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The history of widespread decrease in oak dominance exemplified in a grassland–forest landscape

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HIGHLIGHTS

- Oak establishment is decreasing and open oak ecosystems are remnants.
- We demonstrate loss of open oak ecosystems across a grassland–forest landscape.
- Oaks decreased from 62% of historical composition to 30% of current composition.
- Current forest densities were two times greater than historical densities.
- Prescribed fire with silvicultural methods may help establish oak.

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ABSTRACT

Regionally-distinctive open oak forest ecosystems have been replaced either by intensive agriculture and grazing fields or by denser forests throughout eastern North America and Europe. To quantify changes in tree communities and density in the Missouri Plains, a grassland–forest landscape, we used historical surveys from 1815 to 1864 and current surveys from 2004 to 2008. To estimate density for historical communities, we used the Morisita plotless density estimator and applied corrections for surveyor bias. To estimate density for current forests, we used Random Forests, an ensemble regression tree method, to predict densities from known values at plots using terrain and soil predictors. Oak species decreased from 62% of historical composition to 30% of current composition and black and white oaks historically were dominant species across 93% of the landscape and currently were dominant species across 42% of the landscape. Current forest density was approximately two times greater than historical densities, demonstrating loss of savanna and woodlands and transition to dense forest structure. Average tree diameters were smaller than in the past, but mean basal area and stocking remained similar over time because of the increase in density in current forests. Nevertheless, there were spatial differences; basal area and stocking decreased along rivers and increased away from rivers. Oak species are being replaced by other species in the Missouri Plains, similar to replacement throughout the range of *Quercus*. Long-term commitment to combinations of prescribed burning and silvicultural prescriptions in more xeric sites may be necessary for oak recruitment. Restoration of open oak ecosystems is a time-sensitive issue because restoration will become increasingly costly as oaks are lost from the overstory and the surrounding matrix becomes dominated by non-oak species.
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1. Introduction

In eastern forests of the United States, a wave of widespread and intensive timber harvesting occurred over a relatively short period (e.g., 1800 to 1920) following Euro-American settlement in North America. Extensive harvest promoted oak regeneration in predominantly oak forested ecosystems through release of advance regeneration and stump sprouts (Williams, 1989; Aldrich et al., 2005). The regional scale of forest disturbance resets the age distribution and structure of oak forest ecosystems to dense oak forests by initiating oak regeneration as forests were harvested. Subsequently, suppression of fire in North America changed the disturbance regime to small-scale disturbances, which has promoted the shift to fire-sensitive species in forests of various successional stages at a large scale (Nowacki and Abrams, 2008; Hanberry et al., 2012a). Due to changes in land use, oak recruitment failure and decreasing dominance are occurring throughout eastern North American forests and worldwide (Watt, 1919; Thadami and Ashton, 1995; Humphrey and Swaine, 1997; Niklasson et al., 2002; Svenning, 2002; Li and Ma, 2003; Hofmeister et al., 2004; Götmark et al., 2005; Pulido and Díaz, 2005; Strandberg et al., 2005; von Oheimb and Brunet, 2007; Zavaleta et al., 2007; Hédl et al., 2010; Altman et al., 2013). As a consequence, some light-demanding herbaceous plants,

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and associated wildlife, saproxylic insects, epiphytes, and fungi of open oak ecosystems are declining along with oaks (McShea et al., 2007; Rogers et al., 2008; Lindbladh and Foster, 2010). Oaks, a foundation genus, provide open forested structure, which has become an increasingly rare vegetation type, resulting in biodiversity changes to species that succeed under intensive land use or in closed forests.

The Missouri Plains, in the central United States, are part of the prairie peninsula (Transeau, 1935), a grassland extension into eastern broadleaf forests, where a mosaic of prairies, savannas, woodlands, and forests historically intermingled in patterns influenced by the interaction of soils, topography, and fire disturbances (Nigh and Schroeder, 2002). Prairies were present on flat plains and broad ridges exposed to annual or near-annual fires, oak savannas and woodlands occurred where topographic roughness or wetlands extended fire-free periods to probably at least 5 years, and forests were common on lower and rough slopes and near wetlands including stream networks protected from fire (Nigh and Schroeder, 2002). Stambaugh et al. (2006) reported a mean fire interval of 6.6 years before substantial Euro-American settlement around 1820 in the loess hills of northwestern Missouri. A fire regime that was frequent but not annual favored fire-tolerant oak species and the open structure of savannas and woodlands (Bond et al., 2005). Oak savannas and woodlands had open or simple canopies and fire removed midstories, permitting sufficient light to reach the ground to support a diverse ground cover of forbs and grasses (Nuzzo, 1986).

During the past 150 years, human culture and land use have changed in the Missouri Plains. The final transfer of Osage lands in Missouri by treaty to the US government in 1825 (Rollings, 1992) represented a historical shift in land ownership from Native American to European occupation and use. Stambaugh et al. (2006) observed that the mean fire interval decreased to 1.6 years during initial Euro-American settlement (1825–1850). The use of fire as a tool was continued by Euro-American settlers; in fact, fires were more frequent during initial Euro-American settlement. However, increased development and human densities led to fire suppression by the 1920s. Since the 1950s, wildfires have become rare and average about 4 ha in size during non-drought years in the Missouri Plains region (Westin, 1992). Agricultural development rapidly increased in the midwestern US, including Missouri, as corn and wheat farming developed between 1850 and 1910 (Ramankutty and Foley, 1999). Prairies, savannas, and woodlands of the Missouri Plains were converted to pasture and crop fields (Schroeder, 1981; Ramankutty and Foley, 1999). Later, farm abandonment that occurred during 1930 to 1990 initiated old field succession (Ramankutty and Foley, 1999).

Today, less than 1% of the original savannas in the midwestern prairie peninsula region remain due to conversion to intensive and extensive agriculture and grazing or rapid transition to (relatively) closed canopy forests following fire suppression (Nuzzo, 1986). Although oak forests still dominate xeric sites, oaks are declining on higher quality sites throughout eastern North America and communities are shifting to a range of fire-sensitive species that once were confined to sites protected from fire (Nowacki and Abrams, 2008; Fralish and McArdle, 2009; Hanberry et al., 2012a). Current forest densities and composition show less variation along large scale ecological gradients than in the past due largely to fire suppression and land use events such as exploitative logging and the conversion of forestlands to agriculture and subsequent agricultural abandonment; however, at small scales logging and land abandonment may produce a very high contrasting structure and composition (e.g., edges; Williams, 1989; Hanberry et al., 2012a, 2014).

Although there is a conceptual process of how eastern forests have changed over the past 100 to 150 years (Williams, 1989), there is little quantitative research on historical forest conditions and how they have changed in current times in the Missouri prairie peninsula region. To quantify historical forests, we used General Land Office (GLO) records from the Missouri Plains as a reference for historical forest communities and densities immediately before Euro-American settlement. To determine long term and large scale changes, we compared historical values to current forest communities and densities from USDA Forest Inventory and Analysis (FIA). In addition to the provision of 1) historical ranges of structural values and 2) large scale forest change over time, we present management approaches to address widespread decrease of oak dominance in the eastern United States that may be useful in other regions with oak dominance declines.

2. Methods

2.1. Ecological units

The Missouri Plains cover about 8 million ha and are located in the northwestern part of Missouri (Fig. 1). The Missouri Plains are composed of two ecological sections, the Osage and Till Plains, and further divided into ecological subsections by climate, soils, topography, vegetation, and then divided into land types, such as hills or plains (Nigh and Schroeder, 2002; Fig. 2). We used ecological units, composed of ecological subsections divided into land types, to provide a detailed spatial range of communities and densities across the landscape.

2.2. Community rules

We grouped some tree species into the following categories primarily because of genus-only identification in the GLO surveys: ashes (*Fraxinus americana*, *Fraxinus pennsylvanica*); cherries (*Prunus* spp.); elms (*Ulmus alata*, *Ulmus americana*, *Ulmus rubra*); hickories (*Carya cordiformis*, *Carya glabra*, *Carya laciniosa*, *Carya ovata*, perhaps *Carya texana* and *Carya tomentosa*); maples (primarily *Acer saccharum*, *Acer negundo*, *Acer saccharinum*); red oaks (*Quercus rubra*, *Quercus falcata*, *Quercus coccinea*); walnuts (*Juglans nigra*, *Juglans cinerea*); cottonwoods and willows (*Populus* spp., *Salix* spp.); and mulberry and locusts (*Morus rubra*, *Robinia pseudoacacia*, *Gleditsia triacanthos*).

To determine community composition, we set a threshold of ≥200 trees per ecological unit, resulting in a total of 14 units that met that threshold during each time period (Appendix A). To be classed as a dominant species in a community, percent composition (of species) had to be ≥10% per ecological unit in order to limit communities to no more than 6 species/species groups and yet have species representation. The order of tree species reported within a community was based on descending mean percent composition for all GLO trees to make comparisons more straightforward. For example, black oak had the overall greatest percent composition across all ecoregions and was therefore the first species listed where it exceeded >10% in composition.

2.3. Current surveys and forest density

Every five years, the USDA Forest Inventory and Analysis program surveys long-term forest plots located about every 2400 ha across the country. Each plot contains four 7.31 m radius subplots, configured as a central subplot surrounded by three outer subplots. We used data from the latest complete cycle of 2004 to 2008. We selected live trees with a diameter ≥12.7 cm to correspond with diameters present in GLO surveys; additionally, smaller diameter trees are surveyed in a fraction of each subplot. We selected plots that were 100% forestland, which FIA defines as land at least 1 acre in area and 120 ft wide with at least 10% cover by live trees of any size, "including land that formerly had such tree cover and that will continue to have forest use", and contained at least two trees to exclude some plots that were harvested recently. We calculated trees per hectare using the supplied FIA expansion factor of 6.02 (i.e., one tree represents the inverse of the plot area in acres; $1 / (4 * 0.042)$), and summed the values for each plot.

To predict total density from discrete plots to a continuous surface, and ultimately comparable to historical densities, we used Random Forests regression trees (Breiman, 2001; Cutler et al., 2007) with the

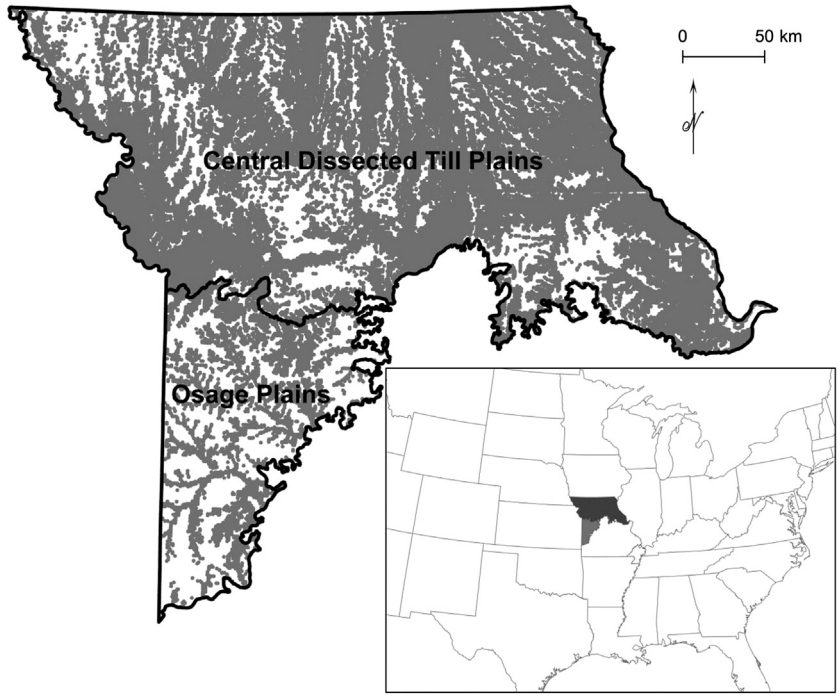

Fig. 1. The two ecological sections of the Missouri Plains. Gray shading shows historical forested extent of the Missouri Plains.

Random Forest package (Liaw and Wiener, 2002) in R statistical software (R Development Core team 2010). We selected 21 predictor variables representing a combination of SSURGO (Soil Survey Geographic) soil and physiographic variables, topographic variables from DEM (digital elevation model), and subsection and geology variables, contained within SSURGO soil polygons (mean polygon area of 23 ha) as spatial units. The predictor variables were a comprehensive set of attributes that influenced tree densities. The 12 soil variables included landform type (bottomlands, protected backslope, exposed backslope, and uplands), parent material kind (e.g., alluvium, colluvium, residuum),

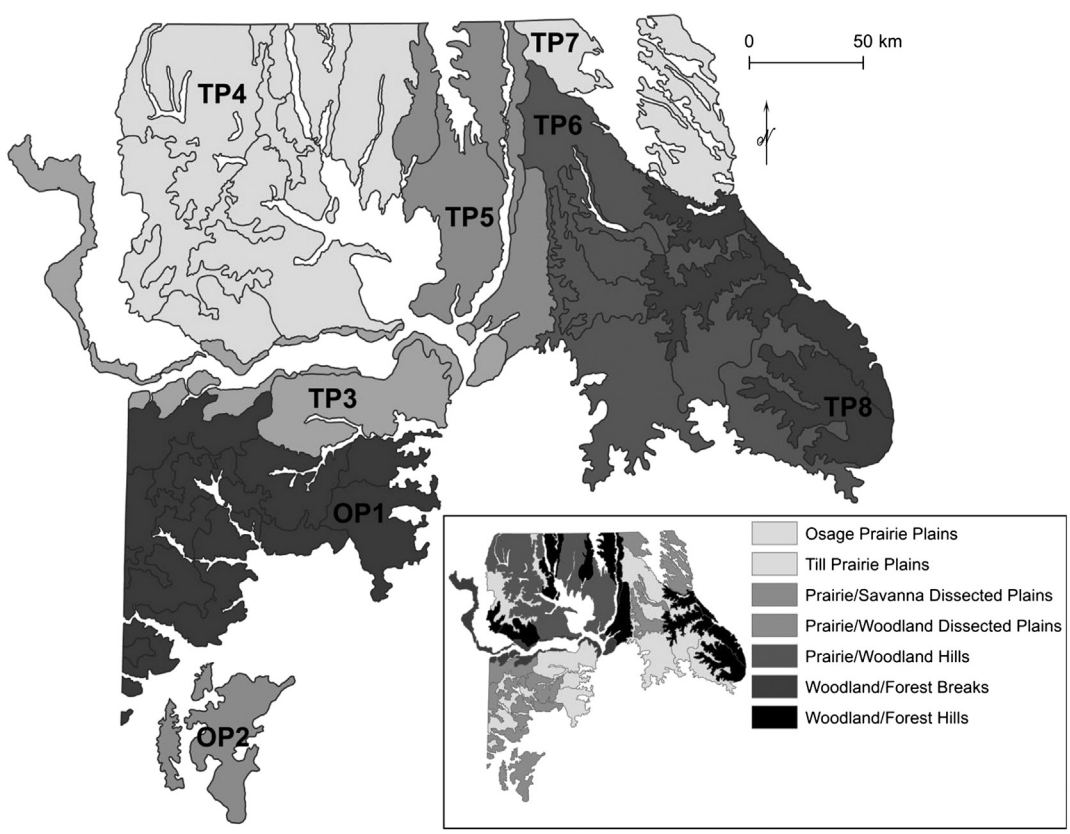

Fig. 2. Ecological subsections (numbered and shaded; Nigh and Schroeder, 2002) of the Osage Plains (OP) and Till Plains (TP) of Missouri, with outlined land types, where there are a sufficient number of large diameter trees (DBH ≥ 12.7 cm) to compare historical and current forests. Land types are shaded in panel.

drainage class (very poorly drained to excessively drained), taxonomic order, and flooding frequency. We also used depth (cm) to either the bottom of the soil profile or soil restriction. We calculated mean water holding capacity (cm/cm), pH, base saturation (sum of bases/effective cation exchange capacity), organic matter (%), clay (%), and sand (%) to the depth and then weighted the values by the percent of each soil series in a soil map unit, or a collection of soil polygons with similar properties. From a 30 m DEM (digital elevation model), we calculated seven variables: elevation (m), slope (%), transformed aspect ($1 + \sin(\text{aspect} // 180 \times \pi + 0.79)$; Beers et al., 1966), solar radiation, topographic roughness (Sappington et al., 2007), wetness convergence, and topographic position index (T. Dilts, http://arcscripts.esri.com). We then calculated the mean value for each variable by prediction zones (mean area of 800 ha) that were soil map units of soil polygons with similar soil characteristics divided into smaller extents by land type association within ecological subsections and geology. The prediction zones were the prediction spatial unit that matched soil and topography values using a smaller ecological area than the soil map units, which shared the same soil values, albeit in discontinuous soil polygons. We also joined ecological subsections and bedrock geology designations to each individual polygon.

We compared the predicted density estimates to observed densities at the FIA plots (about 46 trees ha^{-1} difference). We calculated the standard deviation of the density estimates within an ecological unit and determined a range based on the mean ± standard deviation.

2.4. Historical density

In 1812, the General Land Office developed the Public Land Survey System of townships and ranges; townships measure 9.6 km on a side and contain 36 1.6 × 1.6 km (square-mile) sections (White, 1983). Surveyors recorded species, distance, bearing, and diameter for two to four trees every 0.8 km at the corners and middle of each section line. We selected trees with a diameter ≥12.7 cm, due to surveyor bias against smaller diameter trees, surveyed mostly between 1813 and 1860 in the Osage and Till Plains sections of Missouri (J. Harlan, Geographic Resources Center, http://msdis.missouri.edu; Nigh and Schroeder, 2002). Some of the extent was prairie, or non-forested, where surveyors did not mark trees (Fig. 1).

Because survey points contained only 2 to 4 trees, we could not calculate the density of each plot without error, which precluded use of Random Forests for continuous density predictions. We calculated density using a point-quarter method (Morisita, 1957),

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

where λ (density) is the number of trees/unit area, q is the number of quadrants with surveyed trees (2, 3, or 4), n is the number of plots, and *r* is the survey point-to-tree distance. We estimated density by the number of trees per point for all points within an ecological unit, or land types within an ecological subsection. To increase accuracy, we quantified density only for ecological units with at least 200 points for points with two trees and 50 points for points with three trees (Hanberry et al., 2011). Density estimates were affected strongly by distances with small values, thus we excluded any points that had more than one tree with a distance of '0'. Due to variability of density estimates when there is a clustered spatial pattern for points with 4 trees (Hanberry et al., 2011), we removed the most distant point to convert points with 4 trees into points with 3 trees. We then produced a low value and a high value based on correction for potential spatial patterns (Hanberry et al., 2011).

Surveyors probably did not always select the nearest trees (a distance rank from the survey point of 1), which will result in underestimated densities. Using a rank-based method (sensu, Hanberry et al., 2012b) we calculated two density estimates: (1) a low value using spatial pattern correction and assuming a mean tree rank of 1.4, and (2) a mean value using no spatial pattern correction and assuming a mean tree rank of 1.8. Using a complementary bias method, we found the frequencies by ecological unit for quadrant location, quadrant configuration, and azimuth and we compared species and five diameter classes to line trees, which were recorded when surveyors encountered these trees along section lines, presumably with less bias than trees selected at survey points. We corrected for non-random frequencies by determining the adjustment quotient based on frequencies in regression equations (Hanberry et al., 2012b). We calculated a mean value and a high value, using the high value from the spatial pattern correction. We also set a maximum high value of the value corrected for an unvarying rank of 2 (varying rank of about 2.8).

We then averaged the two mean values and retained the low value (from the rank-based method) and high value (from the bias method). To equilibrate the density estimates from points with two trees and points with three trees, we took into account the type of survey point (density estimates from survey points with three trees are more accurate than points with two trees) and total number of points for each type of point (density estimates become more accurate with more points). We multiplied the count of points with three trees by two, giving it twice the weight of points with two trees. We then multiplied each density estimate by a weight of the number of points over the total number of points and summed the two values.

2.5. Diameter, basal area, and percent stocking

The GLO surveyors selected trees of medium diameter that were healthy (White, 1983) and historical diameter distributions of trees may differ from diameters recorded in GLO surveys (Bouldin, 2010; Rhemtulla and Mladenoff, 2010). Nonetheless, we used GLO data to compare historical and contemporary forest structure for trees ≥12.7 cm DBH (diameter at breast height). For basal area estimates, we used the quadratic mean diameter (square root of the mean DBH^2) to calculate the arithmetic mean tree basal area and multiplied this by the number of trees per ha. We also calculated percent stocking (Gingrich, 1967), a measure of relative growing space occupancy that accounts for the number of trees per ha, tree diameter, and total basal area. A stocking percent of 60 represents the threshold between open and closed canopies and 100 represents average maximum growing space that a stand of trees can occupy but because we included only trees ≥12.7 cm DBH, stocking estimates were not expected to approach 100%. We estimated overall stocking by calculating the stocking contribution of the tree of arithmetic mean diameter and multiplying this by the number of trees per ha.

3. Results

3.1. Communities

No communities currently were the same as in the past (Table 1). Black oak (*Quercus velutina*) and white oak (*Quercus alba*) historically were the dominant species in all but one of the 14 ecological units where there were enough FIA trees to make comparisons (see Appendix B for density and composition of GLO trees for other ecological units). Black oak was no longer a dominant species in any of the current communities throughout the Osage and central dissected Till Plains sections. Fire-tolerant oaks (i.e., dominant species of upland forests, as opposed to for example, pin oak) were no longer compositionally dominant in eight of the 14 ecological units of subsection and land type. White oak maintained its compositional dominance in only five ecological units. Bur oak (*Quercus macrocarpa*) and blackjack oak (*Quercus marilandica*) were dominant species in historical communities but were no longer dominant. Osage-orange

Table 1
Communities and estimated mean densities (Dens; trees ha^{-1}), with low (Lo) and high (Hi) values of historical (GLO) and current (FIA) forests by ecological unit (subsection and land type).

Ecological unit	GLO community[1]	FIA community[1]	GLO			FIA			Density increase
			Dens	Lo	Hi	Dens	Lo	Hi	
OP1 prairie plains	BO–WO–Hi–PO	El–Ma–OO	190	112	226	362	316	409	1.91
OP1 prairie/savanna dissected plains	BO–WO–Hi–PO	El–M_L–OO	115	63	146	360	320	401	3.12
OP2 prairie/savanna dissected plains	BO–Hi–PO–BjO	PO	102	69	109	277	253	300	2.71
TP3 prairie plains	BO–WO–Hi	Ma–M_L–OO–Ha	90	52	108	331	312	350	3.67
TP3 woodland/forest breaks	BO–WO–El	Hi–El–M_L–Ha	190	107	237	318	296	341	1.67
TP4 prairie plains	BO–Hi–El–BuO–RO	El–M_L–Wa–Ha	94	49	123	322	297	347	3.43
TP4 prairie/woodland hills	BO–WO–Hi–El–BuO–PiO	Hi–El–M_L–OO	113	74	124	315	294	335	2.78
TP4 woodland/forest hills	BO–WO–Hi–El–BuO	WO–Hi–El–M_L	181	105	220	314	291	337	1.73
TP5 prairie/woodland hills	BO–WO–Hi	WO–El–PO	117	72	135	335	292	378	2.87
TP5 woodland/forest hills	BO–WO–BuO	WO–Hi	169	104	195	334	299	369	1.98
TP6 prairie plains	BO–WO–Hi	WO–Hi	122	72	144	282	252	312	2.32
TP6 prairie/woodland dissected plains	BO–WO–Hi	Hi–PiO	133	69	173	275	244	306	2.06
TP7 prairie/woodland dissected plains	BO–WO–Hi	Hi–El	259	153	314	281	241	321	1.08
TP8 woodland/forest hills	BO–WO	WO–Hi	205	99	282	301	269	332	1.46

[1] BO = black oak (*Quercus velutina*); BuO = bur oak (*Quercus macrocarpa*); PiO = pin oak (*Quercus palustris*); WO = white oak (*Quercus alba*); PO = post oak (*Quercus stellata*); BjO = blackjack oak (*Quercus marilandica*); Hi = hickories (*Carya cordiformis*, *Carya glabra*, *Carya laciniosa*, *Carya ovata*, *Carya texana*, *Carya tomentosa*); Ma = maples (primarily *Acer saccharum*, *Acer negundo*, *Acer saccharinum*); El = elms (*Ulmus alata*, *Ulmus americana*, *Ulmus rubra*); OO = Osage-orange (*Maclura pomifera*); M_L = mulberry and locust (*Morus rubra*, *Robinia pseudoacacia*, *Gleditsia triacanthos*); Ha = hackberry (*Celtis occidentalis*); and Wa = walnuts (*Juglans nigra*, *Juglans cinerea*)

(*Maclura pomifera*), mulberry and locusts, maples, hackberry (*Celtis occidentalis*) and walnuts have become new dominant species (>10% of species composition) in current forests. Elms, maples, Osage-orange, mulberry and locusts, hackberry, and walnuts have replaced black oak and white oak. With the loss of black and white oaks, hickories have become relatively more dominant, but hickories also were displaced as a dominant species in six ecological units.

About 71% of all tree stems were represented by the dominant species of GLO communities but only 43% of all tree stems were represented in FIA communities. In the GLO surveys (DBH ≥ 12.7 cm), about 62% of species were oaks, in FIA surveys (DBH ≥ 12.7 cm), about 30% of species were oaks, and in FIA surveys for trees <12.7 cm, 13% of species were oak.

3.2. Structure

Historical forest densities averaged about 150 trees ha^{-1} (DBH ≥ 12.7 cm), ranging from a mean low of 85 to a mean high of 180 trees ha^{-1} (Table 1, Fig. 3). Current forest densities average about 315 trees ha^{-1} and range from a mean of 280 to 345 trees ha^{-1}, about 2 times greater than historical densities on average. Twelve of the 14 ecological units had high historical densities that were lower than the low current densities. Historical tree densities were most similar to current densities only in the northeastern portion of Missouri. Density was significantly different between time intervals ($p = 0.0001$, Wilcoxon signed rank test; Proc Univariate, SAS software, version 9.1, Cary, North Carolina, USA).

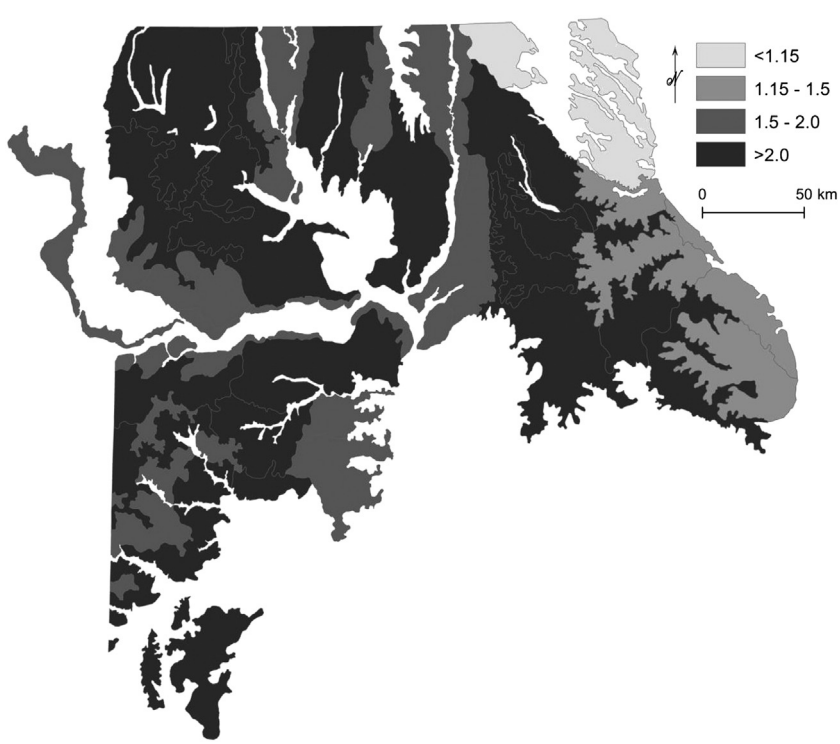

Fig. 3. Current density as a fraction of historical density (trees DBH ≥ 12.7 cm) in the Missouri Plains.

Basal area historically averaged 18.7 m^2 ha^{-1} (8.1 to 31.9 m^2 ha^{-1}), but has since decreased to an average of 16.3 m^2 ha^{-1} (14.8 to 17.9 m^2 ha^{-1}) in current forests of the Osage and Till Plains sections (Table 2). Despite greater tree densities in current forests, average basal area is lower today because tree diameters are smaller than in the GLO surveys. However, spatial changes in basal area were distinctive, with overall decreases along riparian networks (e.g., the Missouri River along subsection TP3 and the Mississippi River along subsections TP7 and 8; Fig. 2) and increases generally in historically less forested areas, including the Osage Plains (Figs. 1 and 4). Due to spatial conflicts in change, basal area was not significantly different between time intervals (based on the Wilcoxon signed rank test).

Similarly to basal area, average stocking has remained relatively stable from the GLO (54%) to the FIA (55%) surveys. Average stocking among the ecological units was more varied (24 to 93%) in the historical survey than it is today (43 to 67%). Although trees today are smaller in diameter they occur in more dense forests than previously and this has resulted in similar levels of stocking of trees ≥12.7 cm DBH. Also similar to basal area, decreases occurred along riparian networks and increases occurred in most upland areas. Due to spatial conflicts in change, stocking was not significantly different between time intervals (based on the Wilcoxon signed rank test).

4. Discussion

4.1. Compositional changes

Current community composition is substantially different than it was in the early to mid-19th century, probably related to fire suppression and land use. Fire-tolerant oaks decreased from historical widespread dominance after fire suppression permitted fire-sensitive species to grow in woodland and forest understories (Pallardy et al., 1988; Westin, 1992; Stambaugh et al., 2006). Black and/or white oaks historically were dominant across 93% of the landscape while these species currently were dominant across 42% of the landscape, based on the area of ecological units where the species were dominant. The greatest changes in composition have been the loss of black oak species as a dominant species, dominance of white oak currently limited to forests on the more topographically dissected areas that are less suited to agriculture, and decline of minor oak species such as bur oak and blackjack oak. White oak is more shade-tolerant than black oak species and has been able to persist somewhat better under the changing disturbance regimes, maintaining its dominance primarily in woodland and forest hills ecological units (see Table 1). White oaks can be long-lived, i.e., dominant mature oaks today established 100 years ago or longer when fire was still part of the disturbance regime. Thus, there is uncertainty in this era of fire suppression whether white oak can be sustained at present stocking levels into the future under current management and disturbance regimes.

Oak forested ecosystems were cleared for agriculture, and subsequently a percentage was abandoned to old field succession because of declining crop production after severe soil erosion, drought, or poor farming practices (e.g. Bazzaz, 1968). When farm fields and pastures were abandoned in the plains, they were reforested by fire-sensitive and colonizing elms, maples, Osage-orange, mulberry, locusts, hackberry, and walnuts, which have doubled in compositional dominance since the mid-1800s (Hanberry et al., 2014, Table 1). These pioneer species have multiple adaptations that promote their establishment in abandoned fields. Osage-oranges, mulberry, locusts and walnuts are shade-intolerant, grow vigorously in open conditions, produce seed at early ages, and seed dispersal is aided by animals (Burns and Honkala, 1990). These species are well-suited to colonize overgrazed pastures with eroded soils that are abandoned after agricultural use. They are common in fencerows and along field borders, which facilitated the delivery of seed to recently abandoned fields, and the establishment of seedlings in advance of pasture abandonment. Osage-orange was planted widely near agricultural fields to produce fence posts, which facilitated the spread of its seed. Hackberry, elms, and maples tend to develop under established trees. These species produce good seed crops nearly yearly starting from a relatively early age and have seed that is wind-borne or disseminated by animals.

4.2. Structural changes

The study area lies within the historical eastern tallgrass prairie–broadleaf forest transition area described by Transeau (1935), where fire, modified by topography, soils and human population, determined vegetation structure, composition and distribution of prairies, savannas, woodlands and forests (Anderson, 1983; Stambaugh and Guyette, 2008). Schroeder (1981) estimated that prairies covered from 50% to 80% of the land area for most counties in the study area based on analysis of GLO survey data; however, surveyors were able to record trees at densities that indicated open forested ecosystems throughout most of the Missouri Plains (Fig. 1). We estimated overall historical mean basal area (for trees ≥12.7 cm DBH) to be greater than the thresholds commonly used to define savannas (e.g., <7 m^2 ha^{-1}; MTNF, 2005). Nonetheless, the low values of historical basal area were within the range typical of savanna structure, whereas the greater values were

Table 2
Mean diameter, basal area, and stocking of historical (GLO) and current (FIA) forests by ecological unit (subsection and land type). Diameter at breast height (DBH) is in cm, basal area (BA) is m^2 ha^{-1} and stocking (Stock) is in percent.

Ecological unit	GLO							FIA						
			Low	High		Low	High			Low	High		Low	High
	DBH	BA	BA	BA	Stock	Stock	Stock	DBH	BA	BA	BA	Stock	Stock	Stock
OP1 prairie plains	34.3	21.0	12.3	24.9	61.6	36.1	73.2	22.6	16.6	14.5	18.7	58.3	50.9	65.7
OP1 prairie/savanna dissected plains	36.2	14.4	7.9	18.3	41.2	22.6	52.2	22.2	16.8	14.9	18.7	56.2	49.8	62.6
OP2 prairie/savanna dissected plains	39.4	14.7	9.9	15.6	42.2	28.6	44.9	24.0	14.8	13.5	16.0	49.2	45.0	53.3
TP3 prairie plains	30.8	8.1	4.7	9.7	24.3	14.0	29.3	25.9	19.8	18.6	20.9	66.7	62.9	70.5
TP3 woodland/forest breaks	40.7	32.0	18.0	39.9	83.4	46.9	103.9	23.7	17.2	16.0	18.4	55.2	51.3	59.2
TP4 prairie plains	34.3	9.9	5.2	13.0	30.5	15.8	39.9	25.7	19.7	18.1	21.2	64.0	59.0	68.9
TP4 prairie/woodland hills	36.0	13.8	9.0	15.1	39.9	26.0	43.7	22.8	15.4	14.4	16.4	51.4	48.1	54.7
TP4 woodland/forest hills	37.2	24.3	14.1	29.4	67.9	39.5	82.2	23.5	15.5	14.4	16.7	53.9	49.9	57.8
TP5 prairie/woodland hills	34.7	13.6	8.3	15.8	38.7	23.7	44.8	21.5	14.2	12.3	16.0	49.6	43.2	56.1
TP5 woodland/forest hills	35.8	20.1	12.4	23.2	59.0	36.5	68.2	23.1	16.4	14.6	18.1	55.4	49.6	61.3
TP6 prairie plains	36.0	14.4	8.5	17.1	42.9	25.3	50.8	25.3	17.4	15.5	19.2	54.8	49.0	60.6
TP6 prairie/woodland dissected plains	35.9	16.1	8.4	21.0	46.9	24.4	61.0	24.4	15.5	13.8	17.3	50.1	44.4	55.8
TP7 prairie/woodland dissected plains	36.3	31.5	18.6	38.2	93.0	54.9	112.9	22.1	12.8	11.0	14.6	43.4	37.3	49.6
TP8 woodland/forest hills	37.5	28.4	13.6	39.0	78.0	37.4	107.2	24.3	16.5	14.8	18.2	54.3	48.7	60.0

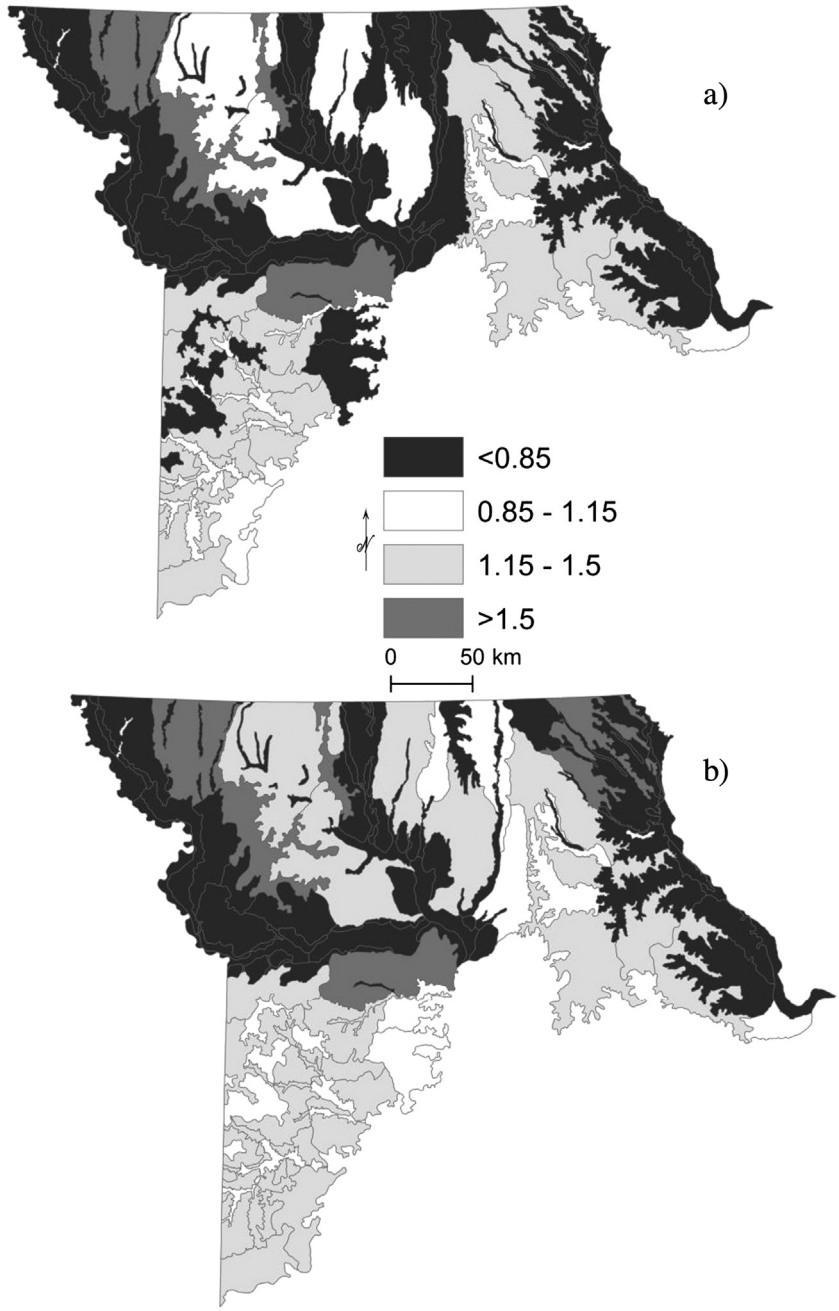

Fig. 4. Current basal area (a) and stocking (b) as a fraction of historical basal area and stocking (trees DBH ≥ 12.7 cm) in the Missouri Plains (all subsections and landforms with current data included).

representative of denser floodplain forests. For example, Dollar et al. (1992) inventoried floodplain forests in northern Missouri and reported an average density of 27 m^2 ha^{-1} in basal area with some stands achieving 85 m^2 ha^{-1} for trees >6.6 cm DBH.

Because of the variation intrinsic to historical landscapes, mean structural values for the entire ecological section or for an ecological unit were not very representative compared to the range of values. Firebreaks provided by stream networks and wetlands helped determine tree presence, structure, and composition in the plains (see Fig. 1) and riparian forests contained denser forests with a greater composition of fire-sensitive species. Therefore, dense forests of riparian or near-riparian species probably occurred alongside closed oak woodlands, which likewise graded into open woodlands, savannas, and prairies within most ecological units. Many of the small streams and wetlands have been filled or drained, so that some of the historical features that influenced forest composition and structure disappeared.

Historically, there was greater variability in the range of average structural values among ecological units than during the current period. Gradients in topography, water and rock firebreaks, and soils influenced fire return intervals, which in turn produced great variation in forest structure (Schroeder, 1981; Anderson, 1983). Even though overall current basal area and stocking were similar to historical structure because increases in tree density have offset reductions in tree diameters, historical basal area and stocking varied with environmental gradients. Therefore, basal area and stocking decreased compared to historical values along the Missouri and Mississippi rivers and major tributaries and basal area and stocking increased compared to historical values in subsections where the historical fire regime removed trees (Fig. 4).

Structural estimates would be greater in current forests, which have multiple midstory layers, with inclusion of trees <12.7 cm in diameter, but in savannas and woodlands, trees in the 2 to 12 cm diameter class would have been largely eliminated and relegated to be sprouts by fires every 6 to 7 years in the Native American period (Stambaugh et al., 2006; Arthur et al., 2012).

Prairie and savanna communities have been eliminated from the landscape either by conversion to agriculture or transition to forests (Nuzzo, 1986). Current forest density was approximately two times greater than historical densities, demonstrating loss of savanna and woodlands and transition to dense forest structure. The typical transition following fire suppression is for prairies to be invaded by trees and for savannas and woodlands to become closed forests over several decades (Cottam, 1949; Grimm, 1984; Heikens and Robertson, 1994). Soils and climate in the prairie peninsula are capable of supporting tree growth and thus, forested ecosystems develop in the absence of fire. Current forest structure in the plains, although similar to values reported by Stambaugh et al. (2006), was lower than values for current fully-stocked mature forests in the state (Pallardy et al., 1988), which indicated that forests may be recovering from cycles of clearing for agriculture followed by agricultural abandonment.

4.3. Ecological considerations

With continued changes in land use, whether fire suppression or changes in land use intensity, non-oak species are expected to continue replacing oaks in the overstory (Abrams, 1998, 2003; Fei and Steiner, 2009). Oak forests are converting primarily to broadleaf forests composed of a variety of species in the eastern United States (Nowacki and Abrams, 2008) and Europe (Humphrey and Swaine, 1997; Niklasson et al., 2002; Svenning, 2002; Hofmeister et al., 2004; Strandberg et al., 2005; von Oheimb and Brunet, 2007; Hédl et al., 2010). Where land use is intensive and trees are removed frequently for agriculture and grazing, as in the Missouri Plains, non-oak species tend to be early-successional species tolerant of exposure, and sometimes planted for fencerows and landscaping purposes. Where land use is for residential and forestry purposes, non-oak species tend to be mid-successional species with greater shade tolerance; red maple in particular has increased in composition in the eastern US (Nowacki and Abrams, 2008; Fei and Steiner, 2009). In both land use scenarios, and even where oaks remain dominant, trees are present at greater densities than historical open oak forested ecosystems.

Foundation species are dominant species that define ecosystems and support biological communities (Dayton, 1972). Open oak-dominated ecosystem covered part of the central eastern United States for thousands of years and provided light and structure to associated herbaceous plants and animals. Herbaceous species present in oak savannas and open woodlands have declined due to decreased available light at the ground from increased tree density (Rogers et al., 2008). A combination of loss of open structure, herbaceous ground story, and light contributes to declines in animals dependent on oak ecosystems (McShea et al., 2007; Lindbladh and Foster, 2010).

Where oak species still remain dominant in forests throughout their worldwide distribution, there are reports of recruitment failure and thus, sustaining or increasing levels of oak stocking is problematic throughout its range (Watt, 1919; Thadami and Ashton, 1995; Li and Ma, 2003; Götmark et al., 2005; Pulido and Díaz, 2005; Zavaleta et al., 2007; Altman et al., 2013). Restoration of open oak ecosystems is an urgent issue because oak recruitment potential declines as forests transition to non-oak species. In healthy mature oak forests, acorn production is periodically sufficient to establish a population of oak seedlings in the understory. Sustaining oak stocking then currently is more of a problem of recruitment of oak advance reproduction into the overstory; recruitment often is limited due to weak competitiveness in heavily shaded understories (Franklin et al., 2003; Alexander et al., 2008; Iverson et al., 2008a; Holzmueller et al., 2011).

Identification of sites that have the greatest potential for restoration is important to efficiently use limited budget and staff resources. Priority sites should contain an oak overstory with the potential to establish oak advance regeneration, or pine forests that are converting to oak; across the Missouri Plains landscape, the ecological units that still contain dominant white oak and post oak should be targeted for restoration. In addition, not all sites have the same potential for restoration due to different disturbance and land use histories, degree of soil erosion, problems with invasive species and other factors that limit the potential or complicate the ability to achieve quality ecosystems inexpensively. For example, regenerating and sustaining oaks on xeric sites is easier than more productive sites, which may have more intact native ground flora than mesic sites that were converted to agricultural use. If restoring woodlands and savannas is the goal, then an assessment of the potential to recover ground flora diversity can aid in site selection. Size of restoration project area, its connectivity to other restoration properties, and landscape objectives for restored natural communities should be considered. Restoration is expensive and often involves treating vegetation that does not produce any marketable commodities, and hence, revenues. Agency and landowner budgets are limited, as are government cost-share and tax incentive programs.

4.4. Management approaches

Combinations of prescribed burning and timber harvesting or stand thinning are proving promising for oak restoration in the eastern United States (Brose et al., 1999; Franklin et al., 2003; Alexander et al., 2008; Hutchinson et al., 2008; Povak et al., 2008). Single prescribed fire effects on hardwood regeneration can persist for up to 10 years especially when the fire is medium to high intensity and done in the early spring when the leaves of competitors are just expanding and oaks are still dormant (Brose, 2010). Additional reductions in stand density may be needed to maintain sufficient light for oak seedling growth. However, reducing stand density to encourage oak sprouts and saplings also promotes non-oak species and necessitates their control. A series of prescribed fires is effective in controlling small diameter (<15 cm DBH) competitors that are less tolerant of burns than oaks, which allocate resources to underground reserves for continued re-sprouting (Brose et al., 2013).

Oak reproduction establishment and development to competitive status is a process that may require 10 to 30 years (Arthur et al., 1998; Iverson et al., 2008a; Waldrop et al., 2008; Holzmueller et al., 2011; Brose et al., 2013). It takes years for small oak seedlings to build competitive root systems and high overstory density and shade prolongs the development of root mass (Brose, 2008). One set of disturbances (e.g., thinning followed by two prescribed burns, or several prescribed fires followed by group selection harvesting) may be enough to improve oak regeneration potential and dominance, but probably will not be enough to ensure oak recruitment into the overstory in the long-term or to achieve savanna or woodland structural reference conditions in the short-term (Waldrop et al., 2008; Hutchinson et al., 2012). Open oak forests developed from disturbances repeated over hundreds or thousands of years that produced a predominantly oak matrix, unlike current forests which provide a steady supply of non-oak propagules. Thus, long-term commitments to active management will be needed to restore and sustain oak savannas, woodlands and forests within an increasingly non-oak matrix. The time required to plan and manage the oak regeneration process is challenging due to changing staff, brief land ownership tenure, vacillating agency directives, and uncertain budgets.

Integration of prescribed fire with other traditional silvicultural methods to regenerate oak, to sustain oak stocking at maturity, or to restore savanna/woodland structure is a relatively new endeavor. Multiple types of treatments can be arranged in any number of various sequences and timings. Vegetation responses may differ in various silvicultural systems across a diversity of ecological units throughout the

eastern United States. Therefore, monitoring and research projects to assess treatment effectiveness should be designed using an ecological framework (Dey et al., 2009) and used to inform adaptive management after assessing the success of oak regeneration and development, or achievement of natural community desired future conditions (Yaussy et al., 2008). Meta-analyses such as Brose et al. (2013) are invaluable for understanding what appears to be confusing or inconsistent results from prescribed fire and regeneration experiments.

5. Conclusions

Similar to the fate of oak throughout the world, composition of oaks has decreased substantially in the Missouri Plains since the mid-1800s. Black and white oak historically were dominant across 93% of the landscape while these species currently were dominant across 42% of the landscape. The decline of oak dominance was accompanied by loss of open ecosystems either though conversion to agriculture or transition to closed, dense forests, similarly to other regions. The former landscape contained a continuum of prairie, savanna, woodland, and forest. In contrast, the current landscape contains agricultural crops, tall fescue pastures, or dense forests, generally the size of small woodlots and sometimes in the form of field rows.

Our research has provided much needed quantitative metrics describing historical composition and structure in a spatially explicit way within an ecological framework. These findings provide quantitative targets that may help managers define the desired future conditions in restoration. By comparison to current forest inventories, we have been able to demonstrate change in composition and structure over a large landscape that is representative of the agricultural midwestern United States and once was part of the grassland–broadleaf forest transition region that covered about 90,000 km^2 (Transeau, 1935). Understanding the extent and location of changes in composition and structure helps to determine the amount of deviation from historical conditions, which may be used to identify priority areas for restoration, set restoration targets, design restoration prescriptions, and assess costs.

Loss of oak is expected to continue under current management practices and trends in land use, even though species distribution projections of climate change scenarios indicate that oak will be favored over its competitors (McKenney et al., 2007; Iverson et al., 2008b). The fate of oak and presence of diverse natural communities across the landscape are dependent largely upon human action at local scales and public policy and cooperation at landscape and regional scales, a daunting task given that most of the land is privately owned. However, active, purposeful management is needed to reverse the densification process that contributed to the loss of savannas and woodlands, and that continues to favor the replacement of oak by fire-sensitive species. The unfavorable economics of restoration currently limits efforts. Innovative silvicultural prescriptions are being developed in the eastern United States that combine fire with other practices to sustain oak in forested settings, or that regulate woody structure and favor ground flora typical of savannas and woodlands. The key to successful restoration of oak ecosystems will include the social adoption of needed silvicultural prescriptions, development of new markets that are able to use currently unmerchantable biomass, and identification of priority areas for restoration that collectively meet landscape and regional conservation goals. Land in the six ecological units that contain dominant white or post oak probably will require the fewest resources to restore. The Missouri Plains is a landscape critical for agricultural production in the midwestern United States. However, regional planning and land use policies that provide for restoration of natural communities and sustaining oak on the landscape are needed.

Conflict of interest

The authors have approved the final article and have no conflicts of interest. Funding was provided by the National Fire Plan of the USDA Forest Service, Northern Research Station; however, the work was completed without any contact with the sponsoring agency. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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Appendix A. Area and number of trees by ecological unit of ecological subsection and land type

Ecological unit	Area (ha)	GLO tree count	FIA tree count
OP1 prairie plains	350,589	1288	550
OP1 prairie/savanna dissected plains	552,413	5443	950
OP2 prairie/savanna dissected plains	209,007	2416	487
TP3 prairie plains	245,013	1408	221
TP3 woodland/forest breaks	272,700	8026	453
TP4 prairie plains	248,941	893	226
TP4 prairie/woodland hills	880,173	11,996	973
TP4 woodland/forest hills	265,485	7958	317
TP5 prairie/woodland hills	227,054	4438	337
TP5 woodland/forest hills	403,417	11,211	959
TP6 prairie plains	908,629	8892	1135
TP6 prairie/woodland dissected plains	133,780	3905	247
TP7 prairie/woodland dissected plains	277,134	6634	576
TP8 woodland/forest hills	508,817	13,456	1426

Appendix B. Communities and densities for historical forests by ecological unit (subsection and land type) where there were <200 trees for current forests

Ecological unit	Density	Low	High	Community
OP1 alluvial plains	122	68	153	BO–Hi–El
OP2 alluvial plains	138	83	164	Hi–El–BuO–PiO
OP2 prairie plains	99	59	119	BO–Hi–PO–BjO
TP1 alluvial plains	214	119	269	El–C_W
TP2 loess prairie hills and blufflands	62	35	76	BO–Hi–El–BuO
TP3 alluvial plains	328	185	402	El–C_W–Ma
TP3 loess prairie hills and blufflands	84	49	102	BO–Hi–El–BuO
TP3 prairie/woodland hills	193	121	219	BO–WO–El
TP4 alluvial plains	209	120	254	Hi–El–BuO–PiO
TP4 low prairie plains	133	70	173	BO–WO–Hi–BuO–PiO
TP5 alluvial plains	154	76	207	BO–Hi–El–PiO
TP7 prairie plains	130	77	155	BO–WO–Hi–El–BuO–PiO
TP8 prairie/woodland hills	200	116	241	BO–WO–PO
TP9 alluvial plains	221	113	293	BO–El–Ma

BO = black oak (*Quercus velutina*); BuO = bur oak (*Quercus macrocarpa*); PiO = pin oak (*Quercus palustris*); WO = white oak (*Quercus alba*); PO = post oak (*Quercus stellata*); Hi = hickories (*Carya cordiformis*, *Carya glabra*, *Carya laciniosa*, *Carya ovata*, *Carya texana*, *Carya tomentosa*); Ma = maples (*Acer saccharum*, *Acer negundo*, *Acer saccharinum*); El = elms (*Ulmus alata*, *Ulmus americana*, *Ulmus rubra*); and C_W = cottonwood and willow (*Populus* spp., *Salix* spp.).

References

Abrams MD. The red maple paradox. Bioscience 1998;48:355–64.
Abrams MD. Where has all the white oak gone? Bioscience 2003;53:927–39.
Aldrich PR, Parker GR, Romero-Severson J, Michler CH. Confirmation of oak recruitment failure in Indiana old-growth forest: 75 years of data. For Sci 2005;51:406–16.
Alexander HD, Arthur MA, Loftis DL, Green SR. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. For Ecol Manage 2008;256:1021–30.
Altman J, Hédl R, Szabó P, Mazůrek P, Riedl V, Müllerová J, et al. Tree-rings mirror management legacy: dramatic response of standard oaks to past coppicing in Central Europe. PloS One 2013;8:e55770.
Anderson RC. The eastern prairie–forest transition — an overview. In: Brewer R, editor. Proceedings 8th North American Prairie Conference. Kalamazoo, MI: Western Michigan University; 1983. p. 86–92.
Arthur MA, Paratley RD, Blankenship BA. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak–pine forest. J Torrey Bot Soc 1998;125:225–36.

Arthur MA, Alexander HD, Dey DC, Schweitzer CJ, Loftis DL. Refining the fire–oak hypothesis for management of oak-dominated forests of the eastern United States. J For 2012;110: 257–66.
Bazzaz FA. Succession on abandoned fields in the Shawnee Hills, southern Illinois. Ecology 1968;49:924–36.
Beers TW, Dress PE, Wensel LC. Aspect transformation in site productivity research. J For 1966;64:691–2.
Bond WJ, Woodward FI, Midgley GF. The global distribution of ecosystems in a world without fire. New Phytol 2005;165:525–38.
Bouldin J. Issues in estimates of relative metrics of historic forest conditions from bearing tree data. Ecol Appl 2010;20:1183–7.
Breiman L. Random Forests. Mach Learn 2001;40:5–32.
Brose PH. Root development of acorn-origin oak seedlings in shelterwood stands on the Appalachia Plateau of northern Pennsylvania: 4-year results. For Ecol Manage 2008;255:3374–81.
Brose PH. Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. For Ecol Manage 2010;260:1516–24.
Brose PH, Van Lear DH, Cooper R. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. For Ecol Manage 1999;113: 125–41.
Brose PH, Dey DC, Phillips RJ, Waldrop TA. A meta-analysis of the fire–oak literature: does prescribed burning promote oak reproduction in eastern North America? For Sci 2013;59:322–34.
Burns, R.M., Honkala, B.H., tech. coords., 1990. Silvics of North America: 2. Hardwoods. Agriculture Handbook 654. USDA, Forest Service, Washington, DC.
Cottam G. The phytosociology of an oak woods in southwestern Wisconsin. Ecology 1949;30:271–87.
Cutler DR, Edwards Jr TC, Beard KH, Cutler A, Hess KT, Gibson J, et al. Random Forests for classification in ecology. Ecology 2007;88:2783–92.
Dayton PK. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC, editor. Proceedings of the Colloquium on Conservation Problems in Antarctica. Lawrence, KS: Allen Press; 1972. p. 81–96.
Dey DC, Spetich MA, Weigel DR, Johnson PS, Graney DL, Kabrick JM. A suggested approach for design of oak (*Quercus* L.) regeneration research considering regional differences. New For 2009;37:123–35.
Dollar KE, Pallardy SG, Garrett HE. Composition and environment of floodplain forests of northern Missouri. Can J For Res 1992;22:1343–50.
Fei S, Steiner KC. Rapid capture of growing space by red maple. Can J For Res 2009;39: 1444–52.
Fralish JS, McArdle TG. Forest dynamics across three century-length disturbance regimes in the Illinois Ozark Hills. Am Midl Nat 2009;162:418–49.
Franklin SB, Robertson PA, Fralish JS. Prescribed burning effects on upland *Quercus* forest structure and function. For Ecol Manage 2003;184:315–35.
Gingrich SF. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. For Sci 1967;13:38–53.
Götmark F, Berglund Å, Wiklander K. Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. Scand J For Res 2005;20:223–34.
Grimm EC. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. Ecol Monogr 1984;54:291–311.
Hanberry BB, Dey DC, He HS. Regime shifts and weakened environmental gradients in open oak and pine ecosystems. PLoS One 2012a;7:e41337.
Hanberry BB, Yang J, Kabrick JM, He HS. Adjusting forest density estimates for surveyor bias in historical tree surveys. Am Midl Nat 2012b;167:285–306.
Hanberry BB, Fraver S, He HS, Yang J, Dey DC, Palik BJ. Spatial pattern corrections and sample sizes for forest density estimates of historical tree surveys. Landscape Ecol 2011;26:59–68.
Hanberry BB, Kabrick JM, He HS. Densification and state transition across the Missouri Ozarks landscape. Ecosystems 2014;17:66–81.
Hédl R, Kopecký M, Komárek J. Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. Divers Distrib 2010;16:267–76.
Heikens AL, Robertson PA. Barrens of the Midwest: a review of the literature. Castanea 1994;59:184–94.
Hofmeister J, Mihaljevič M, Hošek J. The spread of ash (*Fraxinus excelsior*) in some European oak forests: an effect of nitrogen deposition or successional change? For Ecol Manage 2004;203:35–47.
Holzmueller EJ, Groninger JW, Ruffner CM, Ozier TB. Composition of oak stands in the Illinois Ozark Hills 2 decades following light harvesting and no cutting. North J Appl For 2011;28:50–3.
Humphrey JW, Swaine MD. Factors affecting the natural regeneration of *Quercus* in Scottish oakwoods. I. Competition from *Pteridium aquilinum*. J Appl Ecol 1997;34: 577–84.
Hutchinson TF, Long RP, Ford RD, Sutherland EK. Fire history and the establishment of oaks and maples in second-growth forests. Can J For Res 2008;38:1184–98.
Hutchinson TF, Long RP, Rebbeck J, Sutherland EK, Yaussy DA. Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. Can J For Res 2012;42:303–14.
Iverson LR, Hutchinson TF, Prasad AM, Peters MP. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. For Ecol Manage 2008a;255:3035–50.
Iverson LR, Prasad AM, Matthews SN, Peters M. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For Ecol Manage 2008b;254:390–406.
Li Q, Ma K. Factors affecting establishment of *Quercus liaotungensis* Koidz. under mature mixed oak forest overstory and in shrubland. For Ecol Manage 2003;176:133–46.
Liaw A, Wiener M. Classification and regression by Random Forest. R News 2002;2:18–22.
Lindbladh M, Foster DR. Dynamics of long-lived foundation species: the history of *Quercus* in southern Scandinavia. J Ecol 2010;98:1330–45.
McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF. Potential impacts of climate change on the distribution of North American trees. Bioscience 2007;57: 939–48.
McShea WJ, Healy WM, Devers P, Fearer T, Koch FH, Stauffer D, et al. Forestry matters: decline of oaks will impact wildlife in hardwood forests. J Wildl Manage 2007;71: 1717–28.
Morisita M. A new method for the estimation of density by the spacing method, applicable to non-randomly distributed populations. Seiri Seitai 1957;7:134–44. [(in Japanese)].
MTNF. 2005 land and resource management plan, Mark Twain National Forest. Mark Twain National Forest: USDA Forest Service; 2005 [Accessed online September 10, 2013: http://www.fs.usda.gov/main/mtnf/landmanagement/planning].
Nigh TA, Schroeder WA. Atlas of Missouri ecoregions. MO: Missouri Department of Conservation Publication; 2002.
Niklasson M, Lindbladh M, Björkman L. A long-term record of *Quercus* decline, logging and fires in a southern Swedish *Fagus–Picea* forest. J Veg Sci 2002;13:765–74.
Nowacki GJ, Abrams MD. The demise of fire and 'mesophication' of forests in the eastern United States. Bioscience 2008;58:123–38.
Nuzzo VA. Extent and status of Midwest oak savanna: presettlement and 1985. Nat Area J 1986;6:6–36.
Pallardy SG, Nigh TA, Garrett HE. Changes in forest composition in central Missouri: 1968–1982. Am Midl Nat 1988;120(2):380–90.
Povak NA, Lorimer CG, Guries RP. Altering successional trends in oak forests: 19 year experimental results of low- and moderate-intensity silvicultural treatments. Can J For Res 2008;38:2880–95.
Pulido FJ, Díaz M. Regeneration of a Mediterranean oak: a whole-cycle approach. Écoscience 2005;12:92–102.
R Development Core team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2010.
Ramankutty N, Foley JA. Estimating historical change in land cover: North American croplands from 1850 to 1992. Glob Ecol Biogeogr 1999;8:381–96.
Rhemtulla JM, Mladenoff DJ. Relative consistency, not absolute precision, is the strength of the Public Land Survey: response to Bouldin. Ecol Appl 2010;20:1187–9.
Rogers DA, Rooney TP, Olson D, Waller DM. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 2008;89:2482–92.
Rollings WH. The Osage: an ethnohistorical study of hegemony on the prairie-plains. Columbia, MO: University of Missouri Press; 1992.
Sappington JM, Longshore KM, Thompson DB. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. J Wildl Manage 2007;71:1419–26.
Schroeder WA. Presettlement prairie of Missouri. Missouri Dept. Conservation, Natural History Series No. 2; 1981.
Stambaugh MC, Guyette RP. Predicting spatio-temporal variability in fire return intervals using a topographic roughness index. For Ecol Manage 2008;254:463–73.
Stambaugh MC, Guyette RP, McMurry ER, Dey DC. Fire history at the eastern Great Plains margin, Missouri River loess hills. Great Plains Res 2006;16:149–59.
Strandberg B, Kristiansen SM, Tybirk K. Dynamic oak-scrub to forest succession: effects of management on understorey vegetation, humus forms and soils. For Ecol Manage 2005;211:318–28.
Svenning JC. A review of natural vegetation openness in north-western Europe. Biol Conserv 2002;104:133–48.
Thadami R, Ashton PMS. Regeneration of banj oak (*Quercus leucotrichophora* A. Camus) in the central Himalaya. For Ecol Manage 1995;78:217–24.
Transeau EN. The prairie peninsula. Ecology 1935;16(3):423–37.
von Oheimb G, Brunet J. Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. Acta Oecol 2007;31:229–42.
Waldrop TA, Yaussy DA, Phillips RJ, Hutchinson TA, Brudnak L, Boerner REJ. Fuel reduction treatments affect stand structure of hardwood forests in western North Carolina and southern Ohio, USA. For Ecol Manage 2008;255:3117–29.
Watt AS. On the causes of failure of natural regeneration in British oakwoods. J Ecol 1919;7:173–203.
Westin S. Wildfire in Missouri. Jefferson City, MO: Missouri Department of Conservation; 1992.
White CA. A history of the rectangular survey system. Washington DC: Bureau of Land Management, Government Printing Office; 1983.
Williams M. Americans and their forests: a historical geography. Cambridge, UK: Cambridge University Press; 1989.
Yaussy DA, Nowacki GJ, Schuler TM, Dey DC, DeGayner EJ. Developing a unified monitoring and reporting system: a key to successful restoration of mixed-oak forests throughout the Central Hardwood region. Gen. Tech. Rep. PNW-733USDA Forest Service Pacific Northwest Research Station; 2008. p. 281–5.
Zavaleta ES, Hulvey KB, Fulfrost B. Regional patterns of recruitment success and failure in two endemic California oaks. Divers Distrib 2007;13:735–45.