Ecosystems
DOI: 10.1007/s10021-013-9707-7

ECOSYSTEMS

Densification and State Transition Across the Missouri Ozarks Landscape

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ABSTRACT

World-wide, some biomes are densifying, or increasing in dense woody vegetation, and shifting to alternative stable states. We quantified densification and state transition between forests ecosystems in historical (ca. 1815–1850) and current (2004–2008) surveys of the Missouri Ozark Highlands, a 5-million ha landscape in southern Missouri, USA. To estimate density of historical forests, we used the Morisita plotless density estimator and applied corrections for surveyor bias. For contemporary forests, we used known densities at plots to predict continuous densities with random forests, an ensemble regression tree method. We also calculated basal area and percent stocking to determine changes in wood volume. Historical forests had densities ranging from about 75 to 320 trees/ha. Current forest densities were about 2.3 times greater and more uniform, at about 300–400 trees/ha (DBH ≥ 12.7 cm). Not all forests have increased in basal area and percent stocking because trees in contemporary forests are smaller in diameter than historical forests. Although oak species still are dominant (as defined by ≥10% composition), oak dominance is being replaced by many fire-sensitive species, of which only eastern redcedar and maples have become dominant. Densification and community changes in functional traits have produced a state transition from open oak forest ecosystems to predominantly closed eastern broadleaf forests in the Missouri Ozarks. This shift is not at equilibrium, as fire-sensitive species are continuing to increase and turnover in long-lived oaks is slow.

Key words: alternative stable state; eastern redcedar; encroachment; facilitation; fire suppression; juniper; mesophication; presettlement; regime shift.

INTRODUCTION

Ecotones are zones of tension between competing alternative stable states. Currently, many vegetation states with lower abundance of woody vegetation are destabilizing, despite persistence for hundreds if not thousands of years. Although deforestation and desertification are well-known processes driven by land use that decrease vegetation (Gonzalez 2001; Lambin and others 2003; Wright 2005), there also is a pattern of encroachment at ecotones by biomes with greater densities of woody vegetation. In some locations, shrubs and trees are increasing in number in grasslands, shrublands, savannas, and tundra (Van Auken 2000; Archer and others 2001; Buitenwerf and others 2012; Kirdyanov and others 2012), the

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Received 25 January 2013; accepted 28 July 2013

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-013-9707-7) contains supplementary material, which is available to authorized users.

Author Contributions: BBH analyzed data and wrote paper; JMK conceived of study and contributed to writing; HSH conceived of study and contributed to writing.

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canopies of savannas and open woodlands are closing (Roitman and others 2007; Nowacki and Abrams 2008; Fulé and others 2009; Bekker and Taylor, 2010; Ikauniece and others 2012), riparian forest species are expanding into uplands (Axelrod 1985; Crow 1988; Briggs and others 2005), treelines are ascending in elevation (Choler and others 2001; Harsch and others 2009; Wakeling and others 2011), and descending in elevation as well (Van Auken 2000; Briggs and others 2002, Cocke and others 2005). We use the term ''densification'' to describe the phenomenon of increases in the number, basal area, stocking, or canopy cover of trees and shrubs, although encroachment, thickening, and equivalent terms are in use.

The most common explanations for woody densification include altered grazing regimes, fire suppression, climate change or weather oscillations, and carbon dioxide enrichment (Van Auken 2000; Bond and Midgley 2012). In biomes defined in part by trees and not heavily stocked by large grazers (that is, not silvopastural woodlands; Plieninger and others 2011), browsing consumers may be at historically high levels and yet are not powerful enough to prevent tree densification at a regional scale (Nowacki and Abrams 2008; Staver and others 2009). In biomes with a documented fire regime and vegetation types that are stabilized by fire, fire suppression is a parsimonious and consistent explanation for densification with concurrent compositional change to fire-sensitive vegetation. Fire reduces biomass and favors fire-resistant species, explaining both large scale regional patterns, differences in vegetation along environmental gradients, and fine scale heterogeneity between adjacent sites with similar moisture levels, soils, and topography. Climate is an important factor explaining vegetation distribution but tree response to climate change is species-specific and unpredictable (Parmesan 2006; Ettinger and others 2011). Increased tree establishment does not always match with increased precipitation, even in more arid regions with cyclical weather oscillations (Belsky 1996; Bekker and Taylor 2010; Kaye and others 2010; Wigley and others 2010; Schoennagel and others 2011). Rising temperatures may apply drought stress to trees, decreasing biomass. Biomes such as temperate oak- and pine-dominated forests in the United States, that appeared to be relatively stable at least in composition for thousands of years (albeit with some change at leading edges; Prentice and others 1991; Grimm and Jacobson 1992; Overpeck and others 1992), now are densifying. Indeed, most biomes that are densifying have a history of fire that has prevented achievement of potential biomass production indicated by climate, as shown by current and pre-historical woody densification, models, and experiments (Bond and others 2005; Lehmann and others 2011). Carbon dioxide enrichment can enhance photosynthetic rates, translating to increased tree growth and woody densification (Higgins and Scheiter 2012), particularly in the absence of fire and in some areas, even with fire (Buitenwerf and others 2012). Although carbon dioxide fertilization may increase vegetation cover (that is, ''greening'') where water is limited and the climate is warm (Donohue and others 2013), increased water stress in boreal forests has limited tree growth during recent decades (Ma and others 2012; Wu and others 2012).

In the eastern United States, open forest ecosystems dominated by large diameter oak and pine trees are converting to closed forest ecosystems comprised of many species with the shared trait of fire-sensitivity but varying tolerance to drought and temperature. Pre-settlement open forest ecosystems allowed light to reach the forest floor, where light along with periodic fire disturbance supported an herbaceous layer and advance regeneration of fire-tolerant oaks and pine (Nowacki and Abrams 2008). After intensive harvest around the turn of the 20th century, release of oak advance regeneration and stump sprouting may have converted oak savannas and open oak woodlands to closed canopy oak forests within a generation after Euro-American settlement (Crow 1988). Paralleling densification due to reduced disturbance of biomass, without a fire regime to reduce competition for oak seedlings in the understory with lower light levels, a variety of fire-sensitive species have reduced oak dominance (Fralish and McArdle 2009). Currently, dense eastern oak forests generally either have an understory dominated by fire-sensitive species or have completed the transition to a mesic overstory (Fralish and McArdle 2009). Fire-sensitive species are present in increasingly dense forests, with multiple woody layers of subdominant trees and shrubs (Rogers and others 2008).

Densification of biomes and switches to alternative stable states have occurred in some regions, and these processes may be related. Densification of open forest ecosystems may represent rapid state transitions in communities, but this connection has not been examined often across a large spatial and temporal scale. We documented densification at a landscape scale and associated changes in community composition to explore whether densification reflected community changes in state. We quantified densification in number of stems, basal

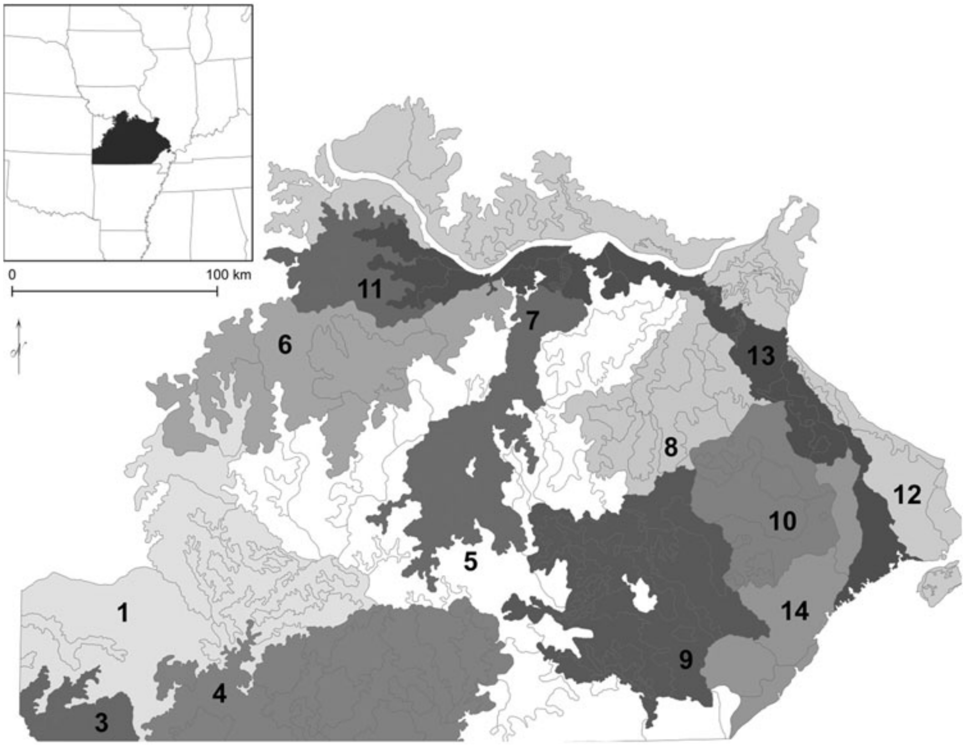

Figure 1. Ecological subsections (shaded and numbered by ecological subsection) and land types (outlined within subsections) in the Missouri Ozarks.

area, and percent stocking across a temperate deciduous forest landscape, incorporating spatial variation by ecological classes, with temporal change between historical General Land Office (GLO) surveys from 1815 to 1850 and USDA Forest Inventory and Analysis (FIA) surveys from 2004-2008.

METHODS

Surveys and Ecological Units

The General Land Office developed the Public Land Survey System of townships and ranges, composed of 1.6-square-km (one square mile) sections, in 1812 (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 border. We selected about 285,000 trees, surveyed mostly between 1815 to 1850, in Missouri's Ozark Highlands section from the GLO dataset (J. Harlan, Geographic Resources Center, http://msdis.missouri.edu).

The USDA Forest Service Forest Inventory and Analysis monitors long-term forest plots across the country at an average density of one plot per 2400 ha. Each plot contains four 7.31 m (24 ft) radius subplots, configured as a central subplot surrounded by three outer subplots. Plots are visited every five years; we used data from the most recent complete cycle of 2004–2008.

To incorporate spatial and ecological variability of forest community types in the GLO and FIA surveys, we divided the study area into ecological subsections (Cleland and others 1997; Figure 1) that were further divided into land types, such as hills or plains. We set a threshold of at least 200 trees per ecological unit to assign density or designate a community to the ecological unit, which included 39 of 55 total ecological units. Due to low representation of small diameter trees in both surveys, we selected only live trees with a DBH of at least 12.7 cm (that is, 5 inches) from accessible plots (resulting in about 280,000 GLO trees and 50,000 FIA trees).

FIA Density

The FIA surveys recorded all trees at a plot, rather than a selected two to four trees in GLO surveys, and we calculated density at each plot and then predicted density from plots continuously across the landscape to estimate density for each ecological unit. We selected plots that contained at least two trees and additionally were 100% forestland. We calculated trees per acre using the expansion factor of 6.02, based on one tree representing the inverse of the plot area in acres (that is, 1/(4*0.0415)), and summed the values for each plot. To predict spatially continuous density, we used random forests regression trees (Breiman 2001; Cutler and others 2007), 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, with the randomForest package (Liaw and Wiener 2002) in R statistical software (R Development Core team 2010). We selected 24 predictor variables including a combination of subsection and geology variables, SSURGO (Soil Survey Geographic) soil and physiographic variables, DEM (digital elevation model)-derived topographic variables, using SSURGO soil polygons as spatial units. The 15 soil variables included landform type (bottomlands, protected backslope, exposed backslope, uplands), parent material kind (for example, alluvium, colluvium, residuum) and origin (that is, no limestone, limestone in combination, limestone), drainage class (very poorly drained to excessively drained), taxonomic order, flooding frequency, and restriction type (that is, none, fragipan or claypan, bedrock). We also used depth (cm) to either the bottom of the soil profile or soil restriction, after removing soil horizon layers below restrictions based on restrictive layer presence (corestriction table) and restrictive layers with suffixes (that is, d, m, r, x). We then calculated mean water holding capacity (cm/cm), pH, base saturation (ECEC/sum of bases), fragments (%), organic matter (%), clay (%), and sand (%) to the depth and weighted values by component. 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 and others 1966), solar radiation (0700–1900 in 4 h intervals on summer solstice for re-sampled 60-m DEM), topographic roughness (Sappington and others 2007), wetness convergence, and topographic position index (Dilts, http://arcscripts.esri.com). We then calculated the mean value for each topographic variable by zones (mean area of 131 ha) based on soil map unit, ecological land type, geology, and landform type (protected backslope, exposed backslope, and other).

GLO Density

The GLO surveyors recorded two to four selected trees per plot, therefore we could not estimate density at each plot, and we additionally had to account for non-random tree selection. We estimated density for each ecological unit with the Morista estimator (Morisita 1957),

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

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 produced density estimates for points with two trees and points with three trees for all points within similar land types for a subsection. For points with four trees, due to the variability of density estimates for a clustered spatial pattern (Hanberry and others 2011), we removed the most distant point, resulting in points with three trees. To produce a reliable density estimate, we excluded estimates where the minimum number of points was less than 200 for points with two trees and the minimum number of points was less than 50 for points with three trees. We then produced a low and high density estimate based on corrections for spatial pattern (Hanberry and others 2011).

Due to surveyor instructions, surveyors probably did not select the nearest tree, which would have a mean distance rank of 1.0, in each survey point quadrant. To adjust density estimates for surveyor error, we produced a low density estimate, assuming trees selected had a mean distance rank of 1.4, and a mean density estimate, assuming trees selected had a mean distance rank of 1.8, using a rank-based method (Hanberry and others 2012a). For a complementary bias method, we found frequencies by ecological unit for quadrant location, quadrant configuration, and azimuth, and we compared species and five diameter classes of trees at survey points to line trees encountered along section lines. We corrected for non-random frequencies by finding the adjustment quotient based on frequencies in regression equations (Hanberry and others 2012a). We produced a secondary set of mean density estimates and a high density estimate. We then averaged the two mean density estimates and retained the low density estimate (from the rank-based method) and high density estimate (from the bias method). To equilibrate the density estimates from points with two trees (earlier surveys overall with mean date of 1827) and points with three trees (later surveys with mean date of 1841), we multiplied the count of points with three trees by two, giving it twice the weight of points with two trees because density estimates from survey points with three trees are more accurate, and we multiplied each density estimate by a weight of the number of points divided by the total number of points, because density estimates become more accurate with more points.

Diameter, basal area, and percent stocking

The GLO records were not a complete census or a random sample; rather, surveyors selected trees of medium diameter that were sound (Bourdo 1956;White 1983). We realize that the historical distribution of trees may have contained a greater percentage of both smaller and larger trees than recorded in GLO surveys (Bouldin 2010; Rhemtulla and Mladenoff 2010). Despite these data limitations, we used GLO data to compare the historic forest structural characteristics to those trees at least 12.7 cm DBH in contemporary forests. To do this we calculated the mean diameter for each ecological unit and estimated the basal area of each ecological unit to better account for growing space occupancy. For the 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 the percent stocking (sensu Gingrich 1967), a measure of relative growing space occupancy that accounts for the number of trees per ha, tree size (diameter), and total basal area. A stocking percent of 100 represents the average maximum growing space that a stand of trees can occupy. However, because the witness tree data included only trees at least 12.7 cm DBH, stocking estimates were not expected to approach 100 percent. 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. Because stocking coefficients differ by species group, we used coefficients of Gingrich (1967) for estimating hardwood stocking and coefficients of Rogers (1983) for estimating shortleaf pine stocking.

Community types

We assigned species that comprised at least 10 percent composition per ecological unit as dominant species in the community. A threshold of 10% limited communities to no more than five species/species groups and yet allowed for adequate species representation. The order of species within communities was based on descending mean percent composition for all GLO trees. That is, white oak (*Quercus alba*) had the overall greatest percent composition and was the first species listed for any ecological unit with white oak composition at least 10%. Because of uncertainty in species identification of historical surveys, we grouped some tree species into the following categories (Table 1 footnote): black oaks (primarily *Quercus velutina*, but also *Q. rubra*, *Q. falcata*, *Q. coccinea*); ashes (*Fraxinus americana*, *F. pennsylvanica*); cherries (*Prunus* spp.); elms (*Ulmus alata*, *U. americana*, *U. rubra*); hickories (*Carya cordiformis*, *C. glabra*, *C. laciniosa*, *C. ovata*, *C. texana*, *C. tomentosa*); maples (primarily *Acer saccharum*, *A. negundo* also *A. rubrum*, *A. saccharinum*); walnuts (*Juglans nigra*, *J. cinerea*). We also calculated oak and pine composition for GLO and FIA surveys and for trees less than 12.7 cm in FIA surveys.

RESULTS

Structure

There were 39 ecological units of subsection and landform that had at least 200 trees in FIA surveys (see supplementary material: Appendix S1 for density and composition of GLO trees for ecological units where there were too few FIA trees). On average for the 39 ecological units, estimated GLO densities were 165 trees/ha ($DBH \geq 12.7$ cm), ranging by ecological unit from 75 to 320 trees/ha (Table 1; Figure 2). In contrast, FIA densities were about 2.3 times greater, averaging 348 trees/ha and ranging by ecological unit from 295 to 395 trees/ha. Thirty-three of the ecological units had high historical density estimates that were less than low current density estimates. Four of the ecological units had some overlap, where the high estimate of historical density was greater than the low estimate of current density, and two of the ecological units had density estimates that roughly were similar. These six ecological units had historical density estimates that were greater than 200 trees/ha.

Trees were about 1.5 times larger in historical (mean of 35 cm DBH) than in contemporary forests (mean of 23 cm DBH), although it was not possible to adjust diameter for potential surveyor bias. Greater densities in contemporary forests compensated for larger diameters in historical forests, so that mean basal area (19 m^2/ha for historical forests and 17 m^2/ha for contemporary forests) and percent stocking (56% for historical forests and 59% for contemporary forests) were estimated to be similar between historical and contemporary forests. Only seven of the ecological units had high historical basal area estimates that were less than the low current basal area estimates, that is, there was no overlap in uncertainty values, although eleven ecological units had current basal area values greater than 1.15 of historical values. Ten of the ecological units had high historical percent stocking

Table 1. Communities, Densities (trees/ha), and Diameters (DBH; cm) of Historical (GLO) and Current (FIA) Forests (trees ≥ 12.7 DBH) by Ecological Unit of Subsection and Land Type

			GLO			FIA			GLO	FIA
Ecological unit	GLO community	FIA community	Density	Low	High	Density	Low	High	DBH	DBH
1 Oak Savanna/Woodland Plains	WO-BO-PO-BjO-Hi	BO-PO-Hi	86	54	98	319	273	365	35	24
1 Prairie/Savanna Plains	BO-PO-BjO	BO-PO-Hi	76	50	86	313	266	360	36	24
3 Oak Woodland Plains and Hills	WO-BO-PO-BjO	WO-BO-PO	111	72	123	332	299	365	36	25
3 Oak Woodland/Forest Hills	WO-BO-PO	WO-BO	206	116	258	326	284	368	32	24
4 Dolomite Glade/Woodlands	WO-BO-PO	WO-BO-Ce	186	114	217	397	340	453	31	22
4 Oak Woodland Plains and Hills	WO-BO-PO	BO-PO-Ce	133	89	143	359	304	414	30	22
4 Oak-Pine Hills	WO-BO-PO-Pi	WO-BO-Hi	162	93	200	349	311	388	35	23
4 Pine-Oak Woodland Plains	BO-PO-Pi-BjO	WO-BO-PO-Pi	175	99	218	389	336	442	34	24
5 Oak Savanna/Woodland Plains	WO-BO-PO-BjO	WO-BO-PO	96	58	113	366	306	426	32	22
5 Oak Woodland Plains and Hills	WO-BO-PO-BjO	WO-BO-PO-Hi	116	69	137	346	294	399	32	22
5 Prairie/Savanna Plains	BO-PO-BjO	PO-Ce	87	57	96	362	304	420	32	24
6 Dolomite Glade/Woodlands	WO-BO-PO	BO-PO-Ce	96	54	121	361	317	405	34	20
6 Oak Woodland Plains and Hills	WO-BO-PO	WO-BO-PO	129	83	142	333	283	384	35	23
6 Oak Woodland/Forest Hills	WO-BO-PO	WO-Ce	229	125	290	333	286	380	35	23
6 Rugged Hills and Forest Breaks	WO-BO-PO	WO-BO-PO	174	98	218	293	242	344	34	24
7 Oak Woodland Plains and Hills	WO-BO-PO	WO-BO-PO	124	72	150	360	302	417	33	23
7 Oak Woodland/Forest Hills	WO-BO-PO	WO-BO-PO-Ce	155	78	207	374	322	426	33	23
7 Oak-Pine Hills	WO-BO-PO-Pi	WO-BO-Pi	162	86	210	378	314	442	33	23
7 Pine-Oak Woodland Plains	WO-BO-PO-Pi	WO-PO-Pi	155	83	197	391	345	437	34	23
7 Rugged Hills and Forest Breaks	WO-BO-PO	WO-BO-Hi	132	75	162	346	293	398	34	22
8 Oak Woodland Plains and Hills	WO-BO-PO	WO-BO-PO	189	110	228	340	291	388	30	24
8 Oak Woodland/Forest Hills	WO-BO-PO	WO-BO-PO	141	84	165	337	292	381	34	25
8 Oak-Pine Hills	WO-BO-Pi	WO-BO-Pi-Hi	320	179	395	342	278	407	34	25
8 Pine-Oak Woodland Plains	WO-BO-Pi	WO-BO-PO-Pi	160	91	196	366	296	435	35	24
9 Oak-Pine Hills	WO-BO-Pi	WO-BO-Pi-Hi	185	96	243	341	295	387	37	23
9 Pine-Oak Woodland Plains	WO-BO-PO-Pi	WO-BO-Pi	156	79	209	361	317	406	39	24
9 Rugged Hills and Forest Breaks	WO-BO-Pi	WO-BO-Pi-Hi	275	129	384	315	272	358	35	24
10 Dolomite Glade/Woodlands	WO-BO-Hi	BO-Hi-Ce	159	85	203	345	292	397	39	22
10 Igneous Knobs	WO-BO	WO-BO-Hi	227	111	309	348	281	414	36	23
10 Oak-Pine Hills	WO-BO-Pi	WO-BO-Hi	247	112	351	315	272	357	38	24
12 Dolomite Glade/Woodlands	WO-BO	PO-Hi-Ce	88	49	108	332	282	382	39	22
12 Oak Savanna/Woodland Plains	WO-BO-Hi	WO-Hi	176	92	230	331	292	369	37	24
12 Oak Woodland/Forest Hills	WO-BO-Hi	WO-Hi-Ce	213	112	274	338	294	381	37	24
12 Rugged Hills and Forest Breaks	WO-BO	WO-BO-Hi-Ma	179	100	222	323	292	353	37	27
13 Dolomite Glade/Woodlands	WO-BO-PO	PO-Ce	146	76	190	395	335	455	34	23
13 Oak Woodland/Forest Hills	WO-BO	WO-BO-PO-Hi-Ce	169	92	215	364	312	417	37	25
13 Oak-Pine Hills	WO-BO	WO-BO-PO-Hi	139	67	191	341	302	380	37	25

estimates that were less than the low current percent stocking estimates, although 22 of the ecological units had current percent stocking values greater than 1.15 of historical values. However, spatial distributions differed, so that increased basal area and stocking in the west and south, where fires historically were more frequent (Hart and Buchanan 2012), offset decreased basal area and stocking in the east and north, where waterways and stream networks protected forests from fire (Figure 3). Furthermore, historical forests had greater variability of basal area (8–37 m^2/ha) and percent stocking (26–105%) values compared to basal area (14–21 m^2/ha) and percent stocking (49–68%) values in contemporary forests.

Communities

White oak, black oak (including three other red oak species), post oak (*Quercus stellata*), blackjack oak (*Quercus marilandica*), shortleaf pine (*Pinus echinata*), and hickories were the dominant (≥ 10% composition) species of historical and contemporary forests. Eastern redcedar (*Juniperus virginiana*) and maples were new dominant species in contemporary forests (Figure 4 shows increased percent composition of eastern redcedar; maples increased along the major Missouri and Mississippi rivers, similarly to where eastern redcedar increased by greater than 15% percent composition in the northern Ozarks). Dominant species (≥ 10% composition) represented about 82% of all individuals in GLO communities but dominant species represented only 63% of all tree species in FIA communities. In the GLO surveys (DBH ≥ 12.7 cm), about 86% of trees were oaks or pine, in FIA surveys (DBH ≥ 12.7 cm), about 57% of trees were oaks or pine, and in FIA surveys for trees less than 12.7 cm, 24% of trees were oaks or pine (Figure 5 shows decreased percent composition of oak and pine).

Of the 39 ecological units, five had the same composition (species ≥ 10% composition) of white oak-post oak-black oak communities as in the past (Tables 1, 2; Figure 6). Historically, all of the ecological units had dominant black oaks and only three ecological units did not contain white oak. Seven of the ecological units lost black oak as a dominant species group and six of the ecological units lost white oak as a dominant species. Thirteen of the ecological units had losses of blackjack oak (7 of 13) or post oak (6 of 13). Eleven of the ecological units had additions of eastern redcedar and one ecological unit gained maple as new dominant species; these two species were not dominant species in the past. Fifteen of the ecological units

Table 1. continued

Ecological unit	GLO community	FIA community	GLO			FIA			GLO	FIA
			Density	Low	High	Density	Low	High	DBH	DBH
14 Oak-Pine Hills	WO-BO-Pi	WO-BO-PO-Pi-Hi	184	96	240	347	311	384	38	23
14 Pine-Oak Woodland Plains	WO-BO-Pi	WO-BO-PO-Pi	302	155	399	366	318	414	35	22

WO = white oak (Quercus alba); BO = black oak (primarily Q. velutina, also Q. rubra, Q. falcata, Q. coccinea); PO = post oak (Q. stellata); BjO = blackjack oak (Q. marilandica); HI = hickories (Carya cordiformis, C. glabra, C. laciniosa, C. ovata, C. texana, C. tomentosa); Pi = shortleaf pine (Pinus echinata); CE = eastern redcedar (Juniperus virginiana); Ma = maples (Acer saccharum, A. negundo, A. rubrum, A. saccharinum).

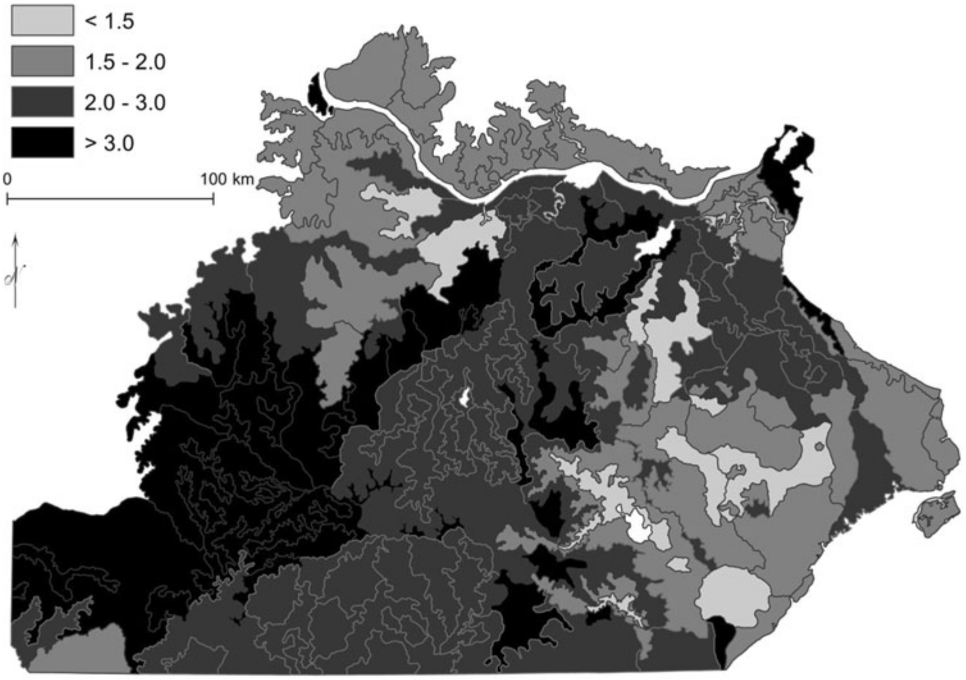

Figure 2. Increased tree density in contemporary forests compared to historical forests (current density/historical density; tree DBH ≥ 12.7 cm).

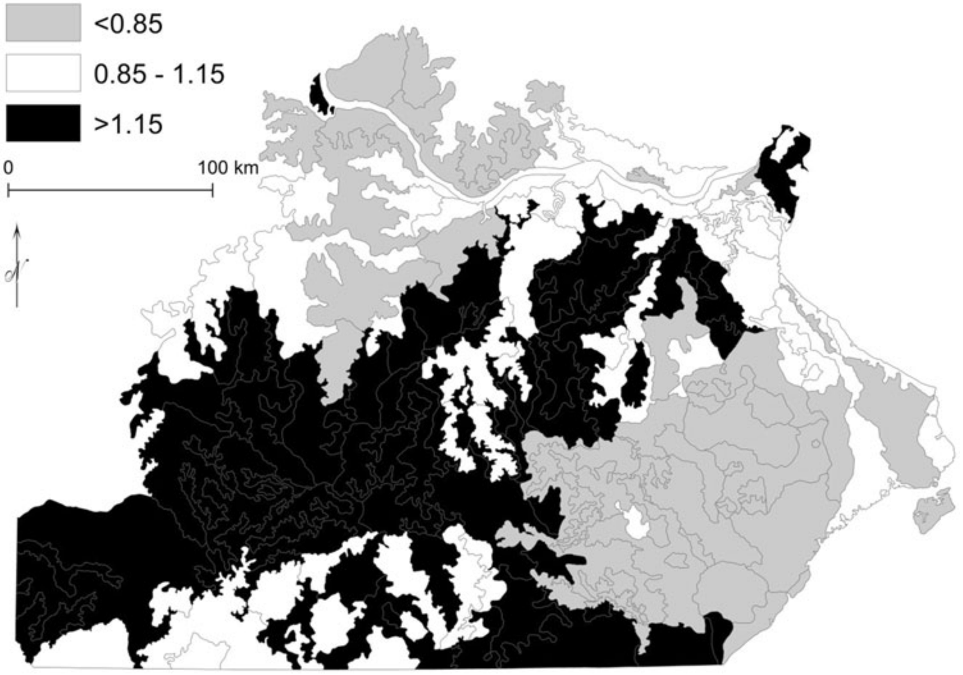

Figure 3. Increased basal area (> 1.15) in contemporary forests of the western and southern Ozarks and decreased basal area (< 0.85) in contemporary forests in the eastern and northern Ozarks compared to historical forests (current density/historical density; tree DBH ≥ 12.7 cm).

gained hickories as a dominant species. Hickories were common historically, but not often dominant.

DISCUSSION

Densification

Forests have densified extensively across the Missouri Ozarks, which paralleled decreased oak dominance and increased prevalence of fire-sensitive species. A variety of open oak ecosystems have densified to eastern broadleaf forests across the landscape. In our study region, forests presently contain about 300–400 trees/ha (DBH ≥ 12.7 cm), with little variation among ecological units. We estimated that historical forests had about 165 trees/ha with much greater variability (ranged from 75 to 320 trees/ha by ecological unit) among ecological units than contemporary forests, due to the

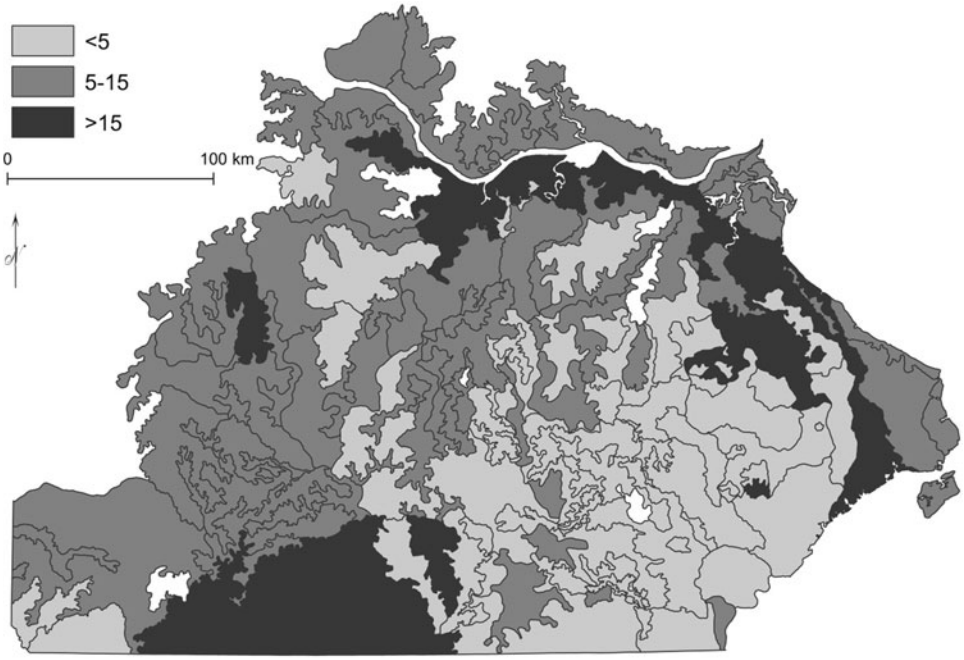

Figure 4. Increased percent composition of eastern redcedar in contemporary forests compared to historical forests (percent eastern redcedar in contemporary forests—percent eastern redcedar in historical forests; tree DBH ≥ 12.7 cm).

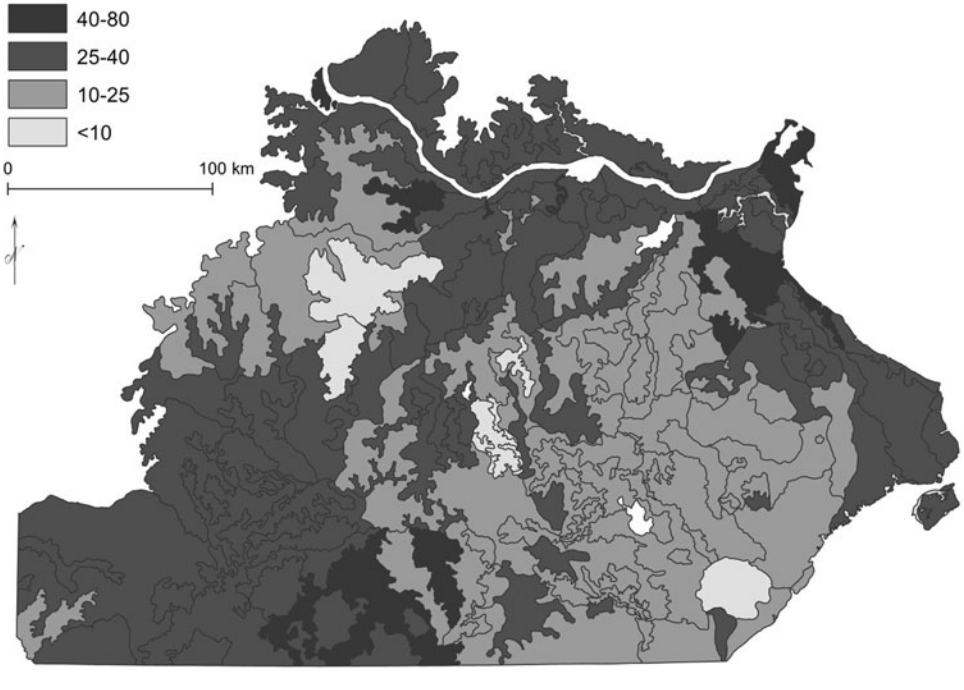

Figure 5. Decreased percent composition of oaks and pine in contemporary forests compared to historical forests (percent oak and pine in contemporary forests—percent oak and pine in historical forests; tree DBH ≥ 12.7 cm).

influence of ecological gradients, such as topography and moisture, on fire return intervals. Density increases were greatest in the drier western Ozarks nearest the prairies where historical densities were least and fires occurred more frequently (Figure 2; Hart and Buchanan 2012). Density increases were least in the northern and eastern Ozarks, within ecological units that are highly dissected and protected by stream networks where historically fires occurred less frequently (Guyette and others 2002).

Densification has not occurred to the same degree for the 39 ecological units of subsection and land types. Although almost all forests have densified in number of tree stems, failing to consider other metrics of forest density may lead to a conclusion that forests in this region have densified to a greater extent than may have occurred. Trees of historical forests had much larger diameters than those in contemporary forests; larger diameter trees require more growing space and contribute more to

Table 2. Basal Area (m^2/ha) and Percent Stocking of Historical (GLO) and Current (FIA) Forests (trees ≥ 12.7 DBH) by Ecological Unit of Subsection and Land Type

	GLO						FIA					
Ecological unit	Basal area	Low	High	Stocking	Low	High	Basal area	Low	High	Stocking	Low	High
1 Oak Savanna/Woodland Plains	10	6	11	29	18	33	17	15	20	56	48	64
1 Prairie/Savanna Plains	9	6	10	27	18	31	17	14	19	56	48	64
3 Oak Woodland Plains and Hills	13	8	14	38	25	43	18	17	20	62	56	68
3 Oak Woodland/Forest Hills	19	11	24	60	34	76	18	15	20	59	51	66
4 Dolomite Glade/Woodlands	17	10	20	52	32	60	17	15	20	60	52	69
4 Oak Woodland Plains and Hills	11	7	12	35	23	37	16	13	18	54	46	62
4 Oak-Pine Hills	18	10	22	52	30	64	16	14	18	55	49	61
4 Pine-Oak Woodland Plains	18	10	22	52	29	65	19	17	22	61	52	69
5 Oak Savanna/Woodland Plains	9	5	10	27	16	32	15	13	18	55	46	64
5 Oak Woodland Plains and Hills	11	6	13	33	20	39	15	13	17	53	45	61
5 Prairie/Savanna Plains	8	5	9	26	17	28	18	15	21	62	52	72
6 Dolomite Glade/Woodlands	10	6	13	31	17	39	14	12	15	49	43	55
6 Oak Woodland Plains and Hills	15	10	16	44	28	49	16	14	19	56	47	64
6 Oak Woodland/Forest Hills	28	15	35	78	42	99	17	15	19	57	49	65
6 Rugged Hills and Forest Breaks	19	10	23	57	32	71	16	13	19	53	44	62
7 Oak Woodland Plains and Hills	12	7	15	37	22	45	17	15	20	59	49	68
7 Oak Woodland/Forest Hills	16	8	22	48	24	64	17	15	20	60	51	68
7 Oak-Pine Hills	17	9	22	48	25	62	18	15	21	57	47	67
7 Pine-Oak Woodland Plains	16	9	21	46	25	59	19	16	21	57	50	64
7 Rugged Hills and Forest Breaks	15	8	18	43	25	53	15	13	18	53	45	61
8 Oak Woodland Plains and Hills	15	9	19	48	28	58	18	15	20	59	51	68
8 Oak Woodland/Forest Hills	15	9	18	45	27	52	19	17	22	63	55	71
8 Oak-Pine Hills	37	21	46	99	56	123	18	15	22	60	49	72
8 Pine-Oak Woodland Plains	18	10	23	49	28	60	19	15	22	60	48	71
9 Oak-Pine Hills	24	12	31	59	31	77	17	14	19	55	48	62
9 Pine-Oak Woodland Plains	23	12	31	54	27	72	19	16	21	60	53	67
9 Rugged Hills and Forest Breaks	32	15	45	86	40	120	17	15	19	56	48	63
10 Dolomite Glade/Woodlands	24	13	31	66	35	84	16	13	18	54	46	62
10 Igneous Knobs	30	14	40	80	39	109	16	13	19	55	44	65
10 Oak-Pine Hills	34	15	48	90	41	128	16	14	18	54	46	61
12 Dolomite Glade/Woodlands	13	7	16	36	20	44	14	12	16	49	42	57
12 Oak Savanna/Woodland Plains	24	13	32	67	35	87	18	16	20	58	52	65
12 Oak Woodland/Forest Hills	29	15	37	80	42	103	18	16	20	59	51	67
12 Rugged Hills and Forest Breaks	23	13	29	66	37	81	21	19	23	68	62	75
13 Dolomite Glade/Woodlands	16	8	21	47	24	62	18	16	21	64	54	74
13 Oak Woodland/Forest Hills	23	12	29	62	34	79	20	18	23	68	58	77
13 Oak-Pine Hills	19	9	26	50	24	69	19	17	21	61	54	68

Table 2. continued

Ecological unit	GLO Basal area	Low	High	Stocking	Low	High	FIA Basal area	Low	High	Stocking	Low	High
14 Oak-Pine Hills	26	14	34	70	36	90	17	15	19	57	51	62
14 Pine-Oak Woodland Plains	35	18	47	90	46	118	16	14	18	54	46	61

basal area and percent stocking than smaller trees. Our analysis indicated that basal area of trees at least 12.7 cm DBH was similar or lower for most contemporary forests compared to historical forests (Figure 3). Percent stocking showed some amount of densification for 22 ecological units, but with no overlap in uncertainty values for only ten ecological units. Corresponding to the spatial variation in stem density increases, basal area and percent stocking increased in southwestern Ozarks, where there was more growing space to fill without frequent biomass removal by fire. Basal area and percent stocking decreased in the north and eastern Ozarks, but there was little net change. The subsections where historic forest basal area or percent stocking were historically high and currently reduced were productive areas protected from fire by stream networks and the locations of extensive harvesting in the Missouri Ozarks beginning in the late 1880s (Cunningham 2007).

Collectively our analyses of forest structure provide insight into changes that have occurred since the onset of European settlement and may serve as the basis for guiding compositional and structural targets for forest restoration in this region. Our results suggest that historical forests may have been denser than previously described (for example, Anderson and Anderson 1975 described pre-settlement open forest ecosystems as less than 16 trees/ha) and composed of open and closed woodlands rather than savannas and open woodlands, at least during the land survey period, 1815–1850. A major release event occurred for oaks during the decrease in Native American populations and initial settlement of the early 1800s in the western portion of eastern oak forests (Beilmann and Brenner 1951; Aldrich and others 2005; Fralish and McArdle 2009). In some areas, dense oak thickets and woods developed within 20–40 years after settlement (Cottam 1949; Crow 1988; Wolf 2004). However, it is equally important to recognize uncertainty, such as surveyor bias in the historical tree surveys and natural range of variability in estimates within and among subsections. Consequently, we generated a range of density values to account for surveyor bias and any spatial and temporal variation associated with moisture gradients, rock outcrops, streams and other water bodies, topography, sinkholes and other karst features, and other natural firebreaks, as well as variation in fire return intervals.

Community Change

Forests did not simply change structure by increasing in stem density to the extent that

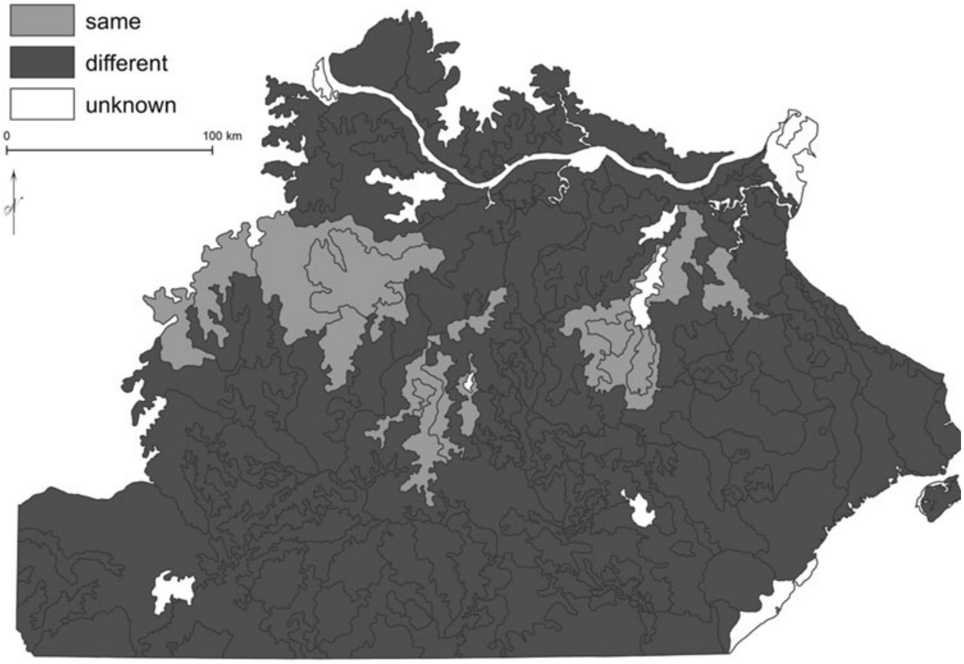

Figure 6. Current communities compared to historical communities (for species ≥ 10% of composition; tree DBH ≥ 12.7 cm).

historical woodlands are no longer present at the landscape scale (Figure 2). Instead, there has been a decrease in oak dominance, which has shifted most communities to eastern broadleaf forest from oak-dominated woodlands (Figures 5 and 6). In Missouri's eastern broadleaf forest, similarly to open oak woodlands, oaks are the most common species and present at greater densities than historically. Nonetheless, oak dominance has been reduced by increases in many fire-sensitive species that historically were dominant in wet or rocky firebreaks or minor components of oak woodlands on upland sites. Given lack of fire and sufficient moisture during wetter years for seedlings to establish, climate and topography are not barriers to most tree species (Axelrod 1985).

The two species that increased enough to become new dominant species (≥ 10% composition), eastern redcedar and maples, also are increasing in dominance to the west (Briggs and others 2002) and east (Nowacki and Abrams 2008; Fralish and McArdle 2009) of the Missouri Ozarks. Maple increases in abundance and distribution are common in eastern forests, although so far are limited in the Missouri Ozarks to ecological subsections along riverways. In contrast, eastern redcedar is colonizing from rocky firebreaks into a variety of ecological subsections and biomes that have open growing space for trees (Figure 4). Eastern redcedar rapidly is increasing in Missouri and perhaps in other eastern broadleaf forests, and westward in tallgrass prairie and eastern Great Plains, where it is planted for landscaping and windbreaks (Briggs and others 2002). Western junipers (*Juniperus osteosperma*, *J. occidentalis*) are expanding eastward in the Great Plains (Van Auken 2009), and in the future, there will be novel communities dominated by both eastern and western juniper species.

State Transitions

We identified a transition in state from oak woodlands to eastern broadleaf forests based on changes in (1) structure through stem densification, (2) composition through a decrease in historically dominant species and increased representation of historically minor species, and (3) functional traits from fire-tolerant oaks and pine to fire-sensitive species such as eastern redcedar and red maple. Changes in composition currently are associated with densification, primarily in stem density, in the Missouri Ozarks and elsewhere in the eastern United States (for example, Hanberry and others 2012b). We differentiate transition in state, which can be indefinitely stable, such as woodlands in the eastern United States and tropical savannas, from succession in state, which occur over time after stand-replacing disturbance.

During the last 100–200 years, some biomes have been transitioning to denser, wooded states that are not easily reversible, due to reinforcement by positive feedbacks (Warman and Moles 2009). In some regions, grasslands are becoming shrublands, savannas, or even tropical forests, whereas savannas and woodlands are thickening to closed forests, with changes in species composition to species that are generally fire-sensitive (Bond and others 2005; Nowacki and Abrams 2008; Warman and Moles 2009). These transition shifts often coincide with (1) fire regime change from use by pre-industrial farmers to effective fire suppression, (2) climate change from the end of the Little Ice Age to the warmest temperatures in a millennium (Mann and others 1999), (3) forestry practice changes (for example, from exploitation to sustainable harvest or from woodland pastures to natural preserves; Götmark 2007), (4) grazing or browsing intensification by heavy cattle stocking and/or increases in native ungulates (Van Auken 2009; Plieninger and others 2011), and (5) carbon dioxide enrichment (Bond and Midgley 2012; Higgins and Scheiter 2012). The temporal and spatial scales of compositional conversion that has been occurring during the past hundred years over large portions of the United States and globally make experimental tests to identify driving factors of state shifts difficult, particularly where alternative forest states are established, such as the eastern United States. Vegetation with shared functional traits different than the previous state has stabilized and will not revert readily to the historical stable state even with restoration of the original characteristics of the driving ecological processes.

Woodlands and forests appear to represent bimodal states in the eastern United States, probably driven by fire (similarly to savannas and forests; Staver and others 2011). Initially in the Missouri Ozarks, after fire suppression, densification resulted from infilling by released oak advance regeneration as open oak woodlands changed to closed oak forests (Beilmann and Brenner 1951; Aldrich and others 2005; Fralish and McArdle 2009). However, dense oak forests are unstable states lasting perhaps one generation, albeit a lengthy generation because oaks are long-lived (Cottam 1949; Crow 1988; Wolf 2004). Fire-tolerant tree species that conserve resources in root systems do not persist in the absence of fire because fire-sensitive species without this trait are more competitive. The state transition from oaks to fire-sensitive species still is progressing. Tree composition in the forest understory (FIA trees < 12.7 cm DBH) in this study and other oak ecosystems (Nowacki and Abrams 2008; Fralish and McArdle 2009), demonstrates the continued trajectory toward a forest increasingly dominated by fire-sensitive species.

Associated with changes in structure, composition, and competitive traits, a state transition includes a cascade reinforced by expanding species that share functional traits different than the original inhabitants (Nowacki and Abrams 2008; Higgins and Scheiter 2012). Vegetation interacts with abiotic conditions to dampen or amplify extremes and maintain the vegetation state. Conversion to a state dominated by fire-sensitive species includes an escalating feedback by which fire-sensitive species engineer more favorable conditions of humidity, shade, and fire proofing (Choler and others 2001; Warman and Moles 2009; Odion and others 2010). Transition shifts by definition are not easily reversible and removal of fire-sensitive species in upland forests that contained oak woodlands and removal of juniper from grasslands is beyond the scale of typical management plans. In eastern forests, use of prescribed fire is an expensive tool that affects a fraction of the landscape and can be ineffective given the moderated climate and discontinuous fine fuels in forests and advance regeneration of fire-sensitive species in the understory (for example, Waldrop and others 2008).

CONCLUSIONS

Densification and associated state transition in the Missouri Ozarks express a pattern of encroachment by denser vegetation states at ecotones. Researchers and managers who detect densification should explore whether there are associated changes in composition and functional traits that will cause transition to an alternative stable state. In the western United States, shrubs, pinyon pine (*Pinus edulis*, *P. monophylla*) and juniper (*Juniperus osteosperma*, *J. occidentalis*) woodlands, ponderosa pine (*P. ponderosa*) parklands, true fir (*Abies* sp.) and Douglas fir (*Pseudotsuga menziesii*) forests are densifying and expanding into the less dense adjacent biome, whereas in the eastern United States, fire-sensitive tree species are densifying and expanding to pine and oak savannas and woodlands (Niklasson and others 2002; Cocke and others 2005; Sakulich and Taylor 2007; Huffman and others 2008; Nowacki and Abrams 2008; Bekker and Taylor 2010). Although expansion of maple species in eastern forests of the United States is common, expansion of eastern redcedar is occurring in forests and grasslands but with less extensive documentation. Eastern redcedar, an eastern juniper, is the current winning competitor in this region, expanding westward into open grasslands and toward western juniper species and eastward, potentially filling clearings in eastern forests.

Regional densification is not at a scale for land management to reverse. However, increased warming and evapotranspiration and variable availability of water may drive some portions of biomes back to less dense states (Ibáñez and others 2007; Frelich and Reich 2010; Ma and others 2012; Wu and others 2012). Drought due to climate warming likely will favor establishment of tree species with underground reserves, similarly to fire (Nowacki and Abrams 2008). A drought regime may partially substitute for a fire regime by sustaining oak dominance in xeric conditions and by determining proportion of oak and drought-sensitive species along steep environmental gradients (Ibáñez and others 2007; Nowacki and Abrams 2008; Klos and others 2009). Nevertheless, where mesic forests have stabilized conditions by increasing moisture and reducing heat and wind, facilitation may allow established drought-sensitive species to exceed typical environmental limits (Warman and Moles 2009).

ACKNOWLEDGMENTS

Funding for this study came from the USDA Forest Service, Northern Research Station and the National Fire Plan. We thank anonymous reviewers, T. Hutchinson, and M. Thomas-Van Gundy for comments and B. Palik for supporting this research.

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