

Modelling the potential for local management practices to offset climate change impacts on freshwater macroinvertebrate communities

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Abstract

1. A robust understanding of the interactions between global and local anthropogenic stressors is crucial for ecosystem management in the Anthropocene. Manipulative experiments in the laboratory or in the field can be used to build knowledge about the physiological and ecological effects of stressors, but predicting the combined landscape-scale effects of global stressors such as climate change, and local stressors such as land-use change requires a different approach.
2. Here we used water quality and hydrology process-based models of entire river catchments in combination with a large biomonitoring dataset to predict the responses of macroinvertebrate communities under different climate change and land-use change scenarios. Using the River Thames in the U.K. as a model system, we predicted changes in water quality (temperature, flow, phosphorus [P], nitrogen, dissolved oxygen [DO]) and subsequent changes in macroinvertebrate communities for two climate change scenarios, individually and in combination with intensified agriculture and reduced P pollution (representing improved wastewater treatment).
3. Our models predicted that water-quality changes associated with climate change may not influence total species richness, but that community composition will shift towards more pollution-tolerant and common taxa based on responses of community indices and taxon-specific responses. We also found that the negative impacts of climate change on water quality (e.g., increased P concentration, decreased DO concentration) accumulate through the catchment, but that local land-use practices influencing P dynamics can modify this trend. Furthermore, although the intensified agriculture scenario was predicted to have minimal impacts on macroinvertebrate communities (a result potentially related to shifting baselines as the Thames is already heavily polluted), we found that reduced P pollution resulting from improved wastewater treatment was able to mostly offset the negative impacts of climate change on macroinvertebrate communities.

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4. Our results demonstrate that using process-based models to study networks of interacting stressors at a landscape scale can provide useful insights into the ecological impacts of anthropogenic global change, and adds support to the idea that management of local stressors has the potential to mitigate some of the impacts of climate change on ecosystems.

KEYWORDS

catchment-scale modelling, ecological forecasts, land-use change, multiple stressors, species turnover

1 | INTRODUCTION

Freshwater ecosystems are particularly vulnerable to anthropogenic global change with higher rates of extinction and population decline compared to other realms (Almond et al., 2020). As low points in the landscape, fresh waters act as sinks where a high diversity of physical, chemical and biological stressors can co-occur. These stressors are caused by drivers of anthropogenic change at global and local scales (Brown et al., 2014; Côté et al., 2016). Even under the most optimistic scenarios, anthropogenic climate change will continue to impact temperature and precipitation patterns for at least the next century with variation in realised effects at local and regional scales (Pörtner et al., 2022). Simultaneously, land-use practices (e.g., agriculture, wastewater treatment, urbanisation, deforestation) will continue to alter the functioning and stability of ecosystems by disrupting nutrient and water cycles, introducing chemical and biological contaminants, and reducing the size and connectivity of habitats (Sage, 2020). A robust understanding of the interplay between these local and global drivers is required to identify which local management practices (e.g., riparian reforestation, enhanced wastewater treatment) will be capable of counteracting the impacts of climate change on freshwater ecosystems.

Ecologists use many tools to study global change. Manipulative experiments in the laboratory or in the field are used to quantify the individual and combined effects of multiple stressors for specific endpoints (Jackson et al., 2016; Orr et al., 2020; Verberk, Durance, et al., 2016), while remote sensing and observational studies are used to correlate anthropogenic activity with changes in biodiversity across larger temporal and spatial scales (Birk et al., 2020; Gilarranz et al., 2022). To complement these approaches, numerical modelling can be used to simulate different scenarios and to make mechanistically informed forecasts at a landscape scale (Lofton et al., 2023). Although anthropogenic stressors may arise from either global or local activities, their effects interact with each other and with the environment at local or regional scales, which can be captured by process-based modelling. For riverine systems, catchment-scale models (e.g., INCA—"Integrated Catchment Model", SWAT—"Soil and Water Assessment Tool") are powerful tools that can be used to study how complex effects of human activities can ripple across the landscape and travel downstream through the catchment (Arnold et al., 2012; Whitehead, Wilson, & Butterfield, 1998). Indeed, these

process-based models have been widely employed to understand the impacts of climate change and land-use change on the physics and chemistry of river systems and are increasingly being used to make biological forecasts and to inform ecosystem management (e.g., Bussi, Whitehead, et al., 2016; Guse et al., 2015; Kuemmerlen et al., 2015; Nelson et al., 2009; Sultana et al., 2020). When these models have been used to predict biological responses, they have typically focused on fish and phytoplankton, whereas other important components of food webs, such as macroinvertebrates, have received less attention (Lofton et al., 2023).

Macroinvertebrate communities are used as bioindicators for river ecosystems around the world as they are easy to identify and comprise a diverse range of taxa that vary in their sensitivity to changes in habitat and water quality (Feld & Hering, 2007; Hawkes, 1998; Windsor et al., 2019). High-quality datasets have therefore been collected for macroinvertebrate communities in many different countries thanks to national and international biomonitoring programs (Hering et al., 2003). Furthermore, the responses of macroinvertebrates to stressor variables such as temperature, pollution and flow have been extensively studied in manipulative experiments, which has built a strong mechanistic understanding of the impacts of climate change and land-use change on the physiology, reproduction, behaviour and phenology of these species (Bonacina et al., 2023; Haxton & Findlay, 2008; Verberk, Overgaard, et al., 2016). At a spatial scale that is more directly applicable to river ecosystem conservation and restoration, some insightful studies have predicted changes in macroinvertebrate communities under different climate change and land-use change scenarios using catchment-scale modelling. However, these studies have either focused primarily on community-level aggregate properties such as richness or diversity that can hide important taxon-specific responses (e.g., Kuemmerlen et al., 2015; Mantyka-Pringle et al., 2014), or on individual stressor variables such as flow (e.g., Kakouei et al., 2018; Sultana et al., 2020) or nutrients (Guse et al., 2015; Vagheei et al., 2022). Understanding community-level responses and taxon-specific responses of macroinvertebrates to multiple, interconnected stressor variables associated with climate change and land-use change (e.g., flow, water temperature, nitrogen [N], phosphorus [P], dissolved oxygen [DO]) is an important next step.

Here, we use water quality and hydrology catchment-scale models in combination with regression models built using a large

biomonitoring dataset to forecast the individual and combined impacts of climate change and land-use change on macroinvertebrate communities. We simulated two climate change scenarios (RCP 2.6 and RCP 4.5 greenhouse gas concentration trajectories, representing an optimistic scenario and a more realistic scenario, respectively) for three different land-use scenarios encompassing activities expected to both increase and decrease nutrient pollution (baseline, intensified agriculture, intensified agriculture with P removal representing improved wastewater treatment) in the Thames catchment, an intensively studied catchment where there is a high quantity and quality of data available. We had three main research questions. Firstly, we asked how community-level (i.e., aggregate properties) and taxon-level (i.e., abundance of specific taxa) responses will be impacted by climate change, agricultural intensification, and reduction of P pollution. Secondly, we asked if anthropogenic impacts accumulate through the catchment, which would lead to deteriorating water quality downstream and could lead to site-specific responses with the greatest effects on macroinvertebrates at the final reaches of the river. Finally, based on the concept of offsetting “climate debt” with management practices (*sensu* Vaughan & Gotelli, 2019), we asked if future changes in water quality driven by climate change (e.g., increased temperature, increased P concentrations, decreased DO concentrations) could be counteracted by a local management strategy that reduced nutrient inputs.

2 | METHODS

In summary, multiple publicly available datasets and two stages of modelling were used to forecast how macroinvertebrate communities may be impacted by the individual and combined effects of climate change and land-use change (Figure 1a). Firstly, process-based catchment-scale models were used to predict changes in the hydrology and water quality of the River Thames under two climate change scenarios and three land-use scenarios for the 2080s. Generalised linear mixed effects models were then constructed to explain how habitat quality and water quality impact macroinvertebrate communities. The results from the process-based modelling were combined with the regression models to predict changes in the macroinvertebrate communities in the Thames catchment under the different climate and land-use scenarios (Figure 1b). The data and code used in this study are available at <https://github.com/jamesaorr/local-global-stressors>.

2.1 | Process-based models

2.1.1 | Description of hydrology and water-quality models

In this study, the INCA (Integrated Catchment) -N and -PEco hydrological and water-quality models were employed to obtain estimates of flow and water-quality parameters of the River Thames

at different sections. INCA-N is a semi-distributed hydrological and N cycle model, which is able to account for diffuse (e.g., atmospheric, fertiliser) and point (mainly from sewage treatment effluents) sources of N, both in nitrate and ammonium forms. It was developed ~25 years ago (Whitehead, Wilson, & Butterfield, 1998; Whitehead, Wilson, Butterfield, & Seed, 1998) and is constantly updated (e.g., Bussi, Whitehead, et al., 2016). INCA-PEco is an extension of the INCA-P model (Wade et al., 2002), which originally reproduced the cycle of P in river catchments, and has been upgraded to include DO, biochemical oxygen demand (BOD) and algal processes (Crossman et al., 2021). Both models were implemented using daily precipitation and temperature for the period 2010–2021 from the UK Met Office as input. Soil moisture deficit and hydrologically-effective rainfall were estimated using the PERSIST model (Futter et al., 2014), which is specifically designed to provide input series for the INCA family of models. Calibration and validation data were obtained from the National River Flow Archive (for river flow data) and from the Environment Agency (for water-quality data). Both models were calibrated through a Monte Carlo generation of a 10,000 sets of model parameter sets, whose results were analysed through a set of goodness-of-fit metrics. The model parameter set that provided the best calibration and validation results was selected and used throughout the study. Goodness-of-fit for the Thames INCA models are reported in Table S1 for flow, P and DO for reaches where there were sufficient observed data and more information about the INCA Thames setup, calibration and validation can be found in a set of specific papers (Bussi et al., 2017; Bussi, Dadson, et al., 2016; Bussi, Whitehead, et al., 2016; Crossman et al., 2013; Jin et al., 2012).

2.1.2 | Climate change scenarios

Climate change impacts on water quality were taken into account by altering the input daily precipitation and temperature with change factors which reflect how much these two atmospheric variables are expected to vary in the future in the River Thames catchment. Altered hydrological and temperature patterns influence the process equations and controlling reaction kinetic parameters in the INCA-N and INCA-PEco models (Whitehead et al., 2009). We used the Thames-averaged river basin UK Climate Projections 2018 (UKCP18; Lowe et al., 2018), a climate analysis tool developed by the UK Met Office (Hadley Centre Climate Programme) as a development of the UK Climate Projections 2009 (UKCP09). This tool includes probabilistic projections that combine information from collections of computer models with observations to provide a result that incorporates the uncertainties of climate projections. These projections are generated using multiple variations of a specific climate model to simulate a wide range of different climate outcomes (i.e., a climate ensemble). A statistical emulator then estimates climate outcomes for a much greater number of climate model variants based on known sensitivities within the model. These outcomes are weighted by comparing

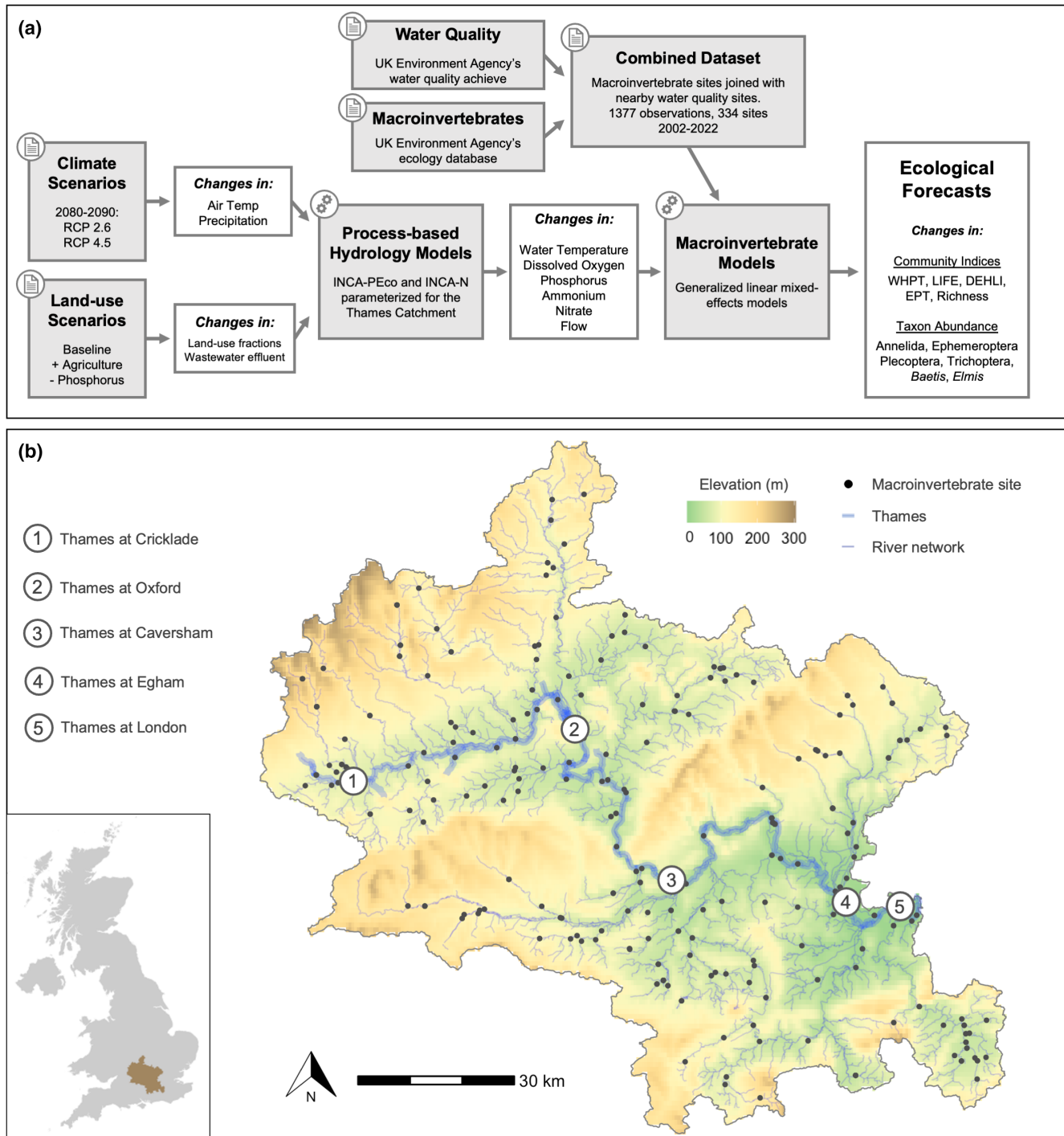


FIGURE 1 (a) Schematic of the modelling approach used in this study. (b) Map of the study site, the Thames catchment west of London. The colour of the map represents the elevation of the terrain in meters. The River Thames is represented by the thick blue line while the thinner blue lines show the wider river network. Black points are macroinvertebrate sampling sites that were used to build the generalised linear mixed-effects models. The five sites along the Thames that we focused on are represented by the numbered white circles.

predictions from historical climate models with historical observations (Lowe et al., 2018). Probabilistic projections are available for several alternative future pathways of emissions, including RCP2.6, RCP4.5, RCP6.0 and RCP8.5, and for time horizons up to 2100 (Van Vuuren et al., 2011). In this paper, 100 sets of monthly precipitation change factors (i.e., precipitation anomalies) and

100 sets of monthly temperature change factors (i.e., temperature anomalies) were downloaded from the UKCP18 web platform (from a broad range of model realisations carried out by the UK Met Office) and were used to generate 100 climate change-affected series of daily precipitation and temperature by altering the baseline precipitation and temperature time series obtained

from measured data across the catchment. RCP2.6 (optimistic scenario described as a “very stringent” pathway) and RCP4.5 (an “intermediate” pathway that more closely aligns with the current trajectory) were used, and the 2080s time horizon was chosen as a reference for measuring the climate change impacts (in particular, the 2070–2099 time slice).

2.1.3 | Land-use change scenarios

The two climate change scenarios were run with a baseline land-use scenario (current land use in the catchment) and with two other land-use scenarios that accounted for potential changes in diffuse and point sources of pollutants. Firstly, the expansion of arable land in the River Thames catchment was implemented into the INCA model by changing the land use fractions used to estimate fertiliser inputs (both in terms of N and P), according to a pre-established arable land expansion scenario defined using the Land-SFACTS model (Castellazzi et al., 2010). This model simulates crop arrangement under increasing population, considering food security as a dominant driving force for land-use change. Arable conversion from other land uses was permitted only on prime land and only from areas previously identified as grasslands (Bussi, Dadson, et al., 2016; Bussi, Whitehead, et al., 2016; Crossman et al., 2013). The baseline scenario had an average of 35% arable land cover across the 22 sub-catchments associated with each reach of the river. In the scenario with intensified agriculture, however, the average cover of arable land is 59%, with greater increases in arable land cover for sub-catchments associated with the earlier reaches of the river (Figure S1). In the INCA models, more agricultural land will lead to more fertiliser usage, thus increasing the input of N and P into the river system. A second scenario, with enhanced P stripping in the sewage treatment plants within the River Thames catchment in addition to agricultural intensification was also considered. Wastewater treatment plants are added to the model by introducing an effluent input into each river reach, which is characterised by its flow rate and the concentration levels of contaminants (e.g., P, nitrates, ammonium). Data for wastewater treatment plants were obtained from the UK Environment Agency's “Urban Wastewater Treatment Directive Treatment Plants” dataset and if there were multiple wastewater treatment plants in a reach the effluents were pooled together in the model (sum of flow rates and weighted mean of concentrations). In line with a recent report by an expert advisory group to the UK Department for Environment, Food and Rural Affairs, which proposed a target of an 80% reduction in P concentrations in wastewater effluent by 2037 (Water Targets Expert Advisory Group, 2022), we reduced the effluent P concentration to 0.3 mg/L in the INCA models to test the potential impacts of a positive local land-use strategy. This P concentration is a typical effluent concentration when P stripping technology is implemented in wastewater treatment plants (Huber et al., 2020). INCA-N and INCA-PEco model how these changes

in nutrients inputs will affect overall water quality (e.g., DO, nitrate, orthophosphate, ammonium).

2.2 | Macroinvertebrate models

2.2.1 | Data collection

On 22 May 2023, macroinvertebrate data were downloaded from the UK Environment Agency's “Ecology” database (<https://environment.data.gov.uk/ecology/explorer/>) and water-quality data were downloaded from the UK Environment Agency's “Water Quality Archive” database (<https://environment.data.gov.uk/water-quality/view/download>). Data from the Thames catchment collected between 2002 and 2022 were selected as these years followed the introduction of the Water Framework Directive, which increased the consistency and accuracy of the sample collection and processing. Data between 2002 and 2020 were used to construct macroinvertebrate models and data from 2021 and 2022 were used to validate these models. For the macroinvertebrate data, only samples where a standard sampling method (“3-min active sampling, 1-min hand search as per BT001”) and a standard analysis method (“Estimate of the log abundance [scale as BT001]”) were considered. A wide range of community-level indices are recorded as well as total abundances of specific taxa (exact abundances for lower values and estimated abundances for higher values) that are typically identified to species or genus level. For the water-quality data, only samples taken from “running surface water” that were inside the Thames catchment were selected. To temporally join macroinvertebrate and water-quality data, macroinvertebrate samples taken in the autumn (September, October, November) were joined to the mean water-quality data taken in the summer of the same year (June, July, August). Explaining variation in macroinvertebrate data in one season using water-quality data from a previous season has been an informative approach employed in previous studies (Durance & Ormerod, 2009; Vaughan & Gotelli, 2019). To spatially join macroinvertebrate and water-quality data, pairs of samples were joined if they occurred in the same river (using the “identifier” variable from the OS “Open Rivers” shapefile) and if they were within 500 m from each other. Only sites that had multiple observations were included in the final dataset so that responses of macroinvertebrate communities could be linked to changes in water and habitat quality within sites, rather than to variation between sites. After filtering the data there were 1,377 observations from 334 sites (with 77 of these observations across 57 sites from 2021 and 2022 used for model validation). On average there were 68.85 (± 6.63 standard error) samples per year. About one third of these sites had only two observations while other sites were sampled almost every year. Additional models were run with a smaller dataset of sites that had been sampled at least eight times (438 observations from 37 sites) to ensure that different filtering procedures did not influence the results (Figure S2a). All data organisation and manipulation was

done in R 4.1.3 (R Core Team, 2020) with *tidyverse* 1.3.0, *lubridate* 1.7.9, *sf* 1.0.0, *raster* 3.4.10 and *ngeo* 0.4.3.

2.2.2 | Response and explanatory variables

Generalised linear mixed effects (GLME) models were constructed using descriptors of habitat quality and water quality to predict the impacts of climate change and land-use change on macroinvertebrate communities. A combination of community indices and abundance of specific taxa were used as response variables. At the community level, the Whalley Hawkes Paisley Trigg (WHPT) index, the Drought Effect of Habitat Loss on Invertebrates index (DEHLI) and the Lotic-invertebrate Index for Flow Evaluation (LIFE) were used. The WHPT index is the primary taxon-specific score used for freshwater macroinvertebrates in England and Wales and is an indicator of water quality (Paisley et al., 2014). Pollution-sensitive taxa such as plecopterans are given higher scores, while pollution-tolerant taxa such as annelids are given lower scores. We used the average score per taxon (WHPT-ASPT) and the total score (WHPT-TOTAL) as response variables. The DEHLI and LIFE indices are used to track the ecological effects of drought making them sensitive to climate change impacts on hydrology (Chadd et al., 2017). We also used traditional biological indicators including total macroinvertebrate richness and the richness and abundance of the EPT taxa: Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies). For taxon-specific responses we used the abundance of orders including Odonata, Diptera, Mollusca, Crustacea, Coleoptera, Annelida and Turbellaria. Using higher taxonomic resolution with the EA data is difficult because samples are analysed to different levels (e.g., order, family) and the highly zero inflated data (e.g., for species or genera) can be challenging to work with. We did, however, fit models for the abundance of five common genera covering a range of WHPT scores (*Asellus*, *Baetis*, *Elmis*, *Gammarus*, and *Glossiphonia*) as responses. For the abundance of genera, the vast majority of zeroes indicate that the genus was not present in the sample, but some zeroes may indicate that a sample was not analysed at that taxonomic depth. Although this is very rare for these five taxa, it may introduce some uncertainty into models for these responses. Basic descriptors of each macroinvertebrate sampling site are available in the database. Of these collinear descriptors, the proportion of the substrate recorded as silt/clay was chosen to account for variation in habitat quality for macroinvertebrates at the different sites. The naturalised mean annual flow (m^3/s), available as a fixed value for each site, was used as a physical measure of habitat quality. From the water-quality samples taken in the summer before the macroinvertebrate samples were collected, we used the mean values of five variables—water temperature (degrees C), DO as percentage saturation, orthophosphate reactive as P (mg/L), nitrate as N (mg/L) and ammonia unionised as N (mg/L)—as further explanatory variables. Finally, site ID was included as a random effect to account for repeated sampling of macroinvertebrates sites and to

account for variability driven by unmodelled differences between sites.

2.2.3 | Generalised linear mixed effects model

The GLME models were fitted with *lme4* 1.1.27.1 (Bates et al., 2014). Owing to the high number of individual sites and an unbalanced number of observations per site, only the intercepts, but not slopes, of individual sites were allowed to vary (Grueber et al., 2011). To reduce the risk of numerical errors during model fitting, highly skewed explanatory variables (flow, ammonia, nitrate and orthophosphate) were log-transformed. A second-order polynomial term for temperature (hypothesising an intermediate optimum temperature for macroinvertebrate communities [Hester & Doyle, 2011]) was ultimately excluded from the models as it was not significant and it did not improve the model's fit. Pairwise interactive terms between temperature, flow, O and P did not significantly improve the fit of the models and were therefore also excluded from the models used for predictions as this would have reduced the interpretability of the ecological forecasting. Although some of the interactive terms were statistically significant (Table S3), fitted values from models including these pairwise interactive terms correlated almost perfectly with fitted values from models without them (Figure S2b). Collinearity of explanatory variables was assessed and found to be low (values in correlation matrix were all <0.4). To test whether even these weak correlations between predictors influenced parameter estimates (Graham, 2003), models were run that either dropped temperature or ammonia (the predictors with the strongest correlation) and their fitted estimates were compared and shown to be almost identical (Figure S2c). Furthermore, DO was expressed as percentage saturation rather than as mg/L to reduce its correlation with temperature. Marginal R^2 (variance explained by fixed effects) were calculated using *MuMIn* 1.43.17 (Barton, 2016). Model residuals were plotted in geographical space to ensure that there were no modelling errors related to spatial autocorrelation. Diagnostic plots were used to ensure that the assumptions of the models (e.g., normally distributed residuals, homogeneity of variance) were met (Harrison et al., 2018). The assumptions of linear mixed effects models (with Gaussian error distributions) were met for models of WHPT-ASPT, WHPT-total, DEHLI and LIFE. Richness and abundance responses are count variables so generalised mixed effects models with Poisson error distributions were used to model them. To confirm that the assumptions of these models were met, DHARMA 0.4.5 was used to create and plot interpretable scaled residuals (Hartig, 2020).

2.2.4 | Model validation and ecological forecasts

In order to ensure that our relatively simple models could predict general changes in macroinvertebrate communities in different climate and land-use scenarios we performed a model validation study using both marginal and conditional model predictions

(Figure S3; Table S4). Data from 2002 to 2020 had been used to build the models, and we used data from 2021 and 2022 to test the performance of these models. The correlation between conditional predicted values and observed values was strong for the community level indices (e.g., 0.81 for WHPT-ASPT and 0.77 for DEHLI) but was moderate-to-weak for the richness and abundance of specific taxa (e.g., 0.43 for EPT richness and 0.34 for annelid abundance). In general, most models for the abundance of taxa that are typically found in lower abundances (e.g., Turbellaria, Plecoptera, *Asellus*, *Gammarus*, and *Glossiphonia*) had low marginal R^2 and weak correlations in the validation study so were not used to make ecological forecasts. The correlation between marginal predicted values—using only fixed effects so therefore expected to be less accurate—and observed values was still moderate for most community-level indices (0.55 for WHPT-ASPT and 0.56 for DEHLI) but was generally weak (or even very weak) for the abundance of specific taxa (Table S4). Furthermore, as orders can contain a diverse range of species and genera with very different sensitivities to water-quality parameters (e.g., some chironomids are very sensitive to pollution and some EPT such as *Cloeon dip-terum* are relatively tolerant to pollution) most of the models with order-level abundances also had low marginal R^2 and weak correlations in the validation study so were therefore also not used to make ecological forecasts. Indeed, only community-level responses and abundance for two common genera (the mayfly *Baetis* and the water beetle *Elmis*) and for Annelida (vast majority of taxa in this phylum in the Thames catchment are tolerant to pollution) were used for the ecological forecasting as these responses all had R^2 values above our a priori threshold of 0.1 and typically had at least moderate correlations in the validation study with conditional model predictions.

We then used our models to predict changes in macroinvertebrate responses for different scenarios. Crossing the two climate change scenarios for the 2080s, the three land-use scenarios (baseline, intensified agriculture, intensified agriculture with P removal) and the five sites in the Thames catchment (from Thames at Cricklade in the upper reaches to Thames at London in the lower reaches; Figure 1b) in a fully factorial design gave us 30 specific scenarios. For each of these scenarios, changes in flow, water temperature, DO, nitrate, orthophosphate and ammonium (as a proxy for ammonia) were obtained from the INCA models. The water quality and hydrology values predicted by INCA did not fall outside the range of values in our dataset. The changes in water quality and hydrology associated with the median, lower (5th) and upper (95th) percentile INCA series were combined with the coefficients of the macroinvertebrate models to make predictions about subsequent changes to macroinvertebrate responses using the “predict” function in R. The “type” argument for this function was set to “response” so that predictions were on the scale of the response variables. Using linear regressions with no polynomial or interactive terms meant that the slope coefficients of the models could be easily interpreted and were the same for all values of the explanatory variables.

3 | RESULTS

3.1 | Changes in hydrology and water quality

Changes in precipitation and air temperature suggest that the climate predicted by UKCP18 projections for 2080 is expected to be warmer than the baseline time period (2010–2018) by around 1°C in winter and 2°C in summer under RCP2.6 and by around 2°C in winter and 3°C in summer under RCP4.5, while both RCPs predict wetter winters and dryer summers, with RCP4.5 projecting more dramatic changes than RCP2.6 (Figure S4). These changes in air temperature and precipitation caused an average increase of ~1.6°C and ~3.3°C in summer water temperature in the Thames under RCP2.6 and RCP4.5, respectively (Figures 2b and S5b). The INCA model suggests that monthly summer flows might be reduced by 28%–37% at London, and by 30%–40% at Oxford and at Cricklade, whereas winter flows should remain unaltered (Figures 2a and S5a). The impacts of climate change on water quality are especially noticeable in summer. Decreased summer runoff is expected to reduce N inputs into the river, although the model suggests that the effect should be relatively small, leading to a reduction in N concentrations between 5% and 10% (Figures 2e and S5e). Lower summer flows also translate into reduced dilution capacity for effluent flows, and therefore increased P concentrations. The model results suggest that monthly P concentrations are expected to increase by up to 33% at London, and up to 31% at Oxford and at Cricklade (Figures 2d and S5d). Similar increases are expected in algal production, as the model predicts increases in chlorophyll-a concentration in the summer by up to 36% at London, up to 37% at Oxford, and up to 43% at Cricklade. Dissolved oxygen concentrations should decrease by around 10% (with stronger effects in summer) due to increased water temperatures (Figures 2c and S5c) because the saturation concentrations of DO in fresh waters fall with increasing temperature. As O concentrations also will be influenced by temperature, nutrients and biological activity (i.e., photosynthesis and respiration) that are modelled by INCA-PEco, the P removal scenario increased O concentrations in the summer but not the winter with stronger effects at lower reaches (Figures 2c and S5c). Expansion of arable land is not expected to bring changes as large as the ones triggered by climate change on the water quality of the River Thames. The most noticeable impacts are on N concentrations, which should increase under a scenario of arable land expansion throughout the whole River Thames catchment by 5%–10% (Figures 2e and S5e). Very small variations are expected in the P concentration of the River Thames as a consequence of agriculture expansion, since the main source of P in the catchment is not agriculture but rather treated wastewater effluents. On the contrary, P stripping down to 0.3 mg/L in every sewage treatment plant in the catchment will have a very significant impact on P concentrations across the river (with knock-on consequences for algal growth and DO concentrations). The model indicates that P concentrations could be reduced in summer months by up to 90% under this scenario (Figures 2d and S5d).

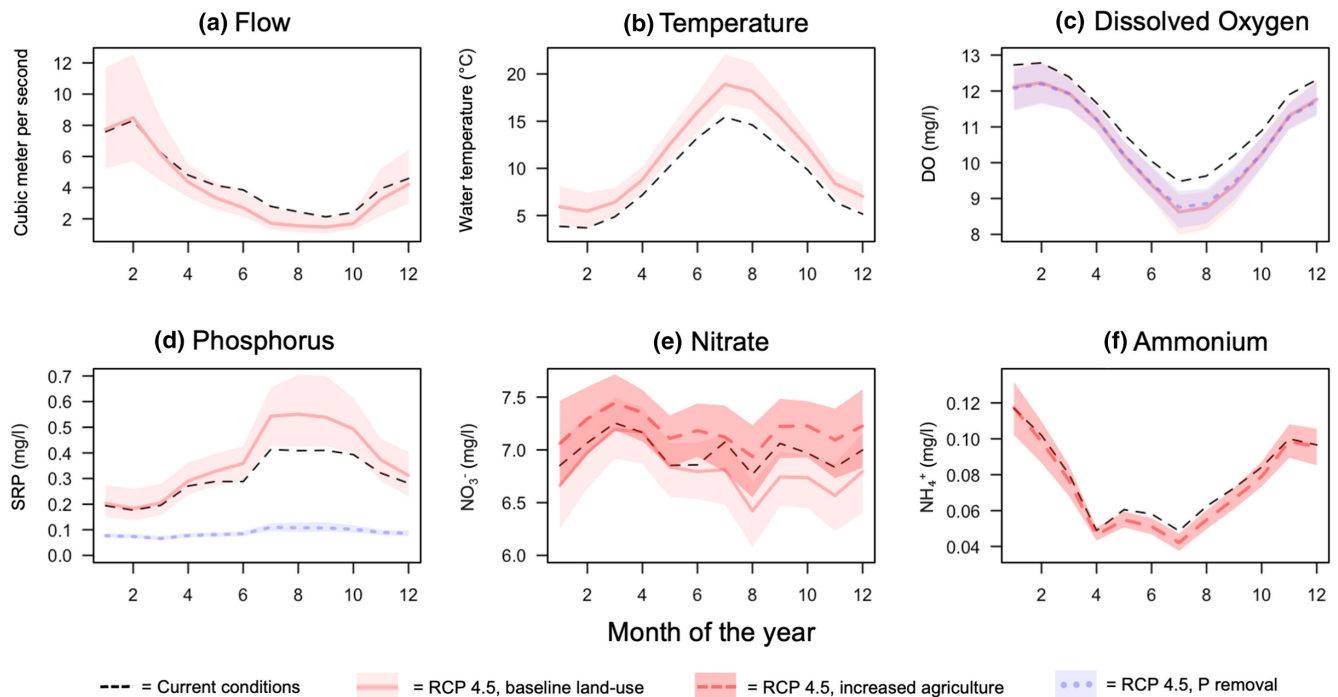


FIGURE 2 Results of hydrology and water-quality models for Thames at Cricklade as monthly series for (a) flow, (b) water temperature, (c) dissolved oxygen (DO), (d) phosphorus (P), (e) nitrate, and (f) ammonium. Dashed black lines show the current conditions. Solid red line represents the RCP 4.5 climate scenario with no changes in land use for the 2080s. Dashed red line represents the RCP 4.5 climate scenario with increased agriculture for the 2080s. Dotted blue line represents the RCP 4.5 climate scenario with the P removal land-use scenario for the 2080s. Lines show median results with the upper and lower bounds of the shaded polygons representing the 5th and 95th percentiles of model results. Not all scenarios are shown for each variable and the purple area in (c) shows an overlap between the baseline and the P removal land-use scenarios.

3.2 | Changes in macroinvertebrate communities

Most of the GLME models had marginal $R^2 > 0.2$ and some models fitted the data surprisingly well considering the simple model structures we used; the model for EPT richness had a marginal $R^2 = 0.35$ (Table S2). Increasing flow had a positive effect on all community-level responses but had no significant effect on the abundance of annelids, *Baetis*, or *Elmis*. Higher proportions of silt/clay decreased all indices. Warmer temperatures increased total richness, the abundance of annelids, EPT taxa, and *Elmis*, but decreased the abundance of *Baetis*, and decreased DEHLI. Increasing DO increased most indices but had no significant effect on WHPT-ASPT, DEHLI, total richness or EPT richness, and decreased the abundance of *Elmis*. Higher levels of P increased the abundance of annelids but negatively impacted all other responses. Nitrate had the opposite effect; it increased all indices except for the abundance of annelids. Finally, increasing levels of ammonia decreased all responses except for the abundance of *Baetis* and *Elmis* (Table S2). For three additional models (WHPT-ASPT, DEHLI, EPT Abundance) that included all pairwise interactive terms between temperature, flow, P and O ($n = 6$), most terms (six of 18) were not significant. However, the effect of temperature became more negative with increasing levels of DO (for WHPT-ASPT and DEHLI), the effect of O became more positive with increasing levels of P (for WHPT-ASPT and DEHLI), and the effect of flow became more

negative with increasing levels of O for DEHLI and with increasing levels of P for WHPT-ASPT.

The climate change scenarios had mixed effects on the community-level responses. Total score of the WHPT index and total macroinvertebrate richness both slightly decreased under the climate change scenarios but only at the final reaches of the river, with stronger impacts under RCP 4.5 compared to RCP 2.6 (Figures 3a and S6a). The average score per taxon of the WHPT index, however, decreased under the climate change scenarios at all sites with a stronger decrease under RCP 4.5 (Figure 3b). The scenarios with intensified agriculture had negligible effects on macroinvertebrate responses, but the P removal scenario showed strong positive increases to all community-level responses under both climate change scenarios. The LIFE index responded to the climate and land-use scenarios in the same way as the WHPT total score (Figure 3c), but the DEHLI index responded more negatively to the climate change scenarios and was less impacted by the P removal strategy (Figure 3d).

Differences between the total WHPT score and WHPT-ASPT can be explained by the variability of taxon-specific responses (Figures 4 and S6). Richness of the EPT taxa was predicted to decrease under climate change scenarios, but to increase when combined with the P removal scenario. Conversely, abundance of annelids increased under both climate change scenarios with a greater increase under RCP 4.5, but this effect was mitigated by the P removal strategy, which led to a reduction in the abundance of

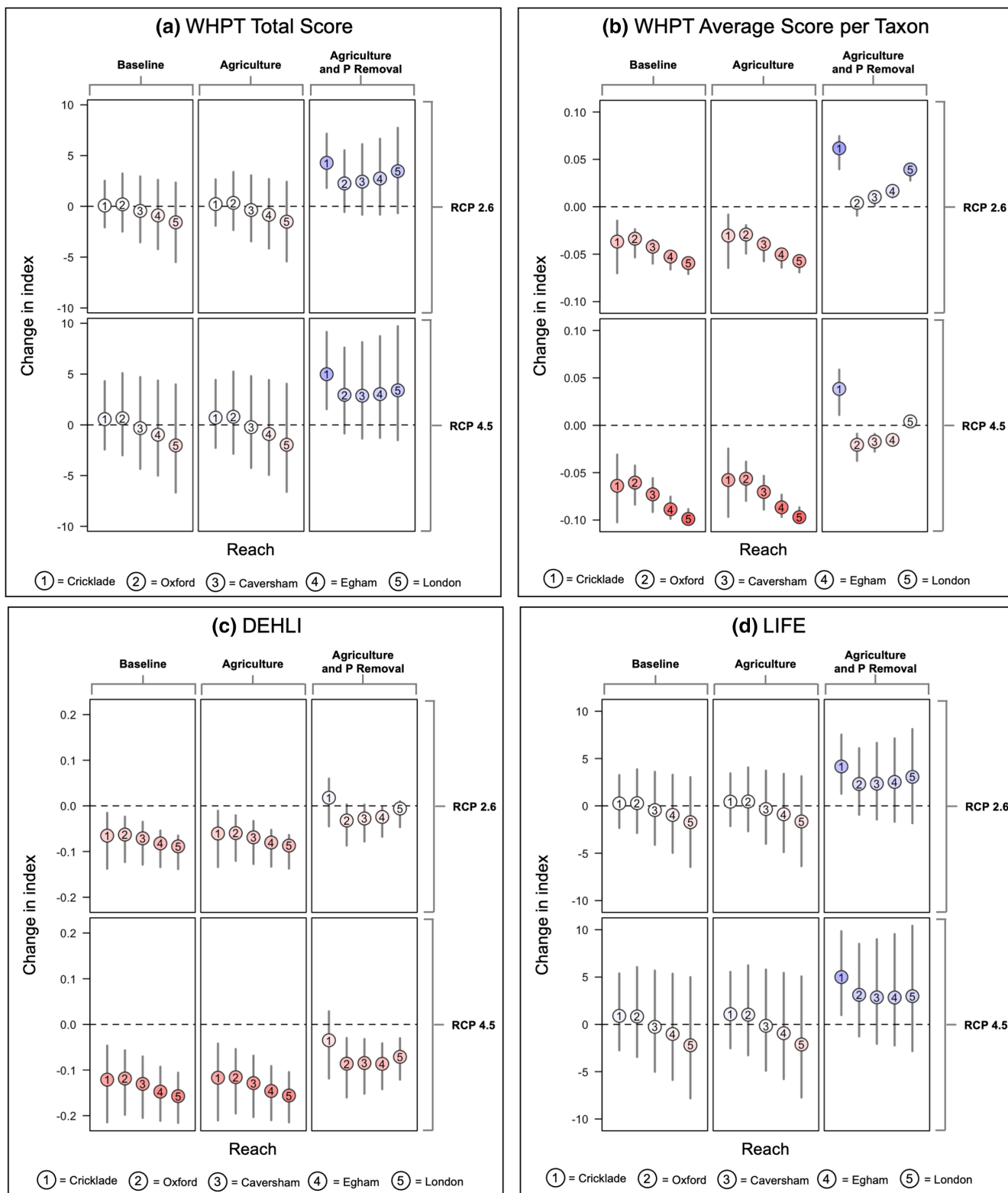


FIGURE 3 Individual and combined effects of climate-change and land-use change on (a) WHPT total score, (b) WHPT average score per taxon, (c) DEHLI and (d) LIFE. For each metric, the six sub-plots are different combinations of climate and land-use change scenarios with the two rows representing the climate scenarios and the three columns representing the land-use scenarios. Each numbered point shows the responses at a different site along the catchment ordered from upstream to downstream. Red depicts a reduction in the index while blue depicts an increase in the index. Error bars show the range of results from the 5th to the 95th percentile of model runs.

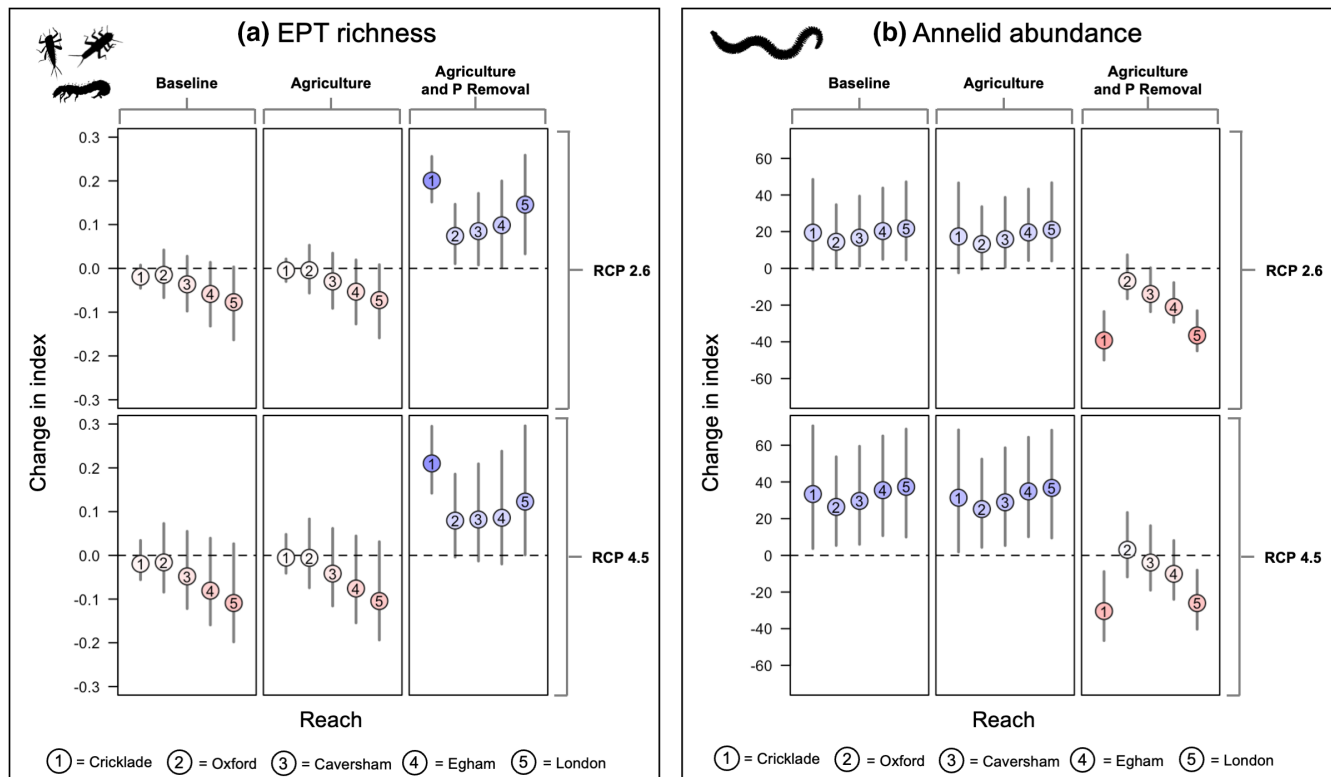


FIGURE 4 Individual and combined effects of climate-change and land-use change on (a) the richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa, and (b) the abundance of annelids. For each metric, the six sub-plots are different combinations of climate and land-use change scenarios with the two rows representing the climate scenarios and the three columns representing the land-use scenarios. Each numbered point shows the responses at a different site along the catchment ordered from upstream to downstream. Red depicts a reduction in the index while blue depicts an increase in the index. Error bars show the range of results from the 5th to the 95th percentile of model runs.

these pollution-tolerant taxa. The abundance of EPT taxa and *Elmis* increased under the climate change scenarios, and was not greatly impacted by the phosphorus removal scenario. However, the abundance of *Baetis* decreased under climate change and responded very positively under the P removal scenario (Figure S6).

4 | DISCUSSION

Our results reveal that climate change will impact macroinvertebrate communities via changes in water quality and habitat quality, but that a reduction in local P pollution through improving wastewater treatment has the potential to mitigate these impacts. Overall, we demonstrate that catchment-scale modelling can give powerful insights into the combined effects of global and local anthropogenic stressors on riverine biodiversity. By modelling many interconnected stressors describing water quality using process-based models we were able to reveal complex interactions between climate change and land-use change. Although total macroinvertebrate richness increased under climate change scenarios, taxon-specific responses suggested that there will be “winners” and “losers” and that the composition of macroinvertebrate communities may shift towards more pollution-tolerant and common

taxa. Indeed, contrasting results for the average score per taxon and the total score of the WHPT index, as well as the variability of taxon-specific responses, illustrate the importance of understanding both community-level and taxon-specific responses (Guse et al., 2015; Jähnig et al., 2021; Mantyka-Pringle et al., 2014; Sultana et al., 2020). Based on the model validation study (Figure S3), our simple models can predict changes in macroinvertebrate indices with high accuracy but are less accurate at predicting changes to the abundance of specific taxonomic groups. It is unsurprising that order-level abundance is not as informative as community indices as there can be great variability even within species from the same family in their sensitivities to different stressors (which may also explain the insignificant effects of temperature and O on EPT richness; Table S2). Nevertheless, when very abundant genera (e.g., *Baetis* and *Elmis*) or more generally pollution-tolerant taxa (e.g., annelids) are considered, taxon-specific responses add important insights into the type of compositional changes that may be expected. For instance, the contrasting responses of *Baetis* and *Elmis* (genera that receive similar scores on the WHPT scale) is driven by differences in their responses to temperature, O and P (Table S2). In a study such as ours, however, results may become more specific to the study system as taxonomic resolution increases as a result of local adaptation and species pools (e.g., pollution-tolerant

taxa may be particularly common in the Thames). Although the WHPT and LIFE indices are designed to be sensitive to specific stressors (nutrient pollution and low flow, respectively) their almost identical responses to scenarios (Figure 3) highlight how some stressor-specific indices can be confounded by other stressors or how different stressors can impact macroinvertebrate communities via similar pathways such as deoxygenation (Jones et al., 2023; Simmons et al., 2021). Conversely, the strong response to climate change but weak response to P removal of the more recently developed DEHLI index suggest that this index is more capable of tracking the specific ecological impacts of low flow. While agricultural intensification was not predicted to impact macroinvertebrate responses, the P removal strategy had a very large effect that was able to offset the impacts of even the more severe climate change scenario. These results add to the growing body of evidence that local land-use practices can either mask or counteract the direct impacts of climate change (Durance & Ormerod, 2009; Ibáñez et al., 2023; Kuemmerlen et al., 2015; Morris et al., 2022; Vaughan & Gotelli, 2019).

The macroinvertebrate responses across the five sites supported the idea that climate change impacts can accumulate along the catchment, but the exact results were nuanced and revealed the importance of P. The four sites between and including Thames at Oxford and Thames at London showed a monotonic trend for most community-level and taxon-specific responses. Although temperature increases are consistent across the catchment, reductions of flow during summer months are proportional to the flow at a given site along the river (compare scales in Figures 2a and 55a). As a result, absolute reduction of flow increases along the catchment, which subsequently causes increases in the absolute concentration of P (resulting from reduced dilution capacity of effluent) and increases in the absolute concentration of Chlorophyll-*a* (resulting from algal growth following eutrophication). Therefore, the impact of climate change on macroinvertebrate communities via changes to water quality increases along the main river channel, which creates spatial context-dependency of responses with strongest effects at the lowest reaches (e.g., Figure 3a). However, this causal chain appears to be strongly influenced by the P removal strategy and by local sources of P. Thames at Cricklade does not follow this monotonic trend as the modelled baseline P concentrations are overestimated at this site. Furthermore, between Thames at Oxford and Thames at London the trends in macroinvertebrate responses are reversed by the P removal strategy, as absolute reductions in P and associated improvements in water quality build up along the catchment. This reinforces the idea that although climate change is predicted to have widespread impacts on water quality that will build up along catchments, local land-use practices and re-oligotrophication will still be extremely important in determining the realised ecological status of freshwater ecosystems (Ibáñez et al., 2023; Vaughan & Gotelli, 2019).

Our simulation approach was able to model some, but not all, of the effects of climate change on macroinvertebrate communities.

The increases in macroinvertebrate richness and abundance of most taxa associated with the climate change scenarios were driven by increases in water temperature, which is a result that has previously been found in manipulative experiments (e.g., Piggott et al., 2015), field observations (e.g., Castella et al., 2001) and modelling studies (e.g., Kuemmerlen et al., 2015). Positive effects of warming—up to some limit—on species richness and total abundance are expected based on the metabolic theory of ecology and the expansion of species ranges (Woodward et al., 2010), but these community-level properties can hide important information regarding species turnover and changes in beta-diversity (Larsen et al., 2018; Milner et al., 2023). We also focused on mean changes to temperature and flow rather than on their variability or on the frequency of extreme events such as droughts or heatwaves, which can have larger impacts on biodiversity compared to gradual changes (Sabater et al., 2023). Furthermore, our goal was to understand and predict the direct impacts that climate change has on macroinvertebrate communities via changes to water quality. However, indirect effects of climate change, including the increased frequency and success of species invasions (Walther et al., 2009), the rewiring of ecological networks (O'Gorman et al., 2019), and potential additional pressures on agricultural and wastewater-treatment systems, also will contribute to the ultimate impacts of climate change on riverine ecosystems.

The predicted impacts of agricultural intensification on macroinvertebrates were surprisingly small. This counterintuitive result can be explained partly by the data available to us, but also partly by the current ecological state of the study system. Firstly, the INCA-N model that we used to model N levels in the river can generate predictions for ammonium and nitrate but not nitrite, which is a stronger predictor of macroinvertebrate community status that typically has more negative impacts on sensitive taxa at environmentally realistic concentrations (Soucek & Dickinson, 2012). We also did not model the effect that pH can have on the equilibrium between ammonium and ammonia, so we will not have precise estimates for the toxicity of N pollution. Furthermore, nitrate increases primary production which may therefore increase the abundance of many taxa and overall macroinvertebrate richness (Guse et al., 2015). As a result, the increases in N compounds as a consequence of agricultural intensification may be counteracting each other; positive impacts on productivity may negate the negative impacts of toxicity (Table S2). However, agricultural intensification had a small impact on water quality in general and this effect was reduced even further by climate change owing to reduced precipitation leading to reduced fertiliser runoff. The Thames catchment is already a highly impacted area—it is one of the catchments in the UK with the poorest ecological status (Vaughan & Gotelli, 2019)—so the communities present may already be over-represented by tolerant, and even non-native, taxa that are resistant to further anthropogenic stress (Guareschi et al., 2021). Part of the explanation for the negligible impact of agricultural intensification on macroinvertebrate communities may therefore be related to a shifting baseline. Applying our approach in a more pristine catchment, with the same intensity of stressors, would be likely to reveal a larger effect of agricultural intensification.

Our research builds a robust understanding of macroinvertebrate community responses to a network of stressors associated with climate change and land-use change, but there are some improvements that could be made in future studies. As this was the first study integrating macroinvertebrate responses with the INCA family of models, we aimed to maximise interpretability and we wanted to avoid overfitting. This is why we used linear regressions with a relatively low number of variables for the macroinvertebrate models. An exciting next step, however, would be to use modelling approaches for the macroinvertebrate community responses that can include more factors, complex nonlinear responses, and even complex interactions such as nonlinear pairwise interactions or even higher-order interactions (Duncan & Kefford, 2021; Kefford et al., 2023; Ryo et al., 2018). Modelling tools that could accommodate missing data would be particularly useful as some informative water-quality variables such as Chlorophyll-*a* and BOD, which are modelled by INCA-PEco, are often missing from the UK Environment Agency's "Water Quality Archive" records. Interpretable machine learning techniques offer great potential as they aim to maximise predictive power while maintaining high levels of model interpretability (Ryo, 2022). Using more complex models (e.g., that account for the network structure of river systems and the proximity of sites) would presumably have increased model accuracy but would have complicated the ecological forecasts and would have reduced the interpretability and generality of our results. Although our two-stage modelling approach is currently limited by the common issue of propagation of uncertainty and uses relatively simple regression models, its high interpretability makes it a useful step towards integrating macroinvertebrate responses into future process-based models of river ecosystems.

Process-based modelling offers a way of investigating the mechanisms of stressors interactions at a landscape scale. Recognising that these interactions can either be related to direct chemical and physical interactions between stressors that influence their ultimate intensities (i.e., "chain interactions") or to the effects of one stressor modifying the biological effect of another (i.e., "modification interactions") is an important first step (sensu Didham et al., 2007). Chain interactions are dealt with explicitly in our analysis by using process-based models where networks of stressors and biological responses are linked through process equations (that are often temperature-dependent). These chain interactions provide mechanistic insights into some intriguing landscape-scale interactions between global and local stressors (such as how climate change reduced N pollution via a reduction in runoff from agricultural lands as a result of reduced precipitation) and the climate change-by-reach interaction where deteriorations in water quality were predicted to increase along the main river channel. Although some modification interactions are incorporated into the process-based modelling (e.g., temperature dependence of P impacts on algal growth), including interactive terms between key water-quality parameters at the level of the macroinvertebrate responses in the regression models did not change fitted estimates (Figure S2b) and so were excluded from the

ecological forecasts to maximise interpretability. However, some of these interactive terms were significant (e.g., effects of temperature on WHPT-ASPT and on DEHLI became more negative with increasing O levels and the flow by P interaction suggests that nutrient effects may vary with stream order) so future research could use mechanistic knowledge of these modification interactions (e.g., how warming influences the effect of pollutants and *vice versa* [Litchman & Thomas, 2023; Verberk, Durance, et al., 2016]) to build more accurate process-based models for river ecosystems.

Our work has demonstrated the importance of research on the cumulative effects of multiple stressors at the landscape scale, a spatial scale of relevance to conservation biologists and ecosystem managers. It has also shown the importance of long-term monitoring programmes for understanding responses to anthropogenic global change; this research would not have been possible without the EA's water quality and ecology datasets. Using process-based catchment modelling allowed us to predict how the interacting network of stressors associated with climate change and land-use change may impact macroinvertebrate communities in the future. Our work therefore lays a solid foundation for the future integration of macroinvertebrate modules into process-based modelling frameworks such as the INCA family of models. Although it is important not to underestimate the potential ecological impacts of climate change, our results offer some solace given that the P removal strategy we simulated was able to offset some of the impacts of climate change. Robust understanding of the interplay between the unavoidable impacts of global climate change and the management of local land use stressors will be crucial for effective conservation of biodiversity and ecosystem functioning in the Anthropocene.

AUTHOR CONTRIBUTIONS

Conceptualisation: James A. Orr, Michelle C. Jackson. *Developing methods:* James A. Orr, Gianbattista Bussi, Paul G. Whitehead. *Data analysis:* James A. Orr, Gianbattista Bussi, Paul G. Whitehead. *Preparation of figures and tables:* James A. Orr. *Writing:* James A. Orr, Gianbattista Bussi, Paul G. Whitehead, Jocelyne M. R. Hughes, Michelle C. Jackson.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GitHub at <https://github.com/jamesaorr/local-global-stressors>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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