Research Paper

Lake and catchment-scale determinants of aquatic vegetation across almost 1000 lakes and the contrasts between lake types

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Running Head: Variation partitioning and lake macrophytes

ABSTRACT

Aim The factors controlling macrophyte (aquatic plant) composition are complex, recent research having shown that the well-studied effects of lake environmental factors (the so-called "environmental filter") can be constrained by hydrological and landscape factors. We investigated the factors determining macrophyte composition in lakes over water body and catchment- scales and the transferability of this pattern across lake types.

Location Almost 1000 lakes distributed across Britain.

Taxon Lake macrophytes

Methods Lakes were partitioned into five types based on subdivision of alkalinity and elevation gradients. Data from botanical surveys were used to compare the spatial turnover and nestedness components of beta diversity between lake types. The relative importance of lake environment (based on local physicochemical data), hydrology (e.g. lake and stream density), landscape (e.g. fragmentation indices, land cover) and spatial autocorrelation in explaining variation in macrophyte composition were derived from variance partitioning.

Results Species composition showed strong spatial structuring, suggestive of overland dispersal, enhanced by spatially-correlated abiotic factors such as alkalinity and elevation. Catchment-scale factors (e.g. land use, connectivity) promoted the establishment of different communities (more or less diverse, or differing in composition) but were of secondary importance. Turnover in composition between upland lakes was lower than in other lake types, reflecting a more specialist flora and increased potential for propagule exchange due to spatial aggregation and higher hydrological connectivity.

Main conclusions Vegetation composition in lakes is more spatially-structured than previously appreciated, consistent with the importance of dispersal limitation, but this does not apply evenly to all lakes, being most acute in lowland high alkalinity lakes. Thus, spatially-structured abiotic factors, such as alkalinity, influence macrophyte composition most (suggestive of niche filtering) in high alkalinity lakes where human impacts tend to be greatest, although nestedness was also lowest in such lakes. By contrast, hydrological connectivity has a proportionally stronger structuring role in upland lakes.

Keywords

Connectivity, dispersal, hydrology, scale-dependent, metacommunity, nestedness, turnover, variation partitioning

INTRODUCTION

Freshwater ecosystems are complex and hierarchical, being structured by a variety of components, scale multiplicity and spatial heterogeneity (Wu & David, 2002). Macrophyte composition in lakes is determined by factors operating at scales that range from lake to catchment and potentially up to continent (Cottenie, 2005; Viana et al., 2016). The effects of lake-scale factors (i.e. lake environmental filters) on macrophyte composition and distribution have been widely studied and are generally considered to be the primary determinants of the biogeographical distribution of macrophytes (Jones et al., 2003; Alahuhta & Heino, 2013). They include physical factors, such as sediment, shoreline morphology and altitude (Recknagel et al., 2006; Vincent et al., 2006), as well as physico-chemical parameters, including nutrient availability, alkalinity and transparency (Capers et al., 2010; Akasaka & Takamura, 2011; O'Hare et al., 2012; Kolada et al., 2014).

Since environmental filters naturally vary in space, their spatial patterning could itself also structure macrophyte communities (Viana et al., 2016). The relationship between macrophyte composition in lakes and the spatial structure of those lakes thus reflects different but overlapping ecological processes: (i) spatial dependency and (ii) spatial autocorrelation (Leibold et al., 2004; Sharma et al., 2011). Spatial dependency arises from the spatial structure of environmental variables acting on the biotic community through species-environment relationships. Spatial autocorrelation is generated by biotic processes such as distance-decay; dispersal limitation is believed to be a particularly strong factor in reinforcing spatial autocorrelation (Legendre et al., 2009). O'Hare et al., (2012) and Alahuhta & Heino (2013) document how lake macrophyte communities respond to different pressures after accounting for spatial autocorrelation.

In addition to lake-scale factors various catchment-scale factors and processes can influence lake macrophyte composition, including land use (Cheruvelil & Soranno, 2008; Hicks & Frost, 2011), isolation (Rolon et al., 2012), flooding (Sousa et al., 2011), habitat diversity and connectivity (Dos Santos & Thomaz, 2007; O'Hare et al., 2012; Willby et al., 2018) and landscape structure (Sun et al., 2018). A large body of research demonstrates that land use change, particularly intensification of agriculture and urbanisation (Alexander et al., 2008; Alahuhta et al., 2012; Rosso & Cirelli, 2013), can have pronounced effects on lake macrophytes, typically driving the loss of submersed species (Rasmussen & Anderson, 2005) and a shift to floating and emergent plant dominance (Egertson et al., 2004).

Furthermore, because lakes and streams are not closed or isolated systems, their connectivity across the landscape and with the wider hydrological network can also influence the distribution of macrophytes at the catchment-scale. However, recent evidence suggests that regional scale processes

influencing dispersal are strongly linked to lake scale environmental filters in regulating macrophyte composition (Alahuhta & Heino, 2013; Chappuis et al., 2014). The connectivity of lakes influences macrophyte composition indirectly through its impact on the exchange of water or other materials (e.g. pollutants) and directly by affecting ease of dispersal. Here we distinguish two indicators of connectivity: landscape connectivity, which represents the physical proximity of lakes over the land surface, and hydrological connectivity, which reflects connectivity of lakes via the drainage network (Freeman et al., 2007; Bracken et al., 2013). Landscape connectivity is important in determining the biogeographical distribution of species dispersed via terrestrial biological vectors (e.g. birds, mammals) or wind, whereas species dependent on water-based dispersal (hydrochory, or obligately aquatic biological vectors) should be more sensitive to hydrological connectivity (Johansson et al., 1996; Makela et al., 2004). Hydrological variables, such as catchment area, catchment slope, precipitation and runoff, are commonly reported to influence lake macrophyte richness and composition (Cheruvelil & Soranno, 2008; Jeppesen et al., 2009; Kissoon et al., 2013), yet few studies consider the influence of lake and stream density at the catchment scale. Studies of floodplain systems confirm that catchment-scale processes can moderate the influence of lake factors such as water chemistry (Van Geest et al., 2005; Dos Santos & Thomaz, 2007); lakes with stronger connectivity are more likely to have similar biogeochemical conditions and thus greater similarity in vegetation (Thomaz et al., 2007), but diverge in their similarity under low water levels when inter-connectivity is reduced.

The relative importance of lake environmental filters (considered a niche process; Zillio and Condit 2007) and dispersal limitation (considered a neutral process; Hubbell 2001) is key to understanding the mechanisms underlying macrophyte community assembly. More recently, consideration has been given to how the relative importance of these processes varies over different spatial scales, ranging from regional to continental (Heino, 2011; Viana et al., 2016). Goncalves-Souza et al. (2014) proposed that the main mechanisms of community assembly are best considered jointly from metacommunity (assemblages are environmentally structured via niche processes) and biogeography (assemblages are spatially structured via dispersal limitation) perspectives. This and other studies (Ng et al., 2009; Heino et al., 2017) indicate that small but significant spatial effects also occur at the metacommunity scale, as well as environmental effects at the biogeographical scale, highlighting the importance of considering both processes across contrasting scales.

Previous studies have analysed lake macrophytes at a different spatial scale, tending to assume all lakes belong to the same metacommunity (Heino, 2011). This ignores the fact that different lake types may support a more or less distinct flora or experience unique environmental drivers or pressures. For example, lakes at low elevation with naturally low concentrations of NO_3 and SO_4^{-2} are prone to anthropogenic acidification (Arts, 2002), while upland lakes can be heavily influenced by peat erosion as well as hydrological exploitation, which lead to a specific macrophyte assemblage (Mosello et al., 2002). Moreover, alkalinity is widely regarded as one of the most important determinants of lake macrophyte composition (Vestergaard & Sand-Jensen, 2000; O'Hare et al., 2012) because it buffers rapid pH changes while also regulating inorganic carbon availability in the form of bicarbonate which

some species are able to utilise. Vegetation composition therefore also varies naturally between systems with, for example, low alkalinity lakes being dominated by short, evergreen isoetids (Maberly & Madsen, 2002), whilst high alkalinity lakes are characterized by larger, faster-growing elodeids (Sand-Jensen & Sondergaard, 1979; Vestergaard & Sand-Jensen, 2000). Thus, although lakes of a contrasting type may occur side by side or at least in the same region, they may be unlikely to exchange species. Few studies have focused on biogeographical scale analyses incorporating subdivision of the freshwater resource, although one study observed differences in the macroinvertebrate and macrophyte taxa between the upland and lowland lakes in Western Ireland lakes, primarily caused by marine-driven hydro-chemical variation and differences in benthic substrate (Soranno et al., 2010; Drinan et al., 2013). Given that limnologists often focus on specific lake types, while conservation designations and management are often developed with the biota of certain lake types in mind, it is important to understand the limits of generalising across lakes as a whole.

Research on catchment-scale drivers of lake assemblages, and their link with lake scale factors, is often limited by the challenges of acquiring suitable data (e.g. lake and habitat connectivity) at a regional scale. In this study, we used data from a large population of British lakes covering a wide gradient of alkalinity and elevation to compare the relative importance of environmental filtering, connectivity and dispersal limitation for macrophyte community composition. We sought to identify which of these processes most constrains macrophyte composition, how their relative importance differs between lake types differing in key typological variables (namely alkalinity and elevation), and if it is reasonable to make generalisations across lake types. We expected that a high geographical dispersion of water bodies and/or low hydrological connectivity would promote turnover between sites, other things being equal. However, this pattern may be distorted by differences in the size of the species pool or degree of anthropogenic impact between lake types, with smaller species pools and higher impact expected to promote nestedness.

MATERIALS AND METHODS

Study lakes and catchments

The study lakes were selected from a dataset of 2558 British lakes containing archived botanical survey data held by the Joint Nature Conservation Committee (JNCC). The catchment boundaries for the 961 lakes >1ha in size (38% of the original dataset) were digitized using Arc Hydro Tools in ArcGIS (v10.2) using the vectorised lake boundaries and DTM from Ordnance Survey (Fig. 1). The remaining lakes were considered too small for their catchment areas to be determined reliably. There are ~14500 water bodies >1ha in area in Great Britain (Bennion et al., 2005). The 961 lakes supported 145 of the 170 aquatic plant taxa (85%) present in the original dataset (see Table S1 in Appendix S1 in Supporting Information).
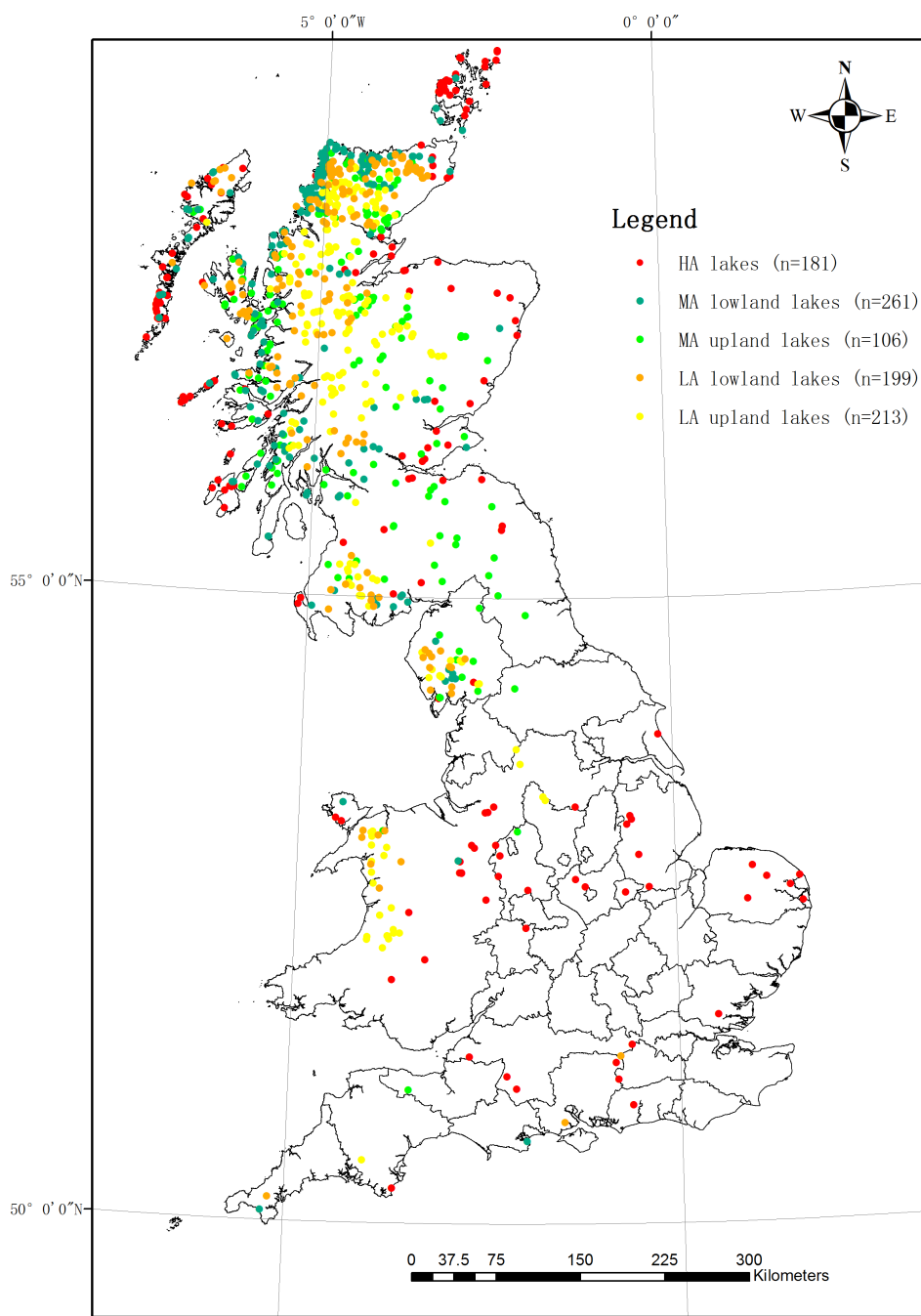
Figure 1. Geographical location of the study lakes (projected coordinate system: British-National-Grid) according to lake type as defined by alkalinity and elevation. HA = high alkalinity; MA = moderate alkalinity; LA = low alkalinity.

To compare the effect of four sets of explanatory variables (environment, hydrology, landscape and spatial) the study lakes (Fig. 1) were then partitioned into five lake types based on subdivision of alkalinity and elevation gradients. These types were low-alkalinity, lowland lakes (alkalinity <10 mg $CaCO_3$ L^{-1}, elevation < 200 m, n=199, labelled as LA-L); low-alkalinity, upland lakes (<10 mg $CaCO_3$ L^{-1}, elevation > 200 m, n=213, labelled as LA-U), moderate-alkalinity, lowland lakes (10-50 mg $CaCO_3$ L^{-1},

elevation < 200 m, n=261, labelled as MA-L), moderate-alkalinity, upland lakes (10-50 mg CaCO$_3$ L^{-1}, elevation > 200 m, n=106, labelled as MA-U) and high alkalinity lakes (>50 mg CaCO$_3$ L^{-1}, elevation < 200 m, n=181, labelled as HA). These lake typologies were established by the UK Technical Advisory Group in accordance with Annex II of the European Water Framework Directive (WFD). The proposed typology approach applies alkalinity boundaries to lake water (Table S2.1a, see Appendix S2) and lake altitude (Table S2.1b, see Appendix S2) as a surrogate for geology to subdivide lakes into types. Alkalinity of drainage water reflects the proportion of calcareous versus siliceous rocks in the catchment. The validity of this lake type classification for the present study was confirmed in advance using Multiple Regression Tree analysis (results not shown).

Sampling of macrophytes and lake water

The original plant survey data were collected mainly between 1985 and 1998 following standard methodologies. Macrophytes were surveyed between July and September by traversing each water body in a boat along multiple transects and by wading in shallower water. The broad time window of the survey data was not considered to be a significant limitation because species occurrence is far more stable over time than species abundance (Sinkeviciene, 2007). Moreover, resurveys of a subsample of the study lakes mostly imply very minor changes on a decadal scale (Willby et al. 2012).

Water samples were taken concurrently with macrophyte surveys for each lake and analysed in the laboratory or linked to independent routine chemical monitoring data collected by the UK environment agencies. Digitised boundaries for the lakes were obtained from the UK Ordnance Survey along with a digitised stream network for the UK (MERIDIAN^{TM} 2). Digital terrain model (DTM) data at a 50 m grid resolution were also obtained from the Ordnance Survey (OS Terrain 50).

Predictors of macrophyte species composition

The resulting catchment boundary for each lake was used to calculate a range of hydrological and landscape variables in ArcGIS. The complete list of explanatory variables, their definition and source are provided in Table 1. Data on lake environment variables was sourced from the GB Lakes Inventory (Bennion et al. 2005). Hydrological variables such as catchment area, mean catchment slope, lake density and stream density were derived specifically for this study. Lake order was also calculated using Arc Hydro Tools (following Martin and Soranno 2006); measures of lake density and spatial structure at the catchment level were derived through analysis of a UK land cover map (LCM2007: http://www.ceh.ac.uk/services/land-cover-map-2007) using FRAGSTATS (v4.1). The landscape dataset included various metrics describing land use and its spatial structure. For simplicity we aggregated agricultural and urban land cover into one class termed 'managed land'.

Table 1. Characteristics of the three environmental datasets in terms of mean, standard deviation (St. Dev) and range (minimum and maximum value) across 961 British lakes; ID is the variable abbreviation used in the results.

| Datasets	ID	Variable	Unit	Definition	Source	Mean ± St.Dev	Range
Lake Environment	L_area	Lake area	km²	Area of water body	GB Lakes	0.69 ± 2.40	0.011 – 38.1
	L_elev	Altitude	m	Lake elevation	GB Lakes	158 ± 138	0.2 - 927
	l_Alk	Alkalinity	mEq/L	Alkalinity concentration of lake water	UK agencies	2.43 ± 0.48	1.09 - 3.81
	L_conduc	Conductivity	µS/cm	Conductivity concentration of lake water	UK agencies	171 ± 384	12-8150
	L_pH	pH	-	pH value of lake water	UK agencies	6.70 ± 0.91	3.74 – 10.09
	L_SDI	Shoreline Development Index	-	Ratio of lake perimeter and area	GB Lakes	1.74 ± 0.66	1.05 – 6.63
	L_MNDP	Mean Depth	m	mean depth of lake basin	GB Lakes	6.00 ± 5.86	0.31 – 69.8
Hydrology	L_order	Lake order	-	Lake order in the outlet point	Ordnance survey	-	0-4
	C_area	Catchment area	km²	Area of lake catchment	Ordnance survey	24.7±92.4	0.12-1764
	C_SDI	Catchment shoreline development index	-	Shoreline development index of catchment	Ordnance survey	1.64±0.24	1.23-2.87
	C_drain_des	Catchment drainage density	km/km²	Total stream length/ catchment area	Ordnance survey	1.49±3.01	0.026-62.8
	C_Slope	Catchment slope	Degree	Slope of catchment	Ordnance survey	7.64±5.34	0.19-29.94
	C_PLAND	Total lake area in catchment	%	Total lake area / catchment area	FRAGSTATS	7.93±6.30	0.08-44.91
	C_PD	Catchment Lake density	1/ km²	number of lakes per 1 km² in catchment	FRAGSTATS	0.89±1.02	0.02-7.80
	C_FRAC	Lake Fractal Dimension index	-	Average degree of complexity of lakes based on a perimeter/ area ratio in catchment	FRAGSTATS	1.07±0.02	1.02-1.20
	C_AI	Aggregation index	%	The number of alike adjacent patches between lakes in catchment	FRAGSTATS	102±270	57.14-8462
Landscape	D_to_sea	Distance to sea	km	Distance to sea	Ordnance survey	12.4 ± 13.1	0.10-85.4
	M_PD	Patch density	1/ km²	Total patch numbers/Catchment area	FRAGSTATS	10.33±7.86	0.23-66.51
	M_LSI	Landscape shape Index	-	provides a standardized measure of total edge or edge density that adjusts for the size of the landscape	FRAGSTATS	6.49±6.20	1.48-57.1
	M_CONTIG	Contiguity Index	-	The mean contiguity value for the cell in a patch minus 1, divided by the sum of the template values minus 1.	FRAGSTATS	0.65±0.08	0.34-0.93
	M_CIRCLE	CIRCLE Index	-	Area (m²) of each patch/1km² around patch.	FRAGSTATS	0.57±0.05	0.28-0.69
	M_DIVISION	Landscape Division Index	Proportion	Measure the fragmentation of the landscape	FRAGSTATS	0.69±0.22	0.03-0.99
	M_PLAND	Land use coverage	%	Managed land area (agriculture + urban)/ Catchment area	FRAGSTATS	0.75±3.46	0.0001-52.26
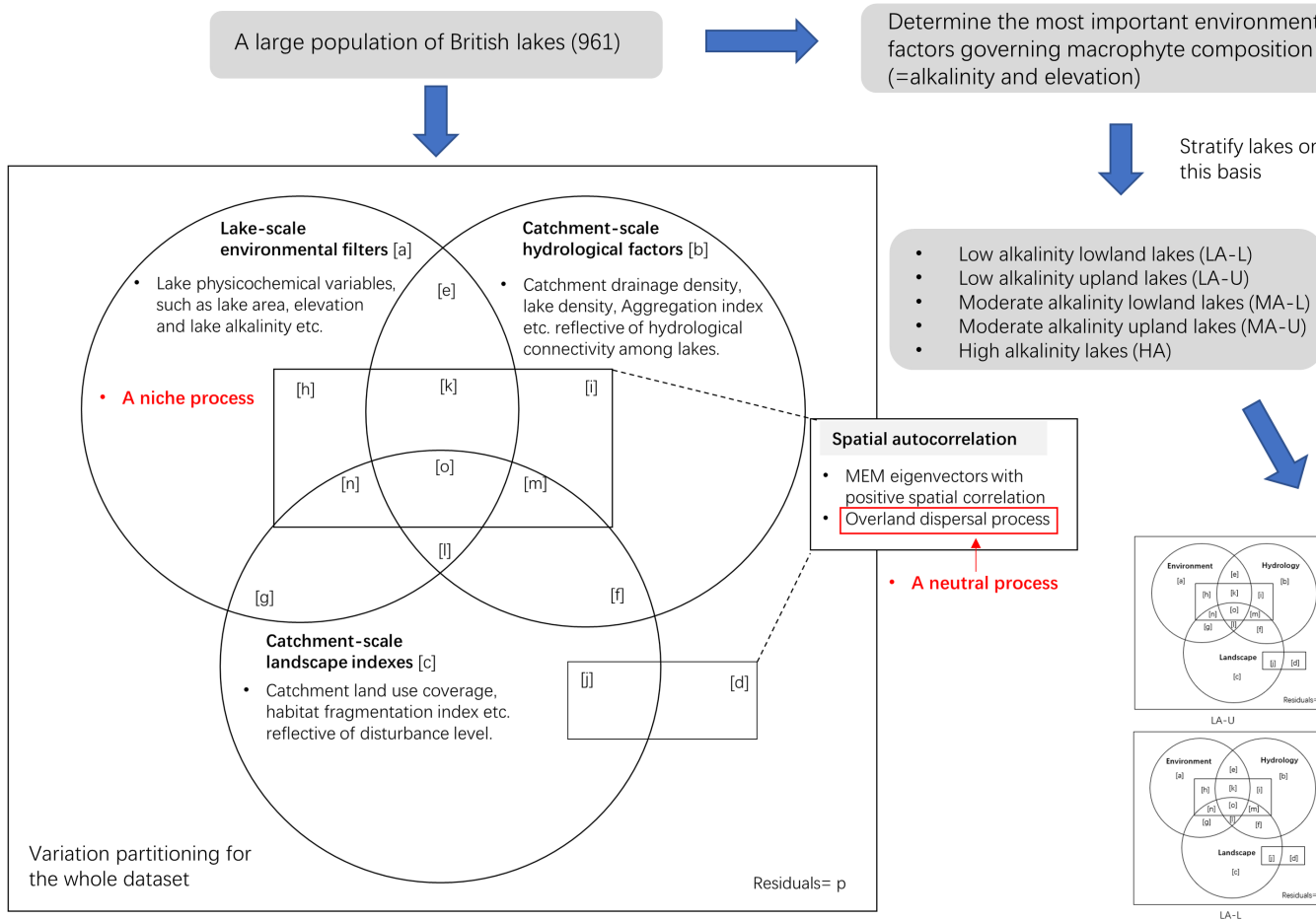
Figure 2 The conceptual model followed to infer the relative importance of environmental filtering and dispersal limitation for macrophyte composition and how this differs between the lake types.

Conceptual model

Our conceptual model (Fig. 2) considers the relative importance of environmental filtering, hydrological connectivity, landscape fragmentation and spatial autocorrelation in determining general macrophyte composition (i.e. variation partitioning for the whole 961 lakes) and, subsequently, how this general pattern compares between individual, and more environmentally homogenous, lake types (i.e. lake type partitioning).

In the variation partitioning analyses, the response variable is lake macrophyte presence/absence data; the explanatory datasets are lake-scale environmental (Fractions [a] in Fig. 2), catchment-scale hydrological variables (Fractions [b] in Fig. 2), catchment-scale landscape factors (Fractions [c] in Fig. 2) and spatial autocorrelation (Fractions [d] in Fig. 2). For passively dispersing organisms such as macrophytes lake connectivity, the degree of spatial connection between individual water bodies, can significantly affect the ability to disperse and colonise new sites. Freshwater bodies may be connected geographically (relative to the ability of species to disperse) if they are sufficiently close relative to the scale of movement of potential dispersal vectors (Ricketts, 2001), or connected hydrologically if they are linked by the temporary or permanent flow of water between sites (Ganio et al., 2005). The Euclidean distance between geographically separated habitats indicates potential overland connectivity between lakes. Spatial autocorrelation (pure fraction of space, fraction [d] in Fig. 2) would thus be expected to more closely reflect overland dispersal processes, whilst hydrological connectivity (pure fraction of hydrology, fraction [b] in Fig. 2) should relate more strongly to dispersal via hydrochory or strictly aquatic biological vectors. Overland dispersal may be the only effective route when lakes are not fully connected.

Note that the spatial filters represent dispersal limitation in the variation partitioning for the 961 lakes, whereas in the lake type partitioning analyses these filters also represent the distribution patterns of sites belonging to each lake type.

Statistical analysis

The total beta diversity (β_{total}), and its components, species turnover ($\beta_{turnover}$) and nestedness ($\beta_{nestedness}$), were estimated for each lake type and the global dataset following Baselga (2010). Turnover indicates species sorting influenced by environmental filtering and dispersal processes, while nestedness is correlated with species loss and extinction-colonization dynamics (Si et al., 2016). The beta-diversity metrics for different lake types were calculated using the functions 'betapart.core' and 'beta.multi' in 'betapart' package (Baselga et al., 2017) in R (v3.1.3) based on the species presence/absence data.

Rarefaction curves were used to derive the mean values of randomized species richness generated by resampling (n=30) with replacement. This allowed the species pool to be compared between lake types containing differing numbers of lakes. Rarefaction curves were plotted using the functions 'rarc' in the package 'rich' (Rossi, 2011) based on the macrophyte species presence/absence matrices. The

beta diversity partitioning and species accumulation curves provide more detailed information on the size of the species pool in each lake group and its heterogeneity, which helps in interpreting variation partitioning results.

For each lake type, variation partitioning (Peres-Neto et al., 2006; De Bie et al., 2012) was performed using a spatial redundancy analysis (spatial RDA) and up to four subsets of data, covering lake environment, hydrology, landscape and spatial structure components respectively, to quantify the unique and combined fraction of macrophyte variation explained by each component.

The latitude-longitude data for each lake were transformed into Cartesian coordinates using the function 'geoxy' from package 'soda' in R (v3.1.3). Macrophyte species presence-absence data were Hellinger-transformed. The spatial RDA model was run using the spatial eigenvectors obtained from Moran's Eigenvector Maps (MEM, Dray et al. 2006; formerly known as Principal Coordinates of Neighbour Matrices (PCNM), Borcard et al. 2004). The resulting spatial eigenvectors were used in the explanatory matrix to account for spatial autocorrelation in the dataset. A total of 7 MEMs, 6 MEMs, 17 MEMs, 8 MEMs and 17 MEMs were derived to form a spatial dataset for each lake type (i.e. LA-L, LA-U, MA-L, MA-U and HA respectively). The truncation distance was determined by using the minimum spanning tree. Then Moran's I (in the first distance class 0 to truncation threshold, no spatial correlation) was determined for each MEM variable. MEM eigenvectors with positive spatial correlation were selected rather than those eigenvalues greater than Moran's I (for more information see Table 2).

For each lake type, we independently ran an RDA with forward selection (Blanchet et al., 2008) on the lake environment, hydrology, landscape and spatial datasets using function 'ordir2step' in R package 'vegan'. Lake order was recoded into a dummy binary variable. Four matrices were composed of the significant forward-selected variables, and a set of positive eigenvectors was generated from principal coordinate analysis (PCoA) based on the presence/absence data of macrophyte species. Variation partitioning with four explanatory matrices has been used in previous studies (e.g., Viana et al. 2016), to investigate the mechanisms accounting for species dissimilarity in aquatic communities over regional (up to 300 km) and continental (up to 3300 km) scales. In the present work, the method was used to compare the relative importance of the four studied components (i.e. lake environment, hydrology, landscape and spatial) in explaining macrophyte composition within different major lake types. Venn diagrams were used to represent the total community variation in that lake type via the rectangle bounding the diagram (Fig. 2). Each circle or overlap region then represented the portion of variation accounted for by a pure or combined explanatory matrix. This generated 16 fractions: 4 pure effects of the lake environment, hydrology, landscape and spatial datasets (Fractions [a] to [d] in Fig. 2), plus 12 joint effects of the two or three separate components (Fractions [e] to [o] in Fig. 2) and 1 unexplained component of the variance (Residuals in Fig. 2). Monte Carlo permutation tests were used to determine the significance of the pure fraction (Fraction [a] to [d]). However, the shared partitions (e.g. Fractions [e] to [o] in Fig. 2) are not interaction terms, and their significance cannot be tested individually.

It is problematic to compare adj-r^2 values for different variance components if the sample sizes of groups are uneven (Dapporto et al., 2014), as in this case. We therefore evaluated the uncertainty of the explanatory power of each component using bootstrapping. Bootstrapping was conducted by random resampling (n= 100 times, using a loop programmed in R to sample 106 lakes for each lake type respectively, corresponding with the minimum sample size across all lake types) with replacement from the original sample (Quinn & Keough, 2004). The bootstrapping procedure allowed the variation partitioning to be repeated using the regenerated lake observations for lake types of a standard sample size. The standardized error of the coefficient of determination (i.e. R^2_{adj}) from the bootstrapped models was calculated to illustrate the uncertainty of each fraction from the variation partitioning.

RESULTS

Beta diversity by lake type

Beta-diversity partitioning provided an enhanced insight to the factors accounting for the spatial variability in macrophyte communities compared with a consideration of total beta diversity alone. Fig. 3 compares the mean value of β_{total}, $\beta_{turnover}$ and $\beta_{nestedness}$ for each lake type. Beta-diversity partitioning for the entire metacommunity is also presented. Total dissimilarity, β_{total}, was much higher for HA lakes than other lake types. The mean value of $\beta_{turnover}$ for each lake type ranged from 0.62 to 0.80, being 5-13 x higher than the equivalent mean $\beta_{nestedness}$. Nestedness-resultant dissimilarity ($\beta_{nestedness}$) was highest in LA-U lakes (mean = 0.149, SD = 0.049, range = 0.045 - 0.271) and lowest in HA lakes (mean = 0.061, SD = 0.018, range = 0.019 - 0.110). The fraction of the total turnover due to differences in species richness was thus almost three times higher in LA-U lakes (19.5%) than in HA lakes (7%).
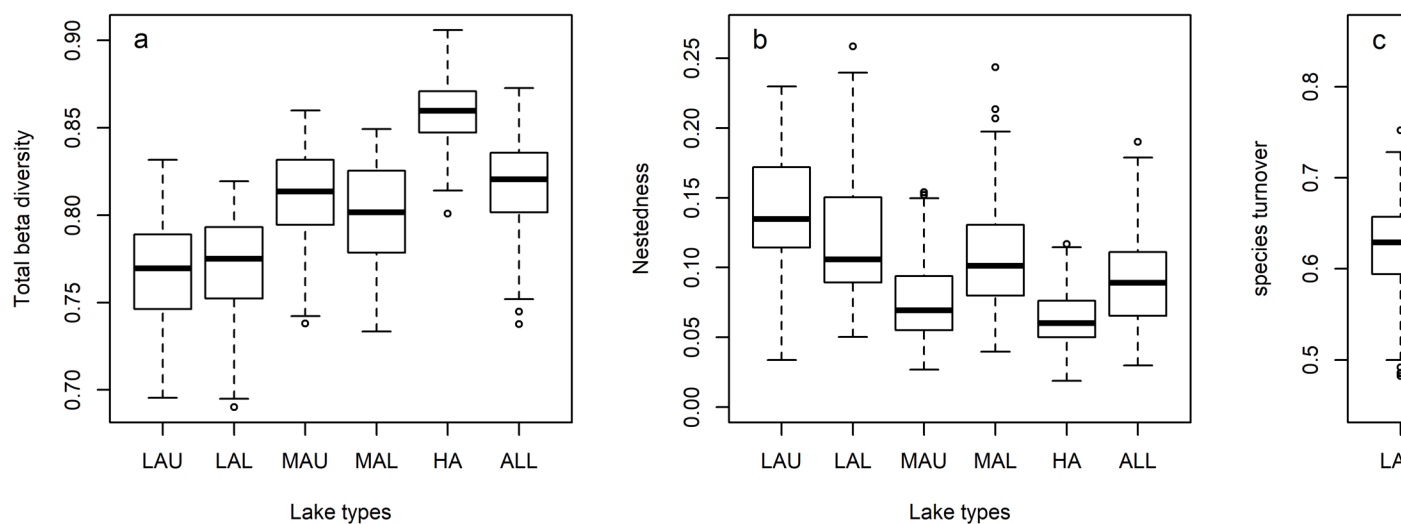
Figure 3. Boxplots comparing components of beta diversity and its components across the five major British lake types (LA-L = low alkalinity and lowland; LA-U = low alkalinity and upland; MA-L = moderate alkalinity and lowland; MA-U = moderate alkalinity and upland; HA = high alkalinity). Lake types are ordered by increasing productivity from left to right. Boxes represent the interquartile range and median with whiskers showing the upper and lower 10th percentiles.

Gamma diversity by lake type

Fig. 4 illustrates the rarefaction curves for macrophyte richness based on the number of sampled lakes in the five different lake types and for the global dataset. The membership of the species pool and their growth forms are given in Fig. S2.1 (see Appendix S2). The cumulative number of species stabilised below approximately 100 sites for all lake types (Fig. 4) suggesting adequate and comparable sampling efficiency. Among different lake types, HA lakes hosted the largest species pool (131 species) for a given number of lakes, consistent with their higher β_{total}. Other lake types were broadly similar (78 to 103 species), with LA-U lakes, the least productive lake type, having the smallest species pool.
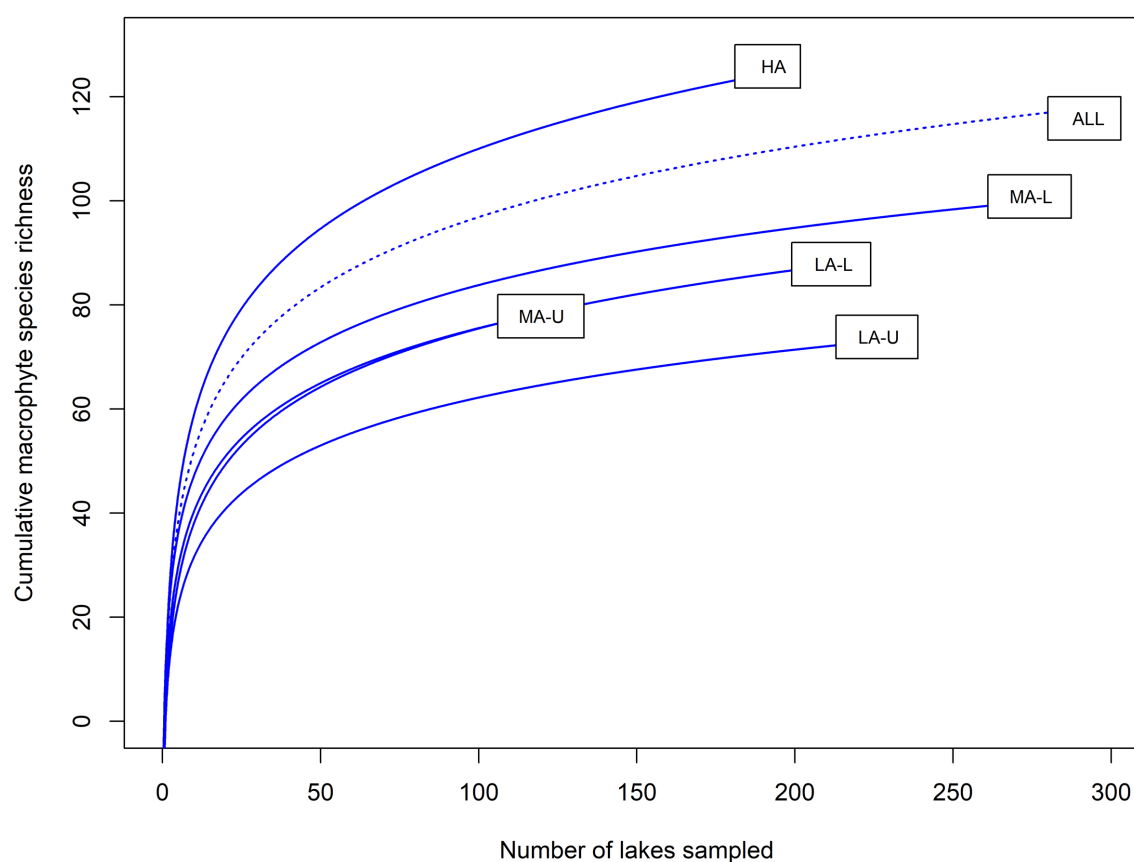

Figure 4. Sample-based rarefaction curves for macrophyte species richness in different British lake types (LA-L = low alkalinity and lowland; LA-U = low alkalinity and upland; MA-L = moderate alkalinity and lowland; MA-U = moderate alkalinity and upland; HA = high alkalinity; ALL = global dataset).

Variation partitioning by lake type

Redundancy Analysis (RDA) (n=961, Fig. S2.2, see Appendix S2) indicated that macrophyte species composition varied strongly depending on lake alkalinity (adj-r^2=7.0%) and elevation (adj-r^2=1.1%), which were included as formal predictors.

The sets of environment, hydrology, landscape and spatial variables collectively explained 11.1%, 13.9%, 16.3%, 18.9% and 23.9% of the total variation in macrophyte composition in LA-L, LA-U, MA-L, MA-U and HA lakes respectively (Fig. 5). These results indicate that the total variation explained independently or jointly by each dataset varies strongly by lake type. Unexplained variation was highest in low alkalinity lakes, suggesting other important ecological processes influence species distribution at a regional scale in these lakes.

For each lake type, most of the explained community variation could be attributed to the pure effect of the spatial patterns (fraction [d] in Fig. 5; 3.5%-11% for each lake type, equivalent to FTVE of 30.5 – 45.9%). The other three sources of variation had unique contributions that differed between lake types: environment alone (fraction [a] in Fig. 5; 0.9%-3.4%), hydrology alone (fraction [b] in Fig. 5; 0.3%-2.4%) and landscape alone (fraction [c] in Fig. 5; <0 -1.7%). All the pure component fractions were significant (p<0.001) except for the landscape fraction in HA lakes (R^2_{adj}=-0.004; p=0.43). The generally low R^2_{adj} for the pure landscape component could reflect the relatively high shared fraction between landscape and spatial components (fraction [j] in Fig. 5; 1.3-2.5%), indicating that a large amount of the variation explained by landscape variables was spatially structured. The significance of the global model for each predictor dataset and the variables retained in the forward selection to be used in the final variance partitioning model are listed in Table 2.

The joint (fully overlapping) contribution of the four explanatory datasets was consistently small (R^2_{adj} <1.3%) across different lake types. The amount of variance shared by some combinations of explanatory datasets revealed greater dependency on lake alkalinity. Thus, the variation explained commonly by environment, hydrology and spatial explanatory datasets (fraction [k] in Fig. 5) increased from <0 to 1.9%, while the contribution of the spatially structured environment fraction (shared space and environment effect; fraction [h] in Fig. 5) increased from <0 to 1.8% from low to high alkalinity.

We repeated the variation partitioning analysis using the randomly-selected lake samples (n=106) to estimate the uncertainty in the explanatory contribution of each component when the sample size is standardised. For different lake types, the standard deviation of the mean R^2_{adj} for each component ranged from 0.001 to 0.1 (values in brackets, Fig. 5), indicating that the uncertainty was sufficiently small to not change the underlying pattern in the contribution of each component.

Triplots of pRDA (Fig. S2.3, see Appendix S2) were used to describe all statistically significant (p<0.05) relationships of environmental, hydrological and landscape variables with macrophyte community composition, after accounting for spatial autocorrelation, for each lake type respectively. Taking LA-L lakes as an example, RDA1 (accounting for 2.1% of variance, Fig. S2.3b, see Appendix S2) was most positively correlated with the spatially structured variables lake alkalinity and lake depth, while the second RDA axis (accounting for 1.2% of variance) was mostly positively correlated with aspects of hydrological connectivity (e.g. lake coverage, stream density).
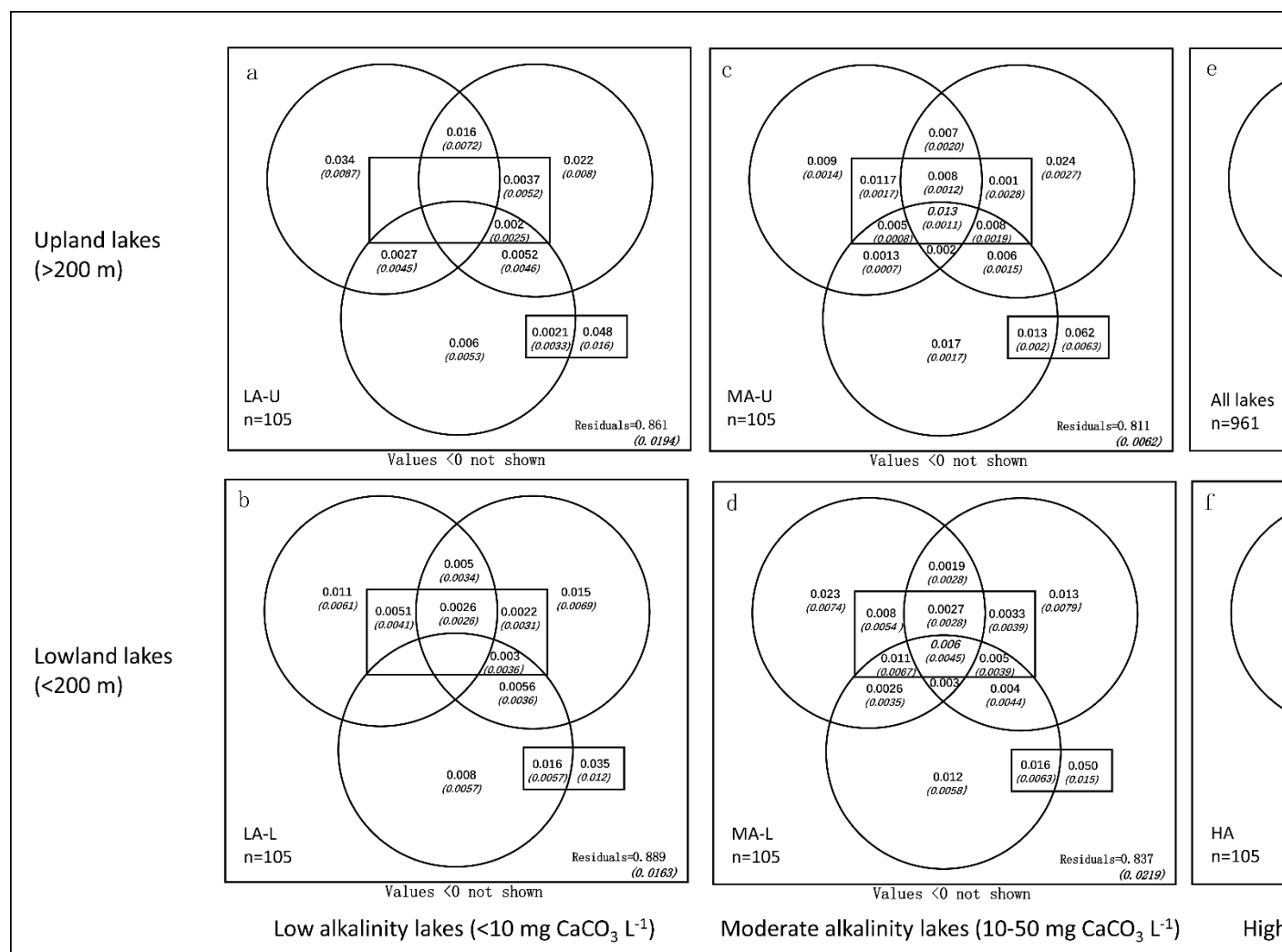
Figure 5. Variation partitioning of the Hellinger-transformed macrophyte data into an environmental component (upper left-hand circle), a hydrological component (upper right-hand circle), a landscape component (lower circle) and a spatial component (disjoined rectangles) (Fig.5e). This generates 16 fractions: 4 pure effects of the environment, hydrology, landscape and spatial datasets (Fractions [a] to [d]) plus 12 joint effects of the two or three separate sets (Fractions [e] to [o]) and 1 unexplained component of the variance (Residuals). Variation partitioning results of the Hellinger-transformed macrophyte data for each lake type (Figure 5a – low alkalinity and upland lakes; Figure 5b – low alkalinity and lowland lakes; Figure 5c – moderate alkalinity and upland lakes; Figure 5d – moderate alkalinity and lowland lakes; Figure 5f – high alkalinity lakes; Figure 5e all lakes). Values indicate the fraction of the explanatory set (as R^2adj). Monte Carlo permutation tests were used to determine significance of the pure fraction (Fraction [a] to [d]) (only significant values are shown). The standard deviation of the mean R^2adj for each component from the bootstrapping procedure is presented within brackets to illustrate the uncertainty. Negative R^2adj values, which explain less of the variation than would be expected by chance, have been excluded. "n" in the lower left corner of each panel refers to the loop programmed resampling from the original lake dataset for each lake type.

Table 2 Details of variation partitioning results covering the significance of the global model for each predictor dataset and the variables retained after forward selection to be used in the final variance partitioning model

Lake type	Datasets	Significance of the global model	Variables retained in the global model after forward selection
LA-L	Environmental	F=1.82, P<0.001***, adj-r^2=0.0283	Alkalinity (adj-r^2=0.015,p=0.0001); Conductivity (adj-r^2=0.012,p=0.0006); Mean depth (adj-r^2=0.011,p=0.0017); SDI (adj-r^2=0.009,p=0.0124)
	Hydrological	F=1.91, P<0.001***, adj-r^2=0.0396	Lake order (adj-r^2=0.011,p=0.0001); Catchment slope (adj-r^2=0.010,p=0.0001); Aggregation index (adj-r^2=0.005,p=0.0014); Lake fractal dimension index (adj-r^2=0.004,p=0.009); Total lake area in catchment (adj-r^2=0.003,p=0.015); catchment SDI (adj-r^2=0.003,p=0.024)
	Landscape	F=1.95, P<0.001***, adj-r^2=0.0325	Landscape shape index (adj-r^2=0.014,p=0.0001); Patch density (adj-r^2=0.010,p=0.0001); Contiguity index (adj-r^2=0.005,p=0.0057);Land use coverage (adj-r^2=0.003,p=0.047)
	Spatial autocorrelation	F=1.52, P<0.001***, adj-r^2=0.0730	7 significant eigenvectors; Truncation distance=274.91; Number of eigenvalues (positive)=43(30); Expected value of Moran's I=-0.00505
LA-U	Environmental	F=2.59, P<0.001***, adj-r^2=0.0502	Elevation (adj-r^2=0.036,p<0.0001); Alkalinity (adj-r^2=0.010,p<0.0001)
	Hydrological	F=2.18, P<0.001***, adj-r^2=0.0478	Catchment slope (adj-r^2=0.017,p=0.0001); Total lake area in catchment (adj-r^2=0.021,p=0.0001); Catchment drainage density (adj-r^2=0.004,p=0.0071)

	Landscape	F=1.51, P=0.002***, adj-r^2=0.0165	Landscape division index (adj-r^2=0.074,p=0.0009); Patch density (adj-r^2=0.048,p=0.0057)
	Spatial autocorrelation	F=1.29, P<0.001***, adj-r^2=0.0429	6 significant eigenvectors; Truncation distance=189.33; Number of eigenvalues (positive)=53(32); Expected value of Moran's I=-0.00474
MA-L	Environmental	F=3.30, P<0.001***, adj-r^2=0.0584	Alkalinity (adj-r^2=0.040,p=0.0001); Lake area (adj-r^2=0.007,p=0.0006); Conductivity (adj-r^2=0.006,p=0.0006); SDI (adj-r^2=0.003,p=0.008); Elevation (adj-r^2=0.002,p=0.015)
	Hydrological	F=2.15, P<0.001***, adj-r^2=0.0383	Catchment lake density (adj-r^2=0.016,p=0.0001); Catchment drainage density (adj-r^2=0.005,p=0.002); Catchment SDI (adj-r^2=0.005,p=0.0007); Catchment slope (adj-r^2=0.004,p=0.0029); Lake fractal dimension index (adj-r^2=0.004,p=0.0034); Total lake area in catchment (adj-r^2=0.004,p=0.0028)
	Landscape	F=3.39, P<0.001***, adj-r^2=0.0606	Landscape division index (adj-r^2=0.029,p=0.0001); Land use coverage (adj-r^2=0.013,p=0.0001); Landscape shape index (adj-r^2=0.007,p=0.0001); Patch density (adj-r^2=0.005,p=0.0002); Circle index (adj-r^2=0.002,p=0.0319); Contiguity index (adj-r^2=0.002,p=0.0142)
	Spatial autocorrelation	F=1.64, P<0.001***, adj-r^2=0.131	17 significant eigenvectors; Truncation distance=257.40; Number of eigenvalues (positive)=81(61); Expected value of Moran's I=-0.00385
MA-U	Environmental	F=2.01, P<0.001***, adj-r^2=0.0633	Alkalinity (adj-r^2=0.045,p<0.0001); Elevation (adj-r^2=0.011,p<0.0001)
	Hydrological	F=1.97, P<0.001***, adj-r^2=0.0766	Catchment area (adj-r^2=0.023,p=0.0001); Catchment slope (adj-r^2=0.018,p=0.0001); Total lake area in catchment (adj-r^2=0.017,p=0.0001); Catchment lake density (adj-r^2=0.009,p=0.0001)
	Landscape	F=2.05, P<0.001***, adj-r^2=0.0655	Landscape shape index (adj-r^2=0.037,p=0.0001); Patch density (adj-r^2=0.017,p=0.0001); Land use coverage (adj-r^2=0.006,p=0.0194); Landscape division index (adj-r^2=0.005,p=0.0239)
	Spatial autocorrelation	F=1.58, P<0.001***, adj-r^2=0.1452	8 significant eigenvectors; Truncation distance=231.84; Number of eigenvalues (positive)=46(31); Expected value of Moran's I=-0.00952
HA	Environmental	F=3.54, P<0.001***, adj-r^2=0.0903	Alkalinity (adj-r^2=0.046,p=0.0001); Lake pH (adj-r^2=0.019,p=0.0001); Elevation (adj-r^2=0.014,p=0.0001); Mean depth (adj-r^2=0.004,p=0.0052); lake area (adj-r^2=0.003,p=0.0154); SDI (adj-r^2=0.002,p=0.0335)

	Hydrological	F=2.05, P<0.001***, adj-r^2=0.0503	Catchment slope (adj-r^2=0.021,p=0.0001); Catchment lake density (adj-r^2=0.020,p=0.0001); Total lake area in catchment (adj-r^2=0.0053,p=0.0042)
	Landscape	F=2.56, P<0.001***, adj-r^2=0.0576	Land use coverage (adj-r^2=0.023,p=0.0001); Landscape shape index (adj-r^2=0.011,p=0.0001); Patch density (adj-r^2=0.012,p=0.0001); Circle index (adj-r^2=0.005,p=0.0034); Contiguity index (adj-r^2=0.003,p=0.0363)
	Spatial autocorrelation	F=2.303, P<0.001***, adj-r^2=0.212	17 significant eigenvectors; Truncation distance=135.84; Number of eigenvalues (positive)=80(37); Expected value of Moran's I=-0.00559
ALL lakes	Environmental	F=14.95, P<0.001***, adj-r^2=0.0926	Alkalinity (adj-r^2=0.070,p=0.0001); Elevation (adj-r^2=0.011,p=0.0001); lake pH (adj-r^2=0.004,p=0.0001); Lake area (adj-r^2=0.003,p=0.0001); Lake SDI (adj-r^2=0.002,p=0.0001); Conductivity (adj-r^2=0.002,p=0.0001); Mean depth (adj-r^2=0.001,p=0.027)
	Hydrological	F=5.550, P<0.001***, adj-r^2=0.041	Catchment slope (adj-r^2=0.011,p=0.0001); Total lake area in catchment (adj-r^2=0.011,p=0.0001); Catchment lake density (adj-r^2=0.011,p=0.0001); Catchment drainage density (adj-r^2=0.011,p=0.0008); lake fractal dimension index (adj-r^2=0.011,p=0.0003); Lake order (adj-r^2=0.011,p=0.0009); Catchment SDI (adj-r^2=0.011,p=0.005); Catchment area (adj-r^2=0.011,p=0.021)
	Landscape	F=7.61, P<0.001***, adj-r^2=0.046	Landscape division index (adj-r^2=0.019, p=0.0001); Land use coverage (adj-r^2=0.014, p=0.0001); habitat patch density (adj-r^2=0.006, p=0.0001); Landscape shape index (adj-r^2=0.004, p=0.0001); Circle index (adj-r^2=0.001, p=0.0001)
	Spatial autocorrelation	F=1.68, P<0.001***, adj-r^2=0.167	62 significant eigenvectors; Truncation distance=99.08; Number of eigenvalues (positive)=458(281); Expected value of Moran's I=-0.00104

DISCUSSION

The composition of freshwater plant assemblages is broadly understood to reflect a balance between niche filtering at the lake-scale and broad-scale hydrological (e.g. flow) and landscape processes (e.g. habitat fragmentation) that can vary independently. Lake factors, such as alkalinity, nutrients, light, water depth and physical disturbance, are well documented influences on aquatic plant distribution (Barendregt & Bio, 2003; Feldmann & Noges, 2007; Weithoff et al., 2010; Keruzoré & Willby, 2014; Steffen et al., 2014). However, equivalent studies on the effect of variables at coarser scales (catchment or landscape) are scarce (Sousa et al., 2011; O'Hare et al., 2012; Rolon et al., 2012), probably in part because of the restricted availability of suitable datasets. In this study we used variation partitioning to assess if elevation and alkalinity gradients form the primary basis for macrophyte beta diversity in lakes and then compared how much of the spatial variation in composition within different lake types is controlled by these lake-scale factors versus a suite of catchment- and landscape-scale variables.

The partitioning of beta-diversity in different lake types

It is instructive to also view nestedness and turnover in the context of lake types since the spatial distribution of lakes within different types varies, while some lake types diverge quite strongly in their floristic composition and, potentially therefore, the dispersal ability of the species they support. In our work, $\beta_{turnover}$ (0.6-0.8, Fig. 3c) caused by compositional change, was the dominant component of macrophyte beta-diversity patterns, rather than $\beta_{nestedness}$ (0.05-0.15, Fig. 3b) based on differences in richness. This conclusion is consistent with most partitioning studies on beta diversity, indicating that species sorting plays a vital role in assembling macrophyte communities (Hill et al., 2017; Soininen et al., 2018).

Both turnover and nestedness contributed to the total dissimilarity, although their relative importance varied depending on lake type, mirroring findings for other aquatic biota (Brendonck et al., 2015; Tonkin et al., 2016; Gianuca et al., 2017). $\beta_{turnover}$ was much higher in HA lakes compared with other lake types (Fig. 3c). Two inter-related facts could explain this pattern; (i) the larger overall species pool of HA compared to LA lakes (Fig. 4); (ii) HA lakes are more geographically dispersed in Britain (Fig. 1) than other lake types and environmental heterogeneity, for example in chemistry and substrate, will therefore be correspondingly greater (Alahuhta et al., 2017). High alkalinity lakes are unquestionably more impacted by anthropogenic pressures than their LA counterparts, being on average 1.2 ecological status classes poorer in the UK based on Water Framework Directive assessments (Willby et al., 2012). However, the argument that this impact will increase turnover (Alahuhta et al., 2017) seems unlikely to apply to the HA lakes in our study; greater impact would be expected to increase nestedness relative to other lake types whereas we found the inverse pattern.

Nestedness was highest in LA lakes and was proportionally almost three times higher than in HA lakes. Alahuhta et al. (2017) also noted in their global study that nestedness tended to be highest where overall beta diversity was low. Nestedness in LA lakes might therefore be indicative of their more

restrictive growing conditions, whereby less productive/poorly connected lakes of this type only contain a subset of the species pool of the more productive/well-connected and therefore most species-rich ones (Henriques-Silva et al., 2013; Bender et al., 2017). Our results suggest that the loss of species will be focussed in areas with low species diversity where stress is high and immigration rates are low. Alternatively, the relatively high nestedness within LA-U lakes could reflect the imprint of widespread historic acidification of British uplands, driven by atmospheric pollution, under which the flora of acidified lakes was reduced to a subset of that of less impacted lakes through the loss of sensitive species which have been slow to recolonise (Monteith et al., 2005; Heino et al., 2018). If so, nestedness might be expected to decline as LA-U lakes recover from acidification.

The importance of lake, catchment and landscape scape variables in explaining species turnover

Spatial structure in community composition can be generated by both spatially correlated environmental variables (shared fraction of space and environment, fraction [h] in Fig. 5e) and spatial autocorrelation (pure fraction of space, fraction [d] in Fig. 5e) (Sharma et al., 2011). Our study indicated that spatial autocorrelation was more important than both lake- and catchment-scale variables in explaining macrophyte composition at a broad (i.e. national) scale. This is probably because spatial autocorrelation is intrinsic to all environment datasets, and can weaken the interpretative strength of species-environment relationships (Tremp, 2007). It could be reflected in the relatively large contribution of the spatially correlated environmental variables (fraction [h] = 0.5% -1.8% in Fig. 5 except LA-U lakes (<0), equivalent to 4.5-8.9% of FTVE) in explaining the macrophyte composition in different lake types. In addition, the effect of spatial structure was found to become progressively more important as alkalinity increased. The spatial autocorrelation component might be more important for HA lakes because of their larger geographical spread, which will magnify distance-decay effects.

Macrophyte composition was strongly determined by lake environment in the different lake types, but catchment-scale variables related to hydrology and landscape structure were proportionally more influential in upland lakes. Typically, upland lakes occur in catchments with a lower coverage of intensively managed land and, generally therefore, less direct human disturbance. Upland lakes located in headwater catchments are characterized by smaller sub-catchments, higher water velocities in the drainage network and shorter retention times (Barendregt & Bio, 2003). The effect of lake physico-chemical variables became progressively more important as the alkalinity of the system increased. Environmental filtering was arguably less important for the flora of LA-L lakes (fraction [a] =1.1%, Fig. 5b) compared with the HA lakes (fraction [a] =2.1%, Fig. 5f), not only because the former systems are generally less impacted by pressures such as nutrient enrichment, but also because, being more aggregated, we would expect lower environmental heterogeneity and thus less species turnover (Fig. 5a) in this type (Viana et al., 2016). This is also perhaps because substantial localised groundwater contact and closer hydrological connectivity in LA-L lakes increases their effective proximity compared to HA lakes (Griffith et al., 1987) or that factors which distort lake vegetation composition have a non-random spatial structure. Interestingly, the contribution of lake

environment was relatively high in LA-U lakes (fraction [a] = 3.4%, Fig. 5a), probably because such lakes are more physically remote from each other, and dispersal vectors such as water birds are naturally scarce, while lake environmental variables are not spatially structured (fraction [h] <0, Fig. 5a). The relatively high contribution of nestedness (Fig. 3b) to beta-diversity in LA-U lakes, compared to species turnover (Fig. 3c), is therefore unsurprising.

The importance of lake chemistry as a determinant of macrophyte composition is widely acknowledged (Kolada et al., 2014) and thus it is to be expected that in HA lakes, which are typically situated in regions of more intensive land use, catchment-scale hydrological and landscape influences are diluted. However, prior to the advent of major human impacts, such catchment-scale variables possibly exerted a stronger influence on community assembly in HA lakes, mirroring the current situation in other lake types.

It should be noted that the explanatory datasets (i.e. environment, hydrology and spatial variables) only accounted for approximately 11% - 24% of the variance in macrophyte species components. In a previous study, abiotic and biotic components explained 16% of the total variance for plants in five different European regions (Viana et al., 2016), whilst de Bie et al. (2012) found that spatial and environmental components explained 5-16% of the variation in distribution of a range of aquatic organisms, including macrophytes, in Belgian ponds. The fraction of total variation explained in our study is thus not abnormally low. Apart from stochastic variation, numerous multi-scale variables influence the spatial distribution of macrophytes on top of those variables we considered, including climate, geomorphology, water level regime, substrate, herbivory and other biotic interactions (Heino, 2011; Wojciechowski et al., 2017).

The importance of lake connectivity and spatial structure in determining species turnover

Our results indicate the important role of dispersal limitation (fraction [b] in Fig. 5e) in macrophyte community assembly, consistent with recent comparative studies of these and other passively dispersing or large bodied organisms in aquatic systems (De Bie et al., 2012; Padial et al., 2014). For the whole 961 lakes, vegetation composition was much more strongly aligned with spatial structure (fraction [d] = 8.1%, Fig. 5e) and was less efficient in tracking hydrological gradients (fraction [b] = 0.67%, Fig. 5e). The large contribution of spatial structuring could imply greater potential for macrophytes to disperse via vectors such as wind (anemochory) or animals (Hartvigsen & Kennedy, 1993), contrary to the conventional view that macrophytes disperse predominantly via water.

Hydrological connectivity depends on a flow path facilitating movement of organisms between water bodies. The greater relative importance of such connectivity for macrophyte composition in upland lakes (fraction [b] = 2.2%-2.4%, Fig. 5a, c) compared with lowland lakes (fraction [b] = 0.03%-1.5%, Fig. 5b,d,e), can be explained, in part, because macrophyte composition in upland lakes is less likely to depend on overland dispersal (due to the low density of suitable vectors) while in lowland lakes water chemistry (and the anthropogenic pressures that influence it) is more likely to act as a direct filter since overland dispersal vectors, such as water birds and humans, are plentiful. This dispersal

limitation is most relevant for submersed species (themselves the major vegetation component in LA lakes) since effective spread as vegetative propagules may be restricted to the hydrological network (Glime, 2007) due to the risk of desiccation associated with aerial dispersal (Keddy, 1976). Conversely, emergent plants, which are relatively more important in HA lakes, readily reproduce from seeds dispersed by water, wind or animals (Soons, 2006). Their establishment elsewhere is thus likely to depend more on lake environmental filtering than on ability to reach a site.

This study highlights that the response of macrophyte communities to the lake environment is complex and moderated by catchment-scale factors such as lake landscape position and connectivity. The importance of catchment-scale factors (e.g. land use, connectivity) in promoting the establishment of different plant communities (more or less diverse, differing in composition) is likely to vary depending on lake alkalinity and elevation. Our findings suggest that the equilibrium state of species composition in lakes is predominantly controlled by overland dispersal and spatially structured environmental gradients. In upland, low alkalinity lakes closer proximity and higher hydrological connectivity might serve to homogenize the environment or associated plant community due to increased potential for exchange of both materials and propagules compared to other lake types. For water bodies smaller than our 1ha size limit, such as ponds, alternative constraints such as shading or permanence may apply and the transferability of conclusions to such water bodies is uncertain.

CONCLUSION

The factors governing macrophyte communities are complex and operate over different scales; this study offers new insights on the relative importance of these factors in different lake types within a diverse region. Our findings suggest that the equilibrium state of species composition in lakes is more spatially structured than previously appreciated. In part this reflects the importance of spatially correlated abiotic factors such as alkalinity, but the strength of the pure spatial effect is suggestive of limitation by overland dispersal. More specifically, the spatial component is strongest in high alkalinity lakes, a lake type that is geographically dispersed and associated with greater environmental heterogeneity, but also higher urban and agricultural land cover and more fragmented landscapes. By contrast, hydrological connectivity has a stronger role in structuring the vegetation composition of upland lakes compared to lowland lakes. Whether this reflects intrinsic differences in drainage network density between the uplands and lowlands, contrasting availability of overland dispersal vectors, or the generally less impacted nature of upland lakes and their more specialist associated species pool, is unresolved.

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REFERENCES

Akasaka, M. & Takamura, N. (2011) The relative importance of dispersal and the local environment for species richness in two aquatic plant growth forms. *Oikos*, **120**, 38–46.

Alahuhta, J. & Heino, J. (2013) Spatial extent, regional specificity and metacommunity structuring in lake macrophytes. *Journal of Biogeography*, **40**, 1572–1582.

Alahuhta, J., Kanninen, A., & Vuori, K.M. (2012) Response of macrophyte communities and status metrics to natural gradients and land use in boreal lakes. *Aquatic Botany*, **103**, 106–114.

Alahuhta, J., Kosten, S., Akasaka, M., et al. (2017) Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude. *Journal of Biogeography*, **44**, 1758–1769.

Alexander, M.L., Woodford, M.P., & Hotchkiss, S.C. (2008) Freshwater macrophyte communities in lakes of variable landscape position and development in northern Wisconsin, U.S.A. *Aquatic Botany*, **88**, 77–86.

Arts, G.H.P. (2002) Deterioration of atlantic soft water macrophyte communities by acidification, eutrophication and alkalinisation. *Aquatic Botany*, **73**, 373–393.

Barendregt, A. & Bio, A.M.F. (2003) Relevant variables to predict macrophyte communities in running waters. *Ecological Modelling*, **160**, 205–217.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Baselga, A.A., Orme, D., Villeger, S., Bortoli, J. De, & Leprieur, F. (2017) Package ' betapart .' *R package ver. 1.4.1*, 31.

Bender, M.G., Leprieur, F., Mouillot, D., Kulbicki, M., Parravicini, V., Pie, M.R., Barneche, D.R., Oliveira-Santos, L.G.R., & Floeter, S.R. (2017) Isolation drives taxonomic and functional nestedness in tropical reef fish faunas. *Ecography*, **40**, 425–435.

Bennion, H., Hilton, J., Hughes, M., Clark, J., Hornby, D., Fozzard, I., Phillips, G. & Reynolds, C. (2005) The use of a GIS-based inventory to provide a national assessment of standing waters at risk from eutrophication in Great Britain. Science of the Total Environment, **344**, 259-273

De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W., & Declerck, S.A.J. (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters*, **15**, 740–747.

Blanchet, F.G., Legendre, P., & Borcard, D. (2008) Forward selection of explanatory variables. *Ecology*, **89**, 2623–2632.

Borcard, D., Legendre, P., Avois-Jacquet, C., & Tuomisto, H. (2004) Dissecting the Spatial Structure of Ecological Data at Multiple Scales. *Ecology*, **85**, 1826–1832.

Bracken, L.J., Wainwright, J., Ali, G.A., Tetzlaff, D., Smith, M.W., Reaney, S.M., & Roy, A.G. (2013) Concepts of hydrological connectivity: Research approaches, Pathways and future agendas. *Earth-Science Reviews*, **119**, 17–34.

Brendonck, L., Jocqué, M., Tuytens, K., Timms, B. V., & Vanschoenwinkel, B. (2015) Hydrological stability drives both local and regional diversity patterns in rock pool metacommunities. *Oikos*, **124**, 741–749.

Capers, R.S., Selsky, R., & Bugbee, G.J. (2010) The relative importance of local conditions and regional processes in structuring aquatic plant communities. *Freshwater Biology*, **55**, 952–966.

Chappuis, E., Gacia, E., & Ballesteros, E. (2014) Environmental factors explaining the distribution and diversity of vascular aquatic macrophytes in a highly heterogeneous Mediterranean region. *Aquatic Botany*, **113**, 72–82.

Cheruvelil, K.S. & Soranno, P.A. (2008) Relationships between lake macrophyte cover and lake and landscape features. *Aquatic Botany*, **88**, 219–227.

Cottenie, K. (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, **8**, 1175–1182.

Dapporto, L., Voda, R., Dinca, V., Vila, R. (2014) Comparing population patterns for genetic and morphological markers with uneven sample sizes. An example for the butterfly Maniola jurtina. *Methods in Ecology and Evolution*, **5**, 834-843

Dray, S., Legendre, P., & Peres-Neto, P.R. (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, **196**, 483–493.

Drinan, T.J., O'Halloran, J., & Harrison, S.S.C. (2013) Variation in the physico-chemical and biological characteristics between upland and lowland (Atlantic) blanket bog lakes in western Ireland. *Biology & Environment*, **113B**, 67–91.

Egertson, C.J., Kopaska, J.A., & Downing, J.A. (2004) A century of change in macrophyte abundance and composition in response to agricultural eutrophication. *Hydrobiologia*, **524**, 145–156.

Feldmann, T. & Noges, P. (2007) Factors controlling macrophyte distribution in large shallow Lake Vortsjarv. *Aquatic Botany*, **87**, 15–21.

Freeman, M.C., Pringle, C.M., & Jackson, C.R. (2007) Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. *Journal of the American Water Resources Association*, **43**, 5–14.

Ganio, L.M., Torgersen, C.E., & Gresswell, R.E. (2005) A geostatistical approach for describing spatial pattern in stream networks. *Frontiers in Ecology and the Environment*, **3**, 138–144.

Van Geest, G.J., Wolters, H., Roozen, F.C.J.M., Coops, H., Roijackers, R.M.M., Buijse, A.D., & Scheffer, M. (2005) Water-level fluctuations affect macrophyte richness in floodplain lakes. *Hydrobiologia*, **539**, 239–248.

Gianuca, A.T., Declerck, S.A.J., Lemmens, P., & De Meester, L. (2017) Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β-diversity. *Ecology*, **98**, 525–533.

Glime J.M. (2007) Bryophyte Ecology Volume 1. Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists.

Goncalves-Souza, T., Romero, G.Q., & Cottenie, K. (2014) Metacommunity versus biogeography: A case study of two groups of neotropical vegetation-dwelling arthropods. PLoS ONE, **9**, e115137. https://doi.org/10.1371/journal.pone.0115.

Griffith, G.E., Kinney, A.J., & Omernik, J.M. (1987) Interpreting patterns of lake alkalinity in the upper midwest region USA. *Lake and Reservoir Management*, **3**, 329–336.

Hartvigsen, R. & Kennedy, C.R. (1993) Patterns in the composition and richness of helminth communities in brown trout, Salmo trutta, in a group of reservoirs. *Journal of Fish Biology*, **43**, 603–615.

Heino, J. (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, **56**, 1703–1722.

Heino, J., Melo, A.S., Jyrkänkallio-Mikkola, J., Petsch, D.K., Saito, V.S., Tolonen, K.T., Bini, L.M., Landeiro, V.L., Silva, T.S.F., Pajunen, V., Soininen, J., & Siqueira, T. (2018) Subtropical streams harbour higher genus richness and lower abundance of insects compared to boreal streams, but scale matters. *Journal of Biogeography*, **45**, 1983–1993.

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., & Virtanen, R. (2017) Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. *Oecologia*, **183**, 121–137.

Henriques-Silva, R., Lindo, Z., & Peres-Neto, P.R. (2013) A community of metacommunities: Exploring patterns in species distributions across large geographical areas. *Ecology*, **94**, 627–639.

Hicks, A.L. & Frost, P.C. (2011) Shifts in aquatic macrophyte abundance and community composition in cottage developed lakes of the Canadian Shield. *Aquatic Botany*, **94**, 9–16.

Hill, M.J., Heino, J., Thornhill, I., Ryves, D.B., & Wood, P.J. (2017) Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. *Oikos*, **126**, 1575–1585.

Hubbell S.P. (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

Jeppesen, E., Kronvang, B., Meerhoff, M., Søndergaard, M., Hansen, K.M., Andersen, H.E., Lauridsen, T.L., Liboriussen, L., Beklioglu, M., Ozen, A., & Olesen, J.E. (2009) Climate change effects on runoff, catchment phosphorus loading and lake ecological state, and potential adaptations. *Journal of Environmental Quality*, **38**, 1930–1941.

Johansson, M.E., Nilsson, C., & Nilsson, E. (1996) Do Rivers Function as Corridors for Plant Dispersal? *Journal of Vegetation Science*, **7**, 593–598.

Jones, J.I., Li, W., & Maberly, S.C. (2003) Area, altitude and aquatic plant diversity. *Ecography*, **26**, 411–420.

Keddy, P. A. (1976) Lakes as Islands: The distributional ecology of two aquatic plants, Lemna minor L. and L. trisulca L. *Ecology*, **57**, 353–359.

Keruzore, A.A. & Willby, N.J. (2014) Avoidance of hydrological disturbance by aquatic vegetation in the floodplain of a large upland river. *Aquatic Botany*, **116**, 19–26.

Kissoon, L.T.T., Jacob, D.L., Hanson, M.A., Herwig, B.R., Bowe, S.E., & Otte, M.L. (2013) Macrophytes in shallow lakes: Relationships with water, sediment and watershed characteristics. *Aquatic Botany*, **109**, 39–48.

Kolada A., Willby N., Dudley B., Noges P., Sondergaard M., Hellsten S., Mjelde M., Penning E., Van Geest G., Bertrin V., Ecke F., Maemets H. & Karus K. (2014) The applicability of macrophyte compositional metrics for assessing eutrophication in European lakes. Ecological Indicators, **45**, 407–415.

Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.F., & He, F. (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology*, **90**, 663–674.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004) The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Maberly, S.C. & Madsen, T. V (2002) Freshwater angiosperm carbon concentrating mechanisms: processes and patterns. *Functional Plant Biology*, **29**, 393–405.

Makela, S., Huitu, E., & Arvola, L. (2004) Spatial patterns in aquatic vegetation composition and environmental covariates along chains of lakes in the Kokemäenjoki watershed (S. Finland). *Aquatic Botany*, **80**, 253–269.

Martin, S.L. & Soranno, P.A. (2006) Lake landscape position: Relationships to hydrologic connectivity and landscape features. *Limnology and Oceanography*, **51**, 801–814.

Monteith, D.T., Hildrew, A.G., Flower, R.J., Raven, P.J., Beaumont, W.R.B., Collen, P., Kreiser, A.M., Shilland, E.M. & Winterbottom, J.H. (2005) Biological responses to the chemical recovery of acidified fresh waters in the UK. Environmental Pollution, **137**, 83-101.

Mosello, R., Lami, A., Marchetto, A., Rogora, M., Wathne, B., Lien, L., Catalan, J., Camarero, L., Ventura, M., Psenner, R., Koinig, K., Thies, H., Sommaruga-Wögrath, S., Nickus, U., Tait, D., Thaler, B., Barbieri, A., & Harriman, R. (2002) Trends in the Water Chemistry of High Altitude Lakes in Europe. *Water, Air and Soil Pollution: Focus*, **2**, 75–89.

Ng, I.S.Y., Carr, C.M., & Cottenie, K. (2009) Hierarchical zooplankton metacommunities: Distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia*, **619**, 133–143.

O'Hare, M.T., Gunn, I.D.M., Chapman, D.S., Dudley, B.J., & Purse, B. V. (2012) Impacts of space, local environment and habitat connectivity on macrophyte communities in conservation lakes. *Diversity and Distributions*, **18**, 603–614.

Quinn, G.P., Keough, M.J., 2004. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Padial, A.A., Ceschin, F., Declerck, S.A.J., De Meester, L., Bonecker, C.C., Lansac-Tôha, F.A., Rodrigues, L., Rodrigues, L.C., Train, S., Velho, L.F.M., & Bini, L.M. (2014) Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. *PLoS ONE*, **9**, e111227.

Peres-Neto, P.R., Legendre, P., Dray, S., & Borcard, D. (2006) Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, **87**, 2614–2625.

Rasmussen, P. & Anderson, N.J. (2005) Natural and anthropogenic forcing of aquatic macrophyte development in a shallow Danish lake during the last 7000 years. *Journal of Biogeography*, **32**, 1993–2005.

Recknagel, F., Cao, H., Kim, B., Takamura, N., & Welk, A. (2006) Unravelling and forecasting algal population dynamics in two lakes different in morphometry and eutrophication by neural and evolutionary computation. *Ecological Informatics*, **1**, 133–151.

Ricketts, T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *The American naturalist*, **158**, 87–99.

Rolon, A.S., Rocha, O., & Maltchik, L. (2012) Do effects of landscape factors on coastal pond macrophyte communities depend on species traits? *Aquatic Botany*, **103**, 115–121.

Rossi, J.P. (2011) Rich: An R package to analyse species richness. *Diversity*, **3**, 112–120.

Rosso, J.J. & Cirelli, A.F. (2013) Effects of land use on environmental conditions and macrophytes in prairie lotic ecosystems. *Limnologica*, **43**, 18–26.

Dos Santos, A.M. & Thomaz, S.M. (2007) Aquatic macrophytes diversity in lagoons of a tropical floodplain: The role of connectivity and water level. *Austral Ecology*, **32**, 177–190.

Sharma, S., Legendre, P., de Cáceres, M., & Boisclair, D. (2011) The role of environmental and spatial processes in structuring native and non-native fish communities across thousands of lakes. *Ecography*, **34**, 762–771.

Si, X., Baselga, A., Leprieur, F., Song, X., & Ding, P. (2016) Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages. *Journal of Animal Ecology*, **85**, 409–418.

Sinkeviciene, Z. (2007) Long-term changes of macrophyte vegetation in lakes of the Dovinė river catchment area. *Ekologia*, **53**, 22–29.

Soininen, J., Heino, J., & Wang, J. (2018) A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, **27**, 96–109.

Soons, M.B. (2006) Wind dispersal in freshwater wetlands: Knowledge for conservation and restoration. *Applied Vegetation Science*, **9**, 271–278.

Soranno, P. A., Cheruvelil, K.S., Webster, K.E., Bremigan, M.T., Wagner, T., & Stow, C. A. (2010) Using Landscape Limnology to Classify Freshwater Ecosystems for Multi-ecosystem Management and Conservation. *BioScience*, **60**, 440–454.

Sousa, W.T.Z., Thomaz, S.M., & Murphy, K.J. (2011) Drivers of aquatic macrophyte community structure in a Neotropical riverine lake. *Acta Oecologica*, **37**, 462–475.

Steffen, K., Leuschner, C., Muller, U., Wiegleb, G., & Becker, T. (2014) Relationships between macrophyte vegetation and physical and chemical conditions in northwest German running waters. *Aquatic Botany*, **113**, 46–55.

Sun, J., Hunter, P.D., Tyler, A.N., & Willby, N.J. (2018) The influence of hydrological and land use indicators on macrophyte richness in lakes – A comparison of catchment and landscape buffers across multiple scales. *Ecological Indicators*, **89**, 227–239.

Thomaz, S.M., Bini, L.M., & Bozelli, R.L. (2007) Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, **579**, 1–13.

Tonkin, J.D., Stoll, S., Jähnig, S.C., & Haase, P. (2016) Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos*, **125**, 686–697.

Tremp, H. (2007) Spatial and environmental effects on hydrophytic macrophyte occurrence in the Upper Rhine floodplain (Germany). *Hydrobiologia*, **586**, 167–177.

Vestergaard, O. & Sand-Jensen, K. (2000) Alkalinity and trophic state regulate aquatic plant distribution in Danish lakes. *Aquatic Botany*, **67**, 85–107.

Viana, D.S., Figuerola, J., Schwenk, K., Manca, M., Hobæk, A., Mjelde, M., Preston, C.D., Gornall, R.J., Croft, J.M., King, R.A., Green, A.J., & Santamaría, L. (2016) Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. *Ecography*, **39**, 281–288.

Vincent, C., Mouillot, D., Lauret, M., Chi, T.D., Troussellier, M., & Aliaume, C. (2006) Contribution of exotic species, environmental factors and spatial components to the macrophyte assemblages in a Mediterranean lagoon (Thau lagoon, Southern France). *Ecological Modelling*, **193**, 119–131.

Weithoff, G., Moser, M., Kamjunke, N., Gaedke, U., & Weisse, T. (2010) Lake morphometry and wind exposure may shape the plankton community structure in acidic mining lakes. *Limnologica*, **40**, 161–166.

Willby, N.J., Pitt, J.A. & Phillips, G. (2012) The ecological classification of UK lakes using aquatic macrophytes. Environment Agency Science report SC010080/R2, Environment Agency, Bristol UK.

Willby. N.J., Law, A., Levanoni, O., Foster, G., Ecke, F. (2018) Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of constrasting biota. Philosophical transactions - Royal Society. Biological sciences, **373**, 20170444.

Wojciechowski, J., Heino, J., Bini, L.M., & Padial, A.A. (2017) The strength of species sorting of phytoplankton communities is temporally variable in subtropical reservoirs. *Hydrobiologia*, **800**, 31.

Wu, J. & David, J.L. (2002) A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. *Ecological Modelling*, **153**, 7–26.

Zillio, T. & Condit, R. (2007) The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. *Oikos*, **116**, 931–940.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 - Table S1 Macrophyte abbreviations in the study

Appendix S2 - Table S2.1a Criteria and types applied under catchment geology typology for Great Britain Ecoregion; Table S2.1b Criteria and types applied under altitude typology for Great Britain Ecoregion; Fig. S2.1 The species pool and contribution of different growth forms for each lake type; Fig. S2.2 Triplot of Partial Redundancy analysis (pRDA) on lake macrophyte data with forward selected lake environmental variables; Fig. S2.3 Triplot of Partial Redundancy analysis (pRDAs) on lake macrophyte data related to lake environmental, hydrological and landscape variables (after accounting for the effects of spatial eigenvectors) for different lake types.

BIOSKETCH

Junyao Sun conducted this work as part of her PhD at the University of Stirling. Her research addresses the processes of environmental filtering and spatial configuration at different scales in determining the distribution of aquatic plants.

Author contributions: In collaboration with the co-authors, JS and NW conceived the idea for the paper and led the data analysis and writing. PH assisted with the GIS modelling and contributed to the editing of the final manuscript. AT assisted with the editing of the manuscript.

TABLES

Table 1. Characteristics of the three environmental datasets in terms of mean, standard deviation (St. Dev) and range (minimum and maximum value) across 961 British lakes; ID is the variable abbreviation used in the results.

Table 2. Details of variation partitioning results covering the significance of the global model for each predictor dataset and the variables retained after forward selection to be used in the final variance partitioning model

FIGURES

Figure 1. Geographical location of the study lakes (projected coordinate system: British-National-Grid) according to lake type as defined by alkalinity and elevation. HA = high alkalinity; MA = moderate alkalinity; LA = low alkalinity.

Figure 2. The conceptual model followed to infer the relative importance of environmental filtering and dispersal limitation for macrophyte composition and how this differs between the lake types.

Figure 3. Boxplots comparing components of beta diversity and its components across the five major British lake types (LA-L = low alkalinity and lowland; LA-U = low alkalinity and upland; MA-L = moderate alkalinity and lowland; MA-U = moderate alkalinity and upland; HA = high alkalinity). Lake types are ordered by increasing productivity from left to right. Boxes represent the interquartile range and median with whiskers showing the upper and lower 10th percentiles.

Figure 4. Sample-based rarefaction curves for macrophyte species richness in different British lake types (LA-L = low alkalinity and lowland; LA-U = low alkalinity and upland; MA-L = moderate alkalinity and lowland; MA-U = moderate alkalinity and upland; HA = high alkalinity; ALL- global dataset).

Figure 5. Variation partitioning of the Hellinger-transformed macrophyte data into an environmental component (upper left-hand circle), a hydrological component (upper right-hand circle), a landscape component (lower circle) and a spatial component (disjoined rectangles) (Fig.5e). This generates 16 fractions: 4 pure effects of the environment, hydrology, landscape and spatial datasets (Fractions [a] to [d]) plus 12 joint effects of the two or three separate sets (Fractions [e] to [o]) and 1 unexplained component of the variance (Residuals). Variation partitioning results of the Hellinger-transformed macrophyte data for each lake type (Figure 5a – low alkalinity and upland lakes; Figure 5b – low alkalinity and lowland lakes; Figure 5c – moderate alkalinity and upland lakes; Figure 5d – moderate alkalinity and lowland lakes; Figure 5f – high alkalinity lakes; Figure 5e all lakes). Values indicate the fraction of the explanatory set (as R^2adj). Monte Carlo permutation tests were used to determine significance of the pure fraction (Fraction [a] to [d]) (only significant values are shown). The standard deviation of the mean R^2adj for each component from the bootstrapping procedure is presented within brackets to illustrate the uncertainty. Negative R^2adj values, which explain less of the variation than would be expected by chance, have been excluded. "n" in the lower left corner of each panel refers to the loop programmed resampling from the original lake dataset for each lake type.

Journal of Biogeography

SUPPORTING INFORMATION

A comparison of local and catchment-scale determinants of vegetation composition across almost 1000 lakes

Junyao Sun, Peter D. Hunter, Andrew N. Tyler & Nigel J. Willby

Appendix S1 the introduction of the lake macrophyte and their growth habit in this work

Table S1 Macrophyte abbreviations and dominant growth habit recorded in this study

Species	ID	Commonest growth habit
Apium inundatum	Api.inu	submersed
Baldellia ranunculoides	Bal.ran	submersed
Batrachospermum spp.	Bat.spp	submersed
Butomus umbellatus	But.umb	emergent
Callitriche agg	Calli.agg	submersed
Callitriche hamulata	Cal.ham	submersed
Callitriche hermaphroditica	Cal.her	submersed
Callitriche obtusangula	Cal.obt	submersed
Callitriche platycarpa	Cal.pla	submersed
Callitriche stagnalis	Cal.sta	submersed
Callitriche truncata	Cal.tru	submersed
Ceratophyllum demersum	Cera.dem	submersed
Chara spp.	Chara.spp	submersed
Chara aspera	Chara.asp	submersed
Chara aspera var.aspera	Chara.asp.a	submersed
Chara aspera var.aspera f.subinermis	Chara.asp.s	submersed
Chara aspera var.curta	Chara.asp.c	submersed
Chara globularis sens.lat	Chara.glo.l	submersed
Chara globularis var.annulata	Chara.glo.a	submersed
Chara globularis var.globularis	Chara.glo.g	submersed
Chara globularis var.virgata	Chara.glo.v	submersed
Chara globularis var.virgata f.barbata	Chara.glo.v.b	submersed
Chara hispida sens.lat.	Chara.his.s	submersed
Chara intermedia	Chara.int	submersed
Chara vulgaris	Chara.vul	submersed
Chara vulgaris sensu Stewart	Chara.vul.s	submersed
Chara vulgaris var. longibracteata	Chara.vul.l	submersed
Chara vulgaris var. papillata	Chara.vul.p	submersed
Chara vulgaris var. contraria	Chara.vul.c	submersed

Chara vulgaris var. vulgaris	*Chara.vul.v*	*submersed*
Crassula helmsii	*Cra.hel*	*submersed*
Elatine hexandra	*Ela.hex*	*emergent*
Elatine hydropiper	*Ela.hyd*	*emergent*
Eleocharis acicularis	*Eleo.aci*	*submersed*
Eleocharis multicaulis	*Eleo.mul*	*emergent*
Eleogiton fluitans	*Eleo.flu*	*submersed*
Elodea canadensis	*Elodea.can.*	*submersed*
Elodea nuttallii	*Elodea.nut.*	*submersed*
Elodea spp.	*Elodea.spp.*	*submersed*
Enteromorpha	*Ent.*	*algae*
Eriocaulon aquaticum	*Eri.aqu*	*submersed*
Filamentous algae	*Fil.alg*	*algae*
Fontinalis antipyretica	*Font.ant*	*submersed*
Fontinalis squamosa	*Font.squ*	*submersed*
Hippuris vulgaris	*Hip.vulg*	*emergent*
Hottonia palustris	*Hot.pal*	*emergent*
Hydrocharis morsus-ranae	*Hyd.mor*	*free floating*
Hydrodictyon.spp.	*Hyd.spp.*	*algae*
Hypericum elodes	*Hyp.elo*	*emergent*
Isoetes indet.	*Iso. Indet.*	*submersed*
Isoetes echinospora	*Iso.ech*	*submersed*
Isoetes lacustris	*Iso.lac*	*submersed*
Juncus bulbosus	*Jun.bul*	*submersed*
Lemna gibba	*Lemna.gib*	*free floating*
Lemna minor	*Lemna.min*	*free floating*
Lemna trisulca	*Lemna.tri*	*free floating*
Limosella aquatica	*Lim.aqu*	*emergent*
Littorella uniflora	*Lit.uni*	*submersed*
Lobelia dortmanna	*Lob.dor*	*submersed*
Ludwigia palustris	*Lud.pal*	*emergent*
Luronium natans	*Lur.nat*	*submersed*
Lythrum portula	*Lyt.por*	*emergent*
Menyanthes trifoliata	*Men.tri*	*emergent*
Myriophyllum alterniflorum	*Myrio.alt*	*submersed*
Myriophyllum spicatum	*Myrio.spi*	*submersed*
Najas flexilis	*Naj.fle*	*submersed*
Nitella spp.	*Nit.spp.*	*submersed*
Nitella confervacea	*Nit.con*	*submersed*
Nitella flexilis agg.	*Nit.fle*	*submersed*
Nitella gracilis	*Nit.gra*	*submersed*
Nitella opaca	*Nit.opa*	*submersed*
Nitella translucens	*Nit.tra*	*submersed*
Nitellopsis obtusa	*Nit.obt*	*submersed*
Nuphar lutea	*Nup.lut*	*floating leaved*
Nuphar lutea x pumila (N. x spenneriana)	*Nup.lut.p*	*floating leaved*
Nuphar pumila	*Nup.pum*	*floating leaved*
Nymphaea alba	*Nym.alb*	*floating leaved*

Nymphoides peltata	*Nym.pel*	*floating leaved*
Oenanthe aquatica	*Oen.aqu*	*emergent*
Persicaria amphibia	*Per.amp*	*emergent*
Pilularia globulifera	*Pil.glob*	*emergent*
Potamogeton alpinus	*Potam.alp*	*submersed*
Potamogeton alpinus x praelongus	*Potam.alp.p*	*submersed*
Potamogeton berchtoldii	*Potam.ber*	*submersed*
Potamogeton coloratus	*Potam.col*	*floating leaved*
Potamogeton crispus	*Potam.cri*	*submersed*
Potamogeton epihydrus	*Potam.epi*	*submersed*
Potamogeton filiformis	*Potam.fil*	*submersed*
Potamogeton filiformis x pectinatus	*Potam.fil.p*	*submersed*
Potamogeton friesii	*Potam.fri*	*submersed*
Potamogeton gramineus	*Potam.gra*	*submersed*
Potamogeton gramineus x lucens (P. x zizii)	*Potam.gra.l*	*submersed*
Potamogeton gramineus x natans (P. x sparganiifolius)	*Potam.gra.n*	*submersed*
Potamogeton gramineus x perfoliatus (P. x nitens)	*Potam.gra.p*	*submersed*
Potamogeton gramineus	*Potam.gra*	*submersed*
Potamogeton lucens	*Potam.luc*	*submersed*
Potamogeton natans	*Potam.nat*	*floating leaved*
Potamogeton obtusifolius	*Potam.obt*	*submersed*
Potamogeton pectinatus	*Potam.pec*	*submersed*
Potamogeton pectinatus/filiformis indet.	*Potam.pec.f*	*submersed*
Potamogeton perfoliatus	*Potam.per*	*submersed*
Potamogeton polygonifolius	*Potam.pol*	*floating leaved*
Potamogeton praelongus	*Potam.pra*	*submersed*
Potamogeton pusillus	*Potam.pus*	*submersed*
Potamogeton rutilus	*Potam.rut*	*submersed*
Potamogeton spp.	*Potam.spp*	*submersed*
Potamogeton trichoides	*Potam.tri*	*submersed*
Ranunculus indet.	*Ranun.indet*	*emergent*
Ranunculus aquatilis agg.	*Ranun.aqu.a*	*emergent*
Ranunculus aquatilis sens.str.	*Ranun.aqu.s*	*emergent*
Ranunculus baudotii	*Ranun.bau*	*emergent*
Ranunculus circinatus	*Ranun.cir*	*submersed*
Ranunculus hederaceus	*Ranun.hed*	*emergent*
Ranunculus lingua	*Ranun.lin*	*emergent*
Ranunculus omiophyllus	*Ranun.omi*	*emergent*
Ranunculus peltatus	*Ranun.pel*	*emergent*
Ranunculus spp.	*Ranun.spp*	*emergent*
Ranunculus trichophyllus	*Ranun.tri*	*submersed*
Riccia fluitans	*Ric.flu*	*free floating*
Ruppia cirrhosa	*Ruppia.*	*submersed*
Ruppia maritima	*Ruppia.*	*submersed*
Sagittaria sagittifolia	*Sag.sag*	*emergent*
Scorpidium scorpioides	*Sco.sco*	*emergent*

Sparganium spp.	*Spar.spp*	*Floating leaved*
Sparganium angustifolium	*Spar.ang*	*floating leaved*
Sparganium emersum	*Spar.emer*	*floating leaved*
Sparganium natans	*Spar.nat*	*floating leaved*
Sphagnum indet.	*Spha.indet*	*submersed*
Spirodela polyrhiza	*Spi.pol*	*free floating*
Subularia aquatica	*Sub.aqu*	*submersed*
Tolypella glomerata	*Tol.glo*	*submersed*
Utricularia spp.	*Utri.spp*	*submersed*
Utricularia australis	*Utri.aus*	*submersed*
Utricularia cf. australis	*Utri.cf.aus*	*submersed*
Utricularia cf. vulgaris	*Utri.cf.vul*	*submersed*
Utricularia intermedia sens. lat.	*Utri.int*	*submersed*
Utricularia minor	*Utri.min*	*submersed*
Utricularia ochroleuca	*Utri.ochr*	*submersed*
Utricularia stygia	*Utri.sty*	*submersed*
Utricularia vulgaris sens. lat.	*Utri.vul.l*	*submersed*
Utricularia vulgaris sens. str.	*Utri.vul.s*	*submersed*
Zannichellia palustris	*Zan.pal*	*submersed*

Appendix S2 the introduction and the statistical analysis of macrophyte composition in term of different lake types

Table S2.1a Criteria and types applied under catchment geology typology for Great Britain Ecoregion

Geological types	Classify each water body into Geological Types using criteria described below and assign a level of confi... (High confidence if based on measured alkalinity, moderate confidence if based on conductivity (except high), low confidence if derived from geology maps)					
Types		Abrev.	Catchment	Alkalinity		Conc
				ueq/l	CaCO$_3$mg/l	
Geology	Organic	P	> 75% Peat			
	Siliceous	LA	> 90% siliceous solid geology	< 200	< 10	
		MA	> 50% siliceous solid geology	200-1000	10-50	
	Calcareous	HA	> 50% calcareous geology	>1000	>50	2
		Marl	> 65% limestone			
	Brackish	B				

Table S2.1b Criteria and types applied under altitude typology for Great Britain Ecoregion

Altitude Types	Classify each water body into Altitude Types using criteria described below and assign a level of confiden... allocation		
Types		Abrev.	Basin altitude (m)
Altitude	Lowland	Low	<200
	Mid-Altitude	Mid	200-800
	High-Altitude	High	>800

Fig. S2.1 The species pool and contribution of different growth forms for each lake type (LAL – low alkalinity and lowland lakes; LAU – low alkalinity and upland lakes; MAL – moderate alkalinity and lowland lakes; MAU – moderate alkalinity and upland lakes; HA – high alkalinity lakes)

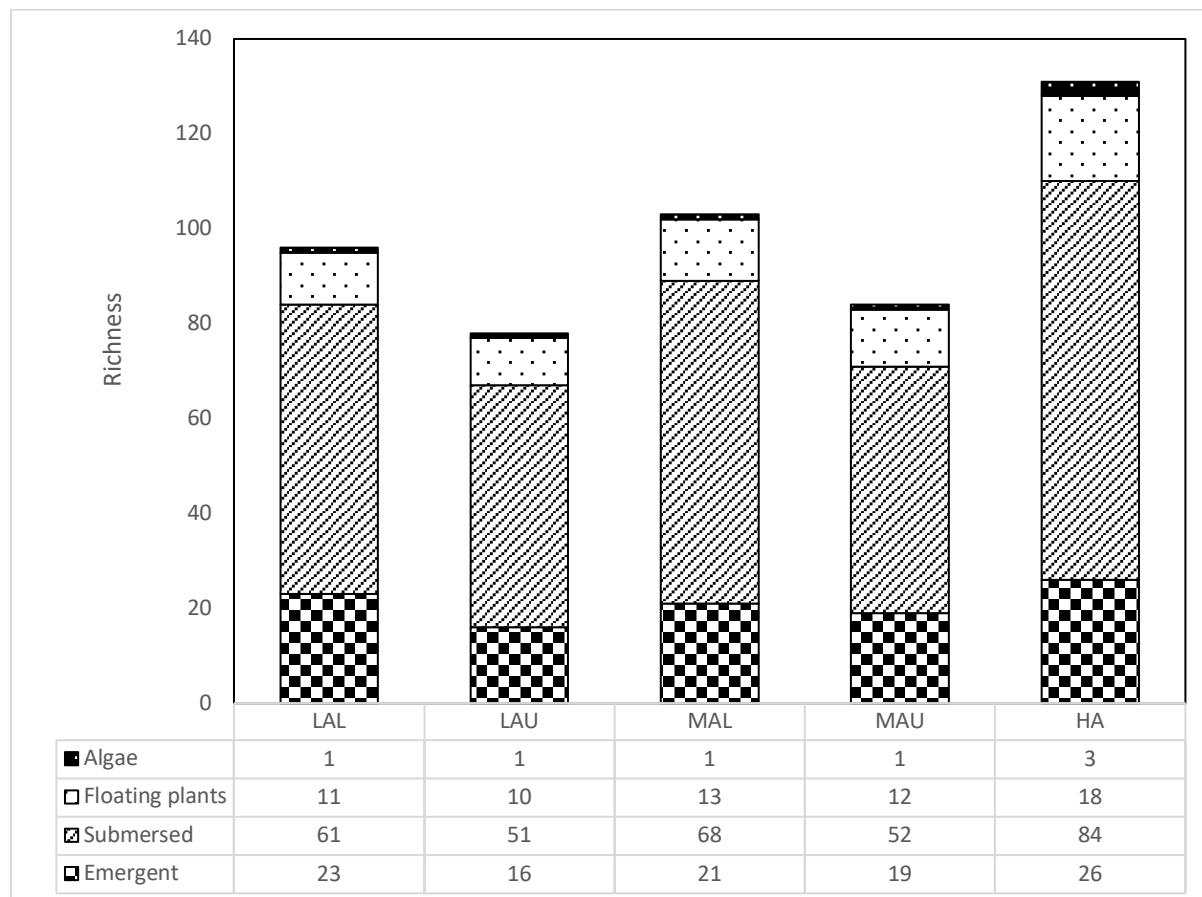|	LAL	LAU	MAL	MAU	HA
■ Algae	1	1	1	1	3
□ Floating plants	11	10	13	12	18
☒ Submersed	61	51	68	52	84
❑ Emergent	23	16	21	19	26

Fig. S2.2 Triplot of Redundancy analysis (RDA) on lake macrophyte data with forward selected significant lake environmental variables, such as lake alkalinity (adj-r^2=7.0%), lake elevation (adj-r^2=1.1%), lake pH (adj-r^2=0.3%), lake area (adj-r^2=0.2%), lake SDI (adj-r^2=0.2%), lake depth (adj-r^2=0.05%). Orange points represent different lakes, and triangles indicate different macrophyte species. Variable abbreviation: SDI- lake shoreline development index.
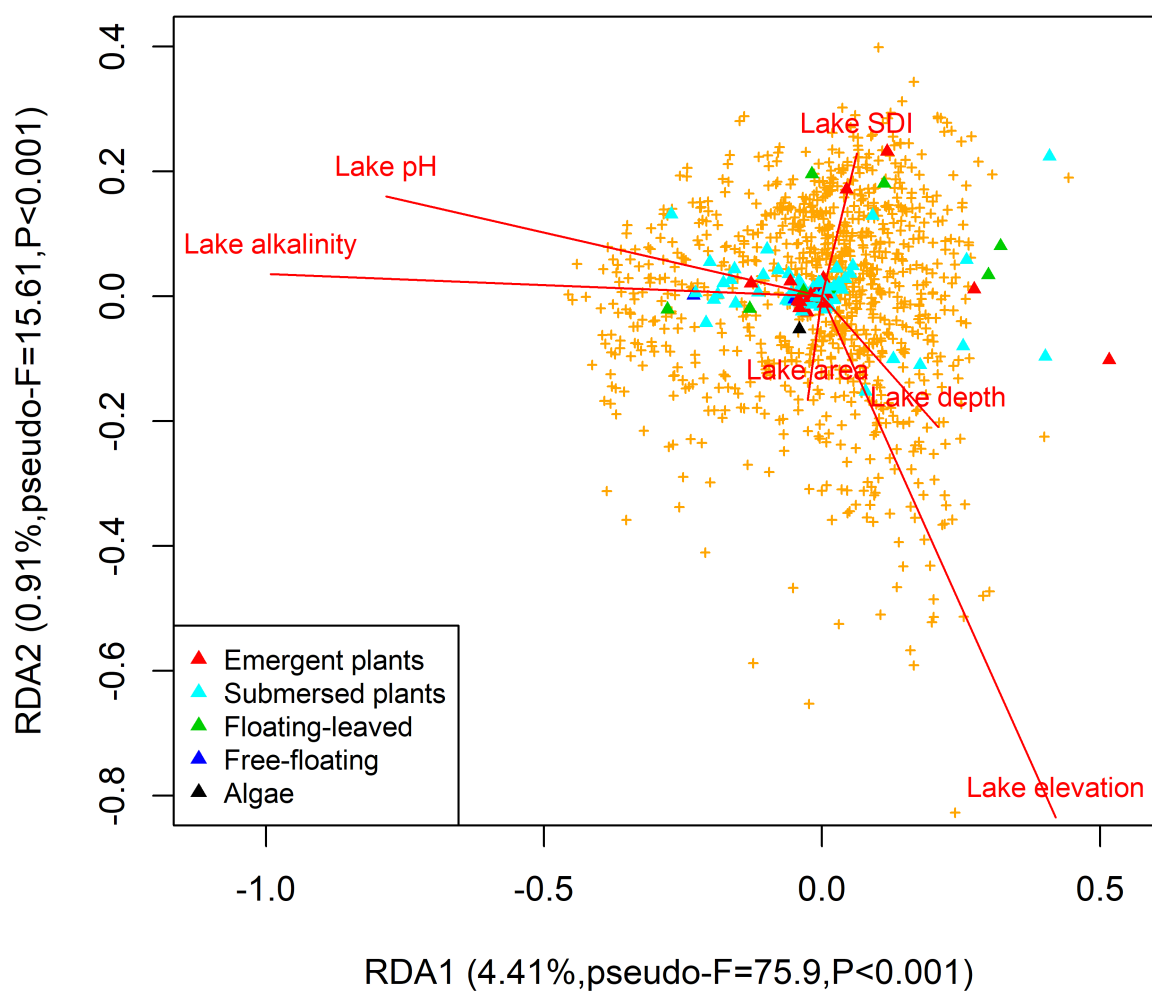
Fig. S2.3 Triplot of Partial Redundancy analysis (pRDAs) on lake macrophyte data related to lake environmental, hydrological and landscape variables (after accounting for the effects of spatial eigenvectors). Orange points represent the lake site scores, and triangles with distinct colours indicate different macrophyte species for different lake types.