval and consent to participate

Not applicable.

#### Consent for publication

Not applicable.

#### Competing interests

The authors declare that they have no competing interests.

### Author details

<sup>1</sup>Faculty of Biology, University of Duisburg-Essen, Essen, Germany. <sup>2</sup>Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Frankfurt, Germany. <sup>3</sup>Conservation Ecology Center, Smithsonian's National Zoo and Conservation Biology Institute, Front Royal, VA, USA. <sup>4</sup>University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátisí 728/II, 389 25 Vodňany, Czech Republic.

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