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Research Article

Rising, falling, stalling: complex biodiversity trajectories in English rivers

Mansi Mungee^{1,2}, Martin Wilkes³, Vicky A. Bell⁴, William E. Kunin⁵, Christopher Hassall⁵ and Lee E. Brown²

¹Azim Premji University, Bhopal, Madhya Pradesh, India

²School of Geography and water, University of Leeds, Leeds, UK

³School of Life Sciences, University of Essex, Wivenhoe Park, UK

⁴UK Centre for Ecology and Hydrology, Wallingford, UK

⁵School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK

Correspondence: Mansi Mungee (mansi.mungee@apu.edu.in)

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Freshwater ecosystems face intense anthropogenic pressures. Yet in parts of Europe, including the UK, studies have documented widespread increases in macroinvertebrate diversity following investments to improve water quality. More recent analyses, however, suggest that these gains have slowed, plateaued, or even reversed. Despite increasing recognition that biodiversity trajectories vary substantially among locations, the majority of analyses are still based on spatially aggregated data which mask important local heterogeneity, complicating interpretation of national-scale trends. Consequently, the mechanisms of local biodiversity dynamics remain poorly resolved. We address this gap using macroinvertebrate time-series data from 803 sites in England's Environment Agency monitoring network. We used an unsupervised clustering approach to group sites with similar temporal trajectories for three community-level metrics: pollution sensitivity (average score per taxon, ASPT), richness, and abundance. We then compared the environmental characteristics and community composition of these groups to identify the factors most strongly associated with different trajectories. Our analyses reveal substantial heterogeneity in temporal trajectories: more than half of the sites (~ 53%) exhibited declining or non-directional trajectories in at least one of the three metrics. Sites that exhibited increases in ASPT and/or richness were strongly associated with a lower distance from source, higher oxygen availability, and lower nutrient concentrations. In contrast, declines were more common in downstream sites with finer sediments and elevated nutrient and pollutant loads. Further, trends varied far more among individual sites than among larger aggregated regions such as catchment or water bodies. Collectively, our findings show that macroinvertebrate community dynamics are a mosaic of non-linear, site-specific trajectories. This reflects the combined influence of multiple processes, likely including species interactions and dispersal dynamics, operating across scales. A stronger mechanistic understanding of these processes is therefore essential for improving river management and conservation strategies, complementing existing catchment- and waterbody-scale management with greater recognition of site-level ecological heterogeneity.

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Introduction

Freshwaters are among the most threatened ecosystems on the planet. Recent headline figures reporting an 85% decline in indicator species abundance (World Wildlife Fund Living Planet Report 2024) have prompted numerous calls to ‘bend the curve of biodiversity decline’ by changing the way rivers are managed and restored (Tickner et al. 2020). Aquatic organisms are particularly sensitive to environmental change due to the spatial structure of river networks, which can limit dispersal (Carrara et al. 2012, Heino et al. 2015, Tonkin et al. 2018, Carraro et al. 2023), and because hydrological pathways act as corridors or sinks for upstream stressor inputs (Vannote et al. 1980, Pringle 2003, Freeman et al. 2007). Together, these factors reduce the availability of refugia or buffer zones from environmental stressors (Revenga et al. 2005, Dudgeon et al. 2006, Reid et al. 2019). Yet, against this global backdrop of concern, studies from several European countries including the UK have reported increases in freshwater macroinvertebrate richness and abundance (Vaughan and Ormerod 2014, Vaughan and Gotelli 2019, Van Klink et al. 2020, Pharaoh et al. 2023), although other recent analyses indicate that these gains have slowed, plateaued, or even reversed (O'Donoghue et al. 2022, Haase et al. 2023, Pharaoh et al. 2024).

Regional improvements in water quality across Europe have followed investments in sewage treatment, driven primarily by the Urban Waste Water Treatment Directive (Directive 1999). Broader regulatory frameworks such as the EU Water Framework Directive, improved treatment of industrial pollution, and recovery from acidification have also contributed to these improvements (Directive 2003, Murphy et al. 2014, Medupin 2020, Whelan et al. 2022, Johnson et al. 2025a, Mining Remediation Authority 2025). However, pollution of certain kinds, such as road runoff, new tyre chemicals, human and veterinary pharmaceuticals may be having an increasing impact through more widespread use, and nutrient and pesticide runoff appear to be increasing over time as agricultural intensification continues (Tull et al. 2023, Halsband et al. 2024, Schürings et al. 2024). At the same time, legacy pressures have not disappeared and long-standing nutrient issues persist in many systems (e.g. increases in chlorophyll-a despite declines in phosphorus; Worrall et al. 2025). Against this backdrop, the extent and generality of the apparent biodiversity recoveries remain contested. Biodiversity estimates are sensitive to methodological choices, including taxonomic harmonization, the diversity metrics used, the treatment of abundance data, trend models, and the spatial scale at which data are aggregated (Demars 2024, Sinclair et al. 2024, Wilkes et al. 2025a, 2025b). Understanding which river systems are either improving or declining, and why this is the case, is vital to developing robust recovery plans for global freshwater biodiversity.

In the UK specifically, the magnitude and even the direction of change differ markedly across studies based upon the same national dataset (Vaughan and Ormerod 2012, 2014, Murphy et al. 2014, Outhwaite et al. 2020, Powell et al. 2023, Qu et al. 2023). Very few works have compared temporal variation at individual sites (but see Vaughan and Ormerod 2012, 2014, Qu et al. 2023), but the end results are typically summarised as directional classes either as single values of slopes, or effect sizes, rather than full trajectories. Yet, management-relevant features of both recovery and decline are often complex and non-linear, with features such as point step-changes after major pollutant incidents or restoration interventions (Johnson et al. 2025a), episodic responses to extreme events (Fornaroli et al. 2020), temporal lags in biodiversity response across taxonomic and functional richness (Pharaoh et al. 2023), and potential tipping points, regime shifts, or alternative states (Carrier-Belleau et al. 2023, Hernández Martínez de la Riva et al. 2023). Methods that reduce trajectories to a single slope or even a sign miss these dynamics, overlooking complex, intervention-sensitive behaviour across individual sites.

National or regional scale trends provide scientists and environmental managers with important ‘big picture’ estimates of change (Outhwaite et al. 2020, Pharaoh et al. 2023, Powell et al. 2023, Johnson et al. 2025a). However, mechanistically, the presence of site-level variation in biodiversity responses is a consequence of interactions among multiple physical, chemical, and biological processes which vary at local scales (Murphy et al. 2014, Verberk et al. 2016, Civan et al. 2018, Pharaoh et al. 2024). For instance, while freshwater biodiversity patterns are often modelled using broad-scale predictors such as land use or climatic gradients (including temperature), local in-stream conditions – particularly water chemistry – can strongly modulate these relationships, resulting in spatially heterogeneous ecological responses along river networks (Fornaroli et al. 2020, Nguyen et al. 2024, Johnson et al. 2025b). Impacts of large-scale drivers such as climate warming can also vary across sites depending on local pollution legacies or flow regime (Durance and Ormerod 2007, Vaughan and Gotelli 2019). Biological drivers of community dynamics, including dispersal events, density-dependent processes, and ecological drift, can further contribute to site-level variation in biodiversity responses (Thompson et al. 2020). Site-level responses can thus depart strongly from catchment or regional means, and national trends can flatten local recovery or decline. Yet, systematic attention to site-level variation in river biological trend studies remains limited.

Cross-scale analyses can help reveal how local stressors shape large-scale biodiversity patterns (Pharaoh et al. 2023, Powell et al. 2023). However, no previous study has examined how freshwater biodiversity responses vary across the full hierarchy of river systems, from individual sites to water bodies, catchments, typology classes, and regions. Nor has

any study compared non-linear site-level time series across multiple metrics within a single, hierarchical, and spatially explicit framework (but see Vercelloni et al. 2014 for a marine ecosystem application). In this study, we address these two important gaps: 1) we identify and delineate clusters of sites that exhibit distinct non-linear temporal trajectories with respect to community-level pollution sensitivity, taxonomic richness, and total abundance, and 2) use variance partitioning across the spatial hierarchy to evaluate site-level patterns in the context of broader catchment and regional characteristics.

We tested the following hypotheses: (H1) macroinvertebrate community indices will not always exhibit simple monotonic increases or decreases; instead, we expected clusters of sites with varied non-linear temporal shapes (i.e. groups of sites sharing similar temporal trajectories, irrespective of geographic proximity) reflecting asynchrony in multiple environmental drivers; (H2) environmental drivers will strongly differentiate cluster membership at the individual-site level, consistent with site-specific chemistry and/or hydromorphology; (H3) taxonomic composition would differ between clusters with increasing, decreasing, or stable trajectories, with declines in pollution sensitivity associated with reduced representation of taxa that are sensitive to stressors, and increases linked to their persistence or recovery; and (H4) the largest share of explainable variation across clusters will sit at the site level, supporting the importance of local drivers and cautioning against over-interpretation of regional or national averages. We harmonised taxonomy (family level), derived explicit shape-based time-series clusters for each metric, and then analysed the environmental and compositional correlates across the clusters. Finally, we used a hierarchical Bayesian variance decomposition analysis to quantify how cluster assignment varies across the (nested) spatial scales. Combining shape-based time-series clustering across multiple community indices with hierarchical variance partitioning provides new insights for freshwater biodiversity patterns across spatial scales from site to national levels.

Material and methods

Macroinvertebrate data

Macroinvertebrate data were sourced from the UK Environment Agency's (EA) long-term monitoring surveys (<https://environment.data.gov.uk/ecology/explorer>). Synonymous taxa were updated to accepted names, abundances aggregated to familial level, and we retained samples from 2002 to 2023, when the EA adopted more accurate abundance estimates, improved quality control, and standardised taxon lists (Murray-Bligh 1999, Wilkes et al. 2025a). Data were filtered to: 1) 3-min kick-sampling protocols (Murray-Bligh 1999); 2) abundances on a linear scale or converted from log scale; 3) sites sampled in spring for ≥ 10 of 20 years, with one spring (March–May) sample randomly selected if multiples were collected per season (to ensure seasonal consistency); 4) sites with data in at least one

of 2002–2004 and one of 2021–2023; and 5) sites without missing samples for ≥ 3 consecutive years.

Statistical analysis

We generated site-specific time series for average score per taxon (ASPT; Chesters 1980, Hawkes 1998), taxonomic richness, and total abundance representing community pollution sensitivity, biodiversity, and assemblage size, respectively. To ensure comparability across the three metrics, we retained only WHPT scoring taxa for all analyses. All metrics were range-normalised (between 0 and 1) and missing values interpolated using the function *na_interpolation* from the R package 'imputeTS' ver. 3.3 (Moritz et al. 2017; www.r-project.org).

ASPT is a biotic index that characterizes the average pollution sensitivity of freshwater macroinvertebrate communities. It is derived from taxon-specific sensitivity scores assigned under scoring systems such as the Walley–Hawkes–Paisley–Trigg (WHPT) index, an updated development of the original Biological Monitoring Working Party (BMWP) system (Armitage et al. 1983, Walley and Hawkes 1997, Paisley et al. 2014). In these systems, each taxon is assigned a score reflecting its tolerance to organic pollution and environmental degradation, with higher scores indicating greater sensitivity and association with higher ecological quality. ASPT is calculated as the mean sensitivity score of all taxa present in a sample, obtained by dividing the sum of individual taxon scores by the total number of taxa recorded:

$$\text{ASPT} = \frac{\sum s_i}{S}$$

where s_i is the sensitivity score of taxon i , and S is the total number of taxa in the assemblage (Armitage et al. 1983). By standardizing the summed sensitivity score by taxon richness, ASPT provides a measure that is widely considered to be independent of variation in richness or sampling effort, and instead reflects the average tolerance of the community. Communities dominated by pollution-sensitive taxa yield higher ASPT values, whereas those composed primarily of tolerant taxa yield lower values (Hawkes 1998).

Taxonomic richness was estimated using coverage-based standardization using the estimateD function in the R package 'iNEXT' (with $q=0$ and base='coverage'; Chao et al. 2014, Hsieh et al. 2016). The metric standardizes samples to a common level of sample completeness (coverage), and accounts for undetected taxa by interpolating or extrapolating richness to the target coverage level. As such, it provided a less biased estimate of true richness under heterogeneous sampling conditions than raw counts (Chao and Jost 2012). For comparison, we also provided a supplementary clustering analysis based on observed taxonomic richness (NTAXA) to assess the consistency of patterns between observed and coverage-standardized richness estimates (Supporting information).

Time-series clustering

Time-series clustering partitions 'n' time series into 'k' clusters ($k \ll n$) such that statistically similar series are grouped together based on some similarity/distance measure (Aghabozorgi et al. 2015). Several methods are available for unsupervised clustering of time series. Here, we used nine commonly used approaches, combining three clustering methods (hierarchical, partitioning k-means, and fuzzy c-means) with three distance measures: Euclidean, dynamic time warping (DTW), and shape-based distance (SBD) (Pavoine 2009, Mannix et al. 2018, Wei et al. 2020, Hegg and Kennedy 2021; see the Supporting information for details on each of these). Since the challenges of clustering complex time-series data are not unique to ecology, analytical approaches from other disciplines may be applicable, including measures to evaluate cluster validity and robustness (Ranacher and Tzavella 2014). Ecological data, however, are typically more heterogeneous, often contain gaps, and rarely span the long temporal scales needed to assess clustering efficiency. In this study, datasets covered ~ 20 years, compared to climatic or financial series that often extend up to more than 100 years (Thomas et al. 2021). To address these limitations, we simulated additional data with statistical properties similar to the empirical macroinvertebrate series. This enabled us to first optimise models and evaluate clustering efficiency on simulated datasets, and then use the 'best-fitting' model for the observed, empirical data. We simulated a large time-series dataset using autoregressive integrated moving average (ARIMA) model parameters (Supporting information). This dataset was used to compare the different methods, evaluate clustering efficiency, and determine the optimal number of clusters (k) (Kim and Ramakrishna 2005, Kaufman and Rousseeuw 2009, Arbelaitz et al. 2013) using a suite of internal cluster validity indices (CVIs; Aghabozorgi et al. 2015; Supporting information). Prior to clustering, time series were smoothed with Nadaraya–Watson kernel regression using Gaussian GCV-optimised bandwidths (λ) to

reduce inter-annual noise (Nadaraya 1964, Watson 1964). Clustering was implemented with the function *tsclust* from the package 'dtwclust' ver. 5.5.12 (Sardá-Espinosa 2019) for all three metrics: ASPT, richness, and abundance.

Linear discriminant analysis (LDA)

We used linear discriminant analysis (LDA) to assess the contribution of different environmental factors in distinguishing the time-series clusters. We assembled a suite of river morphological (e.g. altitude, slope, substrate composition) and water chemistry variables (e.g. nutrients, dissolved oxygen, pH, temperature), for which long-term mean, minimum, and maximum values were calculated for each site (Table 1; Supporting information). Inclusion of both central tendency and extreme values allows representation of episodic conditions (e.g. hypoxia, nutrient pulses, acidification events), which may exert disproportionate ecological effects relative to long-term averages and contribute to non-linear or lagged biological responses. All predictor variables were mean centered and standardized to unit variance before analysis, and variance inflation factor (VIF) analysis was performed to subset to the least correlated variables with independent axes of information. We used 10-fold cross-validation, where in each iteration 90% of the data were used for training and 10% for testing. LDA was performed using the *lda* function from the package 'MASS' ver. 7.3-60.0.1 (Ripley et al. 2013). Model evaluation and goodness of fit were evaluated using a confusion matrix (caret ver. 7.0-1; Kuhn 2008, Kuhn et al. 2020) and Cohen's kappa values (K). Performance was assessed using three standard measures: sensitivity, specificity, and accuracy, using both overall (across all clusters) and class-specific (per cluster) statistics. The entropy-based local indicator of spatial association (ELSA) statistic was calculated to evaluate neighbourhood spatial autocorrelation in the time-series clusters (package 'elsa' ver. 1.1-28; Naimi et al. 2019) and to test for any global spatial structure using enterograms (Naimi et al. 2019).

Table 1. Environmental variables used in linear discriminant analysis (LDA) of time-series cluster membership. Variables represent a combination of geomorphological (Environment Agency datasets) and water chemistry variables (long-term large-scale integrated model; LTLS-IM; Bell et al. 2021). All variables were standardized (mean-centred and scaled to unit variance) prior to analysis, and highly collinear predictors were excluded following variance inflation factor (VIF) analysis to ensure independent axes of information. Only the final set of independent variables used in LDA are shown (Supporting information).

	Variable [LABEL]	Description and unit	Reference
1	Altitude [ALTITUDE]	m above sea level	Environment Agency (2025)
2	Slope [SLOPE]	m km ⁻¹	
3	Distance from the source [DIST_FROM_SOURCE]	Distance from the sampling site to the source (km)	
4	Channel depth [DEPTH]	cm	
5	Boulders and cobbles [BOULDERS_COBBLES]	Percentage of substrate that is recorded as boulders/cobbles in the site base data (%)	
6	Pebbles and gravel [PEBBLES_GRAVEL]	Percentage of substrate that is recorded as pebbles/gravel in the site base data (%)	
7	Total dissolved phosphorous (TDP_MAX)	Dissolved load (g) or pH per 5 × 5 km ² river grid-cell.	Long-term large-scale freshwater ecosystems (LTLS-FE) dataset; Bell et al. (2021)
8	Nitrates (NO3_MAX)		
9	Dissolved oxygen (O2_MIN)		
10	pH (pH_MIN/pH_MAX)		

Non-metric multidimensional scaling (NMDS)

To explore the taxonomic composition of clusters, we used non-metric multidimensional scaling with 100 iterations (NMDS; function *metaMDS* from 'vegan' ver. 2.6-8; Oksanen et al. 2007). We calculated distance matrices using Bray–Curtis distance on a transformed (square-root) community data frame (Cluster ID $\times$ Taxa). Distance-based permutational multivariate analysis of variance (PERMANOVA), which compares the variation between groups to the variation within groups, was performed to test if familial compositions differ significantly across the different time-series clusters for each metric (ASPT, taxon richness, and total abundance). PERMANOVA was implemented with the function *adonis2* ('vegan' ver. 2.6-8; Oksanen et al. 2007).

Hierarchical variance decomposition

We fitted an intercept-only variance-components model using a Bayesian mixed-effects (hierarchical) approach in the 'brms' ver. 2.22.0 package (Bürkner 2017). Our aim was to estimate how much variability in freshwater macroinvertebrate responses was attributable to each level of the monitoring hierarchy:

$$\begin{aligned} \text{Cluster ID} \sim & 1 + (1 | \text{Agency} - \text{area}) + (1 | \text{Agency} - \text{area} : \text{Catchment}) \\ & + (1 | \text{Agency} - \text{area} : \text{Water body}) + (1 | \text{Agency} - \text{area} : \text{Catchment} : \\ & \text{Water body} : \text{Site} - \text{ID}) + (1 | \text{Typology}), \end{aligned}$$

where the agency area represents the geographical administrative divisions used by the Environment Agency in England. Although water bodies are hydrologically associated with catchments, we treated them as separate grouping factors because the monitoring structure did not conform to a strictly nested hierarchy across all sites. In addition, we included Typology (System A typology; Directive 2003; Table 2; Supporting information) as a cross-classified grouping factor. Under this framework, rivers were classified based on a combination of altitude band (< 200, 200–800, > 800 m), catchment size (10–100, 100–1000, > 1000 km²), and dominant geology (calcareous, siliceous, organic), yielding up to 18 discrete 'GB Type' categories.

In our dataset, 13 of these typology classes were represented. This classification captured key physical and geochemical controls on river ecosystems that cut across administrative and hydrological boundaries (Table 2). The hierarchical structure comprised 19 agency areas, within which 240 catchments and 479 water bodies were represented, with a total of 803 unique monitoring sites. The categorical response variable, Cluster_ID, represented groupings of sites with similar temporal trajectories in ASPT, richness, or abundance. For each metric, the baseline category was set to the cluster that did not show either a strong increasing or decreasing trend. A multinomial distribution with a logit link was chosen to model these categorical outcomes.

We fitted an intercept-only model because our focus was not on estimating the effects of predictors (e.g. time or

covariates) on cluster membership, but rather on partitioning the variance in site clustering across multiple hierarchical and cross-linked levels. By excluding fixed predictors, the model attributes variability entirely to the random effects, yielding a direct estimate of the relative contribution of each spatial scale (agency region, typology, catchment, water body, site) to the observed clustering patterns (for a semi-parametric application with fixed effects, see Vercelloni et al. 2014). We used four MCMC chains (parallelised across four cores) with 4000 iterations each (2000 warm-up), setting *adapt_delta* = 0.95 and *max_tredepth* = 12 to improve sampling efficiency and ensure convergence. Convergence was assessed through graphical posterior predictive checks (function *pp_check*), the potential scale reduction factor (*R*), and effective sample sizes (Bulk-ESS and Tail-ESS).

All computations were performed using the R statistical software (ver. 4.4.2; www.r-project.org).

Results

The full Environment Agency dataset comprised 107 937 macroinvertebrate samples from 15 585 sites collected between 2002 and 2023, with a median of 30 samples per site (range: 2–43). After applying the filtering criteria, 27 667 samples from 803 sites were retained for analysis, with a median of 18 samples per site (range: 10–22). These sites were distributed across 19 agency areas, 13 Water Framework Directive typologies (Directive 2003), 240 catchments, and 479 water bodies, and represented a wide variation across all environmental and morphological attributes (Supporting information).

The nine clustering approaches showed variable performance, with k-means using shape-based distance (SBD) performing most consistently across validation indices (Supporting information). Across all three metrics (ASPT, richness, and abundance), the most stable solutions were obtained at *k* = 6. These clusters broadly captured increasing (Clusters 1–2 across all metrics, and Cluster 3 for ASPT), decreasing (Cluster 6 across all metrics, and Cluster 5 for richness and abundance), and more complex or non-linear trajectories (Fig. 1a, 2a, 3a). Monotonic trends formed cohesive clusters with low within-cluster distances (mean distance to centroid *d* = 0.052 ± 0.002), whereas non-linear trajectories were more heterogeneous (*d* = 0.153 ± 0.010). The proportion of sites assigned to increasing or decreasing trajectories varied among metrics, with increasing trends most common in ASPT (54.1%) and least common in richness (17.5%), while declines were most prevalent in abundance (38.0%) and richness (35.7%) (Fig. 4a).

Clusters showed clearer separation in environmental space (Fig. 1c, 2c, 3c), with models achieving moderate to high classification performance (accuracy = 0.72–0.86; specificity = 0.92–0.98; Table 3). For ASPT clusters, the first two discriminant axes explained 60.1% of variation (LD1 = 33.0%, LD2 = 27.1%). LD1 separated strongly increasing (Cluster 1) from strongly decreasing trajectories (Cluster 6) along a

Table 2. River typology classification used in this study (Directive 2003). System A Typology (Directive 2003), which was used in this study, classifies rivers according to fixed physical and chemical descriptors (altitude band, catchment size, and dominant geology) yielding 18 discrete 'GB Type' categories. System B simplifies this framework by grouping sites into six broader classes defined by geology (Calcareous, Siliceous, Organic) and altitude (Low < 200 m, High $\geq$ 200 m). The table lists each System A type, its descriptive category, the corresponding System B class, and the number of monitoring sites from this study that fall within each type. *Great Britain (GB) Type codes follow UKTAG 2003 Work Program – Task 2a. Typology for Rivers; TAG 2003 WP 2a (03) Rivers typology (Pv3-4-02-04). *Type 7 was noted by UKTAG as rare and requiring validation.

Altitude band (m)	Catchment size band (km ²)	Dominant geology	System A Typology [†]	Description	System B Typology	Number of sites in this study
< 200	10–100	Siliceous	I	Lowland, small, siliceous streams	VI (Siliceous Low)	84
< 200	10–100	Calcareous	II	Lowland, small, calcareous streams	II (Calcareous Low)	373
< 200	10–100	Organic	III	Lowland, small, organic streams	IV (Organic Low)	4
< 200	100–1000	Siliceous	IV	Lowland, medium, siliceous rivers	VI (Siliceous Low)	43
< 200	100–1000	Calcareous	V	Lowland, medium, calcareous rivers	II (Calcareous Low)	228
< 200	100–1000	Organic	VI	Lowland, medium, organic rivers	IV (Organic Low)	2
< 200	> 1000	Siliceous	VII*	Lowland, large, siliceous rivers†	VI (Siliceous Low)	3
< 200	> 1000	Calcareous	VIII	Lowland, large, calcareous rivers	II (Calcareous Low)	32
< 200	> 1000	Organic	IX	Lowland, large, organic rivers	IV (Organic Low)	0
200–800	10–100	Siliceous	X	Mid-altitude, small, siliceous streams	V (Siliceous High)	22
200–800	10–100	Calcareous	XI	Mid-altitude, small, calcareous streams	I (Calcareous High)	4
200–800	10–100	Organic	XII	Mid-altitude, small, organic streams	III (Organic High)	4
200–800	100–1000	Siliceous	XIII	Mid-altitude, medium, siliceous rivers	V (Siliceous High)	1
200–800	100–1000	Calcareous	XIV	Mid-altitude, medium, calcareous rivers	I (Calcareous High)	2
200–800	100–1000	Organic	XV	Mid-altitude, medium, organic rivers	III (Organic High)	0
200–800	> 1000	Siliceous	XVI	Mid-altitude, large, siliceous rivers	V (Siliceous High)	0
200–800	> 1000	Calcareous	XVII	Mid-altitude, large, calcareous rivers	I (Calcareous High)	0
> 800	10–100	Siliceous	XVIII	High-altitude, small, siliceous streams	V (Siliceous High)	0

gradient contrasting higher phosphorus (TDP_MAX) and slope with greater distance from source (DIST_FROM_SOURCE) and depth (DEPTH). LD2 further distinguished moderately decreasing trajectories (Cluster 5), reflecting variation in substrate composition and water quality (a gradient of pebbles/gravel [PEBBLES_GRAVEL] to boulders/cobbles [BOULDERS_COBBLES], alongside dissolved oxygen [O2_MIN]). For richness, the first two axes explained 71.8% of variation (LD1 = 54.1%, LD2 = 17.8%), with increasing and decreasing trajectories separated along gradients combining nutrient conditions, channel morphology, and position within the river network. For abundance, separation was weaker (50.0% variance explained), with substantial overlap among clusters. Nevertheless, Cluster 6 remained relatively distinct and was associated with higher phosphorus (TDP_MAX) and lower pH (pH_MIN), while other clusters showed no clear separation along a single dominant gradient (Fig. 3c).

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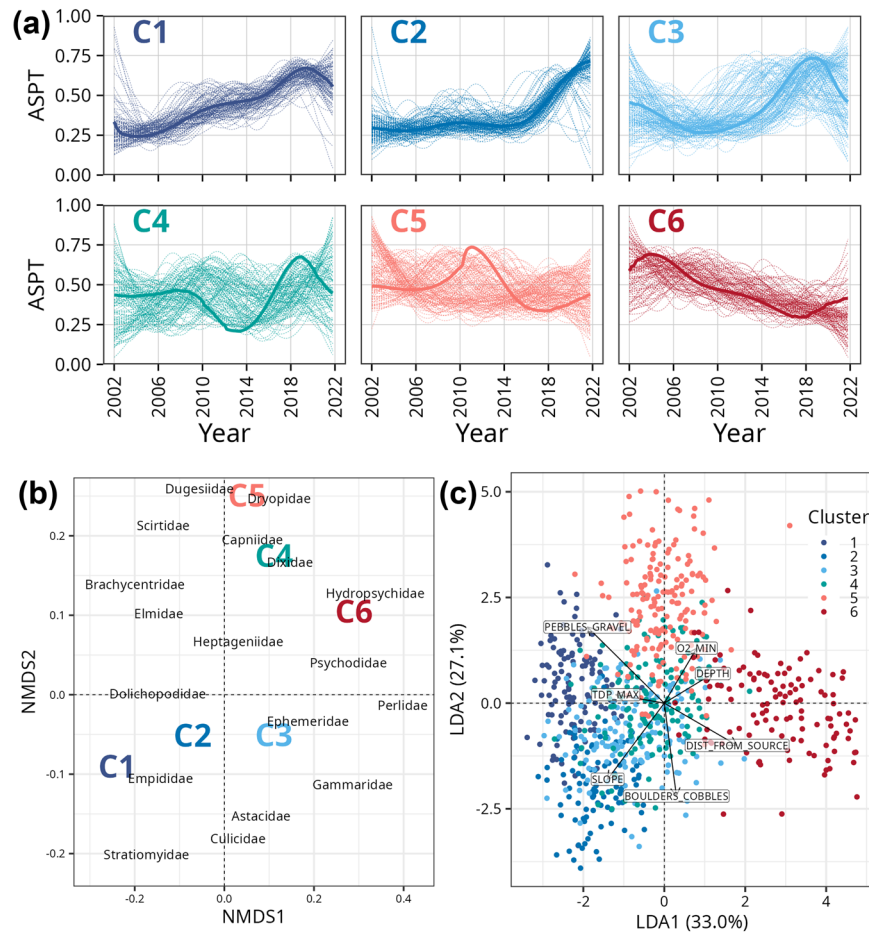


Figure 1. Relationships between clusters of average score per taxon (ASPT) metric time series, environmental variables, and macroinvertebrate community composition. (a) Six distinct clusters were obtained from an unsupervised clustering analysis of the ASPT metric recorded across 803 sites, between 2002 and 2023. Pale dotted lines represent individual time series (i.e. sites); solid thick lines represent the archetypical cluster centroid (i.e. mean temporal trend for each cluster). (b) Non-metric multidimensional scaling (NMDS) plot showing variation in macroinvertebrate community composition across the six ASPT clusters (stress=0.03) (c) Linear discriminant analysis (LDA) of 803 sites based on multiple environmental variables. See Table 1 for environmental variable definitions. Only taxa with the largest NMDS species scores are labelled, to aid interpretation.

and position within the river network. For abundance, separation was weaker (50.0% variance explained), with substantial overlap among clusters. Nevertheless, Cluster 6 remained relatively distinct and was associated with higher phosphorus (TDP_MAX) and lower pH (pH_MIN), while other clusters showed no clear separation along a single dominant gradient (Fig. 3c).

In contrast to environmental space, community composition differed only weakly among clusters (Fig. 1b, 2b, 3b). PERMANOVA indicated a small but significant difference only for abundance-based clusters ($R^2=0.08$), driven primarily by Cluster 6, which showed the most consistent separation in pairwise comparisons (adjusted $p \approx 0.045$; Table 4). This separation was associated with families such as Capniidae, Stratiomyidae, Psychodidae, and aquatic beetles (Dryopidae, Scirtidae), with additional contributions from Ephemeroidea (Fig. 3b). In contrast, ASPT and richness clusters showed no

clear compositional separation (ASPT: $R^2=0.10$, $p=0.055$; richness: $R^2=0.06$, $p=0.311$), and pairwise differences were not significant after correction (Table 4).

Spatial analyses indicated weak spatial autocorrelation across all metrics (mean ELSA ≥ 0.65 ; Fig. 4b), with spatial structure largely confined to neighborhoods below 1 km (Supporting information), suggesting that observed temporal trajectories were shaped primarily by local environmental conditions. Bayesian hierarchical models showed good convergence ($R \approx 1.00$ – 1.02) with high effective sample sizes (Table 5; Supporting information). Variance partitioning revealed that the largest share of unexplained variation occurred at the site level across all metrics, although its importance varied. For ASPT, site-level effects dominated ($\approx 49\%$), indicating strong fine-scale heterogeneity in pollution sensitivity. In contrast, richness was primarily structured by typology ($\approx 35\%$), with a smaller contribution from site-level

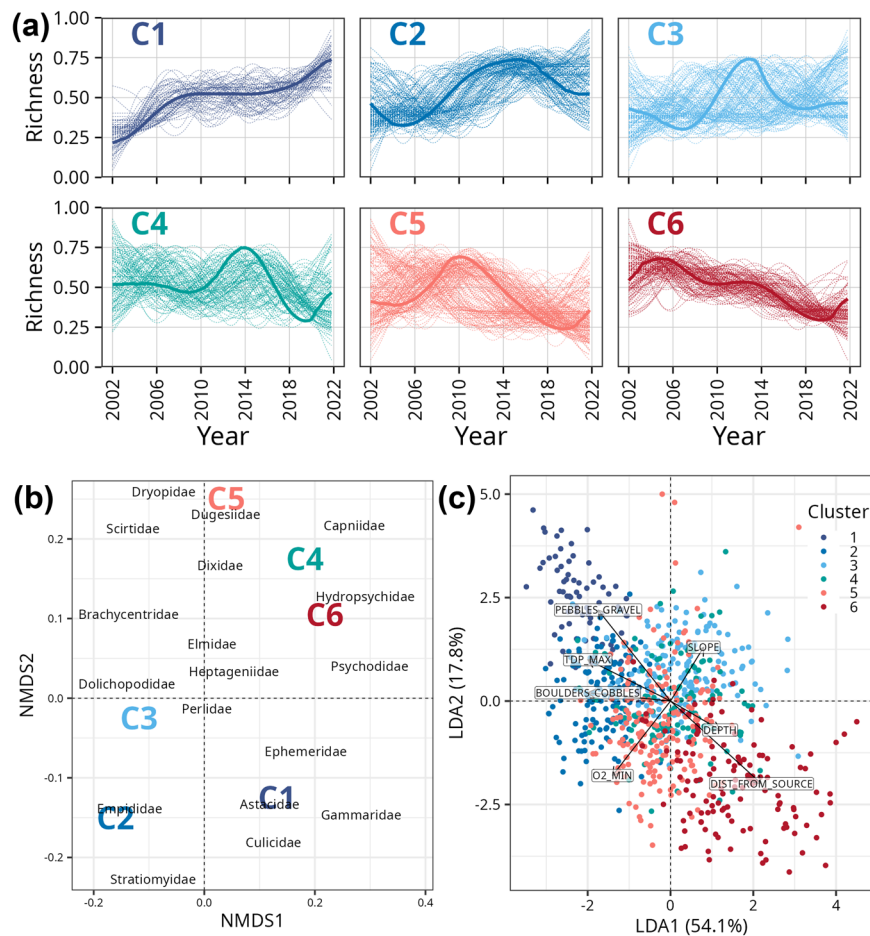


Figure 2. Relationships between clusters of taxonomic richness time series, environmental variables, and macroinvertebrate community composition. (a) Six clusters were obtained from an unsupervised clustering analysis of macroinvertebrate familial richness recorded across 803 sites between 2002 and 2023. Pale dotted lines represent individual time series (i.e. sites); solid thick lines represent the mean temporal trend for each cluster (i.e. the archetypical cluster centroid). (b) Non-metric multidimensional scaling (NMDS) plot showing variation in macroinvertebrate community abundance across the six clusters (stress = 0.02). Only taxa with the largest NMDS species scores are labelled, to aid interpretation. (c) Linear discriminant analysis (LDA) of 803 sites based on multiple environmental variables (Table 1).

variation ($\approx 23\%$). Abundance showed an intermediate pattern, with substantial contributions from both site ($\approx 34\%$) and typology ($\approx 27\%$), as well as additional variation at intermediate spatial scales (catchment and water body; Fig. 5).

Discussion

Across more than 800 long-term monitoring sites, temporal dynamics in three community-level metrics of river ecosystems were highly heterogeneous, with sites exhibiting sharply contrasting patterns, from sustained increases to persistent declines. Our analyses reveal that these dynamics are structured along the river network's longitudinal position, substrate composition, and typology. While these factors are well known to structure spatial variation in freshwater communities, our results reveal that they are also strongly associated with long-term temporal dynamics of several community

metrics. Crucially, sites within the same catchment or water-body often followed markedly different trajectories. This finding challenges the prevailing reliance on regional or national summaries, which can obscure the fine-scale dynamics that ultimately determine ecological outcomes. Rather than a uniform signal of recovery, freshwater change in UK rivers emerges as a mosaic of asynchronous, site-specific pathways.

Environmental drivers of spatio-temporal variation in community metrics

Across sites, temporal dynamics for all three metrics were predominantly non-linear with many trajectories exhibiting peaks, plateaus, and fluctuations through time (Dornelas et al. 2014, Didham et al. 2020). Traditional slope- or effect-size-based approaches would classify both monotonic increases (e.g. C1; Fig. 1a) and trajectories with early plateaus (e.g. C2; Fig. 1a) simply as 'increasing'. In contrast, our shape-based framework when combined with LDA reveals that these two

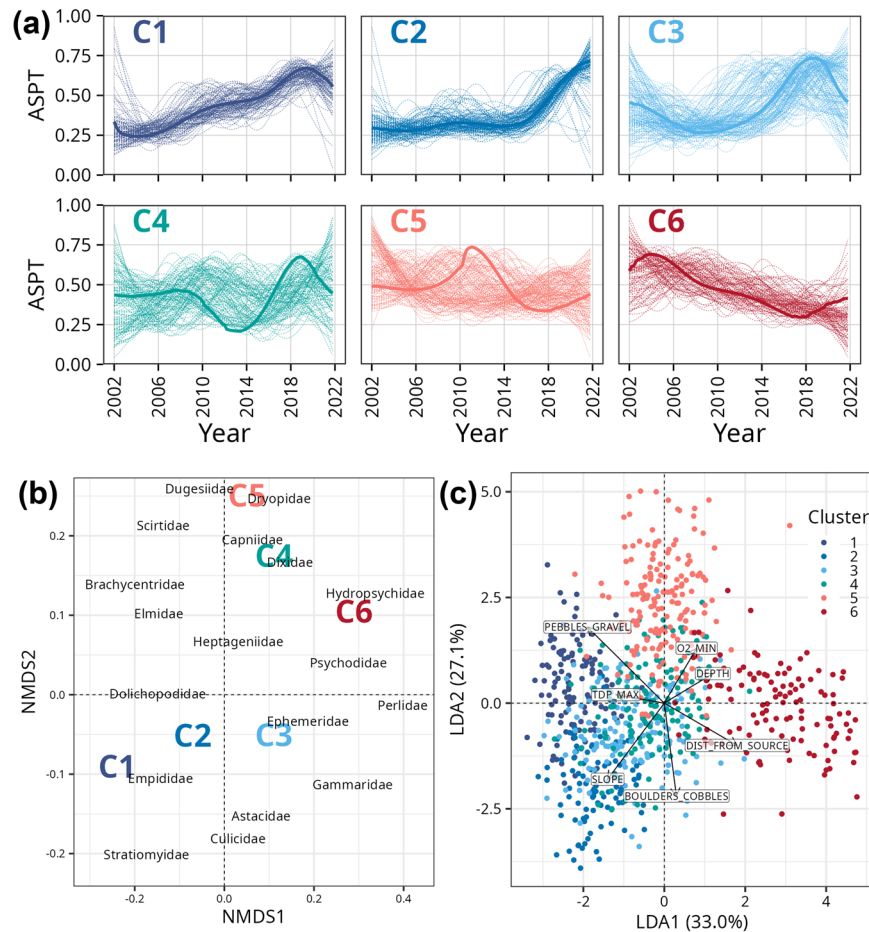


Figure 3. Relationships between clusters of macroinvertebrate abundance time series, environmental variables, and community composition. (a) Six time-series clusters were obtained from an unsupervised clustering analysis of total community abundance recorded across 803 sites between 2002 and 2023. Pale dotted lines represent individual time series (i.e. sites); solid thick lines represent the mean temporal trend for each cluster (i.e. the archetypal cluster centroid). (b) Non-metric multidimensional scaling (NMDS) plot showing variation in macroinvertebrate community diversity across the six clusters (stress = 0.03; only a subset of taxa with the largest NMDS species scores are shown). (c) Linear discriminant analysis (LDA) of 803 sites based on multiple environmental variables (Table 1).

clusters of sites differ in the timing and pathways of recovery, and are also segregated by river network position and local habitat conditions (Fig. 1c). In general, sites exhibiting rapidly increasing trajectories for both pollution sensitivity (ASPT) and taxonomic richness (C1; Fig. 1c, 2c) were more closely associated with higher proximity to a river or stream's source (i.e. low values of 'distance to source'). These environments are typically characterized by higher flow velocities, greater oxygen availability, and reduced retention of fine sediments and associated pollutants, conditions that favor the persistence and recolonization of sensitive and diverse macroinvertebrate communities. In contrast, sites exhibiting more gradual increasing trajectories (C2; Fig. 1c, 2c) tended to occur further downstream than C1 sites, and were associated with shallower slopes and finer substrates. These parts of river networks are likely, in general, to be lowland depositional environments where sediments and associated stressors have longer residence times (Vannote et al. 1980, Allan and Castillo 2007). These factors can increase the

duration of exposure to environmental pressures and are consistent with the more gradual or delayed changes observed in these trajectories. In contrast, declining trajectories (C5 and C6) were predominantly associated with much larger distance from the source. These sites were associated with substantially deeper and more nutrient-enriched waters, which likely indicates an association with agricultural and/or urban run-off (Vannote et al. 1980, Ensign and Doyle 2006, Allan and Castillo 2007). Although we did not explicitly include land use in our analyses, these patterns are consistent with Pharaoh et al. (2024), who showed that the effects of agricultural and urban land cover on macroinvertebrate communities extend beyond average water chemistry, likely reflecting additional stressors associated with these landscapes.

The spatial structuring of trajectories also showed alignment with expectations from meta-community theory, where dispersal processes and network connectivity vary along the river (Carrara et al. 2012, 2015, Altermatt et al. 2013, Tonkin et al. 2018, Carrara et al. 2023). Sites closer to a river's

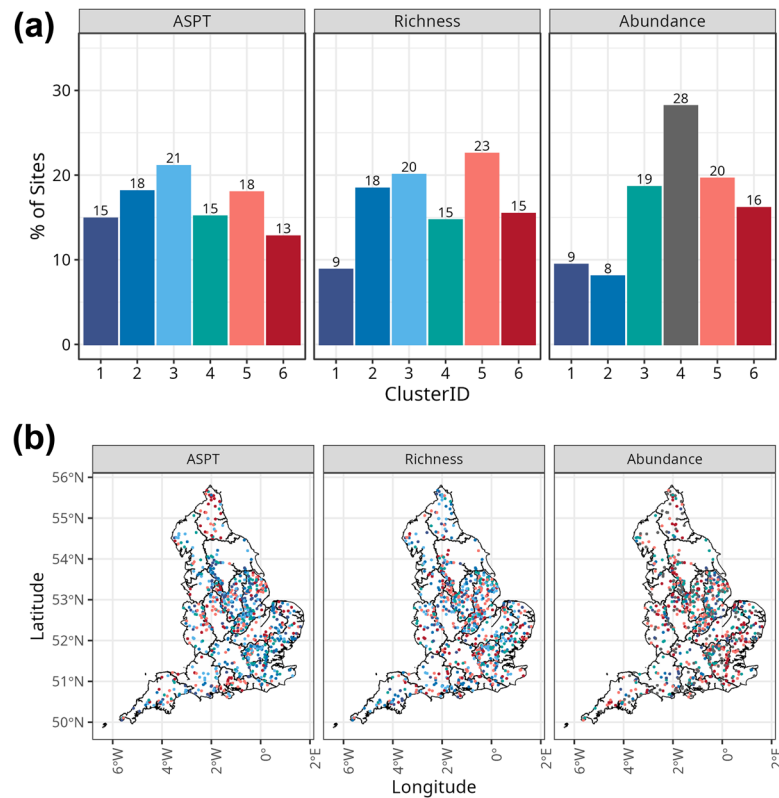


Figure 4. The percentages of sites per cluster, and their geographical distribution across England. (a) Bar plots showing the percentage of sites (individual time series) assigned to different clusters. (b) Spatial distribution of sites and clusters across England. Colors of the points are the same as cluster IDs in panel (a).

source or mid-reaches are more likely to receive colonists from adjacent and upstream reaches, facilitating recovery through dispersal and recolonization, whereas downstream sites may be more isolated from such source populations and increasingly exposed to cumulative catchment stressors (Brown and Swan 2010, Tonkin et al. 2016, 2018). Distance from upstream source populations may therefore partly explain differences in trajectory shapes between C2 and C1 for ASPT (Fig. 1a). However, because pollution-sensitive taxa are also habitat specialists associated with cooler, faster-flowing, well-oxygenated streams and coarse substrates, the different

trajectories are likely to arise from the combined effects of connectivity and environmental filtering.

Total abundance showed comparatively weak and inconsistent segregation in environmental space, in contrast to ASPT and richness (Fig. 3c). The strongly declining trajectories were associated with elevated nutrient concentrations and relatively lower pH conditions than the remaining clusters. This likely reflects the inherently ambiguous ecological interpretation of abundance, which can increase under both improved environmental conditions (e.g. recovery of populations) and enrichment or disturbance (e.g. proliferation of

Table 3. Model diagnostics for linear discriminant analysis (LDA). Models were evaluated using three measures: sensitivity (true positive rate), specificity (true negative rate), and accuracy (overall proportion of correctly classified instances). Cohen's kappa provides a chance-corrected measure of agreement between observed and predicted classifications (−1 = complete disagreement, and 1 = perfect agreement). Asterisks indicate statistical significance for the difference between observed accuracy and the no-information rate [***p < 0.001; **p < 0.01; *p < 0.05].

		C1	C2	C3	C4	C5	C6	Accuracy	Kappa
ASPT	Sensitivity	0.88	0.72	0.75	0.81	0.88	0.79	0.88 ***	0.79 ***
	Specificity	0.69	0.84	0.78	0.80	0.74	0.86		
	Accuracy	0.94	0.92	0.98	0.81	0.92	0.98		
Richness	Sensitivity	0.76	0.76	0.84	0.88	0.71	0.88	0.81 ***	0.79 ***
	Specificity	0.75	0.81	0.77	0.71	0.69	0.79		
	Accuracy	0.98	0.89	0.94	0.98	0.95	0.98		
Abundance	Sensitivity	0.76	0.74	0.73	0.80	0.82	0.72	0.77 ***	0.68 ***
	Specificity	0.63	0.77	0.75	0.81	0.77	0.76		
	Accuracy	0.99	0.96	0.95	0.95	0.93	0.93		

Table 4. Statistics from the multivariate dispersion (betadisper) and permutational multivariate analysis of variance (PERMANOVA) tests of family-level taxonomic composition across the six unsupervised time-series clusters of average score per taxon (ASPT), richness, and abundance metrics. Betadisper evaluates whether the within-cluster dispersion (variance in community composition) differs significantly among clusters, while PERMANOVA tests whether centroids of community composition differ among clusters (i.e. whether overall assemblage structure is more similar within than between clusters). R^2 values represent the proportion of compositional variance explained by cluster identity. Significant pairwise contrasts (adj. p-values) identify which cluster pairs were significantly different compositionally [*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$].

Metric	F-statistic (betadisper)	F-statistic (PERMANOVA)	R^2	Significant pairwise contrasts (adjusted)
ASPT	1.23	3.56	0.10	NA
Richness	1.11	4.68	0.06	NA
Abundance	1.13	2.42	0.08*	C4 versus C6*

tolerant taxa; Vaughan and Ormerod 2012, Verberk et al. 2016). A few sites showed recent plateauing for richness and abundance (e.g. C1 and C2; Fig. 3a), broadly consistent with patterns reported at larger spatial and temporal scales (Haase et al. 2023). However, our shape-based framework reveals substantially greater temporal complexity than the relatively uniform plateau described in that study. These differences may also reflect the temporal extent of analysis. Our study focuses on a relatively recent period (2002–2023), characterized by standardized monitoring protocols and post-regulation conditions, whereas several previous assessments span longer time-frames that include periods of more pronounced environmental degradation and subsequent recovery (Durance and Ormerod 2007, 2009, Vaughan and Ormerod 2012, Murphy et al. 2014). As a result, long-term studies may emphasize broad recovery trajectories, while shorter, contemporary analyses such as ours are more likely to capture emerging declines at finer spatial scales. If UK patterns are representative of broader European trends, then the apparent continental-scale ‘halt’ in biodiversity recovery may conceal considerable local heterogeneity in both the timing and pathways of ecological change.

A lack of strong taxonomic segregation among trajectory groups suggests that divergent temporal dynamics in ASPT,

richness, and abundance were not driven by discrete, non-overlapping assemblages, but instead emerged from substantial compositional turnover and reorganization within broadly shared regional species pools. Increasing and declining trajectories for ASPT and richness frequently retained mixtures of both pollution-sensitive and tolerant taxa, indicating that similar temporal patterns in community metrics can arise from multiple alternative compositional pathways. Such decoupling between biodiversity metrics and community composition is increasingly recognized in long-term ecological datasets, where substantial species turnover may occur despite relatively stable aggregate community properties (Dornelas et al. 2014, Magurran et al. 2018, Powell et al. 2023).

Several mechanisms may contribute to this pattern. First, our family-level analyses may mask substantial species-level turnover within families that differ in ecological tolerances and responses to environmental change. Such taxonomic aggregation can obscure compensatory replacement dynamics, whereby declines in some taxa are offset by increases in ecologically similar taxa (Dornelas et al. 2014). Second, dispersal and metacommunity dynamics may continually reshuffle local assemblages, preventing communities from converging toward stable compositional endpoints (Brown

Table 5. Population-level (fixed) intercepts from Bayesian categorical (multinomial-logit) models of cluster membership for time-series of average score per taxon (ASPT), richness, and abundance. Coefficients are log-odds for the six categories (C_k) relative to the reference category, reported as posterior mean (Estimate), posterior SD (Est.Error), and 95% credible intervals (l-95% CI, u-95% CI). R is the split-chain convergence diagnostic (values ≈ 1 indicate good mixing). Bulk-ESS and Tail-ESS are effective sample sizes for central and tail posterior summaries, respectively. For each metric, the reference category (i.e. the baseline) was set as the cluster where time-series exhibited neither a strong increasing nor decreasing trend.

		Estimate (μ)	Est.Error	l-95% CI	u-95% CI	R	Bulk_ESS	Tail_ESS
ASPT	C1	−1.5	2.1	−7.16	1.31	1.00	1331	1566
	C2	−1.42	2.27	−7.20	1.34	1.00	934	1276
	C3	−2.07	1.45	−5.56	−0.27	1.01	987	878
	C4	−1.25	2.13	−6.53	1.43	1.00	1190	1194
	C5	−1.23	2.09	−5.99	1.09	1.02	896	982
Richness	C2	−1.05	2.01	−5.78	1.6	1.00	1366	1266
	C3	−1.07	2.04	−5.89	1.8	1.02	1992	695
	C4	0.23	1.87	−4.04	3.1	1.02	2369	2463
	C5	−3.21	1.88	−7.87	−0.95	1.00	1092	895
Abundance	C2	−1.89	2.28	−7.61	1.21	1.01	2648	1758
	C3	−1.62	2	−6.49	0.94	1.00	1848	817
	C4	−2.25	1.94	−7.03	0.06	1.01	1808	1509
	C5	−2.66	2.81	−9.34	0.65	1.01	1852	620
	C6	−1.89	2.28	−7.61	1.21	1.01	2648	1758

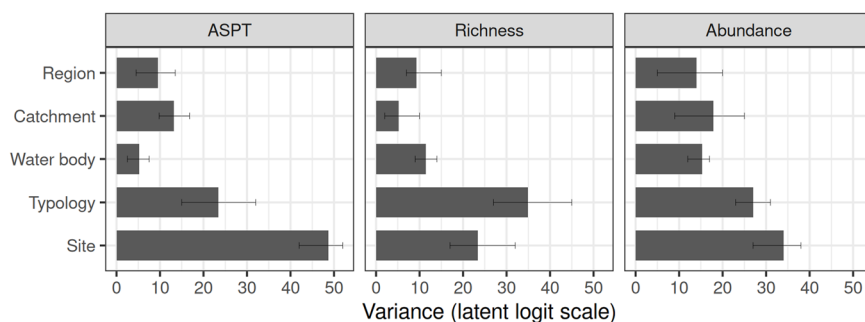


Figure 5. Posterior variance partitioning derived from Bayesian categorical models. Cluster variability was partitioned across hierarchical and cross-linked spatial scales (site, water body, catchment, typology, and Environment Agency region) for three metrics (average score per taxon, ASPT; taxonomic richness; and total abundance). Bars show posterior means of variance components on the latent logit scale (the relative magnitude of heterogeneity in Cluster ID, attributable to each spatial level), with error bars representing 95% credible intervals.

and Swan 2010, Carrara et al. 2012, Tonkin et al. 2018). Finally, the community metrics themselves integrate different aspects of community structure. ASPT is based on average pollution sensitivity scores, such that replacement among taxa with similar tolerance values may generate little change in index structure despite substantial compositional turnover. Likewise, richness may remain relatively stable if local extinctions are balanced by colonization, whereas abundance can increase under both ecological recovery and environmental degradation through the proliferation of tolerant or opportunistic taxa. Together, these results suggest that long-term freshwater change is better interpreted as a dynamic process of continual community reassembly rather than a transition between discrete and taxonomically distinct ecological states. Future work examining these trajectory clusters through the lens of temporal compositional turnover and beta diversity, including functional and phylogenetic turnover, may provide additional insight into the ecological processes underlying divergent community trajectories despite overlapping taxonomic structure.

Overall, the prominence of ‘intermediate’ trajectories, characterized by reversals, plateaus, and non-monotonic fluctuations through time (e.g. C3–C4 in Fig. 1a, 2a, 3a), suggests that ecological change in river systems rarely follows simple directional pathways of recovery or decline. Their substantial overlap in environmental space within the LDA ordination further indicates that these trajectories are unlikely to reflect a single dominant environmental driver. Instead, they likely emerge from the interaction of multiple processes operating asynchronously across river networks, including episodic pollution events, nutrient and sediment loading, hydromorphological modification, restoration activities, and broader climatic variability (Townsend 1989, Palmer et al. 1997, Rice et al. 2001, Durance and Ormerod 2007, 2009, Larsen et al. 2024). We argue that rather than representing noise, these intermediate trajectories may reflect the prevailing mode of contemporary biodiversity change in freshwater ecosystems: dynamic, locally contingent, and characterized by continual community reorganization rather than consistent recovery or decline. This interpretation is also consistent with the inherent challenges of long-term

biodiversity monitoring, including uncertain historical baselines, imperfect detection, taxonomic aggregation, and density-dependent artefacts (Didham et al. 2020, Wilkes et al. 2025a, 2025b). Incorporating such localized and non-linear departures into biodiversity monitoring frameworks will be essential not only for detecting ecological change, but also for disentangling the interacting processes that generate it across spatial and temporal scales.

Scaling ecological variability: from local patches to river networks

Across the spatial hierarchy, temporal trajectories were far more variable among individual sites than among catchments, regions, or administrative units, indicating that neighboring sites can follow markedly different ecological pathways even within the same landscape context (Fig. 5). This finding is supported by a growing recognition that freshwater systems exhibit strong local heterogeneity (Vaughan and Ormerod 2012, Powell et al. 2023, Pharaoh et al. 2024), but we extended current understanding by explicitly quantifying how such variability is partitioned across nested spatial scales. Although strong spatial autocorrelation was not detected at broader neighborhood scales, sites showed notable similarity in trajectory shape at fine spatial extents (~ 1 km²; Fig. 4b), beyond which patterns rapidly diverged. Accordingly, the hierarchical variance-components model did not include an explicit spatial autocorrelation structure, instead accounting for dependence through the nested monitoring hierarchy. However, our autocorrelation analysis did not explicitly incorporate flow direction or network topology, both of which are known to structure ecological connectivity in dendritic systems (Carrara et al. 2012, Altermatt et al. 2013). Incorporating these processes would likely reveal additional structure, reinforcing the role of river networks as directional, connected systems rather than simple spatial grids. We acknowledge that the spatial distribution of monitoring sites was also uneven across England, reflecting the stringent filtering criteria required to obtain long, internally consistent time series. Although the retained dataset spans the major Environment Agency regions, catchments, water bodies, and river typologies, reduced site density in some regions may limit the resolution with which local patterns can be

characterised and should be considered when interpreting regional-scale comparisons.

Despite the overarching result of local site-to-site variability, river typology emerged as an additional key organizing factor. Typology-based approaches form a core component of spatial reference evaluations in environmental monitoring systems such as the EU WFD, reflecting the importance of core variables such as altitude, substrate, and geology that strongly influence macroinvertebrate dynamics (Monk et al. 2008, Vaughan and Ormerod 2012, 2014, Johnson et al. 2025a). However, our results demonstrate that their combined expression, as formalized in typological classifications, provides a meaningful basis for disentangling temporal change. Typology was noted by Powell et al. (2023) as being linked with invertebrate trends in England's rivers, particularly showing divergent responses among organic versus siliceous lowland rivers. Our results broadly support these findings, but also suggest substantially greater temporal complexity within and among river typologies than is captured by directional trend analyses alone. In particular, the prevalence of non-monotonic trajectories, including plateaus, reversals, and asynchronous recovery pathways, indicates that typology structures not only the direction of ecological change, but also its temporal dynamics through time. These findings highlight the value of shape-based approaches for resolving ecological dynamics that may be obscured when trajectories are reduced to net monotonic trends.

Taken together, our results suggest that freshwater ecosystems are best understood as hierarchically structured systems in which broader environmental and spatial templates dominate, but are constrained and modulated by local processes. For ecologists, this underscores the need to move beyond spatially aggregated interpretations of biodiversity change. For managers, it highlights that restoration success, or system degradation, cannot be inferred from broad-scale trends alone, but must be understood in the context of local conditions, connectivity, and position within the river network. This points to a clear need for approaches that retain site-level resolution while explicitly accounting for spatial hierarchy (Pharaoh et al. 2024). In contrast, the ongoing contraction of monitoring capacity threatens this capability; Environment Agency funding fell from approximately GBP120 million in 2010 to around GBP40 million in 2020 (Environment Agency 2025). Without robust, sustained investment in high spatial-resolution monitoring networks, our ability to detect, attribute, and manage biodiversity change in freshwater systems will be fundamentally compromised.

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Author contributions

Mansi Mungee: Data curation (lead); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **William E. Kunin:** Conceptualization (supporting); Funding acquisition (equal); Investigation (equal); Project administration (equal); Supervision (equal); Writing – review and editing (supporting). **Christopher Hassall:** Conceptualization (supporting); Funding acquisition (equal); Investigation (equal); Project administration (equal); Writing – review and editing (supporting). **Vicky A. Bell:** Data curation (supporting); Writing – review and editing (supporting). **Martin Wilkes:** Data curation (supporting); Formal analysis (supporting); Resources (supporting); Writing – review and editing (supporting). **Lee E. Brown:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/ecog.08573>.

Data availability statement

All macroinvertebrate data used for this manuscript are from publicly available UK Environment Agency (EA) long-term monitoring surveys: <https://environment.data.gov.uk/ecology/explorer> (Mungee et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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