







# Complex and nonlinear climate-driven changes in freshwater insect communities over 42 years

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**Abstract:** The ongoing biodiversity crisis becomes evident in the widely observed decline in abundance and diversity of species, profound changes in community structure, and shifts in species' phenology. Insects are among the most affected groups, with documented decreases in abundance up to 76% in the last 25–30 years in some terrestrial ecosystems. Identifying the underlying drivers is a major obstacle as most ecosystems are affected by multiple stressors simultaneously and in situ measurements of environmental variables are often missing. In our study, we investigated a headwater stream belonging to the most common stream type in Germany located in a nature reserve with no major anthropogenic impacts except climate change. We used the most comprehensive quantitative long-term data set on aquatic insects available, which includes weekly measurements of species-level insect abundance, daily water temperature and stream discharge as well as measurements of additional physicochemical variables for a 42-year period (1969–2010). Overall, water temperature increased by 1.88 °C and discharge patterns changed significantly. These changes were accompanied by an 81.6% decline in insect abundance, but an increase in richness (+8.5%), Shannon diversity (+22.7%), evenness (+22.4%), and interannual turnover (+34%). Moreover, the community's trophic structure and phenology changed: the duration of emergence increased by 15.2 days, whereas the peak of emergence moved 13.4 days earlier. Additionally, we observed short-term fluctuations (<5 years) in almost all metrics as well as complex and nonlinear responses of the community toward climate change that would have been missed by simply using snapshot data or shorter time series. Our results indicate that climate change has already altered biotic communities severely even in protected areas, where no other interacting stressors (pollution, habitat fragmentation, etc.) are present. This is a striking example of the scientific value of comprehensive long-term data in capturing the complex responses of communities toward climate change.

**Keywords:** caddisflies, climate warming, discharge alteration, long-term observations, mayflies, rapid abundance decline, stoneflies

Cambios Complejos y No Lineales Causados por el Clima en Comunidades de Insectos de Agua Dulce durante 42 Años

**Resumen:** La continua crisis de la biodiversidad se vuelve evidente en la ampliamente documentada declinación en la abundancia y diversidad de especies, cambios profundos en la estructura de las comunidades y modificaciones en la fenología de las especies. Los insectos se encuentran entre los grupos más afectados; se han

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documentado reducciones en la abundancia de hasta el 76% en los últimos 25–30 años en algunos ecosistemas terrestres. La identificación de los causantes subyacentes es un gran obstáculo porque la mayoría de los ecosistemas están afectados por varios factores estresantes simultáneamente y con frecuencia faltan las medidas in situ de las variables ambientales. Investigamos un flujo naciente perteneciente al tipo de arroyo más común en Alemania ubicado dentro de una reserva natural sin impactos antropogénicos importantes a excepción del cambio climático. Usamos el conjunto más completo disponible de datos cuantitativos de largo plazo para insectos acuáticos que incluye las medidas semanales de abundancia de insectos a nivel especie, las medidas diarias de la temperatura del agua y la descarga del flujo y las medidas de variables físico-químicas adicionales durante 42 años (1969 - 2010). En general, la temperatura del agua incrementó 1.88°C y los patrones de descarga cambiaron significativamente. Estos cambios estuvieron acompañados por una declinación del 81.6% en la abundancia de insectos, pero también de un incremento en la riqueza (+8.5%), la diversidad Shannon (+22.7%), la uniformidad (+22.4%) y la renovación interanual (+34%). Además, la estructura trófica y la fenología de la comunidad cambiaron: la duración del surgimiento incrementó en 15.2 días y el pico del surgimiento ocurrió con 13.4 días de anticipación. Observamos fluctuaciones a corto plazo (<5 años) en casi todas las medidas, así como respuestas complejas y no lineales de la comunidad hacia el cambio climático que podrían haber sido ignoradas si sólo se usaran datos instantáneos o series de tiempo más cortas. Nuestros resultados indican que el cambio climático ya ha alterado seriamente a las comunidades bióticas, incluso en áreas protegidas en las que no están presentes otros factores estresantes en interacción (contaminación, fragmentación del hábitat, etc.). Ésto es un ejemplo notable del valor científico que tienen los datos completos de escalas de tiempo a largo plazo para la captura de las respuestas complejas de las comunidades ante el cambio climático.

**Palabras Clave:** alteración por descarga, calentamiento climático, declinación rápida de abundancia, Ephemeroptera, observaciones a largo plazo, Plecoptera, Trichoptera

**摘要:** 当前的生物多样性危机表现为物种数量和丰度的普遍下降、群落结构的明显变化和生物物候学的转变。昆虫是受影响最严重的群体之一; 记录表明, 过去25-30年间一些陆地生态系统昆虫丰度的下降高达76%。然而, 确定潜在的驱动因素仍阻碍重重, 因为大多数生态系统同时受到多种压力的影响, 且又常常缺少对环境变量的现场测量。本研究调查了德国最常见河流类型中的一条源头溪流, 它位于一个自然保护区内, 除气候变化外没有受到重大的人为影响。我们利用了目前水生昆虫最全面的长期定量数据集, 包括每周测量的昆虫物种丰度、每日水温和溪流流量, 以及42年来(1969-2010年)其它物理化学变量的观测数据。总体而言, 水温升高1.88°C, 流量就会发生明显变化。同时, 昆虫丰度下降81.6%, 但物种多样性增加(+8.5%), Shannon多样性增加(+22.7%), 均匀度增加(+22.4%)以及年际周转率增加(+34%)。此外, 群落营养结构和物候也发生了变化: 物种出现时间增加了15.2天, 出现高峰提前了13.4天。我们发现几乎所有指标都存在短期波动(<5年), 且群落对气候变化存在复杂的非线性响应, 这些变化是简单使用快照数据或更短的时间序列数据难以捕捉的。我们的研究结果表明, 即使在没有任何其它交互压力(污染、栖息地破碎化等)的保护区内, 气候变化也已经严重地改变了生物群落。这个惊人的案例说明综合的长期数据在记录群落对气候变化的复杂响应中具有重要科学价值。【翻译: 胡怡思; 审校: 聂永刚】

**关键词:** 气候变暖, 流量变化, 丰度迅速下降, 长期观测, 蜉蝣, 石蝇, 石蛾

## Introduction

The “Great Acceleration of the Anthropocene” is regarded as one of the biggest threats to the future of the biosphere and humanity (Steffen et al., 2015). Resulting effects on biodiversity comprise losses in species abundance, biomass, diversity, changes in community composition (Dirzo et al., 2014; McCauley et al., 2015), trophic structure (Smol et al., 2005), and shifts in phenology (Stefanescu et al., 2003; CaraDonna et al., 2014). For example, various studies have highlighted that birds (Inger et al., 2015), amphibians (Houlahan et al., 2000), and insects (e.g., Hallmann et al., 2017) have shown a severe decline in abundance or biomass. Similar declining trends were observed in butterflies in the United Kingdom (Warren et al., 2001; Conrad et al., 2006) and Germany (Wenzel et al., 2006), in butterflies and Dipterans in Green-

land (Høye et al., 2013), and in aquatic invertebrates in the United Kingdom (Beche & Resh, 2007; Durance & Ormerod, 2007). A recent meta-analysis by Sánchez-Bayo & Wyckhuys (2019), based on 73 individual studies, showed that “almost half of the [insect] species are rapidly declining and a third are being threatened with extinction.”

Such changes in abundance and diversity are often accompanied by increased temporal community turnover, as shown by an increased instability of chironomid and diatom communities in numerous circumpolar lakes in the last decades due to changes in temperature and niche availability (Smol et al., 2005; Jackson & Sax, 2010). Moreover, changes in community abundance and species richness are often reflected in changes of functional feeding groups, indicating not only taxonomic but also functional alteration of community composition (Jourdán et al., 2018).

However, several of the aforementioned studies are based on meta-analyses compiling data from several long-term studies that focused on the basic question of whether communities are changing, with little or no focus on the pattern of that change (Christensen et al., 2018). Analyses including data on environmental drivers that may explain such changes are even scarcer. Among these drivers is climate change. For example, climate warming often increases primary production (Hejzlar et al., 2003) and accelerates metabolic rates (VanLooy et al., 2016), thereby influencing the developmental time of organisms and their phenology (Hejzlar et al., 2003; Asch, 2015; Jourdan et al., 2019). Changes in an organism's phenology, in turn, can then lead to a disruption of biotic interactions and ecosystem functions via a temporal mismatch between, for example, pollinators and plants, or prey and predators (Roy & Sparks, 2000; Høye et al., 2013). Disentangling the effect of climate change on biodiversity is challenging because ecosystems are often exposed to a variety of interacting anthropogenic stressors (Floury et al., 2013; Larsen et al., 2018; Schäfer & Piggott, 2018). Thus, although we have strong evidence for severe changes in biodiversity in the Anthropocene, identifying and quantifying the underlying patterns and drivers of these changes is still difficult. In addition, as climate change is a long-term phenomenon, disentangling its effects on biota requires very comprehensive data on biodiversity, climate, and other potentially interacting drivers, ideally as continuous long-term data. To date, such data sets are scarce.

Our study utilizes an exceptional quantitative long-term data set comprising 42 years of continuously collected weekly resolution aquatic insect data from a pristine first-order stream within a nature reserve in central Germany—the Breitenbach (Wagner et al., 2011). Insect abundance and diversity (mayflies [Ephemeroptera], stoneflies [Plecoptera], and caddisflies [Trichoptera]—from here on referred to as EPT) were continuously sampled throughout the sampling period and were accompanied by 2 key environmental variables of lotic ecosystems, namely, water temperature and discharge data recorded daily over the same sampling period.

The absence of common anthropogenic pressures (pollution, hydromorphological degradation, pesticides, weirs, etc.), including invasive species, in its catchment allows for addressing a basic question in ecology: what is the impact of climate change on structuring communities without confounding stressors (Schäfer & Piggott, 2018)? We expect that climate change has already increased temperature and altered precipitation patterns subsequently affecting discharge patterns. As the Breitenbach insect communities are adapted to cold water, we hypothesize considerable changes in community composition: Particularly we expect that the shift from cold headwater conditions toward warmer, downstream-like

conditions will lead to an increase in species richness, abundance, and diversity (Maiolini & Lencioni 2001). The changes in abundance, richness, and diversity will be reflected by shifts in the trophic structure of the insect communities due to a shift in the river continuum toward more downstream conditions (Vannote et al., 1980). Moreover, we expect a shift in community phenology by an increased duration of the emergence period driven by increasing temperatures.

## Methods

All data used in this paper were collected on a daily or weekly basis at the Breitenbach stream, located in a German nature reserve (50°39'42N 9°37'26E) between January 1969 and December 2010. The absence of anthropogenic stressors, except for climate change, is shown by the physicochemical variables that never exceed natural background levels and constantly stayed within a “good” water quality class according to the EU Water Framework Directive 2000 (EU Commission, 2000): for example, pH,  $7.2 \pm 0.6$ ; O<sub>2</sub>,  $11 \pm 3$  mg/L; ammonium,  $0.007 \pm 0.01$  mg/L; nitrate,  $0.8 \pm 0.4$  mg/L; and organic orthophosphate,  $0.04 \pm 0.05$  mg/L (Wagner et al., 2011). Further variables and values are given in Wagner et al. (2011). Aquatic insects belonging to the EPT orders (mayflies, stoneflies, and caddisflies that are known to be susceptible to a broad variety of stressors) were collected on a weekly basis throughout the 42 years of observation using a stationary greenhouse-like emergence trap, which covered the whole stream and part of the riparian area over a length of 12 m. All insects were automatically trapped in ethanol jars. Samples were then counted and identified at species level (Wagner et al., 2011). In parallel and at the same site, water temperature and discharge were manually measured several times per day on all days between 1969 and 1984 and, after 1984, by an automated measurement station (Wagner et al., 2011). We used mean annual water temperature as a predictor, and mean annual air temperature to control for the artefacts in our mean annual temperature calculation. Additionally, another 2 traps, labeled “A” and “C,” were operated in identical manner. Trap “A” was operated between 1984 and 1996, and trap “C” between 1974 and 1986, whereas trap “B” covered the entire period (1969–2010) (Fig. S1).

In our analysis, we used 4 standardized discharge patterns (as described in Wagner et al., 2011 and shown in Fig. S3) as categorical variables, instead of mean annual discharge or maximal discharge, because Wagner et al. (2011) showed that the insect community in the Breitenbach responds more strongly to seasonal discharge patterns than to absolute discharge. Accordingly, we used annual discharge patterns that are based on the magnitude of the coefficient of variation of discharge level

during the “hydrological” year (i.e., October to September; Fig. S2). Four annual discharge patterns were identified: “dry” pattern was characterized by low discharge, lower than 20 L/min; “wet” pattern included years with discharge between 20 and 50 L/min; “aseasonal” pattern was characterized by irregular spates; and “spring spates” were characterized by extreme discharge events (spring rain and thawing of high winter snow; Wagner et al., 2011). Initially, we also ran models using mean and maximum annual discharge but we did not find any significant correlations between mean and maximum discharge and the community metrics used in our models.

### Community Metrics Calculation

We used the annual sum of emerged individuals of each of the in total 125 EPT species to calculate overall insect abundance and community metrics. Annual sums are commonly used in studies investigating inter-annual changes in biodiversity (Hallmann et al., 2020). We calculated the proportion of the functional feeding groups using the software ASTERICS, Version 4.04 ([www.fliessgewaesserbewertung.de](http://www.fliessgewaesserbewertung.de)). We further calculated Shannon diversity, species richness and evenness using the *vegan* package (Oksanen et al., 2019) in R, and the interannual abundance-based species turnover, as a measure of qualitative and quantitative change in community composition, using the *turnover* function of the R package *codyn* (Hallett et al., 2016).

Analyses of changes in phenology require a minimum number of individuals per species because a sporadic occurrence of species biases population trend analyses. Thus, we restricted our phenology analysis to those species with a cumulative number of individuals of 500 or more individuals over the entire 42-year collection period. The resulting 31 species accounted for 97% of total abundance of all 125 EPT species in the traps.

To investigate the phenological shifts in species over time, we considered the following phenophases for each species and the whole community: “date of peak emergence” (date of occurrence of the median point of the emergence, i.e., when 50% of individuals had emerged; Asch, 2015) and duration of the emergence (number of days between start and end of the emergence).

### Data Analysis

We fitted linear models using Generalized Least Squares (*gls* function in the R package *nlme*; Pinheiro et al., 2019) to test the impact of the environmental factors (mean annual temperature, annual discharge pattern, and their interactions) on community abundance, diversity (Shannon diversity and species richness), turnover, and trophic structure (proportion of functional feeding

groups). We excluded the time variable (year) from the final models, due to high collinearity of this variable with temperature increase (variance inflation factor = 4.34, *usdm* package in R; Naimi et al., 2014). In order to account for the temporal autocorrelation in the time series, we specified the correlation structure using the *corAR* argument in the *gls* function. Prior to the analysis, we standardized all variables (Asch, 2015) to obtain standardized slopes as effect sizes. We ran 7 *gls* models with the following structure:

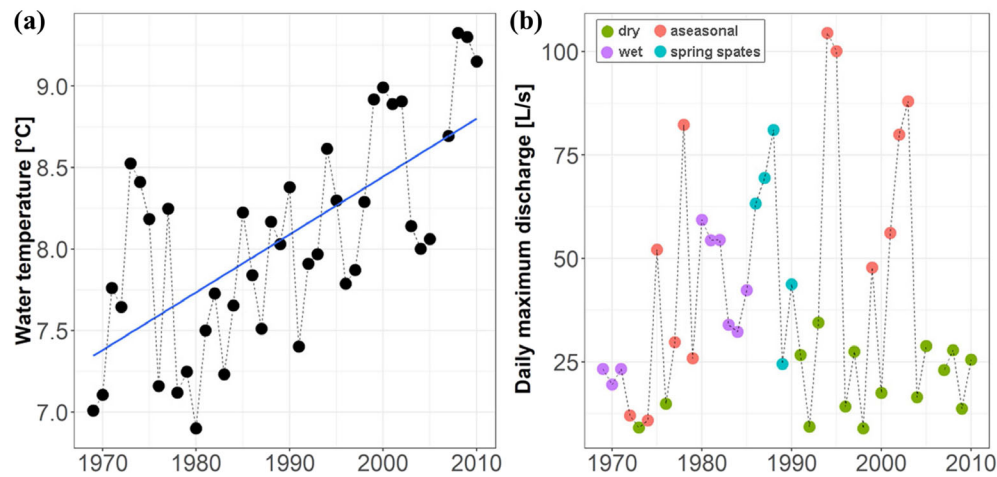
Community abundance/Shannon’s diversity/species richness/total community turnover  $\sim$  mean annual temperature + discharge pattern + mean annual temperature  $\times$  discharge pattern.

Relative abundance of trophic groups  $\sim$  (mean annual temperature + discharge pattern + mean annual temperature  $\times$  discharge pattern)  $\times$  trophic group identity.

Duration of the emergence/date of peak emergence  $\sim$  mean annual temperature + discharge pattern + mean annual temperature  $\times$  discharge pattern + community abundance.

No major violations of model assumptions (e.g., normal errors distribution and homoscedasticity) were detected in any of the models. Model results are reported as ANOVA tables, using ANOVA function in the *car* package and as a standardized effect sizes (Schielzeth, 2010). In each case, for the factorial arguments, one level of the factor was selected as a baseline, which is thus missing in the model output. Additionally, we plotted the interaction effects of temperature and discharge pattern, when significant, using the *visreg* R package (function *visreg*; Breheny & Burchett, 2017; Fig. S5).

Due to the spurious nature of individual species abundance data and nonnormal distribution of the errors, we used the nonparametric Mann–Kendall test to detect the trend and direction of changes in the population abundances of each species over time. Prior to the application of the Mann–Kendall test, data were checked for temporal autocorrelation. In the case that temporal autocorrelation was detected, we applied a modified Mann–Kendall test for serially correlated data following the Hamed and Rao Variance Correction Approach (modified *mk* package and *mmkb* function; Hamed & Rao, 1998; Orlandi et al., 2010). To access a rate of change in the time series, we applied a nonparametric Sen’s slope estimator, using the *mblm* function in the R package *mblm* (Orlandi et al., 2010). We used the Sen’s slope estimator to measure the rates of change in mean annual water temperature, total community abundance, phenology, and functional feeding groups. For species richness, Shannon diversity, and evenness, where trends were nonlinear, the percentage rate change reported in the paper was based on the trend line predicted by the *geom\_smooth* function of *ggplot2* (Wickham et al., 2016). All data analyses were conducted in R version 3.4.1 (R Core Team, 2013).



**Figure 1.** Changes in mean annual water temperature and annual discharge patterns. Four discharge patterns were used in our study: “dry” years (low discharge; green dots), “wet” years (high discharge; purple dots), “aseasional” pattern (irregular spates during the year; red dots), and “spring spates” (blue dots) with at least one extreme discharge event in spring (for a detailed description see Wagner et al. 2011; Fig. S2).

## Results

Although characterized by large fluctuations, during the 42-year period of observation, the annual mean water temperature has increased on average by 0.044 °C per year, resulting in an overall increase of 1.88 °C between 1969 and 2010 (Fig. 1a; Table S1). Mean and maximum annual discharge did not change significantly (Table S1). However, we recorded directional shifts in discharge patterns, particularly toward more “dry” years (Fig. 1b; Fig. S2; Wagner et al., 2011).

Our analyses revealed a decline in the total abundance of insects by 81.6% over the past 42 years (−477 individuals/year slope estimator; Fig. 2a, Table S1), whereas species richness (Fig. 2b), Shannon’s diversity (Fig. 2c), and evenness (Fig. 2d) increased in a nonlinear way: Initially all 3 metrics increased until 1989/1990 by 21.3%, 28.3%, and 24.8%, respectively (Fig. 2), and then started declining by 10.5%, 4.3%, and 1.9%, respectively (Fig. 2). Our gls models revealed that the decrease in abundance is paralleled by increasing temperature (Tables 1 and S2). The increases in Shannon’s diversity, species richness, and evenness are concomitant with increasing temperature and changes in discharge pattern. Specifically, stronger increases in Shannon’s diversity and species evenness with warming occurred during aseasional and wet years, whereas stronger increases in species richness with warming occurred during years with spring spates (Tables 1 and S2; Fig. S5). The interannual turnover rate significantly increased over the observation period (by 34%; Fig. 3a), concomitant with an increase of the water temperature; the stronger increases in turnover with warming occurred during dry years (Tables 1 and S2; Fig. S5). In addition, we examined turnover between decades (Fig. 3b) to illustrate gains and losses of species.

Based on a comparison of the 1st and 4th decade of observation, we found that 20 species were gained, whereas 6 were lost. However, these changes were nonlinear when examined on a decadal basis: species gains were largest between the 1st and 2nd decade and almost matched losses between the 3rd and 4th decade (Fig. 3b). Our analysis on functional feeding group composition revealed an impact of water temperature and discharge patterns on the trophic structure, with predators and passive filter-feeders resulting as “winners,” whereas grazers and scrapers as the main “losers” (in terms of abundance change) (Fig. 3a; Table S3).

Across the community, the mean duration of the emergence period increased by 15.2 days over the 42-year period (Fig. 3c; Table S1). The increase in the mean duration of the emergence period is concomitant with the increase in the mean annual temperature, with stronger increases with warming occurring in dry and aseasional years (Tables S2 and 1; Fig. S5). The peak emergence date (Asch, 2015) shifted to an earlier date by 13.4 days for the whole period of observation (Fig. 3d; Tables 1 and S2). This shift in peak duration comes along with an extended duration of emergence (Fig. 3d). Excessively dry years, high mean annual temperature, high insect abundance and species richness as well as the interaction between high mean annual temperature and wet and aseasional years were all connected to earlier emergence peaks. The interaction of high mean annual temperature and the occurrence of dry years and high Shannon’s diversity were linked to later emergence peaks (Tables 1 and S2; Fig. S5).

The analysis of population trends showed that 17 species (55%) of the 31 most abundant species (representing 97% of the total abundance) exhibited significant shifts in their peak emergence date (Fig. 4a), and

Table 1. Results of generalized least squares models for environmental and community metrics in the Breitenbach.

	Dependent variable						
	Abundance	Shannon's diversity (H)	Richness	Turnover	Duration	Peak emergence	Evenness
Mean T °C	-0.55* (0.25, -2.2)	0.62** (0.10, 6.15)	-0.11 (0.14, -0.81)	-0.01 (0.009, -1.12)	0.47** (0.15, 2.97)	-0.38* (0.17, -2.21)	0.68** (0.10, 6.81)
Pattern dry	-1.91 (3.3, -0.57)	7.95** (1.25, 6.35)	-1.72 (1.72, -0.99)	-0.49** (0.11, -4.41)	1.01 (1.92, 0.52)	-8.01** (2.08, -3.83)	8.84** (1.25, 7.05)
Pattern spring spates	-17.8* (8.0, -2.2)	8.08** (2.58, 3.12)	-8.08* (3.50, -2.30)	-0.07 (0.21, -0.36)	3.03 (3.69, 0.82)	-7.86 (4.0, -1.96)	9.90** (2.60, 3.80)
Pattern wet	2.75 (4.6, 0.6)	3.62* (1.50, 2.40)	0.84 (2.06, 0.40)	0.008 (0.12, 0.06)	9.01** h (2.11, 4.27)	5.42* (2.29, 2.36)	3.94** (1.51, 2.59)
Abundance (stand.)							
Mean T °C × Pattern dry	0.12 (0.32, 0.4)	-0.62** (0.12, -5.17)	0.10 (0.16, 0.62)	-0.006 (0.005, -1.06)	0.16 (0.09, 1.69)	-0.43 (0.10, 4.21)	
Mean T °C × Pattern spring spates	1.8* (0.8, 2.2)	-0.60* (0.25, -2.35)	0.74* (0.34, 2.17)	0.01, 4.69)	-0.06 (0.17, -0.38)	0.691** (0.19, 3.55)	-0.69** (0.12, -5.71)
Mean T °C × Pattern wet	-0.3 (0.48, -0.6)	-0.25 (0.16, -1.54)	-0.07 (0.22, -0.32)	-0.004 (0.013, -0.371)	-0.26 (0.35, -0.73)	0.55 (0.38, 1.43)	-0.77** (0.25, -2.98)
Shannon's diversity (H) (stand.)							
Species richness (stand.)							
Constant	15.7** (2.5, 6.1)	2.64* (1.04, 2.53)	11.4** (1.51, 7.52)	0.55** (0.11, 5.01)	0.04 (0.10, 0.44)	0.30** (0.11, 2.76)	
Observations (df)	41	201	201	200	201		1.93 (1.03, 1.86)
Log Likelihood	-46.4	-52.8	-52.8	454.9753	-112.8		-55.12
Akaike Inf. Crit.	110.8	125.7	125.7	-883.9	251.7		130.2
Bayesian Inf. Crit.	124.3	158.7	158.7	-841.1	294.6		163.2

All variables were standardized, and effects sizes are given. Standard error and t-statistics are in brackets. Pattern ("dry," "spring spates," and "wet"), different discharge patterns; Mean T °C: mean annual water temperature. Pattern "aseasonal" used as a baseline for the model. Significant values are highlighted in bold: \*p < 0.05; \*\*p < 0.01.

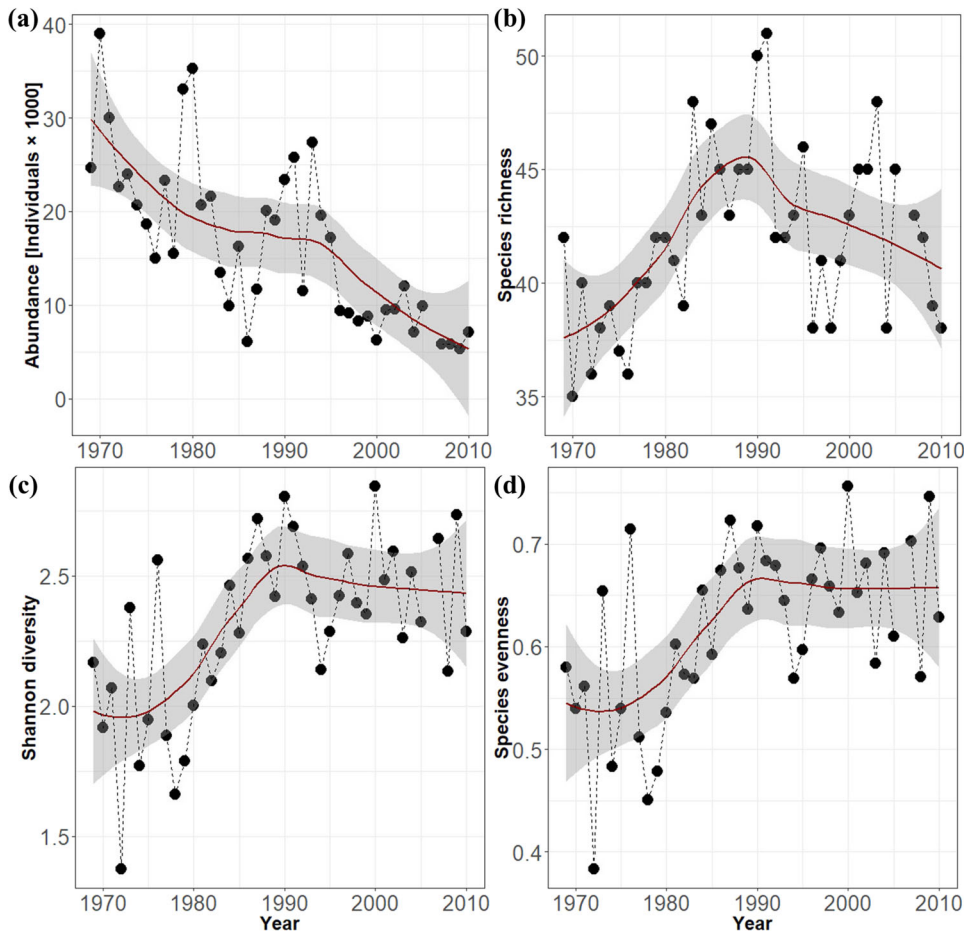


Figure 2. Changes in (a) overall abundance, (b) species richness, (c) Shannon's diversity, and (d) species evenness of the Breitenbach EPT community over time.

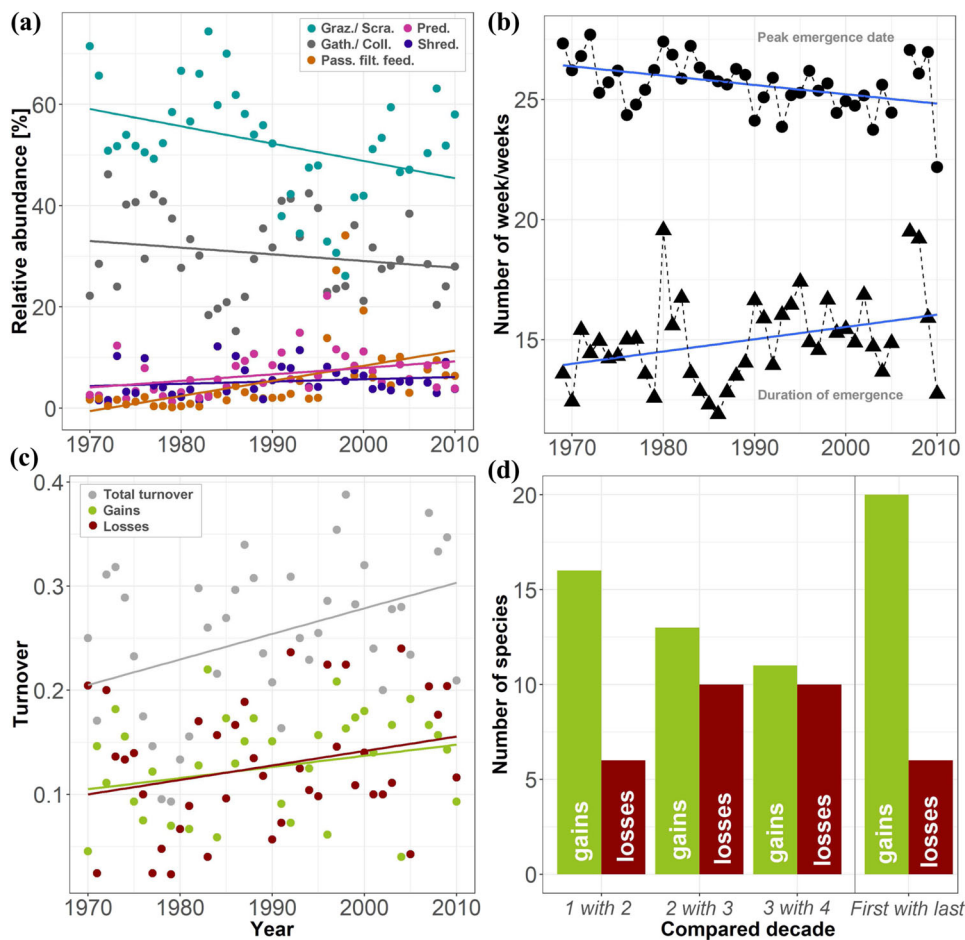
13 (42%) in their emergence duration (Fig. 4b). The analysis of the same 31 species showed that for 11 of these species (35%) abundance decreased significantly, for 3 species (10%) abundance increased, and for 17 species (55%) it remained unchanged (Fig. S3). Greatest losses in abundance were observed in the predominant feeding groups, such as grazers/scrapers, whereas passive filter feeders increased in abundance.

## Discussion

Based on long-term high-resolution biotic and abiotic in situ data, our study provides a striking example of the high complexity and nonlinearity in the response patterns of an aquatic insect community to climate change over a 42-year observation period. Furthermore, our data show severe short-term fluctuations (<5 years) in almost all metrics, clearly emphasizing the necessity of long-term monitoring and questioning the usefulness of time series analyses that also incorporate data covering short time periods (e.g., Dornelas et al., 2014; >3 years).

At the beginning of the observation period, the high abundance of the Breitenbach insect community mainly goes back to very high abundances of the 10 most

dominant species (Fig. S3). This is not unusual for a cold first-order stream with temperatures only allowing a few specialist species to establish larger populations, whereas most other species present in such streams are only able to establish small populations resulting in the overall lower diversity rates initially observed (Wagner et al., 2011). The continuous increase in water temperature allowed further species to establish sizeable populations in the Breitenbach, whereas the previously dominant species declined in abundance (potentially driven by warming and/or increased competition) but did not go extinct. These changes in abundance, richness, and turnover resulted in an increase in Shannon diversity and evenness. However, in the second half of the observation period (starting around 1990), discharge patterns changed significantly: Although the first half of the observation period was characterized by the erratic occurrence of all 4 discharge patterns, the second half was exclusively characterized by "dry" or "aseasonal" discharge conditions, leading to changes in streambed sediment composition and thus in habitat structure (Wagner et al., 2011). Starting around 1990, these changes in discharge patterns together with continually increasing water temperatures altered the response of various community metrics except abundance that continued declining:



**Figure 3.** Changes in turnover, trophic groups and phenology. (a) Interannual turnover of the community. (b) Interdecadal turnover of the community represented by gains and losses of species. (c) Relative abundance of functional feeding groups: “Gra/Scra”: grazers and scrapes, “Pred”: predators, “Gat/Coll”: gatherers and collectors, “Shred”: shredders and “Pass filt”: passive filter feeders. (d) Mean annual shifts in phenology for the 31 most abundant insect species.

richness that had initially increased reached a tipping point and started declining; the same applies to Shannon diversity and evenness but to a lesser extent. A recent study (Kakouei et al., 2018) predicted that an increasing frequency of low-flow events will cause a decline in abundance of rheophilic taxa but an overall increase in abundance in freshwater communities due to increases in low-flow generalists, whereas Smol et al. (2005) have shown that an increase in temperature (approx. 1850–1990) in cold-water ecosystems has already led to an increase in diversity due to increased primary production and immigration of warm-adapted species. Our results show that in cold headwater streams climate change may initially lead to an increase in diversity (confirming Smol et al., 2005), whereas over time, a tipping point might be reached eventually leading to a declining trend (confirming Kakouei et al., 2018).

Although a few species initially dominated the Breitenbach insect community, the severe decline in abundance applies to many more species (Fig. S4). The overall 81.6% decline in total abundance corresponds to an average loss of 1.94% per year, which is similar to the annual loss of 1.88% in forest beetles over 44 years in the United States (Harris et al., 2019). However, in our case richness slightly increased over time (by approximately

10%), meaning that although the vast majority of individuals have been lost, the number of species is now slightly higher in the Breitenbach. Yet, species gains were prominent in the first 2 decades, whereas losses increased significantly in the last 2 decades bringing gains and losses to an equilibrium. This continuous change in interdecadal turnover is masked when only considering the total change over the 42-year period (first and last decade) where gains were much higher than losses. If the observed trend of decreasing gains and increasing losses will continue in the near future, the declining trend in richness—which has already begun—may accelerate. This is a striking example, highlighting that long-term studies need to be continuous if we aim to understand changes in community structure. Some studies on insect population trends only rely upon an initial and a final survey (e.g., Lister & Garcia 2018), which may lead to misinterpretation of the underlying dynamics involved as shown by our study.

In our study, about 35% of the EPT species declined in abundance, a result that agrees with a recent review of Sanchez-Bayo and Wyckhuys (2019; but see Thomas et al., 2019) on global declining trends among Ephemeroptera (37% of species declining) and Plecoptera (35% declining) as well as the average number



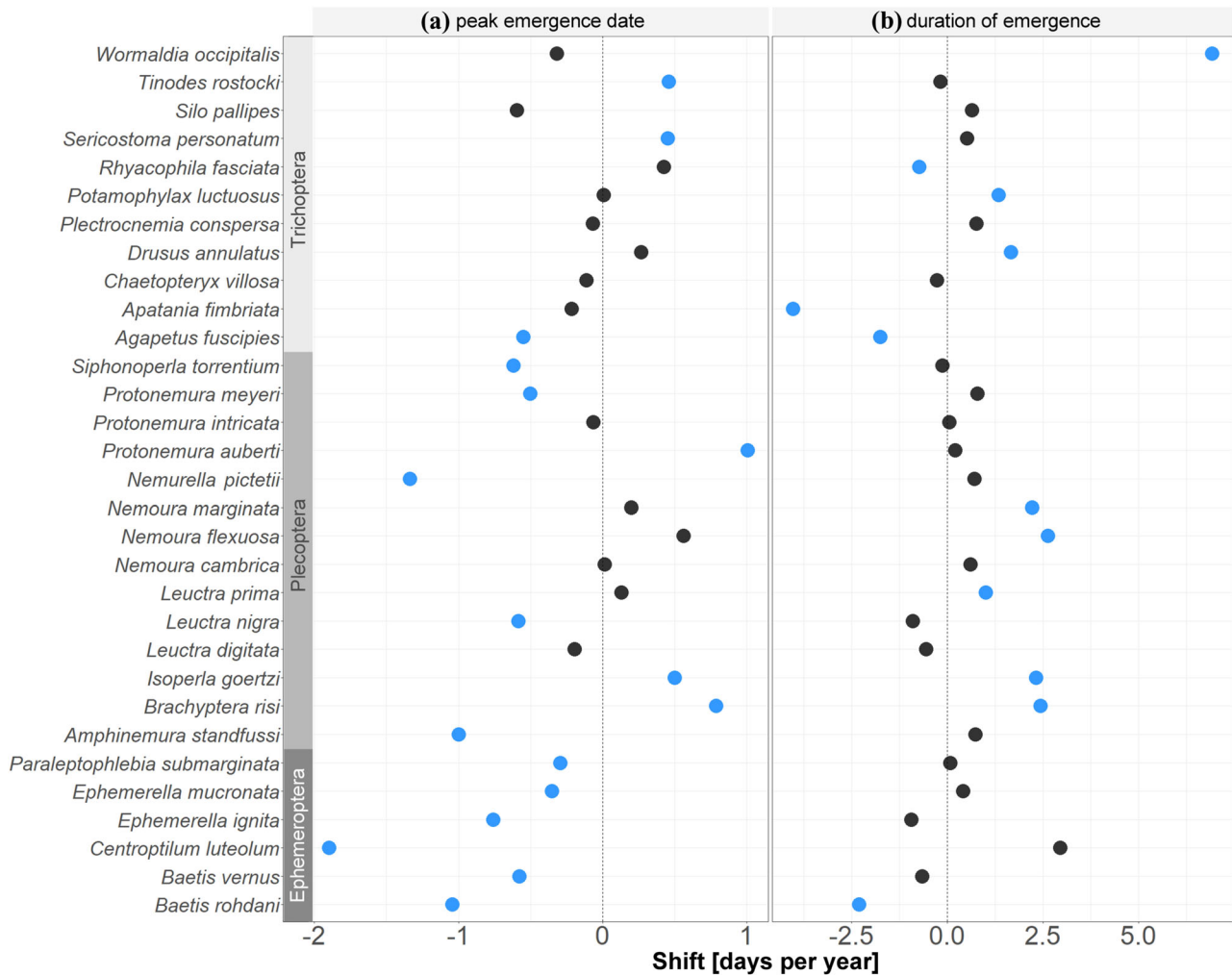


Figure 4. Average annual changes in the phenology of the 31 most abundant EPT-taxa. Blue dots indicate significant changes; black dots represent nonsignificant changes.

of terrestrial insects declining (38% of species). In turn, the proportion of species that increased in abundance (10%) or remained virtually unchanged (55%) is also similar to the temporal trends reported for various insect taxa in the meta-analysis by Sanchez-Bayo and Wyckhuys (2019). Overall, the declines in species abundance of aquatic insects parallel the declines in terrestrial insect species (Sanchez-Bayo & Wyckhuys, 2019). However, reviews or larger-scale studies like those of Sanchez-Bayo and Wyckhuys (2019) either compare start and endpoints or assume monotonic trends. Our data clearly show that community responses over time are often nonlinear.

The observed changes in climate also led to substantial shifts in insect phenology. It is known for plants (CaraDonna et al., 2014), mayflies (Harper & Peckarsky, 2006), and butterflies (Stefanescu et al., 2003) that communities exposed to prolonged warming tend to change their phenology toward an earlier flowering or emergence date. Our study demonstrates similar patterns

among aquatic insects. The protracted emergence of aquatic insects in the Breitenbach might lead to a temporal desynchronization of life histories among interacting species (Høye et al., 2013), for example, between predators (e.g., spiders) and prey (i.e., adult EPT species).

The observed changes in abundance, diversity, and phenology are paralleled by shifts in the trophic structure of the Breitenbach insect community. The changes in discharge pattern toward “dry” or “aseasonal” from 1990 onward improved the conditions for passive filter-feeders (decreased damage of the filtering nets by current; Houghton & Holzenthal 2010; Flourey et al., 2013), with the passive filter-feeding caddisfly *Wormaldia occipitalis* (Pictet, 1834) becoming the biggest winner among all the species in the Breitenbach. In turn, altered discharge patterns also potentially reduced biofilm availability as stones became covered by fine sediment due to increased sedimentation, leading to significant declines of grazers/scrapers (Wagner et al., 2011; Kakouei et al., 2018).

Because there is no evident anthropogenic pressure such as water pollution, land use change, and species invasions in the Breitenbach catchment, climate change is arguably the single most important factor that drove the recorded changes in abundance, community structure, and phenology. Nevertheless, we cannot exclude the impact of other external factors, such as changes in metacommunity structure (Leibold et al. 2004), due to a lack of appropriate long-term data from surrounding streams. If, for example, the insect communities of the neighboring streams are declining due to anthropogenic stressors, this may cause source–sink dynamics affecting the Breitenbach insect community. Such “surrounding” effects have, for example, been described by Seibold et al. (2019). This might be an additional driver of the observed severe decline in abundance, highlighting the need for a comprehensive future long-term monitoring that comprise several sites within a certain metacommunity.

The Breitenbach is a headwater stream belonging to the stream type “small low mountain streams,” which is the most common stream type in Germany and also common in many neighboring countries (e.g., Czech Republic, Slovakia, and France), hence a very representative system for Central Europe. Although we acknowledge the lack of spatial replication in our study, there is always a trade-off between spatial and temporal resolution. Our data set is unique in terms of temporal resolution and length allowing for in-depth analyses to unravel complex response patterns of insect communities toward environmental changes over time that may not be captured by snapshot data, time series with an average length <10 years, or studies investigating only one or a few elements of community structure such as biomass. Just as an example: if our analyses were only based on the first 21 years of the entire 42-year period, the results would have been significantly different compared to analysis of the latter 21 years only. This is important to bear in mind when interpreting large-scale studies in which time series data that cover different time fractions are combined. The importance of the total length of a time series (including the aspect of the starting and end date) may also explain why, for example, Seibold et al. (2019) found an overall decline in terrestrial insect richness from 2008 to 2017, whereas we found an overall increase in insect richness from 1969 to 2010. By restricting our data to the last 2 decades, richness is also declining. We emphasize the importance of high-resolution, continuous long-term data in studying the impact of climate change and urge for caution when interpreting low resolution data. Comprehensive long-term biodiversity data accompanied by comprehensive abiotic data are a treasure that we need to preserve.

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## Supporting Information

Additional figures (Appendix S1) and tables (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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