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Historical trajectories and restoration strategies for the Mississippi River Alluvial Valley

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ABSTRACT

Unlike upland forests in the eastern United States, little research is available about the composition and structure of bottomland forests before Euro-American settlement. To provide a historical reference encompassing spatial variation for the Lower Mississippi River Alluvial Valley, we quantified forest types, species distributions, densities, and stocking of historical forests using General Land Office (GLO) records from Missouri. For modeling historical species distributions, we applied random forests classification and predictor variables included terrain and soil characteristics. Historical forest types predominantly were sweetgum, black and white oak, and elm. Contemporary forests increased in maples and hickories, which are replacing sweetgum and oaks. Forest densities increased from 215 to 350 trees/ha to 350 to 400 trees/ha for trees $\geqslant$12.7 DBH. Basal area historically was greater by a factor of 1.6–2.6 and percent stocking historically was full, except in an open oak-dominated ecosystem, whereas forests today have lower stocking comprised of young, small diameter trees. Land types, elevation, and soil texture determined historical species distributions, and we expect that with loss of fire and flooding, ecological separation by site factors has become less influential for current species distribution. Selection of sweetgum and oaks for planting would restore historical composition better than planting of ash and other shade-tolerant species, which promotes conversion to forest types under undisturbed conditions rather than restoration of forests under historical disturbance regimes. We also recommend managing for large diameter trees by thinning to promote more rapid growth of residual trees. Although there is uncertainty in historical reconstruction, these results provide new information about the presence and spatial variability of sweetgum and oak in historical forests of the Lower Mississippi River Alluvial Valley and post-settlement transformation of alluvial landscapes.

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1. Introduction

The Lower Mississippi River Alluvial Valley, reaching from southern Illinois to the Gulf Coast of Louisiana, is a 10 million ha landscape that historically was composed of bottomland hardwood forests – the greatest representation of this vegetation type in North America (Schoenholtz et al., 2001). The Mississippi River Alluvial Valley consisted of dense hardwood forests on protected slopes, terraces, and deep riparian alluvium, along with cypress swamps and marshes. Natural hydrologic cycles influenced community composition and structure more than fire. Nevertheless, fire was important in maintaining oak woodlands and perhaps even oak savanna and prairie on ridges, exposed slopes, and thin and sandy soils (Nigh and Schroeder, 2002).

Agricultural land use has reduced and modified bottomland forests throughout the world, including the Mississippi River Alluvial Valley. At some point, at least 75% of bottomland forests in the Mississippi River Alluvial Valley have been converted to agriculture (Schoenholtz et al., 2001). After draining, both clearing and conversion to agriculture occurred in bottomland forests, similarly to upland forests of the eastern United States. Suppression of disturbance also occurred, as natural hydrology was controlled by channelization and levees so that floodplains and terraces lost their connection to characteristic disturbance regimes (King et al., 2009). Hydrological suppression was analogous to fire suppression in upland forests (Fralish and McArdle, 2009), and indeed, fire may have been frequent enough to be an influential driver of composition, particularly of oaks and native bamboo, in bottomland forests (Kaufert, 1933; Nelson et al., 2008, 2009; Gagnon, 2009).

Currently, there are extensive programs (e.g., Conservation Reserve and Wetland Reserve Programs, Partners for Fish and Wildlife Program, North American Waterfowl Management Plan,

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Wildlife Habitat Incentives Program) in place to replant approximately 3 million ha of marginal agricultural land, most formerly in soybeans, (King and Keeland, 1999). Hundreds of thousands of acres are enrolled in programs to restore degraded wetland functions through reforestation (King et al., 2006). Other benefits of reforestation include providing suitable conditions for wildlife such as forest-breeding birds, enhanced species heterogeneity, and economic returns through pulpwood and biofuel (Twedt and Portwood, 1997).

Restorationists in the Lower Mississippi River Alluvial Valley initially favored oak species, which is believed to have been the dominant species in the past (Ouchley et al., 2000). Early reforestation efforts used 70–95% oak species, with some pecan and baldcypress, leaving lighter-seeded species to restore naturally (Schoenholtz et al., 2001). More recently, restorationists have made the decision to establish faster growing mixed species stands, planting light-seeded species of sycamore, green ash, and sweetgum to increase the development rate of vertical structure and species diversity (King and Keeland, 1999; Schoenholtz et al., 2001). The oak component of plantings dropped to about 55–80% by 1995–1998 (Schoenholtz et al., 2001).

Reforestation of former agricultural land is an international issue and although natural succession will occur, the length of time required for this process to restore forests may be extreme and the outcome not comparable to historical composition and structure (Stanturf et al., 2009). For active restoration, with little research available about historical bottomland forests in the Lower Mississippi River Alluvial Valley (outside of a National Wildlife Refuge in Louisiana; Ouchley et al., 2000), restorationists must rely on either (1) examples from nearby forests or remnants from mature bottomland hardwood forests that have been disconnected from natural hydrologic disturbance and (2) ecological concepts and beneficial conditions for wildlife (LMVJV Forest Resource Conservation Working Group, 2007). Restorationists decided to shift from predominantly oak forests to diverse forests with complex structure as an outcome without knowledge of historical trajectories. Therefore, to inform restoration decisions, we quantified forest types, species distributions, and densities of historical forests in the Mississippi River Alluvial Valley in Missouri (MMAV) using General Land Office (GLO) records. For some measure of comparison, we used USDA Forest Analysis and Inventory (FIA) plots with the realization that there were a limited number of plots to describe contemporary forests. Unlike site-scale studies, the extent of our study area captures the spatial variation inherent in the Mississippi River Alluvial Valley.

2. Methods

2.1. Tree surveys

The General Land Office founded the Public Land Survey System of townships and ranges in 1812 (White, 1983). Public lands were divided into townships measuring 9.6 km on a side, and townships were divided into 1.6 × 1.6 km sections. Surveyors recorded species, distance, bearing, and diameter for two to four trees at the corners and middle of each section line, i.e., every 0.8 km. In addition to bearing trees, surveyors recorded line trees that they encountered while surveying the section lines. There were about 37,000 GLO bearing trees selected by the surveyors at survey points and line trees encountered along survey lines in the Mississippi River Alluvial Valley in Missouri from 1817 to 1860 (J. Harlan, Geographic Resources Center, http://msdis.missouri.edu). We used ArcGIS (ESRI, version 9.3, Redlands, CA, USA) and SAS (SAS software, version 9.1, Cary, North Carolina, USA) for all data processing.

The USDA Forest Service Forest Inventory and Analysis (FIA) program collects numerous tree measurements for all trees at plots that are visited on a 5 year cycle. We used the latest complete cycle from 2004 to 2008. The USDA Forest Service intersected our environmental variables (see below) to match exact plot coordinates, using GIS (geographic information system) methodology. There were only 5–7 plots per ecological subsection (Nigh and Schroeder, 2002) in the Mississippi River Alluvial Valley in Missouri and about 120–235 trees per ecological subsection.

2.2. Environmental variables for species distribution modeling

We used Soil Survey Geographic Database (SSURGO; Natural Resources Conservation Service, http://soildatamart.nrcs.usda.gov) polygons as our spatial unit (mean polygon area of 39 ha, standard deviation of 233 ha) for species distribution modeling. The SSURGO soil polygons were discrete spatial units but each unique prediction unit (mean area of 1039 ha, standard deviation of 2322 ha) was based on soil map unit for each county (soil polygons with similar soil characteristics in a county), land type association (Nigh and Schroeder, 2002), and bedrock geology. We prepared 11 environmental variables from the SSURGO tables by map unit for each county. Variables included (1) drainage class (very poorly drained to excessively drained), (2) taxonomic order, (3) flooding frequency, and (4) presence of hydric soils. For map units with more than one component (soil series), we used the categorical variable from the dominant component. We also used (5) depth (cm) to either the bottom of the soil profile or soil restriction, after removing soil horizon layers below restrictions based on restrictive layer presence and restrictive layers with suffixes (i.e., *d*, *m*, *r*, *x*). We then calculated (6) mean water holding capacity (cm/cm), (7) pH, (8) base saturation, (9) organic matter (%), (10) clay (%), and (11) sand (%) to the depth and weighted values by component percentage.

From a 30 m DEM (digital elevation model), we calculated seven variables: elevation (m), slope (%), transformed aspect (Beers et al., 1966), solar radiation (from a 60 m DEM), topographic roughness (Sappington et al., 2007), wetness convergence, and topographic position index (T. Dilts, http://arcscripts.esri.com). We then calculated the mean value for each variable by map unit. We also joined land type association, an ecological classification, and bedrock geology designations to each individual polygon (Nigh and Schroeder, 2002).

2.3. Modeling and prediction of species distribution models

We modeled the most common 16 species or species groups (Table 1). We randomly selected 0.67 of polygons with the species, up to 2500 polygons, for modeling, and held back the rest for prediction and validation. For pseudoabsences, we randomly selected up to 2500 polygons without a recorded species presence from the polygons with survey points (Mateo et al., 2010). As our statistical method, we applied random forests (Breiman, 2001; Cutler et al., 2007), a classification method based on bootstrap aggregation (bagging) by the majority vote of many classification trees grown using random samples of both predictor variables and training data. We used the randomForest package (Liaw and Wiener, 2002) in R statistical software (R Development Core Team, 2010), with the sampsize option (which is sampled without replacement), where we set the bag fraction, or subsampling rate, at 0.67 of the selected polygons with the species. We then specified 0.25 of that value for pseudoabsences, resulting in a prevalence of 0.80, or one pseudoabsence for every four known present cases. We set the number of trees at 1000 and the number of variables randomly sampled at each split as the square root of the number of predictors.

We used the ROCR package (Sing et al., 2005) in R to calculate the true positive rate over Receiver Operating Characteristic

Table 1
Tree species/group, counts, and percent composition for GLO (1817–1860) surveys in the Mississippi Alluvial Valley of Missouri. The GLO line trees are encountered by surveyors and GLO bearing trees are selected by surveyors. Black oak and white oak may represent additional species from the Erythrobalanus and Leucobalanus subgeneras, due to misidentification by surveyors.

Species/group		Line trees		Bearing trees	
		Count	%	Count	%
Ashes	*Fraxinus americana, F. pennsylvanica*	725	7.33	2741	11.39
Baldcypress	*Taxodium distichum*	561	5.67	1002	4.16
Blackgum	*Nyssa sylvatica*	318	3.22	797	3.31
Black oak	*Quercus velutina*	1010	10.21	2200	9.14
Cottonwood	*Populus* spp.	773	7.82	909	3.78
Elms	*Ulmus alata, U. americana, U. rubra*	1140	11.53	3338	13.87
Hackberry	*Celtis occidentalis*	190	1.92	830	3.45
Hickories	*Carya cordiformis, C. glabra, C. laciniosa, C. ovata, C. texana, C. tomentosa*	626	6.33	1067	4.43
Maples	*Acer saccharum, A. negundo, A. rubrum, A. saccharinum*	688	6.96	2354	9.78
Mesic (locusts, mulberry, hornbeam)	*Carpinus caroliniana, Robinia pseudoacacia, Gleditsia triacanthos, Morus alba* and *M. rubra*	122	1.23	445	1.85
Post oak	*Quercus stellata*	143	1.45	279	1.16
Sweetgum	*Liquidambar styraciflua*	2175	21.99	4833	20.08
Sycamore	*Platanus occidentalis*	191	1.93	427	1.77
Water tupelo	*Nyssa aquatica*	109	1.10	275	1.14
White oak	*Quercus alba*	912	9.22	1953	8.12
Willow	*Salix* spp.	208	2.10	613	2.55

(ROC) curves for predictions at a 75% threshold. We also grouped the predictions into four bins (0–25%, 25–50%, 50–75%, 75–100%) and mapped the distributions (please contact the authors for maps or GIS layers). Lastly, we examined environmental variable importance, ranked by the statistical method.

2.4. Forest type rules

We identified the historic and contemporary forest types of the region based upon the three to five most abundant tree species. To do this, each ecological subsection (Fig. 1) was divided into land types, such as hills or plains, resulting in a total of 8 units. We selected live trees with DBH $\geqslant$ 12.7 cm from accessible plots. Due to lack of FIA plots, we restricted ecological units to three of the four subsections for current forests. The number of trees had to be $\geqslant$150 per ecological unit and percent composition of tree species or species group had to be $\geqslant$8% per ecological unit to be a dominant species in the forest type. A threshold of 8% limited forest types to no more than 5 species/species groups and yet allowed species representation.

2.5. FIA density

Plots had to contain at least two trees and additionally had to be 100% forestland, which FIA defines as land at least 1.0 acre in size and 120.0 feet wide with at least 10% cover by live trees of any size, "including land that formerly had such tree cover and that will continue to have forest use". We selected live trees with a DBH $\geqslant$ 12.7 cm from accessible plots. We calculated trees per acre using the supplied expansion factor of 6.02, based on one tree representing the inverse of the plot area in acres (i.e., $1/(4 * 0.042)$), and summed the values for each plot. We then found the mean value for ecological subsections with $\geqslant$150 trees.

2.6. GLO density

We estimated density using the Morisita plotless estimator (Morisita, 1957):

$$\lambda = \frac{(kq-1)}{\pi n}\sum_{i=1}^{n}\frac{q}{\sum_{j=1}^{q} r_{ij}^{2}} \qquad (1)$$

where λ (density) is the number of trees/ha, q is the number of quadrants with recorded trees (2, 3, or 4), k is the distance rank of the tree in each quadrant, n is the number of points, and r is the survey point-to-tree distance. We selected trees $\geqslant$12.7 cm DBH and retained only survey points with 2–4 trees. For points with four trees, due to the variability of density estimates for a clustered spatial pattern (Hanberry et al., 2011), we removed the most distant tree, resulting in points with three trees. We also excluded any points that had more than one tree with a distance of '0' because to have two trees filling the same space is an error. To calculate the distance from the survey point to the center of each witness tree we added the tree radius to the distance from the survey point to the witness tree. We estimated density using the Morisita plotless estimator (Morisita, 1957) by the number of tree per point for all points within similar land types for a subsection. To produce a reliable density estimate, we excluded estimates where the minimum number of points was <200 for points with two trees and the minimum number of points was <50 for points with three trees (Hanberry et al., 2011). We then produced a low and high value based on corrections for potential spatial patterns of clustering or regularity.

Surveyors potentially did not select the nearest trees (a distance rank from the survey point of (1), which results in underestimated densities. We corrected density estimates by assuming that surveyors selected trees within a range of mean distance rank from 1.4 to 1.95 (a reasonable range of surveyor bias; Hanberry et al., 2012). We produced a low value, using the low value from spatial pattern correction and assuming trees selected had a mean rank of 1.4, and a mean value, assuming trees selected had a mean rank of 1.8, using a rank-based method (Hanberry et al., 2012). For a complementary bias method, we used adjustment quotients by ecological unit to correct non-random frequencies for quadrant location, quadrant configuration, azimuth, and combined species and diameter classes (Hanberry et al., 2012). We produced a mean value and a high value, using the high value from the spatial pattern correction. We then averaged the two mean values from the rank-based and bias-based methods and retained the low value from the rank-based method and high value from the bias method. To unite the density estimates from points with two trees and points with three trees, we weighted the combined density estimate by the number of trees at each survey point and the total number of survey points.

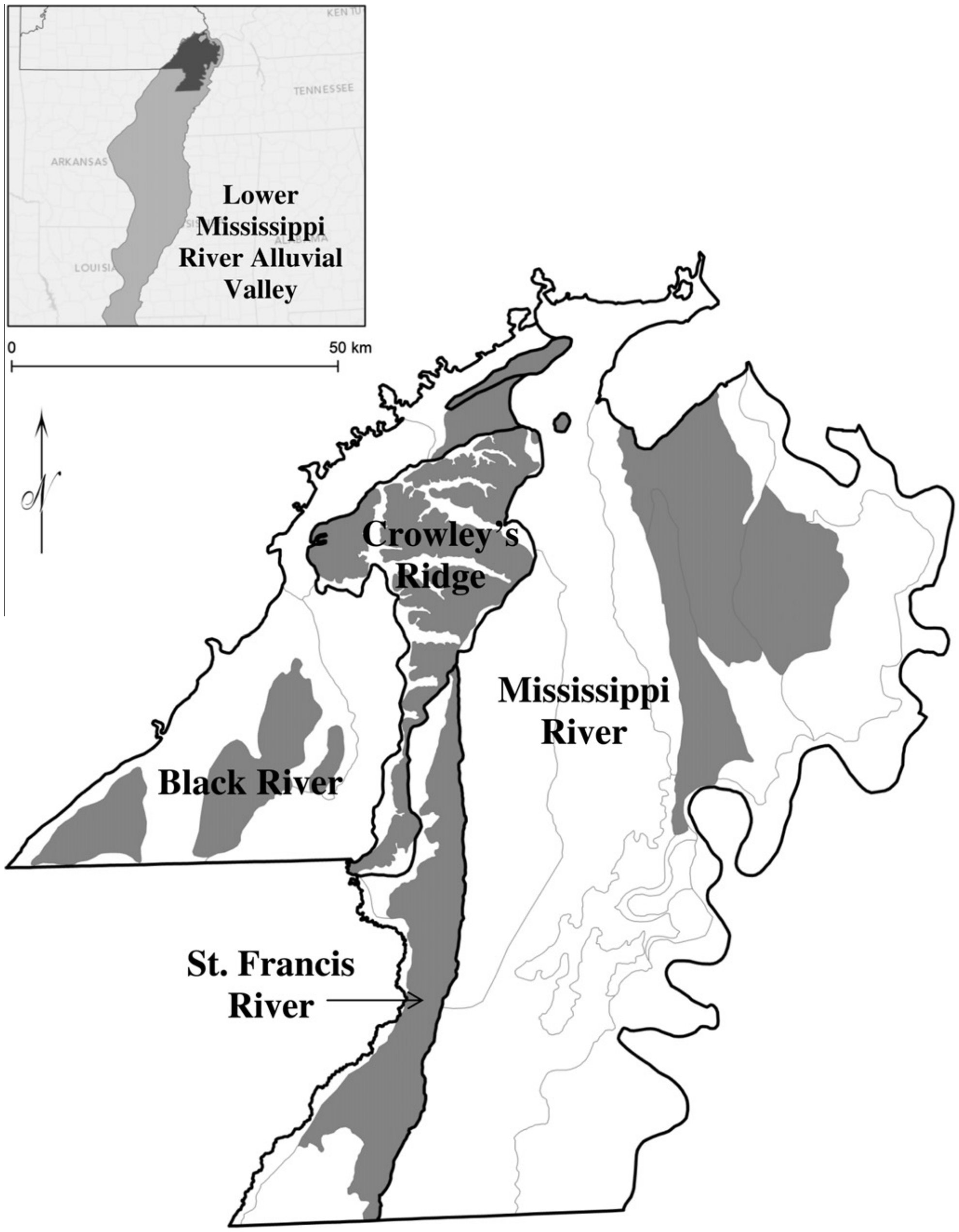

Fig. 1. The four ecological subsections of the Mississippi River Alluvial Valley in Missouri. Areas in white are alluvial plains and dark-shaded areas are sand ridges and hills.

2.7. Basal area and stocking

We used the quadratic mean diameter (square root of the mean DBH^2) to calculate basal area ($0.00007854 \times DBH^2 \times$ density) and mean diameter to calculate percent stocking. We used stocking coefficients for second order polynomial regression equations developed by Goelz (1995) for southern bottomland hardwood forests and Larsen et al. (2010) for midwestern eastern cottonwood-silver maple-American sycamore bottomland forests. A stocking percent of 100 represents full use of growing space.

3. Results

3.1. Composition, species distribution models, and forest types

Historically, the most abundant species were sweetgum, elms, black oak, and white oak (Table 1). Although we interpreted black oak and white oak as single species, i.e., *Quercus velutina* and *Quercus alba*, surveyors may have misidentifed red oaks as black oak and white oaks, particularly overcup oak (*Quercus lyrata*), as white oak. Other abundant species included (in order) ashes, maples, cottonwood, hickories, and baldcypress. There was a discrepancy between the bearing and line trees for cottonwood, ashes, and maples in particular due to the interference by water in bearing tree selection (see Nelson, 1997). Ashes and maples were more commonly selected as bearing trees and cottonwood was encountered more as a line tree. The most common recorded species of about 37,000 trees probably were the most abundant species; it is only the exact frequencies that are questionable. Because this landscape today is largely used for row crop production and other forms of agriculture, there are few remaining forests to be used for comparing to the historic distribution. Our analysis of the remaining forests in this region using FIA data indicated that maples, willows, elms, and sweetgum are the most common species currently.

For species distribution models, mean true positive rate of presence was 84% (65% for sweetgum to 91% for cottonwood and willows). The most common species, sweetgum and elms, were likely to occur everywhere except along the Mississippi River for sweetgum and along some of the ridges for elms (Fig. 2). Similarly to elms, ash and maples were likely to occur everywhere except some of the ridges (Fig. 2). The oaks were probable throughout most of the section, particularly in the western, interior area and away from the Mississippi River (Fig. 3). Cottonwood and willows were common along the Mississippi River floodplain (Fig. 3). The most frequent variables of the top four variables for the 16 species were land type association (top variable in every model), elevation (10 models), percent sand (9 models), and solar radiation (6 models). These variables were important for separating the sandy ridges from bottomland alluvium.

Based upon the most abundant three to five species in each ecological unit, the historical forest types were sweetgum, black and white oak, and elm forests, with some dominance by ashes, maples, hickories, cottonwood, and baldcypress (Table 2). The exception was the predominantly oak, ash, and hickory forests of Crowley's Ridge, the most upland area. Compared to historical forests, current forest types had lower sweetgum and white oak dominance and black oak was no longer a dominant species. Also, our analysis shows that maples and hickories have increased in dominance. Overcup oak, which may have been misidentified by GLO surveyors, water tupelo (*Nyssa aquatica*), and hackberry (*Celtis occidentalis*) were new dominant species. Shortleaf pine (*Pinus echinata*), which is not native the MMAV, was present in the contemporary forest because it was once widely planted.

3.2. Structure

The historic mean density was 279 trees/ha for trees ⩾12.7 cm DBH, with low values of 216 to high values of 351 trees/ha by ecological unit (Table 2). In general, density was lower in the oak

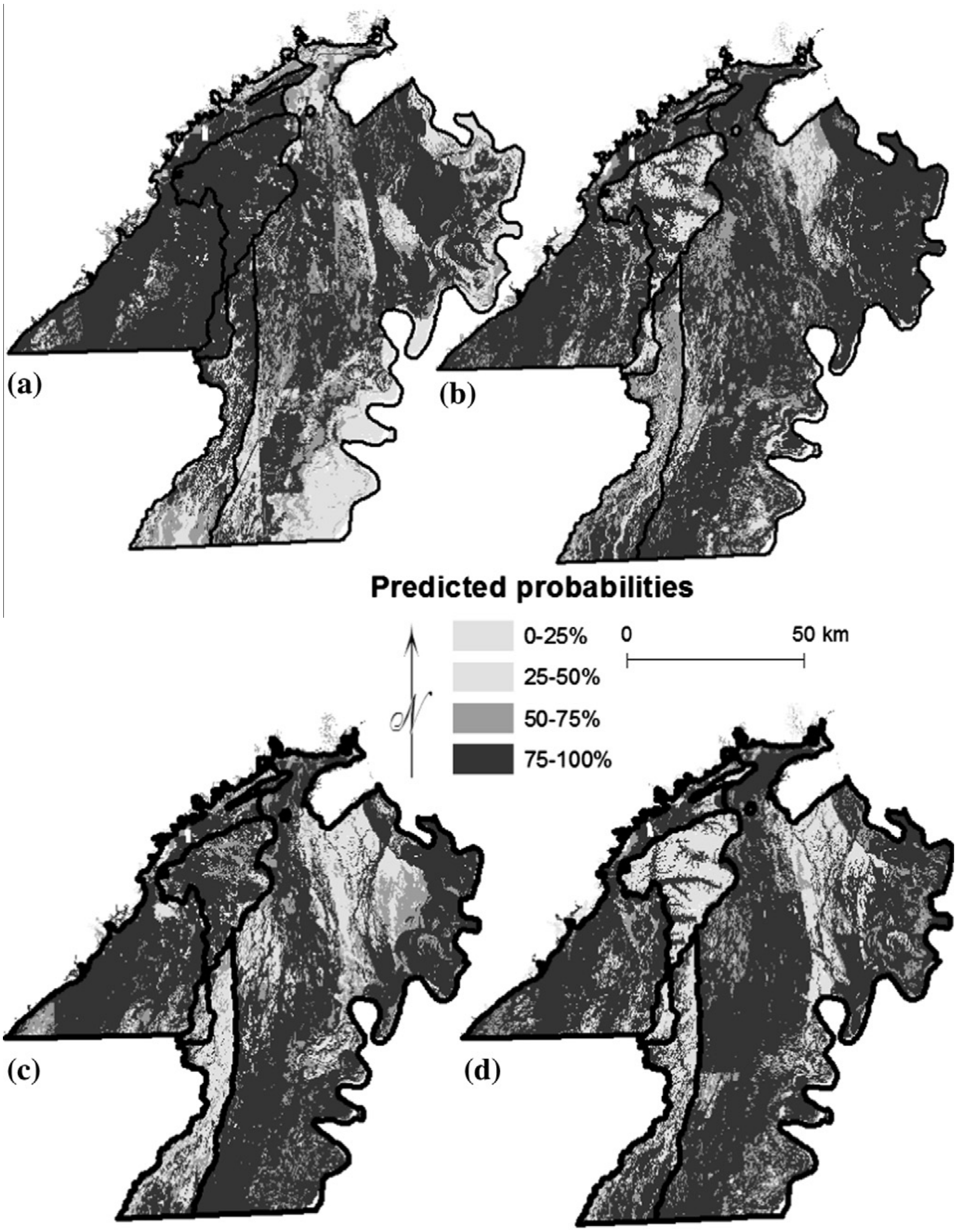

Fig. 2. Species distribution models for (a) sweetgum, (b) elms, (c) ashes, and (d) maples.

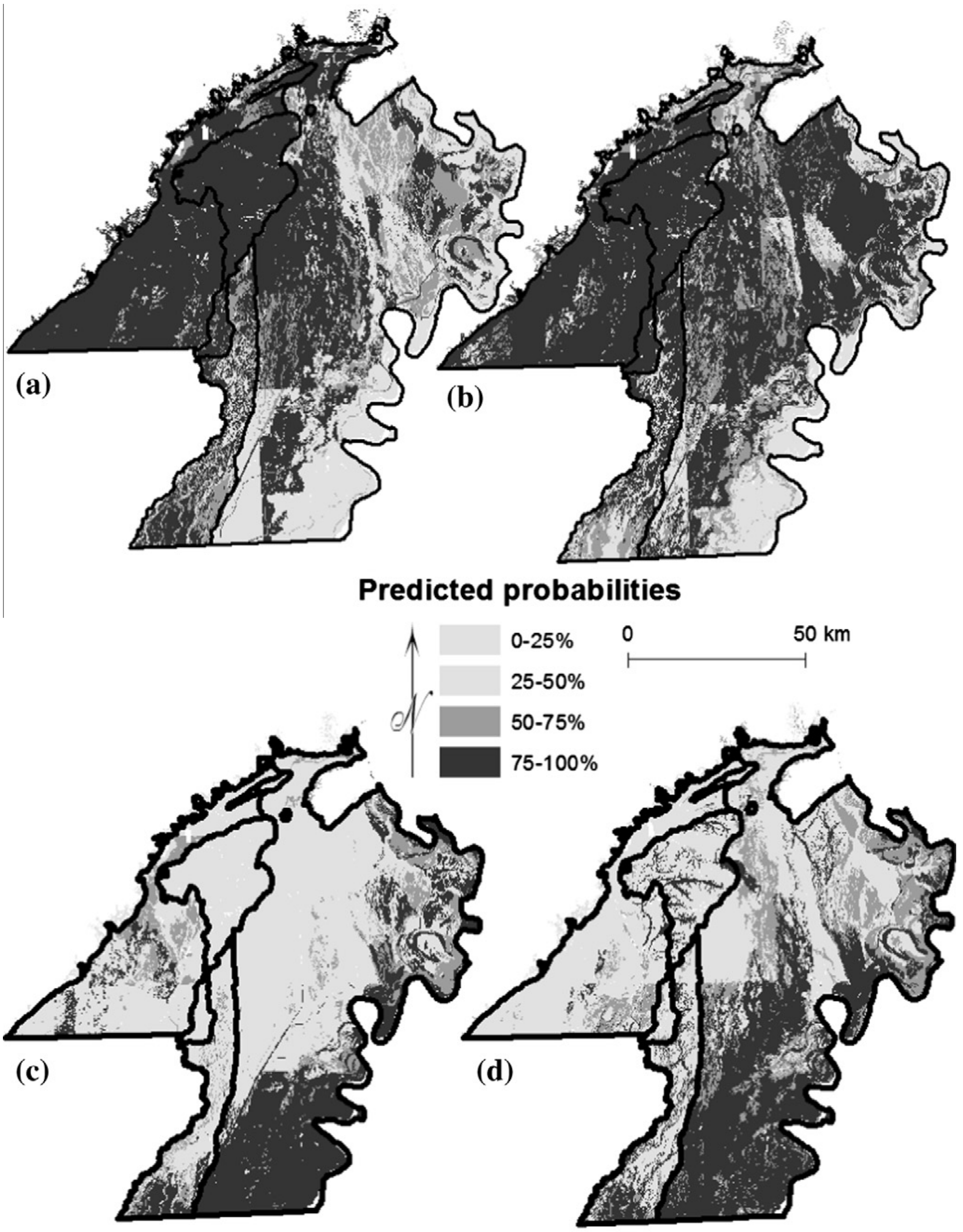

Fig. 3. Species distribution models for (a) white oak, (b) black oak, (c) cottonwood, and (d) willows.

forests and on ridges and sandy soils. Current densities may be greater, at about 350–400 trees/ha. Historically, trees were larger than in contemporary forests. Although unadjusted for potential surveyor bias, GLO tree diameters (mean about 41 cm DBH) were about 1.7 times FIA tree diameters (mean about 24 cm DBH). Trees in the Crowley's Ridge and Mississippi River subsections historically were slightly smaller in diameter than those in the Black River and St. Francis River subsections, perhaps due to greater disturbance.

Although the historical high values for basal area and stocking were unrealistically inflated due to either diameter or density, they provide a range for basal area and stocking. Basal area historically ranged from 30 m^2/ha in the more open oak ecosystem of the Crowley's Ridge hills to 68 m^2/ha along the St. Francis River alluvial plains, whereas current basal area was about 21 m^2/ha, regardless of location (Table 3). Basal area historically was greater by a factor of 1.6–2.6, depending on the historical basal area of the ecological unit. Percent stocking historically ranged from the lower estimates (Larsen et al., 2010) of 52–108 or the greater estimates (Goelz, 1995) of 85–178, which indicated full stocking except in the open oak-dominated ecosystem of Crowley's Ridge hills. Current percent stocking ranged narrowly from 42 to 47 (Larsen et al., 2010) or 64 to 72 (Goelz, 1995). Stocking historically was greater by a factor of 1.2–2.5.

4. Discussion

4.1. Historical trajectory

In the Mississippi River Alluvial Valley of Missouri, forests have changed in extent, composition and structure. Area of the contemporary landscape is much less forested (4% according to FIA estimates) compared to 89% during the historical surveys (Nelson, 1997). Species composition has changed due to decreases in oak

Table 2
Forest types, densities (trees/ha), and diameters (cm) of historical (GLO) and current (FIA) forests (trees ⩾12.7 DBH) by ecological unit (subsection and land type). Listed species order is the same for both GLO and FIA forest types, regardless of frequency. Blank entries are where there were too few FIA trees to evaluate.

Ecological unit	GLO forest type	FIA forest type	GLO density			FIA density	GLO	FIA
			Mean	Low	High		Diameter	Diameter
Black River Alluvial Plains	Sweetgum–black_oak–white_oak–elm	Sweetgum–elm–maple–hickory–overcup_oak	243	137	303	402	45.36	24.06
Black River Sand Ridges & Hills	Sweetgum–white_oak–elm–ash–maple	Sweetgum–elm–maple–hickory–overcup_oak	238	132	301	402	44.75	24.06
Crowley's Ridge Alluvial Plains	Sweetgum–black_oak–white_oak–elm	White_oak–elm–hickory–pine	320	160	428	374	37.59	23.31
Crowley's Ridge Hills	Black_oak–white_oak–ash–hickory	White_oak–elm–hickory–pine	216	113	281	374	37.43	23.31
St. Francis River Alluvial Plains	Sweetgum–elm–cottonwood–cypress		351	191	448		42.92	
St. Francis River Sand Ridges & Hills	Sweetgum–black_oak–elm		267	150	334		44.91	
Mississippi River Alluvial Plains	Sweetgum–elm–cottonwood–ash–maple	Elm–willow–maple–water_tupelo–hackberry	335	171	446	351	39.60	24.66
Mississippi River Sand Ridges & Hills	Sweetgum–black_oak–elm	Elm–willow–maple–water_tupelo–hackberry	262	131	351	351	37.09	24.66

Table 3
Basal area (m^2/ha) and stocking (%) of historical (GLO) and current (FIA) forests (trees ⩾12.7 DBH) by ecological unit (subsection and land type). Blank entries are where there were too few FIA trees to evaluate.

	GLO basal area			FIA basal area	GLO stocking (Larsen et al., 2010)			GLO stocking (Goelz, 1995)			FIA stocking	
Ecological unit	Mean	Low	High		Mean	Low	High	Mean	Low	High	Larsen et al. (2010)	Goelz (1995)
Black River Alluvial Plains	51	29	63	22	83	47	103	137	77	171	47	72
Black River Sand Ridges & Hills	48	27	61	22	79	44	100	131	72	165	47	72
Crowley's Ridge Alluvial Plains	44	22	59	19	78	39	104	127	64	170	42	64
Crowley's Ridge Hills	39	16	39	19	52	27	68	85	45	111	42	64
St. Francis River Alluvial Plains	68	37	86		108	59	138	178	97	228		
St. Francis River Sand Ridges & Hills	54	30	68		89	50	112	148	83	185		
Mississippi River Alluvial Plains	54	27	71	21	89	46	119	147	75	195	43	66
Mississippi River Sand Ridges & Hills	37	18	50	21	62	31	84	102	51	136	43	66

and sweetgum and increases in elms, maples, and hickories. It was possible that GLO surveyors misidentified some of the oaks by for example, recording overcup oak as white oak. Nonetheless, oaks as a genus have decreased in dominance while fast-growing shade-tolerant species (elms and maples) have increased. These species also are recognized as colonizers of abandoned row crop fields and pastureland.

Concurrent with increases in species that thrive in dense forests, density has increased. Without correction for surveyor bias, Nelson (1997) estimated a density of 162 trees/ha from 358 bearing trees in the MMAV. This density estimate was consistent with our low density values, which have only a mild adjustment for surveyor bias. Diameter decreases were not surprising considering that current forests are newly established, but historical diameters were almost twice as large, indicating trees were much larger historically even with some inflation for surveyor bias.

Structurally, historical forests had fewer but larger trees. Metrics of density or basal area alone are poor measures of growing space occupancy because they fail to account for tree size. Growing space occupancy in eastern hardwood forests commonly is estimated as percent stocking (Gingrich, 1967; Goelz, 1995; Larsen et al., 2010). Percent stocking indicated that these forests historically carried greater growing space occupancy than contemporary forests, which were understocked.

Although is not clear how dense the midstory would be when fewer trees in the overstory were so dominant, we suspect that the conditions would be relatively open due to disturbance rather than dense and multi-layered. This does not appear be the same structure that restorationists are envisioning (LMVJV Forest Resource Conservation Working Group, 2007), perhaps rightly so due to the time frame and disturbance intensity that would be required to develop such large trees. However, disturbance by water and fire reduces density and biomass and shifts composition. Fire disturbance in particular likely maintained extensive monotypic canebrakes (*Arundinaria*) and open oak ecosystems with perhaps an understory of canebrakes (Fralish and McArdle, 2009; Gagnon, 2009).

At a smaller scale, the MMAV appeared to reflect the widespread trend in eastern forests where loss of disturbance has allowed disturbance-sensitive species that are fast-growing and shade-tolerant to capture sites where they were historically rare. Species can be adapted for some stress, whether from disturbance or shade. Sweetgum and oaks are relatively shade-intolerant and dependent on disturbance, whether by hydrology or fire, to suppress shade-tolerant competitors that can grow more rapidly under denser, shaded conditions. On mesic to hydric sites with limited fire exposure, loss of periodic flooding has reduced open conditions for sweetgum. Upland sites that were less protected from fire and drought favored oaks in the past, but in the absence of amplification from fire disturbance only dry, infertile soils provide any advantage for oaks against shade-tolerant species. There were not enough trees to model current species distributions. Nevertheless, we expect that the strong influence of land type, soil texture, and elevation on tree species has degraded, at least at coarse scales, in the absence of flooding and fire, which in the past enhanced the effects of topography and soils on vegetation (Hanberry et al., unpublished results).

4.2. Implications for restoration

Restoring the structure of bottomland hardwoods to the MMAV entails managing for large trees grown under high growing-space occupancy levels. This may require periodic but light thinning in stands to increase the growing space for and the growth rate of residual trees while maintaining stands at greater stocking. In addition, restoring native species composition requires planting of sweetgum, bottomland oaks, and where conditions are hydric, cottonwood and baldcypress. Sweetgum was the dominant species of forests and should establish easily in a variety of different sites (Surrettte et al., 2008). *Quercus* as a genus was as common as sweetgum, but the slow growth rate of oaks compared to other species have made oaks less preferable for restoration, at least for the first 10 years after planting (Twedt and Portwood, 1997; Twedt and Wilson, 2002). Interplanting of oaks with fast-growing species or planting of oak after pulpwood harvest (Twedt and Portwood, 1997; Gardiner et al., 2004) have become common strategies to quickly develop well-formed trees, tree height, and canopy cover (Twedt and Wilson, 2002; Lockhart et al., 2006).

Restoration practices that promote fast-growing, shade-tolerant species, such as ash, elm, and maple that were present historically, in order to develop dense, multi-layered forests with an eventual goal of oak forest establishment, may need to be reconsidered. Although there is some confirmation about the ability of oaks to outcompete early successional species that are not shade-tolerant (e.g., Johnson and Krinard, 1988; Lockhart et al., 2006), more probably, given the documented problems of oak restoration in eastern forests in general and specifically the Mississippi River Alluvial Valley (Knutson and Klaas, 1998; Kruse and Groninger, 2003; Oliver et al., 2005; Romano, 2010), oaks cannot outcompete shade-tolerant species without the presence of disturbance. Oak forests in most places will not establish, at least at historical levels, where mesic species are planted without a disturbance regime, and if the objective for restoration is to restore historical conditions and increase overall landscape heterogeneity, hastening landscape conversion to forests without disturbance-dependent species is not compatible with that goal. The benefits of planting oaks, a dominant long-lived species of historical forests and well-known for wildlife and economic values, rather than other species are not questionable given commitment of resources to restoration and suitable sites for reforestation.

There are further considerations for planting oaks rather than disturbance-sensitive, shade-tolerant species. Ash and elm in particular may not be desirable for restoration due to disease (Romano, 2010). Restoration generally is restricted to lower elevations, due to the great economic value of well-drained lands at higher elevations for farmlands. There are a variety of oak species that are adapted to the specific microconditions of topography and flooding. Of course, oak may not always be a good option; site limitations due to hydrology may indicate use of other historically common species, such as baldcypress in wet sites or cottonwood on commonly disturbed sites (Stanturf et al., 1998). Lastly, open herbaceous conditions during lengthier oak establishment are suitable for declining early successional bird species (Twedt and Wilson, 2002).

5. Conclusions

This study presents new information about sweetgum and oak forests in the historical Lower Mississippi River Alluvial Valley landscape on which to base restoration decisions, but the broad applicability of results is uncertain without substantiation from historical and current surveys in other parts of the Mississippi River Alluvial Valley. Historical composition and density reflected surveyor bias for certain species, and bearing trees from the surveys particularly did not represent very wet conditions where there probably were more cottonwood and pioneer species. Flooding and fire disturbance maintained sweetgum and oak species rather than ashes, elms, and maples that were present in undisturbed conditions. We recommend that restorationists continue to favor oak species and increase the amount of sweetgum and cottonwood established, considering the consequences of planting of any non-pioneer, shade-tolerant species that out-compete oaks and sweetgum in the absence of disturbance. Although oaks were never present at greater than 50% of composition in any ecological subsection, planting oaks with greater frequency may allow successful oak restoration. We also recommend management for large diameter trees by conducting light thinning, even though historical composition and structure may be difficult to realize, particularly given the large diameters required in the Mississippi River Alluvial Valley and the complexity of restoring disturbance regimes. Nonetheless, oaks are valuable ecologically and commercially, and efforts should be made to restore oaks rather than assist conversion of historically oak and sweetgum landscapes into forest landscapes of disturbance-sensitive species.

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