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Predicting nature recovery for river restoration planning and ecological assessment: A case study from England, 1991–2042

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Abstract

The Global Biodiversity Framework established ambitious goals for nature recovery which governments must now incorporate into national legislation. In England, legally binding targets require authorities to halt the decline in species abundance by 2030 and reverse the decline by 2042. Riverine invertebrates represent a substantial proportion of the species contributing towards the targets. Thus, understanding the response of these species to potential river restoration actions is key to target delivery. We model counts for 188 riverine invertebrate taxa using zero-inflated generalized Poisson models, applying the models to both inform river restoration planning and set expected values for use in ecological assessment. We identify catchment-specific restoration strategies that combine one or more actions involving the removal of channel modifications, reductions in nitrate concentrations and reductions in total dissolved phosphorus concentrations as the most likely to deliver species abundance targets across three joint climate–socioeconomic scenarios. By hindcasting species abundances under alternative target frameworks, we also demonstrate a new approach to setting expected values in ecological assessment, accounting for changes in water temperature and hydrology that confound historical reference models presently used by regulators. Our findings represent the first systematic attempt to prioritise major actions to deliver species abundance targets in England, providing valuable insights for policymakers, river restoration practitioners and authorities responsible for monitoring river ecosystems.

KEYWORDS

biodiversity modelling, ecological assessment, invertebrates, nature recovery, river restoration, species abundance target

1 | INTRODUCTION

Growing awareness of biodiversity loss has led to the emergence of a global policy agenda on nature recovery, culminating in 2022 with the historic Kunming-Montreal Global Biodiversity Framework (GBF). The GBF has four goals for 2050 and 23 targets for 2030, including to protect 30% of all inland waters by 2030, halt the extinction of threatened species and increase the abundance of native populations. National governments must now align domestic laws and regulations with the GBF. In the United Kingdom, section 2(3) of The Environment Act 2021 included a legally binding target to halt the decline in species abundance by 2030. For England, the species abundance

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target was specified in The Environmental Targets (Biodiversity) (England) Regulations, 2023 (hereafter, 'the regulations'). Section 12 (1:2) of the regulations states that the 'species abundance target is to be measured by calculating the difference between the overall relative species abundance index' and that 'the overall relative species abundance index for a year is derived from the calculation of the geometric mean of the relative species abundance indices for every species listed in Schedule 2 [of the regulations]'. The species abundance index is relative in the sense that it is expressed relative to a baseline. To achieve the 2030 target, the index for the year 2030 must be the same as, or greater than, the index for the year 2029. A further target to reverse the decline in species abundance by 2042 requires that the index for 2042 must be both greater than the index for 2022 and at least 10% greater than the index for 2030.

Of the 1195 taxa listed in Schedule 2 of the regulations, 19.7% are riverine invertebrates. Thus, as policymakers now consider how to deliver the species abundance target, and given that biodiversity is a focus of river restoration projects (England et al., 2021), understanding which restoration actions can have the greatest positive impact on Schedule 2 freshwater invertebrates is key. The policy framework on improving the water system in England provides several potential delivery mechanisms, including statutory targets to reduce nitrogen, phosphorus and sediment pollution from agriculture, phosphorus loadings from treated wastewater, the length of rivers polluted by harmful metals from abandoned mines and per capita use of public water supply. Further non-statutory targets require restoration of 75% of water bodies to good ecological status, reduction of leaks from water infrastructure, elimination of all adverse ecological impacts from sewage discharges and improved drought resilience. The Integrated Plan for Water in England (Defra, 2023) sets out the actions needed to achieve these targets and establishes a new Water Restoration Fund to enable investment of environmental fines and penalties into actions that improve the water environment. However, as yet there is no basis for prioritising these actions in terms of their potential contribution to delivering the species abundance target under alternative future climate and socioeconomic scenarios.

Biodiversity modelling capabilities have improved rapidly in recent decades, to the point that models representing species–environment relationships now underpin key global (Schipper et al., 2020) and national (Hendriks et al., 2016) nature recovery policy. In England, a decades-long history of intensive, large-scale monitoring of river biology offers strong potential for guiding policy through biodiversity modelling, yet this potential remains to be explored. In addition to prioritising actions to improve the water environment by projecting outcomes under alternative policy decisions and climate change scenarios, biodiversity modelling could also provide the basis for a new approach to setting expected values for use in ecological status assessment, a process involving calculation of ecological quality ratios (EQRs), that is, observed:expected values of a given index. Presently, in England, expected values for riverine invertebrate communities are generated using the River Invertebrate Classification Tool (RICT). Underlying RICT is a historical reference condition model, producing expected values based upon data collected between 1978 and 2002 from sites thought to be minimally impacted by anthropogenic stressors at the time. However, the pace and severity of 21st century climate change are such that historical conditions may be an increasingly poor guide to the state of present-day river ecosystems (Tonkin et al., 2019).

River water temperatures in England increased by an average of 0.3°C per decade between 1990 and 2006 (Orr et al., 2015), and this trend is expected to continue under the present climate trajectory (Hannah & Garner, 2015). Hydrological research suggests a general trend of increasing winter flows and decreasing summer flows in the United Kingdom, with an overall increase in mean flows and flow maxima (Christierson et al., 2012; Kay & Kay, 2021; Prudhomme et al., 2012; Sanderson et al., 2012), as well as steadily increasing flood and drought risk (Collet et al., 2017; Kay et al., 2014; Lane & Kay, 2021; Prudhomme et al., 2013, 2014; Schneider et al., 2013; Skoulikidis et al., 2017). Water temperature and discharge are key dimensions of the habitat template of freshwater invertebrates (Jackson et al., 2007; Poff et al., 1997). Thus, observed thermal and hydrological changes are expected to drive significant shifts in the distribution and abundance of freshwater invertebrate species, confounding historical reference models (Chessman, 2021) and potentially undermining nature recovery (Whelan et al., 2022). Indeed, Vaughan and Gotelli (2019) found that the impacts of warming on freshwater invertebrate communities were already limiting the benefits of water quality improvements in English rivers as early as the 1990s. A recent continental synthesis showed that the widely reported recovery of European freshwater biodiversity had come to an end by the 2010s, a result partly attributed to warming (Haase et al., 2023). Biodiversity modelling offers an alternative way to define expected values for ecological assessment by predicting what species abundances would be if environmental targets were achieved, whilst accounting for contemporary thermal and hydrological conditions.

We fitted zero-inflated generalized Poisson models linking >30 million individual count records of Schedule 2 freshwater invertebrate taxa with spatial and temporal data on habitat modification, water quality, water temperature and hydrological anomalies. Focusing on the geometric mean abundance indicator specified in the regulations, we made future projections under joint river restoration, representative concentration pathway (RCP; van Vuuren et al., 2011) and shared socioeconomic pathway (SSP) scenarios (UK Climate Resilience Programme, 2023). We also hindcasted biodiversity outcomes under alternative environmental target frameworks to calculate target-driven expected values of the indicator, comparing these with expected values produced from RICT. We demonstrate how our models can be used to both prioritise actions to improve the water environment and support climate-resilient ecological assessment.

2 | MATERIALS AND METHODS

2.1 | Modelled data

We obtained the full set of publicly available statutory freshwater invertebrate monitoring records for England (Environment

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TABLE 1 Description and sources for environmental data used in species abundance models.

Variable (short name)	Description	Reference
Altitude ('Altitude') Distance from river source ('Distance_from_source') Logarithm of upstream mean altitude ('Log_upstream_mean_altitude') Logarithm of upstream catchment area ('Log_upstream_area') Proportion of upstream catchment area covered by chalk ('Chalk') Proportion of upstream catchment area covered by clay ('Clay') Proportion of catchment area covered by hard rock ('Hard_rock') Proportion of catchment area covered by limestone ('Limestone') Proportion of catchment area covered by peat ('Peat') Discharge category ('Discharge_category') River longitudinal slope ('Slope')	Raster data from the River Invertebrate Classification Tool (RICT) at 50 m resolution covering the river network. Reduced via principal component analysis to yield four synthetic variables ('rict_1', 'rict_2', 'rict_3', 'rict_4')	Clarke & Davy-Bowker, (2018)
Channel resectioning index ('CRI')	Point vector data quantifying the extent of habitat modification through channel resectioning at 500 m intervals along the river network, modelled from the UK River Habitat Survey database	Environment Agency, (2023c)
Water resource availability at the five percentile flow, Q95 ('cams95')	Polygon vector data classifying water resource availability within English water bodies at very low flows using a 'traffic light' classification: green = more water available than required to meet needs of environment; yellow = not enough water to meet needs of environment if all licensed abstractions are carried out in full; red = not enough water to support good ecological status; grey = no classification	Environment Agency, (2023a)
Water temperature ('temp') Nitrate concentration ('NO3') Total dissolved phosphorus ('TDP')	Raster data of modelled monthly means from the Long Term Large Scale (LTLS) Freshwater Model at 5 km resolution, 1990–2017. Values expressed as the mean of the 12 full months preceding the sample date	Bell et al., (2021)
Precipitation anomalies ('rain_anom')	Raster data of monthly precipitation from HadUK-Grid at 5 km resolution, 1960–2020. Values expressed as the mean of monthly anomalies in the 12 full months preceding the sample date, relative to 1960–2020 monthly mean values	Hollis et al., (2019)

Agency, 2023b). Due to the limited temporal coverage of modelled monthly water quality data (Table 1), we filtered the records to include only samples collected between 1991 and 2017. To obtain a more consistent dataset for modelling, we selected only samples collected from rivers using a standard 3-min kick sampling procedure, with abundance recorded on a linear or semi-quantitative log scale (with the latter transformed back to a linear scale by the data owner). We excluded samples collected outside of the statutory monitoring seasons of spring and autumn to minimise any confounding effects of greater variation in sample timing. Samples from water bodies with a sampling frequency <10 were also omitted to allow for model fitting through five-fold cross-validation stratified by water body (see below). After filtering, a total of 160,433 samples collected from 18,728 unique sites within 2999 water bodies remained for modelling. From these samples, we selected records of the 235 Schedule 2 freshwater invertebrate taxa by searching for accepted names and synonyms in the taxonomic database accompanying the original data (Environment Agency, 2023b). Count records for synonymous taxa were aggregated and taxonomy updated to accepted names except in the case of a single taxon, *Baetis niger*, which was classified as *Nigrobaetis niger* to be consistent with the taxon named in Schedule 2 of the regulations. Count data were further aggregated to the taxonomic level specified in Schedule 2, which contains 58 taxa at genus level and 11 at species group level (with the remainder at species level). In these cases, aggregation was performed by summing counts of all child taxa after updating taxonomy.

We matched invertebrate records with spatial environmental datasets covering catchment physiography and geology, habitat modification, water availability, water temperature, nutrient concentrations and hydrological anomalies (Table 1). The 11 catchment physiography and geology variables sourced from the RICT database were highly intercorrelated. Thus, we used principal component analysis (PCA) followed by the broken stick method (Jackson, 1993) to define synthetic RICT variables for modelling (Supplementary Figures 1 and 2). Whilst results indicated that only the second axis explained more variance than the broken stick model, we used the first four axes as a parsimonious set of synthetic variables linked to catchment size, altitude and geology. Together, the first four axes explained 69.4% of the variation in the RICT data. For environmental datasets in raster or polygon vector format, we extracted values for each sample in the filtered invertebrate dataset. For point vector data representing habitat modification via the channel resectioning index (CRI), we extracted values from the nearest point to each unique site in the invertebrate dataset. All numerical environmental variables were centred to mean zero and scaled to unit standard deviation prior to modelling. To enable model predictions to be produced for any part of the river network, we also extracted data from the environmental datasets at the centroid of each 50 × 50 m grid cell in the RICT data (Table 1). Available spatial data on habitat modification and water availability were not available as time series. We therefore assumed that CRI and cams95, variables representing the extent of habitat modification and water availability at very low flows respectively, did not change at individual sites throughout the study period. Further polygon vector data on water bodies (Environment Agency, 2023f) and river basins (Environment Agency, 2023e) were used to reflect the spatial structure of the modelled data.

2.2 | Modelling

Counts for each Schedule 2 invertebrate taxon were modelled as a function of environmental covariates using hierarchical zero-inflated generalized Poisson models. The use of a flexible distributional family was necessary as counts were frequently over- or under-dispersed due to data heterogeneity in terms of sampling effort, observation error and the use of a semi-quantitative log scale before the mid-1990s (see above). We selected generalized Poisson models from among several suitable options (Toledo et al., 2022) as initial tests indicated that runtimes for alternatives (e.g., Conway–Maxwell–Poisson models) were prohibitive for such a large dataset and complex models (McCrea et al., 2023). Counts were modelled as an additive function of the environmental variables described in Table 1, along with interactions between CRI and cams95, water temperature and nitrate concentration and water temperature and total dissolved phosphorus (TDP). Thus, our models reflect potential multiple stressor effects reported in previous studies showing frequent interactions between channelisation and abstraction (Elosegi et al., 2018) and antagonistic effects of temperature and nutrient enrichment (Piggott et al., 2012, 2015). In the absence of discharge records at sufficient spatial extent and resolution, we used precipitation anomalies ('rain_anom') to reflect hydrological variation. Since the relationship between precipitation and river discharge is dependent on catchment characteristics, we included random intercepts and slopes on rain_anom for water bodies nested within river basins.

The use of zero-inflated models was required because the taxonomic resolution of invertebrate recording in the modelled dataset changed during the study period, with the proportion of records at species level generally increasing but also fluctuating over time (Supplementary Figure 3). Taxonomic resolution is a key aspect of observation error. For example, the recording of specimens at the family level results in zeros for the genera and species that those specimens belong to. Thus, we modelled zero inflation using random intercepts on year. We note that there was also variation in taxonomic resolution between operational areas, with the Anglian area showing consistently greater proportions of species level records than other areas. However, during model development, we encountered complete separation when including fixed and random effects on operational area in the zero inflation component.

All models were fitted through five-fold cross-validation, with fold membership stratified by water body, using the *glmmTMB* function from the glmmTMB v1.1.5 package in R (Brooks et al., 2017). In the first instance, we tried fitting models with the 'optim' optimizer algorithm using the 'BFGS' method. If that initial model either failed, returned NA standard error values or returned extreme model coefficients ($|\hat{\beta}| > 10$), we considered a succession of alternative optimization settings. This began with changing the method to 'L-BFGS-B', then 'CG', before switching to the 'nlminb' optimizer algorithm using the 'BFGS', 'L-BFGS-B' and 'CG' methods, until a robust model was found. All models for some taxa either failed or returned NA standard error values and extreme model coefficients ($|\hat{\beta}| > 10$). We excluded these taxa, leaving models for 188 of the 235 taxa covered in Schedule 2 of the regulations. The total number of individual records contributing to our results was therefore 30.2 million (160,433 samples × 188 taxa).

Three types of predictions were made from the fitted models. First, to represent the baseline, we calculated fitted abundances for each taxon and year in the study period. Second, we predicted expected abundances for each year under 15 *alternative target frameworks* constructed by combining four individual restoration actions (Table 2) in all possible single, two-way, three-way and four-way combinations. Finally, following the biodiversity model intercomparison

TABLE 2 Description of individual restoration actions used in constructing restoration scenarios and setting alternative target frameworks. *2009 defined as the start of the period to coincide with cycle 1 of the Water Framework Directive.

Target name	Short code	Description of target
Abstraction	A	Bring all water bodies into 'green' cams95 status
Morphology	M	Remove all channel modifications (CRI = 0)
Nitrates	N	Reduce concentrations to 50% of 2009–2017 mean*
Phosphorus	P	Reduce concentrations to 50% of 2009–2017 mean*

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TABLE 3 Description of RCP-SSP scenarios used in projecting from biodiversity models.

Scenario	Narrative	Description of future changes
RCP2.6-SSP1	Sustainability	Water temperatures and rainfall anomalies return to long-term means (1991–2017)
RCP6.0-SSP2	Middle of the road	Water temperature and rainfall anomalies continue to increase by the long-term rate (1991–2017)
RCP8.5-SSP5	Fossil-fuelled development	Rate of increase in water temperatures and rainfall anomalies doubles relative to the long-term rate (1991–2017)

protocol (Kim et al., 2018), we projected abundances in 2030 and 2042 under each of the 15 alternative target frameworks crossed with each of three RCP-SSP scenarios (Table 3) to yield 45 future scenarios. In each case, predictions were made for spring and autumn in every RICT grid cell within the modelled water bodies. For each taxon, we calculated the mean and standard deviation of predictions across seasons and within water bodies to yield a single set of predicted species abundances for each year and water body, as well as nationally aggregated predictions for each year. We then computed a multi-species indicator (MSI) consistent with the regulations by taking the geometric mean of predicted species abundances within each year and water body, as well as within each year at the national level, under alternative target frameworks and RCP-SSP scenarios.

To define the (optimal) restoration strategy that would maximise MSI within each water body according to our models, we selected the combination of restoration actions with the greatest projected MSI in each future year (2030, 2042) and RCP-SSP scenario. This was achieved by ranking MSI projections using $\mu(MSI) - \sigma(MSI)$, where μ is the mean and σ the standard deviation, to avoid selecting a target framework with a greater projected mean MSI response but wider bounds of uncertainty. We also identified the overall optimal restoration strategy for each water body by selecting the set of targets that most frequently maximised $\mu(MSI) - \sigma(MSI)$ among all future years and RCP-SSP scenarios.

For each restoration strategy, we expressed projections as the probability of achieving the species abundance target at the national level for 2030 and 2042 using the *pnorm* function in the stats v3.6.2 package in R (R Core Team, 2023). We defined the target for 2030 as an MSI value for the year 2030 equal to or greater than the mean baseline MSI value (1991–2017), and for 2042 as an MSI value in 2042 at least 10% greater than mean baseline MSI value (1991–2017). This is different to how the targets are specified in the regulations because observed MSI values for the years 2022, 2029 and 2030 were not yet available. However, our approach provides timely insights that can be used inform large-scale river restoration planning.

2.3 | Other analyses

To allow comparison of expected MSI values from our models with those produced by the historical reference model presently used for statutory ecological status assessment, we obtained RICT species abundance predictions for each 50 × 50 m grid cell in the RICT data using the *rict_predict* function from the rict v3.1.4 package in R (Muyeba et al., 2023). RICT predictions incorporated mean alkalinity values for each water body, which we calculated from the Environment Agency Water Quality Data Archive (Environment Agency, 2023d). RICT predictions were produced for spring and autumn, from which we calculated an annual mean for each site in the invertebrate dataset. Species predicted by RICT were matched to modelled taxa, aggregating to genus or species group level as necessary to match the taxa named in Schedule 2 of the regulations. Some Schedule 2 taxa were not included in RICT predictions. Thus, it was necessary to recalculate MSI values predicted from our models by taking the geometric mean of fitted abundances only for the 168 taxa covered by both the RICT predictions and our models. The recalculated MSI values (MSI_{RICT}) allow direct comparison between expected MSI values under RICT and those produced by our models. Expected MSI values from our models were expressed relative to the baseline (fitted values) in the first year of the timeseries (1991): $MSI_{relative} = \frac{MSI}{MSI_{base}} \times 100$, where MSI is the absolute MSI value for a specific year and MSI_{base} is the absolute baseline MSI value in the first year.

3 | RESULTS

An overview of key effects from our models is provided in Figure 1, with detailed summaries of model coefficients available in the supplementary material (Supplementary Figure 4). Year random intercepts from the zero-inflated portion of our models demonstrated that detection probabilities generally increased but also fluctuated over time (Figure 1a). For example, monitoring in 2013 was associated with lower detection probabilities due to the greater frequency of records at higher ranks (e.g., family) in that year (Supplementary Figure 3). Random slopes and intercepts in the conditional component of our models highlighted the role of catchment-specific effects, with broad variation in hydrologically mediated species abundance responses across water bodies within major river basins (Figure 1b). In terms of predictive performance (mean ± sd) across the 188 taxa modelled, mean error was 0.02 ± 0.09, mean absolute error was 0.67 ± 1.64, root-mean-square error was 6.05 ± 10.47 and the marginal R-squared was 0.37 ± 0.20 (Supplementary Figure 5).

3.1 | Model projections

Individual restoration actions selected in optimal restoration strategies at the water body level varied by future year and RCP-SSP scenario (Figure 2). The reduction of nitrate concentrations contributed to the

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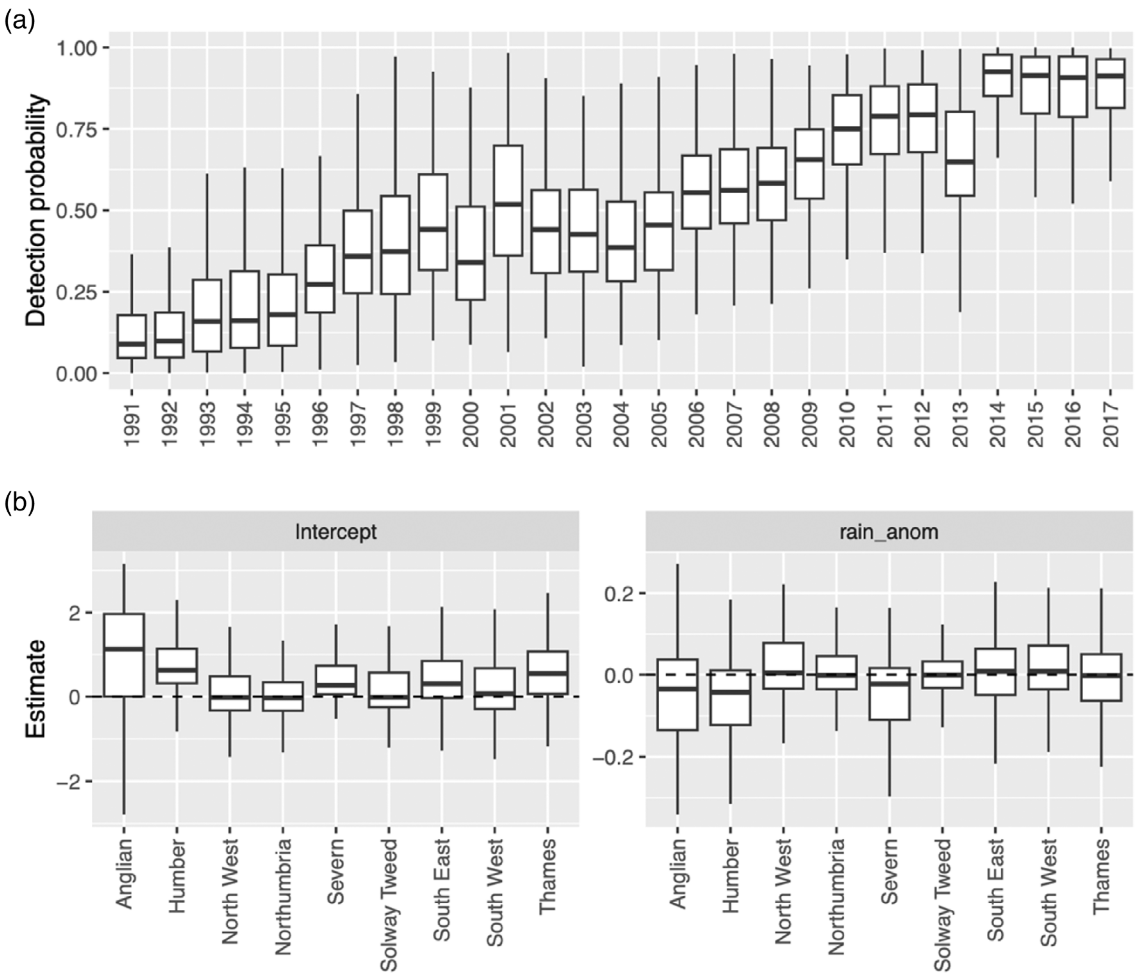

FIGURE 1 Summary of key effects from zero-inflated generalized Poisson models fitted to 188 freshwater invertebrate taxa: (a) year random intercepts from the zero inflated component, expressed as the detection probability (1-*p*, where *p* is the probability of an excess zero); (b) random intercepts (left) and slopes (right) from the conditional component of models. Boxplots show the median (bold horizontal line), interquartile range (box) and 1.5 × the interquartile range (whiskers) of mean values for each species and water body within major river basin. Outliers are not shown.

optimal restoration strategy across 92.8% of the river network by 2030 and 2042 under RCP2.6-SSP1, reducing to 85.6% by 2030 and 77.2% by 2042 under RCP8.5-SSP5 (Figure 2a). In contrast, the contribution of reductions in TDP concentrations increased from 79.8% of the network by 2030 and 2042 under RCP2.6-SSP1, to 92.2% by 2030 and 98.5% by 2042 under RCP8.5-SSP5. Morphological restoration consistently contributed to the optimal strategy throughout 85.6%–87.0% of the network across both future years and all RCP-SSP scenarios. The removal of abstraction pressure was selected as part of an optimal restoration strategy for only a single water body (0.01% of the network) by 2030 and 2042 under RCP2.6-SSP1 and a separate water body (0.14% of the network) by 2030 under RCP8.5-SSP5.

The most frequently selected combination of actions in optimal restoration strategies at the water body level was morphological restoration with reductions in nitrate and TDP concentrations (Figure 2b). This combination was consistently selected across 66.4%–69.4% of the river network, whereas reductions in nitrate and/or TDP concentrations without morphological restoration was the optimal strategy for 9.5%–11.5% of the total stream length. The selection of other combinations involving morphology, nitrates and/or TDP varied by RCP-SSP scenario. The frequency with which morphology with TDP and TDP alone were selected increased from the most optimistic to the most pessimistic RCP-SSP scenario, whereas the selection frequency of other combinations involving morphology and nitrates decreased. Combinations involving the removal of abstraction pressure contributed to the optimal strategy across a negligible proportion of the river network (Figure 2a).

The overall optimal restoration strategy at the water body level (Figure 3), identified as the most frequently selected combination of actions across all future year and RCP-SSP scenarios, involved between one and three restoration actions (Figure 3b) and was projected to increase MSI relative to the baseline in 85.6% of water bodies by 2030 (Figure 3c). The number of actions (mean ± sd) contributing to the overall optimal strategy per unit stream length was 2.58 ± 0.62 (Supplementary Figure 6) and this was projected to lead

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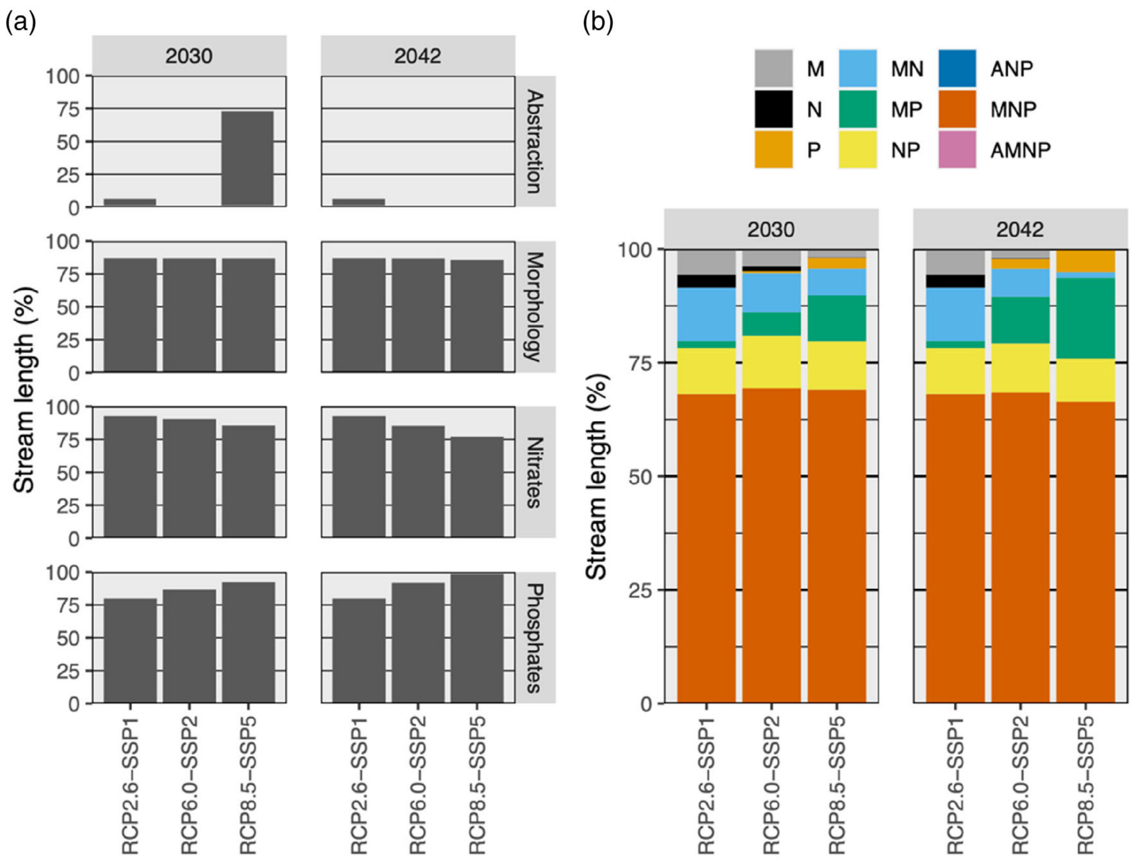

FIGURE 2 Frequency of individual (a) and combined (b) restoration actions identified in optimal restoration strategies at the water body level based on projections for 2030 and 2042 under three In (a), the contribution of individual restoration actions is shown; also note the different scale in the upper row. Key to restoration actions in (b): A = abstraction; M = morphology; N = nitrates; P = total dissolved phosphorus (TDP).

to an increase in MSI nationally of 21.1 ± 21.5% by 2030 and 21.7 ± 23.0% by 2042, relative to the baseline (Supplementary Figure 7). Morphological restoration with reductions in nitrate and TDP concentrations was selected as the overall optimal strategy across the 65.4% of the river network (Supplementary Figure 8). A 50% reduction in TDP concentrations was the single most frequently selected action (Figure 3g). Combinations involving the removal of abstraction pressure were never selected (Figure 3d).

A nationally prescribed restoration strategy, in which the same combination of actions was applied across all modelled water bodies, was projected to lead to the achievement of the 2030 species abundance target with probabilities between 25.6% (removal of abstraction pressure only) and 72.7% (combination of morphological restoration with reductions in nitrate and TDP concentrations) under the RCP6.0-SSP2 (middle of the road) scenario (Figure 4). This compared with a probability of 72.6% by 2030 under the same scenario when the restoration strategy was optimised for each individual water body. Results suggested that the more ambitious 2042 target would be a greater challenge to achieve than the 2030 target, particularly under more optimistic RCP-SSP scenarios. For example, a nationally prescribed restoration strategy combining morphological restoration with reductions in nitrate and TDP concentrations ('MNP') was associated with a 72.3% and 72.7% probability of achieving the 2030 target under RCP2.6-SSP1 and RCP8.5-SSP5, respectively. This reduced to 63.8% and 65.6%, respectively, for the 2042 target.

3.2 | Expected values

Relative MSI values expected under our approach varied over time in response to thermal and hydrological variation (Figure 5). Absolute expected MSI values varied strongly by target framework, with a combination of targets for morphology along with nitrate and TDP concentrations leading to the highest expected values, and abstraction alone the lowest expected values, in line with the projections reported above (Supplementary Figure 9). Target-driven EQRs (mean [95% CI]) under the optimal target framework for each water body (0.80 [0.79, 0.81]) were greater and showed more variability over time than EQRs derived from RICT predictions (0.29 [0.27, 0.30]; Figure 6).

4 | DISCUSSION

By integrating long-term biodiversity monitoring records with spatial environmental datasets within a robust modelling framework, we provide the first national prioritisation of four major restoration actions

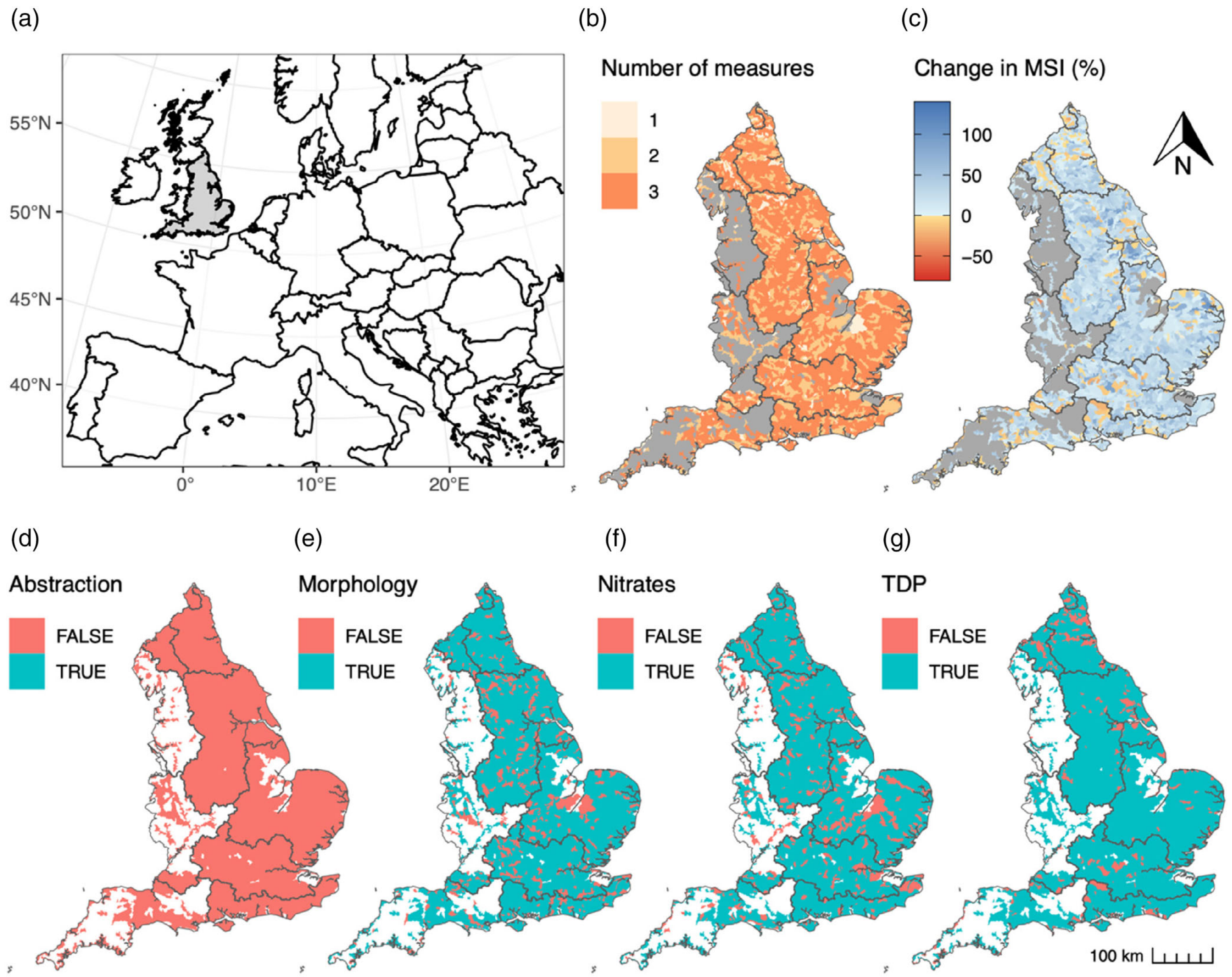

FIGURE 3 Summary of overall optimal restoration strategies at the water body level based on projections for 2030: (a) location of study extent; (b) number of individual restoration actions involved; (c) projected change in the multi-species indicator (MSI) compared with the mean 1991–2017 baseline; (d-g) water bodies for which individual measure were (TRUE) or were not (FALSE) included in the overall optimal restoration strategy. Bold lines in (b-g) show watersheds between major river basins. TDP = total dissolved phosphorus.

under future climate and socioeconomic scenarios. To underpin ecological assessment, we also present a new reference model that sets expected values based upon predicted outcomes under alternative target frameworks, whilst accounting for changes in water temperature and hydrological variability.

Model projections at the national level indicated that morphological restoration and 50% reductions in nitrate and TDP concentrations are priority actions for delivering the species abundance targets for 2030 and 2042. Morphology is a common focus of river restoration projects and may involve channel re-meandering, bank reprofiling, the raising of river bed levels, or barrier removal, among other techniques (van Andel & Aronson, 2012). These aspects of river habitat are implicated in the non-statutory target to restore 75% of water bodies to good ecological status (Defra, 2023). In terms of nutrient concentrations, The Environment Act 2021 targets for water require that nitrogen and phosphorus pollution from agriculture is reduced by at least 40% by 2038 (against a 2018 baseline) and phosphorus loadings from treated wastewater are reduced by 80% by 2038 (against a 2020 baseline). Such reductions could be achieved via catchment restoration programmes focusing on land use and land management practices, as well as mechanisms to increase investment in underperforming sewage treatment works. Whilst we were unable to directly reflect these nutrient targets due to a lack of detailed data on the contribution of agriculture and treated wastewater to nutrient loadings throughout the river network, the morphological restoration and nutrient reductions simulated here are plausible policy outcomes.

Changes to water resources management, which would retain more water for the environment after licensed abstractions are carried out, were identified as a positive contributor to target delivery across a negligible proportion of the river network. This finding suggests that targets aimed at reducing the use of public water supply may not play a major role in delivering the species abundance target. However, we

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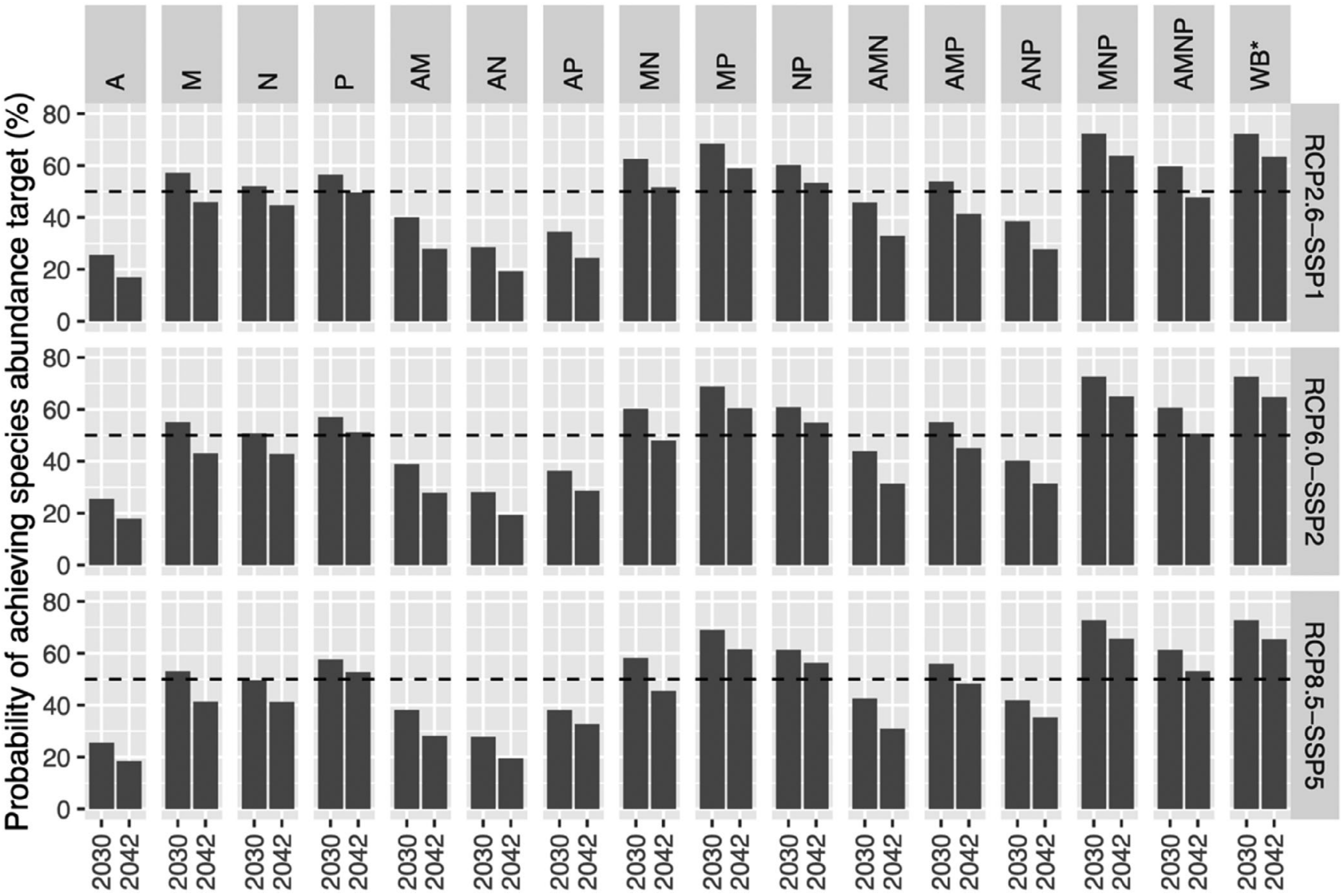

FIGURE 4 Probability of achieving species abundance targets in 2030 and 2042 at the national level under three alternative representative concentration pathway (RCP)-shared socioeconomic pathway (SSP) scenarios (rows) and 16 alternative restoration strategies. Dashed horizonal lines correspond to a 50% probability. Key to individual restoration actions making up alternative restoration strategies: A = abstraction; M = morphology; N = nitrates; P = total dissolved phosphorus. *WB = nationally aggregated change in MSI for restoration strategies optimised at the water body level.

urge caution in the interpretation of these findings as abstraction pressure is widespread in England. Thus, for many water bodies, analogous habitat conditions under low abstraction pressure do not exist in the modelled dataset. Furthermore, our assumption that abstraction pressure did not change during the study period is unlikely to be supported given that human water demands vary over time in many systems (Tijdeman et al., 2018). These factors may explain why, for many taxa, our models indicated higher abundances with greater abstraction pressure (Supplementary Figure 4). On the other hand, our findings are supported by a substantial body of research showing that the impacts of abstraction on riverine invertebrates are difficult to detect in the presence of other pressures (Castella et al., 1995; White et al., 2021).

Optimising the combination of restoration actions required to maximise MSI at the water body level under our models did not lead to an uplift in the probability of achieving the species abundance targets for 2030 and 2042, compared to nationally prescribed restoration strategies. However, restoration planning at the water body level would reduce the number of individual actions required per unit length of the river network (mean = 2.58) by an estimated 14% compared with the combination of three actions projected to result in the greatest probability of achieving the targets via a nationally prescribed strategy. Cost-effectiveness is an important criterion for river restoration (Smith et al., 2014), and our models provide a foundation upon which detailed cost–benefit projections could be based.

The expected MSI values produced from our models are responsive to thermal and hydrological change, in contrast to static expectations produced from RICT (Figure 5). Scientists and practitioners working on freshwater ecological assessment have increasingly argued that reference models used to produce expected values must be adapted to account for climate change or risk generating increasingly confounded results (Chessman, 2021; Feio et al., 2014; Logez et al., 2012). Even under locally unimpacted conditions, it is unrealistic to expect ecological communities to remain static over decades-long periods whilst the global environment undergoes fundamental shifts. Yet, the River Invertebrate Prediction and Classification System (RIVPACS), which is the historical reference model underlying RICT and has inspired many other similar approaches worldwide, incorporates only long-term air temperature means and ranges (Clarke et al., 2003). It therefore fails to account for the severe thermal and

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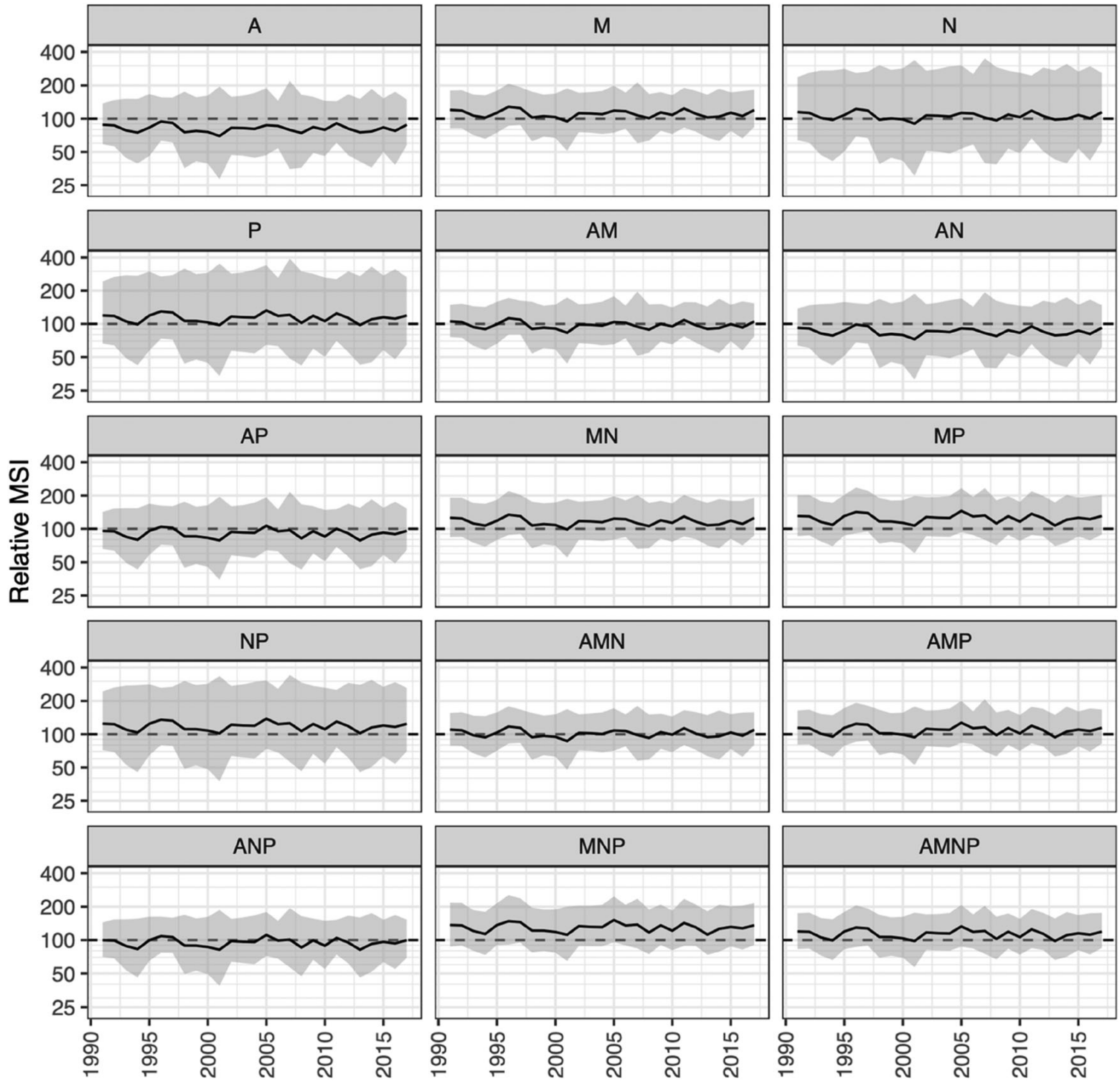

FIGURE 5 Summary of nationally aggregated expected multi-species indicator (MSI) values over time under 15 MSI values are expressed relative to baseline starting (1991) values. Solid lines denote means and shaded areas show means +/− one standard error. Key to individual targets making up alternative target frameworks: A = abstraction; M = morphology; N = nitrates; P = total dissolved phosphorus.

hydrological shifts observed within rivers in England (Christierson et al., 2012; Collet et al., 2017; Hannah & Garner, 2015; Kay et al., 2014; Kay & Kay, 2021; Lane & Kay, 2021; Orr et al., 2015; Prudhomme et al., 2012, 2013, 2014; Sanderson et al., 2012). As climate change contributes to biodiversity loss or offsets the biodiversity benefits of environmental improvements (Vaughan & Gotelli, 2019), regulators must distinguish between those changes they are accountable for (e.g., water quality) and those driven by factors beyond their control (e.g., global greenhouse gas emissions). Our climate-resilient approach provides a foundation upon which regulators can set expected values to support more robust assessment of progress towards environmental targets. Using a notional EQR boundary between 'good' and 'less than good' ecological status of 0.86, our approach suggests 42.6% of water bodies were in good ecological status with respect to MSI by the end of the timeseries (2017). This compares to 18.6% under the RICT approach. Importantly, distributions of EQRs show that many more water bodies would be considered closer to 'good' under our approach (Figure 6), thus motivating restoration efforts to push water bodies over the EQR boundary.

Whilst our models incorporate data covering four major potential pressures on river ecosystems, several further pressures could not be included due to a lack of data at the requisite spatial extent. For example, fine sediment is known to be a significant pressure on freshwater invertebrate diversity (McKenzie et al., 2024). However, sediment pollution across the whole river network of England is presently characterised only by the risk of agricultural fine sediment inputs (Naura, Hornby, et al., 2016) rather than by estimates of actual deposition from any source, including construction, transport and sewage treatment effluent. The concentration of harmful metals from abandoned mines is also identified in the statutory environmental target framework for England, yet time series data on metal concentrations are available for only a small subset of sites in the invertebrate data.

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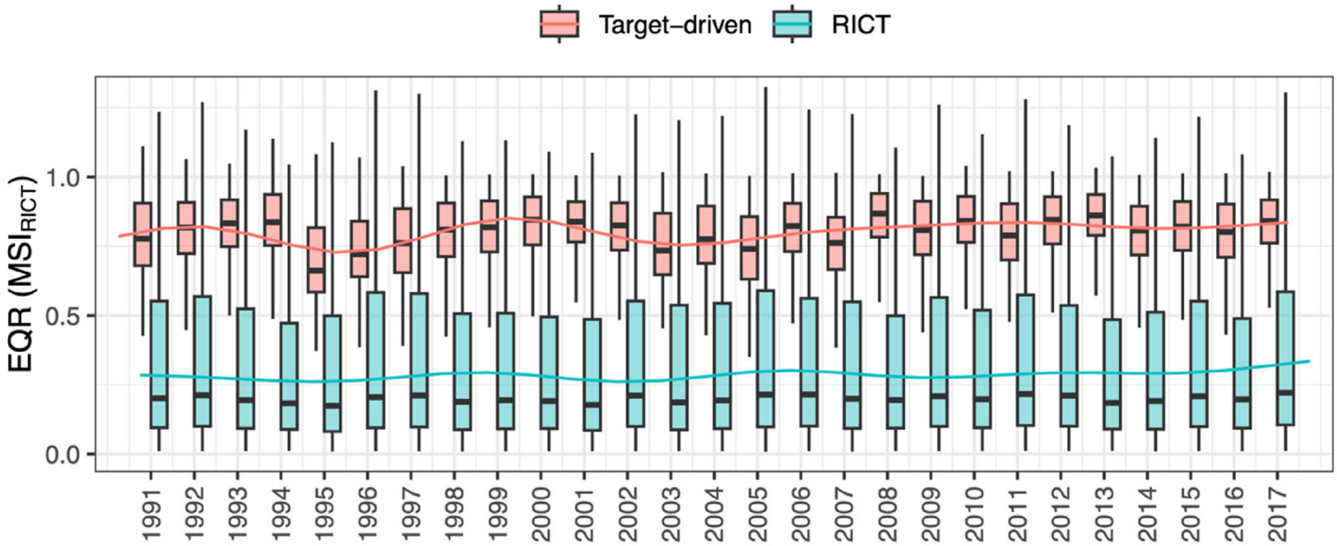

FIGURE 6 Summary of ecological quality ratios (EQRs; observed: expected MSI_{RICT} scores) under the River Invertebrate Classification Tool (RICT) compared with the target-driven framework developed here. Boxplots show the median (bold horizontal line), interquartile range (box) and 1.5 × the interquartile range (whiskers) of EQRs across water bodies for each year. Outliers are not shown. Coloured lines denote mean EQRs from locally estimated scatterplot smoothing (LOESS) models. EQRs under the target-driven framework were calculated based on the overall optimal restoration strategy identified for each water body from the model projections.

Further statutory targets requiring water companies to reduce leaks and the achievement of a greater level of resilience to drought could also potentially contribute to the achievement of biodiversity targets. In particular, the drying of river beds represents a severe disturbance that only specialist invertebrate species can resist or rapidly recover from (Stubbington et al., 2022). The development of spatial datasets relating to the frequency, magnitude and duration of drying events across the river network should therefore be a priority.

Of the pressures we were able to incorporate into predictive models, the corresponding datasets we used are the best available sources of large-scale spatial information for river systems in England, but it is important to note that these are themselves subject to uncertainty which we were unable to fully account for. Data on river habitat modification (CRI) were derived from observations contained within the UK River Habitat Survey database using kriging to generate estimates at 500 m intervals along the river network (Naura, Clark, et al., 2016). The kriging model explained 57% of the variation in the training data. Further uncertainty arises due to the relatively coarse resolution of the CRI data, which risks missing abrupt changes in habitat modification along the river network. Data on abstraction pressure were taken from the national Catchment Abstraction Management Strategy process (Environment Agency, 2023a) which assesses the water resource availability across a whole water body using broad categories derived from a series of models that estimate natural flows, flow scenarios and environmental flow indicators for invertebrates and other freshwater groups. Although based upon ecological responses to water availability, these broad categories of abstraction pressure are somewhat arbitrary (Table 1). Further work would benefit from the development of quantitative indicators of abstraction pressure. Monthly water temperature, nitrate and TDP concentrations originated from a national-scale dynamic macronutrient model associated with spatially variable predictive performance. For example, whilst simulated nitrate concentrations are consistently within 1% of observed values, in some places the model overestimates TDP by up to 100% (Bell et al., 2021). However, our use of long-term mean nutrient concentrations mitigates this source of uncertainty in our models. Precipitation anomalies were derived from climate data interpolated from situ observations to a regular grid (Hollis et al., 2019). Water quality and precipitation data were only available at a relatively coarse (5 km) resolution. If future projects are able to model finer scale variation in water temperature, nutrient concentrations, hydrological anomalies and other pressures, our ecological modelling framework provides the potential for end-users to re-prioritise restoration actions. This would enable application of our approach to guide detailed local river restoration planning.

In constructing RCP-SSP scenarios, we have followed a model intercomparison protocol (Kim et al., 2018) as implemented in a prominent global biodiversity model (Schipper et al., 2020). The specific future changes in water temperature and rainfall anomalies used in our projections were based upon the narratives and semi-quantitative projections developed by the UK-SSP project (UK Climate Resilience Programme, 2023). However, substantial uncertainty around specific environmental trends under the scenarios warrants a full sensitivity analysis in future biodiversity modelling applications. Additional uncertainty is related to the spatial coverage of our models. Due to limited availability of freshwater invertebrate records (particularly in western river basins), we were unable to model every water body; the results reported here represent 75.6% of the land surface of England. Data collection by statutory agencies should focus on filling these gaps to ensure that future models are fully representative of the array

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of England's river basins. Our models could be used to produce population level (fixed effects only) estimates for these understudied water bodies, but we chose not to do this as it would ignore variation in hydrological responses among catchments.

5 | CONCLUSIONS

We offer the first prioritisation of restoration actions to deliver species abundance targets in England, thus providing valuable insights for policymakers and river restoration practitioners. Our findings highlight a critical role for morphological restoration, alongside significant efforts to reduce nutrient concentrations, in delivering nature recovery in English rivers. By introducing a novel approach to setting expected values for ecological assessment, it is now possible to account for shifting thermal and hydrological conditions which confound historical reference models presently used by regulators in the United Kingdom and elsewhere (Chessman, 2021). Some uncertainties and data limitations are currently unavoidable in our models, yet they still present significant potential to underpin a systematic approach to restoration planning and ecological assessment, which is locally adapted whilst accounting for alternative future climate and socioeconomic scenarios.

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CONFLICT OF INTEREST STATEMENT

No conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Catchment physiography and geology data may be requested from the UK Centre for Ecology and Hydrology. Channel resectioning index (M. Naura) and modelled monthly water quality data (V. Bell) may be made available by the respective data owners. Precipitation data, abstraction pressure data, invertebrate records, and other spatial data are publicly available from the sources cited in the main text.

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SUPPORTING INFORMATION

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