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Responses of fish to nationwide improvements in the water quality of a densely populated and heavily modified country over four decades

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ABSTRACT

Globally, fish have been severely affected by the widespread, chronic degradation of fresh waters, with a substantial proportion of species declining in abundance or range in recent decades. This has especially been the case in densely populated countries with an industrial heritage and intensive agriculture, where the majority of river catchments have been affected by deteriorations in water quality and changes in land use. This study used a spatially and temporally extensive dataset, encompassing 16,124 surveys at 1180 sites representing a wide range of river typologies and pressures, to examine changes in the fish populations of England's rivers over four decades (1980s–2010s). The analyses revealed gradual, nationwide increases in mean fish species richness and diversity across the range of pressure gradients. In the majority of cases, increases were most pronounced in the 1980s, since when any further changes have been comparatively minor, but there were no declining trends across the full time series. There were also temporal, nationwide changes in fish assemblage structure, driven largely by variations in the densities of brown trout *Salmo trutta* or roach *Rutilus rutilus*, but no consistent increases in the abundance of sensitive, pollution-intolerant species in response to improvements in wastewater treatment and, consequently, water quality. Although the increases in fish species richness and diversity over the last four decades are encouraging, subtle and contrasting changes in the abundance of a range of species require further investigation, and causal relationships between fish assemblage structure and putative drivers should be modelled at a national scale. This study is the first to examine long-term, nationwide trends in the freshwater fish populations of England, and significantly advances our understanding of the ecological health of rivers in densely populated and heavily modified countries.

1. Introduction

Spatial and temporal variations in animal population sizes and community structure are natural phenomena, but those caused or exacerbated by anthropogenic activities have increased in prevalence and magnitude in the last two centuries, with freshwater ecosystems particularly impacted (Tickner et al., 2020). Some of the most widespread, significant and persistent pressures are overexploitation, habitat loss, invasive species and pollution, but many others, including climate change, novel contaminants and interactive effects, have emerged or increased in severity in recent decades (Birk et al., 2020). In some cases, freshwater ecosystems suffered from severe pollution and habitat degradation as a consequence of industrialisation but are now recovering (Johnson et al., 2019), whereas in others the impacts have persisted or are increasing, and overall biological diversity is still declining on a global scale (Reid et al., 2019).

Fish have been particularly affected by the degradation of fresh waters, with a substantial proportion of species declining in abundance or range in recent decades (Miranda et al., 2022). A wide range of biotic (e.g. competition, predation, disease) and abiotic (e.g. climate,

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hydrology, physico-chemistry) factors influence fish population dynamics. In temperate fresh waters, for example, the recruitment of many fish species is positively correlated with growth in the first year of life and highest in years when water temperatures are higher than average (Nunn et al., 2010). Conversely, elevated river levels can negatively influence population dynamics due to increased mortality and energy expenditure, and reduced food availability and growth (Nunn et al., 2010). In addition, competition can affect fish populations and communities through changes in individual behaviour, and predation and parasitism can have a significant influence on survival and cohort sizes (Longshaw et al., 2010; Nunn et al., 2020). Climate is the most important at large spatial scales, and can result in synchronous fluctuations in population sizes across large geographical areas and, sometimes, multiple species, whereas biotic factors, water chemistry and physical habitat vary widely and so can only be locally influential. In addition to natural variations in climate, hydrology, physico-chemistry, competition, predation and disease, the vast majority of fish populations are exposed to a range of anthropogenic pressures, such as pollution, habitat degradation and land-use change, which may exacerbate or in severe cases exceed the influence of other drivers. Indeed, the extinctions of at least eight species of European freshwater fish have been attributed to pollution (Freyhof and Brooks, 2011), and habitat fragmentation has been identified as one of the key threats to fish populations globally (Miranda et al., 2022). Furthermore, there are concerns over possible additive, antagonistic and synergistic effects, which could exacerbate existing or emerging issues, especially in the face of climate change (Birk et al., 2020).

In densely populated countries with an industrial heritage and intensive agriculture, such as occurs across much of Europe and elsewhere, the majority of river catchments have typically been affected by deteriorations in water quality and changes in land use (Birk et al., 2020; Haase et al., 2023). In England, for example, many fish populations were severely affected or even eradicated by pollution, especially during the 1950s but until as recently as the 1970s, and some of the most sensitive species and those of greatest conservation importance have still not recovered (Nunn et al., 2023). However, despite concerns about diffuse pollution in agricultural landscapes, sewage and persistent or emerging issues in urban areas (Windsor et al., 2019; Perry et al., 2024), benthic macroinvertebrate data suggest that overall water quality has generally improved in the last few decades (Vaughan and Ormerod, 2014; Pharaoh et al., 2023; Qu et al., 2023). Although various studies have documented localised improvements in fish populations following implementation of pollution-abatement measures (e.g. Cowx and Broughton, 1986), whether assemblages have recovered in a similar manner to benthic macroinvertebrates has not yet been fully examined at a national scale. This is important because fishes invariably respond more slowly than invertebrates to environmental changes and so, as a result of the contrasting environmental requirements of particular species and life stages, can be useful indicators of the longer-term ecological quality of fresh waters (Oberdorff et al., 2002). Fish are also sensitive to the mixture of chemicals in wastewater and from agriculture, including pharmaceuticals, so are likely to respond differently to aquatic invertebrates (Hamilton et al., 2016).

This study examined the responses of fish to nationwide improvements in the water quality of a densely populated and heavily modified country (England) over four decades. Long-term trends in fish species richness, diversity, evenness and abundance were investigated in the context of a range of factors known to cause spatial variations in assemblage structure, namely latitude, longitude, altitude, land use, hydrology and wastewater exposure (Wheeler, 1977; Hamilton et al., 2016), the rationale being that temporal changes in fish assemblages may differ according to gradients in covariate attributes. The hypothesis was that the general improvement in the water quality of England's rivers in the last few decades, as indicated by various benthic macroinvertebrate indices (Vaughan and Ormerod, 2014; Pharaoh et al., 2023; Qu et al., 2023), would be reflected by gradual changes in the fish assemblages, such as increases in richness, diversity and the abundance of pollution-intolerant species. Although various studies have investigated either broad spatial or long-term temporal variations in fish populations or assemblages (e.g. Britton et al., 2004; Noble et al., 2007), none appear to have examined both at a national scale. This study will therefore significantly advance our understanding of the long-term ecological health of rivers in densely populated and heavily modified countries in the context of both historical and contemporary anthropogenic pressures.

2. Material and methods

2.1. Fish data collation

This study used the Environment Agency's open-source National Fish Population Database (NFPD), the most comprehensive freshwater fish dataset in England (Environment Agency, 2024). The NFPD is spatially and temporally extensive (>282,000 records of 48 species from >15,000 sites spanning >40 years when accessed on 05/03/2019) and includes quantitative (depletion), semi-quantitative (single catch) and qualitative (no sampling effort reported) surveys at sites representing a wide range of river typologies and pressures across England. For this study, the database was filtered to remove qualitative surveys, which cannot be used to calculate catch-per-unit-effort, and sites with fewer than ten quantitative or semi-quantitative surveys, as one of the objectives was to investigate temporal variations in fish assemblages. The vast majority of surveys were conducted by electric fishing, but seine nets were used at some sites.

Absolute fish counts were available in the vast majority of cases, but it was occasionally necessary to derive abundance for common species historically under-recorded (imprecisely enumerated) in standard fish surveys (bullhead *Cottus gobio* L., minnow *Phoxinus phoxinus* (L.), stone loach *Barbatula barbatula* (L.), three-spined stickleback *Gasterosteus aculeatus* L.) from estimates on a logarithmic scale (Ainsworth et al., 2024). Fish counts from each semi-quantitative survey and the first catch from quantitative surveys were then divided by the sampling area to account for temporal (between survey) and spatial (between site) differences in sampling effort and obtain species-specific densities (no. 100 m^{-2}) (Ainsworth et al., 2024). The 1970s data were excluded due to there being considerably fewer sites and surveys compared to the 1980s–2010s, leaving 90,756 records from 16,124 surveys at 1180 sites in the final dataset. The contributions of individual cohorts to total counts were unknown, so the analyses were conducted on fish of all ages combined.

2.2. Covariate data collation

Covariate data included latitude, longitude, altitude, upstream land use, river discharge and wastewater exposure. Latitude and longitude were included as there are well-documented gradients in fish species richness in England, being highest in the south-east and lowest in the west (Wheeler, 1977). Similarly, species-specific environmental requirements result in shifts in fish assemblage structure according to altitude, with salmonids most abundant in upland areas and cyprinids dominating in the lowlands (Noble et al., 2007). Land use and wastewater exposure were included as they have the potential to cause spatial variations in fish assemblages, and discharge was used as a measure of river size at each site (Hamilton et al., 2016; Qu et al., 2023).

The latitude (°) and longitude (°) of each fish site were included in the NFPD (Environment Agency, 2024), and altitude (m above sea level) was extracted from the Integrated Hydrological Digital Terrain Model (IHDTM) (Morris and Flavin, 1990). Land use (% woodland, urban, arable, semi-natural) in the catchment upstream of each fish site was derived from the UK Centre for Ecology & Hydrology's 2015 Land Cover Map (Rowland et al., 2017) in combination with the IHDTM, and river discharge data (naturalised annual mean, m^3s^{-1}) were obtained from the National River Flow Archive (Gustard et al., 1992). Exposure to the range of contaminants in municipal wastewater was estimated for each site using the LowFlows2000 Water Quality eXtension (LF2000-WQX) model, which combines natural, reach-specific river discharge and the volumes of effluent discharged from treatment works to determine the percentage contribution of wastewater to total river discharge (Williams et al., 2009). Latitude, longitude, altitude and upstream land use were available for all fish sites, and river discharge and wastewater exposure were available for 92 % and 55 % of sites, respectively. The dataset, including how the fish and covariate data were obtained, processed or derived, is described fully and freely available in the supporting documentation (Ainsworth et al., 2024).

2.3. Data analysis

This study followed a similar approach to Qu et al. (2023), with the addition of multivariate analyses, to investigate long-term, nationwide trends in fish assemblages. Thus, covariates were divided into four categories for some of the analyses, namely local polynomial regression (Section 2.3.1) and examination of fish assemblage structure (Section 2.3.3), to facilitate interpretation of any patterns. The selection of the categories was a compromise between similar sample sizes and a meaningful division of the data, with latitude and longitude divided at intervals of ~1.5°, and altitude, land use, river discharge and wastewater exposure split into quartiles (i.e. according to 25th, 50th and 75th percentiles) (Qu et al., 2023). Site latitude, longitude and altitude are necessarily fixed, and although absolute land use, river discharge and wastewater exposure will vary to some extent over time, they are effectively fixed when divided at a national scale into quartiles according to either the single available measurement (land use) or long-term means (river discharge, wastewater exposure). This is convenient as it makes it possible to assess whether any trends in fish assemblages have occurred nationwide or in only some river types (covariate categories). Note that the lack of temporal data for some of the covariates was not an issue as the purpose of the study was to examine trends in fish assemblages, facilitated by splitting the covariates into four categories, not model the impacts of temporal variations in covariates on fish assemblages. The only time when the covariate data *per se* were included in the analyses was for the generalised linear mixed models (Section 2.3.1).

2.3.1. Fish species richness, diversity and evenness

Species richness (number), diversity (Shannon-Wiener, $\log_e$) and evenness (Pielou) were calculated for each fish survey. Trends in mean richness, diversity and evenness over time (1980–2017) were then visualised for each covariate category by local polynomial regression using the LOESS function in the stats R package, with 95 % confidence intervals, weighted to account for annual variations in sampling intensity, represented by grey bands (Zuur et al., 2007).

In addition, employing the code provided by Qu et al. (2023), generalised linear mixed models (GLMM) were computed using the glmmTMB function in the glmmTMB R package. Thus, richness, diversity and evenness were categorised using the nbinom1 function as response variables with negative binomial distributions, with the covariates (latitude, longitude, altitude, upstream land use, river discharge, wastewater exposure) and time (year) used as explanatory variables, and site used as a random variable (Qu et al., 2023). For the entire dataset (i.e. not divided into four categories), separate models were then built for each explanatory variable to determine their influence on fish species richness, diversity and evenness, whilst accounting for random site effects, e.g. Richness ~ Year + Longitude + (1|Site). Explanatory variables were scaled to facilitate interpretation of the coefficients, and the reliability of the models was determined by examining the residuals vs. fitted, normal Q-Q, scale-location and residuals vs. leverage plots. Owing to their reduced complexity, better convergence and lower risk of overfitting, models without interactions were considered most appropriate.

2.3.2. Fish species prevalence, relative abundance and absolute abundance

The prevalence, relative abundance and absolute abundance of each fish species were calculated for each decade (1980s, 1990s, 2000s, 2010s) to examine changes over time, and mean densities (where a species occurred at least once; it was not considered appropriate to include null catches for sites where, for biogeographical reasons, a species was not expected to occur) at the start (1980s) and end (2010s) of the dataset were compared for the most widespread and abundant species using independent samples *t*-tests. Fishes were categorised as tolerant, moderately tolerant or intolerant of reductions in water quality (Oberdorff et al., 2002) for presentation of any changes in mean densities between the 1980s and 2010s. In addition, beta diversity (Whittaker's measure) was calculated for each decade as $\beta = (S/\alpha) - 1$, where S is the total number of species captured from the 1980s-2010s and α is the number of species caught in the 1980s, 1990s, 2000s or 2010s, to examine species turnover.

2.3.3. Fish assemblage structure

Permutational multivariate analysis of variance (PERMANOVA) was used to investigate temporal variations in fish assemblage structure. First, fish densities were multiplied by 100, so that all values were greater than 1, and log ($x + 1$) transformed. Given the focus on long-term changes in this study and its large size, the dataset was then consolidated by calculating mean densities according to a year (1980–2017) × covariate (latitude, longitude, altitude, land use, river discharge, wastewater exposure) category factor. Bray–Curtis similarities were calculated among year × covariate category means, and distances among group centroids were obtained for each decade (1980s, 1990s, 2000s, 2010s) × covariate category factor and ordinated (with trajectories) according to covariate category using non-metric multidimensional scaling (MDS). The year × covariate category means matrices were then tested for homogeneity of dispersions using permutational analysis of multivariate dispersions (PERMDISP; 9999 random permutations), and submitted to PERMANOVA (type III sum of squares, fixed effects for mixed terms sum to zero, permutation of residuals under a reduced model, 9999 random permutations) using a two-way factorial design accounting for covariates and time. In addition, similarity percentages (SIMPER) analysis was used to calculate the contributions of each fish species to differences in assemblage structure over time according to covariate category. Statistical analyses were conducted using R v. 4.3.1 (R Foundation for Statistical Computing, Vienna, Austria), SPSS v. 28.0.1.1 (IBM SPSS Statistics, Chicago, USA) and PRIMER (v. 7) & PERMANOVA+ (PRIMER-E Ltd, Plymouth, UK).

3. Results

3.1. Fish species richness, diversity and evenness

There has been a gradual increase in mean fish species richness in England's rivers in the last four decades. In the majority of cases, the increase was most pronounced in the 1980s, since when any further changes have been comparatively minor, but there have been no declining trends in richness across the full time series (Figs 1 and 2). The increases have occurred across almost the full range of pressure gradients, despite consistent differences in absolute values between covariate categories. The main exceptions are rivers in the far north or south-west of England and at high altitudes, where richness has been relatively stable (Fig. 1). In general, mean species richness was highest in eastern England, at low altitudes and in areas of high urban/arable land use and wastewater exposure (Figs 1 and 2; Table 1). There were no clear linear relationships for latitude, river discharge and woodland coverage, with richness highest in central England, relatively small rivers and moderately wooded catchments, and lowest in northern England, larger rivers and sparsely or extensively wooded catchments (Figs 1 and 2). For river discharge, the similar means for each category resulted in a narrower range of values compared to the other covariates (Fig. 1).

Latitude (°)		**Longitude** (°)		**Altitude** (m.a.s.l.)		**Discharge** (m^3s^{-1})	
1180 sites		1180 sites		1180 sites		1081 sites	
Range	No. sites	Range	No. sites	Range	No. sites	Range	No. sites
50 to 51.5	330	–4.9 to –3.2	184	0 to 19	292	0 to 0.9	216
>51.5 to 53	442	–3.2 to –1.6	374	>19 to 49	296	>0.9 to 2.4	276
>53 to 54.5	303	–1.6 to –0.2	333	>49 to 111	299	>2.4 to 6.7	299
>54.5 to 56	105	–0.2 to +1.6	289	>111 to 410	293	>6.7 to 87.0	290

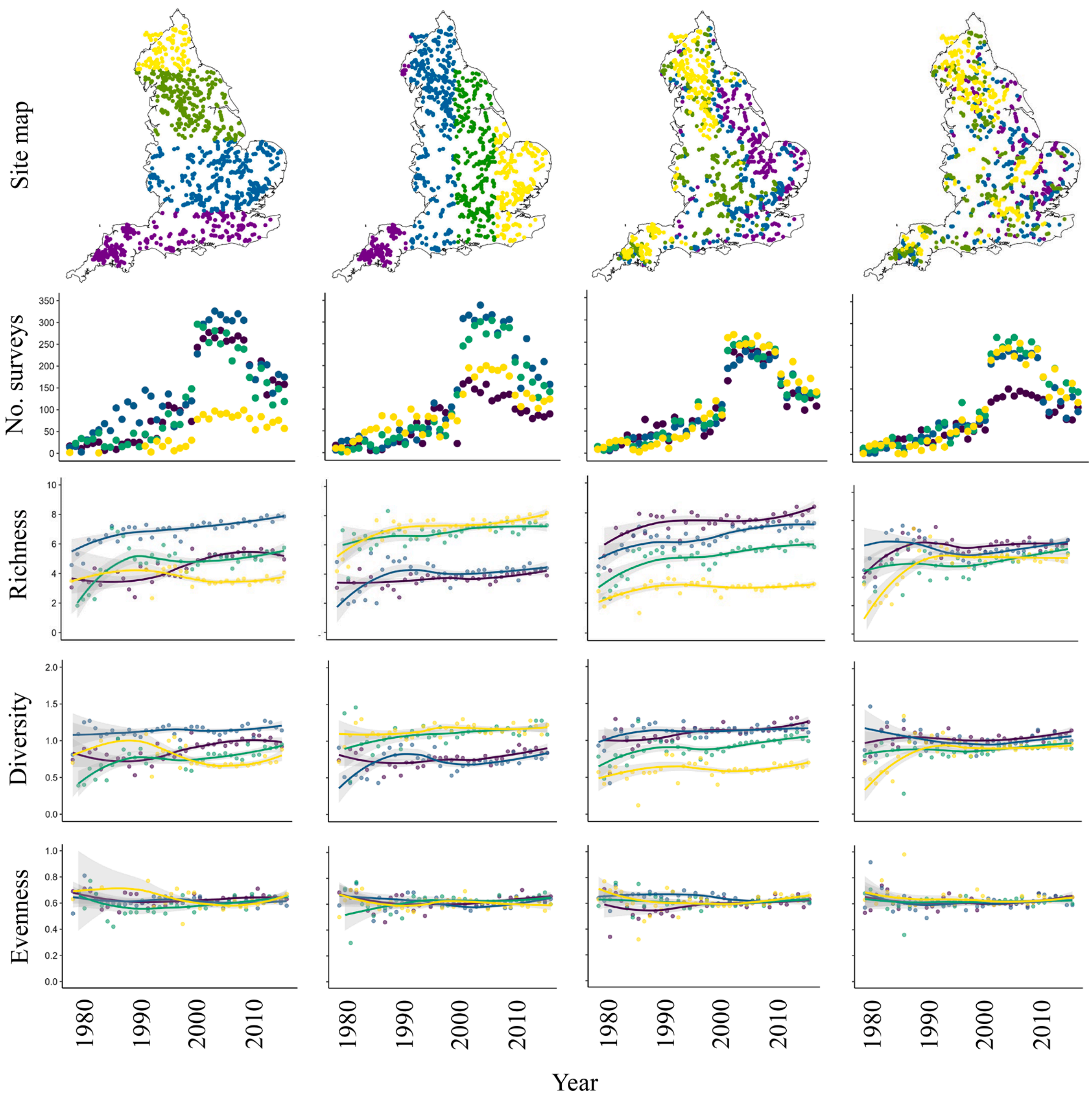

Fig. 1. Fish site locations, survey numbers and mean species richness, diversity and evenness in England's rivers between 1980 and 2017 according to latitude, longitude, altitude and river discharge category.

The patterns were similar, but less pronounced, for fish species diversity, which has been increasing only slowly or remained stable over the last four decades. The greatest increases in diversity over time were in large rivers, sparsely wooded catchments and at sites with very low wastewater exposure in the 1980s (Figs. 1 and 2). There were no apparent temporal trends in fish species evenness (Figs 1 and 2; Table 1).

3.2. Fish species prevalence, relative abundance and absolute abundance

Nationally, there have been some progressive changes in the frequency of occurrence of many fish species over time. The prevalence of bullhead, grayling *Thymallus thymallus* (L.), minnow, stone loach and three-spined stickleback has increased in each of the last four decades, whereas the occurrence of gudgeon *Gobio gobio* (L.), European eel *Anguilla anguilla* (L.) and roach *Rutilus rutilus* (L.) has decreased (Fig. 3a). There were no clear decadal trends for brown trout *Salmo trutta* L., chub

Woodland (%)		**Urban** (%)		**Arable** (%)		**Semi-natural** (%)		**Wastewater** (%)	
1180 sites		1180 sites		1180 sites		1180 sites		644 sites	
Range	No. sites	Range	No. sites	Range	No. sites	Range	No. sites	Range	No. sites
0 to 4	294	0 to 1	293	0 to 1	293	0 to 21	292	0 to 2	158
>4 to 7	296	>1 to 3	296	>1 to 23	296	>21 to 47	296	>2 to 8	159
>7 to 12	297	>3 to 7	296	>23 to 58	296	>47 to 84	295	>8 to 16	163
>12	293	>7	295	>58	295	>84	297	>16	164

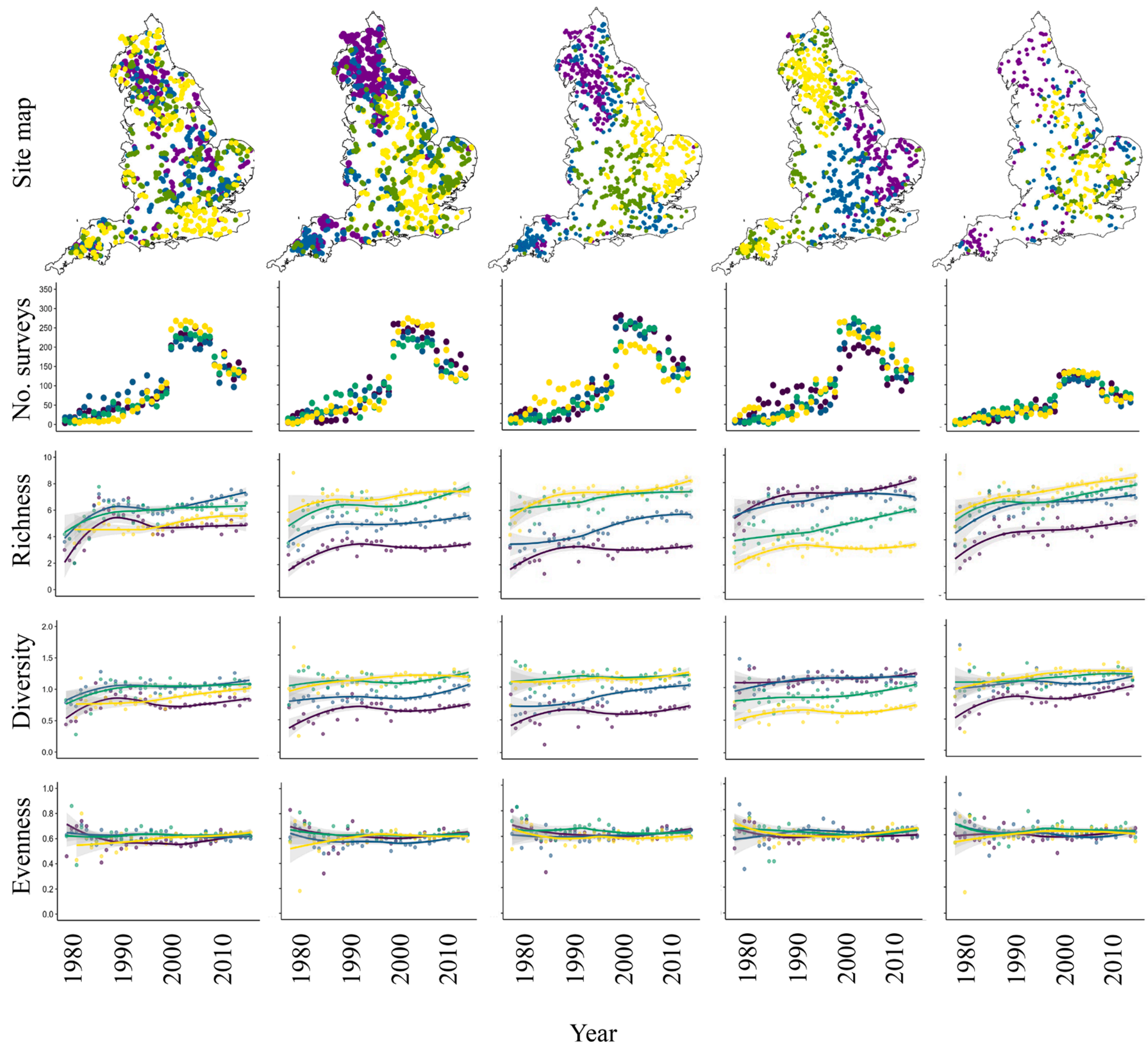

Fig. 2. Fish site locations, survey numbers and mean species richness, diversity and evenness in England's rivers between 1980 and 2017 according to land use (woodland, urban, arable, semi-natural) and wastewater exposure category.

Squalius cephalus (L.), dace *Leuciscus leuciscus* (L.), perch *Perca fluviatilis* L. and Atlantic salmon *Salmo salar* L. (Fig. 3a). Overall, the prevalence of non-native species (bitterling *Rhodeus amarus* (Bloch), common carp *Cyprinus carpio* L., crucian carp *Carassius carassius* (L.), goldfish *Carassius auratus* (L.), ide *Leuciscus idus* (L.), pikeperch *Sander lucioperca* (L.), rainbow trout *Oncorhynchus mykiss* (Walbaum), sunbleak *Leucaspius delineatus* (Heckel), wels catfish *Silurus glanis* L.) declined from 10 % in the 1980s and 1990s to 6 % in the 2000s and 4 % in the 2010s.

Changes in relative abundance have been more marked, with minnow progressively increasing and gudgeon and roach decreasing, but there were no smooth, linear trends over time for the other species (Fig. 3b). The relative abundance of non-native species declined from 0.07 % in the 1980s and 1990s to 0.06 % in the 2000s and 0.01 % in the 2010s.

The mean densities of brown trout, dace, eel, pike *Esox lucius* L., roach, ruffe *Gymnocephalus cernuus* (L.) and salmon significantly declined between the 1980s and 2010s (independent samples *t*-tests, all $P < 0.05$) (Fig. 4; plotted as percentage change due to substantial interspecific differences in densities). By contrast, the mean densities of barbel *Barbus barbus* (L.), bullhead, chub, minnow and stone loach significantly increased (independent samples *t*-tests, all $P < 0.01$), but there were no consistent, between-group changes in the abundance of pollution-tolerant vs. pollution-intolerant species as, in both, some decreased while others increased or remained stable (Fig. 4). Although the mean density of gudgeon declined by 93 % between the 1980s and 2010s (Fig. 4), substantial variation between surveys rendered it not

Table 1
Results of the general linear mixed models examining the influence of latitude, longitude, altitude, river discharge, land use and wastewater exposure on fish species richness, diversity and evenness in England's rivers. Statistically significant results are highlighted bold.

Index	Model	Estimate		
		Variable 1	Variable 2	*P*-value
Richness	R ~ Year + (1|Site)	+0.053		**<0.001**
	R ~ Year + Latitude + (1|Site)	+0.053	−0.107	**<0.001**
	R ~ Year + Longitude + (1|Site)	+0.053	+0.276	**<0.001**
	R ~ Year + Altitude + (1|Site)	+0.054	−0.372	**<0.001**
	R ~ Year + Discharge + (1|Site)	+0.052	−0.018	0.244
	R ~ Year + Woodland + (1|Site)	+0.053	−0.026	0.075
	R ~ Year + Semi-natural + (1|Site)	+0.054	−0.330	**<0.001**
	R ~ Year + Arable + (1|Site)	+0.055	+0.301	**<0.001**
	R ~ Year + Urban + (1|Site)	+0.053	+0.161	**<0.001**
	R ~ Year + Wastewater + (1|Site)	+0.059	+0.119	**<0.001**
Diversity	D ~ Year + (1|Site)	+0.035		**<0.001**
	D ~ Year + Latitude + (1|Site)	+0.035	−0.096	**<0.001**
	D ~ Year + Longitude + (1|Site)	+0.035	+0.171	**<0.001**
	D ~ Year + Altitude + (1|Site)	+0.036	−0.218	**<0.001**
	D ~ Year + Discharge + (1|Site)	+0.033	+0.005	0.654
	D ~ Year + Woodland + (1|Site)	+0.035	+0.003	0.759
	D ~ Year + Semi-natural + (1|Site)	+0.036	−0.200	**<0.001**
	D ~ Year + Arable + (1|Site)	+0.036	+0.172	**<0.001**
	D ~ Year + Urban + (1|Site)	+0.035	+0.101	**<0.001**
	D ~ Year + Wastewater + (1|Site)	+0.039	+0.083	**<0.001**
Evenness	E ~ Year + (1|Site)	+0.001		0.515
	E ~ Year + Latitude + (1|Site)	+0.001	−0.014	**<0.001**
	E ~ Year + Longitude + (1|Site)	+0.004	+0.004	0.297
	E ~ Year + Altitude + (1|Site)	+0.001	−0.002	0.648
	E ~ Year + Discharge + (1|Site)	+0.001	+0.011	**0.005**
	E ~ Year + Woodland + (1|Site)	+0.001	+0.009	**0.010**
	E ~ Year + Semi-natural + (1|Site)	+0.001	+0.002	0.630
	E ~ Year + Arable + (1|Site)	+0.001	−0.006	0.108
	E ~ Year + Urban + (1|Site)	+0.001	+0.002	0.544
	E ~ Year + Wastewater + (1|Site)	−0.001	+0.004	0.375

statistically significant. Of the species that have significantly declined in abundance since the 1980s, the mean densities of brown trout, dace, eel and pike appear to have stabilised, whereas salmon have been variable and roach and ruffe may still be declining (Fig. S1). Of the species that have significantly increased in abundance since the 1980s, the mean densities of barbel, bullhead, chub and minnow peaked in the 2000s, whereas stone loach peaked in the 1990s (Fig. S1). Beta diversity declined from the 1980s (0.41) to the 1990s (0.20) and 2000s (0.07), but increased in the 2010s (0.23).

3.3. Fish assemblage structure

There was a significant difference in fish assemblages according to wastewater category (PERMANOVA, pseudo-F = 91.564, df = 3, P = 0.001) (Fig. 5), with brown trout, bullhead and salmon most important in areas of low or very low wastewater exposure, dace and minnow generally most abundant in low or moderate exposure, and roach dominant in moderate or high exposure (Table 2). However, the differences varied over time (PERMANOVA, pseudo-F = 20.703, df = 3, P = 0.001) (Fig. 5). Salmon contributed most to differences between low and

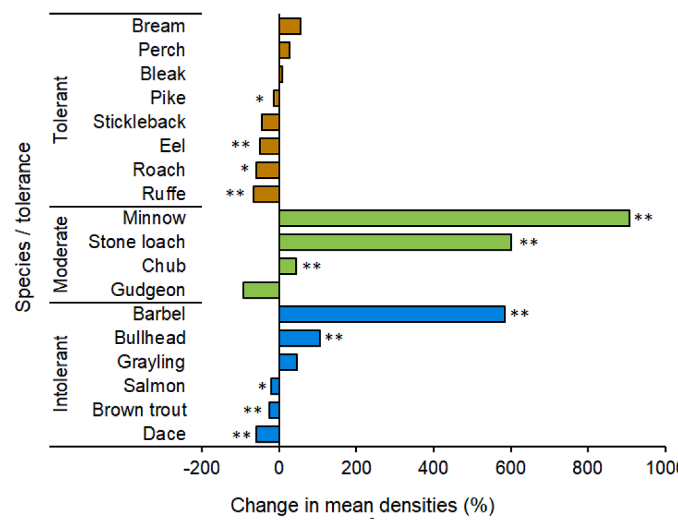

Fig. 4. Changes in the mean densities of the most widespread and abundant fish species captured from England's rivers between the 1980s and 2010s. Statistically significant differences in mean densities are denoted by asterisks (*P < 0.05, **P < 0.01).

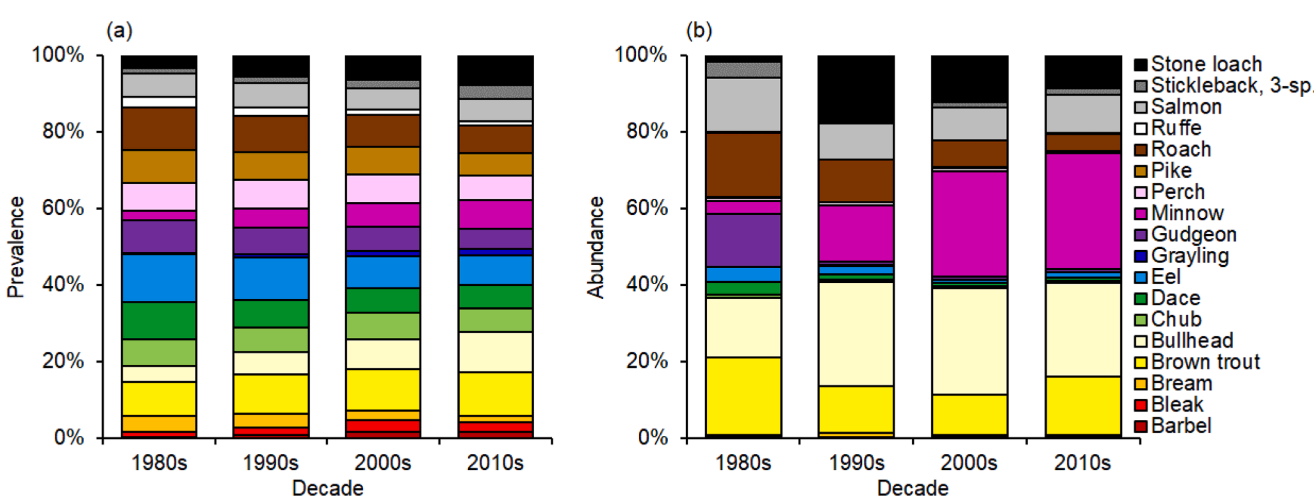

Fig. 3. Relative (a) prevalence and (b) abundance of the most widespread and abundant fish species captured from England's rivers over four decades (1980s, 1990s, 2000s, 2010s).

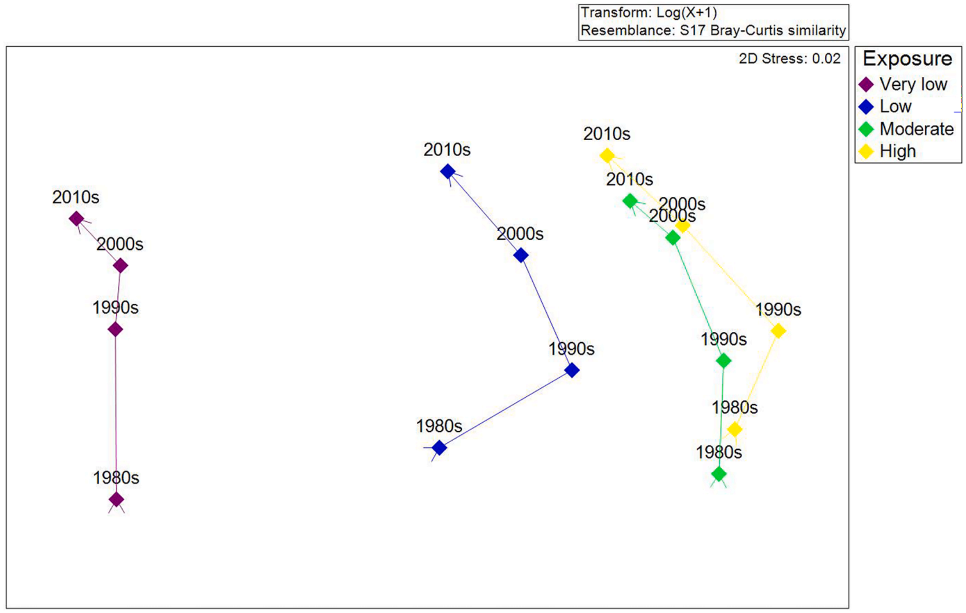

Fig. 5. Non-metric multidimensional scaling ordination plot (group centroids with trajectories) comparing the fish assemblages in England's rivers over four decades (1980s, 1990s, 2000s, 2010s) according to wastewater exposure (very low, low, moderate, high; categories as in Fig. 2).

Table 2
Similarity percentages (SIMPER) analysis of the contributions (%) of key fish species to dissimilarities in assemblage structure according to wastewater exposure (very low, low, moderate, high) and decade (1980s, 1990s, 2000s, 2010s).

		Wastewater exposure					Wastewater exposure		
Species	Decade	V vs. L	L vs. M	M vs. H			V vs. L	L vs. M	M vs. H
Brown trout	1980s	21	10	–	**Minnow**	1980s	–	–	–
	1990s	16	9	–		1990s	10	5	–
	2000s	16	6	–		2000s	17	21	19
	2010s	18	9	–		2010s	19	**25**	**27**
Bullhead	1980s	11	9	–	**Roach**	1980s	13	**28**	**37**
	1990s	13	–	–		1990s	14	**15**	**41**
	2000s	**18**	11	8		2000s	11	**23**	**26**
	2010s	**21**	15	10		2010s	–	20	23
Dace	1980s	–	16	19	**Salmon**	1980s	**27**	–	–
	1990s	–	10	11		1990s	**21**	–	–
	2000s	–	5	6		2000s	17	–	–
	2010s	–	6	6		2010s	15	–	–

V = very low, *L* = low, *M* = moderate, *H* = high wastewater exposure (categories as in Fig. 2).
Green cells indicate that mean densities were highest in the relatively low wastewater exposure category, and blue cells indicate they were highest in the relatively high exposure category.
Species contributing most to dissimilarities in each wastewater exposure × decade category are denoted with a bold border.

very low exposure categories in the 1980s and 1990s, whereas bullhead were more important in the 2000s and 2010s (cells with a bold border in Table 2). Differences between the low-moderate and moderate-high exposure categories were caused largely by roach in the 1980s, 1990s and 2000s, with minnow more important in the 2010s (Table 2). There was no significant interaction between wastewater exposure and time (PERMANOVA, pseudo-$F = 0.775$, df $= 9$, $P = 0.850$), but there was a difference in multivariate dispersions between centroids, with mean distance-to-centroids highest in the 1980s (26 %) and declining in the 1990s (14 %), 2000s (7 %) and 2010s (6 %) (PERMDISP, $F = 11.989$, df $= 15$, $P < 0.001$).

There were also significant differences in fish assemblage structure between covariate categories for latitude, longitude, altitude, river discharge and land use (PERMANOVA, all $P < 0.05$) (Figs S2–S9; Tables S1–S8). With respect to latitude, brown trout, bullhead and salmon were least common in central England (blue cells in the C vs. N column), whereas minnow and roach were relatively abundant (green cells in the C vs. N column) (Table S1). In addition, brown trout, bullhead, minnow and salmon were generally commonest in western England and at higher altitudes, whereas dace and roach were most abundant further east and at low altitudes (Tables S2 and S3). There were no clear linear associations between fish assemblage structure and river discharge or woodland upstream land use, as indicated by the inconsistent distribution of green and blue cells in Tables S4 and S5. However, brown trout and salmon were negatively associated with urban and arable upstream land use, whereas roach were most abundant at sites with moderate urban or high arable coverage (Tables S6 and S7). By contrast, brown trout, bullhead, minnow and salmon were positively associated with semi-natural upstream land use, whereas there was a negative association for dace and roach (Table S8).

The differences in assemblage structure were most frequently driven by the densities of brown trout or roach (cells with bold borders in Tables S1–S8), with other species rarely identified as being responsible, but occasionally varied over time. For example, brown trout contributed most to differences between southern and central England in the 1980s and 1990s, whereas bullhead was marginally more important in the 2000s and 2010s (Table S1). For central vs. northern England, salmon was most important in the 1980s, but this changed to roach in the 1990s and subsequently brown trout (Table S1). Finally, for the north vs. far north of England, differences in brown trout densities were the main reason for dissimilarities in assemblage structure in the 1980s, 1990s and 2010s, but salmon was of greater importance in the 2000s (Table S1).

By contrast, there were no marked temporal variations for longitude, with brown trout contributing most to differences between western and eastern England in all four decades, and roach more important in the far east (Table S2). Similarly, brown trout and roach were of greatest importance in the uplands and lowlands, respectively, throughout the study period (Table S3). In the majority of cases, the abundance of brown trout was the main reason for differences in fish assemblage structure between river discharge categories, although roach and bullhead were also important in small watercourses (Table S4). Throughout the study period, brown trout was of greatest importance in areas characterised by woodland and semi-natural upstream land use, whereas roach was generally most important in urban and arable areas (Tables S5–S8). Non-native species, present in 6 % of surveys but representing <0.1 % of the fish in the dataset, were not responsible for changes in assemblage structure at national level. There were significant interactions with time for latitude, river discharge and woodland, arable and semi-natural upstream land use, suggesting that the temporal changes in fish assemblage structure differed between covariate categories (PERMANOVA, all $P < 0.05$), and also differences in multivariate dispersions between centroids, with mean distance-to-centroids highest in the 1980s and declining over time in all cases (PERMDISP, all $P < 0.001$). The most notable changes were increases in similarity between southern and northern England, and all river discharge categories (Figs S2 and S5).

4. Discussion

4.1. Nationwide increases in fish species richness and diversity

The value of long-term datasets is becoming increasingly recognised, particularly for monitoring phenological, demographic and ecosystem responses to climate change and environmental degradation or recovery. This study found a gradual increase in mean fish species richness and, to a lesser extent, diversity in England's rivers over a period of four decades. In the majority of cases, the increase was most pronounced in the 1980s, since when any further changes have been comparatively minor. Notably, however, there were no declining trends in richness or diversity across the full time series.

The pattern observed in this study contrasts with France, where there was a steady increase in fish species richness between 1990 and 2009 (Poulet et al., 2011), but is similar to studies on riverine macroinvertebrates, which found that the rates of recovery in both England and mainland Europe slowed or plateaued after the 2000s and 2010s, respectively (Haase et al., 2023; Qu et al., 2023). The asynchronous trends for fish (this study) and macroinvertebrates (Qu et al., 2023) in England's rivers, visualised using a similar approach to enable a fair comparison, could be because there is a relatively larger number of pollution-sensitive macroinvertebrates, meaning that fish responded to improvements in water quality more rapidly, but it is likely that other complicating or confounding factors (Section 4.5) were also involved. Although fewer fish surveys were conducted in the 1980s than in later decades, the number was still considerable and all covariate quartiles were well represented in the analyses, providing assurance that the observed trends were genuine, and not simply a consequence of lower sampling intensity. Furthermore, the increases in richness in the 1980s cannot be explained by improved density estimates for species historically under-recorded in standard fish surveys, driven by EC Water Framework Directive (WFD) targets, in the 2000s.

The increases in species richness and diversity over time observed in this study have occurred across almost the full range of pressure gradients, despite consistent differences in absolute values between covariate categories, suggesting an underlying climatic driver has been important and/or that there has been a nationwide improvement in water quality. Although climatic variability can influence fish cohort strength and result in temporal fluctuations in population sizes (Nunn et al., 2010), it is unlikely to cause a gradual, nationwide increase in *species richness*. By contrast, it is possible that general improvements in water quality could underpin such a trend, most likely, given their comparatively restricted distributions, due to pollution-intolerant species gradually recolonising recovering river reaches, either naturally or through stocking (Section 4.5). Indeed, studies on riverine macroinvertebrates revealed that the most pollution-sensitive taxa, such as Ephemeroptera, Plecoptera and Trichoptera, continued to recover after overall family richness ceased to increase (Vaughan and Ormerod, 2014; Qu et al., 2023). Notwithstanding, given the positive influence of water temperature on the recruitment success of many temperate freshwater fishes, it is possible that climate change, specifically the trend of increasing river temperatures (Johnson et al., 2024), contributed to gradual increases in mean cohort sizes and, consequently, *species diversity* at a national scale. There were very few significant results for fish species evenness, suggesting that gradients in latitude, longitude, altitude, land use, river discharge and wastewater exposure had no appreciable influence on the occurrence of rare species, and also that the densities of existing species and those driving the increase in richness were comparable.

4.2. Complex changes in fish assemblage structure

Given the biogeography of freshwater fish in England, their respective habitat requirements and limited capacity to colonise new river catchments naturally, the slower rates of increase in recent decades could suggest that species richness and diversity are approaching their maxima or, in the case of diversity, potentially a flexion point. By contrast, there were significant differences in assemblage structure throughout the study period, demonstrating the importance of including multivariate, as well as composite univariate, analyses. It is theoretically possible, for example, for there to be a complete change in species composition, but no changes in richness and diversity, and for pristine and grossly polluted sites to have identical richness and diversity, but completely dissimilar fish assemblages.

The differences in assemblage structure observed in this study were most frequently driven by the densities of brown trout or roach, two of the most widespread and abundant fish species in England, but there were some variations between covariates and over time. For example, salmon contributed most to differences between low and very low wastewater exposure categories in the 1980s and 1990s, whereas bullhead were more important in the 2000s and 2010s. By contrast, differences between the low-moderate and moderate-high exposure categories were caused largely by roach in the 1980s, 1990s and 2000s, with minnow more important in the 2010s. Non-native species, although established and potentially important locally, were not responsible for the changes in richness, diversity or assemblage structure at national level. This contrasts with the national fish-monitoring datasets in some other countries, such as France, where non-native species have increased markedly in both occurrence and abundance (Poulet et al., 2011; Kuczynski et al., 2018).

Although mean salmon densities at sites with very low wastewater exposure have marginally declined in the last four decades (17, 18, 16 and 12 fish 100 m^{-2}, respectively, in the 1980s, 1990s, 2000s and 2010s), the switch also coincided with an increase in bullhead abundance (10, 18, 31 and 20 fish 100 m^{-2}, respectively). The changes at sites with higher wastewater exposure were largely explained by reductions in roach and increases in minnow densities. Although it is reasonable to expect improvements in wastewater treatment (Johnson et al., 2019) to lead to increases in minnow densities (and/or biomass), an increase in recording effort could also cause such a result as the species has historically been under-recorded in standard fish surveys (Cowx et al., 2009). Improved sampling efficiency probably also partly explains increases in bullhead densities at sites with very low wastewater exposure and the prevalence of three-spined stickleback (pollution tolerant) and stone loach (less tolerant) over time, especially given that there were no clear trends for the majority of species usually targeted by standard fish surveys.

4.3. Declining abundance of some fish species in spite of improving water quality

The gradual decline in salmon densities at sites with very low wastewater exposure over time, and significantly lower mean national density in the 2010s compared to the 1980s, does not contradict studies suggesting that there has been a nationwide improvement in biological water quality. Indeed, the species has been declining globally due to a range of issues, especially during the marine phase of the life cycle, and has recently been classified as Endangered in England (Nunn et al., 2023). Similarly, the global abundance of European eel has declined markedly over the last four decades, due to a range of threats but especially migration barriers, and the species is classified as Critically Endangered in England (Nunn et al., 2023).

Possible explanations for the declines in the densities of brown trout, dace and roach since the 1980s, in spite of improving water quality, include increases in the frequency and magnitude of interspecific competition with increasing species richness/diversity and diminishing primary and secondary production, increased predation, reduced stocking intensity, changes in population structure and deteriorating physical habitat quality. For example, reductions in the contributions of roach and dace to angler catches have been attributed to elevated competition in a more diverse, but less productive, fish community following improvements in water quality (Cowx and Broughton, 1986). In addition, predation pressure, especially by piscivorous birds on brown trout and roach, has increased considerably in recent decades (Russell et al., 2021) while, simultaneously, the extent, frequency and intensity of stocking fish into rivers has declined. Ruffe are rarely stocked or targeted by piscivorous birds, but could have been affected by competition.

Populations of some fish species are prone to stunting, especially where or when environmental conditions are poor. Conversely, it is possible that the observed declines in brown trout, dace and roach densities coincided with changes in population structure, such as increases in body length range, biomass and the proportion of large individuals. It is also possible that pike exhibited similar changes in population structure following a reduction in persecution. Unfortunately, no individual fish length, biomass or age data were available in this study, rendering it impossible to calculate cohort-specific metrics for examination of population structure at a national scale. This is potentially important because it is possible for populations of identical numerical size to have markedly different biomass and age structures. The implication of this is that the declines in the densities of some fish species since the 1980s are not necessarily a cause for concern, especially as those of brown trout, dace and pike appear to have stabilised in recent decades, but further research is required to determine whether changes in population structure have occurred. It is recommended, therefore, that long-term patterns in population structure are examined for rivers that have the data necessary to calculate cohort strengths (Britton et al., 2004), to account for any differences during ontogeny or between cohorts. It is also recommended that the possibility of a general degradation of physical habitat quality (Moore et al., 2021) is investigated in the context of species-specific requirements.

4.4. Biogeography, land use and wastewater exposure

There was an increase in mean species richness and diversity with increasing longitude and decreasing altitude, with brown trout, bullhead, minnow and salmon generally commonest in western England and at higher altitudes, and dace and roach most abundant further east and at low altitudes. Counterintuitively, however, there was also an increase in richness and diversity with increasing urban/arable land use and wastewater exposure. This contrasts with the results of a study on benthic macroinvertebrates in England's rivers, which found that sites with high wastewater exposure or arable land use tended to have a relatively low richness (Qu et al., 2023), possibly because there are relatively larger numbers of pollution-sensitive taxa. Importantly, this does not imply that urban/arable land use or wastewater exposure *per se* are beneficial to fishes. Indeed, brown trout and salmon, both of which require clean, fast-flowing and highly oxygenated water, were negatively associated with urban and arable land use, whereas roach – a less sensitive, eurytopic and lowland species – were most abundant at sites with moderate urban or high arable coverage. These results, therefore, are likely the consequence of a combination of biogeographical factors, including longitude and altitude.

There were significant interactions with time for latitude, river discharge and woodland, arable and semi-natural upstream land use, with decadal increases in similarity between southern and northern England and all river discharge quartiles the most notable changes. The former was due to brown trout decreasing and increasing, respectively, in southern and northern England, but more complex changes occurred in the case of river discharge. Given the improvements in biological water quality in recent decades (Vaughan and Ormerod, 2014; Pharaoh et al., 2023; Qu et al., 2023), it is perhaps surprising that there was no interaction with time for wastewater exposure, with no increase in the similarity of the fish assemblages in areas of high and lower wastewater exposure being apparent. This is possibly related to the relatively small number of sites for which municipal effluent dominated total river discharge and, consequently, the wide range of the high wastewater exposure quartile. It is also likely that a substantial proportion of the sites in areas with high wastewater exposure, largely in central and eastern England, are unsuitable for pollution-sensitive species for other reasons, such as hydrological and physical habitat characteristics (Noble et al., 2007).

4.5. Complicating or confounding factors

Some fish populations are maintained or supplemented by occasional or regular stocking. Currently, fish are invariably only released into rivers where the species are already present, so stocking is unlikely to influence species richness. In addition, although intensive stocking can increase fish abundance and diversity at a local level, it is unlikely to have a significant effect at a national scale as the prevalence and relative numbers of fish released (i.e. compared to the numbers of wild fish) into England's rivers are low (Nunn et al., 2023). Possible exceptions are barbel and chub, both of which were widely translocated and re-introduced (following local extirpations) in the 1980s and 1990s (Britton and Pegg, 2011; Warren et al., 2024), are still frequently stocked and have increased significantly in abundance in the last four decades. However, although translocations and re-introductions undoubtedly led to the establishment of self-sustaining populations and increases in species richness in the 1980s and 1990s, enhanced and more regular natural recruitment in response to nationwide improvements in biological water quality and increasing water temperatures (Johnson et al., 2024) has likely been more important than stocking in recent decades. Notwithstanding, it is likely that multiple and potentially divergent drivers have occurred simultaneously, thereby complicating the situation and making it difficult to disentangle genuine and confounding factors. In addition, it is possible that climate change may lead to an increase in the importance of non-native species in the future, potentially leading to biotic homogenisation, as observed elsewhere (Kuczynski et al., 2018).

5. Conclusions

- Pollution-intolerant fish species were most abundant in areas of low or very low wastewater exposure, but there have been no consistent increases in their densities in response to nationwide improvements in wastewater treatment and biological water quality.
- A complex range of factors influence fish population and community dynamics, and it is recommended that causal relationships with putative drivers, including physical habitat quality, are modelled at a national scale.
- Considering recent concerns over increases in the frequency of combined sewer overflows and volumes of untreated sewage discharged into England's rivers, it is also recommended that more recent data are analysed for areas of high pressure or conservation importance.
- Although the increases in fish species richness and diversity over the last four decades are encouraging, subtle and contrasting changes in the abundance of a range of species require further investigation, especially as they could affect assessments of ecological or conservation status.
- This study significantly advances our understanding of the long-term ecological health of rivers in densely populated and heavily modified countries in the context of both historical and contemporary anthropogenic pressures.

CRediT authorship contribution statement

Andy D. Nunn: Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rachel F. Ainsworth:** Writing – review & editing, Visualization, Validation, Investigation, Formal analysis, Data curation. **Yueming Qu:** Methodology, Conceptualization. **Virginie D.J. Keller:** Writing – review & editing, Validation, Funding acquisition, Data curation. **Nuria Bachiller-Jareno:** Writing – review & editing, Validation, Funding acquisition, Data curation. **Vasileios Antoniou:** Validation, Data curation. **Michael Eastman:** Validation, Data curation. **Clarissa Rizzo:** Validation, Data curation. **Graeme Peirson:** Writing – review & editing, Conceptualization. **Frances Eley:** Validation, Data curation. **Andrew C. Johnson:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Ian G. Cowx:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2025.123163.

Data availability

The dataset is freely available at https://doi.org/10.5285/b0afb78e-a0cb-4762-9220-659211ae3a5e.

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