

# The relative role of environmental, spatial, and land-use patterns in explaining aquatic macrophyte community composition

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**Abstract:** Quantifying the relative role of environmental and spatial factors to understand patterns in community composition is a fundamental goal of community ecology. We applied a tested and repeatable point-intercept sampling method to aquatic macrophyte assemblages in 225 Wisconsin lakes to understand the ability of environmental, land-use, and spatial patterns to explain aquatic plant distribution and abundance. Using a variation partitioning framework in conjunction with Moran eigenvector maps we found that environmental, land-use, and spatial patterns explained 31% of total adjusted variation in aquatic macrophyte assemblages across the landscape. Environmental factors were the most important (contributing 34% of the total explained variation), but all sources of variation were statistically significant. Community composition varied from north to south along a gradient of alkalinity and from disturbed to undisturbed lakes, diverging according to whether disturbance was urban or agricultural. The large amount of shared variation among predictor variables suggests causal relationships are complex and emphasizes the importance of considering space and land-use in addition to environmental factors when characterizing macrophyte assemblages. This work is the first to examine the joint and unique effects of environment, land-use, and spatial patterns on aquatic plant communities.

**Résumé :** La quantification des rôles relatifs des facteurs environnementaux et spatiaux afin de comprendre les patrons de composition des communautés est un objectif fondamental de l'écologie des communautés. Nous utilisons une méthode éprouvée et répétable d'échantillonnage de type point-contact dans des peuplements de macrophytes aquatiques dans 225 lacs du Wisconsin afin de comprendre la capacité des patrons de l'environnement, de l'utilisation des terres et de l'espace à expliquer la répartition et l'abondance des plantes aquatiques. À l'aide d'un cadre de partitionnement de la variation conjointement avec des cartes de valeurs propres de Moran, nous avons trouvé que les patrons de l'environnement, de l'utilisation des terres et de l'espace expliquent 31 % de la variation ajustée des peuplements de macrophytes aquatiques dans l'ensemble du paysage. Les facteurs environnementaux sont les plus importants (contribuant 34 % de la variation totale expliquée), mais toutes les sources de variation sont significatives. La composition des communautés varie du nord au sud suivant un gradient d'alkalinité et aussi des lacs perturbés aux lacs non perturbés de manière différente selon qu'il s'agit de perturbation urbaine ou agricole. La quantité importante de variation partagée entre les variables prédictives laisse croire que les relations causales sont complexes et souligne l'importance de considérer l'espace et l'utilisation des terres en plus des facteurs environnementaux lorsqu'on veut caractériser des peuplements de macrophytes. Notre travail est le premier à examiner les effets conjoints et uniques des patrons de l'environnement, de l'utilisation des terres et de l'espace sur les communautés de plantes aquatiques.

[Traduit par la Rédaction]

## Introduction

Biological community composition varies across time and space in response to biotic and abiotic conditions (Jewell 1935; Neill 1975; Miller et al. 2004). Understanding the forces that structure ecological communities allows us to make better management decisions, form predictions about the strength and direction of ecological change, and even understand the collective influence of human behavior on the environment. Many factors that determine species distribution and abundance do so in a very complex way, often

times operating in concert to cause cascading effects on ecological communities (Wagner and Fortin 2005). One of the primary goals of ecologists is to quantify and compare these interactions.

Aquatic plants are affected by local environmental conditions (e.g., alkalinity, sediment type), broader spatial limiting factors (climate, dispersal), as well as anthropogenic pressures (watershed development, direct removal of plants). All of these factors simultaneously influence species abundance and distribution. In upper midwestern lakes of the United States, urban or agricultural development in a watershed is

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often associated with eutrophic systems with lower species richness and fewer floating-leaf plants (Radomski and Goeman 2001; Hatzembeler et al. 2004; Sass et al. 2010). However, in Wisconsin, watershed disturbance is also negatively correlated with latitude. Latitude in turn is negatively related to presence of non-native Eurasian watermilfoil (*Myriophyllum spicatum*, originally introduced in southern Wisconsin), which has been shown to decrease native species richness in lakes (Boylen et al. 1999). Additionally, a shift from small rosette-form isoetid communities to larger, more species-rich elodeid communities occurs with increased residential development (Borman 2007). The presence of isoetid communities is also predicted by low bicarbonate concentrations associated with lakes high in the drainage network (Alexander et al. 2008). It is obvious, then, that land use can influence environmental factors and both can be spatially structured. The relative contribution of environmental conditions, space, and land use to the structure of aquatic plant communities has not yet been documented.

Relating environmental conditions or land use to plant community composition involves statistical approaches familiar to most community ecologists (Legendre and Legendre 1998), but the use of spatial data in ecological models is more recent (Borcard and Legendre 2002; Borcard et al. 2004; Dray et al. 2006). Ecological patterns and processes vary across space, and the scale at which a researcher chooses to express spatial variation can have a strong impact on the outcome of analysis (Wiens 1989). Indeed, different species of aquatic macrophytes exhibit contrasting environmental associations and respond to environmental conditions on multiple scales (Cheruvilil and Soranno 2008). Fortunately, multiscale methods exist that allow for more comprehensive investigations of the influence of spatial variation (Burrough 1983; Franklin and Mills 2003), including Moran eigenvector maps (MEM; Dray et al. 2006), which can be used to reflect spatial structure at any scale that exists in the data. The present study is the first to employ MEM in a variation partitioning framework to quantify multiscale spatial variation in aquatic plant communities.

Predicting species assemblages and their response to a changing landscape requires a better understanding of the factors that drive variation in species abundance and distribution. Niche-based processes like environmental filtering (Keddy 1992) and dispersal limitation (Hubbell 2001) can be invoked to explain species patterns on a landscape scale; these processes are linked to variation in environmental conditions and space. Several studies (e.g., Santamaría 2002; Alexander et al. 2008; Cheruvilil and Soranno 2008) have considered the influence of environmental, anthropogenic, and spatial factors on aquatic macrophytes independently, but none have yet considered the relative influence of all these factors and their combined effects in a quantitative framework. Our objective was to employ a variation partitioning analysis to quantify the relative role of environmental, land-use and spatial variables in explaining the composition of submersed aquatic macrophytes in Wisconsin lakes.

## Materials and methods

### Aquatic macrophyte data

Submersed aquatic plant communities in 225 Wisconsin

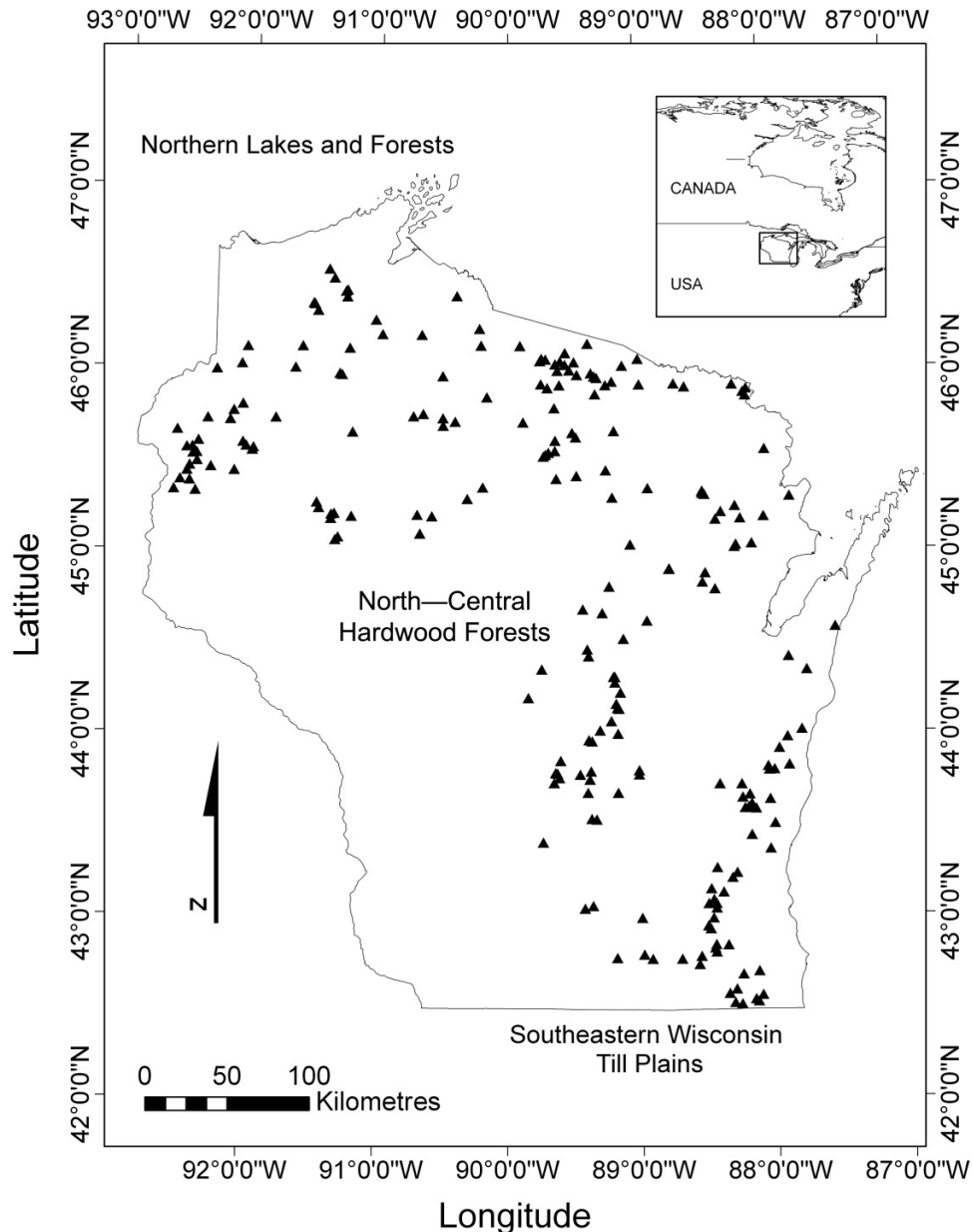
lakes were sampled throughout the three lake-rich ecoregions of Wisconsin from 2005 to 2008 (Omernik et al. 2000; Fig. 1). To ensure that the gradient lengths of environmental and land-use variables were sufficiently long for constrained ordination, the lakes sampled in 2008 were strategically selected according to the 2001 version of the National Land Cover Database (NLCD; Homer et al. 2007) to fully represent the range of watershed disturbance that exists in Wisconsin. The resulting data set includes lakes that are most or least impacted for their region with proportions of disturbed (urban plus agricultural) land in the watershed ranging from 0 to 0.86 in the north, 0 to 0.94 in central Wisconsin, and 0.22 to 1 in the south. To reduce bias due to interannual variation, the lakes sampled in each year were balanced with respect to ecoregion and lake order (Riera et al. 2000). Lakes were sampled from a boat mid-June through August using the point-intercept survey methodology outlined by Hauxwell et al. (2010). This methodology has been shown to return robust and predictable species frequency data and is suitable for making comparisons among lakes (Mikulyuk et al. 2010). Following this protocol, survey grids were constructed based on littoral area and shoreline complexity. Littoral area was estimated using lake area shallower than 6 m, and shoreline complexity was captured using the ratio of the length of the shoreline to the circumference of a circle equal in area to that of the lake (Wetzel 2001). Survey grids were scaled to produce more points on increasingly large and complex lakes and ranged from 44 to 3098, with an average of 305 points per lake, resulting in 68 633 points total. At each point, a double-sided rake was used to record depth and collect plants from a ~0.4 m<sup>2</sup> area. A similar rake attached to a rope was used to collect plants in water deeper than 4.5 m. Plants were identified to species following Crow and Hellquist (2000a, 2000b).

Species data were subjected to the Hellinger transformation prior to multivariate analysis. This transformation consists of taking the square root of each species occurrence expressed as a proportion of the sum of all species occurrences in each lake. The square-root step of the transformation decreases the importance of the most abundant species (Legendre and Gallagher 2001). Furthermore, species present in fewer than 5% of lakes were discarded prior to analysis. Rare species can have a disproportionate effect on multivariate analyses, as they contribute little to understanding general community relationships (Jackson and Harvey 1989).

### Environmental conditions

We qualitatively estimated sediment type as muck, sand, or rock at each sample point. We obtained data on maximum depth, stratification status (Lathrop and Lillie 1980), satellite-predicted Secchi depth, and presence of the invasives rusty crayfish (*Orconectes rusticus*) and Eurasian watermilfoil from the Wisconsin Department of Natural Resources' surface water integrated monitoring system (SWIMS 2010). We estimated littoral area, maximum depth of plant colonization, and average depth of submersed plants from the macrophyte survey data. We used Riera et al.'s (2000) method to calculate lake order and classified negative-order lakes with no or intermittent connectivity to the larger surface-water drainage network as seepage lakes, lakes with one permanent outlet as headwater lakes, first-order lakes with one first-

**Fig. 1.** Map of 225 Wisconsin study lakes throughout the three lake-rich ecoregions of Wisconsin. Lakes were sampled with a point-intercept methodology from mid-June through August 2005 to 2008.



order inlet and at least one outlet as high drainage lakes, and lakes with one or more higher-order inlets and at least one outlet as lowland drainage lakes. Additionally, lakes were classified as reservoirs if the hydraulic height of a dam was greater than half the lake's maximum depth. We delineated watersheds based on flow direction and topography using 30 m resolution digital elevation raster coverage from which we determined total watershed area and the ratio of land to water in the watershed. We obtained data on conductivity, alkalinity, and pH from Wisconsin Department of Natural Resources Surface Water Inventory Surveys (1967–1972) and filled gaps with data collected through the Citizen Lake Monitoring Network. Correlation analysis on a subset of lakes for which we have current data shows modern and historical values to be highly correlated (Pearson's  $r = 0.89, 0.93,$  and  $0.64$  for conductivity, alkalinity, and pH, respectively). Fi-

nally, we used the US Department of Agriculture, Natural Resources Conservation Service's US General Soil Map (STATSGO; Soil Survey Staff 2011) to estimate watershed soil erodibility and clay, sand, and organic content as well as the watershed's dominant soil taxa particle size. Data were transformed in several ways to satisfy the assumptions of statistical analysis; proportional data were arcsin square-root-transformed and variables with skewness greater than one were log-transformed.

#### Land use

Land use was assessed at both 100 m buffer and watershed scales. Watersheds for drainage and seepage lakes, respectively, were delineated to include all land drained by the upstream hydrological network or all land that drains directly into the lake. The 100 m buffers include all land within

100 m of the lakes' perimeter. Land-use composition at each scale was obtained from the 2001 version of the NLCD. The NLCD uses classification algorithms to interpret satellite data from Landsat Thematic Mapper imagery, producing a raster coverage with a resolution of 30 m in which the primary type of land use is designated for each pixel. After quantifying the area at each scale belonging to NLCD standard land-use categories, we collapsed land-use classes into urban (including high-, medium-, low-intensity, and open urban space), agriculture (grassland, pasture-hay, cultivated crops), forested (deciduous, evergreen, mixed forests), and undisturbed (forested, wetlands, grasslands) categories. We also calculated percent impervious surface in both watershed and buffers. All values were expressed in the form of arcsin square-root-transformed proportions.

### Spatial variation

Moran eigenvector maps (MEM) were used to quantify how distances among sampled lakes influenced the similarity of aquatic plant communities after accounting for the influence of environmental and land-use variables. MEM variables were calculated using neighborhoods constructed following Dray (2010a), where competing spatial models are evaluated based on their power to explain variation in species abundance data. MEM variables, or eigenfunctions, are obtained from a spectral decomposition of a distance matrix of the spatial relationships among sampling locations. MEM eigenfunctions can be used to describe symmetric spatial structures at all spatial scales that can be expressed by the sampling design. The MEM variables are in the form of a series of sine waves with decreasing periods that are orthogonal to one another, irrespective of sampling design. The first MEM variables model broad spatial structures, and subsequent MEM variables represent finer spatial patterns. The last eigenfunctions accommodate fine-scale spatial structures (see Borcard and Legendre 2002; Borcard et al. 2004; and Dray et al. 2006 for details). There was no statistically significant linear pattern in the plant community data, obviating the need to detrend. A linear trend is an indication of spatial structure acting at a broader scale than the sampling extent. If present, it may obscure another structure in the data set that could be better modelled by MEM variables. MEM eigenfunctions were constructed using distance matrices based on lake neighborhoods defined using linear distance, Delaunay triangulation, Gabriel graphs, and minimum spanning trees. We considered 200 neighborhoods based on linear distances ranging from 35.6 km (the smallest distance that keeps all neighbors connected, resulting in neighborhoods with an average of 12 links) to 350 km (approximately half the maximum distance between sites, yielding neighborhoods with a mean of 193 links). We also tested various spatial weighting matrices for their ability to improve the spatial model, using a simple binary connectivity model as well as two monotonic decreasing functions (linear and concave-down) to describe the influence of distance on site similarity. We then used a selection procedure based on Akaike's information criterion (AIC; Akaike 1974) to select the most parsimonious neighborhood model. The spatial weighting matrix defined by a concave-down linear decay function and neighborhoods defined by simple linear distance (64 km) ultimately produced the best model (AIC = -129.55 versus -100.57 for the null

hypothesis, with neighborhoods containing an average of 25 links). The simple linear function was nearly as good as the decay function at describing the influence of distance on site similarity. This model included neighborhoods defined by a much greater distance (176 km; AIC = -129.48, with neighborhoods containing an average of 99 links). From the best linear decay model, we retained 39 eigenfunctions associated with positive values of Moran's index of spatial autocorrelation (Moran's  $I$ ; Dray et al. 2006) for further analysis. Analyses were conducted using the `spacemaker` package (Dray 2010b) for the R environment for statistical computing (R Development Core Team 2010).

### Redundancy analysis and variation partitioning

We identified the relative importance of environmental conditions, land use, and spatial structure (MEM variables) by partitioning the variation explained by each subset of predictors into fractions using redundancy analyses (RDA; van den Wollenberg 1977). A forward selection procedure was used to select significant predictor variables that explained the most variation in response variables (Borcard et al. 1992; Blanchet et al. 2008), and variation partitioning was performed using a series of canonical ordinations. This procedure, called partial redundancy analysis, is the multivariate equivalent of partial linear regression and is conducted by performing RDA on meaningful combinations of predictor variables. The analysis identifies common and unique sources of variation in the species response data to compare the relative strengths of different groups of explanatory variables. The three suites of predictor variables in this analysis required seven separate canonical analyses to estimate the major fractions of variation (e.g., space vs. environment plus land use) with 10 subtraction equations to estimate the isolated effects (e.g., influence of space and environment combined, but independent of land use). For instance, the shared variation explained by both environmental variables and spatial descriptors is produced by induced spatial dependence that is generated by the spatial structure of environmental factors acting indirectly on biological communities. The overall significance of the ordination as well as that of each major fraction of variation was tested using an ANOVA-like permutation test with 999 permutations. We summarized the variation explained by calculating the adjusted coefficient of determination ( $R^2_{adj}$ ). While  $R^2$  is biased and increases with the number of explanatory variables even if they are random,  $R^2_{adj}$  provides unbiased estimates of the variation of the response data explained by the explanatory variables (Peres-Neto et al. 2006).

### Results

The sampled lakes exhibited a broad range of environmental conditions (Table 1). Similarly, aquatic macrophyte frequency of occurrence and species richness varied considerably. Mean species richness was 18, with a range of 2 to 46 and with more species-rich systems occurring in the north versus the south. The mean frequency of occurrence of plants within the littoral zone was 75.3%, ranging from 1% to 100%. The most common species sampled included musk grasses (*Chara* spp.), wavy waterlily (*Najas flexilis*), and white waterlily (*Nymphaea odorata*), recorded in 168, 156,



**Table 1.** Chemical, morphometric, biological, geologic, and land-use parameters of 225 Wisconsin lakes surveyed for aquatic macrophyte community composition.

| Parameter                                     | Unit                   | Mean | Range                |
|---|------------------------|------|----------------------|
| <b>Chemistry</b>                              |                        |      |                      |
| Conductivity                                  | ppm                    | 204  | 12–833               |
| Alkalinity                                    | MPA <sup>a</sup> (ppm) | 91   | 2–280                |
| pH  | Unitless               | 7.52 | 5.1–9.9              |
| MDC <sup>b</sup>                              | m                      | 4.8  | 0.9–12               |
| Average SAV <sup>c</sup> depth                | m                      | 2.1  | 0.5–5.7              |
| <b>Morphometry</b>                            |                        |      |                      |
| Lake size                                     | ha                     | 83   | 5–3205               |
| Littoral area                                 | ha                     | 49   | 2–1313               |
| Maximum depth                                 | m                      | 9.8  | 1.2–71.9             |
| Watershed area                                | ha                     | 3608 | 26.3–80473           |
| Watershed land:water                          | Ratio                  | 16   | 0.3–501              |
| Mix:stratify                                  | Ratio                  | 6.5  | 0.6–57.2             |
| <b>Lake soil characteristics</b>              |                        |      |                      |
| Muck  | %                      | 71   | 0–100                |
| Rock  | %                      | 5    | 0–68                 |
| Sand  | %                      | 22   | 0–100                |
| <b>Watershed soil and geologic characters</b> |                        |      |                      |
| Sand  | %                      | 36   | 0–54                 |
| Clay  | %                      | 26   | 0–52                 |
| Fine-loamy over sand                          | Binary                 |      | 39 watersheds        |
| Fine-loamy                                    | Binary                 |      | 24 watersheds        |
| Sandy   | Binary                 |      | 71 watersheds        |
| Fine  | Binary                 |      | 8 watersheds         |
| Coarse-loamy or coarse-loamy over sand        | Binary                 |      | 80 watersheds        |
| Bedrock–sandstone                             | Binary                 |      | 62 watersheds        |
| Bedrock–dolomite                              | Binary                 |      | 51 watersheds        |
| Bedrock–basalt                                | Binary                 |      | 37 watersheds        |
| Bedrock–granite                               | Binary                 |      | 19 watersheds        |
| <b>Invasives</b>                              |                        |      |                      |
| <i>Orconectes rusticus</i>                    | Binary                 |      | Present in 19 lakes  |
| <i>Myriophyllum spicatum</i>                  | Binary                 |      | Present in 116 lakes |
| <b>Lake type</b>                              |                        |      |                      |
| Seepage <sup>d</sup>                          |                        |      | 101 lakes            |
| Headwater <sup>d</sup>                        |                        |      | 40 lakes             |
| High drainage <sup>d</sup>                    |                        |      | 26 lakes             |
| Lowland drainage <sup>d</sup>                 |                        |      | 58 lakes             |
| <b>Land use</b>                               |                        |      |                      |
| Watershed                                     |                        |      |                      |
| Impervious surface                            | %                      | 1    | 0–21                 |
| Urban   | %                      | 10   | 0–83                 |
| Agriculture                                   | %                      | 23   | 0–82                 |
| Crops   | %                      | 15   | 0–68                 |
| Undisturbed                                   | %                      | 67   | 4–67                 |
| Forest  | %                      | 51   | 2–98                 |
| 100 m buffer                                  |                        |      |                      |
| Impervious surface                            | %                      | 10   | 0–41                 |
| Urban   | %                      | 15   | 0–88                 |
| Agriculture                                   | %                      | 8    | 0–85                 |
| Crops   | %                      | 5    | 0–61                 |
| Undisturbed                                   | %                      | 77   | 6–100                |
| Forest  | %                      | 51   | 0–97                 |

<sup>a</sup>Methyl purple alkalinity.<sup>b</sup>Maximum depth of plant colonization.<sup>c</sup>Submersed aquatic vegetation.<sup>d</sup>Lake order following Riera et al. (2000).

and 156 lakes, respectively. After removing extremely rare species present in fewer than 5% of sampled lakes, slender waterweed (*Elodea nuttallii*), variable-leaf watermilfoil (*Myriophyllum heterophyllum*), and water lobelia (*Lobelia dortmanna*) were the next least common species. Where present, musk grasses, followed by Robbins' pondweed (*Potamogeton robbinsii*) and coontail (*Ceratophyllum demersum*) on average had the highest within-lake frequency of occurrence; and small waterwort (*Elatine minima*), water lobelia, and pipewort (*Eriocaulon aquaticum*) were most sparsely distributed within lakes. Communities composed of low-growing rosulate species such as dwarf watermilfoil (*Myriophyllum tenellum*), needle spikerush (*Eleocharis acicularis*), and quillwort species (*Isoetes* spp.) tended to be found in northern lakes and were associated with low alkalinity, low anthropogenic development, and high position in the drainage network. Caulescent species found in similar environments included stonewort species (*Nitella* spp.), small pondweed (*Potamogeton pusillus*), and large-leaf pondweed (*Potamogeton amplifolius*). Tolerant caulescent species like coontail, musk grasses, and sago pondweed (*Stuckenia pectinata*) and non-natives curly pondweed (*Potamogeton crispus*) and Eurasian watermilfoil were found more frequently in the south and were associated with increased agricultural disturbance and low water clarity, as were floating-leaf and free-floating species like white waterlily, common duckweed (*Lemna minor*), and giant duckweed (*Spirodela polyrrhiza*).

Forward selection of environmental variables yielded 17 factors that were statistically significant predictors of aquatic plant community composition, including latitude, alkalinity, pH, maximum depth of plant colonization, average depth of submersed plants, Secchi depth, percentage of sites with mucky sediment, presence of invasive Eurasian watermilfoil, percent littoral area, maximum lake depth, likelihood of stratification, watershed area, lake order (seepage, headwater, high drainage, or low drainage), soil erodibility, whether soil texture was fine and loamy over sand, and percent organic matter in the soil. The five land-use variables selected included percent urban, row-cropped, and undisturbed land in the watershed and percent urban and forested land in the 100 m buffer. Finally, 13 eigenfunctions associated with positive spatial autocorrelation were selected from the original 39. The most important eigenfunctions primarily distinguish low from high conductivity lakes in northern (E1 and E3) and southern (E2) Wisconsin (Fig. 2). A competing spatial model defined by larger neighborhoods and employing a simple linear spatial weighting matrix was nearly as strong in explaining aquatic plant community structure; its most important eigenfunction roughly divided the state into a northern and southern component. Subordinate vectors of both models described finer scales of spatial variation.

RDA was used to describe the statistically significant ( $p < 0.05$ ) influence of environmental, spatial, and land-use variables on aquatic macrophyte community composition (a biplot of all significant variables is shown in Fig. 3). RDA axis 1 is most strongly negatively correlated with alkalinity and most strongly positively correlated with latitude. The second most important RDA axis was most positively correlated with maximum depth of colonization. Spatial eigenfunction 24, representing fine-scale spatial variation, was moderately negatively correlated with RDA axis 2. The total effects of land

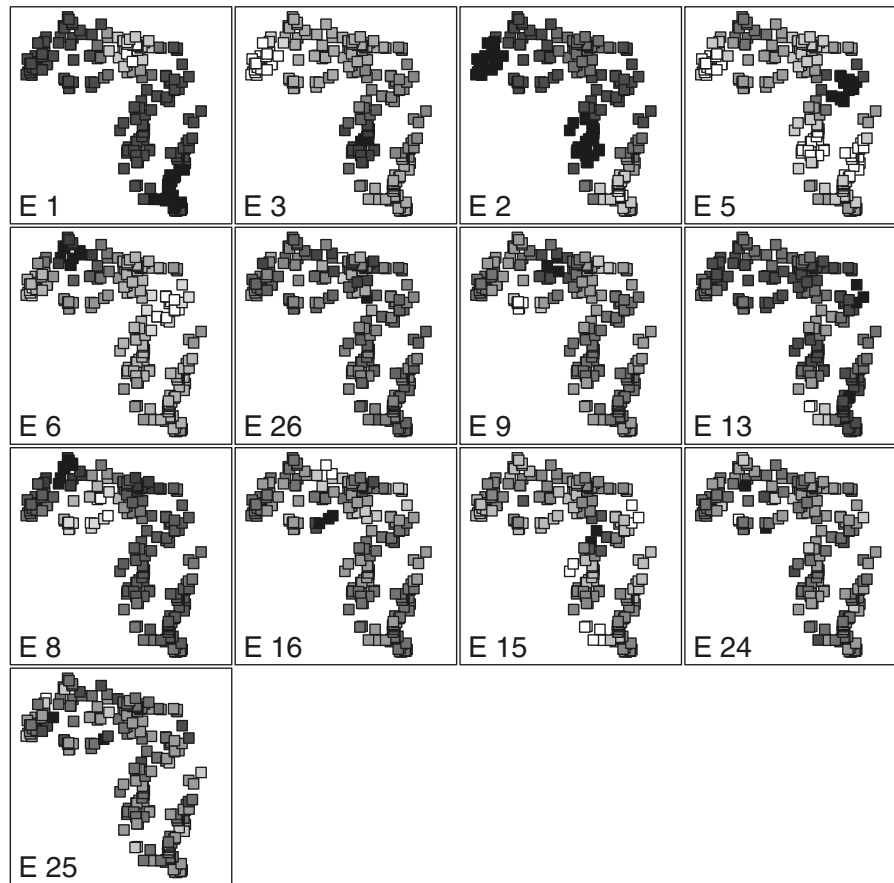
use are reflected by a gradient of watershed disturbance, moving from disturbed watersheds on one side to forested watersheds on the other. The second most important land-use gradient captured the contrasting impacts of agricultural versus urban development. Contrasting plant community types were also evident along RDA axes in each of the associated biplots. Thus, we can describe a gradient with disturbed high-conductivity southern lakes on the negative end and undisturbed northern lakes with low conductivity on the positive end of the first RDA axis. The second most important gradient describes movement from clearer, urban lakes to lakes with reduced water clarity and increased agricultural activity in their watersheds. The results of the partial RDAs on the total effects of each suite of predictor variables are summarized (Table 2).

Variation partitioning revealed that land-use, environmental, and spatial factors were acting independently and in conjunction with one another to explain the variation in macrophyte communities in lakes. RDA found that each testable fraction of variation explained a significant portion of variation in aquatic plant community composition ( $p \leq 0.05$ ). Overall, the combined model including all factors with their conditional effects explained 31% of the total variation observed in aquatic macrophyte community composition. Environmental factors alone accounted for the largest percentage of explained variation (34%, or 11% of total variation), followed by pure spatial (12%, or 4% of total variation) and pure land-use factors (2%, or 0.4% of total variation). Joint effects of all variables explained the second largest portion of any of the constituent fractions (23%, or 7% of total variation; Fig. 4). To better understand the effect of land use, we further partitioned the variation in aquatic macrophyte communities due to watershed- and buffer-scale disturbance in this four-way partitioning of observed variation among spatial, environmental, watershed land use, and buffer land use; the combined effects of buffer- and watershed-scale land use explained more variation than did either scale alone.

## Discussion

The largest proportion of explained variation was due to variation in environmental factors. The second largest proportion was explained by the joint effects of environment, land use, and space, pointing to the overlapping and interdependent nature of the forces that influence lake ecosystems. More specifically, lake macrophyte communities were primarily influenced by environmental conditions that were spatially structured on a latitudinal gradient. Communities were secondarily influenced by factors related to water clarity and landscape position and also by urban versus agricultural land use. Low-growing rosulate species were typical of clear northern seepage lakes, while caulescent species were found more often in disturbed southern lakes with high alkalinity. The structural differences between these functional groups are vast, and as a result, they provide strikingly different habitat for fish and invertebrates. Indeed, plants can be stronger predictors of the fish community than water quality variables (Cvetkovic et al. 2010). Plants can directly influence dissolved oxygen levels, light attenuation, and temperature and can provide sediment stabilization, resulting in indirect impacts to other aquatic life forms (Scheffer 1998; Wetzel

**Fig. 2.** The 13 forward-selected eigenfunctions modelling the spatial distribution of 225 Wisconsin lakes (e.g., E1, E25) in order (left to right, top to bottom) of explanatory power. All eigenfunctions are associated with positive spatial autocorrelation; distance weighting function and neighborhood configurations were determined following Dray et al. (2006) and chosen with an AIC-based forward selection procedure. Squares are located at lake geographic coordinates; boxes represent eigenfunctions, with darker colors symbolizing higher values. Higher-number eigenfunctions represent finer-scale spatial variation. The most important vectors (E1, E3) represent the broadest spatial scale and differentiate northern low-alkalinity lakes.



2001). The impact of aquatic plants on dissolved oxygen concentrations, for example, can substantially change the nutrient and gas chemistry that determines habitat quality for aquatic animals, even on time courses as short as 1 day (Caraco et al. 2006). Habitat complexity, particularly as measured by functional diversity of aquatic macrophytes, is significantly related to summer species richness of varying fish assemblage groups (Tonn and Magnuson 1982), and isoetid communities tend to be less complex and species-rich than the larger-stature elodeid groups. Vegetation in general also tends to increase biomass of macroinvertebrates and reduce foraging efficiency of omnivorous fish (Diehl 1992). The cascading trophic effects resulting from altered macrophyte habitat are many; thus, an understanding of the factors that drive plant community variation will help us to understand dynamics of other trophic groups.

Land use was a statistically significant driver of variation in plant communities and was often correlated with measured environmental variables. Land use has been associated with direct impacts to macrophytes but may also in part capture variation due to unmeasured environmental conditions. Increased development is commonly associated with eutrophication, lower water clarity, and higher conductivity, and our results show that different kinds of anthropogenic develop-

ment have contrasting effects on aquatic macrophyte community composition. Specifically, agricultural development is likely to be found lower in the watershed and is associated with decreased clarity as reflected by reduced maximum depth of plant colonization. Coontail was strongly positively correlated with watershed area, lake order, and agricultural development, reflecting this species' broad environmental preferences and tolerance to disturbance (cf. Nichols 1999; Canny 2007). Also, floating-leaf species such as white water-lily and yellow pond-lily (*Nuphar lutea variegata*) were associated with higher agricultural disturbance and negatively correlated with urban development, reflecting a possible direct effect of manual removal or boat traffic-related disturbance on these species (cf. Hatzenbeler et al. 2004; Radomski and Goeman 2001; Borman 2007). Musk grasses, on the other hand, were positively correlated with urban development and tended to be found in areas with high urban disturbance in the buffer.

The scale at which disturbance is evaluated can be important. Jennings et al. (2003) found the abundance of submerged vegetation responded to watershed-scale but not buffer-scale development. However, variation partitioning between watershed- and buffer-scale disturbances in this study revealed that each factor considered alone explained less var-

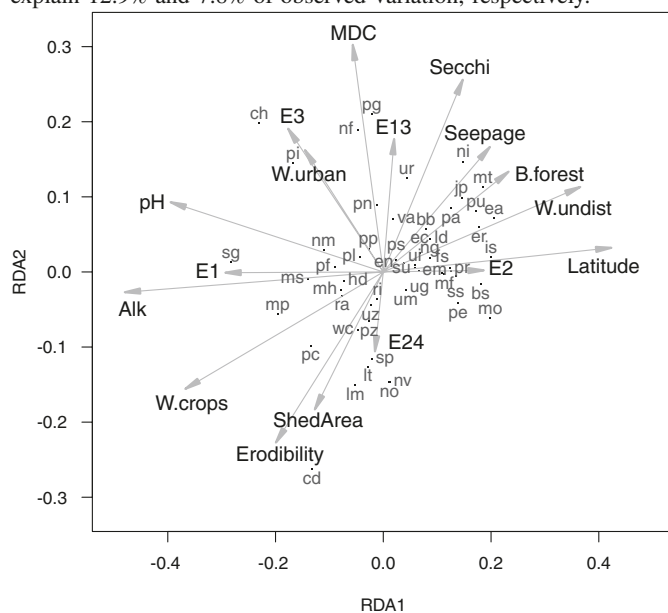
**Table 2.** Results of partial redundancy analysis (RDA) considering the total effects of local environmental, land-use, and spatial factors on aquatic macrophyte abundance and distribution.

| Suite       | Axis  | $\lambda$ | Variation explained (%) | Strongest positive correlate | Strongest negative correlate |
|-------------|-------|-----------|-------------------------|------------------------------|------------------------------|
| Environment | RDA 1 | 0.08      | 12                      | Latitude                     | Alkalinity                   |
|             | RDA 2 | 0.04      | 6                       | MDC <sup>a</sup>             | Soil erodibility             |
| Land use    | RDA 1 | 0.05      | 8                       | Watershed undisturbed (%)    | Watershed crops (%)          |
|             | RDA 2 | 0.02      | 3                       | Watershed urban (%)          | Watershed crops (%)          |
| Space       | RDA 1 | 0.07      | 11                      | E2                           | E1                           |
|             | RDA 2 | 0.03      | 5                       | E13                          | E24                          |

**Note:** Eigenvalues of the first two RDA axes are shown along with the amount of variation they explain. Variables with the strongest correlations with each axis are listed. Spatial eigenfunctions were determined following Dray et al. (2006) using a doubly centered weighting matrix based on a concave-down linear decay function with neighborhoods defined by a distance of 64 km.

<sup>a</sup>Maximum depth of colonization.

**Fig. 3.** Biplot of partial redundancy analysis (RDA) investigating the effect of environmental, land-use, and spatial variables on aquatic plant macrophyte species measured in 225 Wisconsin lakes. Ordination space represents sites distributed based on Euclidean similarity as determined by species abundance. Arrow length is proportional to the strength of correlation between each variable and the RDA axes. Species centroids (points) are labeled with abbreviations defined in Appendix A, Table A1. Centroids occur in ordination space where that species is most likely to be found with high abundance given underlying structure of sites. RDA axes 1 and 2 explain 12.9% and 7.8% of observed variation, respectively.



iation in aquatic plant communities than when both were considered together. We may have been able to detect this effect because our study likely included more highly impacted lakes. Our findings indicate that development at buffer and watershed scales may have a synergistic effect on aquatic plant assemblages, thus illustrating the appropriateness of multiscale management approaches.

Regional processes occurring over spatial scales broader than that of the lake or watershed helped explain aquatic plant community composition. Whereas environmental variables like water chemistry or hydrology can be invoked to explain local trends, the most important spatial eigenfunctions revealed large-scale spatial gradients, and latitude was one of the most important environmental variables. These broad spa-

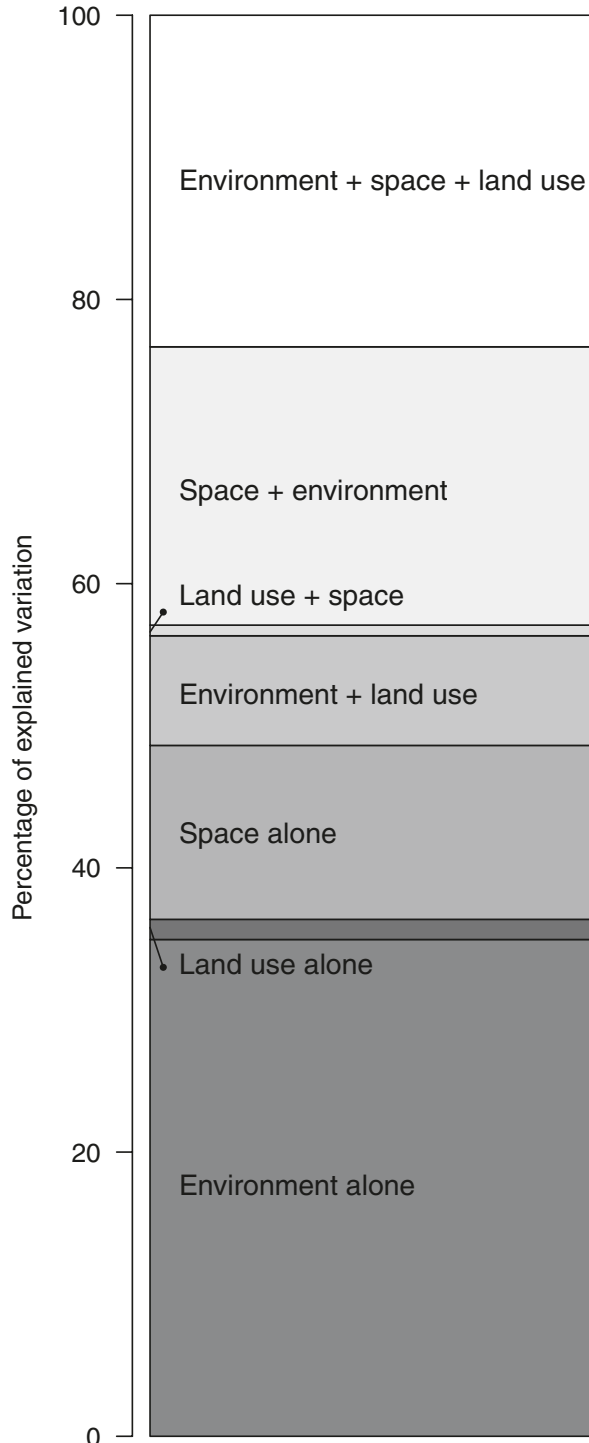
tial patterns may reflect climatic and geologic processes (Omernik et al. 2000) and include regional effects related to dispersal limitations (Svenning et al. 2004; Flinn et al. 2010). A number of less important eigenfunctions captured spatial structuring on a finer scale. While not as important as broader spatial gradients, they may yet signify important structuring factors related to hydrologic connectivity, elevation, or fine-scale geologic patterns. The use of MEM in this context allowed us to explore the influence of spatial variation at multiple scales and incorporate different spatial weighting matrices to best express spatial variation inherent in the data. Gilbert and Bennett (2010) have shown that MEM approaches can inflate the spatial component of explained variation. Although we cannot, for example, infer the exact strength of contribution of dispersal versus environmental processes, the partitioning of variation among spatial, land-use, and environmental variables is a valuable first step to defining more specific and precise models of aquatic macrophyte community composition.

Our results mirror those found by Sass et al. (2010), although their study was conducted on a smaller data set (53 lakes) and employed more intensive diver-assisted transect survey methods. Of particular note, they observed a divergence in plant communities due to the contrasting influences of agricultural and urban development and also captured a gradient from low to high nutrient levels. Phosphorus, which in their study was highly correlated with agricultural development, could further explain the gradient observed between agriculture and urban land use in this study. Unfortunately, this was not available for a sufficient number of our study lakes. Sass et al. (2010) also found a significant relationship between species richness and watershed development statewide, but did not find a significant relationship within ecoregions. Likely the significant statewide effect they observed was driven by the induced spatial dependence generated by the spatial structure of environmental factors acting indirectly on aquatic plant communities. Their data revealed no linear relationship between development and richness at a regional level, likely because the response is unimodal. In minimally developed lakes, disturbance tends to increase species richness, typically manifested in a shift from isoetid to elodeid plant communities (Borman 2007). However, the opposite trend can be found in very developed systems, where extremely high levels of disturbance can cause decreased species richness as the system becomes increasingly inhospitable for plant life.

If we hope to refine plant-based ecological indicators (e.g.,



**Fig. 4.** Proportional contribution of environmental, land-use, and spatial factors and their combined effects to adjusted coefficient of determination ( $R^2_{adj} = 0.31$ ), describing variation among 225 Wisconsin macrophyte communities.



Nichols et al. 2000), it is imperative that we understand how different stressors and environmental factors impact macrophyte community structure. We identified space as a significant driver of plant community dynamics and advocate for the application of spatially informed management strategies instead of a single statewide approach, which has been advocated elsewhere (Beck et al. 2010), but lacked a quantitative

basis. For example, the existence of isoetid communities in northern Wisconsin soft water seepage lakes may be constrained by watershed development. If restoring isoetids becomes a management priority, efforts to support buffer naturalization to mitigate input from agricultural activities may be an appropriate management approach. Alternatively, if a system in southern Wisconsin is dominated by free-floating macrophytes (indicative of hypereutrophic conditions; Vaithyanathan and Richardson 1999), restoration of submersed aquatic plant communities may be best supported by management activities intended to increase water clarity or ameliorate the impact of agricultural land use. Currently, the classification scheme employed by managers in Wisconsin involves grouping lakes by hydrology and stratification status. Our work suggests a regional nesting of these categories would be more appropriate for managing and evaluating macrophyte communities statewide.

The analysis presented here explained only 31% of observed variation in aquatic macrophyte communities. While this number is comparable to the amount of variation explained in other broad-scale ecological studies of freshwater aquatic community composition (Beisner et al. 2006; Soininen and Weckstrom 2009; Capers et al. 2010), it does suggest the existence of other influential but unmeasured factors. The effect of land use, for example, may be underestimated in this study. Land-use variables estimated by satellite on a 30 m × 30 m grid likely relate to coarse effects that are already largely captured by measured environmental variables. Smaller scale within-lake land-use stressors unrelated to water chemistry (e.g., shoreline alteration or manual macrophyte removal) may explain additional portions of the total observed variation. Unmeasured environmental data (e.g., water and sediment phosphorus) would likely increase the amount of variation explained. It is also possible that the influence of pure spatial factors is overestimated because of the ability of spatial patterns quantified in the study to reflect patterns in unmeasured environmental variables. The variation introduced among growing seasons or due to dispersal patterns, combined with the influence of other random stochastic events, may explain other important patterns in community composition.

Aquatic macrophyte communities are managed for a variety of reasons, including biodiversity, recreation, habitat for fisheries, and invasive species control. This work quantifies the importance of spatial, environmental, and land-use factors that define the larger context within which a single community occurs. By developing a greater understanding of the factors that structure aquatic plant communities both locally and regionally, managers are better able to define constraints to and opportunities for restoration, set realistic management goals, and effectively prioritize management options.

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## Appendix A

Table A1 follows on the next page.

**Table A1.** List of species name abbreviations used in Fig. 3.

| Abbreviation | Common name                | Scientific name   |
|--------------|----------------------------|---|
| bb           | Water-marigold             | <i>Bidens beckii</i>  |
| bs           | Watershield                | <i>Brasenia schreberi</i>                                     |
| cd           | Coontail                   | <i>Ceratophyllum demersum</i>                                 |
| ch           | Musk grasses               | <i>Chara</i> spp.   |
| em           | Small waterwort            | <i>Elatine minima</i>   |
| ea           | Needle spikerush           | <i>Eleocharis acicularis</i>                                  |
| ec           | Common waterweed           | <i>Elodea canadensis</i>                                      |
| en           | Slender waterweed          | <i>Elodea nuttallii</i>                                       |
| er           | Pipewort                   | <i>Eriocaulon aquaticum</i>                                   |
| hd           | Water star grass           | <i>Heteranthera dubia</i>                                     |
| is           | Quillworts                 | <i>Isoetes</i> spp.   |
| jp           | Brownfruit rush            | <i>Juncus pelocarpus</i>                                      |
| lm           | Common duckweed            | <i>Lemna minor</i>  |
| lt           | Forked duckweed            | <i>Lemna trisulca</i>   |
| ld           | Water lobelia              | <i>Lobelia dortmanna</i>                                      |
| mo           | Aquatic moss               | Various species   |
| mf           | Farwell's watermilfoil     | <i>Myriophyllum farwellii</i>                                 |
| mh           | Variable-leaf watermilfoil | <i>Myriophyllum heterophyllum</i>                             |
| ms           | Northern watermilfoil      | <i>Myriophyllum sibiricum</i>                                 |
| mp           | Eurasian watermilfoil      | <i>Myriophyllum spicatum</i>                                  |
| mt           | Dwarf watermilfoil         | <i>Myriophyllum tenellum</i>                                  |
| nf           | Wavy water nymph           | <i>Najas flexilis</i>   |
| ng           | Slender water nymph        | <i>Najas gracillima</i>                                       |
| nm           | Spiny naiad                | <i>Najas marina</i>   |
| ni           | Stoneworts                 | <i>Nitella</i> spp.   |
| nv           | Yellow pond-lily           | <i>Nuphar lutea variegata</i>                                 |
| no           | White waterlily            | <i>Nymphaea odorata</i>                                       |
| pa           | Large-leaf pondweed        | <i>Potamogeton amplifolius</i>                                |
| pc           | Curly pondweed             | <i>Potamogeton crispus</i>                                    |
| pl           | Leafy pondweed             | <i>Potamogeton foliosus</i>                                   |
| pe           | Ribbonleaf pondweed        | <i>Potamogeton epihydrus</i>                                  |
| pf           | Fries' pondweed            | <i>Potamogeton friesii</i>                                    |
| pg           | Variableleaf pondweed      | <i>Potamogeton gramineus</i>                                  |
| pi           | Illinois pondweed          | <i>Potamogeton illinoensis</i>                                |
| pn           | Floatingleaf pondweed      | <i>Potamogeton natans</i>                                     |
| pp           | White-stem pondweed        | <i>Potamogeton praelongus</i>                                 |
| pu           | Small pondweed             | <i>Potamogeton pusillus</i>                                   |
| ri           | Richardson's pondweed      | <i>Potamogeton richardsonii</i>                               |
| pr           | Robbins' pondweed          | <i>Potamogeton robbinsii</i>                                  |
| ps           | Stiff pondweed             | <i>Potamogeton strictifolius</i>                              |
| pz           | Flatstem pondweed          | <i>Potamogeton zosteriformis</i>                              |
| ra           | Whitewater crowfoot        | <i>Ranunculus aquatilis</i>                                   |
| ss           | Arrowheads                 | <i>Sagittaria</i> spp.  |
| su           | Swaying bulrush            | <i>Schoenoplectus subterminalis</i>                           |
| fs           | Floating-leaf sparganiums  | <i>Sparganium angustifolium</i> , <i>Sparganium fluctuans</i> |
| sp           | Giant duckweed             | <i>Spirodela polyrrhiza</i>                                   |
| sg           | Sago pondweed              | <i>Stuckenia pectinata</i>                                    |
| ug           | Humped bladderwort         | <i>Utricularia gibba</i>                                      |
| ui           | Flat-leaf bladderwort      | <i>Utricularia intermedia</i>                                 |
| um           | Small bladderwort          | <i>Utricularia minor</i>                                      |
| ur           | Small purple bladderwort   | <i>Utricularia resupinata</i>                                 |
| uz           | Common bladderwort         | <i>Utricularia macrorhiza</i>                                 |
| va           | Watercelery                | <i>Vallisneria americana</i>                                  |
| wc           | Watermeal                  | <i>Wolffia columbiana</i>                                     |