Hydrobiologia
https://doi.org/10.1007/s10750-025-05886-2

PRIMARY RESEARCH PAPER

Mitigating the effects of extreme low-flow on stream macroinvertebrates: the role of woody riparian vegetation and groundwater

Hannah-Marie Stappert · Philipp Blanke · Daniel Hering · Jochem Kail

Received: 28 October 2024 / Revised: 15 April 2025 / Accepted: 17 April 2025

Abstract We investigated the role of woody riparian vegetation (WRV) in reducing the detrimental effects of extreme low-flow conditions on macroinvertebrate communities in Central European streams. We hypothesized that WRV decreases water temperature, thereby lessening the impacts of drought on streams. The study was conducted in the Lippe catchment in northwestern Germany at 26 study sections during the summer drought of 2022. Water temperature and macroinvertebrate communities were analyzed. WRV cover, groundwater influx, cross-section form and flow velocity were considered as predictors in structural equation models. We investigated how the immediate effects of extreme summer low-flow on water temperature and macroinvertebrates were mitigated by the four predictors. Shading by WRV and groundwater influx caused a significantly lower mean daily maximum water temperature of 6.6 °C and 4.8 °C, leading to a higher share of stream-type specific and temperature-sensitive macroinvertebrate taxa and feeding types typical for rhithral stream reaches. These results indicate that both WRV and groundwater influx play a crucial role in regulating stream temperature and maintaining stream-type specific macroinvertebrate communities under extreme low-flow conditions. The study highlights WRV management as a key tool for protecting stream ecosystems from the increasing frequency of droughts and related low-flow due to climate change.

Keywords Climate change · Buffer strips · Structural equation modeling · Macroinvertebrates · Water temperature

Introduction

In Central Europe, precipitation in summer is predicted to decrease due to climate change (Cook et al., 2018) leading to a decrease in discharge accompanied by increased low-flow (van Vliet et al., 2013). Usually three phases are distinguished with decreasing discharge: The flowing, pool, and dry phase (Stubbington et al., 2017). Already in the flowing phase, extreme low-flow affects macroinvertebrates through different pathways, especially by reducing the extent of habitats for rheophilic species, by disconnecting riparian habitats, sedimentation of fine sediments,

Handling editor: Verónica Ferreira

H.-M. Stappert (✉) · D. Hering · J. Kail
Department of Aquatic Ecology, University of Duisburg-Essen, Essen, Germany
e-mail: hannah-marie.stappert@uni-due.de

D. Hering
e-mail: daniel.hering@uni-due.de

J. Kail
e-mail: jochem.kail@uni-due.de

P. Blanke
Planning Office Koenzen, Hilden, Germany
e-mail: blanke@planungsbuero-koenzen.de

increasing conductivity and nutrient concentration as well as increasing water temperature (see review in Dewson et al., 2007). These effects of reduced discharge and the effects on macroinvertebrates were documented, among others, for streams in Denmark and U.K. (Dunbar et al., 2010). The pool and dry phases cause even more severe environmental changes and a dramatic decrease in taxa richness (Verdonschot et al., 2015; Stubbington et al., 2017). Other than in intermittent streams, invertebrate communities in Central European perennial streams are not yet adapted to extreme low-flow periods and climate change will potentially cause major shifts in community composition. Presently, seasonal flow intermittence with pool and dry phases does not occur regularly in perennial streams by definition and is restricted to phases of extreme droughts. As a result of ongoing climate change, extreme low-flow, flow cessation and drying will occur more frequently in the future. While flow cessation and drying will most probably have the most obvious and detrimental effects on invertebrate communities, the effects of permanent but extreme low-flow are less-well studied and still likely to cause considerable changes in habitat conditions and macroinvertebrate community composition. These changes will potentially affect large parts of Central European river networks in the future.

To assess the future shifts in invertebrate community composition caused by more frequent extreme low-flow in presently perennial streams, it is important to focus on the immediate effects after single low-flow events. In perennial streams, recovery of invertebrate communities from single extreme low-flow events is assumed to be rapid (Wood and Petts, 1994; Wright and Symes, 1999) and in the range of one to a few years (Ladle and Bass, 1981; Wood and Armitage, 2004). This is mainly because less affected stream sections remain, which serve as refuge and source for recolonization (Boulton, 2003). However, with the expected increase in drought frequency and severity due to climate change, these possible sources for recolonization will decrease. Therefore, the effects presently observed immediately after an extreme low-flow event are probably a better indication of how macroinvertebrate communities will change in future compared to presently observed long-term effects mitigated by recolonization from refuges. This is supported by Sarremejane et al. (2020) who demonstrated the crucial role of source-sink dynamics in the recovery of communities following disturbances.

Low flow is frequently accompanied by an increase of summer water temperatures. Water temperature increases given that (i) extreme low-flow events are usually accompanied by sunny weather with high direct solar radiation input, which governs water temperature in summer (Webb and Zhang, 2004), (ii) lower flow velocities increase residence time and the time the water body is exposed to solar radiation energy input (White et al., 2023), and (iii) the smaller water volume potentially heats faster in rectangular cross-sections, because wetted width and the water surface receiving direct solar radiation input remains rather constant (White et al., 2023). However, in case of high groundwater influx, water temperature might even decrease during extreme low-flow due to the higher share of cold groundwater (Mosley, 1983; Kinzie et al., 2006). Higher water temperatures induces a main pathway through which extreme low flows immediately affect macroinvertebrates, by increasing metabolic rate and oxygen demand of macroinvertebrates (Verberk et al., 2011).

However, even in streams affected by droughts, this increase in water temperature could be mitigated by addressing the key stream characteristics governing summer water temperature. Direct solar radiation input can be substantially reduced by shading by woody riparian vegetation (WRV), e.g., by about 95% under broadleaved forests (Rutherford et al., 1997; 1999). This results in a reduction of mean daily water temperature in small streams in summer by about 0.5 to 1.5 °C (Bowler et al., 2012), and a much more pronounced reduction in maximum daily water temperature by about 3 to 5°C (Bowler et al., 2012; Kail et al., 2021). Therefore, shading by WRV is widely considered the most important factor which can easily be influenced by river management (White et al., 2023). There are, however, other options to mitigate the effects of low flow that are less often explored and used in management. In particular, landscape water balance might be improved to increase groundwater recharge and groundwater influx during meteorological droughts. Groundwater influx is known to reduce water temperature especially during summer low-flow, for example by about 0.7°C in a lowland mid-sized river in south-east France (Wawrzyniak et al., 2017). Furthermore, river morphology might be restored to create a less rectangular cross-section with a deeper part (thalweg). This would modify cross-sections, wetted width and width/depth ratios susceptible to high water temperatures, but there is limited empirical evidence for this effect (White et al., 2023). In addition, there is evidence for the positive effect of natural stream morphology on macroinvertebrates during low flows by providing refugia (Dunbar et al., 2010).

While multiple studies investigated the influence of these relationships, including the effects of WRV on water temperature and of water temperature on macroinvertebrates, only few studies considered the full cause-effect chain from WRV via shading and water temperature (including possible influences of groundwater discharge) on macroinvertebrates. Several studies treat this cause-effect chain as a black box and demonstrated the large positive effects of WRV on macroinvertebrates (see review in Sweeney and Newbold, 2014). These positive effects can potentially be attributed to many different functions of WRV like nutrient, fine sediment and pesticide retention, input of organic material like leaf litter and large wood, habitat provision for terrestrial species, its role as migration corridor, and the functions related to shading like promoting natural riverbank stability and river morphology, regulating primary production and water temperature (reviews in Broadmeadow and Nisbet, 2004; Sweeney and Newbold, 2014). Some studies and reviews indicated that the positive effect of WRV can mainly be attributed to the functions related to shading and especially to the decrease of water temperature (Parkyn et al., 2003; Feld et al., 2011; Palt et al., 2023), but this has rarely been empirically tested. The effect of water temperature on macroinvertebrate community composition has often been investigated in the field using mean water temperature as a predictor (Lessard and Hayes, 2003; Rivers-Moore et al., 2012; Li et al., 2012). However, daily water temperature fluctuations increased mortality in laboratory studies on thermal limits (Cox and Rutherford, 2000), indicating that mean daily maximum water temperature might be the water temperature parameter most strongly affecting macroinvertebrate communities.

Given the above considerations, the main objective of this study was to investigate the immediate effects of a summer drought with extreme low flows on macroinvertebrates in perennial streams and the possible mitigating effects of WRV. More specifically, the following hypotheses were tested: First, high water temperature, particularly high daily maximum water temperature, during extreme low-flow has immediate detrimental effects on macroinvertebrates. Second, daily maximum water temperature during extreme low-flow can most strongly be decreased by reducing solar radiation input via shading by WRV; this effect is higher than the effect of groundwater influx, cross-section form and flow velocity. Third, macroinvertebrates mainly benefit from reduced water temperature induced by WRV during extreme low-flow, while other functions of WRV are less relevant.

Material and methods

Study area

The study area is located in the western part of the Lippe catchment within the central European lowlands in northwestern Germany (Fig. 1). The streams investigated are lowland sand-bed streams and organic streams which irreversibly developed into sand-bed streams after lowering of the groundwater table or peat extraction (Pottgiesser and Sommerhäuser, 2014). Naturally, type 14 streams are heavily meandering with shallow cross-sections, low valley slope (2–7 ‰) and therefore low-flow velocities. The channel bed mainly consists of sandy substrate with patches of gravel, alder roots, macrophytes, coarse-particulate organic matter, and large amounts of large wood, leading to the formation of pools.

Study sections and period

First, 34 study sections, each 100 m in length, were selected to cover a gradient in the four stream characteristics potentially mitigating low-flow effects on water temperature and used as predictors (WRV cover and related solar radiation input, flow velocity, cross-section form and groundwater influx).

Second, to ensure comparability in respect to other stream characteristics not used as predictors, the study was restricted to (i) a single stream type, lowland sand-bed streams (type 14 and degraded type 11), (ii) stream sections not being affected by other relevant pressures like impoundments and bank or bed fixation with riprap (i.e. no boulders as

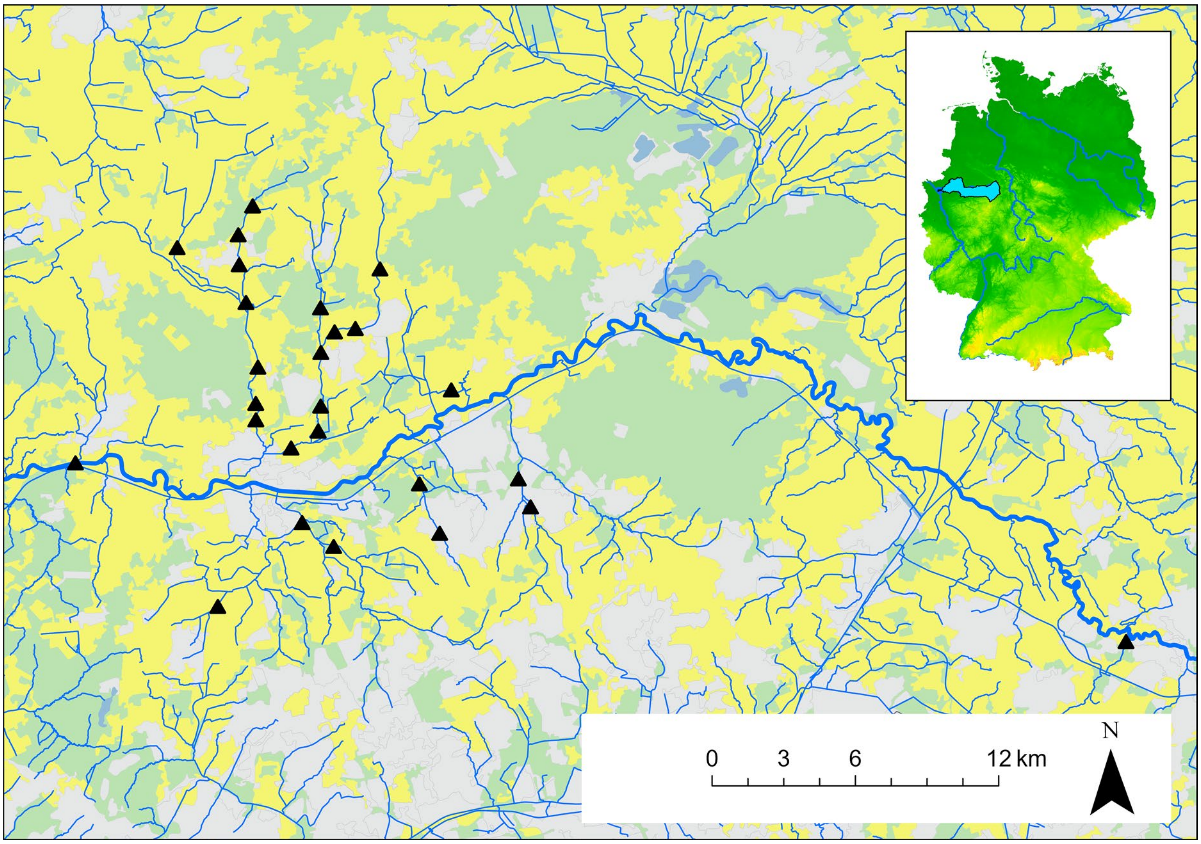

Fig. 1 Study section locations. Gray: Built up area (CLC1 (CORINE Land Cover 1)); Yellow: Agricultural area (CLC2); Green: Forest and natural area (CLC3); Blue: Water (CLC5); Light blue: Lippe catchment

non-natural bank or bed substrate, artificially increasing the share of sensitive EPT taxa), and (iii) sections with a similar cover of natural WRV on both banks up to 500 m upstream, given that it took about 400 m to reach a new equilibrium summer water temperature downstream of a change in WRV cover in similar lowland sand-bed streams (Kail et al., 2021).

Catchment size of the study sections ranged between 4.69 and 72.28 km^2 (mean size of 31.04 km^2). Landcover in the catchment was mainly agricultural area (mean 55%, SD 9%) and forest and natural area (mean 26%, SD 13%), but also built up area (mean 19%, SD 14%), with six study sections located in urban catchments with > 38% built up area. Water samples were taken once per month in the 3 months before macroinvertebrate sampling. Nutrient concentrations were within the typical range in agricultural lowland catchments with mean total nitrogen concentrations ranging from 0.4 to 6.2 mg/L (mean 3.4 mg/L) and mean total phosphorus ranging from 0.01 to 0.23 mg/L (mean 0.05 mg/L).

The study was conducted during an extraordinarily hot and dry summer from July to August 2022. Mean discharge at a gauging station in one of the study streams (Hammbach) was about 0.06 m^3/s in July to August 2022 and almost five times lower compared to the years 1999 to 2023 (without 2022, mean 0.29 m^3/s, SD 0.14 m^3/s).

Responses

Water temperature was measured every 20 min from July 10th until August 28th 2022 at the downstream end of each of the 34 study sections, right before macroinvertebrates were sampled. HOBO Pendant MX2202 temperature loggers were used. The loggers were installed at roots or iron pins at the lower end of the study sections as deep as possible to prevent the loggers from falling dry at low water levels. For one study section, temperature data are only available for July 7th until July 30th, because the logger could not be found afterward. The raw temperature data were checked for obvious measurement errors: Values > 30 and < 10 °C (only exceeded at sites that dried completely and were excluded from the analysis) as well as temperature changes > 4 °C within the 20 min interval (did not occur). These pre-processed data were then used to calculate mean water temperature (T_{mean}) and mean daily maximum water temperature (T_{max}) during the study period.

Macroinvertebrate samples were taken between August 28 and September 7, 2022, right after three months of an extraordinary drought with almost no precipitation, except for five study sections which completely dried. Thus, 29 macroinvertebrate samples remained. Sampling was conducted following the multi-habitat sampling method (Meier et al., 2006a, b), which was modified in the following way: Instead of collecting 20 subsamples, 10 subsamples were taken in order to reduce the number of sampled individuals and allow for determination of each individual. Still, each substrate with an estimated coverage of at least 5% was sampled. The remaining number of samples was split between the substrates with greater coverage, leading to overrepresentation of rare substrates. Since type 14 streams usually contain few other substrates than sand, overrepresenting rare substrates may increase and emphasize differences between study sections. Samples were fixed in 96% ethanol and taken to the laboratory for sorting and determination. Each individual was determined to the lowest taxonomic level possible. Only for groups with an extremely high number of individuals, one half or quarter of the individuals was sorted and determined and total abundance extrapolated, which only applied to Crustaceans in five samples. Taxa lists were adjusted by bringing the same taxa to the same taxonomic level to prevent double counting of the same taxon caused by different taxonomic levels. The following metrics were computed using the software Perlodes (app version 5.0.9 and taxa database version 3.6.0): (i) The stream-type specific German Fauna Index (GFI). Here, each taxon that is characteristic for a specific stream type and/or indicates the presence of ecologically valuable structures is assigned a value of + 2 or + 1, while taxa who indicate disturbances are assigned a value of − 1 or − 2. To obtain the GFI of a study section, the mean value of the entire community is calculated, including the abundance of each taxon. The higher the GFI, the more representative the community is of a typical macroinvertebrate community for near-natural conditions in a specific stream type—in this case type 14. The GFI ranges from − 2 to 2 (Lorenz et al., 2004; Meier et al., 2006a, b). (ii) The KLIWA index reflects the quality of the respiratory habitat conditions in summer (July, August, and September) for macroinvertebrates in streams, considering water temperature, flow, and oxygen content. It has the unit °C and includes the focus temperature of each taxon of the given community, its specificity, and abundance (Halle et al., 2016). (iii) The RETI indicates how close the feeding-type composition to values typical for rhithral reaches. For each taxon, 10 points are distributed among the different feeding types according to its feeding characteristics. The RETI of a community is calculated as the sum of the points for feeding types typical for rhithral reaches (grazers, xylophagous taxa, and shredders) multiplied with the abundance of each associated taxon, divided by the sum of the points of all feeding types multiplied with the abundance of each associated taxon. Higher RETI values indicate a feeding-type composition closer to values typical for rhithral reaches. RETI values range between 0 and 1 (Schweder, 1992).

Predictors

WRV cover and resulting solar radiation input were quantified based on a 1 m resolution digital surface model from summer (DSM; 2018 to 2022) and a digital elevation model of the region (DEM; 2019 to 2020). Subtracting height values of the DEM from height values of the DSM resulted in a difference raster representing the height of features in summer such as trees or buildings. First, the water surface of the 100 m study sections plus 500 m upstream was demarcated on orthophotos. In case, the water surface was not visible on the orthophotos, the stream network was buffered with the mean width. All cells of the difference raster with values largen than 4 m in a 30 m buffer along the water surface were considered WRV. Visual inspection revealed that virtually all these features were indeed bushes and trees. WRV percentage cover was calculated for a 10 m wide buffer along the stream network, because this was a better predictor for water temperature compared to WRV cover in the 30 m buffer in comparable lowland streams (Kail et al., 2021). Total solar radiation input in the summer period (May 1st until October 31st) to each raster cell of the water surface was calculated in kWh/m^2, considering the shading of the surrounding raster cells of the DSM in the 30 m wide buffer, i.e. including all features on the bare-Earth surface as massive opaque objects (using the ESRI ArcPro tool Area Solar Radiation with a transmittivity of 0.5 and a diffuse proportion of 0.3 for generally clear sky conditions, i.e., without clouds). To consider the shading of overhanging tree canopies directly above the water surface, the solar radiation input received by these tree canopies was reduced by a factor of 0.5 and 0.75 for WRV 4–10 m and > 10 m in height to assess the solar radiation input received by the water surface raster cell below them. For each study section, WRV cover and solar radiation input were calculated for the 100 m study section as well as a 600 m section including 500 m upstream, because this was approximately the length necessary to reach equilibrium water temperature in comparable lowland streams (Kail et al., 2021). The calculation of WRV cover and solar radiation input was carried out by the planning office Koenzen. For one study section, the DSM used did not represent the conditions during the study period given that the pollard trees—which had just been cut prior to when the DSM was measured—had fully grown again when this study was conducted. For that study section, solar radiation input was estimated based on the values of similar fully shaded study sections.

Groundwater influx (m^3/ha/year) was calculated by dividing groundwater leakage (m^3/year) at the study sections by catchment size of each study section (ha). The catchment upstream of the study sections was demarcated and catchment size calculated in GIS based on a digital elevation model with a 10 m resolution. Modeled groundwater leakage was provided by the responsible water association and a related hydrological engineering company, based on two SPRING groundwater models (König et al., 2022). The first was a steady-state groundwater model calibrated using a quasi-steady state derived from measured groundwater levels from 1989 to 2018, kindly provided by the Lippeverband. The second was a transient groundwater model considering the dynamics of groundwater surface water interaction and calibrated using measured groundwater levels and measured surface water discharge rates from 2011 to 2023, provided by the engineering company Delta H. For reasons of comparability, annual means were calculated from the daily values of the transient model. As output, both models provided leakage values (m^3/year) for 2022 at model nodes irregularly spaced along the river network. For each study section, a mean value was calculated for the nodes (3–5) located up and downstream of the study section in a river reach approximately 100–150 m in length.

The influence of cross-section form on water temperature was assessed by calculating the ratio between wetted width receiving solar radiation input and wetted cross-section area representing the water volume to be heated (referred to as width/area ratio in the following). At each study section, three representative cross-sections were mapped and daily discharge and related water levels in these cross-sections extracted from existing hydrological and hydraulic models developed for the KliMaWerk project (www.eglv.de/klimawerk-wasserlandschaft/). Based on these daily water levels, mean wetted width, wetted area, and width/area ratio during the study period (July 10th to September 28th) was calculated for each study section. It was not possible to assess flow velocity in the study period the same way, because not all of the hydraulic models provided this as standard output.

Flow velocity was measured monthly in July, August, and September 2022 at five, approximately evenly spaced locations in a representative cross-section at each study section. Measurements were taken for 30 s approximately 2 cm below the water surface using a Schiltknecht MC20 flow velocity meter, and mean values calculated for each month ($n = 5$) and the whole study period ($n = 15$).

Statistical analysis

RStudio (version 4.3.1 and 4.3.3) was used for all following calculations.

For the statistical analyses, three of the 29 study sections were excluded due to missing water temperature data (SE01, WI09) or distinctly higher conductivity (PI02) than the other study sections, which limited comparability, leaving 26 study sections for analysis (Table 1).

Given that statistical methods to quantify variable importance of correlated predictors like conditional inference models need a much larger sample size,

Table 1 Selection criteria for the study sections. SE01 and WI09 were excluded due to missing temperature data. PI02 was excluded due to its high mean conductivity indicating a high ion load. GA01, HA10, HA11, SO02, and SO04 were excluded because no macroinvertebrate samples could be taken as they dried out

SiteID	Conductivity [µS/cm]	Dried out	Temperature data incomplete
GA01	0.343	yes	no
GE01	0.388	no	no
HA03	0.427	no	no
HA04	0.419	no	no
HA06	0.425	no	no
HA10	0.592	yes	no
HA11	0.588	yes	no
HA12	0.594	no	no
LO01	0.734	no	no
LO03	0.717	no	no
MM02	0.388	no	no
MM03	0.400	no	no
MM05	0.384	no	no
NL01	0.966	no	no
PI02	1.225	no	no
RA01	0.984	no	no
RM02	0.404	no	no
RM03	0.395	no	no
RM04	0.389	no	no
RM05	0.404	no	no
SE01	0.842	no	yes
SM01	0.851	no	no
SO01	0.846	no	no
SO02	0.778	yes	no
SO03	0.837	no	no
SO04	0.837	yes	no
WE01	1.340	no	no
WE02	0.786	no	no
WI01	0.400	no	no
WI03	0.409	no	no
WI05	0.411	no	no
WI07	0.413	no	no
WI08	0.477	no	no
WI09	0.410	no	yes

correlations between the four predictors were quantified and visualized using simple Spearman rank correlation and a PCA biplot, respectively, to ease interpretation of the single regression model results. For the PCA calculated with the "prcomp" function of the "stats" package, predictors were standardized to a mean of zero and standard deviation of one because they were measured on different scales.

To investigate the first hypothesis (higher maximum daily water temperature during extreme low-flow has immediate detrimental effects on macroinvertebrates), six regression models were set up, one for each of the three invertebrate response variables (GFI, KLIWA, and RETI index) with the mean daily water temperature T_{mean} and the mean daily maximum water temperature $T_{\max}$ as predictor, respectively. For the RETI index, a beta-regression model was set up as this variable ranges between 0 and 1. Similarly, two beta-regression models were set up for the GFI metric after transforming the metric values—originally ranging from -2 to 2—to range between zero and one. Given that the KLIWA index values are not restricted to a specific range, a linear regression model with a Gaussian distribution was used and a variance structure added if necessary to ensure homogeneity of residuals. In all models (beta regression and linear regression), catchment ID was considered as a random effect (random intercept), to account for potential differences between catchments in water temperature or other catchment characteristics. However, given that including the random effect did not significantly improve any of the models, the random effects were finally not implemented. Linear regression models were set up using the functions "lm" from the "stats" package and "lme" from the "nlme" package. When a variance structure was necessary, the function "gls" from the "nlme" package was used. For beta regression, the function "betareg" from the "betareg" package was utilized. If the water temperature variable was significant at $p < 0.05$ and the regression coefficient negative for GFI and RETI and positive for the KLIWA index, it was considered a detrimental effect. The water temperature variable $T_{\max}$ or T_{mean} resulting in the regression model with the higher (pseudo) R^2 value was considered to be more strongly related to the respective macroinvertebrate metric (Table 2).

To investigate the second hypothesis (importance of shading by WRV in decreasing water temperature during extreme low-flow compared to other stream characteristics), five single linear regression models with a Gaussian distribution were set up with $T_{\max}$ as response and the following

Table 2 Summary results of the four regression models with mean daily maximum water temperature in summer T_{max} as response and one of the three macroinvertebrate community metrics as predictor, respectively

Macroinvertebrate community metric	p-value (T_{mean})	Pseudo R^2 (T_{mean})	p-value (T_{max})	Pseudo R^2 (T_{max})
GFI	<0.05	0.1458	<0.05	0.2201
KLIWA index	0.001	0.3635	<0.001	0.3119
RETI	<0.001	0.3697	<0.001	0.4054

predictors: groundwater influx (m^3/ha/year), mean width/area ratio during the study period to consider cross-section form, mean flow velocity in the study period (m/s), as well as WRV cover and resulting solar radiation input in the study period in the 100 m and 600 m section (kWh/m^2). Again, a variance structure was added if necessary to ensure homogeneity of residuals and catchment ID included as random effect (random intercept) to consider the nested study design. For the random effect models, the marginal R^2 of the fixed effect was quantified, i.e. the variance explained by the random effect excluded, using the function "multilevel.r2" of the "misty" package. Selection of the most important predictors by coefficient values was not possible since the predictors were not standardized in the single regression models. Alternatively, a parameter was considered more important if its effect on water temperature was higher. The effect of a parameter on water temperature was quantified by calculating the change in water temperature predicted by the regression equation along the range of values of the stream characteristic in the dataset. Additionally, the coefficient signs were implemented in the decision. If the coefficient sign was not logically consistent, then the correlation was considered non-causal.

The third hypothesis assumes that the positive effect of WRV on macroinvertebrates during extreme low-flow mainly occurs through the pathway via water temperature and is not related to other functions of WRV. To investigate this hypothesis, a piecewise structural equation model (SEM) was set up. In an SEM, a set of different predictors can be linked to a response variable through multiple pathways, i.e., the predictors can also be linked among each other. This allows to distinguish between (i) the indirect link of a predictor like 'WRV cover' via other predictors like 'solar radiation input' and 'water temperature' with the response (here: macroinvertebrate community metric), representing a specific cause-effect relationship, (ii) the direct link, subsuming all other pathways and effects of the predictor on the response not explicitly included in the SEM, and (iii) its total effect on the response through all pathways (Fig. 2). In piecewise SEMs, only the variables directly pointing to one specific response variable are included in a respective, independent regression model. The

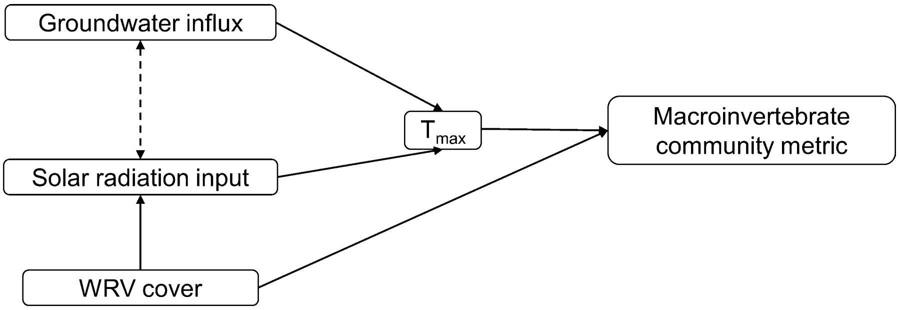

Fig. 2 General structure of the structural equation model showing how the variables are linked. All variables with arrows directly pointing to another variable were included in a respective, independent regression model. The dashed line indicates a non-causal correlation between solar radiation input and groundwater influx implemented in the SEMs as an error term

regression coefficients of all models are then combined to calculate direct, indirect, and total effects for each predictor. For the technical implementation, all data were normalized to make coefficients of the different regression models comparable. Using a bootstrapping approach implemented in the function “bootEff” from the “semEff” package, it was possible to obtain 95% confidence intervals including 95% of the effect values calculated in 1000 bootstrapping runs for the direct, indirect and total effects. Effects were considered relevant if confidence intervals did not include zero. Instead of showing the means of the bootstrap samples—which are close to the center of the respective confidence interval—the original model estimates were given in the figures. The difference between these two values is the bootstrap bias, indicating how representative the original non-bootstrapped dataset is compared to the population. Based on the previous analyses, all stream characteristics which had significant effects on water temperature were included in the SEM, resulting in the following set of single and independent regression models: (i) WRV cover in the 100 m study section—solar radiation input to the 100 m study section, (ii) solar radiation input to the 100 m study section and groundwater influx—mean daily maximum water temperature in the study period, (iii) mean daily maximum water temperature in the study period and WRV cover in the 100 m study section—macroinvertebrate index (Fig. 2). These regression models were set up in the same way as described for hypotheses one and two but using the standardized data. However, since the “bootEff” function cannot handle gls models with a variance structure, it was not possible to include such a variance structure in the regression model with WRV cover as predictor and solar radiation input as response. This was considered an acceptable limitation, because the model including a variance structure was only slightly better compared to the model without ($p = 0.048$).

After setting up the SEM, the global goodness-of-fit test was used to check if the so-called basis set of independence claims (all relationships between the variables not included in the SEM) can be considered independent, i.e., is not significant with a model-wide $p < 0.05$, or if additional relationships may exist as indicted by the data. In addition, the more detailed test of directed separation was used to see if any of the independence claims was significant (Lefcheck, 2016).

Results

Water temperature and macroinvertebrates [Hypothesis 1]

Higher mean daily maximum water temperature (T_{max}) had immediate detrimental effects on all three macroinvertebrate metrics. GFI and RETI significantly decreased with increasing T_{max} (Fig. 3). The observed difference between the study sections in

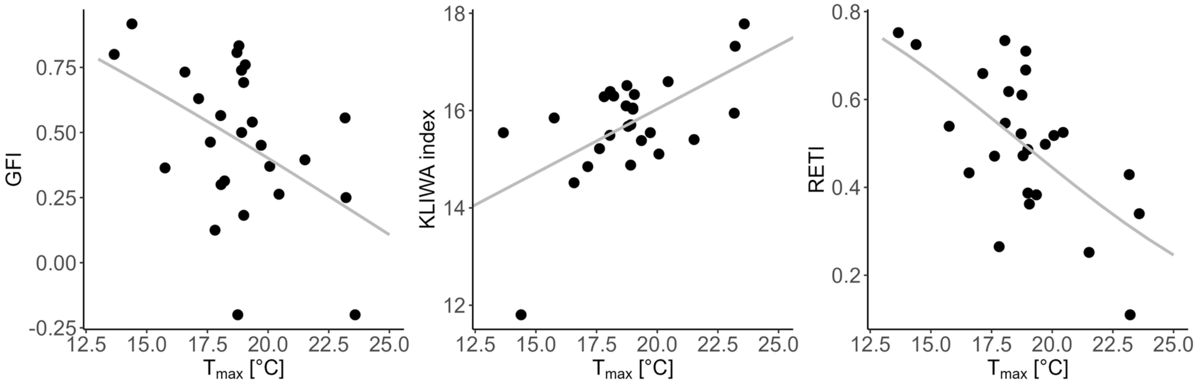

Fig. 3 Scatterplots and regression lines of mean daily maximum water temperature in summer T_{max} prior to biological sampling versus three macroinvertebrate community metrics (German Fauna Index GFI increasing with the share of natural, river-type specific species, the RETI index being higher if the feeding-type composition corresponds to rhithral reaches, the KLIWA index based on water temperature preferences)

T_{max} from 14 to 24 °C corresponded to a difference of the GFI index values of about 0.75 (scale ranging from − 2 to + 2) and of the RETI index values of about 0.5 (scale ranging from 0 to 1). The KLIWA index increased with T_{max}. A change in T_{max} by 10 °C from 14 to 24 °C corresponded to an increase in the KLIWA index by about 3 °C.

WRV and water temperature [Hypothesis 2]

The reduction of solar radiation input by WRV cover was the most important stream characteristic and had the largest effect and more strongly decreased mean daily maximum water temperature in summer (T_{max}) compared to the three other stream characteristics investigated. Solar radiation input resulting from WRV cover in the 100 m reach had a significant effect on T_{max} ($p < 0.01$, Fig. 4) and a change in T_{max} of 6.6 °C was predicted by the regression equation for the range of solar radiation values in the dataset of 91.4–750.9 kWh/m^2 (corresponding to a range of WRV cover values of 0–99%, Table 3). When considering WRV cover and related solar radiation input of a longer 600 m upstream reach, this predictor was not more strongly related to T_{max}, but even not significantly related to T_{max} at all. In contrast, groundwater influx was again significantly correlated with T_{max} ($p < 0.001$; Fig. 5), but the effect on T_{max} of 4.8 °C predicted by the regression equation for the range of groundwater influx values in the dataset (− 0.8–146.8 m^3/ha/year) was smaller. Width/area ratio and flow velocity were also significantly correlated with T_{max} ($p < 0.01$ and $p < 0.001$), but the signs of the correlation coefficients were opposite to the expected and higher width/area ratios (i.e., wider cross-sections) related to lower T_{max} and higher flow velocities (i.e., shorter residence times) to higher T_{max}.

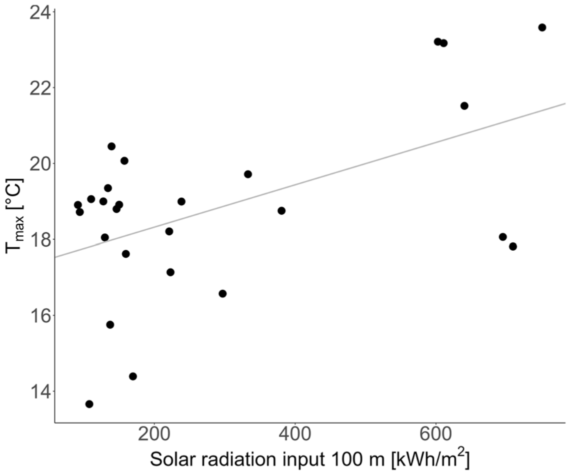

Fig. 4 Scatterplot and regression line of total solar radiation input to the water surface in summer (01.05. − 31.10.) for generally clear sky conditions but considering shading by woody riparian vegetation WRV along the 100 m study sections versus mean daily maximum water temperature T_{max} in the study sections

Correlations between the predictors have to be considered for the interpretation of the single regression models. While solar radiation input was not related to any of the three other predictors, the other three predictors were indeed correlated (Fig. 6). Width/area ratio and flow velocity were significantly correlated ($r_s = 0.524$, $n = 26$, $p < 0.01$), as well as flow velocity and groundwater influx ($r_s = -0.447$, $n = 23$, $p < 0.05$), while groundwater influx and solar radiation input were not significantly correlated.

WRV and macroinvertebrates [Hypothesis 3]

The positive effect of WRV on macroinvertebrates during extreme low-flow mainly occurred indirectly through the pathway via water temperature and was less strongly related to other functions of WRV.

Table 3 Model summary output for linear regression and beta regression of environmental parameters versus T_{max}

Parameter	Coefficient	*p*-value	(Marginal) R^2	Difference T_{max}
Solar radiation input 100 m [kWh/m^2]	0.00558	< 0.01	0.277	6.6
Solar radiation input 600 m [kWh/m^2]	0.00449	0.135	0.091	2.4
Groundwater influx [m^3/ha/year]	− 0.03220	0	0.749	4.8
Width/area ratio	− 0.10669	< 0.001	0.711	5.1
Flow velocity [m/s]	14.84468	< 0.01	0.618	4.3

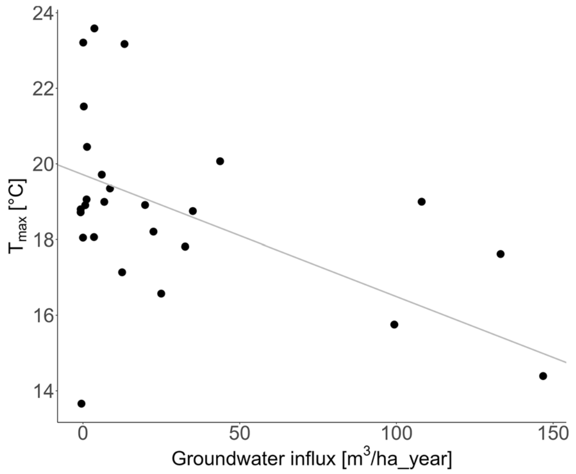

Fig. 5 Scatterplot and regression line of groundwater influx in m^3 per hectare and year versus mean daily maximum water temperature T_{max} in the study sections

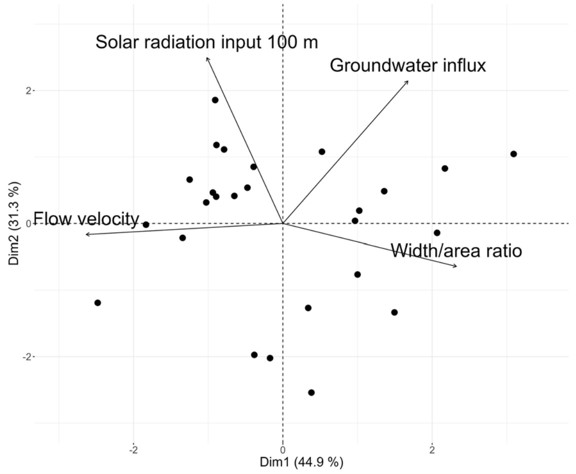

Fig. 6 PCA biplot of the stream characteristics used as predictors for mean daily maximum water temperature in summer prior to the biological sampling T_{max}. Solar radiation input refers to the conditions along the 100 m study section

WRV cover had an ecologically positive mean indirect effect on the GFI, RETI, and KLIWA index via solar radiation input and mean daily maximum water temperature T_{max}, with the confidence intervals not including zero (Fig. 7). For the GFI and RETI index, the mean direct effect of WRV cover—representing effects of WRV on the indices via other functions—was even larger, but the confidence intervals included zero.

Besides WRV cover, also groundwater influx had a relevant indirect effect on most macroinvertebrate metrics via T_{max} as already indicated by the linear regression model with groundwater influx as predictor and T_{max} as response using the unstandardized data (see section on hypothesis 2). Groundwater influx had an ecologically positive mean indirect effect on the GFI, RETI, and KLIWA index via solar radiation input and mean daily maximum water temperature T_{max}, with the confidence intervals not including zero (Fig. 7). The mean indirect effect of groundwater influx is similarly small compared to the mean indirect effect of WRV cover and confidence intervals again clearly include zero.

Test of directed separation revealed a significant correlation between solar radiation input (100 m) and groundwater influx ($p < 0.05$), which had not been considered in the SEM so far. As this was not a causal correlation, a correlated error term between solar radiation input and groundwater influx was added to the SEMs, to consider that solar radiation input and groundwater influx were correlated but not part of the unidirectional set of assumed causal relationships or paths in the network. This resulted in a model fulfilling the global goodness-of-fit test (Chi-Squared and Fisher´s C $p > 0.05$).

Discussion

The main objectives of this study were (i) to investigate, if the immediate detrimental effects of extreme low-flow and high water temperature during a drought in 2022 on invertebrates were mitigated by woody riparian vegetation (WRV), (ii) to compare the mitigating effect of WRV to other stream characteristics (groundwater influx, cross-section form and flow velocity), and (iii) to find out if this mitigating effect mainly occurred through the dampening effect of shading on solar radiation input and water temperature. This might help river management selecting appropriate measures to mitigate the effect of extreme low flows caused by climate change.

Water temperature and macroinvertebrates [Hypothesis 1]

As assumed, higher water temperature during extreme low-flow had immediate detrimental effects

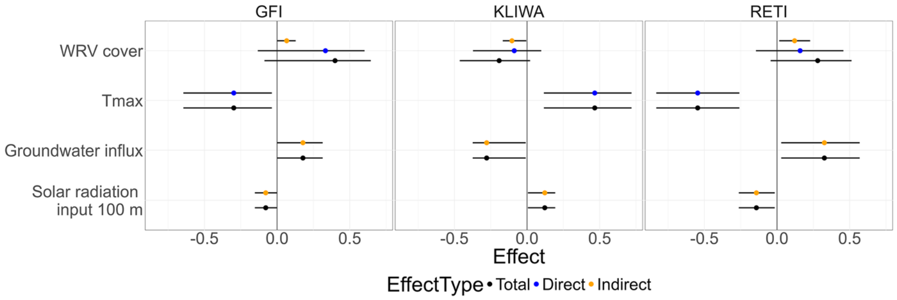

Fig. 7 Standardized regression coefficients (path coefficients) for the indirect, direct, and total effects of the three stream characteristics and mean daily maximum water temperature T_{max} on macroinvertebrate metrics in the structural equation model (SEM). Original path coefficients of the non-bootstrapped dataset (dots) and 95% confidence intervals (gray lines) of the 1000 bootstraps are given. Effects were considered relevant if confidence intervals did not include zero

on macroinvertebrates, and mean daily maximum water temperature (T_{max}) had a stronger effect than mean water temperature (T_{mean}) on all macroinvertebrate metrics investigated, except the KLIWA index. This points out the high importance of temperature extremes for macroinvertebrate communities under drought conditions. Life cycles of aquatic insects are frequently synchronized with water temperature, and at higher water temperature, emergence might occur earlier (Hynes, 1970) and possibly at inappropriate times for adult survival. Higher temperature leads to an increase in respiration and oxygen demand of macroinvertebrates and simultaneously decreased oxygen solubility in water (Bonacina et al., 2023). Macroinvertebrate taxa have specific water temperature limits and if they are exceeded, they retreat and/or die and are replaced by more temperature tolerant species (Steward et al., 2013). Higher T_{max} significantly affects the GFI, KLIWA index, and RETI. The KLIWA index reflects the quality of the respiratory habitat conditions in summer (July, August, and September) for macroinvertebrates in streams and is—among other parameters—based on the mean focus water temperature of each taxon of a given community. Therefore, it is directly associated with water temperature. It is positively correlated with T_{mean} and T_{max}, which is reasonable, as the reference time period for the index and the time period in which water temperature was measured before macroinvertebrate sampling is similar. Even within the short period of about 2 months extreme low-flow duration, differences in water temperature resulted in differences in the macroinvertebrate communities, i.e., extreme low-flow and related increase in water temperature had very immediate detrimental effects. The higher the RETI, the more typical is the feeding-type structure of the macroinvertebrate community for a rhithral stream section. In this study, WRV cover indirectly affected the RETI via a reduction in water temperature. With increasing T_{max}, the RETI decreased, stressing that global warming may shift the feeding-type composition of macroinvertebrate communities further away from their natural state. In our study, the RETI values cover about half of the entire possible range of the RETI (0 to 1) with a range of 10 °C mean daily maximum water temperature difference, which underlines the strong influence of water temperature on the RETI. We expected WRV to also directly influence the RETI, for example by input of dead wood and leaves. As the RETI is based on the feeding-type composition, it is reasonable that differences in WRV cover leading to differences in food and habitat availability act on the RETI as well. Still, we did not find a significant direct effect of WRV on the RETI index. This could be caused by the fact that the study sections were selected by the amount of shading and not by the naturalness of the WRV. Therefore, it is possible that non-native tree species made the majority of WRV at some study sections, with their leaves and wood being a poorer food basis for macroinvertebrates than the one of native tree species. The GFI describes the proximity of the observed macroinvertebrate community to the expected community of the stream type. In our study, we found that the higher the T_{max}, the lower (and further from the natural state) the GFI. The GFI has a range of about 0.75 within a T_{max} range of 10 °C. This means that with further progression of climate change and increase in water temperature, macroinvertebrate communities will change away from their natural state. This was concluded in many studies: A shift in macroinvertebrate community composition due to global warming was predicted by Pedreros et al. (2020) for Andean watersheds. Long-term climate change-induced water temperature increase and discharge reduction in a river in France lead to the decline and extinction of rheophilic, temperature sensitive taxa (Floury et al., 2013). Domisch et al. (2011) set up models predicting that new conditions due to climate change will alter species composition and community structure along the river continuum. Since macroinvertebrates are part of complex food webs, this may lead to changes across the entire food web including higher and lower positions and other organism groups in the web.

Not only small-scale parameters influence the macroinvertebrate community composition, but also larger scale parameters such as land use (Sponseller et al., 2001). Since the study focuses on extreme low-flow and not every prevailing factor could be included in the analysis due to sample size, macroinvertebrate community metrics were selected, which are connected to water temperature and flow conditions in order to evaluate extreme low-flow effects on macroinvertebrates. We did not include general macroinvertebrate community characteristics, such as taxa richness or the Saprobic Index which is strongly connected to nutrient concentration. As the utilized metrics are connected to drought influenced environmental parameters, we do not expect a strong effect of other environmental parameters such as land use. Additionally, we considered land use indirectly by checking on conductivity as a proxy for substance input and intentionally excluding one study section with distinctly higher ion concentrations that probably result from the high percentage of urban land use in the catchment (Table 1).

Even though not all prevailing environmental parameters could be implemented in the models, we were able to demonstrate that higher water temperature, especially higher mean daily maximum water temperature, had immediate detrimental effects on macroinvertebrate communities.

WRV and water temperature [Hypothesis 2]

As hypothesized, shading by WRV and its reduction of solar radiation input most strongly decreased T_{max} in our study (change in T_{max} by 6.6 °C and $p < 0.01$) compared to other stream characteristics. The relationship between shading and water temperature was shown in several other studies (Kalny et al., 2017; Kail et al., 2021; Rutherford et al., 1997, 2004) and is mainly caused by a reduction of solar radiation reaching the water surface.

In comparable lowland streams, a new lower equilibrium water temperature was reached after a sharp increase in shading by WRV within about 400 m, corresponding to a travel time of 45 min (Kail et al., 2021). In contrast, correlation between WRV cover and water temperature was stronger in our study when implementing WRV cover of the 100 m study section than for an additional 500 m upstream. This indicated that—at least in our case–WRV in close surroundings is more important in determining water temperature than conditions further upstream. This is supported by findings of another study: high rates of temperature change can occur over short distances if the amount of shading changes (Rutherford et al., 2004). A possible reason for this fast temperature adaptation to the WRV cover levels could be the prevailing drought conditions and the accordingly smaller water volume that heats up faster, underlining the outstanding role of WRV in reducing water temperature, especially under drought conditions.

Another important factor governing T_{max} in our study was groundwater influx (T_{max} difference of 4.8 °C; $p < 0.001$). Groundwater temperature in the study area is approximately 10 °C (LANUV), as mean yearly air temperature can be seen as a proxy for groundwater temperature (O'Driscoll and DeWalle, 2004). Due to its constant and low temperature, it has the potential to cool down water temperature in summer, depending on its share in the stream, and to reduce diurnal water temperature fluctuations (Constantz, 1998; O'Driscoll and DeWalle, 2004). Based on that, it can be concluded that conservation of high groundwater levels is of similar importance compared to conservation and restoration of WRV along streams. If groundwater levels keep on dropping, this may lead to a substantial increase in water temperature which in turn negatively affects macroinvertebrates. In addition, it increases the risk of complete drying with much larger detrimental effects on macroinvertebrates. Additionally, global warming does not only affect air temperature, but also groundwater temperature (Menberg et al., 2014). This may have devastating consequences for groundwater-fed streams and their inhabitants as it reduces the potential of groundwater to mitigate a strong increase in water temperature in groundwater-fed streams.

Flow velocity impacts water temperature by determining the distance water in a stream needs to flow through a higher shaded section in order to reach equilibrium temperature (Kail et al., 2021). The slower the flow velocity, the shorter the distance the water needs to flow through to reach equilibrium temperature. By flowing through an unshaded stream section, the water constantly gains temperature by solar radiation input (if no clouds are present). If it flows through a shaded stream section, water temperature does not increase but approaches equilibrium temperature, as no solar radiation reaches the water surface. Still, in our study, flow velocity was significantly positively correlated with water temperature, which is counterintuitive, and seems to result from non-causal negative correlation with groundwater influx. Study sections with low-flow velocity that were expected to have higher $T_{\max}$ than sections with high flow velocity had high groundwater influx, which decreased water temperature and probably masked the influence of flow velocity on $T_{\max}$. We cannot think of any other possible or plausible reason for this correlation.

Similarly, width/area ratio was also negatively related to $T_{\max}$, contrary to our expectation. Study sections with a high width/area ratio were expected to heat up faster, because a larger surface exposed to solar radiation receives more energy to heat the same volume of water (Poole and Berman, 2001). These counter intuitive results may have been due the selection criteria for the study sections: They cover a gradient of shading, with a substantial part of the sections being strongly shaded. At these shaded sites, solar radiation input was low, which prevents width/area ratio from taking effect. The sample size was too low to investigate the potential interaction between shading and width/area ratio, but a scatterplot restricted to the nine study sections with low WRV cover (less than 30%) showed some indication for the expected positive correlation between width/area ratio and $T_{\max}$.

To sum up, solar radiation input reduction via shading by WRV was the main and groundwater influx another important parameter governing water temperature in our study.

WRV and macroinvertebrates [Hypothesis 3]

We assumed that macroinvertebrates mainly benefit from reduced water temperature induced by WRV during extreme low-flow, while other function of WRV, subsumed by the direct link in the SEM, is less relevant.

This hypothesis was partly confirmed for the KLIWA index and RETI, while it was partly rejected for the GFI. For the KLIWA index and RETI, the indirect effect of solar radiation input reduction by WRV and the other effects subsumed in the direct link in the SEM were similar, but only the bootstrap confidence intervals of the indirect effect did not include zero, which we considered a relevant effect. This is reasonable for the KLIWA index, given that it is based on the summer temperature preferences of the macroinvertebrates. Furthermore, we assumed that factors like leaf litter and dead wood input lead to a strong positive effect of WRV cover on macroinvertebrates by providing food (Oester et al., 2023) and habitat (Valente-Neto et al., 2015) for shredders and xylophagous taxa. Additionally, we expected WRV to directly influence the RETI through other factors, such as shading limiting macrophyte growth and affecting biofilm development, which serve as the food basis for grazers (Vannote et al., 1980). All those effects apart from the indirect effect via solar radiation input reduction are subsumed in the direct link in the SEM and it is unexpected that those effects of WRV on the RETI are weaker than the effect of solar radiation input reduction, given that it reflects the feeding-type composition of the macroinvertebrate community (Schweder, 1992). The study sections were selected against the amount of WRV cover but not the naturalness of the WRV, thus possibly limiting other positive WRV effects.

For the GFI, the other effects of WRV subsumed as the direct link in the SEM were much larger than the indirect effect via solar radiation input reduction, but again, the bootstrap confidence intervals for the larger other effects (direct link) included zero, representing what we consider a non-relevant effect. Such large bootstrap confidence intervals result from extreme values in the data. Still, the much larger value for other effects than solar radiation input reduction implies that other functions of WRV have a stronger effect on the GFI than reduction in solar radiation input. Those include substrate input (leaf litter and dead wood) and the role of WRV as a migration corridor for species. The GFI represents how typical a macroinvertebrate community is for lowland sand-bed streams. In this stream type, other functions of WRV seem to be more important for macroinvertebrate community formation and continuance than the reduction in water temperature via shading. This could be due to the fact that in low-land streams, water temperature is usually higher than in other stream types, for example mountain streams. Therefore, under extreme low-flow conditions, we find species that are adapted to higher temperatures (as indicated by the KLIWA index) but are still typical for low-land streams (no relevant indirect effect via solar radiation input reduction of WRV cover on the GFI).

In summary, water temperature reduction and other effects of WRV cover shape different components of macroinvertebrate communities during extreme low-flow.

Conclusion

High water temperature has immediate detrimental effects on macroinvertebrates. However, WRV cover and groundwater influx can reduce water temperature during extreme low-flow events. WRV cover has a stronger potential in reducing water temperature (T_{max}) than groundwater influx (6.6 °C from 0 to 99% WRV cover versus 4.8 °C from 0 to 150 m^3/ha/year). Additionally, increasing the amount of WRV cover at the shores of streams is more practicable than increasing groundwater influx, making it an easily and quickly applicable measure which can strongly reduce water temperature, especially during drought conditions. Furthermore, WRV supports macroinvertebrates through other important functions, such as provision of food and habitat. In groundwater-fed streams, groundwater is another important factor decreasing stream water temperature and eventually avoiding a deterioration of biota under drought conditions. This highlights the importance of halting the drop of groundwater levels in order to limit the increase in water temperature resulting from climate change. Preventing a further drop of groundwater levels is also crucial for macroinvertebrate communities of perennial streams as groundwater influx may inhibit complete drying of streams during drought phases. A combination of high WRV cover and high groundwater influx holds the highest potential to mitigate a strong increase in water temperature and by that negative consequences for macroinvertebrates during extreme low-flow events.

Acknowledgements The planning office Koenzen provided the WRV cover and solar radiation input data, and the engineering company Delta H and the water association Lippeverband the groundwater influx data. The German Federal Ministry of Education and research funded the KliMaWerk project (Nachhaltige Bewirtschaftung des Landschaftswasserhaushaltes zur Erhöhung der Klimaresilienz: Management und Werkzeuge; grant number 02WEE1626B), within which this research was carried out. Furthermore, we wish to express our gratitude to the anonymous reviewers for their constructive feedback, which significantly contributed to enhancing the quality and clarity of this manuscript.

Author contributions All authors, except Philipp Blanke, contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Hannah-Marie Stappert, Jochem Kail, and Daniel Hering. The first draft of the manuscript was written by Hannah-Marie Stappert and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. Funding was provided by Bundesministerium für Bildung und Forschung DE, 02WEE1626B, Daniel Hering

Data availability Data will be available on request.

Declarations

Conflict of interests There are no financial or non-financial interests that are directly or indirectly related to the work submitted for publication.

References

Bonacina, L., F. Fasano, V. Mezzanotte & R. Fornaroli, 2023. Effects of water temperature on freshwater macroinvertebrates: a systematic review. Biological Reviews of the Cambridge Philosophical Society 98: 191–221. https://doi.org/10.1111/brv.12903.

Boulton, A. J., 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. Freshwater Biology 48: 1173–1185. https://doi.org/10.1046/j.1365-2427.2003.01084.x.

Bowler, D. E., R. Mant, H. Orr, D. M. Hannah & A. S. Pullin, 2012. What are the effects of wooded riparian zones on stream temperature? Environmental Evidence 1: 3. https://doi.org/10.1186/2047-2382-1-3.

Broadmeadow, S. & T. R. Nisbet, 2004. The effects of riparian forest management on the freshwater environment: a literature review of best management practice. Hydrology and Earth System Sciences 8: 286–305.

Constantz, J., 1998. Interaction between stream temperature, streamflow, and groundwater exchanges in alpine streams. Water Resources Research 34: 1609–1615. https://doi.org/10.1029/98WR00998.

Cook, B. I., J. S. Mankin & K. J. Anchukaitis, 2018. Climate Change and Drought: From Past to Future. Current Climate Change Reports 4: 164–179. https://doi.org/10.1007/s40641-018-0093-2.

Cox, T. J. & J. C. Rutherford, 2000. Thermal tolerances of two stream invertebrates exposed to diurnally varying temperature. New Zealand Journal of Marine and Freshwater Research 34: 203–208. https://doi.org/10.1080/00288330.2000.9516926.

Dewson, Z. S., A. B. W. James & R. G. Death, 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. Journal of the North American Benthological Society 26: 401–415. https://doi.org/10.1899/06-110.1.

Domisch, S., S. C. Jähnig & P. Haase, 2011. Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe. Freshwater Biology 56: 2009–2020. https://doi.org/10.1111/j.1365-2427.2011.02631.x.

Dunbar, M. J., M. L. Pedersen, D. Cadman, C. Extence, J. Waddingham, R. Chadd & S. E. Larsen, 2010. River discharge and local-scale physical habitat influence macroinvertebrate LIFE scores. Freshwater Biology 55: 226–242. https://doi.org/10.1111/j.1365-2427.2009.02306.x.

Feld, C. K., S. Birk, D. C. Bradley, D. Hering, J. Kail, A. Marzin, A. Melcher, D. Nemitz, M. L. Pedersen, F. Pletterbauer, D. Pont, P. F. M. Verdonschot & N. Friberg, 2011. From Natural to Degraded Rivers and Back Again. Advances in Ecological Research 44: 119–209.

Floury, M., P. Usseglio-Polatera, M. Ferreol, C. Delattre & Y. Souchon, 2013. Global climate change in large European rivers: long-term effects on macroinvertebrate communities and potential local confounding factors. Global Change Biology 19: 1085–1099. https://doi.org/10.1111/gcb.12124.

Halle, M., A. Müller & A. Sundermann, 2016. KLIWA Temperatur-MZB-Projekt: Ableitung von Temperaturpräferenzen des Makrozoobenthos für die Entwicklung eines Verfahrens zur Indikation biozönotischer Wirkungen des Klimawandels in Fließgewässern. Final report on behalf of the working group KLIWA. KLIWA-Berichte 20.

Hynes, H. B. N., 1970. The ecology of stream insects. Annual Review of Entomology 15: 25–42.

Kail, J., M. Palt, A. Lorenz & D. Hering, 2021. Woody buffer effects on water temperature: The role of spatial configuration and daily temperature fluctuations. Hydrological Processes 35, Article e14008. https://doi.org/10.1002/hyp.14008.

Kalny, G., G. Laaha, A. Melcher, H. Trimmel, P. Weihs & H. P. Rauch, 2017. The influence of riparian vegetation shading on water temperature during low flow conditions in a medium sized river. Knowledge and Management of Aquatic Ecosystems 418: 5. https://doi.org/10.1051/kmae/2016037.

Kinzie, R. A., C. Chong, J. Devrell, D. Lindstrom & R. H. Wolff, 2006. Effects of Water Removal on a Hawaiian Stream Ecosystem. Pacific Science 60: 1–47. https://doi.org/10.1353/psc.2005.0058.

König, Ch. M., M. Becker, K. Brömme, A. Diehl, T. König, B. Rosen, O. Rüber, S. Schröder, T. Seidel & C. Zimmermann, 2022. SPRING Benutzerhandbuch 6.1. 584 S. ISBN 978–3–00–073433–5, delta h Ingenieurgesellschaft mbH.

Ladle, M. & J. A. B. Bass, 1981. The ecology of a small chalk stream and its responses to drying during drought conditions. Archiv Für Hydrobiologie 90: 448–466.

Lefcheck, J. S., 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution 7: 573–579. https://doi.org/10.1111/2041-210X.12512.

Lessard, J. L. & D. B. Hayes, 2003. Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. River Research and Applications 19: 721–732. https://doi.org/10.1002/rra.713.

Li, F., Q. Cai, W. Jiang & X. Qu, 2012. Macroinvertebrate relationships with water temperature and water flow in subtropical monsoon streams of Central China: implications for climate change. Fundamental and Applied Limnology 180: 221–231. https://www.researchgate.net/profile/Qinghua-Cai/publication/272213267_Macroinvertebrate_relationships_with_water_temperature_and_water_flow_in_subtropical_monsoon_streams_of_Central_China_Implications_for_climate_change/links/550540da0cf2d60c0e6b76ff/Macroinvertebrate-relationships-with-water-temperature-and-water-flow-in-subtropical-monsoon-streams-of-Central-China-Implications-for-climate-change.pdf.

Lorenz, A., D. Hering, C. K. Feld & P. Rolauffs, 2004. A new method for assessing the impact of hydromorphological degradation on the macroinvertebrate fauna in five German stream types. Hydrobiologia 516: 107–127.

Meier, C., J. Böhmer, R. Biss, C. K. Feld, P. Haase, A. Lorenz, C. Rawer-Jost, P. Rolauffs, K. Schindehütte, F. Schöll, A. Sundermann, A. Zenker, & D. Hering, 2006. Weiterentwicklung und Anpassung des nationalen Bewertungssystems für Makrozoobenthos an neue internationale Vorgaben. Final report on behalf of the Federal Environment Agency. http://www.fliessgewaesserbewertung.de.

Meier, C., P. Haase, P. Rolauffs, K. Schindehütte, F. Schöll, A. Sundermann & D. Hering, 2006. Methodisches Handbuch Fließgewässerbewertung.

Menberg, K., P. Blum, B. L. Kurylyk & P. Bayer, 2014. Observed groundwater temperature response to recent climate change. Hydrology and Earth System Sciences 18: 4453–4466. https://doi.org/10.5194/hess-18-4453-2014.

Mosley, M. P., 1983. Variability of water temperatures in the braided Ashley and Rakaia rivers. New Zealand Journal of Marine and Freshwater Research 17: 331–342. https://doi.org/10.1080/00288330.1983.9516007.

O'Driscoll, M. A. & D. R. DeWalle, 2004. Stream-Air Temperature Relationships as Indicators of Groundwater Inputs. Watershed Update 2. https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=bfd36e05e0a2c97940b99fb448659a13175e9501.

Oester, R., P. C. Dos Reis Oliveira, M. S. Moretti, F. Altermatt & A. Bruder, 2023. Leaf-associated macroinvertebrate assemblage and leaf litter breakdown in headwater streams depend on local riparian vegetation. Hydrobiologia 850: 3359–3374. https://doi.org/10.1007/s10750-022-05049-7.

Palt, M., D. Hering & J. Kail, 2023. Context-specific positive effects of woody riparian vegetation on aquatic invertebrates in rural and urban landscapes. Journal of Applied Ecology 60: 1010–1021. https://doi.org/10.1111/1365-2664.14386.

Parkyn, S. M., R. J. Davies-Colley, N. J. Halliday, K. J. Costley & G. F. Croker, 2003. Planted Riparian Buffer Zones in New Zealand: Do They Live Up to Expectations? Restoration Ecology 11: 436–447. https://doi.org/10.1046/j.1526-100X.2003.rec0260.x.

Pedreros, P., M. Guevara-Mora, A. Stehr, A. Araneda & R. Urrutia, 2020. Response of macroinvertebrate communities to thermal regime in small Mediterranean streams (southern South America): Implications of global warming. Limnologica 81. https://www.sciencedirect.com/science/article/pii/S0075951119301872.

Poole, G. C. & C. H. Berman, 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management 27: 787–802. https://doi.org/10.1007/s002670010188.

Pottgiesser, T. & M. Sommerhäuser, 2014. Fließgewässertypologie Deutschlands: 1–61. https://onlinelibrary.wiley.com/doi/abs/https://doi.org/10.1002/9783527678488.hbal2004005.

Rivers-Moore, N. A., H. F. Dallas & V. Ross-Gillespie, 2012. Life history does matter in assessing potential ecological impacts of thermal changes on aquatic macroinvertebrates. River Research and Applications 29: 1100–1109. https://onlinelibrary.wiley.com/doi/full/https://doi.org/10.1002/rra.2600.

Rutherford, J. C., S. Blackett, C. Blackett, L. Saito & R. J. Davies-Colley, 1997. Predicting the effects of shade on water temperature in small streams. New Zealand Journal of Marine and Freshwater Research 31: 707–721. https://doi.org/10.1080/00288330.1997.9516801.

Rutherford, J. C., N. A. Marsh, P. M. Davies & S. E. Bunn, 2004. Effects of patchy shade on stream water temperature: how quickly do small streams heat and cool? Marine and Freshwater Research 55: 737–748. https://doi.org/10.1071/MF04120.

Rutherford, J. C., 1999. Stream shade. Towards a restoration strategy. Wellington, N.Z.: NIWA; Department of Conservation.

Sarremejane, R., J. England, C. E. M. Sefton, S. Parry, M. Eastman & R. Stubbington, 2020. Local and regional drivers influence how aquatic community diversity, resistance and resilience vary in response to drying. Oikos 129: 1877–1890. https://doi.org/10.1111/oik.07645.

Schweder, H., 1992. Neue Indizes für die Bewertung des ökologischen Zustandes von Fließgewässern, abgeleitet aus der Makroinvertebraten-Ernährungstypologie. Limnologie Aktuell 3: 353–377.

Sponseller, R. A., E. F. Benfield & H. M. Valett, 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshwater Biology 46: 1409–1424. https://onlinelibrary.wiley.com/doi/pdf/https://doi.org/10.1046/j.1365-2427.2001.00758.x.

Steward, B. A., P. G. Close, P. A. Cook & P. M. Davies, 2013. Upper thermal tolerances of key taxonomic groups of stream invertebrates. Hydrobiologia 718: 131–140. https://doi.org/10.1007/s10750-013-1611-9.

Stubbington, R., M. T. Bogan, N. Bonada, A. J. Boulton, T. Datry, C. Leigh & R. V. Vorste, 2017. Intermittent Rivers and Ephemeral Streams The Biota of Intermittent Rivers and Ephemeral Streams: Aquatic Invertebrates Elsevier 217–243.

Sweeney, B. W. & J. D. Newbold, 2014. Streamside Forest Buffer Width Needed to Protect Stream Water Quality, Habitat, and Organisms: A Literature Review. JAWRA Journal of the American Water Resources Association 50: 560–584. https://doi.org/10.1111/jawr.12203.

Valente-Neto, F., R. Koroiva, A. A. Fonseca-Gessner & F. O. Roque, 2015. The effect of riparian deforestation on macroinvertebrates associated with submerged woody debris. Aquatic Ecology 49: 115–125. https://doi.org/10.1007/s10452-015-9510-y.

van Vliet, M. T. H., W. H. P. Franssen, J. R. Yearsley, F. Ludwig, I. Haddeland, D. P. Lettenmaier & P. Kabat, 2013. Global river discharge and water temperature under climate change. Global Environmental Change 23: 450–464. https://doi.org/10.1016/j.gloenvcha.2012.11.002.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Verberk, W. C. E. P., D. T. Bilton, P. Calosi & J. I. Spicer, 2011. Oxygen supply in aquatic ectotherms: partial pressure and solubility together explain biodiversity and size patterns. Ecology 92: 1565–1572. https://doi.org/10.1890/10-2369.1.

Verdonschot, R. C. M., A. M. Van Oosten-Siedlecka, C. J. F. Ter Braak & P. F. M. Verdonschot, 2015. Macroinvertebrate survival during cessation of flow and streambed drying in a lowland stream. Freshwater Biology 60: 282–296. https://doi.org/10.1111/fwb.12479.

Wawrzyniak, V., P. Allemand, S. Bailly, J. Lejot & H. Piégay, 2017. Coupling LiDAR and thermal imagery to model the effects of riparian vegetation shade and groundwater inputs on summer river temperature. Science of the Total

Environment 592: 616–626. https://doi.org/10.1016/j.scitotenv.2017.03.019.

Webb, B. W. & Y. Zhang, 2004. Intra-annual variability in the non-advective heat energy budget of Devon streams and rivers. Hydrological Processes 18: 2117–2146. https://doi.org/10.1002/hyp.1463.

White, J. C., K. Khamis, S. Dugdale, F. L. Jackson, I. A. Malcolm, S. Krause & D. M. Hannah, 2023. Drought impacts on river water temperature: A process-based understanding from temperate climates. Hydrological Processes 37, Article e14958. https://doi.org/10.1002/hyp.14958.

Wood, P. J. & P. D. Armitage, 2004. The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream. Archiv Für Hydrobiologie 161: 1–20. https://doi.org/10.1127/0003-9136/2004/0161-0001.

Wood, P. J. & G. E. Petts, 1994. Low flows and recovery of macroinvertebrates in a small regulated chalk stream. Regulated Rivers: Research and Management 9: 303–316.

Wright, J. F. & K. L. Symes, 1999. A nine-year study of the macroinvertebrate fauna of a chalk stream. Hydrological Processes 13: 371–385.