TRADEOFFS AMONG ECOSYSTEM SERVICES IN RESTORED WETLANDS

BY

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THESIS

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ABSTRACT

Recently restoration ecology and land management have found new focus and direction by emphasizing the value of ecosystem services to society. Resource management decisions frequently involve choices that reflect tradeoffs among ecosystem services. Tradeoffs occur when one service changes at the expense of another. These tradeoffs are not always explicit, and can exist without our knowledge. As a consequence, land managers may make decisions that diminish the value of some services while enhancing the value of others. Wetlands provide many ecosystem services, such as water quality maintenance, carbon storage, flood water abatement, and biodiversity support. Current compensatory wetland mitigation policy relies on the assumption that wetlands can be restored to provide a full suite of services. The goal of this study was to determine what tradeoffs exist among ecosystem services in restored wetlands, and identify the abiotic and biotic drivers underlying these tradeoffs. Thirty compensatory mitigation wetlands from across Illinois were included in this study. We measured denitrification potential, soil organic matter decomposition, aboveground herbaceous biomass, and soil organic content as proxies for nutrient-storage and removal services. Additionally, flood water storage potential was calculated using detailed LiDAR and topographic data. Since wetlands provide valuable biodiversity support, we determined plant, anuran, and avian diversity for each site. We found a clear tradeoff between biodiversity support and nutrient-cycling processes. Additionally, we found a positive relationship among the biodiversity indicators, as well as positive relationship between denitrification potential and flood water storage potential. Our findings indicate that designing wetlands to maximize nutrient storage and removal may likely come at the expense of biodiversity. Restoration policy makers and practitioners should consider these tradeoffs when planning wetland restoration and conservation at a watershed or landscape scale. Given these tradeoffs, it is unrealistic to expect all services to be maximized; therefore, restoration practitioners should prioritize services depending upon local site and watershed context.

ACKNOWLEDGMENTS

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Introduction

Wetland ecosystems are valued for the many benefits they provide society such as water filtration, carbon storage, and flood abatement. Additionally, they provide significant plant and animal biodiversity support (MEA 2005, Zedler 2003, Brinson and Malvarez 2002, Mensing et al. 1998, Findlay and Houlahan 1997). Several states, including Illinois, have lost over 90% of their original wetlands since the eighteenth century (Dahl 1990). Today, agricultural land use dominates the Midwestern United States; in fact, the land-cover across some watersheds in Illinois is 90-95% corn and soybean (David et al. 2010). The rampant drainage of wetlands has led to the widespread loss of the benefits they provide to society (Fennessy and Craft 2011, Zedler 2003, Turner et al. 2001, NRC 2001). Additionally, the alteration of surface hydrology through tile drainage and urban development has degraded many remaining wetlands, further impairing the benefits they provide (Fennessy and Craft 2011).

Concern over the rapid loss of wetlands, and an increased understanding of their value to society led to the creation of federal and state laws meant to counteract pervasive dredging and filling (Hough and Robertson 2008). Under Section 404 of the Clean Water Act (CWA), 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 (Hough and Robertson 2008). Concurrently with the establishment of mitigation requirements, the federal government adopted a national goal of “no-net-loss” of both wetland area and functions (NRC 2001, NWPF 1987). The no-net-loss policy goal is meant to ensure that wetland mitigation replaces both the physical area of wetlands lost, as well as the associated ecosystem functions. Encapsulated within this goal is recognition of the inherent value of wetlands to society. However, research over the past decade indicates that in many cases mitigation leads to the creation of low-quality wetlands (Gebo and Brooks 2012, Moreno-Mateos et al. 2012, Stefanik and Mitsch 2012, Hossler et al. 2011, Matthews and Spyreas 2010, NRC 2001, Zedler and Callaway 1999). Current compensatory mitigation policy relies on the assumption that wetlands can be restored to provide a whole suite of services. Similarly, the restoration of ecosystem services has become a major goal for many restoration projects.

Since the landmark work by Costanza et al. (1998) 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 (Costanza et al. 2008, Naidoo et al. 2008, MEA 2005, Woodward and Wui 2001). Restoration ecology may have found new focus and direction by emphasizing the importance of ecosystem services (Jackson and Hobbs 2009), however before the concept can be effectively applied to management and practice, it is necessary to first clearly define the term (Jax et al. 2013, Wallace 2007).

Many different terms and definitions have been used interchangeably in the literature, conflating ecosystem services with ecosystem functions, processes, or ecosystem structure (Wallace 2007, de Groot et al. 2002). Ecosystem processes and ecosystem structure are the means to attaining services, but are not the services themselves (Wallace 2007). For example, denitrification is not an ecosystem service per se, but it is a process that contributes to a service (water filtration and water quality control).). By measuring the relevant ecosystem processes and structures, it is possible to get an indication of the services provided by a given system (Hossler et al. 2011, Wallace 2007). 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 (Wallace 2007, MEA 2005). The ecosystem functions and processes measured in this study we consider to be supporting these wetland ecosystem services (Table 1).

Natural resource management decisions frequently involve choices that reflect tradeoffs among ecosystem services. Tradeoffs occur when one service changes at the expense of another service (Bennett et al. 2009). Additionally, synergies occur when two or more services simultaneously increase or decrease (Bennett et al. 2009). For example, managers of freshwater ecosystems face decisions that result in conflicts among provisioning, regulating, supporting, and cultural services (Rodriguez et al. 2006, MEA 2005). Water extraction from rivers and lakes for drinking, irrigation, or industry can conflict with services that depend upon stream flow or depth, such as fisheries maintenance (Rodriguez et al. 2006). In a terrestrial context, logging creates extractive goods that come at the expense of recreational chances offered by original forest (Rose and Chapman 2003). Tradeoffs among services are not always explicit, they can occur unintentionally and without our knowledge (Rodriguez et al. 2006).

Land use decisions are often based on immediate societal needs, without fully weighing the potential ecosystem consequences and can result in unintended ecosystem services tradeoffs (Palmer and Filoso 2009, DeFries et al. 2004). Ecosystem services may sometimes be linked or bundled together, and these bundles may respond in different or similar ways to changes in environmental pressures (Mitchell et al. 2013, Raudsepp-Hearne et al. 2010). Tradeoffs among ecosystem services have been examined in several different systems; however, previous work has primarily been done using simulation models and conceptual reviews (Briner et al. 2013, Maskell et al. 2013, McInnes 2013, Raudsepp-Hearne et al. 2010, Nelson et al. 2009, Bennett et al. 2009, Carpenter et al. 2009, Rodriguez et al. 2006, DeFries et al. 2004, Rose and Chapman 2003; for more details see Appendix A). Comparing differences and tradeoffs among ecosystem services provides a helpful framework for land managers, but these conceptual models need to be tested .

It is well established that wetlands can provide a complex suite of ecosystem services, including flood abatement, water quality maintenance through nutrient and sediment storage, valuable avian and amphibian habitat, while also supporting diverse plant communities. However, it is likely that many of these services occur at the expense of other services; bundles of services depend upon landscape context and site design (Raudsepp-Hearne et al. 2010). For example, Hansson et al. (2005) found that large basin surface area is strongly associated with nitrogen removal (primarily through denitrification), but not phosphorus retention. Additionally, they found a clear tradeoff between phosphorus retention in wetlands with small deep basins and plant biodiversity. Recent research has identified the need to examine potential tradeoffs among water quality improvement and other ecosystem services in restored and created wetlands (Fennessy and Craft 2011). Uncovering these tradeoffs and the underlying interactions that cause tradeoffs or synergies is a crucial first step in developing effective policy and management using the ecosystem services concept.

Given the widespread use of the compensatory mitigation process and other similar biodiversity offset programs, there is an urgent need to determine the underlying relationships among services. (Georgio and Turner 2012, Walker et al. 2009, Robertson 2004). Due to the inherent difficulty and complexity associated with ecological restoration, there may be unknown relationships among landscape and local abiotic and biotic factors that lead to unintended restoration outcomes with varying bundles of ecosystem services (Raudsepp-Hearne 2010, Petterson, and Bennett 2009). A prerequisite to preventing unintended ecological consequences is to quantify potential tradeoffs between ecosystem responses (DeFries et al. 2004). Additionally, in order to determine how to restore the delivery of specific ecosystem services, it is necessary to identify the primary biotic and abiotic drivers underlying these tradeoffs. Assessing wetland restoration outcomes and ecosystem structure and functional development is necessary if we are to determine the implications of current mitigation policy and practices on the national no-net-loss goal.

The objectives of this study were:

1.) To determine the tradeoffs that exists among ecosystem services in restored wetlands, and the implications for mitigation policy.

2.) Identify the abiotic and biotic factors underlying these tradeoffs in order to improve wetland restoration policy and practice.

Methods

Study Approach

Since the goal of this study is to examine tradeoffs among ecosystem services in restored wetlands, we measured ecosystem processes and indicators of ecosystem structure that are supportive to the delivery of important wetland ecosystem services (Table 1). To quantify the biodiversity support value of each wetland we measured the community composition of anuran, avian, and plant species and calculated diversity. To examine the floodwater abatement potential of each site, detailed topographic data were used to calculate the basin surface volume per area of each wetland. To further examine the nutrient removal-related services of these wetlands, we estimated several nutrient cycling ecosystem processes and components. Specifically, we measured soil organic matter content, organic matter decomposition rates, and aboveground herbaceous biomass, all of which directly relate to nutrient cycling and the release of carbon sources used for bacterial metabolism in biogeochemical processes such as denitrification (Fennessy et al. 2008). Additionally, denitrification enzyme assay was used to directly measure the denitrification potential of each wetland.

Study Sites

Wetlands selected for study had been restored by the Illinois Department of Transportation (IDOT) as mitigation for wetlands impacted in the course of road construction. Thirty mitigation wetlands located across Illinois were included in this study (Fig. 1 and Appendix B). Detailed information on the study sites can be found in Matthews et al. (2009a, 2009b) and Matthews and Spyreas (2010).

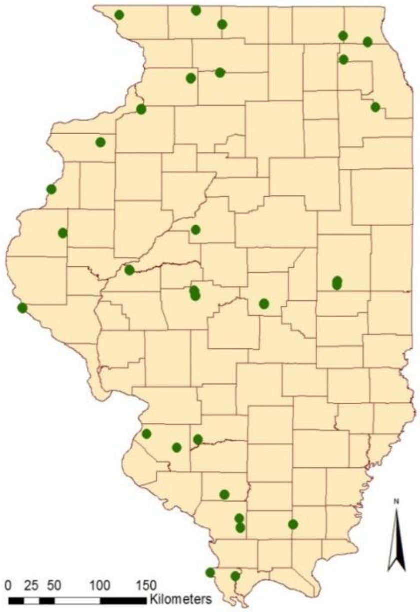


Fig. 1. Locations, within Illinois, of compensatory mitigation projects used in this study.

Methods

Table 1. Wetland ecosystem services considered in this study and the variables measured as proxies of each service.

Ecosystem Services	Associated Supporting Wetland Ecosystem Functions
Climate regulation and carbon storage	Soil organic matter content Herbaceous biomass Soil organic matter decomposition Basin morphology
Water filtration and hydrologic regulation	Denitrification potential Basin morphology
Flood water storage	Basin morphology
Biodiversity support	Avian diversity Anuran diversity Woody plant diversity Herbaceous plant diversity
Recreation and cultural/aesthetic fulfillment	Woody plant diversity Herbaceous plant diversity Anuran diversity Avian diversity Basin morphology

Sampling Design

At each site, a baseline was placed on the longest axis of the wetland divided into four equal segments. At a random point within each segment a transect was placed perpendicular to the baseline, creating four transects along which sampling was conducted (Fig. 2). Along each transect, ten 0.25 m^2 plots were placed at equal distances, for a total of forty plots per wetland. All sampling was conducted between May and September of 2012, with the exception of the anuran call surveys, which were done between March and August of 2013. At two of the ten plots along each transect additional sampling was conducted: soil samples were collected for nutrient analysis, herbaceous biomass samples were collected, and light penetration was measured. Additionally, at one of these two plots along each transect, soil bulk density samples were collected, and organic matter decomposition was measured using the cotton strip assay method. For each variable, additional specific methodological details are provided below.

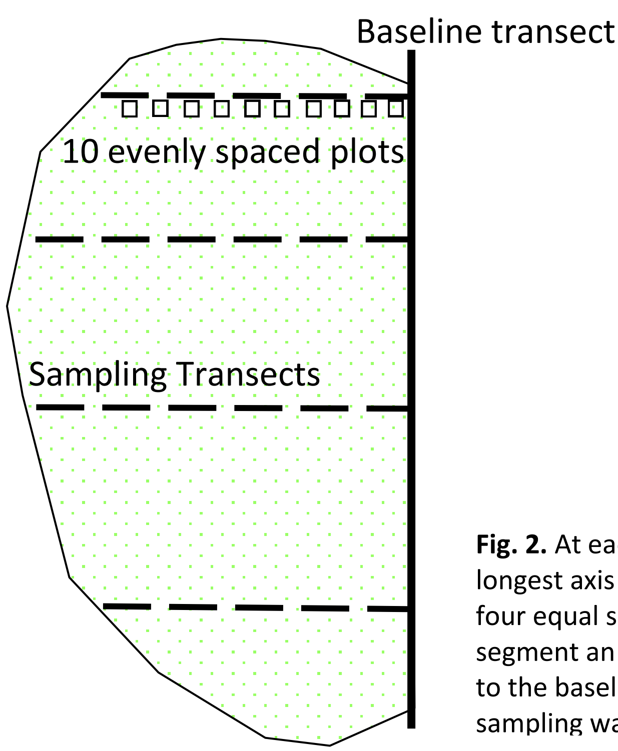


Fig. 2. At each site, a baseline transect was placed on the longest axis of the wetland. This transect was divided into four equal segments. At a random point within each segment an additional transect was placed perpendicular to the baseline, creating four transects along which sampling was conducted

Vegetation Sampling

At each of the forty plots, herbaceous-layer vegetation (<1 m tall) was quantitatively sampled by recording every species and assigning each a cover class based on a visual estimate (<1%, 1-5%, 6-25%, 26-50%, 51-75%, 76-98%, 96-100%). The number of woody stems taller than 1 m was recorded in a 4x30-m belt randomly placed along each of the four transects. Stem density was averaged across each transect to estimate stem density for each site. For each site, Shannon diversity index was calculated for woody and non-woody plant species (Spellerberg and Fedor 2003). Plant species nomenclature followed Mohlenbrock (2002).

Decomposition

Since soil organic matter decomposition directly relates to nutrient cycling, carbon sequestration, and the release of carbon to fuel bacteria for biogeochemical processes such as denitrification, we measured decomposition rates at each wetland. General rates of soil organic matter decomposition were measured using the cotton strip assay (CSA) method (Geatz et al. 2013, Slocum et al. 2007, Latter and Walton 1988). The CSA method uses the decomposition of a standard cotton fabric as a proxy for organic matter decomposition. Decay rates are based on the loss of tensile strength over time compared to a reference strip. The Fredrix brand 12-ounce artistry cotton canvas was used in this study, which was tested and proposed by Slocum et al. (2007) to replace the former standard Shirley Cotton, which has been discontinued (Mendelssohn et al. 1999).

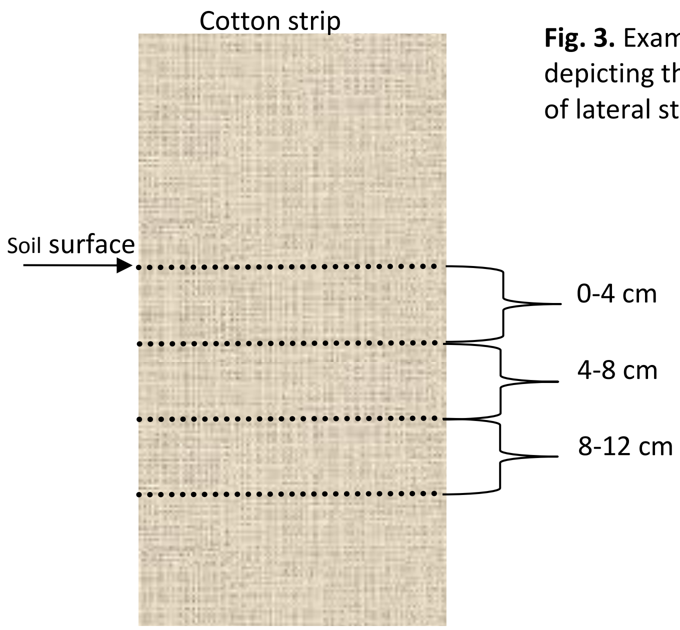


Fig. 3. Example cotton strip depicting the configuration of lateral strips

At each designated plot, a strip 10 cm wide by 20 cm long, was inserted into the soil by first creating a pilot hole with a flat-shovel spade, and then putting the strip against the back of the shovel and inserting it into the hole, typically at least 8 cm deep. The soil surface level on each strip was marked for reference during sample processing (Fig. 3). Fifteen reference cotton strips were inserted into the soil at six sites and immediately removed. Three replicate strips were inserted in one plot per transect, for a total of twelve strips per site. Each strip was left in the soil between 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. Each strip was carefully extracted from the soil by digging around the strip and gently peeling or pulling off the soil. In the lab, each strip was carefully washed by soaking and using a gentle stream of water to remove soil and debris (Latter et al. 1988). The strips were then air-dried for at least 72 hours and stored in a refrigerator. Each strip was laterally cut into 4-cm depth increments (Fig. 3). Each lateral strip was then cut and frayed thread by thread down to the 2.5-cm X 10-cm center section of each strip to standardize strips and to fit them evenly into tensometer grip bits (Slocum et al. 2007). The lateral strips were broken using a Tinius Olsen Series 5000 UTM tensometer machine (maintained at the University of Illinois Department of Materials Science and Engineering teaching laboratory). Each strip was placed between the tensometer grip bits so that there were 5 cm between the bits, and 2.5 cm on each side of the strip was within each bit. The breaking force for each strip was measured in kilograms-force and was calculated relative to the mean of the reference strips, and expressed as a percent of strength-loss compared to the reference mean (Geatz et al 2013).

Soil Bulk Density

To compare differences in soil structural development, we collected, using an Uhland Sampler, 7 cm deep soil samples for determination of bulk density from the same four plots as the CSA (Doran and Mielke 1984). The aluminum ring inside the Uhland sampler, from which the soil is extracted, has a volume of 331.5 cm^3. Each sample was placed in a gallon-size Ziploc bag and stored until processing. Samples were weighed in the lab, and subsamples were dried and weighed to calculate soil bulk density (bulk density = dry weight (g)/volume (cm^3)).

Soil Nutrient and Microbial Analysis

To examine differences in nitrogen and soil organic matter, eight soil cores (1.9-cm diameter and 10-12 cm deep) were collected and composited from two plots along each transect at each site. Soil samples were air-dried and passed through a 2-mm sieve. Available ammonium (NH_4^+) and nitrate (NO_3^-) were determined for each composite sample using the Berthelot reaction method for colorimetric analyses (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 urban or agriculture, the denitrification potential of each site was estimated (Hossler et al. 2011, David et al. 2010). Denitrification potential (DNP) was determined by denitrification enzyme activity assay (Peralta et al. 2010). Soil organic matter content was measured by combustion (Rhine et al. 1998).

Light Availability and Herbaceous Biomass

To quantify differences in plant community structure and canopy light penetration, photosynthetically active radiation (PAR) was measured at two plots along each transect (LI-COR LI-250A Light Meter). Measurements were taken at the soil surface and 1 m above ground-level. Light penetration data were relativized for each site to light measurements collected in the open, under no canopy vegetation. To estimate aboveground herbaceous plant biomass at each site, samples were collected from the same plots as the light measurements and soil nutrient samples. Aboveground plant material was trimmed to ground level within a fixed PVC template (30x30 cm). Each sample was oven-dried at 60°C for at least 48 hours and weighed.

Avian Sampling

To measure avian diversity at each wetland, five-minute unlimited distance avian point counts were conducted at each site between May and August 2013. As many point counts as possible were done at each site, with a minimum distance of 250 m between points. Partners in Flight (PIF), a private-public sector conservation partnership program, developed a system to score and rank birds based on conservation need (Panjabi et al. 2005). PIF scores are derived from six global and/or regional elements: population size, breeding and non-breeding distribution, threats to breeding and non-breeding, and population trends (Panjabi et al. 2005). The avian conservation significance score used provides a standard quantifiable method to examine a given area's relative value for avian conservation (Twedt 2005). Conservation scores were assigned to each species found, and a total avian conservation score was calculated for each site (Fig. 4) to assess its value as bird habitat (Twedt 2005). The conservation significance of each species was derived as the product of each species' concern rating and TDR divided by 1000. Each site's avian conservation significance (ACS) was obtained from the sum of the measures of conservation significance of all species (from Twedt 2005). Avian Conservation Significance (AS) is calculated as:

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

for species *i* = 1 to *n*, CR = LOG GAMMA(PIF Concern)^2, and TDR= 10*LOG_2(observed density).

Anuran Call Surveys

Anuran call surveys (ACS) are a commonly used, cost-effective technique for evaluating anuran species population trends and patterns of distribution (Pierce and Gutzwiller et al. 2004). Call surveys were conducted from mid-March until the first week of August 2013, to correspond with the breeding times of anuran species present in Illinois (Table 3). The ACS method used was adapted from Pillsbury and Miller (2008) and Pierce and Gutzwiller (2004). At each wetland, 15-minute surveys were conducted at least 30 minutes 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 (NAMP 2012, Pillsbury and Miller 2008). For each species, a call index was recorded as: 0, no individuals of a given species heard; 1, one individual heard; 2, multiple individuals with no overlap in calls; and 3, a full chorus (NAMP 2012, Pillsbury and Miller 2008). Due to time and geographic constraints, each site was sampled twice across the breeding season, this may have led to underrepresenting community composition. The total calling rank, or sum of call values at each site for all species, was calculated to compare anuran species abundance and diversity among sites (Pillsbury and Miller 2008, Pope et al. 2000).

Flood Water Storage Potential

Flood water storage potential was calculated by estimating the volume of the wetland basin(s) at each site using Illinois LiDAR data from the Illinois State Geological Survey (ISGS) Height Modernization Program (ISGS 2012). LiDAR-derived digital terrain models (DTM) were used in the analysis (Fig. 4). The LiDAR coverage for Illinois is still incomplete, so precise (2-3 cm accuracy of XYZ data) GPS data were collected using a Fast Survey GPS ProMark 200 for five of the sites. The Surface Volume tool in ArcMap 10.1 3D Analyst was used to calculate basin volume below a reference plane defined by the lowest outlet point for each basin. To relativize between sites, volume was compared per area (Lane and D'Amico 2010).

Fig. 4. Mitigation site in Stephenson County Illinois, outlined in pink. Left: digital terrain model (DTM) derived from LiDAR data used in calculating floodwater storage potential. Right: Orthographic image of study area.

Land Cover

To examine the effects of landscape context on the ecosystem function response variables, the USDA National Agricultural Statistics Service (NASS) 2012 Cropland Data Layer (CDL) data was used to calculate the proportion of wetlands, forest, open water, developed land, and agriculture within buffers around each study site (Appendix C). Land cover was calculated at multiple buffer radii (500, 1000, 1500, 2000 m) and was found to be tightly correlated across scales ($r^2 > 0.73$), therefore 1000 m was used in the analysis. For each site, outside-only buffers were created using ArcMap 10.1 (ESRI, Redlands

California, USA), and any buffer overlap was dissolved. The program Geospatial Modeling Environment (GME), which interfaces with R, was used to calculate the proportion of each land cover class (Spatial Ecology LLC 2012). The GME intersect- polygons-with-raster tool (isectpolyrst) was used to summarize raster cell values contained by the buffer. To reduce the number of land cover variables to orthogonal principal components and describe the primary gradients in land use, we used principal components analysis (PCA) on a correlation matrix followed by varimax rotation (using XLSTAT Pro) (Abdi and Williams 2010, Matthews et al. 2009).

Statistical Analysis

Ordination is often used in ecological research to summarize multivariate data and uncover the underlying structure in a dataset (Jongman et al. 1995). We used principal component analysis (PCA) to identify whether a latent tradeoff structure exists among wetland ecosystem services. Principal components analysis is ideal for answering this type of question because it can effectively take a large dataset and express the variables in a way that clearly highlights similarities and differences, as well as identify specific patterns (Abdi and Williams 2010, Gotelli and Ellison 2004). The mean of each variable was calculated at the site level to make comparisons at the site scale. Every variable was standardized prior to analysis (woody H', herbaceous H', total avain score, total anuran call rank, denitrification potential, soil organic matter content, flood water storage potential, herbaceous biomass, decomposition). A scree plot of the eigenvalues vs. the principal components was studied to decide which components to report (Abdi and Williams 2010).

Redundancy analysis (RDA) is a multivariate multiple regression technique used in conjunction with PCA. RDA was used to quantify the amount of variation in the ecosystem service variables that can be explained by the abiotic and biotic predictors (Borcard et al. 1992). Forward selection was used (CANOCO 4.5) to remove non-significant ($p > 0.1$) predictor variables (Matthews et al. 2009, Heikkinen et al. 2004, Borcard et al. 1992). Partial Monte Carlo permutation tests (*n* = 499) were used to examine each potential predictor variable (Leps and Smilauer 2003). The composite land cover variables (riparian and developed), ground-level photosynthetically active radiation, soil bulk density, and percent non-native plant cover were retained.

Results

Land cover

Principal components analysis of the land cover variables resulted in two components explaining 69.32% of variation in land cover among sites (Table 2). Similar to the results of Matthews et al. (2009), the first axis described a gradient from riparian settings, characterized by high cover of forest, 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.

Table 2. Land cover variable (1000m) loadings on PCA axes after Varimax rotation.

Variable	PC axis 1	PC axis 2
Proportion of open water	0.635	-0.113
Proportion of developed land	-0.408	-0.905
Proportion of forest	0.794	0.042
Proportion of wetland	0.687	0.066
Proportion of agriculture	-0.354	0.912
Variance explained (%)	35.95	33.37

Ecosystem services

Two principal components were retained from the PCA of ecosystem service proxies (Table 3). Principal component vectors that cluster together and point in the same direction correspond to the latent tradeoff among the variables (Fig. 5). The nutrient-cycling related principal component vectors point opposite of the biodiversity vectors (Fig. 5), indicating that wetlands which tend to support higher rates of biodiversity also tend to provide less support to nutrient-cycling ecosystem functions. Specifically, soil organic matter content, herbaceous biomass, denitrification potential and organic matter decomposition variables are negatively loaded on PCA axis 1 (Fig. 5, Table 3). Non-woody plant diversity, woody plant diversity, avian conservation score, and anuran species richness were strongly positively loaded on PCA axis 1. Additionally, the floodwater storage (volume/ha) and denitrification vectors were positively loaded on the second PCA axis (Fig. 5, Table 3).

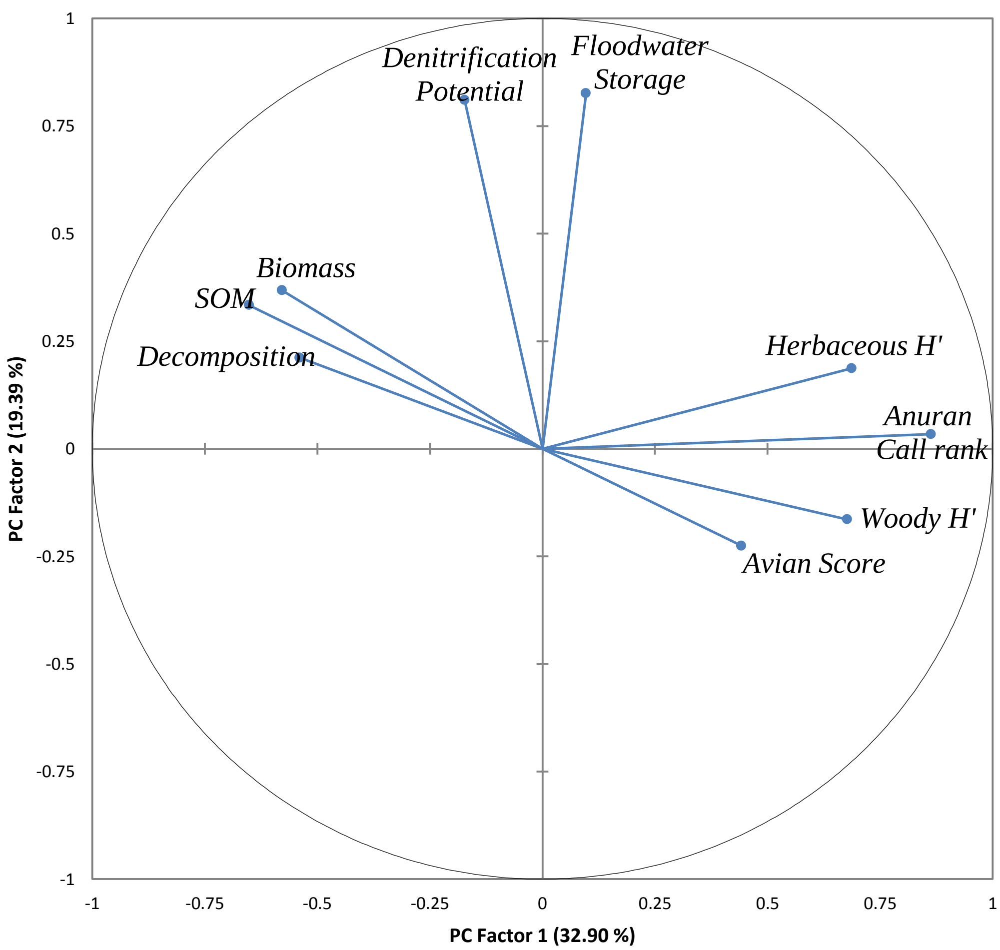


Fig. 5. Biplot from principal components analysis (PCA) of service variables, after applying a Varimax rotation for interpretation. Combined, both axes account for 52.29% of the variation explained.

Table 3. Variable loadings from principal components analysis (PCA) of service variables, after applying a Varimax rotation for interpretation.

Variable	PC axis 1	PC axis 2
Soil organic matter (SOM)	-0.652	0.334
Biomass (g/m^2)	-0.578	0.368
Denitrification potential (mol/g/hr)	-0.173	0.811
Decomposition	-0.539	0.211
Herbaceous Shannon Index (H')	0.687	0.187
Woody Shannon Index (H')	0.677	-0.164
Total avian score	0.442	-0.226
Total anuran Call rank	0.863	0.034
Floodwater storage (vol ha^{-1})	0.097	0.826
Variance explained (%)	36.09	16.20

Seven predictor variables were retained in the redundancy analysis (Fig. 6) following forward selection ($p < 0.1$), explaining 45% of the variation in ecosystem service variables. Total nitrogen explained the most variation, followed by soil bulk density, percent non-native plant cover, land cover PCA axis 1 (riparian gradient), and PAR availability at ground level. The riparian PCA axis was positively associated with the biodiversity indicators (woody and non-woody vegetation, anuran and avian diversity) (Fig. 6). Additionally, soil bulk density was negatively associated with nutrient-cycling related ecosystem functions, specifically denitrification potential (DNP), organic matter decomposition, and soil organic matter content (SOM). Total soil nitrogen was positively correlated with the nutrient cycling related wetland functions, specifically herbaceous biomass, SOM, DNP and decomposition (Fig. 6).

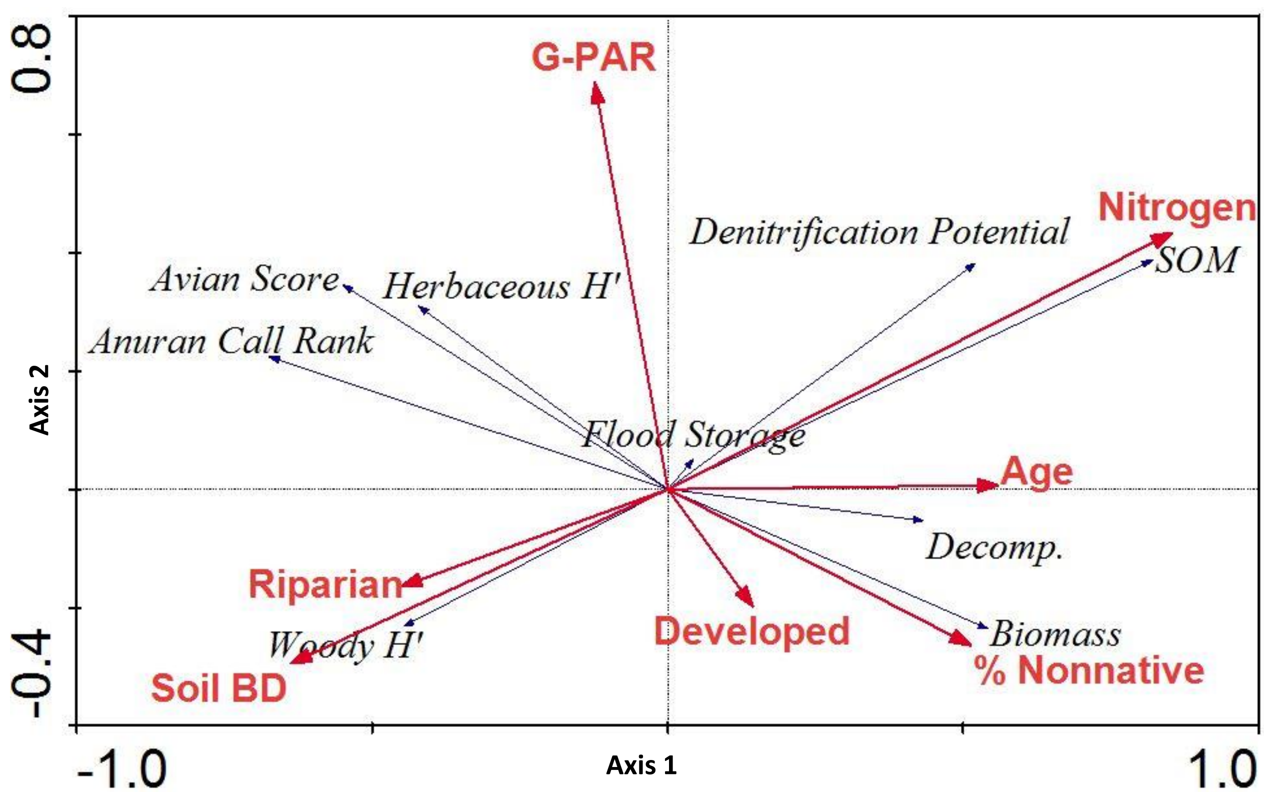


Fig. 6. Redundancy analysis (RDA) biplot of the predictor and function variables. Red vectors: predictor variables, blue vectors: response variables. *Riparian* and *Developed* refer to the PCA-composite land cover variables. *G-PAR* refers to available ground-level photosynthetically active radiation. *Age* is the wetland site age, *%Nonnative* is the percent cover of non-native plants, *Soil BD* refers to soil bulk density, and *Nitrogen* is total soil N.

Discussion

Our results show a clear tradeoff between biodiversity indicators and nutrient-cycling related ecosystem functions. Consequently, our findings indicate that wetland restoration and management decisions may involve choices that reflect tradeoffs among ecosystem services. These tradeoffs occur across continua, represented by the latent structure we found in the two retained PC factors.

Tradeoffs and synergies among ecosystem services

The first axis of the PCA of ecosystem service variables characterized a gradient from nutrient-cycling and storage functions to biodiversity support. Additionally, our results indicate a strong positive relationship among the plant, avian, and anuran indicators of biodiversity support. Similarly, Maskell et al. (2013) found strong positive relationships among plant, insect, and aquatic invertebrate diversity across Great Britain. Other authors examining the relationship among ecosystem services, found potential synergies among biodiversity components (Maes et al. 2012). In this situation, it is unclear whether the pattern we observed among the biodiversity components is due to a synergistic effect, where plant diversity enhances anuran and avian diversity. However, if this pattern is due to an underlying synergistic interaction, it would imply that plant community data are useful for assessing the biodiversity of other taxa at restoration sites. Identifying tradeoffs and enhancing potential synergies among ecosystem services could yield considerable benefits. Determining the factors that link synergies would be helpful to restoration practitioners and policy makers (Bennett et al. 2009).

Contrary to previous studies which have reported a positive relationship between biodiversity and ecosystem function, we found diversity to be negatively correlated with indicators of function. Much research has focused on the connection between plant diversity and ecosystem stability and function (Hooper et al. 2005, Tilman 2001, Tilman et al. 1996). Ecosystem functions, such as productivity and nutrient retention, have been found to be positively correlated with plant species richness in some ecosystems (Hooper et al. 2005, Tilman et al. 2001). Most studies focus on the connection between plant diversity and due to ease-of-measure; assess biomass production as the sole ecosystem function (Hooper et al. 2005). Biomass production alone, while it is an ecosystem function, may not strongly relate to ecosystem service delivery. Recent work conducted in wetlands contradicts the hypothesized positive relationship between biodiversity and ecosystem function, and suggests that certain ecosystem functions, such as nitrogen retention and productivity may sometimes be maximized at lower levels of diversity (Doherty and Zedler in press, Weisner and Thiere 2010, Hansson et al. 2005). The tradeoff between nutrient-removal services and biodiversity support we found appears to support these recent findings.

Maximizing nutrient attenuation functions that are associated with ecosystem services like water quality maintenance appears to conflict with biodiversity support services. We found non-native plant species cover, herbaceous biomass, soil organic matter content, and soil nitrogen to be positively correlated with one another, but also negatively associated with each diversity component (Fig. 6). Nitrogen loading is a major concern in the Midwest, and because of the transitional position wetlands occupy on the landscape, they receive high input rates of nitrate and other pollutants through surface water runoff (Hefting et al. 2012, David et al. 2010). High N levels in our study wetlands may create conditions favorable to aggressive non-native plant species (Hogan and Walbridge 2009, Matthews et al. 2009, Zedler and Kercher 2004, Brooks et al. 2005). Some of these dominant species, such as *Phalaris arundinacea, Phragmites australis,* and *Typha angustifolia,* are highly productive and may contribute to the higher levels of soil organic matter we found to be associated with herbaceous biomass and non-native cover. Spyreas et al. (2009) found reed canary grass dominance to decrease plant diversity and insect abundance in Illinois wetlands. Similarly, we found non-native plant cover to be negatively associated with diversity components. Based on these results, there appears to be a clear tradeoff between plant diversity and nutrient removal, maximizing one may come at the expense of the other. Similar to our results, Weisner and Thiere (2010) found that wetlands which were less diverse, dominated by a few plant species, tended to be more efficient at removing nitrogen. Land managers and policy makers need to be aware of this relationship in order to make informed decisions relating to restoration, conservation, and ecosystem service provisioning.

Landscape setting can have strong effects on wetland restoration outcomes, and the ecosystem services associated with them, especially biodiversity. We found a strong positive relationship between riparian settings, which in Illinois are associated with higher proportions of wetland and forests, to plant, avian and anuran diversity. Simultaneously, we found avian, anuran, and herbaceous plant diversity to be negatively associated with the proportion of developed land surrounding each site. Previous authors have found that, across multiple taxa, landscape context is an important controlling factor in determining biodiversity. Avian species richness has been found to increase in wetlands that are situated in a landscape context with a higher surrounding proportion of wetlands and forest (Fairbairn and Dinsmore 2001, Naugle et al. 1999). A similar landscape-context relationship has been observed in anuran communities in the Midwest (Pillsbury and Miller 2008, Houlahan and Findlay 2003, Knutson et al. 1999). 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. Pesticides and nitrate fertilizers are known to have toxic effects on amphibians (Camargo et al. 2005, Hecnar 1995). Specifically, the effects of nitrate on four of the common species we observed in these mitigation sites (*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. 2009). For example, landscape fragmentation can eliminate plant propagule sources, reducing recruitment within restoration sites (Galatowitsch et al. 2000). Based on previous findings and our results, it appears that landscape context contributes to the tradeoff we found between biodiversity and nutrient removal services.

Our results provide support for previous work which found that soil structural development may hinder the restoration of ecosystem functions related to nutrient cycling. We found that denitrification potential, soil organic matter content, and decomposition rates were negatively correlated with soil bulk density (BD). Similarly, previous authors found soil BD to be negatively correlated with denitrification and other nutrient cycling processes (Wolf et al. 2011, Hossler et al. 2011, Hossler and Bouchard 2008, Meyer et al. 2008). Since soil BD directly relates to soil organic matter content, root penetration, porosity, redox, and soil biotic activity, it has been recommended as a an indicator of physical and biological soil recovery following wetland restoration (Hossler et al. 2011, Meyer et al. 2008). 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 examined.

Flood abatement 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. For example, we found that wetlands with basin morphology conducive to storing large amounts of flood water may also experience higher rates of denitrification, acting as important nutrient sinks. The positive relationship we found between denitrification and the “pondedness” of a site may be due to the abiotic and biotic factors that control the process. 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 higher denitrification potential than higher elevation areas with lower soil moisture (Peralta et al. 2010). The denitrification process is partially controlled by the availability of soil carbon, which is used by bacteria as a metabolic energy source (Bowden 1987). We found a positive relationship among soil organic matter content, soil nitrogen, and denitrification potential. Our findings also are consistent with previous work that found nitrate to increase denitrification rates in wetlands (Kjellin et al. 2007, Sirivedhin and Gray 2006, Hanson et al. 1994). Prioritizing restoration and management to exploit linkages between ecosystem services, such as between flood abatement and nutrient removal, could provide substantial benefits, especially in agricultural settings like the Midwest.

Conclusions

The differences we observed among ecosystem service proxy variables demonstrate that not all services occur simultaneously. Some occur at the expense of others (water quality maintenance and biodiversity support), whereas others may occur synergistically (biodiversity of different taxa). Therefore, restoration practitioners should prioritize services depending upon local site and watershed context (Zedler et al. 2012, Mitchell et al. 2012). In a recent review, Macfadyen et al. (2012) found that management options meant to increase biodiversity can sometimes maintain or enhance ecosystem services, but solely focusing on improving 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 that randomly selected areas. In some situations, particularly in landscapes such as Illinois, where water quality maintenance services are much-needed, restoring sites for the primary purpose of nutrient removal at the expense of biodiversity might be considered acceptable. However, restoration efforts solely focused on nutrient attenuation services must be balanced with projects managed for biodiversity support. As a consequence, restoration policy balancing these tradeoffs should occur at ecologically appropriate scales, such as the watershed level (Mitchell et al. 2013, Zedler et al. 2012, Zedler 2003, Woltemade 2000).

The current metrics used to determine success in compensatory mitigation context are inadequate to assess and manage for ecosystem services. The majority of performance standards used in compensatory mitigation are vegetation-based (Matthews and Endress 2008), and provide little to no indication of ecosystem function development (Cole 2002). Our results support the findings and conclusions of Cole (2002) that more useful metrics for wetland functional and structural development are needed. For example, Hossler et al. (2011) and Meyer et al. (2008) have suggested using soil bulk density as an indicator of soil structural and functional development in restored wetlands. Our finding that soil bulk density was negatively associated with nutrient cycling functions supports this suggestion. The ecosystem services concept may provide a new framework for restoration ecology and 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). A deeper understanding is needed to determine how ecosystem service provisioning in restored wetlands compares to services provided by natural sites, and what factors drive these differences. Environmental offset programs like compensatory wetland mitigation rely on the assumption that wetlands can be restored to provide a whole suite of services, but it is clear that tradeoffs among services are occurring without our explicit knowledge. Additional research is needed to reveal the relationships among ecosystem services, in order to take advantage of potential synergies and prevent unintended tradeoffs.

References

Ballantine, K., & Schneider, R. (2009). Fifty-five years of soil developlment in restored freshwater depressional wetlands. Ecological Applications, 19(6), 1467–1480.

Bennett, E. M., Peterson, G. D., & Gordon, L. J. (2009). Understanding relationships among multiple ecosystem services. Ecology Letters, 12(12), 1394–404.

Bowden, W. B. (1987). The biogeochemistry of nitrogen in freshwater wetlands. Biogeochemistry, 4(3), 313-348.

Briner, S., Huber, R., Bebi, P., Elkin, C., Schmatz, D. R., & Grêt-Regamey, A. (2013). Trade-offs between ecosystem services in a mountain region. Ecology and Society, 18(3).

Brinson, M. M., & Malvárez, A. I. (2002). Temperate freshwater wetlands: types, status, and threats. Environmental Conservation, 29(02), 115–133.

Brooks, R., Wardrop, D., Cole, C., & Campbell, D. (2005). Are we purveyors of wetland homogeneity? A model of degradation and restoration to improve wetland mitigation performance. Ecological Engineering, 24(4), 331–340.

Camargo, J. A., Alonso, A., & Salamanca, A. (2005). Nitrate toxicity to aquatic animals: a review with new data for freshwater invertebrates. Chemosphere, 58(9), 1255-1267.

Cole, C. A. (2002). The assessment of herbaceous plant cover in wetlands as an indicator of function. Ecological Indicators, 2(3), 287–293.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Sutton, P., Limburg, K., Naeem, S., O'Neill, R., Paruelo, J., Raskin, R., van den Belt, M. (1998). The value of the world's ecosystem services and natural capital. Ecological Economics, 25(1), 3-15.

Costanza, R., Pérez-Maqueo, O., Martinez, M. L., Sutton, P., Anderson, S. J., & Mulder, K. (2008). The value of coastal wetlands for hurricane protection. Royal Swedish Academy of Sciences, 37(4), 241–8.

Dahl, T. E. (1990). Wetlands losses in the United States, 1780's to 1980's. Report to the Congress. National Wetlands Inventory, St. Petersburg, FL (USA).

David, M. B., Drinkwater, L. E., & McIsaac, G. F. (2010). Sources of nitrate yields in the Mississippi River Basin. Journal of Environment Quality, 39(5), 1657-1667.

De Groot, R. S., Wilson, M. A, & Boumans, R. M. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. Ecological Economics, 41(3), 393–408.

DeFries, R. S., Foley, J. A., & Asner, G. P. (2004). Land-use choices: balancing human needs and ecosystem function. Frontiers in Ecology and the Environment, 2(5), 249–257.

Ellison, G. N., & Gotelli, N. J. (2004). A primer of ecological statistics. Sinauer, Sunderland, Massachusetts, USA.

Fairbairn, S. E., & Dinsmore, J. J. (2001). Local and landscape-level influences on wetland bird communities of the prairie pothole region of Iowa, USA. Wetlands, 21(1), 41–47.

Fennessy, S., & Craft, C. (2011). Agricultural conservation practices increase wetland ecosystem services in the Glaciated Interior Plains. Ecological Applications, 21(3), 49–64.

Fennessy, M. S., Rokosch, A., & Mack, J. J. (2008). Patterns of plant decomposition and nutrient cycling in natural and created wetlands. Wetlands, 28(2), 300–310.

Galatowitsch, S., Whited, D., Lehtinen, R. M., Husveth, J., & Schik, K. (2000). The vegetation of wet meadows in relation to their land-use. Environmental Monitoring and Assessment, 60, 121–144.

Geatz, G. W., Needelman, B. A., Weil, R. R., & Megonigal, J. P. (2013). Nutrient availability and soil organic matter decomposition response to prescribed burns in mid-atlantic brackish tidal marshes. Soil Science Society of America Journal, 77(5), 1852-1864.

Gebo, N. A., & Brooks, R. P. (2012). Hydrogeomorphic (HGM) assessments of mitigation sites compared to natural reference wetlands in Pennsylvania.Wetlands, 32(2), 321-331

Georgiou, S., & Turner, R. K. K. (2012). Valuing ecosystem services: the case of multi-functional wetlands. Earthscan. London, United Kingdom.

Hanson, G. C., Groffman, P. M., & Gold, A. J. (1994). Denitrification in riparian wetlands receiving high and low groundwater nitrate inputs. Journal of Environment Quality, 23(5), 917-922.

Hansson, L.-A., Bronmark, C., Anders Nilsson, P., & Abjornsson, K. (2005). Conflicting demands on wetland ecosystem services: nutrient retention, biodiversity or both? Freshwater Biology, 50(4), 705–714.

Hecnar, S. J. (1995). Acute and chronic toxicity of ammonium nitrate fertilizer to amphibians from southern Ontario. Environmental Toxicology and Chemistry,14(12), 2131-2137.

Hefting, M. M., van den Heuvel, R. N., & Verhoeven, J. T. A. (2012). Wetlands in agricultural landscapes for nitrogen attenuation and biodiversity enhancement: opportunities and limitations. Ecological Engineering, (September 2011), 1–9.

Hogan, D. M., & Walbridge, M. R. (2009). Recent land cover history and nutrient retention in riparian wetlands. Environmental Management, 44(1), 62–72.

Hooper, D.U, Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs, 75(1), 3–35.

Hossler, K., & Bouchard, V. (2010). Soil development and establishment of carbon-based properties in created freshwater marshes. Ecological Applications, 20(2), 539–553.

Hossler, K., Bouchard, V., Fennessy, M. S., Frey, S. D., Anemaet, E., & Herbert, E. (2011). No-net-loss not met for nutrient function in freshwater marshes: recommendations for wetland mitigation policies. Ecosphere, 2(7), art82.

Hough, P., & Robertson, M. (2008). Mitigation under Section 404 of the Clean Water Act: where it comes from, what it means. Wetlands Ecology and Management, 17(1), 15–33.

Houlahan, J. E., & Findlay, C. S. (2003). The effects of adjacent land use on wetland amphibian species richness and community composition. Canadian Journal of Fisheries and Aquatic Sciences, 1094, 1078–1094.

Jackson, S. T., & Hobbs, R. J. (2009). Ecological restoration in the light of ecological history. Science 325(5940), 567–569.

Jax, K., Barton, D. N., Chan, K. M. A., de Groot, R., Doyle, U., Eser, U., Wichmann, S. (2013). Ecosystem services and ethics. Ecological Economics, 93(May 2011), 260–268.

Jongman, R. H., Ter Braak, C. J., & Van Tongeren, O. F. (Eds.). (1995). Data analysis in community and landscape ecology. Cambridge University Press. Cambridge, United Kingdom.

Kjellin, J., Hallin, S., & Wörman, A. (2007). Spatial variations in denitrification activity in wetland sediments explained by hydrology and denitrifying community structure. Water Research, 41(20), 4710–4720.

Knutson, M. G., Sauer, J. R., Olsen, D. A., Mossman, M. J., Hemesath, L. M., & Lannoo, M. J. (1999). Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, U.S.A. Conservation Biology, 13(6), 1437–1446.

Lane, C. R., & D’Amico, E. (2010). Calculating the ecosystem service of water storage in isolated wetlands using LiDAR in North Central Florida, USA. Wetlands, 30(5), 967–977.

Latter, P. M., Bancroft, G., & Gillespie, J. (1988). Technical aspects of the cotton strip assay in soils. International Biodeterioration, 24(1), 25–47.

Lepš, J., & Šmilauer, P. (2003). Multivariate analysis of ecological data using CANOCO. Cambridge University Press. Cambridge, United Kingdom.

Macfadyen, S., Cunningham, S. A., Costamagna, A. C., & Schellhorn, N. A. (2012). Managing ecosystem services and biodiversity conservation in agricultural landscapes: are the solutions the same? Journal of Applied Ecology, 49(3), 690–694.

Maes, J., Paracchini, M. L., Zulian, G., Dunbar, M. B., & Alkemade, R. (2012). Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. Biological Conservation, 155, 1–12.

Maskell, L. C., Crowe, A., Dunbar, M. J., Emmett, B., Henrys, P., Keith, A. M., Smart, S. M. (2013). Exploring the ecological constraints to multiple ecosystem service delivery and biodiversity. Journal of Applied Ecology, 50(3), 561–571.

Matthews, J. W., Peralta, A. L., Flanagan, D. N., Baldwin, P. M., Soni, A., Kent, A. D., & Endress, A. G. (2009). Relative influence of landscape vs. local factors on plant community assembly in restored wetlands. Ecological Applications, 19(8), 2108–2123.

Matthews, J. W., & Spyreas, G. (2010). Convergence and divergence in plant community trajectories as a framework for monitoring wetland restoration progress. Journal of Applied Ecology, 47(5), 1128–1136.

Matthews, J. W., Spyreas, G., & Endress, A. G. (2009). Trajectories of vegetation-based indicators used to assess wetland restoration progress. Ecological Applications, 19(8), 2093–107.

Mendelssohn, I. A., Sorrell, B. K., Brix, H., Schierup, H.-H., Lorenzen, B., & Maltby, E. (1999). Controls on soil cellulose decomposition along a salinity gradient in a Phragmites australis wetland in Denmark. Aquatic Botany, 64(3-4), 381–398.

Mensing, D. M., Galatowitsch, S. M., & Tester, J. R. (1998). Anthropogenic effects on the biodiversity of riparian wetlands of a northern temperate landscape. Journal of Environmental Management, 53(4), 349-377.

Meyer, C. K., Baer, S. G., & Whiles, M. R. (2008). Ecosystem recovery across a chronosequence of restored wetlands in the Platte River Valley. Ecosystems, 11(2), 193–208.

Mielke, L. N., Doran, J. W., & Richards, K. A. (1986). Physical environment near the surface of plowed and no-tilled soils. Soil and Tillage Research, 7(4), 355-366.

Millennium Ecosystem Assessment. (2005). Ecosystems and human well-being: our human planet: summary for decision-makers (Vol. 5). Island Press. Washington D.C.

Mitchell, M. G., Bennett, E. M., & Gonzalez, A. (2013). Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. Ecosystems, 16(5), 894-908.

Moreno-Mateos, D., Power, M. E., Comín, F. A, & Yockteng, R. (2012). Structural and functional loss in restored wetland ecosystems. PLoS Biology, 10(1), e1001247.

Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R. E., Lehner, B., … Ricketts, T. H. (2008). Global mapping of ecosystem services and conservation priorities. Proceedings of the National Academy of Sciences of the United States of America, 105(28), 9495–94500.

Naugle, D. E., Higgins, K. E., Nusser, S. M., & Johnson, W. C. (1999). Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecology, 14, 267–276.

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D. R., … Shaw, M. R. (2009). Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment, 7(1), 4–11.

NRC (National Research Council) (2001) Compensating for wetland losses under the Clean Water Act. National Academy Press, Washington, DC.

NWPF (National Wetland Policy Forum). (1987). Protecting America's wetlands: an action agenda. The Conservation Foundation, Washingon, DC.

Palmer, M. A, & Filoso, S. (2009). Restoration of ecosystem services for environmental markets. Science, 325(5940), 575–576.

Panjabi, A. O., E. H. Dunn, P. J. Blancher, W. C. Hunter, B. Altman, J. Bart, C. J. Beardmore, H. Berlanga, G. S. Butcher, S. K. Davis, D. W. Demarest, R. Dettmers, W. Easton, H. Gomez de Silva Garza, E. E. Inigo-Elias, D. N. Pashley, C. J. Ralph, T. D. Rich, K. V. Rosenberg, C. M. Rustay, J. M. Ruth, J. S. Wendt, and T. C. Will. 2005. The Partners in Flight handbook on species assessment. Version 2005. Partners in Flight Technical Series no. 3.

Peralta, A. L., Matthews, J. W., & Kent, A. D. (2010). Microbial community structure and denitrification in a wetland mitigation bank. Applied and Environmental Microbiology, 76(13), 4207–4215.

Pierce, B. A., & Gutzwiller, K. J. (2004). Society for the study of amphibians and reptiles auditory sampling of drogs : detection efficiency in relation to survey duration auditory sampling of frogs: detection efficiency in relation to survey duration. Journal of Herpetology, 38(4), 495–500.

Pillsbury, F. C., & Miller, J. R. (2008). Habitat and landscape characteristics underlying anuran community structure along an urban-rural gradient. Ecological Applications, 18(5), 1107–18.

Pope, S. E., Fahrig, L., & Merriam, H. G. (2000). Landscape complementation and metapopulation effects on leopard frog populations. Ecology, 81(9), 2498-2508.

Raudsepp-Hearne, C., Peterson, G. D., & Bennett, E. M. (2010). Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proceedings of the National Academy of Sciences of the United States of America, 107(11), 5242–5247.

Rhine, E. D., Mulvaney, R. L., Pratt, E. J., & Sims, G. K. (1998). Improving the Berthelot reaction for determining ammonium in soil extracts and water. Soil Science Society of America Journal, 62(2), 473-480.

Robertson, M. (2004). The neoliberalization of ecosystem services: wetland mitigation banking and problems in environmental governance. Geoforum, 35(3), 361–373.

Rodríguez, J. P., Beard, T. D., Bennett, E. M., Cumming, G. S., Cork, S. J., Agard, J., Dobson, A. P., Peterson, G. D. (2006). Trade-offs across space, time, and ecosystem services. Ecology and Society, 11(1), 28.

Rose, S. K., & Chapman, D. (2003). Timber harvest adjacency economies, hunting, species protection, and old growth value: seeking the dynamic optimum. Ecological Economics, 44(2), 325-344.

Slocum, M. G., Roberts, J., & Mendelssohn, I. A. (2009). Artist canvas as a new standard for the cotton-strip assay. Journal of Plant Nutrition and Soil Science, 172(1), 71–74.

Spellerberg, I. F., & Fedor, P. J. (2003). A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener'Index. Global Ecology and Biogeography, 12(3), 177-179.

Spyreas, G., Wilm, B. W., Plocher, A. E., Ketzner, D. M., Matthews, J. W., Ellis, J. L., & Heske, E. J. (2009). Biological consequences of invasion by reed canary grass (*Phalaris arundinacea*). Biological Invasions, 12(5), 1253–1267.

Stefanik, K. C., & Mitsch, W. J. (2012). Structural and functional vegetation development in created and restored wetland mitigation banks of different ages. Ecological Engineering, 39, 104–112.

Suding, K. N. (2011). Toward an era of restoration in ecology: successes , failures , and opportunities ahead. The Annual Review of Ecology, Evolution, and Systematics, 42, 465–487.

Tilman, D. (2001). Effects of diversity and composition on grassland stability and productivity. Ecology: Achievement and Challenge, Chapter 9. 183-210. Blackwell Science, Oxford, United Kingdom.

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. Science, 294 (5543), 843-845.

Tilman, D., Wedin, D., & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature, 379(6567), 718-720.

Turner, R. E., Redmond, A. M., & Zedler, J. B. (2001). Count It by acre or function — mitigation adds up to net loss of wetlands. National Wetlands Newsletter, 23(6), 5-16.

Twedt, D. J. 2005. An objective method to determine an area's relative value for avian conservation. Pages 71–77 in C. J. Ralph and T. D. Rich, editors, Bird conservation implementation and integration in the Americas. Proceedings of the Third International Partners in Flight Conference, 20–24 March 2002, Asilomar, California, USA. U.S. Forest Service, General Technical Report PSW-GTR-191, Albany, California, USA.

Walker, S., Brower, A. L., Stephens, R. T. T., & Lee, W. G. (2009). Why bartering biodiversity fails. Conservation Letters, 2(4), 149–157.

Wallace, K. J. (2007). Classification of ecosystem services: problems and solutions. Biological Conservation, 139(3-4), 235–246.

Weisner, S. E. B., & Thiere, G. (2010). Effects of vegetation state on biodiversity and nitrogen retention in created wetlands: a test of the biodiversity-ecosystem functioning hypothesis. Freshwater Biology, 55(2), 387–396.

Wolf, K. L., Ahn, C., & Noe, G. B. (2011). Development of soil properties and nitrogen cycling in created wetlands. Wetlands, 31(4), 699–712.

Woltemade, C. J. (2000). Ability of restored wetlands to reduce nitrogen and phosphorus concentrations in agricultural drainage water. Journal of Soil and Water Conservation, 55(3), 303-309.

Woodward, R. T., & Wui, Y.-S. (2001). The economic value of wetland services: a meta-analysis. Ecological Economics, 37(2), 257–270.

Zedler, J. B. (2003). Wetlands at your service: reducing impacts of agriculture at the watershed scale. Frontiers in Ecology and the Environment, 1(2), 65-72.

Zedler, J. B., & Callaway, J. C. (1999). Tracking wetland restoration: do mitigation sites follow desired trajectories? Restoration Ecology, 7(1), 69–73.

Zedler, J. B., Doherty, J. M., & Miller, N. A. (2012). Shifting restoration policy to address landscape change , novel ecosystems , and monitoring. Ecology and Society, 17(4).

Zedler, J., & Kercher, S. (2004). Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences, 23(5), 431–452.

Appendix A

Table A1. Studies examining the issue of ecosystem service tradeoffs.

Ecosystem Service Tradeoffs Studied	Ecosystem Service Synergies Studied	Type of Analysis	Citation
Provisioning, Biodiversity	Biodiversity and C sequestration	Model	Briner et al. (2013)
Provisioning, Regulating , Cultural	Regulating services	Empirical model	Raudsepp-Hearne et al. (2010)
Provisioning , Regulating, Biodiversity	Biodiversity components	Empirical analysis	Maskell et al. (2013)
Provisioning, Supporting, Regulating, and Cultural	——	Model	Rodríguez et al. (2006)
Provisioning , Regulating, Biodiversity	——	Model	Nelson et al. (2009)
Provisioning, Supporting, Regulating, and Cultural	——	qualitative	McInnes (2013)
Provisioning and Recreation	——	Economic model	Rose and Chapman (2003)
Provisioning, Supporting, Regulating	——	Model	Lautenbach et al. (2010)
Provisioning, Supporting, Regulating, and Cultural	——	Conceptual review	Foley et al. (2005)
Provisioning, Supporting, Regulating, and Cultural	Cultural, Biodiversity	Conceptual review	Tallis et al. (2008)
Provisioning, Supporting, Regulating, and Cultural	——	Conceptual review	DeFries et al. (2004)
Provisioning, Supporting, Regulating, and Cultural	——	Conceptual review	Bennett et al. (2009)
Provisioning, Supporting, Regulating, and Cultural	——	Conceptual review	Carpenter et al. (2009)

Appendix B

Table B1. General study site information

Site code	County	Hydrologic Characteristics	Forest (F) or Herbaceous(H)	Age
1	Cook	Excavated depression	H	19
2	St.Clair	Excavated depression	H	17
3	Hancock	Floodplain	F	19
4	Whiteside	Excavated depression	H	16
5	Ogle	Floodplain, excavated	H	16
5	Ogle	Floodplain	F	16
7	Lake	Excavated depression	H	15
8	Cook	Excavated depression	H	15
9	Champaign	Depression	H	15
10	Cass	Floodplain	F	14
11	Clinton	Floodplain	H/F	14
12	St.Clair	Depression	F	14
13	Alexander	Floodplain	F	14
14	Tazewell	Floodplain	F	13
15	Sangamon	Floodplain, excavated	H/F	13
16	JoDaviess	Floodplain	F/H	13
17	Henry	Floodplain	F/H	13
18	Saline	Excavated depression	H/F	13
19	Pike	Floodplain	F	13
20	Henderson	Floodplain, excavated	H	13
21	Mercer	Floodplain	F	13
22	Stephenson	Excavated depression	H	12
23	Stephenson	Floodplain	F	12
24	Sangamon	Floodplain	H	11
25	Perry	Floodplain	F/H	10
26	Jackson	Floodplain, excavated	F	10
27	Macon	Excavated depression	H	10
28	Jackson	Floodplain	H/F	10
29	Alexander	Floodplain	H	8
30	Winnebago	Floodplain, excavated	H	7

Appendix C

Table C1. NASS Cropland Data Layer categories were combined into four land cover categories used in this study (and open water).

Developed Land	Wetlands	Forest	Agriculture
Developed/Open Space	Woody Wetlands	Deciduous Forest	Grassland Herbaceous
Developed/Low Intensity	Herbaceous Wetlands	Evergreen Forest	Pasture/Hay
Developed/Med Intensity		Mixed Forest	Every crop category
Developed/High Intensity		Shrub land	
Barren			

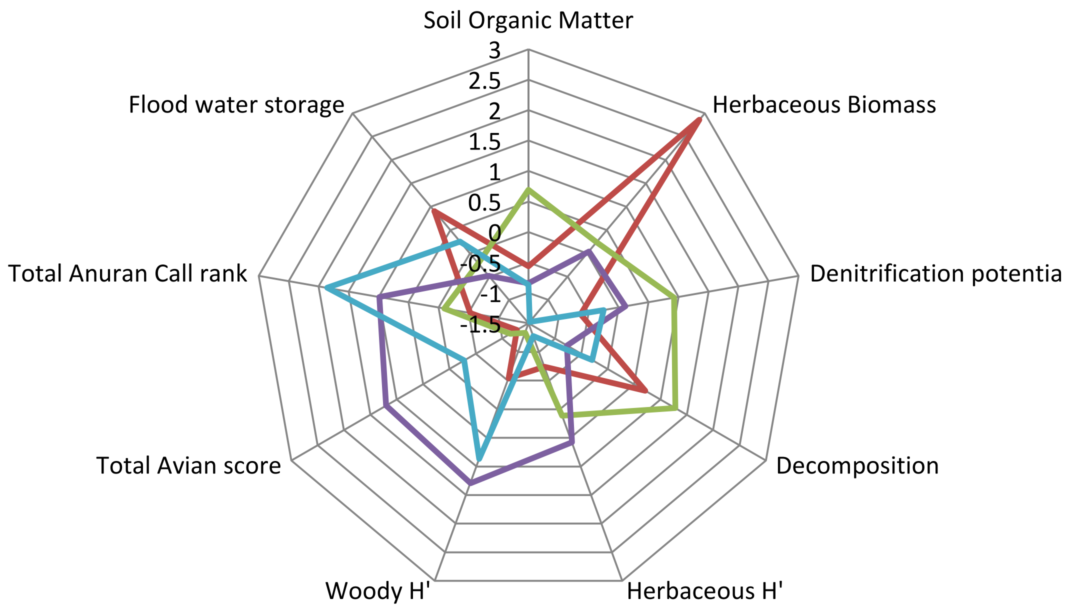
Appendix D

Table D1. Anuran species of Illinois and breeding timeframes (IL DNR 2012).

Species	Breeding Information
Bufo americanus	March to July
Bufo woodhousei	Primarily between May and June
Acris crepitans	Late-April and throughout the summer
Pseudacris triseriata	Early March into May
Hyla cinerea	Mid-May to August
Hyla crucifer	Early March to early June
Hyla versicolor	Later April to August
Rana areolata	Early March to mid-April
Rana catesbeiana	Late April to August
Rana palustris	April to mid-June
Rana pipiens	Mid-March to May
Rana sylvatica	March

Appendix E

Figure E1. Radar graph depicting tradeoffs among ecosystem service variables (standardized). Each line represents a separate site.



Appendix F

Table F1. Site-level data used in PCA and RDA analysis. Table continued on following pages.

Site	Area(ha)	Soil BD (g/cm^3)	G-level ($\mu mol\ s^{-1}\ m^{-2}$)	1-meter ($\mu mol\ s^{-1}\ m^{-2}$)	Nitrogen ($mg\ N\ L^{-1}$)	Age
1	0.7992	1.015818	0.410214	0.531989	0.415	19
2	0.2096	0.740117	0.279123	0.437789	0.18375	17
3	1.3533	1.15545	0.002846	0.024408	0.12375	19
4	1.0388	0.584425	0.241959	0.454711	0.3525	16
5	2.2776	1.014525	0.025948	0.588748	0.2875	16
6	1.1878	0.960715	0.208858	0.887226	0.33625	16
7	0.871	0.730821	0.556522	0.730433	0.33875	15
8	0.9437	0.678748	0.332978	0.844832	0.2675	15
9	1.3307	0.946594	0.109506	0.303788	0.29625	15
10	2.5142	1.276033	0.014687	0.008292	0.10625	14
11	2.7778	1.142373	0.096319	0.525496	0.16875	14
12	0.4736	1.320948	0.21712	0.260691	0.1325	14
13	0.9001	1.190369	0.035154	0.140339	0.0825	14
14	0.2553	1.241387	0.111461	0.143293	0.1025	13
15	3.5363	1.252496	0.41246	0.612407	0.125	13
16	3.1382	0.709188	0.835632	0.939883	0.23	13
17	6.5268	0.785183	0.004424	0.445264	0.29875	13
18	1.5513	1.035813	0.05862	0.024132	0.14625	13
19	7.876	1.066657	0.150671	0.373316	0.175	13
20	3.5534	1.030189	0.25481	0.917614	0.1225	13
21	0.6882	0.793472	0.015313	0.076913	0.295	13
22	4.4724	0.728676	1.313731	1.794613	0.2275	12
23	3.0059	1.058289	0.140944	0.535061	0.2725	12
24	2.3762	1.118851	0.414364	0.77192	0.15375	11
25	1.4337	1.16337	0.016168	0.167111	0.175	10
26	0.6933	1.228968	0.070026	0.236446	0.11375	10
27	4.3858	0.945197	0.030215	0.820281	0.195	10
28	2.273	1.214054	0.263443	0.47206	0.11	10
29	3.1227	1.142951	0.33677	0.740052	0.14625	8
30	7.9832	0.854595	0.38465	0.786524	0.215	7

RCG cover	%nonnative	Woody Stem Density	SOM (%)	Herbaceous Biomass g m^{-2}	DEA potential (mol g^{-1} hr^{-1})
6.357457017	53.85845662	0	7.65625	365.5139	4.9349E-10
0	45.69202566	0.045833333	2.1675	755.1806	1.35133E-10
0	1.92	0.433333333	1.6675	390.9167	2.73388E-10
19.905608	41.67129373	0.179166667	4.32	152.7778	1.51125E-09
4.735013032	5.886185925	0	4.4975	375.3889	4.29025E-09
13.21709038	13.35684813	1.041666667	5.13	436.4722	1.86239E-09
0	52.9454901	0.052083333	4.62875	529.3472	4.54822E-09
11.64929491	43.77682403	0	4.04	306.0952	1.8892E-09
9.118214975	40.16305514	0.183333333	5.21125	449.75	2.93666E-10
0	0	0.439583333	1.71375	13.625	5.66478E-10
9.668943773	36.6001051	0.56875	1.95375	324.1528	2.14899E-10
0	32.47191011	0.414583333	1.67	153.3611	2.73884E-10
0	3.874376284	0.272916667	1.39	169.5556	2.23977E-10
47.43230626	52.41830065	0.160416667	2.6	326.8056	4.93811E-11
0	5.647840532	0.829166667	2.78	202.2361	-2.6277E-10
26.96302451	39.17739925	0.05625	3.12875	29.18056	7.22408E-10
94.38372799	94.8391014	0.222916667	4.5275	338.9167	9.55296E-10
0	29.89690722	0.872916667	1.75375	271.4861	9.74842E-10
6.775067751	28.55691057	0.541666667	2.2025	303.7778	1.62902E-09
0	5.893476205	0	1.63875	312.5278	-2.1792E-10
67.91907514	67.91907514	0.520833333	3.97125	49.49206	8.91244E-10
18.44743016	30.17701002	0.00625	2.82375	74.51389	1.17757E-09
84.5814978	87.33480176	0.1875	3.58	429.7222	6.14668E-10
0	17.60530052	0.045833333	1.92375	130.5139	4.72047E-10
7.805305854	38.87305415	0.710416667	2.07875	72.11111	5.31401E-11
0	28.30286306	0.997916667	1.49875	73.15278	2.24538E-10
0	50.29761905	0.039583333	3.3825	416.1806	8.43016E-10
0	0.923787529	0.2625	1.455	87.79167	1.43243E-10
0	37.59036145	0.004166667	1.98125	196.6389	3.60382E-11
95.1066961	95.1066961	0.00625	2.8475	214.0556	5.39111E-10

%CTSL	Herbaceous Shannon Index	Woody Shannon Index	Basin Volume (m^3)/Ha	Sum of Avian score	Anuran Call Rank	PC axis Riparian (1000m)	PC axis Developed (1000m)
64.53125	2.109272	0	3262.354	49.90867	1	-0.38919	-1.828141014
87.63889	1.561296	0.62549	37888.69	29.63768	4	-0.77786	-0.756220755
91.77083	2.28016	0.31061	1863.296	47.23197	0	1.135221	-0.036804015
80	2.968053	1.49288	3076.984	32.1752	5	-1.18089	1.249127035
82.15909	2.166053	0	119477.2	47.41275	9	0.866071	-0.361530141
83.39286	1.051379	0.056	46.78812	31.58375	1	0.866071	-0.361530141
85	2.559826	1.56742	1691.465	40.78322	1	-1.68978	-2.715900956
97.14286	2.288459	0	7350.269	31.64459	6	-1.17391	-1.935775569
88	3.052341	0.92816	19900.43	45.14179	4	-1.6715	0.945604539
70.72917	1.103583	1.73036	20048.12	45.41437	15	2.264308	0.118282206
42.41667	2.473996	1.87829	2067.224	54.30507	9	0.364402	0.219605833
59.75	3.053127	2.69519	34708.44	31.29384	6	0.556463	0.685074251
87.5	2.107824	1.61515	23101.73	56.05982	4	1.190901	-0.182466356
84.6875	2.442176	1.44572	7927.057	57.15994	3	0.044152	0.714888692
63.06818	2.621309	1.71097	4945.277	50.40272	8	0.2259	-1.730051711
89.16667	2.661739	0	6422.784	74.0183	8	0.300413	0.408792501
75.75	0.343739	0.83322	288.3374	25.27324	2	1.172447	0.200659288
62.8125	2.683497	2.06419	213.6808	68.79739	11	0.701107	0.287053816
69.79167	3.07617	1.83664	2976.936	42.50119	13	0.84586	-0.15826293
78.86364	2.343301	0	93357.14	38.3116	10	0.898103	0.000117813
77.375	1.085086	1.03823	3890.909	35.10741	0	0.108301	0.638671754
83.95833	3.118842	1.09861	4542.452	99.54059	10	-1.40397	0.79043011
86.25	0.646852	0.67686	3806.541	68.0848	2	-1.29706	0.924645507
66.875	2.794982	1.1466	683.4832	61.91174	12	-0.09365	0.724552017
78.64583	2.300153	1.6306	676.7854	46.9131	11	-0.9056	1.011735648
86.25	3.341312	2.16545	1558.159	57.09673	9	0.171682	-1.501737268
75.20833	1.835652	0.51465	3624.629	51.8818	2	-1.47421	0.889699158
11.875	2.565312	1.72167	508.9986	62.5144	13	0.607795	0.116069988
73.125	2.933088	0.69315	3720.143	60.5658	13	-0.58521	0.907568313
87.5	0.229372	0	131.187	52.33721	1	0.32363	0.735842384

openwater1000	dev1000	For1000	Wet1000	Ag1000
0.013523	0.813243	0.091863	0.025414	0.055957
0.012969	0.582815	0.016752	0.031613	0.35585
0.00146	0.064736	0.712095	0.039669	0.182039
0	0.059406	0.060149	0.000743	0.879703
0.102317	0.218858	0.360863	0.012159	0.305804
0.102317	0.218858	0.360863	0.012159	0.305804
0	0.996723	0.000252	0	0.003025
0.001514	0.899041	0.020697	0.005553	0.073195
0.000246	0.142705	0.000328	0	0.856722
0.020674	0.001004	0.299478	0.584303	0.09454
0.009202	0.173903	0.16588	0.163049	0.487966
0.002329	0.043726	0.21837	0.200259	0.535317
0.231899	0.144051	0.215443	0.027342	0.381013
0.020712	0.066118	0.237387	0.014339	0.661445
0.022192	0.673913	0.26087	0.019475	0.023551
0.000679	0.066727	0.487446	0.010405	0.434743
0.132674	0.08426	0.230326	0.094767	0.457973
0.055773	0.055528	0.462084	0.000489	0.426125
0.124116	0.220538	0.077219	0.15848	0.419648
0.088262	0.172009	0.175621	0.129571	0.434537
0.005455	0.096623	0.161039	0.109091	0.627792
0.001539	0.167143	0.014955	0	0.816362
0.00357	0.130299	0.021196	0	0.844935
0.014288	0.083221	0.194246	0.022398	0.685847
0.012075	0.085644	0.05814	0.000224	0.843918
0.024457	0.585725	0.343898	0.00025	0.04567
0.005668	0.144534	0	0.00081	0.848988
0.036967	0.126303	0.402844	0.01564	0.418246
0	0.081775	0.15499	0.018923	0.744312
0.006192	0.035916	0.342711	0.037509	0.577672

Variable notes: Soil BD: soil bulk density, G-level and 1-level: light availability at ground and 1 meter, RCG cover: reed canary grass cover, SOM%: percent soil organic matter content, DEA potential: denitrification potential, %CTSL: percent cotton tensile strength loss.