

Changing tree composition by life history strategy in a grassland-forest landscape

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Abstract. After rapid deforestation in the eastern United States, which generally occurred during the period of 1850–1920, forests did not return to historical composition and structure. We examined forest compositional change and then considered how historical land use and current land use may influence forests in a grassland-forest landscape, the Missouri Plains, where frequent surface fire was the historical land use and intensive agricultural is the current land use. We compared composition, distribution, and environmental relationships during historical (1813–1860) and current (2004–2008) forest surveys. We also examined changing composition of life history strategies of (1) stress tolerators based on fire tolerance, (2) colonizers based on shade intolerance, and (3) competitors based on shade tolerance. Open forest ecosystems of fire-tolerant oaks have been replaced by forests of fire-sensitive species, such as ashes, hackberry, and maples that expanded from riparian firebreaks and osage-orange and eastern redcedar that expanded from planted windbreaks and rocky firebreaks. Colonizing species increased from 7% to 32% of total composition, with assisted tree migration from planting; we expect continued expansion particularly by eastern redcedar into areas unoccupied by trees. Competitive species have increased slightly to 38% of total composition although the trajectory of current forests suggested competitors may increase to 56% of total composition by replacing oaks in forest ecosystems. Changed success of life history strategies in an agricultural landscape without fire resulted in increased composition and extent of fire-sensitive colonizers compared to fire-tolerant oaks. We suggest that patterns of loss of fire-tolerant oaks and increased distribution of fire-sensitive species reflect suppression of fire, the historical land use. In addition, we suggest that subsequent land use dictates the success of either shade-intolerant colonizers or shade-tolerant competitors in current forests. Forests will be composed of shade-intolerant colonizers where land use disturbance is frequent, such as in agricultural landscapes, and forests will be composed of species with greater shade tolerance where land use disturbance is less frequent.

Key words: fire; fire suppression; functional; historical forests; land use; regime shift.

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INTRODUCTION

Forests of the United States have changed since European immigration, westward expansion, and the Industrial Revolution due to deforestation, fire suppression, and land uses including

agriculture, grazing, and development of modern infrastructure. Most forests of the eastern United States were harvested rapidly during the period of 1850–1920 when increased demand for cleared land, fuel, and lumber coincided with the ability of steam-powered tools to provide a supply of

forest products. Although forests were not quantified before they were harvested, extensive historical tree surveys exist that can be used to reconstruct historical forest conditions.

Recent research that has compared historical and current forests in the eastern United States showed two types of patterns. For the first pattern, open forested ecosystems have densified, or increased in number of trees per hectare, in the eastern United States and to some extent, biomes world-wide (Hanberry et al. 2014). Open oak or pine-dominated forested ecosystems have converted to closed forests composed of many species (Nowacki and Abrams 2008, Hanberry et al. 2012a). As a result of shading, tree species in forests are becoming increasingly shade-tolerant (i.e., mesophication; Nowacki and Abrams 2008, Hanberry et al. 2012b). Conversely, for the second pattern, in colder portions of the Northeast and Appalachian mountains, tree species of mature, undisturbed forest have been replaced by less shade-tolerant species (Foster et al. 1998, Fuller et al. 1998, Cogbill et al. 2002, Wang et al. 2010, Thompson et al. 2013). Historical forests with shorter growing seasons were composed of extremely shade-tolerant and long-lived sugar maple, American beech, and eastern hemlock, whereas current composition contained species that are not late successional (Foster et al. 1998, Fuller et al. 1998, Cogbill et al. 2002, Wang et al. 2010, Thompson et al. 2013). Regionally, mid-successional red maple has increased in abundance throughout the eastern United States (Fei and Steiner 2007) due to convergence of the two types of patterns.

Fire suppression (e.g., Nowacki and Abrams 2008, Hanberry et al. 2014) and land use (Foster et al. 1998, Thompson et al. 2013) appear to be the most likely driving factors for forest changes. Fire, which was the historical land use, explains dominance by fire-tolerant oak and pine species in historical forests, rather than dominance by species that have traits that match climate. Fire suppression has occurred and offers a direct explanation for loss of open oak or pine ecosystems and increased biomass of fire-sensitive species; however, fire can not explain composition of current forests. Conversely, current land use can explain the composition of current forests but can not account for loss of open oak or pine ecosystems, that is, relative

increase of fire-sensitive species and increased biomass of specifically fire-sensitive species.

We used this study in an agricultural landscape to demonstrate the potential influences of fire, the historical land use, followed by fire suppression and current land use on forest change. Historically, a continuum of open oak-dominated ecosystems ranging from prairie, savanna, woodlands, and forests occurred across the Missouri Plains, part of the central North American prairie peninsula, which is a grassland extension into eastern broadleaf forests. Fine fuels from herbaceous grasses carried frequent surface fires across a continuous, flat landscape. The mean fire interval was 6–7 years during 1671 to 1820 in northwestern Missouri (Stambaugh et al. 2008). Currently, 70% of the Missouri Plains landscape is used for agriculture and grazing (Fry et al. 2011). Increased development, human densities, and conversion to agriculture resulted in fire suppression during the 1920s and wildfires now average about 4 ha during non-drought years in the Missouri Plains (Westin 1992).

We evaluated forest changes in tree composition, distribution, species-environmental relationships, and tree life history strategies during the past 150 years in the Missouri Plains landscape to examine how historical fire regimes followed by fire suppression and current land use influence forests. After effective fire exclusion began during the 1920s and cycles of agricultural cultivation and abandonment developed in an agricultural landscape, we expected to detect compositional and distributional changes, which may reflect underlying influential processes that filter species assembly. We also explicitly examined traits of tree species. We selected fire tolerance and shade tolerance as simple and generalizable traits of different life history strategies (Grime 1977) that vary depending on disturbance. We hypothesized that suppression of the historical fire regime should decrease fire tolerators, the oak genus. If current land use is influential on forests, then frequent human disturbance through agricultural cycles of cultivation and abandonment that remove rootstock, as well as tree harvest removals, may favor pioneering species that colonize old fields and forest clearings and that tolerate dessication of open early-successional forest ecosystems. Alternatively, if frequent land use is not influential,

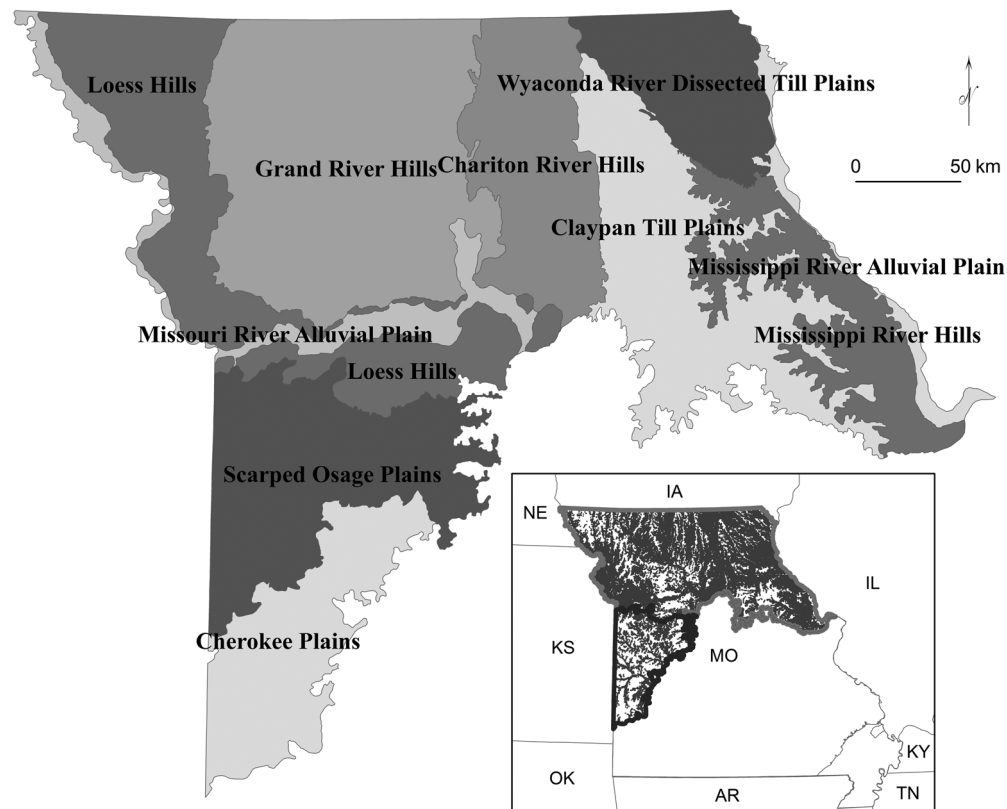


Fig. 1. Ecological subsections of the Missouri Plains. In the inset, the black outlined area is the Osage Plains ecological section, the grey outlined area is the Till Plains ecological section, and the shaded area represents extent of historical forest.

then increased tree density in current forests should select competitive species that harvest light and out-compete colonizer species.

METHODS

Tree surveys and composition

The General Land Office initiated the Public Land Survey System, in which undivided land was measured into townships measuring 9.6 km on a side, and townships were subdivided into 1.6×1.6 km (one square mile) sections. Surveyors recorded species, distance, bearing, and diameter for two to four trees at the corners and middle of each section line (i.e., every 0.8 km). We selected trees, surveyed mostly between 1813 to 1860, in the Osage and Till Plains ecological sections of Missouri from the GLO dataset (Fig. 1; J. Harlan, Geographic Resources Center, <http://msdis.missouri.edu>). We deter-

mined percent composition of 21 species or species groups (inherited from GLO notes where identification was limited to genus; Table 1), as an approximate measure of relative abundance. We used 29,000 line trees, which surveyors encountered along the section lines, and 123,000 bearing trees, which surveyors selected at survey points and recorded by bearing and distance. We quantified line species composition by ecological subsections, or relatively homogenous spatial regions that are subdivisions of the ecological sections of the Missouri Osage and Till Plains (Nigh and Schroeder 2002; Fig. 1).

The USDA Forest Service Forest Inventory and Analysis program records information for all trees at plots that occur about every 2500 ha in the Missouri Plains. The FIA completes a paneled survey on a five-year cycle and we used the latest complete cycle, 2004–2008. We determined percent composition of the species groups for the

Table 1. Tree species/group, counts, and percent composition for trees with diameter ≥ 7.6 cm in GLO (1813–1860) and FIA (2004–2008) surveys in the Missouri Plains. The GLO line trees are encountered by surveyors and GLO bearing trees are selected by surveyors. Shade and drought are tolerance values, increasing from 1 to 5.

Species/group name		GLO line		GLO bearing		FIA		Shade	Drought
Common	Scientific	N	%	N	%	N	%		
American basswood	<i>Tilia americana</i>	822	2.8	2158	1.8	42	0.4	3.98	2.88
American sycamore	<i>Platanus occidentalis</i>	293	1.0	1249	1.0	80	0.7	2.86	2.25
ashes	<i>Fraxinus americana</i> , <i>F. pennsylvanica</i>	273	0.9	1707	1.4	531	4.9	2.46–3.11	2.38–3.85
black oak	<i>Quercus velutina</i>	5182	17.8	24035	19.6	302	2.8	2.72	3
blackjack oak	<i>Quercus marilandica</i>	166	0.6	1271	1.0	18	0.2	3	4
bottomland	<i>Populus deltoides</i> , <i>Salix nigra</i>	691	2.4	3216	2.6	196	1.8	1.34–1.76	1.57–1.77
bur oak	<i>Quercus macrocarpa</i>	1877	6.5	8572	7.0	152	1.4	2.71	3.85
cherries	<i>Prunus</i> spp.	59	0.2	465	0.4	183	1.7	2.46	3.02
chinkapin oak	<i>Quercus muehlenbergii</i>	54	0.2	200	0.2	136	1.3	2.22	4.97
eastern redcedar	<i>Juniperus virginiana</i>	2	0.0	5	0.0	367	3.4	1.28	4.65
elms	<i>Ulmus alata</i> , <i>U. americana</i> , <i>U. rubra</i>	2911	10.0	12840	10.5	1183	11.0	3.14–3.31	2.92–3.00
hackberry	<i>Celtis occidentalis</i>	807	2.8	3001	2.4	749	7.0	3.17	3.85
hickories	<i>Carya cordiformis</i> , <i>C. glabra</i> , <i>C. laciniata</i> , <i>C. ovata</i>	4409	15.2	14912	12.2	1526	14.2	2.07–4.42	2.0–4.0
maples	<i>Acer negundo</i> , <i>A. saccharum</i> , <i>A. saccharinum</i>	350	1.2	2341	1.9	695	6.5	3.47–4.76	2.25–3.03
mesic	<i>Gleditsia triacanthos</i> , <i>Robinia pseudoacacia</i> , <i>Morus rubra</i>	285	1.0	1479	1.2	983	9.1	1.61–2.34	2.88–4.98
osage-orange	<i>Maclura pomifera</i>	0	0.0	0	0.0	631	5.9	1.45	4.22
pin oak	<i>Quercus palustris</i>	1291	4.4	7524	6.1	322	3.0	2.49	2.38
post oak	<i>Quercus stellata</i>	720	2.5	3675	3.0	359	3.3	2.16	4.5
red oaks	<i>Quercus coccinea</i> , <i>Q. falcata</i> , <i>Q. rubra</i>	1242	4.3	3827	3.1	236	2.2	2.07–2.75	2.88–4.00
river birch	<i>Betula nigra</i>	78	0.3	511	0.4	72	0.7	1.45	1.53
shingle oak	<i>Quercus imbricaria</i>	0	0.0	1	0.0	481	4.5	2.09	3.85
swamp white oak	<i>Quercus bicolor</i>	39	0.1	173	0.1	121	1.1	2.98	3.35
walnuts	<i>Juglans nigra</i> , <i>J. cinerea</i>	755	2.6	2784	2.3	565	5.3	1.93	2.38
white oak	<i>Quercus alba</i>	6752	23.2	26769	21.8	829	7.7	2.85	3.56

entire study extent and by subsection as well, using available plots (FIA DataMart, www.fia.fs.fed.us/tools-data). We selected 11,000 live trees that were ≥ 7.6 cm in diameter to make diameter distributions comparable at least to the minimum diameter in GLO surveys. We needed specific FIA plot locations for species distribution modeling. Although available FIA plot coordinates are perturbed to protect landowners, the USDA Forest Service joined environmental variables (see below) to unidentified plots in a table.

Species distribution modeling

To model species distributions, we applied random forests (Breiman 2001, Cutler et al. 2007; see Hanberry et al. 2012c for further details), a classification method based on bootstrap aggregation (bagging) by the majority vote of many trees grown using random samples of both predictor variables and training data. Random forests classification is accurate, nonparametric,

non-linear, user-friendly, and generally avoids predictor collinearity issues, particularly to predict distributions with the range of sampled data (Hanberry et al. 2012c). Model fit depends on the number of strongly predictive variables, regardless of the number of total variables (Biau 2012), and therefore, we used a complete suite of influential predictor variables that were available.

We used the Soil Survey Geographic (SSURGO) Database (Natural Resources Conservation Service, <http://soildatamart.nrcs.usda.gov>) for soil variables and soil polygons for spatial mapping units. After processing, there were about 336,000 polygons for the study area (7,592,550 ha, mean polygon area of 23 ha). Each unique prediction unit represented one of about 10,000 ecological zones (mean area of 800 ha) that were soil map units (discontinuous soil polygons with similar soil characteristics in a county) divided by land type association and geology.

From the SSURGO tables by map unit, we calculated a comprehensive set of soil attributes indicative of water and nutrient supply, which have been shown to influence tree distributions (Van Breeman et al. 1997, Fei and Steiner 2008, Kabrick et al. 2011, Hanberry et al. 2012a, 2012c). Variables used in these calculations included landform, parent material kind (e.g., alluvium, colluvium, residuum), drainage class, taxonomic order, flooding frequency, and the depth to either the bottom of the soil profile or soil restriction. We then calculated mean water holding capacity (cm/cm), pH, base saturation (sum of bases/ECEC), organic matter (%), clay (%), and sand (%) to the depth and weighted values by component percentage. Because terrain variables influence water and light availability related to tree species composition and productivity (Stage and Salas 2007), we used a 30-m digital elevation model (DEM) to calculate topographic variables that also may influence tree distributions: elevation (m), slope (%), transformed aspect ($1 + \sin(\text{aspect}/180\pi + 0.79)$; Beers et al. 1966), solar radiation (0700 to 1900 in 4-hour intervals on summer solstice for re-sampled 60-m DEM), topographic roughness (Sappington et al. 2007), wetness convergence (T. Dilts, <http://arcscrip.esri.com>), and topographic position indices. We then calculated the mean value for each variable by 10,000 ecological zones (mean area of 800 ha) that were divided by map unit, land type association, and geology. We also joined subsection, an ecological land classification, and geology designations to each individual polygon (Nigh and Schroeder 2002). Subsections, and to some extent geology, inform the model about climate, spatial location, and expert opinion. There is some error involved when matching location of trees to environmental data. However, we located trees within soil polygons (mean area of 23 ha), allowing a wide range of locational error.

We modeled species distributions based on presence and absence to examine changes in location and influential variables. We randomly selected 67% of polygons that contained plots with the species, up to 2500 polygons, for modeling, and held back the rest for prediction and validation. For pseudoabsences, we randomly selected 2500 polygons that contained plots without a recorded species presence from poly-

gons with surveys. We then used the random-Forest package (Liaw and Wiener 2002) in R statistical software (R Development Core team 2010), with the sample size option (which is sampled without replacement), where we set the bag fraction, or subsampling rate, at 67% of the selected polygons with the species. We then specified 25% of that value of the selected polygons with unknown presence or absence of the tree species. We set the number of classification trees at 1000 and the number of variables randomly sampled at each split as the square root of the number of predictors. We used the ROCR package (Sing et al. 2005) in R to calculate the true positive rate over receiver operating characteristic (ROC) curves for predictions. We compared predicted probabilities of species presence for each species in GLO and FIA surveys using Pearson's correlation coefficient (SAS software, version 9.1, Cary, North Carolina; Proc Corr).

Variable importance

We examined the five most influential environmental variables for species distribution models, ranked in importance by random forests. We re-scaled variable importance values, by assigning the greatest value as 1, and dividing other values by the greatest original value. We assigned 75% predicted probability as the threshold for presence (i.e., a value similar to modeling prevalence and convenient for mapping; Hanberry and He 2013). We averaged the variables by predicted probabilities $\geq 75\%$ for species presence and compared these values to means of variables for predicted probabilities $< 50\%$ for species presence. We grouped probabilities for species presence into 4 bins (0–25%, 25–50%, 50–75%, 75–100%) to map distributions (please contact the authors for maps or GIS layers). We then assessed changes in distribution based on changes in predicted probabilities $\geq 75\%$ for species presence.

Plant strategies

We applied Niinemets and Valladares' (2006) continuous measurements of shade and drought tolerance based on a scale of increasing tolerance from 1 to 5. We calculated mean values for trees of diameter ≥ 12.7 cm in historical forests and current forests and the potential trajectory of

future forests using diameter <12.7 cm. We adjusted the previous threshold of 7.6 cm to increase sample size of the potential trajectory. We also determined the percent composition of three life history strategies for trees of diameter ≥ 12.7 cm in historical forests and current forests, and potentially the trajectory of future forests using diameter <12.7 cm. We defined early-successional, shade-intolerant colonizer species by shade tolerance <2.5 (Niinemets and Valladares 2006) and later-successional competitors with greater shade tolerance by shade tolerance ≥ 2.5 . We defined the oak genus as disturbance-stabilized tolerators of a continuous surface fire regime. We ran a simple paired t-test (SAS software, version 9.1, Cary, North Carolina; Proc Ttest) to test for significance. We also ran a regression (Proc Reg) between mean shade tolerance and percent of the landscape in agriculture, grazing, and broadleaf forest (Fry et al. 2011).

RESULTS

Composition

Tree species composition, for the entire study extent and within smaller subsections, is a measure of relative abundance (Table 1). White and black oaks historically were about 40% of species composition, but in modern forests, they are 11% of species composition (see Burns and Honkala 1990 for authority names and Table 1 for species groups and scientific names; we grouped to genus when the species commonly was not identified and we combined species into bottomland and locust/mulberry groups). In contemporary forests, many minor species increased in composition, including the locust/mulberry group (relative increase of 8% in composition from 1% historically to 9% currently), osage-orange (increased 6% in composition from 0% to 6%), maples (increased 5% in composition), shingle oak (5%), ashes (4%), hackberry (4%), eastern redcedar (3%), and walnuts (3%). Changes varied by ecological subsection although in most subsections, black oak and white oak historically were the two most dominant species and in all subsections these species decreased by 13–30% in composition (e.g., white oak decreased from 44% historically to 15% currently in the Mississippi River Hills; Fig. 1).

Species distributions

Continuous maps of historical and current species distributions demonstrated fine and coarse scale shifts. Species distributions, with a presence threshold probability $\geq 75\%$, generally became more evenly distributed in current forests across the landscape. However, probabilities predicted presence not density; forests may not have been common historically or currently throughout the prairie peninsula. Ashes (Fig. 2), hackberry, locust/mulberry, and walnuts historically were present along waterways, but they became as likely to be present in the uplands. A similar but less pronounced pattern occurred for American sycamore, birch, maples (Fig. 2), and bottomland species distributions. American basswood and elms were more probable in the north and along waterways, and now are more uniformly distributed. Black oak (Fig. 3), white oak (Fig. 3), post oak, red oak, and hickories were highly probable throughout most of the Missouri Plains historically, but probability of presence reduced to a few locations, mostly in the northeastern, or more forested, portion of the Missouri Plains. Blackjack oak was present along the Missouri Ozarks border historically, but currently is present in few locations. Correlations between predicted probabilities for the same species in GLO and FIA surveys generally were not high, and ranged from -0.02 (pin oak) to 0.75 (river birch), with a mean value of 0.38 . For true positive rates at a 75% threshold, GLO surveys averaged 0.81 (range = 0.59 – 0.92) and FIA surveys averaged 0.89 (range = 0.72 – 1).

Variable importance

Historical and current associations between tree species and site factors showed changes in species-environmental relationships. Wetness convergence, index, slope, subsection, and topographic roughness were the most common variables, shared by at least seven species, of the most influential five variables in GLO and FIA surveys (Appendix). For GLO surveys, subsection (mean rank was 3.8 including all models), wetness index (mean rank was 3.3 including all models), and slope (mean rank was 5.1 including all models) were among the most influential five variables of models for at least 16 species, followed by geology and topographic roughness that were among the

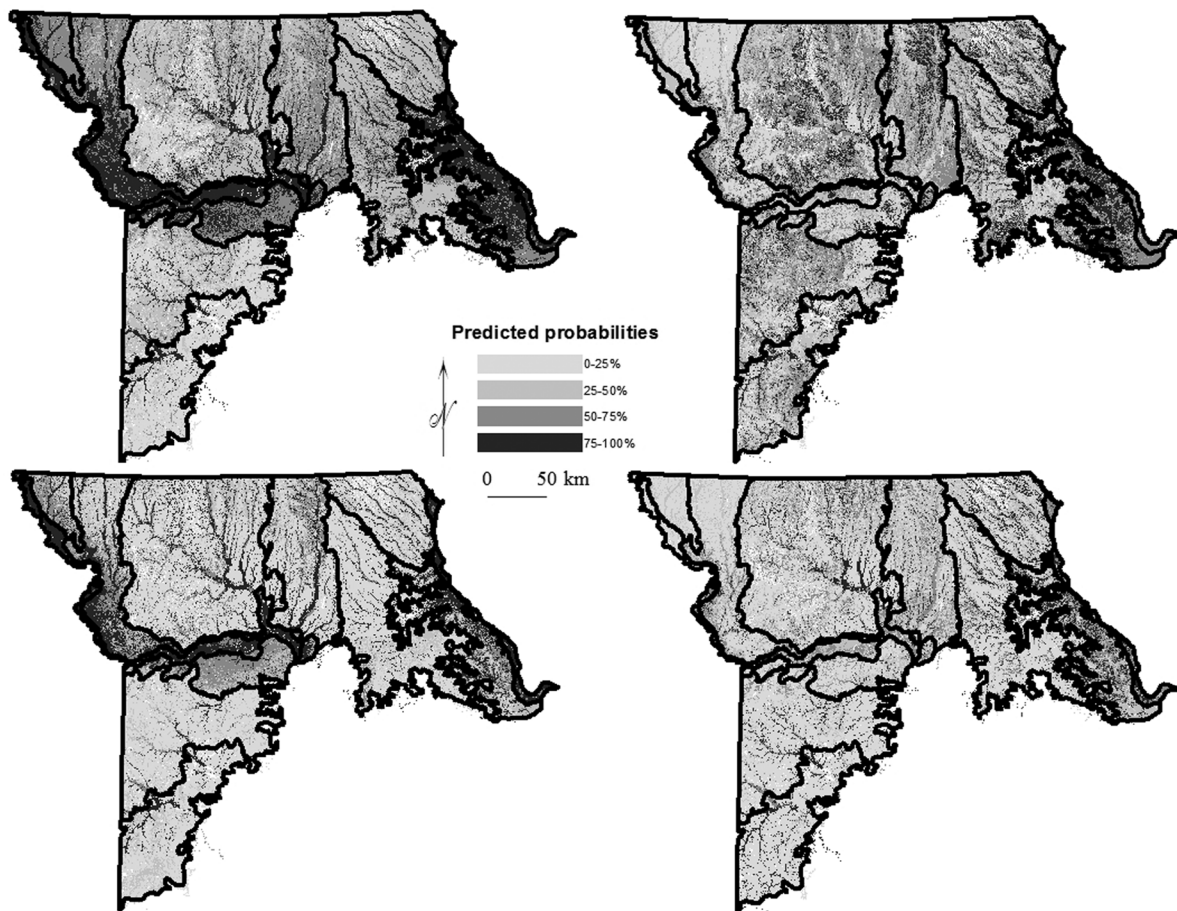


Fig. 2. Predicted probabilities for fire-sensitive species that historically were limited to protected river hills and stream networks: (top left) historical distribution of ashes, (top right) current distribution of ashes, (bottom left) historical distribution of maples, and (bottom right) current distribution of maples.

most influential five variables of models for nine species. For FIA surveys, topographic roughness (mean rank was 4.1 including all models), wetness index (mean rank was 5.3 including all models), slope (mean rank was 4.2 including all models), and topographic position index were among the most influential five variables of models for at least 11 species. Subsection was among the most influential five variables for 8 species (mean rank was 5.6 including all models).

By comparing mean values $\geq 75\%$ predicted probability (i.e., the threshold for presence), between GLO and FIA surveys, values have changed over time, indicating current presence of vegetation in drier and steeper sites. The mean wetness index value associated with presence of most species in current sites has decreased,

particularly for American basswood, ashes, birch, blackjack oak, pin oak, and swamp white oak. Most species increased in presence where slope values were greater (e.g., hickories increased from 6.6% historically to 8.5% currently in slope) along with concomitant increases in roughness. Current forests may be limited to less productive and less accessible areas. In general, distributions of increasing and mesic species (American basswood, American sycamore, birch, locust/mulberry) currently occurred 10 m higher in elevation than historically, whereas distributions of oaks (black oak, bur oak, chinkapin oak, red oak, post oak, pin oak, white oak, also hickories and cherries) currently occurred 10 m lower in elevation than historically.

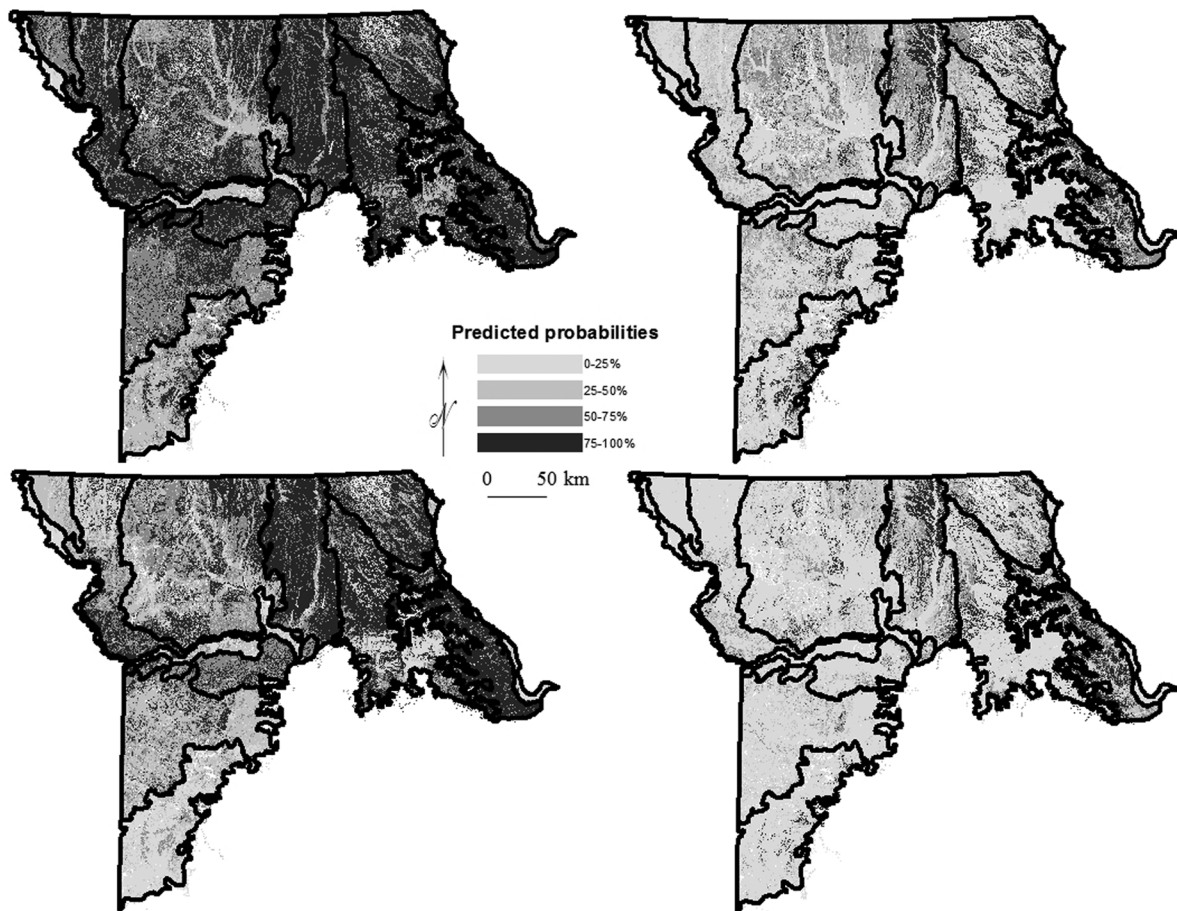


Fig. 3. Predicted probabilities for fire-maintained oaks: (top left) historical distribution of black oak, (top right) current distribution of black oak, (bottom left) historical distribution of white oak, and (bottom right) current distribution of white oak.

Plant strategies

Shade tolerance decreased from 2.78 ± 0.001 (mean $\pm$ SE) in GLO surveys to 2.60 ± 0.007 in FIA surveys ($P = 0.0025$). The regression between current mean shade tolerance and the percent of the landscape in agriculture, grazing, and broadleaf forest was strong ($R^2 = 0.70$), but not significant ($P = 0.1522$). By comparison, regression between historical mean shade tolerance and the percent of the landscape in agriculture, grazing, and broadleaf forest was weaker ($R^2 = 0.41$) and not significant ($P = 0.5099$). Although historical land use was not the same as current land use, land that is suitable for agricultural and grazing would have been more exposed to fires than land where there is currently forest, resulting in species with fire tolerance. Shade

tolerance increased to 2.75 ± 0.017 for trees of diameter <12.7 cm in FIA surveys. Drought tolerance increased from 3.21 ± 0.002 in GLO surveys to 3.51 ± 0.019 in FIA surveys ($P = 0.0150$). Drought tolerance decreased to 3.43 ± 0.048 for trees of diameter <12.7 cm in FIA surveys. The stress-tolerator (i.e., oak) percent composition decreased from 62% in GLO surveys to 30% in FIA surveys for trees ≥ 12.7 cm and 15% for trees <12.7 cm in FIA surveys (Fig. 4). Colonizer percent composition increased from 7% in GLO surveys to 32% in FIA surveys for trees ≥ 12.7 cm and 30% for trees <12.7 cm in FIA surveys. Competitor percent composition increased from 31% in GLO surveys to 38% in FIA surveys for trees ≥ 12.7 cm and 56% for trees <12.7 cm in FIA surveys.

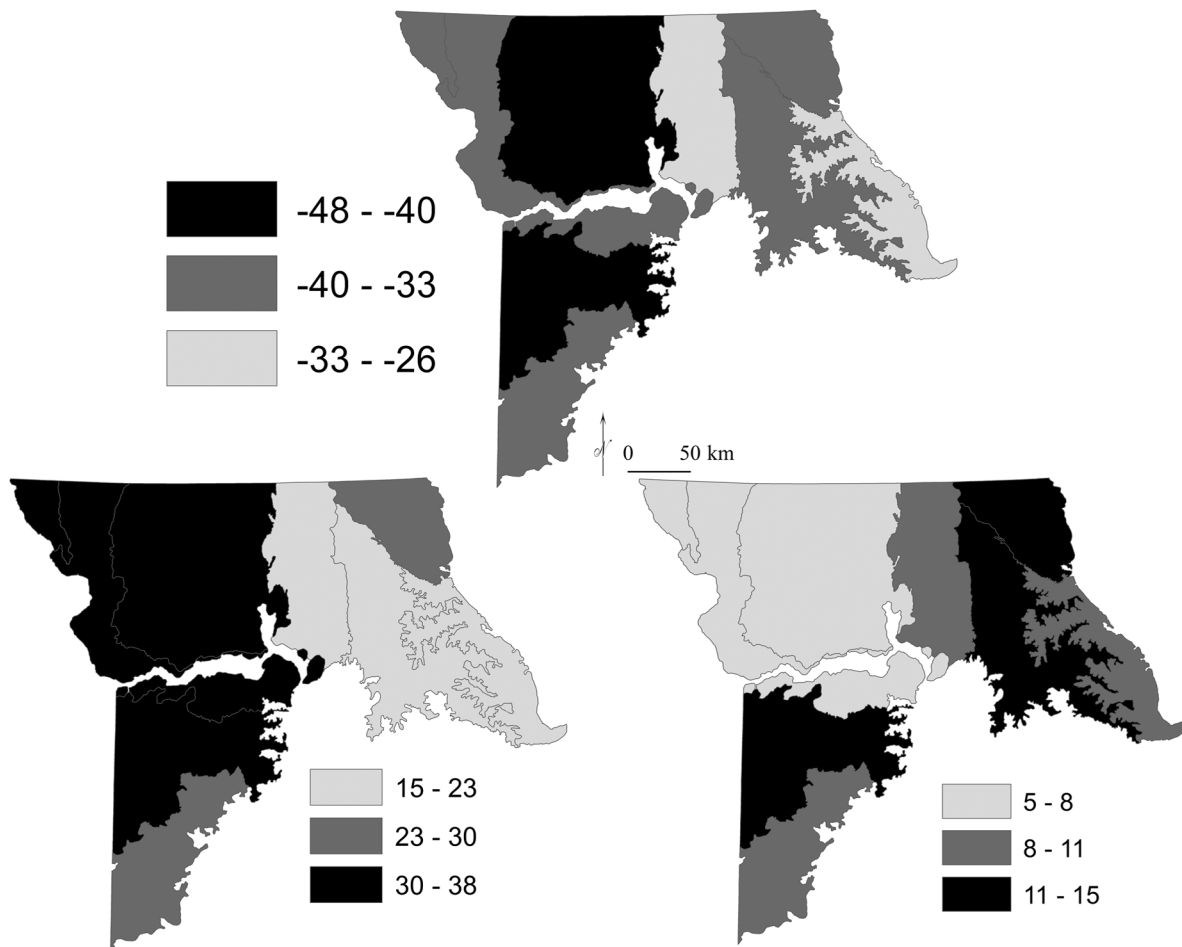


Fig. 4. Relative change in percent composition of (top) fire-tolerant oaks, (bottom left) shade-intolerant colonizers, and (bottom right) shade-tolerant competitors.

DISCUSSION

Changes in composition, distribution, and environmental relationships

Composition has not remained stable in the grassland-forest landscape of the Missouri Plains. Oak abundance has decreased, with the magnitude of decrease varying by ecological subsection, and open oak ecosystems have been replaced by broadleaf forests composed of (less dominant) oaks, hickories and a variety of fire-sensitive species (Table 1). Species that were located predominantly along stream channels and dissected slopes, such as ashes, hackberry, maples, the locusts and mulberry group, and walnuts, increased from transient representation in upland sites to at least 5–10% of composition

throughout the landscape (Fig. 2). These species dispersed from protected riparian areas to successfully colonize upland forests and abandoned fields in the absence of fire. Oak removal without replacement was hastened by agricultural development, which eliminated oak rootstock, followed by invasion of abandoned fields by species including eastern redcedar (Blewett 1986, Briggs et al. 2002), which formerly was limited to firebreaks such as rocky outcrops. Colonizer tree species, which included eastern redcedar, osage-orange, locusts, and mulberry that tolerate open conditions, also were planted for field borders, windbreaks, erosion control, and ornamental purposes, and therefore these species probably would not have increased in composition as greatly without assistance.

Fire disturbance by frequent surface fires probably was a primary factor that determined and stabilized vegetative patterns historically, allowing open oak forest ecosystems to dominate the landscape. Fire exclusion reduced competitiveness of oak species and permitted expansion of fire-sensitive species across the Missouri Plains. Without a fire regime, fire-sensitive species no longer were constrained to locations that were sheltered from fire and therefore were distributed more uniformly in upland areas away from firebreaks. Ecologically-differentiated areas (i.e., ecological subsection and geology designations) have become less restrictive to distributions across the landscape. There was no apparent trend of northerly movement in species distributions even though climate has warmed from the Little Ice Age to record high temperatures during the past 150 years.

Along with changes in species distribution across the landscape, historical species-environmental relationships also have become less influential at a fine scale. Site factors have become favorable, with less specificity, to more species without the physiological constraint of fire tolerance. Altitudinal range shifts along oak/non-oak groupings and expansion of fire-sensitive species into historical oak savannas and woodlands indicated tolerance of drier locations for most species, similarly to other research (Ozier et al. 2006, Morrissey et al. 2010). Soil moisture apparently was never a limiting constraint on mesic species such as maples, which now are present in relatively dry uplands. Rather, soil moisture reflects the likelihood of fire disturbance. Indeed, it may be appropriate to re-define mesic species primarily as fire-sensitive with varying degrees of shade tolerance rather than restricted by edaphic factors.

Although GLO surveys were not complete or random selection of species and surveyors favored overstory species and mis-identified oak species (White 1983), the compositional shifts in in our study were similar to findings of research conducted elsewhere in the prairie peninsula, which showed increased capture of open prairie or oak forest ecosystems by fire-sensitive species formerly limited to either riparian or rocky firebreaks (e.g., Auclair and Cottam 1971, McCune and Cottam 1985, Crow 1988, Briggs et al. 2002). Additionally, the

composition percentages of GLO line tree and bearing tree surveys generally were similar, despite different methods and biases, with a mean absolute difference between composition percentages of 0.7, excluding differences for historically absent eastern redcedar, osage-oak, and shingle oak. In contrast, the mean absolute difference in composition percentage between GLO (either line or bearing) and FIA surveys was 3.5, excluding historically absent species.

Changing plant strategies

Historically, tree species were distributed along gradients according to life history strategies. Fire disturbance formed a gradient congruent with the environmental gradient; more xeric and open conditions facilitated fire and in contrast, hydric and protected sites inhibited fire. In the presence of fire stress, interaction between fire and abiotic conditions organized distributions. Oaks or stress-tolerators dominated the landscape, even though upland sites are suitable for most species. Shade-intolerant colonizers and shade-tolerant competitors were subordinate or transient species on upland sites and only dominant on protected sites, where the ratio of colonizers and competitors depends on time since last disturbance. Most protected sites were near stream networks and wetlands and generally were stable, as colonizer species comprised only 7% of the historical landscape.

After release from fire stress after effective fire suppression, dominance by plant strategy group shifted because of new dynamics between oaks and fire-sensitive species along weakened environmental gradients (Fig. 4). Replacing the primary filter of disturbance interactions with environmental gradients, tolerance to land use and increased competition have become the limiting factors in most eastern forests. Colonizers are successful after field abandonment and harvest. Indeed, currently tolerance to anthropogenic disturbance is the most successful strategy, as the colonizer group has increased from 7% to 32% of total composition, with associated increases in mean drought tolerance and decreases in shade tolerance, while the competitor group has increased only from 31% to 38% of total composition. In a comparison of forest change between pre-settlement and present tree surveys

in western New York, increasing species were earlier successional species rather than late-successional species of American beech, sugar maple, eastern hemlock, and American basswood; increasing species shared traits characteristic of earlier successional species after land use such as forest clearance (Wang et al. 2010).

Many of the currently successful colonizer species were planted; if planting is discontinued, then success of the colonization strategy may be limited for some species if seeds are not spread by wildlife. Eastern redcedar, which is dispersed by wildlife as well as planted, probably will continue to expand into open ecosystems and densify into dense groves that may be self-replacing (Briggs et al. 2002, Belden and Pallardy 2009). Eastern redcedar is the predominant colonizer species, particularly in landscapes that are disturbed by agricultural cycles and unfilled by trees (i.e., grassland ecosystems).

The trajectory indicates that in future forest ecosystems, competitors increasingly may replace oaks. Although colonizers and eastern redcedar in particular are likely to represent a greater proportion of the agricultural and formerly prairie landscape of the Missouri Plains, in the absence of stress by regular disturbance, competition for light by above-ground growth determines composition (Brooker and Callaghan 1998). Furthermore, environmental conditions are influenced by interactions with vegetation. In humid regions, fire-sensitive species can remodel sites to enhance mesic conditions simply by establishing dense, multi-layered forests that resist moisture loss, heat, and wind (Nowacki and Abrams 2008). Consequently, forest ecosystems transition over time from open early-successional forests of colonizers to closed late-successional forests of competitors competing for resources.

Connecting fire suppression with land use

Fire was the major historical land use that shaped vegetation. Unlike current land use that causes vegetation to become uniformly distributed across landscapes, fire strengthened the relationship between vegetation and environmental gradients of climate, soils, and topographic variables. Fire favored the fire tolerance strategy of some oak and pine species. Fire-tolerant species were present in open ecosystems

due to frequent biomass removal where there is exposure to fire, which correlates with warmer, drier, and flatter sites, whereas fire-sensitive species were present in forests on protected sites, which are cooler and wetter, with either more rugged lower slopes or flat, near-riparian sites.

Fire suppression ended a type of land use that stabilized widespread open oak and pine ecosystems that are relatively unchanging in composition and structure. Without fire, composition of fire-tolerant oaks decreased and fire-sensitive species increased, along with a change in state from open forested ecosystems to closed forests (Hanberry et al. 2014). In closed forests, composition of species with any range of shade tolerance is possible. The frequency of land use determines the shade tolerance of species composition. Disturbance from current land use, if frequent, favors a colonizing strategy and if less frequent, favors a shade tolerance strategy. Accordingly, in agricultural areas where cycles of land cultivation and abandonment occur, species composition is less shade-tolerant than historically.

Outside of agricultural areas, in most of the central eastern US (i.e., the eastern broadleaf forests between the broadleaf-pine forests of the Southeast and spruce-fir forests of the Northeast), forests are composed of mid-tolerant species, particularly red maple, which appears to be favored by forestry practices (Fei and Steiner 2007). Late-successional sugar maple and eastern hemlock are increasing (B. B. Hanberry, *unpublished data*); American beech may be prevented from increasing by beech bark disease and eastern hemlock may decline due to hemlock wooly adelgid (*Adelges tsugae*). Despite increases in late-successional species, forests remain composed of less shade-tolerant species than historically due to greater disturbance in colder portions of the Northeast and Appalachian mountains where there was not a fire regime (Foster et al. 1998, Fuller et al. 1998, Cogbill et al. 2002, Wang et al. 2010, Thompson et al. 2013).

The most common terms for the increasing species, which historically were limited to protected areas between fire and flooding regimes, are 'mesic' or 'mesophytic'. However, as discussed above, these species have expanded across the landscape and are able to grow under a wide range of climate and soil conditions,

including into non-forested ecosystems. Although most of the increasing species will not survive a drought in xeric sites, eastern redcedar is extremely drought-tolerant. The species exhibit a wide range of shade and drought tolerance, but share the common traits of fire- and flood-sensitivity. Consequently, we refer to these species as fire-sensitive because they are limited to protected, mesic conditions by fire stress.

Climate and forests

Historical forests dominated by fire-tolerant oak and pine species and current forests dominated by eastern broadleaf species with a range of traits do not appear particularly to reflect the influence of climate and climate change. Climate during the 1920s, when forest changes began (Cottam 1949) and about the time of fire suppression, probably was not outside of the range of previous climate experienced by open oak and pine ecosystems, which were relatively stable in composition for thousands of years including the relatively recent Medieval Warm and Little Ice Age (Prentice et al. 1991, Overpeck et al. 1992, Jackson 2013). There are many tree species in the eastern US and regional climate, similarly to soil and site conditions, is suitable for these species. Climate consists of multiple attributes and temporal and spatial variability that make recent trends in climate variable (i.e., perhaps not warmer and drier in time and space; McEwan et al. 2011). Whether climate has warmed to historical levels and potentially, precipitation has decreased (or the length between precipitation events has increased), or counter-intuitively, growing season temperatures have cooled and growing season precipitation has increased (McEwan et al. 2011), tree species that have increased in current forests show a range of shade and drought tolerance, from early-successional eastern redcedar to mesic, near-riparian tree species (Hanberry et al. 2012a). Further patterns that conflict with climate change as a driving factor of forest change include (1) historically dominant oaks and pine are decreasing and contracting in range, not shifting in range to track climate, (2) although climate outlines species distributions, most species do not realize their potential distribution, as evidenced by naturalization outside of ranges, (3) tree establishment and growth do not always

match with weather oscillations (e.g., Bekker and Taylor 2010, Kaye et al. 2010, Schoennagel et al. 2011). However, changes that (1) began at least a century ago, (2) occur across a continent, (3) operate on a temporal scale of tree generations, (4) and have little documentation make experimental and even correlational studies difficult. We can not disprove the influence of climate change relative to fire suppression and land use on historical and changing forests and we welcome research that can reconcile inconsistencies between climate and forest change.

CONCLUSIONS

Long-term transformation of stable states from open oak forest ecosystems to eastern broadleaf forest has occurred in the Missouri Plains. Fire-tolerant oak species decreased in dominance across the landscape while fire-sensitive species expanded into old fields and oak forest ecosystems. Historical tree interactions with the abiotic environment no longer limit species distributions, as expanded distributions of fire-sensitive species showed reduced restrictions by subsection delineations and environmental gradients. Furthermore, changes in tree composition, distribution, and environmental relationships both reflected and affected disturbance history and site conditions.

Rather than filtration of species by fire disturbance, which intensifies environmental gradients that in turn influence fire return rates, land use and competition currently control community composition and species distributions by favoring fast-growing pioneers and shade-tolerant competitors over fire-tolerant species. Disturbance change therefore affected the effectiveness of life history strategies, by shifting greater success (i.e., growth and reproduction, resulting in greater composition) to aboveground growth for rapid establishment and dispersal or competition for light rather than root reserves to survive stress. Unlike Martínez-Meyer and Peterson (2006), we did not find that ecological niches were stable, because there was a change in the disturbance regime, resulting in convergence to increasingly successful functional traits.

Although current land use can not explain the change from open oak or pine-dominated forested ecosystems to closed forests composed of

numerous fire-sensitive species, discontinuation of historical land use can explain these patterns. However, if fire suppression occurred without disturbance by other land uses, probably late-successional forests of sugar maple and eastern hemlock, and to some extent American beech, would have established in the central eastern US. Instead, the cumulative effects of land uses such as agricultural cultivation and abandonment and harvest resulted in forests of shade-intolerant species where disturbance is frequent and mid-successional forests where disturbance is less frequent.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Most influential two predictor variables for GLO and FIA models of present (probabilities $\geq 75\%$) and absent (probabilities $< 50\%$) trees species in the Missouri Plains.

Species	Variable	GLO				FIA			
		$\geq 75\%$		$< 50\%$		$\geq 75\%$		$< 50\%$	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
American basswood	slope (%)	7.42	3.72	4.91	2.43	9.46	2.54	3.87	1.77
	wetness	4.37	1.07	4.39	0.71	3.89	0.70	4.62	0.75
	position	-0.15	0.47	0.10	0.33	-0.35	0.38	0.13	0.23
	roughness	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ashes	wetness	4.68	1.16	4.25	0.67	4.13	0.93	4.41	0.74
	subsection								
	roughness	0.0009	0.0010	0.0006	0.0006	0.0014	0.0010	0.0004	0.0004
Birches	position	-0.02	0.37	0.06	0.39	-0.17	0.44	0.11	0.30
	wetness	5.92	0.71	4.16	0.65	5.55	1.11	4.18	0.67
	landform								
	subsection								
Black oak	position	-0.21	0.21	0.07	0.39	-0.33	0.25	0.09	0.37
	wetness	4.07	0.63	5.08	0.87	3.79	0.40	4.64	0.86
	aspect	0.99	0.10	1.08	0.24	1.01	0.09	1.01	0.17
	roughness	0.0009	0.0007	0.0004	0.0006	0.0015	0.0009	0.0004	0.0005
Blackjack oak	slope (%)	6.61	2.64	3.62	2.91	8.80	2.75	4.43	2.30
	subsection								
	geology								
Bottomland	water content	0.16	0.03	0.16	0.04	0.14	0.02	0.17	0.03
	wetness	4.20	0.58	4.42	0.95	3.72	0.35	4.65	0.88
	wetness	5.52	0.91	4.23	0.70	5.18	1.20	4.16	0.60
	landform								
Bur oak	position	-0.25	0.27	0.09	0.38	-0.35	0.31	0.15	0.34
	elevation (m)	277.38	29.06	247.06	36.86	260.82	36.07	260.71	34.40
	subsection								
Cherries	position	-0.05	0.45	0.07	0.35	-0.40	0.29	0.22	0.24
	roughness	0.0010	0.0007	0.0006	0.0007	0.0014	0.0009	0.0004	0.0003
	roughness	0.0008	0.0005	0.0004	0.0007	0.0010	0.0008	0.0004	0.0004
	aspect	0.95	0.09	1.13	0.19	0.97	0.11	1.08	0.19
Chinkapin oak	slope (%)	6.55	2.21	3.36	2.89	7.21	2.87	3.82	2.44
	elevation (m)	288.82	15.03	246.33	32.97	241.34	33.23	262.70	37.30
	subsection								
	roughness	0.0013	0.0008	0.0006	0.0007	0.0015	0.0010	0.0004	0.0003
Elms	slope (%)	8.47	2.65	5.02	2.86	9.22	2.88	3.98	1.94
	wetness	4.48	0.99	4.31	0.73	4.34	0.96	4.38	0.78
	position	-0.09	0.34	0.11	0.42	-0.25	0.37	0.19	0.29
	roughness	0.0008	0.0007	0.0006	0.0007	0.0012	0.0010	0.0004	0.0004
Hackberry	wetness	4.71	1.17	4.26	0.69	4.63	1.07	4.30	0.80
	subsection								
	position	-0.03	0.39	0.06	0.38	-0.27	0.32	0.22	0.34
Hickories	roughness	0.0009	0.0009	0.0007	0.0006	0.0011	0.0010	0.0005	0.0005
	aspect	0.98	0.11	1.08	0.25	1.00	0.10	1.01	0.16
	wetness	4.18	0.78	4.71	0.90	3.97	0.74	4.49	0.79
	roughness	0.0009	0.0007	0.0005	0.0007	0.0014	0.0010	0.0004	0.0004
Maples	slope (%)	6.59	2.86	4.46	3.12	8.46	3.39	4.64	2.19
	wetness	5.15	1.21	4.21	0.64	5.20	1.29	4.23	0.68
	landform								
Mesic	position	-0.13	0.42	0.06	0.37	-0.30	0.25	0.10	0.36
	subsection								
	wetness	4.46	1.05	4.27	0.70	4.37	0.95	4.36	0.77
	roughness	0.0009	0.0009	0.0006	0.0006	0.0013	0.0010	0.0004	0.0004
	position	-0.03	0.37	0.06	0.39	-0.31	0.34	0.20	0.28

Table A1. Continued.

Species	Variable	GLO				FIA			
		$\geq 75\%$		$< 50\%$		$\geq 75\%$		$< 50\%$	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pin oak	subsection								
	solar radiation	5966.79	27.74	5986.45	64.97	5972.95	54.27	5981.29	45.32
	elevation (m)	263.21	31.70	253.92	40.28	230.14	23.09	272.28	35.60
Post oak	position	0.01	0.38	0.03	0.42	-0.16	0.21	0.10	0.41
	subsection								
	wetness	4.22	0.66	4.41	0.97	3.85	0.36	4.44	0.87
Red oaks	water content	0.16	0.02	0.17	0.04	0.14	0.03	0.17	0.03
	slope (%)	5.91	2.83	5.72	3.17	8.22	3.16	5.26	2.73
	aspect	0.98	0.11	1.05	0.20	1.00	0.11	1.03	0.17
Swamp white oak	roughness	0.0010	0.0008	0.0004	0.0005	0.0015	0.0009	0.0004	0.0003
	slope (%)	6.98	2.93	4.21	2.52	8.97	2.79	4.10	2.09
	slope (%)	3.13	2.20	7.26	2.77	7.66	2.93	5.09	2.69
Sycamore	wetness	5.51	0.89	3.96	0.61	4.27	0.85	4.37	0.81
	solar radiation	5983.37	52.33	5967.17	47.32	5930.39	28.78	6001.68	46.14
	subsection								
Walnuts	wetness	6.05	0.59	4.17	0.64	5.95	0.67	4.11	0.60
	landform	-0.22	0.28	0.06	0.39	-0.32	0.30	0.16	0.35
	position	4.55	1.07	4.33	0.71	4.22	0.91	4.42	0.80
White oak	wetness	-0.12	0.36	0.15	0.36	-0.30	0.36	0.20	0.29
	roughness	0.0009	0.0008	0.0005	0.0006	0.0013	0.0010	0.0004	0.0003
	roughness	0.0012	0.0009	0.0004	0.0004	0.0018	0.0010	0.0005	0.0004
White oak	wetness	3.98	0.68	4.63	0.82	3.73	0.46	4.49	0.83
	slope (%)	7.54	2.99	4.22	2.29	9.43	2.80	4.94	2.40