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RESEARCH ARTICLE

Wetlands Reserve Program restorations improve floristic quality of understory plant community over time, but community differs from reference wetlands

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The lower Mississippi River Valley and connecting tributaries have lost an estimated 80% of original bottomland hardwood forested wetlands to agricultural conversion. For the past three decades, the Wetlands Reserve Program has restored thousands of wetlands with the objective of recovering wetland functions and supporting wildlife diversity. To inform future restoration decisions, we assessed the recovery of the naturally colonizing understory plant community in wetlands restored from row-crop agriculture in western Kentucky, U.S.A. We measured six floristic variables in 16 wetlands along a gradient of disturbance (degraded, restored, and reference) and a chronosequence ranging from 0 to 13 years since restoration. We found that reference wetlands had significantly higher floristic quality and a higher proportion of woody and perennial species than restored wetlands. Over time, the proportion of non-native species decreased in restored wetlands and floristic quality increased. The successional trajectory of naturally colonizing plant communities in restored wetlands was likely inhibited by dispersal limitations, thus future projects should focus on optimizing project locations to increase recruitment, continue afforestation efforts for heavy seeded trees, and consider planting native understory species. Long-term project monitoring, approximately three decades, will likely provide deeper insight into recovery trajectory. With ongoing biodiversity loss and the effects of climate change, the success of wetland restorations has important local and global implications.

Key words: bottomland hardwood forest, plant community, restoration, understory, wetland, Wetlands Reserve Program

Implications for Practice

- The naturally regenerating understory plant community in WRP restored wetlands on agricultural lands needs more than 6 years to resemble the understory of mature bottomland hardwood forests. Restoration timelines and monitoring checkpoints should be designed to correspond with a long recovery period.
- To facilitate dispersal and recruitment of desirable naturally colonizing wetland plant species, restored wetlands should be located near remnant forested wetlands, or restoration efforts should include plantings of dispersal limited understory species.

Introduction

The floodplains of the lower Mississippi River and connecting tributaries were once covered by an unbroken expanse of wetlands that provided valuable ecosystem services such as flood attenuation and nutrient retention (Jenkins et al. 2010; De Groot et al. 2012). The ridge and swale topography and seasonal flooding pattern of these floodplains created ideal conditions for the development of a specific wetland type, the bottomland hardwood forest, which supported a diverse wildlife community, including migratory birds (King & Keeland 1999). Since European settlement, an estimated 80% of the original bottomland hardwood forest has been converted to agriculture (King & Keeland 1999) and the remaining wetlands exist in a landscape that has been severely altered hydrologically to support agriculture. The loss of bottomland hardwood forested wetlands comes at the cost of lost ecosystem services in a region where nutrient run-off is highest in the nation (Jenkins et al. 2010; Cheng et al. 2020).

For over three decades, wetland restoration efforts, spearheaded by the Wetlands Reserve Program (WRP), have endeavored to reestablish historic bottomland hardwood wetlands in the Mississippi River watershed (Faulkner et al. 2011; U.S. Department of Agriculture 2021). The WRP is a partnership between the federal government and private landowners

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designed to restore wetlands on marginal agricultural lands. The objectives of the WRP are to maximize wetland functions and values with a focus on improving water quality and increasing benefits to wildlife (U.S. Congress 1990, 2018). Under the program, over 2.5 million acres of wetlands in the United States have been restored (U.S. Department of Agriculture 2020) and project density is especially high along the lower Mississippi River where agricultural development has diminished the historic extent of bottomland hardwood forests (U.S. Department of Agriculture 2021). Restoration efforts have largely been found to improve ecological integrity, biodiversity, and function of wetlands (Stryszowska-Hill et al. 2019; Lee et al. 2020), but it is unclear whether restored wetlands can fully mitigate historical wetland losses (Moreno-Mateos et al. 2012). For example, numerous studies have found that restored wetlands differed floristically from reference wetlands (Moreno-Mateos et al. 2012; Stefanik & Mitsch 2012; Salaria et al. 2019).

Early restoration efforts of bottomland hardwood forests in the Mississippi Alluvial Valley were primarily focused on afforestation: planting heavy-seeded, dispersal-limited, wetland-adapted tree species like *Quercus* spp. (oak) and *Carya* spp. (hickory) (King & Keeland 1999; Schoenholtz et al. 2001; Haynes & Egan 2004) to increase overstory diversity (Twedt 2004). Hydrologic wetland restoration was infrequent at first, but is now common, after studies showed that altered hydrology leads to the failure of planted areas (Haynes & Egan 2004; King et al. 2006). After afforestation and hydrologic modifications are completed, restoration then transitions to a passive form, where natural succession is expected to develop mature bottomland hardwood forests, including the understory and herbaceous communities (Hodges 1997; Middleton 2003; Battaglia et al. 2008; De Steven et al. 2015). The recovery of the forest community in WRP restored bottomland hardwood wetlands thus depends on a combination of afforestation and natural colonization. Despite the importance of natural colonization in the succession process, especially to the understory community, research on the trajectory of plants that establish from regional and on-site seed banks in restored bottomland hardwood wetlands is scarce (Battaglia et al. 2002; De Steven et al. 2015). Furthermore, although the WRP has been active along the lower Mississippi River for over three decades, the recovery of the naturally regenerating plant community in wetland restorations has rarely been evaluated (Faulkner et al. 2011; Wortley et al. 2013). We are aware of only a single study addressing the natural regeneration of the understory community of WRP restored bottomland hardwood wetlands (De Steven et al. 2015).

Existing research indicates that some barriers to full recovery of the naturally colonizing tree community are agricultural disturbance history (Middleton 2003), dispersal limitations (Twedt 2004; Battaglia et al. 2008), and site conditions like flooding regime (Matthews et al. 2019), but we know very little about what factors limit the naturally colonizing understory community in bottomland hardwood forests. The success of future WRP restorations is contingent upon understanding the limitations of the developing plant community and adapting management techniques to address these limitations. Therefore, our study aimed to determine the recovery trajectory of the naturally colonizing understory plant community of restored wetlands enrolled in the WRP. The objectives of our study were to (1) determine if the vegetation composition of restored wetlands resembles mature bottomland hardwood forests and (2) determine the trajectory of plant recovery with time since restoration. We hypothesized that the naturally colonizing understory plant community of restored wetlands would be different from reference wetlands, and as wetlands aged, the plant community would become increasingly similar to that of reference wetlands.

Methods

Study Area

Our study was conducted in the Mississippi Alluvial Plain and the Mississippi Valley Loess Plain ecoregions of western Kentucky, which are characterized by relatively flat topography and poorly draining soils (Woods et al. 2002). The Mississippi River, which runs along the western border of Kentucky, drains three tributaries in our study area (Fig. 1). The region is dominated by cultivated crops and pasture (64%) and, to a lesser extent, by forested wetlands and upland forests (25%) (Dewitz 2019). Remnant wetlands in the region are classified as riverine wetlands (U.S. Department of Agriculture 2008), are dominated by flood-tolerant hardwoods like oaks, gums, and hickories, and are confined by widespread agriculture to the floodplains of regional tributaries. The region's mean annual rainfall of 1,200 mm is seasonal, with higher amounts in the winter and spring and declining amounts in summer and fall (National Climatic Data Center, Climatological Summaries, http://www.ncdc.noaa.gov/).

Wetland Selection

All study wetlands were located in the floodplains of three tributaries draining to the Mississippi River (Mayfield Creek, Obion Creek, and Bayou de Chien Creek). Although the region is extensively cultivated, remnant floodplain wetlands persist along tributaries and WRP restoration projects have targeted wetland coverage in floodplain areas. Our study was designed to capture the floodplain wetland disturbance gradient (degraded, restored, reference) with the goal of assessing the ecological condition and restoration progress of the understory plant community and ultimately making recommendations to improve the administration of WRP projects.

We sampled a total of 16 wetland sites: two degraded, nine restored, and five references (Fig. 1). We obtained WRP easement information from the Natural Resources Conservation Service (NRCS) to guide our wetland selection process. We used the following criteria for selecting restored sites: (1) location along one of three western Kentucky tributaries to the Mississippi River, and (2) similarity of attributes among wetlands in terms of wetland type (floodplain), hydroperiod (semi-permanent to permanent as per Cowardin et al. 1979), and size. Prior to restoration, selected easements were in various states of

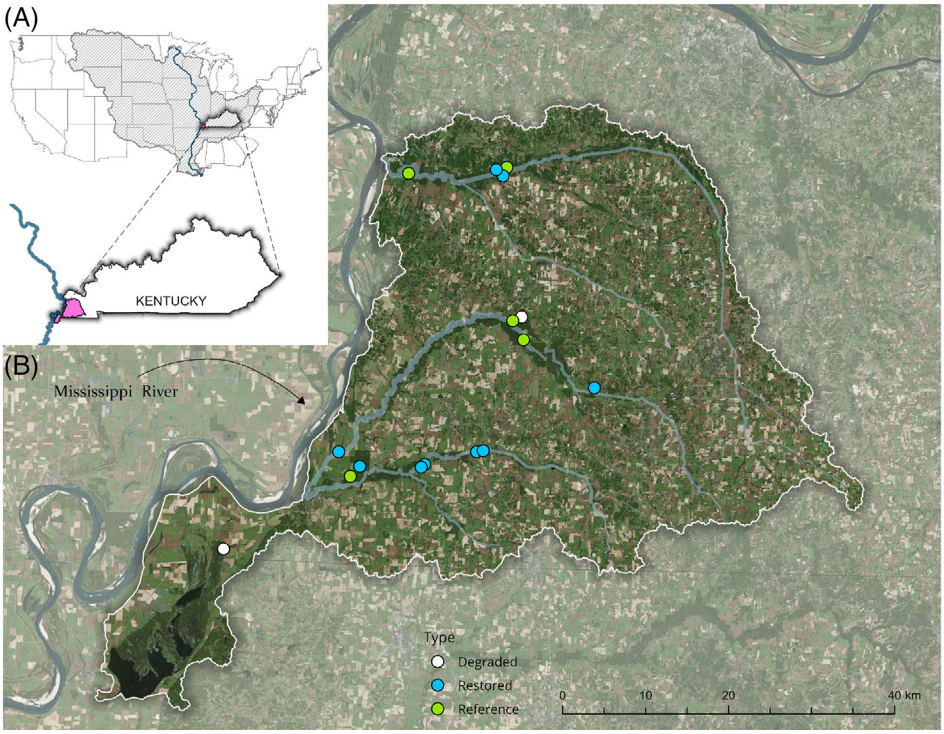

Figure 1. Aerial imagery of the study area (Esri et al. 2017) located in (A) the Mississippi River watershed in western Kentucky. (B) Sixteen study wetland sites; including nine WRP restored wetlands, two degraded wetlands, and five reference wetlands; located along three tributaries to the Mississippi River.

cultivation and were intersected by networks of drainage ditches. Easements were restored using a variety of engineering techniques to reestablish hydrology: levee breaks, excavation of shallow water areas, and ditch plugs. Some wetlands were planted to initiate forest growth, a process that included mowing, applying herbicides, and planting bare-root seedlings of oaks, hickories, and baldcypress. Some easements are managed under Compatible Use Agreements, which include food plot planting, mowing, and water level management (J. Pieper 2021, NRCS, personal communication). Selected WRP wetland easements ranged in area between 14 and 317 ha and in age since hydrologic restoration between 2 and 13 years. Restored wetlands older than 20 years are rare in the region because the WRP was initiated only 30 years ago. Currently, most easements are in the early succession phase post-restoration and are dominated by herbaceous vegetation.

To compare our restored sites to wetlands on the extremes of the disturbance gradient, we also selected sites that were classified as having either low ecological integrity (degraded wetlands) ($n = 2$) or high ecological integrity (reference wetlands) ($n = 5$). Degraded wetlands are areas that were historically wetlands but were drained for agricultural use. Although severely altered hydrologically, degraded wetlands continue to exhibit some wetland characteristics, like hydrophytic vegetation. Both degraded wetlands were low areas adjacent to actively row-cropped fields and were chosen to characterize the condition of restored wetlands prior to restoration. The hydrology, geomorphology, and plant community composition of degraded wetlands represents the baseline condition for the restoration sites. Reference wetlands are natural wetlands that are not hydrologically altered, although they do exist in a generally hydrologically modified landscape. All of our reference sites were floodplain forests; four were located in Wildlife Management Areas managed by the Kentucky Department of Fish and Wildlife Resources, and one was a hydrologically undisturbed wetland on one of the enrolled easements. To control for landscape position, we attempted to select reference and degraded wetlands close to restored sites.

Plant Sampling

Degraded and restored wetlands lacked a developed forest overstory, so for these sites, we sampled the emergent, shrub, and aquatic plant communities. For reference forested wetlands, we focused our sample collection on the understory community only (all herbaceous and woody species with DBH < 10 cm).

We sampled vegetation once per wetland in July–September of 2020 and 2021, which corresponded to peak growing season in the region. We followed a relevé method originally described by Braun-Blanquet (1932). Prior to sampling, we visited each wetland and identified dominant plant communities, that is, emergent, shrub, or aquatic. In each wetland we laid out four 10×10–m plots at least 50 m apart. Each plot was placed to be uniform in vegetation composition (i.e., representative of one of the identified community types) and structural components such as slope, substrate, and hydrology within each plot.

Table 1. Summary of the plant community metrics of degraded ($n = 2$), restored ($n = 9$), and reference ($n = 5$) wetlands in floodplains of western Kentucky.

	Degraded				*Restored*				*Reference*			
	Mean	*SD*	*Min*	*Max*	*Mean*	*SD*	*Min*	*Max*	*Mean*	*SD*	*Min*	*Max*
Richness and diversity												
Total taxa richness	33.0	2.8	31.0	35.0	32.2	11.3	19.0	51.0	32.0	8.2	24.0	45.0
Adjusted floristic quality index	34.3	1.1	33.5	35.1	37.4	2.3	32.5	40.6	48.5	2.4	46.9	52.2
Proportion of species in functional group												
Non-native	0.16	0.04	0.13	0.18	0.13	0.05	0.06	0.22	0.06	0.05	0.00	0.12
Hydrophytic	0.73	0.11	0.65	0.80	0.74	0.13	0.52	0.87	0.60	0.16	0.41	0.81
Perennial	0.63	0.04	0.60	0.65	0.73	0.07	0.62	0.83	0.93	0.03	0.89	0.96
Woody	0.17	0.06	0.13	0.21	0.21	0.14	0.03	0.43	0.49	0.16	0.37	0.75

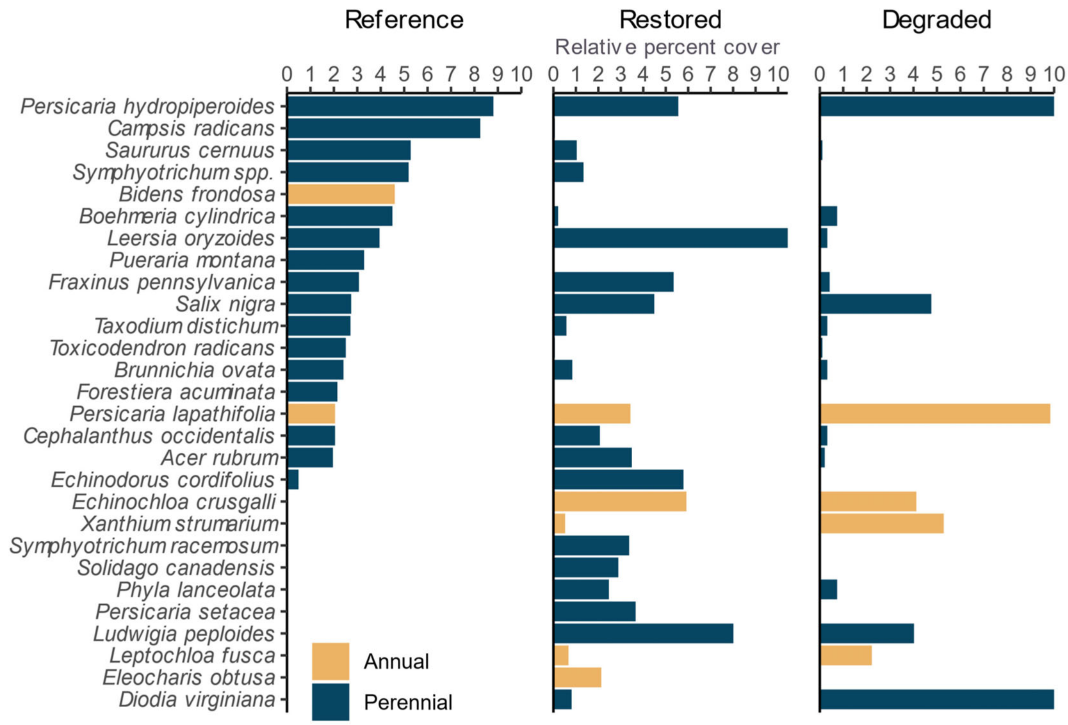

Figure 2. Relative percent cover of the 28 most common understory plant species in reference, restored, and degraded wetlands. Relative cover of a species for each wetland type was calculated by summing the mid-points of the cover classes for that species across all plots in one wetland type and dividing by total species cover for that wetland type. For each wetland type, species with relative percent cover greater than 2% were selected as most common (28 of 198 taxa).

In each sampling plot, all species were identified to the lowest taxonomic level and the abundance of each taxon was visually estimated using six cover classes (<1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–100%). We calculated the relative cover of each species in each wetland by summing the mid-points of the cover classes for that species across the four plots and dividing by the total species cover for each wetland.

Plant Classification and Metrics

Plant species names were based on the United States Department of Agriculture (USDA) Plants database (http://plants.usda.gov). Plants were classified as (annual/perennial and woody/herbaceous) based on the USDA Plants database. Nativity status (native/non-native) was determined using the Tennessee-Kentucky Plant Atlas (https://tennessee-kentucky.plantatlas.usf.edu/) and supplemented by the USDA Plants database. We grouped species into wetland-fidelity categories obtained from The National Wetland Plant List for the Atlantic and Gulf Coastal Plain region (U.S. Army Corps of Engineers 2018). Plants classified as "hydrophytic" species included all OBL (obligate wetland) and FACW (facultative-wet wetland) species. Each species was assigned a coefficient of conservatism (C) value (Swink & Wilhelm 1994), which expresses the propensity of plants to occupy the least-altered habitat.

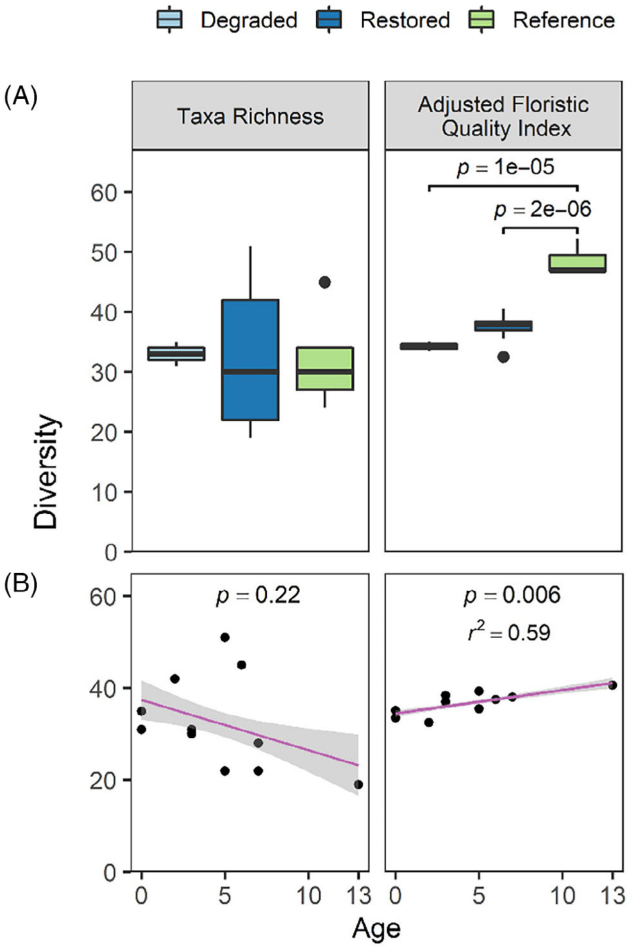

Figure 3. (A) Understory plant community richness and diversity metrics for degraded, restored, and reference floodplain wetlands of western Kentucky. Plotted values for the box are median (50% quantile) ±25% quantile. Statistically significant results are indicated as *p* values on the plot. (B) Linear relationships between richness/diversity metrics and wetland age. Red line represents the fitted regression line, and the shaded region represents the 95% confidence interval of the fitted values. Degraded sites are represented by an age of 0 and restored sites by years since hydrologic restoration. Reference sites are not included in the models. *p* Values are reported for all regressions, and r^2 values only for significant results.

C values are developed regionally by expert botanists, and we used a database developed for southeastern U.S. wetlands (Gianopulos 2014). All non-native species were assigned a *C* value of zero. Plants only identified to genus were not assigned a wetland-fidelity category or *C* value, but some were assigned nativity status when possible and classified into functional groups based on the known species occurring in Kentucky.

To compare the floristic composition of wetland disturbance categories, we assessed plant metrics that encompassed function, composition, and conservation value. To explore indicators of diversity and floristic quality, we calculated total taxa richness and the adjusted floristic quality index. The adjusted floristic quality index is an index of biotic integrity developed by Miller and Wardrop (2006) as an adjustment to the more widely used floristic quality index. Both indices determine the biotic integrity of the plant community using *C* values of native species, but the adjusted index is less sensitive to species richness than the floristic quality index (Miller & Wardrop 2006). The adjusted floristic quality index is calculated as $100\left(\frac{\underline{C}_n}{10}\right)\left(\frac{\sqrt{N_n}}{\sqrt{N_t}}\right)$ where $\underline{C}_n$ is mean *C* of native species, N_n is species richness of native species, and N_t is total species richness (Miller & Wardrop 2006; Freyman et al. 2016). The adjusted floristic quality index ranges from a score of 1–100, where 100 indicates optimal floristic integrity. To examine the contribution of plant functional groups to community assembly, we calculated the proportion of species per wetland belonging to three functional groups: perennial, woody, and hydrophytic.

Statistical Analysis

To address our first objective and compare plant metrics among wetlands in different disturbance categories (degraded, restored, and reference) we performed a one-way analysis of variance (ANOVA) followed by Tukey's honest significant difference post hoc test. To address our second objective and determine how plant metrics changed with age of restoration projects, we performed ordinary least squares regression analysis where our response variables were each plant metric, and our predictor variable was the age of degraded (age $= 0$) and restored wetlands (years since hydrologic restoration). Model assumptions were confirmed by way of QQ plots, the Shapiro–Wilk normality test (rstatix library; Kassambara 2020), the Levene's test for homogeneity of variances (car library; Fox & Weisberg 2019), and the Breusch–Pagan test for homoscedasticity (car library). Significance values were evaluated at the $\alpha = 0.05$ level.

A Non-Metric Multidimensional Scaling (NMDS) analysis ("metaMDS" function from the "vegan" library; Oksanen et al. 2020) was performed to support our first objective and to visualize the separation of wetlands in ordination space. As an input to the NMDS, we used the relative abundance of each taxon ($n = 102$). To reduce the influence of uncommon taxa, we removed taxa that were found at only one site. Abundance values were transformed prior to analysis using the Bray–Curtis dissimilarity matrix. We performed a Pearson correlation between the abundance of each species and the NMDS ordination. All statistical analysis was performed using R statistical software (v. 4.1.0: R Core Team 2020; Wickham et al. 2019) and figures were produced using the package ggplot2 (Wickham 2016).

Results

We identified a total of 198 plant taxa, 11% of which could be identified only to genus. The number of taxa at each site ranged from 19 to 51. In general, wetlands had a low proportion of non-native species and a high proportion of hydrophytic species (Table 1). The most common plant species in degraded and reference wetlands was the perennial *Persicaria hydropiperoides* (swamp smartweed) and in restored wetlands, the perennial graminoid *Leersia oryzoides* (rice cutgrass) (Fig. 2). Relative cover of early successional tree species such as *Fraxinus pennsylvanica* (green ash)

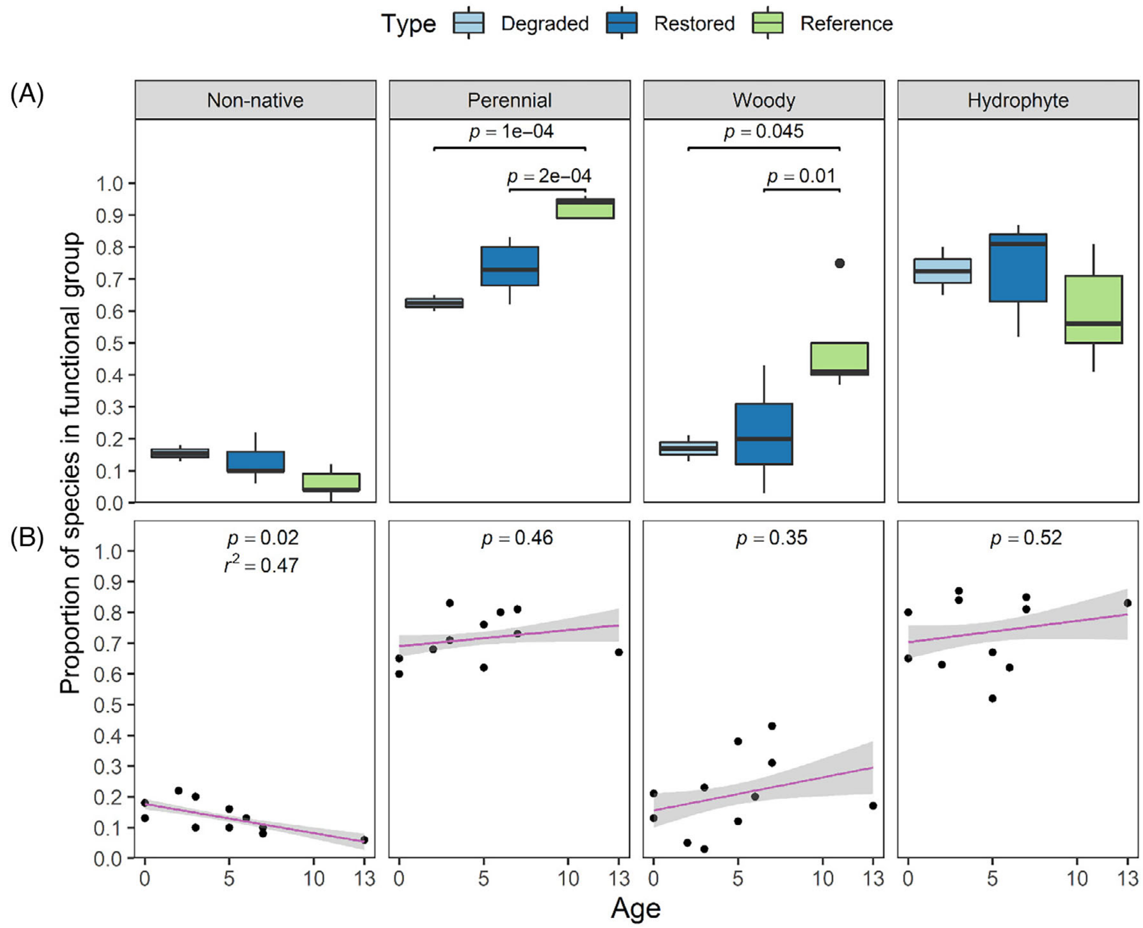

Figure 4. (A) Proportion of understory plant species in four functional groups for degraded, restored, and reference floodplain wetlands of western Kentucky. Plotted values for the box are median (50% quantile) ±25% quantile. Statistically significant results are indicated as p values on the plots. (B) Linear relationships between functional groups and wetland age. Red line represents the fitted regression line, and the shaded region represents the 95% confidence interval of the fitted values. Degraded sites are represented by an age of 0 and restored sites by years since hydrologic restoration. Reference sites are not included in the models. p Values are reported for all regressions, and r^2 values only for significant results.

and *Salix nigra* (black willow) were highest in restored wetlands, whereas the woody vine *Campsis radicans* (trumpet creeper) was completely absent from restored and degraded wetlands.

Objective 1

Restored wetlands showed a higher variability in taxa richness than either degraded or reference wetlands (Table 1; Fig. 3A). Restored wetlands located closest to the Mississippi River and subject to deep seasonal flooding had the lowest taxonomic richness. ANOVA results revealed a significant difference in adjusted floristic quality index ($F_{[2,13]} = 47.0$, $p = 0.000001$), and the proportion of perennial ($F_{[2,13]} = 24.3$, $p = 0.00004$) and woody ($F_{[2,13]} = 7.0$, $p = 0.009$) species among levels of disturbance (Table S1; Figs. 3A & 4A). Pairwise comparisons indicated that reference wetlands had a significantly higher adjusted floristic quality index (48.5 ± 2.4) than degraded wetlands (34.3 ± 1.1, $p = 0.00001$) and restored wetlands (37.4 ± 2.3, $p = 0.000002$). Reference wetlands also had a higher proportion of perennial species (0.93 ± 0.03) and woody species (0.49 ± 0.16) than degraded (perennial 0.63 ± 0.04, $p = 0.0001$, woody 0.17 ± 0.06, $p = 0.045$) and restored wetlands (perennial 0.73 ± 0.07, $p = 0.0002$, woody 0.21 ± 0.14, $p = 0.010$). We did not detect a significant difference in any plant metrics between degraded and restored wetlands (Tables 1 & S1; Figs. 3A & 4A).

Objective 2

Linear regression analysis showed that as restored wetlands aged, the adjusted floristic quality index increased (Fig. 3B), whereas the proportion of non-native species decreased (Fig. 4B). None of the four other plant metrics showed a significant relationship with restoration age (Figs. 3B & 4B). Based on our significant linear models, restored wetlands would match the means of proportion of non-native species and adjusted floristic quality index of reference wetlands in 12 and 28 years, respectively.

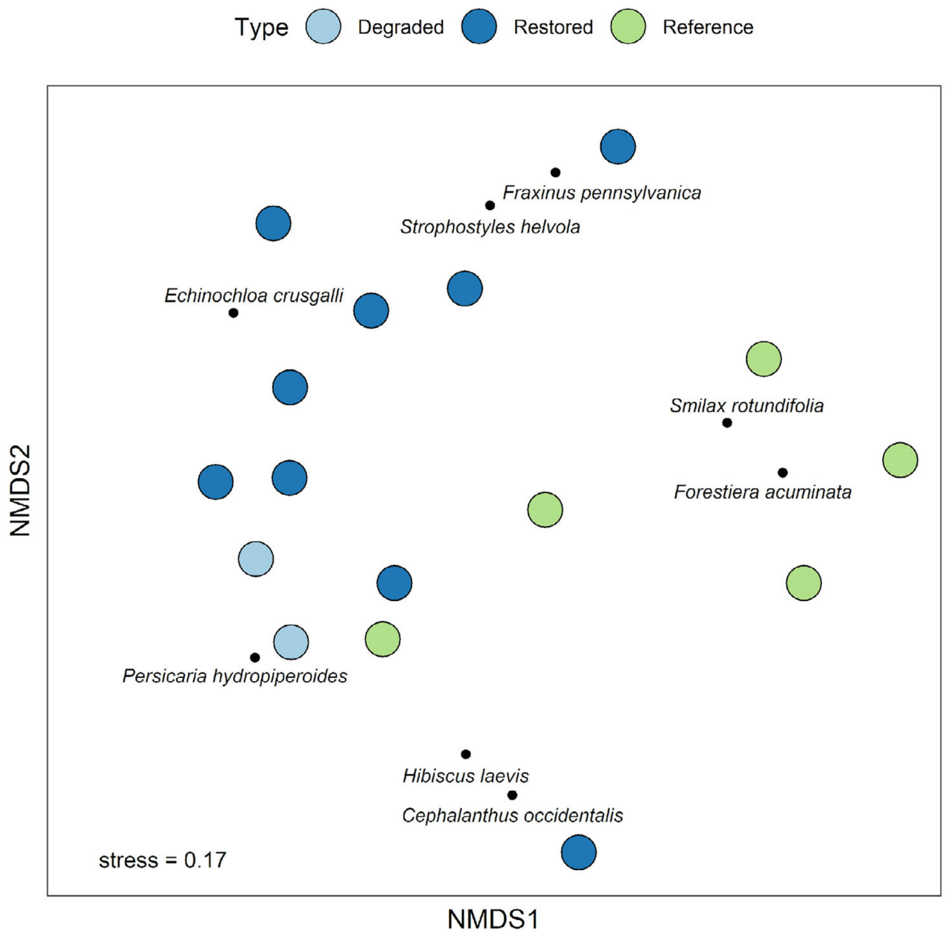

Figure 5. Non-metric multidimensional scaling (NMDS) ordination of understory plant communities in two degraded, nine restored, and five reference wetlands. We correlated the abundance of each species with the NMDS ordination and plotted the eight species with the highest correlation coefficients.

Non-Metric Multidimensional Scaling

The optimal NMDS solution was two-dimensional (Procrustes: RMSE < 0.000003, max residual = 0.000003, stress = 0.17) (Fig. 5). Restored and degraded wetlands separated from reference wetlands along the horizontal axis. Restored wetlands were strongly associated with the abundance of the non-native *Echinochloa crusgalli* (barnyard grass) and some pioneering and early successional woody species (*Fraxinus pennsylvanica* [green ash], *Cephalanthus occidentalis* [common buttonbush], and *Hibiscus laevis* [halberdleaf rosemallow]). Reference wetlands were strongly associated with the shrub *Forestiera acuminata* (eastern swampprivet) and woody vine *Smilax rotundifolia* (roundleaf greenbrier).

Discussion

Bottomland hardwood floodplain forests have disappeared from the lower Mississippi River valley at an alarming rate, although loss has slowed and restoration has increased over the last three decades. Outcomes of wetland restorations rely on adaptive management informed by empirical data gathered about past and present restoration projects. For this reason, the objective of our study was to evaluate restoration success by examining the naturally colonizing plant communities in restored floodplain wetlands along tributaries to the Mississippi River. We found that understory plant communities in restored wetlands differed from those in reference wetlands. As restored wetlands aged, however, the proportion of non-native species decreased and the adjusted floristic quality index increased, suggesting a recovery process. Since restored wetlands were mostly younger than 8 years, we predict that restored wetland plant communities would become more similar to those of reference wetlands over a longer period; further research on older restored wetlands is needed to confirm this prediction.

We failed to determine if our hypothesis that restored wetland plant communities would differ from degraded wetlands was supported. The low sample size and high variability of degraded wetland metrics limited the power to detect differences between these disturbance categories. It is possible that the incomplete drainage of degraded wetlands and the young age of restored wetlands contributed to the development of similar plant communities. The degraded wetlands in our study were flooded year-round as a form of hydrologic modification and retained high proportions of hydrophytic species. Both restored and degraded wetlands were dominated by a mix of annual and perennial hydrophytes with low-to-intermediate conservatism values representative of the early-successional community. The restored wetlands in our study ranged in age from 1 to 13 years but were mostly under 8 years old. Since the plant community of restored wetlands is developing from a disturbed state and is dependent on site and regional seed banks, it can be expected that early-successional vegetation will prevail for some time.

Over time, restored wetlands gained species with higher conservatism values and lost non-native species, which contributed to an increase in the adjusted floristic quality index. Species with higher conservatism values have high fidelity to native remnant habitats and an increase in the adjusted floristic quality index suggests a developing resemblance to the reference ecosystem type. Our results showed that the proportion of non-native species in all wetlands was generally low. In our oldest restored wetland (13 years), the proportion of non-native species was similar to the mean of reference wetlands (mean 13-year-old = 0.10, mean reference = 0.06). The prevalence of non-native species in young, restored wetlands could be due to specific restoration techniques and practices (Hausman et al. 2007; Schultz et al. 2020; Winikoff et al. 2020), hydrologic disturbance (Zedler & Kercher 2004), or landscape setting (Zedler & Kercher 2004; Matthews et al. 2009). Non-native species loss over time might be the result of a shift from colonizing to perennial species—related to a decrease in disturbance in the form of removal of chronic stressors from row crop agriculture—where species adapted to native remnant ecosystems begin to outcompete opportunistic species (Byun et al. 2013). The decrease in the proportion of non-native species over time might also have been related to hydrology. Some of our oldest restored sites experienced deep seasonal flooding, which may have limited the growth of non-native plants (Casanova & Brock 2000; Magee & Kentula 2005).

Despite the increase in the adjusted floristic quality index in restored wetlands over time, we observed a significantly higher adjusted floristic quality index in reference wetlands. We also observed that reference wetlands had a significantly higher proportion of woody and perennial species, especially woody vines. Taken together, these findings indicate that the naturally colonizing understory community of restored wetlands takes longer than 6 years (mean age of our restored wetlands) to resemble bottomland hardwood forest communities. Older restored wetlands (7–13 years) had dense stands of naturally colonizing pioneer tree species such as *Salix nigra* (black willow) and *Fraxinus pennsylvanica* (green ash), a finding similar to previous studies (Hodges 1997; Twedt 2004; Yin et al. 2009; De Jager et al. 2012). These colonizing communities represent the early stages of the bottomland hardwood successional process (Hodges 1997) and highlight the youth of the restored sites. The willow and ash community can persist for 30 years (Hodges 1997; Twedt 2004) followed by succession of the climax community of *Taxodium distichum* (baldcypress), *Quercus* spp. (oaks), and *Carya* spp. (hickories) and associated understory (De Steven et al. 2015). From our study, it is difficult to conclude if restored wetlands are failing to match reference condition or if they need more time to develop the anticipated forest community. Because the WRP became active nationally only 30 years ago, most restorations in the region are relatively young. To determine if wetland restorations are on track to resembling the mature forest community of reference ecosystems, long-term monitoring, beyond the commonly used 5-year period, should be incorporated into adaptive management plans of WRP restorations. Our linear models estimate approximately three decades for restored wetlands to match reference wetlands in floristic quality, but that is assuming a linear trajectory, which is unlikely in dynamic wetland ecosystems, particularly over a longer time scale (Zedler & Callaway 1999). For example, studies of slightly older (approximately 30 years) restored bottomland hardwood forests in the region found that although some variables like tree density increased over time, others like ground vegetative cover peaked and then decreased (Berkowitz 2013, 2019). For a long-lived plant community like a bottomland hardwood forest, the more likely successional timeline might extend to approximately 80 years (Berkowitz & White 2013).

It is important to note that reference wetlands had closed forest canopies and restored wetlands were open fields, which undeniably contributed to the differences in understory community composition. For example, bottomland hardwood forest herbaceous species like *Saururus cernuus* (lizard's tail) and *Chasmanthium latifolium* (inland sea oats) are restricted to closed canopy forests. Woody vines like *Campsis radicans* (trumpet creeper) and *Smilax rotundifolia* (roundleaf greenbrier) require the structural support of a forest canopy for growth. In general, shaded closed canopies reduce herbaceous growth and recruit more woody seedlings (Battaglia et al. 2008; De Steven et al. 2015). The absence of a forested overstory in restored wetlands is likely limiting on-site seed availability of woody species. Furthermore, seed dispersal from outside the restored wetlands might be inhibited by the intensively agricultural surroundings (Matthews & Endress 2010; O'Connell et al. 2013; Roy et al. 2019) and distance from other forests (Battaglia et al. 2008; Kroschel et al. 2016). The undeveloped overstory in restored wetlands may inhibit the development of a reference-level understory and thus call for a more active management and planting approach for the understory community.

Management

The WRP is the largest program restoring wetlands on agricultural lands nationally. Wetland restorations in agricultural settings face numerous challenges and the outcomes of current and future projects will depend on adaptive management strategies. Based on our findings, we make recommendations that could improve the success of restored understory plant communities in resembling forested reference wetlands. We found that restored wetlands have low proportions of naturally colonizing woody and perennial species compared to the understory of reference bottomland hardwood forests and these proportions did not increase with time since restoration. Although afforestation is widely used in bottomland hardwood wetland restorations, we recommend that practitioners also explore planting understory species to aid the development of a target plant community. Planting native understory species can increase community similarity to reference wetlands (Matthews & Spyreas 2010). Furthermore, when choosing locations for future restoration projects, practitioners should prioritize locations that are near remnant wetlands to increase the potential for the natural dispersal of native understory plant species adapted to closed canopy communities (Zedler 2003). This strategy does not mean moving away from agricultural landscapes for which the WRP was designed, but purposefully establishing projects to fill gaps in the floodplain rather than exist in isolation. If potential properties meet program enrollment criteria but are located far away from natural seed banks, extra effort should be expended on afforestation and native herbaceous plantings.

We observed a change in some components of the plant community with time, but since most of our restored wetlands were under 8 years old, and the restoration trajectory toward bottomland hardwood forest takes place over several decades, monitoring check-ins over long time frames are needed as a component of the adaptive management program. Monitoring specifically to observe the change in the proportion of woody, perennial, and high conservatism species is important to determine if restored wetlands are starting to resemble the reference plant community.

Altogether, restoration programs should develop well-defined goals and benchmarks for project success integrated into an adaptive management framework. If wetland restorations continue to target agricultural regions, as they should due to historic wetland losses, the developing plant community might be permanently affected by the agricultural setting. When establishing success benchmarks, restoration practitioners should take into account that restored plant communities might remain dissimilar to reference communities. Long-term restoration plans should define a wide range of acceptable outcomes with a greater emphasis on ecosystem function rather than community composition.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Result of ANOVA and Tukey's post hoc tests for metrics of floristic quality and plant functional groups between degraded ($n = 2$), restored ($n = 9$), and reference ($n = 5$) wetlands in floodplains of western Kentucky streams.

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