

Piecing together the past floodplain forests of the Yazoo Basin in the Mississippi Delta, Lower Mississippi Alluvial Valley, USA

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ABSTRACT

Productive, large alluvial basins have been converted to agriculture, with limited retained vegetation and concomitant incomplete information about the historical vegetation before land use changes. The Yazoo Basin, a 1.7 million ha study extent as defined by 11 counties in the Mississippi Delta of the Lower Mississippi Alluvial Valley (LMAV) in the southeastern United States, currently is 70% croplands, but the historical forests of the region have not been quantified. Therefore, we recovered historical tree species composition and forest structure from land surveys conducted during years 1823 to 1845, and contrasted historical forest composition to limited samples from current tree surveys, given that current forest extent has been minimized by land use. Overall, 75% of 42,105 historical trees (≥ 12.7 cm in diameter at breast height; DBH) showed unique dominance by sugarberry (*Celtis laevigata*) along with oaks (*Quercus*), sweetgum (*Liquidambar styraciflua*), elms (*Ulmus*) and ashes (*Fraxinus*), and moderate components of hickories (*Carya*) and maples (*Acer*). While current tree composition was similar, current inventories indicated decreased proportion of sweetgum (-4.1 percentage points) and oaks (-2.9; likely white oak, *Quercus alba*, in uplands) with increased proportion of loblolly pine (*Pinus taeda*, +3.1), although probably most historical tree species have decreased, due to agricultural conversion. Because upland oaks have decreased to less than 2% of all trees, with only a small change in overall oak percentages, lowland oaks, including Nuttall's oak (*Quercus texana*) and willow oak (*Quercus phellos*), may have increased. Historical density estimates suggested that forests were dense. However, based on surveyor descriptions, overall forests were embedded in an inundated, rivercane (*Arundinaria gigantea*)-filled landscape in the Yazoo Basin, indicating disturbance by flooding and fire. Ecosystem services can be supplied by the remaining floodplain forests, which are located in marginal lands for agriculture.

1. Introduction

Floodplains contain fertile alluvial soils on flat topography, which are ideal conditions for agriculture (Tockner and Stanford 2002). Therefore, floodplains have been converted to croplands world-wide, but primarily in Europe and North America, after clearing native vegetation of trees, shrubs, and herbaceous plants (Tockner and Stanford 2002). Coverage of trees, shrubs, and herbaceous vegetation typically fluctuates with agricultural use and abandonment of marginal soils in lower wetter sites, depending on crop prices (Yang et al. 2020). Drainage and disconnection of wetlands are part of the agricultural conversion process to increase agricultural areas (Andersen 2000; Simon and Rinaldi 2000; Sass and Keane 2016). Moreover, suppression of natural hydrological cycles is a consequence of protecting agricultural fields

from flooding. River control structures, levees, dikes, and channelization regulate dynamics in river locations and water levels (Tockner and Stanford 2002; Gagnon et al. 2021). Floodplains have been converted from infiltrative hydrological networks of wetlands composed of native vegetation to semi-impervious surfaces with drainage channels around current agricultural land use (Andersen 2000; Simon and Rinaldi 2000; Sass and Keane 2016).

The Mississippi River in the eastern United States has one of the largest river basins in the world. The Lower Mississippi Alluvial Valley (LMAV; Figure 1) in the southeastern U.S. covers about 11 million ha, with 5630 km of levees (Gagnon et al. 2021). After flood control, particularly following the 1928 Flood Control Act, the active Mississippi River floodplain became a small corridor in a flood control system (De Steven et al. 2015). Prior to Euro-American land use, the LMAV had

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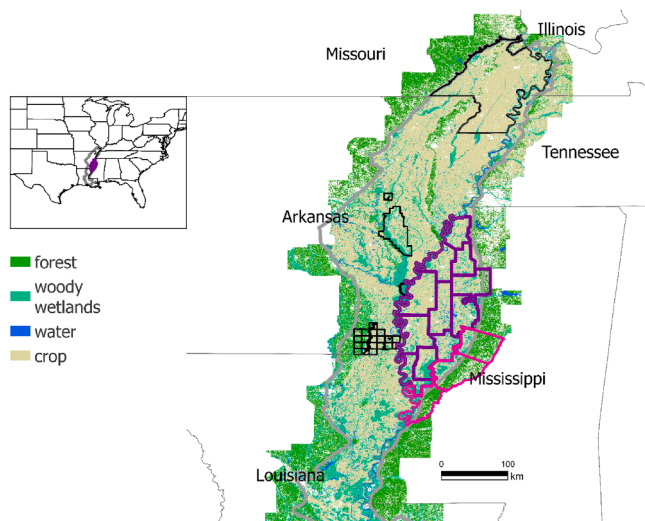


Fig. 1. Location of historical surveys in Mississippi (purple county outlines), the 1947 forest survey in Mississippi (pink and purple county outlines), and the Arkansas and Missouri historical surveys (black outlines), with landcover background of crop (tan), woody wetlands (light green), and forest (dark green) in the Lower Mississippi Alluvial Valley (gray outline).

been used for agriculture for thousands of years; the Mississippian Culture relied heavily on floodplain conditions for agriculture, cultivating maize and bean staples (Carroll et al. 2002). Agricultural use of the LMAV increased with Euro-American settlement and became extensive and intensive during the 1900s, and specifically for soybean production in recent decades (Oswalt 2013; Yang et al. 2020). During 1947 to 1954, forestlands covered about 38% of the LMAV, already encompassing agricultural abandonment and reforestation, but with anticipated continual forest reduction due to agricultural land use (Sternitzke and Putnam 1956). The LMAV has lost an estimated 80% of floodplain forests during cycles of agriculture and abandonment, coupled with timber extraction and other land uses (Yang et al. 2020).

Floodplain forests of the Lower Mississippi Alluvial Valley historically were diverse in tree species, characterized by oaks (*Quercus*) and sweetgum (*Liquidambar styraciflua*), with cypress (baldcypress, *Taxodium distichum*) and tupelo (water tupelo, *Nyssa aquatica*) swamps, and moderate components of sugarberry (historically known as hackberry, *Celtis laevigata*), maples (primarily boxelder, *Acer negundo*), green ash (*Fraxinus pennsylvanica*), elms (primarily American elm, *Ulmus americana*), and hickories (*Carya*, e.g., Sternitzke and Putnam 1956; Hanberry et al. 2012a). Cypress and tupelo were located in swamps, with increased flooding regimes (e.g., duration, frequency; Bragg and Bragg 2016). Black willow (*Salix nigra*), eastern cottonwood (*Populus deltoides*), sugarberry, green ash, boxelder, elms, wetland hickories (primarily *Carya aquatica*), and wetland oaks (primarily *Quercus lyrata*) were common along stream channels and at lower elevation sites in the floodplain and terraces, where flooding was more frequent (Sternitzke and Putnam 1956; King 1982; Rolingson 1993; Hodges 1997). Sweetgum and less water-tolerant oak and hickory species were located on higher elevation sites, such as higher terraces, ridges, and loess bluffs (Sternitzke and Putnam 1956; King 1982; Rolingson 1993; Hodges 1997). In contrast, surrounding upland forests of the northern southeastern U.S. were dominated by oak and pine species, which were tolerant of the historical frequent surface fire regimes in the eastern U.S. (Tatina et al. 2024). Consequently, floodplain forests at higher sites had a greater component of oak and pine species, including loblolly pine (*Pinus taeda*) in the southern LMAV and a variety of oak species in the northern LMAV (e.g., Hanberry et al. 2012; Bragg and Bragg 2016).

Historical tree densities in floodplain forests may have been variable due to large diameters of trees, the presence of permanent water,

wetlands with varying levels of inundation, grasslands, and natural disturbances (Hanberry et al. 2012a; Allen et al. 2019; Hanberry and Noss, 2022). In general, floodplain forests typically had high site quality, resulting in growth of large trees, including cypress and oaks >200 cm in diameter (DBH; Leitner and Jackson 1981; Rolingson 1993; Bragg 2003; Hanberry et al. 2012a). Large diameter trees fill the growing space and out-compete tree seedlings for resources, resulting in lower tree densities but fully or even overstocked forests (Goetz and Meadows 1997; Shear et al. 1996; Hanberry et al. 2012a; Self 2023). Additionally, permanent water restricts tree species to cypress and tupelo, limiting tree densities (Allen et al. 2019). Moreover, flooding in floodplains and fires spreading from the uplands reduced tree densities (Allen et al. 2019; Hanberry and Noss, 2022). Wetlands and grasslands are seasonally dry, permitting frequent fires from uplands to spread into wetlands and grasslands intermixed with floodplain forests (Frost et al. 1986; Gagnon et al. 2021; Hanberry and Noss, 2022). Occasional drought helps make trees vulnerable to fire, while drawing down protective water levels (Mitchell et al., 2014). Rivercane (*Arundinaria gigantea*, a native bamboo), vines, shrubs, and herbaceous species historically filled the understory rather than young trees (Rolingson 1993; Bragg and Bragg 2016; Gagnon et al. 2021). For example, Adair (1775:360) wrote: “Lands of a loose black soil, such as those of the Mississippi, are covered with fine grass and herbage, and well shaded with large and high trees of hickory, ash, white, red and black oaks, great towering poplars, black walnut trees, sassafras, and vines. The low wetlands adjoining the rivers chiefly yield cypress trees, which are very large and of a prodigious height.” Floodplains had a component of herbaceous vegetation, which is critical for increasing biodiversity, not only in plant richness but as a supporting resource for wildlife (Noss et al. 2015; Gagnon et al. 2021).

The Yazoo Basin, also known as the Mississippi Delta, is a 1.7 million ha region that occurs in the LMAV between the Yazoo and Mississippi Rivers (Hudson 1979). In the Yazoo Basin, agriculture covered 5% of area during the 1850 United States census, 26% during the 1900 census, about 55% between the 1945 and 1949 censuses, and increased from 58% to 67% between the 1965 and 1969 censuses (Maizel et al. 1998). As the area of agricultural land increased in the Yazoo Basin, forestlands decreased to 38% of area by 1947 (Sternitzke and Putnam 1956) and 27% of area by 1967 (Sternitzke 1976). This forestlands definition probably included woody wetlands as classified in remotely sensed imagery, because current crop cover remains at 70% of area, with most of the remainder (20%) in woody wetlands, and only 2% forest cover (during year 2013; Dewitz 2023). Woody wetlands are fragmented and concentrated in the Delta National Forest of the southern Yazoo Basin and along the Mississippi River, with other scattered locations (Figure 1). Agricultural conversion has occurred in prime soil locations of historical forests, away from the marginal lands of remaining woody wetlands.

Historical land surveys provide the only source for quantitative and comprehensive representation of historical landscapes. Our primary question was what were tree composition and landscape conditions of the Yazoo Basin at the time of Euro-American settlement, which we answered by using General Land Office Surveys conducted during 1823 to 1845. To provide perspective for historical forests, a secondary question was how has the landscape changed over time, which we documented through multiple sources, including current tree surveys. Due to surveyor bias in historical surveys, resulting from selection of trees near survey points rather than complete surveys, and small samples in current surveys of limited forest extent, results particularly require evaluation and support from other studies (Table 1). We relied on the 1947 forest survey (Sternitzke and Putnam 1956) of the Yazoo Basin, and publications about historical surveys conducted during years 1815 to 1860 in other locations of the LMAV, including about 10,000 trees from six studies of historical surveys in Arkansas during 1815 to 1855 (King 1982; Rolingson 1993; Foti 2001; Tingle et al., 2001; Bragg 2003, 2005; we combined the species compositions of these studies). The 1947

Table 1
Data sources, location, and years.

Source	Location	Survey years	Publication
General Land Office surveys	Yazoo Basin	1823 to 1845	N/A (Analysis)
Forest Service surveys	Yazoo Basin	2009 to 2015	N/A (Analysis)
Forest Service surveys	Yazoo Basin	1947	Sternitzke and Putnam 1956
General Land Office surveys	Arkansas	1815 to 1855	King 1982; Rolingson 1993; Foti 2001; Tingle et al., 2001; Bragg 2003, 2005

forest survey of the Yazoo Basin did include three additional counties, which were not predominantly within the Yazoo Basin. This research will extend information about historical landscapes of the Lower Mississippi Alluvial Valley.

2. Methods

2.1. Study area

The Lower Mississippi Alluvial Valley includes the channel of the Mississippi River and its floodplain from Cairo, Illinois, to the Gulf of Mexico, a distance of 800 km bordered on the east side by loess bluffs (sandy loams of aeolian origin; Saucier 1994). The Mississippi LMAV has a humid subtropical climate, with annual rainfall of 135 cm, heavy rainfall, and rain associated with occasional hurricanes, which may result in flooding (PRISM Climate Group 2020). Soils are alluvial and vary from medium textured, sandy loams to heavy textured clays. The LMAV comprises six basins, the largest of which is the Yazoo Basin, also called the Delta, approximately 320 km in length and up to 100 km east to west, located in the state of Mississippi (Saucier 1994). We extracted historical and current tree information from surveys covering 1.7 million ha from eleven counties of Bolivar, Coahoma, Humphries, Issaquena, Leflore, Quitman, Sharkey, Sunflower, Tallahatchie, Tunica, and Washington Counties, given that historical and modern surveys are provided in county units.

2.2. Data

Historical surveys do not conform to modern sampling designs, resulting in uncertainty (Rhemtulla 2010). Both historical and current surveys indicate representative landscape conditions. However, limitations in quantifying landscapes precisely (and we do not compare stand-level metrics) arise from a maximum of four trees recorded at survey points with lack of random or complete sampling in historical surveys and a small number of plots and lack of continuous forest coverage currently, particularly in the agricultural landscape of the LMAV. Historical land surveys provided methodical coverage for most of the United States before 1900, with survey points every 0.8 km for trees within 60 m, along with general notes about land and vegetation (White 1983). While the large number of trees at landscape scales provide relative representations of historical landscapes (Rhemtulla 2010), the lack of random sampling by surveyors results in unknown uncertainty in species composition estimates, diameter distributions biased for moderately sized trees of the time, and a wide range of density estimation (Hanberry 2011, 2012b).

After transcription of historical General Land Office surveys, we used 21,508 survey points, which were surveyed during 1823 to 1845 (Bureau of Land Management 2025). These survey points excluded about 30 points with no recorded trees due to water (e.g., inundated, 'overflowed', swamps), inaccessibility, or other reasons, noted or unnoted. Surveyors recorded diameters, distances, and directions of up to four

trees at survey points every 0.8 km apart along section lines of townships (i.e., each township was 9.7 km by 9.7 km composed of thirty-six 1.6 km by 1.6 km sections; White 1983). About 44,430 trees were recorded at the survey points, of which 5.3% were less than 12.7 cm, which we excluded. Specifically, surveyors in historical land surveys were instructed to select trees of moderate diameters for longevity, avoiding the largest trees (White 1983), and likely some bias in selection of tree species occurred, at minimum to avoid water and low branches (Hanberry et al. 2011). Therefore, about 42,105 trees were available for determining historical composition. In addition, we recorded surveyor notes about the vegetation or land for about 8500 survey points. We identified survey points with cane; vines, briars or briars (e.g., green-brier, *Smilax*); prairies or open woods; and aquatic indicators (e.g., lake, river, swamp, overflow, inundated), including baldcypress.

Due to issues with species identification and naming, along with changing taxonomy, we generally grouped any genera with multiple species, excepting *Nyssa*. For unknown 'gums' (sweetgum, *Liquidambar styraciflua*; blackgum, *Nyssa sylvatica*), we assigned to species based on relative proportions of identified sweetgum and blackgum. We simply combined 'locusts' (*Gleditsia* and *Robinia*).

For density estimates, we used 17,471 survey points with at least the two nearest trees (trees ≥ 12.7 cm) recorded, or about 80% of the total survey points had at least two trees. We excluded survey points with one tree, which, for example, commonly occurred along river margins that would impede the presence of trees. Conversely, for stipulated upland ecosystems, we included about 230 survey points with no or one trees recorded due to low tree densities in grasslands or other terrestrial ecosystems clearly specified by surveyors. We assigned a distance of 60 m to survey points without two trees within 60 m, including any recorded distances greater than 60 m, albeit at these distances, density estimates are barely affected whether values are 60 m or greater. We calculated density estimates using the Morisita estimator (Hanberry et al. 2011). Based on simulations, density estimates are too great (by a factor of 1.22) for survey points with two trees, requiring an adjustment quotient (Hanberry et al. 2011).

Then we provided a range of uncertainty around the density estimate. We calculated a low spatial density estimate from the adjusted density estimate by correcting for possible clustered trees (adjustment quotient of 1.10) and calculated high spatial density by correcting for possible regular tree distribution (adjustment quotient of 0.97). To correct for possible tree selection bias by surveyors (i.e., not selecting the nearest tree as determined from quadrat location, quadrat configuration and azimuth) we applied adjustment quotients to the high and low spatial density values (Hanberry et al. 2012b). This resulted in a low value, which was about 0.85 of the initial, completely unadjusted density estimate. A moderately low value was the mean of the adjusted low and high spatial density values, which was about equal with the unadjusted density estimate. The low and high spatial density values were also adjusted based on potential ranks and were averaged to yield a moderately high density value, about 1.35 greater than the unadjusted density estimate. A moderate density value was determined from the average of the moderately low and the moderately high density values, which was about 1.15 of the unadjusted density estimate. Lastly, a high density estimate was calculated by adding in another adjustment for potential species and diameter bias to the mean of the adjusted low and high spatial density values (i.e., the moderately low value) and averaging with the moderately high value. This value was about 1.45 of the initial unadjusted density estimate. This range of values likely occurs across the landscape. As the number of survey points without two trees increases, lesser density values become more probable.

While there is limited forest remaining in the Yazoo Basin, we quantified tree composition for 3000 trees (≥ 12.7 cm DBH) from 215 plots in the 11 counties of the Yazoo Basin from USDA Forest Inventory and Analysis (FIA) data during years 2009 to 2015 (cycle 9; USDA FIA Datamart 2021). Long-term forest plots are sampled typically around every five years in the eastern U.S. (Bechtold and Patterson 2005). Each

plot includes four 0.0168 ha circular subplots in which trees are enumerated. Additionally, we isolated 205 trees in 12 plots of the easternmost study extent (Tallahatchie County), to ensure that tree species composition was compatible with the Yazoo Basin. These 205 trees did not include sugarberry, and contained greater abundance of oaks and loblolly pine, but otherwise, consisted of moderate percentages of sweetgum, hickories, elms, ashes, and maples. We retained these plots as generally representative of tree species in the upland, loess bluff edge of the Yazoo Basin.

To compare similarity between historical and current tree composition, we calculated the squared-chord distance metric between surveys. The squared-chord distance metric is used to identify analogous samples, with values ranging from 0 to 2 (higher indicates less similarity; squared-chord distance = $\sum (\sqrt{P_i} - \sqrt{Q_i})^2$; where i is the ith percentage of tree groups in the two different sources, of Q and P; package philentropy; Overpeck et al. 1985; Ewing 2002; Drost, 2018; R Core Team 2025). Divergence in composition is indicated by squared-chord distance ≥ 0.15 , and to account for thresholds for continuous data, values between 0.12 and 0.15 suggest initial divergence

3. Results

Out of 42,105 trees, historical forests of the Yazoo Basin were comprised of sugarberry (18.7% of all trees), oaks (18.8%), sweetgum (12.7%), elms (11.4%), ashes (9.6%), hickories (6.6%), and maples (5.0 %; Table 2; Figure 2). Although a relatively small sample size, at 3000 trees, the current forest inventories indicated loss of sweetgum (-4.1 percentage points), oaks (-2.9), and elms (-2.6; Figure 3). Black willow (*Salix nigra*, +3.8), hickories (+3.2), and loblolly pine (+3.1) gained in percentage points. Overall, historical and current composition was similar, with a squared-chord distance of 0.07.

Historical tree density estimates of forests in the Yazoo Basin may have ranged from 232 trees/ha to 378 trees/ha, with 261 trees/ha as a moderately low value, 310 trees/ha as a moderate value, and 360 trees/

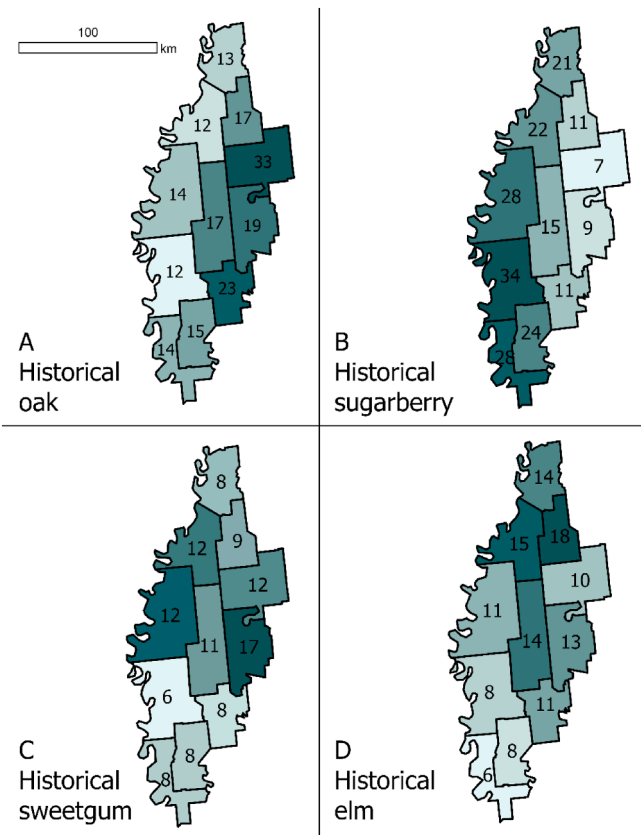


Fig. 2. Spatial representation of historical species composition in the Yazoo Basin, percentages of all trees by county, for *Quercus* (A), *Celtis laevigata* (B), *Liquidambar styraciflua* (C), and *Ulmus* (D).

Table 2
Composition of species or species groups ($\geq 1\%$ of all trees ≥ 12.7 cm in diameter) for historical (years 1823 to 1845) and current (years 2009 to 2015) surveys in the Yazoo Basin, Lower Mississippi Alluvial Valley, Mississippi.

Species/group	Historical		Current		Change	Common species	Count	%
	Count	%	Count	%				
Quercus	7930	18.8	478	15.9	-2.9	Quercus lyrata	128	4.3
						Quercus texana (nuttallii)	122	4.1
						Quercus phellos	62	2.1
						Quercus nigra	54	1.8
						Quercus alba	36	1.2
						Quercus pagoda	35	1.2
Celtis laevigata	7886	18.7	510	17.0	-1.7			
Liquidambar styraciflua	5362	12.7	258	8.6	-4.1			
Ulmus	4811	11.4	265	8.8	-2.6	Ulmus americana	187	6.2
						Ulmus rubra	38	1.3
						Ulmus alata	33	1.1
Fraxinus	4050	9.6	274	9.1	-0.5	Fraxinus pennsylvanica	266	8.9
Carya	2783	6.6	293	9.8	3.2	Carya aquatica	168	5.6
						Carya illinoensis	67	2.2
Acer	2118	5.0	172	5.7	0.7	Acer negundo	120	4.0
						Acer rubrum	32	1.1
Diospyros virginiana	1230	2.9	52	1.7	-1.2			
Gleditsia/Robinia	783	1.9	34	1.1	-0.7	Gleditsia triacanthos	24	0.8
						Robinia pseudoacacia	10	0.3
Taxodium distichum	711	1.7	36	1.2	-0.5			
Nyssa sylvatica	579	1.4	11	0.4	-1.0			
Cornus florida	556	1.3	10	0.3	-1.0			
Sassafras albidum	479	1.1	20	0.7	-0.5			
Populus deltoides	292	0.7	46	1.5	0.8			
Salix nigra	255	0.6	131	4.4	3.8			
Platanus occidentalis	235	0.6	33	1.1	0.5			
Nyssa aquatica	203	0.5	50	1.7	1.2			
Carpinus caroliniana	193	0.5	35	1.2	0.7			
Pinus taeda	161	0.4	106	3.5	3.1			
Liriodendron tulipifera	85	0.2	56	1.9	1.7			

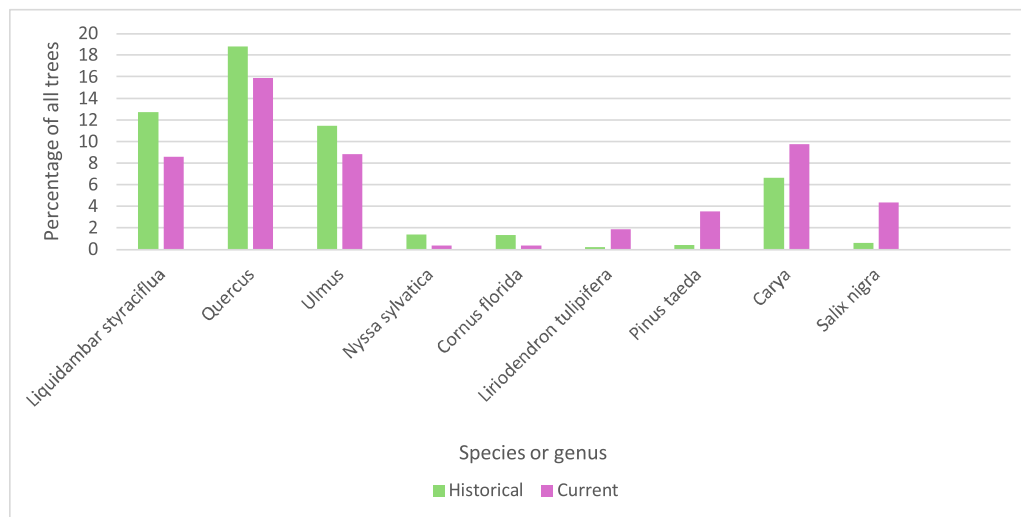


Fig. 3. Change in tree composition (percentage of all trees; for species/genera that exhibited change) between historical and current surveys in the Yazoo Basin.

ha as a moderately high value. Density estimates are based on spatial locations and cannot be accurately extrapolated to species, given differential spatial effects of disturbances on densities. About 20% of survey points were excluded from density analysis due to lack of at least two trees, likely due to standing water, but about 40% of descriptions about land and vegetation included cane, 65% of descriptions included aquatic and wetland descriptors, and 5% of descriptions of the land or vegetation noted prairies or open woods. Therefore, areas where trees occurred may have been at forested densities (overall, greater than 250 trees/ha), but forests were described by surveyors as embedded in a watery, cane-filled landscape.

4. Discussion

4.1. Key findings

We gathered and analyzed historical tree species composition and forest structure from land surveys conducted during years 1823 to 1845, which occurred before extensive land use that resulted in 2% forest cover and 20% woody wetlands remaining in the current agricultural landscape of the Yazoo Basin (Fickle 2001; Dewitz 2023). Historical tree composition in eleven counties of the Yazoo Basin was predominantly sugarberry, oaks, sweetgum, elms, and ashes, with moderate amounts of hickories and maples. Although limited in coverage and sample size due to agricultural conversion, current tree inventories indicated overall similar tree composition, with some compositional changes. However, tree species strongly associated with locations near active river channels and permanent aquatic systems may not have been comprehensively recorded by surveyors in historical surveys and the comparison of current forest surveys is targeted to forested extents. Historical tree density estimates suggested forest tree densities where trees occurred, and abundance of colonizing species such as sweetgum also indicated greater tree densities. Nonetheless, based on surveyor descriptions of land cover recorded in the land surveys, overall forests were embedded in an inundated landscape, with extensive growing space occupied by rivercane. Historical forests, and changes to current forests, with decreased oaks in lowlands and uplands and sweetgum in floodplains, and increased planted loblolly pine, were consistent with other studies, but the abundance of sugarberry may be unique to the Yazoo Basin (Leitner and Jackson 1981; King 1982; Rolingson 1993; Hanberry et al. 2012a).

4.2. Historical composition and change

Sugarberry was the dominant species of forests in the Yazoo Basin, at

about 19% of all trees, which may be the distinctive feature of this basin of the LMAV, both in the past and currently. To the north of our study extent, historical composition of sugarberry was 2% of 16,000 trees in the southern Illinois LMAV, albeit including surrounding areas (Leitner and Jackson 1981), 3% of 26,000 trees in the Missouri LMAV (Hanberry et al. 2012a), and 4% of 10,000 trees in parts of the Arkansas LMAV (i.e., not a comprehensive study extent but combined from King 1982, Rolingson 1993, 2001, Tingle et al., 2001, Bragg 2003 in four townships that did not overlap with Rolingson 1993, Bragg 2005). Sugarberry was not recorded as abundant in the Yazoo Basin during the 1947 survey, but the smaller tree diameters (i.e., mean = 26 cm relative to 39 cm of all trees without sugarberry) may have caused sugarberry to be discounted as a valuable forest product (Sternitzke and Putnam 1956). In current limited surveys, the Yazoo Basin (i.e., the Mississippi LMAV) continued to have the greatest percentage of sugarberry (17%), followed by the Tennessee LMAV (13.5% but for 46 trees; and then also a high percentage for another small sample of an Oklahoma ecological unit outside of the LMAV), and the Louisiana LMAV (8%; USDA FIA Datamart 2021).

Oaks also were a dominant component of the Yazoo Basin, at about 19% of all trees, based on historical surveys, and additionally throughout the LMAV, with dominance in surrounding uplands of the northern southeastern U.S (Hanberry et al. 2012, 2019). Oaks historically were 20% of the Missouri LMAV and about 40% of at least parts of the Arkansas LMAV, albeit samples may not be representative of the entire Arkansas floodplain (King 1982; Rolingson 1993; Foti 2001; Tingle et al., 2001; Bragg 2003, 2005). The 1947 survey of the Yazoo Basin listed upland and lowland oak and hickory species as 35% of commercial forestland area, with about 19% of area as upland oak and hickory, although three additional, mostly upland counties were included in the 1947 inventory (Sternitzke and Putnam 1956). If smaller diameter non-commercial tree species, such as sugarberry, are removed from historical surveys, then oaks become 27% of all trees and hickories become 9.5% of all trees, or 36% of all trees total, relatively similar representation to the oak-hickory area in the 1947 survey, even though tree percentages do not translate directly to area due to differential effects of disturbance on tree densities. Upland oaks occurred particularly on the eastern margin of the Yazoo Basin, in the rugged loess bluffs (Sternitzke and Putnam 1956). White oak (*Quercus alba*) was the primary upland oak species in the Yazoo Basin, with perhaps some northern or southern red oak (*Quercus rubra* and *Q. falcata*), but with non-commercial, small diameter oak species specifically noted as excluded (e.g., *Quercus marilandica* and *Q. stellata*; Sternitzke and Putnam 1956). Oaks now are about 16% of current trees, which is a slight difference from historical composition, considering biases and

sample size issues. Nevertheless, in current surveys, white oak was a minor species at only 1.2% of all trees, with trace amounts of other characteristic upland oaks (*Quercus falcata*, *Q. rubra*), and 3.7% upland hickories (i.e., excluding *Carya aquatica*). Based on support from the 1947 survey, upland oaks, specifically white oak, have declined while other oak species, such as Nuttall's oak (*Quercus texana* previously *nuttallii*, which has a recent classification) along with willow oak (*Quercus phellos*), planted for restoration purposes likely have increased (Allen 1990).

Agricultural conversion of higher elevation sites offers a direct explanation for loss of upland oaks, but a secondary reason is fire exclusion. Upland oak ecosystems, with frequent surface fires, historically surrounded the Yazoo Basin, resulting in exposure to fire and upland oak propagules in the Yazoo Basin (Sternitzke and Putnam 1956; Tatina et al. 2024). Even as late as 1956, after general fire suppression, Sternitzke and Putnam (1956) cautioned: 'The numerous fires that damaged Delta forests during the recent dry years emphasized once again that large areas can and do burn over in what is commonly thought of as swampland.' The loess bluffs in the uplands particularly were exposed to fire, without water to act as a firebreak (Johnson 1958).

Likewise, sweetgum was abundant historically in the Yazoo Basin (12.7% of all trees) and throughout the historical LMAV. Sweetgum was about 17% of the Missouri LMAV (Hanberry et al. 2012a) and 11% of the Arkansas LMAV (King 1982; Rolingson 1993; Foti 2001; Tingle et al., 2001; Bragg 2003, 2005). Loss of higher and drier sites again explains species declines in current surveys. Conversely, sweetgum has increased in upland locations surrounding the Mississippi LMAV, after fire exclusion (Hanberry et al. 2019).

Elms were abundant historically in the Yazoo Basin (11.4% of all trees) and throughout the historical LMAV (13% of the Missouri LMAV and 7% of the Arkansas LMAV; King 1982; Rolingson 1993; Foti 2001; Tingle et al., 2001; Bragg 2003, 2005; Hanberry et al. 2012a). However, decreases were relatively slight (-2.6 percentage points), considering limitations in surveys, with surveyor bias in the historical surveys and small sample sizes in the current surveys. Nonetheless, within elms, species have changed over time. The dominant historical elm species (American elm, *Ulmus americana*) has decreased due to Dutch elm disease (*Ophiostomataceae*), with replacement by other elm species, which have increased (Hanberry 2022).

Although all tree species probably have decreased in overall numbers due to loss of native vegetation to agricultural conversion of 70% of the Yazoo Basin, species that have increased in current surveys relative to historical surveys generally reflected planting of preferred species, disproportional loss of other species in higher elevation sites, or sampling errors. Loblolly pine was a trace species in the historical surveys. Pine, mixed with other upland tree species, was almost 3% of area in the 1947 survey (which excludes less commercial species and includes three additional upland counties) of the Yazoo Basin. Loblolly pine was 3.5% of all trees in current surveys, reflecting current status as the most common tree species in the southeastern U.S., where loblolly pine plantations are common (Hanberry 2021). Lowland oaks, rather than the more historically dominant white oak, are preferred for plantings with restoration objectives (King and Keeland, 1999; Allen 1990). Sternitzke and Putnam (1956) and Sternitzke (1976) reported that species in the lowest and wettest sites, such as overcup oak (*Quercus lyrata*) and water hickory (*Carya aquatica*) did not decrease as much as other species because these species had low commercial value for forest products and the land was too wet for agricultural crops. Willow was not recorded as more than a trace species in the Yazoo Basin and the Arkansas LMAV (King 1982; Rolingson 1993; Foti 2001; Tingle et al., 2001; Bragg 2003, 2005), although a minor species at 2% of all trees in the Missouri LMAV (Hanberry et al. 2012a). Surveyors may have not favored willows for various reasons, including locations along rivers, where surveyors characteristically recorded only one tree for these surveys, based on the transcribed surveys.

Cypress was well-known historically as valuable timber, reaching

large diameters, and associated with the LMAV, and yet not abundantly recorded in the past or current forests (King 1982; Rolingson 1993; Foti 2001; Tingle et al., 2001; Bragg 2003, 2005; Hanberry et al. 2012a). In the Yazoo Basin, cypress was less than 2% of all trees, which was demonstrated in other historical surveys (4% of all trees in the Missouri LMAV, 2.5% in the Arkansas LMAV; King 1982; Rolingson 1993; Foti 2001; Tingle et al., 2001; Bragg 2003, 2005; Hanberry et al. 2012a). In the 1947 survey, about 5% of commercial forestland area was cypress and tupelo, with recent increases in cypress second growth stands (Sternitzke and Putnam 1956). Cypress and tupelo recorded in historical surveys of the Yazoo Basin, with less commercial species (primarily sugarberry) excluded, were about 4.5% of all species, or relatively similar to the 1947 survey of the Yazoo Basin. For recorded trees, which were selected for moderate diameters, historical cypress mean DBH was 78.8 cm, which was the greatest of all tree species. Of tree species with at least minor abundance (> 2% of all trees), sweetgum had the next greatest diameter of 54.3 cm. Therefore, cypress may have been notable, for example, mentioned in about 7% of notes about land and vegetation in the historical surveys, based on diameter and isolation in swamps rather than abundance in most of the LMAV. However, cypress may have been more abundant in Louisiana, where cypress harvest was initiated and cypress gained a reputation as a valuable commercial species, or cypress may have never recovered from early commercial harvest during the 1700s, which progressed up the valley from Louisiana to Mississippi by the early 1800s (Moore 1983).

4.3. Historical structure and disturbance

Tree densities where surveys occurred, excluding where no trees were surveyed due to water, may have ranged from 232 trees/ha to 378 trees/ha (densities > 250 trees/ha indicate closed forests; Hanberry et al., 2014). Tree densities ranged from 215 to 350 trees/ha in the Missouri LMAV, with the least tree densities on ridges where oaks were a greater component of species, because higher elevation sites with fire-tolerant oak species typically reflected exposure to frequent surface fires (Hanberry et al. 2012a). Forests mostly were dense and closed, as may be expected in a floodplain generally protected from fires and comprised of fire-sensitive tree species.

Nevertheless, the Yazoo Basin as a landscape overall may have appeared open, based on surveyor notes about land cover. About 65% of descriptions included aquatic and wetland descriptors and 40% of descriptions included cane, which were not mutually exclusive descriptions. Similar to frequent surface fire disturbance, increased flooding frequency and duration decreased tree densities, in particular by affecting younger and smaller trees, which for example, may not be tall enough to exceed inundation depth (Broadfoot and Williston 1973; Yin 1998; De Jager 2012; Allen et al. 2019). Species with less flood tolerance may die after submergence for a few days (Broadfoot and Williston 1973; Hosner 1958), particularly in lower elevation sites and younger sites near active channels that experience deeper flood depths (De Jager 2012; Boever et al. 2019). Nevertheless, tree species, such as cypress and willows, adapted to inundation can grow well under flooding regimes, especially because competition for resources is reduced (Allen et al. 2019). As for cane, extensive canebrakes were the main indicator of frequent surface fires in floodplains, generally appearing where fire frequencies were less than 10 years (Frost 1995; Platt and Brantley 1997; Taylor 2006; Gagnon et al. 2021). Based on surveyor notes, forests appeared to be embedded in a watery, cane-filled landscape, with disturbances by flooding and fire, in the Yazoo Basin (Frost 1995; Platt and Brantley 1997; Gagnon et al. 2021).

Fire frequency and severity are related to hydroperiod and tree densities in wetlands (Mitchell et al., 2014). Both water and coarse fuels (i.e., trees) provide resistance to fire, but short hydroperiods and fine fuels (i.e., grasses, sedges, and forbs) may produce an annual cycle of growth followed by curing (i.e., drying of vegetation) that offer conditions to burn frequently, and which may spread to forests (Hanberry and

Noss, 2022). Wet grasslands or marshes of herbaceous vegetation, such as canebrakes, generally are ideal sites for frequent fire, because they will be both inundated and dry by turn during spring and fall seasons of typical years, allowing productive vegetation growth followed by curing, which permits ignition when fuel moisture is low (Frost 1995; Platt and Brantley 1997; Hanberry and Noss, 2022). Fire frequency in wet grassland ecosystems may have been less than three years before Euro-American settlement, particularly in large, flat areas that easily spread fires without topographic resistance to spread (Taylor 2006).

Euro-American settlers typically adapted Native American burning practices, but with increased frequencies, and occupied already cleared farmed lands (Fowler and Konopik 2007; Coughlan and Nelson 2018). In addition to agriculturally productive sites on wide floodplains, settlers may have preferred areas with cane, which provided excellent forage for livestock (Coughlan and Nelson 2018). After Euro-American settlement, frequency and extent of fires tended to increase, due to annual burns to increase quality and quantity of livestock forage by removing senescent vegetation (Brantley and Platt 2001). Trappers also set frequent fires in wetlands to prevent destructive fires and accelerate spring growth (Penfound 1952). Cane will re-grow rapidly following disturbance, whether by fire, flooding, or herbivores, but can be depleted without sufficient replacement if disturbance occurs without pause (Frost 1995; Platt and Brantley 1997; Anderson and Oakes 2011; Gagnon et al. 2021). During early Euro-American settlement, very frequent disturbance by both abundant free-ranging livestock and annual burns reduced canebrakes without allowing replacement (Brantley and Platt 2001). Particularly, interactions among disturbances are compounding, because removal of aboveground parts by fire and herbivory will increase susceptibility to flooding (Shull 1921). Similar to forestlands in the Yazoo Basin, more than 98% of all large canebrakes in the U.S. have been lost since the time of Euro-American settlement (Taylor 2006).

Since about 1979, agricultural area has covered about 70% of the Yazoo Basin, indicating remaining lands are marginal for agriculture, which may provide greater ecosystem services if maintained in native vegetation rather than cycles of soybean production (King and Keeland 1999). Native vegetation performs a valuable role in stabilizing soils on land and protecting water quality, while slowing and holding excess flood waters (King and Keeland 1999; Andersen 2000; Simon and Rinaldi 2000; Taylor 2006; Sass and Keane 2016). These regulating ecosystem services are critical in agricultural landscapes with chemical inputs in runoff water, to the magnitude of causing hypoxic zones in the ocean and consequent loss of provisioning services; annual harvest of vegetative cover, which exposes soil to erosion; and semi-impermeable surfaces that direct water rapidly to primary river channels (King and Keeland 1999; Andersen 2000; Simon and Rinaldi 2000; Taylor 2006; Sass and Keane 2016). The LMAV also is crucial for wildlife; for example, the LMAV is part of the Mississippi Flyway, where more than 40% of North America's waterfowl and 60% of all U.S. bird species migrate or winter (LMVJV 2015; Gagnon et al. 2021).

5. Conclusions

The Lower Mississippi Alluvial Valley has been used for crop production for thousands of years, but the LMAV in Mississippi was converted to 70% agricultural area during the 1900s, with most of the remaining lands in woody wetlands cover. As an answer to the question of historical tree composition and forest structure of the Yazoo Basin at the time of Euro-American settlement and landscape change over time, since historical surveys conducted during 1823 to 1845 in the LMAV of Mississippi, higher elevation species of sweetgum and white oak have decreased the most, whereas planted loblolly pine has increased. Disproportional loss of species in higher elevation sites affected tree species recorded in current surveys. Trees were dense where they occurred, but surveyor notes indicated an inundated and overflowed landscape with extensive canebrakes. Land not in agricultural use probably is marginal for agriculture, and may provide greater ecosystem

services, including protection of croplands from flooding and protection of fisheries from hypoxic zones, if maintained and restored in native vegetation.

CRedit authorship contribution statement

Brice B. Hanberry: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Robert Tatina:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data are publicly available.

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