Received: 11 January 2021 | Revised: 22 April 2021 | Accepted: 30 April 2021
DOI: 10.1111/fwb.13733

Freshwater Biology WILEY

ORIGINAL ARTICLE

Local habitat is a strong determinant of spatial and temporal patterns of macrophyte diversity and composition in boreal lakes

Richard K. Johnson[1] | **Vildan Toprak**[2]

[1]Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

[2]School of Natural and Applied Sciences, Ankara University, Ankara, Turkey

Correspondence
Richard K. Johnson, Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, P.O. Box 7050, SE-750 07 Uppsala, Sweden.
Email: richard.johnson@slu.se

Funding information
The Swedish Environmental Protection Agency; Swedish Agency for Marine and Water Management; Erasmus+ Student Mobility Traineeship

Abstract

1. Macrophyte species and trait assemblages from 104 minimally disturbed boreal forest lakes, covering broad environmental and geographic gradients were analysed to identify associations with environmental variables at different spatial scales: geographic context (GEO) and catchment (CATCH) and lake (LOCAL) characteristics.
2. Constrained ordination and variation partitioning were used to quantify variation in species (canonical correspondence analysis [CCA] and pCCA) and trait (redundancy analysis [RDA] and pRDA) compositions that could be explained by environmental variables, and to rank the main environmental factors associated with spatial and temporal patterns.
3. Diversity and assemblage composition correlated with spatial context and variables related to the length of the growing season, catchment forest type and with lake characteristics such as ecosystem size, lake productivity and alkalinity.
4. Variation partitioning showed that lake characteristics alone explained 53% (species) and 73.5% (traits) of the variability in macrophyte assemblages. Contrary to predictions, the shared variance component between latitude and catchment forest type (GEO&CATCH $< 0.1\%$ for both species and traits) and between latitude and lake characteristics (GEO&LOCAL $= 6.7\%$ for species and 3.9% for traits) was low.
5. Temporal variability, measured as changes in species richness, diversity and a pollution-specific index (the Trophic Macrophyte Index), using a subset of the lakes sampled on two occasions (19 lakes sampled in 2012 and 2018 and five lakes sampled in 2013 and 2019) did not differ ($p > 0.05$, paired t-test). Ordination showed that among-year variability in macrophyte assemblage composition was also negligible (0.3%) compared to the variability explained by GEO, CATCH and LOCAL variables. Combined, these findings indicate low species turnover in the boreal lakes of our study.

6. Responses of macrophyte species and trait assemblages and the TMI index were predictable and significantly correlated with lake characteristics associated with nutrient enrichment (Chl *a*, nutrients) and alkalinity supporting their use in monitoring eutrophication of boreal lakes.

KEYWORDS
land use, ordination, primary producer, species and trait composition, variation partitioning

1 | INTRODUCTION

Understanding how patterns and changes in biodiversity relate to local and regional environmental variables has been at the forefront of ecological research for decades (García-Girón et al., 2020; Gaston, 2000). Not only for understanding fundamental questions related to biological organisation but also as this knowledge is critical for managing and mitigating the effects of global change (Heino et al., 2020). For freshwater ecosystems, understanding the variables most strongly associated with biodiversity are especially important as these systems account for a disproportionate amount of the global biodiversity (Palmer et al., 2000) and declines are exceeding those of many other systems (Dudgeon et al., 2006). Natural variables associated with local patterns of lake biodiversity may be related to species sorting processes associated with catchment land cover, ecosystem size and productivity, while regional patterns are often associated with climate and geology (Heino et al., 2009; Stendera et al., 2012). The main anthropogenic pressures affecting the biodiversity of lakes can be summarised as catchment land use, altered hydrology, elevated nutrients, invasive species and climate change (Moss et al., 2011; Poikane et al., 2020). Many studies have addressed how lake communities respond to anthropogenic pressures, whilst fewer have focused on the importance of environmental variables that underpin the natural spatial and temporal patterns of biodiversity.

Macrophytes are an important structural and functional component of many lake ecosystems (Carpenter & Lodge, 1986), not only as a primary producer but also for their role in creating habitat for other organisms and in altering biogeochemical conditions (Jeppesen et al., 2012; Johnson & Hering, 2010; Manatunge et al., 2000; Schriver et al., 1995). In shallow lakes, macrophytes account for a number of ecosystem services (Janssen et al., 2020) and are often a deciding factor maintaining a lake's clear-water state (Moss, 1990). Eutrophication often results in biodiversity loss and lower abundances of submerged species due to light limitation, resulting in a shift in primary production from littoral to pelagic habitats (Jupp & Spence, 1977; Lachavanne et al., 1992; Sand-Jensen et al., 2008). In deeper lakes, their functional importance depends more on intrinsic in-lake characteristics that affect population growth and abundance, such as lake morphometry, depth and light conditions (Jeppesen et al., 1997; Moss, 1990; Søndergaard et al., 2010).

Macrophyte assemblages have often been used in characterising boreal forest lake types (e.g. Linkola, 1933; Lohammar, 1938, 1965). Early focus was on identifying lake types using the presence/absence of selected indicator species (e.g. Lohammar, 1965). However, with the implementation of the European Water Framework directive (WFD) (European Commission, 2000), the number of approaches and biological indices used in lake classifications has markedly increased (Birk et al., 2006; Poikane et al., 2015). Although macrophyte-based indices are primarily used for assessing eutrophication (Kolada et al., 2014; Penning, Dudley et al., 2008; Penning, Mjelde et al., 2008), other environmental pressures have been assessed such as water regulation and drawdown (Mjelde et al., 2013; Rørslett, 1991), catchment ditching (Ecke, 2009), acidification (Baastrup-Spohr et al., 2017; Crowder, 1991), heavy metals (Bonanno & Giudice, 2010; Crowder, 1991) and biological invasions (Strayer, 2010). Macrophyte assemblages have been shown to correlate strongly with variables related to productivity (Alahuhta et al., 2018; Fu et al., 2019), ecosystem size and depth (Lacoul & Freedman, 2006; Middelboe & Markager, 1997; Rørslett, 1991), light conditions (Jeppesen et al., 2000) and alkalinity (Vestergaard & Sand-Jensen, 2000) as well as other biological assemblages (Johnson & Hering, 2010; Kelly et al., 2016). A prerequisite of developing biological response metrics is understanding not only species' responses to disturbance but also responses to the natural environmental gradients underpinning patterns in biodiversity.

We used a spatially extensive dataset of macrophyte assemblages from 104 Swedish boreal lakes situated across a relatively broad latitudinal gradient (climate) and in predominantly forested catchments to better our understanding of the importance of natural environmental variables for structuring macrophyte assemblages. The main objectives were (a) to quantify and rank the main environmental factors associated with spatial and temporal patterns of macrophyte assemblages in boreal lakes, (b) to disentangle the importance of spatial, catchment and local-scale environmental variables and (c) to determine the importance of temporal variability for macrophyte assemblages and on the trophic macrophyte index (TMI, Trophic Macrophyte Index, Ecke, 2007) used in classifying ecological status of Swedish lakes. Building on previous work, we predicted that macrophyte diversity and species richness would be positively correlated with lake productivity (chlorophyll *a*) and alkalinity, and negatively correlated with light conditions (water colour) and length of the growing season (latitude and altitude) (Alahuhta et al., 2018; Heino & Toivonen, 2008; Jeppesen et al., 2000; Toivonen & Huttunen, 1995; Vestergaard & Sand-Jensen, 2000). Furthermore, we predicted that local-scale environmental variables and geographic position would be better predictors of macrophyte assemblages than catchment-scale variables (Alahuhta et al., 2018; Heino et al., 2017). Finally, given the relatively slow turnover time of macrophyte assemblages (Dittrich et al., 2016), we determine whether species richness, diversity, assemblage composition and TMI have changed between two six-year sampling events.

2 | METHODS

2.1 | Sampling

The study lakes ($n = 104$) are part of the Swedish national lake monitoring programme (Fölster et al., 2014) and cover relatively broad environmental gradients in climate and vegetation ranging from the Central Plains ecoregion in the south to the Borealic Uplands ecoregion in the north (Table 1; Figure S1). Macrophytes surveys were performed between 2012 and 2019. The number of macrophyte surveys per lake varied from: a single survey (80 lakes) to two surveys with six years in-between sampling events (24 lakes).

Macrophyte assemblages in each lake were quantified using a standardised sampling protocol (SEPA, 2007, 2015). A transect method was used with the number of transects per lake based a priori on a relationship between lake surface area and species accumulation curves (SEPA, 2015). The number of transects sampled per lake ranged from 5 to 15 (mean = 10). The transects (0.5 m wide) were situated perpendicular to the lake shoreline, and along each transect the presence of macrophytes was recorded using quadrats (25–50 cm) with a distance of 20 cm between sampling plots. Sampling was stopped when no macrophytes were recorded in at least three consecutive sampling quadrats. Both hydrophytes and helophytes were included in the surveys. Using this method, we were able to calculate species frequencies for each lake and year by dividing the number of plots with presence of the respective species by the total number of sampling plots per lake. Macrophytes were surveyed by wading, snorkelling or diving, or by using hydroscopes and a Luther rake from a boat.

Surface-water samples (0.5 m) were collected seasonally four times per year (spring, summer, autumn and winter) at a mid-lake station in each lake. Mean values of the four sampling events were used in our analyses. Secchi depth transparency and water temperature were measured at the time of sampling. Water was collected with a Plexiglas® sampler and kept cool during transport to the laboratory. Samples were analysed for variables characterising, e.g. lake productivity (chlorophyll *a* [Chl *a*], nutrients: total nitrogen [TN] and total phosphorus [TP], water transparency [Secchi depth transparency, water colour], alkalinity/acidity [hereafter referred to as alkalinity]), pH, conductivity and Fe concentration (Fe was included in our analyses as it has been shown to increase water colour [Weyhenmeyer et al., 2014] and decrease P availability [Immers et al., 2014]) (Table 1). All analyses were done according to international (ISO) or European (EN) standards (Fölster et al., 2014). More information on these lakes is available from http://www.slu.se/vatten-miljo.

TABLE 1 Mean ± 1 *SD*, minimum and maximum values of selected environmental variables for 104 boreal Swedish lakes

	Mean ± 1 *SD*	Min.	Max.
Latitude (degrees)	60.61 ± 3.41	55.49	68.35
Longitude (degrees)	15.86 ± 2.56	11.61	23.35
Catchment area (km^2)	78 ± 382	0.25	2,900
Shoreline length (km)	7.5 ± 12.8	0.96	104
Lake surface area (km^2)	1.9 ± 5.6	0.05	52
Surface/catchment area	0.12 ± 0.08	0.005	0.322
Altitude (m a.s.l.)	224 ± 210	2	974
Depth (m)	11 ± 8.6	1	42
Coniferous forest (%)	47 ± 22	0	82
Mixed forest (%)	10 ± 8.6	0	51
Deciduous forest (%)	4.8 ± 6.0	0	31
Other surface water (%)	13 ± 7.8	1.4	32
Mires (%)	4.8 ± 8.1	0	43
Secchi depth (m)	3.5 ± 2.6	0.23	17
Chlorophyll *a* (μg/L)	5.7 ± 6.5	0.6	48
Water temperature (°C)	9.9 ± 1.0	5.15	14.2
Conductivity (mS/m)	5.73 ± 7.2	0.84	48
pH	6.6 ± 0.68	4.9	8.4
Water colour (AbsF)	0.139 ± 0.139	0.011	0.85
Alkalinity/acidity (meq/L)	0.256 ± 0.519	−0.036	2.5
Fe (μg/L)	485 ± 697	7.8	4,150
TN (μg/L)	453 ± 296	79	1,549
TP (μg/L)	14.0 ± 15.6	1.4	87

Land cover/use data were retrieved from Corine (Commission of the European Communities). Climate data (mean annual temperature [°C] and precipitation [mm] for 1961–1990) was obtained from the Swedish institute for meteorology and hydrology (http://www.smhi.se/). Geographical data (altitude [m a.s.l.], catchment size [km^2], lake surface area [km^2], shoreline length [km]) were taken from digital maps from the National Land Survey of Sweden (http://www.lantmateriet.se/).

2.2 | Response indices

Three diversity indices (species richness, Simpson's diversity, evenness) and one pollution-specific index (Trophic Macrophyte Index, Ecke, 2007) were used to quantify variability of macrophyte assemblages between two surveys at six-year intervals. Species richness, Simpson diversity (1-D) and evenness (e^H/S where H is Shannon diversity and S the number of taxa) were calculated using the PAST 4.0 software (Hammer et al., 2001). The Trophic Macrophyte Index (Ecke, 2007), commonly used to assess effects of elevated nutrients on Swedish lakes, was calculated as a weighted average of the indicator values of all taxa present using the niche breadth of the taxa along the phosphorus gradient as a weighting factor. Here we used both the TMI values and the number of TMI scoring taxa as response variables. Helophytes were not included in calculating TMIs. In addition, we quantified the importance of among-year variability using partial constrained ordination (see below).

As many studies have shown that integral multivariate analyses of community structure reveal patterns between species assemblages and environmental variables better than other measures of community diversity (e.g. Johnson & Hering, 2010), macrophyte species and trait composition were included as response variables. The use of trait-based approaches in environmental assessments has increased markedly, chiefly due to the understanding that species traits more accurately reflect functional patterns and processes than taxonomic metrics (Truchy et al., 2015). Here we selected four functional traits to characterise macrophyte assemblages and determine responses to environmental variables: (a) Macrophytes were classified according to six classes of growth form: free floating surface (frflsr); free floating submerged (frflsu); anchored floating leaves (anflle); anchored submerged leaves (ansule); anchored emerging leaves (ansule) and anchored heterophylly (anhete). (b) Three classes for apical growth were used: single apical growth point (siapgr); single basal growth point (sibagr) and multiple apical growth point (muapgr) (Willby et al., 2000). (c) Ellenberg nutrient scores were used as a measure of nutrient preference (Hill et al., 1999): species scores range from 1 (nutrient poor) to 8 (nutrient rich). (d) The Aquaticity score is a measure of each species affinity for aquatic systems and ranges from a score of 1 for exclusively aquatic to 8 for very terrestrial. Both Ellenberg nutrient and Aquaticity scores were obtained from the online database www.freshwaterecology.info (Schmidt-Kloiber & Hering, 2015). Finally, filamentous algae and bryophytes were included as two additional macrophyte classifications.

2.3 | Statistical analyses

Principal component analysis (PCA) and correlation were used to reduce the dimensionality of environmental variables and select a parsimonious set of variables for modelling and ordination (e.g. variation partitioning). PCAs and correlation analysis were done using JMP® (version 14.0.0, SAS Institute Inc., 2018) and Canoco software (version 5.12, ter Braak & Smilauer, 2002). Most environmental variables were log10 transformed before the analyses to approximate normal distributions.

In preliminary analyses, detrended correspondence analysis of 248 macrophyte species (Table S1) showed turnover or gradient lengths of 7.46 for axis 1 and 3.29 for axis 2 indicating a unimodal distribution (ter Braak, 1995). Consequently, canonical correspondence analysis (CCA) and partial CCA (pCCA) were used to quantify variation in the species composition that could be explained by environmental variables, and to rank importance of individual environmental variables for quantifying spatial and temporal patterns (see below). For macrophyte trait composition, linear models were fitted: redundancy analysis (RDA) for calibrating a parsimonious model and for ranking the importance of the individual environmental variables and pRDA for quantifying spatial and temporal variation. Spatial patterns were analysed using one macrophyte assemblage per lake ($n = 104$ lakes). For lakes having two surveys ($n = 24$), we used mean values. Temporal patterns were analysed using a subset of the lakes sampled on two occasions in 2012 and 2018 ($n = 19$) and in 2013 and 2019 ($n = 5$).

Constrained ordinations with single variables were used to assess and rank species responses to selected environmental gradients. The independent (marginal) effects of the 23 environmental variables on macrophyte species (CCA) and trait (RDA) composition were tested using forward selection without selecting covariables. Marginal effects show the amount of variability that can be explained using a single variable in a constrained ordination. Significance of the individual environmental variables on species and trait composition were tested using 999 Monte Carlo permutations.

Using forward selection, we quantified the relative importance of the environmental variables. The most parsimonious model for explaining variability in among-lake macrophyte species and trait compositions was constructed by selecting the environmental variable that explained the greatest amount of variability in species and traits. In subsequent steps, the influence of other variables was quantified, where applicable, by running any variables already selected as covariables to determine the conditional effects, that is, the importance of variables after factoring out the variance explained by variables already included in the model. Partial Monte Carlo permutation tests were used to determine the importance of explanatory variables with 999 permutations.

Partial canonical correspondence analysis (pCCA) and partial redundancy analysis (pRDA) and variation partitioning (Peres-Neto et al., 2006) were used to partition among-lake variability in macrophyte species and traits that could be explained by environmental variables and by time (year). pCCA (species) and pRDA (traits) were run using spatial context (GEO), catchment land cover (CATCH) and local variables characterising the individual lakes (LOCAL) to quantify among-lake variability in macrophyte assemblages that could be explained by these three groups of variables and their shared variance. In pCCA and pRDA, only variables that were selected in model calibration using forward selection were used. The relative importance of the three groups was evaluated using the adjusted R^2, providing unbiased estimates of the explained variation (Peres-Neto et al., 2006). For quantifying variability in macrophyte species and trait composition between the two six-year sampling intervals, year was run as covariable and the variables included in the most parsimonious CCA (species) or RDA (traits) model were used as predictor variables in pCCA and pRDA. Constrained ordinations regressing species (CCA) against single environmental variables were used to quantify and aid in the interpretation of individual species responses along environmental gradients (e.g. latitude, alkalinity, productivity).

3 | RESULTS

The study sites covered broad geographic (latitude 55.45–68.35°, longitude 11.61–23.35°) and environmental gradients (Table 1; Figure S1). The lakes were mostly relatively small (1.9 ± 5.6 km^2), lowland (224 ± 210 m a.s.l.), nutrient poor (TP = 14.0 ± 15.6 μg/L, TN = 453 ± 296 μg/L), with low productivity (Chl *a* = 5.7 ± 6.5 μg/L) and situated in forested catchments (47 ± 22%).

Principal component analysis of 23 environmental variables revealed that the primary environmental gradient in our lake dataset (PC1, accounting for 30.7% of the variability) was related to variables indicative of productivity (Chl *a*, nutrients) and length of the growing season (latitude, altitude) (Figure 1; Table S2). The second PC axis (PC2, 18.7%) was related to water chemistry (alkalinity, pH, conductivity) and ecosystem size (lake surface area and length of the shoreline). The third axis (PC3, 12.5%) was interpreted as representing water retention time (e.g. ratio of lake surface area to catchment area) and the amount of surface water in the catchment.

3.1 | Species responses

Species richness (19.1 ± 8.1) was positively correlated with variables related to alkalinity, ecosystem size, deciduous forest cover and Secchi depth transparency, and negatively correlated with coniferous forest cover, Fe concentration, water temperature and water colour, but not significantly related to lake productivity (Chl *a*), nutrients (TP and TN) or latitude ($p > 0.05$) (Table S3). Similar relationships were found for Simpson's diversity (0.850 ± 0.084): positively correlated with alkalinity, ecosystem size and negatively correlated with water temperature, coniferous forest cover and Fe concentration, but not related to lake productivity or latitude ($p > 0.05$). Hill's diversity (N2, effective number of species) was significantly correlated with DCA axis 2 (Spearman $\rho = -0.368$, $p = <0.001$) but not DCA axis 1 (Figure 2). Correlation also showed that N2 was positively related to ecosystem size (lake surface area, shoreline length) and alkalinity, and negatively correlated with coniferous forest cover, water colour and Fe concentrations ($p < 0.01$) (Table S3).

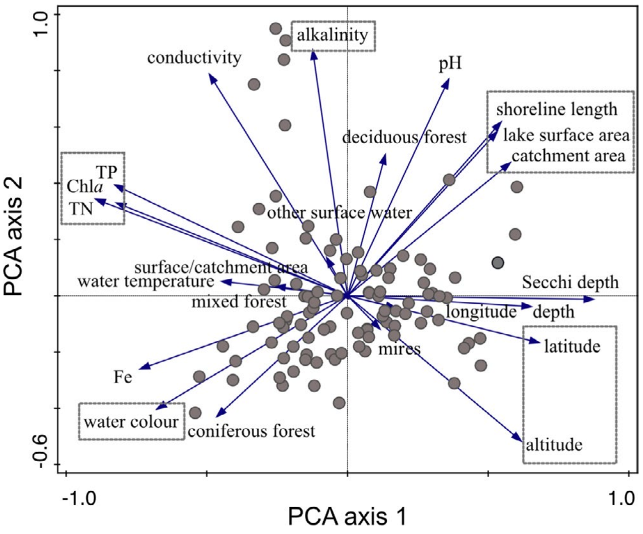

FIGURE 1 Principal component analysis of 23 environmental variables in 104 boreal Swedish lakes. Dashed boxes show the main environmental gradients related to alkalinity, ecosystem size, length of the growing season, water colour and lake productivity. Eigenvalues = 0.3067 for axis 1 and 0.1872 for axis 2 [Colour figure can be viewed at wileyonlinelibrary.com]

Multivariate regression showed that macrophyte species and trait composition were significantly related to all 23 environmental variables (Table 2). The amount of variance explained ranged from ca. 4% for the proportion of other surface water in the catchment area to 16.0% (species) and 40.3% (traits) for alkalinity. Ranking environmental variables by their individual contribution (lambda) revealed that alkalinity and conductivity were the single best predictors (16.0% and 15.5%, respectively) of species composition, followed by variables associated with lake productivity (Chl *a* [12.0%], nutrients: TN [14.4%] and TP [12.7%]), variables related to length of the growing season (altitude [12.0%], latitude [9.9%]), forest cover (coniferous forest [11.4%]) and water transparency (Secchi depth, 10.2%). For trait composition, similar patterns were noted; both alkalinity and conductivity were the best predictors of trait composition. The variation explained and the rankings differed, however, between species and traits for the top five predictors: for species composition rankings were alkalinity > conductivity > TN > TP > altitude; whilst for trait composition rankings were alkalinity > conductivity > pH > altitude > catchment area.

Forward selection resulted in a significant ($p < 0.05$ with Holm *p*-value correction) eight-variable model for species composition (Figure 3a; Table 2) and a five-variable model for trait composition (Figure 3b; Table 2). For species composition, the first variable selected was alkalinity (16.0%), followed by TN (11.3%), coniferous (5.69%) and deciduous (5.57%) forest cover, latitude (5.48%), conductivity (4.40%), TP (4.10%) and lake surface area (4.15%). For trait composition, the most parsimonious model was comprised of alkalinity (40.3%), TN (13.1%), lake surface area (11.8%), coniferous forest cover (5.02%) and latitude (5.34%).

Partitioning the pure effects of the eight (species) or five (traits) variables selected in forward selection modelling by spatial context (GEO: latitude), catchment land cover (CATCH: forest type) and local (LOCAL: e.g. alkalinity) (Table 3), showed that LOCAL variables explained the greatest amount of variation in macrophyte species assemblages (53.0% of explained variance), followed by CATCH (19.1%) and GEO (9.4%) (Table 3A). The shared variance between CATCH & LOCAL was slightly higher (8.7%) than for GEO & LOCAL (6.7%), while GEO & CATCH component did not contribute to the variance partitioning

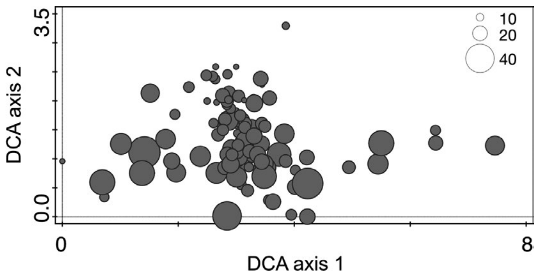

FIGURE 2 Detrended correspondence analysis (DCA) of macrophyte species richness (Hill's diversity, N2) in 104 boreal lakes. DCA gradient lengths of 7.46 for axis 1 (eigenvalue 0.6983) and 3.29 for axis 2 (eigenvalue 0.2738). The size of the circles represents N2 values

TABLE 2 CCA (species) and RDA (traits) analysis of macrophyte assemblages and 23 environmental variables in 104 lakes boreal lakes in Sweden

	Species			Traits			Category	
	λ	*F*	*p*	λ	*F*	*p*	pCCA	pRDA
Latitude	$9.9^{(5)}$	3.4	***	$10.1^{(5)}$	6.0	***	GEO†	GEO†
Longitude	4.6	1.6	**	4.5	2.6	*	GEO	GEO
Catchment area (km^2)	6.2	2.1	***	20.9	13.4	***	LOCAL	LOCAL
Shoreline length (km)	5.6	1.9	**	18.0	11.3	***	LOCAL	LOCAL
Lake surface area (km^2)	$6.6^{(8)}$	2.3	***	$20.7^{(3)}$	13.2	***	LOCAL†	LOCAL†
Surface/ catchment area	4.7	1.6	**	5.7	3.3	*	LOCAL	LOCAL
Altitude (m a.s.l.)	12.0	4.2	***	25.2	16.6	***	LOCAL	LOCAL
Depth (m)	5.8	2.0	***	5.7	3.3	*	LOCAL	LOCAL
Coniferous forest (%)	$11.4^{(3)}$	4.0	***	$9.1^{(4)}$	5.4	**	CATCH†	CATCH†
Mixed forest (%)	5.2	1.8	**	5.0	1.67	**	CATCH	CATCH
Deciduous forest (%)	$4.6^{(4)}$	1.6	*	4.4	1.47	*	CATCH†	CATCH
Other surface water (%)	4.0	1.4	*	4.1	1.37	*	CATCH	CATCH
Mires (%)	4.9	1.7	*	4.9	1.64	*	CATCH	CATCH
Secchi depth (m)	10.2	3.6	***	8.0	4.7	**	LOCAL	LOCAL
Chlorophyll *a* (μg/L)	12.0	4.2	***	11.5	6.9	***	LOCAL	LOCAL
Water temperature (°C)	6.5	2.3	***	5.2	3.0	*	LOCAL	LOCAL
Conductivity (mS/m)	$15.5^{(6)}$	5.5	***	32.0	22.2	***	LOCAL†	LOCAL
pH	11.3	4.0	***	31.4	21.6	***	LOCAL	LOCAL
Water colour (AbsF)	6.5	2.2	***	10.6	6.3	**	LOCAL	LOCAL
Alkalinity (meq/L)	$16.0^{(1)}$	5.7	***	$40.3^{(1)}$	29.6	***	LOCAL†	LOCAL†
Fe (μg/L)	8.7	3.0	***	6.1	3.6	*	LOCAL	LOCAL
TN (μg/L)	$14.4^{(2)}$	5.1	***	$18.8^{(2)}$	11.3	***	LOCAL†	LOCAL†
TP (μg/L)	$12.7^{(7)}$	4.5	***	17.2	10.7	***	LOCAL†	LOCAL

Note: Marginal effects (lambda, λ) and numbers in parentheses show results of forward selection. Category shows classification and the variables used in variation partitioning are marked with †. $^*p < 0.05$.; $^{**}p < 0.01$.; $^{***}p < 0.001$.

(0.1%). For trait assemblages, LOCAL variables explained 73.5% of the variation but, in contrast to species, GEO explained more variation than CATCH (8.9% and 4.5, respectively) (Table 3B). For shared variance, GEO & LOCAL > CATCH & LOCAL > GEO & CATCH.

3.2 | Temporal variability

pCCA (species) and pRDA (traits) with Year as a covariable and the significant (model) environmental variables as predictors revealed that Year did not explain a significant amount of variability in species or trait composition between the two macrophyte surveys ($p > 0.05$). By contrast, environmental variables explained 12.1% of the total variability in species composition (eight predictor variables) and 17.2% of the total variability in trait composition (five predictor variables) between the two sampling events.

Similar to variation partitioning, the three measures of macrophyte diversity and the two measures of the pollution-specific index (the Trophic Macrophyte Index [TMI] and TMI scoring taxa) did not differ between the six-year sampling intervals (2012 to 2018, 2013 to 2019) (paired *t*-test, $n = 24$ lakes).

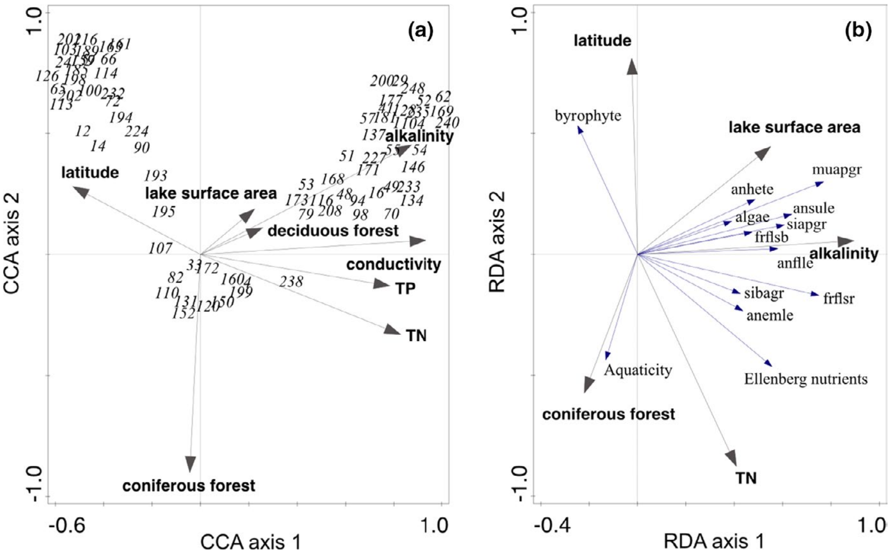

FIGURE 3 Canonical correspondence and redundancy analysis biplots of macrophyte species (a) and traits (b) with eight and five environmental variables, respectively, in 104 boreal lakes. Only the species numbers are shown for clarity (see Table S1 for species numbers and names). For trait abbreviations see text [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Variation partitioning of pure effects of spatial context (GEO), catchment land cover (CATCH) and within-lake (LOCAL) variables on species (A) and traits (C) and shared variance between GEO, CATCH and LOCAL for species (B) and traits (D) for macrophyte assemblages in 104 boreal Swedish lakes

(A) Species, pCCA	**GEO**	**CATCH**	**LOCAL**
Adj. R^2	0.122	0.249	0.692
% of Explained	9.4	19.1	53.0
Pseudo-*F*	2.3	2.4	2.6
df	1	2	5
p	0.0001	0.0001	0.0001
(B) Species, pCCA	**Adj. R^2**	**% of Explained**	
GEO & CATCH	0.0016	0.1	
GEO & LOCAL	0.087	6.7	
CATCH & LOCAL	0.114	8.7	
(C) Traits, pRDA	**GEO**	**CATCH**	**LOCAL**
Adj. R^2	0.029	0.015	0.239
% of Explained	8.9	4.5	73.5
Pseudo-*F*	5.1	3.1	12.6
df	1	1	3
p	0.0018	0.0225	0.0001
(D) Traits, pRDA	**Adj. R^2**	**% of Explained**	
GEO & CATCH	−0.0004	−0.1	
GEO & LOCAL	0.0126	3.9	
CATCH & LOCAL	0.0220	2.5	

4 | DISCUSSION

Understanding how patterns in biodiversity relate to environmental gradients is important for conservation and for implementing best management practices. Here we quantified lake macrophyte diversity and species and trait composition across relatively broad environmental gradients in a boreal forested landscape. Our main findings revealed that diversity and species and trait composition were significantly related to alkalinity, lake productivity, length of the growing season, ecosystem size and catchment forest type. Variation partitioning showed that local-scale variables were better predictors of both species and trait composition than catchment land cover or geographic position. Temporal variability of diversity and turnover of species and trait composition in these minimally disturbed boreal lakes was low and did not differ between the two surveys. Below we address biogeographic patterns in relation to spatial context, ecosystem size, water chemistry and lake productivity.

Many studies have shown that global patterns in biodiversity are related to physiological constraints on growth and reproduction (Chown et al., 2010; Willig et al., 2003). At high latitudes seasonal variability in water temperature and light conditions are two important constraints regulating the timing and rate of seasonal growth (Lacoul & Freedman, 2006). Consequently, latitude is frequently used as a proxy for variables that are associated with patterns in biodiversity and many ecological processes (Hillebrand, 2004; Kinlock et al., 2018). Situated across a 12.9° range in latitude (55.49–68.35°N) correlation of the environmental variables in our study lakes showed that lake productivity (Chl *a*, TP and TN) and water temperature were inversely related to latitude, whilst ecosystem size (lake surface area) and altitude were positively related to latitude. Contrary to our expectations macrophyte species richness and diversity did not decrease with latitude. Species richness and diversity were negatively correlated with coniferous forest, Fe concentration and water temperature. Multivariate regression showed, however, that latitude alone was a significant predictor of species and trait composition. This finding implies that latitude remains an appropriate proxy for important environmental variables not included in our study. Not surprisingly, two bryophyte *Sphagnum* mosses (subg. *Cuspidata* and subgen. *Acutifolia* sect. *Acutifolia*) and the liverworts *Scapania hyperborea* and *Racomitrium fasciculare* were positively associated with the high latitude, low productivity lakes in our study. Both groups are also known to withstand harsh environments, and there is now strong empirical evidence that *Sphagnum* mosses originated in the cooler high latitude climates of the Northern Hemisphere (Shaw et al., 2018). The shorter growing season and slow growth rates in the colder climates benefit plants that can effectively use low levels of photosynthetically active radiation (Loisel et al., 2012).

Alkalinity was the single best predictor of macrophyte assemblages in our boreal lakes, accounting for 16% (species) and 40.3% (traits) of the among-lake variability, and as predicted both species richness and diversity were positively correlated with alkalinity, supporting earlier studies (Alahuhta et al., 2017; Vestergaard & Sand-Jensen, 2000). That numerous studies have shown alkalinity (or dissolved inorganic C) to be a robust predictor of macrophyte distributions is not surprising as some species such as characeans and elodeids are able to efficiently use HCO_3^- in addition to CO_2, whilst others such as mosses and isoetids are restricted to the use of free CO_2 for photosynthesis (Maberly & Spence, 1983; Vestergaard & Sand-Jensen, 2000). Constrained ordination of species frequencies with alkalinity showed that many species such as *Chara* spp. (e.g. *C. polyacantha*, *C. tomentosa*, *C. contraria*) and *Potamogeton* spp. (e.g. *P. friesli*, *P. pusillus*) were positively correlated, while other species such as *Isoëtes lacustris*, *Juncus bulbosa*, *Lobelia dortmanna* and the invasive *Elodea nuttallii* were negatively correlated with alkalinity. From previous studies several of these species are known to exhibit clear growth optima associated with either low or high alkalinity (Spence, 1967; Vestergaard & Sand-Jensen, 2000). Finding that alkalinity was a robust predictor of macrophyte assemblages in a landscape predominated by poorly buffered humic lakes was expected and reinforces the importance of free and bicarbonate bound C as a strong predictor of distribution patterns (i.e. isoetids being predominantly found in poorly buffered lakes, whilst elodeids are found in lakes with varying alkalinity) (Vestergaard & Sand-Jensen, 2000).

Consistent with earlier studies our analyses revealed significant relationships between macrophyte species and trait assemblages and lake productivity (e.g. Alahuhta et al., 2018; Fu et al., 2019; Johnson et al., 2014; Viana et al., 2014). Shifts in macrophyte assemblages and biodiversity loss are often inversely related to an increase in phytoplankton, epiphytes and filamentous algae (Sand-Jensen & Borum, 1991; Sand-Jensen et al., 2008), that is, factors limiting incident light and nutrient availability, with highly productive lakes frequently characterised by only a few highly competitive tolerant species (Sayer et al., 1999). However, other factors such as lake morphometry (Søndergaard et al., 2013; Vestergaard & Sand-Jensen, 2000), and seasonality and internal-population dynamics (Sayer et al., 2010) also contribute to species turnover with elevated nutrients. Poikane et al. (2018), in a relatively large European study, found diverse macrophyte assemblages, characterised by many charophytes and *Potamogeton* species, in lakes classified as having good ecological status, whilst poor quality (eutrophied) lakes had assemblages often comprised of lemnids, nymphaeids and elodeids. As anticipated, Ellenberg nutrient scores ($\rho = 0.501$) and the frequency of certain growth forms such as free-floating, surface species (frflsr, $\rho = 0.445$) and anchored, floating-leaved species (anflle, $\rho = 0.196$) were positively correlated with Chl *a* ($p < 0.05$). Free-floating species were characterised by *Lemna minor* and *Hydrocharis morsus-ranae*, while anchored, floating-leaved species were represented by two *Potamogeton* species (*P. friesii* and *P. pusillus*), *Zannichellia palustris*, *Ranunculus circinatus* and *Callitriche hermaphroditica*. Although a number of studies have shown the occurrence and abundance of submerged species to decline with lake productivity (e.g. Jeppessen et al., 2000; Phillips et al., 1978, 2016; Poikane et al., 2018; Sayer et al., 2010), in our study, anchored species with submerged leaves were not correlated with productivity (Chl *a*, $\rho = 0.071$, $p = 0.477$). However, not finding a significant effect might be due to the oligo- and mesotrophic conditions of our study lakes: the majority of our lakes were nutrient poor (median 9.4 μg TP/L) and only 10 lakes had TP values >30 μg/L and only one lake had Chl *a* > 25 μg/L.

Our prediction that macrophyte assemblages would be more correlated with species-sorting processes at local scales (lake characteristics) than with large-scale variables such as catchment land cover or biogeographic position was supported. Partitioning among-lake variation in macrophyte assemblages by geographic position, catchment land cover and local variables showed that local within-lake characteristics alone explained 53% (species) and 73.5% (traits) of the variability in macrophyte assemblages. Local variables used in variation partitioning of species comprised water quality (alkalinity, nutrients, conductivity) and ecosystem size (lake surface area). Similarly, for traits local variables comprised measures of water quality (alkalinity, TN) and lake surface area. That species and trait composition correlated with nutrients and ecosystem size was expected due to well-known relationships between species richness and productivity (Mittelbach et al., 2001) and habitat size (Drakare et al., 2006). Given the relatively large latitudinal distribution of our study sites we expected latitude to be a significant predictor and also that the shared latitude and catchment and local components would be relatively large. However, this assumption was not supported: for species, CATCH & LOCAL explained more variation than GEO & LOCAL, while the inverse was found for traits (GEO & LOCAL > CATCH & LOCAL). These findings agree with a recent analysis of global patterns in macrophyte metacommunities (Alahuhta et al., 2018; García-Girón et al., 2020). These authors showed that ecosystem size, productivity and alkalinity were robust predictors of macrophyte species richness and composition at regional scales, whilst climate variables were better predictors at global scales.

Among-year variability in macrophyte diversity and assemblage composition was negligible (0.3%) compared to the variability explained by GEO, CATCH and LOCAL variables. This finding implies that the variables structuring macrophyte diversity and assemblage composition were relatively stable over the eight years of this study. That temporal, among-year variability was low can be partly explained by the relatively undisturbed condition of the study lakes and the ecological memory (Padisák, 1992) inherent in macrophyte assemblages, that is, propagules of past assemblages shape present or future assemblages. By contrast, a number of studies have shown relatively high seasonal and among-year variability associated with productivity and water-level fluctuations (e.g. Bunch et al., 2010; Salgado et al., 2018; Valley & Drake, 2007). Diversity metrics, the TMI and the TMI scoring taxa did not differ between the two surveys at six-year intervals, lending further support to low species turnover in these boreal lakes.

Key to the successful management of lakes is the selection of indicators responding at appropriate time scales and with known uncertainties to the pressure(s) of interest. Although resilience to anthropogenic disturbance is desirable for key ecosystem functions, time lags between disturbance and change in a response variable can be costly for biodiversity if substantial loss is allowed to occur before ecological change (status) is established. Our study showed that although macrophyte species richness and diversity were not significantly correlated with Chl *a* and nutrient concentrations, macrophyte species and trait compositions did change significantly with nutrient status, and importantly the index currently used for assessing ecological status (TMI) was correlated to TP ($\rho = -0.48$, $p = 0.016$). These findings support the use of macrophytes in monitoring and assessment of boreal lakes.

However, when designing monitoring programmes to detect human-induced change, careful consideration should be given to the selection of the most robust and cost-effective response indicator (Johnson et al., 1993, 2007). Studies comparing the responses of different taxonomic groups to nutrient enrichment have often shown that macrophyte assemblages respond predictably to eutrophication, but that responses are not as strong as those of other primary producers such as phytoplankton and benthic diatoms (Johnson & Angeler, 2014; Johnson et al., 2014; Johnson & Hering, 2009; Kelly et al., 2016). Studying responses of primary producers to eutrophication in lakes, Kelly et al. (2016) showed that benthic diatoms and phytoplankton tended to have stronger relationships with TP. Moreover, similar findings have been found when comparing responses of primary producers to nutrients in streams. Benthic diatoms have been shown to be more strongly correlated with nutrient concentrations than macrophytes (Johnson & Hering, 2009), and Johnson and Angeler (2014) argued that macrophyte responses to nutrients were confounded by responses to habitat (substratum). Based solely on generation times, macrophyte assemblages are also expected to react to environmental variables over much longer time scales (years) than phytoplankton and benthic diatoms (hours or days) (Schaumburg et al., 2004), resulting in substantial time-lag responses to degradation and recovery (Kleindl & Steinman, 2021). Considerable time lags in recovery have been noted for macrophytes after nutrient reductions, whilst phytoplankton recovery closely tracked decreases in TP concentrations (Eigemann et al., 2016). These authors argued that longer generation times and the predominance of a few competitive macrophyte species may have prevented the reestablishment of weaker competitors. In summary, findings from our study and those of others suggest that macrophytes are reliable response indicators to eutrophication. However, macrophyte responses to nutrient enrichment and other concomitant environmental changes are complex and may not always be related to first principal relationships with nutrients.

ACKNOWLEDGMENTS

The Swedish Environmental Protection Agency and the Swedish Agency for Marine and Water Management are acknowledged for the financing of national and regional monitoring programmes. The many people involved in the monitoring programmes are gratefully acknowledged for making the analyses of these data sets possible. Financial support for VT was provided by an Erasmus+ Student Mobility Traineeship.

DATA AVAILABILITY STATEMENT

Data used in this study are available at https://miljodata.slu.se/mvm/.

ORCID

Richard K. Johnson https://orcid.org/0000-0001-7979-6563
Vildan Toprak https://orcid.org/0000-0003-0730-7315

REFERENCES

Alahuhta, J., Lindholm, M., Bove, C. P., Chappuis, E., Clayton, J., de Winton, M., Feldmann, T., Ecke, F., Gacia, E., Grillas, P., Hoyer, M. V., Johnson, L. B., Kolada, A., Kosten, S., Lauridsen, T., Lukács, B. A., Mjelde, M., Mormul, R. P., Rhazi, L., … Heino, J. (2018). Global patterns in the metacommunity structuring of lake macrophytes: Regional variations and driving factors. *Oecologia*, *188*(4), 1167–1182. https://doi.org/10.1007/s00442-018-4294-0

Alahuhta, J., Toivanen, M., Hjort, J., Ecke, F., Johnson, L. B., Sass, L., & Heino, J. (2017). Species richness and taxonomic distinctness of lake macrophytes along environmental gradients in two continents. *Freshwater Biology*, *62*(7), 1194–1206. https://doi.org/10.1111/fwb.12936

Baastrup-Spohr, L., Sand-Jensen, K., Olesen, S. C., & Bruun, H. H. (2017). Recovery of lake vegetation following reduced eutrophication and acidification. *Freshwater Biology*, *62*(11), 1847–1857. https://doi.org/10.1111/fwb.13000

Birk, S., Korte, T., & Hering, D. (2006). Intercalibration of assessment methods for macrophytes in lowland streams: Direct comparison and analysis of common metrics. *Hydrobiologia*, *566*(1), 417–430. https://doi.org/10.1007/s10750-006-0080-9

Bonanno, G., & Giudice, R. L. (2010). Heavy metal bioaccumulation by the organs of *Phragmites australis* (common reed) and their potential use as contamination indicators. *Ecological Indicators*, *10*(3), 639–645. https://doi.org/10.1016/j.ecolind.2009.11.002

Bunch, A. J., Allen, M. S., & Gwinn, D. C. (2010). Spatial and temporal hypoxia dynamics in dense emergent macrophytes in a Florida lake. *Wetlands*, *30*(3), 429–435. https://doi.org/10.1007/s13157-010-0051-9

Carpenter, S. R., & Lodge, D. M. (1986). Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany*, *26*, 341–370. https://doi.org/10.1016/0304-3770(86)90031-8

Chown, S. L., Hoffmann, A. A., Kristensen, T. N., Angilletta, M. J. Jr, Stenseth, N. C., & Pertoldi, C. (2010). Adapting to climate change: A perspective from evolutionary physiology. *Climate Research*, *43*(1–2), 3–15. https://doi.org/10.3354/cr00879

Crowder, A. (1991). Acidification, metals and macrophytes. *Environmental Pollution*, *71*(2–4), 171–203. https://doi.org/10.1016/0269-7491(91)90032-R

Dittrich, J., Dias, J. D., Bonecker, C. C., Lansac-Tôha, F. A., & Padial, A. A. (2016). Importance of temporal variability at different spatial scales for diversity of floodplain aquatic communities. *Freshwater Biology*, *61*(3), 316–327. https://doi.org/10.1111/fwb.12705

Drakare, S., Lennon, J. J., & Hillebrand, H. (2006). The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecology Letters*, *9*(2), 215–227. https://doi.org/10.1111/j.1461-0248.2005.00848.x

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. https://doi.org/10.1017/S1464793105006950

Ecke, F. (2007). *Bedömningsgrunder för makrofyter i sjöar: Bakgrundsrapport*. Luleå tekniska universitet. (In Swedish).

Ecke, F. (2009). Drainage ditching at the catchment scale affects water quality and macrophyte occurrence in Swedish lakes. Freshwater Biology 54:119–126. *Hydrobiologia*, *704*, 141–151.

Eigemann, F., Mischke, U., Hupfer, M., Schaumburg, J., & Hilt, S. (2016). Biological indicators track differential responses of pelagic and littoral areas to nutrient load reductions in German lakes. *Ecological Indicators*, *61*, 905–910. https://doi.org/10.1016/j.ecolind.2015.10.045

European Commission. (2000). Directive 2000/60/EC of the European Parliament and of the Council of 23rd October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities, L327/1. European Commission, Brussels.

Fölster, J., Johnson, R. K., Futter, M. N., & Wilander, A. (2014). The Swedish monitoring of surface waters: 50 years of adaptive monitoring. *Ambio*, *43*(1), 3–18.

Fu, H., Yuan, G., Li, W., Ge, D., Zou, D., & Huang, Z. (2019). Environmental effects on community productivity of aquatic macrophytes are mediated by species and functional composition. *Ecohydrology*, *12*(8), e2147. https://doi.org/10.1002/eco.2147

García-Girón, J., Heino, J., Baastrup-Spohr, L., Clayton, J., Winton, M., Feldmann, T., Fernández-Aláez, C., Ecke, F., Hoyer, M. V., Kolada, A., Kosten, S., Lukács, B. A., Mormul, R. P., Rhazi, L., Rhazi, M., Sass, L., Xu, J., & Alahuhta, J. (2020). Elements of lake macrophyte metacommunity structure: Global variation and community-environment relationships. *Limnology and Oceanography*, *65*(12), 2883–2895. https://doi.org/10.1002/lno.11559

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, *405*(6783), 220–227. https://doi.org/10.1038/35012228

Hammer, Ø., Harper, D. A., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, *4*(1), 9.

Heino, J., Alahuhta, J., Bini, L. M., Cai, Y., Heiskanen, A.-S., Hellsten, S., Kortelainen, P., Kotamäki, N., Tolonen, K. T., Vihervaara, P., Vilmi, A., & Angeler, D. G. (2020). Lakes in the era of global change: Moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. *Biological Reviews*, *96*, 89–106. https://doi.org/10.1111/brv.12647

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*(1), 121–137. https://doi.org/10.1007/s00442-016-3750-y

Heino, J., & Toivonen, H. (2008). Aquatic plant biodiversity at high latitudes: Patterns of richness and rarity in Finnish freshwater macrophytes. *Boreal Environment Research*, *13*, 1–14.

Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, *84*(1), 39–54. https://doi.org/10.1111/j.1469-185X.2008.00060.x

Hill, M. O., Mountford, J. O., Roy, D. B., & Bunce, R. G. H. (1999). *Ellenberg's indicator values for British plants*. ECOFACT Volume 2 Technical Annex (Vol. *2*). Institute of Terrestrial Ecology.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, *163*(2), 192–211. https://doi.org/10.1086/381004

Immers, A. K., Vendrig, K., Ibelings, B. W., Van Donk, E., Ter Heerdt, G. N., Geurts, J. J., & Bakker, E. S. (2014). Iron addition as a measure to restore water quality: Implications for macrophyte growth. *Aquatic Botany*, *116*, 44–52. https://doi.org/10.1016/j.aquabot.2014.01.007

Janssen, A. B., Hilt, S., Kosten, S., de Klein, J. J., Paerl, H. W., & Van de Waal, D. B. (2020). Shifting states, shifting services: Linking regime shifts to changes in ecosystem services of shallow lakes. *Freshwater Biology*, *66*(1), 1–12.

Jeppesen, E., Peder Jensen, J., SØndergaard, M., Lauridsen, T., & Landkildehus, F. (2000). Trophic structure, species richness and biodiversity in Danish lakes: Changes along a phosphorus gradient. *Freshwater Biology*, *45*(2), 201–218. https://doi.org/10.1046/j.1365-2427.2000.00675.x

Jeppesen, E., Søndergaard, M., & Christoffersen, K. (Eds.). (1997). *The structuring role of submerged macrophytes in lakes*. *Ecological studies* (Vol. *131*, pp. 423). Springer.

Jeppesen, E., Søndergaard, M., Søndergaard, M., & Christoffersen, K. (Eds.). (2012). *The structuring role of submerged macrophytes in lakes* (Vol. *131*). Springer Science & Business Media.

JMP®, Version 14.0.0. SAS Institute Inc., Cary, NC, 1989-2018

Johnson, R. K., & Angeler, D. G. (2014). Effects of agricultural land use on stream assemblages: Taxon-specific responses of alpha and beta diversity. *Ecological Indicators*, *45*, 386–393. https://doi.org/10.1016/j.ecolind.2014.04.028

Johnson, R. K., Angeler, D. G., Moe, S. J., & Hering, D. (2014). Cross-taxon responses to elevated nutrients in European streams and lakes. *Aquatic Sciences*, *76*(1), 51–60. https://doi.org/10.1007/s00027-013-0311-x

Johnson, R. K., Furse, M. T., Hering, D., & Sandin, L. (2007). Ecological relationships between stream communities and spatial scale: Implications for designing catchment-level monitoring programmes. *Freshwater Biology*, *52*(5), 939–958. https://doi.org/10.1111/j.1365-2427.2006.01692.x

Johnson, R. K., & Hering, D. (2009). Response of taxonomic groups in streams to gradients in resource and habitat characteristics. *Journal of Applied Ecology*, *46*(1), 175–186. https://doi.org/10.1111/j.1365-2664.2008.01583.x

Johnson, R. K., & Hering, D. (2010). Spatial congruency of benthic diatom, invertebrate, macrophyte, and fish assemblages in European streams. *Ecological Applications*, *20*(4), 978–992. https://doi.org/10.1890/08-1153.1

Johnson, R. K., Wiederholm, T., & Rosenberg, D. M. (1993). Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. In D. Rosenberg & V. Resh (Eds.), *Freshwater Biomonitoring and Benthic Macroinvertebrates* (pp. 40–158). Chapman & Hall.

Jupp, B. P., & Spence, D. H. N. (1977). Limitations on macrophytes in a eutrophic lake, Loch Leven: I. Effects of phytoplankton. *The Journal of Ecology*, *65*(1), 175–186.

Kelly, M. G., Birk, S., Willby, N. J., Denys, L., Drakare, S., Kahlert, M., Karjalainen, S. M., Marchetto, A., Pitt, J.-A., Urbanič, G., & Poikane, S. (2016). Redundancy in the ecological assessment of lakes: Are phytoplankton, macrophytes and phytobenthos all necessary? *Science of the Total Environment*, *568*, 594–602. https://doi.org/10.1016/j.scitotenv.2016.02.024

Kinlock, N. L., Prowant, L., Herstoff, E. M., Foley, C. M., Akin-Fajiye, M., Bender, N., Umarani, M., Ryu, H. Y., Şen, B., & Gurevitch, J. (2018). Explaining global variation in the latitudinal diversity gradient: Meta-analysis confirms known patterns and uncovers new ones. *Global Ecology and Biogeography*, *27*(1), 125–141. https://doi.org/10.1111/geb.12665

Kleindl, P. M., & Steinman, A. D. (2021). Contrasting trajectories in macrophyte community development after shoreline restoration: Water level obscures trends. *Aquatic Botany*, *169*, 103327.

Kolada, A., Willby, N., Dudley, B., Nõges, P., Søndergaard, M., Hellsten, S., Mjelde, M., Penning, E., van Geest, G., Bertrin, V., Ecke, F., Mäemets, H., & Karus, K. (2014). The applicability of macrophyte compositional metrics for assessing eutrophication in European lakes. *Ecological Indicators*, *45*, 407–415. https://doi.org/10.1016/j.ecolind.2014.04.049

Lachavanne, J. B., Perfetta, J., & Juge, R. (1992). Influence of water eutrophication on the macrophytic vegetation of Lake Lugano. *Aquatic Sciences*, *54*(3–4), 351–363. https://doi.org/10.1007/BF00878147

Lacoul, P., & Freedman, B. (2006). Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews*, *14*(2), 89–136. https://doi.org/10.1139/a06-001

Linkola, K. (1933). Regionale Artenstatistik der Süsswasserflora Finnlands. *Annales Botanici Societatis Vanamo*, *3*(5), 3–13.

Lohammar, G. (1938). Wasserchemie und höhere Vegetation Schwedischer Seen. Doctoral thesis. Uppsala Universitet, Uppsala.

Lohammar, G. (1965). The vegetation of Swedish lakes. Acta Phytogeographica Suecica, 50, Svenska Växtgeografiska Sällskapet, Uppsala.

Loisel, J., Gallego-Sala, A. V., & Yu, Z. C. (2012). Global-scale pattern of peatland Sphagnum growth driven by photosynthetically active radiation and growing season length. *Biogeosciences*, *9*, 2737–2746.

Maberly, S. C., & Spence, D. H. N. (1983). Photosynthetic inorganic carbon use by freshwater plants. *The Journal of Ecology*, *71*, 705–724. https://doi.org/10.2307/2259587

Manatunge, J., Asaeda, T., & Priyadarshana, T. (2000). The influence of structural complexity on fish–zooplankton interactions: A study using artificial submerged macrophytes. *Environmental Biology of Fishes*, *58*(4), 425–438. https://doi.org/10.1023/A:1007691425268

Middelboe, A. L., & Markager, S. (1997). Depth limits and minimum light requirements of freshwater macrophytes. *Freshwater Biology*, *37*(3), 553–568. https://doi.org/10.1046/j.1365-2427.1997.00183.x

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig, M. R., Dodson, S. I., & Gough, L. (2001). What is the observed relationship between species richness and productivity?. *Ecology*, *82*(9), 2381–2396.

Mjelde, M., Hellsten, S., & Ecke, F. (2013). A water level drawdown index for aquatic macrophytes in Nordic lakes. *Hydrobiologia*, *704*(1), 141–151. https://doi.org/10.1007/s10750-012-1323-6

Moss, B. (1990). Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. In R. D. Gulati, E. H. R. R. Lammens, M.-L. Meyer, & E. van Dock (Eds.), *Biomanipulation tool for water management* (pp. 367–377). Springer.

Moss, B., Kosten, S., Meerhoff, M., Battarbee, R. W., Jeppesen, E., Mazzeo, N., & Scheffer, M. (2011). Allied attack: Climate change and eutrophication. *Inland Waters*, *1*(2), 101–105. https://doi.org/10.5268/IW-1.2.359

Padisák, J. (1992). Seasonal succession of phytoplankton in a large shallow lake (Balaton, Hungary) – A dynamic approach to ecological memory, its possible role and mechanisms. *Journal of Ecology*, *80*, 217–230. https://doi.org/10.2307/2261008

Palmer, M. A., Covich, A. P., Lake, S., Biro, P., Brooks, J. J., Cole, J., Dahm, C., Gibert, J., Goedkoop, W., Martens, K., Verhoeven, J., & Van de bund, W. J. (2000). Linkages between aquatic sediment biota and life above sediments as potential drivers of biodiversity and ecological processes: A disruption or intensification of the direct and indirect chemical, physical, or biological interactions between aquatic sediment biota and biota living above the sediments may accelerate biodiversity loss and contribute to the degradation of aquatic and riparian habitats. *BioScience*, *50*(12), 1062–1075.

Penning, W. E., Dudley, B., Mjelde, M., Hellsten, S., Hanganu, J., Kolada, A., van den Berg, M., Poikane, S., Phillips, G., Willby, N., & Ecke, F. (2008). Using aquatic macrophyte community indices to define the ecological status of European lakes. *Aquatic Ecology*, *42*(2), 253–264. https://doi.org/10.1007/s10452-008-9183-x

Penning, W. E., Mjelde, M., Dudley, B., Hellsten, S., Hanganu, J., Kolada, A., van den Berg, M., Poikane, S., Phillips, G., Willby, N., & Ecke, F. (2008). Classifying aquatic macrophytes as indicators of eutrophication in European lakes. *Aquatic Ecology*, *42*(2), 237–251. https://doi.org/10.1007/s10452-008-9182-y

Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, *87*(10), 2614–2625.

Phillips, G. L., Eminson, D., & Moss, B. (1978). A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Botany*, *4*, 103–126. https://doi.org/10.1016/0304-3770(78)90012-8

Phillips, G., Willby, N., & Moss, B. (2016). Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? *Aquatic Botany*, *135*, 37–45. https://doi.org/10.1016/j.aquabot.2016.04.004

Poikane, S., Birk, S., Böhmer, J., Carvalho, L., de Hoyos, C., Gassner, H., Hellsten, S., Kelly, M., Lyche Solheim, A., Olin, M., Pall, K., Phillips, G., Portielje, R., Ritterbusch, D., Sandin, L., Schartau, A.-K., Solimini, A. G., van den Berg, M., Wolfram, G., & van de Bund, W. (2015). A hitchhiker's guide to European lake ecological assessment and intercalibration. *Ecological Indicators*, *52*, 533–544. https://doi.org/10.1016/j.ecolind.2015.01.005

Poikane, S., Herrero, F. S., Kelly, M. G., Borja, A., Birk, S., & van de Bund, W. (2020). European aquatic ecological assessment methods: A critical review of their sensitivity to key pressures. *Science of the Total Environment*, *740*, 140075. https://doi.org/10.1016/j.scitotenv.2020.140075

Poikane, S., Portielje, R., Denys, L., Elferts, D., Kelly, M., Kolada, A., Mäemets, H., Phillips, G., Søndergaard, M., Willby, N., & van den Berg, M. S. (2018). Macrophyte assessment in European lakes: Diverse approaches but convergent views of 'good' ecological status. *Ecological Indicators*, *94*, 185–197. https://doi.org/10.1016/j.ecolind.2018.06.056

Rørslett, B. (1991). Principal determinants of aquatic macrophyte richness in northern European lakes. *Aquatic Botany*, *39*(1–2), 173–193. https://doi.org/10.1016/0304-3770(91)90031-Y

Salgado, J., Sayer, C. D., Brooks, S. J., Davidson, T. A., Goldsmith, B., Patmore, I. R., Baker, A. G., & Okamura, B. (2018). Eutrophication homogenizes shallow lake macrophyte assemblages over space and time. *Ecosphere*, *9*(9), e02406. https://doi.org/10.1002/ecs2.2406

Sand-Jensen, K., & Borum, J. (1991). Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany*, *41*(1–3), 137–175. https://doi.org/10.1016/0304-3770(91)90042-4

Sand-Jensen, K., Pedersen, N. L., Thorsgaard, I., Moeslund, B., Borum, J., & Brodersen, K. P. (2008). 100 years of vegetation decline and recovery in Lake Fure, Denmark. *Journal of Ecology*, *96*(2), 260–271. https://doi.org/10.1111/j.1365-2745.2007.01339.x

Sayer, C. D., Burgess, A. M. Y., Kari, K., Davidson, T. A., Peglar, S., Yang, H., & Rose, N. (2010). Long-term dynamics of submerged macrophytes and algae in a small and shallow, eutrophic lake: Implications for the stability of macrophyte-dominance. *Freshwater Biology*, *55*(3), 565–583. https://doi.org/10.1111/j.1365-2427.2009.02353.x

Sayer, C., Roberts, N., Sadler, J., David, C., & Wade, P. M. (1999). Biodiversity changes in a shallow lake ecosystem: A multi-proxy palaeolimnological analysis. *Journal of Biogeography*, *26*(1), 97–114. https://doi.org/10.1111/j.1365-2699.1999.00298.x

Schaumburg, J., Schranz, C., Hofmann, G., Stelzer, D., Schneider, S., & Schmedtje, U. (2004). Macrophytes and phytobenthos as indicators of ecological status in German lakes—a contribution to the implementation of the Water Framework Directive. *Limnologica*, *34*(4), 302–314. https://doi.org/10.1016/S0075-9511(04)80003-3

Schmidt-Kloiber, A., & Hering, D. (2015). www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, *53*, 271–282.

Schriver, P. E. R., Bøgestrand, J., Jeppesen, E., & Søndergaard, M. (1995). Impact of submerged macrophytes on fish-zooplanl phytoplankton interactions: Large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biology*, *33*(2), 255–270. https://doi.org/10.1111/j.1365-2427.1995.tb01166.x

SEPA. (2007). *Status, potential and quality requirements for lakes, water courses, coastal and transitional waters: A handbook on how quality requirements in bodies of surface water can be determined and monitored* (p. 4, 421). Swedish Environmental Protection Agency.

SEPA. (2015). Handledning för miljöövervakning – Undersökningstyp: Makrofyter i sjöar. Version 3:0, 2015-06-26. (In Swedish).

Shaw, A. J., Carter, B. E., Aguero, B., da Costa, D. P., & Crowl, A. A. (2018). Range change evolution of peat mosses (Sphagnum) within and between climate zones. *Global Change Biology*, *25*(1), 108–120.

Søndergaard, M., Johansson, L. S., Lauridsen, T. L., Jørgensen, T. B., Liboriussen, L., & Jeppesen, E. (2010). Submerged macrophytes as indicators of the ecological quality of lakes. *Freshwater Biology*, *55*(4), 893–908. https://doi.org/10.1111/j.1365-2427.2009.02331.x

Søndergaard, M., Phillips, G., Hellsten, S., Kolada, A., Ecke, F., Mäemets, H., Mjelde, M., Azzella, M. M., & Oggioni, A. (2013). Maximum growing depth of submerged macrophytes in European lakes. *Hydrobiologia*, *704*(1), 165–177. https://doi.org/10.1007/s10750-012-1389-1

Spence, D. H. N. (1967). Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. *The Journal of Ecology*, *55*, 147–170. https://doi.org/10.2307/2257723

Stendera, S., Adrian, R., Bonada, N., Cañedo-Argüelles, M., Hugueny, B., Januschke, K., Pletterbauer, F., & Hering, D. (2012). Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: A review. *Hydrobiologia*, *696*(1), 1–28. https://doi.org/10.1007/s10750-012-1183-0

Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*, 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

ter Braak, C. J. F. (1995). Ordination. In R. H. J. Jongman, C. J. F. ter Braak, & O. F. R. van Tongeren (Eds.), *Data analysis community and landscape ecology* (pp. 91–173). Cambridge University Press.

ter Braak, C. J., & Smilauer, P. (2002). CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). www.canoco.com

Toivonen, H., & Huttunen, P. (1995). Aquatic macrophytes and ecological gradients in 57 small lakes in southern Finland. *Aquatic Botany*, *51*(3–4), 197–221. https://doi.org/10.1016/0304-3770(95)00458-C

Truchy, A., Angeler, D. G., Sponseller, R. A., Johnson, R. K., & McKie, B. G. (2015). Linking biodiversity, ecosystem functioning and services, and ecological resilience: Towards an integrative framework for improved management. In G. Woodward & D. A. Bohan (Eds.), *Advances in ecological research* (Vol. *53*, pp. 55–96). Academic Press.

Valley, R. D., & Drake, M. T. (2007). What does resilience of a clear-water state in lakes mean for the spatial heterogeneity of submersed macrophyte biovolume? *Aquatic Botany*, *87*(4), 307–319. https://doi.org/10.1016/j.aquabot.2007.07.003

Vestergaard, O., & Sand-Jensen, K. (2000). Alkalinity and trophic state regulate aquatic plant distribution in Danish lakes. *Aquatic Botany*, *67*(2), 85–107. https://doi.org/10.1016/S0304-3770(00)00086-3

Viana, D. S., Santamaría, L., Schwenk, K., Manca, M., Hobaek, A., Mjelde, M., Preston, C. D., Gornall, R. J., Croft, J. M., King, R. A., Green, A. J., & Figuerola, J. (2014). Environment and biogeography drive aquatic plant and cladoceran species richness across Europe. *Freshwater Biology*, *59*(10), 2096–2106. https://doi.org/10.1111/fwb.12410

Weyhenmeyer, G. A., Prairie, Y. T., & Tranvik, L. J. (2014). Browning of boreal freshwaters coupled to carbon-iron interactions along the aquatic continuum. *PLoS One*, *9*(2), e88104. https://doi.org/10.1371/journal.pone.0088104

Willby, N. J., Abernethy, V. J., & Demars, B. O. (2000). Attribute-based classification of European hydrophytes and its relationship to habitat utilization. *Freshwater Biology*, *43*(1), 43–74. https://doi.org/10.1046/j.1365-2427.2000.00523.x

Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032

SUPPORTING INFORMATION

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

How to cite this article: Johnson RK, Toprak V. Local habitat is a strong determinant of spatial and temporal patterns of macrophyte diversity and composition in boreal lakes. *Freshw Biol*. 2021;66:1490–1501. https://doi.org/10.1111/fwb.13733