

## Eutrophication homogenizes shallow lake macrophyte assemblages over space and time

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**Abstract.** Eutrophication is commonly implicated in the reduction in macrophyte species richness in shallow lakes. However, the extent to which other more nuanced measures of macrophyte diversity, such as assemblage heterogeneity, are impacted concurrently by eutrophication over space and time and the joint influences of other factors (e.g., species invasions and connectivity) remains relatively poorly documented. Using a combination of contemporary and paleoecological data, we examine how eutrophication influences macrophyte assemblage heterogeneity and how nutrient enrichment interacts with watercourse connectivity, lake surface area, and relative zebra mussel abundance over space (within and among lakes) and time (decades to centuries) at the landscape scale. The study system is the Upper Lough Erne, Northern Ireland, UK, which is composed of a large main lake and several smaller satellite lakes that vary in their hydrological connectivity to the main lake. By applying homogeneity analysis of multivariate dispersions and partial redundancy analysis, we demonstrate that contemporary lake macrophyte heterogeneity and species richness are reduced in lakes with intensified eutrophication but are increased in lakes with greater zebra mussel abundance and lake surface area. Watercourse connectivity positively influenced assemblage heterogeneity and explained larger proportions of the variation in assemblage heterogeneity than local environmental factors, whereas variation in species richness was better related to local abiotic factors. Macrophyte fossil data revealed within- and among-lake assemblage homogenization post-1960, with the main lake and connected sites showing the highest rates of homogenization due to progressive eutrophication. The long-term and contemporary data collectively indicate that eutrophication reduces assemblage heterogeneity over time by overriding the importance of regional processes (e.g., connectivity) and exerts stronger pressure on isolated lakes. Our results suggest further that in connected lake systems, assemblage heterogeneity may be impacted more rapidly by eutrophication than species richness. This means that early effects of eutrophication in many systems may be underestimated by monitoring that focuses solely on species richness and is not performed at adequate landscape scales.

**Key words:** assemblage heterogeneity; hydrological connectivity; lake isolation; landscape ecology; metacommunity; paleolimnology; spatial variation; temporal variation; zebra mussel.

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## INTRODUCTION

Aquatic macrophyte stands are a key component of shallow lake ecosystems, providing structurally complex habitats for many co-occurring organisms (Jeppesen et al. 1998) and contributing to biogeochemical cycling in shallow lakes (Davidson et al. 2015). However, intensification of anthropogenically driven processes (e.g., eutrophication and the introduction of exotic species and habitat fragmentation) over the last two centuries has commonly resulted in the loss of macrophyte stands and the development of turbid waters and algal blooms (Jeppesen et al. 2000, Scheffer et al. 2001). Many studies have now demonstrated how eutrophication influences species diversity and turnover (Scheffer 1998, Jeppesen et al. 2000, Scheffer et al. 2001, Sand-Jensen et al. 2008), but the extent to which eutrophication influences assemblage heterogeneity within and among lakes is poorly understood (Donohue et al. 2009). Even less known is how factors such as connectivity among sites and invasive species may interact concurrently with eutrophication to jointly influence macrophyte assemblage heterogeneity, although, as outlined below, research suggests that these are likely to be important.

Populations of the invasive zebra mussel (*Dreissena polymorpha* Pallas) can favor plant development and biomass because their suspension-feeding activities increase water clarity (Griffiths 1992, Zhu et al. 2006, Ibelings et al. 2007). These processes are likely to explain how zebra mussels can promote shifts from pelagic- to benthic-dominated food webs (Higgins and Vander Zanden 2010) and may thus potentially counter eutrophication effects.

Dispersal and connectivity may also compensate for eutrophication impacts. For example, source-sink dynamics may counter or delay extinction. In this scenario, dispersal from high ecological quality lakes (sources) may promote colonization and the maintenance of viable populations of sensitive species in low-quality lakes (Mouquet and Loreau 2002). Dispersal may additionally facilitate the ability of species to track variation in local environmental conditions according to preferred nutrient enrichment conditions (species sorting; Leibold and Norberg

2004). Dispersal and connectivity could therefore be major drivers of macrophyte diversity both within lakes and among highly connected lakes, while environmental processes such as eutrophication may exert greater influences on macrophyte diversity in more isolated sites because of diminished dispersal-mediated rescue effects (Brown and Swan 2010). A strong eutrophication pulse may also have more impact in small, disconnected lakes if there is no dilution from elsewhere in the catchment (Strecker and Brittain 2017). Connectivity, however, may also be detrimental. For example, recurrent flooding may act as a homogenizing force, decreasing variation in species composition and environmental conditions between lakes and increasing the spread of both native and non-native species (Levine 2000).

This study aims to identify factors driving macrophyte assemblage heterogeneity in a large central lake and in a set of associated well-connected, smaller satellite lakes (Loughs) in the Upper Lough Erne (ULE) system, Northern Ireland, by collecting and analyzing present-day and paleoecological data. In particular, we used homogeneity analyses of multivariate dispersions and partial redundancy analyses to (1) examine how watercourse connectivity, relative abundances of invasive zebra mussels, and lake surface area interact regionally with eutrophication to influence macrophyte diversity within and between the water bodies in this system over time (last 150 yr) and space; and (2) how spatial and temporal patterns of macrophyte assemblage heterogeneity may differ from those associated with other common measures of macrophyte diversity, such as species richness. Our study provides important insights into the combined effects of environmental change and connectivity on macrophyte diversity across multiple lakes at a time-scale (decades to centuries) relevant to the widespread, eutrophication-driven deterioration of biodiversity in shallow lakes.

## METHODS

### Study site

The study system is a complex and dynamic riverine system comprising the River Erne that feeds a main central lake (ULE) in Co. Fermanagh

Northern Ireland (54.2154° N, 7.5103° W), UK (Fig. 1). The main lake (ULE) is a large (34.5 km<sup>2</sup>), shallow (mean depth 2.3 m), and eutrophic (total phosphorus [TP] ~70 µg/L) lake. It is surrounded by a series of interconnected, smaller, shallow (<5 m) satellite lakes that vary in degree of enrichment (TP ~ 30–400 µg/L). The ULE system is a special area of conservation (SAC) under the EC Habitats Directive and supports several species with restricted distributions in the UK. Nevertheless, the ULE system has been affected by progressive eutrophication since the 1960s (Zhou et al. 2000). Prior to the 1900s, the ULE system was characterized by lower productivity and greater variation in hydrological connectivity (Salgado et al. 2018). Water-level regulation schemes implemented in the late 1800s and 1940s acted to reduce water-level fluctuation in the main lake but were unsuccessful in preventing flood events, which periodically inundate much of the ULE area. The zebra mussel invaded the system in the 1990s (Minchin et al. 2003).

#### Data collection

Nineteen satellite lakes and three basins in the Belleisle, Trannish, and Crom areas within the main lake were selected for the study (Fig. 1). Selection criteria included replication along a gradient of enrichment (TP, total nitrogen [TN], and chlorophyll *a* [Chl-*a*]), water transparency (Secchi disk), and a gradient in watercourse connectivity between the satellite lakes and the main lake. Data for Chl-*a*, TN, and TP and for lake surface areas were obtained from lake condition assessments of the ULE system made for the Northern Ireland Environmental Agency (NIEA) during 2006–2007 (Goldsmith et al. 2008, Table 1). The Water Management Unit of NIEA provided additional water chemistry data for the Belleisle, Crom, and Trannish areas of the main lake. Water chemistry sampling and laboratory protocols are presented in Appendix S1.

Submerged and floating-leaved macrophyte (angiosperms, bryophytes, and charophytes) abundances and species data were derived from assessments of lake conditions in the ULE system for the NIEA by Goldsmith et al. (2008). Standard Joint Nature Conservation Committee (JNCC) protocols for site monitoring (JNCC 2009) were followed. This methodology allows

for the characterization of macrophyte assemblages within lakes based on shoreline and boat surveys. Accordingly, data were collected from different sectors of a lake using a combination of two sampling approaches (shoreline and deeper water transects) in each sector to give good spatial coverage (Gunn et al. 2010). In particular, macrophyte data were collected along a 100 m wader-depth shoreline transect by sampling at four depths (25, 50, 75, and >75 cm) at each 20-m interval (20 points in total per shoreline transect). Macrophytes in deeper water were surveyed using a boat to collect data (at depths >75 cm) along a transect starting at the midpoint of the shoreline transect and running toward the center of the lake. Macrophytes were sampled at every 5 m along this 100 m deeper water transect (20 points in total). At each point, we used a combination of bathyscope and grapnel sampling, and all aquatic macrophyte species occurring within a 1-m<sup>2</sup> area were recorded using an abundance scale of 0–3, where 0 = absent and 3 = highly abundant. Between two and three sectors were sampled per satellite lake (see Table 1 for details). Representation of the main macrophytes present in each lake was the basis for selecting sectors for sampling—a selection requiring expertise in macrophyte identification and field-work experience. This JNCC method has been demonstrated to adequately characterize macrophyte communities in small lakes (<50 ha) by sampling two to three sectors (Gunn et al. 2010). Accordingly, we sampled two to three sectors in the majority of our sites. Exceptions were made for Sarah and Pound Loughs whose small size (<2 ha) precluded surveying more than one sector and for Lough 904, where site accessibility prevented surveying more than one sector (Goldsmith et al. 2008). The main lake was divided into three separate study basins and, due to their large size, eight sectors per basin were surveyed. It should be stressed that such sampling along representative transects in a lake will almost certainly not identify all macrophyte species within lakes, but the approach can provide relative data on variation in distributions and abundances (i.e., heterogeneity) of the most typical species within lakes (Gunn et al. 2010). At the same time as surveying for macrophytes, we also collected data on relative zebra mussel abundance. Thus, at each macrophyte sampling point, we noted

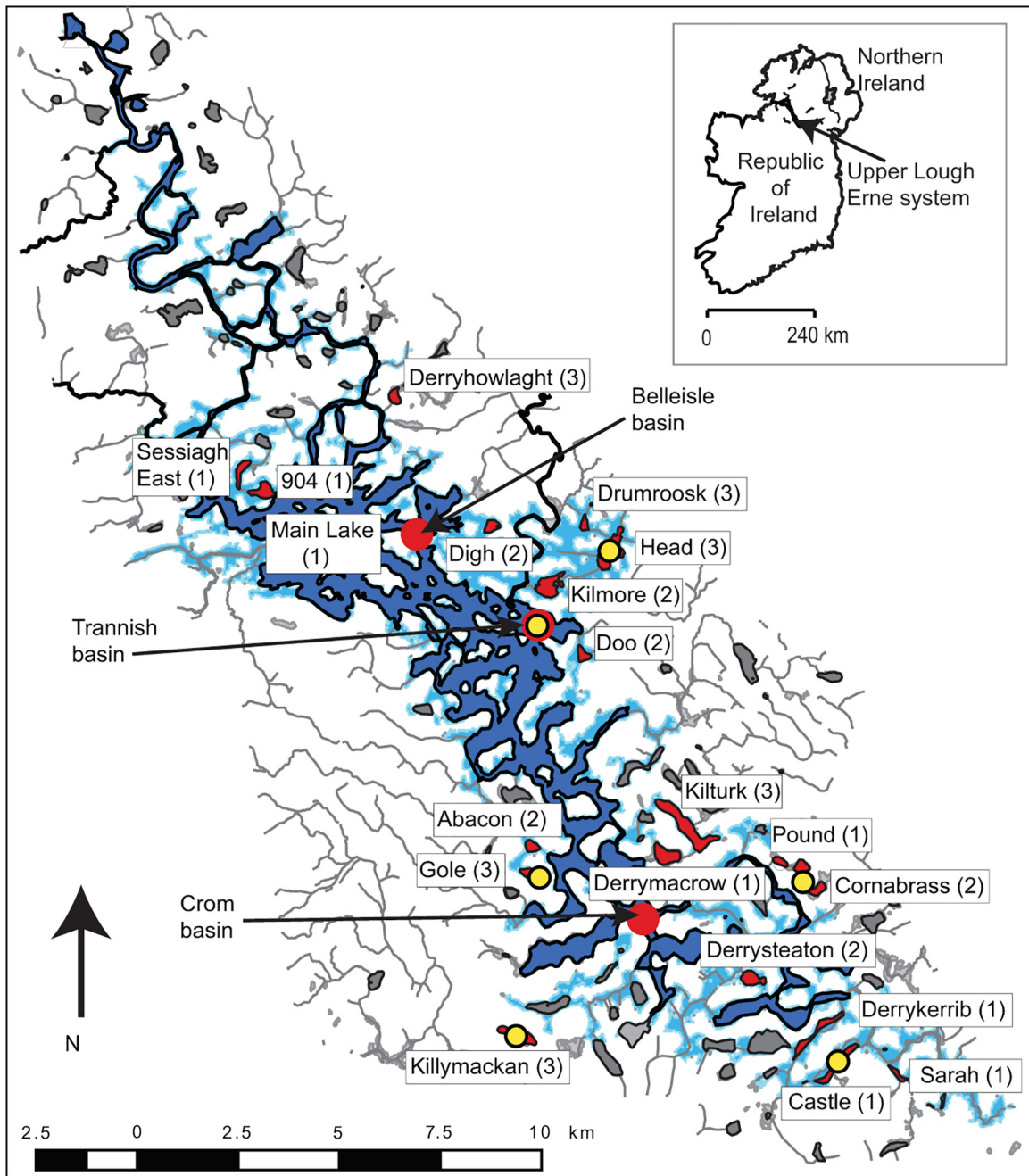


Fig. 1. Map of the Upper Lough Erne system. The main lake is indicated in dark blue with three studied basins, Crom, Trannish, and Belleisle, indicated by a red circle. Contemporary studied satellite lakes are presented in red, and lakes having paleoecological data are highlighted with a yellow circle. A number in parenthesis identifies three connectivity groups according to the water flow direction. These are Group 1, lakes directly connected to the main lake via the River Erne flow; Group 2, lakes with a direct lateral connection to the main lake; and Group 3, lakes connected laterally to the main lake via 1 or more intermediate lakes. Water layers obtained from Ordnance Survey Northern Ireland <https://www.nidirect.gov.uk/services/osni-online-map-shop> and reproduced with the permission of Land & Property Services © Crown Copyright 2018.



Table 1. Macrophyte diversity measures (MAH; assemblage heterogeneity, MSR; species richness), relative zebra mussel abundance, summer and annual averages of total phosphorus (TP), total nitrogen (TN), and chlorophyll a (Chl-*a*), surface area (SA), and number of sectors (NS) sampled in 22 sites (19 satellite lakes and in three basins in the main lake [ML]–Upper Lough Erne).

Lake	MAH	MSR	Zebra mussel (abund.)	Average summer			Average annual			SA (ha)	NS
				TP (µg/L)	TN (µg/L)	Chl- <i>a</i> (µg/L)	TP (µg/L)	TN (µg/L)	Chl- <i>a</i> (µg/L)		
Sarah	0.55	12	0	84	0.98	11.5	61	0.98	7	1.6	1
Castle	0.45	18	1	22	0.47	5.9	29	1.03	4.2	13	2
Derrykerrib	0.46	15	1	44	0.45	13.1	33	0.97	8.6	10.5	2
Derrysteaton	0.57	7	1	202	0.76	11.1	123	1.03	7.1	12	2
Cornabrass	0.55	15	0	86	0.54	6.1	96	1.05	5.3	18	3
Pound	0.39	13	0	285	2.76	12	185	2.25	9	1.25	1
Crom (ML)	0.59	19	3	65	0.28	5.4	65	0.28	5.4	862.5	8
Killymackan	0.48	17	0	159	0.4	30.1	111	0.8	17.4	19.2	3
Derrymacrow	0.54	13	1	78	0.56	12.8	83	1	8.2	21	3
Kilturk	0.54	17	2	92	0.56	14.7	111	0.92	9	43	3
Abacon	0.55	6	1	105	0.84	18	100	1.64	24.2	7	2
Gole	0.43	7	0	172	0.47	22	128	1.35	13.8	8	3
Trannish (ML)	0.60	21	3	70	0.22	7.2	79	0.22	7.2	862.5	8
Doo	0.56	13	0	45	0.6	5.9	54	1.18	5	5	2
Kilmore	0.55	14	0	228	0.45	11.5	186	1.09	6.5	20	2
Head	0.42	10	0	327	0.51	8.7	383	1.79	9	31	3
Drumroosk	0.43	9	0	238	2.22	14.5	168	1.99	12.9	4	2
Digh	0.60	14	0	62	1.2	11.9	81.5	1.4	10.2	9	2
Belleisle (ML)	0.59	15	3	66	0.24	3.1	66	0.24	3.1	862.5	8
904	0.59	12	1	28.5	1.55	6.8	43	1.2	6.4	11	1
Sessiagh East	0.50	11	1	39	0.6	10.8	45	0.9	7.9	8	3
Derryhowlaght	0.54	9	0	161	1	32.3	158.8	1.7	18.3	4	2

the presence of zebra mussels through direct observations using the bathyscope and/or through individuals collected along with macrophytes when using the rake. Mussel relative abundances within lakes were then quantified using a semi-quantitative scale (0–3) as follows: 0 = no zebra mussels observed in any sampling point; 1 = zebra mussels observed in <10 sampling points; 2 = zebra mussels observed in 10–20 sampling points; and 3 = zebra mussels observed in >20 sampling points. Consistent sampling of zebra mussels within and among lakes provided comparative data of their relative abundances.

To characterize temporal variation in within-lake macrophyte assemblage heterogeneity, we used paleoecological methods spanning the last ~200 yr. We analyzed plant macrofossils from short sediment cores (~1 m long) collected during the summers of 2008 and 2009 from six of the 21 sites surveyed for present-day data: Trannish basin of the main lake (core code ULET2), Castle

Lough (NCAS3), Cornabrass Lough (CBRAS1), Gole Lough (GOLE1), Killymackan Lough (KILL2), and Lough Head (HEAD1; Fig. 1). One short sediment core was collected near a basin in the Trannish area from the main lake (ULET2) using an adapted Livingstone corer (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). Cores were collected from similar macrophyte rich and shallow basins (water depths 90–180 cm). Lithostratigraphic changes in the cores were noted, and cores were then extruded in the field at 1-cm intervals.

The cores were dated using a combination of techniques. For the five satellite lakes, we used radionuclide measurements of <sup>210</sup>Pb (half-life 22.3 yr) and <sup>137</sup>Cs and <sup>241</sup>Am (Appleby et al. 1986). Dates at specific levels were ascribed using the constant rate of supply (CRS) model (Appleby and Oldfield 1978, see Appendix S2: Tables S1–S8, Fig. S1). Due to high sedimentation

rates in the top 20 cm of core HEAD1, the CRS dating model covered only the last 23 yr. Thus, we cross-correlated the remaining selected sediment samples with the dated profiles of two cores taken from two similar hypertrophic lakes (GOLE1—Gole Lough, included in this study; and DHOW1—Derryhowlght Lough, unpublished data), which had relatively similar sedimentation rates but greater chronological resolution (Appendix S2: Tables S1–S8, Fig. S1). As funds were not available for dating the core from the main lake (ULET2), selected levels were estimated from the core ULET3 (unpublished data; Appendix S2: Tables S1–S8, Fig. S1), an extra  $^{210}\text{Pb}$  dated core obtained from Castle Lough (NCAS1; Salgado et al. 2018) and three of the study satellite lakes (NCAS3, CBRAS1 and KILL2) which had relatively similar sedimentation rates and similar ranges of total phosphorus concentrations to those observed in the main lake (Table 1).

A selected number of sediment slices of 1 cm were analyzed from all lake cores (NCAS3,  $n = 10$ ; CBRAS1,  $n = 13$ ; ULET2,  $n = 9$ ; KILL2,  $n = 12$ ; GOLE1,  $n = 8$ , and HEAD1,  $n = 11$ ). Sampling resolution was dictated by intrinsic sedimentation rates within each core (Appendix S2: Tables S1–S8). All samples were disaggregated in 10% potassium hydroxide (KOH) before sieving. Macrophyte fossils were retrieved from the residues of the sieved core material (using mesh sizes of 355 and 125  $\mu\text{m}$ ) following standard methods (Birks 2001) and were identified by comparison with reference material and various taxonomic guides (Birks 2001). Macrophyte fossil abundances were estimated by counting seeds, leaves, and spines, and the data were standardized as the numbers of fossils per 100  $\text{cm}^3$ .

### Statistical methods

To understand how variation in macrophyte assemblage heterogeneity among lakes differs from variation in other measures of macrophyte diversity, we conducted analyses on both assemblage heterogeneity and species richness. Species richness was measured as the total number of species recorded per site during the contemporary surveys. We defined lake assemblage heterogeneity as the variation in macrophyte species occurrences and abundances between different sampling points within a lake (Anderson

et al. 2006), and it was calculated as the mean distance to group median (DGM) in ordination space using homogeneity analysis of multivariate dispersions (HMD) on Bray-Curtis dissimilarities (Anderson 2006). Homogeneity analysis of multivariate dispersions applies an ANOVA under the null hypothesis of no difference in multivariate dispersion among sets of lakes (Anderson 2006). Lakes with greater multivariate dispersion (higher values of mean distance to group median) were characterized by greater species dissimilarities and more heterogeneous macrophyte assemblages; more homogenous macrophyte assemblages characterized lakes with low multivariate dispersion. To assess differences in assemblage heterogeneity among lakes, we conducted an overall HMD analysis (each lake being treated as an independent group) using ANOVA. Homogeneity analysis of multivariate dispersions analysis was performed in R using the betadisper package (R Development Core Team 2016). We pooled shoreline and boat data for each lake transect, and, with exceptions of Sarah and Pound Loughs, 40 randomly chosen points (set.seed and sample algorithms in R; R Development Core Team 2016) per lake (20 littoral and 20 open water from all transects) were selected for the analysis. We used this stratified sampling design because the variability within a chosen subset of data is lower compared to variation in the entire population and hence has a high statistical precision while requiring smaller sample sizes in comparison with other approaches (Legendre and Legendre 2012). The absence of macrophyte species in some areas within a lake was common, especially for lakes with high TP and TN concentrations. Because such absences can be equated to reductions in plant heterogeneity, the absence was included in our analyses and coded as pseudo-species with an abundance value of 0.01.

To identify the unique contributions of eutrophication, relative zebra mussel abundance, watercourse connectivity, and lake surface area in determining contemporary macrophyte assemblage heterogeneity and species richness, we conducted partial regression analysis (pRA; Borcard et al. 1992, Legendre and Legendre 2012) using the varpart package in R (R Development Core Team 2016). Watercourse connectivity predictors were calculated through asymmetric eigenvector

maps (AEM) analysis (Blanchet et al. 2008a) using the AEM package in R (R Development Core Team 2016). Asymmetric eigenvector maps variables were derived from a matrix of hydrological connectivity (Fig. 1b), based on the presence/absence of links such as rivers and streams between two given sites (Blanchet et al. 2008a, 2011). Due to a lack of detailed hydrological knowledge about each watercourse, we assumed that all connecting links shared the same ease of water movement between sites (Appendix S3: Fig. S1, Table S1).

Significant environmental variables (log-transformed TP, TN, and Chl-*a* data, zebra mussel abundance and log-transformed lake surface area) and AEM connectivity predictors were detected through forward selection analysis (*packfor* in R; R Development Core Team 2016) by following Blanchet et al. (2008b). Unfortunately, Secchi disk measurements strongly correlated with the other variables (such as nutrients and zebra mussels) making it very difficult to disentangle the unique effects of each parameter. Secchi disk data were therefore excluded from the analysis. The explained variation in each independent and shared fraction in the pRA was corrected following Peres-Neto et al. (2006) and expressed as adjusted  $R^2$  ( $_{adj}R^2$ ) values. The significance of each component was tested through 999 random Monte Carlo permutations under the reduced model. We plotted the data to visually assess the direction of the relationships. To observe spatial patterns in significant predictors, we divided the macrophyte assemblage heterogeneity and the species richness data sets into three connectivity groups according to water flow directions as follows (Fig. 1): Group 1, comprising lakes directly connected to the main lake via the River Erne (e.g., Castle Lough); Group 2, comprising lakes with a lateral connection to the main lake via tributaries (e.g., Kilmore Lough); Group 3, comprising isolated lakes or those laterally connected to the main lake via one or more intermediate lakes (e.g., Killymackan Lough).

We calculated the temporal variation in macrophyte assemblages in each lake by splitting the paleoecological data into two time intervals on the basis of the environmental history of the system. These were (1) c. pre-1900 and (2) post-1960 for cores NCAS3, CBRAS1, ULET2, and KILL2. The macrofossil data for GOLE1 core only

spanned the last ~110 yr so for this core, we characterized temporal variation in the plant community for (1) 1959–1880 and (2) post-1960. Each temporal lake group contained four to six sediment samples per core. Macrofossil abundance data were transformed to a DAFOR (dominant, abundant, frequent, occasional, rare) scale (Salgado et al. 2018) to reduce bias associated with differential production and preservation of plant structures (e.g., spines, leaves, and seeds). We conducted HMD analysis on assemblage heterogeneity both within and among sites (between time periods) using Bray-Curtis dissimilarities. Among-site variation between time periods was calculated by grouping all data at each time period (each time period treated as an independent group) and tested via ANOVA. To visualize temporal variation in lake assemblages, we ran non-metric multi-dimensional scaling analysis (NMDS) on Bray-Curtis dissimilarities. We identified characteristic species in each time period using the IndVal method (*labdsv* in R; R Development Core Team 2016) of Dufrêne and Legendre (1997).

## RESULTS

### *Variation in contemporary macrophyte diversity*

Forty-five submerged and floating-leaved macrophyte species were sampled across the study sites (Appendix S4: Table S1). Homogeneity of multivariate dispersion analysis revealed significant variation in contemporary macrophyte assemblage heterogeneity among the study sites ( $F = 5.5245$ ,  $P < 0.001$ ). Total nitrogen (TN; annual average measurements), relative zebra mussel abundance, and lake surface area were identified by forward selection as significant ( $P < 0.05$ ) explanatory variables for both macrophyte assemblage heterogeneity and species richness. Three watercourse explanatory variables (AEM1, AEM7, and AEM14) for assemblage heterogeneity and two watercourse explanatory variables (AEM2 and AEM6) for species richness were also identified.

Partial regression analysis (pRA) showed that watercourse connectivity alone explained a significant ( $P < 0.001$ ) 50% of the adjusted variation in macrophyte assemblage heterogeneity among sites (Fig. 2a). Spatial structure and shared variation between environmental variables explained

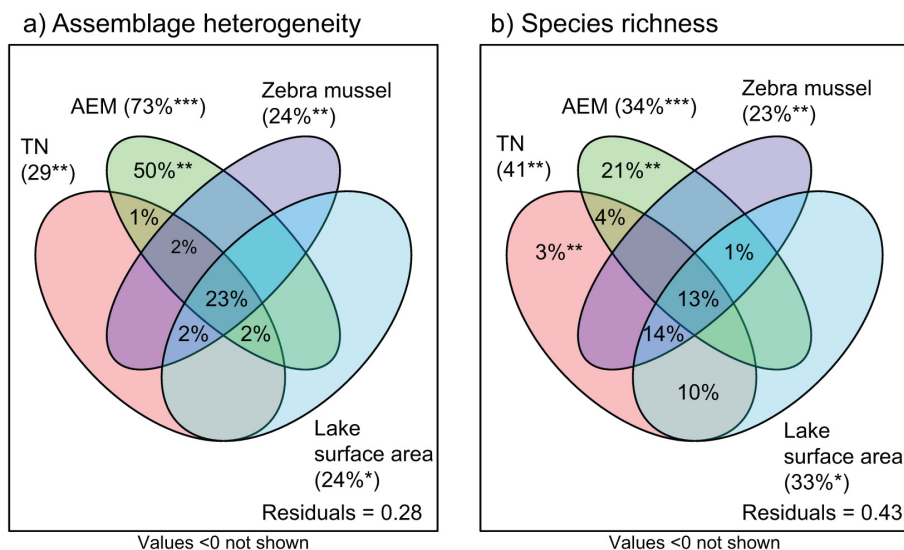


Fig. 2. Venn diagrams of partitioning redundancy analysis performed on the relative contribution of total nitrogen (TN), zebra mussel abundance, and lake surface area on (a) contemporary lake macrophyte assemblage heterogeneity (measured as distance to group median in the multivariate space); and (b) contemporary macrophyte species richness. \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$ .

the following adjusted variation in macrophyte assemblage heterogeneity: (1) watercourse connectivity and TN (1%); (2) watercourse connectivity, TN, and zebra mussel abundance (2%); (3) watercourse connectivity, TN, relative zebra mussel abundance, and lake surface area (23%); (4) TN, relative zebra mussel abundance, and lake surface area (2%); and (5) watercourse connectivity, TN, and lake surface area (2%). Unexplained residual variation accounted for 28% of the variation in macrophyte assemblage heterogeneity among sites.

Partial regression analysis (pRA) on macrophyte species richness resulted in TN and watercourse predictors explaining a significant ( $P < 0.01$ ) 3% and 21% of the adjusted variation, respectively (Fig. 2b). Spatial structure and shared variation between environmental variables together explained the following variation in macrophyte species richness among sites: (1) watercourse connectivity and TN (4%); (2) TN, zebra mussel abundance, lake surface area, and watercourse connectivity (13%); (3) zebra mussel abundance, watercourse connectivity, and lake surface area (1%); (4) TN, lake surface area, and zebra mussel abundance (14%); and (5) TN and lake surface area (10%). Unexplained residual

variation accounted for 43% of the adjusted variation in macrophyte species richness.

Regression plots of the contemporary macrophyte data revealed that concentrations of TN increased while macrophyte assemblage heterogeneity and species richness declined with lake isolation (Fig. 3). In turn, greater macrophyte species richness and more heterogeneous plant assemblages were associated with greater zebra mussel abundance and larger lake surface areas (Fig. 3).

#### Temporal trends in macrophyte assemblage variation

Homogeneity of multivariate dispersion analyses of lake macrophyte fossil data indicated a strong homogenization of macrophyte assemblages within the lakes post-1960 (Fig. 4a). We observed greater rates of post-1960 assemblage homogenization in the main lake (68%;  $\Delta\text{DGM} = -0.15$ ;  $\text{DGM}_{\text{pre-1900}} = 0.22$ ; and  $\text{DGM}_{\text{post-1950}} = 0.07$ ), in Cornabass Lough (40%;  $\Delta\text{DGM} = -0.13$ ;  $\text{DGM}_{\text{pre-1900}} = 0.32$ ; and  $\text{DGM}_{\text{post-1950}} = 0.19$ ), and in Castle Lough (35%;  $\Delta\text{DGM} = -0.05$ ;  $\text{DGM}_{\text{pre-1900}} = 0.16$ ; and  $\text{DGM}_{\text{post-1950}} = 0.10$ ) than in the more isolated lakes Killymackan Lough (22%;  $\Delta\text{DGM} = -0.04$ ;  $\text{DGM}_{\text{pre-1900}} = 0.20$ ; and



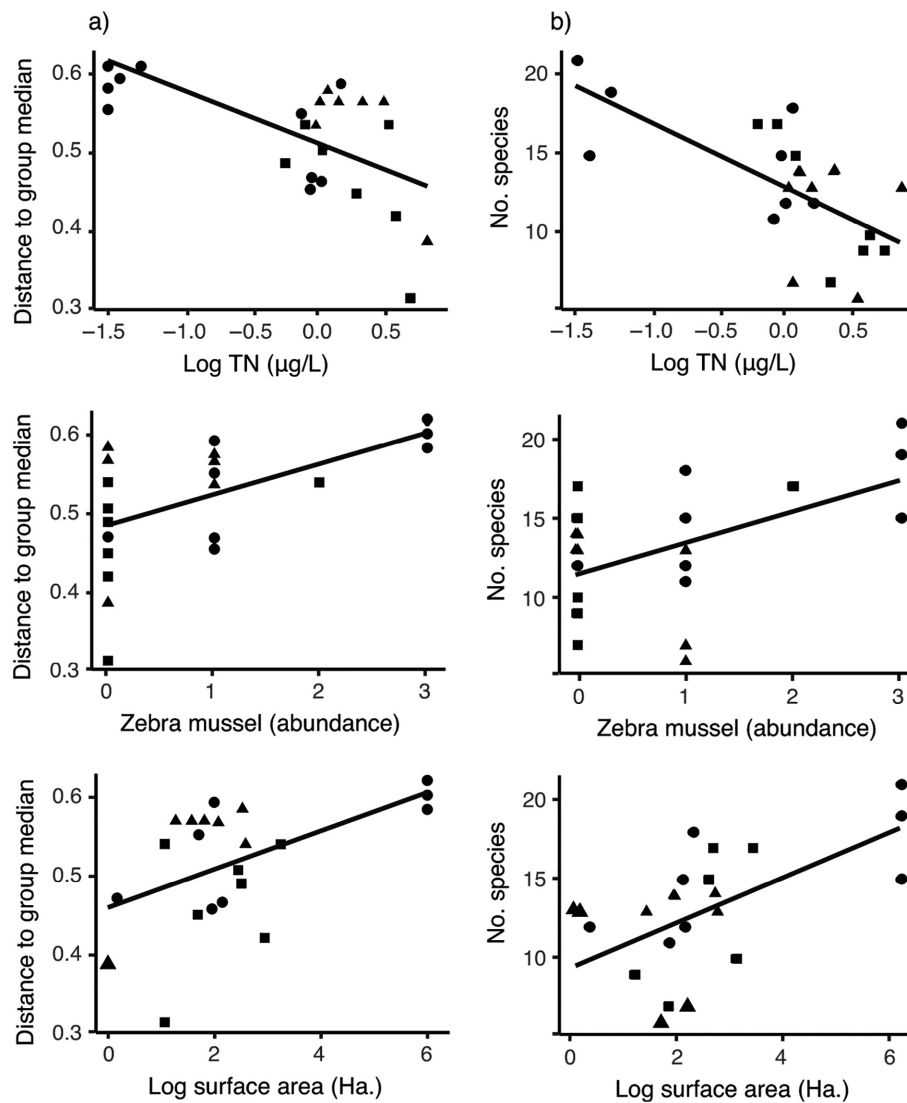


Fig. 3. Linear relationships of (a) lake contemporary macrophyte assemblage heterogeneity (measured as distance to group median in the multivariate space) vs. total nitrogen (TN), zebra mussel abundance and lake surface area; and (b) contemporary lake macrophyte species richness vs. TN, zebra mussel abundance and lake surface area. Circles (Group 1), triangles (Group 2), and squares (Group 3) identify the lakes in the three water-course connectivity groups (Fig. 1).

$DGM_{\text{post-1950}} = 0.15$ ), Gole Lough (14%;  $\Delta DGM = -0.04$ ;  $DGM_{\text{pre-1900}} = 0.25$ ; and  $DGM_{\text{post-1950}} = 0.21$ ), and Lough Head (22%;  $\Delta DGM = -0.04$ ;  $DGM_{\text{pre-1900}} = 0.28$ ; and  $DGM_{\text{post-1950}} = 0.24$ ). Among-lake analysis revealed significant ( $F = 6.8939$ ;  $P = 0.01$ ) post-1960 homogenization and convergence toward similar macrophyte assemblages across lakes (Fig. 4b). IndVal analysis (Fig. 5)

revealed that this post-1960 homogenization of macrophyte assemblages was generally due to declines in abundances of oligo-mesotrophic taxa (including bryophytes, *Isoetes lacustris* L., *Lobelia dortmanna* L., *Najas flexilis* Willd. Rost & Schmidt, *Potamogeton praelongus* Wulfen., and *Potamogeton lucens* L.) and increases in the abundances of species associated with more eutrophic environments (such

as *Lemna minor* L., *Potamogeton pusillus* L., *Potamogeton berchtoldii* Fieber., *Nuphar lutea* L., and *Nymphaea alba* L.).

## DISCUSSION

### Impacts of eutrophication on macrophyte assemblages in space and time

Our analyses reveal that gradual and progressive nutrient enrichment strongly erodes lake macrophyte assemblage heterogeneity across spatial and temporal scales. Both contemporary and paleoecological data reveal changes indicative of macrophyte homogenization. These changes were manifested post-1960 in the paleoecological data and at TN values  $>1.1 \mu\text{g/L}$  in the contemporary data and are characterized by increases in the dominance of fine-leaved *Potamogeton* species (e.g., *P. pusillus* and *P. berchtoldii*), *E. canadensis* Michx., and floating-leaved taxa (water-lilies and *Lemna minor*) and decreases in nutrient-intolerant taxa such as *Isoetes lacustris*, *Najas flexilis*, and several broad-leaved *Potamogeton* taxa (Fig. 5; Appendix S4: Table S1; Kolada et al. 2014).

The decline of macrophyte cover and species richness in shallow lakes caused by eutrophication is well documented (Scheffer 1998, Jeppesen et al. 2000, Kolada et al. 2014). Eutrophication may stimulate a range of responses including gradual vegetational shifts (e.g., from isoetid to more diverse stands of submerged elodeid macrophytes; Arts 2002, Willby et al. 2012), decreases in the seasonal duration of elodeid macrophyte coverage (Sayer et al. 2010a), and apparently sudden shifts from clear water (with abundant and diverse macrophytes) to turbid water conditions (with low transparency and fewer macrophytes; Scheffer 1998, Scheffer et al. 2001, Scheffer and Carpenter 2003). However, despite this relatively large body of research, eutrophication-driven changes in assemblage heterogeneity have received relatively little attention in comparison with studies focusing on patterns of macrophyte abundance and species richness (Jeppesen et al. 2000, Scheffer et al. 2001, Scheffer and Carpenter 2003, Sayer et al. 2010a). Our analyses of contemporary and paleoecological data provide novel and nuanced insights into eutrophication impacts across the landscape, revealing that satellite lakes connected to the

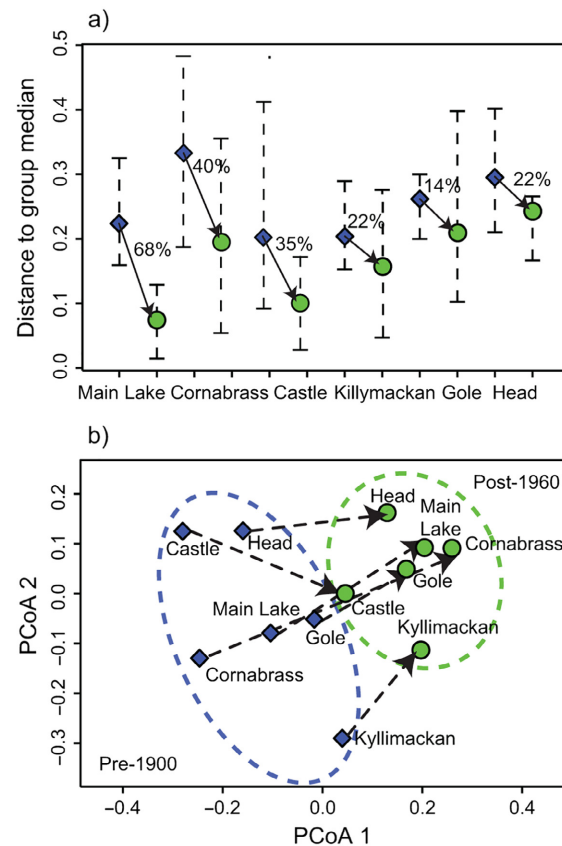


Fig. 4. (a) Variation in lake macrophyte assemblage heterogeneity (measured as distance to group median DGM in the multivariate space) during two time periods across the lakes. For the main lake and the satellite lakes Castle, Cornabross, Killymackan, and Head, the time periods are c. pre-1900 (blue diamonds) and 1960-present (green circles). For Gole Lough, the time periods are 1900–1959 (blue diamonds) and 1960-present (green circles). Rates of variation in macrophyte assemblages between periods ( $\Delta\text{DGM}$ ) were calculated as  $\text{DGM}_{\text{pre-1900}} - \text{DGM}_{\text{post-1950}}$  expressed in percentage. (b) Non-metric multi-dimensional scaling (NMDS) analysis showing each lake distance to group median over the periods c. pre-1900 (blue diamonds) and 1960-present (green circles). Dotted lines denote the lake groups at the two time periods showing a significant ( $F = 6.8939$ ;  $P = 0.01$ ) homogenization among lakes at post-1960.

main lake experienced higher post-1960s rates of macrophyte assemblage homogenization than the more isolated lakes (Fig. 4a). These patterns suggest that prior to 1900, regional processes (e.g.,

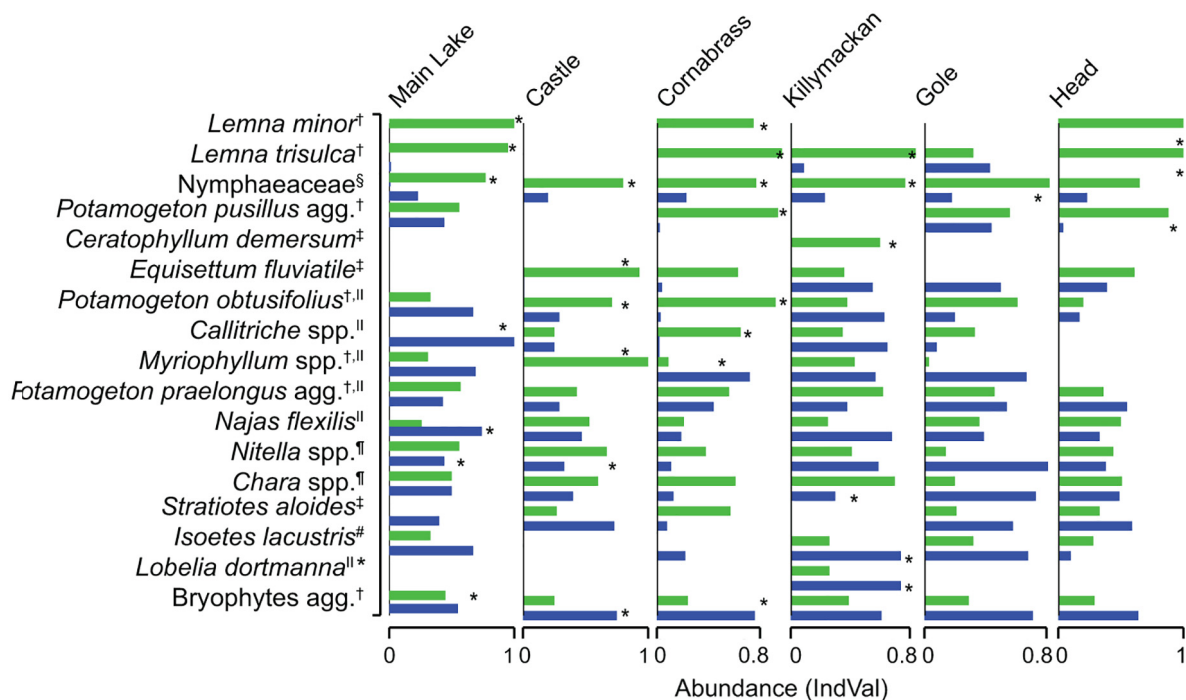


Fig. 5. Characteristic macrophyte fossil taxa revealed by maximum IndVal abundance values for two time periods in the lakes. For the main lake and the satellite lakes Castle, Cornabráss, Killymackan, and Head, the time periods are c. pre-1900 (blue) and 1960-present (green). For Gole Lough, the time periods are 1900–1959 (blue) and 1960-present (green). † leaves, ‡ leaf-spines, § leaf sclereid cells, # megaspores, oospores, || seeds; \* $P \leq 0.05$ ; Agg. (aggregate of closely related species).

seasonal flooding and variation in water level) were influential in maintaining assemblage heterogeneity concurrently in the main lake and in proximal satellite lakes (Castle and Cornabráss), but eventually (post-1960s) these influences were overridden by progressive nutrient enrichment. A paleoecological study by Salgado et al. (2018) addressing macrophyte assemblage variation across three basins in Castle Lough revealed similar nutrient effects over a decadal to centennial scale (10–100 yr), with former drivers of assemblage heterogeneity (e.g., water depth) gradually being displaced by nutrient enrichment, leading eventually to dominance by a few highly competitive macrophyte species. Potential drivers of homogenization include gradual increases in phytoplankton concentrations that restrict macrophyte distributions within lakes and decreases in seasonal duration with macrophytes developing over shorter periods during summer (Sayer et al. 2010a, b). Other mechanisms

are reductions in photosynthetic rates and plant growth due to reduced water transparency (Spence 1967) and selection for taxa (e.g., *E. canadensis*) that can grow at lower light levels (Spence and Chrystal 1970).

#### Homogenization of macrophyte assemblages across sites

The theory of island biogeography (MacArthur and Wilson 1967) and the metacommunity concept (Leibold and Norberg 2004) predict that biodiversity patterns in well-connected landscapes are driven by patch size, habitat quality, environmental heterogeneity, and connectivity. Our results support these predictions, revealing that current macrophyte assemblage homogenization and species loss by eutrophication involve interactions of lake surface area, relative zebra mussel abundance, and watercourse connectivity (Fig. 2). We found positive effects of lake surface area and relative zebra mussel abundance on both macrophyte

assemblage variation and species richness in the main lake and in directly connected satellite lakes (connectivity Group 1). The positive effect of habitat size on plant diversity is one of the most supported patterns in ecology (MacArthur and Wilson 1967) and may be explained by greater diversity of niches and a larger area for colonization. Our analyses also revealed reductions in both macrophyte diversity measures associated with increases in nutrient inputs in more isolated sites (Fig. 3).

Zebra mussel abundance was higher in the main lake than in most satellite lakes, and this may have improved conditions for macrophyte communities by enhancing water transparency (Griffiths 1992, Ibelings et al. 2007). The capacity of zebra mussel populations to filter substantial volumes of water year-round (Strayer 2009) can lead to significant loss of phytoplankton (as suggested by our measurements of Chl-*a*; Higgins and Vander Zanden 2010). The higher concentrations of TN, lower mussel abundances, and elevated levels of Chl-*a* in more isolated sites (Fig. 3) may promote domination by macrophytes species that tolerate nutrient enrichment (e.g., fine-leaved *Potamogeton* species and *E. canadensis*) and the reduction/displacement of intolerant species (e.g., broad-leaved *Potamogeton* species), resulting in more homogenous assemblages. The rarity of zebra mussels in most isolated lakes could be the result of dispersal limitation (Heino and Muotka 2006) or less favorable conditions for zebra mussel establishment in the organic-rich and silty sediments that characterize most satellite lakes (Strayer 2009).

In freshwater systems, connectivity has been characterized as a double-edged sword, promoting diversity but also homogenizing regional communities and abiotic factors and accelerating the spread of invasive species (Strecker and Brittain 2017). In keeping with previous studies (Grant et al. 2012, Strecker and Brittain 2017), we found that increasing connectivity was associated with the occurrence of common taxa, thus increasing local species richness. Highly connected lakes harbored the highest number of species and were characterized by an average of five to six more species than more isolated lakes (Fig. 3). Disentangling the unique effects of dispersal on species richness is challenging and requires further investigation given the interacting effects of connectivity,

relative zebra mussel abundance, and lake surface area.

#### *Responses of diversity measures: assemblage heterogeneity vs. species richness*

Our results revealed declines in both macrophyte assemblage heterogeneity and species richness with increasing eutrophication (Fig. 3). However, the importance of local vs. regional factors in explaining variation associated with these diversity measures differed (Fig. 2). Watercourse connectivity was positively associated with macrophyte assemblage heterogeneity and explained a larger proportion of the variation in assemblage heterogeneity than local abiotic factors. Macrophyte species richness, however, was positively associated with zebra mussel abundance and lake surface area and was negatively associated with eutrophication. In addition, local abiotic factors explained a greater proportion of variation in species richness than connectivity. These contrasting patterns indicate that eutrophication effects are variable but sufficiently large to influence species composition in the ULE system while dispersal among hydrologically connected sites may ultimately maintain macrophyte species abundances that are sensitive to nutrient enrichment within the system (Amarasekare and Nisbet 2001, Mouquet and Loreau 2002). By analyzing measures of both macrophyte assemblage heterogeneity and species richness, our study highlights how regional environmental heterogeneity and spatial gradients in connectivity can influence diversity and dominance and rareness (relative abundance) of plant species in connected landscapes (Amarasekare and Nisbet 2001, Mouquet and Loreau 2002).

## CONCLUSION

By combining landscape-scale contemporary and paleoecological perspectives, we provide evidence that increasing eutrophication has reduced macrophyte diversity over space and time but that watercourse connectivity moderates eutrophication effects. Isolated lakes were characterized by greater impacts of eutrophication but lower rates of macrophyte assemblage homogenization. In connected lakes, rates of macrophyte assemblage homogenization have been higher, but heterogeneity in macrophyte assemblages has



persisted to the present day. This heterogeneity enables the main lake and associated satellite lakes to act collectively as a biodiversity hub, contributing to the integrity and richness of the system through hydrological connections that promote biotic exchange. Our analyses additionally suggest that invasive zebra mussels, large surface areas, source–sink, and species-sorting dynamics all contribute to maintaining the relatively high macrophyte assemblage heterogeneity in these connected water bodies. However, our analyses also reveal that eutrophication impacts have been countering some diversity-generating processes, such as connectivity, over time. There is thus a danger of eventual convergence to homogenous macrophyte assemblages across the Upper Lough Erne system. It would be of interest to determine how changes in the relative abundances of component species in this connected landscape have already impacted ecosystem function (Chapin et al. 2000).

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