



# Submerged macrophytes in Danish lakes: impact of morphological and chemical factors on abundance and species richness

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**Abstract** We analysed long-term monitoring data on submerged macrophytes and water chemistry from 666 Danish lakes > 1 hectare and mean depth < 3 m, encompassing a total of 1447 lake years. Our aim was to describe how plant cover (COV), plant volume inhabited (PVI) and species richness related to physical and chemical and environmental variables. Boosted regression tree (BRT) analyses revealed that chlorophyll *a*, Secchi depth and depth were the strongest predictors of COV and PVI. Chlorophyll

had a strong negative effect up to 50 µg/l, whereas the changes related to Secchi depth and depth were more gradual and covered more of the gradient. Macrophyte species richness was best predicted by lake area and alkalinity, with chlorophyll *a*, nutrients and colour having significant but less marked effects. For chlorophyll *a*, 78% of the observed variance could be explained by the BRT model, with the most powerful predictors being both phosphorus and nitrogen, but with significant additional effects of plant cover and alkalinity. Our analyses revealed limited direct effect of nutrients on macrophyte abundance, but an indirect hierarchical effect of nutrients mediated through chlorophyll *a* with additional interactive effects by plant cover itself, alkalinity, mean depth and colour.

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## Introduction

For decades, human activities and increased eutrophication have resulted in higher turbidity and a decrease or even loss of submerged macrophytes in lakes all over the world (Sayer et al., 2010; Phillips et al., 2016; Zhang et al., 2017; Stefanidis et al., 2019). Following external nutrient loading reduction, lake recovery with re-establishment of submerged macrophytes is a key

target, particularly in shallow lakes where submerged macrophytes may help ensure clear-water conditions due to several positive feedback mechanisms (Scheffer et al., 1993; Kosten et al., 2009; Li et al., 2020). Submerged macrophytes are also important for the overall biodiversity, as many fish, invertebrates, attached algae and microorganisms are associated with the plants (Declerck et al., 2005; Bolduc et al., 2016). In addition, submerged macrophytes play a significant role for lake managers, as their sensitivity to eutrophication makes them useful indicators of ecological status (Søndergaard et al., 2010; Kolada et al., 2014; Verhofstad & Bakker, 2019). Accordingly, in EU's Water Framework Directive macrophytes are one of the four biological elements that are used to define whether measures should be taken to reduce the external loading of nutrients to lakes in order to improve their status (Poikane et al., 2018).

Submerged macrophytes represent a diverse group of organisms, and they contribute to a number of vegetation-turbidity feedback mechanisms (Jeppesen et al., 1998; Hilt et al., 2018; Ersoy et al., 2020). Macrophytes interact with, for instance, fish and macroinvertebrates (Schultz & Dibble, 2012), waterbirds (Larson et al., 2020), zooplankton (Burks et al., 2001) and phytoplankton (Sayer et al., 2010), and they affect the food chain length, ecosystem function (Ziegler et al., 2015), biogeochemical processes, such as the redox potential around the sediment–water interface (Boros et al., 2011), as well as methane emissions (Sorrell et al., 2002). Thus, besides being affected by nutrient loading-induced changes in turbidity, submerged macrophytes also respond to and depend on a number of biological interactions. Spatial and temporal variability in macrophyte abundance is often high and large differences in macrophyte communities occur, even under relatively comparable environmental conditions (Gillard et al., 2020; Yang et al., 2020). The mechanisms behind this variability are not always clear but may, among other factors, be induced by yearly climatic variations or a delayed response to changed environmental conditions (Jeppesen et al., 2005; Ejankowski & Lenard, 2015; Sand-Jensen et al., 2017).

Here, we used a dataset from 666 Danish lakes covering a large gradient in morphological and chemical characteristics and including data on submerged macrophyte composition and abundance. The lakes comprise lowland, temperate, shallow and meso-

to hypertrophic lakes where submerged macrophytes can be both very abundant and very sparse. Our aim was to examine how the direct and indirect effects of lake morphometry and nutrients shape three central aspects of submerged macrophytes—cover, plant volume inhabited and species number—with the aim to better identify the factors structuring the submerged macrophyte community in shallow lakes along a gradient of morphological and chemical factors.

## Methods and data

### Sampling and lake characteristics

Chemical and biological data were collected by regional and national authorities as part of the nationwide Danish monitoring program on the aquatic environment, NOVANA, running since 1989 with the inclusion of macrophytes in 1993. According to the program, physical and chemical variables are sampled using well-defined and comparable techniques and analytical procedures (Svendsen et al., 2005). The physical data include lake area, mean water depth and Secchi depth, and the chemical data encompass total nitrogen (TN), total phosphorus (TP), total alkalinity (TA) and chlorophyll *a* (Chl<sub>a</sub>). Each lake is sampled from one location from the deepest part of the lake at least four times during summer, and mean summer (1 May to 30 September) concentrations are calculated. See Søndergaard et al. (2005) for more detailed descriptions.

A total of 666 lakes with an area > 1 ha and a mean depth < 3 m were included in the data analyses. About half of these lakes (338 lakes) were visited twice or several times during the monitoring period (25 years), which increased the total dataset to 1447 lake years. Most of the lakes sampled multiple times were visited with an interval of at least three years, but some of the lakes were included in a more comprehensive sampling program, and nine lakes were, thus, visited 10–22 times with an interval of 1–3 years. In the analyses and presentations, we used data from all lake years (hereafter mainly referred to as “lakes”).

Submerged macrophytes were monitored during their maximum abundance between 1 July and 15 August. In each lake, 30–375 observation points located along a number of transects in each lake where numbers were lake size dependent. All lakes >

5 ha had at least 150 sampling points. The transects covered the whole lake area and all depth zones which potentially could sustain the growth of macrophytes. The number of transects were adjusted according to the shape of the lake in order to give an overall description of the whole lake area. At each sampling point, water depth, species presence, total coverage of submerged species, and mean plant height were estimated using either a water glass or a rake. Macrophyte coverage was estimated using a scale from 0 to 6 representing: 0% (no plants), 0–5%, 6–25%, 26–50%, 51–75%, 76–95%, and 96–100%. For each lake year, mean macrophyte coverage (COV, %) was calculated based on how large a depth zone and area each sampling point represented relative to the whole lake area. The proportionate mean plant volume inhabited (PVI, %) at each sampling point was calculated as follows:  $PVI = COV * \text{mean plant height} / \text{water depth}$ . The calculation of COV and PVI did not include filamentous algae or floating-leaved species. A total taxa list and taxa number were obtained from transect observations supplemented with additional observations of extra taxa in selected areas. Macrophyte taxa included floating-leaved species of which submerged forms were observed.

The lakes cover large gradients in morphological and chemical characteristics, but most are small (median area = 15 ha), shallow (median mean depth = 1.1 m), non-humic (median colour = 38 mg Pt/l), freshwater (median conductivity = 42 mS/m) and eutrophic (median Chla = 40 µg/l and median TP = 0.112 mg/l) (Table 1). Median COV was 11%, median PVI 3% and median taxa number five. Submerged macrophytes were absent in 11.6% of the lakes and in 13.2% of the observed lake years.

## Data analyses

Analyses were performed using boosted regression tree analysis (BRT) (Elith et al., 2008; Beaulieu et al., 2020; Jarvis et al., 2020), which is a machine learning technique that tests for relationships between predictors (in this case, physical and chemical variables, see Table 1) and response variables (here three macrophyte indicators in shallow lakes and Chla) in a dataset. The principle is that a second model is “boosted” from the previous one by minimising its errors in order to achieve the best new model derived through a model simplification process, where each

predictor is left out sequentially and the reduction in the predictive power is used to determine if it should stay in or not. The method can deal with highly collinear data and provides a good estimate of the relative influence of each predictor and the shape of the relationship between predictor and response variable. The outcome of the BRT analyses is presented as partial dependency plots that show the pattern between the predictor and the response independent of all the other predictors. The predictive power is represented by the total variance explained together with the relative importance of the most important explanatory variables. In this study, BRT analyses were used to test the influence of environmental factors on three main macrophyte indicators: COV, PVI and taxa number. A BRT analysis was also conducted for Chla because of its strong impact on all macrophyte indicators (see for example Søndergaard et al., 2010). A few extreme outliers with Chla above 1000 µg/l and TA above 10 meq/l were removed prior to the analyses. The analyses were conducted on the whole data set as well as a subset of lakes with TP < 2 mg/l (when analysing Chla) and Chla < 200 µg/l (when analysing COV) in order to avoid extreme high values of TP and Chla.

The BRT analysis was carried out following the guidelines of Elith et al. (2008); tree complexity and learning rate were set so as to ensure at least 5000 trees in the analysis. Tree complexity was set at three with a learning rate of 0.005 and with the bag fraction set at 0.75, and only results from the simplified trees are presented. A cost-complexity measure was used to eliminate non-influential predictors by sequentially dropping the least important each variable and assessing the loss in predictive power, no more predictors were dropped if there was a loss in predictive power larger than a standard error of the original model. The predictors that are retained in the simplified model can, therefore, be thought of as significant predictors. Partial dependence plots of fitted function versus observed values for variables significantly predicting the response variables were prepared; these seek to present the influence uniquely attributable to a single predictor. BRT analysis was carried out using gbm package (Greenwell et al., 2018) with additional code from Elith et al. (2008), and standard regression trees were constructed using the rpart package (Therneau et al., 2019), using R v. 4.0.2 (R Core Team, 2020).

**Table 1** Morphometric and chemical characteristics and macrophyte data on the lakes (lake years) included in this study represented by mean, minimum, 10% percentile, 25% percentile, median, 75% percentile, 90% percentile and maximum values

Variable	Number of lake years	Mean	Min	10%	25%	Median	75%	90%	Max
Area (ha)	1447	55.3	1.0	3.0	6.4	14.7	43.8	134	1713
Mean depth (m)	1446	1.2	0.03	0.38	0.66	1.1	1.7	2.3	3.0
Max depth (m)	1447	2.7	0.04	0.90	1.40	2.1	3.5	5.5	10.1
TA (meq/l)	1438	2.24	-0.07	0.14	1.15	2.24	3.19	4.00	10.1
Colour (mg Pt/l)	1293	60	0	17	25	38	61	117	1001
Conductivity (mS/m)	1324	266	0.7	15	27	42	72	945	7568
Secchi depth (m)	1431	1.03	0.08	0.37	0.56	0.84	1.29	1.85	6.13
TP (mg/l)	1352	0.224	0.004	0.034	0.061	0.112	0.220	0.461	6.31
TN (mg/l)	1353	1.73	0.27	0.70	0.94	1.38	2.00	3.09	51.0
Chla ( $\mu\text{g/l}$ )	1442	63	0.0	7.2	15.6	40.1	83.4	141	1199
COV (%)	1447	22.0	0	0	0.6	10.7	37.9	62.7	97.5
PVI (%)	1327	10.6	0	0	0.1	2.9	14.5	34.0	89.3
Taxa no	1336	7.4	0	0	2	5	11	17	53

TA total alkalinity, TP total phosphorus, TN total nitrogen, Chla chlorophyll *a*, COV coverage of submerged macrophytes, PVI plant volume inhabited

We also conducted multiple regression analyses between taxa number, COV and PVI as dependent variables and  $\log_{10}$  of the variables mentioned in Table 1 using SAS PROC REG with forward selection and *p* value correction. The multiple regression was first run on all the variables shown in Table 1 and then, in a second step, conducted only for the variables where the partial  $R^2$  was  $> 0.01$ .

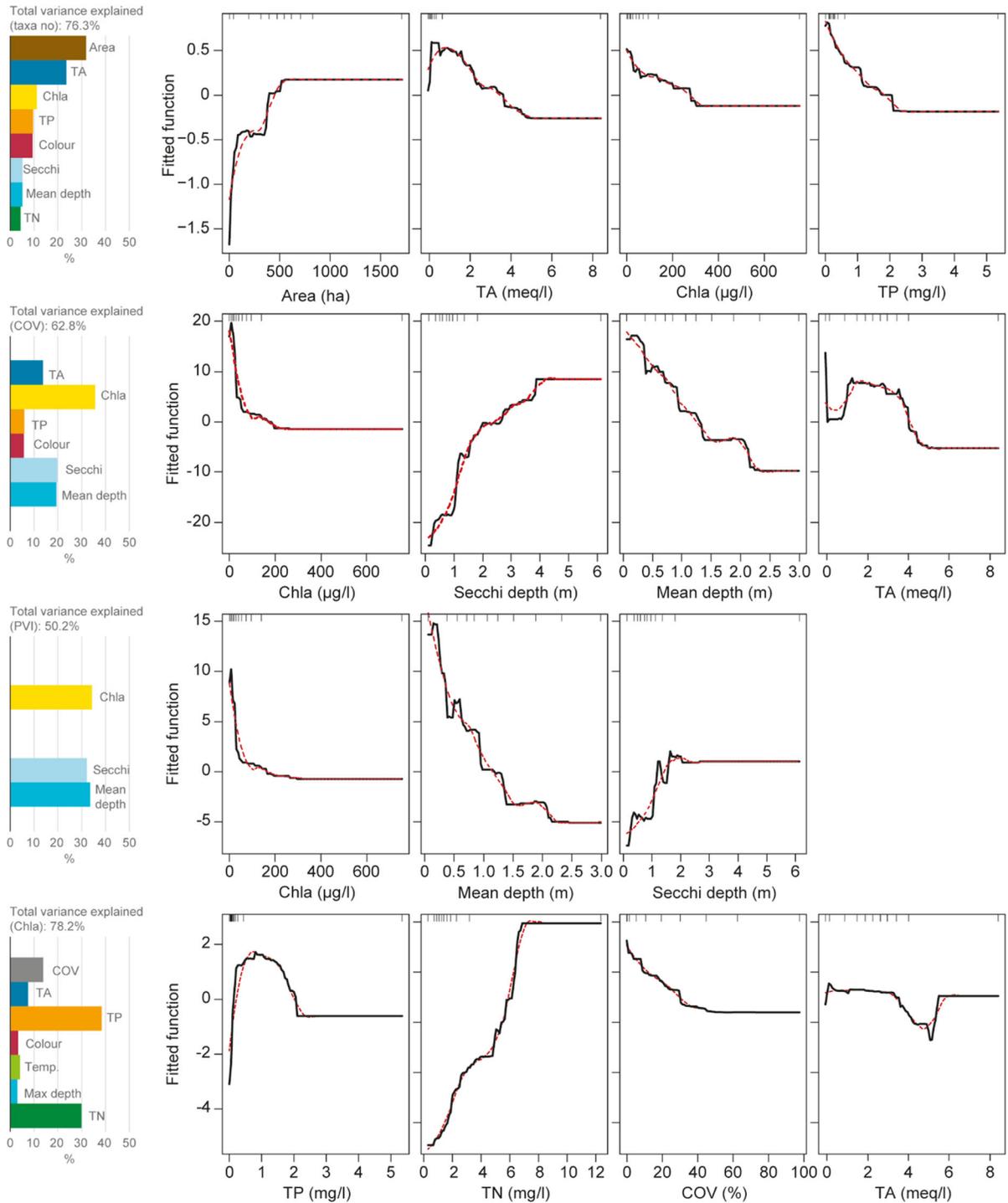
As phosphorus regulation often is used by lake managers to improve lake water quality, sometimes as the only measure (e.g. in Denmark), we also specifically addressed the relationship between TP and COV. The frequency distribution of lakes with COV  $> 1\%$  and lakes with COV  $> 20\%$  was ordered along a TP gradient. Lakes with COV  $< 1\%$  were used to represent lakes with no or very low macrophyte cover, lakes with COV  $> 1\%$  to represent lakes with the presence macrophytes and lakes with COV  $> 20\%$  to represent shallow lakes where submerged macrophytes are abundant and considered to have a significant impact on the overall biological structure in Danish lakes (Søndergaard et al., 2016). In lakes with high TP ( $> 0.2$  mg/l), differences in environmental factors in lakes with high COV ( $> 20\%$ ) or low COV ( $< 1\%$ ) were tested using the SAS PROC TTEST.

## Results

### BRT and regression analyses

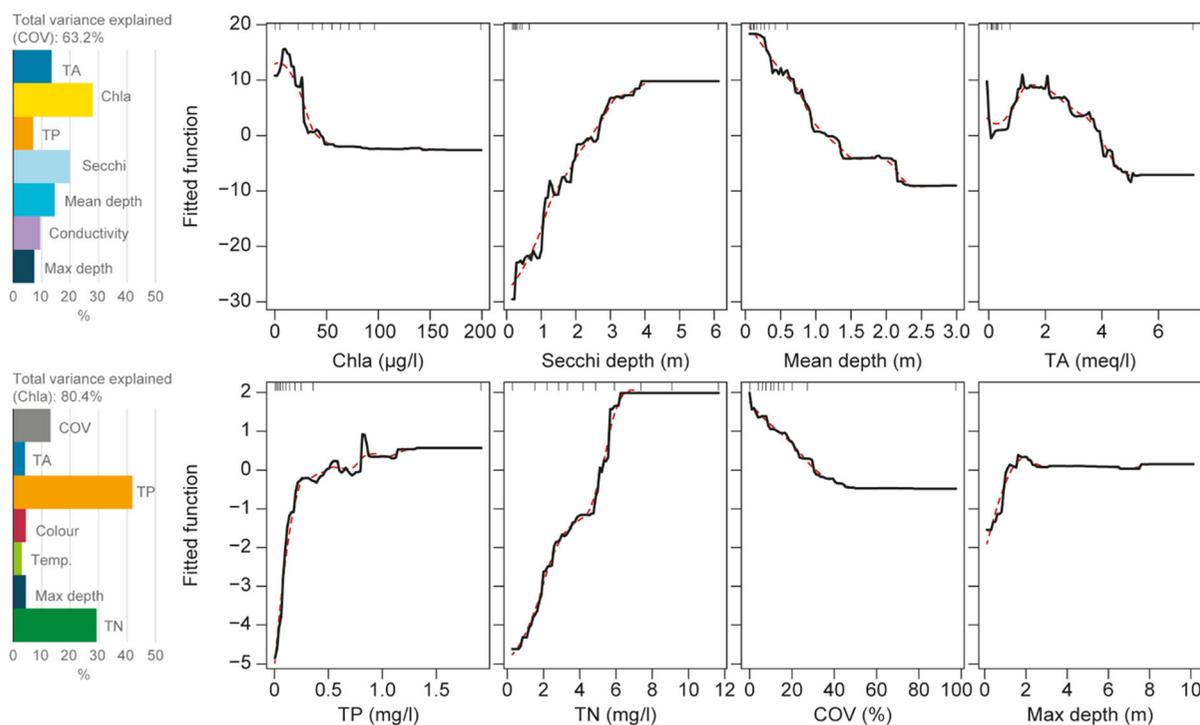
The total variance explained by the BRT analyses for the three macrophyte indicators relevant for shallow lakes ranged from 50% for PVI, 62% for COV to 76% for taxa number (Fig. 1). The relative importance of the predictor variables differed, Chla was most important for COV (36%) and PVI (34%), while lake area was most important for taxa number (32%). For COV and in particular PVI, Secchi depth and mean depth were almost as important as Chla, while the second-most important predictor for species richness was alkalinity (24%). For Chla, 78% of the variance was explained using the predictors in Table 1 (not including the three macrophyte indicators). TP was the most important predictor with a relative importance of 38%, followed by TN with 30% and COV with 14%. Restricting the analyses to TP  $< 2$  mg/l for Chla and to Chla  $< 200$   $\mu\text{g/l}$  for COV increased the total variance explained to 63% and 80%, respectively (Fig. 2).

The BRT plots also illustrate the changes in importance along a gradient of the different predictors (Figs. 1 and 2). For taxa number, lake area was



**Fig. 1** Partial dependence plots of the boosted regression tree analyses for the four most influential predictor variables. The analyses were conducted for lakes with a mean depth < 3 m and included the three macrophyte indicators shown from above: taxa numbers, COV and PVI and Chla (the lower figure). The

plots show the fitted function (solid line) and the smooth function (dashed line) relative to the predictor variables, all other predictor variables being averaged out. The left part of the figure shows the total variance explained and the relative influence of the predictor



**Fig. 2** As Fig. 1 but shows the analyses of COV including only data with Chla < 200  $\mu\text{g/l}$  and the analyses of Chla including only data with TP < 2 mg/l

especially important up to ca. 100 ha, but above 500 ha, there was no further effect of area. For TA, the second-most important predictor for taxa number, an optimum appeared around an alkalinity of 1 meq/l. For COV, there was a strong effect of Chla up to about 50  $\mu\text{g/l}$  but none at higher concentrations, while the effect of Secchi depth continued up to 4 m. For PVI, the response to increasing Chla was similar to that of COV. A sharp decline in the fitted function for mean depth was seen up to ca. 1.5 m. For Chla, the fitted function increased up to a TP of ca. < 0.2 mg/l, with a relatively short range up to 0.1 mg/l being the most important, whereas TN had a more gradual impact up to about 7 mg/l. COV was the third-most important predictor with a relative importance of 13%, and the fitted function particularly decreased up to a COV of 30–40%, after which higher COV had little effect on the fitted function.

In the multiple regressions using the three macrophyte indicators as dependent variables and  $\log_{10}$  transformed environmental variables from Table 1 as predictors, the highest model  $R^2$  was obtained for taxa number ( $R^2 = 0.36$ ) and the lowest for PVI

( $R^2 = 0.22$ ) (Table 2). For COV and PVI, the highest partial  $R^2$  was obtained for Chla, while area had the highest partial  $R^2$  for taxa number and Secchi depth. The parameter estimate for Chla was negative for all macrophyte indicators, whereas area and Secchi depth were positive. Only for taxa number, partial  $R^2$  was > 0.01 for TP or TN.

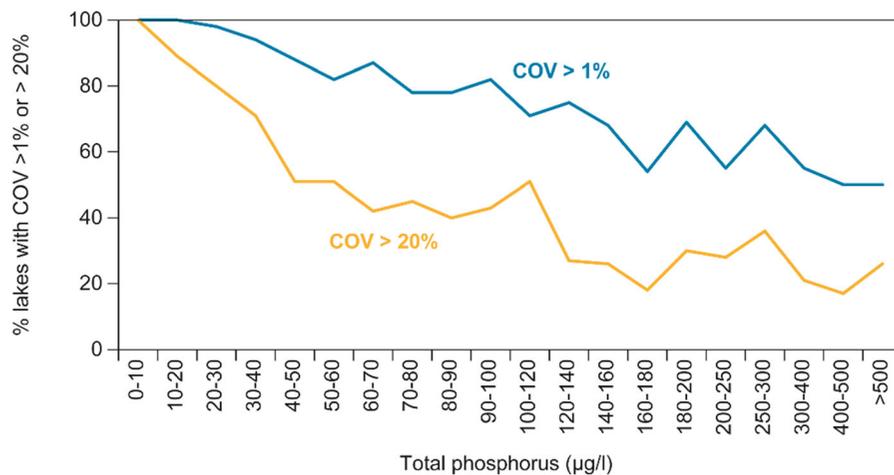
#### Frequency distribution of low and high COV at increasing TP

The number of lakes with COV above 1% or 20% decreased with increasing TP (Fig. 3). The reduction in lakes with COV > 20% occurred particularly when TP increased from < 10 to 40–50  $\mu\text{g/l}$ , where the percentage with high COV decreased from 100 to 50%. Even at TP > 200  $\mu\text{g/l}$ , 20–40% (average 26%) of the lakes still had a COV > 20% and, on average, 54% a COV > 1%. Submerged macrophytes were present (COV > 1%) in all lakes with TP < 20  $\mu\text{g/l}$  and in 94% of the lakes with TP < 50  $\mu\text{g/l}$ . Submerged macrophytes were still found in about 50% of the shallow lakes at TP > 400  $\mu\text{g/l}$ . At TP

**Table 2** Multiple regressions between taxa number, COV and PVI as dependent variables and  $\log_{10}$  of the variables mentioned in Table 1

Dependent variable	N	Intercept	Variable entered	Parameter estimate	Partial R-square	Model R-square
Taxa no	1182	8.39	$\log_{10}$ area	6.11	0.17	0.17
			$\log_{10}$ Chla	- 4.52	0.14	0.31
			$\log_{10}$ colour	3.99	0.03	0.34
			$\log_{10}$ TP	- 3.67	0.03	0.36
COV	1424	42.4	$\log_{10}$ Chla	- 15.6	0.26	0.26
			$\log_{10}$ mean depth	- 31.3	0.02	0.28
			$\log_{10}$ Secchi depth	32.1	0.04	0.32
			$\log_{10}$ area	4.77	0.01	0.34
PVI	1279	22.9	$\log_{10}$ Chla	- 7.97	0.12	0.12
			$\log_{10}$ mean depth	- 19.2	0.08	0.20
			$\log_{10}$ Secchi depth	10.8	0.01	0.21
			$\log_{10}$ alkalinity	2.92	0.01	0.22

In all regressions and for all variables,  $P$  was  $< 0.0001$ . Only variables where partial R-square  $> 0.01$  are shown



**Fig. 3** Percentage of lake year observations with COV above 1% (blue line) and above 20% (yellow line) at increasing TP concentrations. Number of lake years = 1351. The blue line with COV  $> 1\%$  also includes lake years with COV  $> 20\%$  (yellow line)

concentrations  $> 0.2$  mg/l, lakes with COV  $< 1\%$  as a mean had a significantly lower area, higher mean and maximum depths, higher conductivity, lower Secchi depth and higher Chla than lakes with COV  $> 20\%$  (Table 3). TP and TN did not differ significantly between lakes with high and low COV at high TP.

## Discussion

Our results underline the significant negative impact that eutrophication has on submerged macrophytes in shallow lakes (Phillips et al., 2016). At increasing Chla and decreased Secchi depth, the two abundance indicators, COV and PVI, both decreased. The response to eutrophication was hierarchical—nutrients impacted Chla, and Chla causes turbidity and thereby COV and PVI. The direct effect of nutrients on macrophyte abundance was nearly absent and

**Table 3** Mean physical and chemical values for lakes with summer mean TP > 0.2 mg/l shown for lakes with COV ≤ 1% and lakes with COV > 20%

Variable	COV ≤ 1%		COV > 20%		Difference
	Mean	N	Mean	N	
Area (ha)	20.4	181	97.1	102	***
Mean depth (m)	1.15	180	0.73	102	***
Max depth (m)	2.35	181	1.59	102	***
TA (meq/l)	3.23	180	3.17	102	–
Colour (mg Pt/l)	62.5	160	72.3	93	–
Conductivity (mS/m)	274	157	645	99	**
Secchi depth (m)	0.62	181	0.78	101	**
TP (mg/l)	0.65	181	0.50	102	–
TN (mg/l)	2.92	181	2.29	102	–
Chla (µg/l)	149	181	66.7	102	***

Significant differences (t-test) between the two means are shown in the right column with significance levels: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , – = not significant

mediated through water clarity (Chla/Secchi depth) with additional interactive effects of alkalinity, mean depth and colour. Chla, on the other hand, was predicted to a high degree by nutrient concentrations, where nitrogen was almost as important as phosphorus and with some effects of COV and alkalinity. The high importance of nitrogen on Chla and then subsequently on macrophyte abundance suggests that lake managers should not only focus on phosphorus-loading reductions, but also nitrogen loading in order to improve the ecological quality of lakes and their biodiversity, as also concluded in other studies (e.g. Barker et al., 2008; Olsen et al., 2015; Søndergaard et al., 2017a, b).

The multiple regression analyses also suggest that turbidity- and eutrophication-related factors, Chla and Secchi depth, were important factors having the highest explanatory power for the submerged macrophyte community in shallow lakes. For all three macrophyte indicators, however, lake area and/or depth were also important. The empirical relationship using Chla, Secchi depth and mean depth as the three main predictors of COV, as found by the BRT analyses, however, only explained 32% of the variability in COV. Use of the regression models to estimate target concentrations of Chla and nutrients to obtain a certain COV and ecological quality is, therefore, more uncertain than the BRT models.

For most predictors, their effect on macrophyte abundance changed considerably and often non-linearly along an eutrophication gradient in the BRT analyses, for Chla and TP particularly at low concentrations. For example, the effects of Chla on COV and PVI were marked at Chla below ca. 50 µg/l, after

which a further increase in Chla did not affect the fitted function. Similarly, Chla was particularly affected at TP up to ca. 0.2 mg/l, whereas a gradual response was found for TN, supporting the general perception that both phosphorus and nitrogen can be important limiting factors for phytoplankton growth (Seip, 1994; Barker et al., 2008; Olsen et al., 2015; Liang et al., 2020) and that the individual importance of the two nutrients varies with concentration levels and seasons (Søndergaard et al., 2017a). The inadequacy of phosphorus as a predictor of macrophyte abundance, particularly at high TP as seen in the BRT analyses, was also illustrated by the presence of macrophytes in almost half of the shallow lakes with TP > 0.2 mg TP/l and the fact that COV even exceeded 20% as an average in 26% of these lakes. The BRT analyses also revealed a unique cover effect on Chla up to a COV of about 40%, where COV was the third-most important predictor after TP and TN. This allows quantification of the relative importance of plant-related feedback effects of cover in reducing Chla independent of nutrients. Thereby, it feeds into the discussion of at which level of COV, a major impact on the overall biological structure in shallow lakes, including Chla, can be anticipated (Canfield 1983; Wang et al., 2014; Gao et al., 2020). The effect of increasing COV on Chla was gradual up to 40% COV, and the existence of a COV threshold, as indicated earlier, is, therefore, not supported (Søndergaard et al., 2016). Any increase in COV up to 30–40% could be a target for lake managers in order to create more clear water in shallow lakes, whereas a higher COV would not have any further impact on Chla. High

COV in shallow lakes has been associated with reduced conditions close to the sediment which can impact the biogeochemical nutrient cycling and lead to increased internal phosphorus release (Stephen et al., 1997; Boros et al. 2011; Waters & Webster-Brown, 2020).

Species richness (taxa number) depends on different factors in different regions of the world (Alahuhta et al., 2017), but here we found that area was the most important, with effects mainly up to around 100 ha. The inclusion of lakes down to 1 ha in this study probably amplifies the area effect on species richness compared to other studies analysing large lakes only. Alkalinity was the second-most important factor with a maximum effect on species richness around 1 meq/l and with a decreasing effect up to around 4 meq/l. This optimum may reflect that species richness is higher in lakes with high than low alkalinity and that intermediate alkalinity from ca. 0.2 to 1 meq/l allows co-occurrence of elodeids and isoetids (Vestergaard & Sand-Jensen, 2000; Søndergaard et al., 2020). The eutrophication indicators, Chla, TP and Secchi depth, also added significantly to the total variance of taxa number explained, but they contributed much less than area and alkalinity. Our analyses could, therefore, not confirm that vertical expansion was higher than horizontal expansion and thereby that high Secchi depth increased species richness more than lake area (Vestergaard & Sand-Jensen, 2000). Colour had only a minor effect on species richness, but the number of highly coloured lakes in our study was small, implying that potential colour effects and shading by dissolved organic carbon on macrophyte communities cannot be ruled out (Reitsemá et al., 2020).

There are several potential caveats in our study. First, we focused on physical and chemical factors for predicting macrophyte communities despite the numerous interactions with other biological components. As effects of chlorophyll and the cover feedback on chlorophyll are included in the analyses, and as the BRTs explain a large amount of variance, we do not expect that these caveats have great importance for the overall picture. Second, we do not know to which extent the lakes included in the analyses represent lakes in equilibrium. Some of them may still be in recovery after changed environmental conditions (Kozak & Goldyn, 2016; Søndergaard et al., 2017b) or the expansion of macrophytes may not immediately follow changes in abiotic conditions, as also the

occurrence of propagules, herbivory and plant competition may play a role (Bakker et al., 2012). Moreover, for macrophytes, there may be a carryover effect from previous years as opposed to phytoplankton biomass for which there is little “memory” from year to year (Rooney & Kalff, 2000; Cobbaert et al., 2014). Third, in the search for nutrient–macrophyte interactions, it may be difficult to discriminate between causes and consequences, since the presence of submerged macrophytes has significant effects on the internal nutrient cycling (Dai et al., 2015; Søndergaard et al., 2017b; Li et al., 2020). These effects may differ depending on which species dominate; meadow-forming species have strong effects on turbidity and reduce nutrient concentrations, whereas canopy-forming species are less significant in controlling the internal nutrient cycling (Gao et al., 2020). Finally, differences in the winter survival of macrophytes, timing of the spring clear-water phase, local weather conditions during winter and spring, and a number of biological interactions are all factors that can add to the variability in macrophyte abundance (Jeppesen et al., 1998; Mämetts et al., 2006; Phillips et al., 2016), but data were not available in this study to further evaluate their importance. Again, the large predictive power of the BRT analyses suggests that this is not a serious problem for the general conclusions.

Overall, the effect of eutrophication on the macrophyte indicators was hierarchical and primarily depended on water clarity (Chla/Secchi depth) interacting with alkalinity, depth and area. In contrast, TP and TN were not good predictors, because their effects were mediated through water clarity with interactions of area, mean depth, colour and alkalinity. The Chla concentration was highly predictable based on nutrient concentrations but limited to a rather short TP range (up to 0.2 mg/l), whereas the TN effect was much more stable across the length of the gradient. For lake managers, the gradual changes in impact of different nutrients and environmental factors may be used to develop lake-specific management plans.

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**Data availability** The datasets generated during and/or analysed in the current study are available from the corresponding author upon reasonable request.

**Code availability** Not applicable.

## Declarations

**Conflicts of interest** No conflict of interest.

**Consent to participate** Not applicable.

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