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The effect of water temperature changes on biological water quality assessment

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ABSTRACT

Increasing temperatures caused by anthropogenic climate change are leading to changes in the composition of local communities across biomes. This has implications for ecological assessment methods that rely on macroinvertebrates as bioindicators of water quality. To investigate the influence of changing water temperature on these assessment methods, we analysed macroinvertebrate data from Swiss national monitoring programs. We used a species distribution model to simulate temperature change effects on macroinvertebrate communities and estimated the resulting changes on three biological indices commonly used in Switzerland, namely the species richness of Ephemeroptera, Plecoptera and Trichoptera (EPT), the Swiss biological (IBCH) index along with its components, as well as the species at risk pesticides ($\text{SPEAR}_{\text{pesticides}}$) index. While results vary by temperature scenario and index, our model results for the most realistic water temperature increase scenario of + 2 °C across most sites in Switzerland suggest no, or only a minor, influence of temperature (not accounting for other hydrological changes). Our model projection predicted only a small increase in the probability of occurrence for 70 % of the studied families. The sensitivity to temperature as captured in our model is generally not very high and varies among the biological indices: on average across all sites, a + 2 °C increase in temperature resulted in a 7 % increase in EPT species richness, a 4 % increase in the IBCH index, and a less than 1 % increase in the $\text{SPEAR}_{\text{pesticides}}$ index. Our study suggests the robustness of these biological indices to moderate warming and points towards the usefulness of these biological indices for the next few decades as tools for water quality assessment. Despite some limitations of statistical species distribution models (e.g., not accounting for dispersal limitation or biotic interactions, predictive performance varying by taxon), the study provides valuable insights into the complex relationships between environmental factors and macroinvertebrate communities, and the potential impacts of future temperature change. These findings can inform conservation and management efforts for these important ecological systems.

1. Introduction

Biodiversity monitoring programs are important to inform ecosystem management, which can have significant impacts on biodiversity (Bowler et al., 2017; Vaughan and Gotelli, 2019). Freshwater environments harbour a disproportionate amount of the global biodiversity (Dudgeon et al., 2006; Reid et al., 2019) and the data accumulated through monitoring programs is valuable for assessing changes in biodiversity and the habitat quality of freshwater ecosystems (Antão et al., 2020; Bowler et al., 2017; Rios and Bailey, 2006). Biological indices are effective tools for monitoring the ecological status of ecosystems. Compared to methods that directly assess physical and chemical aspects of water as a reflection of habitat quality, biological indices integrate over time and indicate indirect or unknown effects through the presence, absence or relative abundance of taxa, thus providing complementary information. Although these biological indices have been successful in providing insights into biodiversity and habitat status in the past (Birk et al., 2012; Knillmann et al., 2018), one intriguing aspect

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that still requires exploration is how anthropogenic climate change may affect our understanding of their effectiveness in indicating habitat quality in general as well as the impact of specific anthropogenic stressors.

Over time, researchers have accumulated a wealth of knowledge on the relationships between species and their habitats, as well as how they respond to external stressors (Jaureguiberry et al., 2022; Jetz et al., 2019; Pimm, 1985; Tilman, 1999), which has led to the development of various biological indices for monitoring ecological status and biodiversity (Birk et al., 2012). In general, there are three main categories of biological indices commonly used in ecological studies. Firstly, there are indices that describe fundamental aspects of the ecological community at a given location, such as species richness (Dornelas et al., 2014). Secondly, there are indices that assess the deviation of the ecological community from reference conditions (Stoddard et al., 2006), such as the Rivpacks approach in the UK (Wright, 2000) or the Swiss biological index IBCH (Stucki, 2010). Lastly, there are indices designed to identify specific stressors, such as the saprobic system (Rolauffs et al., 2004), or the Biotic Index in the USA (Hilsenhoff, 1998, 1988), which both focus on organic pollution, and the $SPEAR_{pesticides}$ (Liess and Von Der Ohe, 2005), which targets pesticide pollution levels in water bodies.

The IBCH and the $SPEAR_{pesticides}$ indices, along with taxonomic richness, are widely used by the cantonal and federal authorities that are in charge of river management in Switzerland. These indices are commonly used indicators of general habitat quality (IBCH) and pesticides pollution ($SPEAR_{pesticides}$). Both indices simplify the complex nature of responses of biodiversity to external stressors into a single value for easy communication. These biological indices are based on the presence or absence of pollution-sensitive taxa, without reference to the average water temperature of their habitat. Limited knowledge exists regarding how robust or sensitive they are to temperature changes (Chiu et al., 2017). Therefore, it is crucial to assess the impact of warming on the ability of these indices to accurately reflect the quality of waterbodies, to ensure their appropriate implementation in the future under a changing climate. Macroinvertebrate community composition, upon which the IBCH and the $SPEAR_{pesticides}$ indices are based, is dependent on external temperatures (Angilletta, 2009; Angilletta and Dunham, 2003). Changes in environmental temperature can impact macroinvertebrate species distributions (Sunday et al., 2012). For example, a moderate increase in temperature may be beneficial for warm adapted taxa and they could be expected to expand their ranges to higher altitudes (Gebert et al., 2022) or latitudes (Sunday et al., 2012). Rising temperatures can also adversely affect populations of many aquatic insects, especially EPT taxa (Baranov et al., 2020; Piggott et al., 2015). Moreover, the negative impact of daily maximum temperature on the dispersal traits of aquatic insects may counterbalance the positive effects of temperature on species richness (Jourdan et al., 2019). At the same time, warming may reduce the ranges of cold adapted taxa, if cold temperature refugia are lost. Temperature can have effects on macroinvertebrate community composition that are independent of the effects of organic or pesticide pollution, and may therefore falsely impact our interpretation of biotic indices with respect to water quality if not acknowledged and corrected. Therefore, assessing the impacts of temperature change on biotic indices, such as the species richness of Ephemeroptera, Plecoptera, Trichoptera (EPT), and the IBCH and the SPEARpesticides indices, is essential to ensure correct interpretations of water course assessment.

With the growing concern about environmental change and physicochemical changes in water bodies impacting biological communities, it is important to understand the ensuing effects on different biological indices (Liess and Von Der Ohe, 2005; Schuwirth et al., 2015; Zhang et al., 2018; Markert et al., 2023). This can be achieved by utilizing existing knowledge of species or communities' relationships with environmental factors to simulate future communities under change (Thuiller et al., 2005, Elith and Leathwick, 2009). Applying this approach to temperature, we can then re-calculate various biological indices to obtain a quantitative evaluation of their response to water temperature increases due to global warming. While temperature is a dominant factor in shaping species distributions (Caradima et al., 2020; Hawkins et al., 2003), other drivers such as land-use, habitat structure, water flow velocity, sewage water treatment plants and other landscape-related factors can also play important roles (Liess and Von Der Ohe, 2005; Knillmann et al., 2018; Burdon et al., 2019; Caradima et al., 2020; Wiberg-Larsen et al., 2021; Haase et al., 2023; Markert et al., 2023). When simulating future communities to evaluate biodiversity indices, it is therefore crucial to consider these additional factors in order to obtain more realistic projections of the impact of temperature changes on biodiversity.

In recent years, species distribution modelling approaches have become popular tools for predicting future changes in species distribution and community composition (Hof et al., 2018; Voskamp et al., 2020). By incorporating various climatic, environmental, and biological variables, species distribution modelling offers a valuable opportunity to evaluate the impact of temperature change and other drivers on biological indices within a multivariate framework (Elith and Franklin, 2013; Caradima et al., 2019). While simulated future communities can provide quantitative information on the impact of temperature on species richness, the IBCH index and the $SPEAR_{pesticides}$ index, it is important to acknowledge that species distribution modelling is an approximation of future communities and its output relies heavily on the input data and model assumptions (Elith and Leathwick, 2009; Lee-Yaw et al., 2022). Nevertheless, the multivariate framework of species distribution modelling allows us to understand the potential changes in community structure and their effects on different biological indices, while accounting for abiotic factors that affect biodiversity. Such insight is increasingly important in helping us prepare for and adapt to future global change.

In this study, we specifically selected three biological indices that ranged from non-stressor-specific to stressor-specific biological indices and are widely applied by local authorities: EPT species richness, the IBCH index and its components, diversity class and indicator group, as well as the $SPEAR_{pesticides}$ index. We aim to examine the impact of water temperature change on these indices using a species distribution model calibrated with data collected between 2010 and 2019. In addition to temperature, we consider water flow velocity, insecticide application rate (IAR), habitat quality and land-use variables as predictors. We aim to simulate the response of the communities and resulting biological indices to a range of temperature change scenarios. One class of scenarios assumes a uniform change from -1 to $+\ 8\ ^{\circ}C$. In addition, we analyse the responses to more realistic, spatially resolved scenarios for future water temperature increases in 12 catchments (Michel et al., 2021). Since the indices are based upon multiple taxa, and previous studies have shown that some taxa respond positively and other negatively to increasing temperature (Caradima et al., 2020; Vermeiren et al., 2020), we hypothesize that the indices are more robust to temperature changes than the probability of occurrence of individual species, since positive and negative responses may partly cancel out each other.

2. Materials and methods

2.1. Macroinvertebrate monitoring data

We used data of stream macroinvertebrates collected within the framework of the Swiss Biodiversity Monitoring Program (BDM), the National Surface Water Quality Monitoring Program (NAWA) and cantonal monitoring programs from the year 2010 up to 2019. In the BDM and NAWA data, the Ephemeroptera, Plecoptera, and Trichoptera (EPT) are resolved to species level, while the other taxa are mostly available at the family level. In total, we selected 1,802 sites across Switzerland. These sites were sampled with a standardized multi-habitat sampling method described in Stucki (2010). The sampling protocol includes eight kick-net samples covering a 25 * 25 cm area each within a reach that is ten times longer than the river width. The eight samples are placed on substrate types that are prioritized based on their suitability for macroinvertebrates. The eight sub-samples are then pooled for the taxonomic identification in the lab. The different monitoring programs had different designs regarding site selection and temporal resolution. In this regard, the BDM monitoring data is exceptional, because the site selection was based on a regular grid across Switzerland with a spatial resolution of 1 km. In each year, 20 % of the sites were sampled, leading to a five-year interval of the samplings at each site and accordingly to two samplings within 10 years.

2.2. Temperature model and scenarios

For different analyses, we used either air temperature or modelled water temperature data. For the analysis of macroinvertebrate occurrences from 2010 up to 2019, we related maximum morning summer air temperatures to the presence/absence of each species. For this analysis, we used air temperature (Karger et al., 2017) as water temperature was not available for all the sites and years. We used modelled water temperature for the species distribution modelling. Since water temperature measurements were not available for the biomonitoring sites, we used a temperature model that was calibrated to 59 sites in Switzerland (Vermeiren et al., 2020). We modelled water temperature as a function of log-transformed catchment area and catchment elevation. We found high congruence between observed and modelled temperature data (Fig. S1).

We applied two different approaches for forward-simulating communities: in a first step, we assumed uniform temperature changes at all sites from −1 to + 8 °C with increments of 0.5 °C. As a baseline for these changes, we used the temperature for year 2019. This is equivalent to a sensitivity analysis of the whole modelling procedure to temperature. In a second step, we used temperature projections based on Michel et al., (2021) that were available for 12 catchments within Switzerland. We used three Representative Concentration Pathways (RCP) scenarios of greenhouse gas emission, i.e., RCP2.6, RCP4.5 and RCP8.5 and three future time periods (2030–40, 2055–65 and 2080–90). The RCP2.6 is a very strict scenario with net zero greenhouse gas emissions by 2100, whereas RCP4.5 is an intermediate scenario with reduction in greenhouse gas emissions to half by 2100. Lastly, RCP8.5 is the worst-case scenario with a business-as-usual continued greenhouse gas emissions throughout the 21st century. Projected water temperature increases for the RCP2.6 scenario ranged from 0.7 to 1.1 °C, for RCP4.5 from 1.4 to 2 °C and for RCP8.5 from 2.9 to 4.2 °C across 12 different catchments within Switzerland for the 2080–90 period (see Table S1 for more details).

2.3. Statistical analyses

2.3.1. Temporal data

First, we analysed existing monitoring data from the past decade (2010–2019) to assess whether changes in temperature during this time have already resulted in observable changes in biological indices. We restricted the analysis to the BDM data due to its systematic spatial and temporal sampling design. We examined the relationship between changes in biological indices and the corresponding temperature difference between two sampling years separated by a five-year interval. Since the sites were grouped into five blocks to be sampled in five consecutive years, we added the identity of the block as a random factor to address the potential influence of baseline year variations. Since water temperature measurements corresponding to the sites and sampling time points of the biological samplings were not available, we tested the impact of the use of a number of different estimates of temperature change. For instance, we calculated the absolute difference in maximum morning summer air temperature between the first and the second sampling year. Additionally, we computed the absolute difference in modelled maximum morning summer water temperature between these two years. Lastly, we assessed the rate of change in annual maximum morning summer air temperature at each site from 2010 to 2019 (by taking the absolute difference and dividing the difference with the number of years).

2.3.2. Generalized mixed-effects model for biological indices

In order to understand how the biological indices respond to the abiotic factors included in the SDM on a spatial scale, we applied a mixed-effects model, with the biological index as dependent variable and the same explanatory variables that were used in the SDM, i.e. mean annual flow velocity, fraction of agricultural land use in the riparian zone, livestock unit density, insecticide application rate (sum of crop type fractions in the catchment weighted by the number of crop type specific insecticide treatments per year), fraction of urban land use in the catchment, fraction of forest in the catchment and intersecting the river, and width variability of the stream channel. We added the year of sampling as a random factor. For temperature and flow velocity, we added quadratic terms in addition to linear terms in the model to account for known unimodal relationships. Prior to running the models, we z-score standardized the explanatory variables by subtracting the mean and dividing by the standard deviation, to facilitate the comparability of the effects of the different explanatory variables. This direct model of the indices served also for comparing the predictive performance with the SDM approach explained in the next section.

2.3.3. Species distribution modelling approach

In addition to the direct indicator model mentioned in the previous section, we used a species distribution model to predict changes of species occurrence from temperature and other explanatory variables, the predictions of which were then used to calculate the biological indices. This approach allows us to improve our understanding about how temperature may affect the biological indices.

We predicted the probability of occurrence of each taxon using a hierarchical generalized linear model (hGLM) based on the same nine environmental factors as explanatory variables that were used above (see (Caradima et al., 2019) and (Chollet et al., 2023) for a detailed description). The hGLM is a generalized linear model with a logistic link function that is fitted jointly to multiple taxa and where the regression coefficients of each taxon are constrained by an overarching community distribution. This approach prevents overfitting for taxa with unbalanced data (i.e., low or high prevalence). We selected the nine environmental factors as explanatory variables based on expert knowledge and previous studies applied to a similar macroinvertebrate dataset (see Table S2 in the Supporting Information for more details on their definition, (Caradima et al., 2020). We used the model parameters from calibration to the whole dataset (for a performance assessment of the model based on cross-validation see Chollet et al., 2023) and then applied the temperature scenarios described above, while the other factors were kept constant, to predict the change in probability of occurrence of all taxa. To assess the change in occurrence probabilities of each taxon, we took the difference in probability of occurrence between the baseline temperature and the + 2 °C scenario. We chose a water temperature increase of + 2 °C because it aligns with the majority of realistic RCPs and future scenarios, indicating that temperatures are projected to rise by approximately + 2 °C at most sites across Switzerland ((Michel et al., 2021) Table S1).

To assess the quality of fit of both approaches (the linear mixed-effects model for the indices and the SDM approach), we compared the observed and modelled values of the biological indices.

2.3.4. Community sampling and index calculation

To derive presence/absence samples from the predicted probability of occurrence by the SDM that are needed to calculate the biological indices, we draw 100 random samples from a Bernoulli distribution, where the probability p equals the predicted probability of occurrence.

We then calculated the different indices for each sample as described below and averaged the index value over the 100 realizations.

Since the $SPEAR_{pesticides}$ index depends on abundance and not only presence/absence data, we estimated the abundance for each species determined as present by the above procedure, by random sampling from taxon-specific empirical abundance distributions that were derived from the whole biomonitoring data set. Note that implicitly assumes that the typical abundances for sites where a taxon is present will remain the same as they have been in the observed data, i.e., even under future scenarios of temperature change. We then calculated the index for each sample and averaged their values over the 100 realizations.

2.3.5. EPT species richness

The EPT species richness was calculated as the sum over all presence values for the EPT species within each sample.

2.3.6. IBCH index

The IBCH index (BAFU, 2019) is an adaptation of the French IBGN index (Index Biologique Global Normalisé, AFNOR T 90–350). The index relies on presence/absence information of 142 taxa found within Switzerland, mostly on the family level. It consists of two parts. The first is the diversity class (ranging between 1 and 14) which is based on the number of taxa present and the hydrological river type and is converted to an assessment value between 0 and 1. The second part is the indicator group that is based on the sensitivity of 38 taxa divided into 9 groups (ranging between 1 and 9) the value of which is increasing with their general sensitivity to pollution (which is not further specified). The most sensitive taxon present determines the indicator group value, which is also converted to an assessment value between 0 and 1. The IBCH is then calculated from the weighted mean of the assessment of the diversity class and the indicator group:

$$\text{IBCH} = 0.62 * \text{diversity class} + 0.38 * \text{indicator group},$$

with values ranging from 0 and 1 and higher values indicating a better ecological status.

2.3.7. $SPEAR_{pesticides}$ index

The $SPEAR_{pesticides}$ index is based on the “species at risk concept” (Liess and Von Der Ohe, 2005). It uses a binary classification of taxa based on whether or not they are at risk due to pesticide use. The classification is based on a combination of four traits, i) sensitivity to organic pollution, ii) generation time, iii) ability to disperse and re-establish from non-polluted refuge areas and iv) presence of an aquatic life-stage during the pesticide application season. The index is then calculated as follows:

$$\text{SPEARpesticides} = \frac{\sum_{i=1}^{n} \log(4^* x_i + 1) y_i}{\sum_{i=1}^{n} \log(4^* x_i + 1)}$$

where x_i indicates the abundance of taxon i and y_i the classification into the group of sensitive ($y = 1$) or insensitive ($y = 0$) taxa. We used the most recent trait classifications (from https://www.systemecology.de/indicate/, accessed 16.12.2022).

3. Results

3.1. Temporal analysis

We first analysed existing biomonitoring data from the last decade (2010 to 2019), where the same sites were sampled twice with a time interval of 5 years. The aim was to analyse whether there are associations between changes in the index values and changes in maximum morning summer air temperature (Fig. S2) between those years. Although we found that EPT species richness, IBCH index and diversity class have increased significantly over the last decade (Fig. S3), there was no association between the change in air temperature and the change in EPT species richness, $SPEAR_{pesticides}$ index, IBCH index or its components, diversity class and indicator group over this short time period (Fig. S2 a-e). The effect on EPT species richness, $SPEAR_{pesticides}$ and indicator group remained stable even when utilizing modelled water temperatures (Fig. S4), and also remained non-significant though positively related when assessing the change in temperature over a 10-year period from 2010 to 2019 at each site (and thereby smoothing over the variability among years), with the exception of the $SPEAR_{pesticides}$, which showed a significant increase with the slope of temperature change over these 10 years (Fig. S5).

3.2. Spatial analysis

Temperature was a significant predictor for all five biological indices (i.e. EPT species richness, IBCH index, $SPEAR_{pesticides}$, indicator group and diversity class) and explained part of their spatial variation (Figs. 1, S6). We found a unimodal relationship between all five indices and temperature in the multivariate mixed-effect regression model (Fig. 1a). However, the effect size of temperature varies by indicator, with larger effects on $SPEAR_{pesticides}$ and EPT species richness, and a relatively small effect size on the IBCH and its components. All the tested predictors in addition to temperature showed variable influence on the spatial variation in the five indices both in terms of direction and magnitude (Figs. 1, S6). We also noted a higher temperature variance in the spatial data compared to the temporal data (Fig. S7). Flow velocity has a unimodal relationship with $SPEAR_{pesticides}$, EPT species richness, and with indicator group but no relationship with IBCH index and diversity class (Fig. 1b). Insecticide application rate, urban area and riparian agricultural intensity had a negative relationship with all of the indices, especially with $SPEAR_{pesticides}$ and EPT species richness (Fig. 1c, 1d, 1h). The only index not negatively impacted by insecticide application rate (IAR) in the model was the diversity class. Livestock density had a positive influence on EPT species richness, IBCH index and indicator group but no significant effect on $SPEAR_{pesticides}$ and diversity class (Figs. 1g, S6).

3.3. Species distribution model output

The species (Fig 2) distribution model predicted different responses of taxa to temperature changes. For a + 2 °C change scenario, on average over all sites, 70 % of the families were predicted to increase in their probability of occurrence, while 30 % were predicted to decrease (Figs. 2, S8). The largest change in occurrence probabilities was predicted for Erpobdellidae and Hydroptilidae, with a + 0.10 and + 0.11 change in average occurrence probabilities, respectively.

3.4. Scenario analysis

Since more taxa show an increased probability of occurrence than a decrease, it can be expected that the local richness increases in a + 2 °C scenario, which would have positive effects on EPT species richness, Diversity class and IBCH index. This is confirmed by the analysis of the temperature scenarios on modelled indicators based on the SDM approach (Fig. 3), while the indicator group and $SPEAR_{pesticides}$ exhibit only a minor response to temperature changes. On average across all sites, a + 2 °C increase in temperature resulted in 7 % increase in EPT species richness, 4 % increase in IBCH, 6 % increase in diversity class and less than 1 % increase in indicator group and $SPEAR_{pesticides}$ index (Fig. 3).

3.5. Model performance

The analysis of model performance showed significant positive relationships between modelled and observed EPT species richness, IBCH, diversity class, indicator group and $SPEAR_{pesticides}$ index (Figs. S9 and

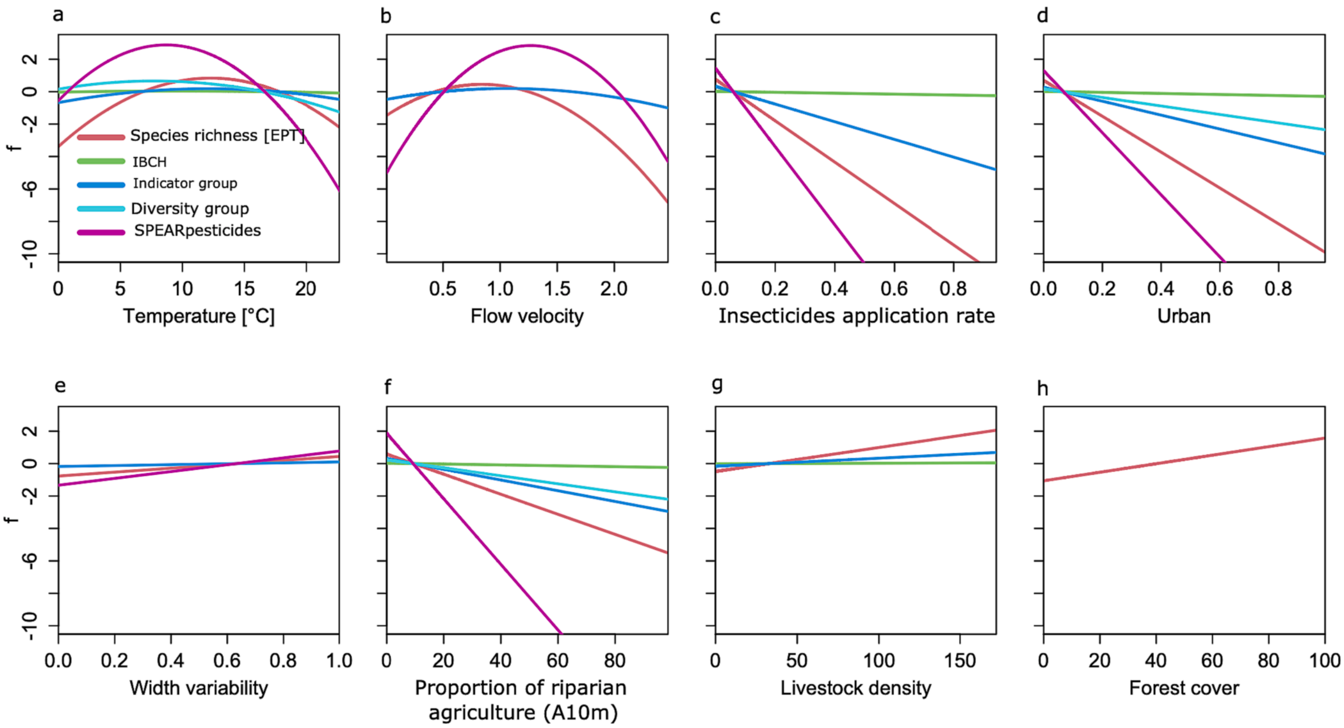

Fig. 1. Response curves of the three indicators and the components of the IBCH index with respect to the 8 predictor variables in the general linear mixed-effects model. The model was calibrated with monitoring data from the year 2010 to 2019. Response curves for temperature, flow velocity generates with a quadratic term. For other predictors, i.e., insecticide application rate, % forest cover in the catchment, livestock density, urban area, stream width variability, the response curves show a linear relationship. Plot for forest cover in the buffer zone is not shown (but see Fig. S6). Only response curves for significant predictors are shown.

S10). However, both approaches (the direct model for indicators based on linear mixed-effects model as well as the SDM approach) tended to over-predict indices at lower values and under-predict at higher values.

The spatial distribution of warming-induced changes in species richness, IBCH, diversity class and indicator group predicted by the SDM model generally showed larger increases at warmer sites (Figs. S11-12). For the $\text{SPEAR}_{\text{pesticides}}$ index, increased values were predicted for cold and warm sites, while decreased values were predicted for sites that had intermediate baseline temperatures (Fig. S12).

Further analyses used the more realistic climate scenarios for water temperature in 12 catchments in Switzerland. The mean water temperature increases predicted across the 12 Swiss catchments using more realistic and mechanistic models of thermal variation in response to climate change range from + 0.7 °C to 4.2 °C, i.e. well with the range of our sensitivity analysis approach above, (Michel et al., 2021) (Fig. 4). Using these scenarios for the SDM in those 12 catchments predicts minimal change in the EPT species richness, IBCH index, indicator group, diversity class and $\text{SPEAR}_{\text{pesticides}}$ index within time horizons of 2030–2040 and 2055–2065 across all three RCPs scenarios (Figs S13, S14). We only started to observe significant predicted increases in IBCH, $\text{SPEAR}_{\text{pesticides}}$ and in diversity for the period of 2080–2090 (but still no significant change in the indicator group) (Fig. 4).

4. Discussion

The primary objective of our study was to assess the impact of water temperature changes on five indices used in biological water assessment, including EPT species richness, IBCH index, diversity class, indicator group, and $\text{SPEAR}_{\text{pesticides}}$ index, both for existing monitoring data and for future simulations under different climate change scenarios. We found a net increase in these indices over the last decade of observed community data, but no dependency between the temporal changes in index values and the temporal changes in temperature. However, our analyses revealed that temperature can explain part of the spatial differences of all the biological indices, especially EPT species richness and $\text{SPEAR}_{\text{pesticides}}$, which show a unimodal response to temperature.

The impact of temperatures on macroinvertebrates has been documented in Switzerland and other regions of the world, consistently showing a positive effect on species richness within the temperature range of 0° to 25 °C (Piggott et al., 2015; Baranov et al., 2020; Niedrist and Fureder, 2020; Timoner et al., 2020, 2021). Our findings of spatial differences of biological indices are consistent with these previous reports. In this context, we would like to emphasize the distinct responses observed in the abundances and species richness of aquatic insects to temperature variations. While the abundances of aquatic insects exhibit a negative correlation with increasing temperatures, species richness demonstrates a positive trend (Piggott et al., 2015; Baranov et al., 2020). Furthermore, the responses of EPT taxa to temperature are region-specific, suggesting the influence of additional factors such as dissolved oxygen concentration in water or land-use-related factors, which may interact with temperature (Jourdan et al., 2018; Baranov et al., 2020; Verberk et al., 2023). Overall, the existence of a unimodal relationship between temperature and biological indices suggests that as temperatures surpass an optimum, negative impacts on these indices may become more pronounced, although this may not occur within the next few decades at most sites.

Intensive land-uses that can be associated with negative effects on water quality (urban land use in the catchment and agricultural land use close to the river – including insecticide application) had negative effects on the indices as expected, especially on the $\text{SPEAR}_{\text{pesticides}}$ index, the EPT species richness and also the IBCH index and its components, confirming the general usefulness of the indices to indicate anthropogenic impacts on water and watershed quality (Fahrig, 2017; Knillmann et al., 2018; Liess and Von Der Ohe, 2005; Zhang et al., 2018). In contrast, the unimodal response of $\text{SPEAR}_{\text{pesticides}}$ index and EPT species richness to flow velocity indicates that there may be hydrological effects on these indices that should be taken into account. For instance, in various montane regions, multiple water bodies are experiencing drying

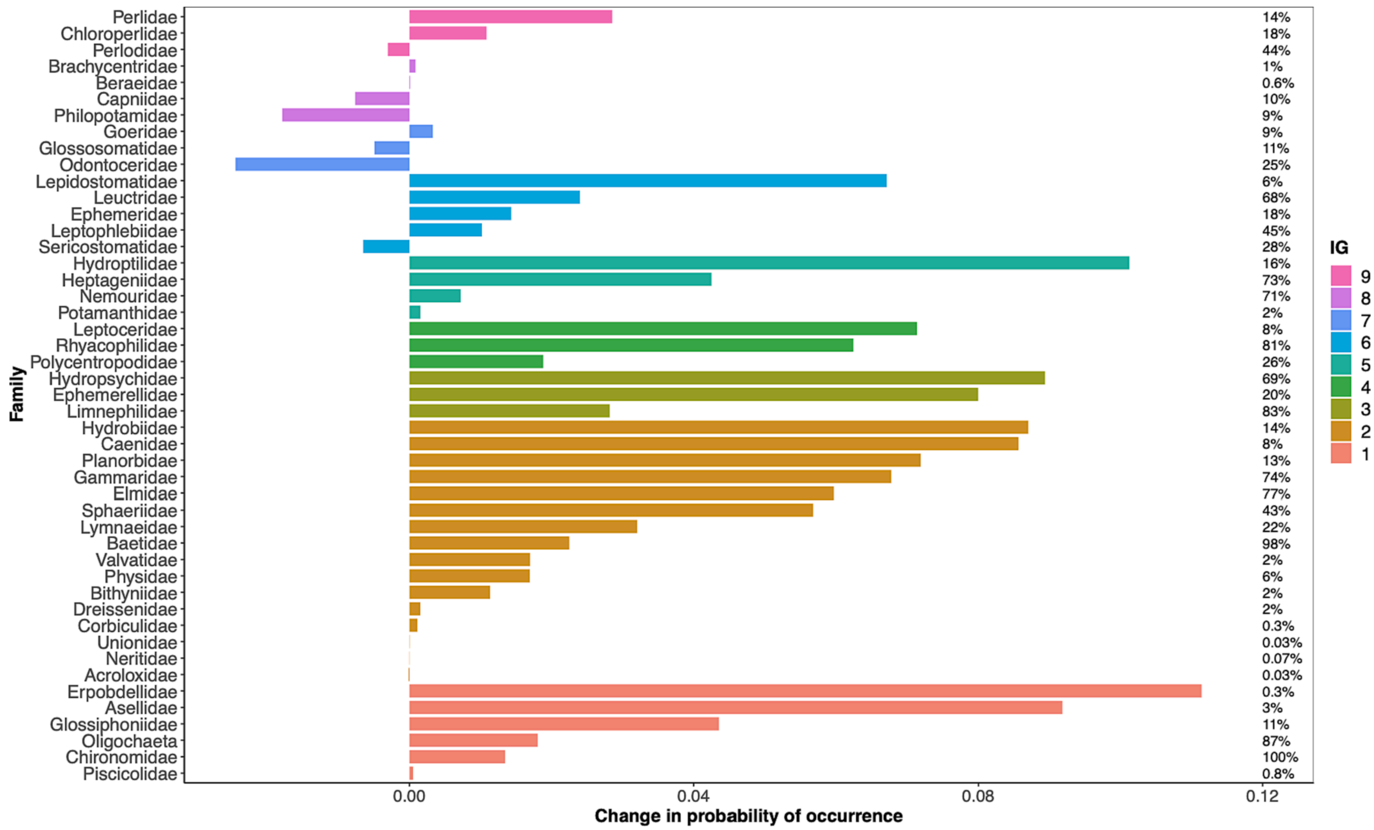

Fig. 2. The change in probability of occurrence (x-axis) for taxa that belong to the nine IBCH indicator groups (see legend for the color-coding) in response to a temperature increase of + 2 °C. On the y-axis, the taxa are sorted by increasing indicator group, corresponding to increasing sensitivity. Positive values on the x-axis indicate an overall increase in the occurrence probability and negative values an overall decrease in the occurrence probability on average over all sites. The labels next to the bars indicate the prevalence of each taxon in the monitoring data.

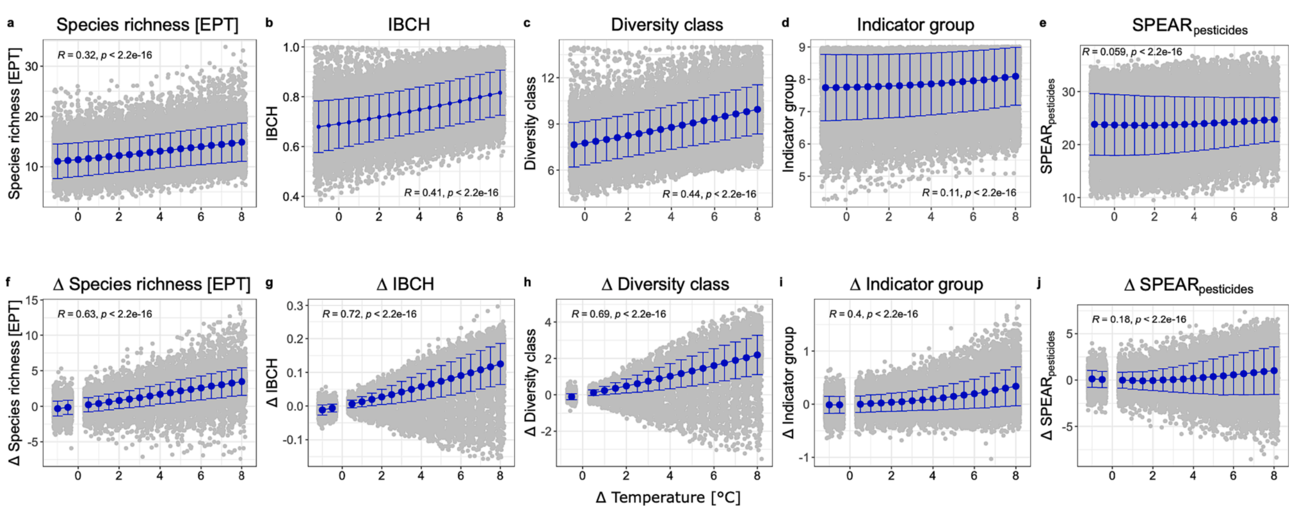

Fig. 3. Relationships of index values (first row) and changes in index values (second row) on the y-axis versus temperature change scenarios from −1 to + 8 °C (x-axis) for EPT species richness (a, b), IBCH (b, g), diversity class (c, h), indicator group (d, i), and $SPEAR_{pesticides}$ (e, j). The grey dots in the background show the values at each site for each of the temperature scenarios. The blue dots represent the mean value of each of the biological index at each temperature. The error bars indicate the 95 % confidence interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

or significant reductions in water discharge. Conversely, in other regions, water runoff may intensify, potentially impacting aquatic insect communities (Schneider et al., 2013). Future changes in flow regimes may have serious impacts on community composition (Schneider et al., 2013). In our analyses, we have partially taken flow velocity into account in our modeling of current spatial differences of the indicators. However, accounting for potential climate change effects on hydrological variables in the future scenarios were beyond the scope of this study. We acknowledge that detailed information of future flow regimes is important to predict future changes on macroinvertebrate communities and biotic indices. The influence of flow velocity along with other physical water quality parameters has also been recognized as an

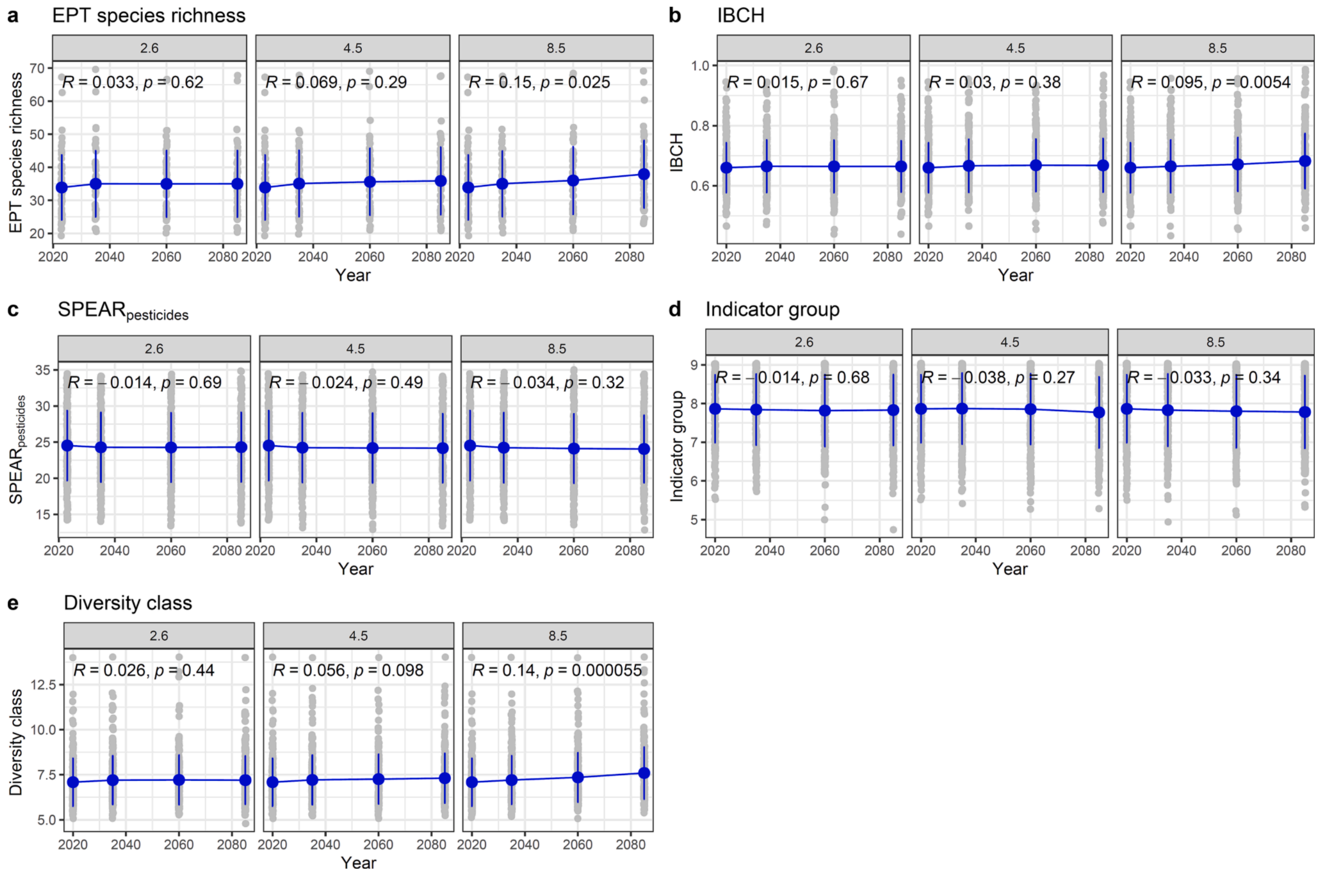

Fig. 4. Predicted EPT Species richness, IBCH index, SPEAR$_{pesticides}$ index, diversity class and indicator group based on the SDM approach for temperature scenarios based on three representative concentrations pathways (RCP) i.e., RCP2.6, RCP4.5 and RCP8.5, and for three time periods, 2030–40, 2055–65 and 2080–90. The changes are modelled only for the 12 catchments for which temperature change was mechanistically modelled in Michel et al. (2021).

important predictor of macroinvertebrates in previous studies similar to our study and it interacts with the temperature as well (Markert et al., 2023; White et al., 2017; Woznicki et al., 2016). The last revision of the IBCH index was intended to reduce effects of natural differences of different stream types, especially on the IBCH diversity group (Küry et al., 2019). Therefore, the absence of a response of the IBCH to flow velocity can be seen as a positive sign that this was successful. However, contrary to the original intention, we did not observe any effect of width variability on the IBCH index or the diversity class. These findings highlight the complexity of using macroinvertebrate communities as ecological indicators, but in this case may also indicate the need to improve the quality of predictor variables to describe habitat variability and morphology of the river.

To assess potential effects of future temperature changes on the indices, we used a multi-variate species distribution model calibrated to historical data and applied different temperature scenarios. As expected, we see that the different taxa respond differently to temperature changes. Specifically, we found that a general + 2 °C temperature increase (expected for majority of sites across Switzerland by the end of this century) is likely to increase the probability of occurrence for 70 % of the studied families on average over all sites (especially those with low sensitivity according to the IBCH indicator group) resulting in an overall positive trend in the probabilities of occurrences. The anticipated increase in species richness can be attributed to the potential benefits warmer waters may provide to ectotherms (Angilletta, 2009; Deutsch et al., 2008) because biological activities of ectotherms rely upon the temperature of their environment. It was also observed in a previous study, that mainly warm-adapted taxa contribute to observed positive trends in local richness (Gebert et al., 2022). However, based on our results, some families can be expected to respond negatively to a + 2 °C temperature increase (especially some with high sensitivity according to the IBCH indicator group), leading to some turnover in taxa, which indicates that the indices itself are more robust than the individual taxa. Furthermore, it is important to emphasize that several taxa exhibited a unimodal shape in their thermal response curves. This indicates that if temperatures surpass the thermal optimum, the probability of occurrence for these species will decrease, potentially leading to an overall negative response to temperature increase.

When projecting different temperature scenarios through the species distribution model to assess their effects on the indices, overall, we see rather minor effects in the range of temperature changes (i.e., 0.7–4.2 °C) that can be expected to happen in this century. For example, we observed positive responses of EPT richness and diversity class (and therefore also IBCH), but minor change on indicator group and the SPEAR$_{pesticides}$ index. A change in temperature of + 2 °C is predicted to lead to minor changes also on diversity measures (on average 7 % increase in EPT richness, 4 % increase in IBCH, 6 % increase in diversity class). Although the observed increase in the values of IBCH during the last decade may suggest an improvement in water and habitat quality, it is important to note that our results indicate that these changes are partially driven by other environmental factors and not necessarily entirely by changes in water quality. For example, changes in dissolved oxygen in water bodies can have a large impact on aquatic insect communities (Verberk et al., 2021, 2023) and we emphasize that in future studies the effect of such factors should also be considered while evaluating future responses of aquatic communities.

Our analysis based on realistic temperature change scenarios indicates that biological indices are quite robust to temperature changes for RCP2.6 and RCP4.5 scenarios. A significant influence of temperature change was noted only under the extreme scenarios of RCP8.5 on the

IBCH index, the diversity class and $SPEAR_{pesticides}$ index. The reason for the very limited influence of temperature change for these realistic scenarios may be attributed to the fact that the temperature increase for the realistic scenarios ranged from + 0.7 °C to 4.2 °C for all the three scenarios and for the three time periods (Michel et al., 2021). For RCP2.6 and RCP4.5, temperature increase ranged from + 0.7 °C to + 2 °C for the three time periods (Michel et al., 2021). Similar to realistic scenarios, for forward-simulated communities, we observed a large influence of temperature on biological indices only when temperature increases beyond + 2 °C. Our results showed that the biological indices were robust to initial temperature changes for both realistic scenarios and for our uniform temperature increase approach. This may be because the IBCH and $SPEAR_{pesticides}$ indices use family-level information, which may mask the interspecific variation in responses to temperature changes. Geographically, our analysis indicates differences in the magnitude of change in all indices, with more positive changes predicted to occur at sites with warmer baseline conditions, which is against our expectations. We could assume that the warming of currently cold sites would lead to the immigration of warm-adapted taxa, but this appears to be compensated by the loss of cold-adapted taxa. Furthermore, we expected a further warming of already warm sites would lead to the local extirpation of many taxa. However, we have to be careful when extrapolating beyond the temperature range that was covered in the calibration data (Chollet et al., 2023). It is possible that the models' estimates are more uncertain for the indices at the warmest sites under extreme warming scenarios because the temperature values may lie outside the range of the calibration data for those sites.

We have observed discrepancies in our findings while investigating the temporal, spatial, and future analysis of biological responses to temperature. These inconsistencies most likely stem from notable differences in temperature variances between our analyses conducted over time and in different spatial contexts. Specifically, our species distribution models (SDM) predominantly rely on spatial data, in which we also observed relatively large thermal variance. Consequently, this spatial perspective encompasses a wider spectrum of thermal fluctuations and exhibits a more pronounced correlation between temperature and biological indices. On the other hand, our temporal analysis indicates relatively small variability in temperature and in other explanatory factors. Hence, we observed weaker or absent relationships of the biological indices to temperature change.

We would like to acknowledge some limitations of our study. First, we only assessed temperature changes and did not include future hydrological or land-use changes in our scenario analysis that can be expected with global warming. Especially for scenarios with large temperature changes, it can be expected that precipitation, flow velocity and land use will change as well (Schwarzwald et al., 2021). The extreme scenario of up to + 8 °C largely served the purpose of a sensitivity analysis and should not be considered as realistic. Second, the SDM does not explicitly account for dispersal limitation or biotic interactions among taxa, assuming that taxa will all be able to track their environmental niches perfectly. Especially for scenarios with fast changes, we can expect an overestimation of local richness if taxa are dispersal limited. Third, our model's predictive performance varies among taxa and the resulting modelled indices have a narrower range than the observed ones (as shown by the regression lines with a slope below 1 in Fig. S9). Therefore, we can expect the sensitivity of the indices to temperature to be rather underestimated than overestimated. Fourth, we can expect that part of the noise in the model predictions can be attributed to limitations in the predictor variables, such as the water temperature being modelled and not measured. Last, our data has two data points per site, with a 5-year gap between site sampling; our conclusions may change once longer timeseries are available.

5. Conclusions

Our study highlights the importance of considering temperature as a significant driver of macroinvertebrate community indices, and the need for a comprehensive assessment of multiple environmental factors to understand the complex relationships at play. We provide valuable insights into the potential direct impacts of temperature changes on different macroinvertebrate indices that are used to inform river management actions. However, it should be noted that indirect effects of temperature via changes in hydrological variables are not considered in this study. While we see a response of richness indicators to increasing temperatures (EPT species richness and the family diversity class that is part of the IBCH index), the indicators that aim to indicate water quality effects (the $SPEAR_{pesticides}$ index and the indicator group contributing to IBCH index) are rather robust to expected temperature changes. A future warming of water temperatures around 2 °C can be expected to lead to only minor change in biological indices, as far as we can tell given the model limitations. These results suggest that on average, macroinvertebrate-based bioindicators will still be useful for surface water quality assessments in the next decades, even under climate change-induced warming. However, we should keep in mind that changes in richness/diversity indicators at any particular site could be partly explained by warming. Overall, our findings underscore the importance of understanding the drivers of macroinvertebrate community dynamics and the potential impact of environmental change, including climate change, in order to develop effective strategies for conserving and managing these ecological systems and the ecosystem services they provide.

CRediT authorship contribution statement

Imran Khaliq: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Emma Chollet Ramampiandra:** Methodology, Validation, Writing – original draft, Writing – review & editing. **Christoph Vorburger:** Writing – review & editing, Funding acquisition, Conceptualization. **Anita Narwani:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Nele Schuwirth:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

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References

Angilletta, M.J., 2009. Thermal adaptation: A theoretical and empirical synthesis. Oxford University Press, Oxford, New York.

Angilletta, M.J., Dunham, A.E., 2003. The temperature-size rule in ectotherms: Simple evolutionary explanations may not be general. Am. Nat. 162, 332–342.

Antão, L.H., Bates, A.E., Blowes, S.A., Waldock, C., Supp, S.R., Magurran, A.E., Dornelas, M., Schipper, A.M., 2020. Temperature-related biodiversity change across temperate marine and terrestrial systems. Nat. Ecol. Evol. 4, 927–933.

BAFU, 2019. Methoden zur Untersuchung und Beurteilung von Fliessgewässern (IBCH_2019). Makrozoobenthos – Stufe F. 1. aktualisierte Ausgabe, November 2019; Erstausgabe 2010. Bundesamt für Umwelt, Bern. Umwelt-Vollzug Nr. 1026: 59 S.

Baranov, V., Jourdan, J., Pilotto, F., Wagner, R., Haase, P., 2020. Complex and nonlinear climate-driven changes in freshwater insect communities over 42 years. Conserv. Biol. 34, 1241–1251.

Birk, S., Bonne, W., Borja, A., Brucet, S., Courrat, A., Poikane, S., Solimini, A., van de Bund, W., Zampoukas, N., Hering, D., 2012. Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive. Ecol. Ind. 18, 31–41.

Bowler, D.E., Hof, C., Haase, P., Kröncke, I., Schweiger, O., Adrian, R., Baert, L., Bauer, H.-G., Blick, T., Brooker, R.W., Dekoninck, W., Domisch, S., Eckmann, R., Hendrickx, F., Hickler, T., Klotz, S., Kraberg, A., Kühn, I., Matesanz, S., Meschede, A., Neumann, H., O'Hara, R., Russell, D.J., Sell, A.F., Sonnewald, M., Stoll, S., Sundermann, A., Tackenberg, O., Türkay, M., Valladares, F., van Herk, K., van Klink, R., Vermeulen, R., Voigtländer, K., Wagner, R., Welk, E., Wiemers, M., Wiltshire, K.H., Böhning-Gaese, K., 2017. Cross-realm assessment of climate change impacts on species' abundance trends. Nat. Ecol. Evol. 1, 1–7.

Burdon, F.J., Munz, N.A., Reyes, M., Focks, A., Joss, A., Räsänen, K., Altermatt, F., Eggen, R.I.L., Stamm, C., 2019. Agriculture versus wastewater pollution as drivers of macroinvertebrate community structure in streams. Sci. Total Environ. 659, 1256–1265.

Caradima, B., Schuwirth, N., Reichert, P., 2019. From individual to joint species distribution models: A comparison of model complexity and predictive performance. J. Biogeogr. 46, 2260–2274.

Caradima, B., Reichert, P., Schuwirth, N., 2020. Effects of site selection and taxonomic resolution on the inference of stream invertebrate responses to environmental conditions. Freshwater Sci. 39, 415–432.

Chiu, M.-C., Hunt, L., Resh, V.H., 2017. Climate-change influences on the response of macroinvertebrate communities to pesticide contamination in the Sacramento River, California Watershed. Sci. Total Environ. 581–582, 741–749.

Chollet, R.E., Scheidegger, A., Wydler, J., Schuwirth, N., 2023. A comparison of machine learning and statistical species distribution models: Quantifying overfitting supports model interpretation. Ecol. Model. 481, 110353.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. PNAS 105, 6668–6672.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A. E., 2014. Assemblage time series reveal biodiversity change but not systematic loss. Science 344, 296–299.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. Camb. Philos. Soc. 81, 163–182.

Elith, J., Franklin, J., 2013. Species Distribution Modeling. Encyclopedia of Biodiversity: Second Edition 6, 692–705.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697.

Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. Annu. Rev. Ecol. Syst. 48, 1–23.

Gebert, F., Obrist, M.K., Siber, R., Altermatt, F., Bollmann, K., Schuwirth, N., 2022. Recent trends in stream macroinvertebrates: warm-adapted and pesticide-tolerant taxa increase in richness. Biol. Lett. 18, 20210513.

Haase, P., Bowler, D.E., Baker, N.J., Bonada, N., Domisch, S., Garcia Marquez, J.R., Heino, J., Hering, D., Jähnig, S.C., Schmidt-Kloiber, A., Stubbington, R., Altermatt, F., Álvarez-Cabria, M., Amatulli, G., Angeler, D.G., Archambaud-Suard, G., Jorrín, I.A., Aspin, T., Azpiroz, I., Bañares, I., Ortiz, J.B., Bodin, C.L., Bonacina, L., Bottarin, R., Cañedo-Argüelles, M., Csabai, Z., Datry, T., de Eyto, E., Dohet, A., Dörflinger, G., Drohan, E., Eikland, K.A., England, J., Eriksen, T.E., Evtimova, V., Feio, M.J., Ferréol, M., Floury, M., Forcellini, M., Forio, M.A.E., Fornaroli, R., Friberg, N., Fruget, J.-F., Georgieva, G., Goethals, P., Graça, M.A.S., Graf, W., House, A., Huttunen, K.-L., Jensen, T.C., Johnson, R.K., Jones, J.I., Kiesel, J., Kuglerová, L., Larrañaga, A., Leitner, P., L'Hoste, L., Lizée, M.-H., Lorenz, A.W., Maire, A., Arnaiz, J.A.M., McKie, B.G., Millán, A., Monteith, D., Muotka, T., Murphy, J.F., Ozolins, D., Paavola, R., Paril, P., Peñas, F.J., Pilotto, F., Polášek, M., Rasmussen, J.J., Rubio, M., Sánchez-Fernández, D., Sandin, L., Schäfer, R.B., Scotti, A., Shen, L.Q., Skuja, A., Stoll, S., Straka, M., Timm, H., Tyufekchieva, V.G., Tziortzis, I., Uzunov, Y., van der Lee, G.H., Vannevel, R., Varadinova, E., Várbíró, G., Velle, G., Verdonschot, P.F.M., Verdonschot, R.C.M., Vidinova, Y., Wiberg-Larsen, P., Welti, E.A.R., 2023. The recovery of European freshwater biodiversity has come to a halt. Nature 620, 582–588.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorf, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84, 3105–3117.

Hilsenhoff, W.L., 1988. Rapid Field Assessment of Organic Pollution with a Family-Level Biotic Index. J. North Am. Benthol. Soc. 7, 65–68.

Hilsenhoff, W.L., 1998. A Modification of the Biotic Index of Organic Stream Pollution to Remedy Problems and Permit Its Use Throughout the Year. Great Lakes Entomol. 31, 1.

Hof, C., Voskamp, A., Biber, M.F., Böhning-Gaese, K., Engelhardt, E.K., Niamir, A., Willis, S.G., Hickler, T., 2018. Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. PNAS 115, 13294–13299.

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., Purvis, A., 2022. The direct drivers of recent global anthropogenic biodiversity loss. Sci. Adv. 8, 1–12.

Jetz, W., McGeoch, M.A., Guralnick, R., Ferrier, S., Beck, J., Costello, M.J., Fernandez, M., Geller, G.N., Keil, P., Merow, C., Meyer, C., Muller-Karger, F.E., Pereira, H.M., Regan, E.C., Schmeller, D.S., Turak, E., 2019. Essential biodiversity variables for mapping and monitoring species populations. Nat. Ecol. Evol. 3, 539–551.

Jourdan, J., O'Hara, R.B., Bottarin, R., Huttunen, K.-L., Kuemmerlen, M., Monteith, D., Muotka, T., Ozoliņš, D., Paavola, R., Pilotto, F., Springe, G., Skuja, A., Sundermann, A., Tonkin, J.D., Haase, P., 2018. Effects of changing climate on European stream invertebrate communities: A long-term data analysis. Sci. Total Environ. 621, 588–599.

Jourdan, J., Baranov, V., Wagner, R., Plath, M., Haase, P., 2019. Elevated temperatures translate into reduced dispersal abilities in a natural population of an aquatic insect. J. Anim. Ecol. 88, 1498–1509.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Peter Linder, H., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4, 1–20.

Knillmann, S., Orlinskiy, P., Kaske, O., Foit, K., Liess, M., 2018. Indication of pesticide effects and recolonization in streams. Sci. Total Environ. 630, 1619–1627.

Küry, D., Stucki, P., Martinez, N., Roth, T., Schuwirth, N., Michel, C., Schindler Wildhaber, Y., 2019. Vom IBCH zum IBCH_2019. Methoden-Update des Moduls 'Makrozoobenthos Stufe F' im Modul-Stufen-Konzept. Aqua & Gas 99, 47–54.

Lee-Yaw, A.J.L., McCune, J., Pironon, S.N., Sheth, S., 2022. Species distribution models rarely predict the biology of real populations. Ecography 2022. https://doi.org/10.1111/ecog.05877.

Liess, M., Von Der Ohe, P.C., 2005. Analyzing effects of pesticides on invertebrate communities in streams. Environ. Toxicol. Chem. 24, 954–965.

Markert, N., Guhl, B., Feld, C.K., 2023. Water quality deterioration remains a major stressor for macroinvertebrate, diatom and fish communities in German rivers. Sci. Total Environ. 907, 167994.

Michel, A., Schaefli, B., Wever, N., Zekollari, H., Lehning, M., Huwald, H., 2021. Future water temperature of rivers in Switzerland under climate change investigated with physics-based models.

Niedrist, G.H., Fureder, L., 2020. Real-time warming of Alpine streams: (re)defining invertebrates' temperature preferences. River Res. Appl. 37, 283–293.

Piggott, J.J., Townsend, C.R., Matthaei, C.D., 2015. Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. Glob. Chang. Biol. 21, 1887–1906.

Pimm, S.L., 1985. The complexity and stability of ecosystems. Nature 315, 635–636.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. Camb. Philos. Soc. 94, 849–873.

Rios, S.L., Bailey, R.C., 2006. Relationship between riparian vegetation and stream benthic communities at three spatial scales. Hydrobiologia 553, 153–160.

Rolauffs, P., Stubauer, I., Zahrádková, S., Brabec, K., Moog, O., 2004. Integration of the saprobic system into the European Union Water Framework Directive – Case studies in Austria, Germany and Czech Republic. Hydrobiologia 516, 285–298.

Schneider, C., Laizé, C.L.R., Acreman, M.C., Flörke, M., 2013. How will climate change modify river flow regimes in Europe? Hydrol. Earth Syst. Sci. 17, 325–339.

Schuwirth, N., Kattwinkel, M., Stamm, C., 2015. How stressor specific are trait-based ecological indices for ecosystem management? Sci. Total Environ. 505, 565–572.

Schwarzwald, K., Poppick, A., Rugenstein, M., Bloch-Johnson, J., Wang, J., McInerney, D., Moyer, E.J., 2021. Changes in Future Precipitation Mean and Variability across Scales. J. Clim. 34, 2741–2758.

Stoddard, J.L., Larsen, D.P., Hawkins, C.P., Johnson, R.K., Norris, R.H., 2006. Setting expectations for the ecological condition of streams: the concept of reference condition. Ecol. Appl. 16, 1267–1276.

Stucki, P., 2010. Methoden zur Untersuchung und Beurteilung der Fliessgewasser. Makrozoobenthos - Stufe F (flächendeckend). Umwelt-Vollzug Nr. 1026.Bundesamt für Umwelt, Bern, 61 S.

Sunday, J., Bates, A.E., Dulvy, N.K., 2012. Thermal tolerance and the global redistribution of animals. Nat. Clim. Chang. 2, 686–690.

Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O., Rouget, M., 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob. Chang. Biol. 11, 224–2250.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80, 1455–1474.

Timoner, P., Marle, P., Castella, E., Lehmann, A., 2020. Spatial patterns of mayfly, stonefly and caddisfly assemblages in Swiss running waters in the face of global warming. Ecography 43, 1065–1078.

Timoner, P., Fasel, M., Ashraf Vaghefi, S.S., Marle, P., Castella, E., Moser, F., Lehmann, A., 2021. Impacts of climate change on aquatic insects in temperate alpine regions: Complementary modeling approaches applied to Swiss rivers. Glob. Chang. Biol. 27, 3565–3581.

Vaughan, I.P., Gotelli, N.J., 2019. Water quality improvements offset the climatic debt for stream macroinvertebrates over twenty years. Nat. Commun. 10, 1–8.

Verberk, W.C.E.P., Atkinson, D., Hoefnagel, K.N., Hirst, A.G., Horne, C.R., Siepel, H., 2021. Shrinking body sizes in response to warming: explanations for the temperature-size rule with special emphasis on the role of oxygen. Biol. Rev. Camb. Philos. Soc. 96, 247–268.

Verberk, W.C.E.P., Hoefnagel, K.N., Peralta-Maraver, I., Floury, M., Rezende, E.L., 2023. Long-term forecast of thermal mortality with climate warming in riverine amphipods. Glob. Chang. Biol. 29, 5033–5043.

Vermeiren, P., Reichert, P., Schuwirth, N., 2020. Integrating uncertain prior knowledge regarding ecological preferences into multi-species distribution models: Effects of model complexity on predictive performance. Ecol. Model. 420, 108956.

Voskamp, A., Hof, C., Biber, M.F., Hickler, T., Niamir, A., Stephen, G., 2020. Climate change impacts on the phylogenetic diversity of the world ' s terrestrial birds : more than species numbers.

White, J.C., Hannah, D.M., House, A., Beatson, S.J.V., Martin, A., Wood, P.J., 2017. Macroinvertebrate responses to flow and stream temperature variability across regulated and non-regulated rivers. Ecohydrology 10, 1–21.

Wiberg-Larsen, P., Nørum, U., Rasmussen, J.J., 2021. Repeated insecticide pulses increase harmful effects on stream macroinvertebrate biodiversity and function. Environ. Pollut. 273, 116404.

Woznicki, S.A., Nejadhashemi, A.P., Tang, Y., Wang, L., 2016. Large-scale climate change vulnerability assessment of stream health. Ecol. Ind. 69, 578–594.

Wright, J.F., 2000. Assessing the Biological Quality of Freshwaters: RIVPACS and Other Techniques.

Zhang, M., Muñoz-Mas, R., Martínez-Capel, F., Qu, X., Zhang, H., Peng, W., Liu, X., 2018. Determining the macroinvertebrate community indicators and relevant environmental predictors of the Hun-Tai River Basin (Northeast China): A study based on community patterning. Sci. Total Environ. 634, 749–759.