Inland Waters

ISSN: 2044-2041 (Print) 2044-205X (Online) Journal homepage: https://www.tandfonline.com/loi/tinw20

The relative roles of dispersal and establishment for shaping whole-lake aquatic macrophyte richness, diversity, and community structure in hemiboreal lakes

Angela A. De Palma-Dow & Kendra Spence Cheruvelil

To cite this article: Angela A. De Palma-Dow & Kendra Spence Cheruvelil (2019): The relative roles of dispersal and establishment for shaping whole-lake aquatic macrophyte richness, diversity, and community structure in hemiboreal lakes, Inland Waters, DOI: 10.1080/20442041.2018.1522224

To link to this article: https://doi.org/10.1080/20442041.2018.1522224

INLAND WATERS
https://doi.org/10.1080/20442041.2018.1522224

The relative roles of dispersal and establishment for shaping whole-lake aquatic macrophyte richness, diversity, and community structure in hemiboreal lakes

Angela A. De Palma-Dow [a] and Kendra Spence Cheruvelil [a,b]

[a]Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA; [b]Lyman Briggs College, Michigan State University, East Lansing, MI, USA

ABSTRACT

Aquatic macrophyte diversity and structure play an important role in freshwater communities, yet little research on macrophytes has focused on native communities in the undisturbed hemiboreal lakes of North America. We used data collected from 15 inland lakes on Isle Royale National Park (Michigan, USA) to identify relationships among macrophyte metrics that describe dispersal and introduction potential (richness, diversity, community structure via growth form, and connectivity) and lake metrics that control establishment and growth potential. Results from partial least square regression analyses found that the most important and recurring predictors were those corresponding to establishment and growth. Alkalinity was the major contributor to the variation seen in richness, Shannon evenness, and Simpson inverse diversity metrics. Sediment phosphorus also contributed significantly to richness and diversity, but negatively. For growth form, half of the variation in submersed species related to alkalinity while almost half of variation in emergent species related to alkalinity and water color. Most of the variation in floating-leaved species was negatively related to alkalinity and water color. Our results suggest a high relative importance of establishment and growth metrics compared to introduction and dispersal metrics for understanding native macrophyte communities in North American hemiboreal lakes.

ARTICLE HISTORY
Received 23 September 2017
Accepted 24 August 2018

KEYWORDS
connectivity; Isle Royale National Park; lake morphometry; partial least squares regression (PLSR); undisturbed lakes

Introduction

Aquatic macrophytes (herein referred to as “macrophytes”) are photosynthetic aquatic organisms that can be seen with the naked eye (Crow and Hellquist 2000a, 2000b, Chambers et al. 2008). A diverse and structurally complex macrophyte community provides food resources and a heterogeneous habitat for a variety of organisms such as fish, turtles, waterfowl, invertebrates, and mammals such as moose and beaver (Aho and Jordan 1979, Carpenter and Lodge 1986, Sousa et al. 2011). Although many environmental lake features can influence diversity and complexity within and among macrophyte communities, most North American lake research has focused on north-temperate lakes under the influence of some form of human-mediated hydromodification, such as dam or weir installation, channelization, cultural eutrophication, or biological manipulation by the intentional or nonintentional introduction of nonnative and invasive species (Kissoon et al. 2013). The combined impacts of temperature increases, ice cover regime shifts, and changes in both evaporation rates and hydrological processes will likely contribute to the loss of important ecosystem services in lakes of higher latitudes (Angeler et al. 2013, Summers et al. 2017). Therefore, studies of macrophyte communities residing in relatively undisturbed aquatic ecosystems in hemiboreal regions are needed to quantify natural variation in communities, understand the drivers of such heterogeneity, and best predict how communities will respond to stressors such as climate change, land use modification, and further movement of invasive species (Beja and Alcazar 2003, Millennium Ecosystem Assessment 2005, Baattrup-Pedersen et al. 2006, Lindo and Gonzalez 2010, Mikulyuk et al. 2010, Chiarucci et al. 2011, O’Hare et al. 2012).

Two factors most influence the distribution and composition of macrophytes within lakes: (1) hydrological surface connectivity that facilitates species introduction and dispersal (i.e., the physical connections between aquatic ecosystems), and (2) features of the lake and watershed that promote or inhibit plant establishment and growth once a species has been introduced (i.e., the physical, chemical, and biological characteristics of a lake and its watershed; Leibold et al. 2004, Mikulyuk et al. 2010, Sousa et al. 2011, Akasaka and Takamura 2012, Kissoon et al. 2013). However, information about

---

CONTACT Angela A. De Palma-Dow ✉ adepalmadow@gmail.com
Supplemental data for this article can be accessed here. https://doi.org/10.1080/20442041.2018.1522224.

the relative importance of these 2 classes of drivers affecting the species diversity of native macrophyte communities is limited, in part because accurately characterizing these communities is challenging. No single metric captures all the important information needed to understand diversity and community structure. For example, some metrics focus on numbers of species or species groups, some incorporate abundance estimates, some examine growth form or functional groups, and others focus on the contribution of rare and/or common species to the overall macrophyte community (Chiarrucci et al. 2011, Engloner 2012, Alahuhta et al. 2014, Joniak et al. 2017). In fact, no single "best index" can capture the aggregate biodiversity and functioning of a given macrophyte community; the appropriate macrophyte metric to measure depends heavily on the research question being asked and varies depending on the approach, available materials and funds, and time frame of the study (Titus 1993, Giller et al. 2004, Capers et al. 2009, Mikulyuk et al. 2010). To date, most studies have employed a single diversity index, such as richness or percent coverage, to characterize the entire macrophyte community, leaving a knowledge gap about the ability of multiple or different metrics to contribute to scientific understanding of the relative roles of introduction and dispersal versus establishment and growth factors for macrophyte communities.

Few studies have quantified the roles of introduction and dispersal as measured by hydrological connectivity for shaping macrophyte communities (O'Hare et al. 2012). However, the presence of hydrological connections is known to be increasingly important—and essential—for macrophyte species dispersal (Barrett et al. 1993, Dahlgren and Ehrlen 2005, Honnay et al. 2010, Akasaka and Takamura 2011, 2012, Sousa et al. 2011, Viana 2017). For example, in a system of manmade ponds, macrophyte richness was lower in isolated ponds than in interconnected ponds (Akasaka and Takamura 2012). Ponds in regions dominated by agriculture experienced shifts in native macrophyte communities with artificial connections that facilitated the movement of invasive species, such as crayfish (Beja and Alcazar 2003). This combination of aquatic connectivity and the introduction of aggressive exotic and native plants contribute to drastic changes in aquatic biodiversity (Akasaka and Takamura 2012). Although these previous studies suggest that the dispersal of macrophytes can be affected by connectivity, especially in highly disturbed systems with connections facilitating the movement of invasives, the role of connectivity in driving native macrophyte diversity and community structure of undisturbed systems is relatively unknown.

In contrast to the relatively few studies of macrophyte–connectivity relationships, previous studies have investigated the roles of environmental lake and landscape features related to macrophyte establishment and growth, establishing that lake morphometry (e.g., size, shape, and depth) influences macrophyte distributions, diversity, and presence (Squires et al. 2002, Håkanson 2005, Søndergaard et al. 2005, Cheruvelil and Sorrano 2008, Capers et al. 2009, Mikulyuk et al. 2010, Kissoon 2013). Also established is that water and sediment characteristics (e.g., lake water color and clarity, alkalinity, pH, and sediment and water column nutrients) are important for understanding both native and invasive macrophyte presence, diversity, and dominance (Hellquist 1980, Håkanson and Boulion 2002, Søndergaard et al. 2005). However, further research is needed to examine the relative roles of introduction versus establishment metrics to understand both macrophyte diversity and community structure, especially in undisturbed hemiboreal lakes.

Our study aimed to fill these research gaps by identifying (1) the macrophyte diversity and community structure within and among relatively undisturbed hemiboreal lakes using multiple metrics and (2) the relative roles of dispersal/introduction and establishment/growth in shaping these communities. We sampled 15 undisturbed hemiboreal lakes on a remote, isolated archipelago, Isle Royale National Park (Michigan, USA), to quantify dispersal via hydrologic connections and characterize multiple macrophyte metrics. We applied partial least squares regression (PLSR) analyses to quantify the most important and recurring predictors of macrophyte communities. This study elucidates the relative importance of establishment/growth metrics compared to introduction/dispersal metrics to understand and predict undisturbed lake macrophyte communities and establishes baseline conditions to identify and understand future responses to pressures such as climate change and invasive species introductions in hemiboreal North America.

Methods

Study site

We studied pre-invasion and undisturbed macrophyte communities in the isolated freshwater lakes in the wilderness area of Isle Royale National Park (Isle Royale), a hemiboreal archipelago located just south of the Canadian border in the northwestern portion of Lake Superior, Michigan, USA (Fig. 1a). The island is 1.2 billion years old and composed of basalt bedrock scoured by glaciers until about 11 000 years ago, when their

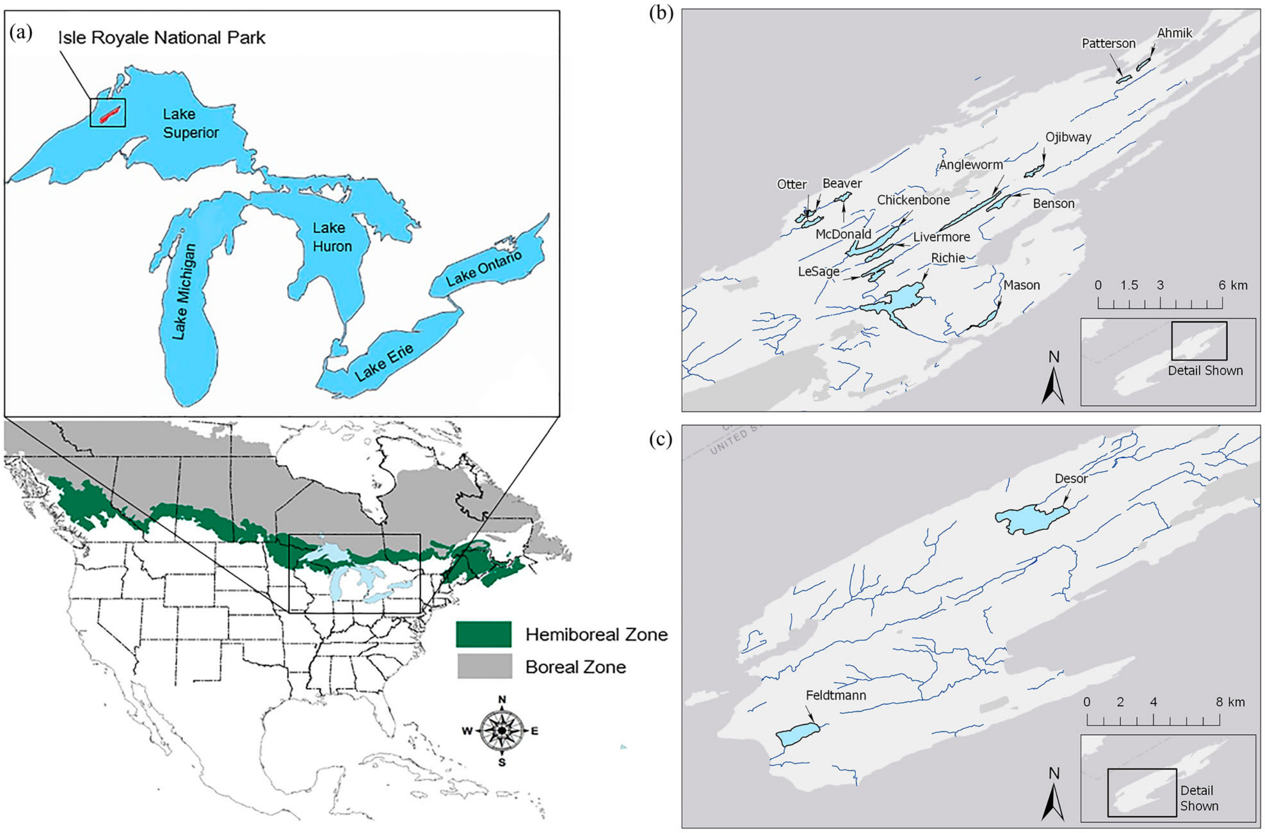

Figure 1. Location of study area in the isolated archipelago, (a) Isle Royale National Park, located in northern Lake Superior, Michigan, USA. The box outlines the specific study area, and study lakes are labeled from (b) the eastern portion and (c) the western portion of Isle Royale National Park. Boreal and hemiboreal zone layers were derived from Brandt (2009).

recession left some of the many lakes that still exist today. Lake Superior influences the climate of Isle Royale, resulting in short cool summers and long cold winters. A typical year has 120–140 frost-free days, and precipitation averages ~75 cm per year (Kraft et al. 2010). This wilderness area is a destination location for ~15 000 boaters, backpackers, kayakers, fishers, and divers every year; and while it possesses one of the lowest visitor rates, it also has the highest visitor-return rate of any National Park in the United States (DuFresne 2002, NPS 2014). The remoteness and wilderness nature of Isle Royale provided an excellent opportunity to better understand the factors that drive macrophyte diversity in relatively undisturbed and remote North American lake systems not yet invaded by exotic plants or animals and with little influence from altered or highly variable land use.

Field research was conducted during summers of 2012 and 2013. Of the 278 inland lakes and ponds on the island (USGS 2008), we chose 15 sample lakes that have minimal seasonal and yearly water fluctuations due to beaver activity and that best represent the most likely long-term and diverse populations of macrophytes for the island (sensu Van Geest et al. 2003). We sampled permanent lakes that are relatively large (>10 ha), relatively deep (>2 m), and not formed by beaver structures, and thus likely contain higher numbers of macrophyte species and resident population pools (e.g., Vestergaard and Sand-Jensen 2000, Squires et al. 2002). In addition, sample lakes were both connected and unconnected (hereafter isolated) to other lakes in the study, as determined by GIS (ESRI 2011; 6 isolated and 9 connected lakes; Fig. 1b–c). Lakes were considered connected if they were located within the same watershed and shared a surface aquatic corridor such as a connecting stream, creek, or adjoining wetland that could allow propagule movement from site to site (Larson et al. 1995, Dahlgren and Ehrlen 2005). Final lake connectivity determinations were made by visual inspection of the National Hydrological Dataset (NHD) HUC 9 flow line layer (USGS 2008).

Lakes were sampled during the warmest months, July and August, to maximize the probability of documenting the largest number of macrophyte species and to avoid spring-specific snow melt dilution effects on chemical and physical water measurements (Larson et al. 1995, Wetzel 2001). Because of unseasonably long ice duration and colder water temperatures through June 2013, sampling for that year was postponed until August.

Macrophyte sampling

Macrophytes were sampled by snorkel survey as described and recommended by Capers et al. (2009). For the purposes of our study, macrophytes included any obligate aquatic plant species found actively growing submerged below, floating on or below, or up through the water surface (Chambers et al. 2008). Macrophyte determination included microalgae genera such as *Chara* and *Nitella* spp. Species richness was determined by recording the presence of each plant species observed growing within the lake (Egertson et al. 2004); a voucher specimen for each was collected and pressed for final identification according to Crow and Hellquist (2000a, 2000b). Some common aquatic plant fragments were classified to genera only (e.g., *Carex* sp.) because they were not flowering or bearing fruit at the time of collection and could not be differentiated from other positively identified species found in the same lake. Nomenclature followed that of Field Manual of Michigan Flora (Voss and Reznicek 2012), and all voucher specimens were submitted to the Michigan State University Herbarium as part of the NPS Interior Collection Management System.

Relative abundance of each species within each lake was measured using a combination of transects and quadrats. Sample locations for abundance estimates were chosen using a semi-stratified design similar to the methods described by Titus (1993) and Capers et al. (2007, 2009); each lake was divided into 4 quadrants to include every cardinal direction (N, S, E, W; or NE, NW, SE, SW, depending on lake orientation). Within each lake quadrant, one 50 m field-based "informed" transect was placed perpendicular to shore in an area that best represented that quadrant's most common littoral zone community. The 50 m transect was marked at predetermined intervals of 0, 5, 10, 15, 20, 30, 40, and 50 m, with the 50 m marker weighted with a rope to a depth of 4.57 m (Capers et al. 2007, 2009). This depth was the maximum dive depth of the research snorkeler and close to the 5.0 m maximum depth of colonization (MDC) of macrophytes in Wisconsin lakes (Mikulyuk et al. 2010) similar in latitude to Isle Royale.

Macrophyte species abundance from the sediment level to the water surface was estimated from a 50 × 50 cm^2 quadrat randomly tossed near each of the 8 marked intervals along the transect line. Abundance of each known species present within, in, on, intersecting, floating, sitting in, rooted in, or resting on the quadrat was estimated using the Braun-Blanquet subjective cover class (i.e., <5%, 5–25%, 25–50%, 50–75%, 75–100%; Braun-Blanquet 1964, Ilmavirta and Toivonen 1986, Titus 1993, Capers et al. 2007, Engloner 2012).

Characterizing macrophyte communities

We used the field-collected data to calculate a variety of macrophyte metrics. To estimate macrophyte abundance, the Braun-Blanquet percentages and range values for each species from each quadrat were converted to single mean values. We used an aggregation method that averages abundance estimates from each quadrat to determine the relative abundance of each species per lake (sensu Egertson et al. 2004). For each lake, a single species abundance metric was calculated from quadrat data. These data were then used to calculate 2 community diversity metrics: the Shannon evenness metric that emphasizes rare species and the inverse Simpson metric, a proportional abundance metric that emphasizes common species. Both community diversity metrics followed Chiarucci et al. (2011) and were calculated using the Vegan package in R (Oksanen et al. 2013).

Species were also categorized into one of the following growth types: emergent, submersed, floating-leaf, or free-floating (sensu Arber 1920, Sculthorpe 1967, Borman et al. 1997). These categories were used to characterize macrophyte community structure for each lake as the percent of each growth type calculated from lake richness values.

Dispersal and introduction potential – connectivity metrics

We employed binomial determination to describe a lake as either connected or isolated, using National Park Service (NPS) topography maps and on-site verification during sampling. We identified and classified connected lakes by their placement within a lake chain to account for the potential of macrophyte fragments moving from one lake to another among lake chains (e.g., 1 = headwater, upstream, or first lake in the chain; 2 = middle; and 3 = terminal, downstream, or last lake in chain). We also used the number of inflowing and outflowing hydrological connections present for each lake to further identify the potential for new macrophyte material to enter or exit a lake.

Establishment and growth potential – lake features

Lake morphometric data used in this study included lake surface area, lake perimeter, lake maximum depth, and watershed area (Meeker et al. 2007). We calculated the shoreline development ratio (SDF) using lake perimeter and lake surface area by the method of Kalff (2002), which represents the irregularity of a lake, with a "1" value representing a perfect circle lake shape. We collected water samples for chemical analysis and measured water clarity using Secchi disk depth (m) at one site per quadrant in each lake. Sample locations were chosen randomly in the field to account for potential bias caused by prevailing wind or fetch effects.

Samples for sediment chemistry, water color, and alkalinity were collected from the littoral zone of each quadrant at ~1 m water depth, usually within 5–10 m from the shoreline. Water samples were surface samples, taken ~10 cm below the surface. Water column alkalinity and water color analyses were conducted immediately on site using a LaMott Alkalinity Titration Kit WAT-MO-DR (Chestertown, MD, USA) and a HACH color test kit CO-1 (item 2234-00; Loveland, CO, USA), respectively. We collected interstitial pore water for chemical analysis using a 1 m tall PVC pore-water syringe-powered extractor inserted to a soil depth of ~10 cm (Winger and Lasier 1991). We stored samples for chemical analysis in portable coolers with multiple instant cold packs until preserved in freezers at Isle Royale National Park Service headquarters. We then transported and thawed samples for analysis in the limnology laboratory at Michigan State University. Nitrogen, measured from ammonium (NH_4^+), was analyzed from filtered water samples following a modified Solorzano (1969) protocol. Total phosphorus (TP) concentrations were determined from unfiltered water samples following the protocol outlined in Menzel and Corwin (1965).

Statistical analysis

We used PLSR to understand how macrophyte species richness, diversity, and community structure were related to connectivity and lake features using the PLS package in R ($n = 15$ lakes; Mevik and Wehrens 2007, R Core Team 2013). PLSR models account for a lower number of observed response variables than the number of predictor variables and highly correlated variables (identified at absolute value $r > 0.6$ using the CARET package in R) and yet provide an ecologically meaningful R^2 value (Carrascal et al. 2009). PLSR involves a 2-step process whereby correlated predictor variables are first consolidated into descending-value contributing "components." Component scores are then used in multiple regressions against responses (e.g., richness, percent emergent, or Shannon index), allowing multiple highly correlated predictor variables to explain the variation observed in each response variable. We considered contributing predictor variables "most important" when their squared loading weight values equaled ≥0.14, allowing us to identify consistent explanatory predictors across response variables and the relative importance of introduction or dispersal (i.e., connectivity) and establishment or growth (i.e., lake features).

When choosing which predictor variables to include in PLSR models of macrophyte diversity metrics, we considered both multicollinearity and a priori understanding of what drives macrophyte communities. Because connectivity type was strongly correlated with chain location ($r = 0.85$), we excluded this variable from our PLSR models, reducing the number of connectivity dispersal variables to 3. We also reduced the number of lake morphometric variables to include in any one model because they were highly correlated ($r > 75$). Therefore, the final list of lake variables included in models was position in lake chain, number of connecting inflows, number of connecting outflows, maximum depth, lake area, SDF, watershed area, alkalinity, water color, Secchi depth, ammonium, water column TP, and sediment TP (Tables 1 and 2).

Results

Characterizing macrophyte communities

We identified 52 macrophyte species belonging to 29 genera across the 15 sample lakes in Isle Royale. McDonald and Otter lakes were the most species-rich, and Lake Ojibway was the least rich (richness = 23 and 9, respectively; Fig. 2). Of all the genera, *Potamogeton* was the most commonly observed, with at least one *Potamogeton* species found in all lakes. *Potamogeton gramineus* was the most common species, present in all but Ojibway Lake, while *P. zosterformis* was the most abundant species, found in quadrats and transects in the highest percent cover (relative abundance at 9%). Seventeen species were considered "rare plants," found in just one of the sample lakes (see Supplemental Table S1 for species list). The distribution of submersed, emergent, and floating-leaved plants was variable across lakes (Fig. 3; no free-floating species were present in our study lakes). Submersed species composed the majority of the macrophyte structure, with emergent species secondarily adding to the majority of community structure, and floating-leaved species contributing the least to community structure (Fig. 3).

Shannon evenness diversity index, which emphasizes rare species, was relatively homogeneous across lakes with a mean of 0.8 (SD 0.1) and a range from 0.4 to 0.9. The inverse Simpson diversity index, which best characterizes common species, was relatively more heterogeneous across lakes, with a mean value of 5.9 (SD

Table 1. Isle Royale National Park study lake descriptive statistics. Coordinates are provided for identification of the general lake location and not specific to any one particular sample location; connectivity types are: 1 = connected, 0 = isolated/unconnected lake; and position in lake chain classes are: 0 = unconnected lake, 1 = top/headwater lake, 2 = bottom/terminal lake for 2-lake chains, and 2 = middle lake, and 3 = bottom/terminal lake for 3-lake chains. Lakes are in alphabetical order. SDF = shoreline development factor (i.e., approximate perimeter/lake area ratio describing lake shape), Max = maximum, No. = number. Sample size was 15 inland lakes sampled during 2012 and 2013 on Isle Royale, Michigan, USA.

Site information			Morphometric metrics					Connectivity metrics			
Lake Name	Sample Year	Lat/long (#/#)	Lake area (ha)	Lake perimeter (m)	SDF	Watershed area (m^2)	Max depth (m)	No. inflow	No. outflow	Connectivity	Lake chain
Ahmik	2012	48.149453, −88.539367	10.3	715.9	62.9	455.1	3.0	0	0	1	1
Angleworm	2012	48.084702, −88.64783	50.4	2271.2	90.3	2265.1	9.1	1	1	1	1
Beaver	2012	48.081261, −88.754432	20.1	936.6	58.9	447.7	5.2	1	1	1	2
Benson	2012	48.087282, −88.632166	24.1	961.4	55.3	276.2	4.3	0	1	0	0
Chickenbone	2012	48.065433, −88.72452	92.6	2696.5	79.0	1698.5	6.4	5	1	1	2
Desor	2013	47.975099, −88.987396	427.8	3925.1	53.5	2428.1	16.8	1	1	0	0
Feltdman	2013	47.855675, −89.171246	185.8	2006.9	41.5	1342.6	3.0	1	1	0	0
LaSage	2012	48.05766, −88.710529	45.0	1741.5	73.2	2265.1	9.1	1	1	1	2
Livermore	2012	48.064716, −88.708427	30.1	1166.8	60.0	1698.5	5.8	2	1	1	1
Mason	2013	48.037721, −88.635942	22.8	1201.8	71.0	612.5	7.9	1	1	0	0
McDonald	2012	48.08883, −88.73203	14.8	730.0	53.5	447.7	4.3	0	1	1	1
Ojibway	2012	48.101614, −88.609721	15.7	933.1	66.4	815.3	4.6	0	0	0	0
Otter	2012	48.077419, −88.752071	20.2	883.1	55.4	447.7	4.3	0	1	0	0
Patterson	2012	48.142637, −88.551013	10.1	606.9	53.8	455.1	4.0	0	0	1	2
Richie	2013	48.043632, −88.696067	216.2	3852.4	73.9	2265.1	11.9	4	1	1	3

2.3) and a range from 1.7 to 10.2 (Table 3). Although both diversity metrics found Chickenbone to be the most diverse lake and Feldtman to be the least diverse lake, there were some discrepancies between the 2 metrics of diversity for other lakes (Table 3). For example, Otter Lake was the eighth most diverse lake when characterized by Shannon evenness but the second most diverse using the inverse Simpson metric. Therefore, consistent with expectations, our employment of multiple macrophyte metrics of diversity and community structure suggested no single metric best characterized all aspects of these macrophyte communities.

Table 2. Chemistry and clarity data characteristics from 15 sample lakes on Isle Royale National Park. Average chemical values in are calculated from 4 replicate samples taken from each lake, except where noted. SD = standard deviation.

Parameter	Units	Mean	SD	Min	Max	Range
Water color	Co/Pt	142.9	93	12.5	325.0	312.5
Secchi depth	m	1.8	1	0.9	2.7	1.9
Alkalinity, water column	mg/L $CaCO_3$	66.4	16	31.0	91.5	60.5
NH_4^+-N, water column[a]	µg/L	143.1	349	11.3	1343.1	1331.8
TP, water column	µg/L	34.6	25	6.9	86.2	79.3
NH_4^+, sediment	µg/L	293.1	418	5.4	1515.8	1510.5
TP, sediment[b]	µg/L	90.8	55	38.2	199.8	161.6

[a] One lake (McDonald) had unusually high nitrogen values ($n = 4$) typical of a highly eutrophic lake and are quite uncommon from a lake on Isle Royale National Park. This lake was sampled once during 2012, and we analyzed nitrogen by spectrophotometer analysis on 2 separate occasions to account for processing errors. This result is unexplained, and NPS does not regularly sample this lake in their annual monitoring and therefore the result cannot be confirmed (Elias and Damstra 2011). However, the variable did not interact or seem to influence statistical output of models, despite its unusually high values.

[b] Sediment TP for Lake Ojibway based on ($n = 2$) and McDonald based on ($n = 3$).

Drivers of macrophyte communities

The PLSR models resulted in first components explaining 63%, 60%, and 56% of the cumulative variation in species richness, Shannon evenness, and inverse Simpson, respectively ($p < 0.001$). For community structure, the first component significantly ($p < 0.05$) explained 50% of the cumulative variation in submersed species, 40% in emergent species, and 61% in floating-leaved species.

Establishment and growth potential, characterized by lake features, were stronger contributors in explaining macrophyte community metrics than were introduction and dispersal potential (i.e., connectivity features). Generally, alkalinity, sediment TP, and water color most consistently contributed to the variation observed in these lakes (Fig. 4a–c, 5a–c). Alkalinity was the most consistent contributing factor of macrophyte richness, diversity, and growth form, although its directional influence varied. Although lower contributors than lake features, at least one connectivity metric was included in the first or second component of the macrophyte models, with a total range of 39–82% variation explained (Fig. 5a–c). Interestingly, the combination of lake and connectivity predictors for each model differed by macrophyte response metric.

For species richness and the 2 measures of diversity (Shannon evenness and inverse Simpson), introduction and dispersal variables played little or no role in explaining variation. Connectivity metrics were not important contributing predictors for component one (loading weights <0.14), with the exception of lake chain location contributing to Shannon evenness (0.14). Although

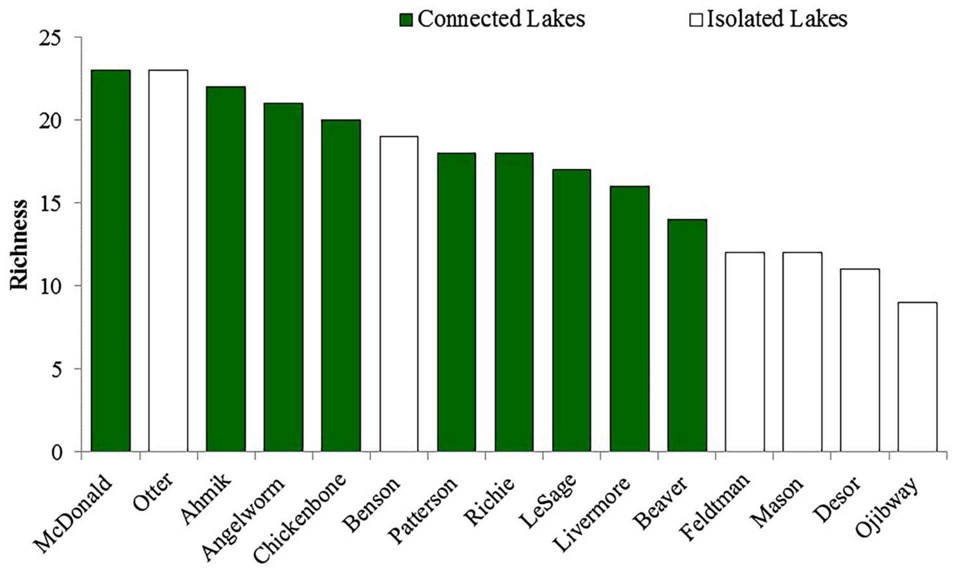

Figure 2. Macrophyte richness per lake (number of species found in each of $n = 15$ lakes on Isle Royale National Park 2012–2013) in order of decreasing richness from left to right. Clear columns represent nonconnected or isolated lakes, and shaded columns represent the connected lakes.

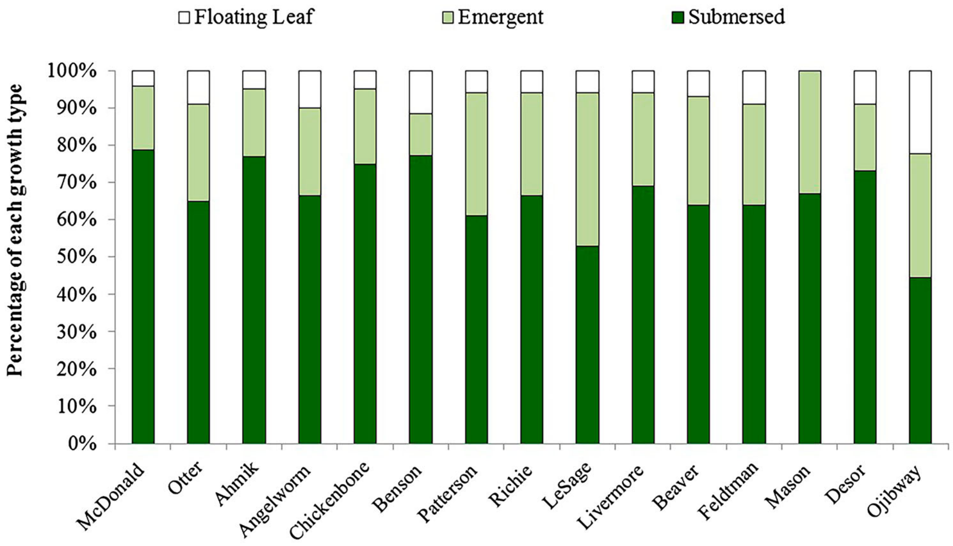

Figure 3. Macrophyte community structure of sampled lakes on Isle Royale National Park, in order of highest richness lake to lowest richness lake left to right.

number of outflows and lake chain location contributed to the second components for Shannon evenness (−0.16) and inverse Simpson (−0.34), respectively, these components were not significant (Fig. 4b–c; $p = 0.08$). By contrast, establishment and growth features explained variation in all macrophyte richness and diversity metrics. For richness, the first component included sediment TP (−0.29), alkalinity (0.17), and lake area (−0.13). For Shannon evenness, in addition to lake chain location, the model included alkalinity (0.31) and sediment TP (−0.22; $p < 0.01$; Fig. 4b). For inverse Simpson, water column alkalinity (0.31) and SDF (0.14) significantly contributed to the models ($p < 0.01$; Fig. 4). Therefore, alkalinity and sediment TP, which had different directional effects, were the most important contributing variables to overall variation in macrophyte richness and diversity metrics.

Establishment and growth features contributed most to overall variation in macrophyte community structure; only 1 of the 3 growth forms was partially explained by introduction and dispersal features (Fig. 5). For submersed species, variation was explained by

Table 3. Study lake macrophyte diversity measures: Shannon evenness and inverse Simpson index ($n = 15$ inland lakes sampled during 2012 and 2013 on Isle Royale National Park). Values are listed in ascending order from least diverse near top of table to most diverse toward the bottom. Mean and standard deviation (SD), and minimum and maximum values across all lakes are located at the bottom of the table.

Shannon Evenness	Lake Name		Lake Name	Inverse Simpson
0.42	Feldtman	Least diverse	Feldtman	1.69
0.60	Benson		Benson	3.13
0.61	Ojibway		Ojibway	3.15
0.73	LeSage		LeSage	3.85
0.74	Beaver		Desor	4.49
0.75	Livermore		Livermore	4.63
0.78	Angelworm		Beaver	5.31
0.79	Otter		Angelworm	5.97
0.81	Mason		Patterson	7.21
0.82	Richie		Richie	7.24
0.83	Desor		McDonald	7.88
0.83	Ahmik		Mason	8.05
0.84	Patterson		Ahmik	8.22
0.84	McDonald		Otter	8.26
0.87	Chickenbone	Most diverse	Chickenbone	10.16
0.8	Mean		Mean	5.9
0.1	SD		SD	2.3
0.4	Min		Min	1.7
0.9	Max		Max	10.2

the first ($p < 0.01$) and second components (marginally significant at $p = 0.08$). The first component included solely alkalinity (0.51), whereas the second component included water column TP (−0.19), watershed area (−0.15), water color (0.15), and maximum depth (−0.16). For emergent species, component one included only alkalinity (−0.34, $p < 0.01$). Two components were significant in explaining variation in floating-leaved species. The first component ($p = 0.001$) included alkalinity (−0.34) and water color (−0.14), whereas the second component (marginally significant at $p = 0.08$) included water color (−0.35). For floating-leaved species, outflow (−0.14) and lake chain location (−0.15) negatively contributed to the significant first component ($p < 0.001$). Although lake chain location (0.19) contributed to the second component for emergent species, that component was not significant ($p = 0.127$). Therefore, all 3 growth forms were mostly explained by establishment and growth metrics (Fig. 5) but with different combinations of most important contributing predictor variables. For total PLSR output results, refer to Supplemental Tables S2 and S3.

Discussion

In North America, few scientists have studied relatively undisturbed or protected hemiboreal aquatic systems when identifying the factors influencing native macrophyte communities (Chambers et al. 2008, O'Hare et al. 2012). Our study of relatively undisturbed and native macrophyte communities on a northern freshwater archipelago provided 2 main insights. First, we found that the lake features that control macrophyte establishment and growth potential, specifically water and sediment chemistry, more often explained variation in macrophyte metrics than did connectivity metrics that facilitate macrophyte introduction and dispersal. Second, we found that no single or combination of predictor variable(s) drove all macrophyte metrics. Therefore, further research of both undisturbed and disturbed systems should include multiple measures of macrophyte communities as well as lake and connectivity predictor variables that affect macrophyte dispersal/introduction and establishment/growth.

Characterizing macrophyte communities

The most important contributing variables differed for each measure of macrophyte richness, diversity, and growth form. Additionally, no single environmental variable was related to all metrics, although alkalinity was a strong contender. For variables related to macrophyte establishment and growth potential, our results corroborate previous findings that water chemistry, especially alkalinity, plays a strong role in determining macrophyte metrics (Vestergaard and Sand-Jenson 2000, Søndergaard et al. 2005, Cheruvelil and Soranno 2008, Capers et al. 2009, Kissoon et al. 2013). Alkalinity moderates and regulates fluctuations in pH, contributing to a stable habitat suitable for a wide range of macrophytes, and can directly influence the bicarbonate used by some macrophytes instead of CO_2 for completing metabolic processes (Kalff 2002, Kahara and Vermaat 2003, Capers et al. 2009). Interestingly, although softwater lakes have been shown to contain lower species richness for other taxa groups (Magnussen et al. 2006), we found no difference in species richness between the 5 softwater lakes ($CaCO_3 < 60$ mg/L) and the 10 moderately hardwater lakes ($CaCO_3 = 61–120$ μg/L; Briggs and Ficke 1977; $t = −0.78$, $p = 0.44$). Softwater lakes may, however, play a role in driving particular macrophyte species (Vestergaard and Sand-Jenson 2000). Although we did not have extensive data to explore this role for Isle Royale lakes, our results generally corroborate the idea that species richness and macrophyte diversity are mostly related to alkalinity and sediment TP (e.g., Vestergaard and Sand-Jenson 2000, Brönmark and Hansson 2005, Søndergaard et al. 2005).

In addition to water chemistry, we found that sediment chemistry was related to macrophyte metrics. For example, richness increased with decreasing

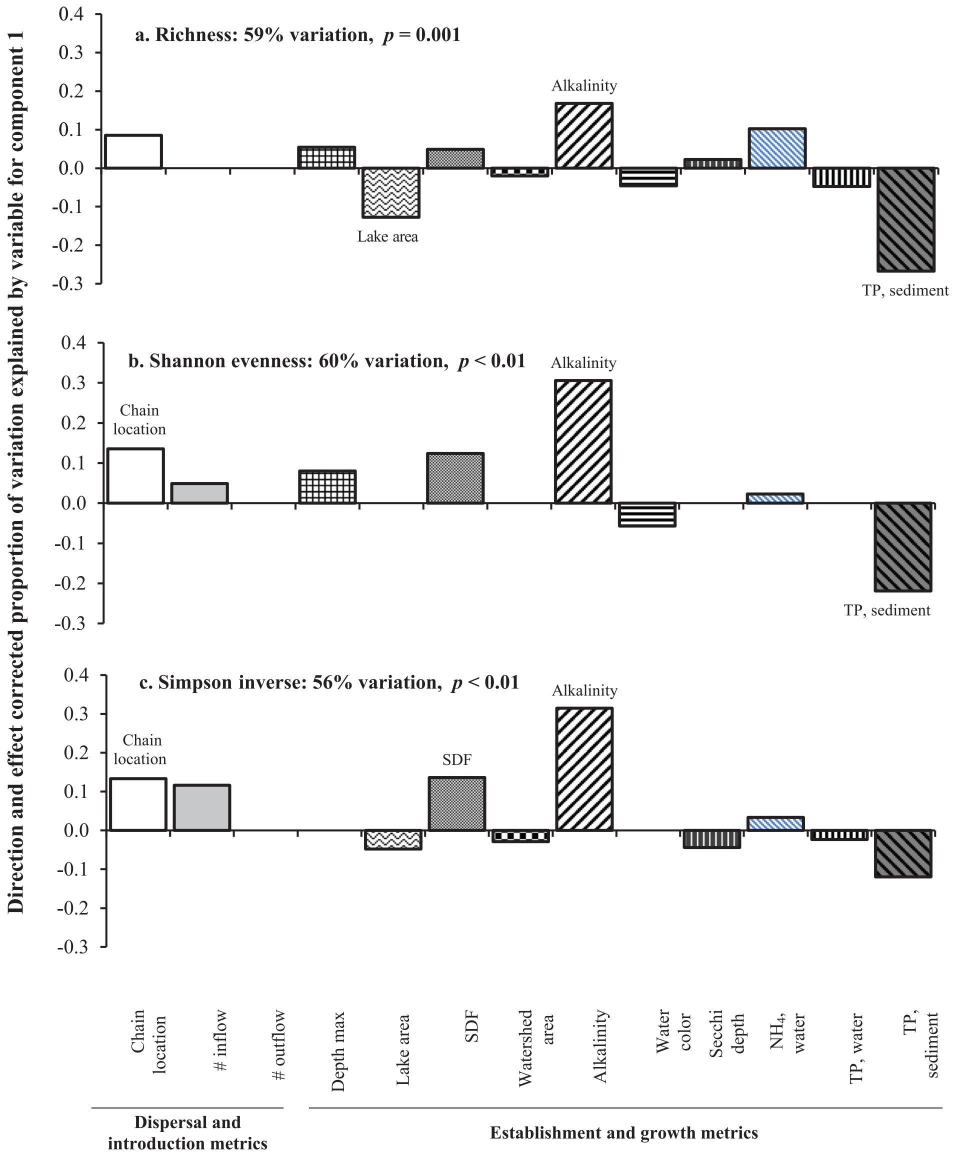

Figure 4. Partial least squares regression (PLSR) proportion plot corrected for effect and direction for measures of diversity: (a) richness, (b) Shannon evenness, and (c) inverse Simpson. The bar heights represent the strength of the variable; the location, above or below the axis line denotes direction (+/–) of the effect. The most important contributing variables are labeled with text ($R^2 > 0.14$). Introduction and dispersal metrics are on the left and shown in solid bars; establishment and growth metrics are on the right with patterned bars. SDF = shoreline development factor.

sediment TP. Research has shown that although certain macrophyte species can acquire up to 72% of their P from the sediment (Carignan and Kalff 1980), other studies indicated that submersed species are not limited by P availability from the sediment or the water column and that macrophytes can effectively bioremediate excess P (Barko et al. 1991). Although sediment nutrients are seldom sampled in most limnological studies, our results indicate they may influence macrophyte communities, particularly macrophyte structure (Li et al. 2010, Kissoon et al 2013). Therefore, we suggest that sediment chemistry measurements may help to better establish the relationships between macrophytes and lake features and should be included in future limnological investigations.

Although multiple variables characterizing macrophyte dispersal and introduction were related to macrophyte metrics, multicollinearity among these variables makes it difficult to tease apart the influence of any one driver from another. For example, lake chain location was related to Shannon evenness, which may be indicative of its relationship with water chemistry. Lakes downstream or terminal within a chain tend to have higher nutrient levels than upstream origin lakes because downstream lakes receive runoff from a higher area of the watershed than upstream origin lakes (Soranno et al. 1999). However,

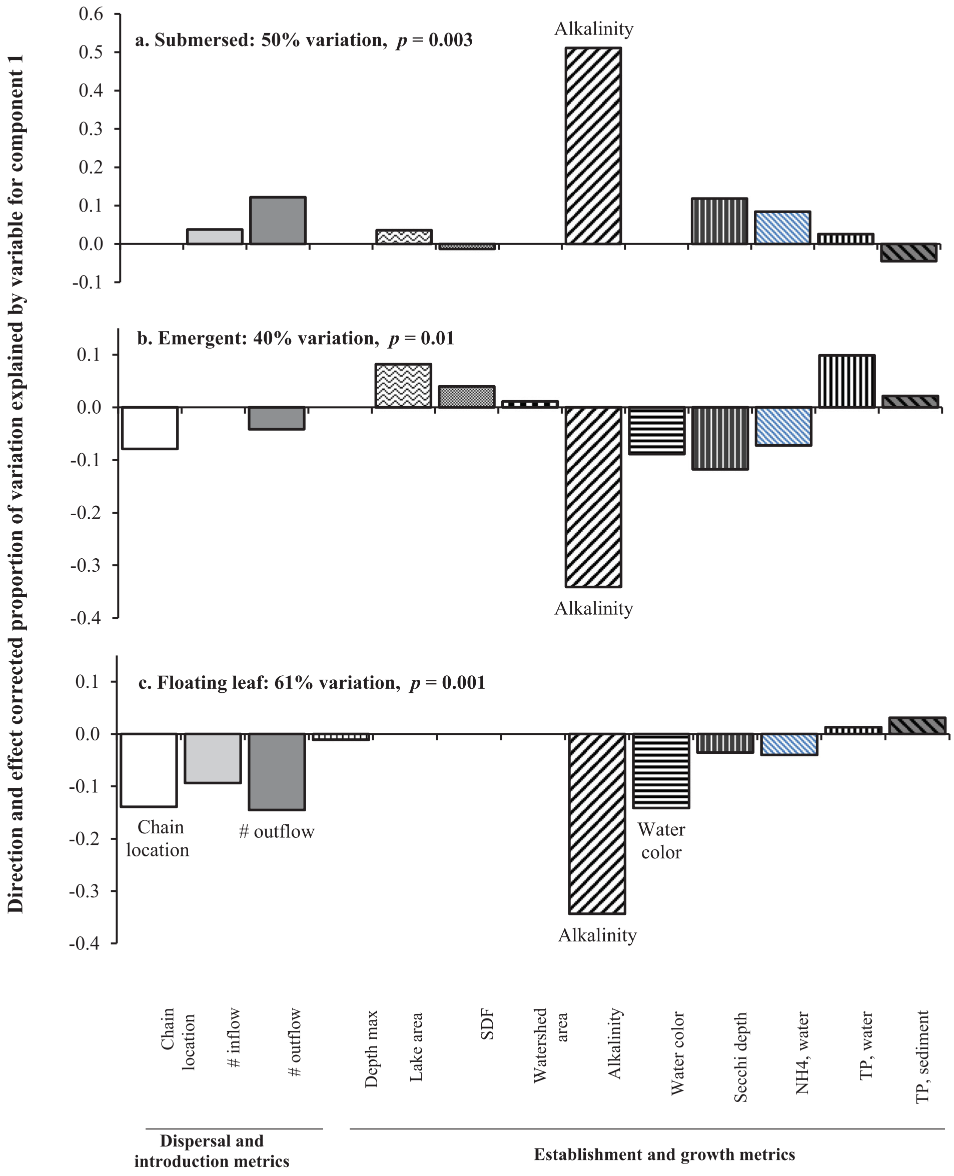

Figure 5. Partial least squares regression (PLSR) proportion plots corrected for effect and direction for measures of community structure: (a) submersed, (b) emergent, and (c) floating-leaf growth forms. The bar heights represent the strength of the variable; the location above or below the axis line denotes direction (+/–) of the effect. The most important contributing variables are labeled with text ($R^2 > 0.14$). Introduction and dispersal metrics are on the left and shown in solid bars; establishment and growth metrics are on the right with patterned bars. SDF = shoreline development factor.

watershed area was not a significant contributing factor for the first component for any of our macrophyte metrics, and alkalinity did not differ along lake chains or between connectivity types ($p = 0.48$ and 0.10, respectively). This finding is in contrast to previous research that found alkalinity to vary with lake chain and landscape position (Magnusson et al. 2006).

Our findings that community structure is influenced by different combinations of dispersal/introduction and establishment/growth variables demonstrate the importance of including macrophyte growth forms as response variables to understand drivers of macrophyte communities. Macrophyte growth forms have different requirements and fill different niches. For example, submersed plants are mainly influenced by alkalinity because they grow entirely under the water surface and are sensitive to and rely on the chemistry composition of the water more than other growth forms (Barko et al. 1991, Brönmark and Hansson 2005, O'Hare et al. 2012). Contrary to previous studies demonstrating that submersed macrophytes are affected by measures of the photic zone (Håkanson and Boulion 2002, Squires et al. 2002, Håkanson 2005, Cheruvelil and Sorrano 2008, Capers et al. 2009), Secchi depth and water color did not contribute to the variation we observed in submersed species (Fig. 5a). This result may be due to the undisturbed nature of these study lakes, or because these lakes are mainly shallow, humic, and represent a relatively narrow range of Secchi and water color (Table 2).

Because both emergent and floating-leaved species rely on a complex and heavy root system and maintain most of their biomass above the water surface, these growth forms are not reliant on water condition and are less sensitive to water column measures of alkalinity or clarity (Kalff 2002, Alahuhta and Heino 2013, Joniak et al. 2017). We found that emergent species were negatively related to alkalinity and Secchi depth (Fig. 5b), whereas floating-leaved species were negatively related to alkalinity, water color, connecting number of outflows, and lake chain location (Fig. 5c). The reasons for the relationship with outflow and chain location is unclear but might be explained by differences in turbidity near outflowing aquatic connections. Disturbed and turbid waters are poor habitat for rooted and quiet-water species, such as the majority of floating-leaved genera (Squires et al. 2002, Kissoon et al. 2013). In addition, increasing turbidity with progression down a lake chain may negatively affect these species (Kratz et al. 1997, Soranno et al. 1999). Therefore, we suggest that further research of macrophyte communities investigating connectivity drivers should include a larger number of lake chains with more complex networks and longer lake chains to test the relationships between connectivity and macrophyte metrics.

Our study did not find hydrologic connectivity to have a strong, consistent relationship with macrophyte metrics. Three potential reasons can explain the presence of additional aquatic plant introduction/dispersal methods other than those that depend on hydrological surface–water connections. First, although measuring the effect of animal-mediated dispersal of macrophyte species (i.e., moose or bird consumption and transport) was beyond the scope of this study, these forms of movement may be important for macrophyte community composition, especially in studies of isolated islands (Dalhgren and Ehlren 2005, Viana 2017). Therefore, further research could examine the role of endozoochorous, epizoochorous, or anemochorous processes that could be contributing to dispersal patterns on the island. Second, others have demonstrated that because many macrophyte species are widely distributed globally, with the same group of species found across large regions, communities in neighboring lakes situated in close proximity are likely to contain similar, if not overlapping, species (Santamaria 2002). Spatial autocorrelation was not a factor in this study, possibly because our study lakes are relatively close to one another on an island that is remote, relatively homogeneous (i.e., experiences similar land cover and management), and just 74 km at its longest point. Third, these remote study lakes are relatively highly connected, facilitating the homogenization of native macrophyte communities through time. Therefore, future research that focuses on the spread of invasive and exotic species in disturbed areas or on species enlarging their ranges because of climate change may well find stronger effects of hydrological connectivity of macrophyte communities.

Studying undisturbed macrophyte communities

Characterizing the relative roles of dispersal/introduction versus establishment/growth metrics for native macrophyte communities on Isle Royale supplies information that will help aquatic ecologists and managers recognize natural and anthropogenic shifts in current lake communities. We found 8–23 species in the Isle Royale sampled lakes compared to 12–31 in a 2007 Isle Royale aquatic resource study completed by NPS staff (Meeker et al. 2007) that found a range of species richness. We cannot make direct comparisons between these 2 studies, however, because the sample lakes were not the same, and the field methods and determinations of vegetated aquatic zones differ. Our information on species present in Isle Royale undisturbed and protected lakes, along with 450+ herbarium vouchers collected as part of our study, will allow managers to efficiently monitor these native aquatic communities and better gauge the effect of an aquatic invasive species introduction to these lakes.

While our records of macrophyte species diversity are important for future community assessments, more evidence of these assessments exists in neighboring regions and in lakes with higher levels of disturbance than in undisturbed hemiboreal lakes. For example, a comparison study of Ontario Canadian Shield lakes demonstrated a decrease in macrophyte biomass with increased cottage density (Hicks and Frost 2011). While species richness ranged from 6 to 10 in any given study lake, shifts in community structure were also observed, in which developed lakes contained more submersed species and less floating-leaved and emergent species than lakes with less cottage development. Another assessment of a highly disturbed Iowa lake revealed a dramatic decrease in species richness from 30 in 1951 to 12 in 2002 (Egerston et al. 2004). This lake experienced shifts from native submersed- and floating-leaf-dominated to invasive emergent-dominated communities, which are more tolerant of the eutrophic conditions that have changed the Iowa landscape during the 50 years between lake surveys (Egerston et al. 2004). This example highlights the need for pre- and postdisturbance data on lake communities as well as the collection of information from multiple measurement metrics such as richness, diversity, and community structure or growth form of these macrophyte communities.

Comparing native systems on Isle Royale to more disturbed lakes and landscapes of similar latitudes and regions can not only provide insight into effects from localized disturbance but also how changing climatic conditions may be affecting aquatic communities. For example, a 75-year study on biotic assemblages in Canadian lakes near large industrial oil sands extraction zones discovered that while aerial contamination is contributing to nutrient increases in prairie lakes, most shifts in primary productivity and diatom assemblages observed result from climate change processes (Summers et al. 2017). This finding is important for protected places like Isle Royale, which may not be subjected to direct disturbance such as land use change and eutrophication but will be subjected to the effects of broad-scale climatic change such as temperature warming and precipitation variability.

To date, few North American macrophyte studies have focused solely on native macrophyte communities in protected and relatively undisturbed hemiboreal lakes. Investigating both relatively untouched and disturbed systems is called for to better understand anthropogenic and climatic influences on macrophyte communities (Millennium Ecosystem Assessment 2005, Baattrup-Pedersen et al. 2006, Mikulyuk et al. 2010, Kissoon et al. 2013, Summers et al. 2017), and categorizing and monitoring reference lakes is considered a priority according to the European Union Water Framework Directive. In a constantly changing and adapting world, documenting reference distributions from native landscapes, such as those on vulnerable ecoregion boundaries like Isle Royale, is imperative. Our information provides important baseline data that can be used to better understand the effects of local and global anthropogenic disturbances and the implications of changes to native diversity and community structure.

Acknowledgements

This research was funded by the Institute of Water Research at Michigan State University (United States Geological Survey Project # 2012MI203B) and Michigan State University College of Agricultural and Natural Resources. We are especially grateful for the support of Lyman Briggs College and Jo Latimore of the Cooperative Lakes Monitoring Program at Michigan State University. Field data were collected by Kimberly Schoch, Sarah Schaffer, Charlotte Lee, Jennifer Hollen, Hannah Meikerjohn, Hayley Sisson, Kaitlin Clark, and Rachel Mistak. Special thanks to Joe Bump and Brenda Bergman at Michigan Technological University, the NPS staff at Isle Royale National Park for providing transportation and field support, Paul Bourdeau and Caren Scott for statistical guidance, and Dr. Kim Scribner and Dr. Garrett Crow for assistance with sampling design and plant identification.

ORCID

Angela A. De Palma-Dow http://orcid.org/0000-0002-6825-0028

Supplementary data

Supplemental data for this article can be accessed at https://doi.org/10.1080/20442041.2018.1522224

References

Aho R, Jordan P. 1979. Production of aquatic macrophytes and its utilization by moose on Isle Royale National Park. US Department of the Interior, National Park Service Transactions and Proceedings, Serial No. 5:341–348.

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

Akasaka M, Takamura N. 2012. Hydrologic connection between ponds positively affects macrophyte α and γ diversity but negatively affects β diversity. Ecology. 93:967–973.

Alahuhta J, Heino J. 2013. Spatial extent, regional specificity and metacommunity structuring in lake macrophytes. J Biogeogr. 40:1572–1582.

Alahuhta, J, Kanninen A, Hellsten S, Vuori K.M, Kuoppala M, Hämäläinen H. 2014. Environmental and spatial correlates of community composition, richness and status of boreal lake macrophytes. Ecol Indic. 32:172–181.

Angeler DG, Allen C, Johnson R. 2013. Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales. J Appl Ecol. 50:572–584

Arber A. 1920. Water plants; a study of aquatic angiosperms. Cambridge (UK): University Press.

Baattrup-Pedersen A, Szoszkiewicz K, Nijboer R, O'Hare M, Ferreira T. 2006. Macrophyte communities in unimpacted European streams: variability in assemblage patterns, abundance and diversity. Hydrobiologia. 566:179–196.

Barko JW, Gunnison D, Carpenter SR. 1991. Sediment interactions with submersed macrophyte growth and community dynamics. Aquat Bot. 41:41–65.

Barrett S, Eckert C, Husband B. 1993. Evolutionary processes in aquatic plant populations. Aquat Bot. 44:105–145.

Beja P, Alcazar R. 2003. Conservation of Mediterranean temporary ponds under agriculture intensification: an evaluation using amphibians. Biol Conserv. 114:317–326.

Borman S, Korth R, Temte J. 1997. Through the looking glass: a field guide to aquatic plants. Stevens Point (WI): Wisconsin Lakes Partnership.

Brandt JP. 2009. The extent of the North American boreal zone. Environ Rev. 17:101–161.

Braun-Blanquet J. 1964. Pflanzensoziologie: Grundzüge of der vegetationskunde. Zweite, umgearbeitete und vermehrte Auflage [Plant Sociology: fundamentals of vegetation science. 2nd ed.]. Berlin (Germany): Springer-Verlag.

Briggs JC, Ficke JF. 1977. Quality of rivers of the United States, 1975. Water year – based on the National Stream Quality Accounting Network (NASQAN). Reston (VA): US Geological Survey Report. No. 78–200.

Brönmark C, Hansson LA. 2005. The biology of lakes and ponds. Oxford (UK): Oxford University Press.

Capers R, Selsky SR, Bugbee GJ, White J. 2007. Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. Ecology. 88:3135–3145.

Capers R, Selskey R, Bugbee GJ. 2009. The relative importance of local conditions and regional processes in structuring aquatic plant communities. Freshwater Biol. 55:952–966.

Carignan R, Kalff J. 1980. Phosphorus sources for aquatic weeds: water or sediments? Science. 207:987–989.

Carpenter SR, Lodge DM. 1986. Effects of submersed macrophytes on ecosystems processes. Aquat Bot. 26:341–370.

Carrascal LM, Galván I, Gordo O. 2009. Partial least squares regression as an alternative to most currently used regression methods in Ecology. Oikos. 118:681–690.

Chambers PA, Lacoul P, Murphy KJ, Thomaz SM. 2008. Global diversity of aquatic macrophytes in freshwater. Hydrobiologia. 595:9–26.

Cheruvelil KS, Soranno PA. 2008. Relationships between lake macrophyte cover and lake and landscape features. Aquat Bot. 88:219–227.

Chiarucci A, Bacaro G, Scheiner SM. 2011. Old and new challenges in using species diversity for assessing biodiversity. Philos T Roy Soc. 366:2426–2437.

Crow GE, Hellquist CB. 2000a. Aquatic and wetland plants of northeastern North America. Vol. 1. Pteridophytes, gymnosperms, and angiosperms: Dicotyledons. Madison (WI): University of Wisconsin Press.

Crow GE, Hellquist CB. 2000b. Aquatic and wetland plants of northeastern North America. Vol. 2. Angiosperms: monocotyledons. Madison (WI): University of Wisconsin Press.

Dahlgren JP, Ehrlen JP. 2005. Distribution patterns of vascular plants in lakes – the role of metapopulation dynamics. Ecography. 28:49–58.

DuFresne J. 2002. Isle Royale National Park: foot trails and water routes 3rd ed. Seattle (WA): Mountaineers Books.

Egertson CJ, Kopaska JA, Downing JA. 2004. A century of change in macrophyte abundance and composition in response to agricultural eutrophication. Hydrobiologia. 524:145–156.

Elias JE, Damstra RA. 2011. Monitoring water quality of inland lakes, Great Lakes Network, 2009 and 2010: data summary report. Fort Collins (CO): National Park Service. Natural Resource Data Series NPS/GLKN/NRDS—2011/163.

Engloner AI. 2012. Alternative ways to use and evaluate Kohler's ordinal scale to assess aquatic macrophyte abundance. Ecol Indic. 20:238–243.

[ESRI] Environmental Systems Research Institute. 2011. ArcGIS Desktop: release 10. Redlands (CA).

Giller P, Hillebrand PH, Berninger UGO, Gessner M, Hawkins S, Inchausti P, Inglis C, Leslie H, Malmqvist BT, Monaghan MJ, et al. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. Oikos. 104:423–436.

Håkanson L. 2005. The importance of lake morphometry for the structure and function of lakes. Int Rev Hydrobiol. 90:433–461.

Håkanson L, Boulion V. 2002. Empirical and dynamical models to predict the cover, biomass and production of macrophytes in lakes. Ecol Model. 151:213–243.

Hellquist BC. 1980. Correlation of alkalinity and the distribution of *Potamogeton* in New England. Rhodora. 82:331–344.

Hicks AL, Frost PC. 2011. Shifts in aquatic macrophyte abundance and community composition in cottage developed lakes of the Canadian Shield. Aquat Bot. 94:9–16.

Honnay O, Jacquemyn H, Nackaerts K, Bteyne P, Looy KV. 2010. Patterns of population genetic diversity in riparian and aquatic plant species along rivers. J Biogeogr. 37:1730–1739.

Ilmavirta V, Toivonen H. 1986. Comparative studies on macrophytes and phytoplankton in ten small brown water lakes of different trophic status. Aqua Fenn. 16:125–142.

Joniak TN, Kuczyńska-Kippen N, Gąbka M. 2017. Effect of agriculture landscape characteristics on the hydrobiota structure in small water bodies. Hydrobiologia. 793:121–133.

Kahara SN, Vermaat JE. 2003. The effect of alkalinity on photosynthesis-light curves and inorganic carbon extraction capacity of freshwater macrophytes. Aquat Bot. 75:217–227.

Kalff J. 2002. Limnology. Upper Saddle Hill (NJ): Prentice-Hall.

Kissoon LTT, Jacob DL, Hanson MA, Herwig BR, Bowe SE, Otte ML. 2013. Macrophytes in shallow lakes: relationships with water, sediment and watershed characteristics. Aquat Bot. 109:39–48.

Kraft GJ, Mechenich DJ, Mechenich C, Cook JE, Seiler SM. 2010. Assessment of natural resource conditions: Isle Royale National Park. Fort Collins (CO): National Park Service. NPS/NRPC/WRD/NRR—2010/237.

Kratz TK, Webster KE, Bowser CJ, Magnuson JJ, Benson BJ. 1997. The influence of landscape position on lakes in northern Wisconsin. Freshwater Biol. 37:209–217.

Larson G, McIntire CD, Thomas EK, Hoffman CH. 1995. Limnology of isolated and connected high-mountain lakes in Olympic National Park, Washington State, USA. Arch Hydrobiol. 134:75–92.

Leibold MA, Holyoak M, Mouquet M, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, et al. 2004. The metacommunity concept: a framework for multiscale community ecology. Ecol Lett. 7:601–613.

Li KY, Liu ZW, Guan BH. 2010. Effects of nutrient levels in surface water and sediment on the growth of the floating-leaved macrophyte *Trapa maximowiczii*: implication for management of macrophytes in east bay of Lake Taihu, China. Limnology. 11:95–101.

Lindo Z, Gonzalez A. 2010. The bryosphere: an integral and influential component of the Earth's biosphere. Ecosystems. 13:612–627.

Magnuson JJ, Kratz TK, Benson BJ. 2006. Long-term dynamics of lakes in the landscape. Oxford (UK): Oxford University Press.

Meeker JA, Harris A, Hoffman V, Judziewicz E, Marr J. 2007. Assessment of wetland communities at Isle Royale National Park. Fort Collins (CO): National Parks Service Great

Lakes Inventory and Monitoring Network Report GLKN/2007/04.

Menzel DW, Corwin N. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol Oceangr. 10:280–282.

Mevik BH, Wehrens R. 2007. The pls package: principal component and partial least squares regression in R. J Stat Softw. 18:1–24.

Mikulyuk A, Hauxwell J, Rasmussen P, Knight S, Wagner KI, Nault ME, Ridgely D. 2010. Testing a methodology for assessing aquatic plant communities in temperate inland lakes. J Lake Reserv Manage. 26:54–62.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Washington (DC): Island Press.

[NPS] National Park Service. 2014. About us and cultural resources. Isle Royale National Park (USA); [accessed June 2014]. http://www.nps.gov/aboutus/index.htm

O'Hare MT, Gunn IDM, Chapman DS, Dudley BJ, Purse BV. 2012. Impacts of space, local environment and habitat connectivity on macrophyte communities in conservation lakes. Divers Distrib. 18:603–614.

Oksanen J, Blanchet JFG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H. 2013. Vegan: community ecology package [R package]. Version 2.0-10; [accessed Nov 2013]. http://CRAN.R-project.org/package = vegan

R Core Team. 2013. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. ISBN 3-900051-07-0. http://www.R-project.org/

Santamaria L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. Acta Oecol. 23:137–154.

Sculthorpe CD. 1967. The biology of aquatic vascular plants. London (UK): Edward Arnold.

Solorzano L. 1969. Determination of ammonium in natural waters by the phenol hypochlorite methods. Limnol Oceangr. 14:799–801.

Søndergaard M, Jeppesen E, Jensen JP. 2005. Pond or lake: does it make any difference? Arch Hydrobiol. 162:143–165.

Soranno PA, Webster KE, Riera JL, Kratz TK, Baron JS, Bukaveckas P, Kling GW, White D, Caine N, Lathrop RC, Leavitt PR. 1999. Spatial variation among lakes within landscapes: ecological organization along lake chains. Ecosystems. 2:395–410.

Sousa WTZ, Thomaz SM, Murphy KJ. 2011. Drivers of aquatic macrophyte community structure in a Neotropical riverine lake. Acta Oecol. 37:462–475.

Squires MM, Lesack LFW, Huebert D. 2002. The influence of water transparency on the distribution and abundance of macrophytes among lakes of the Mackenzie Delta, Western Canadian Arctic. Freshwater Biol. 47:2123–2135.

Summers JC, Kurek J, Rühland KM, Neville EN, Smol JP. 2017. Assessment of multi-trophic changes in a shallow boreal lake simultaneously exposed to climate change and aerial deposition of contaminants from the Athabasca oil sands region, Canada. Sci Total Environ. 592:573–583.

Titus JE. 1993. Submersed macrophyte vegetation and distribution within lakes: line transect sampling. Lake Reserv Manage. 7:155–164.

[USGS] United States Geological Survey. 2008. National hydrography dataset (NHD) – high resolution; [accessed 2011 Dec 18]. http://nhd.usgs.gov/

Van Geest GV, Roozen F, Coops H, Roijackers R, Buijse A, Peeters E, Scheffer M. 2003. Vegetation abundance in lowland flood plain lakes determined by surface area, age and connectivity. Freshwater Biol. 48:440–454.

Vestergaard O, Sand-Jensen K. 2000. Aquatic macrophyte richness in Danish lakes in relation to alkalinity, transparency, and lake area. Can J Fish Aquat Sci. 57:2022–2031.

Viana DS. 2017. Can aquatic plants keep pace with climate change? Front Plant Sci. 8:1906.

Voss E, Reznicek A. 2012. Field manual of Michigan flora. Ann Arbor (MI): University of Michigan Press.

Wetzel RG. 2001 Limnology, 3rd ed. Lake and river ecosystems. Cambridge (MA): Academic Press.

Winger PV, Lasier PJ. 1991. A vacuum-operated pore-water extractor for estuarine and freshwater sediments. Arch Environ Contam Toxicol. 21:321–324.