

A century of change in Minnesota's lake plant communities

Donna J. Perleberg*, Paul J. Radomski

Minnesota Department of Natural Resources, 1601 Minnesota Drive, Brainerd, MN, 56401, USA

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ABSTRACT

Aquatic plant communities are good indicators of lake conditions, and persistent changes to those communities are indicative of environmental change. Our study used historical and recent lake plant surveys to detect changes in Minnesota's lake plant communities over the last century. We did not find taxa richness estimates useful for change detection and suggest that recent richness values were higher than historical due to increased search effort rather than real change. The primary signal of change was the failure to relocate taxa in lakes where they were historically common. In 55 % of the lakes, surveyors did not relocate at least one taxon that was reported in an historic survey. We found that emergent plant taxa were most likely to have been lost; for lakes where emergents were reported historically, 45% had at least one emergent taxon that was not redetected compared to 30% of lakes where at least one floating-leaf taxon was not redetected and 42% of lakes where at least one submerged taxon was not redetected. Lakes in the southwestern and central ecoregions of the state were most likely to have gross and persistent aquatic plant losses. Eutrophication was the most likely reason for losses, with substantial declines in the probability of presence of many taxa with greater increases in lake phosphorus concentrations. We identified limitations with these datasets and recommend survey method changes to improve future collection of lake plant lists.

1. Introduction

The quality and function of freshwater ecosystems continue to be compromised by human disturbances that change trophic status, water clarity, water chemistry, hydrology, and aquatic life. Changing climate further alters the physio-chemical features of these habitats and species growth, distribution and phenology patterns (Dhir, 2015). Shifts in environmental conditions generally favor species with broad environmental tolerance, and geographically widespread species are generally favored over species with narrow geographical ranges (Xu et al., 2019). This leads to biotic homogenization, and ultimately, the loss of biotic communities that help create ecologically functioning ecosystems.

Aquatic plant communities are good indicators of these changes because they are stationary and because there is a good understanding of how abiotic conditions determine aquatic plant occurrence and composition (Nichols, 2001; Bornette and Puijalón, 2011). Anthropogenic eutrophication is a leading cause of lake plant changes because increased nutrients facilitate planktonic algae growth which results in reduced light availability and ultimately can shift a lake from macrophyte dominated to algal dominated (Scheffer and Jeppesen, 1998). As lake clarity declines, dominant plant life forms shift from low growing

submerged plants to species that can escape low light conditions such as larger-stature submerged species (Borman et al., 2009; Sand-Jensen et al., 2000) and floating and emergent species (Egertson et al., 2004). For Minnesota, Radomski and Perleberg (2012) were able to identify biologically impaired lakes using a suite of predictive models for aquatic plant richness and floristic quality because both metrics decreased predictably with increasing lake phosphorus concentrations. Aquatic plants may also be more sensitive than terrestrial plants to climate changes (Dieffenbacher-Krall and Jacobson, 2001). However, the lack of long-term aquatic plant datasets has limited the detection and description of these events.

Other human activities that impact lake plant communities include direct vegetation destruction and land use alterations that result in water chemistry and hydrologic changes, introductions of fish, plants and other organisms, and management activities to control unwanted organisms (Lesiv et al., 2020; Mikulyuk et al., 2020). Because these stressors differ geographically across the landscape and locally within a given waterbody, aquatic plant community changes may be more pronounced in some habitats and within specific ecotones. For example, vegetation in the shallow water, nearshore zone of developed lakes may be more at risk for human destruction than are deep water communities

* Corresponding author.

E-mail addresses: donna.perleberg@state.mn.us (D.J. Perleberg), paul.radomski@state.mn.us (P.J. Radomski).

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or sites on undeveloped lakes.

In the Great Lakes Region of North America, several long-term studies have linked aquatic plant community changes within individual waterbodies with increasing human disturbances including eutrophication. [Stuckey and Moore \(1995\)](#) used species lists, recorded between 1898 and 1970, to reveal a 50 % decline in plant species richness of Put-in-Bay, Lake Erie, Ohio. In Lake East Okoboji, Iowa, [Volker and Smith \(1965\)](#) reported a 60 % loss in all plant species and a 78 % loss of submerged species from 1915 to 1961. [Nichols and Lathrop \(1994\)](#) reported a loss of one third of plant species found in Madison, Wisconsin lakes between the 1870's and 1991. In northwestern Wisconsin lakes, [Borman et al. \(2009\)](#) associated increased submerged plant richness between the 1930's and 2000's with increased residential land use and lake sediment shifts from sand to silt/muck.

Other regional studies have assessed long-term changes in a single taxon or life form. For north-central Minnesota lakes, [Radomski \(2006\)](#) determined that between 1939 and 2003, shoreline development significantly negatively affected floating-leaf and emergent vegetation and estimated a 15 % cover loss for these life forms. In Wisconsin, [Gabriel and Bodensteiner \(2002\)](#) studied historical changes in abundance of the emergent plant, common reed (*Phragmites australis*), and suggested declines were influenced by water level management, damage by boats and common carp. [Biesboer \(2019\)](#) attributed declines in the emergent plant, wild rice (*Zizania palustris*), to humans through changes in climate, hydrology, and pollution, increased seasonal housing along lakeshores, and habitat loss. In Ohio, [Wentz and Stuckey \(1971\)](#) described distribution shifts in species of the submerged genus, *Najas*, as northern, cooler and clearer water species declined while southern and European species expanded; they suggested this trend may be related to increased turbidity, warming, and eutrophication.

Over the last century, surveyors have conducted and repeated aquatic plant inventories on thousands of Minnesota lakes. These datasets present a unique opportunity to evaluate region-wide long-term biological changes in freshwater ecosystems. In this study, we evaluated the use of these plant taxa lists to assess both individual and regional aquatic plant community changes through time. A primary limitation of taxa lists is that the types and total number of taxa recorded (taxa richness) are dependent on search effort (area searched and time spent searching) and surveyor expertise. [Wintle et al. \(2004\)](#) cautioned that differences in observed taxa richness may reflect true differences in taxa richness as well as differences in sampling effort or dissimilarity in the underlying distributions of species abundance. [Fleishman et al. \(2006\)](#) further warned that field measurements tend to underestimate taxa richness. In an earlier review of Minnesota lake plant data ([Radomski and Perleberg, 2012](#)), we found that taxa richness estimates increased with multiple surveys and this was at least partly attributable to increased search effort and increased surveyor botanical expertise. Despite these shortcomings historical taxa lists are still valuable records that may be used to evaluate long-term changes in individual taxa and community composition.

First, we evaluated long-term changes in taxa richness by comparing Minnesota lake plant lists collected from 1917 to 1971 with plant lists collected from the same lakes in recent years. Second, we used data collected from 1940 to 2019 to explore how human eutrophication might have influenced lake plant occurrence. We also identified limitations with these datasets and recommend survey method changes to improve the usefulness of future data.

2. Methods

2.1. Study lakes and datasets

In Minnesota, statewide aquatic plant datasets are available from 1917 to present. Data are from disparate studies that were widespread in time, space, and technique, but all surveys produced a plant taxa list. We divided the data into four periods based on methods used to collect taxa

lists: 1917–1939 (“historic”), 1940–1970 (“mid-century”), 1971–1992 (“late-century”), and 1993–2019 (“recent”). The specific lakes included in each dataset varied but each dataset included a statewide representation of lakes with deep and shallow waterbodies ranging in surface area from a few hectares to those that exceed 10,000 ha.

Historic data are available from two sources: 530 surveys conducted from 1917 to 1931 by waterfowl biologists with the United States Department of Agriculture (USDA) Bureau of Biological Survey ([Moyle and Hotchkiss, 1945](#)) and 197 surveys completed from 1934 to 1939 by Dr. John Moyle as part of his doctorate research on Minnesota's aquatic plants ([Moyle, 1939](#)). Both studies were statewide and focused on lake-rich regions of the state; 70 lakes were surveyed by both research projects. The USDA surveys targeted lakes considered to be prime waterfowl lakes with few surveys in northeastern soft-water lakes. Moyle selected lakes along a water chemistry gradient. Both studies were descriptive and did not estimate abundance or report specific locations of taxon. These were relatively rapid assessments with no standard search time or area. Surveyors included well-known botanists with high botanical skills. Taxa were reported using scientific names and voucher specimens were collected for many taxa. The same suite of species was reported in both surveys but within individual lakes, USDA surveys only reported taxa that were observed to be common and/or were considered to be important for waterfowl habitat and food.

In 1940, the State of Minnesota initiated statewide lake monitoring that included lakewide aquatic plant assessments. These surveys continue today and protocols vary and change based on specific program objectives and advances in technology. Mid-century and late-century surveys were limited in search effort and were conducted by fisheries and wildlife biologists with moderate botanical expertise. From 1940–1970, surveyors traversed the lake, recorded the common names of frequently observed plant taxa, and created hand-drawn maps of major plant stands. Beginning in 1971, surveyors were required to use scientific names and estimate relative abundance.

Recent surveys (1993–2019) included both qualitative surveys similar to the historic period and quantitative methods with increased search effort. Semi-quantitative surveys began in 1993 as consumer grade GPS became available; these lakewide surveys included systematically selected sample stations along belt transects or at points on a grid (point-intercept) ([Perleberg et al., 2019](#)). These established protocols often increased survey effort to multiple days and helped ensure that surveyors sampled sites around the entire lake and in a range of water depths. Plant identification training increased in 2000 through annual workshops and the availability of additional field guides. During this same period, botanists also collected plant species lists at many of these same waterbodies; these surveys were descriptive and were typically restricted to less than a hectare of search area.

There was overlap of lakes included in each dataset. During the historical period (1917–1939), 560 surveys were conducted with most study lakes surveyed once and 12 % of the lakes surveyed twice. In the recent period (1993–2019), each of the original, undrained, study lakes were resurveyed between one and 13 times for a total of 1492 surveys; 79 % of the lakes have multiple recent surveys with a mean of three recent surveys per lake.

2.2. Plant taxonomic groupings and analysis

We assembled data from all survey efforts and combined them into one long-term data set (“combined data set”). The combined data set included a total of 314 shoreland and aquatic plant taxa. To facilitate comparisons across time, we converted all taxa lists to a common set of modern taxonomic concepts, based on [Flora of North America \(1993+\)](#). To reduce the influence of differing taxonomic experience, we identified 24 species that can be easily distinguished by non-botanists and combined other taxa to a species complex or genus level. We combined several small, easily overlooked taxa as “rosettes.” We excluded shoreland and wetland emergent taxa such as *Typha*, *Equisetum* and *Sagittaria*

because we could not determine if surveyors observed these taxa in the study lake or if they were sampled from adjacent wetlands. Volker and Smith (1965) recognized this similar issue where emergent species were documented differently during different time periods (an emergent documented as an “aquatic” in one survey may have been considered “non-aquatic” in another). We also removed free-floating taxa in the Lemnaceae family because they were inconsistently recorded in all surveys. The final combined set included data on 39 taxa including three life forms: 7 emergent taxa, 4 floating-leaf taxa, and 28 submerged taxa (Table 1). All 39 taxa were reported during each of the four study time periods.

2.3. Historical and recent taxa list comparisons on the same lakes

We analyzed plant taxa lists from 502 Minnesota lakes where both

Table 1

Reporting of 39 aquatic plant taxa in historic (1917-1939) and recent (1993-2019) lake plant surveys.

Life Form	Taxa	Report rate		Redetection rate
		Historic	Recent	
Emergent	<i>Phragmites australis</i>	0.15	0.34	0.41
	<i>Bolboschoenus fluviatile</i>	0.10	0.36	0.44
	<i>Zizania palustris</i>	0.28	0.30	0.54
	<i>Eleocharis</i> spp. ^A	0.14	0.34	0.54
	<i>Schoenoplectus pungens</i>	0.04	0.15	0.60
	<i>Sparganium</i> spp.	0.07	0.38	0.62
	<i>Schoenoplectus</i> spp.	0.60	0.75	0.82
Floating-leaved	<i>Brasenia schreberi</i>	0.03	0.14	0.50
	<i>Nymphaea</i> spp.	0.13	0.51	0.81
	<i>Nuphar</i> spp.	0.18	0.56	0.82
	<i>Potamogeton natans</i>	0.12	0.45	0.82
	<i>Potamogeton nodosus</i>	0.02	0.07	0.12
	<i>Najas marina</i>	0.02	0.05	0.22
	<i>Ranunculus aquatilis</i>	0.02	0.27	0.33
	<i>Hippuris vulgaris</i>	0.02	0.06	0.33
	<i>Najas</i> spp. (excluding <i>N. marina</i>)	0.27	0.68	0.35
	<i>Eleocharis</i> spp. ^B	0.05	0.27	0.36
	<i>Ruppia occidentalis</i>	0.04	0.07	0.38
	<i>Stuckenia</i> spp.	0.36	0.82	0.42
Submerged	<i>Zannichellia palustris</i>	0.03	0.15	0.44
	<i>Heteranthera dubia</i>	0.07	0.43	0.61
	<i>Potamogeton epiphydrus</i>	0.04	0.09	0.64
	Rosettes [*]	0.04	0.13	0.64
	<i>Potamogeton gramineus</i>	0.09	0.32	0.69
	<i>Bidens beckii</i>	0.04	0.20	0.70
	<i>Potamogeton zosteriformis</i>	0.19	0.63	0.77
	<i>Potamogeton</i> spp. (narrowleaf) ^{**}	0.14	0.76	0.79
	<i>Potamogeton richardsonii</i>	0.23	0.53	0.80
	<i>Myriophyllum</i> spp. ^{***}	0.23	0.66	0.82
	Characeae	0.28	0.66	0.83
	<i>Potamogeton amplifolius</i>	0.07	0.38	0.84
	<i>Potamogeton praelongus</i>	0.05	0.40	0.85
	<i>Utricularia</i> spp.	0.07	0.52	0.85
	<i>Potamogeton illinoensis</i>	0.06	0.32	0.86
	<i>Ceratophyllum</i> spp.	0.30	0.78	0.86
	<i>Vallisneria americana</i>	0.17	0.48	0.87
	<i>Elodea</i> spp.	0.11	0.57	0.91
	<i>Potamogeton robbinsii</i>	0.02	0.17	0.92
<i>Potamogeton crispus</i>	0.01	0.41	1.00	

Redetection rate is the percent of lakes where a taxon was detected both in historic and recent surveys.

^A *Eleocharis* species included as “emergent” include *Eleocharis palustris* and taxa reported using the common name “spikerush”.

^B *Eleocharis* species included as “submerged” include *Eleocharis acicularis* and taxa reported using the common name “needlerush”.

^{*} Rosette species include *Elatine* spp., *Isoetes* spp., *Juncus pelocarpus*, *Myriophyllum tenellum*, *Ranunculus flammula*, *Subularia aquatica*.

^{**} “Narrow-leaved pondweeds” include *Potamogeton foliosus*, *P. freisii*, *P. pusillus*, *P. spirillus*, *P. strictifolius*, *P. vaseyi*.

^{***} (excluding *M. spicatum*, *M. tenellum*).

historical (1940–1970) and recent (1993–2019) vegetation surveys were conducted. For lakes with more than one historic or recent survey, data were pooled for the period and if a taxon was observed in any survey during the historic or recent period, that taxon was considered detected in the lake for that entire period. For each lake, taxa present in historical data were compared to taxa reported in recent surveys. We made no judgement of change if a taxon was reported in a recent survey but not in historical surveys of the same lake (i.e., we were not confident that this was a true recent addition to the lake). Redetection rates for all taxa were calculated as the percent of lakes where an historically observed taxon persisted through the most recent survey effort. Taxa loss for each individual lake was calculated as the number of historically observed taxa that did not persist through the most recent survey effort. We mapped historical occurrences and redetection occurrences to assess potential geographical patterns of change.

We also conducted the same comparison of taxa lists for 309 lakes that were surveyed during both the historic and late-century (1970–1992) period. We found that redetection rates in this comparison were lower than for the historic to recent comparison. We attributed this result to the decreased search effort that occurred during the 1970–1992 period. Therefore, we present only results comparing the historic to recent taxa lists.

2.4. Using predictive models to assess statewide lake plant communities through time

To understand environmental factors contributing to taxa occurrence, we analyzed lake plant surveys conducted between 1940 and 2019 (this includes mid-century, late-century, and recent time periods). The dataset includes 6751 surveys from 3542 mostly deep-water lakes across the state. Models were developed to predict the probability of detecting aquatic plant taxa within a given lake using generalized linear mixed models (GLMM; Pinheiro and Bates, 2000) and random forest classifier models. All statistical analyses were conducted using R (R Core Team, 2019) with glmer from the lme4 package (Bates et al., 2015) and the randomForest package (Liaw and Wiener, 2002). There were 6751 surveys used in these analyses that had a full complement of predictor variable values.

The GLMM development strategy followed the suggestions of Zuur et al. (2009). The influence of lake surface area (ln transformed), alkalinity (square root transformed), year/survey type period, ecoregion classification, lake depth (shallow or deep), and predicted change in total phosphorus from predevelopment (square root transformed) were analyzed as fixed effects. The predicted change in lake total phosphorus (TP) was the predicted mean lake TP for pre-disturbance (Jacobson et al., 2017, equation 2) minus the observed mean lake TP, and it represents the increase in lake TP from anthropogenic watershed disturbance or hydrologic load increases from climate change. After initial testing to determine significant fixed effects, several candidate models were developed that incorporated fixed effects for the response variable (probability of a specific taxa’s occurrence in a lake). The changes in the AIC score were used to select a set of preferred variables to build random forest models (Burnham and Anderson, 2002). GLMMs were fit using restricted maximum likelihood, and in an effort to incorporate some lake-level attributes into the analysis, lakes were modeled as random effects. The analysis assumed that data from different lakes were statistically independent.

The random forest classifier, a type of recursive partitioning method for constructing classification trees (Breiman, 2001), was used to understand the relationship between probability of taxon occurrence and an increase in lake TP. This approach was applied to taxa of interest from the comparison of the historic and recent surveys. For random forest models, the random subset of variables at each node of a tree was set at three with 500-classification tree forests constructed. Based on the GLMM work, the importance of lake surface area, alkalinity, time/survey type period, ecoregion level II classifications (U.S. Environmental

Protection Agency, 2006), and predicted change in total phosphorus from predevelopment were analyzed. The measures of variable importance from the random forest calculations, computed by the mean decrease in the Gini index for each variable over all trees in the forest, were compared to the explanatory variables from the GLMMs. We used the area under the curve (AUC) of the receiver operating characteristic and Cohen’s kappa statistic to evaluate the predictive accuracy of the models developed (Fielding and Bell, 1997; Pearce and Ferrier, 2000; Manel et al., 2001). Patterns in partial dependence plots, which are plots of the marginal effect of a predictor variable when other variables are held constant, were inspected to assess the likely consequences of increased TP loading from watershed disturbance and climate change to the probability of taxa occurrence. Of particular interest was the plot area between the first and tenth deciles as the patterns at both of the margins are influenced by few data.

3. Results

3.1. Catastrophic changes to subset of lakes through time

Draining resulted in catastrophic changes to 16 of the original study lakes (Fig. 1). Twelve lakes had already been drained before 1930 and four lakes were drained after 1930. These sites are present day agricultural fields.

3.2. Individual lake plant community comparison through time

For the 530 lakes with historical and recent plant data, reporting of aquatic plants increased through time. Historical surveys reported vegetation in 93 % of the lakes compared to 99 % in recent years. For 87 % of lakes, more taxa were reported in recent surveys than in historic surveys and the reported mean number of taxa per lake increased from five in historic surveys to 10 in recent surveys. All 39 taxa were reported

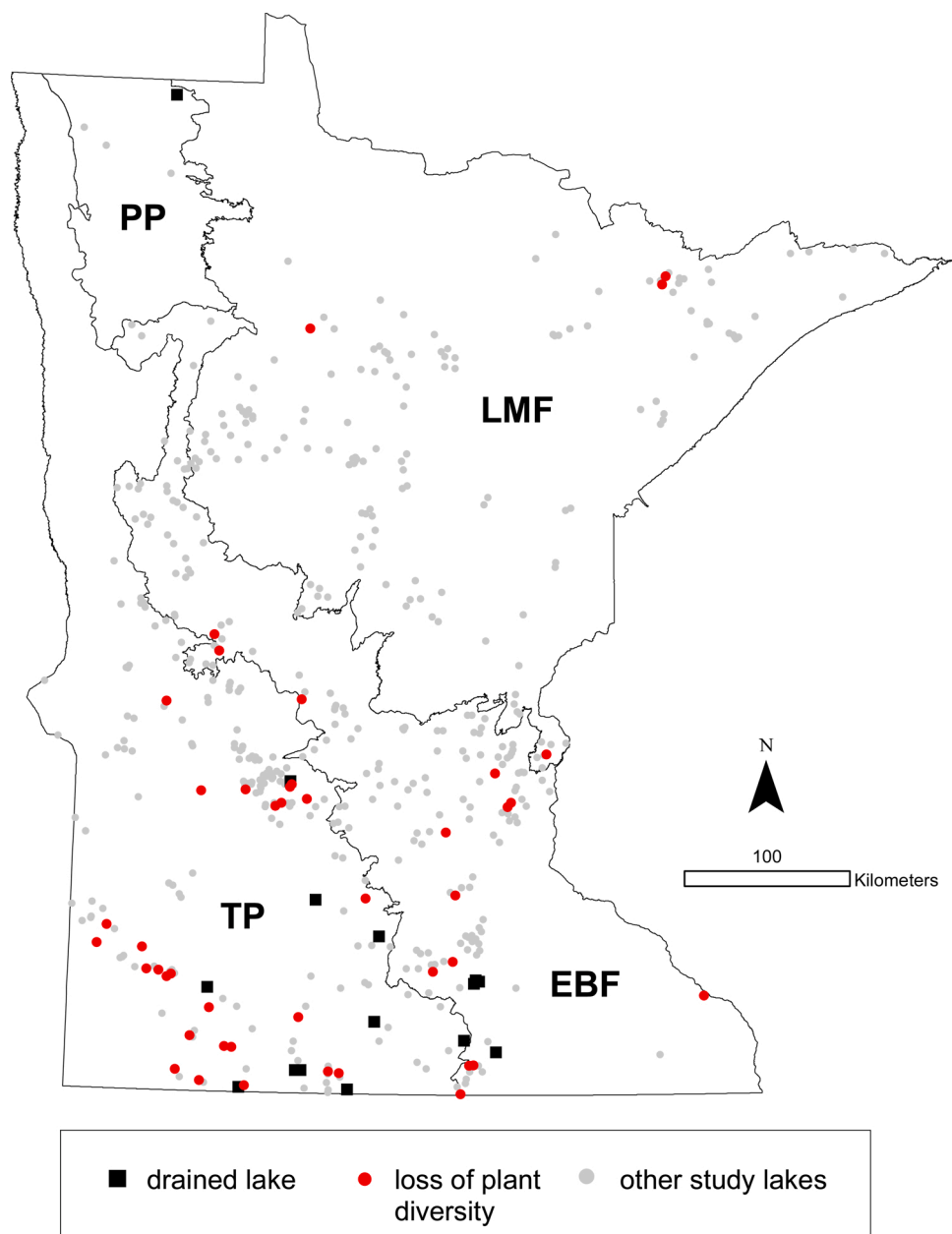


Fig. 1. Distribution of disturbed lakes by Ecological Region. (PP = Prairie Parkland, LMF = Laurentian Mixed Forest, EBF = Eastern Broadleaf Forest, TP = Tallgrass Prairie). Loss of plant diversity is defined as lakes where recent surveys detected fewer plant taxa than historical.

at a higher frequency in the recent surveys than in the historical survey dataset, with 32 taxa reported in at least 15 % of the lakes in recent years compared to only 12 taxa found in at least 15 % of the historic surveys (Table 1). The percentage of lakes within which each life form was reported also increased from historic to recent surveys: emergent taxa, 77%–87%; floating-leaf taxa, 34%–72%; submerged taxa, 76%–97%.

Despite overall increased reporting of plants, losses were detected within individual lakes. In 55 % of the lakes, at least one taxon that was reported in historic surveys was not redetected in recent surveys. Emergent plants were most often not redetected. For lakes where emergent taxa were historically reported, 45 % lost at least one taxon by 2019, and in 22 % of the lakes, surveyors found none of emergent taxa that were originally reported (Fig. 2). Emergent taxa redetection rates varied from 41 % (*Phragmites*) to 82 % (*Schoenoplectus* spp.) (Table 1). For lakes where floating-leaf taxa were historically reported, surveyors failed to redetect at least one taxon in 30 % of the lakes and found none of the historically reported floating-leaf plants in 23 % of the lakes (Fig. 2). Redetection rate for waterlilies were high (about 80 %), but for *Brasenia schreberi* it was 50 % (Table 1). For lakes where submerged plants were historically reported, 42 % of the recent surveys failed to relocate at least one taxon, and in 7% of these lakes, recent surveyors found no submerged plants (Fig. 1). Individual submerged taxonomic group redetection rates were generally high (ranging from 77 % to 95 %) for taxa that were originally reported in at least 15 % of historic surveys (Table 1).

Taxa redetection rates varied by ecoregion. Most lakes with low redetection rates (recent surveys detected fewer taxa than historical surveys) were in the southwestern and central ecoregions of the state (Fig. 1). Percentage of lakes where recent surveys reported more taxa than historical surveys are 15 % in the Prairie Parkland, 8% in the Eastern Broadleaf Forest, and 3% in the Laurentian Mixed Forest. Failure to redetect floating-leaf taxa most often occurred in lakes in the south half of the state. There was no clear geographical pattern for lakes where recent surveys failed to redetect emergent and submerged life forms (Fig. 3). Most individual emergent and floating plant taxonomic groups had a lower redetection rate in the southern half of the state than in the northern part of the state (Fig. 4). Geographical distribution for submerged taxa losses varied; most lakes where Characeae and *Myriophyllum* were not redetected occurred in the south half of the state and patterns for other taxa were less clear.

3.3. Predictive models

The random forest classifier models were applied to 14 taxa to predict probability of presence. The change in lake TP was the most

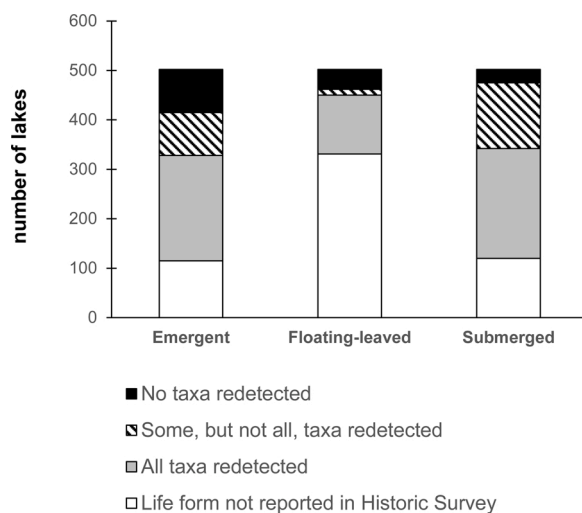


Fig. 2. Redetection rates of plant taxa by life form.

important predictor variable for 12 taxa and the second most important variable for three taxa (*Ceratophyllum*, *Elodea*, and *Phragmites*). The random forest models generally had high accuracy as estimated by AUC, with the mean AUC being 0.84 (range: 0.76–0.91). The partial dependence plots showed mostly negative, mostly nonlinear trends in taxa probability of occurrence for change in lake TP for the interdecile range of the data (Fig. 5). Each value shown in the plots represents the prediction for the occurrence probability for change in TP while averaging out the effects of the other model variables.

Several patterns were observed in the partial dependence plots (Fig. 5). First, three emergent taxa, *Schoenoplectus*, *Eleocharis* and *Phragmites* (not shown), appeared to have a minor negative linear trend in presence for a change in TP. Second, most taxa (*Zizania*, Nymphaeaceae, *Elodea*, *Vallisneria americana*, Characeae, and *Myriophyllum* (native feather-leaf milfoil species)) had negative linear or nonlinear trends in presence for a change in TP. Presence generally increased with small changes in TP followed by substantial declines in the probability of presence with increases in lake TP, especially so for *Zizania*, Characeae, and *Myriophyllum*. This pattern was extenuated with *Najas*, *Potamogeton zosteriformis* (not shown), and the broad-leaf species of *Potamogeton* (*P. richardsonii*, *P. amplifolius*, *P. illinoensis*, and *P. praelongus*). Two taxa had distinctive patterns. *Stuckenia* had lower probability of presence with little change in TP and a zero slope, linear trend with increasing change in TP, likely reflecting the fact that this aquatic plant genus is more tolerant of turbidity than other plant taxa. Lastly, *Ceratophyllum* probability of presence increased with small to modest increases in the change of lake TP.

4. Discussion

Our study suggests that over the past century, human alterations to Minnesota lake environments have resulted in substantial changes to aquatic plant communities. The primary signal of this change was the failure to relocate taxa in lakes where they were historically common. Change was most detectable in the south half of the state where humans have disturbed lakes and their watersheds for a longer period of time (Heiskary and Wilson, 2008). Our modeling supports existing research that human-caused eutrophication negatively influences many aquatic plant taxa.

4.1. Increased search effort of recent surveys led to increased taxa detection

Taxa richness estimates in our datasets were not useful for change detection. Unlike other studies of disturbed lakes that tracked declines in plant taxa richness through time, we found that taxa counts in recent surveys often exceeded historical counts. Borman et al. (2009) also found more taxa in recent surveys but their historical to recent taxa list comparisons were the results of surveys of similar search effort. In our comparison, search effort was greater in recent surveys (larger area searched and multiple searches conducted) and recent surveys reported all taxa observed compared to historic surveys that often reported only taxa that occurred at high frequency. Therefore, we suggest that, for our study, taxa absence from an historic survey has limited meaning. By contrast, we feel confident concluding that many taxa that were reported in historic surveys but not detected in recent surveys have declined in occurrence. Because we standardized taxa lists and focused on changes in taxa that were both easy to detect and to identify, we have additional confidence that these were real changes and less likely due to observer biases. We recognize that there may be true taxa richness increases through time but these are challenging to interpret from a simple comparison of taxa lists. We also emphasize that our analysis may not detect moderate declines in taxa because increased search efforts of recent surveys are more likely to detect taxa at low occurrences. A related suggestion was made by Lindholm et al. (2020) when they failed to detect decreasing trends in spatial beta diversity nor signs of biotic

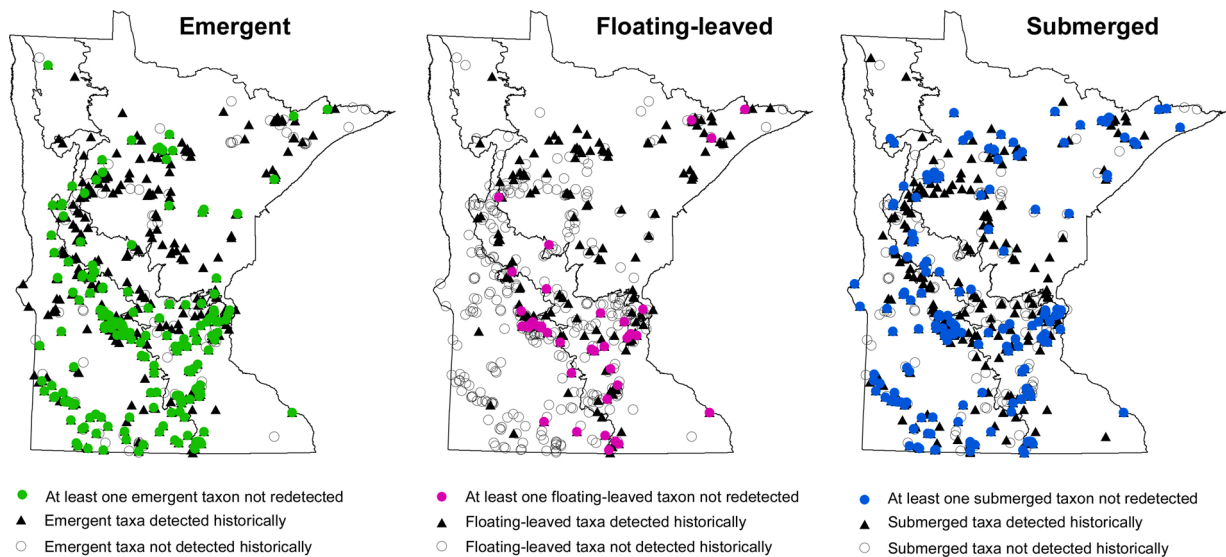


Fig. 3. Redetection success by lifeform.

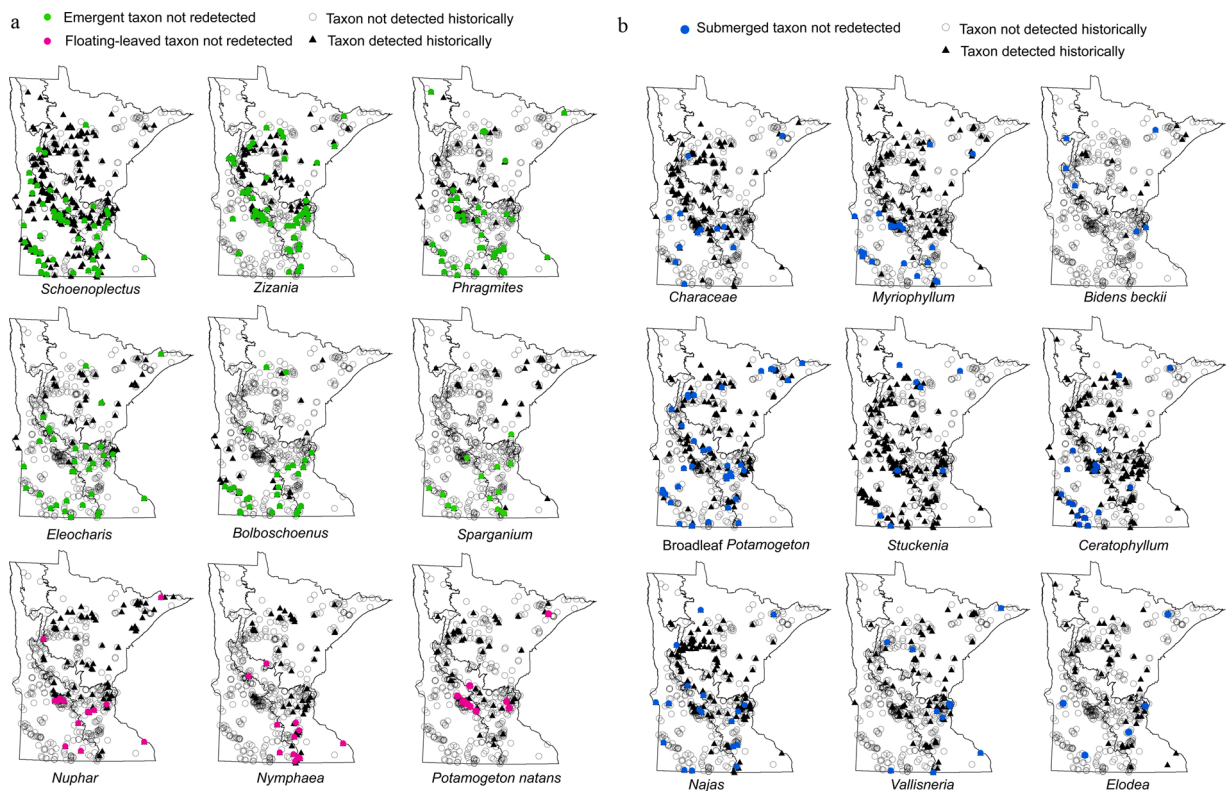


Fig. 4. Redetection success by taxon.

homogenization in Finland lakes during the past 70 years. They proposed that presence-absence data alone may not be sufficient to detect altered lake plant communities caused by relatively modest changes in land use.

4.2. Genus level reporting limits change detection

Our analyses were limited because, for many taxa reported, we could not be confident in some field-level species identifications. Within a genus, aquatic plant species often physically resemble each other but vary greatly in their stress tolerances. When these look-a-like species co-

occur in a region, genus level data are not adequate to determine change. For example, as Minnesota climate continues to change, we anticipate species range shifts based on winter habitat adaptations. Within the *Najas* and *Elodea* species indigenous to Minnesota, *Najas guadalupensis* and *Elodea canadensis* are adapted to year-round open water conditions while *N. gracillima*, *N. flexilis* and *E. nuttallii* are adapted to ice-covered winter conditions (Bowmer et al., 1995; Les et al., 2015). Historical herbarium specimens document *N. guadalupensis* and *E. canadensis* in southern Minnesota while specimens of the other species are primarily from northern Minnesota. We expected our long-term field data analyses would detect a northward advance of the

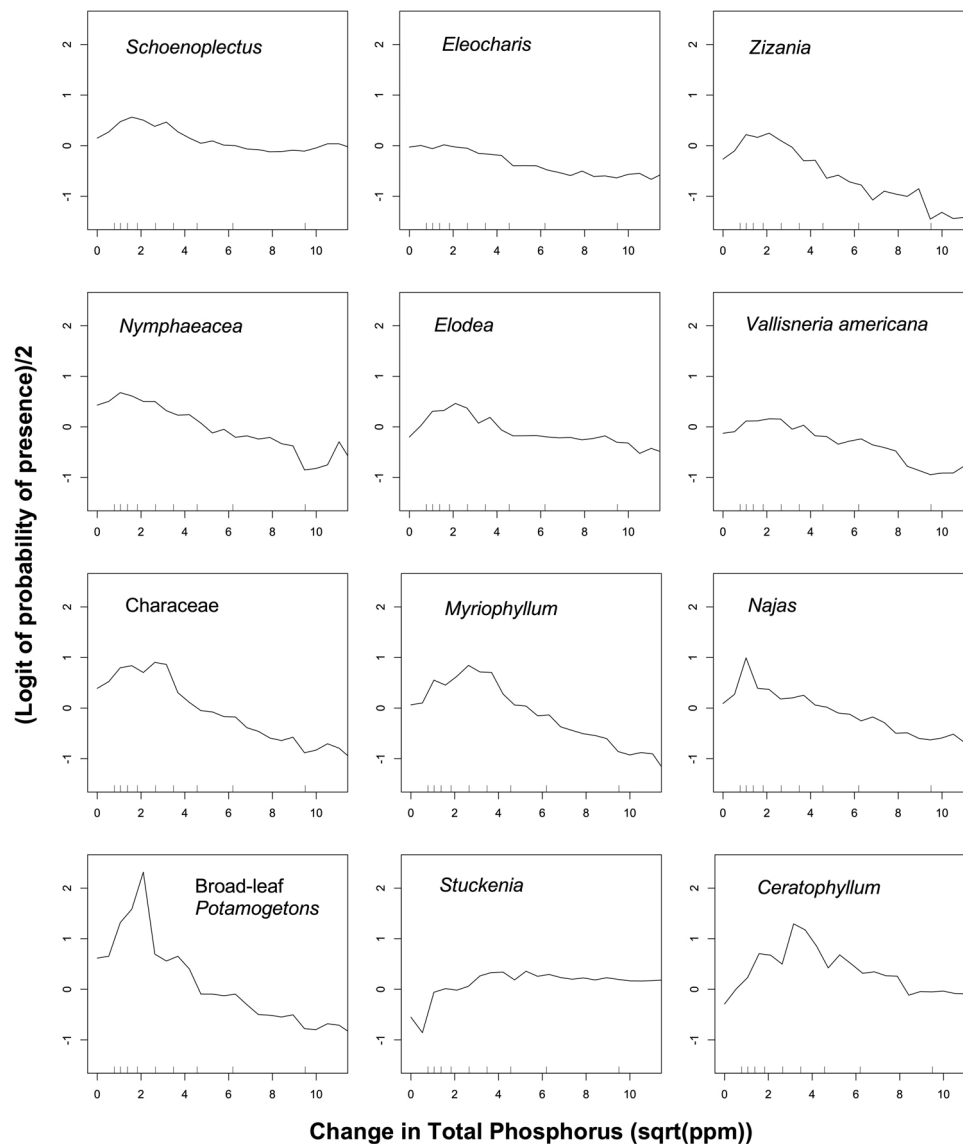


Fig. 5. Partial dependence plots for variables of a random forest classifier of lake plant taxa presence. Small ticks on the x-axis indicate deciles of the variables. The y-axis is one-half the logit of the occurrence probability.

“southern” species, but without verified species-level identifications this was not possible. Similarly, the pondweed genus, *Potamogeton*, includes species that physically resemble each other but differ in their tolerance of turbidity. For several turbidity intolerant species, such as *P. amplifolius* and *P. praelongus*, we were not certain whether the failure to redetect them in some lakes was due to actual declines or if surveyors mis-identified taxa within the genus. For Characeae, [Sleith et al. \(2017\)](#) revealed that water chemistry strongly influences distribution patterns of different species of Characeae and concluded that climate change patterns may differentially affect species. Although Characeae are a dominant component of many Minnesota lake flora, for our datasets we were confident only to the family level for this keystone group.

4.3. Recommendations to improve aquatic plant taxa detection

Natural resource agencies invest funding and time to conduct and repeat lake plant surveys with the objective of assessing change. [Alahuhta et al. \(2014\)](#) suggested that it may be adequate for surveyors to only report common species in lake monitoring, thus saving time and funding. Alternatively, [Kapfer et al. \(2016\)](#) emphasized the need for observers to maintain a high level of experience to keep observer bias

low and thus reduce error; they also recommend standardizing datasets prior to analyses. [Goulder \(2018\)](#) reviewed the value of providing taxa checklist to plant surveyors to help maintain consistency in taxonomic reporting. There is merit in all of these approaches, particularly because non-botanists conduct many aquatic plant surveys and some taxa are difficult to identify.

We suggest additional steps to improve data quality. First, aquatic plant identification training should be provided to surveyors and should include the broad range of taxa they may encounter in the field. Surveyors should record plants to the taxonomic level where they are confident and should be cognizant of look-a-like taxa. Recording a plant to the genus level with confidence is more informative than incorrectly identifying and recording a plant to the species level. Second, recent advances in electronic field data entry provide additional opportunities for in-field taxonomic data proofing. Minnesota Department of Natural Resources has created electronic field data forms for aquatic plant surveys that ensure nomenclatural consistency and that also alert surveyors when questionable taxa are entered (i.e., taxa that may require a voucher specimen for identification or taxa that may be uncommon). Third, many surveyors use a grid-based sample design to conduct lake-wide, semi-quantitative surveys ([Madsen, 1999](#)). On lakes with narrow

littoral zones, this design can under-sample the nearshore zone where the highest plant diversity occurs. We have found that adding sampling plots at the shore-water interface (Perleberg et al., 2019) can increase taxa detection. Finally, collection of voucher specimens can largely reduce the taxa identification challenges we encountered (Hellquist, 1993; Culley, 2013), and we strongly encourage expanding this practice.

4.4. Aquatic plant loss is a call for action

In their analysis of statistical methods to estimate species richness, Xu et al. (2012) state, “Darwin showed how species originate but we are still unable to count how many there are and how many are disappearing due to irresponsible human activities.” While our study also found difficulty estimating true richness from varied surveys, we have documented negative changes in lakes plants as extensive land use alterations occurred across Minnesota. Plant community composition and richness are not only useful indicators of change but can be important metrics to justify habitat protection or restoration within a lake. Minnesota utilizes plant taxa richness estimates as a metric to categorize the biological significance of lakes, with the highest category of outstanding often assigned to lakes with high richness values (Radomski and Carlson, 2018). Our analyses can provide additional protection strategies by identifying remnant populations of plants that have declined across a region, for example, Phragmites populations that have persisted in southern Minnesota and wild rice populations near the Twin Cities metropolitan area. More broadly, our analyses have implications for lake restoration work as these projects often aim to increase plant taxa richness and ideally, restore the historic plant community. For many submerged taxa, our study suggests that moderate human disturbance does not completely eliminate them from a lake but rather they may find refuge in shallow nearshore zones where adequate light is still available (thus resulting in “redetection” in recent, thorough searches). In these situations, restoration of water quality alone may lead to re-establishment of a diverse plant community without replanting. Emergent taxa declines are more difficult to mitigate because, even if remnant stands remain in a lake, most emergents spread by rhizome or seed during low water years. Removing current stressors and replanting may have limited success. Aquatic plants are not valued by many lake users but humans often do value items that are limited or rare. We hope that highlighting the drastic loss of this resource will motivate protection of what remains.

Author statement

Donna Perleberg: Conceptualization, Data curation, Formal analysis, Writing – original draft, review & editing; **Paul Radomski:** Conceptualization, Data curation, Formal analysis, Writing – original draft, review & editing.

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Declaration of Competing Interest

The authors report no declarations of interest.

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References

- Alahuhta, J., Johnson, L.B., Olker, J., Heino, J., 2014. Species sorting determines variation in the community composition of common and rare macrophytes at various spatial extents. *Ecol. Complex.* 20, 61–68. <https://doi.org/10.1016/j.ecocom.2014.08.003>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Biesboer, D.D., 2019. The ecology and conservation of wild rice, *Zizania palustris* L. North America. *Acta Limnol. Bras.* 31, e102. <https://doi.org/10.1590/s2179-975x2319>.
- Borman, S.C., Galatowitsch, S.M., Newman, R.M., 2009. The effects of species immigrations and changing conditions on isoeitid communities. *Aquat. Bot.* 91, 143–150. <https://doi.org/10.1016/j.aquabot.2009.05.001>.
- Bornette, G., Puijalón, S., 2011. Response of aquatic plants to abiotic factors: a review. *Aquat. Sci.* 73, 1–14. <https://doi.org/10.1007/s00027-010-0162-7>.
- Bowmer, K.H., Jacobs, S.W.L., Sainty, G.R., 1995. Identification, biology and management of *Elodea canadensis*. *Hydrocharitaceae. J. Aq. Plant Manage.* 33, 13–19.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 5–32. <https://doi.org/10.1023/A:1010933404324>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, NY.
- Culley, T.M., 2013. Why vouchers matter in botanical research. *Appl. Plant Sci.* 1 (11), 1300076. <https://doi.org/10.3732/apps.1300076>.
- Dhir, B., 2015. Status of aquatic macrophytes in changing climate: a perspective. *Environ. Sci. Technol.* 8 (4), 139–148. <https://doi.org/10.3923/jest.2015.139.148>.
- Dieffenbacher-Krall, A.C., Jacobson, G.L., 2001. Post-glacial changes in the geographic ranges of certain aquatic vascular plants in North America. *Biology and Environment: P. Roy. Irish Acad. B.* 1/2, 79–84. <https://www.jstor.org/stable/20500107>.
- Egertson, C.J., Kopaska, J.A., Downing, J.A., 2004. A century of change in macrophyte abundance and composition in response to agricultural eutrophication. *Hydrobiologia.* 524, 145–156. <https://doi.org/10.1023/B:HYDR.0000036129.40386.ce>.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Fleishman, E., Noss, R.F., Noon, B.R., 2006. Utility and limitations of species richness metrics for conservation planning. *Ecol. Ind.* 6, 543–553. <https://doi.org/10.1016%2Fj.ecolind.2005.07.005>.
- Flora of North America Editorial Committee, eds. 1993+. *Flora of North America North of Mexico*. 21+ vols. New York and Oxford.
- Gabriel, A.O., Bodensteiner, L.R., 2002. Historical changes in mid-water stands of common reed in the Winnebago pool lakes. *Wisconsin J. Freshw. Ecol.* 17, 563–573. <https://doi.org/10.1080/02705060.2002.9663934>.
- Goulder, R., 2018. Checklists and their importance for recording freshwater vascular plants: the British experience. *Freshw. Rev.* 1 (2), 205–225. <https://doi.org/10.1608/FRJ-1.2.5>.
- Heiskary, S., Wilson, C.B., 2008. Minnesota’s approach to lake nutrient criteria development. *Lake Reserv. Manage.* 24, 282–297. <https://doi.org/10.1080/07438140809354068>.
- Hellquist, C.B., 1993. Taxonomic considerations in aquatic vegetation assessments. *Lake Reserv. Manage.* 7 (2), 175–183. <https://doi.org/10.1080/07438149309354269>.
- Jacobson, P.C., Hansen, G.J.A., Bethke, B.J., Cross, T.K., 2017. Disentangling the effects of a century of eutrophication and climate warming on freshwater lake fish assemblages. *PLoS One* 12 (8), e0182667. <https://doi.org/10.1371/journal.pone.0182667>.
- Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F.H., Grytnes, J., 2016. Resurveying historical vegetation data – opportunities and challenges. *Appl. Veg. Sci.* 20, 164–171. <https://doi.org/10.1111/avsc.12269>.
- Les, D.H., Peredo, E.L., King, U.M., Benoit, L.K., Tippery, N.P., Ball, C.J., Shannon, R.K., 2015. Through thick and thin: cryptic sympatric speciation in the submersed genus *Najas* (Hydrocharitaceae). *Mol. Phylogenet. Evol.* 82, 15–30. <https://doi.org/10.1016/j.ympev.2014.09.022>.
- Lesiv, M.S., Polishchuk, A.I., Antonyak, H., 2020. Aquatic macrophytes: ecological features and functions. *Stud. Biol.* 14 (2), 79–94. <https://doi.org/10.30970/sbi.1402.619>.
- Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. *R News* 2, 18–22.
- Lindholm, M., Alahuhta, J., Heino, J., Toivonen, H., 2020. No biotic homogenisation across decades but consistent effects of landscape position and pH on macrophyte communities in boreal lakes. *Ecography* 43, 294–305. <https://doi.org/10.1111/ecog.04757>.
- Madsen, J.D., 1999. *Point Intercept and Line Intercept Methods for Aquatic Plant Management*. APCRP Technical Notes Collection (TN APCRP-M1-02). U.S. Army Engineer Research and Development Center, Vicksburg, Mississippi.
- Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *J. Appl. Ecol.* 38, 921–931. <https://doi.org/10.1046/j.1365-2664.2001.00647.x>.

- Mikulyuk, A., Kujawa, E., Nault, M.E., Van Egeren, S., Wagner, K.I., Barton, M., Hauxwell, J., Vander Zanden, M.J., 2020. Is the cure worse than the disease? Comparing the ecological effects of an invasive aquatic plant and the herbicide treatments used to control it. *Facets* 5, 353–366. <https://doi.org/10.1139/facets-2020-0002>.
- Moyle, J.B., 1939. *The Larger Aquatic Plants of Minnesota and the Factors Determining Their Distribution*. Doctoral Thesis. University of Minnesota, Minneapolis, Minnesota, U.S.A.
- Moyle, J.B., Hotchkiss, N., 1945. *The aquatic and marsh vegetation of Minnesota and its value to waterfowl*. Minnesota Department of Conservation. Tech. Bull. 3. St. Paul, Minnesota. 122 pages.
- Nichols, S.A., 2001. Long-term change in Wisconsin lake plant communities. *J. Freshwater Ecol.* 16 (1), 1–13. <https://doi.org/10.1080/02705060.2001.9663782>.
- Nichols, S.A., Lathrop, R.C., 1994. Cultural impacts on macrophytes in the Yahara lakes since the late 1800s. *Aquat. Bot.* 47, 225–247. [https://doi.org/10.1016/0304-3770\(94\)90055-8](https://doi.org/10.1016/0304-3770(94)90055-8).
- Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* 133, 225–245. [https://doi.org/10.1016/S0304-3800\(00\)00322-7](https://doi.org/10.1016/S0304-3800(00)00322-7).
- Perleberg, D., Radomski, P., Simon, S., Carlson, K., Millaway, C., Knopik, J., Holbrook, B., 2019. *Minnesota Lake Plant Survey Manual, Version 3, for Use by Fisheries Section, EWR Lake Unit, and EWR Minnesota Biological Survey Unit*. Minnesota Department of Natural Resources. Ecological and Water Resources Division, Brainerd, Minnesota. <https://doi.org/10.13140/RG.2.2.34673.74084>, 150 pages including Appendices A-D.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag, New York, NY.
- R Core Team, 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Radomski, P., 2006. Historical changes in abundance of floating-leaf and emergent vegetation in Minnesota lakes. *N. Am. J. Fish. Manage.* 26, 932–940. <https://doi.org/10.1577/M05-085.1>.
- Radomski, P., Carlson, K., 2018. Prioritizing lakes for conservation in lake-rich areas. *Lake Reserv. Manag.* 34 (4), 401–416. <https://doi.org/10.1080/10402381.2018.1471110>.
- Radomski, P., Perleberg, D., 2012. Application of a versatile aquatic macrophyte integrity index for Minnesota lakes. *Ecol. Indic.* 20, 252–268. <https://doi.org/10.1016/j.ecolind.2012.02.012>.
- Sand-Jensen, K., Riis, T., Vestergaard, O., Larsen, S.E., 2000. Macrophyte decline in Danish lakes and streams over the past 100 years. *J. Ecol.* 88, 1030–1040. <https://doi.org/10.1046/j.1365-2745.2000.00519.x>.
- Scheffer, M., Jeppesen, E., 1998. Alternative stable states. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), *The Structuring Role of Submerged Macrophytes in Lakes*. Ecological Studies (Analysis and Synthesis), vol 131. Springer, New York, NY. https://doi.org/10.1007/978-1-4612-0695-8_31.
- Sleith, R.S., Werth, J.D., Karol, K.G., 2017. Untangling climate and water chemistry to predict changes in freshwater macrophyte distributions. *Ecol. Evol.* 8 (5), 2802–2811. <https://doi.org/10.1002/ece3.3847>.
- Stuckey, R.L., Moore, D.L., 1995. Return and increase in abundance of aquatic flowering plants in Put-In-Bay Harbor, Lake Erie. *Ohio J. Sci.* 95 (3), 261–266.
- U.S. Environmental Protection Agency, 2006. *Level III Ecoregions of the Continental United States (revision of Omernik, 1987)*. USEPA – National Health and Environmental Effects Research Laboratory, Map M-1, various scales, Corvallis, Oregon.
- Volker, R., Smith, S.G., 1965. Changes in the aquatic vascular flora of Lake East Okoboji in historic times. *Proc. Iowa Acad. Sci.* 72 (1), 65–72. <https://scholarworks.uni.edu/pias/vol72/iss1/14>.
- Wentz, W.A., Stuckey, R.L., 1971. *The changing distribution of the genus Najas (Najadaceae) in Ohio*. *Ohio J. Sci.* 71, 292–302.
- Wintle, B.A., McCarthy, M.A., Parris, K.M., Burgman, M.A., 2004. Precision and bias of methods for estimating point survey detection probabilities. *Ecol. Appl.* 14, 703–712. <https://doi.org/10.1890/02-5166>.
- Xu, H., Liu, S., Li, Y., Zang, R., He, F., 2012. Assessing non-parametric and area-based methods for estimating regional species richness. *J. Veg. Sci.* 23, 1006–1012. <https://doi.org/10.1111/j.1654-1103.2012.01423.x>.
- Xu, W.B., Svenning, J.C., Chen, G.K., Zhang, M.G., Huang, J.H., Chen, B., Ordóñez, A., Ma, K.P., 2019. Human activities have opposing effects on distributions of narrow-ranged and widespread plant species in China. *Proc. Natl. Acad. Sci. U.S.A.* 116 (52), 26674–26681. <https://doi.org/10.1073/pnas.1911851116>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer, New York, NY.