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Relating Plant Spatial Pattern, Plant Biodiversity, and Ecosystem Function to Management Practices in Experimental Restored Wetlands

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Relating plant spatial pattern, plant biodiversity, and ecosystem function to management practices in experimental restored wetlands

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Abstract

Understanding the effects of management practices on shifting relationships between structure and function over the course of ecosystem development should be a central goal of ecosystem restoration. Yet many of these relationships, such as those between plant biodiversity, spatial pattern of vegetation and community metabolism, remain poorly understood. In a decade-long experiment, we investigated the impact of different initial planting treatments and of nutrient enrichment on relationships among plant biodiversity, plant spatial pattern, and ecosystem function in restored wetland ecosystems. In 2003, six identical and hydrologically-isolated 0.18 ha experimental wetland "cells" were constructed in marginal farmland in northeast Ohio. Cells were subjected to one of three initial planting and management treatments, which were later simplified into two treatment groups. In 2010 and 2011, nitrogen and phosphorus fertilizers were applied to one cell from each of the three treatments to simulate agricultural run-off. Changes and differences in ecosystem function were assessed by measuring aquatic community metabolism, aboveground biomass, soil organic matter, and nutrient concentrations. Structure was characterized through annual plant biodiversity inventories and aerial photographs of plant cover that were analyzed to quantify vegetation spatial patterns. We found significant relationships among plant biodiversity, plant spatial pattern, and planting treatments. We observed significant and sustained differences in plant biodiversity, resulting from both planting treatment and habitat attributes of cells. Relationships between ecosystem function and both biodiversity and spatial pattern were more ambiguous. We found no direct relationships between biodiversity or spatial metrics and any measures of ecosystem function. These findings support the importance of initial wetland structure in achieving plant biodiversity in restored wetlands, but provide little additional evidence that species diversity has a major effect on nutrient retention, primary productivity, or soil organic matter in restored wetland systems. Over multiple years, biodiversity metrics correlated positively with spatial metrics, including mean patch shape complexity and contagion. This suggests that restored wetland landscapes comprised of patches with complex shapes (high edge-to-area ratios) that are highly clumped are home to a more diverse array of plant species. Links between biodiversity and spatial pattern suggest that aerial imagery may provide wetland managers with a robust tool for assessing plant biodiversity.

Introduction

Wetlands are highly diverse and productive ecosystems with important ecological functions, such as purifying water, sequestering carbon, and providing habitat for ecologically and economically important species (DeSteven and Gramling 2012; Mitsch and Gosselink 2007; Zedler and Kercher 2005). Unfortunately, these ecosystems are also highly threatened (Mitsch and Gosselink 2007). About half of global wetlands (Zedler and Kercher 2005) and 86% of wetlands in the United States have been destroyed (Balcombe et al. 2005; Dahle 2011; McKenna 2003). Some of the worst wetland loss has occurred in Ohio, where only one tenth of original wetlands

have escaped conversion into farmland, resulting in substantially reduced ecosystem services (Mitsch and Day 2005). Agricultural expansion is the most widespread cause of wetland destruction. Conventional agriculture relies heavily on fertilizers and pesticides that pollute receiving bodies of water (Zedler 2003). If left intact, wetlands are capable of mitigating such pollution, but since conventional agricultural practices involve converting and draining wetlands, negative environmental impacts are compounded (Zedler 2003). Even when agricultural expansion and other anthropogenic land-use changes do not directly drain wetlands, these activities often fragment them, altering habitat structure and reducing biodiversity (Solé et al. 2004).

The loss and degradation of these ecologically important ecosystems has resulted in policies designed to protect and restore wetlands, such as the "no net loss" policy of the late 1980s, which mandates that all wetland destruction must be mitigated by wetland creation or restoration (Balcombe et al. 2005; Robertson 2000). Construction, restoration, and management of wetlands are informed by research in restoration ecology, a field that both applies and tests ecological theory (Falk et al. 2006). Efforts to measure the "success" of restored wetlands have been criticized for being subjective and biased by anthropocentric concerns (Zedler 2007), but quantitative methods of measurement have been developed and debated (Kentula 2000; Kusler and Kentula 1989). Currently, wetland restoration projects are considered successful if desirable functional objectives have been achieved after a specified period of time (Cui et al. 2009; Ruiz-Jaen and Aide 2005). Functional objectives vary by project, but often include such goals as providing habitat for diverse native species or retaining nutrients that would otherwise contaminate rivers (Cui et al. 2009; Zedler 2003). Unfortunately, functional objectives are not always easily achieved. Restoration projects aimed at mitigating wetland loss often fail to reproduce ecological functioning of natural wetlands (Kentula 2000; Moreno-Mateos et al. 2012; Mossman et al. 2012; Zedler and Kercher 2005). Among other things, restored wetlands often prove to be more susceptible to exotic species invasions and provide poorer ecosystem services than their natural counterparts (Kentula 2000; Zedler and Kercher 2005). This reality may be due to an incomplete understanding of the relationships between restoration methodologies, ecosystem structure, and ecosystem function.

Part of this incomplete understanding stems from lack of clarity in defining the meaning of the terms "structure" and "function". Ecosystem structure can be defined as patterns of the interrelations of organisms in both time and spatial arrangements (Odum 1971). Variables that characterize wetland structure include geomorphology, soil properties, and spatial configurations of biotic and abiotic elements. Ecosystem function can be defined as the energy circuits, food chains, diversity patterns in time and space, nutrient cycles, development and evolution, and controls within an ecosystem (Odum 1971). Variables that characterize wetland function include nutrient cycling and retention, primary productivity, biogeochemical activity, and water retention and release. In the last several decades, there has been considerable debate among ecologists regarding the existence and generality of relationships between ecosystem structure, function, and biodiversity (Huston 1997; Reiss et al. 2009; Tilman and Lehman 2002). Ambiguous definitions of structure and function play a role in this debate, and are further complicated by uncertainty about where biodiversity fits in. As evidenced by Odum's definitions, biodiversity can be considered an aspect of both ecosystem structure and function (e.g., Franklin 2006). Furthermore, biodiversity can encompass diversity at multiple scales, including genetic diversity

within populations, species diversity within communities, and functional diversity within communities and ecosystems. Although the field of restoration ecology considers all of these, the emphasis of management is often on species diversity within the plant community and its implications for achieving species diversity within the animal community and achieving desirable ecosystem functioning. Issues of how to achieve high levels of biodiversity and how biodiversity produces key functions such as nutrient retention and primary productivity are fundamental to restoration ecology.

Spatial pattern, an ecosystem attribute that can be more clearly classified as structure than biodiversity, is also thought to affect ecological function (Maestre et al. 2011). While biodiversity is a well-established measure of success in ecological restoration projects (Ruiz-Jaen and Aide 2005; Zedler 2007), ecologists have only recently begun measuring spatial patterns of various environmental characteristics in restored ecosystems (Gebo and Brooks 2012; Piniewski et al. 2012). It is well documented that the spatial configuration of wetlands within multi-hectare landscapes can have an important effect on wetland function (Mitsch and Gosselink 2000). For example, riparian wetlands have far more influence on stream water quality than non-riparian wetlands (Gilliam 1993). However, little is known about how small-scale spatial pattern relates to other measures of ecosystem structure and to functions considered desirable by restoration ecologists. Research to date suggests that spatial patterns of environmental characteristics, such as water, soil, and plant species, are associated with aspects of ecosystem structure and function, including biodiversity and nutrient cycling (Davidson et al. 2012; Franklin and Mills 2006; Wolf et al. 2011). Spatial patterns of vegetation are particularly interesting. Plant distribution affects the biodiversity of both plants and animals (Bergelson 1990; Fairbairn and Dinsmore 2001), as well as influencing and being influenced by other aspects of ecosystem function, like nutrient dynamics and system metabolism (Turner et al. 2011). Nitrate removal in riparian wetlands depends largely on patterns of plant cover (Curie et al. 2011) and spatial patterns of nutrient release rates in floodplains correlate with spatial patterns of plant types (Wassen et al. 2003).

Examining relationships among measures of biodiversity and spatial pattern is potentially useful in understanding the ecology of restored wetlands, but only if the particular measures used are important to ecological structure and function. Part of the challenge of examining relationships between biodiversity, spatial pattern, and ecosystem function is that multiple metrics can be used to characterize these aspects of structure and function, and it is not always clear which metrics are most useful (Li and Wu 2004; Magurran 1988; Reiss et al. 2009). For example, Shannon-Weaver diversity is routinely used to measure species diversity, but this metric could be applied to all species present in a study site or to various subsets of native and/or wetland target species; different metrics and ways of calculating them could tell very different stories about the biodiversity of a place. On the other hand, a wide variety of spatial metrics exist that can be used to characterize spatial pattern (Peng et al. 2010), but the ecological relevance of many of these metrics has often been questioned (Dramstad 2009).

In this study, we examined the relationships among management of restored wetlands, several measures of plant biodiversity and spatial pattern that we deemed ecologically-relevant, and several aspects of ecosystem function, over a period of eight years. We considered plant biodiversity an aspect of ecosystem structure, but we do not discount the idea that maintaining diversity is a desirable function of wetlands as well. By analyzing temporal changes in measures

of structure and function, we aimed to increase understanding of plant community development in restored systems, and by exploring correlations between plant spatial patterns and elements of ecosystem structure and function, we sought to discern links between spatial characteristics of plant communities and standard measures of restoration success. Our research was conducted on an experimental restored wetland system that has been subjected to two manipulations: differential planting and management, and nutrient addition. We investigated changes in plant spatial pattern, plant species diversity and several measures of ecological function over time in response to these manipulations. Through this investigation, we sought to determine:

> how different planting/management strategies affect plant biodiversity and ecosystem function,
> how nutrient addition affects plant biodiversity and ecosystem function,
> what relationships exist between plant biodiversity and ecosystem function,
> what relationships exist between plant biodiversity and spatial patterns, and
> what relationships exist between measures of ecosystem function and plant spatial patterns.

In answering these questions, we hope to increase understanding of how management practices influence aspects of ecosystem structure and function in restored wetlands, and how those aspects of structure and function relate to one another. We hope this will enrich theoretical understanding of restored wetland ecosystems and help project managers develop effective approaches to establishing ecosystem structure conducive to eliciting desired ecological functioning.

Methods

Study site

Research was conducted at an experimental restored wetland system on the George Jones Memorial Farm in New Russia Township, Ohio (41º17'38" N, 82º13'03" W). The site is located in the Plum Creek basin of the Black River watershed, which drains into Lake Erie. As in much of northeast Ohio, drainage here is poor due to level topography and post-glacial clay loam soil which allow water to collect in depressions after rainstorms. From 1970 to 2000, mean January temperature was -4.6 ºC, mean July temperature was 21.9 ºC, and mean annual temperature was 9.3 ºC. Mean annual precipitation during this period was 92.02 cm, with precipitation distributed fairly evenly throughout the year (National Climatic Data Center 2004). Prior to wetland restoration, this site was used for conventional corn and soy agriculture. Before that, post-glacial beech-maple (*Fagus grandifolia* Ehrh.-*Acer* sp. Marshall) forests and swamp forests dominated the region (Braun 1967). Oberlin College owns the George Jones Memorial Farm and the New Agrarian Center, a non-profit organization, manages it with the goal of demonstrating and promoting sustainable agriculture and ecological restoration.

The wetlands were constructed in July 2003. The tile drainage system used when the land was farmed was blocked, depressions were excavated and berms were built on the downslope northern side in a series of north-south divisions to create six hydrologically-isolated, rectangular wetland "cells" (Fig. 1A). Each cell is 60 m long, 30 m wide, and approximately 0.18 ha in area. The cells were designed to be as uniform as possible in basin morphology, with basins

approximately 1.5 m deep at the north ends (designed to retain water even in dry years) that slope downward toward seasonally wet meadows on the southern ends. This shape was designed to provide habitat for a variety of obligate and facultative wetland plant species. Adjustable weirs are located in each wetland that can control water levels. The watershed draining into each cell is between 0.5 and 1 ha, dominated by annual grasses that were mowed annually in the spring during the first four years of restoration. No addition of fertilizers occurred in the watershed during this experiment. A permanent rebar grid was established within each cell to create a fixed reference system for sampling and spatial analysis (Fig. 1B, C). East-west rebar are spaced 5 m apart and north-south rebar are 10 m apart.
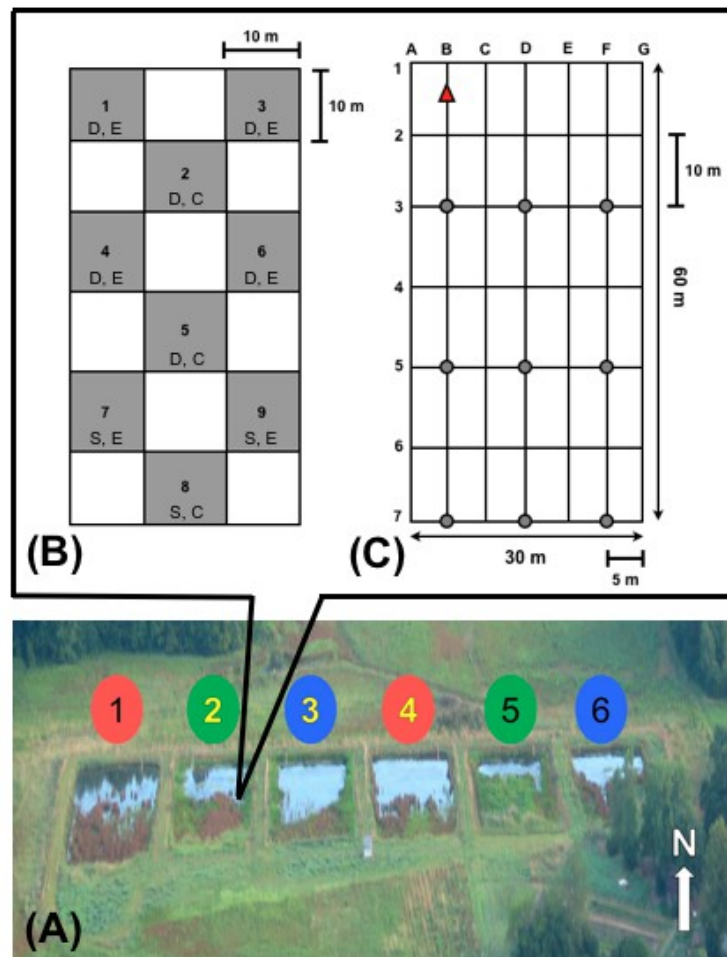
Figure 1. A) Cells 2 and 5 were subjected to **high-intensity** plantings in 2003 and subsequent years. Cells 3 and 6 had **low-intensity** planting in 2003 and were not replanted. Cells 1 and 4 were **unplanted**. Cells 2, 3, and 4 were fertilized in 2010 and 2011. **B)** Sampling pattern used to measure spatial pattern and plant biodiversity. Shaded quadrats were surveyed. Each quadrat was assigned a number to aid in identification. Quadrats were also grouped into central and edge and shallow and deep zones. "D" indicates cells are in deep zone vs. "S" for shallow. "E" indicates cells are in edge zone vs. "C" for central. **C)** Schematic of the rebar grid delineating 5 x 10 m plots in each cell. Circles indicate soil sampling locations. The triangle indicates the water sampling location.

Two invasive plant species, reed canary grass and cattail (*Phalaris arundinacea* L. and *Typha* spp. L.), and one animal species, muskrat (*Ondatra zibethicus*), were controlled during the study period. *P. arundinacea* was controlled with Roundup in dry regions of wetlands (2004-2006; no overspray entered the water) and selective removal and mowing (2004-2007). *Typha* spp. was removed by hand-pulling during the summers of 2004 and 2005. In northeast Ohio, cattail often becomes a dominant species, even a monoculture, if uncontrolled in early stages of wetland restoration (Galatowitsch et al. 1999). Cattail removal was discontinued once populations remained relatively low. Reed canary grass, however, continued to dominate some regions of cells once removal ceased. In total, 36.5 hours were spent weeding in 2004, 16.3 hours in 2005, and 13.8 hours in 2006. Muskrats invaded several cells in 2004 and inflicted considerable damage through herbivory and extensive excavation of berms. We attempted to control muskrat population by using conibear traps, primarily during the winter, but the muskrat population and herbivory have persisted throughout the remainder of the experiment.

The cells were subjected to two experimental treatments (Fig. 1A). In the first treatment, cells were assigned one of three planting/management treatments. Cells were 1 and 4 were left unplanted; colonization occurred through natural recruitment alone. High-intensity cells (2 and 5) and low-intensity cells (3 and 6) were extensively planted in 2003 with a mixture of locally-collected and commercially-acquired seeds and seedlings of native wetland species (Appendix: Table 1). seedlings that did not survive initial planting were replanted in both high- and low-intensity treatments in summer 2004. In the high-intensity treatment, missing seedlings were replanted again in summers 2005 and 2006 (Appendix: Table 2). Seeds were not resown in either treatment, as they were much less successful at establishing than seedlings.

The second treatment was a nutrient addition designed to simulate runoff from a watershed dominated by corn and soy conventional agriculture. In summers 2010 and 2011, commercial agricultural fertilizers containing high concentrations of nitrogen (N) and phosphorus (P) were spread onto one cell from each planting/management treatment. We wanted to simulate runoff into the cells that would come from a 4.5 ha watershed, as this yielded a wetland:watershed ratio of 0.04, which is the mean value calculated from many constructed wetland studies (Appendix: Table 3). Quantities of N (59.4 kg/cell) and P (8.69 kg/cell) applied were determined from average nutrient loads in agricultural runoff (kg/ha/yr) (Appendix: Tables 4 and 5). In 2011, these amounts were doubled in an attempt to elicit a stronger response from the fertilized wetland cells.

Data collection and processing

Surveys of plant biodiversity took place from 2004 to 2012 in late July or early August. Our methodology was based on Ohio EPA procedures adapted from the North Carolina Vegetation Survey (Peet et al. 1998, Smith 2006). Within each cell, we surveyed nine quadrats covering half of the total area of each cell in a checkerboard pattern, for a total of 54 quadrats per year (Fig. 1B). Each quadrat consisted of two of the 5 x 10 m rebar rectangles previously described. Quadrats were also characterized as belonging to four, sometimes overlapping, "zones" based on location within the cell. The "central" zone has no adjacency to upland regions, while the "edge"

zone is bordered by upland terrain (Fig. 1B). The "deep" zone encompasses areas of deeper water in cells, while the "shallow" zone is seasonally dry (Fig. 1B).

We recorded percent cover of all plant species within each quadrat. Plant identification and nomenclature followed Gleason and Cronquist (1991) and records of all plants identified were stored at Oberlin College. Percent cover was determined according to the system of Peet et al. (1998). There are ten levels of cover in this system that are progressively larger and encompass wider ranges of cover. For example, level 2 was used for areas with 0-1% cover by a particular species, while level 7 encompassed 25-50% cover. This allowed for better resolution in identifying categories of cover than a system with equally-sized cover classes (Smith 2006). Percentages of emergent plant cover, total plant cover, algae cover, open water, and open land were approximated for each quadrat as well.

We assigned attributes that characterized each plant species present in the wetlands using the classification scheme published by Andreas et al. (2004). Species were classified as either native or non-native to Ohio, and as obligate wetland, facultative wetland, facultative (equally amenable to either upland or wetland habitat), facultative upland, or obligate upland. In our analyses of plant species biodiversity, we treated all obligate wetland, facultative wetland, and facultative species as "wetland species." The "coefficient of conservativism" (C) is a classification attribute used to weight the relative value of species in biodiversity assessments. We used the weighting values of Andreas et al. (2004), which assigns high C values to endemic species with narrow ranges and low values to exotic or generalist species. While native upland species have higher C values than non-native upland species, species endemic to wetland habitats often have the highest C values, making this a useful classification attribute for assessing wetland biodiversity (Bourdaghs et al. 2006; Chamberlain and Ingram 2012).

In preliminary analyses, we used cover data from our biodiversity surveys to calculate several metrics of biodiversity for treatments, whole cells, zones, and quadrats. Metrics calculated include standard metrics like species richness and Shannon-Weaver diversity (SWD), both of which were calculated for all diversity data, as well as subsets of the original dataset that included only certain species (native species only, wetland species only, species that are both native and wetland only, and exotic species only). We also calculated less common metrics, such as the Floristic Quality Assessment Index (FQAI), and Whittaker's Beta (B_W). We settled on three metrics for our final analyses, which capture important and distinct aspects of the biodiversity of our study site: FQAI, SWD calculated for the native species dataset (native SWD), and B_W.

FQAI and SWD are measures of alpha-diversity (Magurran 1988), meaning they measure diversity without reference to the spatial arrangement of plants. FQAI is a specialized species richness metric. Like species richness, it does not incorporate abundance data, and can thus be skewed by non-uniform distributions of species in a community (Magurran 2005), which may limit its usefulness as a management tool (Jennings et al. 2008). However, FQAI is more complex than basic species richness, as it incorporates C values of species, giving extra weight to rare, native, and specialist species over common and generalist species. Exotic species, which have C values of zero, are excluded from FQAI. FQAI is a widely used biodiversity metric in studies of wetland plant communities (DeBerry 2006; Matthews 2003; Mushet et al. 2002), as its

emphasis on "quality" of plant species makes it a useful indicator of the desirability of plant species composition in wetland ecosystems (Johnston et al. 2009). We calculated FQAI scores for quadrats and cells following Smith (2006). Andreas et al. (2004) define FQAI as $\Sigma[(C_i)/(S)^{0.5}]$, where C_i is the coefficient of conservativism for species i and S is the total species richness of the area being evaluated.

SWD is perhaps the most familiar measure of community biodiversity and has been used for over sixty years (Lopez and Fennessy 2002). SWD incorporates relative abundance data as well as composition data (Magurran 2005). We used native SWD, as we felt this more closely paralleled FQAI, which also emphasizes native species. Furthermore, preliminary analysis revealed similar patterns in native SWD, wetland SWD, and native and wetland SWD, so we deemed using all three metrics in our analyses unnecessary. Our complete dataset included observations of the abundance of 98 species. To calculate native (55 species) SWD, we excluded species from the original dataset based on Ohio EPA classification of species attributes (Andreas et al. 2004) before calculating SWD. We used the Multivariate Statistical Package (Kovach Computing Services; Pentraeth, Wales) to calculate native SWD (Kovach 1999; Krebs 1999). This package calculates SWD using the standard formula $SWD = -\Sigma p_i \ln(p_i)$ and treats p_i as the percent cover (calculated by averaging range of percentages within a given cover class) in the surveyed area attributable to species i, as in Kovach (1999) and Smith (2006). We calculated native SWD for each quadrat assessed and averaged native SWD scores from individual quadrats within each cell to get native SWD scores for entire cells.

Beta-diversity (B_W), or spatially explicit diversity (Magurran 1988), is derived from compositional data and allows for examination of spatial heterogeneity of species diversity within a defined area (Wiersma and Urban 2005; Reilly et al. 2006). The metric has not been widely used in biodiversity studies, but we employed it in our examination of relationships between biodiversity and spatial metrics since, unlike SWD and FQAI, it considers variation over space, and might therefore be more related to spatial metrics than these other biodiversity metrics. We calculated average B_W values for whole cells and zones (Fig. 1B). $B_W = S/\alpha - 1$, where S is the total number of species found in the whole system and α is the mean species richness of all subunits within the system (Magurran 1988). For example, we calculated quadrat-scale B_W values by considering species richness within a given quadrat and average species richness of the whole cell within which that quadrat was nested.

Aerial photographs of vegetation in the cells were taken from 2008 to 2012 in late August using a remote-controlled camera mounted on a large helium-filled balloon (e.g., Miyamoto et al. 2004). The balloon was controlled manually from the ground with kite strings. Aerial photographs were taken of each cell in its entirety and have a sub-meter resolution. Close-up photographs of the cells were taken as well, to be used along with diversity surveys for ground-truthing when necessary. Photographs were imported into ArcMap (ESRI 2011) and georeferenced to GPS points taken at each node of the rebar grid. Polygons representing areas of different cover types (plant species *Lemna/Wolfia* spp., *Juncus effusus*, *Nymphaea odorata*, *Malva moschata, Peltandra virginica, Phalaris arundinacea, Pontedaria cordata, Polygonum* spp., and *Sagittaria latifolia*, as well as open water and open land) were delineated in each photograph (Fig. 2). Some polygons were delineated manually, while others were first assigned automatically using the Maximum Likelihood Classification tool in ArcMap 10 and then

corrected by hand.
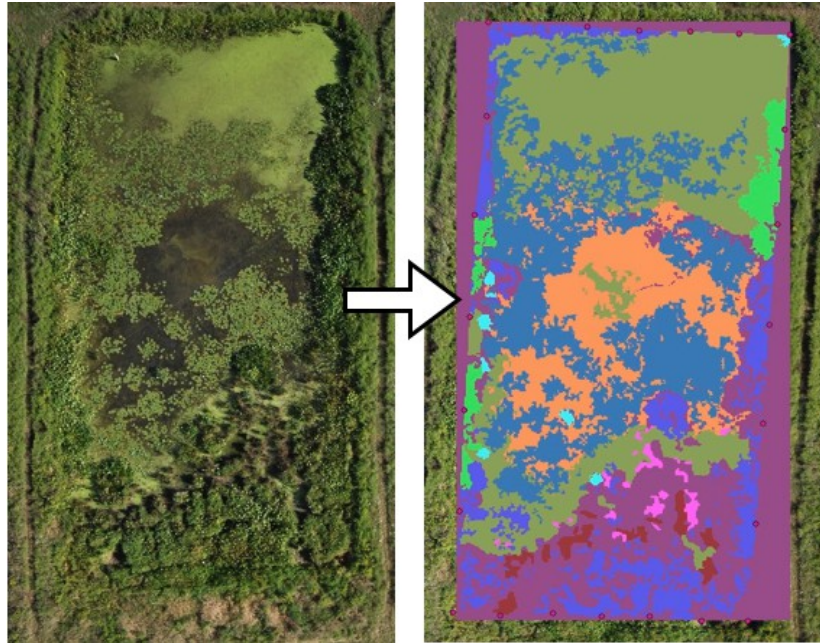
Figure 2. An aerial photograph and subsequent delineation of cover types. This example is of cell 3, a high-intensity planted cell, from 2010.

In order to minimize human error from hand delineation, each patch was delineated in fine detail, then aggregated and simplified by standard normalization parameters at a more relaxed degree of precision. Polygons were first aggregated (aggregation distance = 0.1 m, minimum area = 0.1 m^2, minimum hole = 0.25 m^2), then simplified (simplification algorithm = point_remove, maximum allowable offset = 0.05 m, minimum area = 0 m, keep collapsed points = no). Polygons were converted to raster (grid) files, then to text files and imported into FRAGSTATS (McGarigal et al. 2012).

Spatial metrics of the wetland landscapes were computed in FRAGSTATS. What constituted a "landscape" in this study differed depending on the scale of examination (Fig. 3). Specifically, spatial pattern was assessed for each whole cell, for each of the four separate zones defined within each cell (central, edge, shallow, and deep), and for each of the nine quadrats within each cell (Fig. 1B). In a preliminary analysis, we computed multiple different landscape spatial metrics, several of which were highly correlated with each other. We chose three that that we felt characterized distinct aspects of spatial pattern, including shape, distribution, and diversity of patches of different cover types, each of which is potentially important for ecological function. One spatial metric, percentage of landscape, was calculated at the class (i.e., cover type) scale. This metric was only calculated for the "open water" cover type, in order to enhance our understanding of relationships between biodiversity, which we hypothesized would correlate negatively with percent open water, and ecosystem function. The three landscape spatial metrics used to explore relationships between plant spatial pattern and biodiversity are Shannon's diversity index (SHDI), area-weighted mean patch shape index (SHAPE_AM), and contagion (CONTAG).
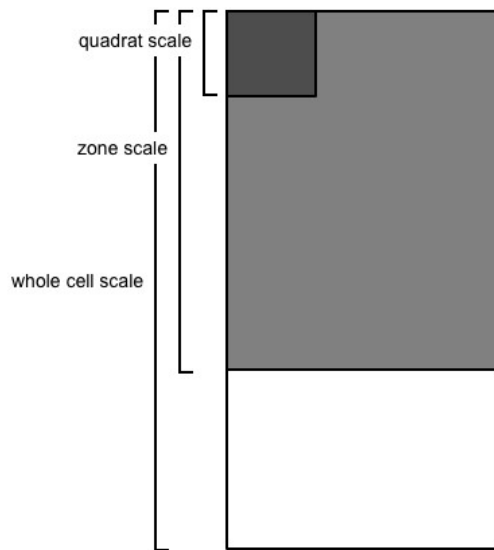
Figure 3. Three different scales used in calculating plant biodiversity and spatial metrics. In this example, quadrat 1 represents the quadrat scale and the deep zone represents the zone scale.

SHDI is a combined measure of cover type richness and evenness in a landscape. Higher values indicate higher diversity and more even distribution of cover types, while lower values indicate lower diversity and less even distribution. SHDI considers the proportion of a landscape occupied by patches of different cover types, but not the spatial configuration of those patches within the landscape. It is similar to the standard Shannon-Weaver diversity index used to quantify species diversity, but quantifies diversity based on the smaller number of cover types identified through aerial photography rather than on complete plant species diversity identified through on-the-ground assessment. In this study, we delineated 11 cover types from our aerial photographs, versus the 98 distinct species identified in our species diversity inventories.

SHAPE_AM is a landscape-scale metric that measures the mean complexity of patch shape within a landscape. To accomplish this, the actual shape of a patch is compared to a standard (square) shape of the same area, and SHAPE_AM quantifies the degree to which its edge-to-area ratio differs. An advantage of using SHAPE_AM over other similar metrics like perimeter-to-area ratio is that it is standardized to account for patch size.

CONTAG is a landscape-scale metric that measures how clumped patches are within a landscape. It quantifies both patch interspersion, or intermixing of patches of different cover types, and dispersion, or the spatial distribution of a given cover type, at the landscape scale. Lower CONTAG values indicate landscapes made up of many small, dispersed patches, while higher CONTAG values indicate landscapes with relatively fewer, larger, and more contiguous patches.

Percentage of landscape (PLAND) measures the percentage of a landscape occupied by a given cover type (in our study, open water). Descriptions of spatial metrics provided above are adapted from FRAGSTATS documentation. More detailed descriptions of metrics, discussion of their

usefulness, and their formulas can be found in FRAGSTATS documentation (McGarigal and Marks 1995).

Methods for assessing soil organic matter using the loss-on-ignition method followed procedures described in *Methods of Soil Analysis* (Soil Science Society of America 1996). Annual soil samples were collected in August from 2009 to 2012 using a soil corer to a depth of 8 inches. Sampling occurred at nine locations in each cell, spaced in order to capture soil heterogeneity based on water depth and distance from edge (Fig. 1C). At each location, a 1 m^2 sampling area was delineated. This sampling area was rotated around a central point each year to avoid sampling at the exact same locations every year (Fig. 4). Four cores were collected (one from each corner of the sampling area) and homogenized. Aboveground stems were excluded from soil samples, but roots and litter were included.
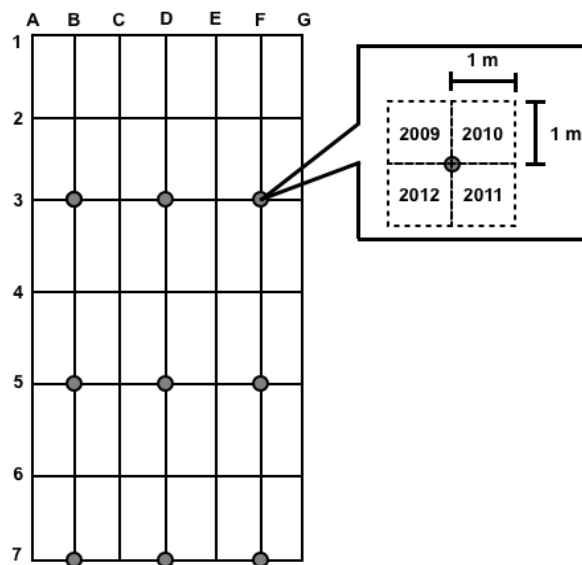
Figure 4. Schematic of the rebar grid delineating 5 x 10 m plots in each cell. Circles indicate soil sampling locations. Dashed-line squares indicate sampling areas and numbers inside squares indicate the year each sampling area was used.

Aboveground biomass was measured in 2009, as a pre-fertilization baseline, and again in 2010, after fertilization. In this study, aboveground biomass is an aggregate measure of all macrophyte tissue that is above the soil or sediment surface, including submerged macrophytes. In each cell, we harvested 1 m^2 plots centered at B3, F3, B5, F5, B7, and F7 (Fig. 1C). Samples were collected in plastic bags and then dried. Plant matter was dried at 105°C in a drying oven until there was no more weight loss, then grouped by sampling plot and massed. Biomass from 2009 was used to assess the potential effect of planting treatment on primary productivity before fertilization, but we found no significant differences between planted and unplanted cells that needed to be controlled for. Change in biomass per cell from 2009 to 2010 was calculated and compared between fertilized and unfertilized wetlands in order to measure response to fertilization.

Water quality was assessed by measuring dissolved oxygen (DO), dissolved inorganic nitrogen

(DIN), dissolved inorganic phosphorus (DIP), and turbidity. These were measured weekly during the growing season. Monitoring occurred at a single point in the deep end of each cell (Fig. 1C), as analysis of water samples from multiple locations and depths within cells indicated that water quality did not vary significantly within cells. Methods for assessing water quality were based on *Standard Methods for the Examination of Water and Wastewater* (Clesceri 1998). We measured temperature and DO using a model 550A YSI probe *in situ* (YSI Inc.; Yellow Springs, Ohio) and collected water samples for laboratory analysis of DIN, DIP, and turbidity. Turbidity was measured in unfiltered samples using an 890 nm infrared light turbidity sensor (Vernier Software and Technology; Beaverton, OR), which reported turbidity in Nephelometric Turbidity Units (NTU). Samples for nutrient analysis were filtered through 435 µm thick glass microfiber filters (North Central Laboratories; Birnamwood, Wisconsin) and then frozen until analysis took place. Concentrations of dissolved nitrate (NO_3), nitrite (NO_2), and phosphate (PO_4) were measured using an ASRS-II Suppressed Conductivity Ion Chromatograph (Dionex Corporation model DX500 with ED40 Conductivity Detector; Sunnyvale, California) and a 4 x 250 nm IONPAC AS9-HC Analytical anion column. We measured concentration of dissolved ammonium (NH_4) with a Thermo Orion 720 ammonia probe (Thermo Fisher Scientific, Inc.; Pittsburgh, Pennsylvania). NH_4 analysis of a subset of water samples from all seasons over multiple years consistently showed NH_4 concentrations in all samples that were substantially lower than NO_3 concentrations. We therefore treat dissolved NO_2 and NO_3 measurements as reflective of total dissolved inorganic nitrogen (DIN). Median values of nutrient concentrations (DIN and DIP) and turbidity over the duration of each summer were used to characterize those variables for particular years so that these point measures could be compared with annual assessments of species diversity and spatial pattern.

Metabolic activity within the water column and benthos was assessed using *in situ* Oxyguard DO probes (Oxyguard International; Birkerød, Denmark) equipped with mechanical mixers during summers of 2010 to 2012. *In situ* DO probes were deployed in each wetland cell in early June and data loggers recorded readings every 15 minutes for the duration of the summer. Probes in each pair of adjacent wetlands shared a battery-charging and data-logging station. DO probes were tethered to flotation buoys approximately 5 m from either the east or west berm and 10 m from the north berm. A tether anchored the probes approximately 0.3 m below the water surface in the deepest section of each wetland cell. DO probes were cleaned and calibrated every week until removal from wetlands in early September each year.

Measured changes in DO were used to calculate primary productivity and respiration of the aquatic community (including phytoplankton, benthic algae, submerged macrophytes, and benthic and planktonic heterotrophs) (Petersen et al. 1997). Respiration (R) in the water column and benthos was assessed by tracing diurnal fluctuations of DO in the water column (Fig. 5). R was defined as the rate of change in DO during the dark period of a day and net primary productivity (NPP) was defined as the rate of change in DO during the lit portion of the day. R was calculated for every 15-minute interval unless change in DO was no longer linear due to hypoxic conditions (below 2 mg/L). NPP was calculated for each 15-minute interval during the day.
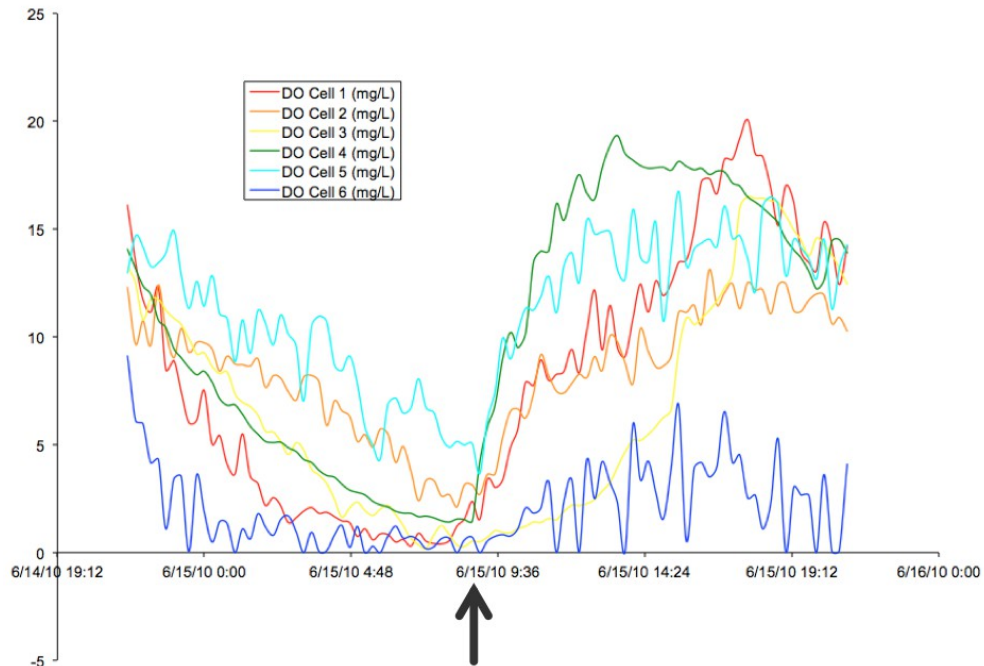
Figure 5. Example of diurnal DO fluctuations from June 2010. Arrow indicates where the switch from day to night (NPP to R) occurs.

Median rates were used to summarize R and NPP for each day. The absolute amount of photosynthesis before any carbon is respired, or gross primary productivity (GPP), was calculated by adding NPP to an average of the median rate of R from the night before and the night following that day. After calculating GPP for each 15-minute NPP measurement, median GPP was used to find a central tendency for each day's data. Median values of R, GPP, and NPP for each growing season were used to evaluate relationships with annual measures of biodiversity and spatial heterogeneity.

Nutrient removal rates following fertilization were calculated for DIN and DIP for each fertilized cell (2, 3, and 4) for each year of fertilization (2010 and 2011). These rates were calculated by fitting exponential decay equations to nutrient concentration data; in the exponential decay equation $N(t) = N_0 e^{-rt}$, the nutrient removal rate variable is r (Fig. 6).

13

DIN 2010 Cell 4
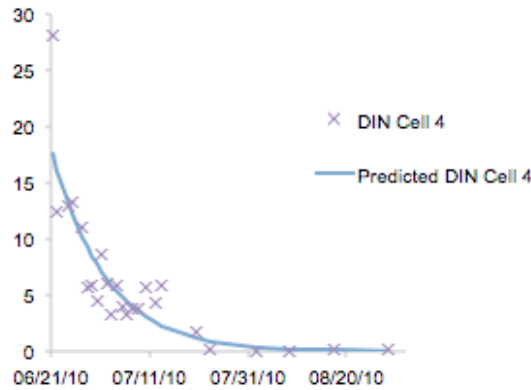
Figure 6. Example of a nutrient depletion rate (line labeled "Predicted DIN Cell 4") fit to DIN data from cell 4 in 2010. For these data, the exponential decay equation is $N(t) = 28.18e^{-0.09t}$, and the nutrient removal rate variable (r) = 0.09 hr^{-1}.

Statistical analysis

We assessed differences in biodiversity metrics and in mean annual change in biodiversity metrics, based on planting treatments and time during our study period, using t-tests conducted in GraphPad QuickCalcs, an online statistical software (GraphPad Software; La Jolla, California). Mean annual change was calculated by measuring change between each pair of years (e.g., change from 2004 to 2005, change from 2005 to 2006, etc.) and averaging these values. Preliminary analyses revealed that differences in biodiversity between high- and low-intensity planted cells were not detectable, so we only examined two levels of planting and management treatment—planted (including both high- and low-intensity) and unplanted—in order to add more statistical power to our analyses.

In order to examine the effects of planting treatment and habitat attributes on plant biodiversity, we created a three-factor nested analysis of variance (ANOVA) model with repeated measures on two cross-factors (Doncaster and Davey 2007) in R (R Foundation for Statistical Computing; Vienna, Austria). The general equation for this model's structure is:

$$y = p \mid d \mid c(t)$$

In this equation, y is the biodiversity value of a given quadrat, p is the proximity of a given quadrat within a cell to upland terrain (edge or central zone), d is the depth of the quadrat within its cell (deep or shallow zone), c is the cell a given quadrat is in, and t is the treatment associated with that cell. In other words, this model examines the biodiversity of quadrats (y) as a function of depth (d) and proximity to upland (p) in six cells (c) nested in a treatment (t) (unplanted or planted), and can attribute differences in y to each of these explanatory variables. We used this nested ANOVA model in order to avoid pseudoreplication effects that might occur from treating quadrats as independent observations without acknowledging when they are situated within the same zones or cells. We ran this ANOVA on FQAI and native SWD data averaged over all years

of our study period.

We used GraphPad to analyze differences in plant biodiversity, spatial pattern and ecosystem function, as well as changes in biodiversity, spatial pattern and ecosystem function, based on nutrient addition treatment (GraphPad Software; La Jolla, California). For absolute (non-change) measures, data were averaged over all years and differences in these values were assessed using a t-test. To quantify change, differences in the values of biodiversity and spatial metrics from 2009 (pre-fertilization) to 2012 (post-fertilization) were quantified, and differences in these changes between fertilized and unfertilized cells were assessed with t-tests. Changes in the values of ecosystem function measures were quantified and analyzed similarly. Changes in aquatic community metabolism (R, GPP, and NPP) from 2009 to 2010 were calculated and differences in change between fertilized and unfertilized cells were assessed, but 2009 data were subsequently misplaced. Thus, 2010 was used as the starting point, rather than 2009, in assessment of overall changes (2010-2012) in aquatic metabolism and DIN and DIP. Similarly, for aboveground biomass, 2010 was used as the end point rather than 2012, due to lack of 2012 data.

We performed linear regressions in R (R Core Team; Vienna, Austria) to characterize relationships among biodiversity, spatial pattern, and ecosystem function. We created a mixed model in which a primary explanatory variable (independent variable) acts on a response variable (dependent variable), with the effects of year and of interaction between the explanatory variable and year being accounted for as well. In this model, the primary explanatory variable (e.g., FQAI) is continuous, while year and interaction between the explanatory variable and year are both categorical. The equation for this is:

$$y = b_0 + b_1 * x + b_2 * year + b_3 * x * year$$

In this equation, y is the response variable, x is the primary explanatory variable, b_0 is the y-intercept, b_1 is the slope, b_2 is the coefficient for the effect of year by itself, and b_3 is the coefficient for the effect of interaction between x and year. Year effect, b_2, changes the intercept of the regression (shifts the line up or down) while interaction effect, b_3, changes the slope of the regression. Only the directions of correlations (positive or negative slope) are reported in results rather than actual values, because there were no standardized units among variables, rendering numeric values unhelpful in interpreting the relative strengths of correlations for different variables.

Before addressing relationships between spatial pattern and other measures of structure and function, it is important to note that spatial metrics are often highly correlated with one another (Hargis et al. 1998; Turner et al. 2001; McGarigal et al. 2009), which can interfere with interpreting relationships between spatial metrics and other variables. We regressed SHAPE_AM and CONTAG on SHDI in order to gauge correlation among spatial metrics. We chose only to regress SHAPE_AM and CONTAG on SHDI, rather than regressing all metrics on each other, because we deemed SHDI to be a fundamental variable of interest, as it is most likely to correlate with biodiversity metrics due to its similarity to SWD. Spatial metrics (SHDI, SHAPE_AM, and CONTAG) were also regressed on biodiversity metrics (FQAI, native SWD, and B_W) at varying scales, ranging from quadrat to whole cell. We also regressed spatial metrics on measures of

ecosystem function (R, GPP, NPP, DIN Removal Rate, DIP Removal Rate, median annual DIN and DIP, and SOM). This was done at the whole cell scale for all ecosystem function measures except SOM, as this was the only scale at which we had measurements of these variables, and at the quadrat, zone, and whole cell scales for SOM. Finally, we regressed biodiversity metrics (FQAI and native SWD) on measures of ecosystem function, to complement other analyses of biodiversity effects on ecosystem function.

Results

Planting effects on plant biodiversity

We measured biodiversity and changes in biodiversity during early and later succession in our study period. Mean biodiversity metric values were calculated by averaging biodiversity metric values of cells within each planting/management treatment for all years within each successional time block (Fig. 7). Mean values of both FQAI and native SWD were significantly different in planted and unplanted wetlands in both early and later succession ($p < 0.004$). Neither FQAI nor native SWD differed significantly between early and later succession in either planted or unplanted cells.
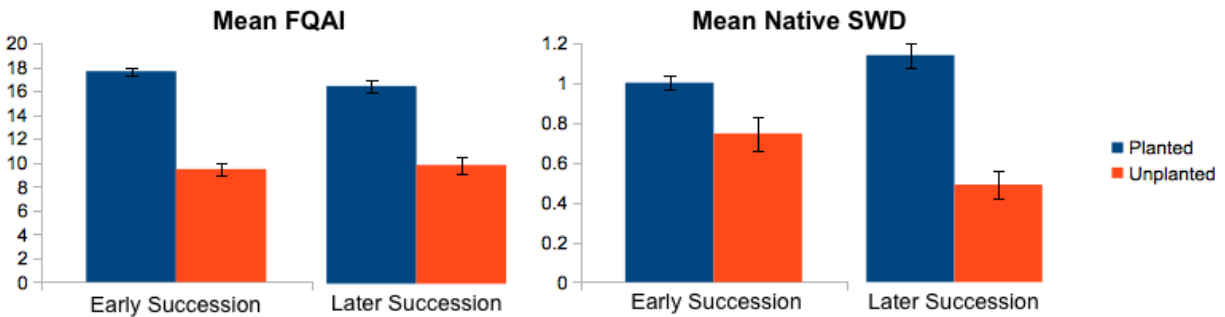
Figure 7. Mean values of biodiversity metrics during early and later succession. Early succession here is defined as the first half of our study period (2004-2008) and later succession is the second half of our study period (2009-2012). Metrics are dimensionless. Error bars represent standard error of the mean among replicates.

We examined mean annual changes in values of biodiversity metrics to determine whether planted and unplanted cells were experiencing similar patterns of change (Fig. 8). Planted and unplanted cells both appeared to experience annual increases in FQAI and native SWD during early succession, and annual decreases in both biodiversity metrics during later succession, but these trends were not statistically significant. Likewise, mean annual changes in biodiversity metrics were not significantly different in planted and unplanted cells in early or later succession.
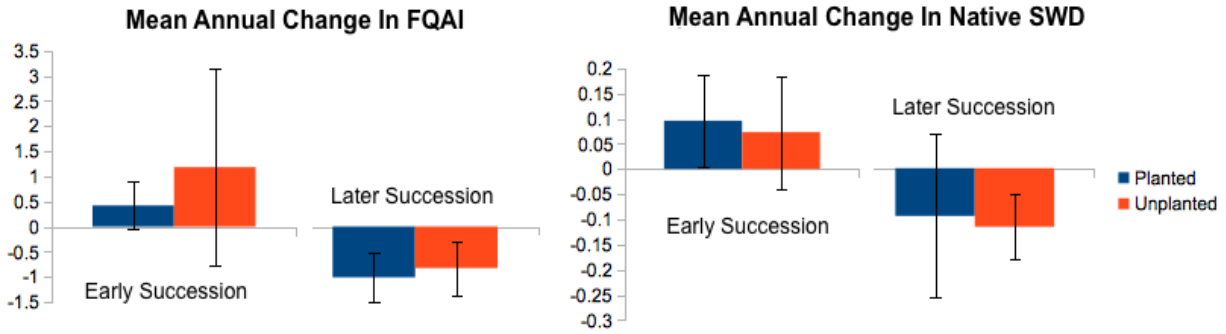
Figure 8. Mean annual changes in biodiversity metrics during early and later succession. Early succession here is the first half of our study period (2004-2008) and later succession is the second half of our study period (2008-2012). Metrics are dimensionless. Error bars represent standard error of the mean among replicates.

We found that planting treatments, as well as habitat attributes and various interactions among treatments and habitat attributes, resulted in significant differences in biodiversity among the surveyed quadrats. Differences in both FQAI and native SWD could be partially attributed to differences in planting treatment (Table 1). Differences in FQAI could also be partially attributed to differences in proximity of surveyed quadrats to upland (edge vs. central zones) and to interactions between quadrat depth and proximity (Table 1). Differences in native SWD could also be partially attributed to differences in depth, and to interactions between planting treatment and depth (Table 1). Interactions between planting treatment and proximity, and among planting treatment, depth, and proximity did not result in significant differences in either biodiversity metric (Table 1).

Table 1. F-statistics for nested ANOVAs of biodiversity between quadrats subjected to two levels of planting. "Treatment" column contains ANOVAs when planting treatment is the only factor considered, "Treatment:Depth" column contains ANOVAs when interactions between treatment and depth are considered, and so on. P-values were adjusted with a Bonferroni correction to account for multiple comparisons. Significant differences at $\alpha = 0.05$ are bolded.

Biodiversity Metric	Treatment	Depth	Proximity	Treatment: Depth	Depth: Proximity	Treatment: Proximity	Treatment: Depth: Proximity
FQAI	**p < 0.001**	p = 1	**p = 0.056**	p = 0.686	**p = 0.042**	p = 1	p = 1
Native SWD	**p = 0.014**	**p = 0.028**	p = 1	**p = 0.098**	p = 1	p = 1	p = 1

Effects of planting, plant biodiversity, and spatial pattern on ecosystem function

We found no significant differences in any measure of ecosystem function (R, GPP, NPP, DIN, DIP, N removal rate, P removal rate, or SOM) between planted and unplanted cells. Likewise, we found no significant correlations between biodiversity metrics or landscape spatial metrics and measures of ecosystem function. We hypothesized that greater shading by macrophytes in planted cells, which prevents sunlight from reaching submerged plants that process nutrients in the water column and drive aquatic metabolism might result in lower rates of aquatic metabolism in planted cells. To further investigate this hypothesis, we examined relationships between the percentage of cell area occupied by open water, a habitat feature associated with low macrophyte

shading, and biodiversity metrics, to see if higher diversity cells had lower percentages of open water within cells. Our hypothesis was not supported, as we found that percent open water did not correlate consistently with biodiversity metrics over time. We also examined relationships between percent open water and measures of ecosystem function. We found that percent open water was significantly negatively correlated with P removal rate ($p = 0.003$).

Nutrient addition effects on plant biodiversity, spatial pattern, and ecosystem function

Fertilization had no discernible effect on plant biodiversity or spatial pattern; we found no significant differences in biodiversity or spatial metrics, or change in biodiversity or spatial metrics, between fertilized and unfertilized cells. However, fertilization did have a significant effect on several variables that we used to characterize function. Fertilization caused significant decreases in aquatic community metabolism (GPP, NPP and R) in fertilized cells during the summer following the first nutrient addition (2010), relative to unfertilized cells ($p = 0.037$). However, these differences did not persist into later years. We observed significant differences in change in DIN ($p < 0.001$) and DIP ($p = 0.033$) based on fertilization. Fertilized cells experienced greater reductions in both DIN and DIP from 2009 to 2012. We found that the fertilized cells were significantly more turbid than unfertilized cells ($p = 0.002$), indicating a relatively higher abundance of phytoplankton in fertilized cells. We found no difference in change in aboveground biomass between fertilized and unfertilized cells. Likewise, there were no significant differences in SOM or in changes in SOM in response to fertilization. Nutrient removal rates for N and P (for each individual summer of fertilization, as opposed to changes in DIN and DIP between pre- and post-fertilization years) were not correlated with change in aquatic community GPP or change in aboveground biomass. Likewise, DIN and DIP were not causally related to change in GPP or change in aboveground biomass.

Relationships between plant biodiversity and spatial pattern

Before examining relationships between biodiversity and spatial metrics, we looked for and found significant correlations among spatial metrics. At both the quadrat and zone scales, SHDI was significantly positively correlated with SHAPE_AM ($p = 0.013$; $p = 0.063$), but the correlation was not significant at the whole cell scale. At the zone and whole cell scales, SHDI was significantly negatively correlated with CONTAG ($p < 0.001$; $p = 0.001$), but the correlation was not significant at the quadrat scale. However, we believe that these metrics characterize different enough aspects of spatial pattern that these correlations do not confound interpretation of other relationships.

When we examined relationships between plant biodiversity and spatial pattern, we found significant correlations between biodiversity and spatial metrics at several scales. FQAI was significantly positively correlated with all three spatial metrics at the quadrat scale, and with SHDI and SHAPE_AM, but not CONTAG, at the zone scale (Table 2). No correlations between FQAI and spatial metrics were significant at the whole cell scale. The nature of the observed correlations varied from year to year. At the quadrat scale, the correlations between FQAI and CONTAG in 2009 and 2011 were significantly different from the correlations between those metrics in other years. In 2009, this difference was attributable to the effects of both year ($p = 0.024$) and interactions between year and FQAI ($p = 0.047$). In other words, some unique

combination of characteristics of the year 2009 and our measure of FQAI in that year contributed to making the correlation between FQAI and CONTAG in 2009 significantly different from the correlations between those metrics in other years. In 2011, this difference was attributable only to effects of year ($p = 0.027$), and not interactions between year and FQAI. At both the quadrat and zone scale, the correlation between FQAI and SHDI in 2010 was significantly different from the correlations between those metrics in other years. At the quadrat scale, this difference was attributable only to interactions between year and FQAI ($p = 0.022$), but at the zone scale, this difference was attributable in part to the effects of year alone ($p = 0.027$), as well as interaction effects ($p = 0.002$).

Table 2. Adjusted r^2-values and directions of significant correlations for linear regressions of spatial metrics on FQAI.

Correlation	Scale	Adjusted r^2	Direction of correlation
FQAI v. SHDI	quadrat	0.30	positive ($p < 0.001$)
FQAI v. SHAPE_AM	quadrat	0.19	positive ($p = 0.002$)
FQAI v. CONTAG	quadrat	0.09	positive ($p = 0.008$)
FQAI v. SHDI	zone	0.56	positive ($p = 0.003$)
FQAI v. SHAPE_AM	zone	0.21	positive ($p = 0.004$)

Native SWD was significantly positively correlated with all three spatial metrics at the quadrat scale, and with SHDI and SHAPE_AM, but not CONTAG, at the zone and whole cell scales (Table 3). As with FQAI, the correlations between native SWD and CONTAG in 2009 and 2011 were significantly different from the correlations between those metrics in other years at the quadrat scale. In 2009, this difference was attributable to the effects of both year ($p = 0.001$) and interactions between year and native SWD ($p = 0.003$). In 2011, this difference was attributable only to effects of year ($p = 0.037$), and not interactions between year and native SWD. At both the zone and whole cell scales, the correlation between native SWD and CONTAG in 2012 was significantly different from the correlations between those metrics in other years. At the zone scale, this difference was attributable to both year effects ($p = 0.031$) and interactions between year and native SWD ($p = 0.003$), while at the whole cell scale, the differences was only attributable to interaction effects ($p = 0.046$). At the zone scale, the correlation between native SWD and SHAPE_AM in 2011 was significantly different from the correlations between those metrics in other years, due to both year effects ($p = 0.047$) and interaction effects ($p = 0.045$). At the quadrat scale, the correlation between native SWD and SHDI was also significantly different in 2011, due to year effects ($p = 0.001$). At the zone scale, this correlation was significantly different in 2010, due to interaction effects ($p = 0.038$).

Table 3. Adjusted r^2-values and directions of significant correlations for linear regressions of spatial metrics on native SWD.

Correlation	Scale	Adjusted r^2	Direction of correlation
Native SWD v. SHDI	quadrat	0.43	positive (p < 0.001)
Native SWD v. SHAPE_AM	quadrat	0.18	positive (p = 0.007)
Native SWD v. CONTAG	quadrat	0.07	positive (p = 0.031)
Native SWD v. SHDI	zone	0.55	positive (p = 0.006)
Native SWD v. SHAPE_AM	zone	0.12	positive (p = 0.049)
Native SWD v. SHDI	whole cell	0.76	positive (p = 0.036)
Native SWD v. SHAPE_AM	whole cell	0.33	positive (p = 0.040)

Despite the spatial component of B_W, we found no significant correlations between B_W and any spatial metrics at any scale.

Discussion

Planting effects on plant biodiversity

We found significant, sustained differences in plant biodiversity between unplanted and planted cells. Planting may have been especially effective in increasing biodiversity in these restored wetlands, as they are not immediately proximate to undisturbed natural wetlands, making natural recruitment of desirable wetland species more difficult (O'Connell et al. 2013). Within planted cells, however, we found that differences in intensity of planting and management did not yield significant differences in biodiversity; both low-intensity and high-intensity planting treatments resulted in similar levels of biodiversity. Whereas some studies, such as Matthews and Spyreas (2010) recommend that increased planting effort yields more desirable species diversity and composition, our findings suggest that planting/management in the early years of wetland restoration has a large impact on long-term plant biodiversity, but that replanting species that struggle with establishment may be a wasted effort; species that do not survive initial planting are unlikely to survive subsequent replanting. However, species with low survivorship were evidently not well suited to the wetlands; replanting efforts would likely have had greater impact on long-term plant biodiversity if better-suited species were chosen.

It is worthwhile to note that muskrat herbivory may be a confounding factor in interpreting patterns of biodiversity over time. We do not have quantitative data on the dietary preferences of the muskrats inhabiting our study site, but it is possible that observed patterns in biodiversity are due at least in part to their herbivory. Anecdotal evidence from a local trapper suggests that muskrats do not have any special preference for native wetland species or for planted versus unplanted cells. Therefore, we are inclined to assume that the effects of muskrat herbivory on plant biodiversity are random rather than systematic.

While we found that differences in biodiversity, especially FQAI, were often attributable to planting treatment, environmental characteristics like proximity to upland terrain and water depth strongly influenced biodiversity as well. These findings are consistent with studies that have found that environmental characteristics of restored wetlands, such as site hydrology and context of the surrounding landscape, influence succession and plant community development (Matthews and Endress 2010; Ahn and Dee 2011). Thus, these factors, as well as planting and management strategies, should be taken into consideration in wetland restoration projects.

Effects of planting, plant biodiversity, and spatial pattern on ecosystem function

We found that P removal rates were negatively correlated with the percent of open water present in cells, contradicting our hypothesis about macrophyte shading resulting in lower aquatic metabolism in planted cells. Our hypothesis rested on the assumption that submerged aquatic plants are responsible for most nutrient uptake in the wetlands. However, our findings suggest that emergent plants may in fact be removing more nutrients from the water column, as cells with faster P removal and less open water necessarily have fewer submerged aquatics and more emergent macrophytes.

We found that planting treatment had no effect on our other measures of ecosystem function. This, coupled with a lack of correlation between both plant biodiversity and spatial metrics and measures of ecosystem function, suggests that plant community structure (composition, spatial pattern, and diversity) is not tightly coupled with many aspects of ecosystem function in these restored wetlands. In a large meta-analysis, Allan et al. (2013) found that plant biodiversity significantly affects a little under half of over 400 measures of ecosystem function, suggesting that the lack of effect we observed is not entirely surprising. It is possible that more relationships could have emerged from our analyses if different metrics were used to assess biodiversity, spatial pattern, or ecosystem function.

Nutrient addition effects on plant biodiversity, spatial pattern, and ecosystem function

We found that fertilization did not significantly affect our measures of biodiversity. This countered our expectations that nutrient addition would induce eutrophication in the wetlands and subsequently lower biodiversity (e.g., Kneitel and Lessin 2010). It is possible that the expected differences in biodiversity require more time to appear, and that we could see significant differences in biodiversity between fertilized and unfertilized cells in several years. Alternatively, it is possible that the impact of nutrient addition on biodiversity would be greater earlier in wetland ecosystem development, before plant communities have become established (Hefferman and Fisher 2012).

Although we did not observe the expected effect of nutrient addition decreasing biodiversity (Venterink et al. 2002), or changing above-ground biomass, we found that fertilized cells had significantly lower rates of aquatic metabolism (R, GPP, and NPP) in the season immediately following nutrient addition and were significantly more turbid than unfertilized cells. This suggests that the nutrient additions led to early stages of eutrophication, in which increased in fertilized wetlands. If subjected to greater or more consistent nutrient influx, it is likely that DO

in the water column would have been drastically reduced, perhaps leading to the drop in plant biodiversity that we expected to observe. Interestingly, fertilized cells also experienced significantly greater decreases in DIN and DIP from 2009 to 2012, although it is likely that this is simply a function of the increased DIN and DIP levels in those cells resulting from fertilization.

Relationships between plant biodiversity and spatial pattern

We saw a pattern of biodiversity metrics correlating positively with SHDI. This correlation is not surprising, since SHDI is basically a variation of SWD intended to capture the diversity of cover types, which strongly reflects plant biodiversity since most cover types represent plant species. The fact that strong correlations exist between remotely sensed data with much fewer cover type categories and on-the-ground measures of biodiversity suggests the potential utility of high resolution remote sensing as a mechanism for assessing relative wetland plant biodiversity.

We also saw positive correlations between biodiversity metrics and SHAPE_AM. This correlation is likely due in part to the fact that the patches whose shape were characterized by SHAPE_AM represented plant species. SHAPE_AM is not entirely independent of number of cover types. It is possible that a landscape might be comprised of patches of only a few cover types with very complex shapes, but the correlations we observed between SHDI and SHAPE_AM suggest that greater number of cover types increases the probability that patches of those cover types will have complex shapes, compared to patches in landscapes with fewer cover types. Since most cover types represent plant species, it follows that plant biodiversity metrics would also correlate positively with SHAPE_AM. In this scenario, mean vegetation patch shape complexity might be best understood as a function of plant biodiversity.

However, it is also possible that vegetation patch shape complexity is a driver of plant biodiversity. Landscapes composed of complex patches contain more "ecotones" (that is, places where patches of different cover types meet) than landscapes with simple patches because patches with more complex shapes have higher edge-to-area ratios, and thus more places to come in contact with other patches. Although ecotones are usually defined at a much larger scale than the one we explore in this study (e.g., Jepsen et al. 2012), our findings suggest that the pattern seen at larger scales of ecotones harboring high biodiversity (Kark 2013; Kunmar et al. 2006; Moser et al. 2002) translates to the sub-hectare scale in restored wetlands. It is possible that wetlands with many ecotones between patches of different dominant plant cover types contain a wider diversity of microhabitat and offer more niches to be filled by specialist plant species, leading to higher plant biodiversity.

We also saw a pattern of biodiversity metrics correlating positively with CONTAG at the quadrat scale. This correlation suggests that more diverse wetlands have more clumped distribution of cover types. These findings are consistent with studies that have found links between biodiversity and landscape heterogeneity in other ecosystems (Benton et al. 2003; Priego-Santander et al. 2013). Studies have found both positive and negative heterogeneity-diversity relationships at small scales; positive relationships like the one we observed are usually explained by niche limitation theory (Tamme et al. 2010). However, this pattern did not hold at the zone or whole cell scale. In fact, although the relationships were not quite significant,

correlations between biodiversity metrics and CONTAG tended to be negative at those scales. Tamme et al. (2010) propose several ecological reasons this might be, including microfragmentation theory, which holds that increasing spatial heterogeneity causes species isolation, preventing reproduction and thus reducing diversity. It is possible that the quadrat scale is not ideal for assessing relationships between biodiversity and contagion; quadrats are small enough that they can only contain a few cover types, so aggregation may appear misleadingly high. Year and interactions between year and biodiversity sometimes had significant effects on relationships between biodiversity and spatial pattern, especially in correlations involving CONTAG. This suggests that the effect of contagion on biodiversity is fairly fluid, and may depend on external conditions that change over time.

Conclusions

We observed that plant spatial and species diversity did not directly translate to desirable ecosystem function (defined here as high rates of aquatic community metabolism, low water column nutrient levels, and high soil organic matter). However, high species diversity in itself is often a functional goal of wetland restoration (Cui et al. 2009; Kentula 2000; Zedler 2003).

We observed that intensive initial planting, but not successive replanting, was a more effective strategy for creating diverse restored wetlands than natural recruitment. Likewise, intensive removal of invasive species during early years of restoration greatly limited exotic invasion in the long-term. Our nutrient addition experiment revealed that nutrient influxes in later succession (6 or more years after restoration) did not significantly affect plant biodiversity or biomass production. These observations support the importance of initial conditions in restored wetlands, and suggest that wetland managers' efforts are best focused on establishing favorable conditions for desired ecosystem functioning in the early years of restoration.

This does not mean that restored wetlands are impervious to disturbance after initial establishment, however. We found that nutrient addition lowered rates of aquatic metabolism in the months immediately following fertilization, indicating that more intense or more sustained nutrient addition could eventually lead to eutrophication and subsequent reductions in plant biodiversity. Furthermore, muskrat invasion did considerable damage to the wetlands in the later years of our study period. Beyond possible reductions in plant biodiversity from herbivory, muskrats have significantly altered the hydrological structure of the wetlands by burrowing into banks. We predict that the wetlands will be all but drained in a few years.

We found that plant biodiversity was higher in wetlands comprised of intricately shaped (as opposed to simple) and clumped (as opposed to evenly-spaced) patches of vegetation. This suggests that within restored wetlands, spatially heterogeneous landscape mosaics with many "ecotones" between dominant species patches create beneficial microhabitats for harboring plant biodiversity. We hypothesize that aggregation increases biodiversity because more clumped vegetation distribution may lead to more habitat differentiation, thus attracting a wider variety of species. Patch shape complexity may increase biodiversity by creating small-scale "ecotones" where vegetation patches with very different structures (plant height, root mat density, etc.) meet. These ecotones, like ecotones at larger scales, may foster biodiversity by providing suitable habitat for a wider array of plant species than would be found in the core of one patch or another.

For example, wetlands, themselves a larger-scale ecotone, provide habitat for both aquatic and upland plant species.

Remote sensing has been used to assess certain aspects of wetland restoration success (Abtew and Melesse 2013). Links between plant biodiversity and spatial patterns found in this study suggest that aerial imagery may also provide wetland managers with a robust tool for assessing relative plant biodiversity. With the abundance of high-resolution satellite imagery available for many places, this could prove to be a more efficient method than labor- and time-intensive on-the-ground biodiversity surveys.

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Appendix

Table A1. Species and numbers of seeds and seedlings planted in low- and high-intensity planted cells during initial planting in 2003. Data for seedlings re-planted in these cells in 2004 were lost.

Seeds spread in 2003	seedlings planted in 2003
Carex frankii (215 g/cell) *Carex vulpinoidea* (215 g/cell) *Scirpus validus* (55 g/cell) *Juncus torreyi* (25 g/cell) *Juncus effusus* (26 g/cell) *Malva muscova* (8.5 g/cell) *Asclepius incarnata* (12.5 g/cell) *Decagon vertisalata* (2.7 g/cell) *Rosa palustris* (1.25 g/cell) *Lobillia cardinalis* (0.9 g/cell) *Cephalanthus accidentales* (0.42 g/cell)	*Nymphaea odorata* (10 seedlings/cell) *Saururus cernuus* (8 seedlings/cell) *Peltandra virginica* (17 seedlings/cell) *Sparganium americanum* (15 seedlings/cell) *Sagittaria latifolia* (17 seedlings/cell) *Pontedaria cordata* (6 seedlings/cell)

Table A2. Species and numbers of seedlings re-planted in high-intensity planted cells in 2005 and 2006.

Cell	seedlings planted in 2005	seedlings planted in 2006
2	*Acorus calamus* (16 seedlings/cell) *Iris versicolor* (15 seedlings/cell) *Peltandra virginica* (7 seedlings/cell) *Pontedaria cordata* (2 seedlings/cell) *Saururus cernuus* (8 seedlings/cell) *Sparganium americanum* (1 seedling/cell) *Sagittaria latifolia* (4 seedlings/cell)	*Acorus calamus* (16 seedlings/cell) *Carex stricta* (4 seedlings/cell) *Iris versicolor* (12 seedlings/cell) *Peltandra virginica* (2 seedlings/cell) *Pontedaria cordata* (4 seedlings/cell) *Sagittaria latifolia* (2 seedlings/cell) *Saururus cernuus* (5 seedlings/cell) *Sparganium americanum* (1 seedling/cell) *Spartina patens* (13 seedlings/cell)
5	*Acorus calamus* (14 seedlings/cell) *Iris versicolor* (10 seedlings/cell) *Nymphaea odorata* (4 seedlings/cell) *Peltandra virginica* (16 seedlings/cell) *Pontedaria cordata* (1 seedlings/cell) *Saururus cernuus* (8 seedlings/cell) *Sparganium americanum* (4 seedlings/cell) *Sagittaria latifolia* (3 seedlings/cell)	*Acorus calamus* (16 seedlings/cell) *Carex stricta* (4 seedlings/cell) *Iris versicolor* (9 seedlings/cell) *Peltandra virginica* (2 seedlings/cell) *Pontedaria cordata* (4 seedlings/cell) *Saururus cernuus* (8 seedlings/cell) *Sparganium americanum* (1 seedling/cell) *Spartina patens* (7 seedlings/cell)

Table A3. Wetland-to-watershed area ratios. Ratios are calculated by dividing the area of the wetlands by the area of the watershed that the wetlands are treating.

Wetland-to-watershed area ratio	Reference
0.03	Kovacic et al. 2006
0.12	Lu et al. 2009
0.03	Braskerud 2002
0.30	Braskerud 2002
0.03	McCartney 2010
0.04	Kovacic et al. 2006
0.04*	Kadlec and Knight 1996
0.04	Weighted average** (value used at the George Jones wetlands)

*Mean value from 85 treatment wetland studies compiled by the given reference
**The weighted average was used to account for the number of wetlands in the compiled reference

Table A4. Phosphorus loads in agricultural landscapes. Not all load values were measured in the same way; therefore, a large range of values was produced when they were converted into kg/ha/yr. The studies referenced below were selected for use in the final analysis because they are primarily studies from the midwest. Studies that obviously produced outlier data in the compilation were not included.

Total phosphorus load applied to fields (kg/ha/yr)	Reference	Total phosphorus loads in agricultural runoff (kg/ha/yr)	Reference
16.18	Domagalski et al. 2008	0.31	Domagalski et al. 2008
11.07	Domagalski et al. 2008	0.17	Domagalski et al. 2008
		0.08	Alberts et al. 2006
67.37	D'Ambrosia et al. 2006	1.30	Alberts et al. 2006
56.14	D'Ambrosia et al. 2006	0.69	Domagalski et al. 2008
56.14	D'Ambrosia et al. 2006	7.80	Domagalski et al. 2008
84.0	Council on Environmental Quality 2008	1.11	Crumpton et al. 1993
48.48	Average	4.00	Kadlec and Knight 1996
1.93	Average: The loading value for the proposed research		

Table A5. Nitrogen loads in agricultural landscapes. Not all load values were measured in the same way; therefore, a large range of values was produced when they were converted into kg/ha/yr. The studies referenced below were selected for use in the final analysis because they are primarily studies from the midwest. Studies that obviously produced outlier data in the compilation were not included.

Total nitrogen load applied to fields (kg/ha/yr)	Reference	Nitrogen form and oad in agricultural runoff (kg/ha/yr)	Reference
72.0	Moshiri 1993	15.8 (NO_3-N and NO_2-N)	Alberts et al. 2006
150.0	Moshiri 1993	15.5 (NO_3-N and NO_2-N)	Domagalski et al. 2008
84.0	Borin and Tocchetto 2007	4.9 (NO_3-N and NO_2-N)	Domagalski et al. 2008
32.0	Borin and Tocchetto 2007	12.9 (NO_3-N and NO_2-N)	Fausey et al. 1995
49.0	Domagalski et al. 2008	12.3 (NO_3-N and NO_2-N)	Average for NO_3 and NO_2
63.0	Domagalski et al. 2008	18.3 (total N)	Domagalski et al. 2008
168.4	D'Ambrosia et al. 2006	9.6 (total N)	Domagalski et al. 2008
16.8	D'Ambrosia et al. 2006	15.0 (total N)	Kadlec and Knight 1996
84.2	D'Ambrosia et al. 2006	10.0 (total N)	Borin and Tocchetto 2007
79.9	Average	13.2 (total N)	Average for total N: loading value for proposed research