RESEARCH ARTICLE

Wetland management strategies lead to tradeoffs in ecological structure and function

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Anthropogenic legacy effects often occur as a consequence of land use change or land management and can leave behind long-lasting changes to ecosystem structure and function. This legacy is described as a memory in the form of ecological structure or ecological interactions that remains at a location from a previous condition. We examined how forested floodplain restoration strategy, based on planting intensity, influenced wetland community structure and soil chemical and physical factors after 15 years. The site was divided into 15 strips, and strips were assigned to one of five restoration treatments: plantings of acorns, 2-year-old seedlings, 5-ft bareroot trees, balled and burlapped trees, and natural seed bank regeneration. Our community composition survey revealed that plots planted with bareroot or balled and burlapped trees developed closed tree canopies with little herbaceous understory, while acorn plantings and natural colonization plots developed into dense stands of the invasive species reed canary grass (RCG; *Phalaris arundinacea*). Restoration strategy influenced bacterial community composition but to a lesser degree compared to the plant community response, and riverine hydrology and restoration strategy influenced wetland soil conditions. Soil ammonium concentrations and pH were similar across all wetland restoration treatments, while total organic carbon was highest in forest and RCG-dominated plots compared to mixed patches of trees and open areas. The differences in restoration strategy and associated economic investment resulted in ecological tradeoffs. The upfront investment in larger, more mature trees (i.e., bareroot, balled and burlapped) led to floodplain forested communities, while cheaper, more passive planting strategies (i.e., seedlings, seedbank, or acorns) resulted in dense stands of invasive RCG, despite the similar floodplain hydrology across all sites. Therefore, recovery of multiple ecosystem services that encompass plant and microbial-derived functions will need to include additional strategies for the recovery of plants, microbes, environment, and functions.

Introduction

Anthropogenic legacy effects often occur as a consequence of land use change or land management, and these legacies can have lasting impacts on the structure and function of ecosystems undergoing restoration (Fraterrigo, Turner, et al., 2006; Kulmatiski and Beard, 2011; Hawkes and Keitt, 2015). We define legacy effects as the residual impacts on chemical, physical, and biological factors due to prior land uses such as agriculture or urban development, or previous land management such as restoration activity. Legacies appear as a lingering effect, a memory in the form of ecological structure or ecological interactions that remains at a location from a previous

condition. Restoration outcomes can be unpredictable, and restoration goals may be unmet, due in part to the constraints of lingering legacy effects. Once residual legacy effects are identified, it is critical to consider how restoration strategies can incorporate knowledge of the prior land use in order to enhance restoration outcomes and reduce tradeoffs in ecological functions (e.g., diversity vs. carbon storage) (Jessop et al., 2015; Bürgi et al., 2017). Restoration practices can be modified to improve restoration outcomes in areas that are heavily impacted by humans. Restoration strategies that explicitly address legacy effects can potentially enhance our ability to recover biodiversity and ecosystem functions.

One way to evaluate legacy effects is to study plant, microbial, and soil interactions that directly influence above- and belowground community composition through plant-soil feedbacks. Plants alter microbial community composition by changing resource availability, which can increase plant growth rate. These changes in the microbial community can also feedback to influence plant growth rates (Bever et al., 1997; Reynolds et al., 2003; van der

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Putten et al., 2016). Likewise, enhanced plant growth rate increases plant root exudation which provides carbon and nutrient resources to soil microbes (Stephan et al., 2000; Hooper et al., 2005; Paterson et al., 2009; Dijkstra et al., 2010). However, while some studies have found short-term, rapid microbial responses to these plant inputs (Maul and Drinkwater, 2010; Yan et al., 2017), other studies indicate that the long-term legacy effects of prior land use impact both plants and microbes and may dominate plant-microbial systems for many years (Fraterrigo, Balser, et al., 2006; Kulmatiski and Beard, 2011). Therefore, the holistic recovery of the wetland ecosystems and the monitoring of restoration success should consider the interlocked web of interactions between plants, microbes, and soils (Bissett et al., 2013; Zedler, 2017).

Ecosystem recovery occurs at rates that vary depending on initial conditions and the strategies used to meet project goals (Morrison and Lindell, 2011; Meli et al., 2017), and in some cases, recovery occurs quickly even with minimal input from restoration practitioners. For example, "passive" restoration approaches, including the re-establishment of vegetation through an existing seed bank and natural re-colonization of plants and animals, can be successful in some situations (Řehounková and Prach, 2008; Moreno-Mateos et al., 2015). These passive restoration approaches are low-cost and increase the likelihood that reestablished species are well-suited to the local physical conditions (Mitsch et al., 1998; Prach and Hobbs, 2008). However, passive methods are constrained by the necessity to overcome dispersal limitation and prior land use legacy effects, often making it difficult to achieve specific restoration goals (Dobson et al., 1997; Prach and Hobbs, 2008; Holl and Aide, 2011). In contrast, active restoration approaches provide more control over abiotic conditions and biota, and attempt to "fast-forward" ecosystem recovery. In the case of wetland restoration, active approaches can include physical intervention to restore, create, or enhance wetland ecosystems by altering the topography or hydrology. The active restoration of native vegetation includes intensive planting, often using mature individuals which have a higher survival probability but are more expensive (Stanturf et al., 2004). In addition, active restoration including the removal of invasive species can promote native vegetation reestablishment, but requires additional expenses. Therefore, because active restoration efforts are often more expensive than passive approaches, there is a tradeoff between restoration efficacy and cost.

While direct intervention of land use management can achieve the restoration of wetland communities, natural ecosystem processes such as succession and site hydrology also impact restoration outcomes. For example, the hydrologic dynamics of adjacent river networks regulate floodplain plant and microbial communities due to fluctuations in soil moisture, nutrient, sediment loading, and dispersal (Foti et al., 2012; Foulquier et al., 2013; Konar et al., 2013). Furthermore, flooding can increase sediment loads and deposition rates, especially in low lying riparian areas (Tockner et al., 2010). Changes in soil moisture conditions will directly impact community composition and plant-microbial interactions as microbial

species differ in tolerance to flooded conditions (Peralta et al., 2013; Peralta et al., 2014). In addition, newly deposited sediments can contribute to microbial and plant species pools, which can influence community structure. Therefore, floodplain dynamics have potential to override restoration treatments. In locations where overlapping legacies are found, where a restoration legacy is layered on top of an agricultural legacy, both sets of legacy effects may be erased by flood dynamics.

Land use management and wetland restoration decisions directly impact the reestablishment of soil conditions and biological community composition, but it is unclear whether these decisions introduce a persistent legacy themselves, perhaps on top of a pre-existing land use legacy, especially in a dynamic floodplain setting where present hydrologic influences may eliminate all past legacy effects. Using an experimental approach, we compared how different restoration approaches, which vary in planting intensity, influence microbial and plant community composition after 15 years in a floodplain restoration site. This site was restored as compensatory mitigation for wetlands which were destroyed due to road construction, as mandated under the U.S. Clean Water Act (National Research Council Committee on Mitigating Wetland Losses, 2001). Compensatory mitigation at this site required: (1) 5.9 ha of wetland protection, and (2) the restoration, on former agricultural land, of an additional 6.1 ha of forested wetland which satisfied the federal wetland definition (predominance of hydrophytic vegetation, presence of hydric soils, and present of wetland hydrology), and met minimum floristic quality standards with vegetation characteristic of forested wetland plant communities (Plocher et al., 2003). We addressed the following questions in this study: (1) To what degree does restoration strategy, defined by planting intensity, impact understory plant and soil bacterial community composition and the soil environment? and (2) How does restoration strategy influence wetland plant and soil bacterial community composition compared to reference floodplain wetland conditions? We used a neighboring reference site to determine the efficacy of the different approaches by determining which restoration strategies yielded understory plant and bacterial communities more similar to the reference communities and which strategies were limited by lingering restoration treatment legacy effects. We predicted that, compared to more passive restoration treatments (e.g., relying on an existing seed bank), restoration treatments with an initial investment in planting larger, more mature trees would result in understory plant and soil bacterial communities that were more similar to those of the reference floodplain forest.

Methods
Study site
To address our questions, we used a floodplain restoration site, where past land use was conventional row crop agriculture, located in Henry County, Illinois, USA (41.5525, –90.1849) along the Rock River. This wetland restoration project was established by the Illinois Department of Transportation as compensation
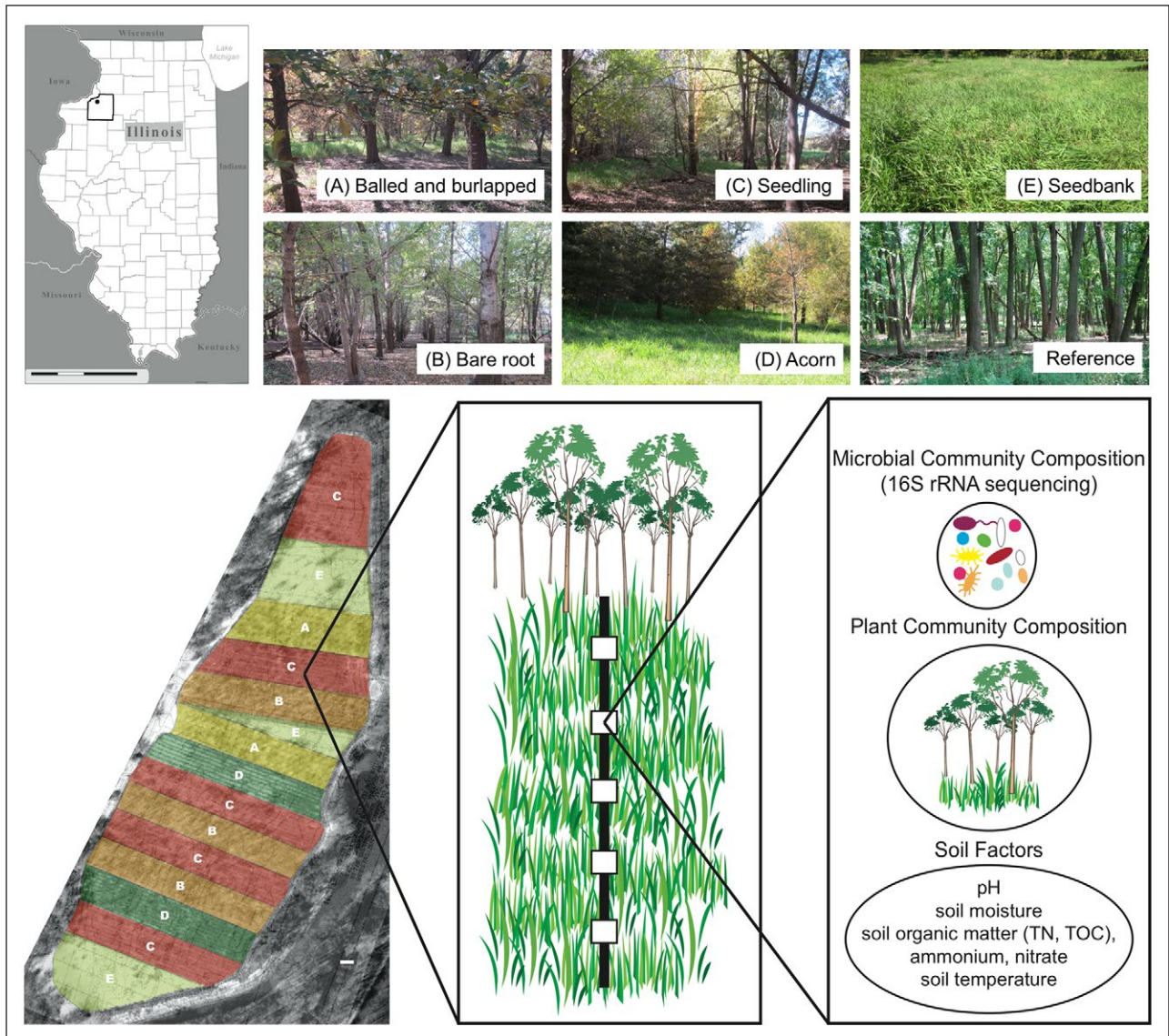
Figure 1: Experimental design of wetland restoration study conducted in Henry County, Illinois, USA. Wetland restoration strategy was replicated at the field scale and sampled after 15 years post-restoration implementation. Images of plant community composition after 15 years of restoration included along with restoration treatments associated with letters on the aerial map A = balled and burlapped, B = bareroot, C = seedling, D = acorn, E = seedbank, and reference floodplain forest wetlands were adjacent to the restored area. DOI: https://doi.org/10.1525/elementa.253.f1

for floodplain forest wetland losses due to bridge construction. The 6.1-ha floodplain wetland site, which was previously used for conventional farming, relies on overbank flooding from the Rock River for hydrologic input, and is adjacent to a 5.9-ha protected floodplain forest. The soils across the wetland were characterized as poorly drained Sawmill silty clay loam, which is a hydric soil type. An experimental mixture of passive and active wetland restoration approaches, which varied in planting method, was applied to the site (Plocher et al., 2003) (**Figure 1**). In 1997 and 1998, the site was divided into 15 strips, and strips were assigned to one of 5 restoration treatments. The five planting methods included replicate plantings of acorns (n = 2), 2-year-old seedlings (n = 5), 5-ft bareroot trees (n = 3), balled and burlapped trees (n = 2), and natural seed bank regeneration (control; n = 3). Site preparation was similar across all treatments.

Planted bottomland trees included silver maple (*Acer saccharinum*), green ash (*Fraxinus pennsylvanica*), sycamore (*Platanus occidentalis*), cottonwood (*Populus deltoides*), river birch (*Betula nigra*), pin oak (*Quercus palustris*), swamp white oak (*Quercus bicolor*), and pecan (*Carya illinoensis*), and the site was managed for 5 years with mowing and herbicide to control invasive species. An adjacent mature floodplain forest and local floodplain dispersal provided natural colonization sources. We revisited the site in 2013, 15 years after planting, and established three, randomly located 50-m transects per treatment type, plus three transects in the adjacent mature floodplain forest as a reference site. Along each transect, a total of five 0.25-m² plots were placed at 10-m intervals (**Figure 1**). At each of the plots, we evaluated plant community composition and collected soil samples for chemical, physical, and microbial analyses.

Soil chemical and physical data

Soil samples representing a composite of eight soil cores, 12-cm deep and 3.0-cm diameter, were collected from each plot. We homogenized soil cores by mixing and passing samples through a 6-mm sieve, and removed plant material prior to soil and bacterial analyses. We measured gravimetric soil moisture by drying 20–30 g of field-moist soil at 105°C for 24 h, and reweighing to quantify moisture as the proportion of water to oven-dried soil mass. We stored a subsample of soil at –20°C for downstream bacterial sequencing. The remaining soil was air-dried and ground to pass through a 2-mm sieve prior to chemical analyses. Air-dried soils were analyzed for soil pH, ammonium, nitrate, carbon, and nitrogen content. The pH of the soil solution (1:1 soil:water) was determined for each composite sample. In addition, exchangeable ions collected from a 2 M KCl soil extraction were analyzed for ammonium (NH_4^+–N) and nitrate (NO_3^-–N) using colorimetric analyses on an auto analyzer (Lachat Instruments/Hach Company, Loveland, CO). Analysis of air-dried soils provides a reliable and reproducible measurement of ammonium and nitrate and appropriate for relative comparisons among wetland soils. This method is broadly used in soil fertility studies (Robertson et al., 1999; Ma et al., 2005; Vandendriessche et al., 2011). Soil organic matter content (total organic C and total N) was analyzed using an elemental analyzer (ECS 4010, COSTECH Analytical Instruments, Valencia, CA, USA). The 18 data points included in analyses represented an average of the five subsamples collected within each of the three replicates for each treatment (five restoration treatments plus the reference wetland). The Iowa State University Soil and Plant Analysis Laboratory conducted analyses of soil pH, total organic carbon, total nitrogen, pH, and inorganic N.

Understory plant community data

To characterize plant communities, we measured understory species percent cover in the five 0.25-m² plot along each sampling transect. All vascular plant species observed in each plot, as well as bare ground, were assigned a cover class (<1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, or 96–100%) to assess plant community composition at the plot-level. In addition, within each sampling plot, all aboveground vegetation from a 30-cm × 30-cm subplot was clipped to the soil surface, dried at 60°C, and weighed to estimate aboveground herbaceous biomass.

Bacterial community data

To characterize bacterial communities, we used a DNA sequencing approach. We extracted and purified soil DNA using the MO BIO d DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, CA) using 0.25 g of homogenized soil. Using ~10 ng of purified DNA for each soil sample, we amplified the V4–V5 region of the 16S ribosomal RNA gene using barcoded primers (bacterial/archaeal 515f/806r primer set) developed by the Earth Microbiome Project (Caporaso et al., 2012). All PCR reactions were run in triplicate, and we cleaned the amplification products using the AMPure XP purification kit, quantified using the QuantIt PicoGreen kit (Invitrogen), and pooled samples at equal molar ratios (final concentration: 10 ng each). We then sequenced the pooled library with the Illumina MiSeq platform using paired end reads (Illumina Reagent Kit v2, 500 reaction kit) at the Indiana University Center for Genomics and Bioinformatics Sequencing Facility. Raw sequences were processed using the mothur software package version 1.39.5 (Schloss et al., 2009).

We used a standard mothur pipeline to process and analyze bacterial sequence data (Kozich et al., 2013). Briefly, we assembled contigs from the paired end reads, quality trimmed using a moving average quality score (minimum quality score 35), aligned sequences to the Silva Database (version 123), and removed Chimeric sequences using the UCHIME algorithm (Edgar et al., 2011). We created operational taxonomic units (OTUs) by first splitting sequences based on taxonomic class and then binning into OTUs based on 97% sequence similarity. For phylogenetic analyses, we picked representative sequences for each OTU based on the most abundant sequence and used FastTree (Price et al., 2010) to generate a phylogenetic tree using the generalized time-reversible model of nucleotide evolution.

Statistical analyses

We tested for differences in soil parameters (soil pH, inorganic nitrogen, total organic carbon, total nitrogen, soil moisture) in response to wetland restoration treatment using analysis of variance (ANOVA) making sure statistical assumptions were met. We used Tukey's Honestly Significant Difference (HSD) to identify between-treatment differences in soil parameters. We compared plant and bacterial communities across the wetland treatments. To visualize the community responses to restoration treatments, we used principal coordinates analysis (PCoA) of plant and bacterial community composition based on the Bray-Curtis dissimilarity. We used a permutational multivariate analysis of variance (PERMANOVA) to examine among-treatment differences in bacterial and plant communities. In addition, we accounted for phylogenetic relationships in the bacterial community by rerunning the PCoA and PERMANOVA using weighted UniFrac distances which accounts for the phylogenetic relationships between organisms and their abundance (Lozupone et al., 2011). To evaluate relationships between communities (plant and bacterial) and between communities and environmental conditions (soil edaphic factors), we used a series of Mantel tests and multivariate linear models. First, we compared community dissimilarity matrices (based on Bray-Curtis dissimilarity) for plant and bacterial communities using a Mantel test. Next, we compared community dissimilarity (based on Bray-Curtis dissimilarity) and environmental distances (based on Euclidean distance for soil edaphic factors) using a Mantel test and distance-based redundancy analysis (dbRDA). Finally, we used indicator species analysis to identify which plant and bacterial species were most representative of each restoration

treatment. For the plant analyses, we included 'bare ground' in addition to the observed plant species to represent the direct impact of shading from floodplain forest cover on herbaceous community composition. For the indicator species analysis, we only included bacterial taxa with a relative abundance greater than 0.05 when summed across all plots.

All statistical calculations were completed in the R environment (R v3.2.3, R Core Development Team 2015) using the vegan and ade4 packages (Dray et al., 2017; Oksanen et al., 2017) and custom function. We performed PERMANOVA using the *adonis* and used the *dbrda* function in the vegan package, we used the *mantel.rtest* function in the ade4 package, and UniFrac distances were calculated using the mothur software package (version 1.39.5).

Results
Wetland restoration strategy altered soils, plant communities, and soil bacterial communities to varying degrees. There were obvious differences in vegetation

structure among specific restoration treatments. Plots planted with bareroot or balled and burlapped trees developed closed tree canopies with sparse herbaceous layers (**Figure 1**). In contrast, acorn plantings and natural colonization plots were dense stands of reed canary grass (*Phalaris arundinacea*). Seedling plantings were spatially variable, with patches of trees and open areas. In general, the restoration treatment and natural successional processes influenced wetland communities.

Soil properties across wetland restoration strategies
Wetland restoration strategy affected soil edaphic factors. Soil moisture differed among treatments (ANOVA, $F_{5,84} = 4.87$, $P < 0.001$) and was highest in the reference wetland compared to restoration treatments, but soil moisture was similar across restoration treatments (Tukey's HSD, **Figure 2**). Soil temperature differed among treatments (ANOVA, $F_{5,84} = 7.14$, $P < 0.0001$) and was highest in the balled and burlapped treatment compared to all other treatments (Tukey's HSD, **Figure 2**). Soil pH
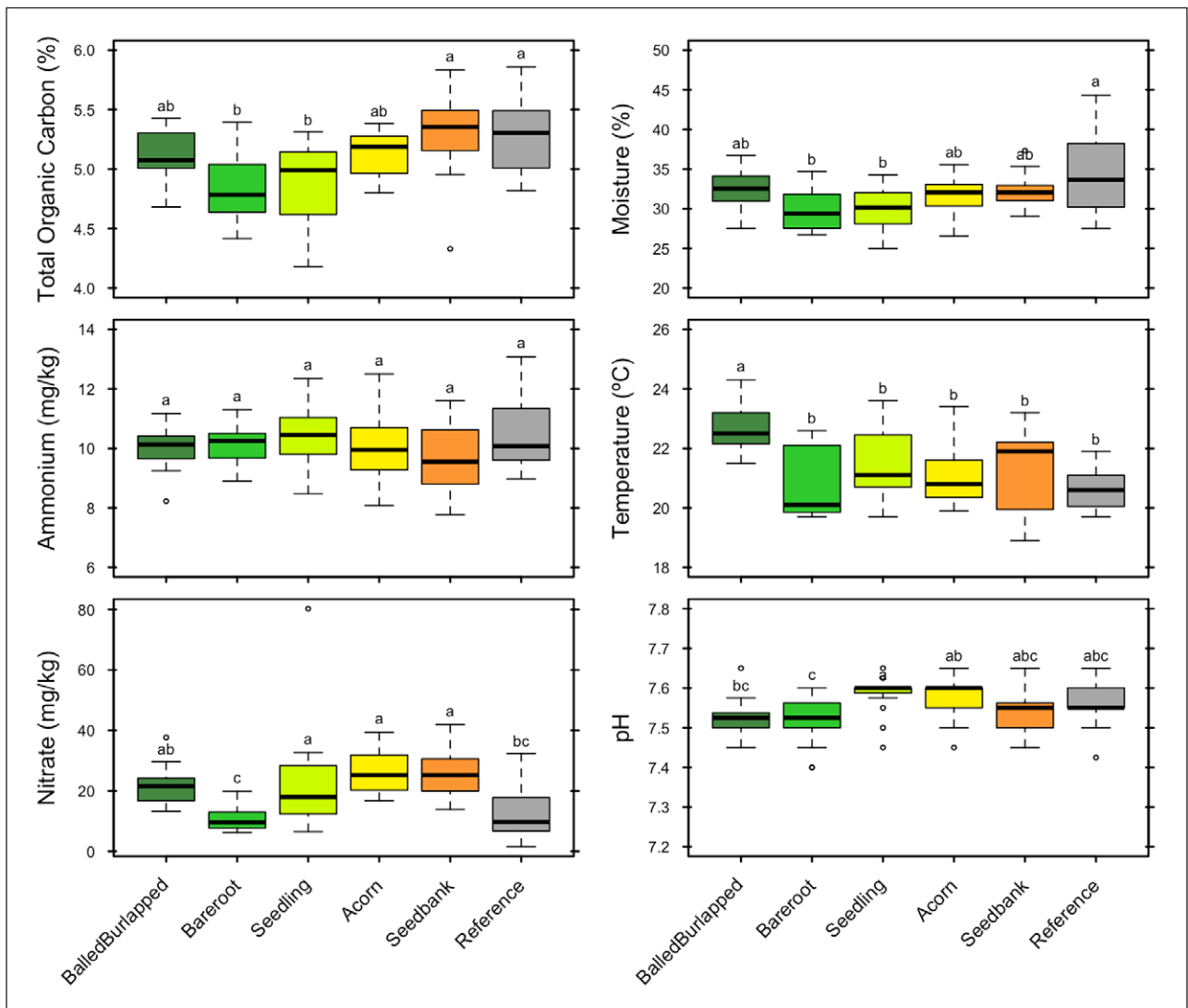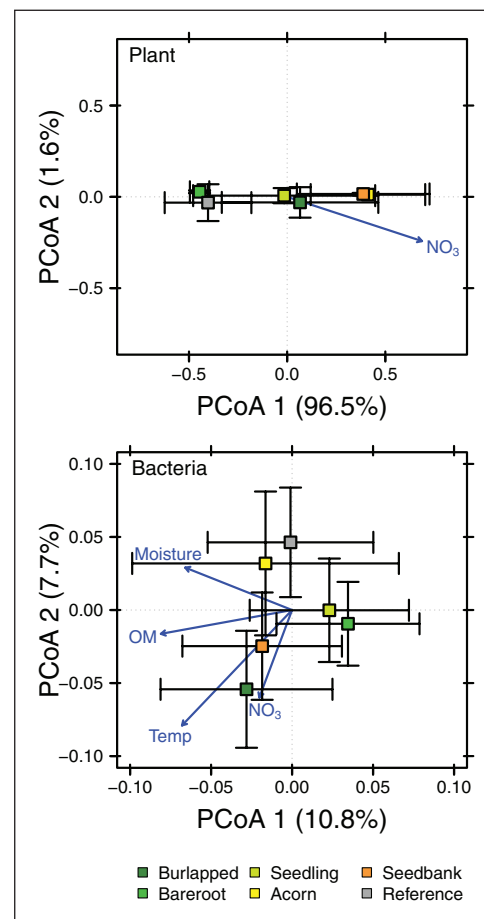

Figure 2: Comparison of soil properties across wetland restoration strategy. Boxplots are colored according to wetland restoration treatments. Different letters above bars are considered significantly different at P < 0.05. DOI: https://doi.org/10.1525/elementa.253.f2

ranged around neutral conditions (pH = ~7.5) for all plots but was slightly higher in the seedling treatment and slightly lower in the bareroot treatment (ANOVA, $F_{5,84}$ = 3.71, P = 0.004, Tukey's HSD, **Figure 2**) For nutrients, ammonium concentrations were similar across treatments (ANOVA, $F_{5,84}$ = 1.47, P = 0.207), while soil total nitrogen (ANOVA, $F_{5,84}$ = 7.15, P < 0.0001) and nitrate differed among treatments (ANOVA, $F_{5,84}$ = 7.11, P < 0.0001), and was highest in seedbank plots and lowest in the bareroot and reference plots (Tukey's HSD, **Figure 2**). Total organic carbon also differed among treatments (ANOVA, $F_{5,84}$ = 5.88, P = 0.0001) and was greatest in the reference plots and seedbank plots, which were dominated by the invasive species *Phalaris arundinacea*. Total organic carbon was lowest in the seedling and bareroot plots (Tukey's HSD, **Figure 2**).

Restoration strategy impacts plant and bacterial communities

Wetland restoration strategy altered the composition of plant and bacterial communities. However, restoration treatment explained more variation in plant community composition than bacterial community composition (PERMANOVA, plant: R^2 = 0.53, P < 0.001; bacteria taxonomic: R^2 = 0.13, P < 0.001; bacteria phylogenetic: R^2 = 0.15, P < 0.001) (**Figure 3**). Based on the principal coordinates analysis (PCoA), the plant communities separated into three groups (group 1: reference and bareroot; group 2: seedling and balled and burlapped; group 3: seedbank and acorn) along the primary axis, which explained 96.5% of the variation among plots (**Figure 3**). Indicator species analysis suggested that the bareroot treatment lacked an understory community, and plots were characterized by bare ground (IndVal = 0.32, P = 0.001), whereas the acorn treatment was characterized by *Phalaris arundinacea* (IndVal = 0.31, P = 0.001), and the reference plots were characterized by *Lemna minor*, an aquatic species apparently deposited by recent flooding, (IndVal = 0.40, P = 0.001), *Acer saccharinum* seedlings (IndVal = 0.20, P = 0.018), and *Bidens frondosa* (IndVal = 0.20, P = 0.02). Finally, *Phalaris arundinacea* biomass differed considerably among treatments (ANOVA, R^2 = 0.401, P < 0.0001) (**Figure 4**).

Based on PCoA, the bacterial communities also separated into three main groups; however, these groups were not as distinct as the plant communities and the primary axis only explained ~10% of the variation among plots (**Figure 3**). Indicator species analysis suggested that there were bacterial taxa (OTUs) unique to each treatment and identified 94 indicator taxa across all treatments (**Tables 1**, S1). The indicator taxa were spread across the restoration treatments with the most being associated with the balled and burlapped treatment (26 OTUs) and the least being associated with the seedling treatment (6 OTUs). The indicators are taxonomically diverse but are especially represented by the Acidobacteria (Gp 3, 4, 6, 7) and Proteobacteria phyla, which included and Bacteroidetes, Flavobacteria Proteobacteria, Gammaproteobacteria, Pseudomonadales, Pseudomonadaceae, Pseudomonas (balled and burlapped),

Figure 3: Ordination from Principal Coordinates Analysis depicting plant (top) and bacterial (bottom) community composition. Symbols are colored according to wetland restoration treatments. Blue vectors represent soil factors that significantly explained patterns in community composition. (NO_3 = nitrate-N, OM = organic matter, Temp = temperature). DOI: https://doi.org/10.1525/elementa.253.f3
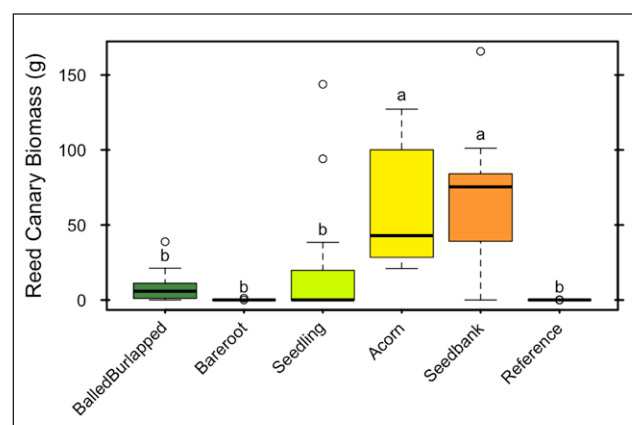
Figure 4: Comparison of invasive species *Phalaris arundinacea* (reed canary grass) biomass across wetland restoration strategy. Boxplots are colored according to wetland restoration treatments. Different letters above bars are considered significantly different at P < 0.05. DOI: https://doi.org/10.1525/elementa.253.f4

Table 1: First five bacterial taxa (OTUs) unique to each wetland treatment according to indicator species analysis. DOI: https://doi.org/10.1525/elementa.253.t1

OTU	Treatment	IndVal	Prob	Phylum/Class/Order/Family/Genus
Otu000173	BalledBurlapped	0.250	0.001	Bacteroidetes/Flavobacteria/Flavobacteriales/Flavobacteriaceae/Flavobacterium
Otu000199	BalledBurlapped	0.244	0.001	Proteobacteria/Gammaproteobacteria/Pseudomonadales/Pseudomonadaceae/Pseudomonas
Otu000180	BalledBurlapped	0.241	0.001	Planctomycetes/Planctomycetacia/Planctomycetales/Planctomycetaceae/Planctomycetaceae_unclassified
Otu000070	BalledBurlapped	0.237	0.003	Bacteria_unclassified/Bacteria_unclassified/Bacteria_unclassified/Bacteria_unclassified
Otu000047	BalledBurlapped	0.226	0.024	Proteobacteria/Gammaproteobacteria/Pseudomonadales/Pseudomonadaceae/Pseudomonas
Otu000030	Bareroot	0.221	0.002	Proteobacteria/Alphaproteobacteria/Rhizobiales/Methylobacteriaceae/Microvirga
Otu000189	Bareroot	0.221	0.002	Bacteria_unclassified/Bacteria_unclassified/Bacteria_unclassified/Bacteria_unclassified
Otu000207	Bareroot	0.215	0.009	Proteobacteria/Deltaproteobacteria/Deltaproteobacteria_unclassified/Deltaproteobacteria_unclassified
Otu000056	Bareroot	0.212	0.009	Acidobacteria/Acidobacteria_Gp6/Acidobacteria_Gp6_order_incertae_sedis/Acidobacteria_Gp6_family_incertae_sedis/Gp6
Otu000211	Bareroot	0.211	0.031	Chloroflexi/Chloroflexi_unclassified/Chloroflexi_unclassified/Chloroflexi_unclassified/Chloroflexi_unclassified
Otu000193	Seedling	0.291	0.017	Proteobacteria/Proteobacteria_unclassified/Proteobacteria_unclassified/Proteobacteria_unclassified
Otu000058	Seedling	0.238	0.001	Proteobacteria/Deltaproteobacteria/Myxococcales/Cystobacteraceae/Anaeromyxobacter
Otu000186	Seedling	0.234	0.033	Proteobacteria/Proteobacteria_unclassified/Proteobacteria_unclassified/Proteobacteria_unclassified
Otu000220	Seedling	0.199	0.040	Proteobacteria/Betaproteobacteria/Betaproteobacteria_unclassified/Betaproteobacteria_unclassified
Otu000078	Seedling	0.197	0.006	Proteobacteria/Deltaproteobacteria/Myxococcales/Myxococcales_unclassified/Myxococcales_unclassified
Otu000119	Acorn	0.260	0.035	Proteobacteria/Gammaproteobacteria/Gammaproteobacteria_unclassified/Gammaproteobacteria_unclassified/Gammaproteobacteria_unclassified
Otu000125	Acorn	0.239	0.001	Proteobacteria/Alphaproteobacteria/Sphingomonadales/Sphingomonadaceae/Sphingomonas
Otu000221	Acorn	0.230	0.004	Bacteria_unclassified/Bacteria_unclassified/Bacteria_unclassified/Bacteria_unclassified
Otu000067	Acorn	0.230	0.002	Acidobacteria/Acidobacteria_Gp4/Acidobacteria_Gp4_order_incertae_sedis/Acidobacteria_Gp4_family_incertae_sedis/Gp4
Otu000212	Acorn	0.227	0.001	Acidobacteria/Acidobacteria_Gp3/Acidobacteria_Gp3_order_incertae_sedis/Acidobacteria_Gp3_family_incertae_sedis/Gp3
Otu000237	Seedbank	0.266	0.029	Proteobacteria/Gammaproteobacteria/Aeromonadales/Aeromonadaceae/Aeromonas
Otu000279	Seedbank	0.263	0.001	Bacteroidetes/Flavobacteria/Flavobacteriales/Flavobacteriales_unclassified
Otu000201	Seedbank	0.258	0.001	Proteobacteria/Deltaproteobacteria/Desulfuromonadales/Desulfuromonadaceae/Desulfuromonas
Otu000268	Seedbank	0.247	0.001	Bacteria_unclassified/Bacteria_unclassified/Bacteria_unclassified/Bacteria_unclassified
Otu000274	Seedbank	0.244	0.008	Proteobacteria/Deltaproteobacteria/Desulfuromonadales/Geobacteraceae/Geobacter
Otu000200	Reference	0.288	0.017	Proteobacteria/Betaproteobacteria/Betaproteobacteria_unclassified/Betaproteobacteria_unclassified
Otu000224	Reference	0.261	0.035	Proteobacteria/Betaproteobacteria/Betaproteobacteria_unclassified/Betaproteobacteria_unclassified
Otu000232	Reference	0.255	0.009	Proteobacteria/Proteobacteria_unclassified/Proteobacteria_unclassified/Proteobacteria_unclassified
Otu000275	Reference	0.233	0.024	Proteobacteria/Proteobacteria_unclassified/Proteobacteria_unclassified/Proteobacteria_unclassified
Otu000117	Reference	0.226	0.005	Acidobacteria/Acidobacteria_Gp7/Acidobacteria_Gp7_order_incertae_sedis/Acidobacteria_Gp7_family_incertae_sedis/Gp7

Proteobacteria, Alphaproteobacteria, Rhizobiales, Methylo bacteriaceae, Microvirga (bareroot), Proteobacteria_unclassified (seedling), Gammaproteobacteria_unclassified (acorn), ProteobacteriaBetaproteobacteria_unclassified (reference) (**Tables 1**, S1).

While restoration treatment influenced plant community composition more strongly than bacterial community composition, a correlated community response between plant and bacterial community composition was detected. A Mantel test indicated that there was a small yet significant correlation between the Bray-Curtis distance matrices for plant and bacterial communities (Mantel r = 0.10, P = 0.001). Likewise, the primary axis in the plant community PCoA correlated with a small yet significant amount of the variation in bacterial community composition (dbRDA: R^2 = 0.04, $F_{1,82}$ = 3.06, P = 0.001).

Soil environment influences plant and bacterial communities

Although wetland restoration strategy altered the soil environment, the soil factors had different relationships with the plant vs. bacterial communities. A comparison of the soil environment which includes all measured chemical and physical soil factors and bacterial community composition revealed no overall relationship (Mantel r = –0.02, P = 0.54). However, when we separated the soil environment into soil edaphic factors and soil nutrients, there was no correlation between the bacterial community and soil nutrient concentrations (Mantel r = –0.04, P = 0.68); but there was a relationship between the bacterial community and soil physical characteristics (Mantel r = 0.16, P = 0.02). In contrast, a comparison of the soil environment and plant community composition revealed a positive correlation (Mantel r = 0.25, P = 0.001), and this relationship was supported by nutrient concentrations (Mantel r = 0.27, P = 0.001) and, weakly, by physical characteristics (Mantel r = 0.04, P = 0.02).

We further examined the relationships between soils factors and biological communities to identify which soil factors correlated to community patterns. Soil nutrients (total organic C, ammonium, nitrate), but not edaphic factors, significantly explained patterns in plant community composition (dbRDA model adjusted R^2 = 0.164; nutrients: $F_{1,80}$ = 13.4, P = 0.001, adjusted R^2 = 0.194; edaphic: $F_{1,80}$ = 1.20, P = 0.282) (**Figure 3**). Nutrients and soil edaphic factors (pH, temperature, and moisture) weakly accounted for bacterial community variation (dbRDA model adjusted R^2 = 0.070; nutrients: $F_{1,76}$ = 2.90 P = 0.001; edaphic: $F_{3,76}$ = 2.14, P = 0.001) (**Figure 3**).

Discussion

In this study, the restored wetland satisfied the federal wetland definition (i.e., predominance of hydrophytic vegetation, hydric soils, and characteristic wetland hydrology), but achieved a floristic quality similar to target forested wetlands only in areas that were free of invasive reed canary grass. Our study provided evidence that the effectiveness of wetland mitigation relies on initial management strategy, resulting in restoration treatment legacy effects. We determined the outcomes of various wetland restoration strategies by comparing community composition of restorations to reference floodplain forest communities. Investment in larger planted trees resulted in a more predictable plant community trajectory toward the intended restoration goal, and bypassed dominance by invasive species. Active restoration strategies, including planting more mature trees, accelerated wetland forest plant community establishment and resulted in distinct plant communities dominated by floodplain forest communities, while less intense planting strategies (e.g., acorn planting and reliance on existing seedbanks) yielded wetlands dominated by an invasive reed canary grass (RCG, *Phalaris arundinacea*).

Hydrology is essential for wetland community composition – for both plants and bacteria. Because hydrology is so important, it has the potential to override restoration treatments. Based on community composition, not all restoration treatments used in this study yielded plant or bacterial communities which resembled reference plots (**Figure 3**). In fact, active human intervention was necessary to achieve restoration of plant communities and avoid dominance by a fast growing invasive species. Despite natural successional processes and the similar hydrology across the site, different treatments led to alternative community structure. Local hydrology is known to affect sedimentation, redox, oxygen, and nutrient availability important for restoration of ecosystem functions (Peralta et al., 2012; Peralta et al., 2014). In turn, variation in the physiological requirements of microorganisms influences the composition of microorganisms that persist under environmentally variable conditions (e Silva et al., 2012; Hawkes and Keitt, 2015). Likewise, plant communities are also strongly driven by hydrology and nutrient flux (Flinn et al., 2010). Nevertheless, our study revealed that development of plant communities similar to reference wetlands was dependent on initial restoration treatment despite similar riverine hydrology across the study site.

Former agricultural land use has its own legacy effects. These effects, we can assume, were also similar across our study site. Despite these similarities in hydrology and former land use, initial restoration treatment left a strong legacy of its own 15 years after restoration. Not all treatments yielded communities similar to the reference site. Specifically, human intervention in the form of active restoration was necessary to achieve restoration and avoid dominance by an invasive species. In this particular restoration context, with stressors from flooding, former agricultural land use, and surrounding agricultural land use, passive restoration was ineffective due to the fact that RCG thrives under these conditions. However, active planting was able to override this default trajectory. As we expected based on our initial prediction, more active intervention (i.e., mature plantings) led to restorations that more closely matched the reference floodplain forest.

Even though managing bacterial community composition is not incorporated into wetland design, monitoring, or evaluation, bacterial communities are

essential for restoration of wetland functions related to nutrient cycling (Peralta et al., 2013; Peralta et al., 2016). Given the importance of microorganisms in plant-soil feedbacks and ecosystem function, monitoring bacterial community composition may provide insights into the relative effectiveness of alternative restoration strategies. Our indicator species analysis found that some taxonomic groups of bacteria were common indicators across treatments, while others were more characteristic of specific restoration treatments. Many of the bacterial taxa identified as indicators were members of the Acidobacteria and Proteobacteria phyla (**Tables 1**, S1). These phyla represent taxonomically and functionally diverse organisms typical in wetland sediments (Newton et al., 2011). For example, taxa in the phyla Acidobacteria have been shown to respond to nitrogen additions (Amend et al., 2016), and Acidobacteria and Proteobacteria are associated with higher potential for biogeochemical cycling of nitrogen, phosphorus, carbon, and sulfur (Li et al., 2014). Given that the restored wetland in this study is located on former agricultural land in an agriculturally dominated watershed (~62% land cover representing continuous corn, corn-soybean, and corn-hay) and thus receives non-point source nitrogen and phosphorus inputs due to fertilizer runoff (Kirsch, Kevin et al., 2002), our findings suggest that current or former local nutrient inputs drive bacterial community responses. However, a more detailed analysis provides further insight into the effects of different restoration strategies. For example, taxa in the order Rhizobiales are representative of nitrogen-fixing microorganisms (Bahulikar et al., 2014; He et al., 2015), and our indicator species analysis found that bacterial taxa belonging to the order Rhizobiales were characteristic of the balled and burlapped, bareroot, and reference plots. The soil nitrate concentrations in these plots were low compared to seedling, acorn, and seedbank plots, possibly due to increased plant N uptake in the plots with more mature trees (**Figure 2**). Furthermore, members of the class Deltaproteobacteria, specifically Desulfuromonales and Geobacter (**Tables 1**, S1), which are indicative of anaerobic sediment processes (Coates et al., 1996), were characteristic in the seedbank plots. These findings suggest that restoration strategy has an impact on bacterial community composition and that investment in more mature plants promoted the plant-microbe interactions which were characteristic of the reference plots.

While wetland restoration strategy strongly influenced plant and bacterial community patterns, other factors such as local hydrology affected the floodplain wetland by transporting and depositing sediment and nutrients. However, the influence of riverine hydrology varied for different wetland soil parameters. For example, while soil ammonium and pH were similar across all treatments, soil nitrate was highest in the RCG-dominated acorn and seedbank treatments (**Figure 2**). Interestingly, soil carbon levels in RCG-dominated plots were observed to approach levels equivalent to those of reference wetlands. Thus, the least successful treatments at restoring plant communities similar to the reference plots were, in fact, the most successful at restoring soil organic C. Usually, soil carbon changes slowly over time (Campbell and Paustian, 2015); however, the combination of wetland restoration and floodplain hydrologic dynamics may be providing faster sedimentation and input of organic carbon and stabilization. While restoration strategy resulted in distinct plant communities, both floodplain forest and invasive RCG-dominated wetlands resulted in similar carbon storage capacity (**Figure 2**). A recent study by Jessop et al. (2015) also found that RCG-dominated restored wetlands to have greater soil organic C relative to wetlands dominated by native species. Two potential reasons for this outcome are: the high *in situ* aboveground biomass of RCG adding soil C, and the dense nature of RCG stands enhancing soil C by trapping and sequestering sediments in flood waters. These results suggest that metrics describing plants, microbes, and soils are needed to evaluate restoration outcomes.

Our study suggested that wetland restoration success is strongly influenced by both hydrologic context and human interventions that included local wetland vegetation plantings. Riverine inputs influenced the entire wetland, however, the restoration treatments imposed a change in plant community composition and helped establish unique plant-microbe interactions locally. Despite the overwhelming influence of hydrology on wetland structure and function in other studies, and the fact that hydrological conditions did not differ systematically among treatments, we observed a strong influence of imposed restoration treatment on plant communities and a subset of soil factors. Furthermore, we found that restoration influenced bacterial communities, and while the overall effect of treatment was less pronounced, perhaps due to hydrological similarity among treatments, we did find characteristic taxa suggesting the development of plant-microbe interactions in the treatments where more mature plants were introduced during restoration.

Restoration strategies which include vegetation plantings are critical for accelerating restoration towards a reference goal. These initial decisions can set up community assembly trajectories, resulting in lingering restoration treatment legacies. However, it is challenging to maximize different components of ecosystem functions using a single restoration strategy. In our study, investment in larger, more mature trees led to forested floodplain communities while more passive planting strategies (i.e., seedbank or acorn plantings) led to invasive species dominated communities. As such, our study suggested that initial management decisions regarding restoration strategy have lasting effects beyond the 5-year mandated monitoring as required by the Clean Water Act, even 15 years after wetland restoration began. The implications of these management decisions resulted in alternative trajectories: either forested communities resembling reference sites or communities dominated by the invasive reed canary grass. Because our sites share common riverine hydrological conditions, it appeared that initial restoration strategy and the use of larger plantings (i.e., balled and burlapped vs. passive

seedbank) played a more significant role in community trajectory than hydrological connectivity.

Data Accessibility Statement

All data analyzed in this study and code for sequence processing and statistical analyses are publicly available at https://github.com/PeraltaLab/IL_Wetlands. Raw sequence files are available on the NCBI SRA (BioProject PRJNA393844).

Supplemental File

The supplemental file for this article can be found as follows:

- **Table S1.** List of 94 indicator taxa (OTUs) that were unique across all wetland restoration treatments based on indicator species analysis, xlsx. DOI: https://doi.org/10.1525/elementa.253.s1

Competing interests

The authors have no competing interests to declare.

Author contributions

- Contributed to conception and design: ALP, JWM
- Contributed to acquisition of data: ALP, JWM
- Contributed to analysis and interpretation of data: ALP, MEM, JWM
- Drafted and/or revised the article: ALP, MEM, JWM
- Approved the submitted version for publication: ALP, MEM, JWM

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