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High aquatic macrophyte diversity in Norwegian lakes north of the Arctic Circle

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Abstract

1. Aquatic macrophytes recolonised inland waters following the last glacial retreat. The resulting diversity and the variables influencing it remain largely unexplored north of the Arctic Circle, including possible effects of past colonisation routes. Our understanding of species diversity north of the Arctic Circle has also been hampered by a lack of control in sampling effort.

2. Here we use a newly assembled set of lake surveys from Norway to test: (1) whether regional richness (γ diversity) as well as turnover, net gain and loss (β diversity) of species differ between bioclimatic zones, latitudinal bands, and geographical regions; (2) how the environment and the spatial structure (e.g. dispersal constraints) may predict lake species richness (α diversity); and (3) how the changes in species β diversity between lakes are related to these environmental and spatial gradients.

3. We expected high species turnover with longitude, net species loss with latitude and higher species richness in north-east compared to mid Norway due to geographical dispersal barriers and past recolonisation routes. However, the regional species richness was similar across all geographical regions after correcting for sampling effort and spatial extent, with slightly lower richness in north Norway (−4%) and north-east Norway (−11%) than expected by the species area relationship. Species β diversity (both turnover and loss) was also surprisingly low between most areas.

4. Species richness per lake increased with lake area and temperature, showed a preferential peak at 10 μg/L total phosphorus, was sensitive to spatial structure, and largely indifferent to calcium (or alkalinity). In contrast, β diversity (mostly turnover) increased with differences in calcium, total phosphorus, and latitude, while not responding much to temperature and lake area. Species loss and gain between lakes were hardly related to any of the selected variables.

5. Overall, species richness (α, γ) was higher than expected north of the Arctic Circle mostly due to species turnover with little net loss. These patterns suggested good dispersal abilities by aquatic plants, after controlling for sampling efforts

and spatial extent. Conservation of aquatic plants should not be driven by the delineation of terrestrial vegetation zones, but through an understanding of the variables affecting aquatic plant diversity. Finally, northern lakes may be increasingly important as reservoirs of macrophyte diversity under global warming.

KEYWORDS
aquatic vascular plants, Arctic Circle, charophytes, deglaciation, richness, turnover

1 | INTRODUCTION

Aquatic plants have long been known for their large distribution range (e.g. Darwin, 1859; Santamaria, 2002; Schenck, 1885) relative to their terrestrial counterparts (Arber, 1920) rather than in absolute terms (Murphy et al., 2019). Aquatic macrophyte ability for short and long distance dispersal has been demonstrated through hydrographic networks (Dahlgren & Ehrlen, 2005; Demars & Harper, 2005) and over land (Capers et al., 2010; Les et al., 2003) by birds (e.g. King et al., 2002; Viana et al., 2013; Viana, Santamaria, et al., 2016) and now increasingly through human activities (e.g. Chapman et al., 2020; Hussner, 2012). The pace of aquatic plant dispersal along bird migratory routes has been estimated to be faster than current climate change velocity (Viana, 2017), thus aquatic plant distribution may closely track climate change (summer temperature) during the Holocene (Väliranta et al., 2015).

Aquatic macrophytes rapidly recolonised Fennoscandia following the last glaciation maximum (e.g. Shala et al., 2014; Väliranta et al., 2005) and indicated warmer summer temperature than present time in northern Fennoscandia in the early Holocene (e.g. Clarke et al., 2019; Helmens et al., 2018; Schenk et al., 2018). Some species recorded from early Holocene have now a more southern distribution (e.g. Väliranta, 2006).

Deglaciation during the last glacial maximum in Fennoscandia happened from the east with the formation of large glacial lakes (e.g., Ancylus lake 10,000 years ago, Helmens et al., 2018; Stroeven et al., 2016). The Norwegian mountain range prevented non-anadromous freshwater fish to migrate to western Norway, still reflected in current species distribution (Økland, 1974; Tammi et al., 2003) and population genetics (e.g. Nesbø et al., 1999; Østbye et al., 2005) with higher fish species diversity in north-eastern Norway than central Norway (Lau et al., 2022). Whether the current latitudinal distribution of aquatic plant diversity in Norway may still reflect historical migration route since the last glacial maximum remains unknown, since plant dispersal is not as constrained as for freshwater fish across topographical barriers. This is obvious in aquatic plant distribution maps (Hultén & Fries, 1986; Langangen, 2007; Mossberg & Stenberg, 2018; Samuelsson, 1934).

Global datasets are now being used to test biogeographical hypotheses previously applied to terrestrial organisms (e.g., Murphy et al., 2019, 2020). However large uncertainties in sampling effort remain in many parts of the world susceptible to alter previous conclusions. A recent synthesis from the Conservation of Arctic Flora and Fauna suggests that there is a gap in knowledge of species distribution and diversity north of the Arctic Circle (Lau et al., 2022; Lento et al., 2019). We are not aware of any study on aquatic macrophyte diversity accounting for regional sampling effort north of the Arctic Circle, on which biogeographical studies and conservation of aquatic plants must rest (Gotelli & Colwell, 2001). The study of regional diversity should include alternative ways to investigate sampling efforts as a basis for multiple investigations in theoretical and applied ecology: e.g., bioclimatic zones (often used in conservation), geographical regions (possible link to historical dispersal pathways), or latitudinal bands (strong interest in biogeographical studies).

The determinants of species richness and spatial turnover, net gain and loss of species in lake ecosystems include lake area (colonisable lake area, habitat diversity), spatial isolation, latitude (length of growing season), pH–conductivity–alkalinity (geological setting), light availability through trophy (planktonic chlorophyll-*a*, coloured dissolved organic matter, Secchi depth), elevation, and fluctuation of water level—e.g. in north-west Europe (Rørslett, 1991; Vestergaard and Sand-Jensen, 2000; Jones et al., 2003; Alahuhta et al., 2013; Viana et al., 2014; Viana, Figuerola, et al., 2016). The relative importance of these individual variables is largely dependent on the data at hand: length of environmental gradients, spatial extent, and resolution and correlations among variables (e.g. Lohammar, 1938; Pip, 1984).

Here we tested: (1) whether regional richness (γ diversity) as well as turnover, net gain and loss (β diversity) of species differed between bioclimatic zones, latitudinal bands, and geographical regions while controlling for sampling effort to see whether correspondence with deglaciation migration routes may be inferred (lower species pool in mid Norway than north-east Norway might be expected—Reiersen, 1942); (2) whether lake area, climate, geological setting, nutrients, and spatial location affected lake species richness (α diversity); and (3) whether the changes in species β diversity (turnover, net gain and loss) between lakes were related to the length of these environmental and spatial gradients to uncover potential environmental mechanisms determining species diversity. We tested these hypotheses with a newly assembled set of lake surveys (1,213 surveys in 909 lakes) from Norway spanning latitude 58–71° N and longitude 5–30° E with long and largely uncorrelated environmental gradients under relatively low human pressures.

2 | MATERIALS AND METHODS

2.1 | Lakes

The data were mainly collected by the Norwegian Institute for Water Research (NIVA) with additional surveys from the literature. The dataset includes 1,213 surveys (with some time series) in 909 Norwegian lakes from 1927 to 2017. The lakes are distributed from lowland to mountain areas, and from coastal to continental areas and covering latitudes 58–71° N. Over 200 lakes are situated north of the Arctic Circle (66° N), some of them in sub-Arctic areas (Figure 1).

2.2 | Aquatic macrophytes

In the present study, we focus on hydrophytes (vascular plants) and charophytes (Table S1). Amphibious plants able to develop different growth forms were only included if the hydrophyte growth form was the most frequent. All together, 94 species and nine hybrids were recorded in the 1,213 summer surveys (late June to early September),

covering about three quarters of hydrophytes recognised in Norway (Mjelde et al., 2022). All macrophyte data were collected based on comparable survey methods, mainly using an aquascope (underwater viewer) and dragging a casting rake from the boat at different localities covering the diversity of habitats (sediment and degree of wave exposure, slope, depth). Surveyors also walked along the shore and recorded all species listed in Table S1, including on temporarily exposed shore due to water drawdown. While most of the area of small lakes (up to 1 km^2) can be investigated, the survey of large lakes was based on localities around the lake covering the full range of habitats (shore exposure, slope, peers, areas close to inlets and outlet). The surveyor may spend 2–8 hr surveying small lakes (up to 5 km^2) and 15–90 min per locality for the very large lakes (with 15–25 localities per lake). The time spent at a single locality is dependent on the number of species. The sampling effort for individual lakes was found to be appropriate using species accumulation curves (SACs; Mjelde & Thrane, 2021). Resurvey of lakes by different investigators returned similar number of species when the environmental conditions remained largely unchanged (on-going monitoring work). Most taxa were identified to species levels. The nomenclature follows the
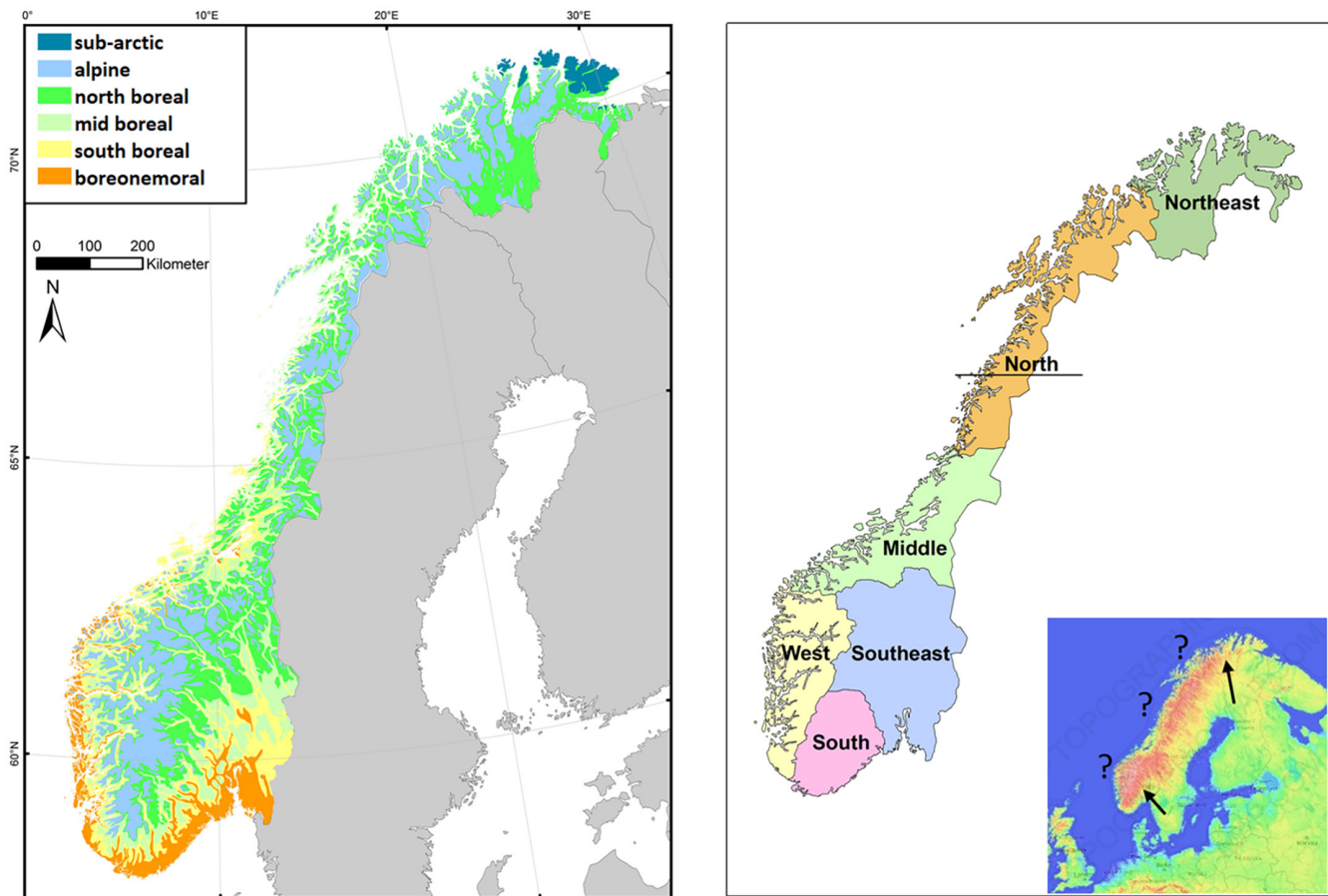

FIGURE 1 Left: Bioclimatic zones in Norway. Modified from Norwegian biodiversity information Centre https://www.biodiversity.no/Pages/205795 (Licence CC BY 4.0. Publisher: NTNU Vitenskapsmuseet). Right: Geographical regions in Norway used in this study with hypothesised plant dispersal routes in inset topographical map modified from https://en-gb.topographic-map.com/maps/d9x/Sweden/ (Licence CC BY 4.0.), derived from Yamazaki et al. (2017). North east, in particular, was hypothesised to have higher species richness than mid Norway. The Arctic Circle (66°33′ north) is shown by a black line in the map

Norwegian flora for vascular plants (Lid & Lid, 2005) and the flora of the Nordic countries for charophytes (Langangen, 2007), with updated names and taxonomy in Mjelde et al. (2022).

2.3 | Spatial and environmental factors

The major spatial and environmental factors likely to determine aquatic macrophyte diversity (see Section 1) were recorded in the NIVA database: latitude, longitude, bioclimatic zones and geographical regions, lake area, calcium, alkalinity, summer temperature, precipitation, elevation, total phosphorus, total nitrogen, Secchi depth, chlorophyll-*a*, and water colour (Table 1), with methods generally following Norwegian national standards (see Direktoratsgruppen, 2018).

Latitude, longitude, lake area, and elevation were collected from the national databases at the Norwegian Water Resources and Energy Directorate (NVE) (https://atlas.nve.no/) and the Norwegian Mapping Authority (https://www.norgeskart.no). The lakes were grouped in different bioclimatic zones (derived from climate and terrestrial vegetation, see explanation of the zones in https://www.biodiversity.no/Pages/205795) and geographical regions reflecting different colonisation route for aquatic plants (Figure 1). The southeast region includes the counties Akershus, Buskerud, Hedmark, Oppland, Oslo, Vestfold, and Østfold; south includes Aust-Agder and Vest-Agder og Telemark; west includes Sogn og Fjordane, Hordaland, and Rogaland; middle includes Møre og Romsdal and Trøndelag; north includes Nordland and Troms, while the north-east region includes Finnmark county. The south, south-east, and north-east of Norway could have been recolonised early from the last glacial maximum and may host higher species diversity (independently of the environment). However, the western part of the country (divided here into west, mid, and north) is isolated from eastern Fennoscandia by a continuous mountain range and may have fewer aquatic plant species than the other regions (Figure 1). The climate

data were derived from WorldClim2 using average July air temperature and precipitation over 1970–2000 (Fick & Hijmans, 2017). Temperature is a good proxy for the duration of ice cover and length of the growing season (Magnuson et al., 2000). The determination of water quality was often part of the macrophyte surveys, and where missing, were derived from various national water quality surveys (mainly from the NIVA Aquamonitor database) in the same lakes and periods.

2.4 | Data preparation

We only used species presence–absence data. We excluded surveys prior to 1980 to narrow the time span and we only selected one survey per lake to avoid temporal pseudo-replication. We selected the earliest survey with the most complete abiotic set of data. This reduced the dataset to 720 lakes (161 north of the Arctic Circle) on which we based our analyses of regional richness, turnover, net gain and loss of species. The dataset was further reduced to 634 lakes (148 north of the Arctic Circle) for which a common set of abiotic variables was available to test how patterns in lake species richness may be explained: geographical coordinates, climate variables, lake area, elevation, calcium, and total phosphorus. The additional inclusion of total nitrogen and water colour would have reduced the dataset to only 314 lakes, and, since both were correlated to total phosphorus (Table S2), they were not included in our statistical analyses. Similarly, pH (509 surveys), electric conductivity (282 surveys) and alkalinity (421 surveys) were strongly correlated ($r > 0.8$) to calcium (1,043 surveys, log transformed) and not selected. Secchi depth (434 surveys) and chlorophyll-*a* (216 surveys) were also strongly correlated ($r \geq 0.75$) to total phosphorus (997 surveys) and not selected. Among the climatic variables we only selected temperature, as precipitation is more relevant on wider gradients including dry areas (e.g., Chappuis et al., 2012; Murphy et al., 2019). We checked the selected variables were not

TABLE 1 Selected environmental variables in the Norwegian Institute for Water Research macrophyte database

Variable	Min	25th	50th	75th	Max	n
Elevation (m)	1	28	114	219	1,234	1,192
Lake area (km²)	0.0001	0.05	0.22	0.95	369	1,192
Electric conductivity (μS/cm)	7	25	47	116	732	282
Alkalinity (mEq/L)	0.01	0.08	0.24	0.75	3.66	421
pH	4.3	6.1	6.6	7.2	9.0	509
Calcium (mg Ca/L)	0.19	2.12	7.72	23.6	183	1,043
Colour (mg Pt/L)	1	13	23	40	338	497
Total organic carbon (mg C/L)	0.6	1.9	3.3	5.0	16.5	156
Secchi depth (m)	0.1	2.7	4.2	6.2	17	434
Chlorophyll a (μg/L)	0.08	1.06	1.8	4.7	95	216
Total nitrogen (μg N/L)	10	202	380	785	4,860	647
Total phosphorus (μg P/L)	0.5	5.0	7.3	16	961	997
Average July air temperature (°C)	9.4	13.1	14.5	15.8	17.6	1,213
Average July precipitation (mm)	46	75	82	92	195	1,213

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strongly correlated (all pairwise correlations below $r = 0.5$, except for latitude–longitude $r = 0.81$ and latitude-temperature $r = -0.68$; see Table S2). We also produced a distance-based matrix (km) between lakes from the latitude and longitude using the geosphere package in R (Hijmans, 2021). The distance between lakes was highly correlated to latitude ($r = 0.88$).

2.5 | Statistical analyses

Data handling and statistics were performed with R version 4.0.0 (R Core Team, 2020). We used the package dplyr to subset the data and ggplot2 to plot results (Wickham, 2016; Wickham et al., 2021). To compare species richness between bioclimatic zones, latitudinal bands, or geographical regions for a given sampling effort (standardised γ diversity), we produced SAC using the procedure of Gotelli and Colwell (2001) finding the expected species richness and its standard deviation by sampling sites at random (function specaccum, vegan package version 2.5.7, Oksanen et al., 2020). The SAC may be affected by the spatial extent (species–area relationship, SAR) of the bioclimatic zones, latitudinal bands or geographical regions (Azovsky, 2011). At equivalent sampling effort (determined from the SAC) we would expect a steeper slope for the SAR with more heterogeneous habitats: geographical regions > latitudinal bands > biogeographical zones (Kallimanis et al., 2008, data compiled in Table S3).

We partition Sørensen β diversity index (range 0–1) by the Simpson species spatial turnover (Lennon et al., 2001) and nestedness (species net gain and loss) between lakes within selected areas (using 100 repeated samples of 25 lakes selected at random from each area) and between areas using the partitioning method of Baselga (2010) with R package betapart (Baselga & Orme, 2012). We also calculated the Sørensen β diversity, Simpson turnover and nestedness of all pairs of lakes to relate it (using generalised additive model [GAM], see below) to the pairwise difference in spatial (only latitude) and environmental variables. The differences in calcium, total phosphorus, and area between pairs of lakes were $\log(x+1)$ transformed for the statistical analyses. The differences in temperature and latitude between pairs of lakes did not need to be transformed.

To visualise the spatial distribution of our data, we used GAMs with latitude and longitude as predictors to display distribution maps of species richness (Poisson distribution, log link) and selected environmental variables (Gaussian distribution, identity link). These maps provide a broad-brushed picture smoothing local heterogeneity not easily rendered on small plots and the maps can be compared with the fitted GAM spatial structure (see below).

For testing the covariation between lake species richness and the spatial and environmental variables we used a GAM with Poisson distribution (response variable is a count of species) and log link function using the mgcv R package (Wood, 2017). GAM uses non-parametric functions (so-called *splines*) able to model non-linear changes in species richness along selected spatial and environmental gradients. We used reduced ranked thin plate regression spline basis, with automatic selection of the effective degrees of freedom for all smooths (Wood, 2017). The smoothness selection was by REML. We plotted partial effect plots to show the prediction (from the fitted GAMs) of the selected variable, assuming other predictive variables were at their average value or geometric mean for log transformed variables. Standard errors on the plots show the 95% confidence interval. All environmental variables were log transformed to improve normality and homoscedasticity. We checked the model converged rapidly towards a solution, the number of nodes for the splines was appropriate, concurvity of individual and pairwise variables (equivalent to collinearity in linear models), and diagnostic plots—(Figure S1; Ross, 2019). We tried to maximise the fit of the model (percentage of deviance explained) while controlling for model complexity (number of predictors) using Akaike information criterion (Table S4, Johnson & Omland, 2004).

We also used GAMs to test the effects of the environmental and spatial variables on β diversity with a gaussian distribution (identity link) for β diversity (continuous variable). Note that a β distribution (logit link) may be more appropriate to a continuous response variable with range 0–1, but it did not perform well (Figure S2), and the explained deviance was only 15%, half of the GAM using the gaussian distribution. The gaussian distribution performed best according to the diagnostic plots (Figure S3), despite a few fitted values slightly above 1. Whatever distribution used, the datapoints in the GAMs for β diversity cannot be seen independent, even though the response variables (Sorensen and its components turnover and nestedness) to selected environmental factors were independent of spatial distance. We should therefore not rely on the p values but more on the amount of explained deviance together with the rate of increase in the response variables along the environmental and spatial gradients. Generally, β diversity should increase with the length of the gradient. A flat wiggly sinusoidal curve basically shows that the given response variable is not sensitive to the environmental or spatial gradient. A large downward trend could indicate that the model is not appropriate (e.g., potential issues with concurvity). Finally, we also calculated the Akaike information criterion of GAMs with fewer predictors, taking out the weakest predictor at each step of model selection (Table S5).

Here we used GAMs to relate distance matrices (β diversity, spatial distance, and environmental differences). Alternative approaches have been applied to model plant compositional changes along spatial and environmental gradients such as partial constrained ordinations (e.g. Demars & Harper, 2005; ter Braak & Šmilauer, 2002), simple and partial Mantel tests (e.g. Demars et al., 2014; Demars & Trémolières, 2009; Legendre & Legendre, 1998), multiple regression on distance matrices (Lichstein, 2007), and generalised dissimilarity modelling (Mokany et al., 2022). The latter produced very similar results to the GAMs (Figure S8). It would be interesting to test a range of approaches with various strengths and constraints in data analyses of β diversity (see e.g. Lichstein, 2007; Righetti et al., 2019).

3 | RESULTS

3.1 | Regional species richness (standardised γ diversity)

3.1.1 | Bioclimatic zones

The regional species richness was highest in the south-boreal and boreonemoral zones, and lower, but still relatively high, in the mid and north boreal zones. While fewer lakes were sampled from the low alpine zone, regional and individual lake species richness were both markedly lower than the other zones (Figure 2, ANOVA test $p < 0.001$, Tukey's HSD test, difference in means up to 2.5 species per lake). The few lakes from the sub-arctic zone are in the analysis included among the low-alpine lakes. Sampled lake area differed a

bit between zones (ANOVA test $p < 0.001$), relatively lower for mid boreal and low alpine zones (Tukey's HSD test). Neither observed nor expected richness were related to the area of bioclimatic zones (Figure S4).

3.2 | Latitudinal bands

Regional species richness was higher south of the Arctic Circle, with over 60 species compared to about 50 species per 3°N latitudinal bands north of the Arctic Circle for the same sampling effort of 75 lakes (as seen in Figure 2). The species richness per lake was only slightly different between latitudinal bands (ANOVA test $p < 0.001$, Figure 2), lower at 61°N and 70°N than 58°N and 64°N (Tukey's HSD test, difference in means not exceeding 0.5 species per
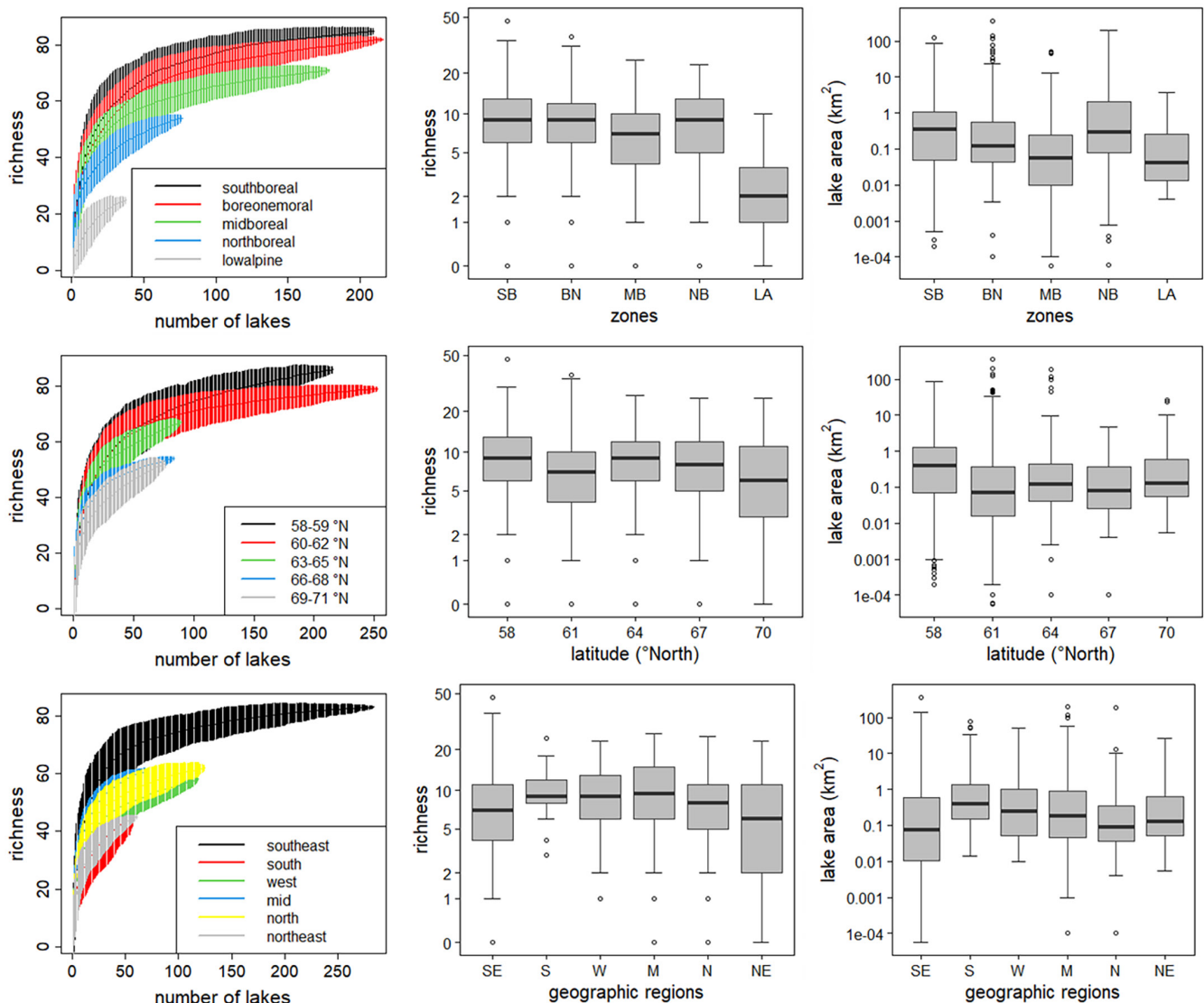

FIGURE 2 Left: expected species richness and its standard deviation (species accumulation curve) to sampling effort (number of lakes surveyed). Centre: boxplot with interquartile of species richness per lake. Right: boxplot with interquartile of lake area, in bioclimatic zones (top), latitudinal bands (middle) and geographical regions (bottom). SB = south-boreal, BN = boreo-nemoral, MB = mid-boreal, NB = north-boreal, LA = low alpine

lake). Differences in lake area between latitudinal bands were slim (ANOVA test $p < 0.001$), only higher at 58°N than 61°N and 67°N (Tukey's HSD test). Neither observed nor expected richness were related to the area of latitudinal bands (Figure S4).

3.2.1 | Geographical regions

Regional species richness was highest in the south-east, which was also the most surveyed area in Norway. At a comparable sampling effort of 50 lakes (as seen in Figure 2), the regional species richness was similar in mid, west and north Norway, and higher than in north-east and south Norway. This was not reflected by differences in species richness per lake (ANOVA test $p = 0.003$, Figure 2). Differences in lake area between regions were small (ANOVA test $p < 0.001$), relatively lower in the south east (Tukey's HSD test). Both observed and expected richness were related to the area of geographical regions (log–log plot). The standardisation of sampling effort reduced the slope of the SAR (Figure S4). Using the SAR standardised by sampling effort the north and north-east regions had 4% and 11% less species than expected, while the other more southern regions had 6%–11% more species than expected from the SAC alone.

3.3 | Species turnover, net gain and loss within and between areas (regional β diversity)

The high β diversity ($\beta_{SØR} > 0.9$ in most cases) between lakes within bioclimatic zones, latitudinal bands and geographical regions mostly comprised species turnover ($\beta_{SIM} > 0.8$ in most cases, Tables 2–4). B-diversity was, however, low ($\beta_{SØR} < 0.25$) between bioclimatic zones, apart from the low alpine zone where high species loss was observed (β_{SNE} 0.32–0.52, Table 2).

TABLE 2 Median multiple-site dissimilarities across sites *within* bioclimatic zones, controlling for the number of sites (top); and Sørensen β diversity components: species turnover (β_{sim}, bold black) and nestedness (β_{sne}, shaded grey) *between* bioclimatic zones (bottom)

Bioclimatic zones	$\beta_{SØR}$	β_{SIM}	β_{SNE}
Boreonemoral (BN)	0.91	0.84	0.07
South boreal (SB)	0.92	0.87	0.05
Mid boreal (MB)	0.92	0.87	0.05
North boreal (NB)	0.91	0.83	0.08
Low alpine (LA)	0.93	0.84	0.09

	BN	SB	MB	NB	LA
BN	—	0.02	0.06	0.20	0.49
SB	**0.09**	—	0.08	0.22	0.52
MB	**0.14**	**0.06**	—	0.13	0.48
NB	**0.04**	**0.02**	**0.06**	—	0.32
LA	**0.08**	**0.04**	**0.00**	**0.12**	—

TABLE 3 Median multiple-site dissimilarities across sites *within* latitudinal bands, controlling for the number of sites (top); and Sørensen β diversity components: species turnover (β_{sim}, bold black) and nestedness (β_{sne}, shaded grey) *between* latitudinal bands (bottom)

Latitudinal bands	$\beta_{SØR}$	β_{SIM}	β_{SNE}
58–59° N	0.91	0.85	0.06
60–62° N	0.93	0.87	0.06
63–65° N	0.91	0.85	0.06
66–68° N	0.91	0.83	0.08
69–71° N	0.91	0.80	0.11

	58	60	63	66	69
58	—	0.04	0.11	0.21	0.22
60	**0.05**	—	0.07	0.17	0.19
63	**0.07**	**0.09**	—	0.10	0.11
66	**0.07**	**0.09**	**0.06**	—	0.02
69	**0.10**	**0.08**	**0.13**	**0.19**	—

The species turnover was low and similar between latitudinal bands ($\beta_{SIM} < 0.1$), except between band 69–71°N and 63–66°N, 66–69°N which had higher species turnover (β_{SIM} 0.13–019) than nestedness (β_{SNE} 0.02–0.11)—Table 3. The somewhat lower species richness north of the Arctic Circle was reflected by higher species loss (β_{SNE} 0.17–0.22) than turnover (β_{SIM} 0.07–0.10) between the southern and northern latitude (Table 3).

Beta-diversity of the south-east geographical region gained in species (β_{SNE} 0.13–0.28) rather than showing species turnover (β_{SIM} 0.04–0.10). In general, β diversity of the other geographical regions was dominated by species turnover and not species net gain or loss (with $\beta_{SNE} < 0.14$, Table 4). The largest turnover in species ($\beta_{SIM} = 0.4$) was between the south and north-east geographical regions, with remarkably no net species loss or gain ($\beta_{SNE} = 0$, Table 4).

3.4 | Individual lake richness across spatial and environmental gradients (α diversity)

The spatial structure of species richness highlights areas of relatively low species richness (notably the northernmost lakes situated in sub-Arctic areas) and many areas of relatively high species richness per lake (Figure 3). It is not obvious how species richness relates to the spatial structure of selected environmental variables (Figure 3). The variable most strongly associated with species richness per lake was lake area, followed by spatial structure, temperature, total phosphorus, and, to a very small extent, calcium (Figure 4, Table 5). The average species richness per lake (back transformed intercept of the model) was 8.2 species. With other variables set at their mean, richness increased markedly with lake area (richness increases by 11% with doubling of lake area) and temperature while presenting a bell shape curve for total phosphorus with an optimum around 10 μg P/L (Figure 4). Overall, this was the most parsimonious model with R^2adj = 0.59 and $p < 2 \times 10^{-16}$ ($n = 634$; Table 5), despite

TABLE 4 Median multiple-site dissimilarities across sites *within* geographical regions, controlling for the number of sites (top); and Sørensen β diversity components: species turnover (β_{sim}, bold black) and nestedness (β_{sne}, shaded grey) *between* geographical regions (bottom)

Geographical regions	$\beta_{SØR}$	β_{SIM}	β_{SNE}
South east (SE)	0.93	0.87	0.06
South (S)	0.86	0.76	0.09
West (W)	0.90	0.82	0.08
Mid (M)	0.91	0.84	0.07
North (N)	0.91	0.84	0.07
North east (NE)	0.92	0.79	0.13

	SE	S	W	M	N	NE
SE	—	0.28	0.17	0.14	0.13	0.28
S	0.07	—	0.11	0.13	0.12	0.00
W	0.05	0.13	—	0.02	0.02	0.09
M	0.07	0.16	0.24	—	0.01	0.13
N	0.10	0.27	0.29	0.18	—	0.14
NE	0.04	0.40	0.31	0.11	0.09	-

some concurvity between spatial structure and temperature. The pure spatial effect on richness (Figure 4) was more homogeneous, notably with a lesser latitudinal gradient than appearing in the unconstrained effect of spatial structure (Figure 3) suggesting that the spatial patterns in richness also reflected spatial heterogeneity in environmental variables (Figure 3). Note the differences in species richness in the south east (Figure 3 vs. Figure 4) may result from concurvity with temperature (equivalent to negative collinearity in linear model). That is, associations could not be ascertained and when spatial structure was removed from the model richness did not increase with temperature above 15°C. Elevation was not significant ($p = 0.32$) nor was it significant after removing temperature or geographical coordinates but the models had higher Akaike information criterion. Thus, elevation was not selected in the final model.

3.5 | Variables associated with pair-wise lake β diversity

Beta-diversity between pairs of lakes was best explained (R^2adj = 0.29, $p < 2 \times 10^{-16}$, $n = 193,131$) by pairwise differences among lakes in calcium concentration, latitude and phosphorus, with temperature and lake area playing relatively minor roles (Figure 5, Table S5). The average species β diversity between lakes was $\beta_{SØR} = 0.78$ and was mostly driven by species turnover ($\beta_{SIM} = 0.66$, Table S6, Figure S5) rather than nestedness (species gain or loss, $\beta_{SNE} = 0.12$, Table S6, Figure S6). Species turnover increased with a pairwise difference in calcium between lakes of 0.1–50 mg/L, latitude 6–12° N and total phosphorus 10–100 µg P/L. The responses in species turnover and nestedness to other variables were weak or even uninterpretable in the case of lake area (Figures S5 and S6). Replacing differences in latitude (°) by distance between sites (km) made virtually no difference in the statistical results (see Figure S7 and Table S7).

4 | DISCUSSION

Bioclimatic zones, latitudinal bands, and geographical regions uncovered complementary aspects of species diversity. The relative influence of these variables on lake species richness and turnover differed markedly. Overall, the substantial sampling effort (north of the Arctic Circle) reported in this study showed relatively high species richness north of the Arctic Circle at two spatial extents (individual lakes and regional distribution).

Bioclimatic zones, a proxy for terrestrial vegetation, were a relatively poor descriptor of species richness and turnover in aquatic plants, except for the low alpine zone (Schenck, 1885). This had been noted in a regional study of lake sediment where aquatic pollen and spores poorly reflected bioclimatic zones (Felde et al., 2014). The conservation of aquatic plants should therefore not solely be driven by the delineation of terrestrial vegetation zones.

Species turnover between latitudinal bands (β_{SIM} 0.07–0.10) was remarkably low (see also Jensen, 1994; Rørslett & Brettum, 1989) and this may be due to the relatively short range of latitude (12° N) compared to other studies at larger spatial extent (e.g. Chappuis et al., 2012; Murphy et al., 2019, 2020), but a sharp decline in species over the same latitudinal range of our study was also presented (from atlas data) in Fennoscandia (Alahuhta et al., 2020; Heino & Toivonen, 2008). This discrepancy is probably due to differences in sampling efforts. In our national scale study, we made a special effort to survey lakes north of the Arctic Circle and were able to quantify sampling effort to produce standardised regional diversity estimates. This is often acknowledged but harder to control at continental to global scale studies (Murphy et al., 2019).

One of the most remarkable results is that species β diversity was dominated by species turnover (β_{SIM}) between geographical regions and not by species loss (β_{SNE}) as had been expected.

FIGURE 3 Spatial distribution of species richness per lake, elevation (m), temperature (°C), total phosphorus (TP; μg/L) and calcium (Ca; mg/L) drawn with simple independent generalised additive models. The range of values was depicted with isolines and colour gradient yellow to red colour representing low to high values. Grey circles represent the 720 lakes included in this analysis, depicted as blue circles in the bottom right map. The Arctic circle latitude line is at 66°30′ N
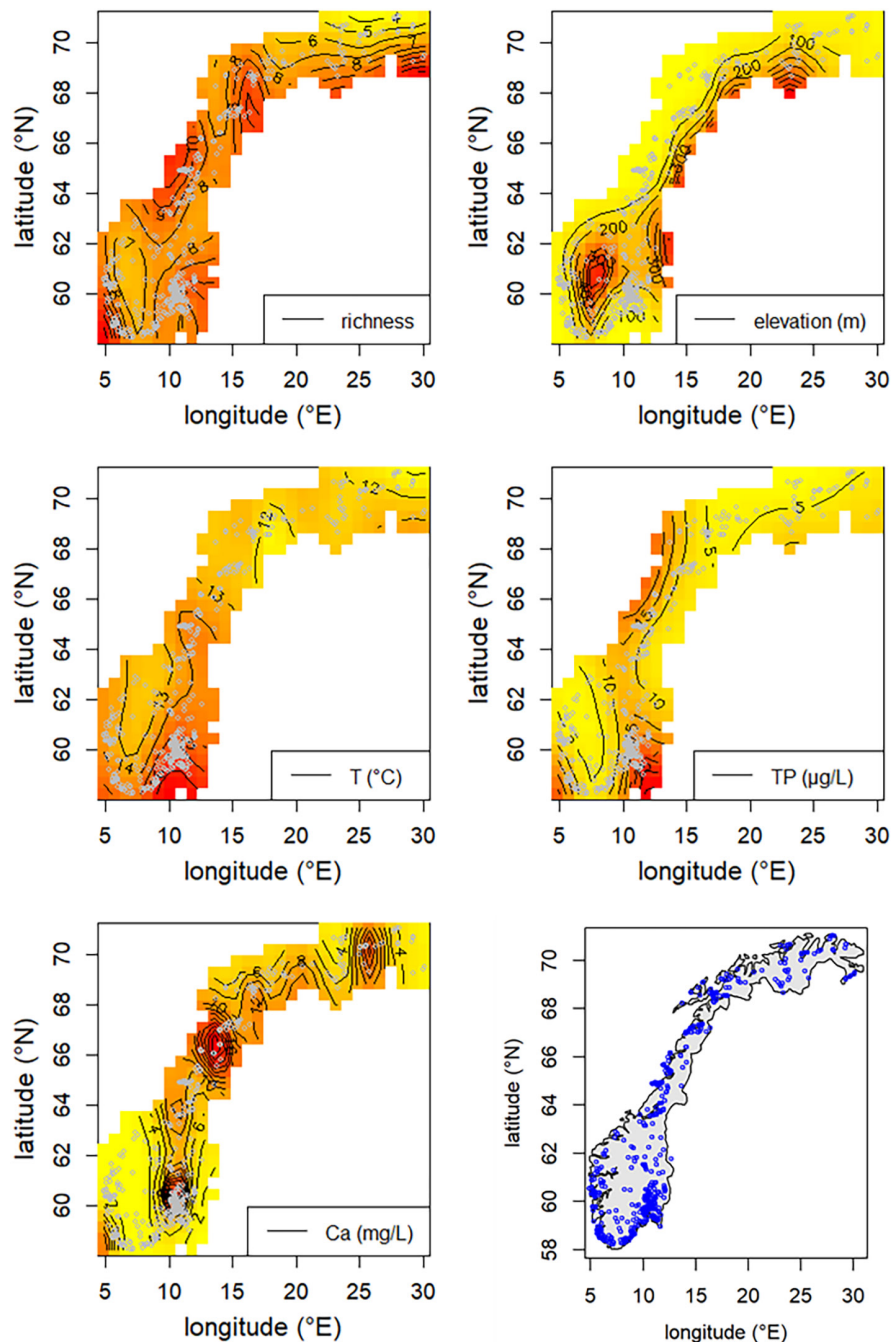
Moreover, the deviation in expected richness from the SAR standardised by sampling effort showed only marginal depletion (4%–11%) in expected species richness in regions north of the Arctic Circle. High species richness north of the Arctic Circle in Norway may be due to the Atlantic meridional overturning circulation currently providing more favourable climatic conditions in that region than at other longitudes around the globe (Murphy et al., 2019). However, the Atlantic meridional overturning circulation is showing signs of slowing down (Boers, 2021) and this is likely to shorten the growing season despite the possible persistence of short warm summers (Schenk et al., 2018). Further studies should strive to integrate high-resolution global climate simulations and predicted plant distribution through a wider range of habitat preference (only temperature for now) or species traits using a species approach.

In northern Fennoscandia (including north-east Norway), terrestrial plant species richness and the regional species pool increased rapidly from the beginning of the Holocene to stabilise about 3 millennia ago (Rijal et al., 2021). Thus, aquatic macrophyte distribution in north-east Norway maybe assumed to reflect the eastern continental flow of species since the last glacial maximum. Aquatic plant species richness was not lower in mid Norway (most isolated by mountain ranges) than north-east Norway as hypothesised, and this despite some species long known to have an eastern distribution
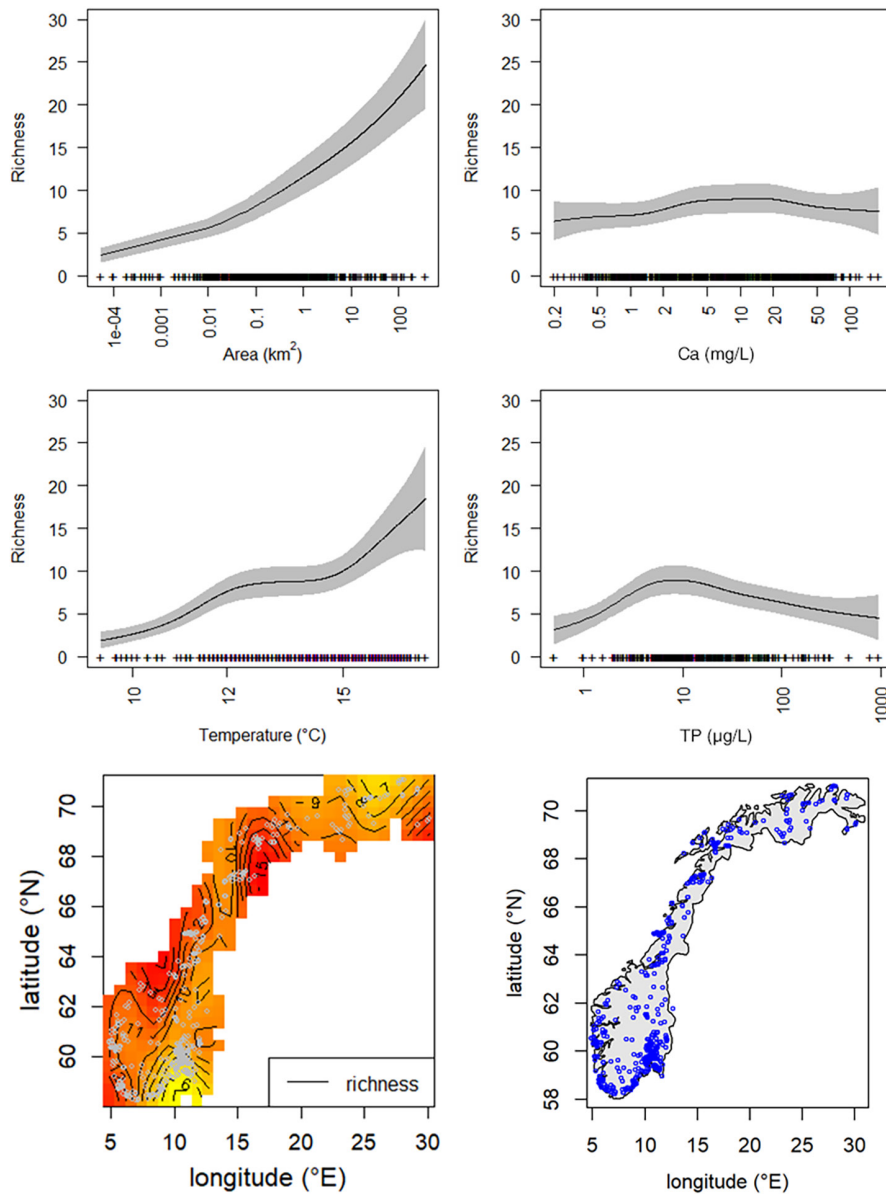
FIGURE 4 Species richness per lake as a function of environmental and spatial drivers. Plots are generalised additive model results (with 95% confidence interval) representing partial effects of individual drivers (setting all other drivers to their geometric mean). Bottom graph represents species richness per lake (range 6–15 species, yellow to red colour) with isolines based on the 634 lakes included for this analysis (grey circles, depicted as blue circle in the bottom right map). See Table 5

TABLE 5 Generalised additive model where richness (number of species per lake) is predicted as a function of lake area, calcium, total phosphorus, average summer temperature and geographical coordinates (longitude, latitude). Estimated degrees of freedom (*edf*) are related to the complexity of trend lines. Richness ~ s(log(area)) + s(log(Ca)) + s(log(TP)) + s(log(T.av)) + s(long, lat)

Poisson distribution with log link function; REML

	Estimate	**SE**	**p**
Intercept	2.10	0.01	$<2\times10^{-16}$
	edf	χ^2	*p*
log (area)	2.6	451	$<2\times10^{-16}$
log (Ca)	4.5	23	7×10^{-4}
log (TP)	5.0	78	$<2\times10^{-16}$
log (T.av)	5.2	116	$<2\times10^{-16}$
Long: lat	22.3	118	$<2\times10^{-16}$

Note: R^2 (adj) = 0.59, deviance 59%, n = 634.

in Fennoscandia (Samuelsson, 1934). The species turnover and nestedness between mid and north-east Norway were also low (β_{SIM} = 0.11, β_{SNE} = 0.13) suggesting that aquatic plants may have dispersed readily throughout Norway since the last glacial maximum despite the dispersal barrier provided by the mountain range that isolates mid Norway.

The main variables affecting lake species richness (α diversity) and turnover, net gain, and loss (β diversity) differed: lake area and temperature were most important for richness, while calcium and phosphorus concentrations influenced species turnover. The strong role of calcium concentration (and alkalinity) in species turnover results from a difference in plant ability to handle very low or high minerality (Sculthorpe, 1967; Smits et al., 1992) and evolution of species ability to use bicarbonate for photosynthesis (Demars & Trémolières, 2009; Iversen et al., 2019). The most salient results were the lack of an effect of calcium concentration on species richness and the unimodal response of species richness to total

FIGURE 5 Beta-diversity (Sørensen index, β_{sor}) predicted by pairwise differences between lakes in calcium (Ca), total phosphorus (TP), latitude, average summer temperature and lake area. Note the difference was log transformed for Ca, TP and area. Plots are generalised additive model results (with 95% confidence interval) representing partial effects of individual drivers (setting all other drivers to their mean or geometric mean). Note the number of pairwise differences represented 193,131 datapoints for this analysis (Table S2)
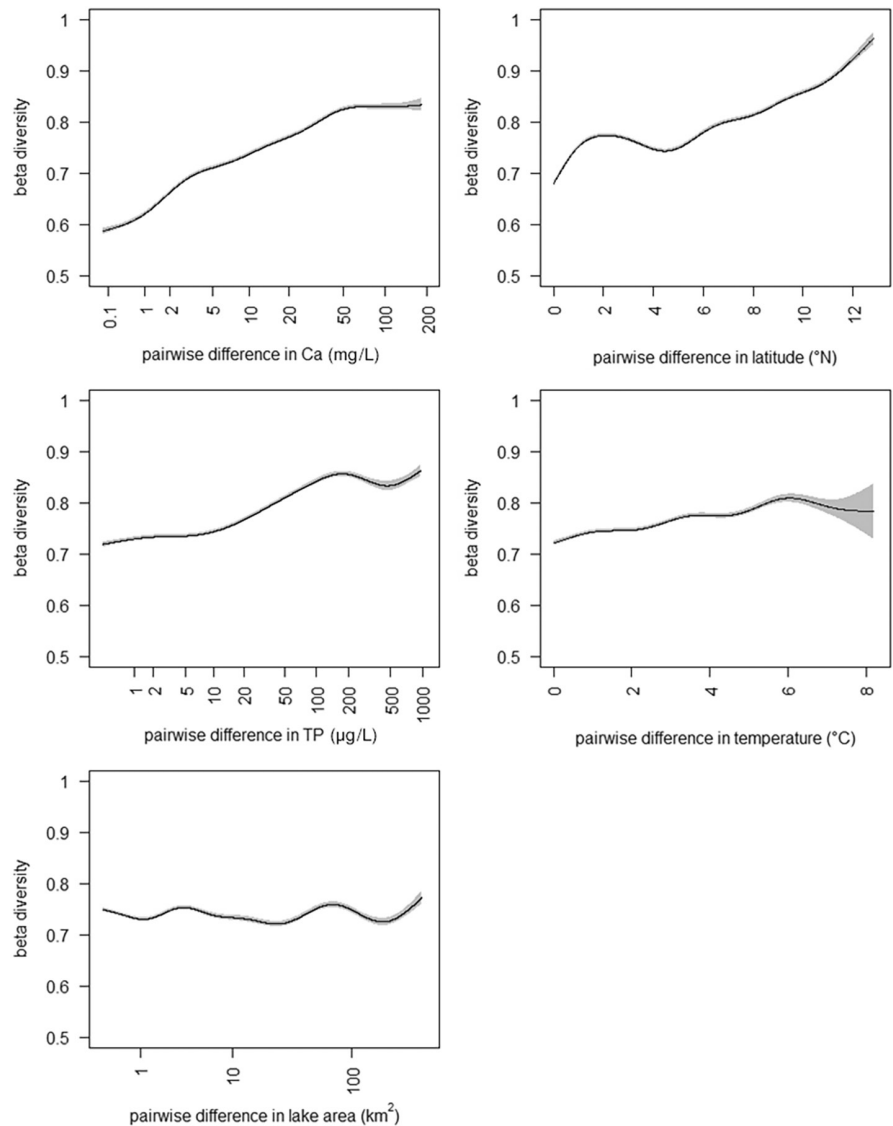
phosphorus concentration peaking at about 10 μg P/L, a finding not available in previous studies where lake trophy integrated both hardness (or alkalinity) and nutrients (N, P) (e.g. Rørslett, 1991). The significant partial effect of spatial structure on richness suggested that there might be differences in species dispersal or other assembly processes (such as biotic interactions); this is something to test using a species trait approach (Demars & Harper, 2005; Elger et al., 2004). Alternatively, spatial structure may be related to unmeasured environmental gradients. Norway has not been affected to the same extent by agriculture and urban development as other European countries (e.g. Sand-Jensen et al., 2018). Instead, it has been more affected by atmospheric deposition leading to acidification (in the south and west), and so it showed long and mostly independent environmental gradients including some of the lowest possible nutrient concentrations. Species turnover was most sensitive to changes in calcium and phosphorus concentrations, thus recovery from acidification (or liming), ongoing nutrient enrichment or darkening of water (recall colour was correlated with

phosphorus in our database) may drive species changes more than temperature in the future.

5 | CONCLUSION

The high sampling effort of the present study showed higher regional species diversity than expected from previous studies north of the Arctic Circle. Aquatic macrophyte diversity in north-east Norway was similar to mid Norway suggesting good dispersal since the last glacial maximum; a pattern contrary to that for freshwater fish. Current species richness in lakes was most strongly associated with lake area, spatial structure, and temperature, while species turnover between lakes was associated with calcium concentration, total phosphorus concentration, and spatial distance (latitude). The conservation of aquatic macrophytes should be based on an understanding of the variables with the most influence on aquatic plant diversity. Finally, northern lakes

may be increasingly important as reservoirs of macrophyte diversity under global warming.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

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