Current and Historical Composition and Size Structure of Upland Forests Across a Soil Gradient in North Mississippi

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Abstract - Comparisons of current and historical tree species composition and size structure along natural productivity gradients are useful for inferring effects of disturbance regimes and productivity on patterns of succession. We tabulated occurrences and estimated diameters of 3483 General Land Office bearing trees across 19 survey townships along an upland soil texture and organic matter gradient in north Mississippi. We then contrasted this presettlement composition and structure with that of 2998 trees in sampling plots within present-day mature (>100 years old) upland forests contained within the survey townships. Presettlement upland communities appeared to consist of non-successional communities, in which the most abundant trees were shade-intolerant, fire-tolerant trees (e.g., *Quercus marilandica* [blackjack oak]) in both large and small size classes across the entire soil gradient. These fire-prone presettlement assemblages differed greatly from present-day mature uplands, which were transitional assemblages of upland and floodplain trees, with mesophytic floodplain species (both early and late-successional) dominating the smaller size classes.

Introduction

Comparisons of current and historical tree species composition and size structure are useful for inferring effects of disturbance regimes on patterns of succession. The differences between pre-colonial (i.e., pre-European-settlement; hereafter presettlement) and current mature forests in North America can be dramatic, and many are related, at least in part, to modern fire suppression and exclusion (Abrams 1992, Beilmann and Brenner 1951, Gilliam and Platt 1999). Accordingly, the current tree species composition of early and late-successional forests that have experienced a long history of fire suppression and exclusion may not be the most desirable reference point for conservation or restoration activities or for testing theories of succession (Brewer 2001, Gilliam and Platt 1999).

Despite increasing knowledge of the composition of presettlement communities in North America, we do not fully understand how succession or patterns of species replacement differed between modern and presettlement forests. Most would agree that fire and other disturbances played a major role in shaping presettlement upland forest communities in North America (Beilmann and Brenner 1951, Braun 1950, Brewer 2001, Dale and Ware 1999, Skeen et

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al. 1993, Van Lear and Waldrop 1989). There is some disagreement, however, about whether these communities represented early successional stages or fire-maintained, non-successional communities (Chapman 1932, Quarterman and Keever 1962). The prevalence of disturbance-dependent species in presettlement landscapes does not imply that plant communities were transitional or comparable to early or mid-successional communities seen today (Brewer 2001). A size- or age-structured forest at middle stages of succession should show evidence of potential replacement of early successional species by mid- or late-successional species (Horn 1975). To our knowledge, however, there have been no attempts to reconstruct size structure of presettlement tree communities and thus interpret potential transitions in species composition.

Historical reconstruction of tree species composition along soil gradients can provide an indirect test of plant life-history theories that focus on soil productivity and disturbances as selection pressures. Traditional theories predict that in the absence of disturbances high, soil productivity should produce late-successional forests of shade-tolerant tree species (Grime 1979, Tilman 1988). In addition, these theories predict that species adapted for surviving and/or competing well in unproductive soils (i.e., stress-tolerators of Grime [1979]; belowground competitors of Tilman [1988]) are at a competitive disadvantage in productive soils. Alternatively, these theories predict that the combination of high productivity and frequent disturbances favors rapidly growing, early successional species. Species adapted to nutrient-poor soils grow slowly and reproduce infrequently and therefore are presumed to be incapable of recovering quickly from disturbances (Grime 1979, Huston 1979). Traditional views of disturbance, however, assume that frequent disturbance is more or less equivalent to frequent density-independent mortality of all species (Huston 1979), as opposed to a selective filter that favors those species adapted for surviving the disturbance (Williamson and Black 1981). The predictions of general theories are complicated further by the fact that some species adapted to nutrient-poor soils are more resistant to disturbance than other species (Grime 1979) and the possibility that variation in soil conditions can indirectly influence disturbance regimes (Brewer et al. 1998, Kellman 1984,).

In this study, we examined variation in tree species composition and size structure along an upland soil texture and organic matter gradient in north-central Mississippi. Our specific objectives were 1) to compare the composition and size structure of tree species in presettlement uplands with those of mature upland forests today and to elucidate differences in patterns of succession, and 2) to examine composition and distributions of xerophytic and mesophytic tree species along an upland soil gradient in presettlement north Mississippi.

Study Area

We quantified presettlement and current upland tree species composition in portions of central Marshall County and central and northeast Lafayette County, which are located along a southeast to northwest gradient of loess in north-central Mississippi (Fig. 1). The region is characterized by rolling hills in the uplands, typically ranging from 10 to 50 m from ridge to hollow, with slightly greater topographic relief in northeast Lafayette County than farther west. The areas we sampled appeared to encompass a clear upland soil productivity gradient in the middle 1800s, as determined by detailed, quantitative soil analyses of soil organic matter (between 1 and 2% higher in central Marshall County than in eastern Lafayette County), along with qualitative assessments of soil texture (Hilgard 1860). Upland areas (including ridges) throughout central Marshall County and in scattered localities in central Lafayette County occurred on deep, loess-based silt-loam organic soils, whereas upland areas in northeast Lafayette County occurred on loamy sand, sandy loam, or sandy clay-loam soils with Eocene parent material, relatively little organic matter, and little or no loess (Harper 1913, Hilgard 1860). The uplands of central Marshall County and parts of central and western Lafayette County supported relatively large cotton plantations from the mid-1800s to the early to mid-1900s; most uplands in northeastern Lafayette County, by contrast, were primarily settled by poor subsistence farmers during this time, and large

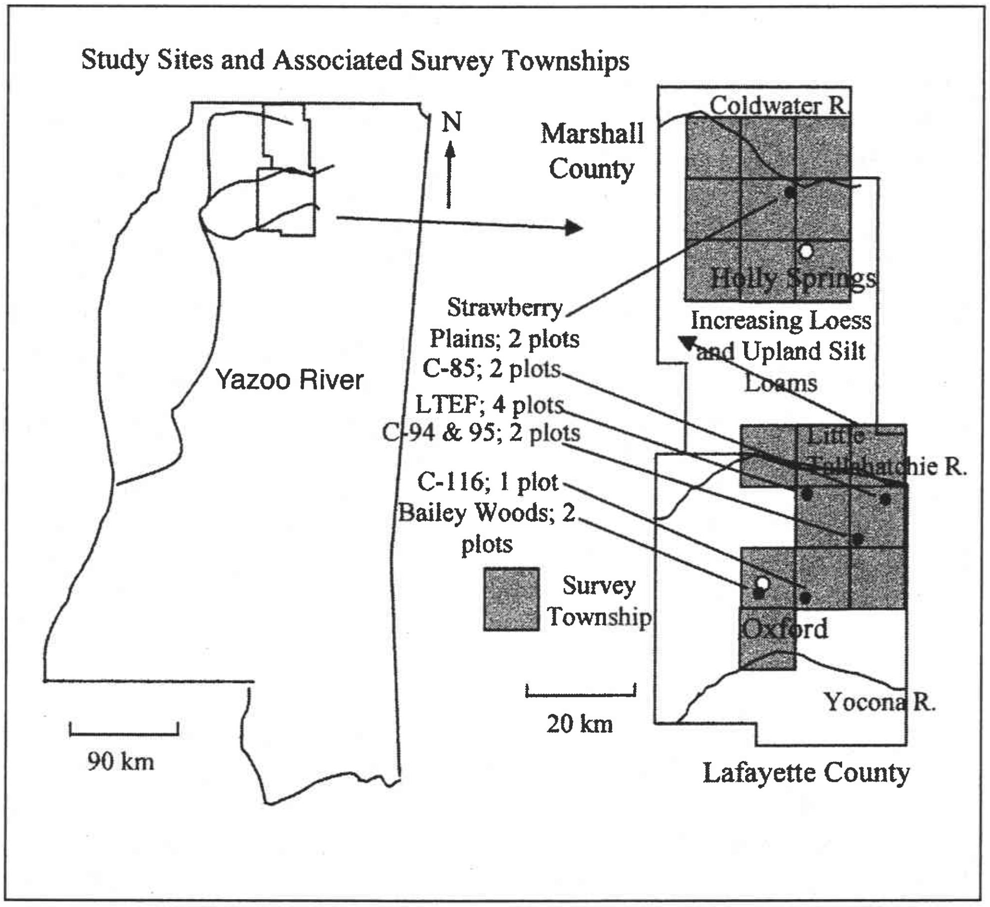

Figure 1. Location of each research site (each containing 1 to 4 plots) in Marshall and Lafayette counties in northern Mississippi. Shaded squares indicate the location of townships used to tabulate bearing-tree species composition.

plantations were rare (Doyle 2001). Today, this soil gradient is undoubtedly not as great as it was historically, due in large part to the massive loss of topsoil following cultivation of the loess-based silt loam soils (Hilgard 1860, Morris 1981, Tyer et al. 1972). Nevertheless, the presettlement signature of this soil gradient is still apparent in the current east–west gradient in soil texture, parent material, and percent organic matter, based on data from county soil surveys (Morris 1981, Tyer et al. 1972) and direct measurements of soil texture at the sites (Surrette 2006; Surrette and Brewer, in press).

All research plots were located in upland, closed-canopy forests and were chosen to meet the following criteria: 1) located on upland soils (i.e., not floodplains or floodplain terraces); 2) contained second-growth stands dominated by mature (100+ years old) trees; 3) burned no more than 3 times since 1978, preceded by a prolonged period (30+ years) of active fire suppression; and 4) contained a ridge and a lower slope or hollow.

The majority of these sites were located in the Little Tallahatchie Experimental Forest (LTEF) and the adjacent ranger district of Holly Springs National Forest (HSNF) in northeastern Lafayette County. Holly Springs National Forest occupies approximately 62,835 ha (155,270 acres) of Forest Service land, which is mostly dominated by second-growth stands of hardwoods and pines (primarily *Pinus echinata* Miller [shortleaf pine], and to a lesser extent *Pinus taeda* L. [loblolly pine]), which grew back after extensive logging in the early 1900s (US Forest Service, Oxford, MS, unpubl. memorandum).

Other sites were located on property managed by the University of Mississippi in central Lafayette County, and at the Strawberry Plains Audubon Center (SPAC) in central Marshall County. Three of our research plots were located on forested land owned by the University of Mississippi since its charter in 1844 (Brewer 2001, Sansing 1999). Strawberry Plains Audubon Center is a 1052-ha (2600-acre) wildlife sanctuary that was bequeathed to the National Audubon Society in 1988 by two private donors. Two of our plots are located in a mature second-growth oak-hickory-gum forest at SPAC, which grew back after cotton farming was abandoned on this portion of the property in the early 20th century (C. Pope, stewardship ecologist at SPAC, pers. comm.).

Methods

Comparing current and presettlement tree species composition

We established between one and four 75- x 70-m research plots at each site (giving a total of 13 plots) and quantified current tree species composition within each research plot by counting stems of each species. All trees $\geq$1.5 m tall and 10 cm diameter at breast height (dbh; measured at 1.5 m above the ground) were identified to species and permanently marked at 1.5 m above the ground using an aluminum tag with a designated identification number secured by an aluminum nail. Tree species, dbh, and topographical location were then recorded, and the frequency of current trees by species along ridges and slopes within central Lafayette, northeastern Lafayette and Marshall counties was then tallied.

Presettlement tree species composition of upland areas and floodplains was estimated in Marshall and Lafayette counties from tallies of bearing trees obtained from survey notes from the Marshall and Lafayette county courthouses. Bearing trees were trees identified by the original land surveyors (in the 1830s and 1840s) associated with the intersection of section lines and at midpoints between section lines. All the records we examined showed that the surveyors marked, identified to common name, estimated the diameter in inches of nearly all bearing trees, and measured the distance to bearing trees when identifying sections and quarter-section corners (one section = 2.59 km^2 or 1 $mile^2$). In Marshall and Lafayette counties, two trees were generally identified at quarter-section corners and four trees at section corners.

Although biases associated with bearing-tree selection certainly existed, original survey records provided the best quantitative sample of trees representative of old-growth upland forests in the vicinity of our current study sites before settlement by US citizens (1830–1840s), but during and following sparse subsistence settlement (primarily near rivers) by Chickasaw livestock ranchers (Brewer 2001, Johnson 2000). Supporting evidence comes from the qualitative assessments of the most common trees made by Nutt (1805 in Jennings 1947), the surveyors themselves, and Hilgard (1860). The earliest quantitative surveys by scientists were not conducted in this region until the late 1800s and early 1900s, well after much of the region had been cleared for agriculture. By this time, species composition began to show the signs of the widespread clearing of forests for agriculture and fire suppression, as exemplified by an increase in the frequency of *Liquidambar styraciflua* L. (sweetgum) in upland areas (Brewer 2001, Dunston 1913, Harper 1913, Lowe 1921). Previous comparisons of bearing-tree composition with quantitative surveys by experts (e.g., R.M. Harper, a botanist) before logging and fire suppression have proven that bearing-tree data can be remarkably reliable indicators of presettlement composition in the southeastern United States (Schwartz 1994).

We corroborated to the extent possible the accuracy and precision of the bearing-tree identification in our region by comparing trees identified by surveyors to those described by Hilgard (1860), whose identification was more precise (see Brewer 2001). Hilgard consulted with botanists and translated common names of trees used by locals in the early to mid-1800s to common and scientific names more widely used at the time (Table 1). A renowned professor of soil science at the University of Mississippi in the mid-1800s, Hilgard was commissioned by the state legislature to conduct a statewide soil and vegetation survey in the 1850s. He was chiefly interested in identifying the most abundant species of forests that had not yet been cleared to use as indicators of soil fertility and flooding frequency and therefore the suitability of these sites for cultivation. He devoted numerous pages to describing the vegetation and soils of Marshall County and Lafayette County (where he resided). Hence, the timing of his survey and its relevance to the current study is ideal.

We tallied bearing trees from nineteen townships in Marshall and Lafayette counties. The location of these townships coincided with the location of each of our sites. This sampling approach provided an accurate, albeit imprecise, comparison of current and presettlement tree species composition (Wang and Larsen 2006). In addition, we tallied bearing trees for several townships that occurred within several major watersheds in Lafayette and Marshall counties. We did this to ensure an accurate estimate of the distribution of presettlement mesophytic and floodplain tree species, some of which are common in upland areas today.

Table 1. List of common names as used by surveyors (spelling is as observed in the survey notes) of trees and their translations to modern common and scientific names (Brewer 2001).

Names used by surveyors	Translation of modern common names (Hilgard 1860)	Scientific names
Ash (including ash and black ash)	Ash	*Fraxinus americana* L., *F. pennsylvanica* Marsh.
Beech	American beech	*Fagus grandifolia* Ehrhart
Black gum	Black gum	*Nyssa sylvatica* Marsh. (possibly including var. *biflora* (Walter) Sargent)
Birch	River birch	*Betula nigra* L.
Black jack	Blackjack oak	*Quercus marilandica* Muenchh.
Black oak	Black oak and northern red oak	*Quercus velutina* Lam., *Q. rubra* L.
Chestnut	American chestnut and possibly chinquapin	*Castanea dentata* Marsh., *Castanea pumila* (L.) Miller
Dogwood	Flowering dogwood	*Cornus florida* L. (possibly other spp.)
Elm (including winged elm, American elm, red elm, and slippery elm)	Elm	*Ulmus alata* Michaux, *U. americana* L., *U. rubra*. Muhl.
Hickory	Hickory	*Carya* L. spp.
Holly	American holly	*Ilex opaca* Aiton
Ironwood	Hop hornbeam, ironwood (possibly blue beech, musclewood)	*Ostrya virginiana* (Miller) K. Koch (possibly *Carpinus caroliniana* Walter
Maple	Maple	*Acer* spp.
Mulberry	Red mulberry	*Morus rubra* L.
Persimmon	Eastern persimmon	*Diospyros virginiana* L.
Pine	Shortleaf pine, bottom (loblolly) pine	*Pinus echinata* Miller *Pinus taeda* L.
Poplar	Yellow poplar, tulip poplar	*Liriodendron tulipifera* L.
Post oak	Post oak	*Quercus stellata* (Wang.)
Red oak (possibly including cherrybark oak)	Spanish oak, southern red oak	*Quercus falcata* Michaux (possibly including *Q. pagoda* Raf.)
Sassafras	Sassafras	*Sassafras albidum* (Nutall) Nees
Spanish oak	Scarlet oak (possibly including shumard oak)	*Quercus coccinea* Muenchh. (possibly *Q. shumardii* Buckley)
Sweetgum	Sweetgum	*Liquidambar styraciflua* L.
Sycamore	Sycamore	*Platanus occidentalis* L.
Walnut (including black walnut, white walnut, butternut)	Black walnut, white walnut	*Juglans nigra* L., *J. cinerea* L.
Water oak	Water oak	*Quercus nigra* L.
White oak	White oak	*Quercus alba* L.

We mapped survey points on soil survey maps for Marshall and Lafayette counties (Morris 1981, Tyer et al. 1972) to determine associations between presettlement forest composition and landscape position (i.e., occurrence in uplands vs. floodplains). These data were then recorded and pooled according to all possible combinations of bearing-tree species, survey points, and landscape position. To determine tree associations with landscape position, soil types were pooled and grouped into the following categories: lower sandy slopes of uplands, all other uplands, and floodplains and alluvial terraces (hereafter, floodplains). Lower sandy slopes of uplands were distinguished from other uplands, because the former currently have the greatest plant diversity of all the types examined (Surrette 2006) and thus are of significant conservation and management concern.

Comparing current and presettlement size structure of co-occurring trees

We compared diameter variation of bearing trees and current trees in areas that today occur in Holly Springs National Forest (where shortleaf pine was and is common) to infer changes in patterns of canopy tree replacement in presettlement and current oak-pine forests. We used a weighted averaging approach to test the hypothesis that presettlement upland forests containing multiple size classes were non-successional communities numerically dominated by fire-tolerant upland pines and oaks in both the large and the small size classes. Using the same approach, we also tested the hypothesis that current upland forests were transitional (i.e., successional) communities, in which larger trees tended to be upland species and smaller trees tend to be floodplain species. We placed all bearing trees with an estimated diameter of 25 cm or greater in the large category and all remaining trees in the small category. Likewise, we placed all current trees with a measured diameter of 25 cm at 1.5 m height in the large category and all current trees 15 to 24.99 cm dbh in the small category. Using a lower bound of 10 cm did not qualitatively change the results; only the results using the 15 to 24.00 cm dbh category are presented here to represent the small category. Sample points were survey points in the case of bearing trees and sampling plots in the case of the current trees. We excluded from consideration all survey points that contained trees from only one diameter category. In the majority of these cases, all trees at the point were small individuals of *Quercus marilandica* Muenchh. (blackjack oak), which even as an older adult tends to be a relatively small tree. Hence, out of a total of 251 survey points with multiple trees in upland soils in northeastern Lafayette County, 72 points contained trees in both diameter categories. For this reason, our analysis can only be used to infer compositional differences at points where multiple size classes existed. It cannot address how common uneven-sized stands were in the presettlement landscape.

Associations of upland pines and hardwoods with soil texture, aspect, and slope position in the presettlement landscape

To determine whether upland areas with organic silt-loam soils supported a greater fraction of mesophytic species than did regions with sandy or sandy-clay soils with less organic matter, we used a weighted averaging approach comparable to that used to differentiate upland and floodplain species. Since nearly all floodplains in Marshall and Lafayette counties were known to contain productive soils (Hilgard 1860), if upland soil type had a significant effect on tree composition, then we might expect a greater floodplain component to tree composition in fertile uplands than in infertile uplands. To infer which soil and/or topographic characteristics favored pines in the presettlement landscape in Lafayette County, we examined current soil types, topography, and bearing-tree records in the following Lafayette County townships: T7R1, T7R2, T8R2, T8R3, and T9R3. According to Hilgard (1860), these townships spanned a clear west-to-east gradient in soil texture and the occurrence of shortleaf pine from central to northeastern Lafayette County. There was only one record of pine in central Marshall County and so these townships, which were disjunct from those in Lafayette County, were excluded from this analysis. Although current soils obviously differed from presettlement soils due to severe erosion and loss of topsoil following cotton agriculture in the mid-to late 1800s, in a relative sense, current variation in soil texture across the region paralleled that of presettlement soils (Hilgard 1860). Exceptions were the severely gullied soil types, which we excluded from our analysis. To test the hypothesis that pine occurrence in northeastern Lafayette County depended on soil texture, we tabulated the presence and absence of pines in different upland soil types using soil survey data as previously described. Silt loam, soils comprised a "silty" soil category, whereas sandy, sandy loam and sandy clay-loam soils were grouped into a "not silty" soil category.

The slope position and aspect at each survey point were determined using Maptech Terrain Navigator 2004® topographical software. To obtain an objective estimate of each bearing tree's position along the slope, the "halfway" point between the nearest ridge and hollow was used to partition the slope into upper and lower halves. Any tree located above that point was placed in the upper slope category; any tree located below that point was placed in the lower slope category. The aspect of the slope on which each bearing tree occurred was determined by rotating Terrain Navigator's 3-dimensional topographic map to the direction the slope was facing and then recording the compass output. We grouped all aspects broadly into either north- or south-facing slopes. We then tabulated the presence and absence of pine and hardwoods at each slope position and aspect.

Data analysis

Relationships between presettlement tree species composition and landscape position (i.e., floodplains, uplands) were quantified statistically using indicator-species analysis (DuFrêne and Legendre 1997). Before doing the analysis, we pooled survey points from central and northeast Lafayette County. We then calculated indicator values for each species in each landscape position category by taking the product of each species' relative abundance and relative frequency in each landscape position. This product was then converted to a percentage by multiplying by 100. The unit of observation for calculating average relative abundance of each species in each landscape position category was each landscape-position by survey-point combination. In most instances, only one landscape position category (e.g., floodplain, upland) occurred at each survey point. However, because more than one tree occurred at each survey point, in a few cases, particularly those in which survey points were located at the upland edge of alluvial terraces, two landscape positions occurred at the same survey point. For this reason, we had more units of observation than survey points. The relative frequency of each species in each landscape position was calculated using survey points as the unit of observation. The statistical significance of the observed maximum indicator value of each species was calculated using a Monte Carlo test with 1000 permutations. A P-value < 0.05 was considered statistically significant.

Size structure and composition of current and presettlement upland trees within the range in which pines occurred were analyzed using a weighted averaging approach. The weighted averages we used to infer patterns of replacement in presettlement and current forests were derived from species' weights produced by an ordination of upland and floodplain samples of bearing trees. Specifically, we used non-metric multidimensional scaling (NMS; Kruskal 1964) of 6 samples of bearing trees (4 upland and 2 floodplain samples) to obtain scores for each tree species. We sorted upland bearing trees within the three townships containing the field sites in Holly Springs National Forest with respect to soil type and topographic position as deduced from the Lafayette County Soil Survey (Morris 1981). One sample included all upland trees that were located within 20 m of a small or intermittent creek or floodplain (as determined from aerial photographs). The other three upland bearing tree samples contained trees that were located farther than 20 m from a creek or floodplain. We classified these three samples with respect to soil type: sandy-loam soils, silt-loam soils, and sandy-clay-loam soils, and grouped trees that occurred on silty-clay-loam soils with the sample of trees on clay-loam soils. We pooled all bearing trees located in floodplains associated with a given watershed into one sample, resulting in two floodplain bearing-tree samples, one for the Tallahatchie River watershed and one for the Yocona River watershed.

The species scores (i.e., soil type/landscape position weights) derived from NMS of bearing trees were used to indicate a species' affinity for upland or floodplain habitat types. We then calculated the average weight for large and small bearing trees at each survey point and examined differences between the size classes with a paired-samples t-test. The null hypothesized difference was zero. To examine differences between bearing and current trees, we calculated averages of species weights for large and small trees for the present-day samples of trees. We then compared differences in average weights of large and small bearing trees in upland areas to an overall average difference in species scores between size classes in present-day forests using a paired-samples t-test. Hence, in this analysis, the null hypothesized difference was the overall average difference in species scores between size classes in present-day forests.

The species scores derived from NMS of bearing trees were also used to calculate weighted averages of upland tree species composition in each of the three major areas known to differ in soil texture and possibly productivity (central Marshall County [silt-loam organic], central Lafayette County [mix of sandy loam and silt loam], and northeastern Lafayette County [loamy sand and sandy-clay loam, with little organic matter]). Here, we calculated weighted averages and weighted standard errors of the percentages of all tree species for each region and examined statistical differences among the three areas using one-way analysis of variance. If floodplain (and thus mesophytic) species represented a greater fraction of all trees present in upland soils with more silt and organic matter (e.g., central Marshall County) than in other soils, then the weighted average percentage should be greater in the organic silt-loam soils.

The NMS of samples of bearing trees was based on Sorensen distances between samples using arcsine-square-root transformed proportions for each sample. We used PC-Ord, version 4 for Windows software (McCune and Mefford 1999) to run NMS, and the "slow and thorough autopilot" routine in PC-Ord assisted us in making multiple randomized runs to assess dimensionality and obtain significant ordination axes. We quantified the proportion of variation in species composition explained by each axis using coefficients of determination (r^2) for the relationships between Sorensen distances and axis scores.

We used log linear models to determine whether the relative occurrence of upland pines and hardwoods was independent of soil texture, slope position, or aspect in Lafayette County. Chi-square tests were performed using Statistix, version 8, for Windows. To determine whether pine occurrence changed with soil fertility, we tested the interaction between pine occurrence and soil-type group (i.e., fertile vs. infertile soil types, the pine presence x soil fertility interaction). We examined the association between pine occurrence and slope position by testing the pine presence x slope position interaction. We examined the association between pine occurrence and aspect (i.e., north- vs. south-facing slopes) by testing the pine presence x aspect interaction. We then tested the three-way interactions between pine presence, soil fertility, and slope position and pine presence, slope position, and aspect.

Results

Presettlement versus current tree species composition

We identified a total of 2998 trees in our current, upland tree sampling plots and tallied a total of 3483 bearing trees across Lafayette and Marshall counties. We found that current upland forests were composed of a mixture of historically upland and mesophytic floodplain species. *Quercus alba* L. (white oak) was the single most common tree species encountered in our upland study plots (Table 2). Shortleaf pine was the second most common species (Table 2). Other common species in uplands were *Carya tomentosa*

(Poiret) Nutall (mockernut hickory), *Carya glabra* (Miller) Sweet (pignut hickory), sweetgum, *Quercus stellata* Wang. (post oak), *Quercus falcata* Michaux (southern red oak), *Cornus florida* L. (flowering dogwood), and *Nyssa sylvatica* Marsh. (blackgum) (Table 2). Blackjack oak, *Quercus coccinea* Muenchh. (scarlet oak), and loblolly pine were not common (Table 2).

With some exceptions, current tree species composition was not that different between upper and lower slopes. Shortleaf pine was the most common species along upper slopes. Other common species along upper slopes were post oak, hickory, white oak, and sweetgum (Table 2). All species commonly found along upper slopes were also common along lower slopes, with the exception of post oak, which was replaced by southern red oak (Table 2).

In contrast to what we encountered in mature upland forests today, "black oak," "blackjack," "post oak," and in some areas, "pine" were the most common bearing trees in upland areas (Table 3). Indicator species analysis revealed that all were significant indicators of uplands (Fig. 2).

Table 2. Average percent abundance of current trees (≥10 cm diameter at breast height) tallied within sixteen forest sites across Lafayette and Marshall counties, MS.

Species	Upper slope % abundance (# stems = 1024)	Lower slope % abundance (# stems = 1974)	Total % abundance (# of stems = 2998)
Acer rubrum L.	1.17	2.84	2.27
Acer saccharinum L.	0.00	0.05	0.03
Acer sp.	0.58	2.69	1.97
Carpinus caroliniana	0.00	0.05	0.03
Carya sp.	12.31	10.34	11.01
Cornus florida	4.98	6.64	6.07
Diospyros virginiana	0.20	0.15	0.17
Fagus grandifolia	0.00	0.86	0.57
Fraxinus sp.			0.33
Juniperus virginiana L.	1.95	2.94	2.60
Liquidambar styraciflua	7.32	11.65	10.17
Lirodendron tulipifera	0.00	0.25	0.17
Magnolia grandiflora L.	0.00	0.05	0.03
Morus rubra	0.00	0.15	0.10
Nyssa sylvatica	6.44	4.71	5.30
Pinus echinata	18.16	10.89	13.38
Pinus taeda	6.25	2.58	3.84
Platanus occidentalis	0.00	0.05	0.03
Prunus serotina Ehrhart	1.56	0.96	1.17
Quercus alba	7.42	17.02	13.74
Q. coccinea	1.37	2.08	1.83
Q. falcata	6.09	8.36	7.57
Q. marilandica	1.47	0.96	1.13
Q. nigra	0.10	0.10	0.10
Q. rubra	0.49	0.46	0.47
Q. stellata	13.18	6.03	8.47
Q. velutina	3.81	4.86	4.50
Sassafras albidum	0.20	0.20	0.20
Ulmus alata	4.88	1.57	2.70
Unknown	0.10	0.00	0.03

Pines were primarily found in upland areas of northeastern Lafayette County and were not common as bearing trees in either uplands or floodplains or terraces in southwestern Lafayette or Marshall counties (Table 4). "White oak," "hickory," "sweetgum," "black gum," and "beech" (*Fagus grandifolia* Ehrhart [American beech]) were common bearing trees in floodplains. Accordingly, indicator species analysis revealed that these species, along with "sassafras," "ironwood," "poplar," "dogwood," "ash," "maple," "holly," and "elm" were significant indicators of floodplains (Fig. 2; see Table 1 for modern translations and scientific nomenclature and authorities). Results associated with red oak should be viewed with caution, since surveyors used "red oak" to refer to both southern red oak and *Q. pagoda* Raf. (cherrybark oak; Hilgard 1860), which today are considered indicative of uplands and floodplains, respectively.

Table 3. Average percent abundance of presettlement trees associated with floodplains and uplands found in eighteen townships across Lafayette and Marshall counties.

Species	Floodplains (# of stems = 929) % abundance	Uplands (# of stems = 2554) % abundance
Ash	2.66	0.04
Bay	0.22	0.00
Beech	7.91	0.04
Birch	0.54	0.04
Black Locust	0.22	0.00
Black oak	7.51	24.16
Blackgum	5.81	0.90
Blackjack oak	1.44	23.25
Cherry	0.47	0.00
Chestnut	0.32	0.47
Chestnut oak	0.11	0.00
Cypress	0.54	0.00
Dogwood	2.27	0.32
Elm	4.20	0.08
Hickory	13.38	8.65
Holly	4.20	0.04
Hornbeam	0.97	0.04
Ironwood	1.11	0.00
Laurel	0.11	0.00
Maple	3.78	0.19
Mulberry	0.00	0.00
Persimmon	0.11	0.00
Pine	0.11	3.92
Poplar	2.60	0.08
Post oak	5.60	23.92
Red oak	8.80	11.23
Sassafras	1.73	0.00
Swamp oak	0.58	0.04
Sweetgum	5.61	0.08
Sycamore	0.22	0.00
Walnut	1.88	0.00
Water oak	0.54	0.00
Willow oak	0.11	0.00
White oak	13.80	2.74

Shade-intolerant upland species, including "red oak," "chestnut" (most likely, *Castanea dentata* Marsh.), "pine," and "black oak" were significant indicators of lower slopes with sandy soils, while "blackjack oak" and "black oak" were indicative of the remaining portions of the uplands (Fig. 3). Bearing-tree species indicative of floodplains included "American beech," "hickory," "sweetgum," "elm," "American holly," "maple," "ash, " "black gum," "sassafras," "ironwood," "yellow poplar," and "white oak" (Fig. 3). When floodplain samples were excluded, "white oak" and "chestnut" were significant indicators of sandy lower slopes, whereas "blackjack oak" was a significant indicator of the remaining upland areas (Fig. 4). "Black oak" (which was a significant indicator of uplands when floodplain samples were included) was not a significant indicator of either upland group when the floodplain samples were removed, indicating that it was a common and abundant bearing tree throughout the upland landscape.

Presettlement versus current size structure of co-occurring trees

The most common large and small bearing trees in upland forests near Holly Springs National Forest in northeast Lafayette County were upland,

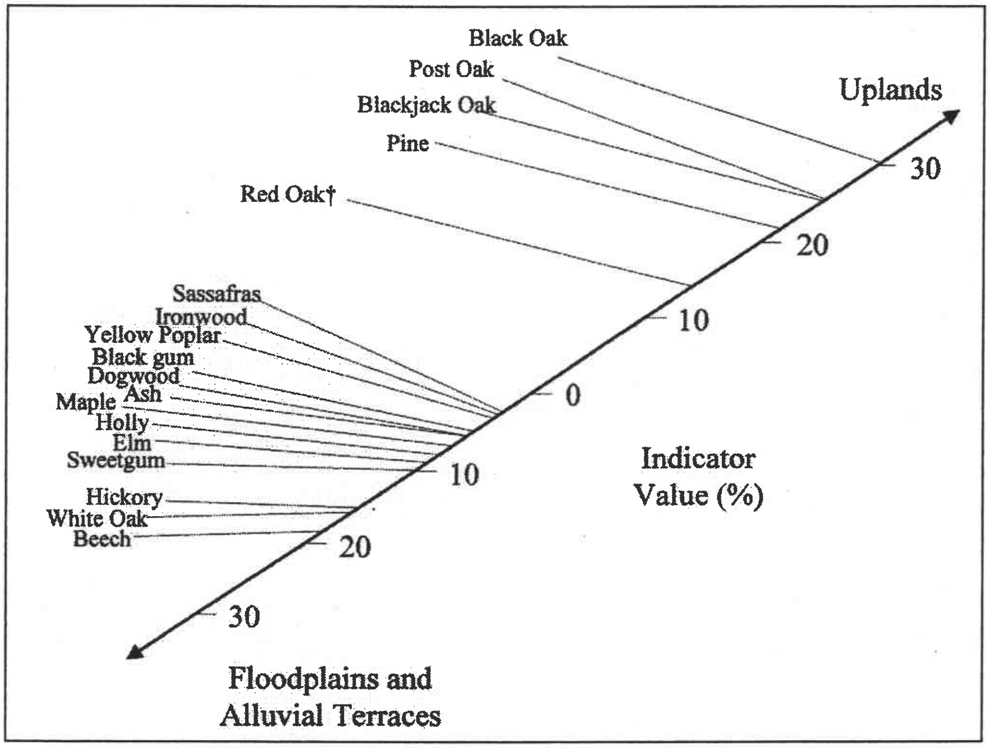

Figure 2. Presettlement tree species that were found to be significant indicators of uplands or floodplains in nine townships across central and northeastern Lafayette County, MS. Positions along "axis" correspond to calculated indicator values (percent of perfect indication) for uplands or floodplains. Statistical significance was determined by Monte Carlo permutation tests. † Red oak values should be interpreted with caution. Surveyors did not distinguish between southern red oak and cherrybark oak. Red oak is likely a combination of both of these species and perhaps others.

Table 4. Percent abundance of presettlement trees associated with well-drained uplands from three areas within eighteen townships in Lafayette and Marshall counties. NEL = northeastern Lafayette County (lowest fertility, # of stems = 671), CL = central Lafayette County (intermediate fertility, # of stems = 392), CM = central Marshall County (highest fertility, # of stems = 1491)

Species	NEL % abundance	CL % abundance	CM % abundance
Ash	0.15	0.00	0.00
Beech	0.00	0.00	0.07
Birch	0.15	0.00	0.00
Black oak	32.04	13.01	23.54
Blackgum	0.60	0.77	0.54
Blackjack oak	17.44	32.65	23.40
Chestnut	0.89	1.28	0.07
Dogwood	0.15	0.77	0.27
Elm	0.15	0.00	0.07
Hickory	4.92	8.16	10.46
Holly	0.15	0.00	0.00
Hornbeam	0.00	0.26	0.00
Maple	0.15	0.51	0.13
Pine	13.11	2.81	0.07
Poplar	0.15	0.00	0.07
Post oak	19.67	19.39	27.02
Red oak	6.41	18.62	11.46
Swamp oak	0.15	0.00	0.00
Sweetgum	0.00	0.00	0.13
White oak	3.73	1.79	2.55
Willow oak	0.00	0.00	0.13

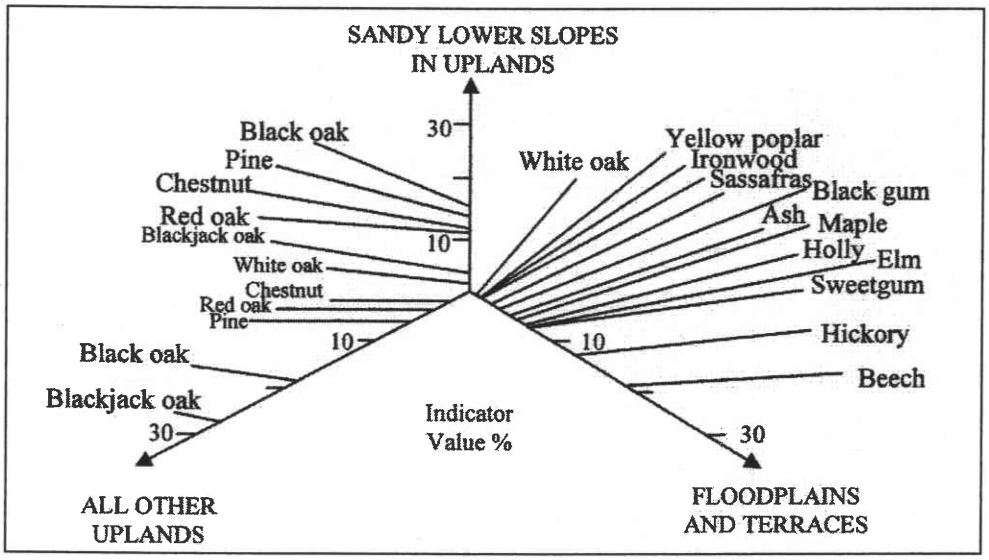

Figure 3. Presettlement tree species that were found to be significant indicators of sandy soils found on lower slopes in uplands, all other uplands, and floodplains in nine townships located in central and northeastern Lafayette County, MS. Positions along "axes" correspond to calculated indicator values (percent of perfect indication) for each of the three habitat types. Species in large bold type were statistically significant indicators of that habitat. Species not shown were not statistically significant indicators of any of the three habitat types.

fire-tolerant, shade-intolerant species. Hence, we found no evidence of transitions in species composition in upland areas in this region in the early 1800s. An NMS ordination of the six presettlement samples of trees produced a single significant axis, which sorted samples according to the relative abundance of upland indicators such as "blackjack oak," "black oak," "pine," and "post oak" (negative axis 1 scores) and floodplain indicators such as "American beech," "American holly," "sweetgum," "black gum," "maple," "yellow poplar," and "white oak" (all with positive axis 1 scores; Table 5). Negative sample scores were associated with all presettlement upland samples, regardless of soil or proximity to small creeks. Positive sample scores were associated with floodplain samples. Using these species scores as species weights, we found that both the large and small size classes of bearing trees at those survey points containing both size classes of trees exhibited similarly negative average (i.e., "upland") scores (Table 5). The small size class did not contain a significantly greater floodplain component than did the large size class (paired-samples $t = 0.75$; $df = 71$; one-tailed $P = 0.228$).

In contrast to presettlement upland communities, present-day samples of upland trees in tree plots showed a very significant floodplain component in

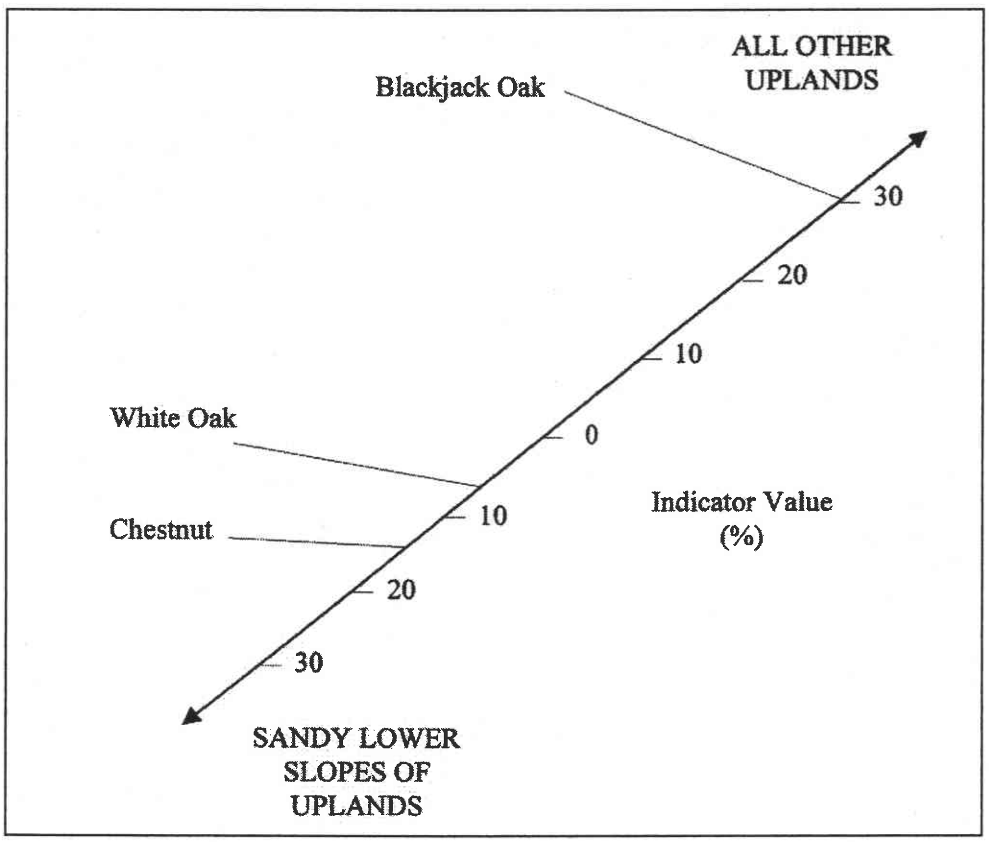

Figure 4. Presettlement tree species that were significant indicators of uplands and loamy sandy soils found on lower slopes in nine townships in Lafayette County, MS after removing floodplain samples. Positions along "axes" correspond to calculated indicator values (percent of perfect indication) for each of the two habitat types.

the small size class (two-sample t = 12.83; df = 998; one-tailed $P < 0.0001$). The large size class of the present-day samples had a significant upland component (although still not as great as either the large or small size classes of presettlement upland tree samples, due in large part to the low abundance of large blackjack oaks and black oak and the greater abundance of white oak in the large size class of present-day forests). The average difference between the composition of the large and small size classes of bearing trees was much less than compositional differences between size classes in present-day forests (paired-samples t = 9.23; df = 1; one-tailed $P < 0.0001$; null hypothesized difference = 0.39; Table 5).

Associations of upland pines and hardwoods with soil texture, aspect, and slope position in the presettlement landscape

Fire-tolerant, shade-intolerant oaks were the most common bearing tree species across a wide range of upland soil types (Table 4; Fig. 5). No one region appeared to have a more mesophytic tree species composition than any other, as determined by similar weighted averages of percent abundance (Fig. 5; $F_{2,39} = 0.132$, $P = 0.88$). The only two species that showed a consistent positive or negative association with soil texture were "pine" (negative) and "hickory" (positive). The presettlement distribution of "pine" was associated with an east–west soil texture gradient in Lafayette County. "Pines"

Table 5. Species composition of large and small trees weighted by their affinity for upland or floodplain samples of bearing trees in the early 1800s in north-central Mississippi. Negative weights indicate a presettlement association with upland habitats. Positive weights indicate a greater presettlement association with floodplain habitats.

Species	Weight (NMS axis 1 species score from analysis of bearing trees)
Eastern red cedar	NA
Blackjack oak	-0.63
Pine	-0.50
Black oak	-0.43
Post oak	-0.30
Scarlet oak	-0.10
Hickory	-0.09
Red oak (includes southern red oak and cherrybark oak)	0.25
White oak	0.33
Blackgum	0.60
Dogwood	0.63
Maple	0.74
Ash	1.01
American beech	1.37
Sweetgum	1.38
Yellow poplar	1.41
Elm	1.45
Cherry	1.58
Water oak	1.58
Average weight overstory: presettlement upland	-0.323
Average weight midstory: presettlement upland	-0.288
Average weight overstory: current upland	-0.120
Average weight midstory (15–24 dbh): current upland	0.279

occurred more often in sandy and sandy clay-loam soils in northeastern Lafayette County than in silt loam soils in central Lafayette County ("pine presence" x soil type interaction $\chi^2 = 54.78$, df = 1, $P < 0.0001$). "Pine" occurrence was independent of both slope position ("pine" presence x slope position interaction: $\chi^2 = 0.01$, df = 1, $P = 0.974$) and aspect ("pine" presence x aspect interaction: $\chi^2 = 1.35$, df = 1, $P = 0.246$), or the interaction between these factors. The position that "pines" occupied along the slope did not depend on soil type ("pine" presence x slope position x soil type interaction $\chi^2 = 2.64$, df = 2, $P = 0.267$) or aspect ("pine" presence x slope position by aspect interaction: $\chi^2 = 1.20$, df = 2, $P = 0.548$).

Discussion

Current versus historical species composition and size structure of trees in north Mississippi

The prevalence of bearing trees of "xerophytic" oaks across a wide range of upland soil types of the presettlement upland landscape of north-central Mississippi (with co-occurring pines in non-silty soils), combined with the near absence of bearing trees of several fire-sensitive species such as "black gum," "maples," "ashes," "walnuts," and "sweetgum" in uplands (while abundant in floodplains), is consistent with the hypothesis that fires were either more frequent or were of greater intensity in the uplands than in the floodplains in northern Mississippi. In southern Missouri, Batek et al. (1999) found that areas of a presettlement landscape with the highest fire frequencies (as determined by fire-scar analyses; Guyette and Cutter 1997) were dominated by mosaic of "oak barrens," consisting primarily of post oak, blackjack oak, and black oak, and open forests of shortleaf pine and black oak. These are precisely the same species that dominated the upland

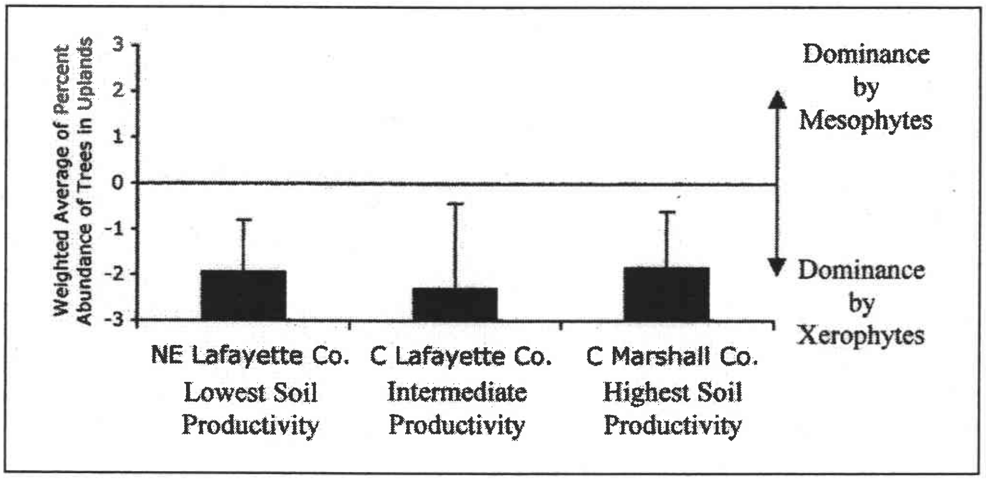

Figure 5. Weighted averages (+ 1 standard error) of percent abundance of all tree species in presettlement uplands in each of three regions that differed in soil productivity. Weights are based on upland versus floodplain affinity in the region with lowest upland soil productivity (northeastern Lafayette County; see Table 4).

landscape in north Mississippi (although we cannot rule out the possibility that some pines encountered in our region were loblolly pine). They also found that a river acted as a fire barrier, which separated a fire-tolerant community (e.g., shortleaf pine, black oak) located near a Native American settlement from a more mesophytic community (e.g. northern red oak, black gum, and maples) located on the opposite side of the river from the settlement. Soil fertility and topographical conditions were not responsible for partitioning these community types.

At those points in the presettlement upland landscape at which large bearing trees co-occurred with small bearing trees, shade-intolerant oaks and pines were the most abundant species in both size classes. Hence, we found no evidence of a forest in transition (i.e., replacement by floodplain or mesic forest species) in the early 1800s. This pattern strongly suggests to us that some combination of canopy openings and fire played an important role in maintaining tree species composition in the presettlement upland landscape in north Mississippi. Although canopy openings can increase sapling densities of oaks and pines (Brewer 2001), most of these do not successfully recruit into the midstory in fire-suppressed forests, due to competition from early successional species that grow rapidly following the formation of canopy gaps (Brose et al. 1999). On the other hand, repeated low-intensity fires within closed-canopy forests do not favor regeneration of light-demanding oaks and pines (Arthur et al. 1998, Brose et al. 1999, Franklin et al. 2003, Hutchinson et al. 2005). Some species regarded as early successional species today (e.g., sweetgum) can grow relatively rapidly in the shade as root sprouts and saplings and are able to respond favorably to large canopy gaps, thereby exhibiting considerable phenotypic plasticity. They were not, however, common bearing trees in the presettlement upland landscape in north Mississippi. We suggest that periodic fires acted as a filter that excluded or suppressed all floodplain tree species (early and late-successional) and maintained relatively open canopies. Indeed, stand densities (as inferred from point-to-tree distances) appear to have been lower in the presettlement upland landscape than in present-day mature upland forests in this region (Brewer 2001). Likewise, the significant occurrence of shade-intolerant *Andropogon* L. spp. ("broomsedges") in the groundcover of these presettlement communities [Nutt's 1805 observations in Jennings (1947)] also suggests an open canopy. Such conditions would have likely favored upland oaks and pines. If this hypothesis is correct, then ecological restoration of presettlement disturbance regimes in mature forests may require a combination of persistent canopy openings and variable fire frequencies to give small saplings of oaks and pines an advantage over fire-sensitive floodplain species that are shade tolerant as root sprouts and small saplings but also responsive to canopy openings (Albrecht and McCarthy 2006, Brose et al. 1999).

The relatively high abundance of fire-dependent and light-demanding species of bearing trees on sandy lower slopes of uplands above small creeks during the early 1800s (e.g., shortleaf pine, black oak) suggests that these areas experienced moderately frequent fires and/or had a more open canopy than what we see today. Nevertheless, the greater occurrence of bearing trees of white oak and chestnut and the relatively low occurrence of blackjack oak bearing trees in these areas also suggest that the canopy was not as open, soil moisture was higher, and the frequency or intensity of fires in these areas might not have been as high as in other areas of the upland landscape. Such conditions might have created a fire/light/moisture regime that favored a mixture of open-habitat/fire-dependent species and some mesophytic species. Hence, sandy lower slopes above creeks may have supported some of the highest plant diversity in the upland landscape.

Presettlement tree species composition along a soil gradient

Slow-growing, shade-intolerant species were the most-abundant bearing trees in the uplands of north-central Mississippi across a wide range of soil texture and organic matter. To the extent that this soil gradient was correlated with soil productivity, our results contradict predictions of general plant life-history theories, at least as they relate to presettlement upland forests in this region (Grime 1979, Tilman 1988). These theories predict that the combination of high soil productivity and frequent stand-replacing disturbances favors rapidly growing, early successional species. We argue that frequent fires were not stand-replacing disturbances and acted a species-specific filter in the presettlement landscape, which excluded or suppressed both fast-growing, early successional species and shade-tolerant, late-successional species across the entire upland soil productivity gradient. On the other hand, the bearing-tree species composition we found in presettlement floodplain forests appears to be at least in part consistent with general plant life-history theories, which predict that high soil fertilities support late-successional forests dominated by shade-tolerant tree species in the absence of frequent or intense disturbances. Presettlement floodplains and terraces, which contained fertile soils and likely experienced fires that were either less frequent or less intense than in upland areas (Beilmann and Brenner 1951), contained large numbers of bearing trees of shade-tolerant and fire-sensitive species such as American beech (as well as less shade-tolerant white oak, hickories, and possibly cherrybark oak) in north Mississippi, and thus appear to have approximated mesic late-successional forests. However, the significant abundance of early successional species such as sweetgum in these floodplain forests suggests that long-lived, phenotypically plastic species capable of rapid growth responses to canopy gaps were also favored in these forests.

Despite the widespread occurrence of fire-tolerant tree species in the presettlement uplands, there was nonetheless some modest variation in tree species composition in relation to soil texture. Bearing trees of pines occurred along ridges and slopes (north- and south-facing) and in hollows in infertile loamy sands and sandy clay-loam soils, but were for the most part absent from organic, loess-based silt-loam soils in central Marshall County and most of central Lafayette County. Also, bearing trees of hickories appeared to occur more frequently in organic silt-loam soils. Our findings agree with Hilgard (1860), who indicated that the occurrence of both shortleaf pine and hickories in north central Mississippi followed an east–west gradient in soil fertility in Lafayette County. The western uplands of Lafayette County were dominated by black oak, post oak, and blackjack oak (with hickories being subdominant), whereas the eastern portion of the county consisted of a mixture of pines and the same species of oaks that were the common bearing trees in the western portion of the County, but with few bearing trees of hickories. We do not have a satisfactory explanation for why the xerophytic oaks occurred throughout the soil gradient, whereas the pines did not. One possibility is that the oaks are more shade-tolerant than the pines and thus were favored in the richer soils. Hilgard (1860) noted that individuals of blackjack oak and post oak growing in fertile soils in Marshall County had relatively straight trunks and few limbs (possibly due to their growing in more dense stands in these areas), in stark contrast to the crooked trunks and numerous lower limbs produced by these species in sandy, nutrient-poor soils in northeast Lafayette County. Therefore, xerophytic oaks may have exhibited enough intraspecific variation in growth patterns to adapt to a wide range of soil fertilities and the associated modest variation in stand density and light availability. Regardless of what limited the distribution of pines in uplands, pines and upland oaks were more similar to one another with respect to environmental requirements than they were to mesophytic hardwoods. Arguments about natural distributions of pine and hardwoods that do not distinguish between fire-tolerant upland oaks and mesophytic hardwoods should be viewed with skepticism.

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