AQUATIC MACROPHYTES AT THE INTERFACE OF ECOLOGY AND MANAGEMENT

By

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ABSTRACT

Macrophyte communities face numerous threats related to eutrophication, shoreline modification, climate change and invasive species. Despite the important ecological roles they play in lakes, stakeholders demonstrate conflicting beliefs regarding their value. Whether, how frequently, and to what endpoint macrophytes should be managed is intensely debated. Management decisions require weighing competing stakeholder values, but science can provide the facts upon which those decisions are based. In this thesis, I explore several angles in support of science-based management of macrophyte communities**. Chapter 1** presents a biological assessment approach for north temperate lakes based on taxon-specific environmental tolerance and macrophyte abundance. I describe the ecological condition of a large number of lakes and identify those that show signs of stress. This method may be used to identify restoration and protection targets and was designed to be accessible and implementable. In **Chapter 2**, I compare the effects of a non-native macrophyte, *Myriophyllum spicatum*, on native macrophyte communities to the effects of large-scale herbicide treatments used in its control. Treatments were associated with greater effects on macrophyte abundance and community composition while the effects of *M spicatum* are indistinguishable from those of native species. These results suggest that lakewide herbicide treatments produce impacts on native macrophyte communities that exceed

the effects of the invader itself. While the effects on *M. spicatum* on native macrophyte communities may not be as problematic as previously thought, its social and economic costs are clear, suggesting the need for ongoing prevention and management. However, we lack an understanding of lake-specific vulnerability to invasion by *M. spicatum*. In **Chapter 3**, I predict *M. spicatum* occurrence and abundance using empirical species distribution and abundance models. By combining occurrence and abundance predictions, I present a simple management prioritization framework that can be used to plan prevention and control. Finally, in **Chapter 4**, I explore science communication and the role of interdisciplinary collaboration between artists and scientists. This chapter describes a collaborative project that blends scientific and filmmaking processes to tell a rich place-based story in which we explore new methods of representing science, policy and the human dimensions of ecology.

INTRODUCTION

In the present era of accelerating ecological change in response to increasing anthropogenic pressure, freshwaters have become one of the most imperiled ecosystems on the planet (Vitousek et al. 1997, Vörösmarty and Sahagian 2000, Vörösmarty et al. 2010). Despite their relatively modest contribution to the global water budget, they are extraordinarily valuable providers of a broad range of ecosystem services (Postel and Carpenter 1997). Unfortunately, they are subject to a diverse and expanding set of stressors, and as a result, increasingly show signs of degradation (Danz et al. 2007, Williamson et al. 2008, Stendera et al. 2012). It is imperative that we develop tools to support the protection and management of freshwater ecosystems.

Macrophytes are important to the structure and function of freshwaters (Jeppesen et al. 1998). But they too suffer from the effects of anthropogenic eutrophication, urbanization, invasive species and climate change.(Roberts et al. 1995, Radomski and Goeman 2001, Egertson et al. 2004, Alahuhta et al. 2011). Over the past several decades, we have refined our knowledge of the autecology of aquatic macrophytes enough to understand the critical role they play in shallow lakes (Scheffer 1998). Past studies cover diverse topics: from productivity, to nutrient limitation, to habitat provision (Anderson and Kalff 1986, Chilton 1990, Nielsen and Sand-Jensen 1991, Bornette and Puijalon 2010).

Macrophytes are important components of lake ecosystems from a biogeochemical perspective. A large proportion of lake gross primary productivity (GPP) occurs in the littoral zone, and GPP is significantly higher in lakes with abundant submerged macrophytes (Brothers et al. 2013). Macrophytes sequester nutrients from the water column, which can result in reduced populations of phytoplankton and clear water (Denny 1972, Chambers 1987, Chambers et al. 1989, Scheffer 1998). In addition, dense plant stands can change hydrologic flow patterns, resulting in increased nutrient burial and decreased rates of sediment resuspension (Barko and James 1998, Clarke 2002). Macrophytes can serve as a source of oxygen as well as dissolved organic and inorganic carbon, which has cascading effects on aquatic food webs (Wetzel and Søndergaard 1998, Caraco et al. 2006)

Macrophytes also directly interact with other aquatic organisms. They provide a daytime refuge for cladocerans and food and cover for macroinvertebrates (Timms and Moss 1984, Engel 1985, Beckett et al. 1992, Lauridsen and Lodge 1996). Diverse and abundant macroinvertebrate communities are an important forage base for fish (Holland and Huston 1985, Rozas and Odum 1988). Macrophytes provide fish spawning cover and refuge from predators (Colle and Shireman 1980, Killgore and

Dibble 1993). Structurally complex macrophyte habitat supports high growth rates and abundance for many fish species (Trebitz et al. 1997, Olson et al. 1998, Cross and McInerny 2006).

Services rendered by healthy macrophyte communities are valuable to humans. Diverse communities of macrophytes support the biodiversity of trophic levels, which is of great importance to conservationists (van Nes et al. 2002). Bird abundance and diversity are higher in vegetated lakes, and sport fish production is enhanced in the presence of diverse macrophyte communities of moderate abundance (Wiley et al. 1984, Scheffer 1998). Sediment stabilization and enhanced water clarity are services that are valued by multiple stakeholder groups (Hershner and Havens 2008). Macrophytes can also directly provide extractive benefits of significant cultural value (e.g. wild rice, *Zizania palustris*; Garibaldi and Turner 2004).

However, despite their many supporting, provisioning, and regulating services, aquatic macrophytes can sometimes cause great controversy (van Nes et al. 2002). Shallow lakes with abundant macrophyte communities are common across Wisconsin, but are not valued by some stakeholder groups because they can interfere with recreation and enjoyment of the lake (Schaall 2014). Unfortunately, anthropogenic nutrient enrichment stimulates plant growth, which often makes this problem worse (Duarte 1995). Management actions intended to reduce the abundance of aquatic macrophytes are often requested by lake users. Some management actions (large-scale herbicide treatments in particular), can lead to massive die-offs that can create an impoverished turbid-water system dominated by phytoplankton and blue-green algae (Wagner et al. 2007, Hilt et al. 2013). Yet the number of permit requests for controlling aquatic macrophytes continues to increase. Managers require additional science-based tools to support informed decisions and prioritization in order to better manage macrophyte communities.

Work situated at the interface of ecology and management for aquatic macrophytes is critically needed to produce better outcomes for freshwaters. In this thesis, I present a set of studies on aquatic macrophytes that address anthropogenic disturbance, herbicide treatments, the effects of invasive species, and lake-specific vulnerability to invasion. In each chapter, I highlight applications to management and present a set of accessible tools that can be immediately applied in a variety of decision-making contexts. It is my hope that this work contributes to our understanding of aquatic macrophytes and supports the adoption of science-based tools to support smart management decisions.

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CHAPTER 1

A MACROPHYTE BIOASSESSMENT APPROACH LINKING TAXON-SPECIFIC TOLERANCE AND ABUNDANCE IN NORTH TEMPERATE LAKES

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Abstract

Bioassessment methods are critically needed to evaluate and monitor lake ecological condition. Aquatic macrophytes are good candidate indicators, but few lake bioassessment methods developed in North America use them. The few macrophyte bioassessment methods that do exist suffer from problems related to subjectivity and discernibility along disturbance gradients. We developed and tested a bioassessment approach for 462 north temperate lakes. The approach links macrophyte abundance to lake ecological condition via estimates of taxon-specific abundance-weighted tolerance to anthropogenic disturbance. Using variables related to eutrophication, urban development and agriculture, we calculated abundance-weighted tolerance ranges for 59 macrophyte taxa and clustered them according to their tolerance to anthropogenic disturbance. We also created a composite index of anthropogenic disturbance using 20 variables related to population density, land cover and water chemistry. We used a statistical approach to set ecological condition thresholds based on the observed abundance of sensitive, moderately tolerant and tolerant taxa in each lake. The resulting lake condition categories were usually stable across multiple survey events and largely agreed with condition rankings assigned using expert judgment. We suggest using this macrophyte bioassessment method for federal water quality reports, restoration and management on north temperate lakes.

1. Introduction

Healthy freshwater ecosystems are essential for life on Earth. They provide water for consumption, regulate water quality, support biodiversity, control floods and provide cultural value (Aylward et al. 2005). Furthermore, freshwaters are sentinels of environmental change that integrate terrestrial, atmospheric and in-water processes (Williamson et al. 2008). Expanding human development threatens both the health of freshwaters and their ability to render valuable ecosystem services (Baron et al. 2002, Vörösmarty et al. 2010, García-Llorente et al. 2011, Dodds et al. 2013). It is imperative that we develop the capacity to track the ecological condition of lakes. There are nearly 100 bioassessment methods currently used in Europe to report on a range of biotic groups, but few lake assessment methods have been developed in the United States, and most of them focus on fish (Beck and Hatch 2009, Brucet et al. 2013).

The central goal of any biological assessment method is to describe the ecological integrity of a system using aspects of its biota. The input variables employed in assessment can take various forms, but may be conceptually divided by those describing taxonomy (in terms of richness, abundance, diversity or composition), and those that describe ecological traits (e.g. disturbance tolerance, trait or condition values, or invasive status; Birk et al. 2012). Depending on the input data, there are two general biological assessment methods (and Collier 2009 combines the two). The first uses an integrated biotic index (IBI), to combine information on multiple biological attributes that respond to anthropogenic disturbance. IBIs thus produce a single score that represents a system's ecological condition (Karr and Chu 1997). The second approach uses multivariate analysis of taxonomic data. For example, a researcher may quantify a community's deviation from that which would be expected under least-disturbed conditions (e.g. Green and Chapman 2011, Raapysjarvi et al. 2016), or categorize communities based on the environmental preferences of their constituent species (Penning et al. 2008a). Unlike IBIs, which often require selecting a subset of responsive species, multivariate techniques allow the use of all data collected from a community. They are often more precise and accurate than IBIs, but they are computationally intensive and can be more complicated to implement (Reynoldson et al. 1997, Kanninen et al. 2013).

Aquatic macrophytes are suitable indicators of ecological condition because they are sensitive to multiple forms of anthropogenic disturbance (Schneider and Melzer 2003, Clayton and Edwards 2006, Seo et al. 2014, Alahuhta and Aroviita 2016). Macrophyte species abundance and community composition respond to nutrient enrichment, which is most often implicated as the cause of lake impairment worldwide (Egertson et al. 2004, Scheffer and van Nes 2007, Herschy 2012). Nearshore urbanization results in decreased macrophyte cover, likely due to shoreline modification, boating activity, and physical removal of vegetation (Radomski and Goeman 2001, Patrick et al. 2016). Macrophyte cover also responds to invasive species while water level regulation and extraction can result in decreased species richness (Chappuis et al. 2011, Gallardo et al. 2016). Furthermore, aquatic macrophytes are widespread, abundant, and quite easy to sample.

Most of the macrophyte bioassessment methods developed for use in North American lakes are IBIs that rely in part on biologists' subjective ranking of macrophyte tolerance to anthropogenic disturbance (e.g. Nichols 1999, Beck et al. 2010). In addition, IBIs can confound relationships among component indicators in a way that makes a single score difficult to interpret (Beck et al. 2013). Some show poor sensitivity to increasing anthropogenic disturbance, especially when disturbance is low (Nichols et al. 2000). While a greater diversity of methods have been developed in Europe, several of the reported 13 macrophyte-based approaches currently in use are IBIs that rely on expert judgment (Benoit 2011). Several other European methods produce single trophic index from scores that reflect species' position along a eutrophication gradient. A third group of assessment methods employs abundance estimates of groups of species that vary with respect to their tolerance of eutrophication or their association with reference conditions (Poikane 2009, Water Information System for Europe (WISE) 2012).

We developed a macrophyte-based ecological assessment method for use in north temperate lakes of North America. We use data-driven estimates of taxon-specific tolerance limits to describe groups of species that vary in their tolerance to multiple anthropogenic variables, but we explicitly include variables that describe nearshore- and watershed-scale land cover in addition to those describing water quality and eutrophication. We then use a statistical approach to define ecological condition across an index of anthropogenic disturbance to ultimately categorize lakes that range in their ecological condition.

2. Methods

2.1 Overview of the approach

We used taxon-specific tolerance to anthropogenic disturbance coupled with abundance estimates (here, frequency of occurrence) to explain patterns in anthropogenic disturbance affecting lakes and watersheds. The constituent steps of the method depicted in Figure 1 were: (a) collect aquatic macrophyte abundance data, (b) relate macrophyte taxon abundance to anthropogenic disturbance, (c) cluster taxa by their tolerance to disturbance and (d) calculate abundance by tolerance clusters in each lake. Concurrently, we used (e) 20 anthropogenic disturbance variables to create an index of lake anthropogenic disturbance. Finally, we combined the results from (a)-(d) with (e) in order to (f) create decision trees that determine ecological condition thresholds (Figure 1).

2.2 Aquatic macrophyte surveys

We collected data on aquatic macrophyte species occurrence between May 25 and September 04, 2005-2012 using 983 point-intercept surveys conducted on 542 unique Wisconsin waterbodies (Fig 1a). Waterbodies were distributed across Wisconsin’s three lake-rich ecoregions with surface area ranging 1.36 - 3958 ha and sampled as part of a monitoring and research program conducted by the Wisconsin Department of Natural Resources (WDNR; Omernik et al. 2000). Watersheds ranged from being almost entirely forested to those that were largely agricultural or urbanized. We observed species presence from a boat at every point on a grid scaled by lake littoral zone size and shoreline complexity (Mikulyuk et al. 2010). Total number of points ranged from 45 to 4149 points per lake. On average, 207 sample points fell within littoral zones, defined per lake by areas equal to or more shallow than the 99th percentile of ordered depths at which aquatic macrophytes were observed. At each sampling point, observers used a double-sided bow rake attached to a 4.5m pole to collect macrophytes from a 0.3m^2 area. A similar rake head attached to a rope was used to collect macrophytes from sites deeper than 4.5m (Hauxwell et al. 2010). All live macrophytes detached by the rake were identified to species, and some cryptic species were lumped by genus (Crow and Hellquist 2000a, b; Supplementary material, Appendix 1, Table A1). The inclusion of cryptic taxa at the genus level enhances the applicability of the approach, but may limit our ability to discern species-specific patterns in the greater macrophyte community. We expressed taxon abundance as relative frequency of occurrence in the littoral zone. We also identified species growth forms following methods used in the National Lakes Assessment, which divides species by growth form and leaf width (USEPA 2012). Growth form categories included floating leaf, free-floating, emergent, submersed-compact (<20cm tall), submersed-wide

($\geq$ 20cm tall with leaves >1mm) and submersed-narrow ($\geq$ 20cm tall with leaves <1mm) groups.

2.3 Taxon tolerance clusters

Next, we explored patterns in taxon-specific tolerance to anthropogenic disturbance gradients across all lakes (Figure 1b). Macrophyte abundance was often distributed unimodally along anthropogenic disturbance gradients, we used an abundance-weighted average to estimate species-specific optimal values of 20 disturbance variables describing population, land use and water quality (See section 2.4 for details; Akasaka et al. 2010, Mikulyuk et al. 2011). We excluded taxa that were not present in at least 15 surveys, resulting in 59 taxa for which we were able to estimate abundance-weighted optimal values (u_k) using the formula:

$$u_k = \sum_{i=1}^{n} \frac{y_{ki} x_i}{\sum_{i=1}^{n} y_{ki}} \tag{1}$$

where y is the abundance of taxa k in lake i, and x is the value of the anthropogenic disturbance variable in lake i (Ter Braak and Prentice 2004). Next, we calculated each taxon's tolerance range:

$$u_k \pm \sqrt{\frac{\sum_{i=1}^{n} (x_i - u_k)^2 * y_{ki}}{\sum_{i=1}^{n} y_{ki}}} \tag{2}$$

using the optima and tolerance functions in the R package ‘analogue’ in R version 3.1.2 (R Core Team 2014, Simpson and Oksanen 2015). We used the disturbed-end limit of the tolerance range (hereafter, tolerance limit) in all succeeding analyses. To prevent biased tolerance range estimates on taxa with low occurrence rates, tolerances were adjusted by 1 – the inverse of a measure of species diversity (Hill 1973).

We sought to cluster taxa into a smaller number of groups with similar tolerance limits (Figure 1c). We mean-centered the set of tolerance limits and scaled them to unit variance. We selected the set of upper tolerance limits that produced the best discrimination among species groups using the package ‘vscc’ in R (Andrews and McNicholas 2013). We allowed the procedure to compare discriminatory power of the full set of upper tolerance limits to define from 3 to 5 species clusters, selecting the set of variables that minimizes variance within species groups and maximizes the variance between species groups (Andrews and McNicholas 2014). We then fit finite Gaussian mixture models where the tolerance limit data was assumed to be a mixture of underlying taxa groups (Fraley and Raftery 2002). Each tolerance cluster was modeled using a normal probability distribution, with cluster means and covariance structure estimated using the expectation-maximization algorithm. The algorithm iteratively determines the probability of cluster membership for each observation to produce a solution of parameters that determine cluster membership wherein each observation’s conditional probability of belonging to its identified group is maximized. Competing models with different covariance structures were ranked using the Bayesian Information Criterion (BIC) and we selected the model with the lowest BIC (Fraley and Raftery 2002). The model returned three groups of taxa that varied with respect to anthropogenic disturbance tolerance.

Finally, we explored how the occurrence of species tolerance clusters within lakes changed along the disturbance gradient (Figure 1d). We developed generalized linear models to describe how the abundance of each tolerance cluster changed along the anthropogenic disturbance gradient. We fit models to the binomially-distributed series of observations within each lake for each tolerance cluster as a matrix of presences and absences. Presences were recorded wherever at least one tolerance cluster representative was present and absences included all sampled littoral points.

2.4 Index of anthropogenic disturbance in lakes

We combined information on anthropogenic disturbance to produce a single index for Wisconsin lakes following methods outlined by Danz et al. (2007, Figure 1e). We assembled 20 anthropogenic disturbance variables and separated them into groups representing human population, water quality, and land cover. Population variables were expressed per watershed with data from the US Census Bureau (2010). For water quality variables, we obtained lake conductivity estimates from a database of chemical and limnological parameters (Papeş and Vander Zanden 2010). We estimated mean summer total phosphorus, chlorophyll *a* and satellite-estimated Secchi depth using data drawn from the WDNR's surface water integrated monitoring system. We included samples collected from May 1 to September 1 and required at least three measurements to estimate summer means, averaging all estimates occurring within five years of a macrophyte survey. We calculated proportional contribution by land use variable at the watershed and 500m buffer scales in ArcGIS using lake and watershed polygons delineated by the Wisconsin DNR (Akasaka et al. 2010, Menuz et al. 2013). We interpreted grassland occurring in the 500m buffer as reflective of anthropogenic disturbance (e.g. landscaping), but did not calculate this variable at the watershed scale where it may reflect natural conditions. In total, we generated 20 individual anthropogenic disturbance variables (Supplementary material, Appendix 1, Table A2). 8% of observations were missing at random and were most often total phosphorus or chlorophyll *a* estimates. We imputed missing values imputed via robust iterative stepwise regression (Templ et al. 2011).

We reduced each anthropogenic disturbance group in Table 1 to its principal components following Falcone et al. (2010) and Danz et al. (2007) using package 'prcomp' in R version 3.1.2 . We retained the orthogonal variables that explained at least 15% of observed variation and examined factor loadings to interpret each component.

The seven land cover variables were reduced to two components that describe agricultural and urban land cover. The two components of water quality describe nutrient enrichment and conductivity. The population variables were reduced to two components explaining population and road density. For each lake, we scored each of the six component values from 1 to 5. Values in the upper 20% of the distribution of scores were assigned a 5, with sequentially decreasing scores assigned at the 80th, 60th, 40th, and 20th percentiles. We then added each lake's component scores and range-standardized the scores to produce a single index of anthropogenic disturbance varying from 0 (least disturbed) to 10 (most disturbed).

2.5 Bioassessment (MAC method)

Lakes in Wisconsin demonstrate strong and collinear north-to-south spatial patterns in anthropogenic disturbance and natural environmental conditions. Natural variation in alkalinity is a strong driver of macrophyte community composition, but alkalinity is also correlated with multiple anthropogenic disturbance variables (e.g. % agriculture in the watershed, conductivity, and nearshore urban land cover; Vestergaard and Sand-Jensen 2000). To decrease the influence of natural environmental variation, we assessed lakes within region and lake type classes. We divided the state into subsets lying north and south of 44.84707°N latitude (Mikulyuk et al. 2011). Within each region, we grouped lakes as 'seepage' or 'drainage' based on the presence of an outlet stream, resulting in four lake type groups. Because water level management should be considered in assessing reservoirs and impoundments and we lacked sufficient data on non-natural lakes, we excluded them from the assessment procedure to produce a final sample set of N = 462 unique lakes. We randomly selected one survey to represent lakes with multiple survey events.

We determined ecological condition category thresholds based on abundance by tolerance cluster using the package 'ctree' in R (Hothorn et al. 2006). We expressed tolerance abundance data as vegetated frequency of occurrence, using the proportion of sites occupied by at least one tolerance cluster member divided by the total number of points at which any taxon belonging to any of the clusters was observed. The conditional inference procedure works recursively, conducting a permutational test of independence among predictors and responses, selecting the predictor with the strongest relationship, and determining a binary split where the variable affords the best discrimination among groups of at least 5 lakes. This process is repeated for each resulting group until the null hypothesis of non-independence between new groups cannot be rejected ($\alpha = 0.95$). The conditional inference framework and its statistical stopping criteria avoids problems of other tree-based methods (e.g. overfitting and variable selection bias; Hothorn et al. 2006).

2.6 Validation

We tested the MAC method in three ways. First, we assessed the ecological condition of lakes that were sampled in multiple years (N = 126 lakes). We explored the variability in lake-specific assessment rankings among years to evaluate index stability. Second, we examined MAC assessments in minimally disturbed lakes as defined by the U.S. Geological Survey's National Network of Reference Watersheds program. Reference-condition watersheds had neither cropland, medium nor high urban development, included less than 10% total urban development (high, + medium + low) and less than 5% pasture (National Water Quality Monitoring Council 2012). Third, we compared the MAC assessment to expert knowledge. We asked 8 regional managers with knowledge of aquatic macrophyte communities to rank macrophyte impairment on the lakes (N = 218) they were familiar with. Managers had no knowledge of the MAC rankings and were asked to assign a score ranging from 1 to 10 (1 indicating 'best condition' and 10 indicating 'most impaired') relative to other lakes in the northern and southern regions. We then explored the concordance between rankings assigned by expert judgment and MAC.

3. Results

3.1 Macrophyte taxon tolerance to anthropogenic disturbance

Seven anthropogenic disturbance variables were selected to discriminate among 3 tolerance clusters that include taxa with similar upper tolerance limits (Figure 2).

Abundance-weighted tolerance limits across taxa were more highly correlated than were the raw anthropogenic disturbance variables used in their calculation. The mean of the absolute value of Pearson's correlation coefficient among the seven underlying variables was r = 0.29, while the mean for the taxon tolerance limits for the same variables was r = 0.66. We hereafter refer to the taxon clusters as tolerant (T), moderately tolerant (M) and sensitive (S; Supplementary material, Appendix 1, Table A2). In general, as anthropogenic disturbance increased, the abundance of sensitive taxa decreased and the abundance of tolerant taxa increased, while the abundance of moderately tolerant taxa was distributed unimodally along the disturbance index (Figure 3; Table 1). We also observed patterns in taxon growth form across S, M and T clusters. All species with compact, short-stature growth forms occurred in the sensitive tolerance cluster. Of the 29 species belonging to the sensitive tolerance cluster, 48% were tall-form submersed species with wide leaves while 24% were compact species that were short in stature. Of the 17 moderately-tolerant species, 71% were tall submersed species, and of those, slightly more than half had wide, as opposed to narrow leaves. Tolerant species were either free-floating (30%) or were taller submersed species with narrow, often finely dissected leaves (40%). A Fisher's exact test led us to reject the hypothesis of non-independence across growth forms and tolerance clusters (p = 0.01).

3.2 Categorizing lakes using macrophyte abundance thresholds

We generated a set of tolerance cluster abundance thresholds via a conditional inference procedure that allowed us to place lakes into groups that experience different levels of anthropogenic disturbance. Seepage and drainage lakes in the south fell into two groups based on the frequency of occurrence of sensitive and tolerant taxa, respectively. Northern seepage and drainage lakes formed three groups dependent on the frequency of occurrence of tolerant and moderately-tolerant taxa (Figure 4). Summary statistics for anthropogenic disturbance variables by ecological condition category are provided in Appendix 1, Table A3.

3.3 Validation

Data were collected in multiple years on a subset of lakes (N=126). Of lakes with repeated surveys, 83 had no change in ecological condition over periods ranging from 2 to 11 years. Of the 43 lakes that switched ecological condition categories over time, 38 demonstrated a shift between two categories, of which 26 shifts were unidirectional, where a lake changed condition at a given point in time and did not change back. Ecological condition improved on 17 lakes and decreased on 9. A shift between end-member categories occurred once (impaired to excellent, surveys were separated by 8 years). Of the 17 lakes that changed categories at more than one point in time most (13) switched between adjacent categories. Four northern lakes were alternately assessed as having excellent, general and impaired ecological condition. Three of those lakes experienced lakewide herbicide treatments targeting the invasive *M. spicatum* and one was unmanaged, but experienced interannual fluctuations as large as 57% in the littoral occurrence of *M. spicatum*.

Seventy-seven lakes, or 22.6% of seepage and 11.8% of drainage lakes met reference watershed criteria statewide. We therefore reserved the 'excellent' designation for seepage and drainage ecological condition categories with median disturbance levels below the 22.6th and 11.8th percentiles respectively. This reflects the 'ambient distribution' approach mentioned by Stoddard et al. (2006). National reference condition watersheds contained lakes that were infrequently impaired. Three of 28 northern drainage reference lakes were assessed as impaired despite being minimally disturbed. Each of these lakes had large populations of tolerant species and are being actively managed for the non-native species *M. spicatum*. Seven of 45 minimally-disturbed northern seepage lakes were assessed as impaired, four of these had populations of non-native *M. spicatum* and several are undergoing active aquatic plant management with herbicides. All four minimally-disturbed lakes in the southern region were in the highest condition category for that region.

Lake condition categories generally reflected the expert judgment of regional lake managers. With no information on the outcome of the MAC assessments, managers gave lower ranks to MAC-impaired lakes and higher ranks to those in excellent or general condition (Figure 5). Kruskal-Wallis rank sum tests revealed significant differences among rankings in southern seepage ($\chi^2(1) = 18.7$, $p < 0.001$), southern drainage ($\chi^2(1) = 4.36$, $p=0.04$), and northern drainage ($\chi^2(2) = 8.35$, $p = 0.02$) lakes, but ranks did not differ for northern seepage lakes ($\chi^2(2) = 2.36$, $p = 0.31$).

4. Discussion

4.1 Methodological considerations

The Macrophyte Assessment of Condition (MAC) method uses abundance-weighted tolerance estimates to cluster taxa into groups with increasing tolerance to disturbance, followed by statistical definition of ecological condition thresholds using tolerance cluster abundance. Lake condition assessments were largely consistent across years and generally agree with expert judgment.

Many IBIs rely on the abundance of one or a few indicator species combined with other variables that can have confounding relationships (Beck et al. 2013). While IBIs are easy to understand and implement, the ability to use most available data on a biological assemblage has advantages. There is a high degree of macrophyte species turnover among lakes due to environmental filtering and stochastic processes (Alahuhta et al. 2017). It would be difficult to select a small set of species to use for assessment because they may be absent from lakes for reasons unrelated to disturbance.

The simplification of species data to tolerance clusters combines abundance estimates across taxa with similar disturbance response patterns, thereby decreasing the influence of species turnover on assessment.

Assessment methods that use all available data often rely on complex methods of multivariate analysis that are difficult to implement (Reynoldson et al. 1997, Green and Chapman 2011). The method we present here simplifies species abundance data using shared patterns in disturbance tolerance among taxa, and the multivariate methods are restricted to method development. Lake condition assessments are conducted using a simple set of taxon frequency of occurrence thresholds, and implementation does not require advanced statistical knowledge. Thus, we address some of the oft-cited problems with IBIs while also simplifying implementation.

Because we used a statistical approach to set thresholds along a regional disturbance gradient, the MAC method necessarily defines lake condition in a relative manner within each of the four lake types. However, the method performs reasonably well when applied to minimally-disturbed lakes. We find the ecological condition criteria in many cases to be more stringent than if impairment were assessed using reference-condition criteria alone. In several cases, MAC assessment identified impairments that may be due to invasive species presence or aquatic plant management activities.

Validation and stability analyses support the use of the MAC across time and suggest the method captures information about ecological condition shared by lake managers in three out of four lake types. Southern lakes experienced more anthropogenic disturbance relative to lakes in the north. However, defining restoration and protection priorities in both regions of the state is important for statewide policy. Regionalizing the lake assessments allowed us to decrease the influence of natural variation occurring between regions, but it also allowed us to identify protection priorities statewide. Lakes likely to meet national reference criteria and occurred almost exclusively in the less-developed north, and assessment groups of overall excellent quality occurred only in the north.

4.2 Relation of growth forms to disturbance tolerance

Species growth forms were unequally distributed across tolerance clusters. Disturbance-sensitive taxa were often short in stature relative to disturbance-tolerant taxa (e.g. *Isoetes* spp. vs. *Ceratophyllum demersum*). This suggests that the replacement of sensitive taxa by moderate or tolerant taxa may be associated with shade intolerance. Most of the carnivorous bladderworts, which are adapted to life in low-nutrient systems, were found in the sensitive tolerance cluster. Conversely, disturbance-tolerant taxa included tall, submersed taxa and free-floating taxa dependent on nutrient-enriched water (e.g. *Lemna* spp.). Some floating-leaf taxa that are tolerant of high nutrients and low water clarity, but sensitive to mechanical disturbance and riparian shoreline modification were grouped with moderately disturbance-tolerant taxa (e.g. *Nymphaea odorata*). Many tall but broad-leaved species (e.g. most of the Potamogetonaceae) occurred in the sensitive and moderately-sensitive clusters. In general, taxon-specific tolerance clusters make sense in light of each cluster's biological requirements and sensitivities to different forms of disturbance (Baattrup-Pedersen et al. 2015).

The trends we observed in growth form across tolerance clusters suggest that data on growth form may be useful as a bioindicator. Due to the substantial time investment required by species-specific surveys, we suggest further investigation into the possibility of using data on species growth form to indicate anthropogenic disturbance or nutrient enrichment (Wagner et al. 2011). Simplification of the survey methodology to examine growth form instead of species identification would allow for quicker surveys and would decrease the training necessary for conducting them, perhaps allowing for the participation of citizen scientists.

4.3 Alkalinity and regionalization

Anthropogenic disturbance and natural environmental variation are collinear and demonstrate a strong north-to-south gradient in Wisconsin, complicating biological assessment (Omernik et al. 2000, Alahuhta and Aroviita 2016). For example, alkalinity is one of the most important drivers of macrophyte community composition, but it is also indirectly linked to agricultural eutrophication by features like flat land with erodible soil that simultaneously make land farmable and productive of high surface water alkalinity (Kolada et al. 2014, Alahuhta 2015). This can make mechanisms of impairment difficult to disentangle. For example, macrophyte species that live in low-alkalinity waters that lack bicarbonate have unique mechanisms of acquiring carbon but fail to successfully compete when bicarbonate levels increase (Maberly and Madsen 2002). These same species also decrease with increasing anthropogenic influences on sediment organic content, water clarity and eutrophication, often due to shading by taller plants (Borman 2007, Penning et al. 2008b, Raun et al. 2010). In this case, the natural and anthropogenic factors in the study region are collinear and may have the same ultimate effect on plant species, making it difficult to distinguish natural from anthropogenic drivers. Our strategy to regionalize assessments was designed to decrease the impact of natural variation. Indeed, taxa included in the sensitive tolerance cluster vary in their ability to utilize bicarbonate. While this suggests that carbon uptake strategy is not solely responsible for the structure of the taxon tolerance clusters, we recognize that natural factors may yet contribute to unquantified variation in lake ecological condition assessment.

5. Conclusion

This paper describes the analytical steps of a macrophyte-based bioassessment method and initially assesses many Wisconsin lakes. Our approach employs empirical estimates of taxon-specific tolerance to anthropogenic disturbance combined with information on taxon abundance. In creating the MAC method, we also produced a single index of lake anthropogenic disturbance that can be used to compare lakes within regions. This work will allow agencies and managers to conduct assessments of macrophyte communities, track environmental quality, set management priorities and fulfill federally-mandated reporting requirements.

6. Supplementary material

Appendix 1 contains supporting information for chapter 1. Table A1 lists macrophyte taxa, abundance, occurrence, and tolerance cluster with frequency of occurrence estimates. Table A2 presents anthropogenic disturbance variables, their scales and sources. Table A3 lists minimum, mean, and maximum values of all anthropogenic disturbance variables by region, lake type and ecological condition category.

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9. Tables

Table 1. Parameters estimated by generalized linear models predict the probability of presence of each tolerance cluster. Intercept and slope parameters are expressed as odds ratios with profile likelihood 95% confidence intervals in parentheses. Separate models developed for Sensitive (S), Moderately tolerant (M) or Tolerant (T) taxa. Models and all parameters statistically significant at $\alpha = 0.05$.

	Tolerance cluster		
Parameter	T	M	S
Intercept	0.45 (0.42 – 0.49)	0.69 (0.64 – 0.74)	9.91 (9.06 – 10.86)
Disturbance index	0.97 (0.94– 1.0)	1.66 (1.61– 1.71)	0.62 (0.60 – 0.65)
Disturbance index^2	1.03 (1.03 – 1.04)	0.95 (0.95– 0.96)	1.01 (1.0 – 1.01)

10. Figure Captions

Figure 1. We joined (a) data on aquatic macrophyte frequency of occurrence with anthropogenic disturbance variables to calculate (b) taxon-specific tolerance to anthropogenic disturbance. We grouped taxa into (c) sensitive (S), moderately tolerant (M) and tolerant (T) clusters based on the upper limit of their abundance-weighted tolerance ranges. We computed (d) the frequency of occurrence of S, M and T taxa by lake. Simultaneously, we combined data on anthropogenic disturbance variables to produce (e) an index of lake anthropogenic disturbance. We then related the abundance of tolerance clusters within each lake from (d) to the anthropogenic disturbance index from (e) to determine (f) tolerance cluster thresholds that categorize lake ecological condition.

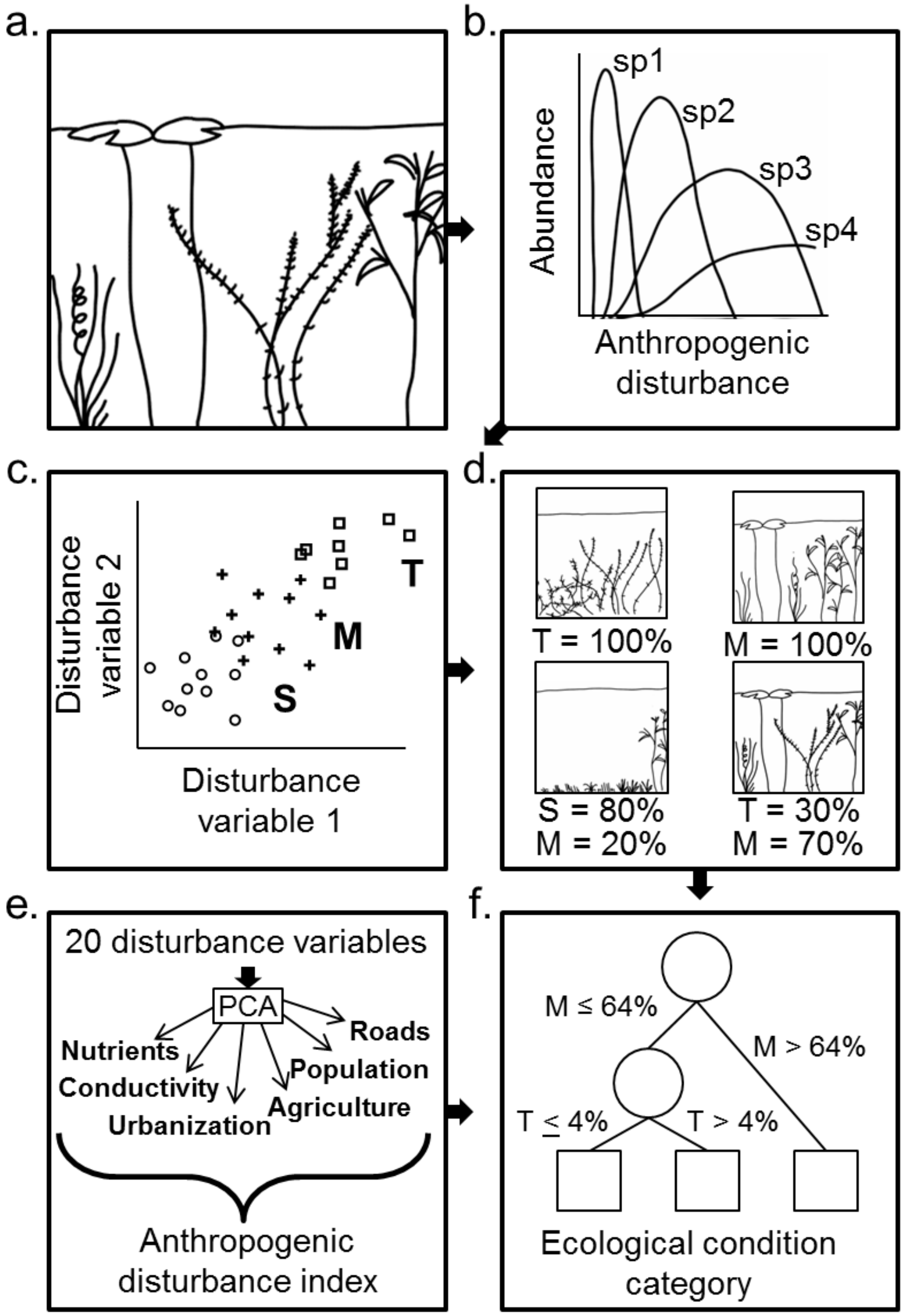
Figure 2. Upper limits of tolerance to anthropogenic disturbance variables for each taxon tolerance cluster. Boxplots show median, 1st and 3rd quartiles and observations falling beyond 1.5 times the interquartile range.

Figure 3. Predicted vegetated frequency of occurrence by tolerance cluster across an index of anthropogenic disturbance. Lines depict expected values of tolerance cluster abundance predicted by the anthropogenic disturbance index estimated by three generalized linear models.

Figure 4. Conditional inference trees relating vegetated frequency of occurrence by tolerance cluster to the anthropogenic disturbance index. Sample size indicated following N, p values are printed in each node, with mean disturbance index and condition categories labels in leaves. Threshold values are printed at each split, indicating Sensitive (S), Moderate (M) and Tolerant (T) variables.

Figure 5. Lake condition ranks assigned by expert judgment for each assessed condition category. Rank values assigned ranged 1 (least disturbed) to 10 (most disturbed) within the lake condition categories determined by the MAC assessment method. Boxes show median, 1st and 3rd quartiles and observations falling outside 1.5 times the interquartile range. Sample size for each condition category is located at the group mean rank value.

11. Figures



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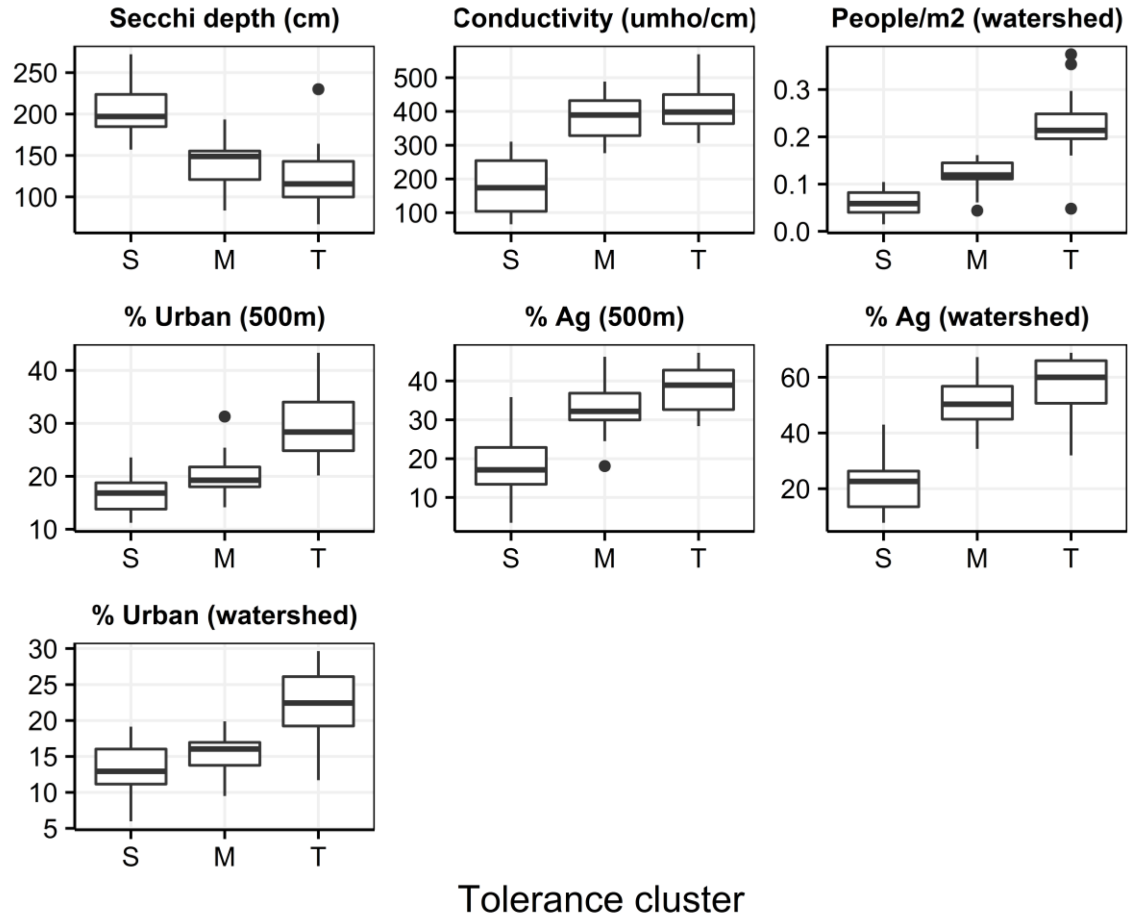

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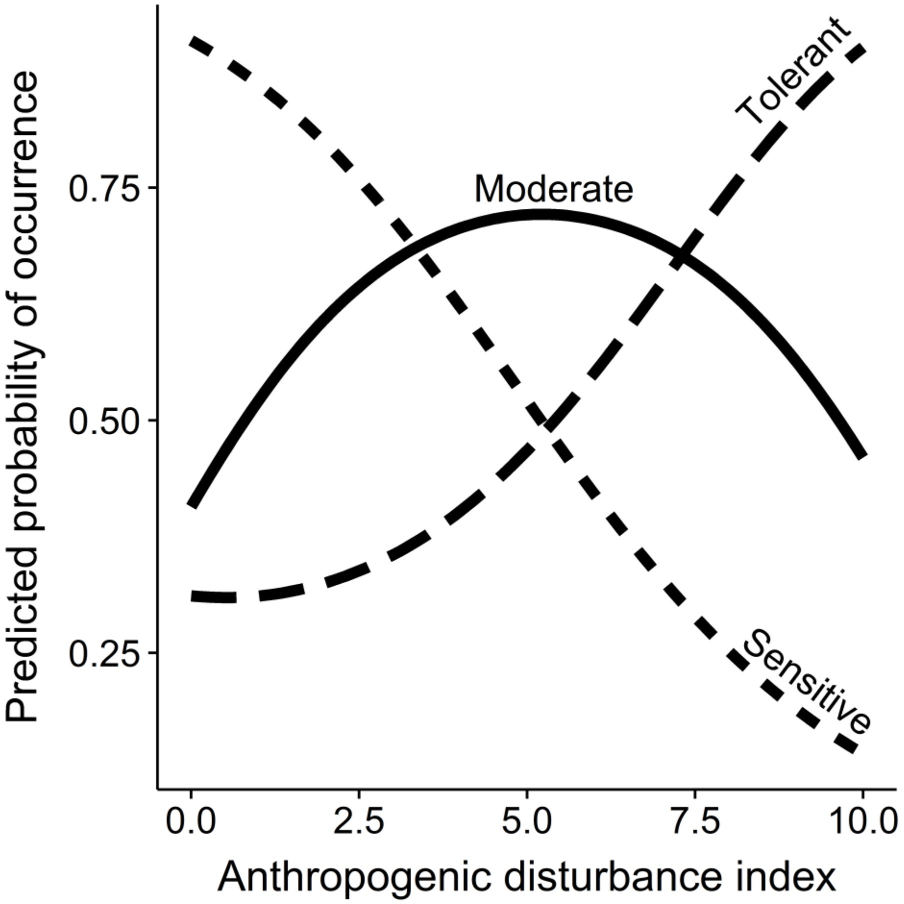

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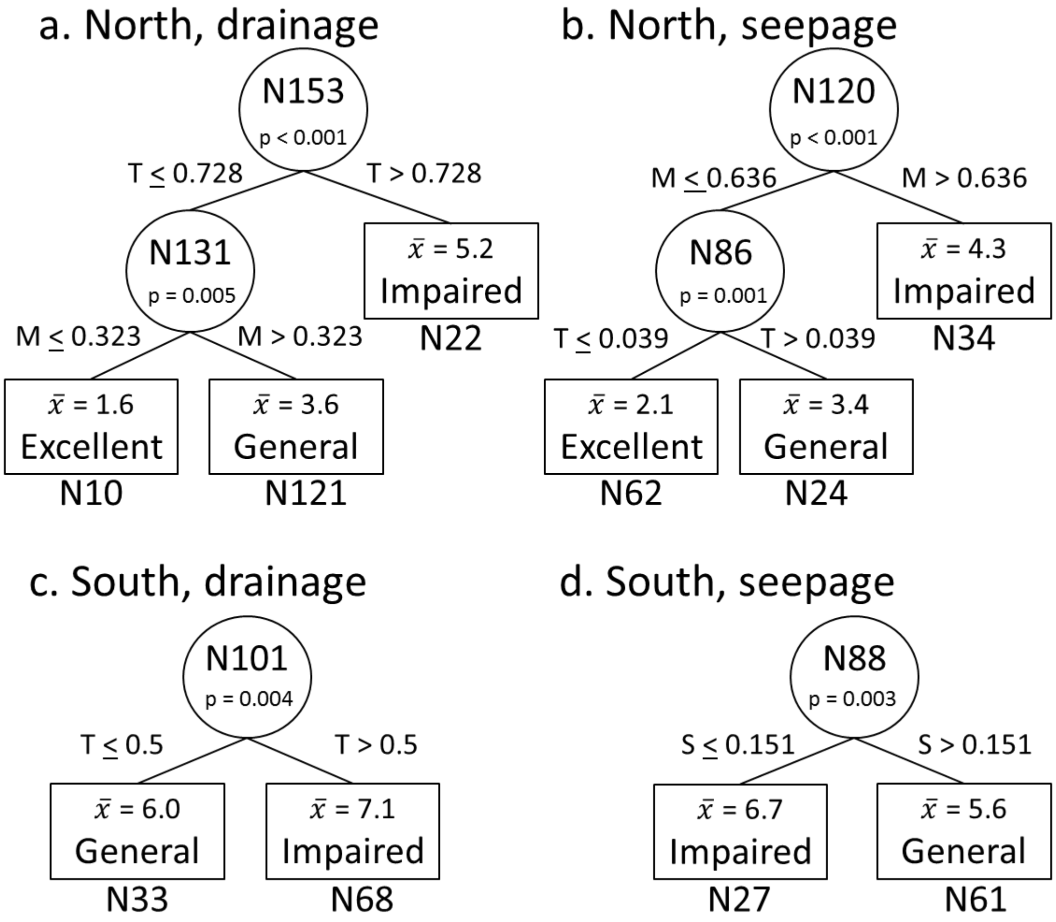

a. North, drainage

b. North, seepage

c. South, drainage

d. South, seepage

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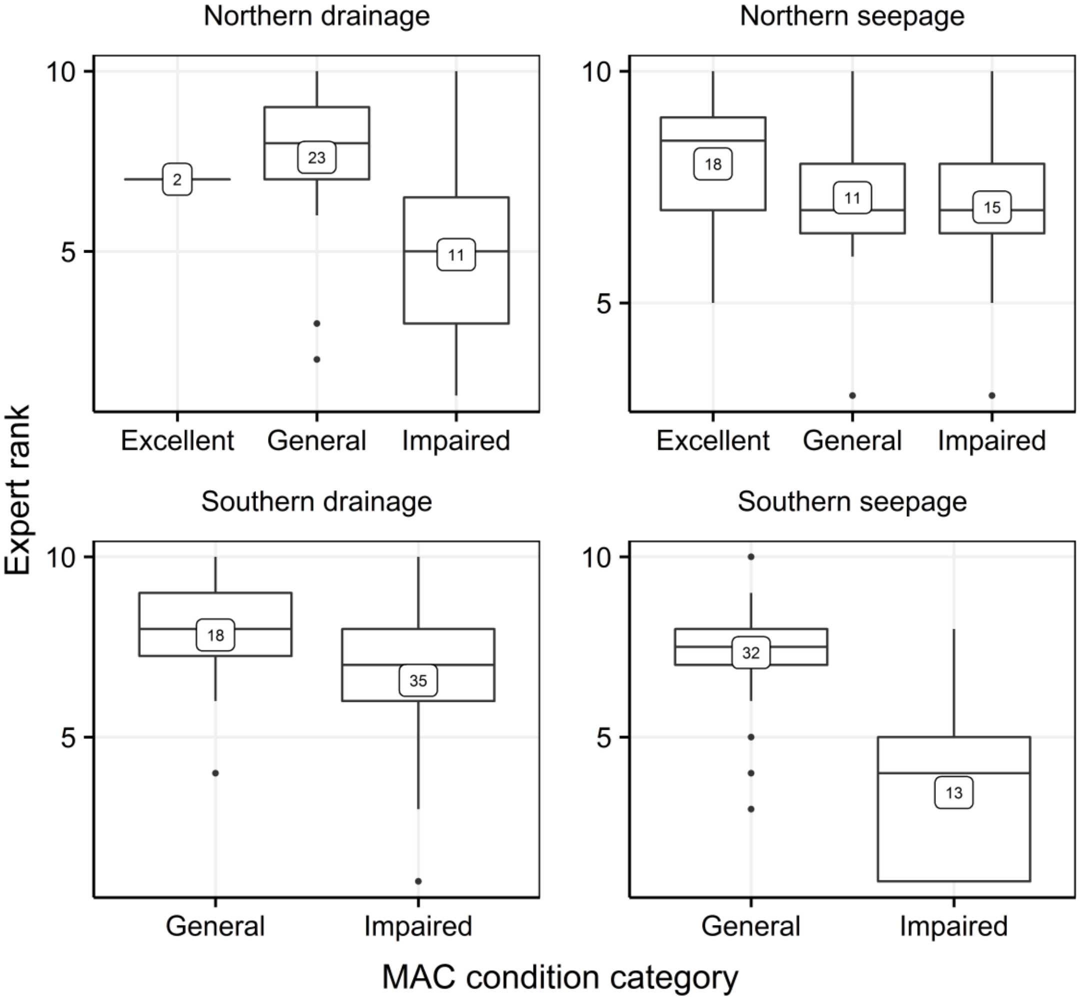

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CHAPTER 2

IS THE CURE WORSE THAN THE DISEASE? COMPARING THE ECOLOGICAL EFFECTS OF AN INVASIVE AQUATIC PLANT TO HERBICIDE TREATMENTS USED IN ITS CONTROL

In preparation for submission with co-authors: Ellen Kujawa, Michelle E. Nault, Scott Van Egeren, Kelly I. Wagner, Martha Barton, Jennifer Hauxwell, M. Jake Vander Zanden

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Abstract

Invasive species can have negative effects on recipient ecosystems, but so can the management actions used to control them. In this study, we compare the effects of the invasive aquatic plant *Myriophyllum spicatum* (Eurasian watermilfoil) to the effects of lakewide herbicide treatments used in its control. Our findings indicate the effects of lakewide herbicide treatment on native macrophyte communities are greater than that of *M. spicatum*. More statistically significant declines in native species cover across years were observed in treated relative to untreated lakes. Multi-level modeling on a large dataset (150 lakes) linked whole-lake herbicide treatments with negative effects on macrophyte cover, while there was no significant effect associated with increasing *M. spicatum*. Additionally, species-specific responses to herbicide treatment were more variable than responses to *M. spicatum*, meaning herbicide treatments will likely have larger effects on macrophyte community composition. Finally, a comparative analysis conducted on 363 untreated lakes revealed that while the invasive *M. spicatum* was associated with community composition effects on native species, those effects were indistinguishable from those of native species. Our results suggest that lakewide herbicide treatments were associated with effects on native macrophytes that generally exceeded those of the invasive species they are intended to control. This finding reveals an important management tradeoff and encourages more careful consideration of the effects of both invasive *M. spicatum* and management when considering lakewide herbicide treatments.

1. Introduction

Humans are transporting species faster, farther, and more frequently than ever before (Hulme 2009). Transport events can lead to the establishment of non-native species that can have major effects on recipient ecosystems (Williamson and Fitter 1996). On a global scale, species invasions reduce native biodiversity and have substantial ecological and economic repercussions (Pimentel et al. 2005, Simberloff et al. 2013, Gallardo et al. 2016). However, invader effects are heterogeneous and complex, making it difficult to generalize across species regarding the magnitude and mechanism of impact (Gurevitch and Padilla 2004, Hejda et al. 2009, Kulhanek 2011). Invaders are capable of negative, positive, or neutral effects on native communities, and understanding invader-specific effects is one path toward better environmental management (Parker et al. 1999, Simberloff et al. 2013).

Because invasive species vary in their potential to cause harm, some advocate a precautionary approach, stressing prevention and control of invaders that are 'guilty until proven innocent' (Brown et al. 2007, Barney et al. 2013). However, management resources are limited, and systematic prioritization of management efforts is often necessary (Vander Zanden and Olden 2008, Januchowski-Hartley et al. 2011). For example, costly eradication efforts may be best applied to small populations or recent invasions (Rejmánek and Pitcairn 2002, Simberloff 2003, Vander Zanden et al. 2010). Established invaders, on the other hand, may require long-term control and containment actions designed to limit further spread or mitigate major impacts (Epanchin-Niell and Hastings 2010). Eradication and suppression programs alike employ management techniques like pesticide application, mechanical removal and biological control, but all of these techniques also have the potential to harm non-target species and ecosystems (Bergstrom et al. 2009, Rinella et al. 2009, Lu et al. 2015). Efforts to control invader populations must therefore carefully weigh the invader's potential to do harm against the possible impacts of management (Zavaleta et al. 2001, van Nes et al. 2002, Kovalenko et al. 2010).

In the United States, over $150 million in public funds per year are used for chemical and mechanical control of invasive aquatic macrophytes, and we lack estimates of likely substantial private investments (Parochetti et al. 2008). *Myriophyllum spicatum* (Eurasian watermilfoil) is a widespread non-native macrophyte species that is often managed via herbicide applications, often with the goal of reducing the species' negative impact on native macrophytes. However, work to quantify the ecological impact of *M. spicatum* on native plant communities reveals contradictory findings. Studies range from detecting no impact, to reporting lagged recoveries following invasion, to revealing food web shifts and sustained native species declines (Trebitz et al. 1993, Duffy and Baltz 1998, Boylen et al. 1999, Kovalenko and Dibble 2010, Ludwig et al. 2012). Several well-cited studies associate *M. spicatum* with depauperate macrophyte communities, but these employed a small number of lakes with uncommonly high *M. spicatum* abundance (Madsen et al. 1991, Madsen 1999). In reality, *M. spicatum* abundance distributions are right-skewed; like most native species, abundance is usually low (Hansen et al. 2013)

In addition to reported ecological effects, *M. spicatum* is also associated with economic and recreational impacts. Several studies highlight the socio-economic impacts of *M. spicatum*. Lakefront property values in the U.S. states of Wisconsin and Washington are on average 13 and 19% lower on lakes with *M. spicatum* populations

(Horsch and Lewis 2009, Olden and Tamayo 2014b). Recreational impacts in one system have been estimated at around $45 million dollars per year (Eiswerth et al. 2000). Herbicide treatments are commonly employed to control *M. spicatum* populations, as they are generally believed to be selective and cost-effective. Herbicide applications designed to have system-wide effects can markedly reduce *M. spicatum* cover. However, lakewide treatments have also been show to negatively affect non-target native species (Kovalenko et al. 2010, Nault et al. 2014, Kujawa et al. 2017, Nault et al. *submitted*). In light of the widespread application of herbicide treatments to control *M. spicatum* populations, it is vitally important to know how the ecological effect of invasive *M. spicatum* compares with the ecological effect of the herbicide treatments used in its control.

We use several complementary approaches to explore the effects of *M. spicatum* and lakewide herbicide treatment on aquatic macrophyte communities. First, we used a pre-post comparison to examine the response of native macrophyte species to lakewide chemical treatment in 25 treated lakes. Next, we identified patterns at the landscape scale using a comparative modeling approach and a large sample of lakes. We directly compared the effects of *M. spicatum* to the effects of lakewide chemical treatment using multi-level models that describe the response of average macrophyte cover as well as macrophyte community composition. Finally, we provide context for understanding the ecological effects of the invader by testing whether the effects of *M. spicatum* and the effects of native species on macrophyte frequency occurrence and community composition differ. We aim to provide insights into the costs and benefits of a common management approach intended to control invasive species, thereby informing management actions, particularly those conducted for the purpose of ecological restoration.

2. Methods

2.1 Aquatic macrophyte surveys

We collected species cover data for floating leaf, free-floating, and submersed aquatic macrophyte species during 634 surveys conducted on 426 Wisconsin lakes between May 14 and October 12, from 2005 to 2012. We used a grid-based point-intercept sampling method to observe macrophyte species presence from a boat at multiple points within a lake (Hauxwell et al. 2010). We scaled the number of points on each lake with lake littoral area and shoreline complexity, resulting in a statistically robust dataset for estimating plant cover and community composition (Mikulyuk et al. 2010). At each littoral sampling point, observers used a double-sided bow rake attached to a 4.5-m pole to remove plants from a 0.3m^2 area. A similar rake head attached to a rope was used to collect plants from sites deeper than 4.5m. We sampled a mean of 199 sample points per lake littoral zone, ranging from 10 to 1017 per lake. All live plants detached by the rake were identified to species (Crow and Hellquist 2000a, b). Certain cryptic species were analyzed at the genus level, including *Isoetes* spp., *Chara* spp., *Nitella* spp., *Najas guadalupensis* and *N. flexilis*, *Elodea canadensis* and *E. nuttallii*, *Sagittaria* rosettes, *Lemna* spp (excluding *L. trisulca*) and *Wolffia* spp. Rare species present in fewer than 5% of lakes were excluded from analysis. We estimated species-specific macrophyte cover in the littoral zone by calculating the proportion of sampled points at which each species was present. This measure can be taken as an unrelativized index of cover in lake littoral zones; hereafter, we will refer to this estimate as 'cover'.

We obtained lake environmental data from a comprehensive database of chemical and limnological parameters for Wisconsin lakes (Papeş and Vander Zanden 2010). Missing values comprised 4% of the total number of observations and were imputed via predictive mean matching (Little 1988). Because water clarity and alkalinity are important drivers of macrophyte abundance and community composition, we used estimates of Secchi depth (m) and alkalinity (mg $CaCO_3$/L) to account for environmental drivers of macrophyte cover (Vestergaard and Sand-Jensen 2000, Mikulyuk et al. 2011).

Of the 426 lakes, regional staff selected 25 that underwent a lakewide herbicide treatment and had both pre- and post-treatment macrophyte data. Treatments varied with respect to herbicide formulation and application rate (Supplementary material, Appendix 2, Table A1). Most employed some form of 2,4-dichlorophenoxyacetic acid

(2,4-D; DMA IV, Aqua-Kleen; Weedar 64; Navigate). From the original set of 426 lakes, we defined a group of reference lakes for which no herbicide treatments were reported prior to the plant survey, resulting in a master set of macrophyte surveys conducted on 363 untreated and 25 treated lakes.

2.2 Pre-post analysis

To compare species cover before and after treatment, we first assembled a pre-treatment/post-treatment dataset. We compiled data on surveys collected before and after treatment where the pre-treatment survey occurred during the growing season 1 to 3 years prior to treatment and where the post-treatment survey occurred no later than in the year following. For each lake, we used Pearson's chi-square test of independence to calculate the number of species for which cover significantly increased, decreased, or showed no change from pre- to post-treatment. We then compared these observations to the interannual changes observed in untreated lakes. We randomly selected two surveys to represent each of the 46 untreated lakes for which had multiple annual surveys. We repeated the Pearson's chi square analysis for the untreated survey pairs, recording the number of species where cover significantly increased or decreased per lake from one year to the next. We tested whether treatment status was significantly related to increases and decreases, fitting generalized linear models (log link, quasi-

Poisson errors) to the count of interannual increases and decreases (function 'glm'; R Core Team 2014).

2.3 Comparative analysis

We generated a comparative dataset to explore the effects of treatment and *M. spicatum* on native macrophyte communities. Because the number of treated lakes was small (N=25) relative to untreated lakes (N = 363), we balanced the dataset using a matched-set approach and 1:5 ratio (Breslow and Day 1987). For each treated lake, we selected the 5 untreated lakes that were most similar to the set of pre-treatment macrophyte surveys according to the Bray-Curtis dissimilarity measure computed on species presence-absence data (Bray and Curtis 1957). We matched multiple control cases per treated lake to increase coverage for individual species and enhance our ability to estimate species-specific slopes. We combined the resulting set of 125 matched untreated lakes with the post-treatment surveys to produce a final set of 150 lakes.

We applied a multilevel modeling (MLM) framework to compare the effects of *M. spicatum* and treatment on macrophyte cover and community composition. Multilevel models are similar to standard regression models that describe relationships among variables, but in addition to estimating fixed-effects coefficients that describe response patterns as a function of the predictors, they include a second set of random effects that model variation in those coefficients according to groups of interest (Gelman and Hill 2007). Thus, when we specify ‘species’ as a group of interest, the random effects portion of the model returns species-specific estimates from which we can infer effects on community composition. For example, when implemented to describe macrophyte communities, a positive fixed-effects slope coefficient for a given predictor indicates that on average, macrophyte cover increases in response to that predictor. The random-effects portion of the model then estimates a slope and intercept coefficient for each species. Slopes that are highly variable across species indicate that species differ greatly in their response to a given predictor. Divergent species responses to a given predictor will lead to changes in community composition, even if average abundance remains the same (Jackson et al. 2012).

We specified a multilevel model to describe macrophyte cover as a function of predictors. We expressed the macrophyte variable as the number of sites within lakes at which a given species was observed to be present and the number of sites at which it was observed to be absent (a binomial variable). We accounted for environmental variation by estimating continuous fixed effects for water clarity (Secchi depth) and its square as well as the linear fixed effect of alkalinity (Barr et al. 2013). We selected the forms for these two predictors based on exploratory scatterplots. We then estimated the fixed effect of *M. spicatum* expressed as pre-treatment cover. We also included a factor to capture whether a lake experienced a lakewide herbicide treatment. We chose to use pre-treatment cover estimates for *M. spicatum* to reduce dependence among the treatment and *M. spicatum* predictors. We estimated species-specific random slopes and their correlations for each of the above predictors. We also fit uncorrelated intercepts for species and lakes and included an observation-level random effect to account for overdispersion (Browne et al. 2005). Prior to analysis, we scaled all continuous predictors to mean zero and unit variance. We assumed a binomial error distribution and employed a logit link function to linearize predictors. All models were fit by maximum likelihood using zero Gauss-Hermite quadrature points with the function 'glmer' in lme4 version 1.1-7 and R version 3.1.2 (R Core Team 2014, Bates et al. 2015). We use likelihood ratio tests conducted on nested models with and without the term in question to report the significance of fixed and random effects. Significance tests for the random effects require testing parameters at the edge of their possible range ($\sigma = 0$) which produces inflated p-values. We adjusted p-values for random effects test by dividing by 2 (Bolker et al. 2009, Bates et al. 2014).

Finally, we compared the statistical effect of *M. spicatum* on native macrophyte species cover to the effects of native species. In essence, we used native macrophyte species as a null model for evaluating the impact of the invader. Using data on each of the 363 untreated reference lakes, we specified a new MLM relating macrophyte cover to water clarity, alkalinity, and *M. spicatum* cover. Then, to compare the effects of *M.*

spicatum to those of natives, we constructed a series of 65 nearly identical MLMs, one for each species in the dataset. In each model, we replaced *M. spicatum* as a predictor with a different native macrophyte species. Whenever a macrophyte species was used as a predictor, it was removed from the matrix of species responses. We compared fixed- and random-effects coefficients for all species and computed standardized Z-scores for *M. spicatum* coefficients.

3. Results

3.1 Pre-post analysis

In untreated lakes, the number of species that significantly increased ($\bar{x} = 1.0$, sd = 2.2) and decreased ($\bar{x} = 1.2$, sd = 2.4) across years was similar. However, lakes that experienced lakewide herbicide treatments experienced more increases ($\bar{x} = 1.6$, sd = 1.9) and more decreases ($\bar{x} = 4.1$, sd = 3.1) following treatment. Treatment status was a significant predictor of the number of interannual decreases ($t = -3.7$, $p < 0.001$), but not increases ($t = -1.2$, $p = 0.23$; Figure 1). Species that decreased following treatment included monocots, dicots, and macroalgae (Table 1).

3.2 Comparative analysis

Large-scale herbicide treatment was negatively related to macrophyte cover ($\beta = -0.35$, $p = 0.047$; Table 2), while *M. spicatum* was positively related to macrophyte cover, though the effect was non-significant ($\beta = 0.11$, $p = 0.22$). Responses to both predictors were highly variable across species, though the responses to increasing *M. spicatum* (sd random effects = 0.34, $p < 0.001$) were less variable and less often negative than those associated with treatment (sd random effects = 0.68, $p = 0.007$; Figure 2a). Consistent with the pre-post analysis, the species with negative coefficients associated with herbicide treatment were both monocots and dicots from a variety of growth forms. Species that responded negatively to *M. spicatum* were often short in stature, while those that responded positively generally had taller growth forms (Figure 2b; Table 3).

Next, we sought to determine whether the effect of *M. spicatum* on average macrophyte cover and community composition differed from that of native species in the 363 untreated reference lakes. We developed a separate MLM for each of the 65 native species, using each native species as a predictor (instead of *M. spicatum*). Estimates associated with *M. spicatum* were not markedly different from those of native species. The fixed effect estimate for *M. spicatum* was within one standard deviation of the mean for all other species ($Z = 0.05$; Figure 3a) and about half of the native species had effects that were larger than *M. spicatum*. For community composition, the random effects describing species-specific responses to *M. spicatum* were not different from the species-specific responses to native species; the Z-score for the random effects expressed as the standard deviation of species-specific coefficients for *M. spicatum* fell within one standard deviation of the mean value for all other species ($Z = -0.74$; Figure 3b). We further examined species-specific *M. spicatum* coefficients and found that approximately 75% of native species responded positively to increasing *M. spicatum* cover (Figure 2b).

4. Discussion

Lakewide herbicide treatments were associated with a decrease in average macrophyte cover and divergent species responses that may lead to shifts in community composition. At the same time, the effects of *M. spicatum* on native macrophyte communities were similar to the effects of many native species. This, in combination with the fact that *M. spicatum* populations in lakes are most often small, we found no evidence that *M. spicatum* has large negative effects on native macrophyte communities on a regional spatial scale.

4.1 Effects of herbicide treatments

We observed a statistical association among lakewide herbicide treatments and declines in macrophyte cover along with divergent species responses that suggest probable effects on macrophyte community composition. The possible decrease in native cover we observed should be carefully considered in conducting lakewide herbicide treatments. *M. spicatum* is fast-growing and tolerant of disturbance (Smith and Barko 1990). It has been observed to successfully colonize de-vegetated sites; care should be exercised lest treatments create conditions that ultimately benefit the invader (Bayley et al. 1978, Galatowitsch et al. 1999). Managers should also be aware of the potential for compounding effects of multi-year treatments. Very few species responded positively to lakewide herbicide treatment. Repeated use of lakewide herbicide applications may favor communities dominated by a few treatment-tolerant species and reduced macrophyte diversity. Repeated 2,4-D treatments have also been associated with increasing herbicide resistance and hybridization (LaRue 2012). The role of lakewide herbicide treatments in a broader lake restoration plan may therefore hinge on whether treatments can produce a progressive decrease in the scale of the management problem such that non-target impacts are minimized over time.

Previous studies range with respect to the magnitude of herbicide treatment effects they report. Some report no or minimal non-target impacts, others demonstrate species declines that recover shortly following treatment, while others reveal evidence for sustained declines (Ortenblad et al. 2006, Kovalenko et al. 2010, Wersal et al. 2010, Nault et al. 2014). Contradictory findings may be explained by treatment scale as well as differences in herbicide concentration and exposure time (CET; Nault et al. 2012, Nault et al. *submitted*). Herbicide efficacy often varies across treatments because of differences in water temperature, trophic status, water chemistry and lake-specific degradation pathways (Frater et al. 2017). We caution against over-generalization of the findings in this study due to the many treatment-specific sources of variability that ultimately determine outcome.

4.2 Effects of *M. spicatum*

M. spicatum did not appear to affect average macrophyte littoral cover in a predictable way. This echoes previous findings that the species is a 'matrix dominant,' capable of co-existing with other species with no negative impacts on native cover (Trebitz and Taylor 2007). However, evidence for effects that range from negative to neutral to positive can be found in the literature (Boylen et al. 1999, Trebitz and Taylor 2007, Gräfe 2014). While at first glance, published results are apparently contradictory, the observed patterns may in part depend on the spatial scale of the study and on sampling design. Studies at the scale of individual lakes or sites within lakes and those that focus on lakes with large *M. spicatum* populations tend to report negative relationships between *M. spicatum* and native species, while landscape-scale studies conducted on multiple lakes report neutral or positive relationships (Madsen et al. 1991, Madsen 1998, Boylen et al. 1999, Gräfe 2014). This study reports on trends observed in an unprecedented number of lakes, and we found no evidence of negative effects of *M. spicatum* on native macrophytes. Additionally, it is important to note that centering and standardizing the predictor variable affects the response units parameterized by the model: the slope coefficient estimated by the MLM describes the change in native macrophyte cover in response to an increase in *M. spicatum* cover of 23 percentage points. This is a relatively large unit of increase in *M. spicatum* cover. On average, interannual changes in *M. spicatum* cover as well as changes occurring over long time scales (10 years) were only half as large (Kujawa et al. 2017). As a result, the real effect of *M. spicatum* may be even smaller than we estimated.

Increasing *M. spicatum* littoral cover is likely to change macrophyte community composition. However, 75% of species-specific responses to increasing *M. spicatum* were positive, suggesting that competitive displacement of native species by *M. spicatum* is not one of the invader's major ecological effects. This trend held for other species too: species-specific responses to increasing cover of natives were mostly positive. In communities where competition is a major structuring force, covariance among population abundances is on average expected to be negative (Houlahan et al. 2007). Our findings suggest that facilitation or environmental filtering, rather than interspecific competition, determines macrophyte species abundance and distribution (McGill et al. 2006). *M. spicatum* has been documented to replace native species in certain lakes, but it remains unclear whether *M. spicatum* was a causal factor, or was simply responding to changing environmental conditions (Davis and Brinson 1983, Nichols 1994, MacDougall and Turkington 2005). The results of our study are more consistent with *M. spicatum* responding to environmental factors rather than engineering macrophyte communities, which echoes observations reported elsewhere (Galatowitsch et al. 1999).

M. spicatum has morphological and physiological traits that are often cited as the reason for displacement of native species (Boylen et al. 1999, Eiswerth et al. 2000, Prather et al. 2007). For example, in certain lakes, *M. spicatum* can form a canopy of branching stems that decreases the amount of light available for native plants lower in the water column (Titus and Adams 1979, Smith and Barko 1990). *M. spicatum* can also efficiently fix carbon and has relatively low nutrient requirements, which is thought to give the species a competitive advantage (Grace and Wetzel 1978). However, natives may have adaptations that allow them to successfully coexist with *M. spicatum*. Some native species maintain high photosynthetic rates despite low light and are thus tolerant of shading (Adams et al. 1974). While *M. spicatum* may have negative local-scale effects on native macrophytes, our findings suggest that the broad-scale effects are more complex and less negative than previously assumed.

There are many ways to quantify the effects of invasive species (Kulhanek 2011). We observed macrophyte response along a gradient of invader cover. Exploring patterns along an abundance gradient is a common approach to assessing invader impacts using observational data. However, we suggest that a stronger design would incorporate an understanding of the effects of native species. Instead of simply asking whether invasive species have a measurable effect, the more germane question is whether and how the effects of invasive species differ from the effects of natives. Failure to understand invader impacts in light of the effects of natives could lead to an overestimation of a species' ecological impact, and would affect management prioritization (Kumschick et al. 2012)

4.3 Management implications

We acknowledge that the effect of *M. spicatum* on native macrophytes is just a part of the larger context within which lake management decisions occur, and that *M. spicatum* may negatively affect other aspects of lake ecology (although this holds for herbicide applications too). For example, *M. spicatum* can change the structural geometry and composition of lake littoral habitat, alter light regimes and influence lake biogeochemistry (Madsen et al. 1991, Barko et al. 1994). There is little evidence that *M. spicatum* directly affects fish abundance, but there is support for a significant effect on the trophic diversity of secondary consumers (Dibble and Harrel 1997, Duffy and Baltz 1998, Kovalenko and Dibble 2010, Kovalenko et al. 2010). While we failed to find evidence for *M. spicatum* effects on macrophyte communities, it is important to recognize these other documented cases of ecological effects of *M. spicatum*, though more work is needed to clarify magnitude and mechanism. In particular, whether or not the reported ecological effects are different from those of native species should be explored in more detail.

Minimizing ecological impacts is not the only reason invasive species are managed. Decisions on how and to what end to manage lakes must consider social as well as ecological effects. Dense canopies formed by some *M. spicatum* populations can interfere with recreation, decrease tourism and agricultural revenue, and affect property values (Eiswerth et al. 2000, Horsch and Lewis 2009, Olden and Tamayo 2014a). While previous work reveals that abundance distributions of *M. spicatum* and native species are statistically similar, it is possible that certain negative effects occur even when invader populations are small (Hansen et al. 2013). However, the relationship between effect and abundance has not been adequately characterized for *M. spicatum*'s socio-cultural impacts. Additional cross-lake work is necessary for a more thorough understanding of the socio-economic costs and benefits of *M. spicatum* and the management actions designed to control it. While lake management decisions must consider diverse stakeholder values, the best decisions should also consider ecological health, and this work reveals a new understanding of the impacts of aquatic invasive species management that should be incorporated into our decision making frameworks (Kumschick et al. 2012).

Given that we revealed strong effects of lakewide treatments but little evidence for ecological impacts related to *M. spicatum*, ecological restoration may not be an appropriate short-term management objective for lakewide herbicide applications because reductions in *M. spicatum* are likely to come at the expense of native cover. Nuisance relief, rather than ecological restoration, though, may be a more appropriate short-term endpoint, but the question remains as to whether lakewide herbicide treatments can be used in a long-term management plan in a way that minimizes non-target impacts over time. Some may weigh these costs and benefits and still find utility in performing lakewide herbicide treatments, especially within the context of an integrated approach to invasive species management (Gill and Goyal 2016). We must simultaneously consider the possibility that disturbance-intolerant natives may fail to recover from lakewide herbicide treatments faster than *M. spicatum*, or that they might fail to recover at all, resulting in less diverse native assemblages in which the invasive species continues to present a substantial management problem (Rinella et al. 2009). We suggest caution in the use of lakewide herbicide treatments for invasive species control. Unless there is strong evidence that the invader's site-specific ecological, social or economic impact is likely to be high, proactive and aggressive management may in fact do more harm than good.

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6. Supporting information

Supporting information appears in Appendix 2. Table A1 lists large scale treatment and macrophyte survey timing, herbicide active ingredient and formulation by waterbody.

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8. Tables

Table 1. Species that demonstrated statistically significant increases (bold) and decreases in littoral cover in more than two of the 25 treated lakes following lakewide application of herbicide. We list the number of lakes in which significant declines were observed as well as the percentage (out of the total number of lakes with pre-treatment populations of the indicated species).

Species	# lakes	% lakes
***Chara* species**	**5**	**20**
***Nitella* species**	**4**	**18**
Vallisneria americana	**3**	**15**
***Elodea* species**	**3**	**14**
Potamogeton pusillus	11	65
Myriophyllum sibiricum	6	46
Potamogeton zosteriformis	7	41
Najas flexilis or *guadalupensis*	11	40
Heteranthera dubia	4	36
Nitella species	7	32
Potamogeton friesii	3	30
Ceratophyllum demersum	6	27
Potamogeton gramineus	4	27
Vallisneria americana	5	25
Chara species	5	20
Suckenia pectinata	3	19
Potamogeton amplifolius	3	17

Table 2. Estimated coefficients for fixed and species-specific random effects from a multilevel glm describing macrophyte cover as a response to environmental variables, *M. spicatum* cover, and herbicide treatment. Data were comprised of macrophyte community surveys on a matched set of 150 lakes. We combined 25 post-treatment surveys with data on 125 untreated lakes where macrophyte communities resembled pre-treatment conditions in the 25 treated lakes. Significant ($p < 0.05$) predictors in bold, as indicated by likelihood ratio tests on nested models without the indicated predictor.

Predictor	Fixed estimate (coefficient)	Species-specific variation (sd random estimates)
Intercept	**-5.98**	**2.18**
Secchi	0.21	**0.82**
Secchi^2	**-0.32**	**0.27**
Alkalinity	**-0.54**	**1.47**
M. spicatum	0.11	**0.33**
Treatment	**-0.35**	**0.68**
N	7,350	
Log likelihood	-13032	

Table 3. Species-level coefficients (random effects) describe the response of individual species to increasing *M. spicatum* frequency of occurrence (*M. spicatum*) or lakewide herbicide treatment (Trt) as estimated by a multilevel generalized linear model that also accounts for the effects of alkalinity and water clarity in 150 lakes. ID corresponds to labels used in Figure 2.

		Species-specific coefficients				Species-specific coefficients	
ID	Species	Trt	*M. spicatum*	ID	Species	Trt	*M. spicatum*
1	*Myriophyllum sibiricum*	-1.32	0.04	26	*Utricularia intermedia*	-0.33	0.17
2	*Potamogeton foliosus*	-1.27	-0.02	27	*L. trisulca*	-0.32	0.45
3	*P. pusillus*	-0.97	0.04	28	*U. resupinata*	-0.32	-0.20
4	*M. heterophyllum*	-0.92	0.29	29	*P. strictifolius*	-0.31	-0.03
5	*P. spirillus*	-0.91	0.04	30	*P. friesii*	-0.29	0.05
6	*P. zosteriformis*	-0.86	0.29	31	*P. epihydrus*	-0.28	0.21
7	*P. robbinsii*	-0.81	0.00	32	*Spirodela polyrrhiza*	-0.22	0.70
8	*Bidens beckii*	-0.70	0.02	33	*U. minor*	-0.19	0.20
9	*P. natans*	-0.69	0.03	34	*Isoetes* spp	-0.16	-0.16
10	*Ceratophyllum demersum*	-0.64	0.48	35	*P. amplifolius*	-0.13	-0.02
11	*Schoenoplectus subterminalis*	-0.64	-0.03	36	*Eleocharis acicularis*	-0.11	-0.09
12	*P. crispus*	-0.55	0.38	37	*Vallisneria americana*	-0.07	0.08
13	*Heteranthera dubia*	-0.55	0.25	38	*P. nodosus*	-0.04	0.37
14	*Najas flexilis* or *guadalupensis*	-0.53	-0.06	39	*N. marina*	-0.04	0.05
15	*Lemna* spp	-0.46	0.62	40	*Brasenia schreberi*	-0.04	0.19
16	*Nuphar variegata*	-0.44	0.25	41	*U. vulgaris*	0.00	0.29
17	*Sagittaria* spp	-0.44	-0.01	42	*Eriocaulon aquaticum*	0.03	-0.21
18	*P. richardsonii*	-0.42	0.27	43	*Stuckenia pectinata*	0.08	0.20
19	*P. praelongus*	-0.40	0.22	44	*N. gracillima*	0.12	0.14
20	*Nymphaea odorata*	-0.40	0.25	45	*U. gibba*	0.14	0.11
21	*Ranunculus aquatilis*	-0.38	0.23	46	*P. illinoensis*	0.21	-0.20
22	*Wolffia* spp	-0.38	0.71	47	*Nitella spp*	0.22	-0.20
23	*Elodea* spp	-0.37	0.24	48	*P. gramineus*	0.36	-0.36
24	*M. tenellum*	-0.37	-0.42	49	*Chara spp*	0.48	-0.15
25	*Juncus pelocarpus*	-0.36	-0.32				

9. Figure captions

Figure 1. Density distribution of the number of species that demonstrated statistically significant increases and decreases pre- to post-treatment in 25 treated lakes compared to background interannual increases and decreases observed across randomly selected pairs of years in 46 untreated lakes.

Figure 2. Frequency distribution (a) of species-specific (random) coefficients for *M. spicatum* (black bars) and treatment (gray bars) estimated by a multilevel generalized linear model that accounts for the fixed effects of alkalinity and water clarity in 150 lakes. Species-specific coefficient biplot (b) identifies overall 'winners' (upper right quadrant) from 'losers' (lower left quadrant). Species, coefficients and ID labels listed in Table 3.

Figure 3. (a) Fixed effects coefficients for each native species as a predictor and (b) the associated standard deviation of species-specific (random) effects. Values estimated by a set of 65 multilevel models describing macrophyte cover as a response to environmental variables and the cover of each of 65 macrophyte species. Data from 363 untreated lakes. Values for *M. spicatum* depicted by dashed lines.

10. Figures

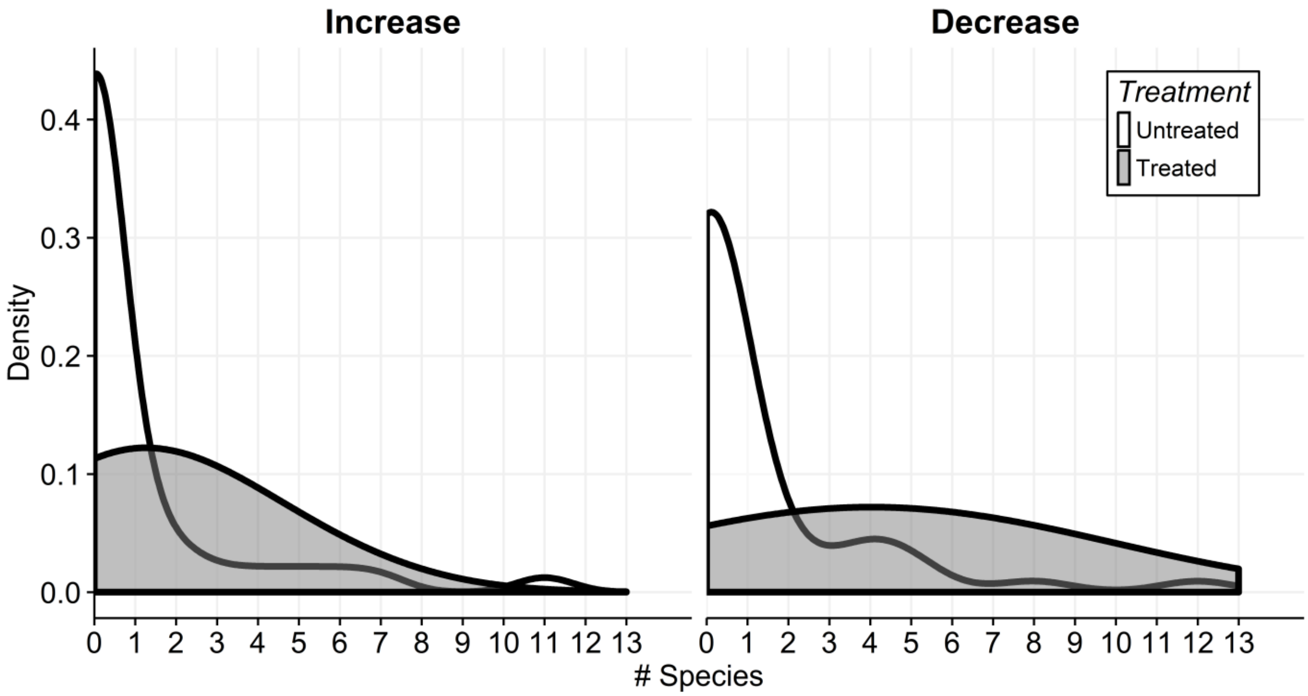

Figure 1. Density distribution of the number of species that demonstrated statistically significant increases and decreases pre- to post-treatment in 25 treated lakes compared to background interannual increases and decreases observed across randomly selected pairs of years in 46 untreated lakes.

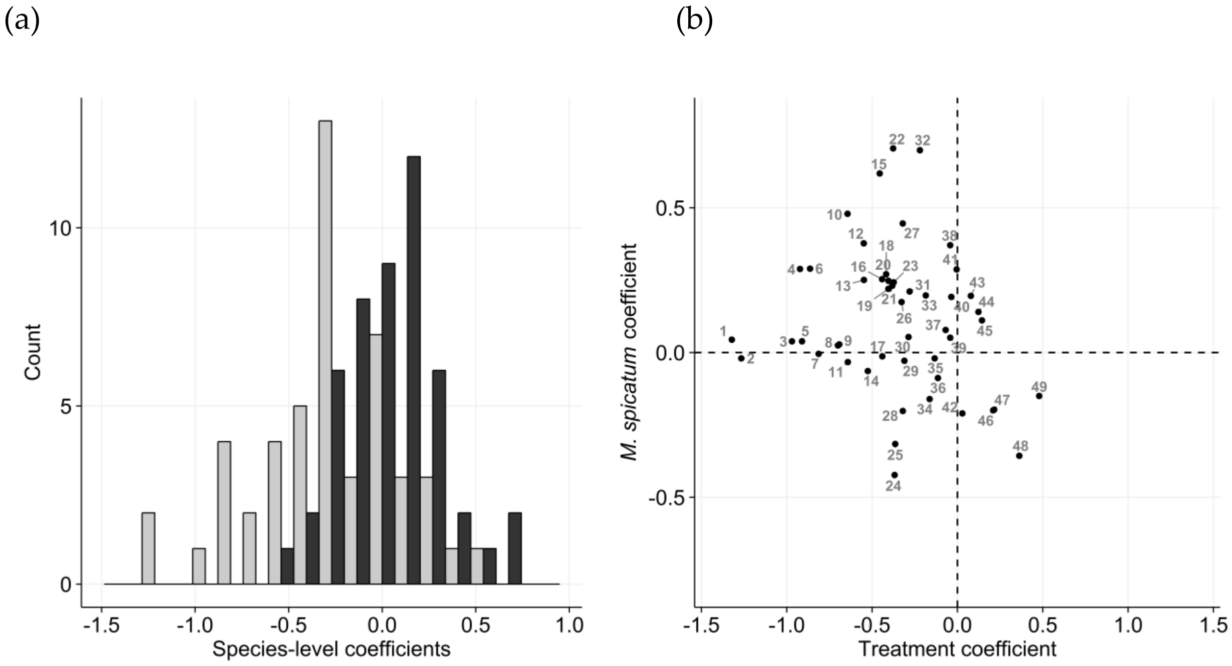

Figure 2. Frequency distribution (a) of species-specific (random) coefficients for *M. spicatum* (black bars) and treatment (gray bars) estimated by a multilevel generalized linear model that accounts for the fixed effects of alkalinity and water clarity in 150 lakes. Species-specific coefficient biplot (b) identifies overall ‘winners’ (upper right quadrant) from ‘losers’ (lower left quadrant). Species, coefficients and ID labels listed in Table 3.

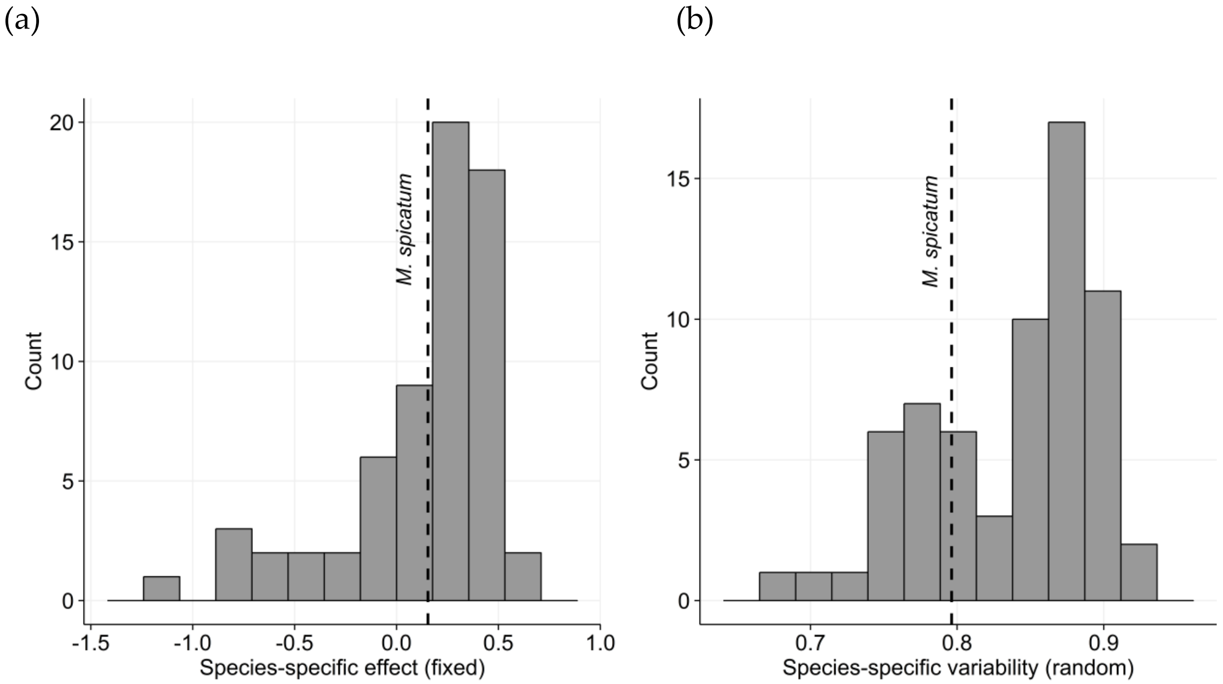

Figure 3. (a) Fixed effects coefficients for each native species as a predictor and (b) the associated standard deviation of species-specific (random) effects. Values estimated by a set of 65 multilevel models describing macrophyte cover as a response to environmental variables and the cover of each of 65 macrophyte species. Data from 363 untreated lakes. Values for *M. spicatum* depicted by dashed lines.

CHAPTER 3

MODELLING INVASIVE *M. SPICATUM* OCCURRENCE AND ABUNDANCE: APPLICATION TO PRIORITIZING PREVENTION AND CONTROL EFFORTS

In preparation for submission with coauthors: Ellen Kujawa, Catherine M. Hein, Scott Van Egeren and M. Jake Vander Zanden.

Abstract

Effective application of limited resources to managing invasive species requires predicting site-specific vulnerability, considering the likelihood of invasion and the probability of adverse effects. While many studies forecast invasive species distributions, few integrate an analysis of invasive species impact, though both factors are relevant for planning prevention and control. We present an empirical predictive model of occurrence and abundance for *M. spicatum*, a non-native nuisance macrophyte that is managed at great expense in the United States. We used generalized linear models to predict occurrence and extended beta regression models to predict cover. *M. spicatum* occurrence was statistically significantly positively related to road density, maximum air temperature, lake surface area and maximum depth. Occurrence was negatively related to near-surface lithological calcium oxide content, annual air

temperature range and average distance to all source populations. *M. spicatum* cover was negatively associated with maximum lake depth and water clarity and positively associated with water conductivity, soil eroibility and maximum air temperature. Variability in cover was related to maximum depth, calcium oxide lithological content , soil erodiblity and water clarity. Cross-validated performance measures revealed that model predictions were highly accurate (AUROC = 0.81), though a large amount of variation was not accounted for by the model (Tjur's R^2 = 0.32). While cover models were informative and statistically significant, they too accounted for a small proportion of the observed variation in cover (pseudo R^2 = 0.25). We used each model to extrapolate predictions of occurrence and cover to all lakes greater than 1 ha (N = 9825). The occurrence model performed well when compared to independent occurrence information (AUROC = 0.94). Finally, we combined modeled occurrence and cover predictions to identify high-priority prevention and control targets. The resulting prioritization matrix has applications to prevention and management. These results may be used to allocate prevention actions to systems at high risk of experiencing an invasion with special priority placed on those that are most likely to experience adverse effects. Likewise, recommendations for pro-active versus conservative aquatic plant management plans may use the prioritization matrix to consider the risk of a population attaining high cover.

1. Introduction

Invasive species are a leading cause of global change. They can alter ecosystem structure and function and decrease global biodiversity (Vitousek et al. 1997, Wilcove et al. 1998, Mack et al. 2000, Simberloff 2011). They are economically costly and can pose hazards to human health (Pimentel et al. 2005, Neill and Arim 2011). Taxonomically, they represent nearly every extant phylum, and their modes of impact are as diverse as the invaders themselves. The vulnerability of a particular site to invasion is thus a central concern for both invasion ecologists and natural resource managers. Assessing invasion vulnerability at a particular site requires understanding three filters that mediate species invasions. The first determines the likelihood of invader introduction, the second determines its probability of establishing a self-sustaining population, and the third assesses its likely impact (Vander Zanden et al. 2004). Sites at which an invader is likely to arrive, survive, and have adverse effects can be considered highly vulnerable. Assessments of site vulnerability are important because they allow the informed application of limited management resources to maximize efficiency and minimize negative effects.

Predicting site-specific vulnerability to a particular invader first requires predicting where it is likely to occur. Species occurrence patterns are determined by many factors, including climate, dispersal ability and resource availability, which are reviewed elsewhere (Guisan and Thuiller 2005). Given knowledge of these theoretical relationships, species distributions may be modelled by statistically relating species occurrence records to a set of variables hypothesized to directly or indirectly explain them (Prushton et al. 2004). Distribution models for range-expanding invasive species should consider dispersal constraints in addition to habitat suitability, but dispersal is not routinely accounted for in SDMs (Elith et al. 2006, Guisan et al. 2006, Vaclavik and Meentemeyer 2009).

The second step in assessing site vulnerability requires understanding whether the invader is likely to adversely affect the recipient ecosystem. The idea of 'effect' can be extremely complicated. On one hand, we may consider direct or indirect effects on biotic and abiotic aspects of the invaded system. But because invasive species can have major social and economic impacts, assessment of effect may also consider ecosystem services and stakeholder values (Pimentel 2005, Kumschick et al. 2012). Invader effects are often more difficult to measure and forecast than species distributions and as a result, they are not often predictively modelled (but see approaches in Kulhanek et al. 2011, Dick et al. 2014, Ward and Morgan 2014). A promising way forward is to use abundance as a proxy for impact because it is more tractably modelled as a function of explanatory variables (Potts and Elith 2006). For most invasive species, abundance and impact are positively related, though the precise shape of that relationship can take several forms. (Parker et al. 1999, Yokomizo et al. 2009, Latzka et al. 2016).

Our central goal was to unite predictions of species occurrence and abundance (as % cover) to describe lake-specific vulnerability to invasion by *M. spicatum*, a non-native nuisance-causing macrophyte. We used empirical data to predict species occurrence and cover as a function of variables that describe environmental conditions, land cover, dispersal, geology and climate. We included as predictors both local (e.g. water conductivity, water clarity, nearshore urban development) and regional predictors (e.g. annual temperature range, watershed land cover). To characterize vulnerability to invasion, we united predictions of occurrence and cover in a prioritization framework to identify lakes with increasing risk of having *M. spicatum* populations that may attain high cover. We separated vulnerable lakes into three tiers of increasing prevention priority, thereby offer a simple tool that can be used in the planning of prevention efforts and management actions designed to decrease the spread and impact of *M. spicatum.*

2. Methods

2.1 Model organism

M. spicatum is an invasive aquatic plant that can grow to high abundance in certain freshwater systems. Native to Europe, Asia and North Africa, the precise date of introduction to the United States is unknown but probably occurred sometime between 1880 and 1940 (Eiswerth et al. 2000). It has since spread throughout the continental US and Canada (EDDMapS 2017). Present in over 800 Wisconsin waterbodies, the invader has steadily expanded its range northward since its initial introduction in south central Wisconsin in the 1960s (Trebitz et al. 1993). EWM at nuisance levels forms thick mats that prevent navigation, reduce property values and impact native species (Boylen et al. 1999, Provencher et al. 2012). In 2011, over half of the total funding for Wisconsin's AIS control grant program was allocated to EWM, amounting to more than $2 million dollars annually, making it a high priority for vulnerability assessment (Asplund 2011).

2.2 Occurrence and cover of *M. spicatum*

We developed occurrence and cover models using data obtained from macrophyte surveys conducted from May 01 to October 01 from 2005-2016 on 657 Wisconsin waterbodies. Waterbodies were distributed across Wisconsin's three lake-rich ecoregions with surface area ranging 1.36 - 3958 ha (Omernik et al. 2000). Surveys were conducted as part of a research and monitoring program by the Wisconsin Department of Natural Resources (WDNR). Watersheds ranged from being almost entirely forested to those that were largely agricultural or urbanized. We observed species presence from a boat at every point on a grid scaled by the estimated size of the littoral zone and shoreline complexity (Mikulyuk et al. 2010). Total number of points ranged from 32 to 4149 points per lake, with a mean of 406. On average, 234 sample points fell within littoral zones as defined by areas equal to or more shallow than the 99th percentile of ordered depths at which macrophytes were observed. At each sampling point, observers used a double-sided bow rake attached to a 4.5m pole to collect macrophytes from a ~0.3m^2 area. A similar rake head attached to a rope was used to collect macrophytes from sites deeper than 4.5m (Hauxwell et al. 2010). All live macrophytes detached by the rake were identified to species (Crow and Hellquist 2000a, b). For a given species, the number of occurrences divided by the total number of points per lake data can be interpreted as an estimate of lakewide % cover.

We also obtained statewide *M. spicatum* occurrence records from the aquatic invasive species program of the Wisconsin Department of Natural Resources (WDNR). Occurrences were drawn from multiple sources including professionally-verified citizen reports, routine monitoring work and formal AIS detection surveys (Figure 1a). A recent probabilistic survey conducted on 458 lakes found 104 populations of *M. spicatum*, 87% of which were already present in the statewide database (Latzka 2015).

2.3 Explanatory variables

We compiled information on predictors hypothesized to predict *M. spicatum* occurrence and cover that were available for over 7000 of the 9285 Wisconsin lakes with surface area greater than 1 ha. Predictors represented a suite of factors related to in-lake patterns in water quality and morphometry as well as regional patterns related to dispersal, land use, geology and climate (Supplementary material, Appendix 3, Table A1). We obtained several WORLDCLIM variables to describe climate, including annual temperature range, the maximum temperature of the warmest week, and the minimum temperature of the coldest quarter, extracting values occurring at lake centroids (worldclim.org). Geological data included % lithological calcium oxide content (CaO) in near-surface geology and soil erodibility (Soil Survey Staff (SSURGO) , Soil Survey Staff (STATSGO2) , Olson and Hawkins 2014). We apportioned the geological values within watersheds delineated by a tracing procedure applied in R to a value-added catchment attribution database produced by the WDNR (Menuz et al. 2013). Percent agriculture (crops and pasture) and percent urban land use were calculated per watershed (Jin et al. 2013). Dispersal factors may be introduced to species distribution models with a simple term reflecting the distance from any given point to all source populations (Allouche et al. 2008). We computed two predictors to represent dispersal probability and propagule pressure as the mean distance (km) between a lake's centroid and all other *M. spicatum* lakes and the density of vehicle roads (m/m^2) in a 500m buffer around each lake (Open Street Map 2014). We extracted lake surface area from the 24K hydrography dataset and maximum depth from the WDNR Register of Waterbodies (Wisconsin Department of Natural Resources 2008). Spatial analyses were conducted using R packages 'rgdal', ‘raster’, ‘sp’, ‘rgeos’ and ArcGIS 10.2.2 (Pebesma and Bivand 2005, ESRI 2011, Hijmans 2015, Bivand et al. 2016, Bivand and Rundel 2016). Finally, we obtained estimates of water conductivity (μS/cm), alkalinity (mg $CaCO_3$), pH and satellite-estimated Secchi depth (m) from a comprehensive database of chemical and limnological parameters (Papeş and Vander Zanden 2010). Missing-at-random values comprised less than 3% of all observations. We imputed missing variables using predictive mean matching and package ‘mice,’ employing 50 iterations (van Buuren and Groothuis-Oudshoorn 2011). We log-transformed highly skewed numeric variables and square-root-transformed skewed percentages (see Table 1). We then computed variance inflation factors (VIF) for each variable in the dataset using function ‘vif’ in package ‘car’ (Fox and Weisberg 2011). We sequentially excluded variables with the largest inflation factor until no inflation factor exceeded 10.

2.4 Predicting *M. spicatum* occurrence

We built species distribution models using logistic regression in a generalized linear modelling framework applied to the 657 surveyed lakes. This approach is similar to multiple linear regression but allows for binomially-distributed response variables. The procedure employs a maximum likelihood optimization algorithm to estimate intercept and slope parameters(β_0 , β_j) for a set of j predictors (X) to determine the probability (p) that a given lake (i) has been invaded. The equation linearizes the response variable via a logit transformation.

$$y = \text{logit}\,(p_i) = \ln\frac{p_i}{1-p_i} = \beta_0 + \sum_{j=1}^{j}\beta_{ij}X_{ij}$$

The probability is subsequently calculated as

$$\text{P}(M.\,spicatum\ \text{presence}) = e^y/(1+e^y)$$

Model fitting was performed using Firth's method of bias reduction in R using the function and package 'brglm' (Firth 1993).

We used a five-fold cross-validation procedure to evaluate model performance. We randomly split the data into 5 approximately equal folds and developed each model five times, once per each unique combination of N = 4 folds. For each combination, we generated predicted values by applying the resulting model on the remaining 20% of data (Fielding and Bell 1997). After each cross-validation, we evaluated model performance. First, we used a receiver operating characteristic analysis (Hosmer et al. 2013). The logistic regression equation estimates probability of presence which can then be translated into predicted presence or absence by setting a threshold of probability at which one would expect the species to actually be present. This threshold can conceivably be set at any point along the probability of presence ranging from 0 to 1. We thus compared predicted probabilities to observed occurrence data and plotted the percentage of true presences against true absences while incrementally increasing the threshold value from 0 to 1. A 1:1 line relating the two factors would describe a model that is no better than random chance; the area under this line is 0.50. Therefore, values for the area under the receiver operating characteristic curve (AUROC) higher than 0.5 reflect increasing predictive power and a value of 1 reflects perfect discrimination. We generated receiver operating characteristics curves using the function 'roc' in package 'pROC' (Robin et al. 2011). We calculated overall model deviance, the percentage of deviance explained by the model (D2) and Tjur's coefficient of discrimination, which can be interpreted much in the same way as an R^2 value for linear regressions (Tjur 2009). All model performance statistics were averaged across cross-validations. Finally, we present maps of predicted probability of presence for all surveyed, uninvaded lakes.

We then used the model developed on the 657 surveyed lakes to predict probability of presence on all lakes larger than 1 ha in surface area (N = 9285), assessing performance against the statewide database of *M. spicatum* occurrences and AUROC. Finally, we produced a statewide map of predicted probability of presence of *M. spicatum*. We selected a threshold value for predicted probability of presence above which we would consider *M. spicatum* likely to occur, choosing the largest value that allowed no more than 1% of predicted absences to be false.

2.5 Predicting *M. spicatum* cover

We generated a *M. spicatum* cover model where observed cover was assumed to be a function of all predictors in the 296 lakes on which *M. spicatum* was observed during macrophyte surveys. Exploratory univariate plots revealed evidence for curvilinear and unimodal distributions, so we included quadratic transformations for all predictors. *M. spicatum* cover was highly heteroskedastic, overdispersed, and right-skewed. Previous work recommends the beta distribution for modeling vegetation cover (Chen et al. 2008). We therefore assume the response to be beta-distributed with the shape of the distribution controlled by mean (μ) and precision (ϕ) parameters (Ferrari and Cribari-Neto 2004). The model thus contains two submodels, one for the mean response and one for precision. We used extended beta regression models with bias correction to estimate mean and precision parameters as a function of predictors, thereby explicitly accounting for patterns in variable dispersion and skewness (Simas et al. 2010). Here, for any fixed μ, greater φ relates to decreased variability in the response variable (Hunger et al. 2011). The expected value and variance of the response variable y is determined by

$$E(y) = \mu$$

$$var(y) = \frac{\mu(1-\mu)}{1+\varphi}$$

Using a logit transformation for the mean submodel and a log link for dispersion, the models are specified as:

$$\text{logit}(\mu_i) = \ln \frac{\mu_i}{1-\mu_i} = \beta_0 + \sum_{j=1}^{j} \beta_{ij} X_{ij}$$

$$\ln \varphi_i = \theta_0 + \sum_{j=1}^{j} \theta_{ij} Z_{ij}$$

The set of predictors (X_i, Z_i) may vary by submodel but need not be mutually exclusive. We allowed all predictors to contribute both submodels. Model fitting was performed using the function and package 'betareg' in R (Cribari-Neto and Zeileis 2010).

We then applied the five-fold cross-validation procedure described previously. After each cross-validation, we evaluated model performance using several metrics. We calculated Pearson's correlation coefficient (r) between observed and predicted values to reflect agreement, while we used Spearman's rank correlation (ϱ) to test the concordance among value ranks. Finally, we calculated the root mean square error among observed and predicted values. We used the model developed on all 657 lakes to report model calibration statistics via the simple linear regression parameters *m* and *b* that describe the relationship between predicted and observed values. Given perfect concordance among observed and predicted values, the intercept (*b*) and slope parameter (*m*) would be 0 and 1, indicating no bias and a comparable range of observed values at all points along the range of predicted values. Different *b* indicates model under- or over- prediction, while different *m* reflects a bias that may differ in magnitude along the range of predictions (Potts and Elith 2006).

We mapped predicted *M. spicatum* cover for all surveyed but univaded lakes. We then used the model developed on the 296 surveyed lakes to predict cover on all lakes larger than 1ha in surface area. Finally, we produced a statewide map of predicted probability of presence of *M. spicatum* for the same lakes on which we mapped predicted probability of presence at the statewide level.

2.6 Defining and prioritizing management targets

We combined estimates of cover and occurrence likelihood for the 1267 uninvaded lakes for which predicted probability of *M. spicatum* occurrence exceeded the previously-etablished 1% false absence threshold (0.417). We grouped lakes into nine categories of prevention priority. Predicted probability of occurrence ranged from 0.417 to 1, and we selected thresholds dividing lakes into three equal groups having low, medium, and high probability of *M. spicatum* occurrence. We did the same for predicted cover values, again trisecting the range of predicted cover. By cross-tabulating the priority categories for both presence and cover, we constructed a three-tiered priority matrix that can be used to plan prevention and management.

3. Results

3.1 Occurrence models

Logistic regression models predicting *M. spicatum* presence performed well, with AUROC = 0.81. The probability of *M. spicatum* occurrence was statistically significantly related to water quality, morphometry, climate, dispersal and geology. *M. spicatum* occurrence was positively related to road density, surface area, maximum temperature of the warmest month and lake maximum depth while occurrence was negatively related to %CaO in the watershed, annual temperature range and mean distance from all source populations. Mean cross-validated deviance was 515, Tjur's coefficient of determination was 0.32, and the model accounted for 22% of deviance. We mapped the predicted probability of occurrence for all surveyed, uninvaded lakes (Figure 1b).

Comparing model-predicted probability of presence to statewide occurrence data collected by WDNR revealed that modeled predictions were highly accurate. The relationship between sensitivity and specificity of the model across the entire range of possible occurrence thresholds indicates high model performance (AUROC = 0.94). In a prevention program, false absences may lead managers to conclude a lake is 'safe' when it is not, while false presences may result in over-cautiousness. Since false absences may be perceived less preferred than false presences, we chose to minimize false absences when selecting the threshold of predicted probability at which we would consider the species to be present. Using the relationship between threshold predicted probability and observed presences and absences, we found that using 0.417 as a threshold to indicate likely occurrence resulted in no more than 1% of predicted absences to be false (Table 2). We mapped the model-predicted probability of occurrence for all lakes exceeding the threshold of 0.417 (Figure 2a).

3.2 Cover models

On average, lakewide *M. spicatum* cover was 13% (Figure 1c). *M. spicatum* cover models explained a statistically significant portion of the observed variation (Log-likelihood = 416, pseudo $R^2 = 0.25$; Table 3). Mean cross-validated deviance was -678, root mean squared error was 0.16, while cross-validated correlation coefficients for observed and predicted values were $r = 0.32$ and $\varrho = 0.34$. Mean *M. spicatum* cover was statistically significantly positively related to conductivity, soil erodibility and the maximum air temperature of the warmest month. *M. spicatum* cover was negatively related to maximum lake depth and water clarity. Variability in *M. spicatum* cover as predicted by the precision submodel was statistically significantly positively related to % lithological calcium oxide content, soil erodibility and maximum lake depth, while variability was negatively related to water clarity.

Observed and predicted *M. spicatum* cover for the final model developed on the subset of 269 lakes with *M. spicatum* populations were highly correlated ($r = 0.51$, $\varrho =$

0.48), though cross-validated performance was lower, indicating some uncertainty in modelled predictions. Model-predicted cover explained a significant amount of variation in observed cover. Predictions were relatively unbiased (b = 0.002) and consistent across the range of predictions (m = 0.94). Model-predicted cover estimates explained 25% of the variation in observed cover (F = 101, df = 294, $p < 0.001$; Figure 3). For all surveyed lakes not yet observed to have EWM populations, we present a map of predicted cover values (Figure 1d). Finally, we used the model developed on the subset of 269 surveyed lakes to predict cover on all lakes over 1 ha. We present predicted cover values for all lakes exceeding the probability of occurrence threshold of 0.417 (Figure 2b).

3.3 Prioritizing management

We describe overall site-specific vulnerability to invasion by combining occurrence and cover risk for uninvaded lakes with predicted probability of *M. spicatum* presence exceeding our previously-established threshold of 0.417. First, we trisected the range of predicted occurrence probabilities into categories of low, medium and high risk (cutoffs were 0.61 and 0.80). Then, using the model predicting *M. spicatum* cover (Fig. 4), we divided lakes into three categories of cover risk (cutoffs were 0.24 and 0.48). Cross-tabulating the three priority categories for presence and cover reveals only a small percentage of lakes fall into the high priority category, that is, few lakes are likely to be invaded and have high cover (Table 4, Figure 5, lakes listed individually in Supplementary material, Appendix 3, Table A2).

4. Discussion

Site-specific invasion vulnerability depends on the probability of introduction, establishment and impact of an invasive species (Vander Zanden and Olden 2008). Knowing where an invader might be introduced, the likelihood with which it persists and its associated impacts are three critical pieces of information that support effective invasive species management. We explored patterns in occurrence and cover of *M. spicatum* in light of the arrival, establishment and impact filters that mediate the invasion process. We built species occurrence and cover models that incorporate factors related to physical and environmental conditions, climate, dispersal, geology and landuse. This is the most extensive modeling effort to date for *M. spicatum* and the first to jointly address factors related to introduction probability, establishment and impact. Finally, we join occurrence and cover estimates in a prioritization matrix that integrates all three aspects of invasion vulnerability that may be used to plan proactive and reactive lake management.

4.1 Occurrence models

The first step in determining the risk of invasion is it to develop an understanding of the likelihood of introduction and establishment. Several variables likely to determine *M. spicatum*'s probability of introduction were significantly related to occurrence—lakes with *M. spicatum* populations tended to be larger, deeper, and had more roads nearby. Roads may be associated with increased propagule pressure via increasing accessibility to humans, who have been implicated as an important vector of invasive species transport (Johnstone et al. 1985). Larger lakes, which tend to be deeper, have more access points and experience higher boating activity, which may also increase the rate of introduction (Reed-Andersen et al. 2000). Deeper lakes are often have clearer water which is considered desirable; large, deep and clear lakes may experience increased visitation by boaters, and thus increased propagule pressure and vegetative spread via plant fragmentation. In addition, higher spatial heterogeneity in larger lakes may reduce the number of stochastic extinction events and enhance population persistence (Brönmark 1985).

Invaded lakes had a smaller average distance to all *M. spicatum* source populations. Dispersal ability tends to decline with distance, and distance from source populations is often helpful in predicting patterns in invasive species occurrence (Havel et al. 2002, Vaclavik and Meentemeyer 2009). Distance from source populations in the occurrence model may capture constraints related to dispersal, but it may also reflect spatially auto-correlated environmental conditions that are difficult to disentangle (Allouche et al. 2008). Annual temperature range was positively associated with invasion status, while annual temperature range was negatively related. *M. spicatum* is capable of growing in a wide range of temperatures with populations extending up to 66.63°N latitude. Temperature is unlikely to be a limiting factor for this species in the spatial extent considered by this study, so climate factors may be better associated co-linear environmental factors, or the earlier introduction of *M. spicatum* in the southern part of the state.

Following introduction, survival of an invasive population is in part determined by local environmental conditions. Calcium oxide surface rock content, which demonstrates a strong spatial pattern associated with the presence of a large dolomite deposit in southeastern Wisconsin, was negatively related to *M. spicatum* occurrence. Marl lakes occur in abundance in this area of the state, and they have unique biogeochemical qualities. Calcium carbonate in high-alkalinity, high-pH marl lakes is plentiful, but rapidly co-precipitates with phosphorus and dissolved organic material. The low concentrations of free CO_2, phosphorus, iron and manganese in the water of marl lakes can limit macrophyte growth (Rech et al. 1971).

Relative to dispersal and climate variables, local environmental conditions were not as important in explaining occurrence patterns. This may be due to *M. spicatum*'s broad environmental tolerances and the fact that measured environmental variables were mostly within published tolerance ranges (Smith and Barko 1990).

Using widely available physical, environmental, climate, geological and landuse factors, we predicted the probability of *M. spicatum* occurrence on the largest set of lakes we know of (9,825). The statewide occurrence model performed well, which may be a result of increased model accuracy produced by a larger sample size (Wisz et al. 2008). AUROC is a threshold-independent performance measure that has been shown to be independent of prevalence, which is significantly lower in the statewide dataset (Manel et al. 2001).

While species occurrence models typically assume a population is at equilibrium, this assumption is violated in the case of a range-expanding species like *M. spicatum*. The inclusion of true absence data along with spatial variables related to dispersal decreases the bias that would otherwise be present (Václavík and Meentemeyer 2009). *M. spicatum* occurrence data on the 657 lakes with macrophyte surveys can be confidently assumed to represent true absences less an amount of unquantified detection error. Error is most certainly higher in the statewide dataset. The statewide model likely underestimates true probability of occurrence, though validation conducted by a previous study revealed few *M. spicatum* populations were missing from the statewide dataset (Latzka 2015). Still, there are certainly a number of false absences that have not yet been detected. While the predictions we present for the statewide set can be useful in planning prevention and management activities, we recommend some degree of caution in their use.

4.2 Cover models

Once probability of introduction and survival is known, the remaining question is one of impact: if the species is introduced, and if it survives, is it also likely to cause problems? While impact is arguably the most important filter to consider, it is often the most difficult to predict (Parker et al. 1999). *M. spicatum* has been associated with varying effects on native flora, macroinvertebrates, habitat, and water quality (Carpenter 1980b, Madsen et al. 1991, Wilson and Ricciardi 2009, Kovalenko et al. 2010). *M. spicatum* has also been associated with recreational impairment and decreased lake property value (Horsch and Lewis 2009, Olden and Tamayo 2014). While more work is needed to adequately quantify the abundance-impact relationship, we can reasonably assume that magnitude of socio-economic and ecological effects are linearly related to abundance (Latzka et al. 2016). Hereafter, we hold cover as a proxy for impact.

The beta regression model predicting *M spicatum* cover explained 25% of the variation observed. Several local environmental variables were important to *M. spicatum* cover. Conductivity and soil erodibility were positively associated with *M. spicatum* cover and Secchi depth was negatively associated. Centered and standardized predictors allow model coefficients to be interpreted as effects sizes, and conductivity had one of the largest effects observed. Conductivity is a strong driver of macrophyte community composition and abundance. *M. spicatum* is capable of using bicarbonate as a source of carbon dioxide, giving it a competitive advantage in high conductivity, high-alkalinity lakes (Hutchinson 1970). In addition, each of the significant environmental factors is related to surface water nutrient enrichment. The plant nutrient phosphorus is primarily derived from rock and is generally higher when watersheds are comprised of highly erodible soil (Verheyen et al. 2015). Erodible soil is also often favored for agriculture, where exogenous additions of fertilizer further enrich surface waters (Parry 1998). Eutrophic relative to oligotrophic waters have higher concentrations of dissolved substances and thus higher conductivity. Finally, as nutrient levels increase so does phytoplankton productivity, resulting in decreased water clarity (Smith 2003, Egertson et al. 2004). *M. spicatum* is considered to be relatively tolerant of nutrient enrichment (Smith and Barko 1990). Nitrogen and phosphorus enrichment and agricultural activity has been associated with increased abundance of *M. spicatum* (Anderson and Kalff 1986, Shuskey et al. 2009).

Relative to the occurrence model, environmental predictors were emphasized in the cover model. While *M. spicatum* is likely to survive (occur) in a large number of lakes considered in this study, conditions that create high abundance may occur less frequently. That the species, like most invaders, shows a highly right-skewed abundance distribution is consistent with this theory (Hansen et al. 2013).

Maximum air temperature was positively related to *M. spicatum* cover and maximum depth was negatively related. The species' optimum temperature for photosynthesis is 35°C which for Wisconsin, is relatively high. Climate in this case may indeed be mechanistically associated with increased *M. spicatum* cover. Alternately, increased cover in the southern portion of the state could be due to increased boat traffic and fragmentation contributing to within-lake population expansion or a history of aquatic plant management actions increasing the populations of disturbance-tolerant species. The earlier data of introduction in the southern part of the state may also explain cover patterns, though declines in populations around 10 years following introduction have been widely reported. Given that the estimated date of introduction to the southern part of the state is in the early 1960s, this variable may be a less likely predictor (Carpenter 1980a, Bates and Smith 1994, Nichols 1994).

Variability in *M. spicatum* cover as captured by the precision submodel of the beta regression was negatively related to Secchi depth. Given the negative of effect of water clarity on mean cover, we can assume that increasing water clarity predicts lower levels of *M. spicatum*, but that relationship, especially in clear lakes, is highly variable. The relationship between nutrient enrichment and water clarity in fact is nonlinear, in part due to the stabilizing effect of aquatic plants and their ability to create conditions of clear water via increased settling and nutrient burial rates (Barko and James 1998, Jeppesen et al. 1998). Thus, clear water in some lakes may be associated with low nutrients and sparse macrophyte populations, but in others, it is a direct result of abundant macrophyte communities. At the other end of the nutrient spectrum, soil erodibility was positively related to the precision parameter, thus positively associated with variability in cover. Nutrient over-enrichment can in certain cases result in catastrophic rigime shifts that are associated with markedly reduced macrophyte cover (Edwards et al. 2013). Thus, non-linear dynamics of macrophyte- and phytoplankton-dominated communities may contribute variability in *M. spicatum* cover along the enrichment spectrum (Hilt et al. 2013).

Maximum depth and lithological calcium oxide content in the watershed were also positively related to the precision parameter and help explain observed variability in the cover response. As lakes get deeper, lakewide cover is highlydependent on the bathymetry of the lake and resulting area of the habitable littoral zone, lakes of the same depth having different bathymetric profiles are likely to vary in lakewide macrophyte cover. As mentioned in section 4.1, calcium oxide content is likely predictive of calcium carbonate substrate and highly altered biogeochemical conditions. When the amount of dolomite in the watershed is high, marl lakes are common. Marl lakes tend to have less suitable environmental conditions for macrophytes and can present start contrast to nearby lakes without marl sediment.

4.3 Prevention prioritization: uniting occurrence and cover

Understanding all levels of the invasion process is necessary to generate realistic predictions of system-specific risk (Vander Zanden and Olden 2008, Bradley 2012). However, few efforts to date have produced integrated risk assessments (but see Kulhanek et al. 2011). We presented empirical predictive models that relate to introduction and establishment probability alongside models that estimate cover. We then defined a prioritization scheme to unite them under a single map of invasion vulnerability. We used simple matrix to assess overall prevention priority, but priorities within this matrix can be assigned by managers using any prioritization scheme that makes sense. We decided here to rank both vulnerability scores from 1:3, but matrix dimensions could theoretically be as complex as is warranted in light of the variability of the predictions. Additionally, we chose to select risk thresholds by simply trisecting the observed range, but the step by which thresholds are selected may be better determined by explicitly defining the shape of the impact-abundance relationship (Yokomizo et al. 2009, Latzka et al. 2016).

Considered separately, occurrence probability is often used to target preventative measures toward lakes with a high likelihood of invader introduction and persistence. However, when the area of high risk is extremely large, monitoring all sites can still be cost-prohibitive. Actions may then be directed at a small set of lakes with the highest probability of occurrence. Here, we suggest an alternative prioritization scheme that considers modeled cover in addition to probability of occurrence. Thus, prevention activities may be directed to the subset of lakes likely to receive and support a species but that are also likely to experience high impact. Alternately, the prioritization framework, in particular the risk of high *M. spicatum* cover can be used to guide reactive management following a new detection. Here, a wait-and-see approach may be advised in low priority lakes, while more aggressive actions may be applied to those of high priority. In this way, prevention dollars can used with maximal effectiveness, while management actions may targeted toward high-impact lakes, thus saving money and minimizing collateral damage to non-target species.

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6. Supporting information

Supplementary material can be found in Appendix 3. Table A1 presents a statistical summary of variables used to predict *M. spicatum* occurrence and cover, their units, description and spatial scale. Table A2 lists overall prevention priority for a set of uninvaded lakes, along with occurrence risk, cover risk and prevention priority.

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8. Tables

Table 1. Estimated coefficients for *M. spicatum* occurrence model developed on 657 surveyed lakes. Coefficients expressed as odds ratios calculated for centered and scaled predictors, profile confidence intervals in parenthesis.

Predictor	Coefficient
Intercept	0.13*** (0.07–0.21)
Road density (log (m/ha +1))	1.93*** (1.42–2.74)
Surface area (log ha)	1.72*** (1.33–2.31)
Max. air temp (°C * 10)	1.69** (1.23–2.40)
Maximum depth (log m +1)	1.55** (1.20–2.06)
Conductivity (log µS/cm)	1.47 (0.72–3.20)
Alkalinity (log mg $CaCO_3$ +1)	1.44 (0.67–3.03)
Soil erodibility (kwfact)	1.17 (0.93–1.49)
Watershed urban ($\sqrt{\%}$)	1.07 (0.77–1.53)
pH	1.06 (0.80–1.41)
Secchi depth (log m +1)	0.85 (0.62–1.16)
Watershed agriculture ($\sqrt{\%}$)	0.81 (0.58–1.10)
CaO ($\sqrt{\%}$)	0.74** (0.57–0.92)
Annual temp range (°C * 10)	0.64* (0.42–0.92)
Mean distance source (log m)	0.61*** (0.45–0.82)

Note: *$p<0.05$, **$p<0.01$, ***$p<0.001$

Table 2. Cross-validated confusion matrix relating observed to predicted *M. spicatum* occurrence using the statewide model for 9285 lakes. We set the threshold for classifying the predicted probability as presence at 0.417, a value that allows no more than 1% of the predicted absences to be false absences.

		Observed	
		Absent	Present
Predicted	Absent	7363	74
	Present	1267	581

Table 3. Parameters estimated using a beta regression model developed using data on 657 surveyed lakes. Coefficients and standard errors for mean (logit link) and precision submodels (log link) describe patterns and variability in *M. spicatum* cover.

	Mean submodel				Precision submodel			
	Linear		Quadratic		Linear		Quadratic	
Predictors	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	-1.64***	0.36			1.55***	0.47		
Conductivity (log µS/cm)	0.87	0.6	-0.49*	0.24	-0.63	0.78	0.4	0.32
Mean distance source (log m)	0.33	0.21	0.05	0.11	-0.15	0.29	-0.13	0.15
Max. air temp (°C * 10)	0.3*	0.14	-0.22	0.11	-0.25	0.19	0.26	0.16
Road density (log (m/ha +1))	0.15	0.24	-0.005	0.1	-0.12	0.31	-0.04	0.12
Watershed urban ($\sqrt{\%}$)	0.15	0.17	0.005	0.05	0.19	0.22	-0.08	0.06
Watershed agriculture ($\sqrt{\%}$)	0.12	0.15	0.01	0.09	-0.34	0.21	-0.03	0.12
CaO ($\sqrt{\%}$)	0.02	0.12	-0.02	0.05	0.39*	0.17	-0.12	0.07
Soil erodibility (kwfact)	0.002	0.09	-0.29**	0.1	0.03	0.13	0.39**	0.14
Secchi depth (log m +1)	-0.1	0.11	-0.25***	0.07	-0.01	0.15	0.22*	0.09
pH	-0.11	0.26	0.04	0.11	0.48	0.33	-0.17	0.13
Surface area (log ha)	-0.21	0.22	0.04	0.06	-0.2	0.29	0.03	0.08
Annual temp range (°C * 10)	-0.31	0.24	-0.01	0.08	0.23	0.33	-0.04	0.11
Maximum depth (log m +1)	-0.35*	0.14	-0.05	0.07	0.49***	0.18	0.11	0.1
Alkalinity (log mg $CaCO_3$ +1)	-0.46	0.66	0.41	0.32	0.72	0.84	-0.47	0.42
Log likelihood	415							
Df	58							
Pseudo R2	0.25							
*Note: *p<0.05, **p<0.01, ***p<0.001*								

Table 4. Management priority matrix for all lakes with probability of presence above the threshold that allows no more than 1% of predicted absences to be false (0.417). High priority (tier 1) can be considered of immediate management concern due to relatively high likelihood of invasion and risk of high cover. Low-priority (tier 3) lakes are less likely to be invaded and are less likely to have *M. spicatum* populations that achieve high cover.

		Cover		
		High	Med	Low
Occurrence	High	▓ 34	▓ 55	▒ 122
	Med	▓ 6	▒ 83	□ 311
	Low	▒ 9	□ 103	□ 561

▓ Tier I	▒ Tier II	□ Tier III

9. Figure captions

Figure 1. (a) Surveyed lakes (N = 657) showing observed presence and absence records for *M. spicatum*; (b) Predicted probability of *M. spicatum* presence estimated by a logistic regression model and mapped in blue for the 272 uninvaded surveyed lakes, grey dots show known EWM populations; (c) Observed *M. spicatum* cover from macrophyte surveys on 296 surveyed lakes with *M. spicatum* populations; (d) Predicted *M. spicatum* cover drawn from a beta regression developed on 296 lakes with *M. spicatum* cover estimates.

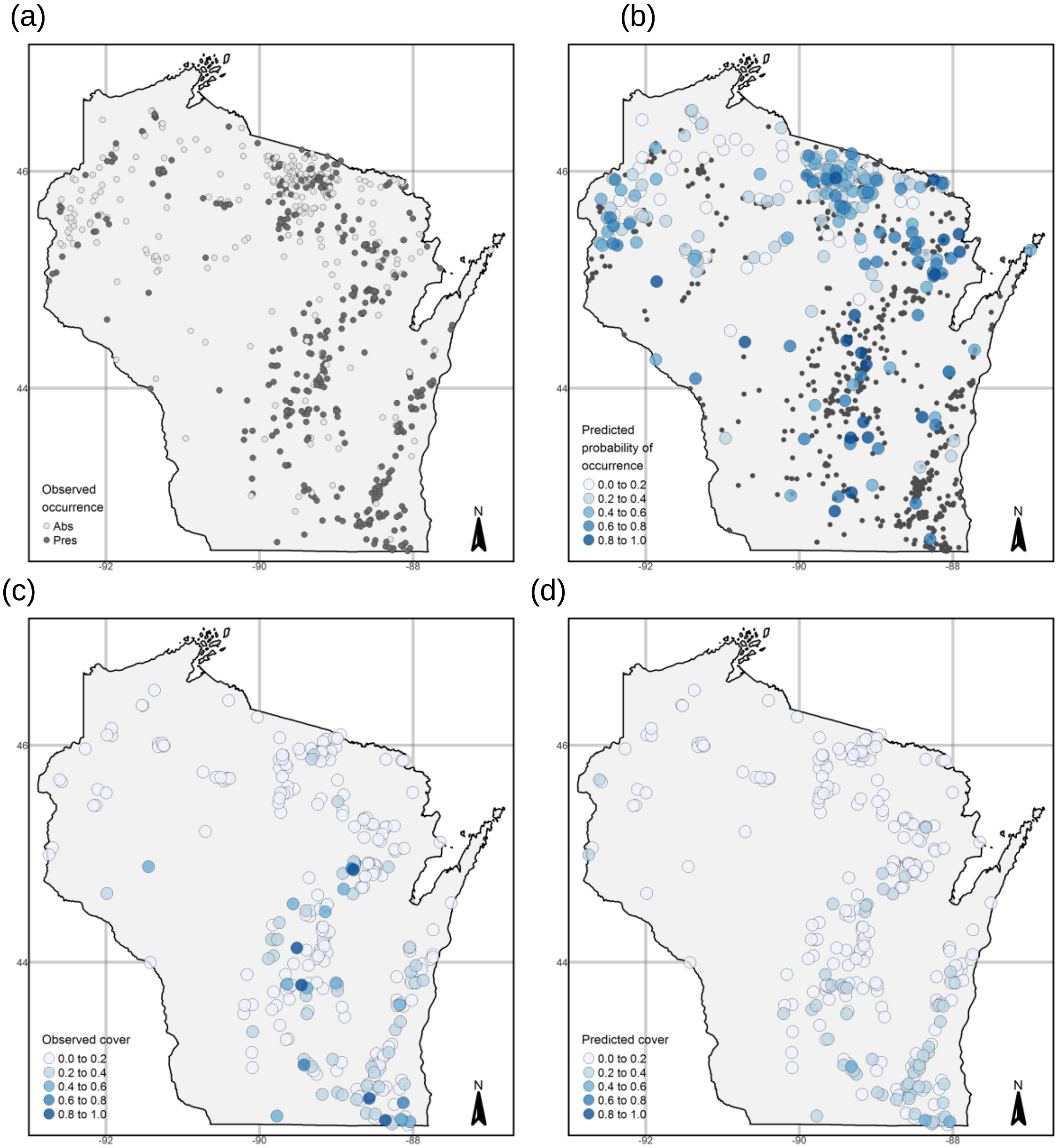
Figure 2. Predicted probability of *M. spicatum* occurrence (a) and cover (b) for all lakes over 1 ha in size (N = 9825) using models developed on the surveyed subset (N = 657). Blue dots indicate lakes with probability of presence exceeding 0.417, the largest threshold at which no more than 1% of predicted absences are false. Grey dots are lakes with probability of occurrence below this threshold.

Figure 3. Linear model relating model-predicted *M. spicatum* cover and observed cover. Line of best fit is solid, while the 1:1 line is dashed. R^2_{adj}, linear model equation, and p value at top left.

Figure 4. Map displaying prevention priority as determined by modelled risk of *M. spicatum* occurrence and abundance and following the prioritization matrix presented in Table 4. Colors indicate management priority tier, where tier 1 indicates the highest

prevention priority, where *M. spicatum* has a high probability of occurring and may attain high cover.

10. Figures



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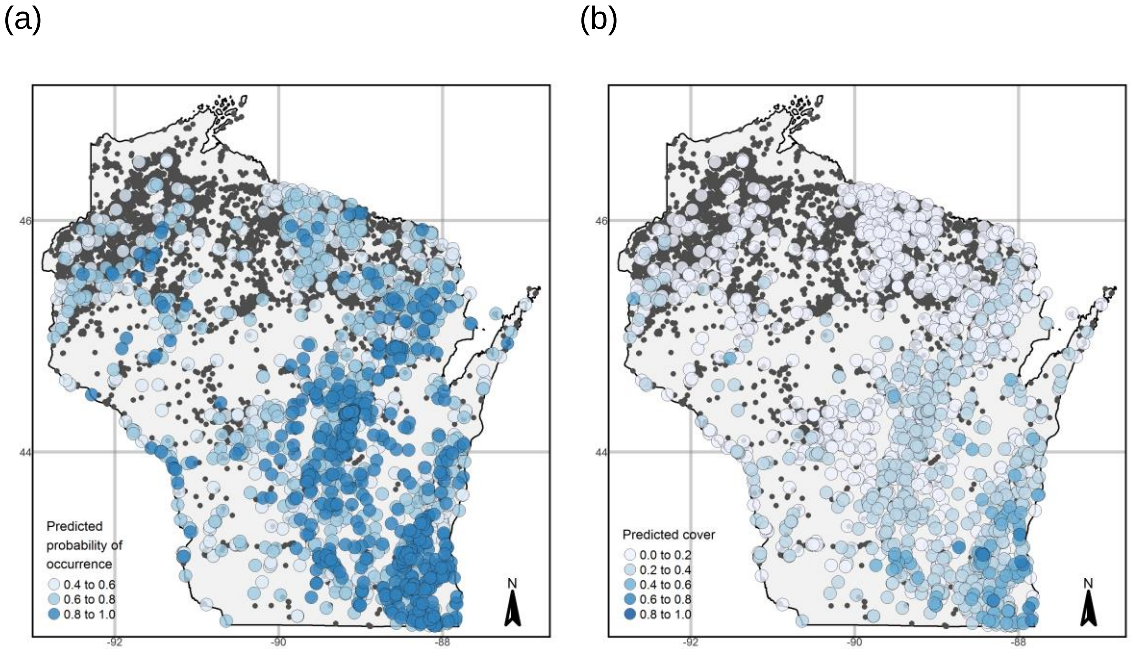

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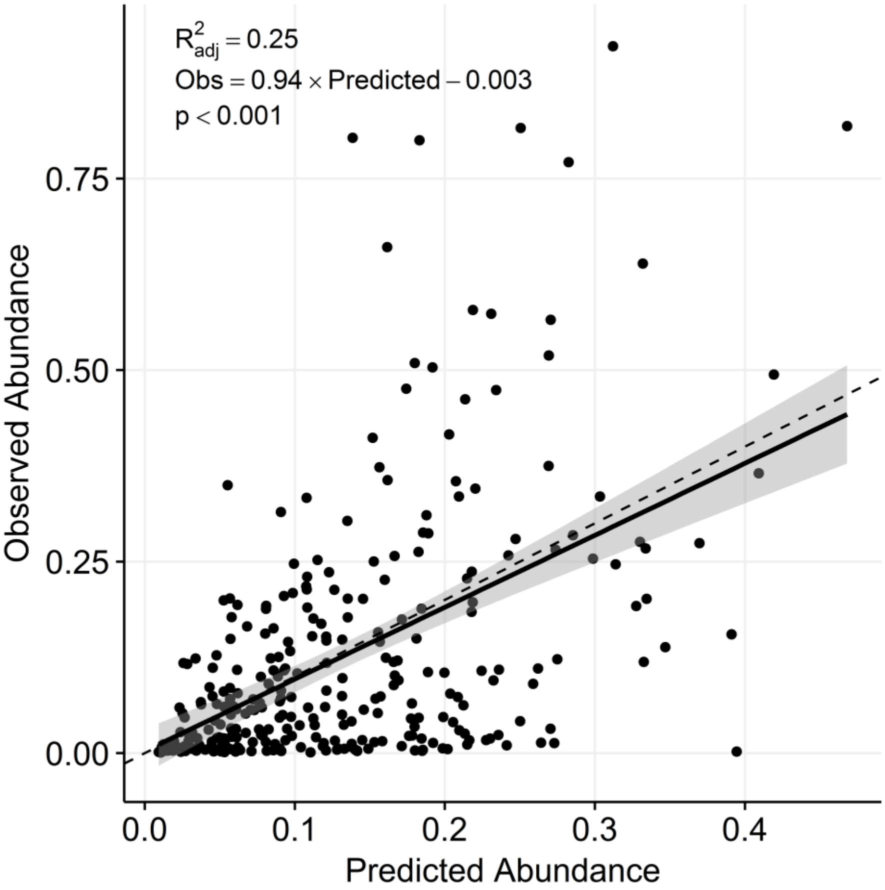

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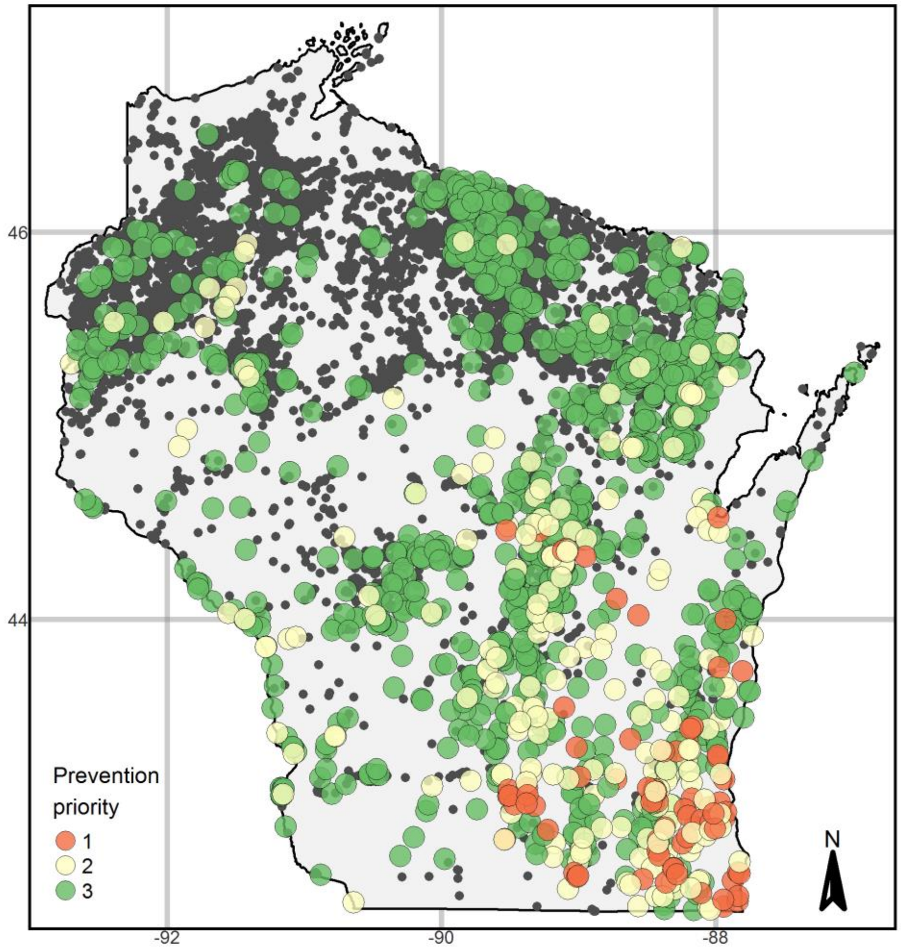

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CHAPTER 4

VOICES OF THE NAMEKAGON: A MULTIMEDIA INTERDISCIPLINARY NARRATIVE

Coauthors: J. Van Winkle, C. Blanke, H. J. Bullard, S. Peterson

Mikulyuk, A. and J. Van Winkle. 2017. Voices of the Namekagon. *Online at:* http://www.naturevoiceswisconsin.org

Mikulyuk, A., H. J. Bullard, S. Peterson, J. Van Winkle, C. Blanke. 2016. At the Confluence of Art and Science. Edge Effects. University of Wisconsin Center for History and the Environment Digital Magazine. 22 Sep 2016.

Abstract

Voices of the Namekagon is an interdisciplinary multimedia project with the central goal of celebrating and disseminating aspects of the social, scientific and natural history of the Namekagon River, a culturally and ecologically significant natural place in northwestern Wisconsin. The *Voices* project blends scientific and filmmaking processes to tell a rich place-based story in which we explore new methods of communicating about science, natural resources policy and human dimensions of ecology. We combined conversations, ecological data, film and images to explore the Namekagon River as a literal and figurative thread connecting people to the land and to each other.

Secondarily, the work exists as a case-study in art-science collaboration. While working on the project, we simultaneously constructed a meta-narrative that reflects on the nature of art-science collaborations in general and our experience of this collaboration in particular. We hope that our work will support continued interdisciplinary research and place-based engagement, having broader impacts that extend beyond the local Namekagon community to the larger interconnected network of people who care about natural places and our shared ecological future.

1. Background

As climate change, environmental degradation and uncertain futures threaten our global ecosystem, political instability and confusion has only increased. Despite the emergent nature of issues like global climate change and decreasing global water security, humans have yet to achieve consensus on the best approach to solving wicked environmental problems (IPCC 2000, Vörösmarty et al. 2010, Foley et al. 2011). The struggle to understand and communicate complex scientific realities unfortunately hampers a constructive engagement with some of the most pressing issues of our time.

Wicked problems by definition defy a simple technological solution, so it is understandable that we lack consensus on what to do about them. But some of the reason for ongoing confusion can be traced to scientists' communication failures. In the case of climate change, the failures may be traced to set of false assumptions about the public as an audience (Moser and Dilling 2011). Ranging from inappropriate framing and inadequate consideration of cultural values to over-emphasizing the role of a public knowledge deficit, several characteristics of early climate change communication likely contributed, at least in part, to the public's resistance to accept climate realities (Nisbet 2009, Kahan 2010, Stoknes 2014).

Fortunately, in reflection on past missteps and with an increased understanding of the evolving nature of the production and consumption of media, the scientific community has produced work aimed at improving scientific communication (Bubela et al. 2009, Olson 2009, Baron 2010). We have collectively begun to define a set of best practices in communication, including, for example, using figurative language to communicate clear, simple concepts that are given adequate context and delivered with consideration of the audience in question (Somerville and Hassol 2011). Simultaneously, we have begun to see the value in interdisciplinary efforts in crafting effective messages that support public understanding and action (Pidgeon and Fischhoff 2011).

Art-science collaborations are one such interdisciplinary endeavor. They have been shown to produce understanding and shared empathy among participants, and they have been observed to lead to innovative approaches to communication (Jacobson et al. 2016, Lesen et al. 2016). Additionally, leveraging narrative in communication has been suggested to increase non-expert comprehension and interest in science.

(Dahlstrom 2014). With little knowledge of each other’s disciplines and no central aim other than to ‘have a life-changing experience’, in 2014, we (an aquatic ecologist and a filmmaker) began an undefined collaborative project to explore opportunities in art-science collaboration.

Over the next several years, we defined, executed, and disseminated a multimedia project titled *Voices of the Namekagon* in which we blended scientific and filmmaking processes to tell a rich place-based story. Working collaboratively, we researched and produced a web-based multimedia collection of film, sounds, data, images, and maps exploring manifold dimensions of a river of great historical and ecological significance to the state of Wisconsin. We made extensive use of narrative and employed multiple communication strategies. In a shared belief that sophisticated development of the affective qualities of communication increases its effectiveness, we also worked to develop and celebrate those qualities in our work.

2. Central Aim

Voices of the Namekagon dwells centrally on discovering and communicating a set of compelling narratives related to the Namekagon River and its watershed. The work contains set of thematically-organized vignettes highlighting the Namekagon’s people, biota, and the ecosystem’s processes and flows. We employed a diverse and changing presentation style in which our communication approach varies from vignette to vignette. In certain cases, we concentrated on compelling narratives told by a few of the Namekagon stakeholders. Often, we used human interlocutors to speak for the river, and sometimes we let the river speak for itself. We presented data, but in an interactive way we hope will lead to exploration and the development of new questions. In addition, we chose to present a positive perspective wherever possible, offering an uplifting tenor as counterpoint to our very real concern regarding future of environmentalism in Wisconsin and the emerging threats of the Anthropocene. In essence, we used multiple strategies to construct a place-based multimedia portrait to support increased engagement with social and ecological realities of the area (Smith 2002).

3. Process

At the beginning of our collaborative work, we struggled to find common ground. Over the course of a year, we employed dialectical and qualitative research methods that ultimately resulted in a shared concept and vision. At first, we cast a wide net, conducting in-depth interviews with a diverse group of ecological professionals, followed by the coding and analysis of that information. Most of our interviewees wanted to speak with us 'off the record', so we found that much of the information we had gathered on individual perspectives of the state of ecology in contemporary socio-political climate could not be made public. It was this qualitative research that led us to focus on narrative in communicating a positive and uplifting message. However, the precise subject and nature of the project was unclear during its entire first year.

Several drastic changes in natural resources policy at the state level in Wisconsin led us to reflect on Wisconsin's legacy of environmentalism written in the histories of Aldo Leopold and Gaylord Nelson. We continued our research at the Wisconsin Historical archives, which ultimately led to our discovery of historical footage of Gaylord Nelson traveling down the Namekagon River in support of its inclusion under the National Wild and Scenic Rivers Act of 1968. We were struck by the simplicity and power of that pro-environmental action and decided to re-perform his trip down the Namekagon, this time collecting images, footage, data, and stories as we traveled. We paddled 92 miles of the river, ultimately settling on an open-ended approach to the project, letting it evolve organically. Over a series of six field trips to the river, we built relationships with the stakeholders in the watershed that ultimately guided our work.

4. Content

The project presents three types of river "voices" represented by humans, nature (biota) and the ecosystem. Our aim was to provide a mixture of cultural, ecological, personal and aesthetic perspectives united under this framework. Here, we briefly outline the content in each of the three areas.

The first vignette in the ‘voices of the ecosystem’ series deals with the challenges and opportunities of watershed-scale ecosystem management (Sabatier et al. 2005). In an interview with Max Wolter and Kathy Bartleson of the Wisconsin Department of Natural Resources, we highlight non-point source pollution as a wicked environmental problem that has no tractable solutions, while celebrating partnerships among the river and lake associations that support ecologically-friendly riparian development models. Second, we explore the 1927 construction of the Trego dam and the resulting exclusion of sturgeon from the upper reaches of the river (Kampa 2014). In this vignette, we present the ecological impacts of altered flow regimes and connectivity on river ecology and present a collaborative fish passage project that aims to restore connectivity (Bunn and Arthington 2002). Finally, we present an interactive data explorer centered on the River Continuum Concept in the Namekagon River and the changes that occur in macroinvertebrate communities as one moves downstream (Vannote et al. 1980).

In the vignettes representing voice of the people, we present personal stories that are deeply connected to the Namekagon. The Namekagon is attended to by a small army of volunteer stewards and naturalists. We explore volunteerism and stewardship in an interview with the National Park Service. Next, we present an interview with Brisbane printmaker Christopher Hagen, whose work is heavily influenced by the ecology of northwestern Wisconsin and the ethos he developed while growing up there.

The Namekagon supports economic prosperity in the region, and we present two stories connected to eco-tourism. Kathy Shattuck in Trego, WI, runs a low-impact hospitality business, and she and her partner Jim explain the connection between their business and the River. Next, we present the story of a four-generation family canoe rental business that outfitted Nelson’s journey in 1966. Finally, we present two vignettes related to outdoor recreation and silent sports, and one on nature-based restorative youth programming. The Namekagon river area has a rich tradition of stewardship, volunteerism, and outdoor engagement. The material in these vignettes captures the activity of local partnerships, organizations, and activists, while exploring the role of the National Park Service in supporting and facilitating environmental stewardship.

Third, we represent the voices of nature. We present information on native turtles in an interview with graduate student researcher Lauren Mitchell. Bob DuBois of the Wisconsin DNR participates in a sound piece describing the diversity and conservation of Namekagon dragonflies and damselflies. We present a vignette on harvesting and processing wild rice with University of Wisconsin-extension outreach specialist John Haack, while we explore the sport of fly fishing with a father and son pair with a long-standing birthday tradition of fishing the River together. Finally, we present a ‘River Portrait’ using film and music to capture the natural beauty of the river.

Together, the series of conversations, images, data and film that comprise the project function as a set of bridges to understanding the River's rich and complex nature.

5. Reflections

While institutionally separated, there is much that unites artistic and scientific disciplines in terms of fundamental goals, epistemology and the creative process. Subjects of scientific inquiry may be fruitful subjects for artistic thought and vice versa. The emerging practice of sci-art emphasizes similarity among scientific and artistic disciplines in their search for greater understanding of the human experience, although the central humanistic mission may not apply to all art-science practice (Magazine 2017). In particular, we see collaborative relationships as a means by which practitioners may achieve critical perspective on their practice by generating and responding to questions not native to their disciplines' lines of reasoning (Kieniewicz 2013). We initiated our collaborative endeavor in hopes of discovering methods and perspectives previously unknown to us, not just to produce a compelling piece of work, but also to critically explore our own practices and our understanding of each other's disciplines. We strove to not just to employ our own methods in pursuit of more effective communication, but to learn with each other to employ new methods and stretch the boundaries of our individual disciplinary and interdisciplinary knowledge.

We immediately recognized listening and communication as two of the central themes of our project, but we began our collaboration with a shared opinion that too often, art-science collaborations result in an artist translating scientific findings for the public, or a scientist dabbling in art. We wished to avoid this outcome by placing equal importance on artistic and scientific approaches to research and communication. However, throughout the project, we had difficulty responding to questions that were strongly rooted in disciplinary language (e.g., Where is the “science” in this project? What does the “art” achieve from a research perspective?). We hoped to generate a different discussion: not, “is this art or science?” but, rather, “what is this work’s individual identity, what is its agency?”

We sought to transcend the rigid disciplinary identities that we at times elected, and at others were cast upon us. We agreed that the first step in this process was developing shared empathy. We built trust and respect for one another first, which ultimately resulted in our designing a project that was novel to each of us: native to neither collaborator’s medium and where neither collaborator’s disciplinary practice overshadowed the other’s. The selection of a river ecosystem by a lake ecologist and the decision to film in nature by a studio-trained filmmaker was intentional. We adopted an egalitarian approach to question development and data collection. We regularly reflected on our relationship to the ecological and social communities of our studies. We feel that overall, our approach led to a mutually fulfilling experience and an effective outcome.

We strove to avoid the simple instrumentalization of ‘art’ by ‘science’ to address a public relations problem or the instrumentalization of ‘science’ by ‘art’ in pursuit of inspiration and subject matter. We reflected carefully on the others’ perspective and attended to the reciprocal influence collaboration had on our individual work. Mikulyuk reports a marked shift in the way she understands the construction and production of scientific knowledge. Close engagement with the narratives at work behind the focus of her inquiry led her to consider her scientific practice from a broader perspective, provoking a consideration of the nature of her research writ large. This led her to develop a new approach to asking scientific questions that considers story earlier in her scientific process. Van Winkle also reported a shift in how she reflects on her artistic practice. During the course of the project, she became SCUBA-certified and invested underwater camera gear to capture images that reflect the inside of the river. While her primary media and basic methods remained unchanged, she found the ways she questions the world expanded with greater exposure to ecological field work and the process of scientific knowledge production. She has developed a deeper understanding of the necessity of repetition and collection of large amounts of data in forming ecological conclusions. This new understanding has led her to begin to explore ways through her future film projects to encourage state and federal funding for ecological research.

6. Conclusion

We found this endeavor to be a transformative experience that influenced our pedagogical approach, practices, and academic interests in positive ways. We brought back to our work the influence of another and as a result have been forever changed. Engaging with and for each other taught us greater facility in navigating disciplinary spaces and we grew more comfortable inhabiting the blurred areas between them. However, during our travels locally and abroad, we engaged a diverse group of thinkers from a variety of backgrounds, and observed a common feeling of frustration with respect to the lack of formal valuation of art-science interdisciplinary work. Indeed, it is often difficult for art-science projects to secure funding, and once funded, students struggle to make time for projects that may be considered extra-curricular. Students of science in particular found engagement in art-science projects to take more time they felt they were permitted to divert from what they considered their core studies. Their struggle for legitimacy was echoed in our constant confrontation of an unyieldingly rigid definition of science and the channels of communication it must necessarily follow. Herein lies one of the most substantial barriers to ongoing interdisciplinary research between the arts and sciences. There can exist no alternate form of valuation within science if the definition of science remains shortsightedly narrow. Science thinking that follows non-traditional modes of inquiry and communication is not formally recognized as science, but rather ‘management’, ‘outreach’, ‘natural history’, or even ‘storytelling’. To confront and solve the emerging problems facing science today, it may help to support an expanded definition of science and increase support for efforts that are often seen as secondary goals by the scientific discipline.

Fortunately, work to increase science literacy and emphasize communication is increasing. Under this effort, it is imperative that we acknowledge radically interdisciplinary endeavors as worthy of support. Wicked problems will require radical solutions, and interdisciplinary exploration may be the best way forward.

7. Acknowledgements

We are grateful to have had the chance to participate in this project, and wholeheartedly thank the Graduate School for its support. We appreciate Dr. Steve Carpenter and Professor Laurie-Beth Clark for securing the grant that supported this work and for their participation and helpful guidance along the way. In what we feel to be a giant step forward in valuing non-traditional scientific production, we sincerely thank advisor Dr. M. Jake Vander Zanden for his support of our efforts and the inclusion of this work in Mikulyuk’s doctoral dissertation. We appreciate the National

Park Service staff granting us filming and research permits on the Namekagon River. We are also very grateful to the individuals who shared their thoughts, knowledge and personal experiences related to the River. Without their collaboration, this project would not be possible. In the near future, we look forward to a community-based screening in Hayward, WI where we will share the results of our project that is currently still in production.

Finally, the most unexpected aspect of the collaborative for which we are grateful is the opportunity for us to spend time together in a variety of settings: on the River, at conferences in Madison and abroad in Uruguay and Australia, in planning meetings on and off-campus, and during our field trips to conduct interviews, document and research. This shared one-on-one time spent in cars, tents, hotels, planes, the canoe, restaurants, coffee shops, and our own homes was when we could talk not only about the project, but get to know each other more by sharing our work histories, our life philosophies and personal stories. We have developed a strong working friendship. We are very grateful to know each other as individuals and to have time to see each other's lives evolve in many different directions over the years. We feel that through this added gift of getting to know and understand each other, we took one small step towards seeking new ways to improve our shared world.

Voices of the Namekagon can be viewed online at: http://naturevoiceswisconsin.org/

The project included a set of public presentations with critical discussion:

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