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ARTICLE

Freshwater Ecology

Aquatic vegetation types identified during early and late phases of vegetation recovery in the Upper Mississippi River

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Abstract

Assemblage patterns and processes of aquatic vegetation in most large floodplain rivers are not well understood, particularly after plant recovery. Identifying vegetation types, which are recurring plant groupings based on species composition, diversity, and abundances, can describe plant assembly patterns and environmental drivers that aid conservation planning and management. We used a 22-year dataset ($n = 18{,}000$ sampling plots) to identify aquatic vegetation types during an "early phase" and "late phase" of plant recovery at multiple spatial scales nested within a 500-km river reach of the Upper Mississippi River, USA. We hypothesized that vegetation types varied according to scale because of the stark environmental differences among riverine habitats and differing regional species pools along the river's latitudinal gradient, and that the late phase of recovery had developed several new vegetation types. We first used cluster analyses at multiple spatiotemporal scales to identify the number of vegetation types and their characteristics, such as indicator species, species compositions and abundances, and diversity index. Then we applied a multivariate regression to pinpoint environmental factors (such as hydrodynamics, system productivity, local habitat, and water quality) that structured those vegetation types. Clustering revealed that ~90% of plots irrespective of recovery phase were not classified into vegetation types, which indicated that most aquatic sampling plots are unique in species composition and unpredictable. However, impounded areas upriver from dams had matured five vegetation types: lotus (*Nelumbo lutea* Willd.), submersed (a mix of 11 common submersed species), watercelery (*Vallisneria americana* Michx.), arrowheads (*Sagittaria rigida* Pursh and *Sagittaria latifolia* Willd.), and a diverse community (with high diversity indices and multiple life forms). The vegetation types were associated with three environmental gradients related to inundation depth and duration, system productivity, and water clarity. These five vegetation types are known to be of high ecological value to fish and wildlife and thus targets for restoration, for example, the watercelery

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community is principal forage for migrating canvasback ducks (*Aythya valisineria*) along the Mississippi River flyway. Our results provide insights on vegetation assembly during recovery and aid habitat conservation by providing quantitative, environmental targets for restoration.

KEYWORDS
aquatic plants, biocoenosis, cluster, community assembly, community type, macrophytes, phytocenosis

INTRODUCTION

Rivers provide high biodiversity and many ecosystem services but have experienced severe disturbances and stresses globally over the past century (Dodds & Whiles, 2019). In most large rivers, humans have altered the natural connectivity and flows by draining wetlands and constructing lock and dams (Nilsson et al., 2005; Sparks et al., 1998) and have amplified nutrient enrichment (Harper, 1992). The synergistic effects of altered hydrology and eutrophication can negatively impact biodiversity, ecosystem services, and the structures and functions of biological assemblages (Datry et al., 2018; Huang et al., 2019; Sparks et al., 1998).

Like all biological communities, riverine macrophyte (aquatic plant) assemblages are structured by multiple spatiotemporal processes and environmental filtering (Alahuhta et al., 2021; Lacoul & Freedman, 2006; Wiens, 1989). The regional species pool is mainly determined by regional processes like climate, geology, biogeography, seedbanks, and dispersal (Keddy, 2017). The regional species pool is subjected to disturbances and stresses that "environmentally filter or sieve" toward a localized species pool, which is a subset of species that can withstand or thrive in the local environmental conditions (Keddy, 2017). Common environmental filters for riverine macrophytes include habitat (e.g., inundation regime, water quality), biotic interactions, and stochastic disturbances (e.g., water quality impairment, floods, droughts, and waves) (Bornette & Puijalon, 2011; Correia Nunes et al., 2021; Haslam, 2006; Liu et al., 2020). Ecologists often seek to understand the patterns and dynamics in assemblages at multiple scales, but large river macrophyte data are sparse (Alahuhta et al., 2021).

Assemblages or "vegetation types" result after the finest environmental filters are applied to a regional species pool. A vegetation type is a collection of species that forms a relatively predictable patch and can be described based on species composition, relative abundances, functional traits, diversity indices, and the physical structure such as canopy heights (Clements, 1916; Keddy, 2017). Vegetation types are assigned by refining existing classification schemes like those of Cowardin et al. (1979), Dieck et al. (2015), and Tiner (2017) or by using models with a site by species' (dis)similarity matrix. Both the environmental niche space and biotic interactions in rivers may lend to structuring riverine macrophytes into discernable vegetation types. Strong habitat gradients in rivers (e.g., sharp changes in water depth and velocity over small spatial scales) create ecological boundaries that can invoke macrophyte responses (Bouska et al., 2022; Carhart & De Jager, 2019). Macrophyte assembly also may be influenced by biotic interactions like facilitation or competition (LeBagousse-Pinguet et al., 2012).

Previous studies have quantitatively described riverine vegetation types that advanced ecological understanding and conservation management (Day et al., 1988; Schaumburg et al., 2004). The conservation applicability of vegetation typing is well-demonstrated in many ecosystems. Vegetation typing visuals like maps, photographs, and conceptual figures are useful communication tools that target audiences such as environmental educators, resource managers, and botanists. Vegetation maps highlight patterns of species co-occurrence, distributions, and rare types, which can then be related to environmental gradients (Day et al., 1988) and aid selection of ecological reserves and management units (Margules & Pressey, 2000). Finally, typology modeling can assess past, current, and future conditions. Once vegetation types are defined, repeated vegetation surveys can detect assembly shifts over time and their likely causes (De Jager & Rohweder, 2017). Future hypothetical modeling may predict the vegetation responses to anticipated environmental changes, which can guide new research and conservation management.

Riverine macrophytes had recent, remarkable recoveries in a few large rivers worldwide, but the structure of macrophyte assemblages and environmental factors shaping recovery remains interesting and perplexing (Bouska et al., 2022; Ibáñez et al., 2012; Ibanez & Penuelas, 2019). Studies are lacking for environmental filtering and spatial processes that affect river macrophyte assembly, and more information is needed to inform generalizations in ecological theory

(Alahuhta et al., 2021). Exploring patterns and processes of vegetation development during the recovery process is challenging with currently sparse data (Ibanez & Penuelas, 2019), but examining long-term assemblage data can promote recovery elsewhere by understanding the environmental filters necessary to manage macrophytes.

Our primary objective was to determine which macrophyte vegetation types occurred within a 500-km river reach of the Upper Mississippi River (UMR), USA in an early phase and late phase of macrophyte recovery that spanned 22 years (Figure 1a,b). This study in the UMR focused on (1) classifying macrophyte vegetation types within multiple study areas, strata, and two phases spanning early and late macrophyte recoveries, (2) identifying indicator species, species abundances, and diversity indices that characterize the vegetation types, and (3) relating the environmental gradients that likely structured the vegetation types during recovery, such as inundation regime, localized habitat, and regional water quality. Hypothesis 1 was that different vegetation types would be distinguishable at two spatial scales: (1) "study areas" (each averaging ~40 km in length) due to slightly different regional species composition and temporal trajectories of species turnover (Bouska et al., 2022), and (2) "strata" (each averaging ~4–15 km length; strata are called floodplain lakes, side channels, and impounded areas) due to strong differences in environmental conditions and disturbance frequency that would reflect lotic and lentic plant assemblages (Carhart & De Jager, 2019). Hypothesis 2 was that the early phase would have few vegetation types, whereas the late phase would have more. In the UMR, the late phase of recovery (years 2015–2019, 15 years after the early phase) was characterized by the greatest macrophyte prevalence and relative stability (Figure 1b, and see Bouska et al., 2022; Drake et al., 2022; Larson, Lund, et al., 2022). Thus, we expected the early phase would have only a few turbid-tolerant and cosmopolitan species (Lougheed et al., 2001), such as *Stuckenia pectinata* (L.) Borner (POPE6), *Potamogeton crispus* L. (POCO3), *Ceratophyllum demersum* L. (CEDE4), and *Elodea canadensis* Michx. (ELCA7). Previous work (Bouska et al., 2022) showed macrophyte dissimilarity between these two phases, and thus our hypothesis 2 was that the late phase would have more vegetation types that had yet to be described.

METHODS

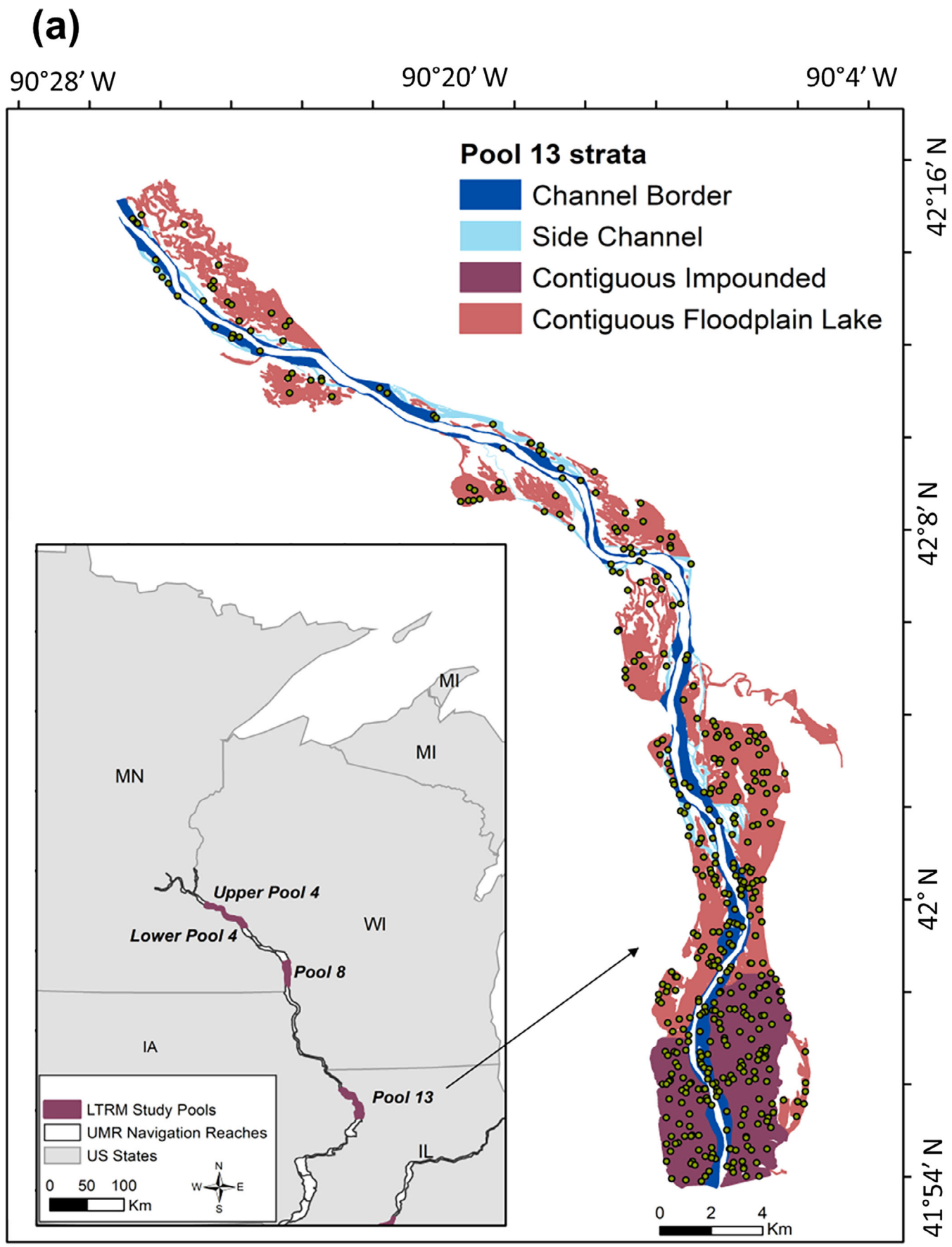
Study area

Our study examined macrophyte vegetation types from four study areas: Upper Pool 4, Lower Pool 4, Pool 8, and Pool 13 (Figure 1a). We examined Upper and Lower Pool 4 (separated by a tributary delta lake that filters suspended solids) due to the strong contrast in environmental conditions (Larson, Lund, et al., 2022). These study areas spanned ~500 km of the UMR and multiple environmental gradients, including geomorphology, hydrology, and water quality (De Jager et al., 2018). We also examined three strata: floodplain lakes, side channels, and impounded areas that contain different habitat and species assemblages.

The UMR has 29 locks and dams that have been operating since installation in the 1930s. The locks and dams divide the river into navigation pools that allow barge traffic on the main channel throughout the ice-free seasons. Each pool (called study areas herein) is composed of a mosaic of aquatic strata that can support macrophytes (Figure 1a). Side channels are hydrologic extensions of the main channel with unidirectional flow, floodplain lakes have varying degrees of connectivity to the main channel with low velocity, and impounded areas are large, open shallow waters with moderate velocity upstream from lock and dams.

Historically, the lock and dams created expansive aquatic areas with stabilized water levels that allowed macrophytes to flourish for decades (Moore et al., 2010). In the late 1980s, severe decline in macrophytes occurred system-wide but the causes are not well understood. Plant loss was speculated as a result of high nutrient and sediment loads, short-term drought (Rogers, 1994), and island erosion (Fischer & Claflin, 1995). A severe flood in 1993 reduced aquatic vegetation abundance further (Spink & Rodgers, 1996). However, seedbanks and overwintering buds remained plentiful during droughts and floods (Kenow & Lyon, 2009; Kimber et al., 1995).

Monitoring aquatic vegetation for the Upper Mississippi River Restoration (UMRR) Program began annually in 1998 in response to plant loss. The data captured an "early" and "late" phases of vegetation recovery (Figure 1b; Larson, Lund, et al., 2022), but the disturbances and reasons for the apparent recovery remain mysterious. All four study areas experienced biologically significant increases in macrophyte prevalence, diversity, and species composition changes from years 2000 to 2015 (Bouska et al., 2022). From years 1998 to 2002, vegetation was in an early phase of recovery and characterized by lower diversity and prevalence of plants. During 2015–2019, macrophyte prevalence, diversity, and community dissimilarity plateaued and became relatively stable in most study areas. Due to these plant assembly changes through time (Figure 1; Bouska et al., 2022; Larson, Lund, et al., 2022), we defined a posteriori the early phase of macrophyte recovery as years 1998–2002 and the late phase of recovery from years 2015 to 2019.


(a)
90°28′ W
90°20′ W
90°4′ W
42°16′ N
42°8′ N
42° N
41°54′ N
Pool 13 strata
Channel Border
Side Channel
Contiguous Impounded
Contiguous Floodplain Lake
MI
MI
MN
WI
IA
IL
Upper Pool 4
Lower Pool 4
Pool 8
Pool 13
LTRM Study Pools
UMR Navigation Reaches
US States
0 50 100
Km
N
W
E
S
0 2 4
Km

Macrophyte and habitat sampling

Long-term resource monitoring of macrophytes occurred since 1998 using consistent, standardized protocols over the 22-year record (Yin et al., 2000) through the UMRR Program. The protocol uses a stratified random sampling design, where the strata included side channels, floodplain lakes, and open impounded areas (Figure 1) and sampling plots are randomly selected within strata. In each study area, a minimum of 450 sampling plots had macrophytes surveyed annually at randomly selected locations within strata. The sampling plot was a 2-m ring around the sides of the airboat but excluded underneath the boat (total area: ~44 m^2). The sampling captured aquatic macrophytes in very shallow depths (~0.1 m), but did not sample the wetland assemblages found in the dewatered floodplains (Dieck et al., 2015). Deep littoral macrophytes (growing in >3 m water depths) were not sampled because of difficulty sampling in deep waters and plants were unlikely to occur due to turbidity (Carhart et al., 2021). Therefore, the vegetation types tested were derived from fully aquatic species inhabiting water depths from 0.1 to 3 m.

Five common life forms were measured at each plot: submersed, filamentous algae, emersed, free-floating, and rooted floating-leaved. We noted presence of any aquatic species detected visually within the plot. Next, we used six subplots around the boat and visually assessed the presence of filamentous algae, emergent, free-floating, and rooted floating-leaved species and raked for the presence of submersed species at each subplot. The plant rake had moderately high detection probability of submersed plants (Gray et al., 2013).

We collected a suite of environmental variables expected to be important for structuring macrophytes. Several environmental characteristics within plots were measured during the macrophyte surveys (Yin et al., 2000), which included location (accuracy of ±5 m), substrate type (nominal variable with six categories: hard clay [category 1], silty clay [category 2], mostly silt [category 3], mostly sand [category 4], all sand [category 5], and rock [category 6]), and average water depth at time of sample (continuous variable; sampling depths ranged from 0.1 to 3 m; average depth = 1.0 m [±0.7 m, 1 SD]). Long-term water quality data were collected for the UMRR Program but independent of macrophyte surveys using standard protocols (Soballe & Fischer, 2004). We selected nine water quality variables from the entire water quality dataset: water clarity (Secchi reading measured in centimeters), total suspended solids (in milligrams per liter), algae (chlorophyll *a* concentration in micrograms per liter), total nitrogen (in milligrams per liter), total phosphorus (in milligrams per liter), water temperature (in degrees Celsius), dissolved oxygen (in milligrams per liter), water velocity (in cubic meters per second), and pH. All water chemistry data were collected near the water's surface between 8:00 and 16:00 h. We used ArcGIS version 10.7.1 to extract water quality values recorded within <60 days and <600 m of each macrophyte sample. The "cost distance function" in ArcGIS ensured that the nearest water quality location was hydrologically connected to the macrophyte plot. The water quality values were appended to each macrophyte plot used in subsequent analyses.

Data analyses

The original macrophyte data frame was converted to a "site by species" matrix that consisted of relative abundance data for 18,178 plots by 86 aquatic macrophyte species. First, we removed plots that lacked vegetation ($n = 22{,}335$ plots) prior to analyses because the research focus was to define vegetation types based on plots with shared taxa, not shared absences. Previous ordinations showed that when unvegetated plots are included, the ecological gradient of no vegetation to high vegetation is so strong (Bouska et al., 2022) that the results highlight shared absences. Next, any species that had less than 15 occurrences were considered rare and removed to improve statistical inferences, which resulted in 72 species for analyses (described in Appendix S1: Table S1). Rare species were members of moist soil communities (Dieck et al., 2015) and their exclusion did not affect our classification results. The data frame contained the species codes created from the standardized U.S. Department of Agriculture's "PLANTS Database" (https://plants.sc.egov.usda.gov/). We retained the original species code names to maintain continuity in the historical dataset and often refer to the species codes in text and figures for brevity. We calculated Shannon's diversity index

FIGURE 1 (a) Map of the Upper Mississippi River (UMR), USA, and the key Long Term Resource Monitoring (LTRM) study areas examined for macrophyte species compositions through time. In each of the four study areas, macrophyte species composition and relative abundance data were collected annually during 1998–2019 at 450 sample plots. The inset is an example from Pool 13 that shows the 450 macrophyte sample plots each year (green dots) that were chosen from a stratified random sampling design. The strata included contiguous floodplain lakes, barge navigation channel borders, side channels, and contiguous impounded areas. (b) Time series graphs from each of the four study areas showing the percent frequency of occurrence for submersed plants through time. The points are pool-wide annual means and the error bars are 95% confidence intervals. For this study, we called years 1998–2002 the "early" phase of macrophyte recovery when plant frequency was <50% and years 2015–2019 the "late" phase of macrophyte recovery when plant frequency was >50% (except Upper Pool 4 that did not show the same magnitude of recovery).

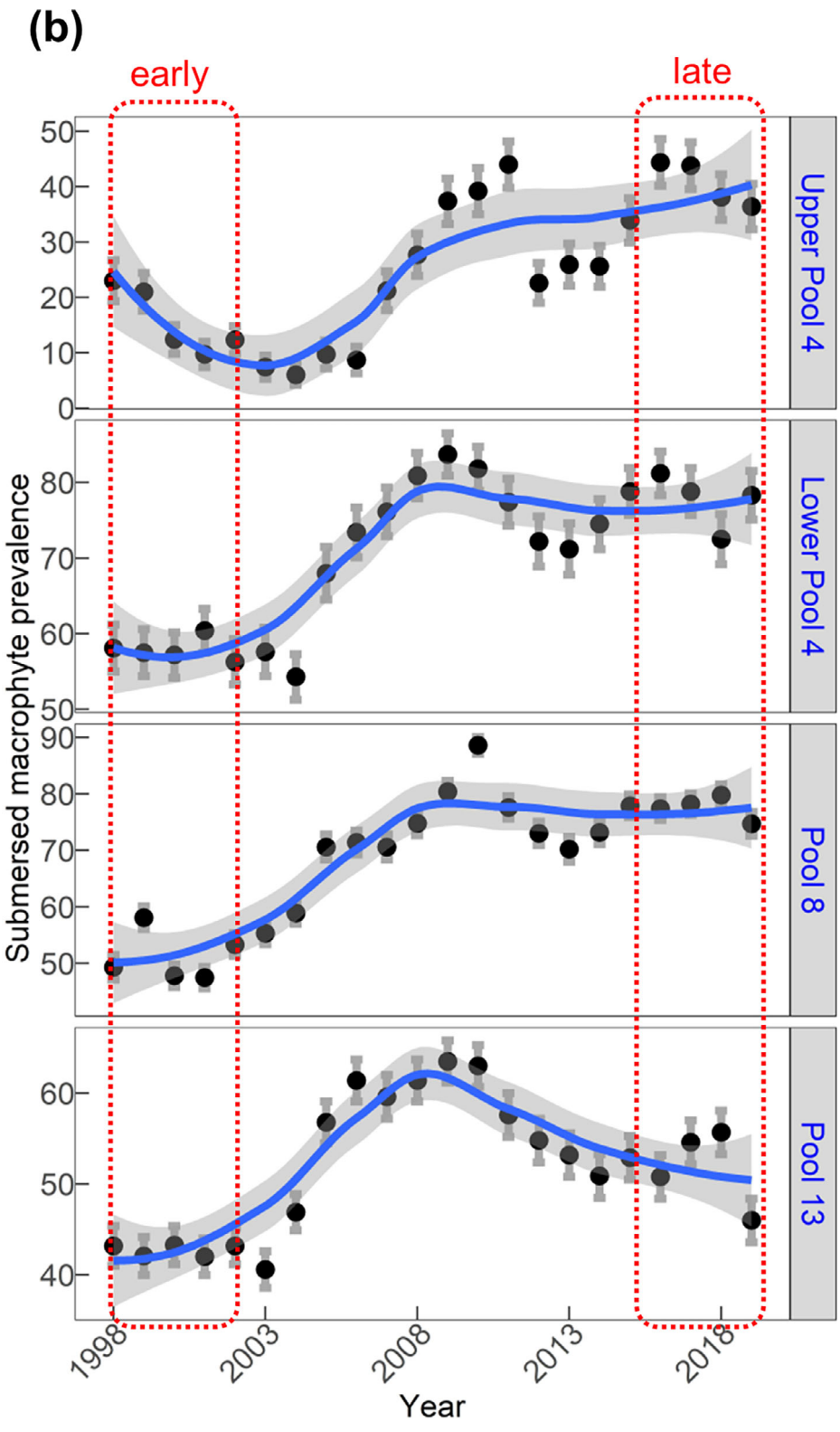


FIGURE 1 (Continued)

using the "vegan" package in R (Oksanen et al., 2019) because vegetation types were differentiated using diversity indices along with species identities and abundances.

Species occurrence data were summarized at the ~44-m^2 plot scale to represent a relative abundance index as follows. Any species that occurred and were detected visually anywhere within the plot were given a score of "1." Then, any species that occurred at a subplot was given a score of "1" for each subplot. Finally, we summed the occurrence data from each of the six subplots and the

visual detection within the entire plot for each species; therefore, each species was assigned a relative abundance index ranging from 0 to 7 based on the species occurrences. Next, the species abundance matrix underwent a Hellinger transformation using the "vegan" package (Oksanen et al., 2019) in software R (R Core Team, 2022) to improve linearity and to group plots by shared species (not joint absences). The transformation allowed for the subsequent Euclidean-based principal components analysis that can identify all species and indicator species in biplots to better interpret results compared with distance-based ordinations (Legendre & Gallagher, 2001).

We ran cluster analyses and sought vegetation types according to study area, strata, and recovery phases for a total of 13 cluster analyses (4 study areas × 2 phases; 3 strata; plus, Pool 8 and Pool 13 impounded areas separately). We subsequently modeled and reported all 13 cluster analysis results. Each cluster analysis used 17–33 species, and a total of 450–1500 plots with complete species composition data were included. We did not identify outliers that could have negatively affected centroid-based clustering. Cluster analyses were carried out with RStudio version 1.3.1093 (R Core Team, 2022) and the packages "vegclust" (De Cáceres & Wiser, 2019) and "pvclust" (Suzuki & Shimodaira, 2006). We ran three common classification techniques and compared results to ensure similar performance that improved our confidence in the classifications. First, we used a "hierarchical cluster analysis" with the average linkage method and the optimum number of clusters defined by the maximum silhouette width criterion. Next, we conducted a "nonhierarchical fuzzy noise cluster analysis" with 999 permutations, a membership value of 1.2, a minimum distance of 0.8 for the plot to be assigned to the noise cluster, and a "defuzzying" level of 0.5. Finally, we ran a principal components analysis and used the first two principal component scores (not raw species abundances) in "*k*-means partitioning," which separated plots into groups by minimizing the sum of the squared Euclidean distances of the plots to the group mean centroids. The optimum number of *k*-means clusters was determined by comparing 30 different indices of clustering validation using the "NbClust" package (Charrad et al., 2014). The optimum number of clusters was consistently similar across all three modeling techniques.

We reported results of *k*-means clustering because of its long-standing use in ecology, robust performance with large datasets, and easily interpretable results for classifying vegetation types (Jongman et al., 1995; Keddy, 2017). Like the original data frame, we removed "rare" species for clustering. For visualizations, we presented a principal component biplot (Figure 2) and *k*-means clustering plots (Figure 3) using tools from the "factoextra" package (Kassambara & Mundt, 2016). To visualize the relative species abundances by cluster, we presented the mean centroid of each species on radar plots (Figure 3). The mean centroid of each cluster is also presented in Table 1, which can be interpreted as the unscaled, average relative abundance score (ranging from 0 to 7) of all species in the cluster. We tested dispersion (variance) differences among clusters using the "betadisper" function in the R vegan package (Oksanen et al., 2019). We named the vegetation types based on species composition, dominant species (radar plots and mean centroid scores), and a diversity index (Appendix S1: Tables S2 and S3).

Next, we conducted a redundancy analysis to examine relationships between the vegetation types and hypothesized environmental predictors using the "vegan" package in R (Oksanen et al., 2019). This analysis is a multivariate extension of multiple regression where the vegetation types are constrained by linear combinations of the predictor variables. The vegetation types identified by cluster analyses were used as the response variables. Environmental predictor variables initially included 11 hypothesized factors that could be important for vegetation typing predictions. The predictors pH and dissolved oxygen were highly correlated (variance inflation factor >200), and so the best predictor (pH) was chosen for the final model based on single-variable elimination and likelihood ratio tests. We applied a Hellinger transformation to the assemblage data to fit linear assumptions and to include species in the biplot. We conducted a permuted, multivariate analysis of variance (perm = 9999) to assess the statistical and biological significances of the overall model, axes, and terms. The final model was structured as:

$$\begin{aligned}\text{Vegetation type} \sim\ & \text{substrate} + \text{velocity} + \text{water depth} \\ & + \text{water clarity} + \text{pH} + \text{chlorophyll } a \\ & + \text{temperature} + \text{total nitrogen} \\ & + \text{total phosphorus} \\ & + \text{total suspended solids}.\end{aligned}$$

We reported the *p* value with degrees of freedom and relative magnitude of differences to assess "statistical significance" of model outputs, and significance was defined at $\alpha = 0.05$. The statistical analysis outputs, graphical trends, and previous literature were used to conclude what constitutes "biologically significant" results and where uncertainty remains (Wasserstein et al., 2019).

RESULTS

Vegetation types at the study area scale (~40–500 km) through time

Vegetation types were not distinguishable at the study area scale or recovery phase. The optimum number of clusters

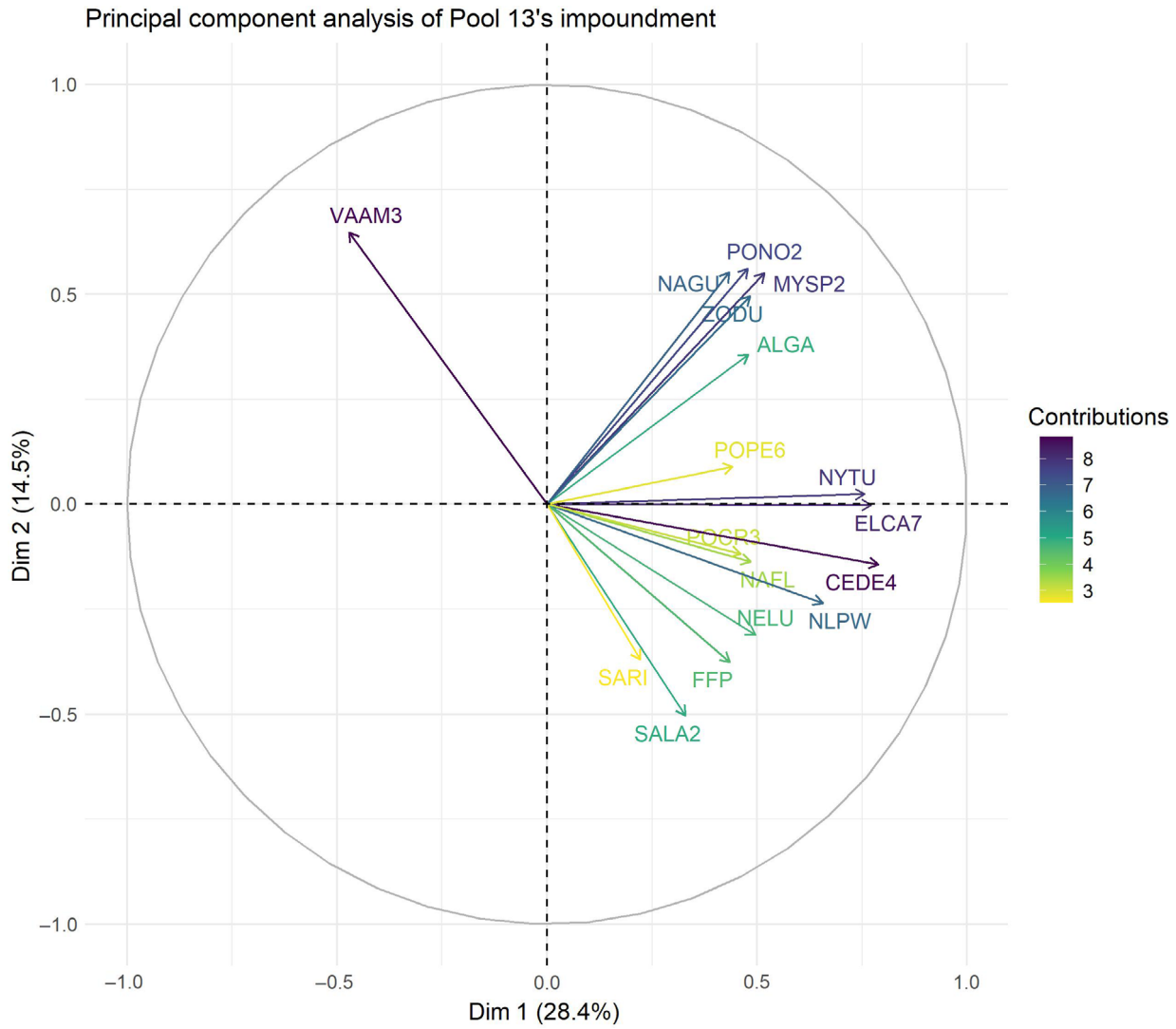


FIGURE 2 The species variables in a principal components analysis of the macrophyte assemblage from the impounded area of Pool 13 during 2015–2019 (the late recovery phase). Axis dimension 1 (Dim 1) explains 28.4% of the community variation and axis dimension 2 (Dim 2) explains 14.5% of the community variation. The species are color-coded according to the relative contributions (%) to explaining the variability in the data. The most prevalent species such as VAAM3, CEDE4, ZODU, and NLPW explain the most variability. VAAM3 is in its own ordination space, indicating this species is uncorrelated or negatively correlated to the other species within the biplot. ALGA, filamentous algae; CEDE4, *Ceratophyllum demersum* L.; ELCA7, *Elodea canadensis* Michx.; FFP, "free-floating plants" including *Wolffia columbiana* Karst., *Spirodela polyrrhiza* (L.) Schleid., *Lemna minor* L.; MYSP2, *Myriophyllum spicatum* L.; NAFL, *Najas flexilis* (Willd.) Rostk. & Schmidt; NAGU, *Najas guadalupensis* (Spreng.) Magnus; NELU, *Nelumbo lutea* Willd.; NLPW, *Potamogeton foliosus* Raf./pusillus L.; NYTU, *Nymphaea odorata* Ait. spp *tuberosa* (Paine) Wiersma & Hellquist; POCR3, *Potamogeton crispus* L.; PONO2, *Potamogeton nodosus* Poir.; POPE6, *Stuckenia pectinata* (L.) Borner; SALA2, *Sagittaria latifolia* Willd.; SARI, *Sagittaria rigida* Pursh; VAAM3, *Vallisneria americana* Michx.; ZODU, *Heteranthera dubia* (Jacq.) MacM.

was always two ($k = 2$; Table 1) for all combinations of the four study areas and the two phases. The relative macrophyte abundance (but not species composition) was the primary differentiating characteristic of the two clusters. One cluster was characterized by low macrophyte abundance (mean abundance index: 0.4–0.6) and the other cluster was characterized by high macrophyte abundance (mean abundance index: 1.2–1.8). Gamma diversity (regional species richness) across the UMR over the 22-year record was 86 aquatic macrophyte species (Appendix S1: Table S1).

The cluster analyses revealed evidence for macrophyte recovery over time. In the late phase, species richness increased in Pool 8 by four new species (MYSI, ZAPA, TYLA, and TYAN) and increased in Pool 13 by six new species (MYSI, NAFL, UTMA, POCO14, SPEU, and

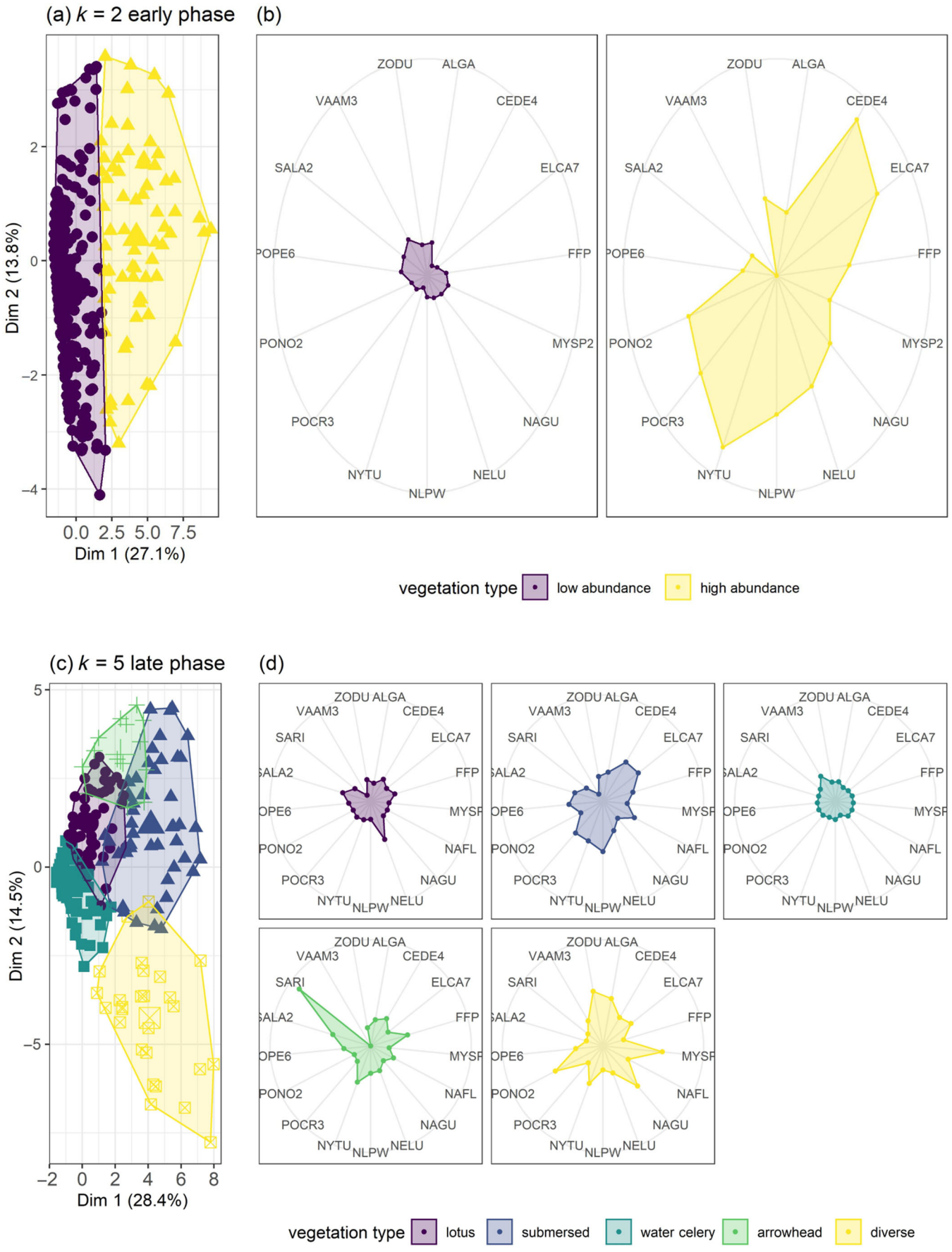


FIGURE 3 Legend on next page.

TYLA). In the late phase, ~25% more plots were within the cluster of high macrophyte abundance, indicating macrophyte abundance increased from the early to late phase in all strata, particularly in floodplain lakes. In Pool 4, the species compositions and number of vegetated plots did not change between the two phases. Species detected in the early phase were always re-detected in the later phase in each study area.

Vegetation types at the strata scale (~4–40 km) through time

Strata did not demonstrate discrete vegetation types, except within impounded areas. The abundance of macrophytes ($k = 2$) but not species composition characterized the clusters through time in floodplain lakes and side channels, like the study area-scale results (Table 1). The impounded strata had discrete vegetation types that matured from the early to late phases of recovery in both Pools 8 and 13. For brevity, the results and discussion focused on the impounded vegetation types in Pool 13, and the results of the vegetation types in Pool 8 are reported in Appendix S1: Text S1 and Appendix S1: Figures S1 and S2.

The principal components analysis biplot of Pool 13 did not clearly discern clusters (Figure 2), other than a possible cluster dominated by watercelery (VAAM3), another by arrowheads (SARI and SALA2), and another at the top right quadrant characterized by submersed species (PONO2, ALGA, MYSP2, NAGU, and ZODU). The biplot showed watercelery (VAAM3) was negatively correlated to the other 16 species. The other 16 species were either not correlated or positively correlated to one another. The highest contributors to explaining assemblage variability were the most prevalent and abundant species, such as watercelery (VAAM3), coontail (CEDE4), narrow-leaved pondweeds (NLPW), Canadian waterweed (ELCA7), and grassleaf mudplantain (ZODU).

In the Pool 13 impounded area during the early phase, 15 species clustered based on low or high macrophyte abundance ($k = 2$; Table 1, Figure 3). In the late phase, two species were added (NAFL and SARI) and three new, additional clusters were identified ($k = 5$; Figure 3). In the late phase, five vegetation types were distinguished based on the abundances, species composition, indicator species, and diversity (Figure 4). The assemblage variation captured by clustering was 44% and all clusters had similar dispersion (variability). Cluster 1 was dominated by lotus (NELU), a rooted floating-leaved species, which coexisted with several submersed species; cluster 2 was named submersed with mix of 11 submersed species, excluding watercelery; cluster 3 represented moderate abundance but dominance of watercelery (VAAM3), a submersed species; cluster 4 was dominated by very high abundance of arrowhead (SARI and SALA2), co-occurring emersed species; and cluster 5 represented diverse plots, as evidenced by a mix of species (Figure 3) and the highest Shannon diversity index (Appendix S1: Figure S3; Figure 4). The diverse, lotus, and arrowhead vegetation types had the greatest relative abundances (>2.5 abundance index) compared with the submersed and watercelery types (Table 1, Figure 3d). Water celery principally occurred in the open impounded area, whereas the other four vegetation types occurred along shorelines and bordering floodplain lakes (Figure 5). Water celery was 3–10 times more common than the other four vegetation types within the impounded area. Although arrowhead (SARI) recently colonized in the late phase and became a novel vegetation type, the arrowhead type was rare and comprised only 3% of plots.

Vegetation types were found in different riverine environments

We used redundancy analysis to associate the environmental factors and the five vegetation types from Pool 13. The full model ($F_{1,469} = 40.11$, $p = 0.001$) and the first

FIGURE 3 Results from *k*-means partitioning that sought discrete vegetation types in the early and late phases of macrophyte recovery in the Pool 13 impounded area of the Upper Mississippi River, USA. (a, b) In the early phase of years 1998–2002, two clusters were differentiated by low and high abundance of macrophyte species. Axis dimension 1 (Dim 1) explains 27.1% of the community variation and axis dimension 2 (Dim 2) explains 13.8% of the community variation. (c) In the late phase of years 2015–2019, five vegetation types were identified. Axis dimension 1 (Dim 1) explains 28.4% of the community variation and axis dimension 2 (Dim 2) explains 14.5% of the community variation. (d) The vegetation types were described by the relative abundance of species (codes on the ends of the radar plots) in each cluster, and clusters were given a vegetation type name based on the dominant indicator species and diversity index. ALGA, filamentous algae; CEDE4, *Ceratophyllum demersum* L.; ELCA7, *Elodea canadensis* Michx.; FFP, "free-floating plants" including *Wolffia columbiana* Karst., *Spirodela polyrrhiza* (L.) Schleid., *Lemna minor* L.; MYSP2, *Myriophyllum spicatum* L.; NAFL, *Najas flexilis* (Willd.) Rostk. & Schmidt; NAGU, *Najas guadalupensis* (Spreng.) Magnus; NELU, *Nelumbo lutea* Willd.; NLPW, *Potamogeton foliosus* Raf./pusillus L.; NYTU, *Nymphaea odorata* Ait. spp *tuberosa* (Paine) Wiersma & Hellquist; POCR3, *Potamogeton crispus* L.; PONO2, *Potamogeton nodosus* Poir.; POPE6, *Stuckenia pectinata* (L.) Borner; SALA2, *Sagittaria latifolia* Willd.; SARI, *Sagittaria rigida* Pursh.; VAAM3, *Vallisneria americana* Michx.; ZODU, *Heteranthera dubia* (Jacq.) MacM.

TABLE 1 Summaries of macrophyte species richness, number of vegetation types, description of the vegetation types, and the average relative abundance score (ranging from 0 to 7) according to various spatial ("study areas" and "strata") and temporal ("early" and "late" phases of macrophyte recovery) scales within the Upper Mississippi River, USA.

Cluster attributes	Study area scale		Strata scale, side channels		Strata scale, floodplain lakes		Strata scale, Pool 13 impounded area	
	Early phase	Late phase	Early phase	Late phase	Early phase	Late phase	Early phase	Late phase
Species richness	14–27	14–32	20	22	32	32	15	17
No. clusters (k) or vegetation types	2	2	2	2	2	2	2	5
Cluster name and percent of plots within each cluster	1: low abundance (68%–94%) 2: high abundance (6%–32%)	1: low abundance (68%–76%) 2: high abundance (24%–31%)	1: low abundance (79%) 2: high abundance (21%)	1: low abundance (68%–76%) 2: high abundance (24%–32%)	1: low abundance (71%) 2: high abundance (29%)	1: low abundance (49%) 2: high abundance (51%)	1: low abundance (85%) 2: high abundance (15%)	1: lotus (17%) 2: submersed (11%) 3: watercelery (63%) 4: arrowheads (3%) 5: diverse (6%)
Mean centroid of cluster as a relative abundance index	1: low abundance (0.4–0.5) 2: high abundance (1.2–1.6)	1: low abundance (0.4–0.6) 2: high abundance (1.2–1.8)	1: low abundance (0.3) 2: high abundance (1.2)	1: low abundance (0.5) 2: high abundance (1.6)	1: low abundance (0.4) 2: high abundance (1.2)	1: low abundance (0.6) 2: high abundance (1.8)	1: low abundance (0.6) 2: high abundance (2.2)	1: lotus (2.5) 2: submersed (2.0) 3: watercelery (1.0) 4: arrowheads (2.7) 5: diverse (2.5)

Note: The study areas scale data show ranges because four study areas are summarized: Upper Pool 4, Lower Pool 4, Pool 8, and Pool 13 (Figure 1).

axis ($F_{1,475} = 284.14$, $p = 0.001$) were statistically significant (Figure 6). The 10 environmental variables explained 30% of the variation in species composition across plots, indicating these environmental factors can somewhat predict vegetation types. Plots classified as vegetation types grouped in ordination space, indicating similar environmental responses with low variability within vegetation types. The vegetation types had statistically significant associations with average water depth, water clarity, substrate, and chlorophyll *a* (Table 2, Figure 6). The five vegetation types were not statistically associated with water velocity, pH, total suspended solids, total nitrogen, total phosphorus, or water temperature, although some patterns were displayed on box plots (Figure 7). In summary, the lotus type was found in relatively shallow water, the lowest water clarity, and variable productivity (i.e., nutrients, pH, and chlorophyll *a*). The submersed type had the greatest environmental variability; although submersed plants were typically found on silty substrate in water depths <1 m, they were associated with large ranges of water clarity, water velocity, and productivity. The watercelery type was found in the deepest water depths, coarsest substrates, a range of water clarity, relatively high pH (indicative of high productivity), and low Shannon's diversity index (Appendix S1: Figure S3). The arrowhead type was found in the shallowest water depths, silty substrates, moderately high water clarity, low total suspended solids, low total phosphorus concentrations, but higher total nitrogen concentrations. The diverse type was positively associated with the highest water clarity, lowest chlorophyll *a*, high pH, high water velocity, high total suspended solids, and highest total nitrogen.

The redundancy analysis and box plots revealed three primary environmental gradients that vegetation types responded to: (1) inundation depth and duration (measured by water depth, velocity, and substrate coarseness), (2) water clarity (measured by total suspended solids, chlorophyll *a*, and Secchi depth), and (3) productivity (measured by pH, nutrients, and chlorophyll *a* concentrations). From these results, we generated a conceptual figure relating the vegetation types to key environmental gradients to visualize the structuring factors and variability (Figure 8). The submersed and watercelery types had the greatest variability in environmental conditions (Figures 7 and 8). The watercelery, arrowhead, and diverse types had the least overlap in environmental niche space compared with the submersed and lotus types.

DISCUSSION

The long-term, spatially comprehensive dataset on macrophyte community composition and distribution provided a

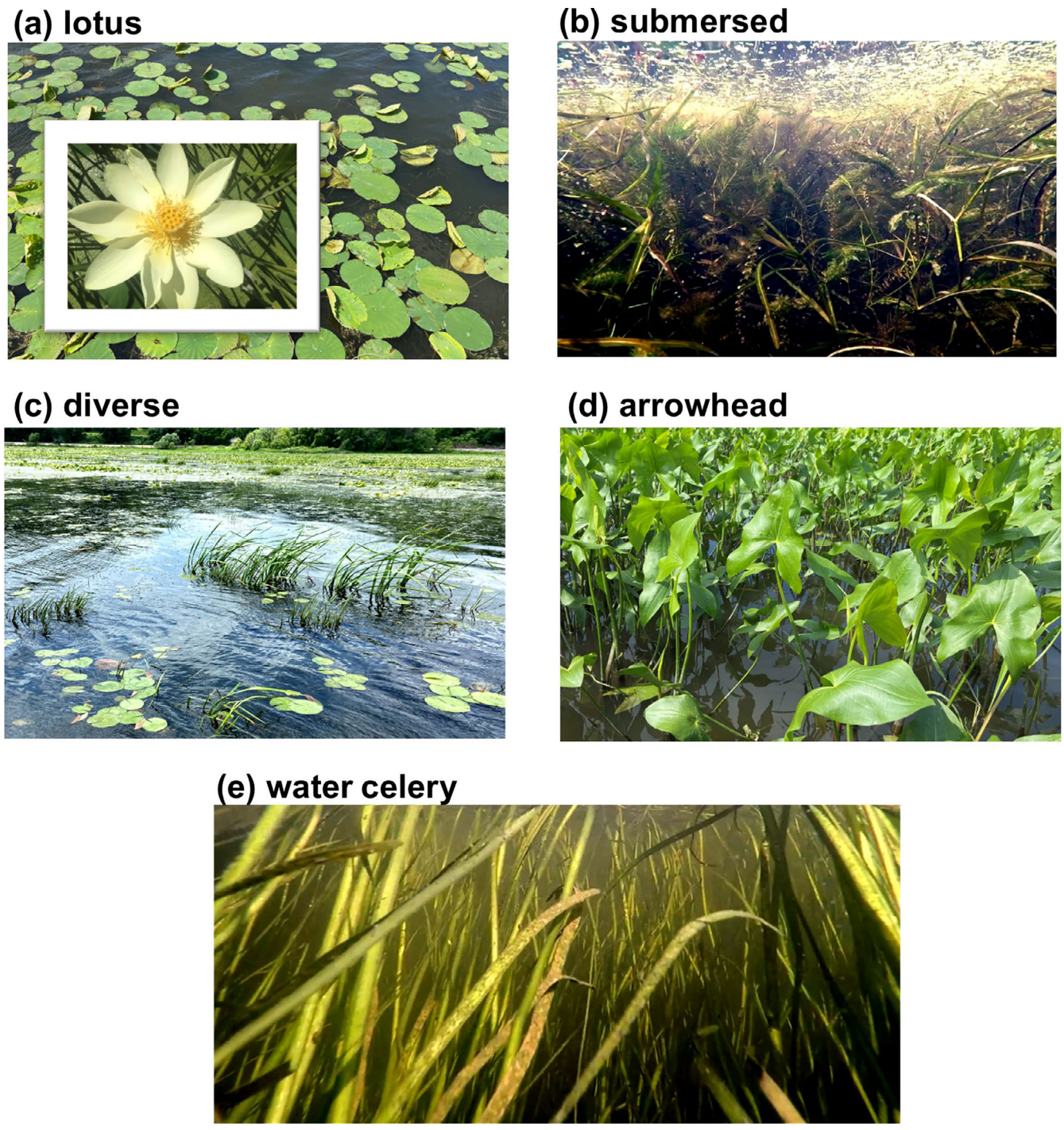


FIGURE 4 A photograph collage of the five vegetation types found in impounded areas of the Upper Mississippi River, USA during years 2015–2019. Vegetation types were named based on the dominance of an indicator species and Shannon's diversity index.

rare opportunity to characterize vegetation types in an internationally significant river exhibiting macrophyte recovery over the past 22 years. The clustering highlighted that macrophyte abundance, species identities, and diversity indices occasionally differentiated vegetation types across the UMR in space and time. About 90% of plots did not have predictable assemblages, indicating most plots are unique in species composition and that perhaps complex ecological processes and randomness structure the assemblages. However, impounded areas (10% of plots) showed five matured vegetation types in the late phase of recovery that were moderately predictable based on commonly measured environmental gradients. These five vegetation types happen to be important restoration targets in this river because of partnership goals of restoring

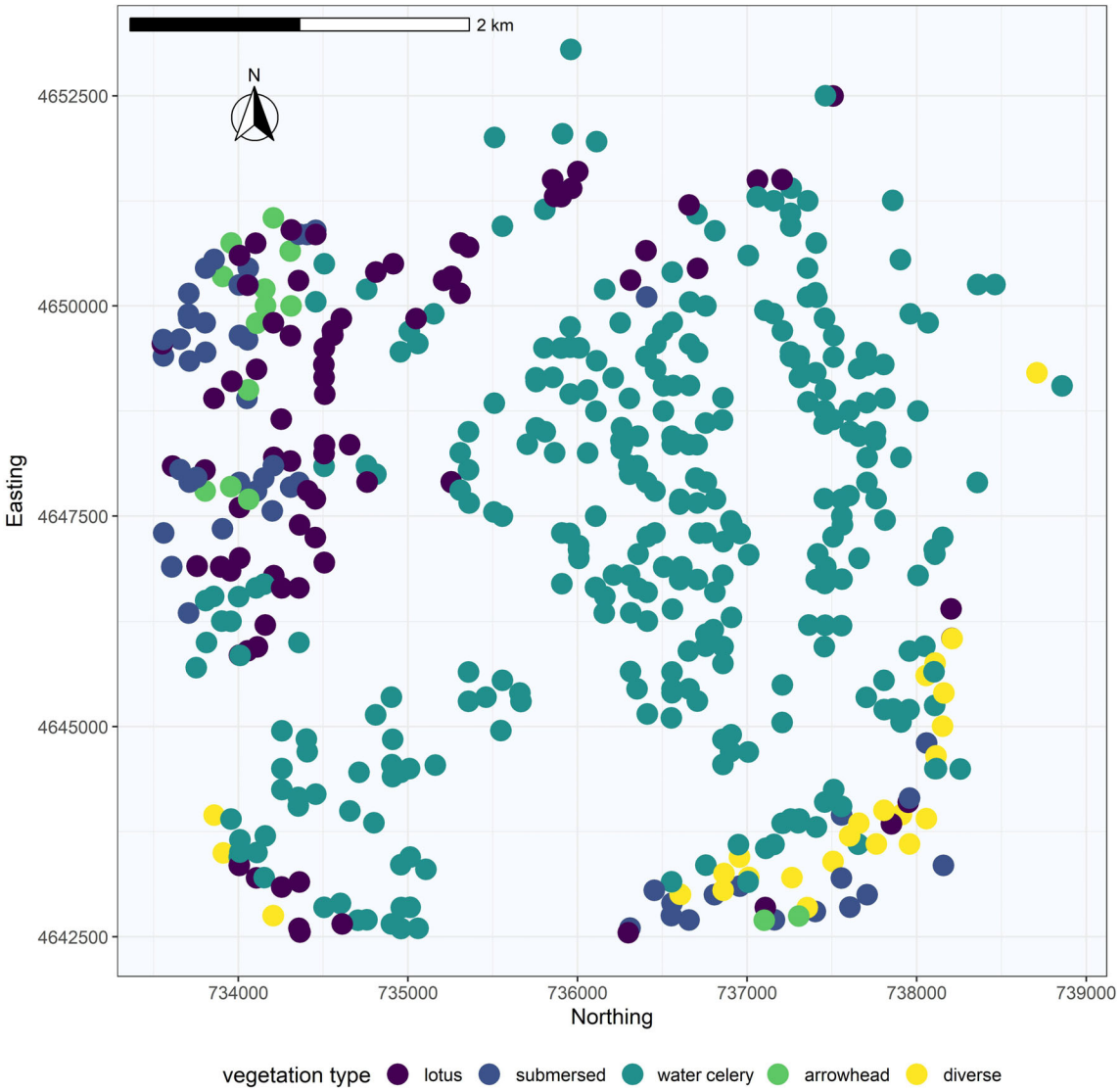


FIGURE 5 A map highlighting the spatial distribution of the five vegetation types in the Pool 13 impounded area of the Upper Mississippi River during the late phase of macrophyte recovery during 2015–2019. Water celery principally occurred in the open impounded area whereas the other four vegetation types were in connected backwaters and side channel strata.

plant diversity and their ecological significance to wildlife (Devendorf, 2013; Korschgen et al., 1988; McCain et al., 2018). Our results provide communication tools for restoration planning that enable managers to describe desired aquatic vegetation goals, as well as quantifiable targets to set environmental conditions for specific typologies. The macrophyte restoration implications from our results include creating habitat heterogeneity for abiotic conditions (e.g., velocity, productivity, and water depth; Figure 8). In more predictable impounded areas, our results provide quantitative restoration targets for specific aquatic vegetation types and their associated abiotic conditions. The newly identified vegetation types can serve as benchmarks for assessment of future changing conditions and vegetation responses to restoration.

Few, but ecologically meaningful, vegetation types were distinguished

Five vegetation types were identified in the riverine impounded areas during late recovery and were predicted and differentiated by gradients of inundation, water clarity, and productivity (Figures 6–8). These five vegetation types are not unexpected because they represent various "life forms" (e.g., submersed, floating-leaved, and emersed vegetation) that are known to strongly respond to inundation regimes based on water depth, water duration, and hydrologic connectivity (Clark & Clay, 1984; Schneider et al., 2018). Previous work also concurred that aquatic plant diversity responds to lower productivity and higher water clarity from low phytoplankton (chlorophyll *a*) biomass

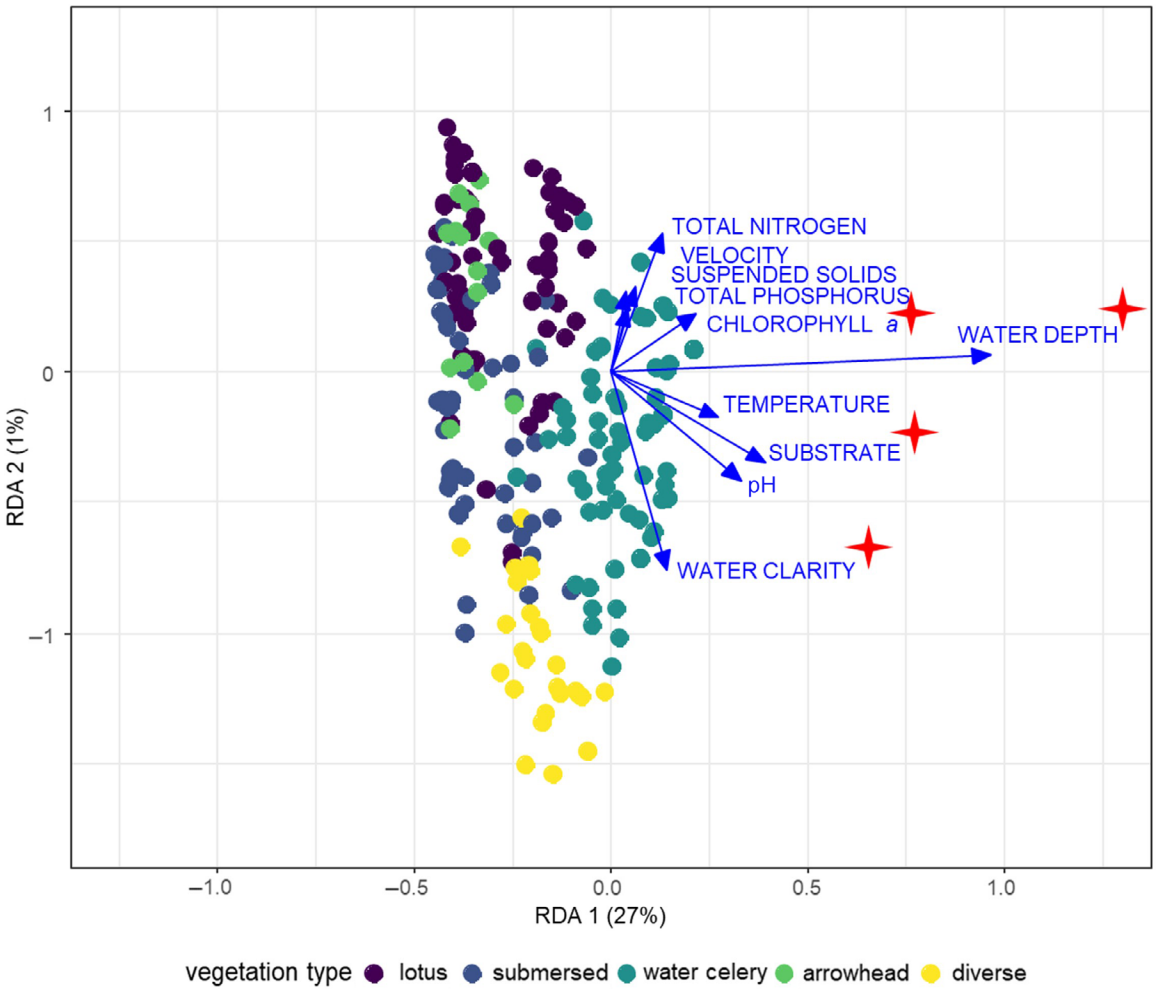


FIGURE 6 A redundancy analysis (RDA) biplot of the Pool 13 impounded area of the Upper Mississippi River. The biplot displays the response variables (the five vegetation types) and the environmental predictors (blue vectors) in ordination space. Axis 1 (RDA 1) explains 27% of the community variation and axis 2 (RDA 2) explains 1% of the community variation. Species abundances had a Hellinger transformation prior to ordination. The RDA scaling reads that species, predictors, or responses have positive associations if at acute angles, no associations if at right angles, and negative associations if at obtuse angles. The overall RDA model, RDA axis 1, and the RDA terms "water clarity," "substrate," "water depth," and "chlorophyll *a*" were statistically significant (red stars).

(Hough et al., 1989). Although these vegetation types are specific to the UMR, they well represent submersed types in regional wetlands (Larson, DeJong, et al., 2022), watercelery types of the North American Laurentian Great Lakes' inland and coastal wetlands and rivers (Schloesser & Manny, 2007), and arrowhead types in rivers worldwide (Ndlovu et al., 2020; Wang et al., 2020).

We expected a few additional vegetation types, but which were not observed. First, our hypothesis 2 was partially supported in that *C. demersum* and *E. canadensis* were often abundant in the early phase, both other expected species like *S. pectinata* and the invasive *P. crispus* were not (Figure 3). We were surprised that wild rice, *Zizania aquatica* L., was not its own vegetation type given its rapid expansion and high abundance in the late recovery phase in some UMR study areas, except in Pool 13 (Larson, DeJong, et al., 2022; Larson, Lund, et al., 2022). Interestingly, invasives (like *P. crispus* and *Myriophyllum spicatum*) were present in low abundance in all vegetation types but were not indicator species (Figure 3) because aquatic plant invasives rarely dominate in this system (Appendix S1: Table S1; Drake et al., 2022; Larson, DeJong, et al., 2022, Larson, Lund, et al., 2022). However, our river experience is that a new and prolific invader as of year 2020, *Butomus umbellatus* L., may soon become a novel vegetation type.

Most plots were not classified into vegetation types. Often complex ecological processes such as hydrologic disturbance, dispersal, and facilitation can interplay and lead to random assemblages in rivers (Boschilia et al., 2008). In the UMR, these ecological processes are likely affecting aquatic vegetation assemblages. As examples, inundation and flooding regimes are complex and

TABLE 2 Results from a multivariate redundancy analysis in which five aquatic macrophyte vegetation types from Pool 13 impoundment area of the Upper Mississippi River were predicted by habitat (full model: $F_{1,469} = 40.11$, $p = 0.001$).

Predictor variable	df	Variance	*F*	*p*
Substrate	1	0.04	21.96	<0.001
Water clarity (Secchi depth)	1	0.04	20.56	<0.001
Chlorophyll *a*	1	0.01	0.02	0.002
Average water depth	1	0.05	31.00	<0.001
Velocity	1	0.00	0.49	0.48
pH	1	0.00	0.93	0.35
Water temperature	1	0.00	0.03	0.87
Suspended solids	1	0.00	0.39	0.54
Total nitrogen	1	0.01	0.88	0.35
Total phosphorus	1	0.00	0.47	0.49
Residual	466			0.81

spatially variable in this system (VanAppledorn et al., 2021), connectivity between the impounded area and the contiguous backwaters may buffer eutrophication and support diversity (Amoros & Bornette, 2002; Salgado et al., 2019), and biotic facilitation in the late phase of recovery may have buffered the effects of eutrophication on submersed plant diversity (LeBagousse-Pinguet et al., 2012).

We suggest several plausible reasons that not more than five vegetation types were identified. First, the late phase had a greater available species pool that was more complex in terms of species richness and abundances, and complexity adds uncertainty in predictive modeling (e.g., see the cluster overlap in Figure 3c). Second, we speculate but do not have sufficient data to test that using biomass (in grams per square meter) would yield more vegetation types because this may allow the inclusion of rare species and have a larger range of abundances than the current coarse abundance scaling. Third, our data collection experiences lead us to suggest that one sample plot (44-m^2 area) regularly straddled multiple vegetation types (e.g., one side of the boat was lotus and the other was submersed). Lastly, our sampling frame was restricted to fully aquatic species with a regional species pool of less than 50 common species (Appendix S1: Table S1) and so few vegetation types would be expected. Likewise, a previous study that spanned multiple German rivers classified only seven aquatic vegetation types (Schaumburg et al., 2004). A previous floodplain vegetation study in the UMR captured a strong inundation gradient that included the emergent and wet meadow zones, and 16 floodplain vegetation types were identified (De Jager et al., 2016). Similarly, a strong inundation gradient across the Danube River floodplain in Austria identified 14 floodplain vegetation types, but only 5 of those types were exclusively aquatic (Schmidt-Mumm & Janauer, 2016).

Ecological relevance of these vegetation types

Our results identified vegetation types that were responsive to environmental conditions that developed during the later phase of plant recovery (Figures 3 and 6), which might indicate possible causes for the recovery. In particular, submersed and diverse vegetation types were affiliated with moderate nutrient concentrations and high water clarity (Figures 6–8), both of which have improved over the past 22 years due to regional watershed management and localized river restoration (Houser et al., 2022). Macrophyte recovery in rivers depends on interactions between the river's geomorphology and degree of eutrophic reduction (Carhart et al., 2021; Hilton et al., 2006). These impounded areas had restored habitat complexity over the past two decades, such as floodplain connectivity and reconstructed islands that likely increased water clarity and reduced eutrophication (De Jager et al., 2018; Drake et al., 2018; Langrehr et al., 2007). The combination of a suitable geomorphic template for aquatic plants (Carhart et al., 2021), improvements to water quality (Burdis et al., 2020; Houser et al., 2022), and time (~22 years) may have allowed vegetation types to "develop and mature" in the later phase of recovery.

These five vegetation types have high ecological value for certain wildlife species and people (Moore et al., 2010). More than 50% of the eastern population of Tundra swans (*Cygnus columbianus columbianus*) use the Upper Mississippi Flyway during autumn migration and consume mostly arrowhead tubers. The canvasback duck (*Aythya valisineria*) is a species of conservation priority (U.S. Fish and Wildlife Service, 2019) that feeds primarily on watercelery and arrowhead tubers and requires substantial energy from these plant sources for migration (Korschgen et al., 1988). Northern pike (*Esox lucius*) is a valued recreational sport fish that has greatest production in submersed vegetation (Holland & Huston, 1984). The flowering lotus and diverse vegetation types can have high aesthetic beauty to humans (Figure 4).

Applications and tools for restoring vegetation

Our classifications helped identify habitat suitable for the recovery or restoration of specific vegetation types such as watercelery and high diversity, which are important and ongoing partnership priorities (McCain et al., 2018; U.S. Fish and Wildlife Service, 2019). Broad management goals in the UMR were stated for arrowhead, watercelery, and diverse vegetation types to improve ecological integrity and waterfowl habitat (Devendorf, 2013; McCain et al., 2018; U.S. Fish and Wildlife Service, 2019). Therefore, our results that classified (Figures 2–4), mapped

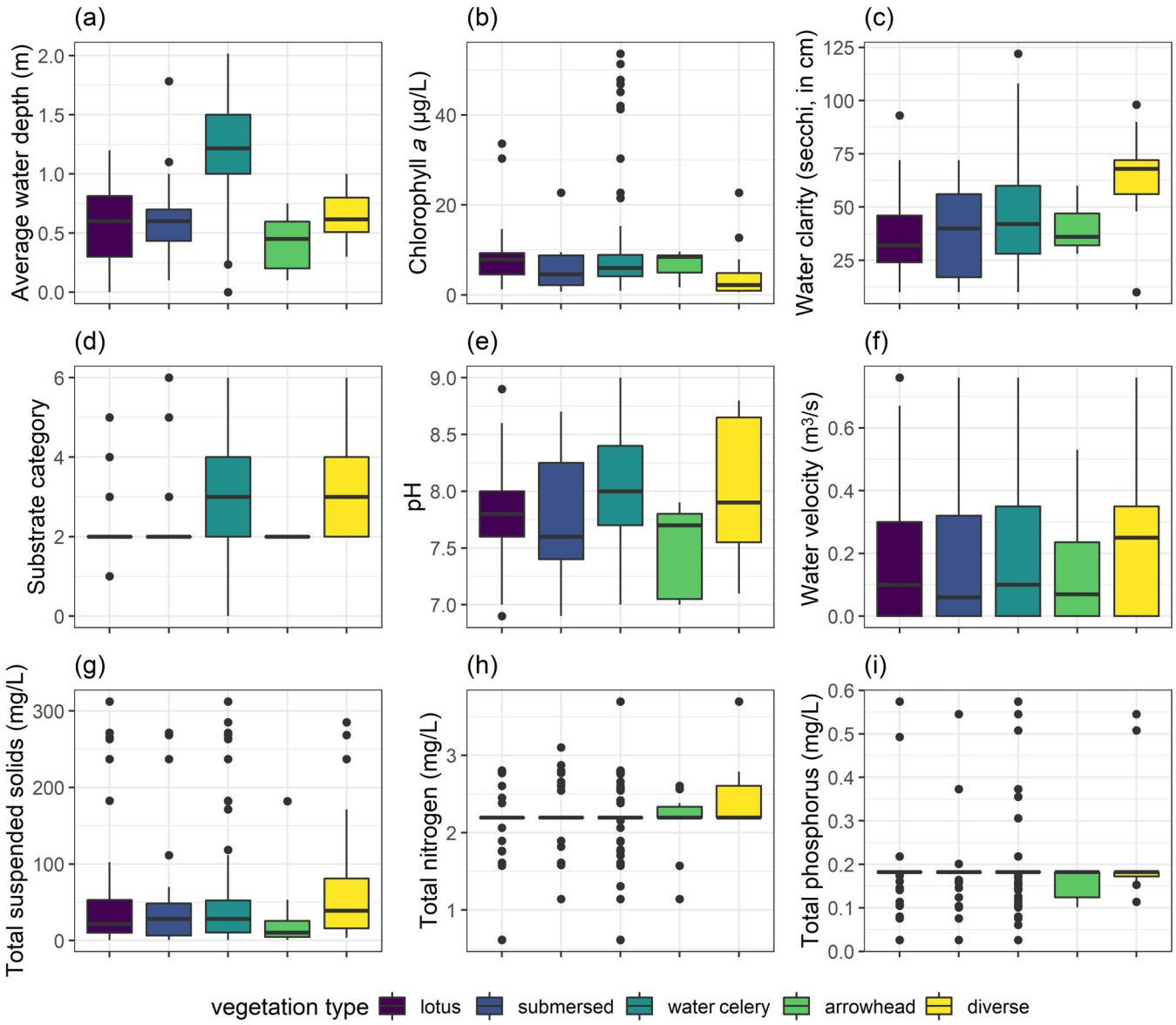


FIGURE 7 Box plots showing the five macrophyte vegetation types from Pool 13 in the Upper Mississippi River in relation to several hypothesized environmental predictors. The boxes encapsulate the interquartile range where the middle line is the median, the whiskers are 1.5 times the interquartile range, and the dots are outliers. The data in panels (a) "water depth," (b) "chlorophyll *a*," (c) "water clarity," and (d) "substrate" were statistically significant predictors for each vegetation type based on redundancy analysis. Substrate categories ranged from 1 to 6 along a gradient of hard clay (category 1), silty clay (category 2), mostly silt (category 3), mostly sand (category 4), all sand (category 5), and rock (category 6).

(Figure 5), and predicted (Figures 6–8) macrophyte communities could be directly applied to manage habitat at strata and study area scales. The classification of vegetation types can facilitate decisions on which vegetation types to restore, the maps may aid in choosing restoration and conservation areas, and the predictive outputs provide a quantitative range of suitable environmental conditions. However, moving toward an ecosystem stewardship framework would require not only managing these vegetation types as "steady-state resources," but also encouraging their adaptive capacities and natural dynamics (Chapin et al., 2010). Adaptive management and resiliency are especially important in this large, modified river that often experiences uncertain and dramatic environmental changes and disturbances (Bouska et al., 2019). As an example, reinstating a natural flow regime and lost natural processes like gap formation in dammed rivers may provide heterogeneity needed for the full array of vegetation types (Keddy, 2017). These dynamic processes may be achieved in the UMR with water level management (Heglund et al., 2022) and other inundation regimes (VanAppledorn et al., 2021).

Given the extent of this large dataset and high priority of macrophyte restoration in the UMR (McCain et al.,

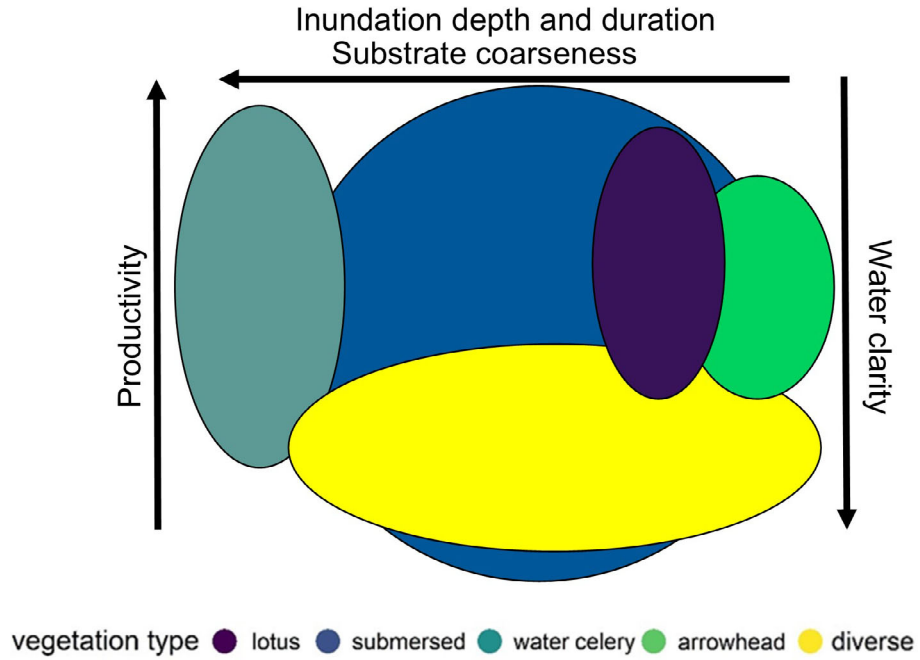


FIGURE 8 A conceptual figure showing the primary aquatic vegetation types of the Upper Mississippi River across three riverine gradients related to inundation depth and duration (average water depth, velocity, and substrate coarseness), productivity (chlorophyll *a* concentration and nutrients), and water clarity (Secchi depth, chlorophyll *a* concentration, and total suspended solids).

2018), future work that models each vegetation type separately would yield further ecological understanding and improved restorations. For example, modeling diversity or watercelery as a single response variable in a model could reveal more information about assemblage optima and tolerances to environmental conditions and perturbations, important functional traits to conserve, environmental "thresholds" that can warn of state changes, and the relative stability and resilience of assemblages through time. Further, predictive modeling for vegetated versus unvegetated plots and the gradient of vegetation abundance would aid our understanding in the recovery of macrophytes and identify existing environmental constraints that still serve as a bottleneck to full macrophyte recovery. Our results had moderate levels of uncertainty and explanatory powers (Figures 6–8) similar to other riverine vegetation typing studies (Day et al., 1988; Schaumburg et al., 2004), so this precludes macrophytes as effective indices of environmental conditions (Demars et al., 2012).

With more detailed and long-term data for each vegetation type, "hypothetical scenarios" could be developed that predict how environmental changes or restoration actions would affect vegetation and resiliency (Gillson et al., 2021). Recent hypothetical scenario modeling on submersed vegetation in the river estimated how major improvements in water clarity would increase submersed aquatic vegetation coverage, and those results can help prioritize restoration locations and the abiotic conditions to focus restoration (Carhart et al., 2021). Similar predictive and scenario modeling using our newly identified vegetation types could further aid restoration and resiliency of other desirable vegetation types (e.g., high diversity and watercelery) in the face of hydrologic fluctuations, climatic changes, or river restoration actions. As another example, the two indicator species in the arrowhead type (*Sagittaria rigida* and *Sagittaria latifolia*) are primary swan forage that can occupy different depth ranges (Clark & Clay, 1984) but also can overlap at the same plot (Figure 3); testing hypothetical scenarios of arrowhead resiliency to hydrologic fluctuations could be valuable to managers seeking to understand available forage to migrating swans. In most instances, vegetation types were not defined in the UMR and so restoration could focus on providing geomorphic complexity that may then support macrophyte species and diversity (Makkay et al., 2008).

CONCLUSIONS

Macrophytes in rivers worldwide can be biological indicators of both localized habitat conditions and anthropogenic effects up to continental scales (Carhart et al., 2021; O'Hare et al., 2011; Steffen et al., 2014), although challenges exist in the use of vegetation types as biological indices of water quality or "ecosystem health" (Demars et al., 2012). Similar to other vegetation typing studies in rivers worldwide (Day et al., 1988; Demars et al., 2012; Makkay et al., 2008; Schaumburg et al., 2004), our results and inferences were limited by moderate predictability but vegetation types were associated

with specific ecological gradients that can inform river restoration and management (Figures 6–8). In conclusion, the newly identified aquatic vegetation types we described can serve as references in the long-term monitoring of macrophytes and enable future assessments of changing conditions and responses to restoration in one of the world's largest rivers.

AUTHOR CONTRIBUTIONS

All authors conceived the study, conceptualized the research, interpreted the results, and edited the paper. Danelle M. Larson ran data analyses, constructed figures, wrote the first paper draft, and addressed peer reviews.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets are publicly available through the Upper Mississippi River Restoration Program's website (Long Term Resource Monitoring element—SRS Vegetation Data Query [usgs.gov]). To query this specific dataset: (1) select "Field Station" *1*, *2*, and *3*; (2) select "Date Range" *January 01, 1998 to January 01, 2019*; (3) select "Map Stratum" *BWC*, *IMP*, *MCB*, and *SC*; (4) select "Vegetation Species" *All Species*; (5) select "Submit Query" button at bottom of page.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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