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Tradeoffs among ecosystem services in restored wetlands

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ABSTRACT

Land management decisions frequently involve choices that reflect tradeoffs among ecosystem services. These tradeoffs are not always apparent, and land managers unknowingly may make decisions that diminish the value of some services while enhancing the value of others. Offset policies, such as wetland mitigation in the United States, rely on the assumption that ecosystems can be restored to provide a full suite of services. Wetlands provide many ecosystem services such as water quality maintenance, carbon storage, flood abatement, and biodiversity support. Our objectives were to describe tradeoffs among ecosystem services in mitigation wetlands and identify abiotic and biotic drivers underlying these tradeoffs. We measured denitrification potential, organic matter decomposition, herbaceous biomass, and soil organic content as indicators of nutrient storage and removal services in 30 mitigation wetlands in Illinois, USA. Additionally, we estimated surface-water storage potential, and, since wetlands provide valuable biodiversity support, we determined the species composition of plant, anuran, and avian communities. We found a positive relationship among biodiversity indicators for different taxa. Denitrification potential and surface-water storage potential were positively correlated. However, there was a tradeoff between biodiversity support and nutrient cycling processes; soil organic matter, biomass, decomposition rates, and potential denitrification were greater at less biodiverse sites. Our findings indicate that optimizing restored wetlands for nutrient storage and removal may come at the expense of biodiversity. It is unrealistic to expect all services to be maximized at a restoration site. Therefore, restoration practitioners should prioritize services based on needs and opportunities given local and watershed contexts.

1. Introduction

Since landmark work in the 1990s (e.g., Costanza et al., 1997; Daily, 1997) brought the concept of ecosystem services to the forefront of ecology, policy, and management, researchers have sought to expand our understanding of the benefits provided by nature (Woodward and Wui, 2001; MEA, 2005; Costanza et al., 2008). The ecosystem services concept offers a framework to consider the impacts of environmental degradation on ecosystems and human wellbeing. Recent emphasis on the importance of ecosystem services also has provided the field of restoration ecology with a new focus and direction (Jackson and Hobbs, 2009; Bullock et al., 2011), as ecosystem restoration is increasingly being used to offset environmental degradation and replace lost ecosystem services (Maron et al., 2012).

Land management decisions, including decisions about restoration, frequently involve choices that reflect tradeoffs or synergies among ecosystem services. Synergies can occur if two or more services simultaneously increase or decrease in response to the same driver (Bennett et al., 2009). Alternatively, tradeoffs occur when one service changes at the expense of another (Bennett et al., 2009). For example, managers of freshwater ecosystems face decisions that result in conflicts among provisioning, regulating, supporting, and cultural services (MEA, 2005; Rodríguez et al., 2006). Water extraction from rivers and lakes for drinking, irrigation, or industry can conflict with services that depend upon streamflow or depth, such as fisheries maintenance (Rodríguez et al., 2006). Although correlations among services have been examined in several systems, previous work has been based primarily on simulation models and conceptual reviews (e.g., Carpenter et al., 2009; Briner et al., 2013; Maskell et al., 2013; McInnes, 2013). These conceptual models need empirical support if they are to provide a useful framework for natural resource management.

Wetlands are notable for providing a complex suite of ecosystem services, including flood abatement and water quality maintenance through nutrient and sediment storage, while also supporting valuable animal and plant habitat (Zedler, 2003). However, it is likely that some of these services occur at the expense of others since bundles of services vary with landscape context and restoration site design (Bennett et al., 2009; Raudsepp-Hearne et al., 2010). Uncovering these tradeoffs, or synergies, and their underlying causes is a crucial first

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step in developing effective restoration strategies using the ecosystem services concept. A prerequisite to preventing unintended ecological consequences through uninformed restoration is to quantify potential tradeoffs among ecosystem responses (DeFries et al., 2004).

Given their value in providing ecosystem services to society, concern over the rapid loss of wetlands in the United States led to the creation of federal and state laws meant to counteract their pervasive destruction (Hough and Robertson, 2008; USACOE and USEPA, 2008). Under Section 404 of the U.S. Clean Water Act, the federal government requires that "unavoidable" impacts on wetlands be compensated for by the creation or restoration of other wetlands. This process is known as compensatory wetland mitigation. Concurrent with the establishment of mitigation requirements, the federal government also adopted a national goal of "no-net-loss" of both wetland area and ecosystem functions (NWPF, 1987). Similar compensatory mitigation strategies have been adopted in several countries to offset losses of critical ecosystems (Madsen et al., 2010).

Implicit in the no-net-loss goal is recognition of the inherent value of ecosystem services to society. However, compensatory mitigation and biodiversity offsetting policies rely on the assumption that destroyed ecosystems can be restored to replace the *entire suite of ecosystem services* that have been lost. Research over the past decade indicates that, in many cases, wetland restoration, including compensatory mitigation, leads to the creation of wetlands that are not ecologically equivalent to naturally occurring wetlands, thereby calling to question the level to which ecosystem services can be replaced (Zedler and Callaway, 1999; Matthews and Spyreas, 2010; Moreno-Mateos et al., 2012; Stefanik and Mitsch, 2012).

Here, we explore tradeoffs among ecosystem services in restored wetlands. Our objectives were to identify the primary tradeoffs that exist among ecosystem services that are being restored and identify the abiotic and biotic factors underlying these tradeoffs. In this paper we consider ecosystem services to be the benefits that people attain from the environment, which are derived from ecosystem structure and processes (MEA, 2005; Wallace, 2007). Therefore, we measured ecosystem processes and indicators of ecosystem structure that support important ecosystem services provided by wetlands (Table 1). In addition to supporting and regulating services described by the Millennium Ecosystem Assessment (2005), we considered biodiversity itself to be an ecosystem service (e.g., Mace et al., 2012). We quantified the biodiversity support value of each wetland, evaluated flood abatement potential, and examined nutrient cycling-related services. In addition, we identified and quantified a second set of variables that we expected to be predictive of the ecosystem services of interest (Table 1). These potential drivers of ecosystem services included variables describing the successional development of the wetland (site age, soil bulk density, woody stem density, and light availability) or representing external stressors or landscape context (site area, surrounding intensive land use, available soil nitrogen, and percent coverage of non-native plant species).

Table 1
Indicators of wetland ecosystem services considered in this study and expected relationships (positive or negative) with potential predictor variables.

Ecosystem service indicator	Associated ecosystem services	Potential predictors
Soil organic matter content	Soil formation, climate regulation	Site age (+), soil bulk density (−)
Herbaceous biomass	Primary production	Available N (+), available light (+), woody stem density (−)
Soil organic matter decomposition	Soil formation, nutrient cycling	Soil bulk density (−)
Denitrification potential	Water purification, nutrient cycling	Available N (+), soil bulk density (−)
Surface water storage potential	Water regulation	Land use intensity (+), site area (+)
Avian conservation score	Biodiversity support	Land use intensity (−), site age (+), site area (+)
Anuran call rank	Biodiversity support	Available N (−), land use intensity (−), Site age (+), Site area (+)
Mean coefficient of conservatism	Biodiversity support	Available N (−), non-native plant cover (−), land use intensity (−), site age (+), site area (+)

2. Materials and methods

2.1. Study sites

Wetlands selected for study had been restored by the Illinois Department of Transportation as mitigation for wetlands impacted by road construction. Thirty mitigation wetlands, ranging from 0.21 ha to 7.98 ha and located across Illinois, USA were included in this study (Fig. 1). Sites were constructed between 1991 and 2002 by excavating, removing drainage structures, and/or creating berms to hold water on site. Some sites were left unplanted, whereas others were planted with trees, shrubs, and/or seeded with wetland species. Thirteen of the sites were herbaceous, ten were forested, and seven included both herbaceous and forested areas. The wetlands occurred in a variety of landscape settings, from urban areas to agricultural and forested areas.

2.2. Sampling design

At each site, we placed a baseline on the longest edge of the wetland and divided it into four equal segments. At a random point along the baseline within each segment, we established a transect perpendicular to the baseline and extending across the entire width of the wetland, creating four sampling transects per wetland. Along each transect, we placed ten 0.25-m^2 sampling plots at equal distances, for a total of 40 plots per wetland. At two of the ten plots, randomly selected along each half of the transect, we collected soil samples for nutrient and denitrification analyses, collected herbaceous biomass samples, and measured light penetration. At one of these two plots along each transect, we collected soil bulk density samples and assayed organic matter decomposition. Additionally, we surveyed anuran, avian, and plant community composition across the entire site. We conducted all sampling

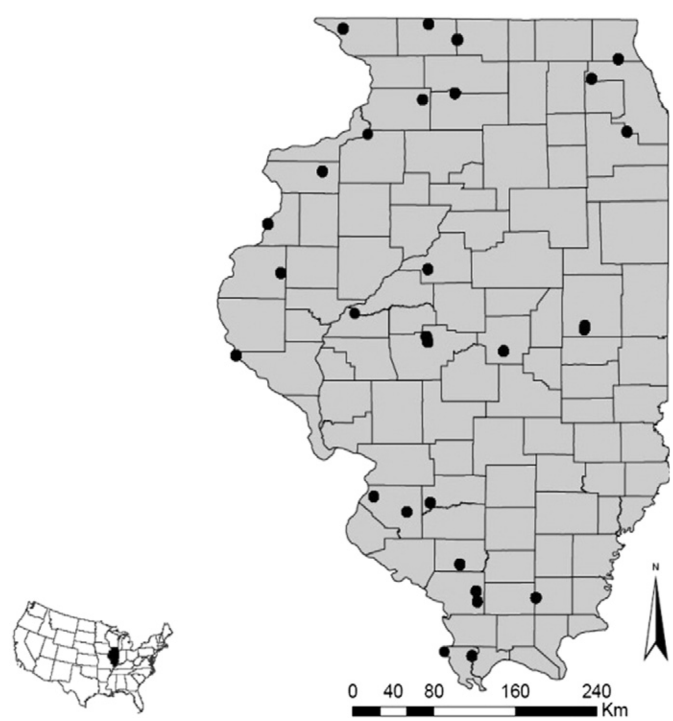

Fig. 1. Locations of 30 restored wetlands within Illinois, USA.

between May and September of 2012, with the exception of the anuran call surveys, which were done between March and August of 2013. Specific methodological details are provided below.

2.3. Vegetation sampling

At each of the 40 plots, we sampled herbaceous-layer vegetation (excluding <1 m tall woody species) by recording every species and assigning each a cover class based on a visual estimate (<1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, 96–100%). Woody stems would not have been adequately captured in small quadrats; therefore we recorded the number of woody stems taller than 1 m in a 4 × 30-m plot randomly placed along each of the four transects, and averaged stem density across transects to estimate stem density for each wetland. Plots were moved slightly if large woody stems interfered. In addition, we performed a timed search (at least 30 min per site) of the entire wetland to record the presence of additional species not detected in herbaceous or woody plots. Vegetation sampling was conducted once at each site during a five-week period in June and July of 2012, when most wetland plant species are detectable and identifiable to species.

We used Mean Coefficient of Conservatism (mean *C*) as an indicator of the floristic conservation value of each wetland. Each native plant species in Illinois has been assigned a "Coefficient of Conservatism" (*C*), a score assigned to each species based on its affinity for undegraded natural environments (Taft et al., 1997). Scores range from 0 to 10, with higher values assigned to plant species less tolerant of anthropogenic disturbance. Non-native plants are assigned $C = 0$. For each wetland, the mean Coefficient of Conservatism (mean *C*) was calculated from the whole-wetland species list.

2.4. Decomposition

Rates of soil organic matter decomposition were measured using the cotton strip assay (CSA) method, which uses the decomposition of a standard cotton fabric as a proxy for organic matter decomposition (Mendelssohn et al., 1999). Decay rates are based on the loss of tensile strength over time compared to a reference strip. We used Fredrix brand 12-ounce artistry cotton canvas, as recommended by Slocum et al. (2009). At each designated plot, we inserted three replicate strips, each 10 × 30-cm, into the soil at least 8 cm deep, for a total of twelve strips per wetland. Strips were installed during a five-week period in June and July of 2012, and each strip was left in the soil for 25–30 days, which we determined based on a pilot study to be the length of time necessary to achieve at least 50% strength loss. Additionally, to account for physical stress resulting from installation, we inserted and then immediately removed 15 reference strips at six sites. All strips were air-dried after removal and stored in a refrigerator. We cut each strip laterally into 4-cm depth increments, and then cut and manually frayed each lateral strip down to its 2.5 × 10-cm center section (Slocum et al., 2009). Lateral strips were broken using a Tinius Olsen Series 5000 UTM tensometer. The breaking force, measured in kilograms-force, for each strip was expressed as a percent of strength-loss relative to the mean of the reference strips (Slocum et al., 2009).

2.5. Soil Analyses

We collected, using an Uhland sampler, 7-cm deep, 331.5-cm^3 soil samples for determination of bulk density from the same four plots prior to installing cotton strips. Samples were dried and weighed to calculate soil bulk density in dry weight per volume (Mielke et al., 1986). To examine differences in nitrogen and soil organic matter, we collected and composited eight soil cores (1.9 × 12-cm) from each of two plots along each transect, during a five-week period in June and July of 2012. Soil samples were air-dried and passed through a 2-mm sieve. We determined available ammonium (NH_4^+) and nitrate (NO_3^-) for each composite sample using the Berthelot reaction method for colorimetric analyses, and measured soil organic matter content by combustion (Rhine et al., 1998). Since the transformation of nitrate (NO_3^-) into inert nitrogen gas (N_2) through denitrification is a key ecosystem process for maintaining water quality, especially in watersheds where land cover is heavily urbanized or agricultural (David et al., 2010; Hossler et al., 2011), we estimated the denitrification potential (DNP) of each site using a denitrification enzyme activity assay (Peralta et al., 2010).

2.6. Herbaceous biomass and light availability

To quantify differences in plant community structure and canopy light penetration, we measured photosynthetically active radiation (PAR) at two plots along each transect using a LI-COR LI-250A light meter. Measurements were taken at the soil surface and 1 m above ground level. We relativized light penetration data for each site to light measurements collected in the open, under no canopy vegetation. To estimate aboveground herbaceous plant biomass at each site, we collected samples from the same plots as the light measurements and soil samples. Aboveground plant material was trimmed to ground level within a 30 × 30-cm subplot. Each sample was oven-dried at 60 °C for at least 48 h and weighed.

2.7. Avian sampling

We conducted five-minute unlimited distance avian point counts at each wetland between May and August 2012. We included as many point counts per site as possible to characterize the entire wetland, with a minimum distance of 250 m between points. We used Partners in Flight (PIF) scores to rank bird species based on their conservation value (Panjabi et al., 2005). PIF scores are assigned to each species in a region based on six global and/or regional elements: population size, breeding and non-breeding distribution, threats to breeding and non-breeding populations, and population trends (Panjabi et al., 2005). Each site was sampled once, and although this may have led to underrepresenting avian richness, it was necessary due to time constraints and the distance between sample sites. A total Avian Conservation Score (ACS) can be calculated based on PIF scores from the total avian community in an area, providing a standard method to assess that area's relative value for avian conservation and bird habitat (Twedt, 2005). We calculated each site's ACS from the sum of the measures of conservation significance of all species as follows:

$$ACS = \sum_{i=1}^{n} \left(\frac{CR \times TDR_i}{1000} \right)$$

for species $i = 1$ to n, where $\mathrm{CR} = \log \text{gamma} (\text{PIF score})^2$ and $\mathrm{TDR} = 10 \times \log_2(\text{observed density})$.

2.8. Anuran call surveys

We conducted anuran call surveys at each wetland from mid-March until the first week of August 2013, to correspond with the breeding times of anuran species present in Illinois. At each wetland, 15-minute surveys were conducted at least 30 min after dusk, with air temperatures greater than 5.6 °C, a wind speed less than 5.8 m s^{-1}, and a water temperature greater than 10 °C (Pillsbury and Miller, 2008). Following the protocols of the North American Amphibian Monitoring Program of the U.S. Geological Survey, we recorded a call index for each species as: 0, no individuals of a given species heard; 1, one individual heard; 2, multiple individuals with no overlap in calls; or 3, a full chorus (Pillsbury and Miller, 2008). Each site was sampled twice during the breeding season, and although this may have led to underrepresenting anuran richness, it was necessary due to time constraints and the distance between sample sites. We calculated the total calling rank, or sum of call values at each site for all species, to compare anuran species abundance and diversity among sites (Pope et al., 2000; Pillsbury and Miller, 2008).

2.9. Surface-water storage potential

To evaluate flood abatement, we calculated surface-water storage potential by estimating the volume of depressional areas within each wetland using Illinois LiDAR data from the Illinois State Geological Survey (ISGS) Height Modernization Program. LiDAR-derived digital terrain models (DTMs) were used in the analysis. Where LiDAR coverage was not available (five of the sites), we conducted on-site elevation measurements using either survey-grade GPS (Leica GPS 1200 system; 10 mm positional and 20 mm height accuracy) or a total station (Leica TC702; 2″ angular measurement accuracy). We used the Surface Volume tool in ArcMap 10.1 3D Analyst to calculate basin volume below a reference plane defined by the lowest outlet point for each basin using either the LiDAR DTM or an elevation model produced from on-site measurements. We analyzed volume on a per site area basis (Lane and D'Amico, 2010).

2.10. Land cover

To examine the effects of landscape context on ecosystem function response variables, we used the USDA National Agricultural Statistics Service 2012 Cropland Data Layer to calculate the proportion of wetlands, forest, open water, developed land, and agricultural land within buffers around each study site. We calculated land cover at multiple buffer radii (500, 1000, 1500, 2000 m) and found cover to be closely correlated across scales ($r > 0.93$). Therefore, we used 1000-m buffers in the analysis. For each site, we generated outside-only buffers using ArcMap 10.1 (ESRI, Redlands California, USA). We used the program Geospatial Modeling Environment (Spatial Ecology LLC) to calculate the proportion of each land cover class within the buffer. To reduce the number of land cover variables to a smaller number of uncorrelated variables and describe the primary gradients in land use, we used principal component analysis (PCA) on a correlation matrix followed by varimax rotation (using XLSTAT Pro).

2.11. Numerical analyses

We used PCA to determine whether a latent tradeoff structure existed among wetland ecosystem services. Principal component analysis is ideal for this purpose because it can efficiently express the correlation structure among a large number of variables (Abdi and Williams, 2010). Each variable (mean C, avian conservation score, total anuran call rank, surface-water storage potential, and site means for denitrification potential, soil organic matter content, herbaceous biomass, and decomposition rate) was standardized by mean and standard deviation prior to analysis. We used a scree plot of the eigenvalues vs. principal components to decide which components to report.

Redundancy analysis (RDA) is a multivariate multiple regression technique used in conjunction with PCA. To determine which ecosystem services were associated with which drivers we used RDA to quantify the amount of variation in ecosystem service indicators that could be explained by the set of environmental predictor variables (Table 1) that included woody stem density, PAR at 1 m above ground, PAR at ground level, available soil nitrogen (NO_3^- plus NH_4^+), soil bulk density, percent cover by non-native plants, site age, total site area, and two composite land cover variables. We used Partial Monte Carlo permutation tests ($n = 499$) and forward selection (in CANOCO 4.5) to remove non-significant ($p > 0.1$) predictors (Lepš and Šmilauer, 2003).

3. Results

3.1. Tradeoffs among ecosystem services

Data for each wetland site are presented in Appendix A. Two principal components were retained from the PCA of ecosystem service indicators (Table 2, Appendix B). Vectors for biodiversity indicators pointed opposite of those related to nutrient-cycling related services in the PCA biplot (Fig. 2), suggesting that wetlands with greater habitat value provide lesser nutrient-cycling ecosystem services. Specifically, soil organic matter content, herbaceous biomass, denitrification potential, and organic matter decomposition loaded negatively on PCA axis 1, whereas mean C, Avian Conservation Score, and anuran call rank loaded positively on the same axis (Fig. 2, Table 2). Additionally, the surface-water storage vector was directly opposite the organic matter decomposition vector on the second PCA axis, indicating that sites with deeper basins tended to have slower rates of decomposition (Fig. 2, Table 2).

3.2. Predictors of ecosystem services

The PCA of land cover variables resulted in two components explaining 69% of variation among sites (Appendix C). The first axis described a gradient from riparian settings, characterized by greater forest cover, wetland and open water, to non-riparian settings, mainly associated with developed land. The second axis described a gradient from developed urban land to rural agricultural settings.

Five predictor variables were retained in the RDA. These five predictors explained 43% of the variation in ecosystem service indicators (Fig. 3). Total available nitrogen explained the most variation, followed by soil bulk density, PAR at ground level, percent non-native plant cover, and land cover PCA axis 1 (riparian gradient). Available soil nitrogen was positively correlated with nutrient cycling related indicators, specifically herbaceous biomass, SOM, DNP, and decomposition rate (Fig. 3). The riparian PCA axis was positively associated with biodiversity indicators (Fig. 3). Additionally, soil bulk density was negatively associated with nutrient cycling related indicators, specifically DNP, SOM, and organic matter decomposition. More than half of the variance in ecosystem service indicators was not explained by the set of predictor variables, suggesting that additional, unmeasured factors may have been important.

4. Discussion

4.1. Tradeoffs and synergies among ecosystem services in wetlands

This study demonstrates the value of examining multiple ecosystem services simultaneously in a restoration context. There is a paucity of empirical data in papers that consider the ecosystem services perspective through a tradeoff and synergy analysis. Instead, most rely on qualitative expert opinion (McInnes, 2013) or simulation models (Rodríguez et al., 2006; Briner et al., 2013), or are conceptual reviews (DeFries et al., 2004; Foley et al., 2005; Tallis et al., 2008; Bennett et al., 2009; Carpenter et al., 2009). Examining tradeoffs and synergies among

Table 2
Loadings of ecosystem service indicators on principal component (PC) analysis axes.

Variable	PC axis 1	PC axis 2
Soil organic matter	−0.716	0.223
Herbaceous biomass	−0.625	0.330
Denitrification potential	−0.428	0.443
Decomposition	−0.652	−0.483
Mean coefficient of conservatism	0.372	−0.052
Avian conservation score	0.532	−0.439
Anuran call rank	0.860	0.118
Surface-water storage potential	0.551	0.711
Variance explained (%)	37.21	16.29

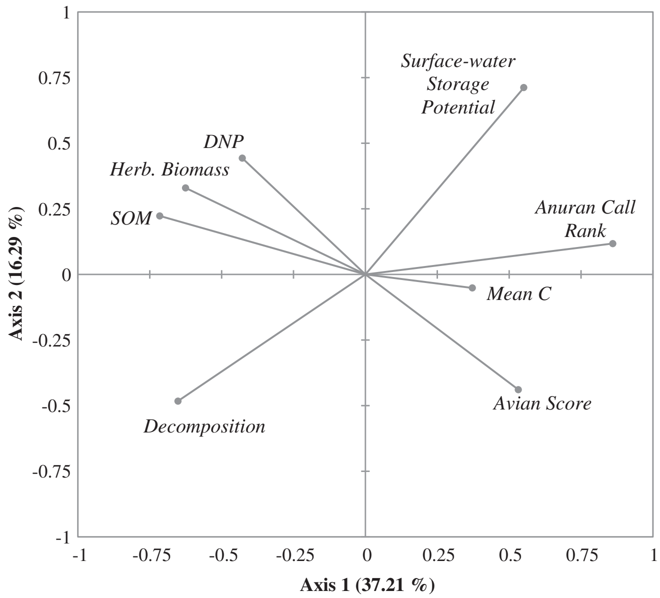

Fig. 2. Principal component analysis biplot for ecosystem service indicators in 30 restored wetlands.

ecosystem services is a useful perspective for considering restoration outcomes, but these conceptual models need further support from empirical data. Our study confirms previous studies which have demonstrated tradeoffs among ecosystem services provided by constructed wetlands (Hansson et al., 2005; Doherty et al., 2014). Other empirical studies conducted at scales ranging from watersheds to continents have shown that ecosystem services are geographically clustered as a result of human land use, with regulating services clustered in high conservation value lands and provisioning services clustered in productive lands (Raudsepp-Hearne et al., 2010; Maes et al., 2012; Qiu and Turner, 2013). Our results suggest that land use effects may determine which bundles of ecosystem services can be provided by restored ecosystems as well. Consequently, wetland restoration decisions likely involve choices that reflect tradeoffs among ecosystem services which are determined by external environmental and socioeconomic drivers.

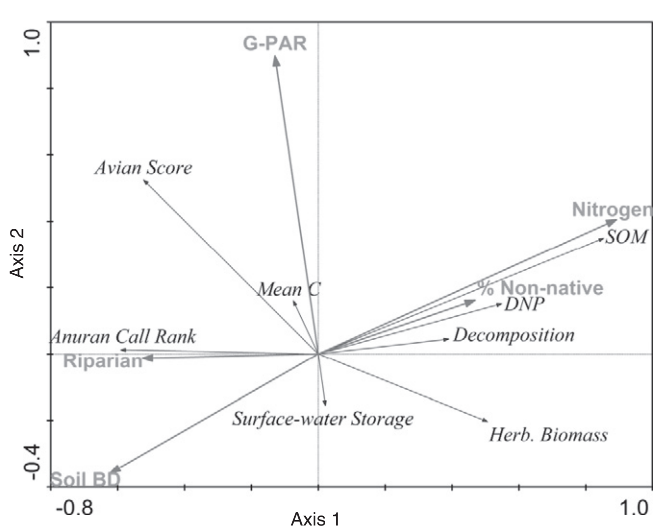

Fig. 3. Redundancy analysis biplot for ecosystem service indicators (italicized) and predictor variables (bold) in restored wetlands. *Riparian* refers to the composite land cover variable (Appendix C), *G-PAR* refers to available ground-level photosynthetically active radiation, *%Non-native* is the percent cover of non-native plants, *Soil BD* refers to soil bulk density, and *Nitrogen* is total available soil N.

We observed a positive relationship among the plant, avian, and anuran indicators of biodiversity support services. Similarly, other authors examining relationships among ecosystem services have found potential synergies among biodiversity components (Maes et al., 2012; Maskell et al., 2013). Identifying tradeoffs and enhancing potential synergies among ecosystem services could yield considerable benefits for restoration (Bennett et al., 2009). However, in a recent review, Macfadyen et al. (2012) found that management meant to increase biodiversity can sometimes maintain or enhance ecosystem services, but solely focusing on improving other services may not increase biodiversity. Similarly, when examining whether services spatially overlap with biodiversity, Naidoo et al. (2008) found that regions selected to maximize biodiversity provide no more ecosystem services than randomly selected areas.

Landscape setting can strongly affect wetland restoration outcomes and the associated ecosystem services, especially biodiversity support. We found a positive relationship between riparian settings, and plant, avian, and anuran conservation value. In our study area, riparian settings were associated with wetland and forest land cover. Likewise, previous authors have found that landscape context is important in determining biodiversity in wetlands. For example, wetlands situated in wetland-rich or forested landscapes have been found to support greater avian species richness (Naugle et al., 1999; Fairbairn and Dinsmore, 2001), and a similar dependency on landscape context has been observed for anuran communities (Knutson et al., 1999; Houlahan and Findlay, 2003; Pillsbury and Miller, 2008). Consequently, habitat fragmentation and loss may be driving the pattern we observed. Additionally, we found anuran diversity to be negatively correlated with total soil nitrogen, which is not surprising considering that pesticides and nitrate fertilizers are known to have toxic effects on amphibians (Hecnar, 1995; Camargo et al., 2005). Specifically, the effects of nitrate on four of the common species we observed (*Pseudacris triseriata*, *Rana clamitans*, *Rana pipiens*, *Bufo americanus*) have been studied experimentally, and significant toxic effects were found at nitrate loading levels common in agricultural settings (Hecnar, 1995). Intensive land use surrounding wetlands can also impact plant community composition and diversity (Matthews et al., 2009a). For example, landscape fragmentation can eliminate plant propagule sources, reducing recruitment within wetlands (Galatowitsch et al., 2000). Although our study suggests that biodiversity support services are associated with intact landscape settings, even in more intensively used landscapes other important ecosystem services may be provided, albeit with lesser biodiversity.

Contrary to previous studies which have reported a positive relationship between plant diversity and ecosystem function (e.g., Tilman et al., 2001; Hooper et al., 2005), we found biodiversity support to be negatively correlated with indicators of function. Similarly, other recent work conducted in wetlands has contradicted the hypothesized positive relationship between biodiversity and ecosystem functions, and suggests that certain ecosystem functions, such as nutrient retention and productivity may be maximized at lower biodiversity (Hansson et al., 2005; Weisner and Thiere, 2010; Doherty and Zedler, 2014). This relationship in wetlands may be driven by the dominance and greater relative productivity of robust, invasive plant species such as *Phalaris arundinacea* and *Phragmites australis* (Martina et al., 2014). Regardless of the specific mechanism, the tradeoff we observed indicates that biodiversity support does not necessarily signify that other ecosystem services are provided at high levels.

As a consequence of this tradeoff, maximizing nutrient attenuation functions that are associated with ecosystem services like water quality maintenance may conflict with biodiversity support. We found non-native plant cover, herbaceous biomass, soil organic matter, and soil nitrogen to be positively correlated with one another, but also negatively associated with each diversity component. High soil N availability in our study wetlands likely created conditions favorable to invasive plant species (Zedler and Kercher, 2004; Hogan and Walbridge, 2009; Matthews et al., 2009b). Some of these dominant species, such as *P. arundinacea*, *P. australis*, and *Typha angustifolia*, are very productive and may have contributed to the greater herbaceous biomass and soil organic matter that we found to be associated with non-native plant cover. As a further consequence, increasing dominance by species such as *P. arundinacea* might decrease diversity of plants and other taxa (Spyreas et al., 2009). Land managers and policy makers need to consider the potential tradeoff between biodiversity conservation value and nutrient removal functions when making decisions regarding wetland restoration, conservation, and ecosystem services establishment.

Our results illustrate that ecosystem services associated with nutrient cycling may be hindered by a lack of soil structural development. Denitrification potential, soil organic matter content, and decomposition rates were negatively correlated with soil bulk density (BD). Similarly, previous authors have found soil BD to be negatively correlated with denitrification and other nutrient cycling processes (Meyer et al., 2008; Hossler et al., 2011; Wolf et al., 2011). Since soil BD directly relates to soil organic matter content, root penetration, porosity, redox status, and soil biotic activity, it has been recommended as an indicator of physical and biological soil recovery following wetland restoration (Meyer et al., 2008; Hossler et al., 2011). Soil BD tends to decrease over time following wetland restoration. For example, soil BD decreased gradually over a 55-year chronosequence of freshwater wetlands as soil organic matter increased (Ballantine and Schneider, 2009). Further research is needed to determine the influences of soil properties on the tradeoff relationships observed in this study. In particular, the effects of wetland soil structural development on nutrient cycling, carbon storage, and invasive species dominance should be more thoroughly examined in the context of ecosystem service provisioning.

4.2. Flood abatement, decomposition, and denitrification

If synergistic relationships can be found among ecosystem services, management practices can be changed to exploit this information to enhance restoration and subsequent service provisioning. This study suggests potential synergistic relationships among wetland basin morphology, nitrogen transformation, and decomposition. The relationship between hydrology and decomposition rates in freshwater wetlands is complex. Generally, decomposition in the wettest, most anoxic, areas tends to be extremely slow, whereas decomposition in the driest areas tends to be much faster (Mitsch and Gosselink, 2007). Our results were consistent with this expected relationship; decomposition was slower in wetlands with basin morphology conducive to storing more surface water, and thus these wetlands may act as important carbon sinks.

Although a strong relationship between surface water storage potential and denitrification was not apparent in this study, denitrification occurs in anoxic conditions, where nitrogen is used as an electron acceptor to facilitate anaerobic respiration. Consequently, more permanently inundated, lower elevation areas within restored wetlands have significantly greater denitrification potential than higher elevation areas (Peralta et al., 2010). We found a positive relationship among soil organic matter content, available soil nitrogen, and denitrification potential. The denitrification process is partially controlled by the availability of soil carbon, which is used by bacteria as a metabolic energy source (Bowden, 1987). Our findings also are consistent with previous work that found nitrate to increase denitrification rates in wetlands (Hanson et al., 1994; Kjellin et al., 2007).

Flood abatement is a valuable ecosystem service provided by floodplains and some depressional wetlands outside of floodplains (Bullock and Acreman, 2003). This is particularly important in landscapes such as the Midwestern United States, where leveeing has greatly reduced floodwater storage capacity (Belt, 1975), and drainage of wetlands has reduced water storage higher in the landscape (Prince, 1997). Prioritizing restoration and management to exploit synergies between ecosystem services, such as between flood abatement and nutrient removal, could provide substantial benefits, especially in agricultural settings (Fennessy and Craft, 2011).

4.3. Implications for offset policies

Offset policies, such as wetland mitigation, rely on restoration as a form of compensation for the loss of ecosystem structure and function, with the assumption that a suite of ecosystem services will be replaced upon restoration (USACOE and USEPA, 2008). Whereas the destruction of the original habitat is permanent, the ultimate quality of the compensation is often unknown, even when a compensation site meets the minimum legal requirements for success (Matthews and Endress, 2008; Suding, 2011). Current U.S. wetland mitigation rules generally require restored wetlands to provide the suite of functions that are “typically provided by the affected aquatic resource” (USACOE and USEPA, 2008). However, there are no standard requirements for measuring ecosystem functions at impacted wetlands prior to impact or at compensatory mitigation wetlands. Most performance standards used to evaluate mitigation wetlands are vegetation-based and provide little indication of whether other ecosystem functions are being replaced (Cole, 2002; Matthews and Endress, 2008). Therefore, it is unknown which ecosystems services are being provided through wetland mitigation. Additional metrics, such as measures of soil bulk density (Meyer et al., 2008; Hossler et al., 2011), are needed for assessing wetland functional and structural development. Furthermore, agencies responsible for implementing offset policies should consider the likelihood of tradeoffs in ecosystem services delivery among restored sites as well as the role of landscape context and local abiotic conditions underlying those tradeoffs.

4.4. Conclusions

This study underscores the need to consider the overall balance among ecosystem services in the context of restoration goals and policies. Land use decisions are often based on immediate societal needs, without fully weighing the potential ecosystem consequences and can result in unintended tradeoffs (DeFries et al., 2004; Palmer and Filoso, 2009). If the ecosystem services concept is to become a dominant paradigm in restoration ecology, restoration practitioners should be aware of which services are being lost, gained, and retained as a result of restoration efforts. Restoration practitioners should prioritize services depending upon which are most needed and achievable given the local and watershed contexts (Zedler et al., 2012; Mitchell et al., 2013). In some situations, particularly in landscapes where water quality maintenance services are critical, it might be considered acceptable to restore wetlands for the primary purpose of nutrient removal at the expense of biodiversity. However, restoration efforts solely focused on nutrient attenuation must be balanced with projects managed for biodiversity support. As a consequence, restoration planning to balance these tradeoffs should occur at ecologically appropriate scales, such as watersheds (Zedler, 2003; Mitchell et al., 2013).

The ecosystem services concept may provide a new framework for restoration ecology and for understanding human impacts on the environment (Jackson and Hobbs, 2009). However, assessing and achieving restoration outcomes in the context of ecosystem service delivery are fraught with complications. Regulatory agencies establish mitigation requirements with the expectation of desirable restoration outcomes, but often overlook the particular ecosystem services being lost or replaced (Suding, 2011). It is clear that tradeoffs among services are occurring without our explicit knowledge. Additional research is needed to reveal relationships among ecosystem services, in order to take advantage of potential synergies and prevent unintended tradeoffs. The issue of ecosystem service tradeoffs and synergies will only become more relevant to restoration ecology as ecosystem service markets continue to expand (Robertson et al., 2014).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.07.006.

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