Check for updates

Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography | A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

Landscape-Scale Responses of Freshwater Biodiversity to Connectivity and Stressors

Craig Wilkie[1] | Alan Law[2] | Stephen J. Thackeray[3] | Charlotte Ward[4] | Tom August[5] | Ambroise Baker[6] | Jafet Belmont[1] | Laurence Carvalho[7,8] | Daniel Chapman[2] | Anne Dobel[8] | Claire Miller[1] | Henrietta Pringle[4,9] | Marian Scott[1] | Gavin Siriwardena[4] | Philip Taylor[8] | Nigel Willby[2]

[1]School of Mathematics and Statistics, University of Glasgow, Glasgow, UK | [2]Biological and Environmental Sciences, University of Stirling, Stirling, UK | [3]Aquatic Ecosystems Group, UK Centre for Ecology & Hydrology, Lancaster, UK | [4]British Trust for Ornithology (BTO), The Nunnery, Norfolk, UK | [5]UK Centre for Ecology and Hydrology, Oxfordshire, UK | [6]School of Health and Life Sciences, Teesside University, Middlesbrough, UK | [7]Norwegian Institute for Water Research (NIVA), Oslo, Norway | [8]UK Centre for Ecology and Hydrology (UKCEH), Penicuik, UK | [9]People's Trust for Endangered Species, London, UK

Correspondence: Craig Wilkie (craig.wilkie@glasgow.ac.uk)

Received: 5 July 2024 | **Revised:** 14 May 2025 | **Accepted:** 18 May 2025

Handling Editor: Janne Soininen

Funding: This research was funded by the NERC Highlight Topic Hydroscape: connectivity×stressor interactions in freshwater habitats (NE/N006437/1, https://hydroscapeblog.wordpress.com/). Laurence Carvalho also acknowledges support for writing from the FutureLakes project, funded by the European Union under Grant agreement ID 101156425.

Keywords: aquatic plants | chlorophyll-*a* | connectivity-stress interaction | dragonflies | freshwater fish | hydrological networks | lakes | water beetles | water snails | waterfowl

ABSTRACT

Aim: There is compelling evidence that drivers and patterns of biodiversity and ecosystem functioning vary across multiple spatial scales, from global to regional, landscape and patch. However, macroecological processes impacting freshwater biodiversity are poorly understood compared to marine and terrestrial ecosystems. Despite step changes in data availability, we have a fragmented view beyond the local scale of how hydrological and landscape connectivity interact with ecosystem stressors to shape freshwater biodiversity and functioning. While macroecological patterns can vary substantially among taxonomic groups, previous studies have focussed on individual habitat types, sites or taxonomic groups within landscapes, hindering direct comparisons. We present a cross-landscape, multi-species analysis of the interactive effects of landscape and hydrological connectivity and stressors on standing freshwater quality and the diversity of several major freshwater taxonomic groups.

Location: Great Britain (United Kingdom).

Time Period: 2000–2016.

Major Taxa Studied: Phytoplankton chlorophyll-*a*, macrophytes, molluscs, Coleoptera, Odonata, fish and birds.

Methods: Using random forests and generalised additive modelling, we quantified the interactive effects of landscape and hydrological connectivity and stressors on water quality (phytoplankton chlorophyll-*a*) and the diversity of selected taxa in standing freshwaters.

Results: We found evidence of connectivity changing from positive to negative relationships with biotic responses with increasing human-induced stress levels. Some species groups showed the inverse, reflecting complexities of modelling at large, cross-landscape scales. Almost all responses were affected by stress or connectivity, often interacting and with non-linear relationships.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

Main Conclusions: Patterns in stressor-connectivity interactions differed across taxa, but were important in shaping 6 of 8 biotic responses. This emphasises the need for taxon-specific analyses to resolve freshwater ecological responses to stressors, connectivity, and their interactions. Our results also highlight that connectivity effects must be integrated in landscape-scale, evidence-led decision-making, designed to reduce impacts of stressors on water quality and biodiversity.

1 | Introduction

Macroecological patterns vary substantially according to taxonomic group and ecosystem type (Heino 2011), yet studies to date have focussed on individual habitat types or taxonomic groups within discrete geographic landscapes or predominant land use types (Stendera et al. 2012). Predictable macroecological patterns in terrestrial and marine environments are well documented (Hillebrand 2004), but the same cannot be said for freshwater environments, despite their global representation, disproportionately high biodiversity and high rates of endemism (Heino 2011; Collen et al. 2014). Freshwater biodiversity is declining at faster rates than in other major environments, primarily due to human-induced stressors (Dudgeon 2019; Reid et al. 2019; Darwall et al. 2018). Furthermore, habitat destruction, pollution, overexploitation, biological invasions and climate change are all key drivers of biodiversity decline in fresh waters (Dudgeon 2019; IPBES 2019; Albert et al. 2021). These impacts are further influenced by changes in hydrological and landscape connectivity being shaped by land use and climate change (Revenga et al. 2005), raising the need to better understand how this connectivity drives species distributions and ecosystem processes (Ormerod et al. 2010).

Connectivity among sites is recognised as a vital attribute of an ecological network, allowing both the exchange of energy and matter, and species to feed, disperse, migrate, reproduce, and avoid or recover from disturbance (Lawton et al. 2010; Fergus et al. 2017). For this reason, enhancing and restoring connectivity is explicitly highlighted in Goal A and Target 2 of the Kunming Montreal Global Biodiversity Framework (United Nations Convention on Biological Diversity 2022). It is often recommended that alongside enhancing connectivity among sites (directly via corridors such as rivers and canals, or indirectly via 'stepping stones' such as lakes and ponds), these sites must be of high quality themselves (Lawton et al. 2010). However, within fragmented landscapes with intense human land use, there is a danger in viewing enhanced freshwater connectivity as universally positive. Connecting poorer quality freshwater habitats can lead to unintended negative outcomes, and under such situations, one might expect a negative association between biodiversity and habitat connectivity (Olden et al. 2018). For example, increased connectivity may facilitate the movement of non-native species (Chapman et al. 2020; Fausch et al. 2009), spread pollutants, or increase homogenisation of biotic communities (Salgado et al. 2018), all of which may exacerbate the loss of biodiversity and ecosystem function (Strecker and Brittain 2017).

The effects of known and emerging, synergistic, antagonistic, and additive stressor combinations on freshwater biodiversity are increasingly recognised as a major concern for freshwater biodiversity (Jackson et al. 2016; Birk et al. 2020), with a growing literature assessing biodiversity responses to stressors (often using land use as a proxy (Stendera et al. 2012)), while also acknowledging the complexity of this issue (Craig et al. 2017). However, despite this interest, the effects and possible interactions between stressors and connectivity are rarely studied. This may be in part due to the difficulty in quantifying the most ecologically meaningful dimensions of connectivity for both habitats and their functionally diverse biota (e.g., temporal vs. spatial, potential vs. realised, incidence vs. regular events). Given this, many studies resort to coarse, simple metrics as proxies, such as connectivity measures within buffer zones around water bodies, or the distances among neighbouring freshwater habitats (Law et al. 2019; Juračka et al. 2019). Simple, single metrics are useful and often significantly explain biodiversity patterns (O'Hare et al. 2012). However, whilst indicative, they may fail to capture the complex, multidimensional nature of connectivity, which might be better reflected via multiple metrics that incorporate habitat extent (e.g., water area), surrounding land quality and fragmentation (e.g., land use) and biological elements, including vectors of dispersal (e.g., by humans and waterfowl).

To protect and restore freshwater habitats, a better understanding of the relationships between freshwater biodiversity, landscape connectivity, and the interactions between this and human-induced stress is urgently needed (Hill et al. 2021; Heino et al. 2021). Yet, a general understanding of whether species' responses to connectivity and stressor interactions are generalisable or taxon-specific is lacking. Therefore, outcomes of habitat restoration and creation efforts remain uncertain. Several decades of work by volunteers, natural history societies, conservation NGOs, and environmental agencies to improve data gathering, standardisation, and accessibility to online databases now make analyses to address this need feasible (Jetz et al. 2012). By utilising long-term and spatially explicit datasets for standing freshwaters, our aim was to quantify how anthropogenic stressors and connectivity act singly and in combination (main and interactive effects) to impact water quality (phytoplankton chlorophyll-*a*) and the biodiversity (species richness) of selected, functionally important freshwater biota (macrophytes, molluscs, beetles, Odonates, fish and birds), representing multiple trophic levels (primary producers to apex predators) across the landscape of Great Britain. Specifically, we hypothesised that:

Hypothesis 1. *Freshwater habitats with low stressor exposure, and high connectivity to other habitats, will support higher water quality and greater biodiversity of each taxonomic group, but*:

Hypothesis 2. *For habitats with high stressor exposure, this directionality will reverse, that is, high connectivity will support lower water quality and low biodiversity.*

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hypothesis 3. *Water quality and taxonomic groups will be most sensitive to different indicators of connectivity (e.g., hydrological or landscape proximity), due to intrinsic differences in mobility and dispersal mechanisms.*

2 | Methods

2.1 | Data

Taking a multi-scale spatial approach (Fergus et al. 2017; Soranno et al. 2017), we used a suite of lake and catchment, connectivity and stressor metrics covering standing freshwater bodies in Great Britain, which are described in detail in Section S2 of the Supporting Information. Our data cover a supra-regional scale, that is, a large area comprising multiple landscape types. Our response data (Figure 1), representing standing freshwater biodiversity, were species richness (i.e., number of species) of macrophytes, molluscs, beetles, Odonata, wetland birds that feed or breed in, or by, standing waters, and freshwater fish. Collectively, these species vary greatly in potential dispersal rates and mechanisms, and trophic position. We also analysed phytoplankton chlorophyll-*a* as a widely used biological indicator of water quality, which is sensitive to land-use stressors such as nutrient pollution. Due to the well-documented effect of lake depth on the response of phytoplankton chlorophyll-*a* to nutrient pollution from catchments (Phillips et al. 2008), chlorophyll-*a* analyses were conducted separately for shallow and deep lakes (i.e., lakes of less than, or greater than, 5 m mean depth to group them into deep lakes, typically stratifying, vs. shallow lakes with mixed water columns and extensive littoral habitat). Data were either collected from each waterbody or within 1 km grid squares and subsequently matched to waterbodies, as described in Subsection S2.5 of the Supporting Information.

2.2 | Statistical Analyses

Due to the large numbers of potential covariates for each response and a lack of prior knowledge about the form of any relationships, we took a variable selection approach that made no assumptions about the shapes of potential relationships, and we used a flexible regression approach to model the complex relationships between the responses and covariates. For each response, we carried out variable selection using conditional inference tree-based Random Forests (Strobl et al. 2007, 2009), using the conditional variable importance method (Strobl et al. 2008), and taking the approach of Genuer et al. (2010). We transformed highly skewed covariates and used only one of each group of highly related covariates in the variable selection. We used generalised additive models, GAMs, (Wood 2017) to flexibly model nonlinear relationships between the response and covariates, allowing for bivariate smooths representing interactions between stressor and connectivity metrics, and allowing for non-Gaussian response distributions. More details of the methods are given in Section S3 of the Supporting Information, while model error distributions and link functions are presented in Table 2.

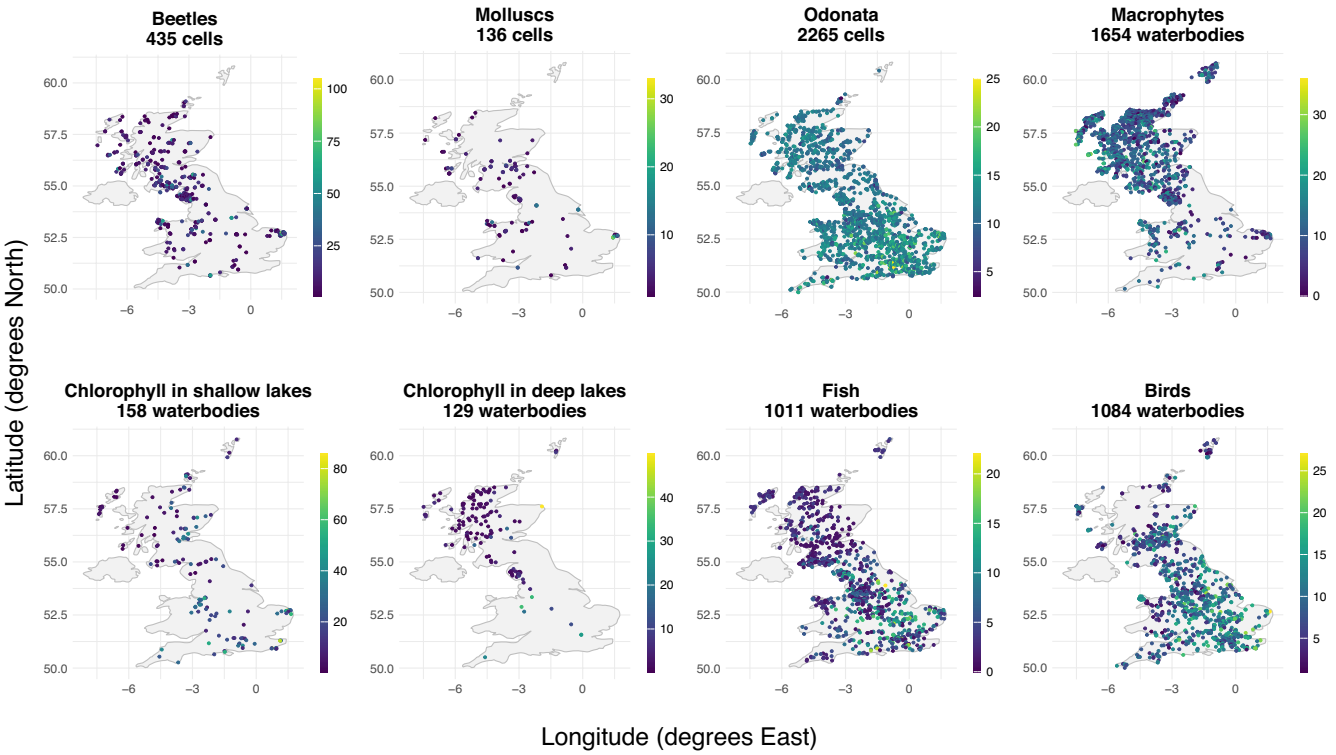

FIGURE 1 | Locations of observations for each biological response within Great Britain, within either standing waterbodies (lakes and ponds) or Ordnance Survey (Great Britain) National Grid 1 km cells, as dictated by the spatial resolution of recording schemes for each response. Points are coloured by species richness for beetles, molluscs, Odonata, macrophytes, fish and birds, or by mean concentration (μg/L) for chlorophyll-*a*. (See Sections S1 and S2 of the Supporting Information for full data details).

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 | Summary of how a biological indicator of water quality (chlorophyll-*a* concentration) and the richness of each species group respond to human stressors (agricultural and urban land use), hydrological connectivity, human connectivity, and the interaction between connectivity and stressors.

Response (columns)	Chlorophyll-*a*, shallow lakes	Chlorophyll-*a*, deep lakes	Macrophytes	Molluscs	Beetles	Odonata	Fish	Birds
Agricultural and urban stress	✗	✓	✓	✓	✓	✓	✓	✓
Hydrological connectivity (not necessarily direct—includes landscape connectivity)	✗	✓	✓	✗	✓	✓	✓	✓
Human connectivity	✗	✗	✓	✓	✗	✗	✓	✓
Connectivity-stressor interactions	✗	✓	✓	✓	✗	✓	✓	✓

Note: A tick (✓) means that there was a statistically significant relationship between the response and at least one variable (or interaction term) in each covariate group within the final statistical model for that group, with a cross (✗) otherwise. See Table S3 for full details of the final models for each response.

3 | Results

All responses, except for chlorophyll-*a* concentration in shallow lakes, showed evidence of association with measures of human pressure, as indicated by extent of agricultural or urban land use (Table 1). Chlorophyll-*a* concentration in deep lakes and the taxonomic richness of macrophytes, beetles, Odonata, fish, and birds also showed evidence of association with hydrological connectivity. Macrophyte, mollusc, fish, and bird richness were additionally associated with human connectivity. All responses except chlorophyll-*a* concentration in shallow lakes and beetle taxonomic richness showed evidence of associations with connectivity–stressor interactions.

Plots of smooth terms from the final models are given in Figures 2 and 3, with summaries of all variables included in Table 2.

3.1 | Chlorophyll-*a* Concentration

Our analysis indicated very different responses in shallow and deep lakes. For shallow lakes, variation in chlorophyll-*a* concentration was associated with characteristics of the lake (River Basin District [RBD] and humic type; Table 2), with the model explaining 21% of the variance in the response. For deep lakes, the model explained 77% of the variance in the response. Chlorophyll-*a* concentration generally decreased with increasing slope of the surrounding landscape (Figure 2a) and there was an interaction between river density and the percentage of agricultural land in the catchment. Chlorophyll-*a* concentration was generally higher in catchments with low river densities, and concentrations increased strongly as percentage agricultural land (catchment scale) increased to about 40%, decreasing slightly at the highest percentage agricultural land (50%–60%). Percent agricultural land had little relationship with chlorophyll-*a* concentrations at high values of river density, and river density had little effect for low percentage agricultural land.

3.2 | Macrophyte Richness

The final model for macrophytes included connectivity, stressor, and lake typology covariates (Table 2, Figure 2b), explaining 24% of the variance in richness. Macrophyte species richness was lower in low alkalinity, humic, isolated, or headwater sites, and higher in small or very small water bodies. Richness increased on average with increasing water body perimeter, catchment mean slope, and 1 km buffer mean temperature. In terms of stressor metrics, richness decreased with increasing catchment urban land use, and from a connectivity perspective, increased on average with increasing catchment visits for watersports.

Connectivity-stressor interactions were apparent for macrophyte richness. The effects of Strahler 1 density and pond area percent both depended on the surrounding agriculture. Figure 2b shows that macrophyte species richness increased on average with increasing Strahler 1 density for very low and very high percentages of surrounding agriculture land use, but this was reversed for around 20%–40% of agriculture in the buffer. Richness was estimated to increase on average with increasing pond area in the buffer (Figure 2b), but with a steeper slope for higher percentages of agriculture.

3.3 | Mollusc Richness

For mollusc richness, 57% of variance was explained by RBD (though not necessarily along a North–South gradient), depth

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

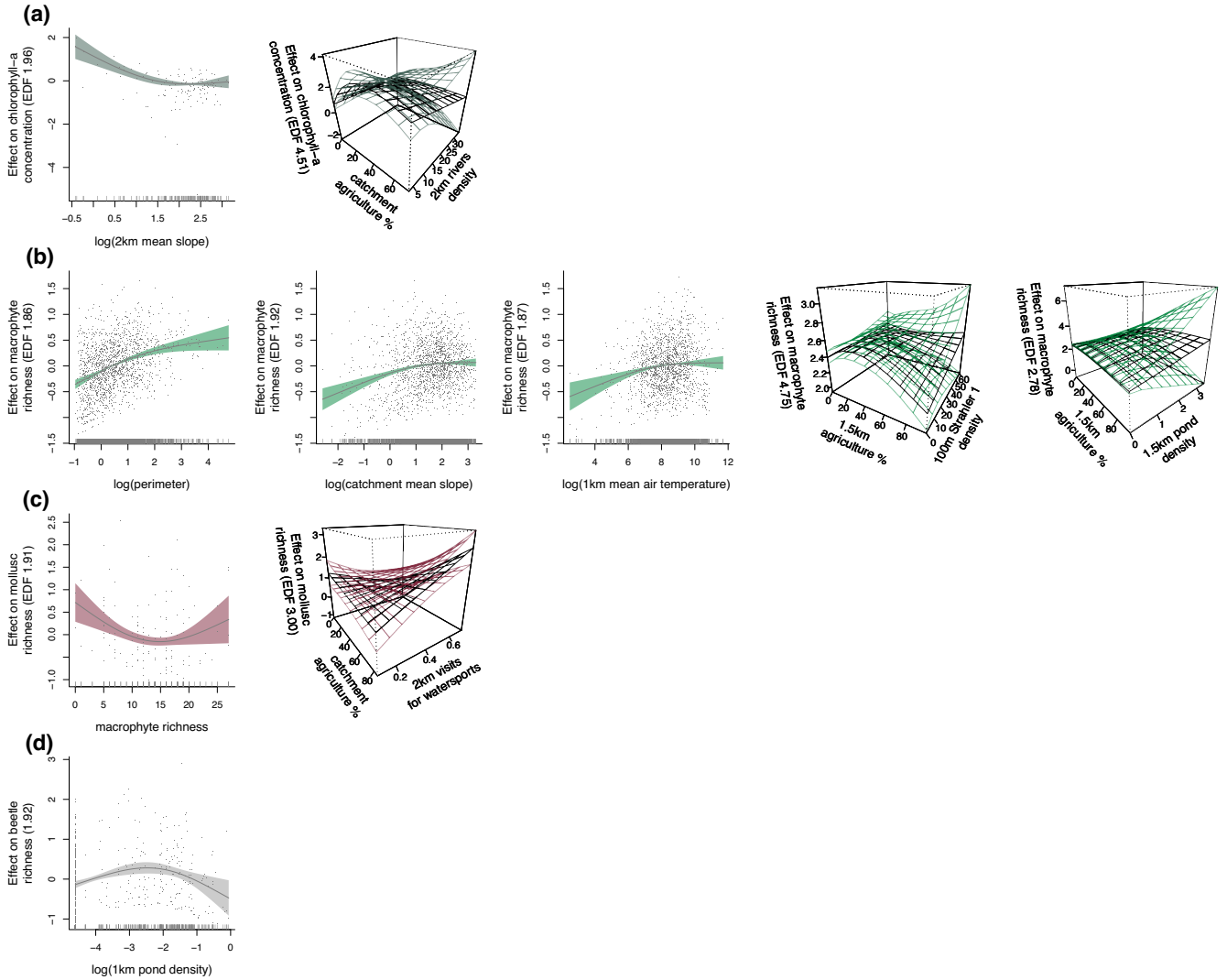

FIGURE 2 | Fitted smooths for each GAM. (a) Chlorophyll-*a* concentration in deep lakes; and the richness of (b) macrophytes, (c) molluscs, and (d) beetles. The model for chlorophyll-*a* concentration in shallow lakes contained no smooth terms. The dark grey lines and black grids represent the estimated smooth relationships, while the coloured shading and grids represent the estimated smooths ±2 standard errors. The dark grey dots represent the partial residuals. These are omitted from the perspective plots, for clarity.

(shallow lakes having lower richness than deep lakes) and geology type (lakes with catchments dominated by limestone having higher mollusc richness than non-limestone-dominated high alkalinity lakes). Mollusc richness was influenced by macrophyte richness, with a small decrease observed at intermediate macrophyte richness (Figure 2c). Catchment agriculture had both negative and positive effects on mollusc richness by interacting with visits for watersports (Figure 2c). Richness was highest in catchments with high agricultural land cover and a high likelihood of watersports visits, and was also relatively high for low agriculture and low watersports visits.

3.4 | Beetle Richness

Approximately 24% of the variance in beetle richness was explained by the model. Grid cells with catchments with a higher mean slope or higher urban land use had lower beetle richness, with significant differences also observed between RBDs (Table 2). Within lake catchments, there was a negative effect of lake density and a non-linear relationship between richness and the area of ponds within a 2 km buffer (i.e., with richness peaking at intermediate pond areas, Figure 2d). Richness was estimated to differ between lake size classes, with small lakes having lower richness than large lakes, but very small lakes having higher richness than large lakes. There was limited evidence of connectivity–stressor interactions for beetle richness.

3.5 | Odonata Richness

Approximately 20% of the variance in Odonata richness was explained. Greater Odonata richness was found where catchments had higher mean temperatures, as the distance from the sea increased, and as the pond density increased in the surrounding buffer (2 km, Table 2, Figure 3a). Richness varied among RBDs, geology types (greater in low to medium alkalinity lakes) and

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

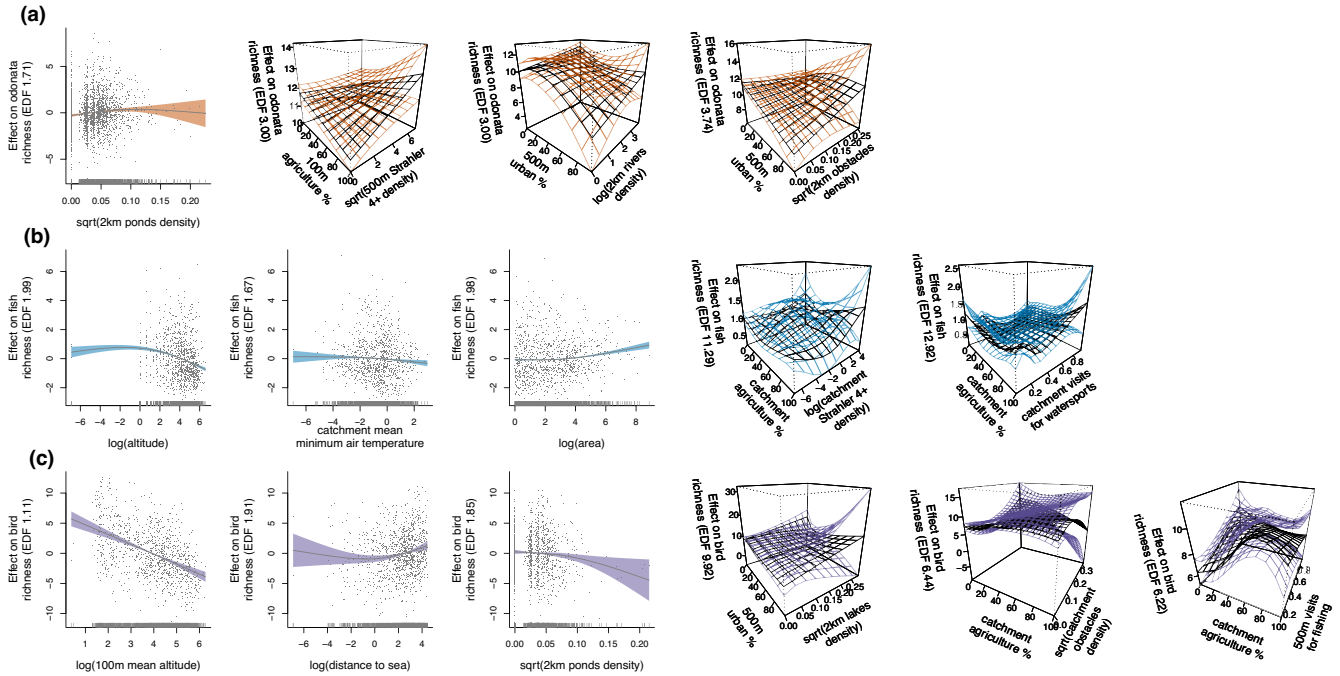

FIGURE 3 | Fitted smooths for GAMs of the richness of (a) Odonata, (b) fish and (c) birds. The dark grey lines and black grids represent the estimated smooth relationships, while the coloured shading and grids represent the estimated smooths ±2 standard errors. The dark grey dots represent the partial residuals. These are omitted from the perspective plots, for clarity.

lakes of different size types (with small and very small lakes having a greater species richness).

Modelling suggested the presence of connectivity-stressor interactions. For high agricultural land use, a positive relationship between Strahler 4+ density and Odonata richness was observed, but no relationship was found under low agricultural land use. For low Strahler 4+ density, there was a negative relationship between Odonata richness and agricultural land use, but for high Strahler 4+ density, the relationship was positive.

For low urban land use, there was no clear relationship between Odonata richness and river density, but where urban land use was high, river density had a positive relationship with richness.

There was an overall positive relationship with increasing obstacle (weirs, dams, lock gates, etc.) density, although the effects were highly variable when obstacle density was at its highest (Figure 3a).

3.6 | Fish Richness

The model for freshwater fish explained approximately 40% of the variation in species richness. Fish species richness varied among Great Britain RBDs and with elevation, being lowest in Scotland and at higher elevations (Figure 3b).

Richness was highest in larger lakes, at greater distances from the sea, and in locations with lower air temperatures and rainfall. However, there was much variability around these general trends, which each explained between < 1% and 7.8% of the total variability in species richness.

Modelling of the fish data suggested interacting effects of human pressure and connectivity. There was generally higher richness where the likelihood of watersports visits was lower, but for high agricultural land cover, higher richness estimates were associated with a greater likelihood of watersports visits. There was also a complex interaction between Strahler 4+ segment density and percentage agriculture, but this explained very little of the variation in fish species richness.

3.7 | Bird Richness

The final model for bird species richness included nine connectivity variables, explaining approximately 42% of the variation in the response, including three interaction terms.

Bird species richness varied among RBDs, was significantly greater in larger lakes (Table 2, Figure 3c), and was negatively related to landscape Strahler 1 density, riparian mean altitude, and landscape ponds density.

Human influence by fishing visits had an interactive effect with agricultural coverage on bird species richness (see Figure 3c). At low agricultural coverage, bird richness increased with increased fishing visits, whilst for high agricultural coverage, there was a weak negative effect of fishing visits.

Under low urban land use, there was a positive relationship between bird species richness and lake density, but increased uncertainty obscured the relationship for higher percentage urban land use. For low lake densities, there was a generally negative relationship between urban cover and bird richness (although very low increasing values of urban cover had a positive effect).

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 | Summaries of the final fitted models for each response, showing response distributions and adjusted R^2 values.

Chlorophyll in deep lakes	Gamma: link=log, R^2 (adj.) = 0.77
Smooth terms	**EDF**
log(2km mean slope)	1.96
catchment agriculture % * 2km river density	4.51
Chlorophyll in shallow lakes	Gamma: link=log, R^2 (adj.) = 0.21
Factor terms	
RBD	(Northumbria, Scotland, Solway Tweed) < Anglian
Humic type	(humic, poly humic and unclassified) < clear
Macrophytes	Quasipoisson: link=log, R^2 (adj.) = 0.24
Linear terms	**Estimate (Standard error)**
Catchment urban %	-0.01 (0.00)
Logit(catchment visits for watersports)	0.08 (0.03)
Smooth terms	**EDF**
log(perimeter)	1.90
log(catchment mean slope)	1.92
1km mean temperature	1.86
1.5km agriculture % * 100m Strahler 1 density	4.72
1.5km agriculture % * 1.5km pond area %	2.79
Factor terms	
Size type	(small, very small) > large
Connectivity type	(drainage upstream, headwater) > drainage; isolated < drainage
Humic type	humic > clear; poly humic < clear
Geology type	low alkalinity < high alkalinity
Molluscs	Quasipoisson: link=log, R^2 (adj.) = 0.57
Smooth terms	**EDF**
Macrophyte species richness	1.91
catchment agriculture % * 2km visits for watersports	3.00
Factor terms	
RBD	(North West, Severn, Solway Tweed, Western Wales) < Anglian
Depth type	(shallow, very shallow) < deep
Geology type	Marl > high alkalinity
Beetles	Negative Binomial(0.892): link=log, R^2 (adj.) = 0.24
Linear terms	**Estimate (Standard error)**
Log(100m mean slope)	-0.34 (0.06)
Log(2km lakes density)	-4.08 (1.39)
Sqrt(100m urban %)	-0.10 (0.04)
Smooth terms	EDF
log(1km pond area %)	1.92
Factor terms	
RBD	Thames < Anglian
Size type	very small > small
Odonata	Gaussian: link=identity, R^2 (adj.) = 0.2
Linear terms	**Estimate**
Catchment mean temperature	0.25
Log(distance to sea)	0.12
Smooth terms	**EDF**
sqrt(2km ponds density)	1.71
100m agriculture % * sqrt(500m Strahler 4+ density)	3.00
500m urban % * log(2km river density)	3.00
500m urban % * sqrt(2km obstacles density)	3.74
Factor terms	
RBD	(Dee, Humber, North West, Northumbria, Scotland, Severn, Solway Tweed, South East, South West, Western Wales) < Anglian
Geology type	low alkalinity > high alkalinity
Size type	(small, very small) > large
Fish	Poisson: link=log, R^2 (adj.) = 0.4
Linear terms	**Estimate (Standard error)**
Log(distance to sea)	0.09 (0.01)
Sqrt(catchment mean minimum monthly rainfall)	-0.06 (0.02)
Smooth terms	**EDF**
log(altitude)	1.99
catchment mean minimum temperature	1.67
log(area)	1.98
catchment agriculture % * log(catchment Strahler 4+ density)	11.29
catchment agriculture % * catchment visits for watersports	12.92
Factor terms	
RBD	(Humber, Scotland, Solway Tweed) < Anglian, Severn > Anglian
Birds	Gaussian: link=identity, R^2 (adj.) = 0.42
Linear terms	**Estimate (Standard error)**
Log(area)	0.95 (0.09)
1.5km Strahler 1 density	-0.11 (0.04)
Smooth terms	**EDF**
log(100m mean altitude)	1.11
log(distance to sea)	1.91
sqrt(2km pond density)	1.85
500m urban % * sqrt(2km lake density)	9.92
catchment agriculture % * sqrt(catchment obstacles density)	6.44
catchment agriculture % * 500m visits for fishing	6.22
Factor terms	
RBD	Northumbria > Anglian, (Scotland, Solway Tweed, Western Wales) < Anglian

Note: Estimates (with standard errors) are given for each linear term, effective degrees of freedom (EDF) are given for each smooth term, and statistically significant relationships among the levels of factors (i.e., categorical variables) are noted. Smooth interactions are denoted by *. Smooth terms are plotted in Figures 2 and 3. Further details for all terms are given in Table S4. All p-values for the effects reported are <0.05.

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

For high lake densities, we instead found a negative relationship between urban cover and bird richness for lakes with up to around 10% urban land use nearby, with the relationship being too uncertain to define as urban land use increased beyond 10%.

4 | Discussion

We believe this to be the first study to investigate the interacting impacts of connectivity and human-induced stress on multiple taxonomic groups at a supra-regional scale. We found evidence that connectivity and stress often interact at the landscape scale to affect biodiversity (an initial condition for our first two Hypotheses). However, these biodiversity responses were far more nuanced than the simple interaction that we initially expected (Hypotheses 1 and 2). We found evidence that species richness for each taxonomic group responded differently to connectivity and stress and that taxonomic groups differed with respect to the connectivity indicators to which they were most sensitive (in support of Hypothesis 3). This result is not unexpected, as freshwater species have a wide range of dispersal mechanisms, both active and passive (Bilton et al. 2001). Active dispersal is more prominent in larger species able to swim (fish) or cross land (amphibia), or with some smaller species that have adult stages that disperse actively through the air (e.g., beetles and Odonata). Passive dispersal occurs through the movement of water, air, or biological vectors. This is largely the case for macrophytes, phytoplankton (e.g., chlorophyll-*a* response) and larval stages of many small invertebrates (e.g., beetles and molluscs). Some macrophytes have developed traits that result in active dispersal by proxy through mobile species such as wetland birds (Figuerola and Green 2002). Generally, dispersal ability across contrasting organism groups declines with body size, particularly in lakes, which tend to be less connected than flowing waters (Shurin et al. 2009).

Despite the expected among-taxa variation in responses, we identified some common patterns across landscapes and ecological responses (species richness and chlorophyll-*a* concentration), which we discuss below.

4.1 | Ecological Responses to Lake and Landscape Characteristics, Stressors and Connectivity

4.1.1 | Interactions Between Connectivity and Human-Induced Stress Are the Norm

All models except those for chlorophyll-*a* concentration in shallow lakes and for beetle richness included connectivity-stressor interactions, suggesting that the effects of anthropogenic stress on ecosystem state will frequently depend on the degree of freshwater connectivity, in agreement with the broad theory behind our Hypotheses 1 and 2. There were few commonly occurring interactions across water quality and biological groups (e.g., agricultural or urban land use and measures of hydrological connectivity), but considering their effects is vital to adequately understand the impacts of both connectivity and stress on freshwater quality and biodiversity. Therefore, our models indicate that it is important not to assume a priori that the same interactions are relevant to all ecological responses. They also emphasise that modifying connectivity may reshape how biota experience and respond to stressors in their environment. These findings agree with our Hypothesis 3 that indicators of connectivity would relate differently to water quality and different taxonomic groups, but they go beyond this in revealing that the directions of the connectivity-stressor interactions also differ between these groups.

Bivariate smooths of connectivity and agricultural land cover appeared in models for chlorophyll-*a* concentration in deep lakes and richness of macrophytes, Odonata, fish and birds. Chlorophyll-*a* in deep lakes and macrophyte richness were higher at intermediate percentages of agricultural land cover, dampened in the presence of greater hydrological connectivity. Plausibly, these responses reflect elevated nutrient runoff from increasingly hydrologically connected agricultural land, which is then tempered by higher lake flushing rates associated with a high surrounding river density, which in turn reduce nutrient retention, as found in cyanobacteria and phytoplankton (Carvalho et al. 2011; Richardson et al. 2019). The complex relationship between the richness of Odonata, Strahler 4+ density and agricultural land cover may indicate that Strahler 4+ density is a proxy for suitable habitat types in the buffer/catchment, not as an indicator of density of flowing freshwater, with the presence of Strahler 4+ segments likely indicating heterogeneous, lowland, floodplain systems that often contain suitable habitats for Odonates (Chovanec and Waringer 2001).

Macrophyte richness was the only ecological variable with evidence of an interacting effect of connectivity to standing freshwater and agricultural land cover. The negative relationship between macrophyte richness and agricultural land use under low values of pond area is unexpected, but small in magnitude. The positive relationship between richness and agricultural land cover for higher values of pond area agrees with Law et al. (2019), who found a positive relationship between nearby agriculture and macrophyte richness in three UK regions, with a negative relationship identified between richness and agricultural pollutant levels. However, at high levels of agricultural land use (*c.* 40%) the impact on richness could be detrimental (Law et al. 2019), with high variability across the supra-regional study area.

For Odonata and birds, species richness was related to connectivity-stressor interactions involving urban land cover. For Odonata, this stressor interacted with metrics of connectivity to flowing freshwaters, while for birds the relevant connectivity metric represented standing water density (lakes density). Odonata richness and obstacle density were potentially positively related under high urban land cover, which we assume reflects variation in water quality, still water habitat availability, or landscape type rather than a direct effect, since obstacles are usually found in urban or human-impacted landscapes (Atkinson et al. 2018). The positive relationship between Odonata richness and river density for high percentage urban land cover agrees with the principle that connectivity can buffer negative land use effects.

Bird species richness was related positively to lake density under low urban land use, agreeing with Hypothesis 1, but there was high uncertainty under high urban land use, possibly due to

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

fewer data points (lake density lower in highly urbanised areas), and/or reflecting the potential difference in relationships in different contexts (e.g., in England lakes are concentrated in the north west (Lake District) and south east (Broads National Park), but landscapes and land uses contrast strongly between these regions). An increasing bird species richness with increasing lake density was expected as waterbirds with high dependence on connectivity utilise available nearby resources (Almeida et al. 2018). The generally positive effect of urban land use (in the interaction with lake density) could be due to benefits of supplementary feeding in urban areas or the greater utilisation of urban areas by common and/or introduced species (Blair 1996; Galbraith et al. 2015; Harrison et al. 2016), and these could counteract potential negative effects of a reduction in habitat specificity on more sensitive species at the community level.

Our models suggest that mollusc, fish, and bird richness were affected by interactions between agricultural land use and human connectivity (visits for watersports or fishing), providing support for the initial condition of our Hypotheses but suggesting some nuances rather than the simple interactions under our Hypotheses 1 and 2. The differing relationship between mollusc richness and likelihood of visits for watersports under contrasting levels of agricultural land use most probably relates to larger lakes generally having more mollusc species (e.g., as found by Harris et al. (2011) and Carlsson (2001) in the context of shoreline length of lake islands) and also being more popular for watersports (e.g., Lake District, Broads National Park). The complexities of relationships between fish species richness, agricultural land use and watersports visits may arise from the combination of multiple interrelationships between human recreational behaviour, site attributes like slipways and car parks, likelihood of stocking, and risks of species introduction, in both natural and human-made water bodies (Nunn et al. 2023; Chovanec and Waringer 2001; Chapman et al. 2020). Bird species richness relates positively to visits for fishing under low agricultural land use, reversing for high agricultural land use. The positive response under low agricultural cover could reflect closer proximity to human habitation, with more fishing visits anticipated close to (but not in) urban areas. In such areas, native and introduced bird species are more likely to be found, so fishing may be a proxy, with direct effects being unlikely unless these reflect a joint attraction of both birds and anglers to fish. These differing interactions between variables provide support for our Hypothesis 3.

4.1.2 | Intensive Land Use Is a Key Source of Ecological Stressors

Chlorophyll-*a* concentration in shallow lakes was the only response to show no statistically significant relationship with the stressor variables (percentage urban and agricultural land use in the surrounding landscape). This may be because internal processes, such as competition with macrophytes for resources (nutrients and light) and top-down effects of fish, are much greater in shallow lakes compared with deep lakes, reducing the effects of land-use stressors on this response (Moss et al. 1997). Efforts to manipulate trophic cascades and nutrient loading in the interests of shallow lake restoration may also increase under more intensive land covers. All other ecological responses included these stressors as significant model components, often in interactions (bivariate smooths) with connectivity variables. For example, urban land use was found to be negatively associated with beetle and Odonata richness. These relationships may be explained by water bodies nearer human populations tending to be less natural and more impacted by human factors (e.g., more likely to have physically modified features, to be subject to higher levels of disturbance and to be exposed to a range of pollutants at higher concentrations arising from waste materials, sewage and road run-off (Gál et al. 2019), or the negative impacts of invasive species (Chapman et al. 2020)). Furthermore, agricultural land use effects, while almost ubiquitous, always appeared as part of interactions with connectivity. Given the large number of stressor–connectivity interactions we detected, integrating the connectivity of water bodies is clearly vital if human-induced stressor impacts on water quality and biodiversity are to be understood and managed.

4.1.3 | Hydrological Connectivity Is the Blueprint for Ecological Responses

All ecological responses, except chlorophyll-*a* concentration in shallow lakes and mollusc richness, had statistically significant relationships with hydrological connectivity metrics. However, the fitted effects for hydrological connectivity differed considerably among ecological responses, in terms of the connectivity metrics selected. Chlorophyll-*a* concentration in deep lakes, and the species richness of macrophytes, Odonata, fish and birds were correlated with connectivity metrics representing linear freshwater connectivity (i.e., connectivity to rivers and canals), and the richness of macrophytes, beetles, Odonata and birds were also related to measures of connectivity to standing freshwaters (i.e., lakes, larger ponds and reservoirs).

We found great variability in the form of the observed ecological responses. For example, there was a hump-shaped relationship between pond density and beetle richness, and a positive relationship between pond density and Odonata richness, which was not maintained at the highest pond densities. Potentially, at the highest pond densities, species and ecological interactions may also play a role in determining richness and composition, for example by changing the attractiveness of the focal water body to some mobile taxa. In contrast, we found a negative, rather than hump-shaped, relationship between pond density and bird species richness. For birds, ponds may be too small to support some water bird species such as cormorants, coots and great crested grebes, so that these species may avoid areas with many ponds rather than larger lakes. Both bird and fish species richness were related to connectivity to running waters. For birds, richness decreased with an increasing density of Strahler 1 streams (e.g., headwater streams) in the surrounding 1.5 km landscape, indicating that upland habitat may be more suited to specialist bird species. The stream connectivity relationship was highly nuanced for fish richness. Fish species richness is known to depend upon hydrological network position, often increasing at higher stream orders (Beecher et al. 1988) due to associated changes in habitat connectivity, extent and stability. However, we found that the relationship between richness and the density of high-order streams in fact had a complex association with human pressure (agricultural land cover).

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

At a basic ecosystem functioning level, landscape connectivity appears to be important for phytoplankton in deep lakes, with river density modifying the more well-established positive effects of percent agricultural land on algal biomass through increased nutrient loading (Dillon and Rigler 1974; Phillips et al. 2008). This was not true for shallow lakes, where it has been widely recognised that internal ecological processes can have a strong effect on phytoplankton biomass (Moss et al. 1994; Jeppesen et al. 1997; Scheffer and Van Nes 2007). However, the exact role of these internal processes remains the focus of active research and debate (Davidson et al. 2023). This basic effect of connectivity in modifying the primary production of deep lakes needs wider consideration in regional, supra-regional and global studies of lake water quality (Stockwell et al. 2020) and is likely to have knock-on effects on the broader biodiversity responses examined in this study.

4.1.4 | Human Activity Is a Common Agent of Connectivity

Macrophyte, mollusc, fish and bird species richness all displayed statistically significant relationships with human connectivity metrics. Macrophyte richness was related positively to visits for watersports, probably through macrophyte introductions via transportation of propagules on watersports equipment, like boats and trailers, a well-known route for dispersal of invasive aquatic plants (Brainard et al. 2021; Tamayo and Olden 2014).

The human connectivity metrics in the models for molluscs, fish, and birds appear as part of interactions with agricultural land use. For molluscs and fish, models include the likelihood of visits for watersports, while for birds, the likelihood of fishing visits is included instead. The absence of visits for fishing specifically from the model for fish suggests that we do not see any clear effect of fish stocking or accidental introduction at a supra-regional scale once the other variables are accounted for. We note that Gimenez et al. (2023) found a positive relationship between stocking and richness in certain lake types, while Arlinghaus et al. (2022) and Eby et al. (2006) found more complex relationships which, with our supra-regional scale analysis including different types of lakes, might explain this result. Inclusion of the likelihood of watersports visits in the models for molluscs and fish could again relate to accidental transportation of species on watersports equipment (for molluscs, Anderson et al. 2015), or there may be some unmeasured variable affecting both mollusc species richness and suitability of lakes for watersports activities, such as availability of hard engineered surfaces.

4.1.5 | Broad Features of Lakes, Climate and Catchments Help to Explain Ecological Responses

We found that all ecological responses (chlorophyll-*a*, macrophytes, molluscs, beetles, Odonates, fish and birds) were associated with at least one lake, buffer or catchment feature or typology metric, with most models including several of these. This highlights that freshwater biodiversity and water quality are impacted by processes operating across multiple spatial scales (Birk et al. 2020). As such, both waterbody and landscape features must be considered when seeking to disentangle the unique and shared effects of stress and connectivity. The frequent inclusion of RBD indicates spatial structuring of water quality and biodiversity at biogeographical scales that could not be explained by the available stressor and connectivity metrics, or the typology features included in our study. Including a district-type metric such as RBD can be beneficial to explain the patterns in biodiversity and water quality, and its inclusion highlights that regional patterns will be further nuanced (Heino 2011). This accords with patterns seen in other studies (e.g., Sandin and Johnson 2000; Santoul et al. 2004) where species richness in freshwater habitats was observed to vary between hydroregions.

Ecological responses were frequently associated with landscape features within catchments or buffers. For example, fish and bird richness were negatively related to altitude, chlorophyll-*a* concentration in deep lakes and beetle richness were negatively related to slope, while macrophyte richness was positively related to slope. Our observation that different taxonomic groups vary in their response to similar environmental variables is likely to reflect among-species variation in traits that shape ecological requirements, tolerances and sensitivities, and to reflect the effects of landscape type on water quality (Biggs et al. 2007), mediated, for example, via likely effects of catchment slope on surface runoff and lake flushing rates. Variability in such traits is likely to relate to taxonomy to some extent. For example, sensitivity to catchment temperatures could limit richness of amphibia, beetles, and Odonata more due to their terrestrial stages. Additionally, we acknowledge that there is likely to be considerable among-species variation even within any specific group. Macrophyte species, in particular, can have widely differing and specialist dispersal mechanisms, with several pondweed species documented to disperse seeds via passage through the guts of wetland birds (Figuerola and Green 2002), whilst the seeds of three species of water lilies have been shown to be destroyed by gut passage (Smits et al. 1989).

Climate variables (rainfall and temperature) were not commonly included in our models, despite climate being known to be a major determinant of the distributions of species and water quality (Markovic et al. 2014; Heino et al. 2009; Richardson et al. 2019). This is probably caused by RBD and landscape features (e.g., slope and altitude) being present in models, already accounting for the main spatial patterns of biodiversity and water quality (See Figure S3), as well as richness relationships obscuring species-level responses.

4.2 | Reflection on the Modelling Approach

We adopted a data-driven, correlative approach, allowing us to explore complex relationships without making assumptions based on previous knowledge. Our novel approach using GAMs accounted for inter-variable correlations and nonlinear relationships to reveal nonlinear connectivity-stress interactions, which many commonly used approaches, that is, linear models, can miss (Duncan and Kefford 2021). The multiple

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

interactions between variables pose difficulties in interpretation, but importantly using a consistent flexible approach has allowed us to identify these. While requiring careful interpretation of fitted relationships due to their nonparametric nature, GAMs fall within a statistically robust modelling framework, with constraints penalising excessive curvature of fitted relationships, improving interpretability while retaining flexibility (Wood 2017). The necessary difficulties introduced by this approach include synthesising results when conceptually similar, but not identical, variables were included in different models. Despite the large numbers of variables available for the models, it is beyond the scope of this study to tease apart causation at the supra-regional scale, and further (experimental) analyses that also consider the most relevant scales of impact for each taxonomic group would be required to infer causality. We note that when modelling different taxonomic groups, lake-, buffer- and catchment-scale variables were included, reflecting the effects of different geographic scales.

Further studies should also consider species- or trait-specific relationships, community composition, and impacts upon functional diversity, all of which are obscured in analyses based on taxonomic richness. In particular, beta and gamma diversity indices could be used to explore further how the spatial distribution of freshwater biodiversity can inform the management of ecosystems under stress (e.g., Alahuhta et al. 2017; Hill et al. 2021; Law et al. 2024). Importantly, our taxa span wide ranges of body size, dispersal potential, reproductive and trophic ecology. Future analyses could benefit from understanding how the impacts of connectivity and stress differentially affect species according to these traits and influence functional diversity.

Our datasets varied in size and spatial intensity/extent among the ecological responses (e.g., 130 1-km grid cells for molluscs, and 2265 cells for Odonates) with model fits varying accordingly (adjusted R^2 0.20–0.77). Dataset differences reflect differences in ease and popularity of recording among groups. Furthermore, the motivations for data collection and the degree of structuring in data collection differed among groups. For example, official data from monitoring ecological or conservation status were available for some responses (chlorophyll-*a* concentrations, macrophytes) and citizen science data for others. As we did not have complete coverage of Great Britain and we sought to capture broad-scale correlations, our models should not be used to make predictions for specific unstudied lakes, but instead to yield general insights into the relationships between our chosen responses and connectivity, stress, and their interactions.

Importantly, we note that the conceptual distinctions between the variables used in our analysis are not always clear, with some that could be viewed as indicators of both connectivity and stress (e.g., watersport visits in relation to mollusc richness). To investigate this, analyses of species composition could elucidate whether the species present in contrasting connectivity scenarios also vary in their resilience to stress (e.g., from invasive non-native species), thus exposing patterns that would be masked when using overall species richness as the biodiversity metric.

5 | Conclusions

We investigated the relationships between hydrological and human-mediated connectivity, human-induced land use stressors, and their interactions on indicators of water quality and biodiversity at a supra-regional scale. Using a data-driven modelling approach, we showed different relationships for different species groups, and that almost all ecological responses were affected by stressors or connectivity, or their interaction. These findings emphasise the need to consider species groups independently when considering the effects of connectivity on freshwater ecosystems, and the importance of considering waterbody connectivity when attempting to understand and manage the impacts of human-induced stress on water quality and biodiversity.

Our research found that broad features of lakes, climate, and catchments helped to explain ecological responses. This reflects the impact of landscape and climate on water quality and quantity, as captured by district-type variables such as river basin district, and hence on species distributions. Intensive land use was, as expected, a key source of ecological stress, but both hydrological and human connectivity were important in regulating the expression of ecological responses.

A key finding was that landscape-scale interactions between connectivity and human-induced stress were the norm across responses, although the forms of these interactions were often complex. We found some support for our Hypotheses that increased connectivity could change from a positive to a negative effect in the presence of high human-induced stress levels. However, the inverse pattern was also detected for some species groups implying that connectivity might offer a 'rescue effect' for some organisms in the face of stress. This probably reflects complexities introduced by modelling at the supra-regional scale, across different landscape types, and that biodiversity responses might not always be apparent through taxonomic richness (e.g., compared to functional richness, and measures of taxonomic and functional composition). Understanding the response of other biodiversity measures (such as beta or gamma diversity) to connectivity and stress will require modelling of these separately.

In summary, we found that the assessment of impacts of human-influenced land cover as a proxy for stressors should integrate the effects of various forms of connectivity. Equally, the complexities of landscape- and taxon group-specific effects should be recognised in evidence-led decision-making, with generalisations being treated with caution.

Acknowledgements

This research was funded by the NERC Highlight Topic Hydroscape: connectivity × stressor interactions in freshwater habitats (NE/N006437/1, https://hydroscapeblog.wordpress.com/). Laurence Carvalho also acknowledges support for writing from the FutureLakes project, funded by the European Union under Grant agreement ID 101156425. We thank our data providers (Aquatic Coleoptera Conservation Trust, Biological Records Centre, Conchological Society of Great Britain & Ireland, British Dragonfly Society, British Trust for Ornithology, Broads Authority, Buglife, Cumbria Wildlife Trust,

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

ENSIS, Environment Agency, Froglife, Glasgow City Council, Norfolk Biodiversity Information Service, Royal Society for the Protection of Birds, Joint Nature Conservation Committee, Scottish Environment Protection Agency, UK Centre for Ecology & Hydrology and UK Upland Waters Monitoring Network). Particular thanks are due to Stephen J Brooks (Natural History Museum), Stewart Clarke (National Trust), Garth Foster (Aquatic Coleoptera Conservation Trust), Ruth Hall (Natural England), Andrea Kelly (Broads Authority), Geoff Phillips (University of Stirling), Jo-Anne Pitt (Environment Agency) and Pam Taylor (British Dragonfly Society). The authors would like to thank the Editors and two anonymous reviewers for thoughtful comments that greatly helped to improve the article.

Disclosure

This work forms part of the Hydroscape project (https://hydroscapeblog.wordpress.com/about/), which aims to determine how connectivity and human-induced stressors interact to influence freshwater biodiversity and ecosystem function. Our team comprises statisticians, data scientists and ecologists, with expertise across freshwater ecology, plant ecology and terrestrial ecology.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets and code used for the analyses in this paper are available on Dryad here, under the CC0 licence: https://doi.org/10.5061/dryad.bcc2fqzn8.

References

Alahuhta, J., S. Kosten, M. Akasaka, et al. 2017. "Global Variation in the Beta Diversity of Lake Macrophytes Is Driven by Environmental Heterogeneity Rather Than Latitude." *Journal of Biogeography* 44, no. 8: 1758–1769. https://doi.org/10.1111/jbi.12978.

Albert, J. S., G. Destouni, S. M. Duke-Sylvester, et al. 2021. "Scientists' Warning to Humanity on the Freshwater Biodiversity Crisis." *Ambio* 50, no. 1: 85–94. https://doi.org/10.1007/s13280-020-01318-8.

Almeida, B. d. A., A. J. Green, E. Sebastián-González, and L. Dos Anjos. 2018. "Comparing Species Richness, Functional Diversity and Functional Composition of Waterbird Communities Along Environmental Gradients in the Neotropics." *PLoS One* 13, no. 7: e0200959. https://doi.org/10.1371/journal.pone.0200959.

Anderson, L. G., S. Rocliffe, N. R. Haddaway, and A. M. Dunn. 2015. "The Role of Tourism and Recreation in the Spread of Non-Native Species: A Systematic Review and Meta-Analysis." *PLoS One* 10, no. 10: e0140833. https://doi.org/10.1371/journal.pone.0140833.

Arlinghaus, R., C. Riepe, S. Theis, T. Pagel, and M. Fujitani. 2022. "Dysfunctional Information Feedbacks Cause the Emergence of Management Panaceas in Social-Ecological Systems: The Case of Fish Stocking in Inland Recreational Fisheries." *Journal of Outdoor Recreation and Tourism* 38: 100475. https://doi.org/10.1016/j.jort.2021.100475.

Atkinson, S., M. Bruen, J. N. Turner, et al. 2018. "The Value of a Desk Study for Building a National River Obstacle Inventory." *River Research and Applications* 34, no. 8: 1085–1094. https://doi.org/10.1002/rra.3338.

Beecher, H. A., E. R. Dott, and R. F. Fernau. 1988. "Fish Species Richness and Stream Order in Washington State Streams." *Environmental Biology of Fishes* 22: 193–209. https://doi.org/10.1007/BF00005381.

Biggs, J., P. Williams, M. Whitfield, et al. 2007. "The Freshwater Biota of British Agricultural Landscapes and Their Sensitivity to Pesticides." *Agriculture, Ecosystems & Environment* 122, no. 2: 137–148. https://doi.org/10.1016/j.agee.2006.11.013.

Bilton, D. T., J. R. Freeland, and B. Okamura. 2001. "Dispersal in Freshwater Invertebrates." *Annual Review of Ecology and Systematics* 32: 159–181. https://doi.org/10.1146/annurev.ecolsys.32.081501.114016.

Birk, S., D. Chapman, L. Carvalho, et al. 2020. "Impacts of Multiple Stressors on Freshwater Biota Across Spatial Scales and Ecosystems." *Nature Ecology & Evolution* 4, no. 8: 1060–1068. https://doi.org/10.1038/s41559-020-1216-4.

Blair, R. B. 1996. "Land Use and Avian Species Diversity Along an Urban Gradient." *Ecological Applications* 6, no. 2: 506–519. https://doi.org/10.2307/2269387.

Brainard, A. S., V. A. Luzadis, and K. L. Schulz. 2021. "Drivers of Species Richness, Biomass, and Dominance of Invasive Macrophytes in Temperate Lakes." *Biological Invasions* 23, no. 4: 1069–1085. https://doi.org/10.1007/s10530-020-02418-y.

Carlsson, R. 2001. "Species-Area Relationships, Water Chemistry and Species Turnover of Freshwater Snails on the Åland Islands, Southwestern Finland." *Journal of Molluscan Studies* 67, no. 1: 17–26. https://doi.org/10.1093/mollus/67.1.17.

Carvalho, L., C. A. Miller, E. M. Scott, G. A. Codd, P. S. Davies, and A. N. Tyler. 2011. "Cyanobacterial Blooms: Statistical Models Describing Risk Factors for National-Scale Lake Assessment and Lake Management." *Science of the Total Environment* 409: 5353–5358. https://doi.org/10.1016/j.scitotenv.2011.09.030.

Chapman, D. S., I. D. M. Gunn, H. E. K. Pringle, et al. 2020. "Invasion of Freshwater Ecosystems Is Promoted by Network Connectivity to Hotspots of Human Activity." *Global Ecology and Biogeography* 29, no. 4: 645–655. https://doi.org/10.1111/geb.13051.

Chovanec, A., and J. Waringer. 2001. "Ecological Integrity of River–Floodplain Systems—Assessment by Dragonfly Surveys (Insecta: Odonata)." *Regulated Rivers: Research & Management* 17, no. 4–5: 493–507. https://doi.org/10.1002/rrr.664.

Collen, B., F. Whitton, E. E. Dyer, et al. 2014. "Global Patterns of Freshwater Species Diversity, Threat and Endemism." *Global Ecology and Biogeography* 23, no. 1: 40–51. https://doi.org/10.1111/geb.12096.

Craig, L. S., J. D. Olden, A. H. Arthington, et al. 2017. "Meeting the Challenge of Interacting Threats in Freshwater Ecosystems: A Call to Scientists and Managers." *Elementa: Science of the Anthropocene* 5: 72. https://doi.org/10.1525/elementa.256.

Darwall, W., V. Bremerich, A. De Wever, et al. 2018. "The Alliance for Freshwater Life: A Global Call to Unite Efforts for Freshwater Biodiversity Science and Conservation: The Alliance for Freshwater Life: A Global Call to Unite Efforts for Freshwater Biodiversity Science and Conservation." *Aquatic Conservation: Marine and Freshwater Ecosystems* 28, no. 4: 1015–1022. https://doi.org/10.1002/aqc.2958.

Davidson, T. A., C. D. Sayer, E. Jeppesen, et al. 2023. "Bimodality and Alternative Equilibria Do Not Help Explain Long-Term Patterns in Shallow Lake Chlorophyll-A." *Nature Communications* 14: 398. https://doi.org/10.1038/s41467-023-36043-9.

Dillon, P. J., and F. H. Rigler. 1974. "The Phosphorus-Chlorophyll Relationship in Lakes." *Limnology and Oceanography* 19, no. 5: 767–773. https://doi.org/10.4319/lo.1974.19.5.0767.

Dudgeon, D. 2019. "Multiple Threats Imperil Freshwater Biodiversity in the Anthropocene." *Current Biology* 29, no. 19: R960–R967. https://doi.org/10.1016/j.cub.2019.08.002.

Duncan, R. P., and B. J. Kefford. 2021. "Interactions in Statistical Models: Three Things to Know." *Methods in Ecology and Evolution* 12, no. 12: 2287–2297. https://doi.org/10.1111/2041-210X.13714.

Eby, L., W. Roach, L. Crowder, and J. Stanford. 2006. "Effects of Stocking-Up Freshwater Food Webs." *Trends in Ecology & Evolution* 21, no. 10: 576–584. https://doi.org/10.1016/j.tree.2006.06.016.

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D. P. Peterson. 2009. "Invasion Versus Isolation: Trade-Offs in Managing Native Salmonids With Barriers to Upstream Movement." *Conservation Biology* 23, no. 4: 859–870. https://doi.org/10.1111/j.1523-1739.2008.01159.x.

Fergus, C. E., J.-F. Lapierre, S. K. Oliver, et al. 2017. "The Freshwater Landscape: Lake, Wetland, and Stream Abundance and Connectivity at Macroscales." *Ecosphere* 8, no. 8: e01911. https://doi.org/10.1002/ecs2.1911.

Figuerola, J., and A. J. Green. 2002. "Dispersal of Aquatic Organisms by Waterbirds: A Review of Past Research and Priorities for Future Studies." *Freshwater Biology* 47: 483–494. https://doi.org/10.1046/j.1365-2427.2002.00829.x.

Gál, B., I. Szivák, J. Heino, and D. Schmera. 2019. "The Effect of Urbanization on Freshwater Macroinvertebrates—Knowledge Gaps and Future Research Directions." *Ecological Indicators* 104: 357–364. https://doi.org/10.1016/j.ecolind.2019.05.012.

Galbraith, J. A., J. R. Beggs, D. N. Jones, and M. C. Stanley. 2015. "Supplementary Feeding Restructures Urban Bird Communities." *Proceedings of the National Academy of Sciences* 112, no. 20: E2648–E2657. https://doi.org/10.1073/pnas.1501489112.

Genuer, R., J.-M. Poggi, and C. Tuleau-Malot. 2010. "Variable Selection Using Random Forests." *Pattern Recognition Letters* 31, no. 14: 2225–2236. https://doi.org/10.1016/j.patrec.2010.03.014.

Gimenez, M., S. Villéger, G. Grenouillet, and J. Cucherousset. 2023. "Stocking Practices Shape the Taxonomic and Functional Diversity of Fish Communities in Gravel Pit Lakes." *Fisheries Management and Ecology* 30, no. 6: 603–614. https://doi.org/10.1111/fme.12621.

Harris, A. T., D. A. Woolnough, and D. T. Zanatta. 2011. "Insular Lake Island Biogeography: Using Lake Metrics to Predict Diversity in Littoral Zone Mollusk Communities." *Journal of the North American Benthological Society* 30, no. 4: 997–1008. https://doi.org/10.1899/11-020.1.

Harrison, P. J., Y. Yuan, S. T. Buckland, et al. 2016. "Quantifying Turnover in Biodiversity of British Breeding Birds." *Journal of Applied Ecology* 53, no. 2: 469–478. https://doi.org/10.1111/1365-2664.12539.

Heino, J. 2011. "A Macroecological Perspective of Diversity Patterns in the Freshwater Realm: Diversity in Freshwater Systems." *Freshwater Biology* 56, no. 9: 1703–1722. https://doi.org/10.1111/j.1365-2427.2011.02610.x.

Heino, J., J. Alahuhta, L. M. Bini, et al. 2021. "Lakes in the Era of Global Change: Moving Beyond Single-Lake Thinking in Maintaining Biodiversity and Ecosystem Services." *Biological Reviews* 96, no. 1: 89–106. https://doi.org/10.1111/brv.12647.

Heino, J., R. Virkkala, and H. Toivonen. 2009. "Climate Change and Freshwater Biodiversity: Detected Patterns, Future Trends and Adaptations in Northern Regions." *Biological Reviews* 84, no. 1: 39–54. https://doi.org/10.1111/j.1469-185X.2008.00060.x.

Hill, M. J., H. M. Greaves, C. D. Sayer, et al. 2021. "Pond Ecology and Conservation: Research Priorities and Knowledge Gaps." *Ecosphere* 12, no. 12: e03853. https://doi.org/10.1002/ecs2.3853.

Hillebrand, H. 2004. "On the Generality of the Latitudinal Diversity Gradient." *American Naturalist* 163, no. 2: 192–211. https://doi.org/10.1086/381004.

IPBES. 2019. "Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services." *Zenodo*. https://doi.org/10.5281/ZENODO.3553458.

Jackson, M. C., C. J. G. Loewen, R. D. Vinebrooke, and C. T. Chimimba. 2016. "Net Effects of Multiple Stressors in Freshwater Ecosystems: A Meta-Analysis." *Global Change Biology* 22, no. 1: 180–189. https://doi.org/10.1111/gcb.13028.

Jeppesen, E., J. P. Jensen, M. Søndergaard, T. Lauridsen, L. J. Pedersen, and L. Jensen. 1997. "Top-Down Control in Freshwater Lakes: The Role of Nutrient State, Submerged Macrophytes and Water Depth." *Hydrobiologia* 342: 151–164. https://doi.org/10.1023/A:1017046130329.

Jetz, W., J. M. McPherson, and R. P. Guralnick. 2012. "Integrating Biodiversity Distribution Knowledge: Toward a Global Map of Life." *Trends in Ecology & Evolution* 27, no. 3: 151–159. https://doi.org/10.1016/j.tree.2011.09.007.

Juračka, P. J., J. Dobiáš, D. S. Boukal, et al. 2019. "Spatial Context Strongly Affects Community Composition of Both Passively and Actively Dispersing Pool Invertebrates in a Highly Heterogeneous Landscape." *Freshwater Biology* 64, no. 12: 2093–2106. https://doi.org/10.1111/fwb.13398.

Law, A., A. Baker, C. Sayer, et al. 2024. "Repeatable Patterns in the Distribution of Freshwater Biodiversity Indicators Across Contrasting Landscapes." *Landscape Ecology* 39: 195. https://doi.org/10.1007/s10980-024-01992-z.

Law, A., A. Baker, C. Sayer, et al. 2019. "The Effectiveness of Aquatic Plants as Surrogates for Wider Biodiversity in Standing Fresh Waters." *Freshwater Biology* 64, no. 9: 1664–1675. https://doi.org/10.1111/fwb.13369.

Lawton, J., V. Brown, C. Elphick, et al. 2010. "Making Space for Nature: A Review of England's Wildlife Sites and Ecological Network. Report to Defra." https://webarchive.nationalarchives.gov.uk/ukgwa/20130402154501mp_/http://archive.defra.gov.uk/environment/biodiversity/documents/201009space-for-nature.pdf.

Markovic, D., S. Carrizo, J. Freyhof, et al. 2014. "Europe's Freshwater Biodiversity Under Climate Change: Distribution Shifts and Conservation Needs." *Diversity and Distributions* 20, no. 9: 1097–1107. https://doi.org/10.1111/ddi.12232.

Moss, B., M. Beklioglu, L. Carvalho, S. Kilinc, S. McGowan, and D. Stephen. 1997. "Vertically-Challenged Limnology: Contrasts Between Deep and Shallow Lakes." *Hydrobiologia* 342: 257–267. https://doi.org/10.1023/A:1017059928028.

Moss, B., S. McGowan, and L. Carvalho. 1994. "Determination of Phytoplankton Crops by Top-Down and Bottom-Up Mechanisms in a Group of English Lakes, the West Midland Meres." *Limnology and Oceanography* 39, no. 5: 1020. https://doi.org/10.4319/lo.1994.39.5.1020.

Nunn, A. D., R. F. Ainsworth, S. Walton, et al. 2023. "Extinction Risks and Threats Facing the Freshwater Fishes of Britain." *Aquatic Conservation: Marine and Freshwater Ecosystems* 33, no. 12: 1460–1476. https://doi.org/10.1002/aqc.4014.

O'Hare, M. T., I. D. M. Gunn, D. S. Chapman, B. J. Dudley, and B. V. Purse. 2012. "Impacts of Space, Local Environment and Habitat Connectivity on Macrophyte Communities in Conservation Lakes." *Diversity and Distributions* 18, no. 6: 603–614. https://doi.org/10.1111/j.1472-4642.2011.00860.x.

Olden, J. D., L. Comte, and X. Giam. 2018. "The Homogocene: A Research Prospectus for the Study of Biotic Homogenisation." *NeoBiota* 37: 23–36. https://doi.org/10.3897/neobiota.37.22552.

Ormerod, S. J., M. Dobson, A. G. Hildrew, and C. R. Townsend. 2010. "Multiple Stressors in Freshwater Ecosystems." *Freshwater Biology* 55, no. s1: 1–4. https://doi.org/10.1111/j.1365-2427.2009.02395.x.

Phillips, G., O. P. Pietiläinen, L. Carvalho, A. Solimini, A. Lyche Solheim, and A. C. Cardoso. 2008. "Chlorophyll–Nutrient Relationships of Different Lake Types Using a Large European Dataset." *Aquatic Ecology* 42: 213–226. https://doi.org/10.1007/s10452-008-9180-0.

Reid, A. J., A. K. Carlson, I. F. Creed, et al. 2019. "Emerging Threats and Persistent Conservation Challenges for Freshwater Biodiversity." *Biological Reviews* 94, no. 3: 849–873. https://doi.org/10.1111/brv.12480.

Revenga, C., I. Campbell, R. Abell, P. De Villiers, and M. Bryer. 2005. "Prospects for Monitoring Freshwater Ecosystems Towards the 2010 Targets." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 360, no. 1454: 397–413. https://doi.org/10.1098/rstb.2004.1595.

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Richardson, J., H. Feuchtmayr, C. Miller, P. Hunter, S. C. Maberly, and L. Carvalho. 2019. "Response of Cyanobacteria and Phytoplankton Abundance to Warming, Extreme Rainfall Events and Nutrient Enrichment." *Global Change Biology* 25, no. 10: 3365–3380. https://doi.org/10.1111/gcb.14693.

Salgado, J., C. D. Sayer, S. J. Brooks, et al. 2018. "Eutrophication Homogenizes Shallow Lake Macrophyte Assemblages Over Space and Time." *Ecosphere* 9, no. 9: e02406. https://doi.org/10.1002/ecs2.2406.

Sandin, L., and R. K. Johnson. 2000. "Ecoregions and Benthic Macroinvertebrate Assemblages of Swedish Streams." *Journal of the North American Benthological Society* 19, no. 3: 462–474. https://doi.org/10.2307/1468107.

Santoul, F., A. Soulard, J. Figuerola, R. Céréghino, and S. Mastrorillo. 2004. "Environmental Factors Influencing Local Fish Species Richness and Differences Between Hydroregions in South-Western France." *International Review of Hydrobiology* 89, no. 1: 79–87. https://doi.org/10.1002/iroh.200310704.

Scheffer, M., and E. H. Van Nes. 2007. "Shallow Lakes Theory Revisited: Various Alternative Regimes Driven by Climate, Nutrients, Depth and Lake Size." *Hydrobiologia* 584, no. 1: 455–466. https://doi.org/10.1007/s10750-007-0616-7.

Shurin, J. B., K. Cotteie, and H. Hillebrand. 2009. "Spatial Autocorrelation and Dispersal Limitation in Freshwater Organisms." *Oecologia* 159: 151–159. https://doi.org/10.1007/s00442-008-1174-z.

Smits, A. J. M., R. van Ruremonde, and G. van der Velde. 1989. "Seed Dispersal of Three Nymphaeid Macrophytes." *Aquatic Botany* 35: 167–180. https://doi.org/10.1016/0304-3770(89)90103-4.

Soranno, P. A., L. C. Bacon, M. Beauchene, et al. 2017. "LAGOS-NE: A Multi-Scaled Geospatial and Temporal Database of Lake Ecological Context and Water Quality for Thousands of US Lakes." *GigaScience* 6, no. 12: gix101. https://doi.org/10.1093/gigascience/gix101.

Stendera, S., R. Adrian, N. Bonada, et al. 2012. "Drivers and Stressors of Freshwater Biodiversity Patterns Across Different Ecosystems and Scales: A Review." *Hydrobiologia* 696, no. 1: 1–28. https://doi.org/10.1007/s10750-012-1183-0.

Stockwell, J. D., J. P. Doubek, R. Adrian, et al. 2020. "Storm Impacts on Phytoplankton Community Dynamics in Lakes." *Global Change Biology* 26, no. 5: 2756–2784. https://doi.org/10.1111/gcb.15033.

Strecker, A. L., and J. T. Brittain. 2017. "Increased Habitat Connectivity Homogenizes Freshwater Communities: Historical and Landscape Perspectives." *Journal of Applied Ecology* 54, no. 5: 1343–1352. https://doi.org/10.1111/1365-2664.12882.

Strobl, C., A.-L. Boulesteix, T. Kneib, T. Augustin, and A. Zeileis. 2008. "Conditional Variable Importance for Random Forests." *BMC Bioinformatics* 9, no. 1: 307. https://doi.org/10.1186/1471-2105-9-307.

Strobl, C., A.-L. Boulesteix, A. Zeileis, and T. Hothorn. 2007. "Bias in Random Forest Variable Importance Measures: Illustrations, Sources and a Solution." *BMC Bioinformatics* 8, no. 1: 25. https://doi.org/10.1186/1471-2105-8-25.

Strobl, C., T. Hothorn, and A. Zeileis. 2009. "Party On!" *R Journal* 1, no. 2: 14. https://doi.org/10.32614/RJ-2009-013.

Tamayo, M., and J. D. Olden. 2014. "Forecasting the Vulnerability of Lakes to Aquatic Plant Invasions." *Invasive Plant Science and Management* 7, no. 1: 32–45. https://doi.org/10.1614/IPSM-D-13-00036.1.

United Nations Convention on Biological Diversity. 2022. "Kunming-Montreal Global Biodiversity Framework, 18 Dec. 2022, CBD/COP/15/L.25." https://www.cbd.int/doc/c/e6d3/cd1d/daf663719a03902a9b116c34/cop-15-l-25-en.pdf.

Wood, S. N. 2017. *Generalized Additive Models: An Introduction With R*. 2nd ed. Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

14668238, 2025, 6, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70069 by Alan Law - University Of Stirling Sonia W , Wiley Online Library on [12/06/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License