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Potential drivers of changing ecological conditions in English and Welsh rivers since 1990

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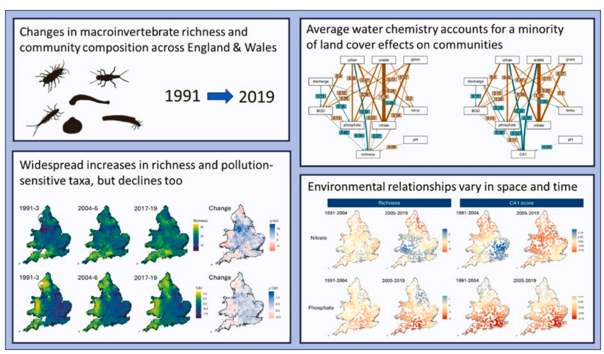
HIGHLIGHTS

- National-scale improvements in river quality can disguise divergent regional changes.
- Pollution-sensitive macroinvertebrates declined in upland streams, 1991–2019.
- Richness declined in several areas, contrasting with widespread increases.
- The roles of climate, water quality and land cover varied temporally and spatially.
- This study captures the complexity of changing river status and its potential drivers.

GRAPHICAL ABSTRACT



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ABSTRACT

River invertebrate communities across Europe have been changing in response to variations in water quality over recent decades, but the underlying drivers are difficult to identify because of the complex stressors and environmental heterogeneity involved. Here, using data from ~4000 locations across England and Wales, collected over 29 years, we use three approaches to help resolve the drivers of spatiotemporal variation in the face of this complexity: i) mapping changes in invertebrate richness and community composition; ii) structural equation modelling (SEM) to distinguish land cover, water quality and climatic influences; and iii) geographically weighted regression (GWR) to identify how the apparent relationships between invertebrate communities and abiotic variables change across the area. Mapping confirmed widespread increases in richness and the proportion of pollution-sensitive taxa across much of England and Wales. It also revealed regions where pollution-sensitive taxa or overall richness declined, the former primarily in the uplands. SEMs confirmed strong increases in average biochemical oxygen demand and nutrient concentrations related to urban and agricultural land cover, but only a minority of land cover's effect upon invertebrate communities was explained by average water

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chemistry, highlighting potential factors such as episodic extremes or emerging contaminants. GWR identified strong geographical variation in estimated relationships between macroinvertebrate communities and environmental variables, with evidence that the estimated negative impacts of nutrients and water temperature were increasing through time. Overall the results are consistent with widespread biological recovery of Britain's rivers from past gross organic pollution, whilst highlighting declines in some of the most diverse and least impacted streams. Modelling points to a complex and changing set of drivers, highlighting the multifaceted impacts of catchment land cover and the evolving role of different stressors, with the relationship to gross organic pollution weakening, whilst estimated nutrient and warming effects strengthened.

1. Introduction

Globally, rivers and other freshwater ecosystems are widely considered to be in poor biological or physico-chemical condition (Dudgeon et al., 2006; Reid et al., 2018), with large declines in many freshwater vertebrates (WWF, 2022). Conversely, for macroinvertebrates – which are often used as an important feature for biomonitoring in rivers – increases in richness, abundance and/or the prevalence of pollution-sensitive taxa over recent decades have been reported in some regions (e.g. Outhwaite et al., 2020; van Klink et al., 2020; Pharaoh et al., 2023; Haase et al., 2023), although this trend is not universal (e.g. Baranov et al., 2020; Rumschlag et al., 2023). Where increases in diversity have occurred, recovery from historically poor water quality is a likely explanation (van Klink et al., 2020), but teasing apart the roles of other potential stressors is difficult. In addition to an often complex and changing mixture of pollutants, rivers are impacted by flow modifications, catchment land use, changing climate and invasive species among other factors (Dudgeon et al., 2006). Coupled with the large temporal variability characteristic of many river systems, disentangling the causes of changing river biodiversity is a complex task.

Two key challenges of identifying the environmental drivers of change in communities of river organisms are the presence of multiple, potentially interacting stressors (Birk et al., 2020), and strong context dependency, making it difficult to identify general relationships (e.g. Burdon et al., 2023). In the latter case, the apparent relationships between river organisms and their environment may vary geographically, depending upon such things as environmental variation or antecedent conditions not captured by the suite of explanatory variables recorded – for example missing geological or pollutant data (Ogle et al., 2015). These factors may alter observed relationships, such as where organisms modulate the mobilisation or effects of fine sediment delivery from agricultural land (Wilkes et al., 2019), where responses to dam removal in a river system are altered by the distribution of other impoundments (Foley et al., 2017), or where past management continues to influence current species composition (e.g. Sawtschuk et al., 2014). In a bid to understand patterns and their drivers more clearly, there is value in looking for geographical variation in species-environment relationships.

There have been large changes in macroinvertebrate communities in UK rivers over the last 30 years, interpreted primarily as biological recovery from historical gross pollution (Outhwaite et al., 2020; Pharaoh et al., 2023). Sanitary indicators such as ammonia, Biochemical Oxygen Demand (BOD) and phosphate concentrations have declined widely since 1990 (Supplementary Fig. 1), as a result of improvements in wastewater treatment arising from the Urban Wastewater Treatment Directive. Taxonomic richness, functional diversity and the prevalence of pollution-sensitive invertebrate taxa have all increased since 1990, although there is some evidence that trends have slowed in recent years (Outhwaite et al., 2020; Pharaoh et al., 2023). Across England and Wales, inter-annual and longer-term changes have been linked to variations in water chemistry, discharge, and land cover, sometimes mediated by catchment geology (e.g. Monk et al., 2008; Vaughan and Ormerod, 2012, 2014; Pharaoh et al., 2023; Powell et al., 2023; Qu et al., 2023). However, one of the weaknesses in existing analyses is that the traditional regression-based approaches might not characterise the complex interactions between multiple stressors (Villeneuve et al., 2018). Moreover, there have been few attempts to disaggregate national-scale changes to reveal more detailed, local-scale patterns within the UK, nor to explore how the observed relationships between communities and the abiotic environment might vary geographically. In England and Wales, biological recovery has been greatest in urban rivers (Pharaoh et al., 2023; Qu et al., 2023), whilst there is some evidence that rivers draining some upland areas and the more diverse streams in southwest Britain have declined in quality (Vaughan and Ormerod, 2012). Obtaining a fuller picture of such spatio-temporal changes, their underlying drivers and how apparent drivers vary across the country, would provide both provide greater insight into current status and inform possible management interventions, from local to national scales.

Using data from 1991 to 2019, collected across England and Wales as part of routine national monitoring, this study aimed to: i) map changes in macroinvertebrate communities over three decades; ii) use structural equation models (SEMs) to examine how annual water chemistry, catchment land cover and climate might account for changing invertebrate community composition and richness; and iii) employ geographically weighted regression (GWR) to investigate how apparent relationships between water quality, land cover, climate and invertebrate communities varied across England and Wales, and if these relationships differed between the first and second halves of the study period.

SEMs are being used increasingly for their ability to handle complex relationships between multiple environmental variables and biological responses, and to test causal hypotheses (Lefcheck et al., 2018). They can disentangle complex relationships by distinguishing direct relationships between two variables from indirect ones, where a variable influences another via one or more intermediaries (Shipley, 2016). In the current study, a key aim was to assess the relative importance of two pathways through which catchment land cover can affect macroinvertebrate communities: via its effect upon water chemistry or 'directly' (either independent of its role in water quality or via other, less widely measured chemical determinands e.g. pesticides). Based on previous studies highlighting the strong impacts of urban land cover (e.g. Pharaoh et al., 2023), we predicted that catchment urbanisation and biochemical oxygen demand (BOD) would have stronger relationships with invertebrate communities than agricultural land cover or nutrient concentrations. GWR is a valuable exploratory tool, complementing 'global' analyses such as conventional regression or SEM by estimating regression coefficients at each sampling location based on the values within a local neighbourhood. This reveals geographical variation in modelled relationships and can highlight possible missing variables or interaction terms, informing future improvements in global models (Foody, 2005). We predicted that modelled relationships between invertebrate communities, and water quality, climate and land cover would vary across England and Wales, which could help to explain the difficulties in resolving multiple stressor effects at large spatial scales and highlight the importance of considering the local or regional context.

2. Methods

2.1. Macroinvertebrate data

The data set used in the current study was based upon that used by Pharaoh et al. (2023), which provides a full description of site selection and filtering criteria: the only difference here was that some additional samples for the study period were available to increase the sample size. Briefly, macroinvertebrate data were collected by two UK statutory agencies – the Environment Agency and Natural Resources Wales, and their predecessor the National Rivers Authority – during routine river monitoring across England and Wales (Environment Agency, 2023a; Natural Resources Wales, 2023). A standardised 3-minute kick sampling protocol was used and a joint quality assurance programme showed near-constant error rate 1991–2011 (Murray-Bligh and Griffiths, 2022), with similar sample processing protocols retained for England and Wales after 2011, allowing meaningful comparisons of change through time. Data were collated for a 29-year period (1991–2019 inclusive) and filtered to retain samples collected in spring (March–May inclusive) and remove locations immediately downstream of effluent outfalls. This resulted in 48,382 samples from 3982 sites (cf. 47,009 in Pharaoh et al., 2023). Data were selected for 78 families or composite taxa, and simplified to presence-absence records to avoid problems due to variations in taxonomy and recording of abundance through time (Pharaoh et al., 2023).

Two descriptors of the invertebrate community were calculated for each sample: i) taxonomic richness and ii) community composition, the latter using the first axis of a correspondence analysis (CA1) calculated from macroinvertebrate presence-absence data. CA1 (eigenvalue = 0.260) explained 9 % of the variance (Pharaoh et al., 2023), with negative CA1 scores representing communities with greater proportions of taxa associated with poorer water quality, slower flow and siltier substrata (e.g. oligochaetes and molluscs) whilst positive scores were indicative of taxa typical of better water quality, faster flows and greater oxygenation (e.g. Ephemeroptera, Plecoptera and Trichoptera i.e. EPT taxa; see Supplementary Fig. 3 for loading coefficients).

2.2. Environmental data

For GWR and SEM, a subset of the 3982 locations was selected where macroinvertebrate sampling locations could be matched to nearby water chemistry sampling locations and discharge gauging stations. Water chemistry data covering 1990–2019 were sourced from routine monitoring by the Environment Agency and Natural Resources Wales. Annual median pH, temperature, biochemical oxygen demand (BOD), orthophosphate (hereafter phosphate) and nitrate were calculated at each site for the 12 months prior to the spring macroinvertebrate sampling period. Where $\geq$50 % of values were below detection limits, regression-on-order-statistics was used to estimate medians (NADA package; Lee, 2020): this, and all subsequent statistical analyses, were carried out using R version 4 (R Core Team, 2021). Missing nitrate concentrations were predicted from total oxidised nitrogen (TON) using a linear regression calibrated using samples where both determinands were recorded (Vaughan and Ormerod, 2012).

Discharge data (1990–2019) were accessed from the UK National River Flow Archive and the median daily discharge for the 12 months prior to the spring sampling period was calculated. Discharge was divided by gauging station catchment area to provide a standardised measure of discharge (units = $m^3\ s^{-1}\ km^{-2}$).

Macroinvertebrate sampling sites were matched to the nearest water quality and gauging locations. Sites were removed where no match was found within 1 km for water chemistry and 5 km for a gauging station (Vaughan and Ormerod, 2012) – these different criteria reflecting the greater density of chemical sampling points (cf. gauging stations) and provided a good compromise between close spatial correspondence and maximising the resulting sample size. Data were filtered so that only years which contained macroinvertebrate, chemistry and discharge data were retained, resulting in a final sample size for this analysis of 672 macroinvertebrate locations, with a mean of 5.4 years sampled per site (Supplementary Fig. 2).

Finally, the catchment for each sampling location was derived from a 50 m resolution digital elevation model (Ordnance Survey Terrain 50) using ArcHydro tools (ESRI ArcGIS 10.7.1). The percentages of urban land cover (combining the urban and suburban categories), improved grassland and arable agriculture within each catchment were calculated from the 1 km resolution UK Land Cover Map 2007 (Morton et al., 2014) – the map closest to the centre of the time series.

2.3. Mapping invertebrate communities

Ordinary kriging (gstat package; Pebesma, 2004) was used to interpolate macroinvertebrate data between the 3982 sampling locations to produce 10 km resolution maps of richness and CA1 scores (Vaughan and Ormerod, 2012). Three time points (1991–1993, 2004–2006, 2017–2019) were used, each with a 3-year window to increase the chances that a site was sampled on each occasion; mean values were calculated where a site was sampled multiple times in a window. Maps were clipped to exclude areas which fell >25 km from the nearest invertebrate site, resulting in some gaps for north-west and south-west England. The final sample sizes were 2639, 3819 and 1664 for 1991–1993, 2004–2006 and 2017–2019 respectively. The same approach was used to generate water chemistry maps from the 672 locations for the same periods to provide context for the biological changes.

2.4. 'Global' structural equation modelling

SEMs were fitted for richness and CA1 across the 672 sites and 29 years. The two models included nine environmental variables: pH, BOD, nitrate, phosphate, water temperature, discharge, and catchment cover by urban land, improved grassland and arable crops. BOD, nitrate, phosphate, discharge and urban land cover were all log-transformed to reduce skewness, and a correlation matrix between all variables was used to assess the potential for collinearity problems. All correlations were $<|0.7|$ – a simple, but effective rule for minimising collinearity issues in data analysis (Dormann et al., 2013) – so all nine variables were used in the SEM and GWR analyses.

SEMs were constructed using the piecewiseSEM package (Lefcheck, 2016) because it is compatible with longitudinal data. Land cover, pH and discharge were treated as exogeneous variables i.e. they were assumed to be unaffected by the other variables in the model (Lefcheck, 2016). In the case of discharge this helped to simplify the model: whilst discharge is affected by catchment land cover, the relationship is complex and strongly influenced by local precipitation and other catchment characteristics (Shaw et al., 2011) which would require extensions to the overall SEM. Land cover relationships with water temperature, by contrast, are generally simpler and more readily captured by statistical models (Wehrly et al., 2009), hence temperature's links to land cover and discharge were included in the model. The nature of the piece-wise SEM fitting meant that the other paths in the model – hence the overall interpretation – were not affected by omitting land cover-discharge linkages (Lefcheck, 2016). The remaining variables were modelled using linear mixed-effects models (LMM; *nlme* package; Pinheiro et al., 2021), breaking the SEM into five LMMs (Table 1). LMMs were fitted with sampling site as a random effect to account for repeated sampling through time and autoregressive moving average error terms, up to second-order, were used to model residual temporal autocorrelation (Lefcheck et al., 2018). The error structure chosen for each model was the one that produced the lowest Akaike information criterion.

The same starting model was constructed for richness and CA1 (Fig. 1). This distinguished 'direct' links, where one variable affected another independent from the other variables in the model (e.g. BOD

Table 1
The response and explanatory variables included in the five mixed-effect models that formed the SEM. LC = catchment percentage land cover.

Model	Response	Explanatory variables
1	Nitrate	Urban LC, improved grassland LC, arable LC, discharge
2	Phosphate	Urban LC, improved grassland LC, arable LC, discharge
3	BOD	Phosphate, urban LC, improved grassland LC, arable LC, discharge
4	Water temperature	Urban LC, improved grassland LC, arable LC, discharge
5	Richness or CA1	Nitrate, phosphate, pH, temperature, BOD, discharge, urban LC, improved grassland LC, arable LC

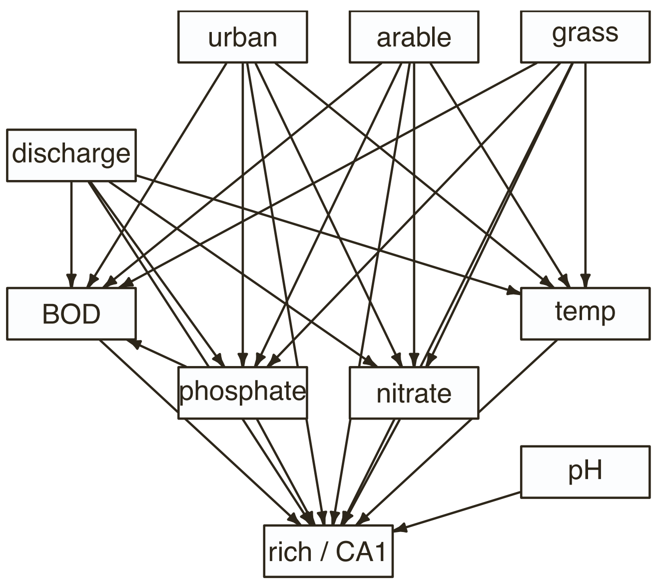

Fig. 1. Conceptual model for the effects of catchment land cover, climate and water chemistry upon invertebrate richness and CA1. Arrows represent hypothesised relationships between the abiotic variables and the invertebrate community.

and phosphorus linked to CA1), from indirect ones mediated via other environmental variables (e.g. urbanisation linked to CA1 via its effect upon BOD). In reality, these direct links are likely to be mediated via other unrecorded variables (e.g. the link from phosphate to CA1 could be via its effects upon primary production), but the SEM approach starts to resolve the causal pathways. Catchment land cover (urban, arable and improved grassland) and discharge were hypothesised to affect nitrate, phosphate and BOD via inputs from the catchment and dilution effects (Models 1–3), and water temperature via thermal effects and dilution (Model 4). For BOD, phosphate was hypothesised to play a role alongside land cover and discharge (Mallin and Cahoon, 2020). Model 6 encapsulated all of the hypothesised 'direct' drivers of richness and CA1, with each of the water chemistry measures, land use and discharge.

The initial fit of the models produced several likely meaningless independence claims, where an improbable relationship is derived between two variables in the model where there is no scientific reasoning (Lefcheck, 2016) e.g. water temperature explaining phosphate concentration. These relationships were specified as correlated errors in the SEMs and the overall fit of the model assessed using the Fisher's C statistic: both models showed adequate fit ($p > 0.05$; Lefcheck, 2016) to the data ($C_6 = 12.278$, $p = 0.056$ for both richness and CA1 models). The outputs of the model were expressed as standardised regression coefficients, making it easier to compare the relative strength of relationships between different pairs of variables (i.e. paths in the model).

2.5. Geographically weighted regression

GWR was used to investigate how invertebrate communities were related to water quality, land cover and climate across England and Wales. Models were fitted separately for 1991–2004 and 2005–2019 to assess whether the relationships varied through time, using mean values for invertebrate and water chemistry variables in each time window. To ensure consistency in spatial coverage between the two time periods, only sites which were sampled in both were retained from the paired water quality and invertebrate biology data ($n = 465$). The same set of nine variables and transformations was used as for the SEMs.

Four GWRs were fitted using the spgwr package (Bivand and Yu, 2022): separate models for 1991–2004 and 2005–2019, for both richness and CA1. Prior to fitting the GWRs, conventional linear regressions were fitted and the residuals assessed to check overall model fit. The optimal bandwidth for each GWR model, the extent of the neighbourhood around each sampling point used for fitting the model, was determined using cross validation (gwr.sel function in spgwr): values equating to 5.1–10.3 % of the data set were selected across the four models and used to fit the GWRs. Two main GWR outputs are presented: i) local R^2 calculated at each sampling site as a measure of explanatory ability and ii) the regression coefficient estimates at each location.

3. Results

3.1. General patterns

Macroinvertebrate communities showed clear geographic structure across England and Wales. Communities in the low nutrient, cleaner, cooler waters of the upland north and west were characterised by pollution-sensitive taxa which shifted to more pollution-tolerant taxa in the warmer, nutrient rich waters with higher BOD in the south and east. Arable and urban land cover also became more extensive along this gradient (Fig. 2 & Supplementary Fig. 4).

The most macroinvertebrate-rich rivers were mostly in rural southwest England and Wales, but richness declined in these areas across the study period by 5–10 % or more (≈2–4 taxa; Fig. 2). Richness also declined between 1991 and 2019 in parts of northern England and central southern England, but otherwise richness increased by up to 14 taxa across most of England and Wales. In 1991–93 there were extensive areas of lower richness in or near to major urban and former industrial centres (e.g. London, Birmingham, Liverpool; Fig. 2 & Supplementary Fig. 4), which showed some of the largest richness increases by 2017–19. This mix of declines and increases reduced geographical variation in richness overall by 2017–19 (standard deviation across the 10 km grid squares = 4.8 families in 1991–3 and 3.2 in 2017–19).

The highest CA1 scores, indicating rivers characterised by pollution sensitive taxa, were in northern and western locations (Fig. 2), corresponding largely to upland areas (Supplementary Fig. 4). Stream communities in these areas typically comprised ≥50 % EPT taxa. CA1 increased through time across the majority of England and Wales, with mean gains of around 0.2 units across much of the English and Welsh lowlands. Similar to richness, declines in CA1 occurred in those areas with the highest values at the start of the study period: upland areas of southwest England, mid-Wales and parts of northwest England (Fig. 2). As with richness, spatial variation declined through time (standard deviation = 0.61 in 1991–3 versus 0.48 units (2017–19)).

Taken together, these data show how overall community composition changed most strongly across former urban areas and the lowlands of central and eastern England (Supplementary Fig. 5a). The changes were driven primarily by increases in ephemeropteran and trichopteran family richness, whilst the declines in CA1 scores across upland areas corresponded to declining plecopteran richness (Supplementary Fig. 5b and d). There was a net decline in non-EPT taxa in many areas which showed increasing richness and/or CA1, highlighting the importance of taxonomic turnover through time (Supplementary Fig. 5c).

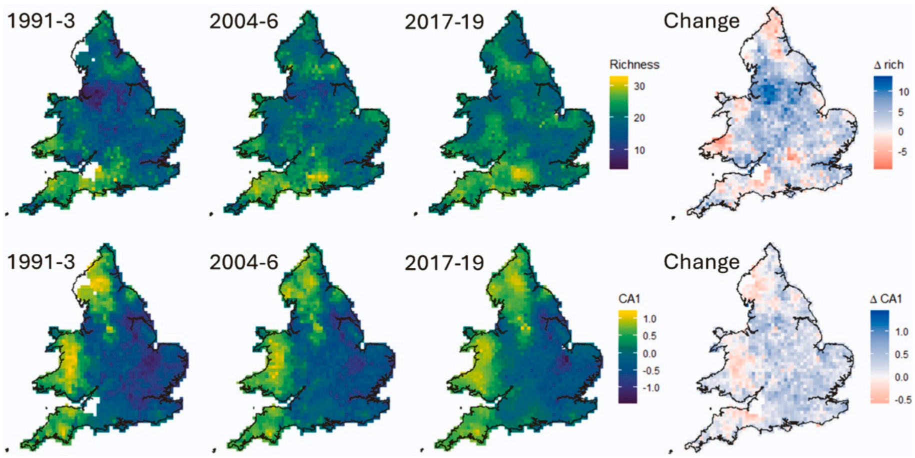

Fig. 2. Kriged maps of macroinvertebrate richness (top row) and community composition (CA1 score; bottom row) for 1991–93, 2004–06 and 2017–19, and change (Δ) from the first to last time period. Blank regions in 1991–1993 and the corresponding change maps were not interpolated due to sparse data.

3.2. Structural equation models

SEMs largely supported the hypothesised relationships between environmental and biological variables (Fig. 3), illustrating how catchment land cover might influence invertebrate communities both via water quality and 'directly' through pathways not mediated via average water chemistry. Notable exceptions were the lack of statistically-significant effects of average water temperatures upon richness or CA1, and of direct nitrate or improved grassland effects upon CA1 (Fig. 3). Increasing extents of urban land and both types of agriculture were linked to increasing nutrient concentrations and BOD, whilst urban and arable were linked to higher water temperatures. Increased discharge led to cooler water and reduced BOD and phosphate concentrations, consistent with dilution effects (Fig. 3). BOD, phosphate and pH all had statistically significant direct links to richness and CA1. Higher pH correlated with higher richness and lower CA1 score, whilst BOD and phosphate had negative effects upon both richness and CA1, and nitrate had a negative effect upon richness.

Larger standardised regression coefficients were estimated for the 'direct' effects of urban and arable land cover upon richness and CA1 than for measured water chemistry, consistent with the multifaceted ways in which land cover can affect stream communities. Urbanisation had consistently negative relationships with richness and CA1, whilst arable land cover had an apparently positive effect upon richness and negative upon CA1 (Fig. 3). Aside from indirect dilution effects on nutrients and BOD, increasing discharge had a direct positive effect upon CA1. Overall, composition (CA1) was more predictable than richness (marginal $R^2 = 0.59$ and 0.23 for CA1 and richness respectively).

3.3. Geographically-weighted regressions

Consistent with the SEM results, CA1 scores were more predictable than richness based on the combination of land cover, water quality and climate (quasi-global R^2 for CA1 = 0.82 in 1991–2004 and 0.74 in 2005–2019, and 0.58 and 0.57 for richness in the equivalent time periods). Underlying this was a strong geographical gradient in the predictability of CA1, with high predictive power in the west (local $R^2 >$ 0.80), declining to <0.30 in southeast England (Supplementary Fig. 6). Richness varied less in local R^2, with slightly higher values in parts of northern England and southwest Wales. The local R^2 patterns were similar in the two time periods for both response variables.

The estimated relationships between invertebrate communities and environmental variables varied greatly across England and Wales, and often between richness and CA1 (Fig. 4). Differences between the two

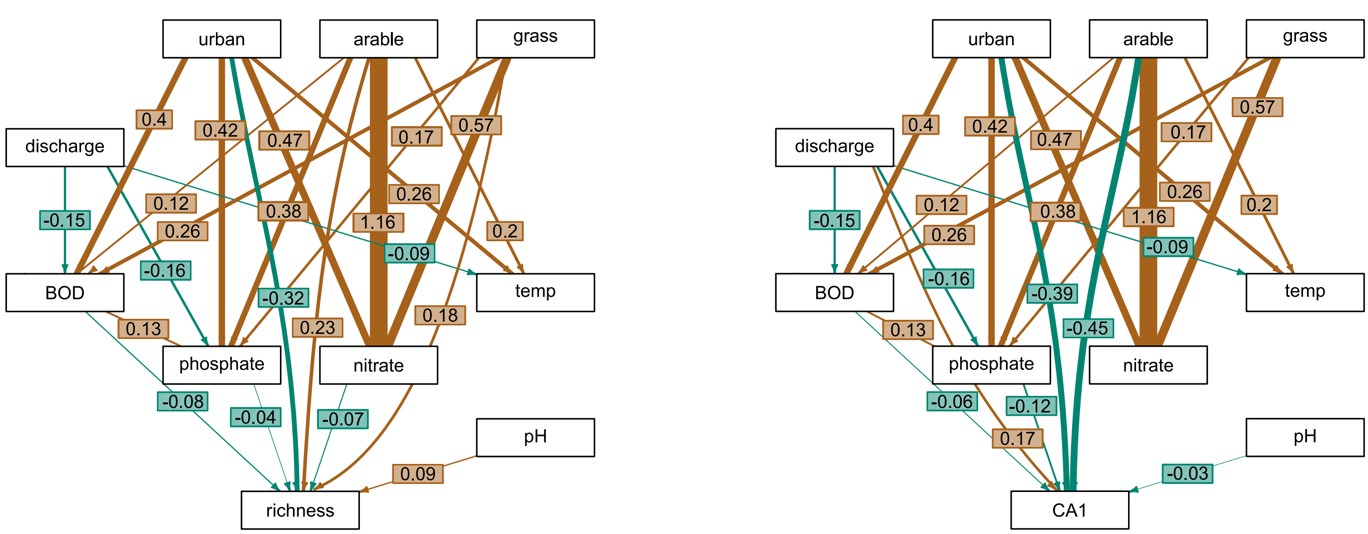

Fig. 3. Structural equation models of water quality, climate and land use effects on macroinvertebrate richness (left) and composition (right). Arrows represent the direction of effects, with only statistically significant paths ($p < 0.05$) shown. Path widths are proportional to the standardised path coefficients, which are also printed in the path labels: green paths and labels = negative effects; brown = positive. See Table S2 for full coefficient estimates and significance test results.

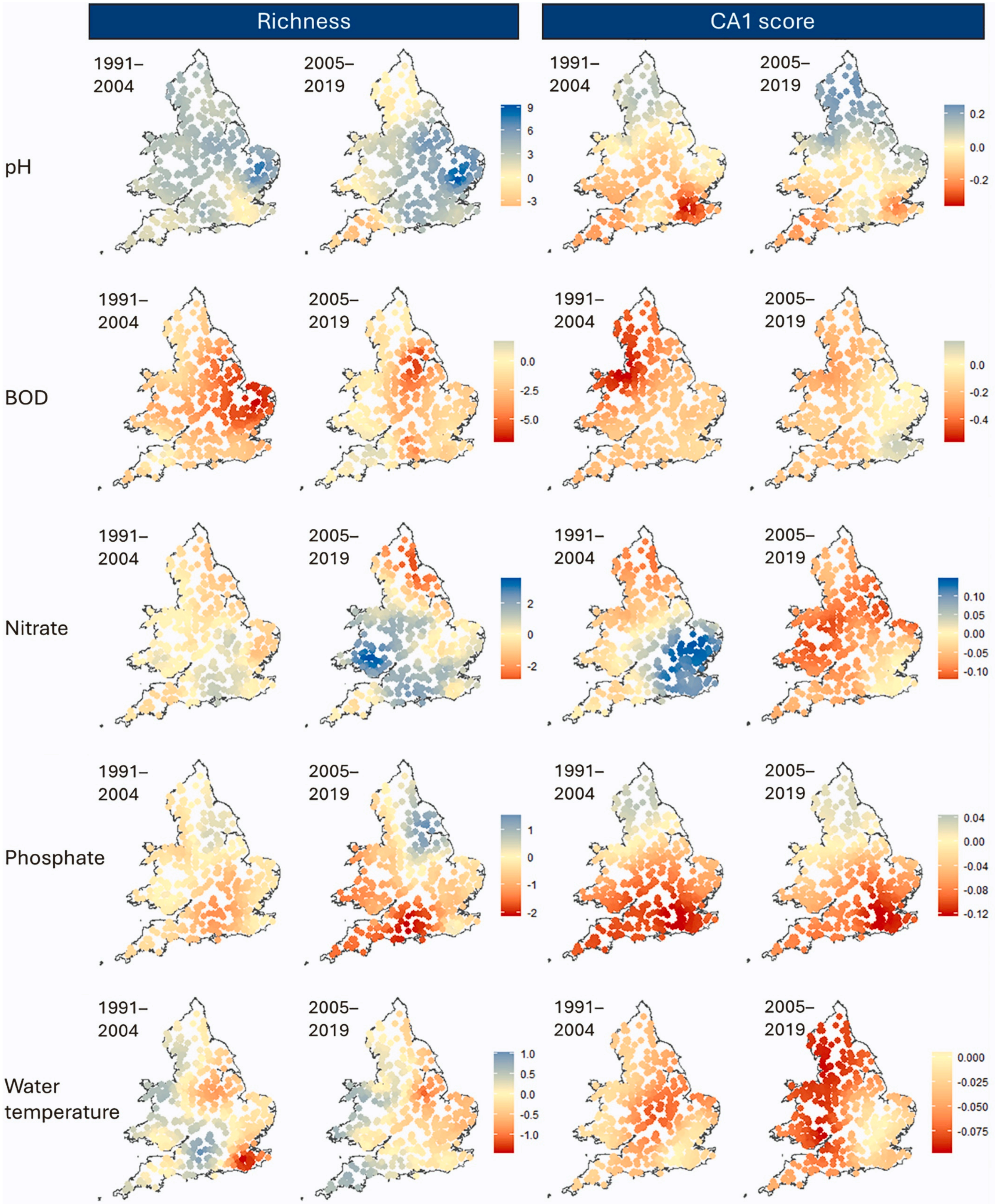

Fig. 4. GWR coefficients (slope coefficients) from richness (two left hand columns) and CA1 score (two right hand columns) models for the two time periods, representing the direction (positive or negative) and strength of the estimated relationships between abiotic variables and biological responses. Note that due to differences in the units and transformations applied to the environmental variables, the intensity scales differ between panels.

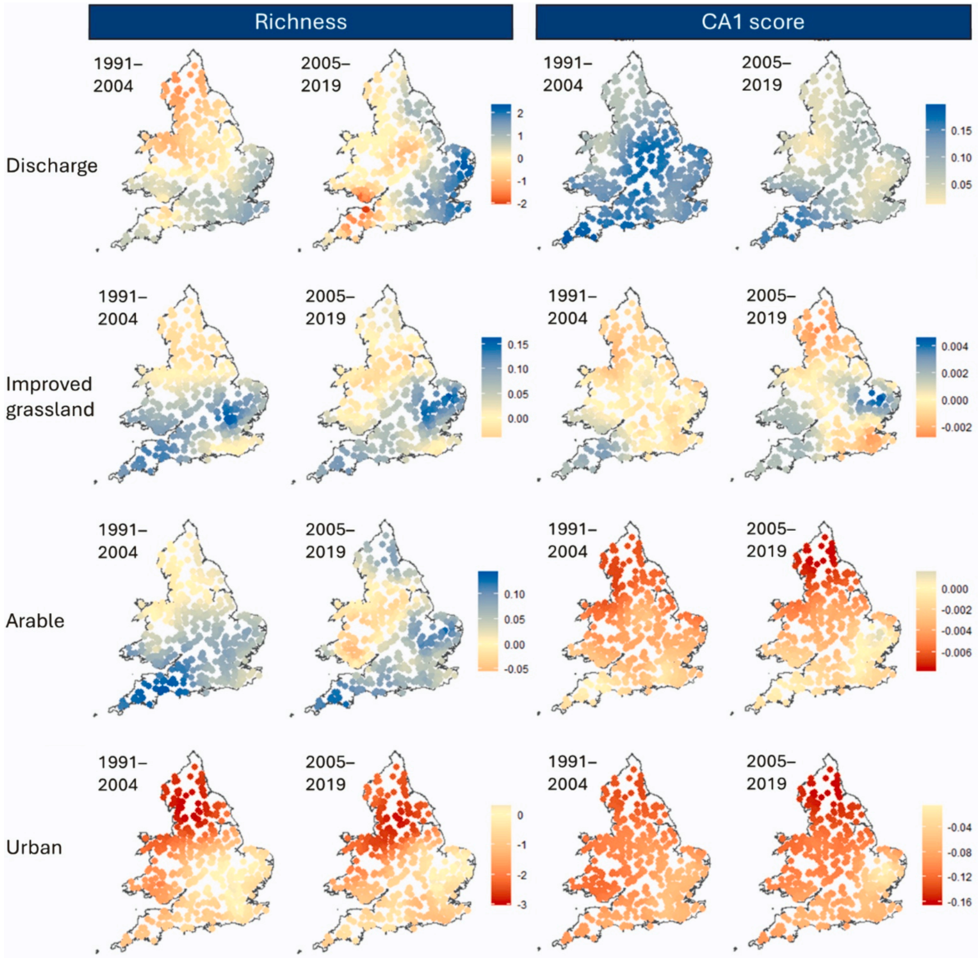

Fig. 4. (*continued*).

time periods were often smaller than geographical variation, with similar spatial patterns and just minor changes in the magnitudes of estimated regression coefficients. Richness and CA1 declined consistently in response to increasing BOD, with exceptions in the southwest (richness) and southeast (CA1). This contrast was stronger in the second half of the time series as the estimated relationship with BOD weakened (Supplementary Fig. 6). Richness was broadly positively correlated with pH in ways that were generally consistent across England and Wales, albeit with a negative relationship emerging in the southwest in later years. The relationship between pH and CA1 varied strongly: positive in the north and negative in large parts of the south (Fig. 4).

Phosphate was estimated to have a primarily negative effect upon richness and CA1, with the exception of northern England, where weak positive relationships were apparent. The strongest negative relationships were estimated in southern and southeastern England (Fig. 4). Nitrate had more complex effects both spatially and temporally: a mixture of weakly positive and negative effects upon richness in the first time window strengthened to larger positive relationships in Wales and central England, and more negative effects in northern England. At the first time point, nitrate had a negative effect upon CA1 in the north and the west, but a positive relationship was estimated in the southeast; in the second time window, nitrate was estimated to have near-universal negative effects upon CA1.

Richness and CA1 showed contrasting geographic relationships with climatic variables (Fig. 4). East-west gradients were evident for richness, with warmer temperatures and drier conditions associated with higher richness in the west, whereas the relationship reversed in the east. CA1 was more consistently related to climate across England and Wales, with evidence that the estimated negative relationship with temperature strengthened through time, whilst the positive relationship with discharge weakened.

Estimated coefficients for land cover varied geographically and between richness and CA1. Richness increased with increasing extents of agricultural land cover across much of England and Wales, with a weaker or negative relationship across parts of northern and western areas. CA1 score near-universally decreased with arable land cover, whilst the relationship with improved grassland was weakly positive in some areas (e.g. southwest England and Wales), but negative in other areas including northern England. Both richness and CA1 decreased near-universally with urban land cover except for slightly weaker relationships in parts of southeast England.

4. Discussion

Investigating changes in invertebrate communities and identifying drivers is complex, especially at large spatial scales. This study revealed not only geographic variation in biological change through time, but also marked variation in apparent causes of changes in time and space. This highlights the complexity of the relationships between communities of river organisms and environmental factors, which serves as a cautionary tale where studies treat large geographical areas as homogenous units with consistent processes. The combination of SEM and GWR expanded our understanding of spatial patterns beyond time series-based analyses (e.g. Pharaoh et al., 2023; Qu et al., 2023) and provided new insights into the possible drivers of macroinvertebrate changes. SEM took a step towards resolving the roles of land cover, water quality and climate by separating out the 'direct' and indirect effects upon stream ecosystems, and better characterising the relationships among variables. GWR emphasised the complexity of the apparent relationships between communities and the abiotic environment, and how this has evolved in space and time. Both approaches indicated differences in the ways that the environment might influence richness and composition, with the former was less predictable than the latter. This may indicate that richness is influenced to a greater extent by factors not captured in our analysis (e.g. pollutants) or reflect the additional methodological challenges in estimating richness, leading to more 'noise' in the data (Gotelli and Colwell, 2001).

We start this section by considering the main limitations of the study, before discussing the broad-scale changes in macroinvertebrate communities, and then focusing on areas where diversity declined and/or sensitive taxa were lost. The latter are of particular interest, as they contrast with average increases in richness and other measures at national and international scales.

4.1. Limitations

Invertebrate data were only resolved to family or higher levels, and were simplified to presence-absence rather than abundance. Whilst these simplifications will have made the analysis less sensitive and potentially masked more nuanced biological responses expressed at the species-level, they were a necessary compromise to ensure spatial and temporal consistency in the data set. Secondly, we had an incomplete picture of potential stressors. In part, this relates to the precision and biological relevance of variables (e.g. calculating average water chemistry from monthly samples; using average climate and water quality, rather than capturing extremes), both of which may lead to underestimates of their importance in our models. More widely, some potential stressors were missing altogether (e.g. excess fine sediment, pesticides, pharmaceuticals, legacy contaminants) and are known to have pervasive effects upon river organisms and ecosystems, such as reduced growth rates and survival, loss of sensitive species, and altered food web structure and ecosystem functioning (e.g. Magbanua et al., 2010; Jones et al., 2012; Windsor et al., 2019). Some of these stressors may be either growing in severity or potentially constraining recovery from historical gross pollution but the effects are still poorly quantified (e.g. Windsor et al., 2019; Whelan et al., 2022). Biological interactions were also not captured by our data, but can affect organisms both directly and through interactions with abiotic stressors (Urban et al., 2016). Our land cover, water quality and climatic variables should therefore be considered as proxies for other stressors implicated in the changing biological status of river ecosystems (Dudgeon et al., 2006).

Finally, any analysis looking at temporal change is conditional upon the start date and time period over which change is measured. This could be particularly relevant to the maps of change, representing periodic 'snapshots' of English and Welsh rivers. This was unlikely to be an important issue in the current study because: i) we combined three years of data at each time point, minimising the potential bias from using single, atypical years as benchmarks (e.g. a particularly hot, dry summer), and ii) the patterns observed in 2004–6 were intermediate between 1991–3 and 2017–19, consistent with long-term directional change.

4.2. Overall changes in macroinvertebrate communities

Taxonomic richness and the prevalence of pollution-sensitive taxa (CA1 score) increased across most of England and Wales over the study period, consistent with average temporal trends in Great Britain and more widely in Europe (e.g. Outhwaite et al., 2020; Pharaoh et al., 2023; Haase et al., 2023). The changes coincided with near-universal declines in BOD and widespread reductions in phosphate (Environment Agency, 2023b; Supplementary Fig. 1). Consistent with previous studies (e.g. Friberg et al., 2010), both SEM and GWR confirmed near-universal negative impacts of BOD on richness and CA1, and widespread negative relationships across Wales and most of England for phosphate. Nitrate had a more complex relationship with macroinvertebrate communities: a direct negative relationship with richness in the SEM, but strong geographical variation in the apparent relationships to both CA1 and richness (GWR). These complexities are likely to reflect the blend of sources of nitrogen released to surface waters from wastewater and agriculture as well as a likely shift in nitrogen species from ammoniacal to oxidised as gross, sanitary pollution has declined with improving wastewater treatment.

SEM confirmed well-established influences of land cover on water quality (Allan, 2004). Simultaneously, the estimated 'direct' effects of average chemistry upon macroinvertebrate communities were relatively weak, and generally smaller than putatively 'direct' links from land cover to community structure. Urbanisation, in particular, had negative direct relationships with richness and CA1 score, consistent with impacts beyond elevated nutrients and organic matter. The suite of urban effects is likely to be complex in its own right – ranging from hydromorphological modifications to novel pollutants such as pharmaceuticals (Walsh et al., 2005) – accompanied by short-term extremes overlooked by annual averages (e.g. road run-off, sewer stormwater overflows). Arable agriculture also had a relatively large 'direct' relationship with composition, potentially indicating the importance of stressors such as excess fine sediment and pesticides relative to average nutrient concentrations in arable catchments, yet both arable and improved grassland cover had positive relationships with richness. The relatively modest relationships with average chemistry, alongside sometimes large geographical variation in the GWRs, suggests that average macro-nutrient or sanitary chemistry may have limited potential to account for or predict changes in macroinvertebrate communities across England and Wales. This emphasises that further work is needed to reveal the missing parts of the relationship: better characterisation of extremes, potentially complex interactions between stressors (Jackson et al., 2016), missing stressors and/or the potential roles of biotic interactions. Uncovering these additional effects could be key to restarting the recovery of British and European rivers from past pollution (Haase et al., 2023).

Both climate variables were linked to community structure, but results varied between SEM and GWR. CA1 score was positively correlated with discharge across England and Wales, with evidence that discharge acted via a dilution effect upon BOD and phosphate (SEM), and also 'directly', with the latter potentially reflecting lower hydrological stress, greater habitat area/volume or a role in the dilution of other potential pollutants. Discharge only influenced richness via mean BOD and phosphate, and showed a complex spatial correlation pattern (GWR): positive to the south and east, and negative to the west and north. Such non-stationarity may make it difficult to estimate discharge's role in a single national model unless the varying relationship could be accounted for by interactions with other variables. With water temperature, again there was a more complex spatial relationship apparent for richness, with more consistent patterns for CA1 (GWR), which seemed to strengthen through time. This geographical variation may account for the lack of a statistically-significant relationship at the national scale (SEM). Declines in other stressors such as organic pollution (BOD) or eutrophication may mean that temperature effects are becoming more prominent, in addition to there being greater cumulative climate change through time.

4.3. Regions of declining quality

Against the background of apparent recovery from poor water quality, coherent regions of decline were evident, especially in areas that had the highest richness or CA1 scores in 1991–1993. This decline in the least degraded areas, coupled with large improvements in urban areas ('closing the gap' on rural rivers; Pharaoh et al., 2023), underlay an homogenisation of invertebrate communities across England and Wales (see also Pharaoh et al., 2023). There was little correspondence between areas where richness and CA1 scores declined, suggesting different causes, and GWR didn't highlight the areas with declining richness or CA1 as having unique relationships with the abiotic variables. Richness declined across large parts of south-west England and western Wales, as well as some other areas of southern and northeastern England. The relatively mild and humid areas of the south and west are dominated by improved grassland and correspond to a concentration of dairy farming and high cattle densities (Animal and Plant Health Agency, 2019), which are associated with declining taxon richness and loss of sensitive freshwater taxa (e.g. Ramezani et al., 2016). However, GWR and SEM suggested a largely positive relationship between improved grassland and richness in the southwest, although increases in both nutrients had negative effects on richness (SEM), with GWR highlighting a negative relationship with phosphate. Further work is needed to tease apart these potentially complex interactions of land cover and water quality at the regional scale. The development of agricultural support schemes intended to deliver environmental gains would benefit from clearer insights into land cover effects, including more precise estimates of agricultural intensity and impacts (Schürings et al., 2024).

There was evidence of losses of pollution sensitive taxa (reduced CA1) across much of the English and Welsh uplands, yet there was little decline in richness in these areas. This suggests that turnover has occurred in the uplands, with more tolerant species replacing pollution sensitive taxa. Uplands in the UK have been historically subject to acid deposition and coniferous afforestation, which has had lasting impacts on hydrology, water chemistry and ecology of upland streams, although evidence now is of recovery (Ormerod and Durance, 2009 and unpubl. data). Moreover, upland streams and their communities are likely to be more sensitive to climate change due to their fast response times to hydrological events and low thermal mass (Gomi et al., 2002; Caissie, 2006), as well as their higher elevation meaning species are limited in their potential to move upstream to cooler conditions. Climate change can also have secondary effects on upland stream conditions (e.g. organic litter dynamics), which can further influence invertebrate communities (Pye et al., 2022). The strengthening negative relationship through time between CA1 and water temperature in northern and western areas (Fig. 4) is consistent with such a climate effect, although the strengthening effect size of nitrate is also worth noting. Plecopterans were the main contributors to the declining CA1 scores and many are primarily cool water taxa that are very sensitive to organic pollution (Friberg et al., 2010). It is also notable that a modest increase in phosphate was detected in many of the upland areas, which could affect algal biomass.

5. Conclusions

Overall, the three strands of our analysis confirmed some aspects of our understanding about English and Welsh rivers (e.g. widespread improvement in biological quality post 1990; roles for water quality, climate and land cover), whilst providing new insights (e.g. identifying regions of decline; possible increasing climate sensitivity; a modest role for average water chemistry relative to land cover; variations in apparent influences on invertebrates in time and space). These results highlight the importance of considering geographically disaggregated changes alongside average (inter-)national trends to gain a better understanding of how rivers are changing, as average trends can disguise regions of decline. Whilst the condition of rivers draining urban areas and large parts of lowland England and Wales have improved over the last 30 years, overall diversity and/or sensitive taxa have declined in areas such as SW Britain and the uplands, and these now represent research and management priorities. Moreover, the SEM and GWR results emphasise the complexity and variability in the apparent drivers of changing biological quality. The changing mix of multiple, interacting stressors in river environments – not all of which were included within this study – has the potential to change the apparent relationships between focal variables and invertebrates. Better characterisation of the changing mix of potential stressors through space and time, and the ways in which they interact, should help to unpick these complex relationships.

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CRediT authorship contribution statement

Emma Pharaoh: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Mark Diamond:** Writing – review & editing, Conceptualization. **Helen P. Jarvie:** Writing – review & editing, Conceptualization. **Steve J. Ormerod:** Writing – review & editing, Funding acquisition, Conceptualization. **Graham Rutt:** Writing – review & editing, Conceptualization. **Ian P. Vaughan:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Ian Vaughan reports financial support was provided by Natural Environment Research Council. If there are other authors, they 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

Environment Agency data are available from the Ecology and Fish Data Explorer (https://environment.data.gov.uk/ecology/explorer/) and Natural Resources Wales data from NBNAtlas (https://registry.nbnatlas.org/public/show/dr2116). Our data sets, derived from these two databases, are available from the Cardiff University data catalogue at http://doi.org/10.17035/d.2024.0326519107.

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Appendix A. Supplementary data

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