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Connectivity and zebra mussel invasion offer short-term buffering of eutrophication impacts on floodplain lake landscape biodiversity

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Abstract

Aim: To investigate if connectivity and zebra mussel (*Dreissena polymorpha*) occurrence can mitigate effects of eutrophication in a lowland lake landscape.

Location: Upper Lough Erne, Northern Ireland, UK.

Methods: Data on environment, macrophytes and invertebrates were assembled for three basins of a large central lake and its satellite floodplain lakes via field surveys and palaeolimnological analyses. Space–time interaction analyses of palaeoecological data were compared pre-1950 and post-1950. Multivariate analyses examined how connectivity, environment and zebra mussels influenced contemporary lake communities, and explain their divergence from historical communities in the past.

Results: Pre-1950, we found high community variation across sites and low within-lake variation in macrophytes, but progressive eutrophication accentuated within-lake community variation after 1950. Partitioning analysis showed larger effects of connectivity than nutrient enrichment on contemporary macrophyte composition, while local effects structured invertebrate communities. Three clusters of lakes were revealed according to variation in macrophyte composition, isolation from the central lake and nutrient enrichment: *Group 1*– the central lake and six nearby lakes were meso-eutrophic (TP = 66.7 ± 47.6 μg/L; TN = 0.79 ± 0.41 mg/L) and had the highest zebra mussel abundances and organismal biodiversity; *Group 2*– Eight eutrophic (TP = 112±36.6 μg/L; TN = 1.25 ± 0.5 mg/L) and connected lakes; *Group 3*– Seven isolated and hypertrophic (TP = 163.2 ± 101.5 μg/L; TN = 1.55 ± 0.3 mg/L) lakes. Pre-1950 palaeolimnological data for macrophytes and invertebrates for 5 lakes and a basin in the central lake most resembled extant lake communities of *Group 1*. However, palaeo-records revealed that macrophytes and invertebrates subsequently converged towards those of *Groups 2* and *3*.

Main conclusions: Our study reveals that the central "mother" lake acts as a hub for preserving biodiversity via shared hydrological connectivity with satellite lakes and high zebra mussel abundances. These may buffer the impoverishing effects

of eutrophication and sustain unexpectedly high biodiversity in the short term. Such protective buffering, however, cannot be relied upon indefinitely to conserve biodiversity.

KEYWORDS
asymmetric eigenvector maps, dispersal, ecosystem resilience, invasive species, invertebrates, macrophytes, palaeoecology, space–time interactions

1 | INTRODUCTION

Floodplain lake systems are characterized by variable environmental and fluvial dynamics that create complex habitats and connectivity gradients (Ward, Tockner, & Schiemer, 1999). Such systems also harbour unique biota, including rare and highly specialized species of high conservation value (Amoros & Bornette, 2002), and provide important ecosystem services, such as flood mitigation and nutrient retention (Schindler et al., 2014). However, as with many other freshwater systems, the ecological integrity of floodplain lake landscapes has been compromised over the last two centuries by anthropogenic degradation (Paillex, Dolédec, Castella, & Mérigoux, 2009). The most pervasive causes of degradation include increasing demands for flow regulation and drainage schemes, invasion and negative impacts from exotic species and eutrophication (Paillex et al., 2009).

The influences of eutrophication and species invasions on aquatic communities and ecosystem resilience are relatively well known (Heino, Virkkala, & Toivonen, 2009; Rahel & Olden, 2008). However, temporal interactions between these factors, and how these may be mediated by hydrological connectivity, have received less attention. This is due to inherent difficulties in measuring joint effects and to complications associated with these processes. For instance, if local populations receive immigration subsidies from associated lakes, connectivity may be beneficial for promoting resilience and recovery through source–sink dynamics (Leibold & Norberg, 2004). In addition, channels that connect lakes may offer spatial and temporal refugia for species (Strecker & Brittain, 2017). Communities may also vary in response to connectivity and environmental variation depending on their position and configuration within the landscape (O'Hare, Gunn, Chapman, Dudley, & Purse, 2012). For example, downstream aquatic communities may benefit from connectivity subsidies, while environmental factors may exert the greatest influence on community structure in more isolated headwaters (Brown & Swan, 2010). However, increased habitat connectivity may also disrupt ecosystem resilience if lake communities become homogenized following hydrological modifications (Grant et al., 2012; Strecker & Brittain, 2017) or through the introduction of invasive species (Rahel & Olden, 2008). Thus, understanding how processes such as eutrophication and species invasions interact with connectivity to influence aquatic communities at the landscape scale, and how such interactions change over time (decades to centuries), is a key issue for managing freshwater systems. A long-term perspective is of particular value as both eutrophication and invasive species impacts take time to be fully manifested (decades–centuries) and hence are typically poorly captured by short-term (typically 2–5 years) monitoring studies.

The aim of this study was to examine the combined and long-term influences of eutrophication, hydrological connectivity and invasion by zebra mussels (*Dreissena polymorpha* Pallas) on submerged and floating-leaved macrophyte (charophytes, gymnosperms and angiosperms) and invertebrate (molluscs, chironomids, bryozoans and daphnids) communities. We focused on a lowland lake landscape exhibiting a gradient of nutrient enrichment and hydrological connectivity. The system comprises a large central "mother" lake with diverse macrophyte communities and numerous (n > 40) satellite lakes that vary in terms of eutrophication impacts and connectivity to the central lake. Our three main objectives were to: (a) examine long-term changes in macrophyte and invertebrate communities at within- and between-lake scales using palaeolimnological data; (b) test the contemporary impacts of eutrophication, hydrological connectivity and invasive zebra mussel abundance on lake communities using selected contemporary chemical variables and lake connectivity predictors; and (c) explore the similarities between present-day and historical biological communities. Despite eutrophic conditions, the system supports relatively high macrophyte diversity. This led us to hypothesise that connectivity and invasion by zebra mussels have delayed biological degradation that would be expected to arise from nutrient enrichment. This delay is likely to be explained by both connectivity-driven subsidies of organismal propagules and the filter-feeding activities of zebra mussels that more than offset the adverse effects of connectivity-driven subsidies of nutrients. These processes improve conditions for macrophytes and associated invertebrates by accelerating colonization and reducing turbidity. Zebra mussels can also affect nutrient stoichiometry and phytoplankton composition with important positive consequences for macrophytes and water column turbidity (Zhu, Fitzgerald, Mayer, Rudstam, & Mills, 2006). To our knowledge this represents the first study to explicitly combine present-day and historical data to test how eutrophication, biological invasion and hydrological connectivity jointly influence biodiversity and ecosystem resilience in space and time.

2 | METHODS

2.1 | Study area

The Upper Lough Erne (ULE) system, located in Co. Fermanagh, Northern Ireland is composed of a large (surface area 34.5 km^2),

generally shallow (mean water depth 2.3 m) central lake, fed by the River Erne, which is linked, by various channels and tributaries, to a network of small (<40 ha), shallow (<5 m) satellite lakes (Figure 1). The central lake is situated in a hilly agricultural landscape and is divided into four main basins: Belleisle, Trannish, Crom and Galloon (Figure 1). The central lake is designated a RAMSAR site (an internationally important site under the Intergovernmental Convention on Wetlands; Ramsar, Iran, 1971) and, along with its satellite lakes, as a Special Area of Conservation (SAC) under the EC Habitats Directive. Since the 1950s, the system has been increasingly affected by eutrophication (Battarbee, 1986; Zhou, Gibson, & Foy, 2000) and currently has high annual mean concentrations of total phosphorus (TP = 29–383 μg/L) and total nitrogen (TN = 0.22–2.25 mg/L). Although the system has been subjected to two drainage improvement schemes (in 1890 and 1946), it remains prone to major floods that increase connectivity with most surrounding satellite lakes (Figure 1). The zebra mussel has recently (early 1990s) invaded the system, resulting in strong reductions in phytoplankton biomass (Minchin, Maguire, & Rosell, 2003).

2.2 | Long-term changes in lake communities

To characterize temporal and spatial changes in macrophyte and invertebrate community composition across the landscape, we undertook palaeolimnological studies of five satellite lakes (Castle, Cornabrass, Killymackan, Gole and Head) and the Trannish area of the central lake (Figure 1). A single sediment core was collected in 2008 from the central lake (ULET2) using an adapted Livingston coring system (7.4 cm diameter; Livingstone, 1955). For the remaining lakes, single sediment cores were collected using a wide-bore (14 cm diameter) "Big-Ben" piston corer (Patmore et al., 2014) during 2008–2009, with lake core codes as: Castle (NCAS3), Cornabrass (CBRAS1), Gole (GOLE1), Killymackan (KILL2) and Head (HEAD1). Cores were taken at water depths of 90–180 cm and extruded at 1-cm intervals in the field. Core chronologies were obtained following Salgado, Sayer, Brooks, Davidson, Goldsmith, et al. (2018), which involved the use of radionuclide measurements of ^{210}Pb (half-life 22.3 years) and ^{137}Cs and ^{241}Am under the Constant Rate of Supply model (CRS; Appleby & Oldfield, 1978; Appleby et al., 1986).

Selected sediment slices (1-cm thickness) were analysed for cores CBRAS1 (n = 16 slices), GOLE1 (n = 8), HEAD1 (n = 20), KILL2 (n = 14), NCAS3 (n = 13) and ULET2 (n = 12), respectively, according to intrinsic sedimentation rates within each core. We analysed all 6 cores for plant macrofossils and 5 cores (CBRAS1, KILL2, ULET1, HEAD1 and NCAS3) for invertebrate macrofossils following the methods of Birks (2007) and Salgado, Sayer, Brooks, Davidson, and Okamura (2018). All macrofossil data were standardized as the number of fossils per 100 cm^3 and macrophyte composition was estimated using a range of vegetative and reproductive macro-remains (Birks, 2007). The phylactolaemate bryozoans, *Cristatella mucedo* Cuvier and *Plumatella* spp., were quantified by enumerating statoblasts

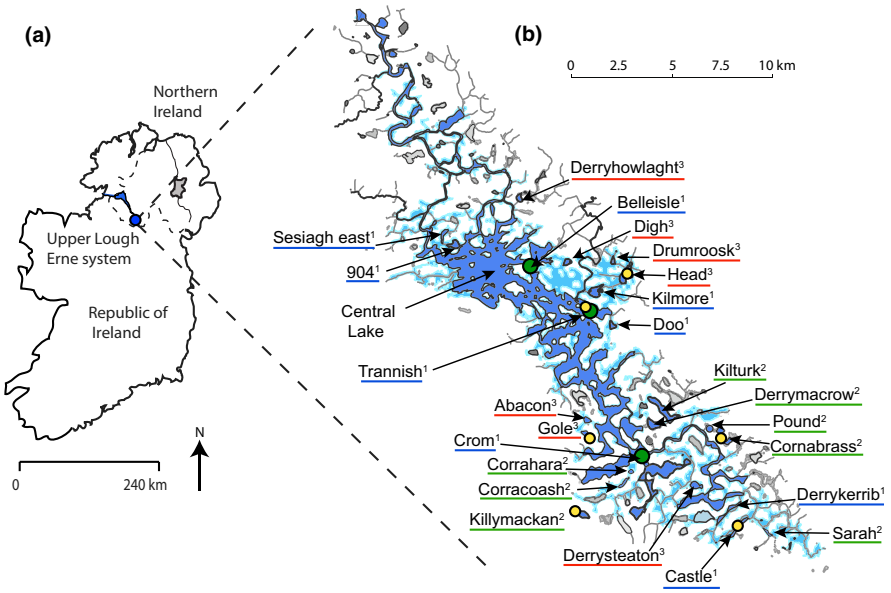

FIGURE 1 (a) Map showing the location of the Upper Lough Erne (ULE) system; (b) map of the ULE system showing the study sites. Lakes clustered into *Groups 1*, *2* and *3* (indicated in superscript) according to our analyses using macrophyte community composition and selected hydrological connectivity predictors and environmental parameters. *Group 1* (blue underline) contains the meso-eutrophic (TP = 66.7 ± 47.6 μg/L; TN = 0.79 ± 0.41 mg/L) central lake (the three study basins Crom, Trannish and Belleisle are indicated by a green circle) and satellite lakes Castle, Derrykerrib, Doo, Kilmore, 904 and Sessiagh East.; *Group 2* (green underline) contains the eutrophic (TP = 112±36.6 μg/L; TN = 1.25 ± 0.5 mg/L) satellite lakes Sarah, Cornabrass, Pound, Kilturk, Derrymacrow, Killymackan, Corraharra and Corracoash.; *Group 3* (red underline) contains the hypertrophic (TP = 163.2 ± 101.5 μg/L; TN = 1.55 ± 0.3 mg/L) satellite lakes Derrysteaton; Abacon, Gole, Head, Drumroosk, Digh and Derryhowlaght. A yellow circle indicates the coring sites. Flooding areas are shown in pale blue. Water layers obtained from Ordnance Survey Northern Ireland (OSNI) https://www.nidirect.gov.uk/services/osni-online-map-shop and reproduced with the permission of Land & Property Services © Crown Copyright 2018

TABLE 1 Effects of space (S), time (T) and their interaction (S-T) on the variation of macrophyte and invertebrate macrofossils composition in sediment cores from the central lake and the satellite lakes Castle, Cornabrass, Killymackan, Gole and Head revealed by S-T analysis. S-T analyses were run using "Model 5" of Legendre et al. (2010)

	Factor	R^2	*F*	*p*
Macrophytes (pre-1950)				
Model 5	S-T	0.18	1.37	0.11
Model 2	Space	0.41	3.42	0.001***
	Time	0.11	1.18	0.21
Macrophytes (post-1950)				
Model 5	S-T	0.17	1.46	0.03*
Model 6a	Space	0.51	0.96	0.59
Model 6b	Time	0.41	2.57	0.001***
Invertebrates (pre-1950)				
	S-T	0.13	1.55	0.03*
Model 6a	Space	0.47	1.16	0.06 (.)
Model 6b	Time	0.38	2.53	0.001***
Invertebrates (pre-1950)				
Model 5	S-T	0.10	1.69	0.01**
Model 6a	Space	0.43	0.99	0.50
Model 6b	Time	0.33	3.36	0.001***

Note: Depending on the outcome, we tested the main spatial and temporal factors using two different strategies: (i) if the interaction was significant, a nested model was used to assess whether a separate spatial (model 6a) and/or separate temporal structure (model 6b) existed; and (ii) if the S-T interaction was not significant, one cannot conclude that changes have occurred in the spatial or temporal structure of the lake communities, thus a test for common spatial and/or common temporal structures were run using Helmert contrasts "Model 2." S-T analyses were assessed over two independent time blocks that correspond to a pre-eutrophication period (pre-1950) and an eutrophication period (post-1950).
*$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$.

(whole and half valves) and the ctenostome bryozoan, *Paludicella articulata* Ehrenberg, by counting the highly distinct fragments of branching colonies. Daphnids (largely *Daphnia* spp. and *Ceriodaphnia* spp.) were quantified by counting ephippial-resting stages. Molluscs (*Bithynia* spp., other gastropods and glochidium larvae of unionid bivalves) were quantified by counting whole shells, shell fragments and glochidia. Chironomids were quantified by counting larval head capsules by standard methods (Brooks, Heiri, & Langdon, 2007).

To make realistic comparisons between macrophyte taxon abundances and to account for the problem of different types of plant remains (e.g., leaf vs. seed fossils) produced by different species, we adopted a similar approach to Salgado, Sayer, Brooks, Davidson, and Okamura (2018) and transformed the plant macrofossil data into a 0–5 abundance scale, where 0 is absent and 5 is highly abundant. In order to compensate between plant structures and production rates, we rescaled the data for each taxon as a proportion of the maximum by assuming 100% for the highest taxon abundance in each core. Percentage frequencies were then classed as follows: 5 (100%–80% abundance frequency); 4 (79%–60%); 3 (59%–40%); 2 (39%–20%); 1 (19%–1%); 0 (0%).

2.3 | Contemporary consequences of eutrophication, connectivity and invasion by *D. polymorpha*

To illustrate how eutrophication, zebra mussels and hydrological connectivity influence contemporary lake dynamics we selected 21 satellite lakes and three basins within the central lake (Belleisle, Trannish and Crom) across a gradient of eutrophication and hydrological connectivity (Figure 1). Macrophyte (submerged and floating plants) occurrences and environmental data for each site were obtained from a site condition assessment of standing water features in the ULE system undertaken for the Northern Ireland Environmental Agency (NIEA) during the summers of 2006–2007 (Goldsmith et al., 2008). Three specific nutrient enrichment indicators (chlorophyll-a, TN and TP as concentrations) were measured along with water colour, secchi depth and conductivity. The NIEA provided additional water chemistry data for the study basins in the central lake. Details of water chemistry sampling and laboratory protocols are presented in Appendix S1.

Macrophyte data were collected using the standard site condition monitoring protocols of the Joint Nature Conservation Committee (JNCC, 2005). Plants were recorded from different sectors of a lake along a 100 m wader-depth shoreline transect by sampling at water depths of 0.25, 0.50, 0.75 and >0.75 m at 20 m intervals along the transect. Macrophytes growing at depths >0.75 m were surveyed at roughly 5 m intervals on a 100 m boat transect starting at the midpoint of each shoreline transect and running towards the centre of the lake. At each macrophyte sampling point, species occurring within a $1m^2$ area were recorded with the assistance of a bathyscope and double-headed rake. The JNCC method has been shown to effectively characterize macrophyte communities in small lakes (<50 ha) by sampling two-three sectors (Gunn et al., 2010). Accordingly, we surveyed between two and three sectors per satellite lake (see Table 1 for details). Exceptions were made for lakes Drumroosk, Corraharra and Sarah (whose small sizes [<2 ha] precluded surveying of more than one sector) and for lake 904 for which only one sector was recorded (Figure 1). Due to the larger size (>100 ha) of each basin in the central lake, we surveyed eight sectors per basin. Recorded macrophyte data at each site were then expressed according to their frequency of occurrence (i.e., [number of observations/total number of sampling points] × 100; Goldsmith et al., 2008). To assess the contribution of macrophytes to contemporary invertebrate dynamics, we calculated a lake plant coverage index as: ([total number of sampling points having macrophytes/total number of sampling points] × 100). Because surface sediments that were collected (see below) can contain invertebrate remains over several years, for the purpose of comparison we also averaged the lake plant coverage index from 2006 to 2007 with equivalent data collected in 2009 (Salgado, 2012).

To quantify contemporary invertebrates, we counted the sub-fossil remains of invertebrate taxa found in collected surface sediment samples (uppermost 2 cm) from 12 of the 25 sites sampled for macrophytes. This approach has been shown to be a reliable integrator of invertebrate communities within lakes (van Hardenbroek, Heiri, Wilhelm, & Lotter, 2011) and can successfully detect community dynamics at the regional scale (Declerck, Coronel, Legendre, & Brendonck, 2011). Surface samples were retrieved during the summers of 2008–2009 using a Glew gravity corer (Glew, 1991) and analysed for daphnids, molluscs, chironomids and bryozoans according to the palaeolimnological methods described above.

Relative abundance data for zebra mussels in each lake were obtained from Salgado, Sayer, Brooks, Davidson, Goldsmith, et al. (2018). In summary, we noted the presence and estimated the abundances of zebra mussels during each macrophyte survey through direct observation with the bathyscope and/or through individuals collected using a rake at each survey point. Subsequently, zebra mussel abundance was expressed on a semi-quantitative abundance scale of 0–3 (3 = abundant and 0 = absent) for each lake. We also used sub-fossil remains to verify recent presence of zebra mussel in each lake providing data that were not reported by Salgado, Sayer, Brooks, Davidson, Goldsmith, et al. (2018).

2.4 | Analyses of long-term changes in lake communities

We quantified the varying temporal effects of local stressors and hydrological connectivity on the compositional palaeoecological records of macrophytes and invertebrates via ANOVA space–time analysis; henceforth referred to as S-T analysis (Legendre, Cáceres, & Borcard, 2010). This analysis is ideal for assessing space–time interactions in repeated ecological surveys (such as the collected sedimentary lake material) that lack replication of sampling units (Legendre et al., 2010). We used the *quickSTI* function of the PCNM package (R development team; Legendre et al., 2010), where the space–time interaction is tested using "Model 5." This model uses information about the physical relationships amongst sampling sites (lakes) over time via distance-based Moran Eigenvector Maps-dbMEM (previously known as principal coordinates of neighbour matrices- PCNM) to assess any interaction between space and time. The use of dbMEMs is ideal as they represent a spectral decomposition of the spatial or temporal relationships amongst sampling sites or times and can fit many nonlinear situations (Legendre et al., 2010). Thus, they can model spatial or temporal variation with any shape and are a more parsimonious representation of spatial and temporal relationships (less degrees of freedom) than that provided by other commonly used dummy variables like Helmert contrasts (Legendre et al., 2010).

Depending on the outcome of the "Model 5" test, we assessed the main spatial and temporal factors using two different strategies according to Legendre et al. (2010): (a) If the interaction was significant, a nested model was used to assess whether a separate spatial (model 6a) and/or separate temporal structure (model 6b) existed, and (b) If the S-T interaction was non-significant (hence one cannot conclude that changes have occurred in the spatial or temporal structure of the lake communities), a test for common spatial and/or common temporal structures was achieved using Helmert contrasts "Model 2."

The palaeo-data on organismal abundances were divided into two time blocks (pre-1950 and post-1950) for independent S-T analyses. The ULE system has been affected by progressive eutrophication since the 1950s (Battarbee, 1986; Zhou et al., 2000). Prior to the 1950s, the system was characterized by lower phytoplankton production and greater variation in hydrological connectivity (Salgado, Sayer, Brooks, Davidson, & Okamura, 2018). Water-level regulation schemes implemented in the late 1800s and late 1940s have reduced widespread flooding and water-level fluctuations in the central lake. Nevertheless, much of the ULE system area is still periodically inundated by winter flooding (Figure 1). A space–time interaction would suggest that macrophyte and/or invertebrate community composition has differentially reacted to changing environmental conditions over time and space (Legendre et al., 2010). We hypothesised that pre-1950 spatial patterns in the system (e.g., lake position and associated hydrological connectivity to the main lake) would impose stronger effects across sites with proportionally weaker local effects. However, we also hypothesized that intensified eutrophication post-1950 increasingly drove sorting of species over time according to local, lake-specific nutrient enrichment. We thus expected to detect a significant space–time interaction where spatial effects have weakened over time.

Invertebrate abundance data were $\log(x + 1)$ transformed prior to S-T analyses and the macrophyte and invertebrate abundance data were tested independently for S-T analyses. Each time block (pre-1950 and post-1950) comprised 30 data points for macrophytes (6 cores × 5 temporal samples) and 25 for invertebrates (5 cores × 5 temporal samples). S-T analyses were assessed using a confidence level of $p < 0.05$ under 499 permutations.

2.5 | Analyses of contemporary consequences of eutrophication, connectivity and invasion by *D. polymorpha*

We conducted partial redundancy analysis (pRDA; VARPART package, R Development Core Team, 2016) to assess the unique contributions of environmental variables, zebra mussel, plant coverage (for invertebrate analyses), and hydrological connectivity in determining contemporary lake community variation (Borcard, Legendre, & Drapeau, 1992).

Hydrological connectivity predictors were designed to represent two characteristic hydrological features of the system: (a) natural water flows across the central lake and from subsidiary tributaries into the central lake; and (b) water flows from the central lake into the satellite lakes resulting from recurrent flooding (Figure 1). For each hydrological feature, we constructed a separate binary connectivity matrix through Asymmetric Eigenvector Maps (AEM) analysis using the AEM package in R (R Development Core Team, 2016) following

Blanchet, Legendre, and Borcard (2008a) and Blanchet, Legendre, Maranger, Monti, and Pepin (2011). AEM analysis transforms a binary matrix into a series of eigenvectors which are orthogonal as dbMEMs that can be used as connectivity predictors (see Appendix S2; Figure S2.1). This method provides an advantage over other more traditional spatial analysis (e.g., dbMEM) as it can model directional asymmetric processes such as water flow direction (Blanchet, Legendre, & Borcard, 2008b).

We achieved parsimonious pRDA analysis for macrophyte and invertebrate community variation by selecting the most important explanatory environmental variables (log-transformed) and AEM connectivity predictors (both hydrological features together) via forward selection analysis (Blanchet et al., 2008b). Prior to pRDA, square root transformed macrophyte and log(x + 1) invertebrate abundance data were subject to Hellinger transformations and each biological group was tested independently. Variation explained by each component in the pRDA was corrected to adjusted R^2 following Peres-Neto, Legendre, Dray, and Borcard (2006). The significance of each component was tested through 999 random Monte Carlo permutations under the reduced model. RDA plots were then used to visually assess how the study sites clustered according to: (a) macrophyte community variation and the selected explanatory AEMS; and (b) macrophyte community variation and the combined selected explanatory AEMS and environmental variables.

To assess further how the distributions of macrophytes and invertebrates linked with hydrological connectivity to the central lake we used IndVal analysis (Dufrêne & Legendre, 1997). IndVal analysis calculates an indicator value for each species based on the product of its relative frequency and relative average abundance in a specific temporal or spatial group cluster under a significance value of $p \leq 0.05$. The IndVal score is maximized (1) where a species occupies all the samples from a group and is unique to that group. Because some macrophyte species of conservation importance (e.g., *Stratiotes aloides* L., and *Potamogeton praelongus* Wulfen) presented marginal significance values (i.e., $p < 0.1$), we included all species with a $p < 0.1$ in our analysis. Macrophyte frequencies of occurrences were square root transformed, and invertebrate abundance data were log (x + 1) transformed prior to analysis.

2.6 | Comparisons of historical and contemporary lake communities

We compared historical and contemporary lake communities by testing for associations using non-metric multidimensional scaling analysis (NMDS) and Bray–Curtis dissimilarities (Faith, Minchin, & Belbin, 1987). We compared characteristic macrophyte and invertebrate species of major temporal zones of biological change (palaeo-data) detected through IndVal analysis against the observed characteristic macrophyte and invertebrate species of three lake connectivity groups (IndVAL contemporary data). We ran independent IndVal analysis for each lake and each biological group (invertebrate abundances were [log (x + 1)] transformed prior to analysis). For each NMDS analysis, we created a binary (0/1) matrix (Tables S3.1 and S3.2 in Appendix S3), using unrecorded historical species (i.e., the macrophytes *Isoetes lacustris* L., *Lobelia dortmanna* L., *Najas flexilis* (Willd.) Rostk. & Schmidt.) and shared species between the palaeo- and the contemporary data. We assigned a value of 1 to the species having the maximum indicator IndVal score at a given temporal and connectivity group. IndVal-selected phases of change in macrophyte and invertebrate species abundances in the palaeo-data were assessed via *Coniss* clustering analysis using the RIOJA Package in R.

3 | RESULTS

3.1 | Long-term changes in lake communities

S-T analysis on pre-1950s plant macrofossils showed a weak interaction between space and time ($F = 1.38$; $p = 0.108$), accounting for 18% of macrophyte compositional variation (Table 1). The test for common spatial and temporal structures (Model 2) showed that space alone explained a significant ($F = 3.77$; $p = 0.001$) 41% of plant compositional variation, whereas time uniquely explained a non-significant ($F = 1.24$; $p = 0.126$) 11%. Macrophyte taxa such as *Chara* spp., *I. lacustris*, *L. dortmanna*, *Najas flexilis*, *Nitella flexilis* (L.) C. Agardh, and *S. aloides* were common during this time interval (Figure S4.1 in Appendix S4). The S-T analysis of post-1950 data revealed a significant ($F = 1.46$; $p = 0.03$) space–time interaction, accounting for 17% of macrophyte variation in composition (Table 1). The test for separate spatial structure (Model 6a) showed that space alone explained a non-significant ($F = 0.96$; $p = 0.596$) 50% of macrophyte compositional variation, whereas the test for separate temporal structure (Model 6b) uniquely explained a significant ($F = 2.57$; $p = 0.001$) 41%. During the post-1950 time-period, there was a general shift towards dominance by macrophytes typical of nutrient-enriched lakes, with increases in floating-leaved plants (*Lemna minor* L., and water lilies) and disappearances or declines in *I. lacustris*, *L. dortmanna* and *N. flexilis* (S4.1 in Appendix S4).

Analysis of pre-1950 invertebrate data revealed a significant space–time interaction ($F = 1.55$; $p = 0.028$) accounting for 13% of variation in invertebrate composition (Table 1). The test for separate spatial structure (Model 6a) explained a non-significant ($F = 1.16$; $p = 0.063$) 46% of invertebrate compositional variation, whereas the test for separate temporal structure (Model 6b) uniquely explained a significant ($F = 2.53$; $p = 0.001$) 37%. Taxa showing strong temporal and spatial compositional variation during this time interval included the bryozoans *P. articulata* and *Plumatella fruticosa* Allman, and the chironomids *Stempellina* spp., *Pseudochironomus* spp., and *Protanypus* spp. (Figure S4.2 in Appendix S4). Analysis of post-1950 data revealed a highly significant ($F = 1.68$; $p = 0.001$) space–time interaction that accounted for 11% of invertebrate compositional variation. The test for separate spatial structure (Model 6a) explained a non-significant ($F = 0.99$; $p = 0.503$) 43% of variation in invertebrate composition, while the test for separate temporal structure (Model 6n) explained a uniquely significant ($F = 3.36$; $p = 0.001$) 33%. Concomitant reductions in chironomid types intolerant of nutrient-rich conditions (e.g.,

Stempellina spp., *Pseudochironomus* spp., *Orthocladius consobrinus* and *Protanypus* spp.) were detected (Figure S4.2 in Appendix S4).

3.2 | Contemporary consequences of eutrophication, connectivity and invasion by *D. polymorpha*

Forward selection in an RDA of contemporary macrophyte data identified TP, TN, water colour, zebra mussel abundance and six AEMs (1, 3, 4 and 5 for the natural water flows model and 1 and 6 for the flooding model) as significant predictors of variation in macrophyte composition (all environmental lake data are presented in Table S1.1 of Appendix S1). For the invertebrate data, the analysis identified water colour, plant coverage and one AEM (AEM10 of the water flow model) as factors contributing to variation in invertebrate composition. Zebra mussel abundances failed to explain a significant portion of invertebrate compositional variation.

The pRDA of macrophyte data showed that only the environmental (TP, TN and water colour) and hydrological connectivity fractions (AEMs) explained a significant (6% and 21%, respectively, at $p < 0.01$) amount of adjusted macrophyte compositional variation (Figure 2a). The shared fraction between AEMS and environmental variables explained 3% of adjusted macrophyte compositional variation, while the shared fraction between AEMS, environmental variables and zebra mussels explained a further 1%. A shared fraction between environmental variables and zebra mussel abundance explained an additional 3%, while a shared fraction between AEMS and zebra mussel abundance explained an additional 3%. Unexplained residual variation accounted for 65% of macrophyte-adjusted compositional variation.

The pRDA of invertebrate data revealed that only the environmental fraction (plant coverage and water colour) explained a significant amount (9%; $p = 0.03$) of adjusted invertebrate variation in composition (Figure 2b). The shared fraction between environmental variables and AEM predictors explained 3% of adjusted invertebrate compositional variation. A non-significant 2% of the invertebrate compositional variation was explained by the unique AEM component. The unexplained residuals of invertebrate adjusted variation in composition accounted for 87%.

Redundancy analysis plots revealed three distinct clusters of lakes according to macrophyte community variation and both the AEM model data (Figure 3a) and the combined AEM and environmental data (Figure 3b): *Group 1* lakes were either directly connected to the central lake via the River Erne (Castle, Derrykerrib, Kilmore, Doo, 904, Sessiagh East) or directly connected via tributaries (Kilmore and Doo; Figure 1). These lakes had high mean values of zebra mussel abundance (1.44 ± 1.23), a mean water colour of 69.5 ± 27.6 mg/L, low-intermediate mean nutrient concentrations (TP = 66.7 ± 47.6 μg/L; TN = 0.79 ± 0.41 mg/L) and a dense plant coverage index (mean = 86.24 ± 6.3%; Table 2). *Group 2* lakes were connected to the central lake via tributaries (e.g., Corraharra, Pound and Derrymacrow) or by flows through one or more intermediate lakes and associated tributaries (Corraharra, Killymackan, Cornabrass and Kilturk lakes; Figure 1). These lakes were eutrophic (TP = 112±36.6 μg/L; TN = 1.25 ± 0.5 mg/L) with mean water colour of 67.6 ± 8.5 mg/L, a low mean zebra mussel abundance of 0.37 ± 0.74 and a high mean plant coverage index of 81.5 ± 14.2% (Table 2). *Group 3* lakes were similarly connected to the central lake as for Group 2 (via flow through one or more

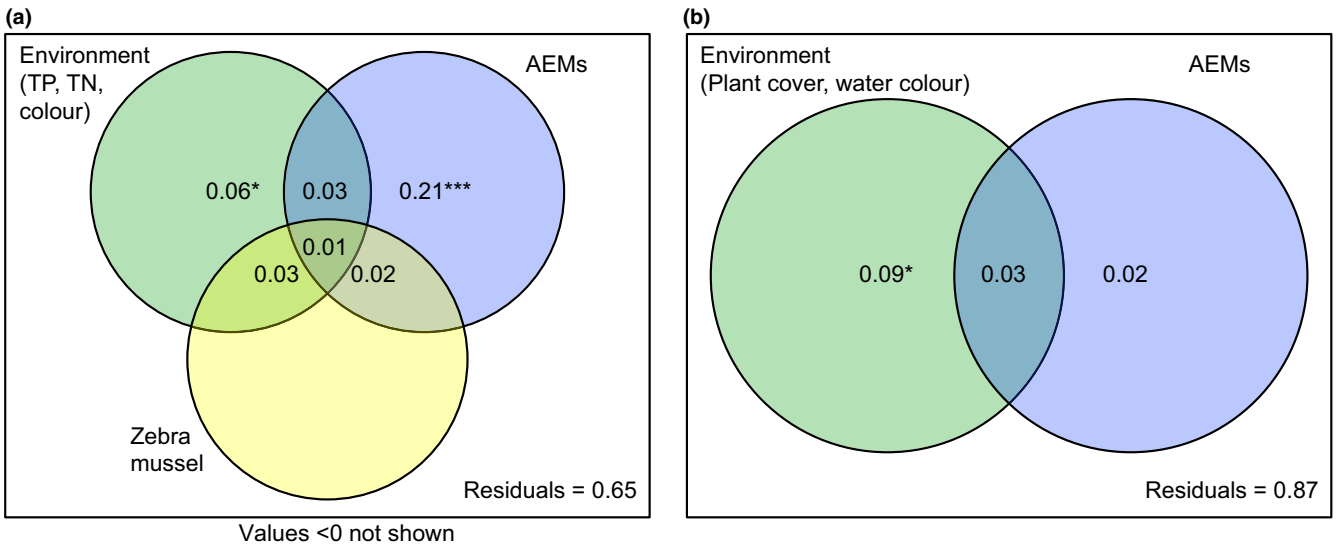

FIGURE 2 Results of partitioning redundancy analysis (pRDA) performed on contemporary compositional variation of macrophytes (a) and invertebrates (b) according to two modelled hydrological features in the landscape: i) natural water flows across the central lake and from subsidiary tributaries into the central lake, and; ii) water flows from the central lake into the satellite lakes resulting from recurrent flooding. The diagrams represent the contributions of the pure environmental, hydrological connectivity and zebra mussel abundance components and their shared contributions on assemblage composition. Explained variation is expressed as adjusted R^2 values × 100. TP = total phosphorus; TN = total nitrogen; AEMs = Asymmetric eigenvectors. Asterisks denote significance levels as follows: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Values < 0 are not shown

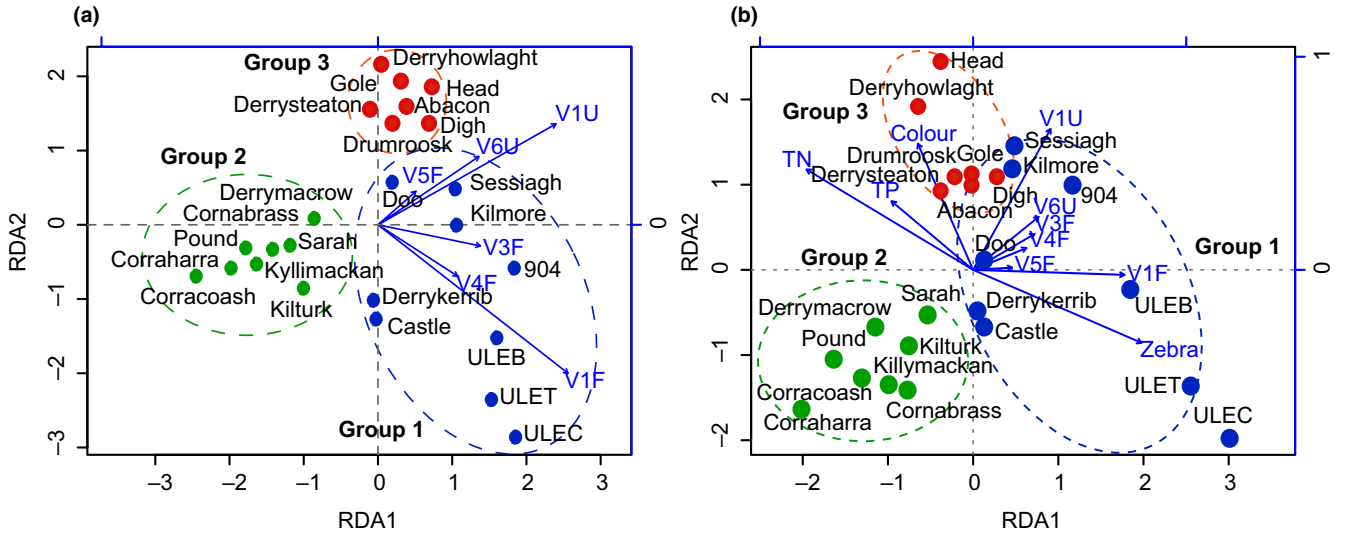

FIGURE 3 Redundancy analysis plots of contemporary macrophyte compositional variation and (a) selected hydrological connectivity predictors (asymmetric eigenvalues-AEMS) related to two hydrological features: i) natural water flows across the central lake and from subsidiary tributaries into the central lake (indicated by an F), and; ii) water flows from the central lake into the satellite lakes resulting from recurrent flooding (indicated by an U); and (b) selected AEMS and environmental and hydrological connectivity predictors showing three distinct lake groups defined according to variation in macrophyte composition—*Group 1* (G1); *Group 2* (G2); *Group 3* (G3)

TABLE 2 Mean annual measurement of environmental variables and plant cover collected over 2006–2007 across three sampling basins in the central lake (Crom, Trannish and Belleisle) and the 21 satellite lakes

Lake	TP* (µg/L)	TN* (mg/L)	Chl-a (µg/L)	Cond. (µS/cm)	Water colour* (mg/L as Pt)	Z_a*	Secchi (cm)	Plant coverage Index (%)*
Group 1	66.7 ± 47.6	0.79 ± 0.41	6.0 ± 1.8	267.2 ± 44.8	69.5 ± 27.6	1.44 ± 1.23	156.2 ± 76.7	86.24 ± 6.3
Group 2	112.3 ± 36.6	1.25 ± 0.5	10.9 ± 5.7	281.6 ± 47.8	67.6 ± 8	0.37 ± 0.74	91.5 ± 21.7	81.5 ± 14.2
Group 3	163.2 ± 101.5	1.55 ± 0.3	13.6 ± 5.9	264 ± 36.1	83.3 ± 28.9	0.28 ± 0.48	86.4 ± 34.2	68.3 ± 26.2

Note: The environmental and plant cover data are presented according to three groups of lakes detected by our analyses using selected hydrological connectivity predictors and environmental parameters*. *Group 1* included the three central lake areas (Crom, Trannish§+ and Belleisle) and the satellite lakes: Castle§+, Derrykerrib§, Doo§, Kilmore, 904 and Sessiagh East; *Group 2* included the satellite lakes: Sarah, Cornabrass§+, Pound, Corraharra, Corracoash, Killymackan§+, Derrymacrow and Kilturk§; *Group 3* included the satellite lakes: Abacon, Derrysteaton§, Digh§, Derryhowlaght§, Drumroosk, Gole§+ and Head§+.

Abbreviations: +, sites sampled for palaeolimnological analysis; §, Sites sampled for contemporary invertebrate compositional variation; Chl-a, chlorophyll-a; Cond., conductivity; TN, total nitrogen; TP, total phosphorus; Z_a, Zebra mussels abundance (0–3 scale).

intermediate lakes and associated tributaries [Head, Gole and Drumroosk lakes] or via tributaries [Derrysteaton, Abacon, Digh and Derryhowlaght lakes]), but were more isolated than lakes in *Groups 1* and *2* due to the presence of intervening small hills, woodlands and roads (Figure 1). Lakes in *Group 3* were the most eutrophic (TP = 163.2 ± 101.5 µg/L; TN = 1.55 ± 0.3 mg/L) and turbid (water colour = 83.3 ± 28.9.3 mg/L) sites. The plant coverage index (68.3 ± 26.2%) and zebra mussel abundance (0.28 ± 0.48) were both low in these sites (Table 2).

Most contemporary macrophyte and invertebrate species had widespread distributions (Appendix S5, Tables S5.1 and S5.2). Twenty macrophytes presented distributions linked with hydrological connectivity to the central lake, including *Chara globularis* Thuill., *Eleocharis acicularis* (L.) Roem, *Potamogeton* × *angustifolius* J. Presl., *Potamogeton lucens* L., and *Sagittaria sagittifolia* L., (Table 3). More species-rich macrophyte communities were detected in *Group 1* lakes (n = 9), which harboured a total of 43 species, including some of high conservation importance, such as *E. acicularis* and broad-leaved pondweed taxa (e.g., *P. lucens*, and *P. x angustifolius*; Table 3; Table S5.1). *Group 2* lakes (n = 8) had 33 species, including several species characteristic of high quality, base-rich shallow lakes such as *Potamogeton alpinus* Balb., *P. praelongus*, and *Myriophyllum verticillatum* L. (Willby, Pitt, & Phillips, 2012) as well as the invasive *Elodea canadensis* Michx. *Group 3* lakes (n = 7) supported 21 species, including *Myriophyllum spicatum* L., *Hippuris vulgaris* L., and *Potamogeton berchtoldii* Fieber. (Table S5.1).

Six invertebrate taxa had non-random distributions in relation to the detected lake groups (Table 3). These were the molluscs *Bithynia tentaculata* L., *D. polymorpha* and gastropods, the chironomid types *Cricotopus intersectus* and *Glyptotendipes pallens*, and oribatid mites. *Group 1* lakes supported 25 taxa (including *D. polymorpha*) compared to 19 and 15 taxa in lakes of *Groups 2* and *3*, respectively (Appendix S5, Tables S5.2).

TABLE 3 Significant macrophyte and invertebrate indicator taxa determined by IndVAL analysis based on its relative frequency and relative average abundance for three groups of lakes detected by our analyses using selected hydrological connectivity predictors and environmental parameters

Biological group	Species	G1	G2	G3
Macrophytes	*Chara globularis**	X		
	*Eleocharis acicularis***	X		
	*Eleocharis palustris**	X		
	*Hydrocotyle vulgaris**	X		
	Nitella mucronata var. *gracillima**	X		
	*Potamogeton lucens****	X		
	*Potamogeton natans**	X		
	Potamogeton X angustifolius (·)	X		
	*Sagittaria sagittifolia**	X		
	*Sparganium emersum***	X		
	*Elodea canadensis***		X	
	*Hydrocharis morsus ranae***		X	
	*Lemna minor***		X	
	*Lemna trisulca**		X	
	*Nymphaea alba***		X	
	Potamogeton praelongus (·)		X	
	*Potamogeton pusillus**		X	
	*Spirodela polyrhiza***		X	
	Stratiotes aloides (·)		X	
	Callitriche c.f. *platycarpa**			X
Invertebrates	*Bithynia tentaculata* (·)	X		
	*Dreissena polymorpha**	X		
	Cricotopus intersectus (·)		X	
	Gastropods (·)		X	
	Glyptotendipes pallens (·)		X	
	Oribatid mites (·)		X	

Note: *Group 1* (G1) included the three central lake areas (Crom, Trannish and Belleisle) and the satellite lakes: Castle, Derrykerrib, Doo, Kilmore, 904 and Sessiagh East; *Group 2* (G2) included the satellite lakes: Sarah, Cornabrass, Pound, Corraharra, Corracoash, Killymackan, Derrymacrow and Kilturk; *Group 3* (G3) included the satellite lakes: Abacon, Derrysteaton, Digh, Derryhowlaght, Drumroosk, Gole and Head.
·$p < 0.1$; *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$.

3.3 | Comparisons of historical and contemporary lake communities

Cluster analysis of the palaeo-data indicated three major phases of change in macrophyte and invertebrate abundances: pre-1900s; 1901–1950; 1951–2009 (Figures S4.1–2). The combined temporal-spatial NMDS analysis of macrophytes and invertebrates indicated strong similarities between historical lake communities (pre-1950) and extant communities in the central lake and those lakes connected via the River Erne (*Group 1* lakes; Figure 4). However, post-1950 macrophyte historical data showed higher similarities with communities presently found in the more degraded lakes of *Group 2*. The invertebrate historical data showed greater compositional similarity with recent sediment samples from the *Group 3* lakes.

4 | DISCUSSION

4.1 | Long-term eutrophication and connectivity

Relative to our first objective, our analyses have revealed that, with increased eutrophication, the relative importance of drivers of community variation across sites changed according to lake-specific nutrient enrichment histories over time. Indeed, our data suggest that eutrophication was the main cause of lake degradation in time, with gradual and progressive biological impacts evident across the ULE landscape. Before 1950, the system was characterized by macrophyte taxa associated with low to intermediate nutrient levels, such as *I. lacustris*, *L. dortmanna* and *N. flexilis* (Kolada et al., 2014), the bryozoans *P. articulata* and *P. fruticosa* (Økland & Økland, 2002) and the chironomids *Stempellina* spp., *Pseudochironomus* spp., and *Protanypus* spp. (Brodersen & Lindegaard, 1999). During this time, there was high between-lake variation in both macrophyte and invertebrate communities, but low macrophyte within-lake compositional variation over time, resulting in a non-significant macrophyte space–time interaction. Temporal within-lake invertebrate compositional variation was observed, however, and is reflected in a significant space–time interaction (Table 1). Together, these patterns suggest that degree of isolation from the central lake may have acted as a key driver of variation in macrophyte and invertebrate composition. However, moderate shifts in within-lake macrophyte composition and/or local environmental factors (e.g., water colour) may have also acted as important drivers of invertebrate compositional variation over time. Invertebrates have been shown to be more sensitive to local environmental changes in lake landscapes than macrophytes perhaps as a result of high dispersal potential, shorter life cycles and the absence of seedbanks (De Bie et al., 2012). The observed spatial variation in both biological communities may also be influenced by other spatially autocorrelated processes such as divergent local environmental histories (Bennion et al., 2018) and/or differences in within-lake features such as variation in water depth (Salgado, Sayer, Brooks, Davidson, & Okamura, 2018).

The drivers of lake communities shifted after 1950, presumably due to the overriding influence of progressive nutrient enrichment. This inference is supported by transitions to dominance by macrophytes commonly associated with nutrient-enriched lakes (e.g., water lilies and fine-leaved *Potamogeton* species; Sayer, Davidson, & Jones, 2010) and reduced abundances of taxa associated with nutrient-poor lakes such as *I. lacustris*, *L. dortmanna* and some broad-leaved *Potamogeton* species (Kolada et al., 2014; Willby et al., 2012). The significant space–time interaction reflects increases in the importance of within-lake variation (time factor) for both macrophytes and

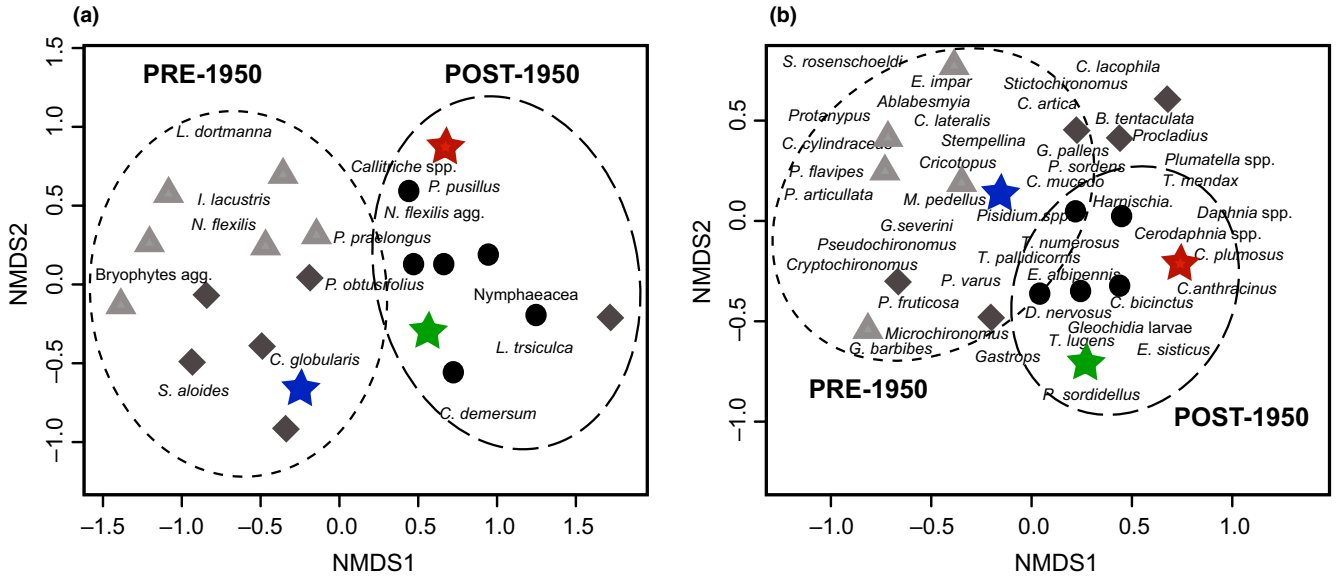

FIGURE 4 Plots of Non-Metric Multidimensional scaling (NMDS) analyses on a binary (0/1) matrix, using shared macrophyte (a) and invertebrate (b) species between the palaeo-data (cores ULET2, NCAS3, CBRAS1, KILL2, GOLE1 and HEAD1) and the contemporary data in the three lake groups (indicated by a star; blue = *Group 1*; green = *Group 2*; red = *Group 3*). A value of 1 was assigned to the species having the maximum indicator IndVal score (measured according to its relative frequency and relative average abundance) at a given temporal and connectivity group. Agg.=aggregate of closely related species. Triangles = pre-1900 palaeo-data; diamonds = 1901–1950 palaeo-data; circles = post-1950 palaeo-data

invertebrates and suggests that lake communities responded independently over time (Legendre et al., 2010), probably according to their individual eutrophication histories (Table 2; Bennion et al., 2018).

4.2 | Connectivity, invasive species and ecosystem resilience

In relation to our second and third objectives, we have constructed what we believe to be a highly realistic representation of inter-lake connectivity for the ULE system using the two AEM models. This approach enabled us to separate sites into three broad lake groups according to isolation to the central lake (Figures 1 and 3). Our analyses revealed that both directional hydrological processes (i.e., water flow from the satellite lakes into the central lake or flooding from the central lake into the satellite lakes) play key roles in driving biodiversity in the lake landscape.

Indeed, hydrological connectivity explained larger proportions of macrophyte compositional variation than any of the other measured environmental variables. Sites hydrologically connected to the central lake (*Group 1*) had the highest species richness and abundances of macrophytes regarded as conservation priorities (Table 2; Table S5.1). A companion study by Salgado, Sayer, Brooks, Davidson, Goldsmith, et al. (2018) showed that macrophyte communities in this group of connected lakes were also more heterogeneous in species relative abundances and composition than in the less specious and eutrophic isolated lakes. Subsidiary natural water flows from the associated satellite lakes with variable nutrient enrichment conditions may therefore introduce a range of different plant propagules to the central lake while recurrent floods likely also transport plant propagules in the opposite direction. Such overriding influences of spatial effects over environmental processes in structuring aquatic communities have been similarly described in dendritic river networks (Dong et al., 2016; Zhao et al., 2017).

Together, our evidence highlights that currently, the central lake and its immediately surrounding satellite lakes (*Group 1*) act as a hub for preserving lake biodiversity in the ULE system as a whole. The large area of this central lake and variation in the extent and timing of flooding may further promote environmental heterogeneity within and amongst the central and satellite lakes over space and time (Van Looy et al., 2019; Ward et al., 1999), thus further stimulating regional lake biodiversity (Salgado, Sayer, Brooks, Davidson, Goldsmith, et al., 2018).

The AEM analysis further showed that directional processes not only influenced the spatial structure of lake communities, but also spatial patterns of environmental variables and invasive species (Figure 2). Zebra mussels were closely associated with the *Group 1* lakes, whereas high values of TP, TN and water colour predominated at the more isolated *Group 3* lakes (Figures 1 and 3). A greater importance of local environmental factors in structuring aquatic communities across more isolated headwater systems has also been described for dendritic river networks (Brown & Swan, 2010; Dong et al., 2016). In addition, Zhao et al. (2017) showed a greater importance of environmental factors for 47 sites along the Ying River in China when sites were more isolated during the dry season (potentially analogous to our *Group 3* lakes). In the wet season, there was a greater importance of subsidiary spatial processes (potentially analogous to our connected *Group 1* lakes).

The higher abundances of zebra mussels in the central lake and its immediately surrounding satellite lakes (*Group 1*) may reinforce the positive effects of hydrological connectivity in preserving lake biodiversity, in this case by improving water clarity (Table 2). When present at high densities, zebra mussels can filter large volumes of water year round (Strayer, 2009), reducing both nutrient concentrations and chlorophyll-a (Higgins & Vander Zanden, 2010), which ultimately increases water transparency (Griffiths, 1992). Similar patterns are suggested by our data (Table 2). Improvements in water transparency have been shown to stimulate macrophyte growth across eutrophic shallow lakes (Ibelings et al., 2007; Zhu et al., 2006). The observed rarity of zebra mussels in the most isolated lakes could derive from more limited boating activity, a population lag phase (Strayer, 2009), or may potentially reflect dispersal limitation due to the direction of flow (Heino & Muotka, 2006). Alternatively, since the more isolated satellite lakes have organic-rich sediments and flatter lake beds (compared to shore-lined gravels and steeper margins of the central lake) they may be less favourable for zebra mussel population establishment and expansion (Strayer, 2009).

Our data show that local factors are more important in structuring invertebrate communities than spatial processes (Figure 2). Furthermore, this and other shallow lake studies (Jones, Moss, & Young, 1998; Langdon, Ruiz, Wynne, Sayer, & Davidson, 2010) collectively demonstrate that spatial dynamics of invertebrate communities are largely tied to those of macrophytes (Figure 2). Indeed, many invertebrates depend on living or decomposing macrophytes as food sources (including epiphytic algae growing on them), substrata, and refugia (Jeppesen, Søndergaard, Søndergaard, & Christoffersen, 1998). Although our results also indicated strong effects of water colour on invertebrate dynamics, this variable was strongly correlated with zebra mussels, TN and TP (Figure 3); hence, any independent effects on invertebrates, or indeed macrophytes, are difficult to separate from those of eutrophication.

4.3 | Caveats

We are aware that the unique contribution of a spatial component in structuring communities may be attributable to other unmeasured variables (Laliberté, Paquette, Legendre, & Bouchard, 2009). Examples include non-linearity in the influence of environmental variables, presence of fish, individual lake histories, priority effects and spatially structured environmental variation (Chang, Zelený, Li, Chiu, & Hsieh, 2013; Logue, Mouquet, Peter, & Hillebrand, 2011). Spatial patterns of psicivorous fish, for instance, can create top down cascading effects by decreasing planktivorous densities, increasing grazer densities and decreasing lake water chlorophyll-a (Carpenter, Kitchell, & Hodgson, 1985), thus yielding potentially similar patterns to those observed for zebra mussels. Studies addressing fish spatial dynamics in the ULE system are therefore imperative to refine interpretation of our observed spatial patterns in environmental and biological variables.

The connectivity AEM models that we conducted are based on a constant connectivity matrix through time. This may be a fair reflection of most on going natural water flows across the central lake and from subsidiary tributaries into the central lake, but could be less realistic for connectivity associated with discrete flooding events. By combining both hydrological connectivity models into a single best predictive model in the pRDA, we attempted to reduce some of these potential temporal underestimations of variation due to discrete floods. Studies incorporating more realistic flood models through time could refine inferences based on the connectivity models employed here.

The use of palaeolimnological data to infer past communities also has limitations. Due to preservational issues and a strong likelihood of missing rare or distantly located macrophyte and invertebrate taxa, (van Hardenbroek et al., 2011; Zhao, Sayer, Birks, Hughes, & Peglar, 2006), not all species present historically will leave remains in sediment cores. Nevertheless a substantial portion of current-day macrophyte species (in this case 60%) was represented in the surface sediments of our six ULE sediment cores (in keeping with previous studies [see Davidson et al., 2005; Salgado, Sayer, Carvalho, Davidson, & Gunn, 2010; Salgado, Sayer, Brooks, Davidson, & Okamura, 2018]). Analyses of the surface sediment samples were also consistent with the contemporary macrophyte surveys in identifying key spatial compositional differences between the three observed lake connectivity groups (Figure 6). Finally, as shown by Heino and Soininen (2010) rare species do not need to be accounted for when analysing metacommunity patterns of species turnover along environmental and/or spatial gradients.

Another further taphonomic caveat is that the plant macrofossil records could over- or under-represent some taxa (e.g., Davidson et al., 2005). The importance of variation in representation was reduced through using a semi-quantitative scale (0–5) and a c. 10-year time series intervals. A further methodological limitation is the lack of data on historical climatic or environmental variables (other than eutrophication and changing water levels and connectivity) that may have played a role in structuring the community over space and time. Nonetheless, as indicated by both macrophyte and invertebrate compositional shifts, it is strongly suspected that these factors were the key drivers of change in the ULE system (Battarbee, 1986; Salgado, Sayer, Brooks, Davidson, Goldsmith, et al., 2018; Salgado, Sayer, Brooks, Davidson, & Okamura, 2018), as is typically the case for Northern Hemisphere lakes.

4.4 | Aquatic conservation implications

Our novel landscape approach using contemporary and palaeoecological data revealed some key features and processes reflecting the complexities of well-connected lake landscapes and how these systems respond to environmental pressures. In particular, we found that, after 1950, eutrophication had similar effects at the within-lake scale to those effects observed at isolated lakes (Figure 4). This suggests that, although eutrophication affected each site over long-time scales (decades to centuries) at the between-lake scale, isolated lakes are

more influenced by surrounding land use than those with greater connectivity and show loss of resilience more quickly. Other forms of connectivity (e.g., subsidies provided when birds act as vectors; Okamura, Hartikainen, & Trew, 2019) require further evaluation, however.

We did not observe strong decreases in local species richness of macrophytes at either spatial or temporal scales (Figure 3; Table 3). Rather a companion study demonstrated that the major compositional changes in lake communities were mostly attributable to variation in dominance (Salgado, Sayer, Brooks, Davidson, Goldsmith, et al., 2018). Such community patterns further suggest that hydrological connectivity, regional environmental heterogeneity and recent invasion by zebra mussels may be sustaining eutrophication-sensitive plant populations across sites, substantially delaying eutrophication impacts at the whole lake landscape level. This phase of delay could be thought of as a form of "eutrophication debt" (Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015). Knowing the duration of this phase is critical for predicting system behaviour and for designing appropriate management strategies for the ULE system and for floodplain lake systems elsewhere in the world. We show that the delay of severe eutrophication effects might be in the order of decades, with both the historical and contemporary data congruently showing that the ULE system is deteriorating. We therefore urge responsible authorities here, and indeed of lake landscapes around the world, to tackle eutrophication issues now, as the buffering effects from high connectivity cannot be expected to last.

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DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3jj548d

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BIOSKETCH

The research team behind this paper focuses on understanding the responses of freshwater ecosystems to environmental change and implications for conservation. The team has strong expertise in contemporary freshwater ecology, palaeolimnology and organismal biology.

Author contributions: J.S. conceived the ideas; J.S., B.G., T.D., S.B., C.S., I.P. and B.O. collected the contemporary and palaeodata; J.S. analysed the data and wrote the first manuscript; B.O., C.S., A.B., N.W., H.B., B.G., T.D., S.B. and I.P. contributed essentially to the interpretation and wording of the final version.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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