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22 Years of Aquatic Plant Spatiotemporal Dynamics in the Upper Mississippi River

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Abstract: Macrophyte (aquatic plant) recovery has occurred in rivers worldwide, but assemblage patterns and habitat requirements are generally not well understood. We examined patterns of species composition and macrophyte abundance in the Upper Mississippi River (UMR), spanning 22 years of monitoring and a period of vegetation recovery. Non-metric multidimensional scaling (NMDS) ordination revealed a gradient of macrophyte abundance and diversity for 25 species, which were associated with water velocity, depth, wind fetch, and water clarity. Three macrophyte genera of ecological and restoration interest (*Zizania aquatica*, *Vallisneria americana*, and *Sagittaria* spp.) occupied different ecological niches. Trends of NMDS values showed that *Z. aquatica* first co-occurred in shallow areas with *Sagittaria* spp. but then expanded into deeper, lotic habitats where *V. americana* often resided. Curve Fit regression analysis identified large areas of significant increases in the relative abundance of *V. americana* and percent cover of *Z. aquatica* in several reaches of the UMR from 1998–2019. *Sagittaria* spp. were more spatiotemporally dynamic, which may indicate specific habitat requirements and sensitivity to environmental gradients. Our analyses showed that these three ecologically important genera are spatiotemporally dynamic but have somewhat predictable habitat associations, which can guide macrophyte management and restoration in the UMR and other large, floodplain rivers.

Keywords: aquatic macrophytes; aquatic plant diversity; aquatic vegetation assemblage; ecological community dynamics; large floodplain river; long-term data; *Sagittaria* spp.; temporal change; *Vallisneria americana*; *Zizania aquatica*

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1. Introduction

Aquatic vegetation (hereafter 'macrophytes') provides critical food, habitat, and refuge for river biota and has a strong influence on water quality in large river floodplains. The composition, abundance, and distribution of macrophytes is affected by complex interactions of physical and biological drivers, although, in many rivers, plants are primarily limited by light availability and water level fluctuations [1–3]. Many riverine systems lack sufficient data to assess long-term dynamics and the roles of environmental and spatial gradients that structure macrophyte communities [4].

Ecologists quantify species distributions and the environmental drivers (both biotic and abiotic factors) to understand limitations and restoration potential for species and communities. The conceptual development and quantification of the 'environmental niche' of species has progressed over the past century [5,6], and assessments today still aim to measure how environmental conditions and the interplay among species (e.g., niche overlap that induces competition) can affect species distributions and how those distributions change over time [7]. Methods for quantifying and defining the environmental niche typically include species distribution modeling or ordination techniques. Ordination quantifies the species–environment relationships (i.e., the environmental niches) by using maximization criteria to construct synthetic environmental gradients (i.e., axes) from the included environmental variables and placing species in ordination space according to their environmental associations [8]. Quantifying the multidimensional environmental niche space can guide restoration targets by revealing environmental drivers and the relative stability or vulnerability of the species niche [9].

There is growing interest in restoring the floodplain habitat and aquatic plants in regulated rivers, such as the Upper Mississippi River (UMR) [10]. Like many large floodplain rivers, the UMR is highly modified and degraded [11–13]. Prior to the construction of the lock and dam system in the 1930s, macrophytes were abundant and diverse [10]. The impoundment of the UMR and subsequent maintenance of a 2.7-m navigation channel changed the distribution of flow and depth throughout the system [12,14], resulting in a change in composition and an increase in the abundance of river vegetation [15]. Macrophytes flourished in these new habitats for decades following the construction. A widespread decline in macrophytes was observed in the UMR during the 1990s [16,17]. However, some areas within reaches (e.g., backwater lakes) maintained aquatic vegetation during this period, while other areas (e.g., impounded areas) experienced a substantial recovery from 2000–2016 [17–19]. Understanding where macrophytes were stable or underwent changes over this time period and identifying the environmental drivers would provide useful information about resilience of large river floodplains.

A considerable portion of the increase in the UMR macrophytes over this period is attributable to four native species: wild celery (*Vallisneria americana* Michx.), wild rice (*Zizania aquatica* L.), and arrowheads (*Sagittaria latifolia* Willd. and *Sagittaria rigida* Pursh.) [20]. Like other submersed species, *V. americana* provides food and shelter for a diverse assemblage of invertebrates, fish, amphibians, reptiles, and water birds [21–23]. *Vallisneria americana* is a predominantly clonal, perennial plant that produces overwintering buds with high energetic value for canvasback ducks (*Aythya valisineria* Wilson) and other migrating waterfowl [23]. *Vallisneria americana* is commonly found growing in open impounded areas with moderate flow [3]. *Zizania aquatica*, an annual aquatic grass, provides excellent cover for many species of water birds, including the federally listed black tern (*Chlidonias niger*), and provides food for waterfowl during the fall migration [24]. *Zizania aquatica* is also a valuable food source for humans, provides cultural connections to the river, and is found in many habitat types of this riverscape [20]. Broadleaf arrowhead (*S. latifolia*) and stiff arrowhead (*S. rigida*) are emergent species that provide critical wildlife food and habitat [15,25]. *Sagittaria* spp. are predominantly clonal, perennial plants that expand through the growth of rhizomes, and the edible tubers are commonly found in shallow, backwater habitats [25,26]. These three ecologically important genera appear to be different vegetation types [27] with differing traits and habitat preferences, yet niche differentiation and the annual to decadal spatiotemporal changes have not been well described.

In this study, we assessed the changes to three key genera within the aquatic vegetation assemblage at several spatiotemporal scales across the UMR. We focused on the dynamics among *Z. aquatica*, *V. americana*, and *Sagittaria* spp. due the recent expansion of *Z. aquatica* in some areas and a concern from river managers that *Z. aquatica* may be outcompeting and replacing other species. Our specific objectives were to: (1) determine if *Sagittaria* spp., *Z. aquatica*, and *V. americana* occupy different ecological niches or overlap, (2) identify the associated environmental gradients for each species, and (3) quantify how these species have changed in abundance and niche space over 22 years. We expected significant changes in abundance of *Sagittaria* spp., *Z. aquatica*, and *V. americana* to have occurred over the 22-year recovery period and that these changes would be associated with geomorphic characteristics, water quality, and hydrology. We hypothesized that the three genera would separate in ordination space, indicating distinct ecological niches. We also hypothesized that nine environmental factors (such as depth, clarity, velocity, and wind fetch) would separate these species into different and somewhat predictable niches across the riverscape. Based on our field experiences, we suspected that large river sections transitioned from the dominance of either *V. americana* or *Sagittaria* spp. into predominantly *Z. aquatica*, and that *Z. aquatica* had shifted its ecological niche to deeper, flowing water.

2. Methods

We used multiple, long-term monitoring datasets of macrophytes, hydrology, and water quality metrics to analyze macrophyte assemblage dynamics and habitat associations across space and time in the UMR. We first used non-metric multidimensional scaling (NMDS) to describe species compositional gradients (n = 13,802 sites) and to observe the niche space of the three primary genera. We then used the Envfit function in R (vegan package, version 2.5-7) to evaluate if species composition was associated with hypothesized environmental factors. Lastly, we mapped changes in relative species abundance for *V. americana*, *Z. aquatica*, and *Sagittaria* spp. from 1998–2019 (at annual and decadal time steps) to identify areas that have shifted or remained stable for macrophyte abundance or composition.

2.1. Study Area

The UMR has 29 locks and dams that separate the river into navigation pools. Each pool contains a mosaic of aquatic habitats including a main channel, channel border, side channels, contiguous and isolated floodplain lakes, and impounded areas upstream from the dams. Each of these riverine habitats span large ecological gradients and have varying degrees of flow velocity, water exchange rates, and substrate type [14].

Our study used macrophyte and habitat data from the Long Term Resource Monitoring (LTRM) element of the U.S. Army Corps of Engineers Upper Mississippi River Restoration Program. The entire study area spans approximately 400 km of the UMR, from Lock and Dam 3 near Red Wing, Minnesota to Lock and Dam 13 near Fulton, Illinois (Figure 1). We focused on Pools 4, 8, and 13, because LTRM has monitored aquatic vegetation and water quality using standardized protocols since 1998 in these pools. Pool 4 (~70 km long and ~15,557 ha aquatic area) is sometimes analyzed as “upper Pool 4” and “lower Pool 4” because Lake Pepin, a natural tributary delta lake (~34 km long) between upper- and lower-Pool 4, acts as a major sediment sink and greatly affects water clarity downstream from the lake in Lower Pool 4 [3]. In Pool 8 (~37 km long and ~9424 ha aquatic area) and Pool 13 (~45 km long and ~13,526 ha aquatic area), the hydrologic effects of the navigation system are most pronounced in open impounded areas upstream from the lock and dams (i.e., mean annual water level fluctuation is generally <0.5 m in these areas). Much of the open impounded areas are shallow with high wind fetch and, therefore, are subject to island erosion and sediment resuspension.

2.2. Macrophyte and Habitat Data

Macrophyte data were collected in Pools 4, 8, and 13 using consistent, standardized sampling protocols over the 22-year record (1998–2019) [28]. A minimum of 450 sites in each pool were sampled annually between 15 June and 15 August using a stratified random sampling design, where strata included main channel borders, side channels, contiguous and isolated floodplain lakes, and impounded areas. In each pool, a 50 × 50 m grid was generated and overlaid onto the stratified aquatic areas, and sites were reselected annually using a random number generator. Five aquatic vegetation lifeforms were measured at each site: submersed, emersed, rooted floating-leaved, free-floating (e.g., duckweeds), and filamentous algae. Submersed species and filamentous algae were sampled at six subsites (0.3 m × 1.5 m) around the boat using a double-sided rake. Relative abundance was estimated for each submersed species and algae present on the rake with scores ranging from 0–5 (0 = no plants retrieved, and 1 = 1–20% rake teeth filled to 5 = 81–100% rake teeth filled). Emersed, rooted floating-leaved, and free-floating lifeforms were recorded as percent cover ranging from 0–5 (0 = no plants retrieved, 1–5 in 20% increments) within a 2 m buffer around the boat (total area = ~44 m^2).

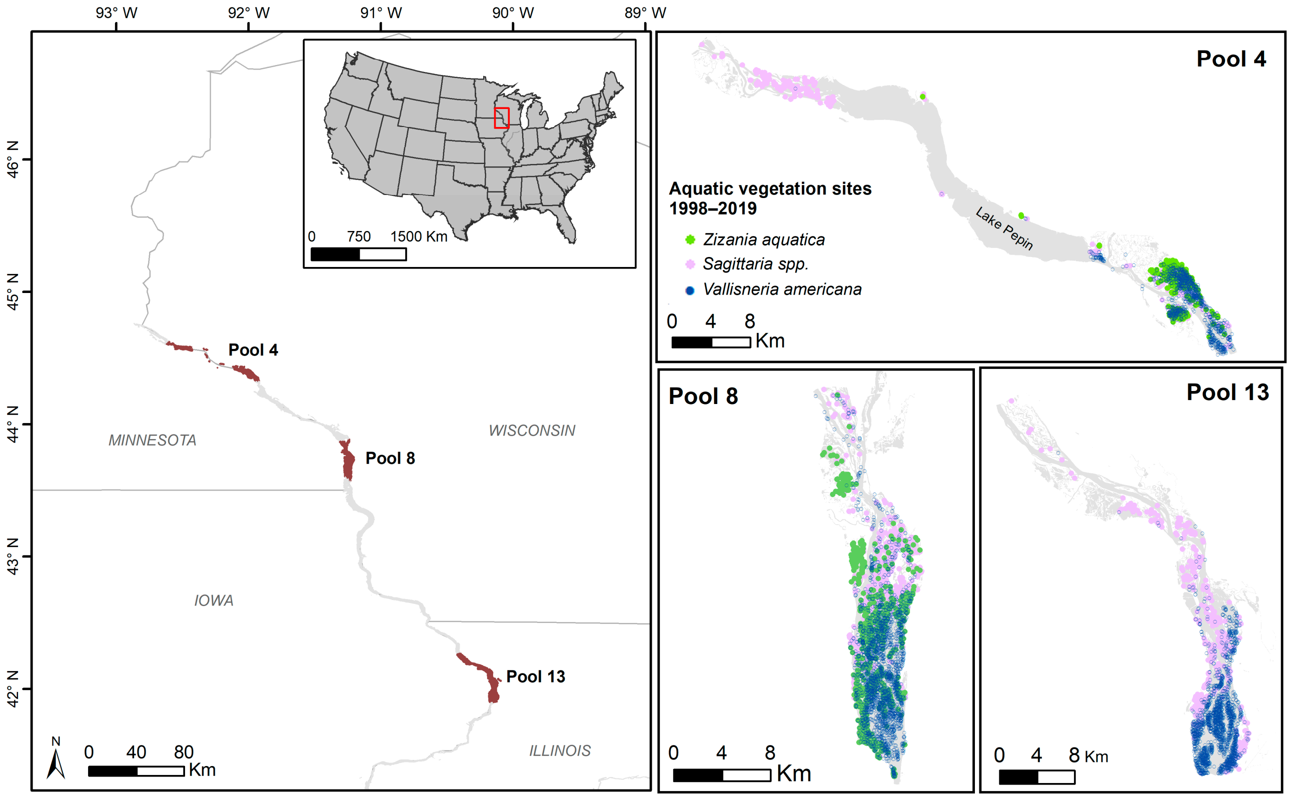

Figure 1. Map of the Upper Mississippi River, USA Left panel shows a map of study reach locations and extent of the three floodplain pools. Right panels show locations of arrowheads (*Sagittaria* spp.; purple), wild rice (*Zizania aquatica*; green), and wild celery (*Vallisneria americana*; blue) in Pools 4, 8, and 13 during 1998–2019. *Zizania aquatica* was absent from Upper Pool 4 and Pool 13.

We standardized all macrophyte lifeforms to the same scale using similar methods published by Bouska [9]. Specifically, for submersed species and filamentous algae, we first summed the rake score of each species across subsites and divided by the maximum possible rake score (30) at each site, and then multiplied by 100 to convert the result into a percentage (0–100%). For emersed, rooted floating-leaved and free-floating lifeforms, we converted % cover to the category's maximum % cover (20% increments from 0–100%).

We held an "aquatic plant vulnerability workshop" in 2021 to gather professional knowledge from scientists and resource managers regarding the environmental predictors of macrophytes in the UMR. Using workshop knowledge and a priori hypotheses, we selected nine environmental predictors expected to be important for influencing macrophytes (Table S1). Selection criteria also included data availability and low multicollinearity (Pearson's $r < 0.35$). Average water depth and substrate type were recorded in the field at each vegetation site. Substrate type was classified as silt/clay, mostly silt with sand, mostly sand with silt, hard clay, gravel/rock, or sand. We recoded substrate to represent a fine- to coarse-scale and velocity gradient (hard clay < silt/clay < sand < gravel/rock). Additional long-term water quality data were collected in these study pools using standardized protocols [29]; however, the location and time of measurement often deviated from that of the vegetation sites. We selected five water quality variables that we expected to be important for structuring plant communities, namely flow velocity (m/s), total nitrogen (mg/L), total phosphorus (mg/L), total suspended solids (mg/L), and chlorophyll *a* (µg/L). We used ArcGIS (version 10.8.1) to extract water quality values recorded within 60 days and 100 m of each vegetation sample and used the cost distance function to ensure that the nearest water quality site was hydrologically connected to the vegetation site. The selected water quality variables were then merged with the vegetation site data. Wind fetch values (m), modeled for the years 2000 and 2010 [30], were extracted from rasters (10-m × 10-m cell size) and merged with the vegetation site data. Wind fetch values from the year 2000 were applied to vegetation sites sampled in 1998–2009, and wind fetch values from the year 2010 were applied to vegetation sites sampled in 2010–2019. Lastly, we summarized mean discharge during the growing season (m^3/s; May–September) at the pool-scale for each year using public data from the U.S. Army Corps of Engineers [31] at Lock and Dams 3, 7, and 12.

2.3. Data Analyses

2.3.1. Using Ordination to Define Niches and Environmental Gradients

We used community ordination and boxplots to address Objectives 1 and 2 for defining the ecological niches and gradients of the three genera. There were 13,802 macrophyte sites across the period of 1998–2019. The final dataset used in the NMDS ordination included 25 species that were detected at >1% of sites (Table 1). This species list included 15 submersed species, 6 emersed species, 2 rooted floating-leaved species, duckweeds (*Lemna*, *Spirodela*, and *Wolfia* spp. combined), and filamentous algae (not identified further). Many of the species that were considered rare were not truly aquatic, so exclusion did not affect the results for the aquatic community analysis. To further improve computation, we removed unvegetated sites and included a dummy variable for each remaining site. We applied a Bray–Curtis dissimilarity measure [32] to the relative abundance dataset, which uses a ranking system to quantify the dissimilarity of species composition among sampling sites. We then ordinated the relationships between sites using NMDS. Sampling sites that were similar to each other with respect to species composition were ordinated closer together on the NMDS biplot. The final NMDS solution had the lowest stress after 20 random starts and 400 iterations. The appropriate number of dimensions for the NMDS was assessed using a scree plot. We then fitted the nine environmental variables to the NMDS ordination and assessed the significance of each factor using the EnvFit function in R [33]. All calculations, including the NMDS ordination, were performed in R version 4.0.3 [33] with the vegan package (version 2.5-7) [34]. Next, we created boxplots for the nine environmental variables to further determine habitat preferences and variation among the three genera.

Table 1. Aquatic vegetation species (n = 25) found at >1% of sites and used in the non-metric multidimensional scaling (NMDS) ordination. Life forms include submersed (S), emersed (E), rooted floating leaved (RFL), free floating (FF), and filamentous algae (A). Species list is ordered by combined number of occurrences in Pools 4, 8, and 13 of the Upper Mississippi River, USA.

Common Name	Scientific Name	Species Code	Life Form	Number of Occurrences	Mean Relative Abundance
Coontail	*Ceratophyllum demersum* L.	CEDE4	S	7975	4.477
Canadian waterweed	*Elodea canadensis* Michx.	ELCA7	S	6802	3.967
American wild celery	*Vallisneria americana* Michx.	VAAM3	S	5734	4.177
Water stargrass	*Heteranthera dubia* (Jacq.) MacMill.	ZODU	S	5126	1.857
Narrow-leaved pondweed	*Potamogeton foliosus* Raf., *P. pusillus* L.	NLPW	S	4486	1.891
Filamentous algae	not identified further	ALGA	A	4212	1.928
Duckweeds	*Lemna*, *Spirodela*, *Wolfia* spp., combined	NRFL	FF	4176	6.811
Sago pondweed	*Stuckenia pectinata* (L.) Börner	POPE6	S	4078	1.403
White waterlily	*Nymphaea odorata* Aiton	NYTU	RFL	3686	4.322
Eurasian watermilfoil *	*Myriophyllum spicatum* L.	MYSP2	S	3279	0.942
Curly pondweed *	*Potamogeton crispus* L.	POCR3	S	3060	0.945
American lotus	*Nelumbo lutea* Willd.	NELU	RFL	2679	4.117
Flatstem pondweed	*Potamogeton zosteriformis* Fern.	POZO	S	2151	0.704
Broadleaf arrowhead	*Sagittaria latifolia* Willd.	SALA2	E	1743	2.855
Stiff arrowhead	*Sagittaria rigida* Pursh.	SARI	E	1257	1.593
Longleaf pondweed	*Potamogeton nodosus* Poir	PONO2	S	1218	0.306
Wild rice	*Zizania aquatica* L.	ZIAQ	E	1073	1.120

Table 1. *Cont.*

Common Name	Scientific Name	Species Code	Life Form	Number of Occurrences	Mean Relative Abundance
Nodding waternymph	*Najas flexilis* (Willd.) Rostk. and Schmidt	NAFL	S	744	0.267
Reed canarygrass *	*Phalaris arundinacea* L.	PHAR3	E	464	0.556
Giant burreed	*Sparganium eurycarpum* Engelm.	SPEU	E	434	0.520
Southern waternymph	*Najas guadalupensis* (Spreng.) Magnus	NAGU	S	433	0.202
River bulrush	*Bolboschoenus fluviatilis* Torr. Soják	SCFL	E	423	0.576
Longbeak buttercup	*Ranunculus longirostris* Godr.	RALO2	S	341	0.113
Brittle waternymph	*Najas minor* All.	NAMI	S	257	0.105
Northern watermilfoil	*Myriophyllum sibiricum* Komarov	MYSI	S	247	0.071

* Indicates not native/invasive to the Upper Mississippi River Basin.

2.3.2. Mapping Spatial and Temporal Changes in *Sagittaria* spp., *Z. aquatica*, and *V. americana*

To address Objective 3, the spatiotemporal dynamics, we examined NMDS scores through time using kernel density estimation and mapped changes in relative abundance and percent cover across the three pools using curve fit regression. We hypothesized that *Z. aquatica* had changed its environmental niche space over time, so we plotted annual average NMDS scores for all sites that had ≥20% *Z. aquatica* coverage at any time within the 22 years. Plotting *Z. aquatica* sites with ≥20% coverage at any time point allows detection of temporal change in the abundance and colonization of new sites not previously occupied by *Z. aquatica*.

We interpolated the percent cover of *Sagittaria* spp. and *Z. aquatica*, as well as the relative abundance of *V. americana* for each sampling year (1998–2019) and each pool. Interpolation used the *inverse distance weighting* (IDW) tool in ArcMap 10.8.1 [35]. The IDW predicts values for cells (10-m × 10-m cell size) in a raster using the average of the eight nearest sampling points within a 2000 m maximum distance search radius. The river's main channel was used as a barrier in the interpolations. This resulted in annual maps for each species for 21 years (1998–2019, excluding 2003 due to limited sampling) in Pools 4, 8, and 13 (n = 168 annual maps; Figures S1–S8). We used raster calculator in ArcMap to aggregate *Sagittaria* spp. maps for each year (e.g., the sum of *S. rigida* and *S. latifolia*, maximum cell value of 100). The strata that were modeled in the interpolations include channel borders, contiguous floodplain lakes, side channels, and tertiary channels. We excluded the main navigation channel, isolated floodplain lakes, tributaries, and tributary delta lake strata (i.e., Lake Pepin) due to the small number of sampling points. We also excluded all data in Upper Pool 4 (i.e., above Lake Pepin) due to few observations of the three genera of interest.

We used Curve Fit (Version 10.1) [36], an extension developed for use within ArcMap, to run regression analyses on the interpolated community raster datasets from 1998–2019. The Curve Fit output showed areas of significant change in macrophyte abundance over the 22-year period for the three genera of interest. A similar method was used in Pool 8 for submersed vegetation [18]; we expand on this with the addition of Pool 4 and Pool 13, the inclusion of emergents, and a longer temporal scale due to additional sampling years. Each explanatory variable (i.e., year) was paired with the corresponding raster (one raster for the sum of *S. rigida* and *S. latifolia*, one raster for *Z. aquatica*, one raster for *V. americana*). Curve Fit estimated the linear relationship between year and pixel value (one relative abundance or percent cover value per year) and created an output raster containing parameter estimates, model error, and r^2. The r^2 was converted to a correlation coefficient (r). The y-intercepts (starting conditions) were then compared to the correlation, or degree of change across the years from 1998–2019. We used a two-tailed t test on the Pearson's correlation coefficient ($t_{(19)} = 0.433$, $p = 0.05$) to define pixels with significant decreases or increases in the relative abundance of *V. americana* and percent cover of *Z. aquatica* and *Sagittaria* spp. The critical value was used to scale and color code the maps to define areas that underwent significant change. A significant positive correlation indicated an increase in relative abundance over time, and a significant negative correlation indicated a decrease in relative abundance over time. Each of these scenarios indicated areas that underwent temporary or perhaps long-term shifts in composition and abundance. Non-significant correlations identified areas that did not undergo significant changes in relative abundance or percent cover over time, and, therefore, may indicate stability or the absence of that species. Standard error estimates were mapped for each Curve Fit analysis to estimate uncertainty and further show relative stability or variability at various spatiotemporal scales.

We repeated the Curve Fit analyses to examine changes between the years 2010 and 2019 when *Z. aquatica* expanded substantially in Pools 4 and 8. We used a two-tailed t test on the Pearson's correlation coefficient ($t_{(8)} = 0.632$, $p = 0.05$) to define pixels with significant decreases or increases in the percent cover of *Z. aquatica* and *Sagittaria* spp. and relative abundance of *V. americana*. Examining change across several temporal scales allowed us to determine whether species were highly dynamic, possibly in response to environmental drivers, or more stable and predictable from year to year.

3. Results

3.1. Defining Ecological Niches and Associated Environmental Gradients

The NMDS of the entire macrophyte assemblage across all three pools (2D Stress = 0.20) showed that the three genera of interest were separated distinctly in ordination space across two main axes (Figure 2, Table S2). The first NMDS axis (NMDS 1) identified a strong gradient of plant abundance and diversity. The second NMDS axis (NMDS 2) identified a gradient of lotic and lentic macrophytes associated with depth, velocity, and wind fetch (Table S3); specifically, positive NMDS 2 values were characterized by lotic habitats that exhibited deeper depths and greater velocity and wind fetch compared to negative NMDS 2 values. *Vallisneria americana* was in the upper left quadrant with negative NMDS 1 values and positive NMDS 2 values; *Z. aquatica* was in the upper right quadrant with positive NMDS 1 and NMDS 2 values; and NMDS 1 values varied by *Sagittaria* spp. but both *S. rigida* and *S. latifolia* had negative NMDS 2 values. The species in the upper portion of the ordination plot with positive NMDS 2 values, such as *V. americana* and *Z. aquatica*, were generally found in greater velocities and deeper water depths, whereas other species, such as *Sagittaria* spp., which were in the lower portion of the ordination plot, were associated with lower velocities, shallower depths, and minimal wind fetch.

Similar associations between environmental variables and macrophytes were presented in boxplots (Figure 3). *Sagittaria* spp. were generally found in shallow, protected areas with minimal wind fetch, low velocity, and a silty substrate. *Sagittaria* spp. were also associated with lower discharge during the growing season compared to *Z. aquatica* and *V. americana*. *Vallisneria americana* had the greatest environmental variability (i.e., a large range of environmental conditions at surveyed sites), although this species was commonly found at sites with the deepest water depths (up to 3 m), largest wind fetch (>2 km), highest water velocity, and silt-sand substrate (Figure 3). *Zizania aquatica* was generally found in silty substrates, areas with high water clarity, and sites with moderate water depths, wind fetch, and water velocity.

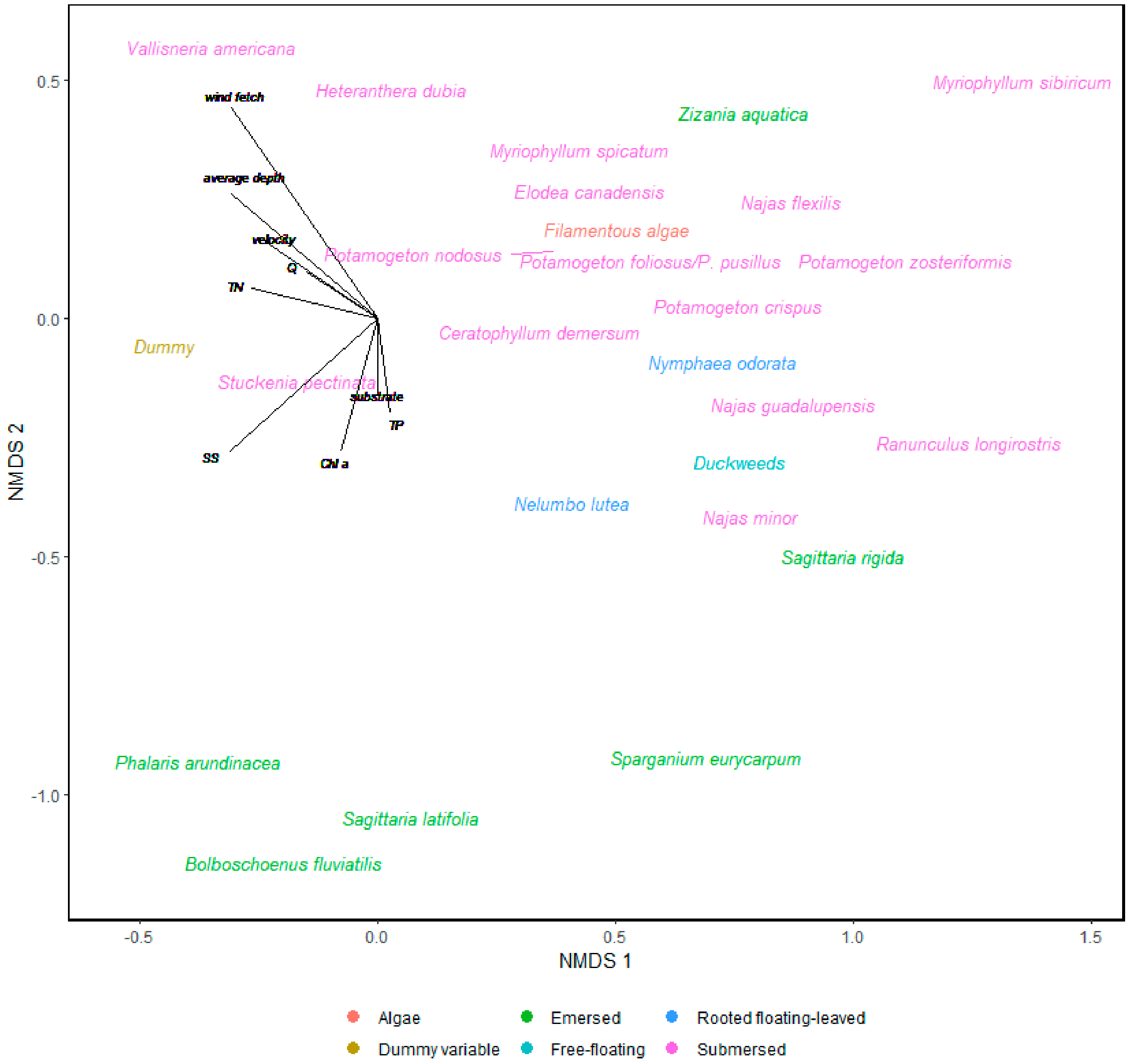

Figure 2. Non-metric multidimensional scaling (NMDS) ordination in two dimensions (NMDS 1, NMDS 2) of the relative abundance of 25 aquatic vegetation species and associated environmental drivers in Pools 4, 8, and 13 in the Upper Mississippi River, USA, from 1998–2019. Drivers occurred along vectors and included TN = total nitrogen, Q = discharge, SS = suspended solids, Chl *a* = chlorophyll *a*, and TP = total phosphorus. Substrate represents a fine- to coarse-scale gradient (hard clay < silt/clay < sand < gravel/rock). Aquatic vegetation species are color-coded based on lifeform, and the common names are cross referenced in Table 1. Bray–Curtis similarity; 2D stress = 0.20.

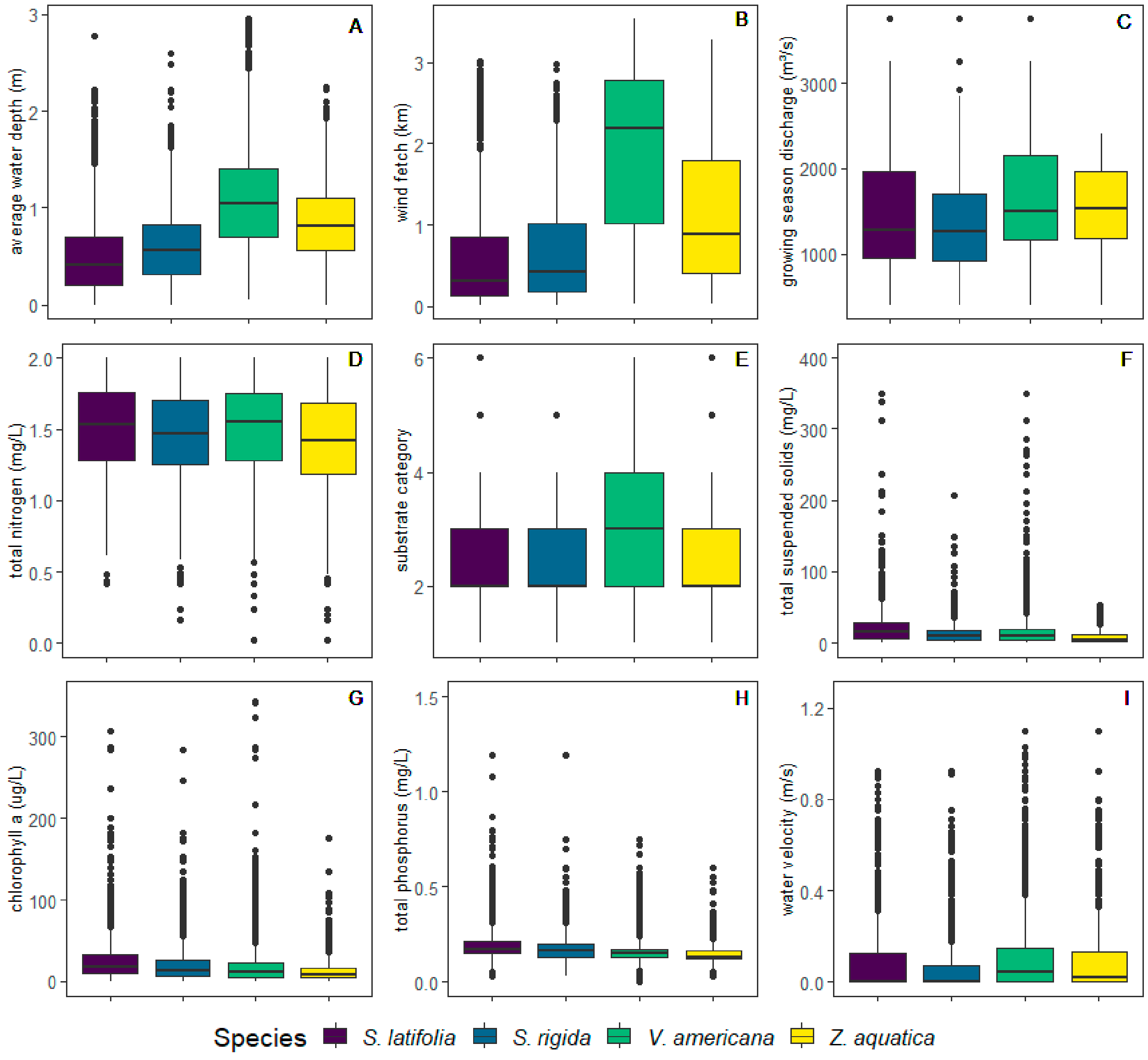

Figure 3. Boxplots of arrowheads (*Sagittaria latifolia* and *S. rigida*), wild celery (*Vallisneria americana*), and wild rice (*Zizania aquatica*) in Pools 4, 8, and 13 in the Upper Mississippi River, USA, in relation to 9 hypothesized environmental predictors (**A**–**I**). The boxes encapsulate the interquartile range where the middle line is the median, the whiskers are 1.5 times the interquartile range, and the dots are outliers. Extreme outliers for concentrations of total suspended solids (1500 mg/L) and chlorophyll *a* (500 µg/L) at *V. americana* sites were not plotted. Substrate categories (E) included hard clay (1), silt/clay (2), mostly silt with sand (3), mostly sand with silt (4), sand (5), and gravel/rock (6).

3.2. Ordination-Quantifying Patterns of Macrophyte Abundance and Niche Space over Time

Ordination scores at the pool-scale showed changes in species assemblages and the dominance of the three macrophyte genera from 1998–2019 (Figure 4). *Zizania aquatica* abundance substantially increased in Lower Pool 4 by 2019, as indicated by more NMDS values in the upper right quadrant in later years (Figure 4). Pool 8 became more vegetated and speciose in later years and had especially high *V. americana* and *Z. aquatica* abundances. Furthermore, Pool 8 had the greatest abundance of *Sagittaria* spp. in the mid-2000s and less *Sagittaria* spp. towards 2019. Pool 13 sites were dominated by either *V. americana* or *Sagittaria* spp. in later years. *Zizania aquatica* was absent in Pool 13 throughout the study period and the ordination space in the upper right quadrant was relatively empty, meaning there may be an unoccupied habitat in Pool 13.

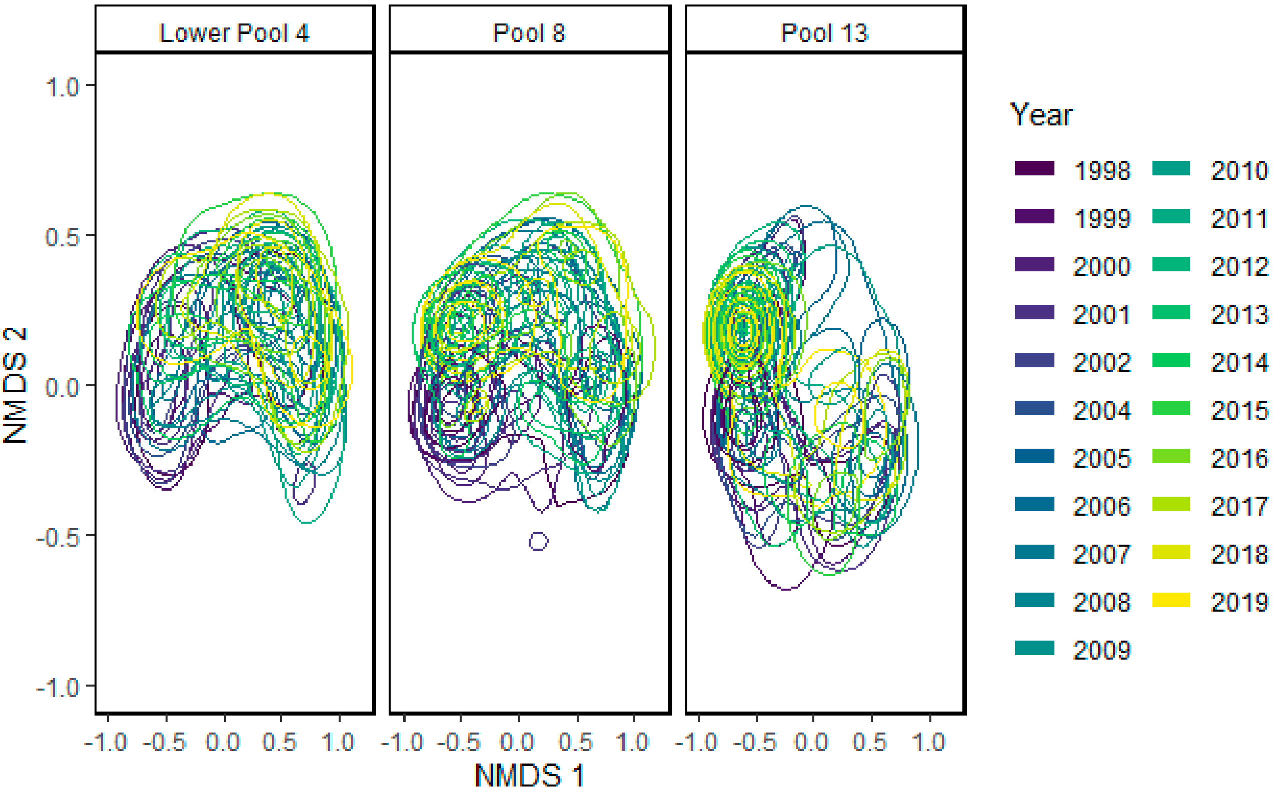

Figure 4. Two-dimensional kernel density estimation of non-metric multidimensional scaling (NMDS) site values in Lower Pool 4, Pool 8, and Pool 13 in the Upper Mississippi River, USA, based on the entire macrophyte assemblage (25 species) included in Figure 2. The color gradient represented annual changes from 1998–2019. Upper Pool 4 was not shown due to the small sample sizes and low macrophyte abundance and diversity.

Zizania aquatica expanded its ecological niche over the 22 years, as indicated by changes in annual mean NMDS values at sites with ≥20% coverage of *Z. aquatica* (Figure 5). Initially, *Z. aquatica* overlapped spatially with several lentic submersed species and emergent species (e.g., stiff arrowhead) and was present at high diversity sites (+ NMDS 1, − NMDS 2). Over time, mean centroid values decreased for NMDS 1 and increased for NMDS 2, showing that *Z. aquatica* initially occupied high-diversity, shallow backwater habitats in 1998 but subsequently expanded to deeper, lotic areas by 2019.

3.3. Curve Fit- Spatial and Temporal Trends of Z. aquatica, V. americana, and Sagittaria spp.

Curve Fit analysis identified large areas with significant increases in percent cover of *Z. aquatica* in Lower Pool 4 and Pool 8 from 1998–2019. Specifically, there was a significant increase in the percent cover of *Z. aquatica* at 1128 hectares in Lower Pool 4 (Figure 6E) and 3657 hectares in Pool 8 (Figure 7E), and no areas had significant decreases from 1998–2019 (Table S4). *Zizania aquatica* prevalence also substantially increased in Pools 4 and 8, particularly in the impounded areas upstream of locks and dams (Figure S9).

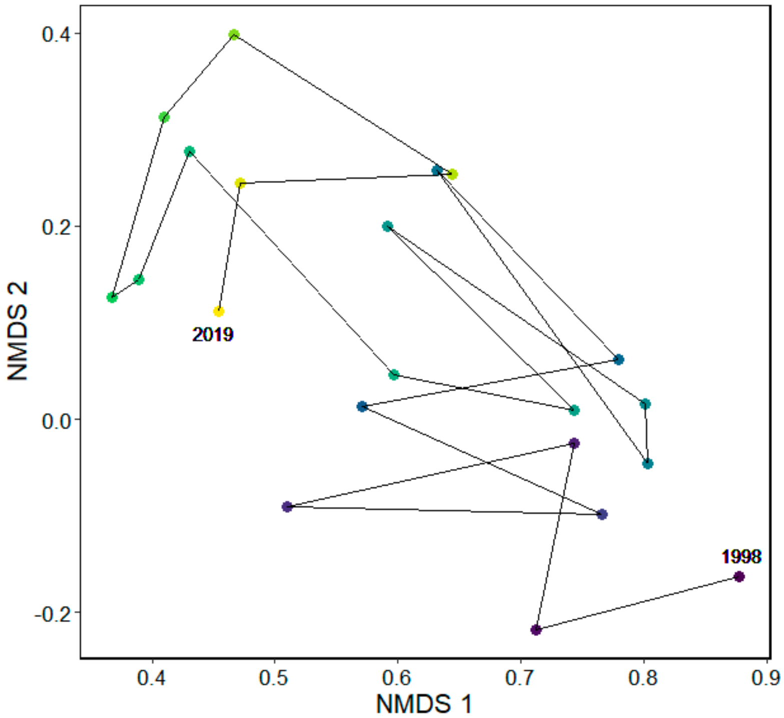

Figure 5. Biplot of annual, mean non-metric multidimensional scaling (NMDS) values at sites with ≥20 percent cover of wild rice (*Zizania aquatica)* detected at any time within the 22 years (1998–2019) in Pools 4 and 8 of the Upper Mississippi River, USA Times series are represented with a purple (1998) to yellow (2019) gradient.

Sagittaria spp. increased in percent cover from 1998–2019, but the total area was much smaller than that of *Z. aquatica* (Table S4); specifically, *Sagittaria* spp. coverage increased by ~46 hectares in Lower Pool 4 (Figure 6D), ~109 hectares in Pool 8 (Figure 7D), and ~130 hectares in Pool 13 (Figure 8C). Small areas in all study pools decreased in percent cover from 1998–2019 (Table S4). The prevalence of *Sagittaria* spp. in the contiguous backwaters of Pools 4 and 8 declined substantially starting in 2010, nearly simultaneously with the expansion of *Z. aquatica* (Figure S9). Over time, the dominant emergent species in Pools 4 and 8 shifted from *Sagittaria* spp. in 1998 to *Z. aquatica* in 2019; however, both *S. rigida* and *S. latifolia* remained the dominant species in Pool 13. Curve Fit results for 2010–2019 (Figures S10–S12) did not identify large areas of significant change in any pool. Furthermore, standard error estimates (Figure S13) were greater for *Sagittaria* spp. compared to *Z. aquatica* and *V. americana*, especially in Lower Pool 4 and Pool 8, showing that *Sagittaria* spp. were more variable at an annual-scale.

Similar to *Z. aquatica*, Curve Fit analysis identified large areas with significant increases in *V. americana* across all study pools, especially Lower Pool 4 and the impounded area of Pool 8 from 1998–2019. There was a significant increase in the relative abundance of *V. americana* of 539 hectares in Lower Pool 4 (Figure 6F), 2514 hectares in Pool 8 (Figure 7F), and 526 hectares in Pool 13 (Figure 8D). There were small, localized areas of decline in *V. americana* from 1998–2019 scattered throughout Lower Pool 4 and the impounded area of Pool 13 ((Figures 6F and 8D). The prevalence of *V. americana* increased over time in all pools; however, *V. americana* declined in Pool 13 from 2014–2019 (Figure S9). Curve Fit analysis for 2010–2019 revealed more areas that experienced a significant decline in the abundance of *V. americana* in Pool 13′s impounded area (434 hectares; Figure S12).

In summary, in terms of the interplay among the three macrophyte genera, Curve Fit maps identified specific locations within each pool that experienced significant changes in *V. americana*, *Z. aquatica*, and *Sagittaria* spp. (Figures 6–8). *Zizania aquatica* increased in Lower Pool 4 and Pool 8, and often overlapped spatially with *Sagittaria* spp. and *V. americana*; however, *V. americana* and *Sagittaria* spp. rarely grew in the same locations. In Pools 4 and 8, increases in *Z. aquatica* and *V. americana* often co-occurred throughout the pool, but *V. americana* often dominated large areas in the impounded area. In Pool 13, one small area showed a decrease in *V. americana* and increase in *Sagittaria* spp.; however, *V. americana* mostly increased in the absence of *Sagittaria* spp. and *Z. aquatica* (Figure 8C,D). Similarly, the substantial decline in *V. americana* in Pool 13 from 2010–2019 did not overlap with the spatial distribution of *Sagittaria* spp. or *Z. aquatica* (Figure S12).

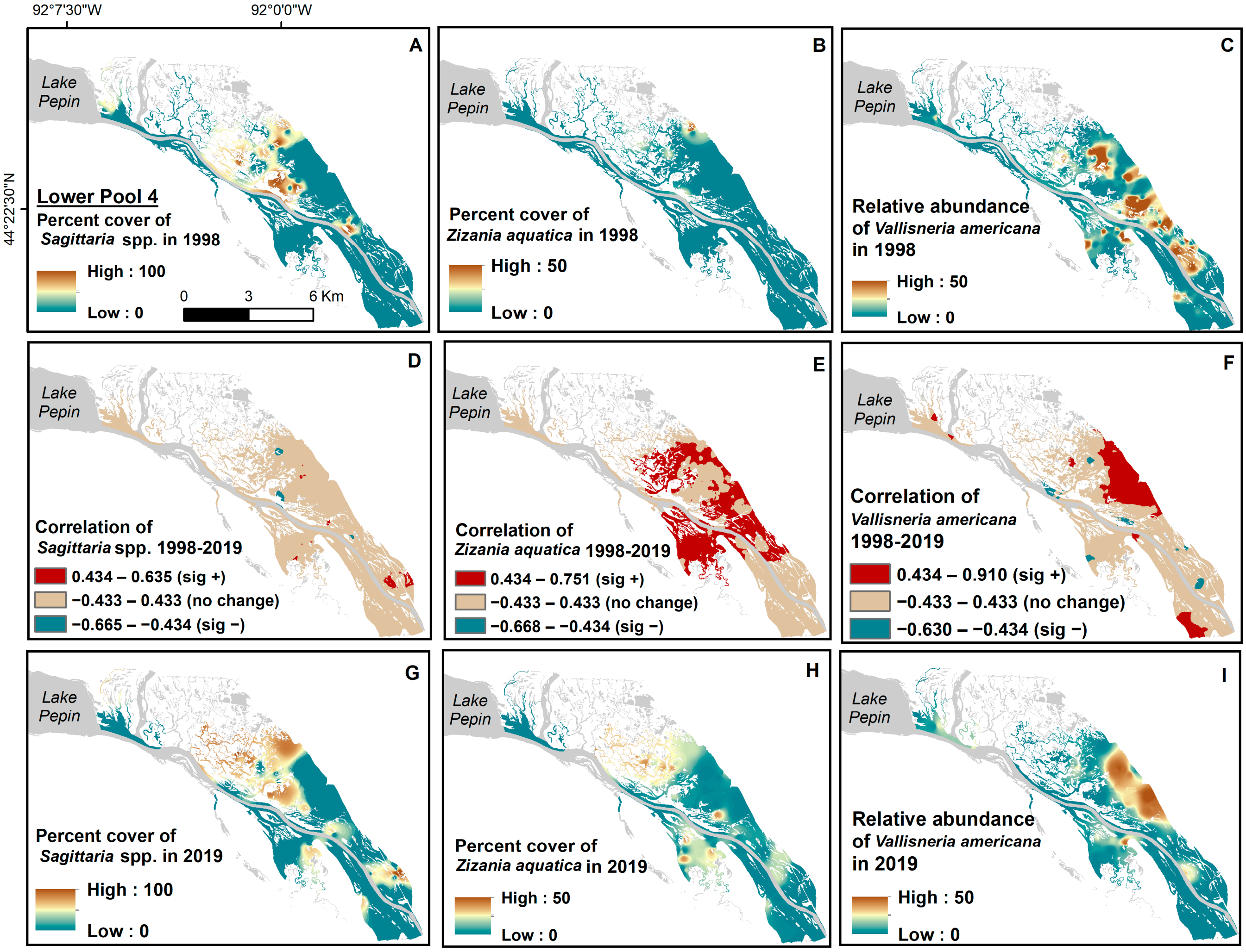

Figure 6. Curve fit regression output for arrowheads (*Sagittaria latifolia* and *S. rigida*, combined), wild rice (*Zizania aquatica*), and wild celery (*Vallisneria americana*) in Lower Pool 4, Upper Mississippi River, USA Y-intercept indicates the estimated percent cover or relative abundance in 1998 (**A**–**C**), correlation indicates the slope of percent cover or relative abundance from 1998–2019 (**D**–**F**), and (**G**–**I**) indicates the estimated percent cover or relative abundance in 2019. Correlation values less than −0.434 are significant negative slopes (blue) and correlation values greater than 0.434 are significant positive slopes (red). Intermediate values indicate no significant change. Areas that are not sampled are shown in gray.

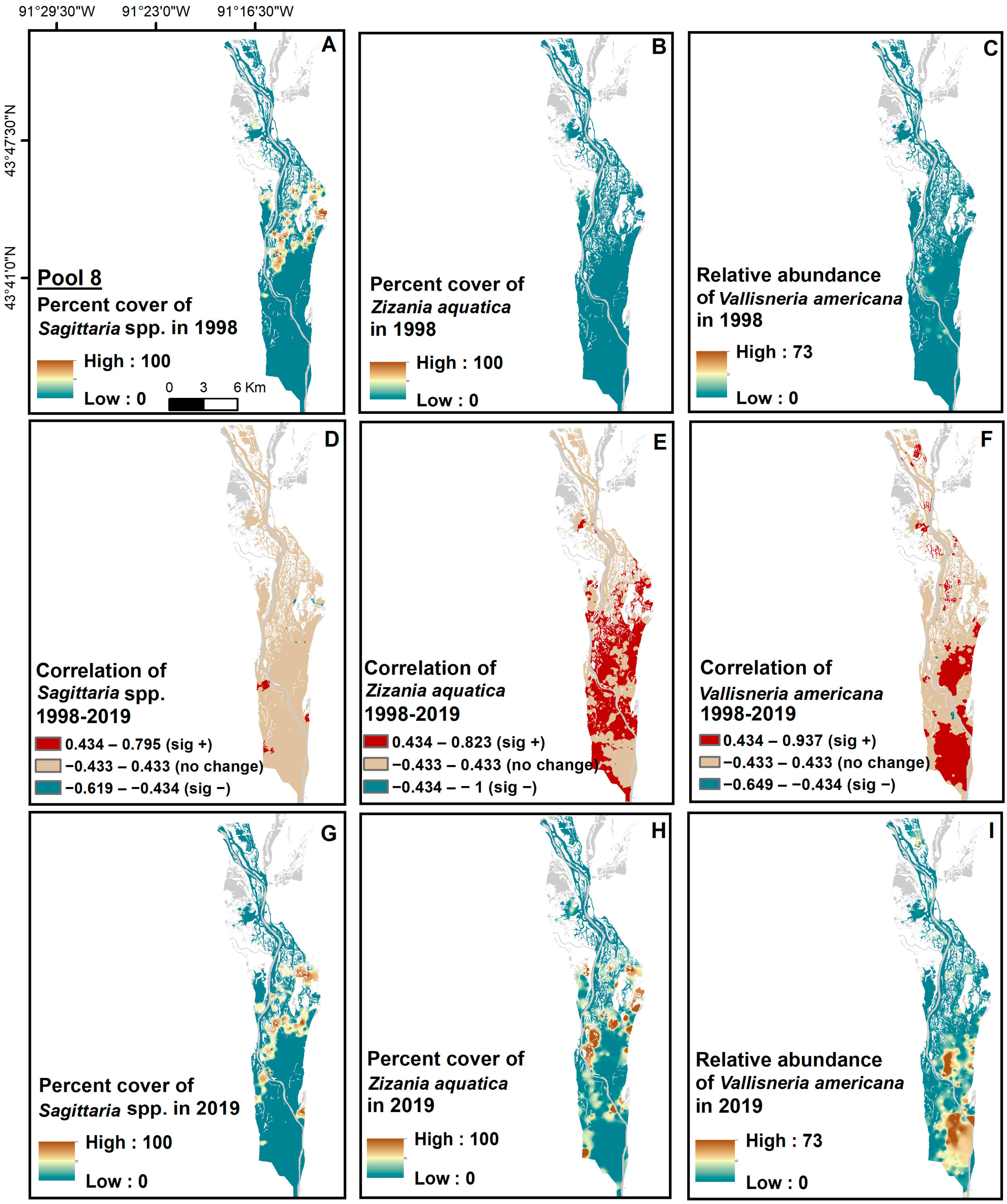

Figure 7. Curve fit regression output for arrowheads (*Sagittaria latifolia* and *S. rigida*, combined), wild rice (*Zizania aquatica*), and wild celery (*Vallisneria americana*) in Pool 8, Upper Mississippi River, USA Y-intercept indicates the estimated percent cover or relative abundance in 1998 (**A**–**C**), correlation indicates the slope of percent cover or relative abundance from 1998–2019 (**D**–**F**), and (**G**–**I**) indicates the estimated percent cover or relative abundance in 2019. Correlation values less than −0.434 are significant negative slopes (blue) and correlation values greater than 0.434 are significant positive slopes (red). Intermediate values indicate no significant change. Areas that are not sampled are shown in gray.

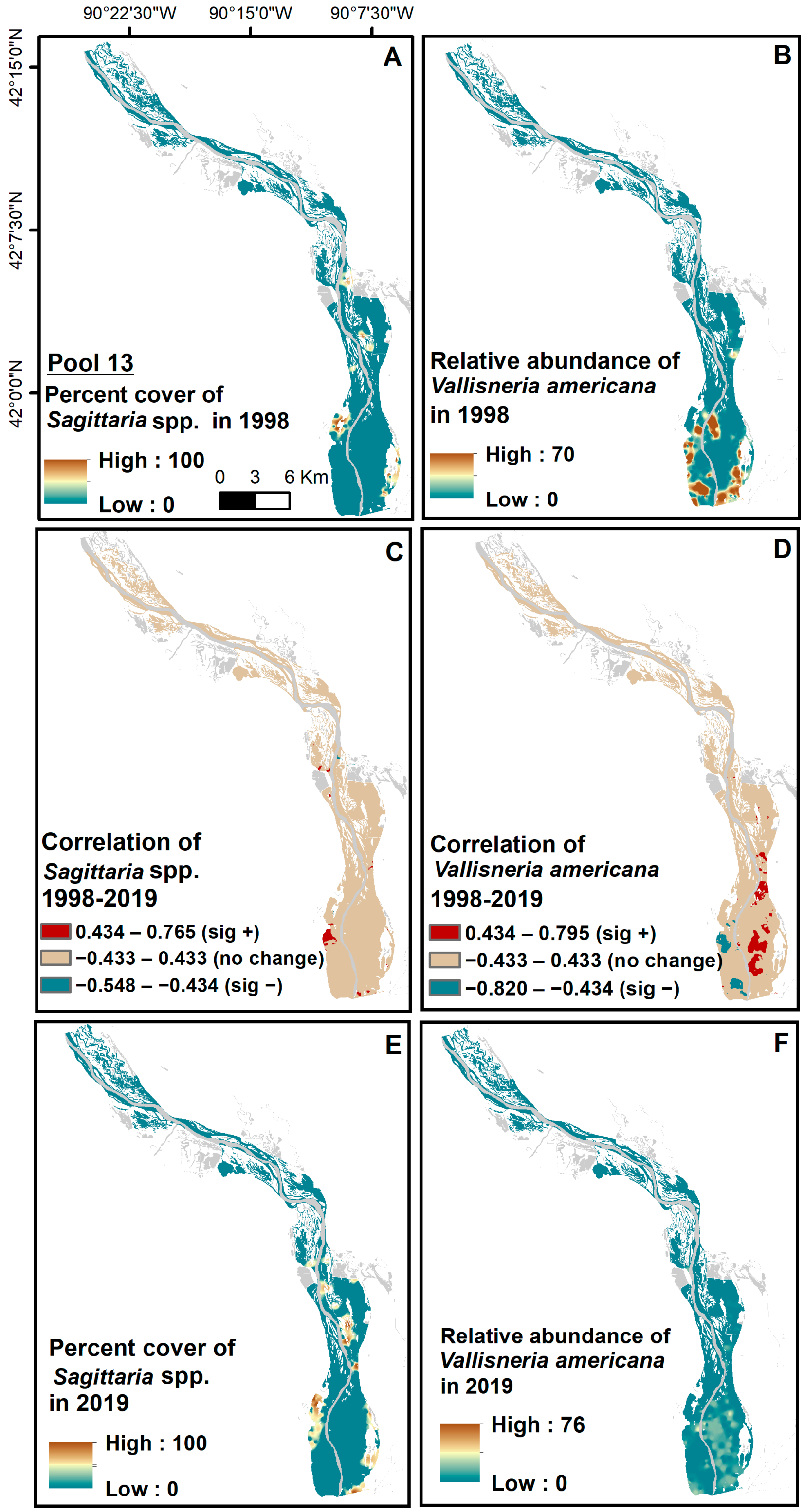

Figure 8. Curve fit regression output for arrowheads (*Sagittaria latifolia* and *S. rigida*, combined) and wild celery (*Vallisneria americana*) in Pool 13, Upper Mississippi River, USA Wild rice (*Zizania aquatica*) was not detected during LTRM sampling in Pool 13. Y-intercept indicates the estimated percent cover or relative abundance in 1998 (**A**,**B**), correlation indicates the slope of percent cover or relative abundance from 1998–2019 (**C**,**D**), and (**E**,**F**) indicates the estimated percent cover or relative abundance in 2019. Correlation values less than −0.434 are significant negative slopes (blue) and correlation values greater than 0.434 are significant positive slopes (red). Intermediate values indicate no significant change. Areas that are not sampled are shown in gray.

4. Discussion

Our results confirmed that *V. americana*, *Z. aquatica*, and *Sagittaria* spp. occupied different ecological niches in the UMR. *Sagittaria* spp. were generally found in shallow, protected backwaters, co-occurring with other lentic aquatic macrophytes, whereas the lotic habitat tends to be dominated by *V. americana*. Notably, *Z. aquatica* separated from all other emergent species in the NMDS ordination. *Zizania aquatica* was found at high densities in shallow backwaters of the UMR, although trends in NMDS values showed that *Z. aquatica* later expanded into deeper, flowing water and suggests that it may be more tolerant of lotic conditions than previously understood [37–39]. *Vallisneria americana* generally increased across the study area, but Pool 13 showed a decline in *V. americana* since 2014. These results can aid restoration and management of the UMR and other large, regulated rivers by providing an understanding of the spatiotemporal dynamics of common species and the likely environmental drivers of species changes and stability.

We found that water depth, water velocity, water clarity, and wind fetch were important drivers for explaining differences in species composition and abundance of the entire macrophyte assemblage and these three genera of interest. This finding was consistent with environmental drivers governing macrophyte growth in other large rivers [2,40]. Many interactions exist between macrophytes, water quality, and the physical environment [41]. For example, wind fetch and water velocity can have a substantial effect on macrophyte growth due to physical stress caused by wind-generated waves and high current velocity. Furthermore, increased erosion and sediment re-suspension reduce water clarity and light availability, which can affect submersed plants, such as *V. americana* [3]. However, once plants become established, depth and flow may be altered enough to support increased coverage and density of macrophytes which, in turn, can feedback to reduce the effects of wind-generated waves and sediment re-suspension [41]. Our field experiences lead us to suggest that feedback among *Z. aquatica*, sediment deposition, water depth, and water clarity occurred in the UMR and possibly facilitated *Z. aquatica* expansion, although more experimental research would be needed to confirm this.

Our hypothesis that *Z. aquatica* has expanded into deeper water and a new niche space was supported (Figures 4–7). The expansion of *Z. aquatica* into deeper water may be a result of the substantial improvement in water clarity that occurred throughout the UMR over the last two decades [42,43], which increased light penetration and may have allowed seedlings to emerge from deeper water [44]. This is supported by the strong negative association with suspended solids (SS) (Figure 2) and low SS measured near *Z. aquatica* sites (Figure 3F). In addition, dense stands of *Z. aquatica* may be effectively reducing water velocity [39], capturing sediment [38], and aiding in natural island formation (A. Carhart, pers. observations, 2022), although the stability of these habitats is unknown. Asaeda [39] found that *Zizania* adapted to greater water velocity by increasing shoot density within patches, thereby reducing overall drag force and altering the flow pattern. Although *Z. aquatica* was not strongly correlated with mean discharge during the growing season, annual plants often benefit from occasional disturbances and water level fluctuations that set back perennial competition and create habitat for re-colonization during low water [38].

Curve Fit results confirmed significant changes in the total area and relative abundance of the three macrophyte genera (Figures 6–8), but there was little support for the hypothesis that *Z. aquatica* had overlapped its niche space and displaced *V. americana* and *Sagittaria* spp. (Figures 2–4 and 6–8). *Zizania aquatica* expanded rapidly in Lower Pool 4 and Pool 8 circa 2010 and became the most prevalent emergent species in these reaches [20]. However, as of 2019, *Z. aquatica* had not been detected in Pool 13 during LTRM surveys. *Sagittaria* spp. remains the dominant emergent species in Pool 13, although the recent invasion of flowering rush (*Butomus umbellatus* L.) may compete for *Sagittaria* spp.'s niche space. Furthermore, trends in percent cover of *Sagittaria* spp. were variable across all pools, which may indicate sensitivity to environmental gradients, such as the lotic and lentic hydrologic gradient in Figure 2. The relative abundance of *V. americana* increased substantially in all study pools over the 22-year study; however, large areas within the Pool 13 impounded area experienced a reduction in the abundance of *V. americana* since 2014. This indicates that restoration and management inventions for *V. americana* in Pool 13 may be helpful to reduce loss and increase resilience.

To prevent vulnerability to macrophyte loss and increase ecosystem resilience, river managers must understand the environmental drivers and community dynamics of the past two decades spanning a period of widespread vegetation recovery. Our analyses showed that *Z. aquatica*, *V. americana*, and *Sagittaria* spp. are spatiotemporally dynamic in the UMR, but have some predictable habitat associations that can help guide future management and restoration efforts. Given the ecological importance of these three macrophyte genera as defined vegetation types [27] and specified as restoration targets in the UMR [13,45,46], modeling the hypothesized ecological drivers and dynamics of each species individually would further aid ecological understanding and management. Although we focused on patterns in relative abundance and defining ecological niches in the UMR, *Zizania, Vallisneria*, and *Sagittaria* are common genera in rivers worldwide [39,47–49], and, therefore, the methods and results provided here may be transferrable to other riverine systems where data may be sparse.

5. Conclusions

The patterns documented here illustrated the importance of analyzing species compositional changes at multiple spatial and temporal scales. As one example from Pool 13, a few large *V. americana* patches increased in total area and abundance since 1998 (Table S4, Figure 8D), yet many small patches had significant decreases since 2014 (Figure S8 and Figure S12) which may signal vulnerability and *V. americana* bed fragmentation. We found that the extent and abundance of *Z. aquatica* and *V. americana* patches significantly increased over time and that *Sagittaria* spp. were more dynamic and experienced very little long-term change. Further research can quantify threshold responses of the determined environmental drivers (Figure 2, Table S3) and associated feedback mechanisms that affected change and stability for each species individually. Our findings contribute to macrophyte restoration and management efforts in the UMR and other large, floodplain rivers worldwide.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15040523/s1, Table S1: A summary of the 9 environmental variables included in the EnvFit model that were important in explaining site-level differences in species composition and relative abundance of aquatic vegetation in the Upper Mississippi River (UMR), USA These predictors were selected following our "aquatic plant vulnerability workshop" in 2021 that gathered professional knowledge from 65 scientists and resource managers regarding the environmental predictors of aquatic vegetation in the UMR. Selection criteria also included data availability and low multicollinearity (Pearson's $r < 0.35$); Table S2: Species centroid values ($n = 25$) for the first 2 non-metric multidimensional scaling (NMDS) axes across Pools 4, 8, and 13 of the Upper Mississippi River, USA; Table S3: Summary of environmental variable ($n = 9$) centroid values for the first two non-metric multidimensional scaling (NMDS) axes across Pools 4, 8, and 13 of the Upper Mississippi River, USA; Table S4: Area (hectares) of significant change in percent cover of arrowheads (*Sagittaria rigida* and *S. latifolia*) and wild rice (*Zizania americana*) and relative abundance of wild celery (*Vallisneria americana)* in Pools 4, 8, and 13 of the Upper Mississippi River, USA, from 1998 to 2019; Figure S1: Spatial changes in percent cover of wild rice (*Zizania aquatica*) in Lower Pool 4, Upper Mississippi River, from 1998 to 2019. Areas not sampled are shown in gray; Figure S2: Spatial changes in percent cover of arrowheads (*Sagittaria* spp.) in Lower Pool 4, Upper Mississippi River, from 1998 to 2019. Areas not sampled are shown in gray; Figure S3: Spatial changes in relative abundance of wild celery (*Vallisneria americana*) in Lower Pool 4, Upper Mississippi River, from 1998 to 2019. Areas not sampled are shown in gray; Figure S4: Spatial changes in percent cover of wild rice (*Zizania aquatica*) in Pool 8, Upper Mississippi River, from 1998 to 2019. Areas not sampled are shown in gray; Figure S5: Spatial changes in percent cover of arrowheads (*Sagittaria* spp.) in Pool 8, Upper Mississippi River, from 1998 to 2019. Areas not sampled are shown in gray; Figure S6: Spatial changes in relative abundance of wild celery (*Vallisneria americana*) in Pool 8, Upper Mississippi River, from 1998 to 2019. Areas not sampled are shown in gray; Figure S7: Spatial changes in percent cover of arrowheads (*Sagittaria* spp.) in Pool 13, Upper Mississippi River, from 1998 to 2019. Areas not sampled are shown in gray; Figure S8: Spatial changes in relative abundance of wild celery (*Vallisneria americana*) in Pool 13, Upper Mississippi River, from 1998 to 2019. Areas not sampled are shown in gray; Figure S9: Annual prevalence (±1 SE) of (A) wild rice (*Zizania aquatica*), (B) arrowheads (*Sagittaria* spp.), and (C) wild celery (*Vallisneria americana*) in Pool 4, Pool 8, and Pool 13 of the Upper Mississippi River, USA Locally weighted regression (LOESS model) trendlines (solids lines) and 95% confidence intervals (shaded areas) depict temporal patterns from 1998 to 2019. Panel A modified from Larson et al. (2022); Figure S10: Curve Fit regression output for arrowheads (*Sagittaria latifolia* and *S. rigida*, combined), wild rice (*Zizania aquatica*), and wild celery (*Vallisneria americana*) in Lower Pool 4, Upper Mississippi River, USA Y-intercept indicates the estimated percent cover in 2010 (A–C), correlation indicates the slope of percent cover from 2010–2019 (D–F), and (G–I) indicates the estimated percent cover in 2019. Correlation values less than −0.632 are significant negative slopes (blue) and correlation values greater than 0.632 are significant positive slopes (red). Intermediate values indicate no significant change. Areas that are not sampled are shown in gray.; Figure S11: Curve Fit regression output for arrowheads (*Sagittaria latifolia* and *S. rigida*, combined), wild rice (*Zizania aquatica*), and wild celery (*Vallisneria americana*) in Pool 8, Upper Mississippi River, USA Y-intercept indicates the estimated percent cover in 2010 (A–C), correlation indicates the slope of percent cover from 2010 to 2019 (D–F), and (G–I) indicates the estimated percent cover in 2019. Correlation values less than −0.632 are significant negative slopes (blue) and correlation values greater than 0.632 are significant positive slopes (red). Intermediate values indicate no significant change. Areas that are not sampled are shown in gray; Figure S12: Curve Fit regression output for arrowheads (*Sagittaria latifolia* and *S. rigida*, combined) and wild celery (*Vallisneria americana*) in Pool 13, Upper Mississippi River, USA Y-intercept indicates the estimated percent cover in 2010 (A,B), correlation indicates the slope of percent cover from 2010 to 2019 (C,D), and (E,F) indicates the estimated percent cover in 2019. Correlation values less than −0.632 are significant negative slopes (blue) and correlation values greater than 0.632 are significant positive slopes (red). Intermediate values indicate no significant change. Areas that are not sampled are shown in gray; Figure S13: Curve fit standard error estimates for arrowheads (*Sagittaria latifolia* and *S. rigida*, combined), wild celery (*Vallisneria americana*), and wild rice (*Zizania aquatica*) in Lower Pool 4 (A–C), Pool 8 (D–F), and Pool 13 (G–H) of the Upper Mississippi River, USA Areas that are not sampled are shown in gray. References [50,51] are cited in the supplementary materials.

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Data Availability Statement: The aquatic vegetation and water quality datasets are publicly available through the Upper Mississippi River Restoration Program website (https://www.umesc.usgs.gov/ltrm-home.html). Daily discharge is publicly provided by the U.S. Army Corps of Engineers for the Mississippi River at Red Wing, Minnesota (Lock and Dam 3), La Crescent, Minnesota (Lock and Dam 7), and Bellevue, Iowa (Lock and Dam 12) and obtained from https://rivergages.mvr.usace.army.mil/WaterControl/new/layout.cfm. The wind fetch data were publicly accessed from https://doi.org/10.5066/P99OVGZB. All spatial datasets (NMDS rasters, Curve Fit outputs) are publicly available at https://doi.org/10.5066/P96A7PC5 [52].

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