RESEARCH ARTICLE

Historical Open Forest Ecosystems in the Missouri Ozarks: Reconstruction and Restoration Targets

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ABSTRACT

Current forests no longer resemble historical open forest ecosystems in the eastern United States. In the absence of representative forest ecosystems under a continuous surface fire regime at a large scale, reconstruction of historical landscapes can provide a reference for restoration efforts. For initial expert-assigned vegetation phases ranging from prairie to forest across the Missouri Ozarks landscape, we reconstructed historical (1815 to 1850) forest densities, basal area, percent stocking or growing space, and canopy cover. After examination of structural means and ranges by initial expected vegetation phases, we classified vegetation phases based on percent stocking boundaries of 30–55% for open woodlands and 55–75% for closed woodlands (diameters ≥ 12.7 cm). We suggest that a percent stocking boundary of 10% may separate prairie and savannas, but we did not identify any large scale prairies in Missouri. We provided structure of each vegetation phase for restoration targets; mean historical densities of vegetation phases ranged from 81 trees/ha in savannas to 285 trees/ha in non-oak/non-pine forests (diameters ≥ 12.7 cm). Due to greater densities than expected and larger diameter trees than current forests, historical forests may have been primarily (about 65%) woodlands with nearly closed canopies, unlike the open canopies presumed during settlement in the Missouri Ozarks. However, a closed yet single canopy layer can transmit enough light to sustain an herbaceous ground cover, given an open midstory due to frequent surface fires. Restoration of open woodlands across all public lands is not practical, but restoration of lower density forests composed of drought-tolerant tree species should translate to management for changing climate.

Keywords: fire suppression, phase, presettlement, range of variability, vegetation state

Open forest ecosystems are mixed tree-herb systems characterized by a continuous herbaceous layer and discontinuous tree canopy (Ratnam et al. 2011). Within open forests ecosystems, tree density varies in space and time, producing a continuum of vegetation phases from open grasslands to closed woodlands (Parr et al. 2012). Although tropical savannas are defined by their abundant C_4 (i.e., warm-season) grasses (Lehmann et al. 2011), open forest ecosystems in temperate zones may not follow this pattern. Temperate open forest ecosystems, which stretch along the length of the United States in a wide transition zone between tallgrass prairie and eastern forests, are recognized for their forb diversity, and C_3 grasses and sedges may be as common as C_4 grasses, at least in northern regions with cooler growing seasons or with overstory shading (Leach and Givnish 1999, Peterson et al. 2007).

Composition in open forest ecosystems varies, but functional traits of plant species adapted to open conditions are similar (Ratnam et al. 2011) because open forest ecosystems share a low severity surface fire regime or other similar disturbance regime that maintains large diameter trees and removes small diameter trees, enforcing the boundary between open and closed forest ecosystems. Variation in fire return intervals produces a gradient of open ecosystem phases (Stringham et al. 2003) ranging from prairies to closed woodlands that are stabilized by fire and additionally promote fire due to the same open conditions that distinguish the biome: fine, continuous fuels from the herbaceous layer and exposure to wind and sun. The transition between the open forest ecosystem state and closed forest ecosystem state is a threshold between two positive feedbacks that are largely governed by vegetation that either reinforces or resists fire (Warman and Moles 2009, Hanberry et al. 2014). Climate often plays a lesser role compared to fire because climate suitable for savannas also is suitable for dense, closed forests (Bond et al. 2005), which may occur in close proximity, separated by the presence of firebreaks such as rivers and streams, large water bodies, and rock outcrops.

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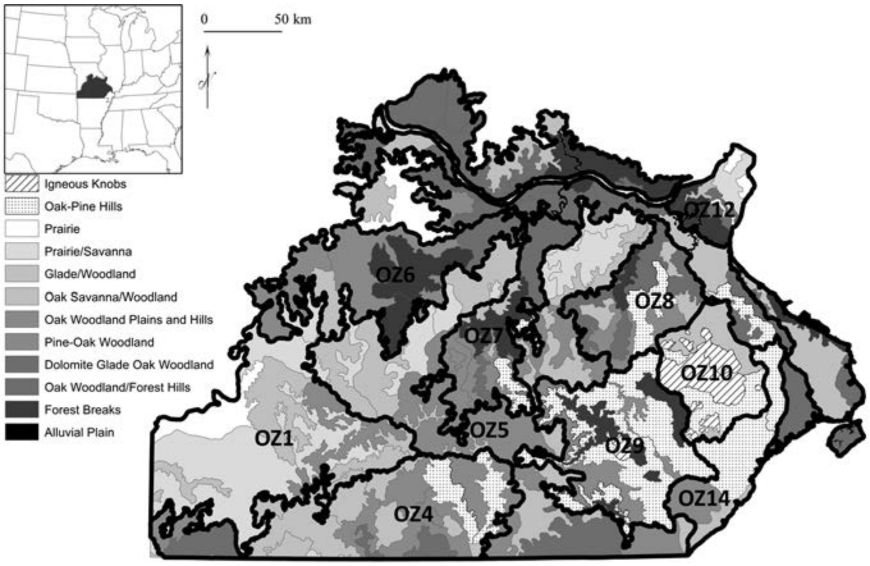

Figure 1. Ecological subsections (outlined and labeled by 'OZ' for Ozarks and unique number) and land types (shaded) of the Missouri Ozarks section, a 9.4 million ha extent. The igneous knobs land type is shaded by hatched lines and the oak-pine hills land type is shaded by stipples.

Effective fire suppression began in the 1920s in the eastern United States, and fire suppression along with conversion to agriculture has been as devastating to oak savannas and woodlands as harvest has been to closed mature forests. Perhaps < 1% of oak savannas remain intact (Nuzzo 1986). Without a continuous fire regime across the landscape, savannas and woodlands "densify" to closed forests; closed forests of fire-tolerant species represent an unstable state transition that is invaded by competitive fire-sensitive species (Hanberry et al. 2014). Furthermore, increased humidity fostered by closed forests facilitates presence of less drought-resistant species in areas that might otherwise be too xeric for establishment of mesic species (i.e., 'edaphic compensation' [Warman and Moles 2009]; although increased densification and evapotranspiration at some level will increase moisture stress). Fires in humid regions extinguish at closed forests, which contain dense, discontinuous fuels of moist shrubs and trees and closed conditions that retain humidity and disrupt wind.

Because there are no landscapes of oak savannas and woodlands under a continuous surface fire regime available to measure, expert models of historical ecosystems generally consist of subjective and unique descriptions of structure and composition. Therefore, even categories that are quantitative vary depending on the expert system. For example, canopy cover, which is difficult to measure accurately, appears to be the most common quantitative metric; oak savannas have been described as having a range of canopy covers from 10 to 80% (Nuzzo 1986, Peterson and Reich 2001, Nelson 2005). However, historical surveys can provide a more ecologically meaningful range of structural targets for restoration. Historical General Land Office (GLO) surveys supply one of the few available baselines prior to fire exclusion during the leading edge of Euro-American settlement and westward expansion. The surveys offer comprehensive, detailed records of American landscapes during the nineteenth century. Although these forests may not be as open across the landscape as the forests that occurred before European contact reduced Native American populations, historical forests nevertheless contained a range of open forest ecosystems (Hanberry et al. 2014). We used GLO surveys conducted from 1815 to 1850 in the 9.4 million ha landscape of the Missouri Ozarks (Figure 1) to reconstruct historical forest densities, basal area, percent stocking, and canopy cover, with a range of low and high values to account for uncertainty in phases ranging in tree density from prairie to floodplain forest. We (the Central Hardwoods Joint Venture; CHJV 2003) elicited expert opinion to assign initial expected vegetation phases by ecological spatial units of ecological subsection, land type, and landform. We used initial restoration targets, or the mean and range of structural values for each initial expected vegetation phase, to develop structural boundaries for vegetation phases. After reassigning any misassigned initial expected vegetation phases based on structural boundaries, we repeated the process to produce restoration targets of quantified structure and composition for each vegetation phase.

Methods

Historical Surveys

The United States General Land Office was responsible for surveying, platting, and selling public domain lands for settlement of Western Territories. The Public Land Survey (PLS) System divided most of the western territories into 1.6 km^2 (1 $mile^2$) square sections, grouped into 36 mile square townships (White 1983). This system allowed settlers to disperse across the country in a reasonably equitable and organized manner.

At survey points along the corners and middle of each section line (every 0.8 km), surveyors recorded species, distance, bearing, and diameter for two to four trees, roughly equivalent to point centered quadrat sampling. There were about 285,000 trees, surveyed between 1815–1850, in Missouri's Ozark Highlands section from the Missouri GLO dataset (J. Harlan, Geographic Resources Center, www.msdis.missouri.edu). Survey instructions mandated selection of medium diameter trees that were sound and of great potential longevity (Bourdo 1956, White 1983); therefore, historical distribution of trees probably contained a greater percentage of both smaller and larger trees (Bouldin 2010, Rhemtulla and Mladenoff 2010). To establish a clear diameter threshold, we selected trees with a DBH ≥ 12.7 cm because recorded trees rarely were smaller than this diameter. We determined percent composition of oak species (*Quercus* spp.), shortleaf pine (*Pinus echinata*), and other species. Other species included primarily hickories (*Carya* spp.), elms (*Ulmus* spp.), walnuts (*Juglans* spp.), hackberry (*Celtis occidentalis*), maples (*Acer* spp.), and ashes (*Fraxinus* spp.).

Ecological Units for Vegetation Phases

We reconstructed structure by ecological subsection (Cleland et al. 1997; Figure 1) divided into land types, such as hills or plains, and further divided into landform, such as floodplains and flat uplands. Subsection and land type were based on climate, geology, topography, soils, hydrology, and vegetation (Cleland et al. 1997). Subsections represented distinctive spatial units across a landscape varying in size from thousands to millions of hectares, whereas land types can be repeated among subsections and vary in size from hundreds to tens of thousands of hectares. Landform was similar to land type, but represents finer scale variation, varying in size from a hectare to hundreds of hectares. Landform designation was based on classification rules for a digital elevation model (DEM) that elucidate differences in landscape position and solar insolation (Diamond et al. 2005). Landscape positions were defined using relative elevation of a pixel compared to its neighbors at multiple spatial extents. Solar insolation was calculated from slope, aspect, shading and exposure indices calculated from the DEM. Calculations were done in ArcGIS 8.3 (ESRI, Redlands, CA).

Density

Briefly, we estimated tree density from GLO surveys with the Morisita plotless estimator (Morisita 1957) by the number of trees per point for all the points within each landform and land type for a subsection. We retained survey points with two to four trees per point. For points with four trees, due to the variability of density estimates for a clustered spatial pattern (Hanberry et al. 2011), we removed the most distant point, resulting in points with three trees. To produce a reliable density estimate, we excluded any density estimates where the minimum number of points was < 200 for points with two trees or the minimum number of points was < 50 for points with three trees. We calculated a raw, unadjusted density estimate with the number of trees per point. We then produced a low and high value based on corrections for spatial pattern, which we proceeded to further adjust (see below) for surveyor bias (Hanberry et al. 2011).

Surveyors probably did not select the nearest tree to each survey point, based on deviations from randomly expected ratios (i.e., there should be a similar number of trees in each of four quadrants). Using a rank-based method for bias correction, we produced a low value, assuming selected trees had a mean distance rank of 1.4 from the survey point, and a mean value, assuming selected trees had a mean distance rank of 1.8 from the survey point (Hanberry et al. 2012). Using a bias-based method, we corrected for non-random frequencies using adjustment quotients from regression equations (Hanberry et al. 2012). We produced a mean value and a high value. 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 mean density estimates from points with two trees (earlier surveys with mean date of 1827) and points with three trees (later surveys with mean date of 1841), we accounted for: 1) the type of survey point, because density estimates from survey points with three trees are more accurate than points with two trees given the same number of points; and 2) the total number of points for each type of point, because 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 determined the combined density estimate using a weight of the number of points of each type divided by the total number of points.

Basal area, Stocking, and Canopy Cover

To better describe structure, we incorporated diameter as well as density into reconstructed structure. We used the quadratic mean diameter (qmd, square root of the mean DBH^2) to calculate basal area per tree and then multiplied this by the density to estimate the total basal are on a per hectare basis. We determined the mean diameter to calculate percent stocking and canopy cover. 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. We used stocking coefficients for a second order polynomial regression equation developed by Gingrich (1967) for upland hardwood forests and by Rogers (1983) for shortleaf pine in Missouri. A stocking percent of 100 represents full use of growing space; sites only can hold a certain number of trees of a certain diameter and thus increases in site quality lead to increased tree height and faster diameter growth. Allometric equations for canopy cover have not been fully developed, probably because of inherent variation. We used the canopy cover equation by Law et al. (1994) with overlap reductions supplied by Crookston and Stage (1999), which appeared to be

Table 1. Reconstruction of initial expected vegetation phases (trees ≥ 12.7 cm diameter) by historical density (trees/ha), percent oak species, percent shortleaf pine, diameter (DBH; cm), basal area (BA; m2/ha), percent stocking, and percent canopy coverage.

Expected vegetation phase[1]	Density	Low	High	% Oak	% Pine	DBH	BA	Low	High	% Stocking	Low	High	% Canopy (low)	Min	Max
Prairie/Grassland	94	51	119	89	0	36	12	6	15	33	18	43	56	48	65
Oak Open Woodland	123	69	154	92	1	33	12	7	15	36	20	46	61	38	88
Oak Closed Woodland	168	85	222	84	0	35	20	10	26	58	29	76	73	56	86
Glade/Savanna Mosaic	192	100	254	80	7	36	23	12	31	67	35	88	80	72	87
Forest	195	97	264	75	14	35	23	11	31	66	33	90	77	55	89
Pine/Oak Closed Woodland	226	113	303	67	28	37	29	14	39	76	38	103	81	62	99
Floodplain Forests	240	119	323	39	4	38	36	18	48	96	48	129	83	67	98

[1] Identified by Central Hardwoods Joint Venture process

the best calculation currently available for eastern woodland canopy cover.

Quantitative Reconstruction of Historical Vegetation Phases

We used an expert model based on assignments of expected vegetation phases by ecological spatial units of ecological subsection, land type, and landform. As part of eco-regional conservation planning efforts for birds to provide estimates of restoration potential at multiple scales, the Central Hardwoods Joint Venture staff developed a map of expected vegetation phases for the Central Hardwoods Bird Conservation Region. The region is approximately 33 million ha in size, covering portions of ten states that straddle the Mississippi River in the center of the conterminous United States (U.S. North American Bird Conservation Initiative Committee 2000), including the Missouri Ozarks. Joint Venture staff developed the map through a series of workshops bringing together well-known community ecology experts from each state in the region. Experts were asked to review maps of land types and landforms (described above) and populate a matrix of land type-landform with vegetation phases based on their knowledge of historic conditions and disturbance regimes. Joint Venture staff then linked the matrix assignments to unique land type-landform combinations in a GIS and provided the map to the experts for review. The final model characterized 11 vegetation phases, including nine forested and woodland vegetation phases, mapped at 30-m resolution (see Table 1 for vegetation phases present in the Missouri Ozarks).

For each initial expected vegetation phase (i.e., the expert designations) in the Missouri Ozarks, we calculated restoration targets of mean, low, and high values of density, percent oak, percent pine, diameter, basal area, percent stocking, and canopy cover. We removed ecological units for vegetation phases with values that were < 50% or > 200% of mean density values. Because the Law et al. (1994) equations overestimated canopy coverage, we provided both a mean value and range for only the low canopy cover estimate, even though in consequence floodplain forests did not have completely closed canopies.

We assessed initial expected vegetation phases (Table 1) for differences in structural means of density, basal area, percent stocking, and canopy cover of the vegetation phases using an ANOVA (SAS software, version 9.1, Cary, North Carolina; Proc Mixed, LSMEANS PDIFF option or Fisher's least significant difference). We also assessed whether structural values increased along the continuum of vegetation phases (i.e., from prairie to forest). We then slightly modified boundaries in percent stocking to classify vegetation phases and re-assigned a vegetation phase to each land type by subsection based on modified boundaries. We provided restoration targets (mean and ranges for density, basal area, percent stocking, canopy cover, percent oak and pine) for reconstructed structure based on reassigned vegetation phases. We mapped reconstructed vegetation phases, extending the study area to Missouri's Plains.

Results

Initial restoration targets, or values of historic structure based on expert designations of expected vegetation phases, generally indicated increases in metrics, including density, basal area, and stocking, with changes to more dense vegetation phases, from prairie/grassland (94 trees/ha) to floodplain forests (240 trees/ha; Table 1). Initial expected vegetation phases of open or closed oak woodlands had lower densities, basal areas, and stocking levels than forests. Estimated canopy cover followed a similar trend with mean canopy cover of 56% for prairie/savanna and 83% in floodplain forests. Initial expected vegetation phases had significant differences ($p < 0.0005$) in density (df = 86, F = 3.91), basal area (df = 86, F = 6.22), percent stocking (df = 86, F = 5.39), and canopy coverage (df = 86, F = 7.97). (See Table S1 for density and stocking of each of the 94 ecological units of subsection-land type-landform comprising the vegetation phases).

Nevertheless, reconstruction of historic structure using initial restoration targets suggested that some of the initial expected vegetation phases did not match with the continuum in density in vegetation phases (Table 1). Presence of pine trees appeared to affect results causing greater density in pine/oak closed woodland than forest. Furthermore, prairies and grasslands were not likely to have tree stocking levels at or above 33%.

The vegetation phase boundary in initial restoration targets between open and closed woodlands occurred at 58% stocking, where stocking equations for upland trees indicates that 'B' level stocking begins (Gingrich 1967). The 'B' line indicates the point where available growing space is filled and closed canopies develop. For final vegetation phase boundaries, we reduced the boundary between open and closed woodlands to 55%, taking into account that we only used trees ≥ 12.7 cm diameter and therefore, there was a missing component to percent stocking (Table 2). The maximum percent stocking for oak closed woodlands and the mean percent stocking for pine/oak closed woodlands was 76%, which we used as our threshold to separate states of closed woodlands from forests, albeit reset at 75%. We reassigned the lowest mean percent stocking of 33% from prairies to savannas and reduced the value to 30%. The Missouri Ozarks did not have large areas of prairie and the low value for percent stocking was 18%. We thus suggest 10% stocking as a value well below that for savannas to represent prairies, but we do not have any reconstruction data for prairies. In addition, we classified forests as oak, pine, or oak/pine based on percent composition ≥ 30% (Table 2).

Table 2. Vegetation phase boundaries (trees ≥ 12.7 cm diameter) using historical percent stocking, density (trees/ha), percent oak species, and percent shortleaf pine.

Vegetation phase	% Stocking	Density	% Oak	% Pine
Prairie/Grassland	< 10	<50	—	—
Oak Savanna	< 30	< 100	≥ 30	—
Oak Open Woodland	< 55	< 175	≥ 30	—
Oak Closed Woodland	< 75	< 250	≥ 30	—
Oak Forest	≥ 75	≥ 250	≥ 30	—
Oak/Pine Savanna	< 30	< 100	≥ 30	≥ 30
Oak/Pine Open Woodland	< 55	< 175	≥ 30	≥ 30
Oak/Pine Closed Woodland	< 75	< 250	≥ 30	≥ 30
Oak/Pine Forest	≥ 75	≥ 250	≥ 30	≥ 30
Pine Savanna	< 30	< 100	—	≥ 30
Pine Open Woodland	< 55	< 175	—	≥ 30
Pine Closed Woodland	< 75	< 250	—	≥ 30
Pine Forest	≥ 75	≥ 250	—	≥ 30
Other Forest	≥ 75	≥ 250	< 30	< 30

After reclassification of vegetation phases based on stocking boundaries and reassignment of each ecological unit, mean historical densities ranged from 81 trees/ha in savannas to 285 trees/ha in non-oak/non-pine forests for larger trees (diameters ≥ 12.7 cm; Table 3). Mean basal area ranged from 8 m^2/ha in savannas to 46 m^2/ha in non-oak/non-pine forests for larger trees. Canopy coverage was about 50% for savanna, 65% for open woodlands, and 80% for closed woodlands.

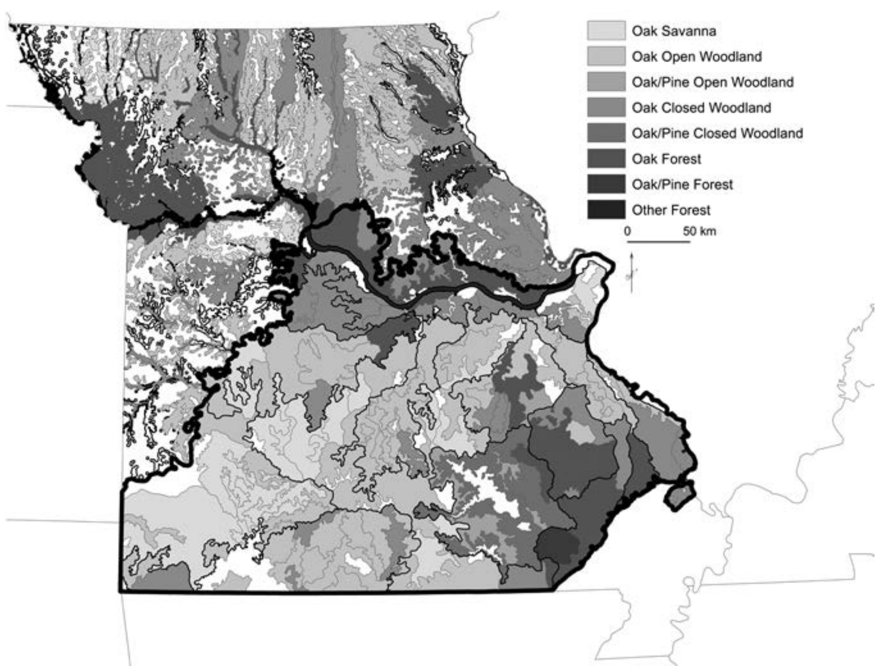

Figure 2. Vegetation phases based on reconstructed structure by subsection and land type in the Missouri Ozarks (delineated by thick black outline) and Plains. White areas in the Missouri Ozarks did not contain enough trees to reconstruct structure and thus may represent prairies in some cases. White areas in the Missouri Plains are the non-forested extent where surveyors were not able to locate trees; outlines indicate where there were trees but not enough to reconstruct structure.

Table 3. Modified reconstruction of vegetation phases (trees ≥ 12.7 cm diameter) assigned using initial restoration targets by percent stocking, percent oak species, percent shortleaf pine, density (trees/ha), basal area (BA; m2/ha), and percent canopy coverage.

Vegetation phase	% Stocking	Low	High	% Oak	Low	High	% Pine	Low	High	Density	Low	High	BA	Low	High	% Canopy (low)	Min	Max
Oak Savanna	25	16	30	92	78	99	0	0	2	81	58	110	8	5	10	51	38	60
Oak Open Woodland	41	30	55	89	75	98	2	0	23	133	85	214	14	9	20	66	50	80
Oak/Pine Open Woodland	51	49	53	48	37	58	49	37	62	158	155	161	21	19	23	77	77	77
Oak/Pine Closed Woodland	63	56	69	47	43	53	46	42	49	200	172	216	25	22	29	81	77	84
Oak Closed Woodland	64	55	75	78	48	95	3	0	28	200	130	246	23	18	29	81	74	87
Oak Forest	88	76	105	69	52	88	6	0	25	247	192	318	32	26	38	87	83	94
Oak/Pine Forest	89	89	89	53	53	53	38	38	38	300	300	300	35	35	35	92	92	92
Other Forest	118	118	118	11	11	11	0	0	0	285	285	285	46	46	46	93	93	93

We were able to reconstruct vegetation structure for about 8.5 million ha of the 9.4 million ha Ozark landscape (Figure 2). Thus, about 10% of the vegetation structure was unknown due to small sample size, and in larger areas, may represent prairies where there were a low number of trees recorded in GLO surveys. After application of restoration targets, about 19% of the reconstructed landscape was savanna, 41% was open woodland, 24% was closed woodland, and 16% was forest. Although restoration targets were based on reconstruction of vegetation phases in the Missouri Ozarks, we extended the application of restoration targets to the Missouri Plains. Rather than detection of prairies based on stocking boundaries of reconstructed structure, the Missouri Plains contained non-forested ecosystems within subsections where surveyors were not able to locate trees.

Discussion

We have developed restoration targets for vegetation phases (i.e., savannas to forests) using stocking, or growing space, boundaries from reconstructed structure of historical forests using surveys that were corrected for surveyor biases. The boundaries that define vegetation phases and associated structure (Tables 2 and 3) can be used to guide restoration activities in oak savannas and woodlands in the central and eastern United States where open oak ecosystems were common prior to European settlement and industrialization. Land managers can use targets to provide structural variation within each ecological subsection. Managers may choose to spend resources to attain savannas or open woodlands, but closed woodlands are easier to maintain, and thus larger areas of closed woodlands can be restored compared to more open phases. A more coordinated restoration effort by multiple managing agencies may achieve a gradient in structure that occurred historically across the landscape.

If restoration produces open forest ecosystems, the need to distinguish between or manage for the specific open vegetation phases may not be great in temperate regions. Temperate open ecosystems support a diversity of light-demanding plants along with animals that use open ecosystems (McShea et al. 2007, Rogers et al. 2008, Fox et al. 2010). Glaciation and colder temperatures affected composition of temperate savannas and woodlands, which have been developing for less than 10,000 years (Axelrod 1985). Temperate savannas and woodlands are not uniquely speciated and instead share species with surrounding biomes, resulting in compositional and functional similarity. In contrast, for some tropical savannas, the transition between two alternative stable phases of vegetation with contrasting functional ecology may occur between savanna and subtropical thicket or dry seasonal forest (Parr et al. 2012), which probably corresponds with woodlands.

Even though greater areal extents of the more open vegetation phases of prairie, savanna, and open woodlands likely occurred before European contact reduced Native American populations, historical forests prior to and during Euro-American settlement nevertheless contained a range of open forest ecosystems not present in current landscapes (Hanberry et al. 2014). Open forest ecosystems occurred across the landscape in a continuum of vegetation phases, which varied spatially and temporally. It is possible that there were increases in forest density during the changing disturbance patterns of the 1800s when the surveys were conducted. However, GLO surveys are perhaps the only benchmark available to quantify forest structure across a landscape and represent a range of historical conditions when open oak systems existed across the Missouri Ozark landscape. Presently, there are no landscapes with low density, large diameter oak forests that developed under an uninterrupted fire regime. Oak-dominated forests growing without a history of fire probably are not representative of historical oak-dominated forests in this region (Fralish et al. 1991, Brewer 2001).

When the stocking boundaries are applied to the survey data to identify vegetation phases (Table 3), the generalized idea interpreted from historical documents of low-density savannas and open woodlands may not have been consistent throughout the Ozarks during the post-European contact period. Although density, basal area, stocking, and canopy closure of historical Ozark forests varied considerably across the landscape, open and closed woodlands may have been widespread. Density ranges for vegetation phases (81 trees/ha in the most open vegetation phase of savannas to 200 trees/ha in closed woodlands for larger trees of DBH ≥ 12.7 cm), as well as basal area and canopy cover ranges, may fall within the high end of typical values for closed woodlands, but are greater than expected for savannas and more open woodlands (Anderson and Anderson 1975, Fralish et al. 1991, M. Leahy, Missouri Department of Conservation, pers. comm.). Our bias corrections may be too strong, and in that case, the lower range of density estimates, which roughly are equal to density estimates uncorrected for surveyor bias, may be more appropriate. Nevertheless, current forest densities in the Missouri Ozarks of about 350 trees/ha generally are 2 to 2.5 times greater than mean historical densities with moderate correction for surveyor bias (Hanberry et al. 2014).

Given greater than expected historical densities and percent stocking for all categories of open oak ecosystems, closed or nearly closed canopies may have existed in a larger portion of the Ozarks than expected. Despite high stocking and closed canopies, it is possible that these ecosystems were relatively open. Generally to achieve high levels of stocking, a stand of trees must be dense and closed and stands with lower stocking are open. However, it is possible for stands containing low densities of large trees to achieve a high level of stocking (e.g., 60% stocking or greater) and to have a closed canopy but be relatively open. Frequent fire intervals reduce density in the understory and overstory, generating a single stratum of large diameter trees spaced widely apart with top-loaded foliage. Although temperate woodlands may have had a connected canopy, high and light shade appears to permit moderate light to reach the forest floor and allow growth of an herbaceous understory (Fralish and McArdle 2009). When sunlight is available, trees develop lower specific leaf areas and foliage is less dense and more permeable to light (Reich et al. 2001, Hoffmann et al. 2005, Ratnam et al. 2011). In addition, shade-intolerant broadleaf tree species produce leaves later in the spring than shade-tolerant species, providing more light for herbs (Brewer 1980). This alternative architecture of thinly connected canopy, open understory, herbaceous ground layer of closed woodlands seems plausible and corresponds with structure of restored oak forests that contain large diameter oak trees.

Because the Missouri Ozarks appeared to be predominantly (65%) woodlands, there is uncertainty about the boundary that we developed between prairie and savanna; however, we propose that 10% stocking may be a functional boundary. We extended our application of restoration targets to GLO surveys in the Missouri Plains, where we also could not identify large extents of prairie based on trees recorded by surveyors (Figure 2). Rather, prairies probably occurred where surveyors could not record trees (i.e. the non-forested extent). Even though the Missouri Plains was exposed to frequent surface fires, historically extensive wetlands and stream networks that drained to the large Missouri and Mississippi rivers provided firebreaks to protect tree establishment and growth. The Missouri Plains in particular likely contained a mosaic of different vegetation phases within subsections, where riparian forests changed to oak woodlands and open prairies within short distances from streams and wetlands (Schroeder 1981). Conversely, high elevation and xeric subsections in the Missouri Ozarks probably contained relatively constant vegetation phases, without heavily timbered stream networks to serve as firebreaks and allow increases in overall stocking. West-East gradients in vegetation phases (Figure 2) likely represented fire exposure from western prairies, or non-forested ecosystems that may have annual surface fires, on the flat, higher elevation Ozark Plateau, before dissected hills leading down to the Missouri and Mississippi Rivers reduced fire exposure. Additionally, the eastern side is within the shortleaf pine distribution, which contributed to increased density and stocking.

There are questions about the validity of reference conditions given the trajectory of climate change away from the Little Ice Age conditions present during pre-settlement forests (Millar et al. 2007). However, oaks and pine open ecosystems dominated the Medieval Warm Period (Matthews and Briffa 2005) and there is no reason to assume that cooler conditions with less moisture stress are necessary to oaks and pine; indeed, drought may favor these genera. The root reserves that allow seedlings of fire-dependent species to resprout following a fire also increase their drought resistance and their ability to respond more rapidly after a drought when soil water becomes available. Therefore, the trajectory of warming and increased moisture stress by evapotranspiration (Brandt et al. 2014) may be exactly the right direction for oak and pine species to become more competitive. If climate warming drives oak and pine recruitment and increases mortality of more drought-sensitive species, reducing resistance and resilience of the closed forest state, then management for open forest ecosystems will require fewer resources to restore and maintain open forests. Managing for open forest ecosystems is thus compatible with strategies for managing for forest resilience to climate change. Additionally, current stand-replacing disturbances by land clearing and harvest may provide processes that can be modified to retain large diameter oak and pine trees, if there is social adoption of silvicultural prescriptions.

One obstacle to future restoration of open forest ecosystems is loss of herbaceous seed banks due to lack of current restoration. Oaks are long-lived and oak seed sources will still be standing. However, open oak ecosystems host a variety of light-demanding herbaceous forbs and grasses that are progressively lost to shading and which may require fire scarification to achieve germination. A variety of invertebrates and wildlife also are declining without the widespread presence of open forest ecosystems (McShea et al. 2007, Fox et al. 2010). Large landscape conservation efforts such as Joint Ventures (www.mbjv.org) and Landscape Conservation Cooperatives (www.fws.gov/landscape-conservation/lcc.html) seek to restore and maintain viable populations of birds and other species. The success of such efforts is dependent in part on the restoration of resilient natural communities across landscapes.

Conclusions

To guide restoration, we quantified structure with a range of variability that was likely for vegetation phases in the Missouri Ozarks and developed smoothed restoration targets for vegetation phases based on stocking or growing space. A frequent, low severity fire regime can produce high stocking by maintaining moderate densities of large diameter trees. Managers may opt to aim for lower densities, although sustaining lower targets will require greater resources due to resistance by a continual influx of propagules from fire-sensitive tree species. Not only is restoration of closed woodlands more attainable than very open forest ecosystems, closed or nearly closed oak woodlands may have been more common than savannas and prairies in Missouri, at least during the 1800s after European contact and before Euro-American settlement. Oak woodlands with a connected yet sparse canopy of thin crowns still allow light penetration through the canopy and if the herbaceous understory and open midstory is achieved, then the structural phase is appropriate for maintaining biodiversity of open forest ecosystems against future conditions. Low-density forest ecosystems composed of relatively drought-tolerant species should endure climate change stresses better than greater density forests composed of species that compete well under mesic conditions.

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Supplementary Table S1 can be found online at: uwpress.wisc.edu/journals/journals/er-supplementary.html.

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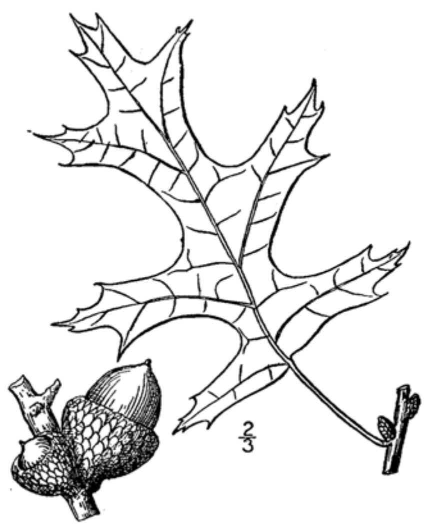

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