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RESEARCH ARTICLE

Understory vegetation as an indicator for floodplain forest restoration in the Mississippi River Alluvial Valley, U.S.A.

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In the Mississippi River Alluvial Valley (MAV), complete alteration of river-floodplain hydrology allowed for widespread conversion of forested bottomlands to intensive agriculture, resulting in nearly 80% forest loss. Governmental programs have attempted to restore forest habitat and functions within this altered landscape by the methods of tree planting (afforestation) and local hydrologic enhancement on reclaimed croplands. Early assessments identified factors that influenced whether planting plus tree colonization could establish an overstory community similar to natural bottomland forests. The extent to which afforested sites develop typical understory vegetation has not been evaluated, yet understory composition may be indicative of restored site conditions. As part of a broad study quantifying the ecosystem services gained from restoration efforts, understory vegetation was compared between 37 afforested sites and 26 mature forest sites. Differences in vegetation attributes for species growth forms, wetland indicator classes, and native status were tested with univariate analyses; floristic composition data were analyzed by multivariate techniques. Understory vegetation of restoration sites was generally hydrophytic, but species composition differed from that of mature bottomland forest because of young successional age and differing responses of plant growth forms. Attribute and floristic variation among restoration sites was related to variation in canopy development and local wetness conditions, which in turn reflected both intrinsic site features and outcomes of restoration practices. Thus, understory vegetation is a useful indicator of functional progress in floodplain forest restoration.

Key words: afforestation, bottomland hardwoods, Conservation Effects Assessment Project, wetland ecosystem services, wetland restoration, Wetlands Reserve Program

Implications for Practice

- On former agricultural floodplains, some floristic differences between afforested sites and mature bottomland forests are a natural result of differing successional age. However, species-composition attributes of understory vegetation offer useful indicators of restoration progress.
- Relative growth form composition (herbaceous vs. woody) reflects the role of tree-planting practices in establishing a forest overstory. Functional-group composition (based on wetland-fidelity rankings) can be an important indicator of hydrologic conditions and practices.
- Active afforestation can restore forest habitat structure, but restoring local hydrology is key to enhancing functional ecosystem services such as nutrient retention and carbon sequestration.

Introduction

The 10-million-hectare Mississippi River Alluvial Valley (MAV) is the largest floodplain feature in the United States (Fig. 1). Historically, much of the MAV was exposed to voluminous floodwaters from the upper Mississippi River drainage basin and was covered by diverse deciduous forests that were important habitats for migratory waterbirds, fish, and other fauna. These seasonally flooded "bottomland hardwood" forests also provided additional ecosystem services such as storing floodwaters, sequestering carbon, and attenuating sediment and nutrient loads (King & Keeland 1999). Today, the River's active floodplain is reduced to a narrow corridor within a continuous main stem levee system constructed in the early twentieth century (Frederickson 2005); major internal tributaries are also confined within secondary levees. Flood control enabled a vast scale of land clearing and drainage,

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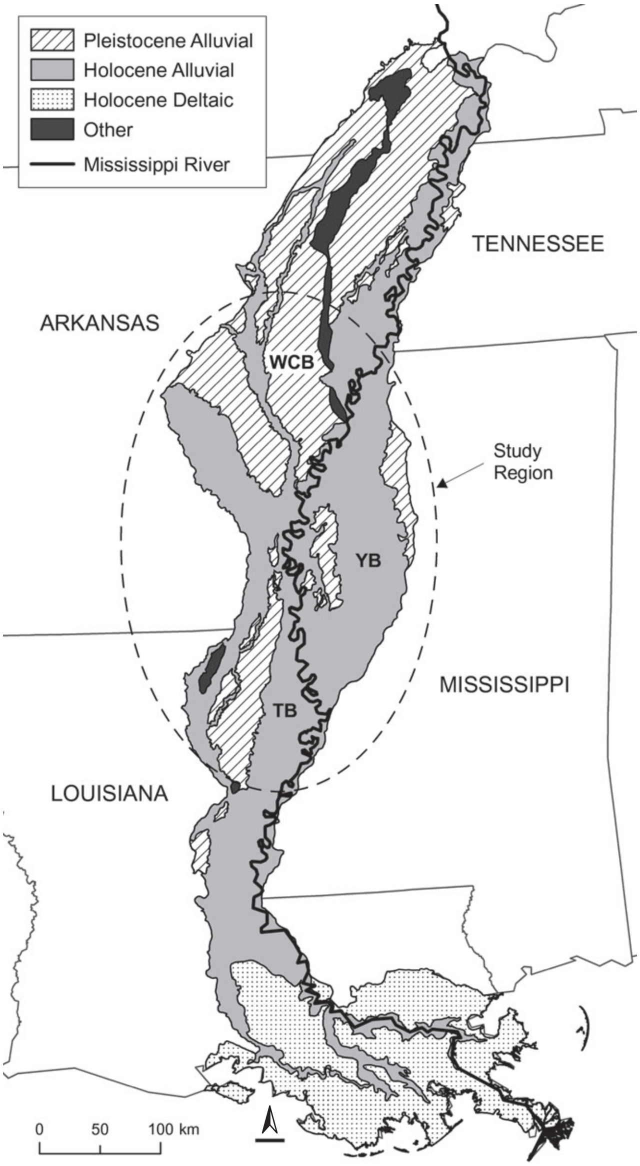

Figure 1. Major physiographic divisions of the Mississippi Alluvial Valley (Autin et al. 1991), and general region of the study. Map is generalized from Chapman et al. (2004). Symbols indicate approximate locations of study sub-basins (TB, Tensas Basin; WCB, lower White–Cache Basin; YB, Yazoo Basin).

which converted the MAV to a region of productive commercial agriculture but resulted in nearly 80% loss of original forest area. Natural flooding in the former floodplain is now limited to rainfall-driven surface run-off or occasional backflooding of internal streams, and remnant forest is highly fragmented (Faulkner et al. 2011).

Wherever large floodplain landscapes have been transformed by human development, the prospects for full-scale reversal are constrained by enormous physical challenges and intensely competing land uses (Moss 2007; Dufour & Piégay 2009). "Restoring" the entire MAV floodplain is not realistic, given the permanence of the flood control system that supports present-day land uses. Instead, local-scale recovery of lost forest ecosystems has been attempted through efforts to reforest (afforest) farmlands that are marginal for crop production (King & Keeland 1999; Haynes 2004). Afforested tracts are intended to increase wildlife habitat within the agricultural landscape but also to provide other ecosystem functions. Many projects were completed from 1992 to 2013 under the U.S. Department of Agriculture's (USDA) Wetlands Reserve Program (WRP), which offered incentive payments to private landowners for restoring marginal cropland to wetlands within protective easements. This program has enrolled over 275,000 ha of land in the MAV (USDA–NRCS 2014). In a typical WRP project, a cropland tract of several hundred hectares is prepared and planted with a limited selection of bottomland tree species, usually oaks and pecans (*Quercus* and *Carya* spp.), green ash (*Fraxinus pennsylvanica*), and baldcypress (*Taxodium distichum*). Other tree and understory species are expected to recolonize naturally. Tree planting is the main restoration practice, but hydrology enhancement may be added to create areas of inundated habitat for migratory waterbirds. Hydrologic practices include blocking drainage ditches, constructing earthen berms and control structures for managed water retention, and excavating swales for passive water retention (King et al. 2006).

The issue of whether afforestation efforts in the MAV are "successful" is ongoing and intertwined with evolving program objectives (Gardiner & Oliver 2005). Initial goals focused on certain tree species with high wildlife and timber value, so early assessments focused on whether tree-planting practices achieved a desired tree density and species composition. Success varied greatly in relation to factors such as planting method, seedling quality, and species-site matching (Allen 1997; Haynes 2004; Stanturf et al. 2004). Conservation-easement programs such as the WRP now emphasize ecological "restoration" for multiple ecosystem functions. Consequently, a broader evaluation of MAV projects was begun as part of the Natural Resource Conservation Service's (NRCS) Conservation Effects Assessment Project (CEAP), a national effort to quantify the ecosystem services gained from USDA conservation programs (cf. Duriancik et al. 2008). The MAV assessment compares active croplands, afforested WRP tracts, and mature bottomland hardwood (BLH) forests to quantify multiple services including pollutant reduction, wildlife habitat, and biodiversity support (e.g. Waddle et al. 2013; Walls et al. 2014). Preliminary data for overstory tree composition suggested that WRP and BLH sites shared about 70% of species (both planted and colonizing), indicating a potential to resemble natural forests with time.

Tree planting may structure the eventual forest overstory on afforested sites, but the understory vegetation ("herbaceous layer"; Gilliam 2007) must establish from seed banks and dispersal after farming ceases. For biodiversity support, a basic question is whether those passive mechanisms will recover an understory flora similar to that of BLH forests. Evaluation is complicated by the young age of WRP sites compared with mature forests; also, multiple factors may affect floristic composition (Battaglia et al. 2002; Middleton 2003). For example, distributions of herb species within natural floodplains are influenced at local scales by factors such as relative elevation, light, and soil texture (Menges 1986; Grell et al. 2005). Because understory vegetation is sensitive to site conditions, compositional variation among sites could be a useful indicator of functional restoration outcomes. Therefore, we examine three questions about the understory of floodplain WRP sites: (1) Does their vegetation composition resemble that of mature BLH forest? (2) What influences among-site variation? and (3) What could such variation indicate about restoration effectiveness?

Methods

Study Sites

Representative WRP and BLH forest sites were surveyed across a three-state area in the central MAV (Fig. 1) encompassing the lower White–Cache River Basin ("Western Lowlands") in Arkansas (AR), Tensas River Basin in Louisiana (LA), and Yazoo River Basin in Mississippi (MS). The MS and LA basins represent mainly Holocene-age meander belt and backswamp deposits. The AR basin is a slightly elevated terrace dominated by Pleistocene-age valley-train deposits plus included Holocene deposits of the White and Cache River floodplains (Chapman et al. 2004). The levee system isolates these areas from Mississippi River flooding except at the outflow points of major tributaries. Thus, site-level hydrologic conditions are locally controlled, in part by hydrogeomorphic features that vary with subregion (Fig. 1), topography, and soil type (e.g. Klimas et al. 2009), but also by the extensive land alterations (levees, land-leveling, stream channelizing, ditch systems) that were used for floodplain de-watering (cf. Frederickson 2005).

The WRP sites were chosen from NRCS-supplied digital maps of completed projects, with final selection contingent on permission for site access. All WRP sites had been withdrawn from row-crop farming and planted with 5–8 bottomland tree species (range 4–13), mainly oaks (*Quercus texana*, *Q. phellos*, *Q. nigra*, *Q. lyrata*, *Q. pagoda*), green ash, baldcypress, persimmon (*Diospyros virginiana*), and pecans (*Carya aquatica*, *C. illinoinensis*). The BLH sites were naturally regenerated forests at least 70 years old with no significant management disturbance and located on public lands (National Wildlife Refuges or State Wildlife Management Areas). They represent examples of mature floodplain forest under present-day conditions, as nearly all remnant forests in the MAV were selectively cut or clear-felled historically. Minimum size for any study site was 40 ha, but most were larger than 100 ha.

Site selection and vegetation sampling occurred in several phases owing to changes in study scope over time. In AR and LA, a stratified-random sample of 16 sites per state (8 WRP, 8 BLH) was selected and sampled in July–August 2006. In MS, 28 WRP sites were selected randomly and sampled in June–September 2008; 21 of those sites were used for the current analyses based on completeness of plant identification. Lastly, 10 BLH sites in MS were sampled in July–August 2012; these were not selected randomly owing to a scarcity of remnant forests, but they were distributed across the same spatial extent as the MS WRP sites. In total, there were 63 sites (37 WRP, 26 BLH) in locations spanning six AR counties, three LA parishes, and nine MS counties. Sites of each type were distributed across the major geomorphic subregions (Pleistocene valley train, Holocene meander belt, Holocene backswamp) and encompassed similar hydrogeomorphic settings (rainfall flat or lowland backwater). Hydrogeomorphic classes of BLH sites were not determined specifically but were selected to resemble the WRP sites with respect to landscape position, soils, and elevation (e.g. deep-water depressional sloughs were not included).

Each WRP site was characterized for geomorphic subregion (from Chapman et al. 2004), soil type (from general soil maps), project age (years since tree planting), distance to the nearest forest tract (a source of colonizing species), and presence of hydrology enhancements (constructed water-retention areas or excavated swales). The LA and MS soils were typically mapped as clays or silty clays (Vertisols and Alfisols), whereas the AR soils were mainly silty clay loams or silt loams (Alfisols and Inceptisols) (NRCS Web Soil Survey; http://websoilsurvey.nrcs.usda.gov/). Project ages ranged between 3 and 14 years (mean = 7 years). Distances to existing forest were measured on digital aerial imagery and ranged between 125 and 2,330 m. Presence of hydrology-enhancement features was determined from the digital aerial imagery; visibly wetter macrotopography features (natural swales) were also noted when they co-occurred with sampled areas.

The region's mean annual rainfall of 1,300–1,400 mm is seasonal, with higher amounts in November–May and declining amounts during June–September. Mid-growing season conditions (April–August) were relatively drier in 2006 and 2012 (rainfall about 90 and 30 mm below average, respectively) and wetter in 2008 (about 100 mm above average) (National Climatic Data Center, Climatological Summaries, http://www.ncdc.noaa.gov/).

Vegetation Sampling

Plot arrays and understory sampling intensity varied by study phase but were matched for WRP and BLH sites within a state. In all AR and LA sites, there were five sample points spaced at least 75 m apart along a randomly located transect. Tree and large-sapling/shrub layers (stem diameters ≥10 and 2.5–10 cm, respectively) were sampled in a 400-m^2 nested plot at each point; the understory layer was sampled in four 1-m^2 quadrats per plot (20 per site). In MS WRP sites, 20 nested plots were placed in a stratified-random array, spaced at least 30 m apart; the understory was sampled in two quadrats per plot (40 per site). In MS BLH sites, the understory was also sampled at 20 points with two quadrats per point (40 per site), but for logistical reasons the points were arrayed along two or three widely spaced transects. Sampling of tree and sapling layers was comparable to that for AR and LA. All sampling was located at least 100 m from the habitat edge and 400 m from paved roads.

The species of herbs, woody vines, low shrubs, and tree seedlings (stems approximately <1 m height or <2.5 cm diameter) in each understory quadrat were given visual cover scores of 1 to 6 (Daubenmire scale; Mueller-Dombois & Ellenberg 1974). Species scores were converted to absolute coverages (%) using the mid-points of the percent range for each score, and then averaged over quadrats to give mean species coverages in each site. Species were classed by growth form, native/non-native status, and also into groups based on wetland-fidelity categories (Reed 1997), where (1) "hydrophytic" species include all OBL (obligate wetland), FACW (facultative wetland), and FAC (facultative) categories (ACOE 2010), (2) true "wetland" species are OBL and FACW only, and (3) "upland" species represent non-hydrophyte categories (FACU, facultative upland; UPL, upland). FAC species occur in both wetlands and uplands but are indicative of wetland habitat where soil and hydrology criteria are satisfied. Species nomenclature is taken from the USDA Plants database (http://plants.usda.gov).

Data Analyses

Analyses evaluated both understory floristic (species) composition and functional vegetation attributes. Because total sample area differed among states, we were cautious in the use of species-number attributes, which tend to be area-dependent. We focused instead on proportional measures that are less area-sensitive, and we avoided interpretation of among-state differences that might not be meaningful. Multivariate floristic data were analyzed in PC-ORD (McCune & Mefford 2011), and univariate attribute data in SYSTAT® (SPSS, Inc., Chicago, Illinois). Significance level was $p < 0.05$ except where noted.

WRP Versus BLH Sites. Two-way analysis of variance (ANOVA) was used to test the effects of land type (WRP vs. BLH) and state on these site-level vegetation attributes: the relative counts (% of total species) and relative covers (% of total cover) of species growth forms, wetland indicator groups, and exotic (non-native) species, respectively. State was a blocking factor because sampling area was matched within states. Most attribute data met ANOVA assumptions; however, the exotic species data could not be normalized owing to many zero values, so we grouped the absolute number and percent cover of exotics into three levels each and tested the land-type effect with likelihood ratio chi-square. We report statistics only for the land-type effect, as there were no substantive state or interaction effects in any analysis.

Floristic composition of all 63 sites was compared using nonmetric multidimensional scaling (NMS) ordination, which arrays sites in low-dimensional space according to their relative dissimilarities. The site dissimilarity matrix was calculated using Sorensen distances on species presence/absence data. Before calculating the matrix, highly similar species in some species-rich genera were aggregated at genus level to reduce data noise. Only taxa occurring in at least three sites (≥5%) were retained in the matrix (McCune & Grace 2002); this resulted in 124 taxa for analysis (80 herbaceous, 44 woody), of which 56 were common (in ≥15% of sites). A three-dimensional solution with orthogonal axis rotation gave an optimal fit (stress = 12.1), with two axes representing most of the variation (cumulative $R^2 = 0.82$). Difference in floristic composition between land types was tested with multiple-response permutation procedures (MRPP). This test compares average within-group similarities of observed and randomized site groups, where p values for the resulting T-statistic are derived from a continuous distribution (McCune & Grace 2002). Individual taxa were tested for association with land type by indicator species analysis (ISA) using the phi coefficient, which ranges from −1 to 1 (perfect negative to perfect positive association) (Tichý & Chytrý 2006). A significance level of $p < 0.01$ ($\Phi \geq 0.40$) was chosen to minimize spurious results for infrequent taxa.

Variation Among WRP Sites. Floristic variation within the group of 37 WRP sites was analyzed in a second ordination using 104 taxa occurring in at least two sites. A three-dimensional solution was optimal (stress = 15.5), with all axes representing important variation ($R^2 = 0.79$). Site-level factors and vegetation descriptors (below) were evaluated as potential explanatory variables for the ordination pattern. Categorical variables were tested with MRPP and continuous variables with Pearson correlations. The vegetation descriptors were also analyzed in relation to site factors using group-mean tests or correlation, as appropriate.

Site factors were geomorphic subregion, distance to the nearest forest tract, potential wetness condition, and project age. Distance to forest was tested for correlation with the ordination array and with the numbers of herbaceous, woody, hydrophytic, and wetland species per site. Possible wetter or drier conditions were inferred from two coarse-scale properties, as the single-visit surveys could not provide real-time hydrologic data. Each site was assigned a binary "hydric soil" score based on whether mapped soils in the sampled area are considered hydric (indicating wet conditions) or partly/wholly non-hydric. Hydric-status designation is based on map-unit soil types and landscape positions (NRCS Web Soil Survey; http://websoilsurvey.nrcs.usda.gov/). A binary "hydrology-enhancement" score was assigned based on the presence/absence of constructed water-retention areas or wet macrotopography located within or adjacent to the sampled areas; such features could influence understory vegetation if ponded waters were to spread into tree-planted areas (Hunter et al. 2008). Project age was scored as a categorical variable (3–5 years, 6–8 years, 9–14 years; $n = 10$, 18, 7 sites); two sites lacked age information.

Site vegetation descriptors included the proportional species-guild attributes plus a binary variable for density of the "overstory" tree stratum (all stems ≥2.5 cm diameter at breast height, dbh). In WRP sites, this overstory consists mainly of saplings of 2.5–10 cm dbh, with densities ranging between 25 and 1,300 ha^{-1} in sites greater than 3 years old. Tree density was scored as "low" (<100 stems/ha; sparse/no overstory) or "high" (>200 stems/ha; denser overstory); the latter approximates a minimum criterion for tree-planting success after 3 years (see King & Keeland 1999).

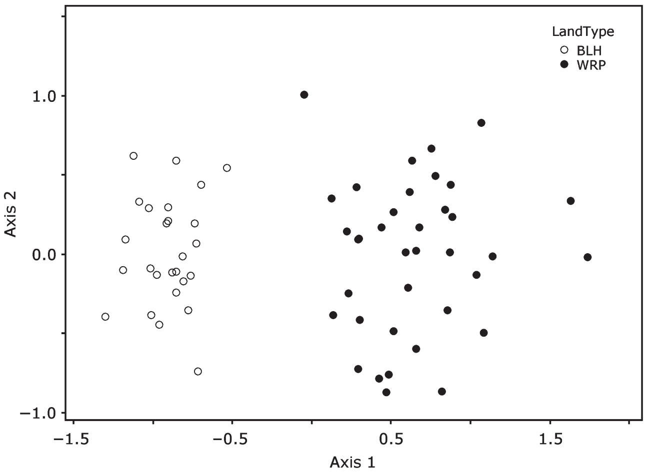

Figure 2. NMS ordination of species composition in 63 sites coded by land type. BLH and WRP sites differ significantly (MRPP test, $T = -36.1$, $p < 0.001$).

Results

WRP Versus BLH Forest Understories

WRP and BLH sites differ substantially in understory species composition (Fig. 2), with dissimilarity averaging 82%. Vegetation attributes of the two land types reflect their contrasting age and canopy development (Table 1). Herbaceous species averaged 74% of species and 76% relative cover in WRP sites compared with 30 and 24%, respectively, in BLH forests. Woody vines were more prevalent in BLH sites. WRP sites had lower representation of hydrophytic species; however, hydrophytes still averaged more than 70% of species and relative cover. The two land types had similar percentages of wetland species, whose relative covers did not differ greatly. WRP sites averaged more exotic species, which were detected in 89% of WRP sites but only 31% of BLH sites. Species composition differed overall among states (MRPP, $T = -8.5$, $p < 0.001$), but this is likely an artifact of greater sampling area in MS. WRP sites in MS had more species (generally 21–40) than those in AR/LA (9–27), whereas BLH forest sites in all states had similar numbers of species (generally 17–36). Within-group dissimilarities averaged 45% in BLH sites and 57% in WRP sites (paired *t*-test on state means, $df = 2$, $p = 0.13$), suggesting that WRP sites are more variable in composition (cf. Fig. 2).

The ISA (Table 2) revealed that WRP and BLH understories differ much more in herbaceous composition than in woody composition (34 vs. 77% of taxa shared). Herb species associated with WRP sites include upland old-field plants (e.g. *Andropogon virginicus*, *Solidago altissima*, *Ambrosia artemisiifolia*, and *Conyza canadensis*) as well as plants of wetland habitats (e.g. *Ludwigia* spp., *Lythrum alatum*, *Juncus* spp., and *Cyperus pseudovegetus*). Herb taxa shared between WRP and BLH sites include hydrophytes in the genera *Polygonum*, *Dichanthelium*, *Eleocharis*, and *Leersia*. Other typical BLH herbs were infrequent or absent in WRP sites (e.g. *Boehmeria cylindrica*, *Justicia* spp., *Polygonum virginianum*, and *Saururus cernuus*). In contrast, WRP and BLH sites share many woody species (Table 2), including early-successional vines and shrubs (e.g. *Brunnichia ovata*, *Campsis radicans*, *Toxicodendron radicans*, and *Rubus* spp.). BLH forests differ mainly in having other woody vines that were uncommon in WRP sites (e.g. *Trachelospermum difforme*, *Berchemia scandens*, *Bignonia capreolata*, and *Smilax* spp.). Of eight exotic species found in more than one WRP site, most were agricultural weeds (e.g. *Sorghum halepense*, *Cardiospermum halicacabum*, and *Verbena* spp.); *Lonicera japonica* was the only woody exotic that also occurred in BLH sites.

Variation Among WRP Understories

Compositional variability among WRP sites reflected several underlying factors and attributes. On NMS axes 1 and 2 (Fig. 3A), understory floristic variation was correlated with percent woody species and distance to forest, such that woody plants are more prevalent (relative to herbs) with greater proximity to forest. Sites with higher versus lower tree density were also differentiated across the understory floristic gradient (Fig. 3A; MRPP, $T = -3.1$, $p < 0.01$). Sites with denser overstory averaged 33% woody species and 32% relative woody cover versus 20 and 16%, respectively, in sites with sparse overstory (*t*-tests, $p < 0.01$). Sites with denser overstory were generally closer to forest (mean distance 535 m vs. 858 m) (*t*-test, $p = 0.09$). The number of woody understory species decreased with distance to forest ($r = -0.41$, $p < 0.05$), principally in sites more than 1,000 m away. The number of herbaceous species per site was uncorrelated with forest distance ($r = -0.07$).

Floristic variation on axes 1 and 3 (Fig. 3B & 3C) reflected a site-wetness gradient. Species composition differed in sites with hydric versus non-hydric soils (Fig. 3B; $T = -4.2$, $p = 0.001$). Although hydrology enhancements were installed on nearly 80% of the projects, hydrologic features (including natural swales) were adjacent to sampled areas in only 35% of sites. Species composition was weakly differentiated in sites with versus without those adjacent features (Fig. 3C; $T = -1.4$, $p = 0.09$). Sites with hydric versus non-hydric soils differed in percent hydrophytic species (84 vs. 69%) and percent wetland species (51 vs. 34%) (*t*-tests, $p < 0.01$). Likewise, percent hydrophytic and wetland species averaged 82 and 50%, respectively, in sites with adjacent hydrologic features versus 74 and 40% in sites lacking those features (*t*-tests, $p \leq 0.05$). The numbers of hydrophyte and wetland species per site were uncorrelated with distance to forest ($r = -0.21$ and -0.19, $p > 0.20$).

There was some floristic differentiation by geomorphic subregion ($T = -5.7$, $p < 0.01$), but it was unrelated to the site-wetness gradient. Floristic composition was partly related to project age ($T = -1.8$, $p = 0.05$). At the site level, percent herb species was higher in the youngest age group (mean 83%) than in older classes (means 70–71%) (ANOVA; $F = 5.2$; $df = 2, 32$; $p = 0.01$). Annual/biennial herbs (vs. perennial) were also more prevalent in the youngest class (23 vs. 14–15% of species) ($F = 4.3$, $p < 0.05$).

Table 1. Mean values (SE) for site-level vegetation attributes by land type, with associated F-tests from two-way ANOVA. $df = 1, 57$ for all F-tests.

Vegetation Attribute	*WRP Sites*	*BLH Sites*	F *Value*	p *Value*
Species count attributes				
Percent herbaceous species	73.8 (1.9)	30.4 (3.0)	228.8	<0.001
Percent woody vine species	10.9 (0.9)	36.4 (2.6)	142.6	<0.001
Percent hydrophytic species	76.8 (2.0)	94.2 (0.9)	77.3	<0.001
Percent wetland species	43.4 (2.2)	49.5 (2.4)	9.8	<0.01[a]
Number of exotic species[b]	2 (0.2)	0.3 (0.1)	[b]	<0.001
Species cover attributes				
Relative cover of herb species (%)	76.2 (2.8)	24.4 (4.1)	163.3	<0.001
Relative cover of woody vines (%)	19.7 (2.6)	53.2 (5.2)	54.8	<0.001
Relative cover of hydrophytes (%)	74.8 (3.2)	96.1 (1.3)	38.3	<0.001
Relative cover of wetland species (%)	24.5 (3.1)	37.6 (4.9)	10.6	<0.01
Percent cover of exotic species[b]	5.7 (1.2)	0.5 (0.3)	[b]	<0.001

[a]Weak ANOVA effect ($p = 0.07$ using a non-parametric Kruskal–Wallis test).
[b]Proportional data did not meet ANOVA assumptions; p values are for chi-square tests with $df = 2$.

Discussion

A frequent basis for assessing restoration outcomes is whether the established vegetation is similar to the flora of a target ("reference") community. Prospects for fully replicating BLH floristic composition in the MAV are constrained, given the magnitude of landscape alteration and scarcity of mature forest. Recovery of functional attributes may be equally or more important (NRC 2001), but wetland functions do not necessarily correlate with "condition" metrics such as departure from reference vegetation (McLaughlin & Cohen 2013). Strict floristic comparisons are especially problematic for forest restorations, as the plant communities of young afforested sites and mature forests would naturally differ in the short term. The Wetlands Reserve Program seeks to recover multiple ecological services that include structural forest habitat and more natural hydrologic function, so we used both floristic and functional-group attributes to assess the developing understories of restored sites. Our findings indicated that understory vegetation reflected several factors that influence restoration progress.

Restored Versus Mature Forest Sites

The answer to the question "are WRP and BLH understories similar?" was mixed. Species composition appeared to differ greatly, but the pattern diverged by plant growth form. Early-successional herbaceous vegetation dominates in WRP sites because afforested sites are establishing from crop fields, whereas the understories of mature BLH sites are predominantly woody because forest canopy reduces herb cover and favors woody regeneration. The herb flora of WRP sites is variable, ranging from upland weedy species of abandoned farmlands (e.g. Battaglia et al. 2002) to hydrophytic species of open and forested wetlands (e.g. Sharitz & Mitsch 1993; De Steven & Gramling 2013). Some hydrophytes are frequent in both land types, whereas other hydrophytes of WRP sites may be infrequent in mature forest because they occur only in unshaded areas such as canopy gaps. In contrast to the herbaceous component, the woody flora of WRP and BLH understories is broadly similar and almost entirely hydrophytic, with many bottomland tree and vine species in common.

WRP and BLH sites were more similar in attributes reflecting wetland function, specifically the wetland-fidelity indicators. WRP sites have relatively more upland species because of agricultural history, but on average their understories are over 70% hydrophytic. This exceeds the 50% threshold that qualifies vegetation as meeting regulatory definitions for "wetland" habitat (cf. ACOE 2010). The two land types were also similar in the prevalence of "true" wetland species, even if such species are mainly herbaceous in restored sites and woody in forest sites.

Herbaceous and woody vine cover can inhibit tree establishment and growth in early stages of afforestation projects (Stanturf et al. 2004); however, observations of bottomland forest succession suggest that tree species can overtop the herb layer after 15–25 years (Battaglia et al. 2002; Twedt 2004). Shading from canopy closure would eventually reduce herbaceous cover and exclude many early-successional upland weeds and exotics (McLane et al. 2012; De Steven et al. 2015). If there are many woody species in common, then understory similarity between restored and mature sites would increase over time as the herbaceous component declined. This outcome depends critically on establishing an adequate density of overstory trees to drive canopy development.

Analogous patterns of understory composition were observed in the California Central Valley, U.S.A., a 5-million-hectare alluvial basin of two major river systems. The historic habitats were grasslands, marshes, and riparian forests along river courses, but flood regimes and land cover were vastly altered for agriculture at a scale comparable to the MAV (Duffy & Kahara 2011). Tree and shrub plantings are used to restore forest overstory on reclaimed riparian areas, whereas passive processes are expected to recover understory vegetation. Similar to our findings, understory diversity in these riparian systems is attributable to a richer and more varied herb flora compared with the woody component (Viers et al. 2012). McClain et al. (2011) found that understory composition of tree-planted sites differed from that of mature riparian forests; however, relative cover of native species increased with greater canopy closure over time, accompanied by floristic shifts to more shade-adapted

Table 2. Differentiated table of the relative frequencies (% of sites) of common understory taxa, by land type. ISA phi values with * denote significant association with land type at $p < 0.01$.

Taxon	*Life Form*	*Wetland Indicator Group*	*WRP (Relative Frequency)*	*BLH (Relative Frequency)*	*ISA (Φ)*
Herbaceous taxa					
Andropogon virginicus	Grass	Facultative	89	0	0.90*
Iva annua	Forb+	Facultative	73	0	0.76*
Solidago altissima	Forb	Upland	89	4	0.86*
Sorghum halepense†	Grass	Upland	59	0	0.65*
Ludwigia spp.	Forb	Wetland	51	8	0.48*
Lythrum alatum	Forb	Wetland	54	0	0.61*
Desmanthus illinoensis	Forb	Facultative	49	0	0.57*
Juncus spp.	Rush	Wetland	46	0	0.55*
Juncus (*coriaceous*, *effusus*)	Rush	Wetland	38	0	0.48*
Cyperus pseudovegetus	Sedge	Wetland	38	0	0.48*
Cardiospermum halicacabum†	Vine+	Facultative	32	0	0.44*
Ambrosia artemisiifolia	Forb+	Upland	30	0	0.42*
Apocynum cannabinum	Forb	Upland	27	0	0.40*
Conyza canadensis	Forb+	Upland	27	0	0.40*
Sida (*rhombifolia*, *spinosa*)	Forb+	Upland	27	0	0.40*
Solanum spp.	Forb+	Upland	32	0	0.44*
Verbena spp.†	Forb	Upland	32	0	0.44*
Symphyotrichum spp.	Forb	Wetland, Facultative	70	15	0.56*
Polygonum spp.	Forb	Wetland	62	15	0.48*
Dichanthelium spp.	Grass	Facultative	32	31	0.02
Eleocharis spp.	Rush	Wetland	27	4	0.32
Oxalis spp.	Forb	Upland	24	4	0.29
Carex vesicaria	Sedge	Wetland	14	27	0.17
Elymus virginicus	Grass	Facultative	16	46	0.32
Leersia (*lenticularis*, *virginica*)	Grass	Wetland	16	35	0.21
Boehmeria cylindrica	Forb	Wetland	5	50	0.50*
Justicia (*americana*, *ovata*)	Forb	Wetland	3	35	0.41*
Polygonum virginianum	Forb	Facultative	0	46	0.55*
Sanicula canadensis	Forb	Upland	3	58	0.60*
Woody taxa					
Brunnichia ovata	Vine	Wetland	84	88	0.07
Campsis radicans	Vine	Facultative	73	69	0.04
Diospyros virginiana	Tree	Facultative	16	38	0.25
Fraxinus pennsylvanica	Tree	Wetland	35	38	0.03
Quercus texana	Tree	Wetland	32	27	0.06
Rubus argutus	Shrub	Facultative	54	69	0.16
Rubus (*hispidus*, *trivialis*)	Shrub	Wetland, Facultative	38	35	0.03
Toxicodendron radicans	Vine	Facultative	62	96	0.42*
Celtis laevigata	Tree	Wetland	43	88	0.48*
Ulmus americana	Tree	Wetland	22	69	0.48*
Ampelopsis arborea	Vine	Facultative	19	65	0.47*
Vitis (*rotundifolia*, *aestivalis*)	Vine	Facultative, Upland	11	81	0.70*
Trachelospermum difforme	Vine	Wetland	8	88	0.80*
Ilex decidua	Shrub	Wetland	5	62	0.60*
Berchemia scandens	Vine	Wetland	5	54	0.53*
Bignonia capreolata	Vine	Facultative	0	73	0.76*
Cocculus carolinus	Vine	Facultative	3	58	0.60*
Parthenocissus quinquefolia	Vine	Facultative	5	50	0.50*
Smilax spp.	Vine	Facultative	3	92	0.90*
Quercus phellos	Tree	Wetland	5	54	0.53*
Ulmus crassifolia	Tree	Facultative	3	38	0.44*
Acer rubrum	Tree	Wetland	5	31	0.33
Sabal minor	Shrub	Wetland	5	31	0.33

†, Exotic species; +, annual species, or includes annuals.

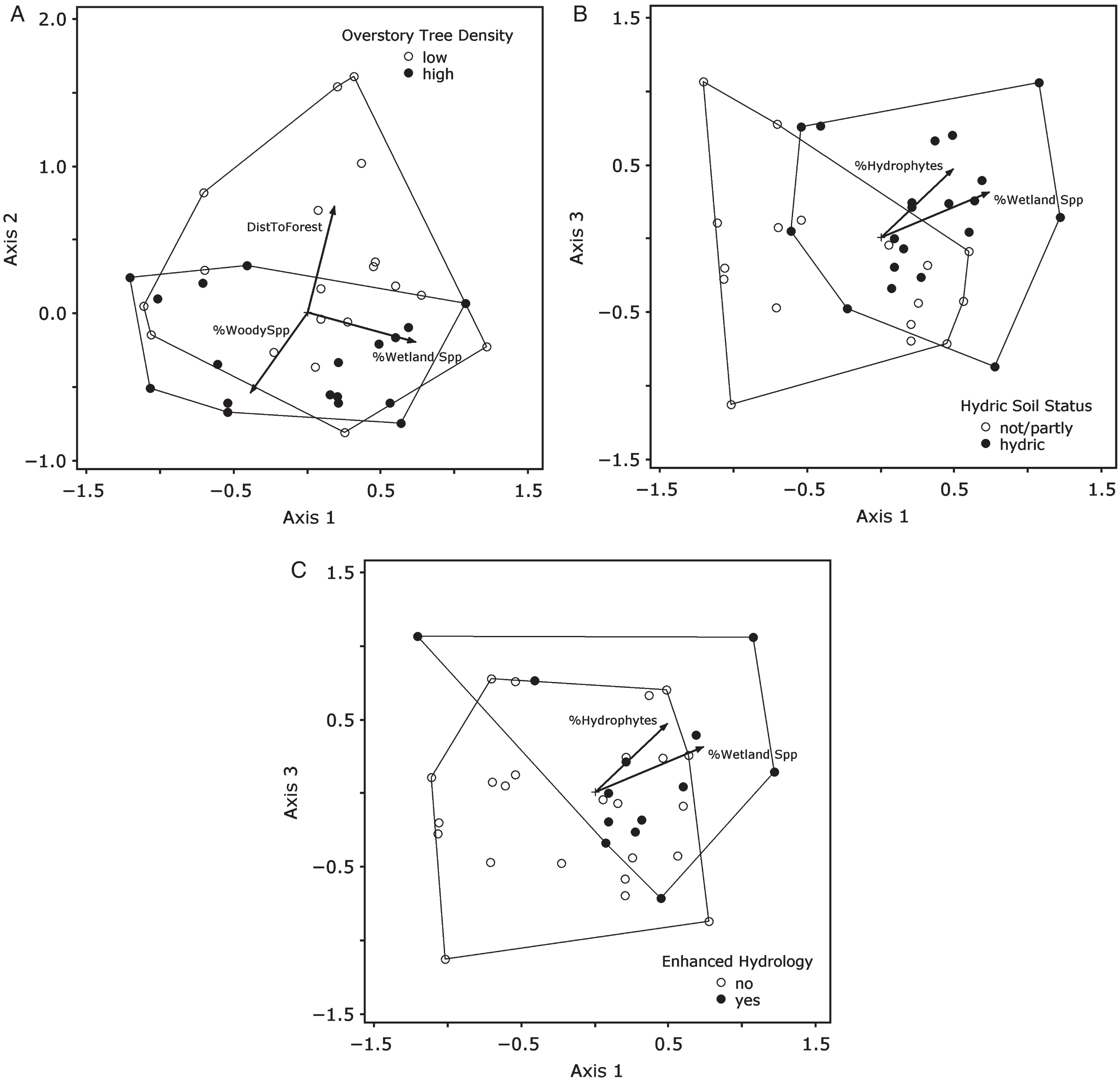

Figure 3. NMS ordination of 37 WRP sites for (A) axes 1 and 2, and (B, C) axes 1 and 3. Site-level binary variables are shown as groups delineated by convex-hull polygons. Significant continuous variables are represented by labeled vector arrows, where values increase with arrow direction and lengths are proportional to joint correlation strength.

species. In contrast to the MAV, exotic species are prevalent across the Central Valley landscape and dominate the understory cover in both restored and mature forest sites. Responses of growth forms or wetland indicator classes have not been evaluated to date.

Variation Among Restored Sites

The answer to the question "what influences variation among WRP sites?" identified several key elements for site-level restoration outcomes; these factors are partly interrelated and in some cases can be influenced by management actions.

The relative prevalence of woody species in the understory was correlated with the linked factors of distance to remnant forest and overstory density. The tree-planting practice seeks to overcome dispersal limitation for heavy-seeded species such as oaks and pecans, while relying on natural colonization to supply a diversity of other tree species with less restrictive dispersal (Allen 1997; King & Keeland 1999). Success of this "semi-passive" approach depends on proximity to existing forests because many woody species lack persistent seed banks and must colonize by dispersal after farming ceases (e.g. Middleton 2003). Studies of afforested sites have noted that density of colonizing trees declines with distance from forest edges (e.g. McCoy et al. 2004; Twedt 2004). We found correlations between forest proximity, overstory tree density, and woody species prevalence in the understory (cf. Fig. 3A), which suggests a self-reinforcing process: sites closer to forest may establish denser overstories that will reduce herbaceous cover and recruit more woody seedlings to the understory (Battaglia et al. 2008). The number of woody species was low if WRP sites were at large distances (>1,000 m) from forest, which suggests a possible landscape-scale effect on forest development. If agricultural landscapes lack forest remnants or if afforested sites are too distant for natural colonization, successful tree planting becomes critical. Monotypic oak plantings may have low survival because of adverse site flooding, poor soils, or intense herbivory, whereas mixed-species plantings may be more successful across a range of conditions (Haynes 2004; Dey et al. 2010).

The numbers of herbaceous and hydrophytic species were unrelated to distance from forest, which may seem paradoxical if BLH forest is regarded as the main source of "typical" floodplain herbs. However, many herb species have long-lived seed banks that enable them to persist even within farmed floodplains (Middleton 2003). Agricultural landscapes also have multiple sources of colonizing herbs; for example, drainage ditches support wet vegetated habitats that can supply propagules of wetland herbs to restored areas (Herzon & Helenius 2008). The entire MAV landscape is covered by an extensive network of open field ditches and drainage channels that contain various herb and hydrophyte species (Bouldin et al. 2004); hydrologically enhanced areas on afforested tracts also support wet-site vegetation (Fleming et al. 2012). Thus, WRP sites have nearby sources of herbaceous hydrophytes other than forest, which may account for lack of correlation with forest distance. Nonetheless, certain BLH herbs may not re-establish because they are restricted to closed forests or depend upon river flooding for dispersal (Middleton 2003; De Steven et al. 2015).

Whereas canopy development influences understory growth form composition, local hydrologic conditions influence the relative prevalence of plant functional types. One factor affecting local hydrology is variability in physical setting. Even though the floodplain is disconnected from Mississippi River flooding, site-wetness potential varies across the MAV owing to substrate and topographic variation (Chapman et al. 2004). Holocene alluvial soils (cf. Fig. 1) are predominantly dense, poorly drained clays that are saturation- or flood-prone, whereas Pleistocene alluvial soils include better drained loams and silt loams that may flood intermittently but lack hydric soil features (Chapman et al. 2004). This contrast may partly explain the weak floristic differentiation between geomorphic subregions, but land alterations can obscure the effects of geomorphic setting on local hydrology. The local factor of hydric soil status had greater explanatory power, as WRP sites with mapped hydric soils tended to have more hydrophytic vegetation than sites lacking such soils.

Another factor influencing site-level wetness condition is the use of hydrology restoration practices (Hunter et al. 2008; Pierce et al. 2012). Enhancements such as water-retention areas will be variably inundated depending on rainfall amounts, type of enhancement, and degree of water-level management. It appeared that afforested areas near to hydrologic features (whether installed or associated with natural swales) had relatively more understory hydrophytes and wetland species. Adding hydrologic practices could promote a more hydrophytic vegetation directly by inundating adjacent tree-planted areas and favoring flood-tolerant species, and indirectly by creating wetter habitats that supply propagules to planted areas.

Implications for Assessment

Evaluations of vegetation restoration often focus on species richness patterns, but additional insight can be gained by examining the responses of meaningful functional groups. On floodplain restoration sites, understory growth form composition reflects the progress of forest development. Successful afforestation depends on suitable tree-planting practices and/or favorable site locations for tree colonization, although specific approaches will vary with land ownerships and project goals. Depending on whether the objective is timber production, wildlife habitat, or multiple ecosystem services, planting and management practices may be chosen to achieve rapid growth of monotypic plantations or slower development that promotes greater biodiversity (Twedt 2004). Differing objectives may also involve trade-offs at the landscape scale; for example, project locations that are best for increasing forest patch size (close to existing forests) may differ from locations that maximize services such as pollutant reduction (Faulkner et al. 2011).

Successful floodplain afforestation can produce structural forest habitat, given sufficient time. Enhancing other ecosystem services requires restoring site hydrology to the extent possible because hydrologic conditions regulate functional processes (e.g. nutrient removal and carbon sequestration) that vary with soil type, topographic position, and land-use practices (Ullah & Faulkner 2006; Hunter et al. 2008). As indicators of hydrologic status, the relative prevalence of hydrophytic and wetland species can suggest whether a restored site has the potential to support these functional processes. Relative hydrophyte cover in WRP sites ranged between 35 and 99% (median 80%); likewise, relative cover of wetland species mostly ranged between 1 and 43% (median 20%). In 6 of 37 sites (16%), relative hydrophyte cover was below the 50% threshold that defines "wetland" vegetation, which suggests that wetness conditions in those sites may be inadequate. Local hydrology restoration is critical to improving functional services, given that recovering the historic flood regime is impractical. Adding hydrology enhancements on otherwise afforested tracts can also increase landscape-scale diversity by supporting a different wetland flora from that which occurs under forest canopies (Haynes 2004; Fleming et al. 2012; cf. Bruland & Richardson 2005).

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