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# Recognizing loss of open forest ecosystems by tree densification and land use intensification in the Midwestern USA

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**Abstract**
Forests and grasslands have changed during the past 200 years in the eastern USA, and it is now possible to quantify loss and conversion of vegetation cover at regional scales. We quantified historical (ca. 1786–1908) and current land cover and determined long-term ecosystem change to either land use or closed forests in eight states of the Great Lakes and Midwest. Historically, the region was 35% grasslands (31 million hectares), 38% open forests of savannas and woodlands (33 million hectares), and 25% closed forests (22 million hectares). Currently, the region is about 85% land use (76 million hectares), primarily agriculture, and 15% closed forests (12 million hectares). Land use intensification removed 75% of open forests, while 25% of open forests have densified to closed forests without low severity disturbance to remove understory trees. Historical forest ecosystems included a gradient of oak savannas and woodlands with open midstories (50 to 250 trees/ha), along with closed old growth forests. Open forests have become dense (200 to 375 trees/ha) and are cut frequently, resulting in the extremes of closed canopy forests and clearcut openings across forested landscapes. We demonstrated that forests have transitioned from a historically wide gradient in canopy closure to either dense young closed forests with clearcut openings or to various land uses (agriculture, grazing, residential and commercial land development). The historical abundance of open forest ecosystems, composed of both forest and grassland layers, often is not recognized, and thus, these forests are undervalued for conservation and management.

**Keywords** Grassland · Historical data · Land cover · Land use · Transition

## Introduction

Oaks historically dominated the central eastern USA. Tree surveys substantiate that oaks were about 53% of total tree composition in the central eastern USA and 65% along the border of the eastern USA (Hanberry and Nowacki 2016). White oak (*Quercus alba*) was most abundant overall, with variable amounts of black oak (*Q. velutina*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), southern red oak (*Q. falcata*), post oak (*Q. stellata*), and bur oak (*Q. macrocarpa*). Dominance by fire-tolerant oaks suggests a historical fire regime, to filter out the hundreds of other potential tree species present in the temperate climate of the eastern USA (Abrams 1992). Fire disturbance also limits tree densities by removing young trees and other small diameter woody stems in the understory and reducing tree establishment even for fire-tolerant species (Arthur et al. 2012). Variation in fire frequency produces open forest ecosystems of savannas, open woodlands, and closed woodlands, which fill a wide gradient of tree density and canopy cover between grasslands and closed forests (Hanberry et al. 2014a).

Open forests have a single canopy layer that increases in continuity from savannas to closed woodlands, in which large diameter open-grown oak trees may have crowns wide

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enough to produce a closed canopy (Hanberry et al. 2014a). Open forests consist of both a simple overstory tree layer and a robust herbaceous understory, comparable to grasslands, that produce unique characteristics that differ from grasslands and closed canopy forests. Rather than development of multiple vertical layers, which is the stand structure of closed old growth forests, open forests develop variation in tree densities horizontally across environmental gradients and landscapes. Despite the presence of an overstory, open forests may be more comparable to grasslands (i.e., open ecosystems composed of grasses and forbs) than closed forests, due to shared dependence on fire and exposure to light and wind. Frequent fires removed woody vegetation in the understory, limiting vegetation entry into the midstory and overstory and allowing high light transmittance to the ground layer. Repeated fires may result in top-killed oak sprouts and other trees in a shrub growth form.

Compositional change from primarily oak species to eastern broadleaf tree species has been well-documented for most forests of the central eastern USA (Nowacki and Abrams 2008). To date, oak has decreased to about 15–30% of total tree composition in the central eastern USA (B. Hanberry, unpublished data). Many formerly minor species (< 2% of historical forest composition) of eastern broadleaf forests that historically were restricted to wetlands, rocky outcrops, and other firebreaks have increased in tree density and expanded in distribution (Hanberry et al. 2014b). Replacement species are fire-sensitive and early- to mid-successional, such as red maple that capture light resources in eastern forest gaps (Nowacki and Abrams 2008). In more open ecosystems and agricultural regions, primarily along the western edge of eastern forests, open spaces have been claimed particularly by eastern redcedar (*Juniperus virginiana*; Briggs et al. 2002). Many oak species currently in the canopy are long-lived, but based on widespread understory dominance by fire-sensitive species (Fralish and McArdle 2009), overstory composition of oak will continue to decrease.

Prior to Euro-American settlement, most open and closed forests were old growth in the eastern USA due to lack of overstory disturbance at landscape scales (excluding areas in the northern US region with a 50–150-year severe fire regime; Lorimer 2001). Successional ecosystems were rare, typically no more than 1–10% of the forested landscape (Lorimer 2001). Currently, most old growth forests are rare ecosystems across the region, and no longer present except as remnants, at no more than 1% of historical distribution (Nuzzo 1986; Noss et al. 1995). With frequent overstory disturbance and fire exclusion, forests across the eastern USA generally are either regenerating clearcuts or mid-successional (i.e., self-thinning or stem exclusion stage) in structure with dense, multiple layers of vegetation and few gaps. Frequent harvest and land use clearings create transient open areas and successional forests. Successional forests result from human land use that creates vegetation that forms over short timescales (Veldman et al. 2015), and early to mid-successional forests have become the new forest standard, replacing old growth forests. Grasslands also were old growth due to lack of soil disturbance. Perennial grasses may live decades to centuries, regrowing from surviving roots after loss of aboveground vegetation, and vegetative reproduction extends individual continuity (Ehrlén and Lehtilä 2002).

Here, our objective is to quantify loss of open forests using land cover maps and additionally, partition loss either to tree densification within current forest extents or to intensification of land use that resulted in conversion away from open forests. We compared land classes and tree density estimates from historical tree surveys (ca. 1786–1908) and current land cover maps for Missouri, Minnesota, Wisconsin, Iowa, Illinois, Indiana, Ohio, and Michigan. Although the historical tree surveys contain error due to surveyor bias in tree selection, the surveys provide the best available information of historical forests at landscape scales due to large, systematic sample sizes (Liu et al. 2011). We test the hypothesis that transition from historic disturbance regimes to modern land use had a bifurcate impact on open forests, resulting in loss to agriculture or transition to closed forests. We conceptualize and discuss potential ecological consequences of divergence to two extreme end points from a historically continuous cover gradient across the eastern USA.

## Methods

### Estimating land cover change

We focused on the Midwestern USA, or the western half of the central eastern US, where General Land Office (GLO) historical tree surveys or land cover maps were available. We excluded northern forests that had a 50–150-year severe fire regime (Lorimer 2001) and the Mississippi Alluvial Valley in southeastern Missouri. This area of about 88 million hectares covers part of the Eastern Broadleaf Forest and Prairie ecological divisions (Ecomap 2007). States included Missouri and Wisconsin with complete GLO surveys; Minnesota with GLO surveys for the eastern forests and historical land cover for the western prairies; and Iowa, Illinois, Indiana, Ohio, and Michigan with historical land cover maps (1786–1908; see Appendix S1 for URL and survey dates by state).

Each land cover map had a unique classification system. Therefore, we reclassified land cover maps as grasslands, open forests, closed forests, wetlands, and water for historical and current land cover (National Land Cover Database 2011 for current land use and cover; Homer et al. 2015; see Fig. 1 for classification steps). We then assigned the most abundant land cover by ecological subsection (i.e., the smallest spatial

**Fig. 1** List of classification steps

1. Obtain historical and current land cover maps
   a. Use composition and density estimates to determine historical land cover for three states with available historical surveys
   b. Use published historical density estimates to separate open and closed forests in states with land cover maps
2. Reclassify historical and current land cover maps to grasslands, open forests, closed forests, wetlands, water, and land use
3. Assign most abundant land cover by ecological subsection
   a. For ecological subsections with similar areas (area of one land cover <1.2 of the other area; four subsections for both historical and current land cover), reassign land cover to better match overall land cover percentage before assignment of one land cover to each subsection.

unit in Ecomap 2007 classification system). For current land cover, we deliberately specified land cover as land use when intensive land use resulted in agricultural or urban land cover; that is, land use represented about 65% agriculture land cover, 20% grazing land cover, and 15% urban land cover.

For the historical land cover maps, we reclassified four ecological subsections that had relatively even grassland and forest land cover (grassland land cover area < 1.2 greater than area of forest land cover) to forest, to match overall land cover percentage before assignment of one land cover to each subsection (i.e., 48% grass and 35% closed forest before and 50% grass and 34% closed forest after subsection assignment, excluding water and wetland designations, for the areas with land cover maps). For the current land cover, we reclassified four subsections that had relatively even land use and forest land cover to forest, to better match overall land cover percentage before assignment of one land cover to each subsection (i.e., 86% land use and 14% closed forest before and after subsection assignment, excluding other classes).

To supplement historical land cover maps, we also used density estimates from Leitner and Jackson (1981) and Lindsey (1961), respectively, to reclassify one subsection in southern Illinois as open forest (175 trees/ha; 65% oak) and to classify northern and central Indiana as open forests (oak prairies of 30 trees/ha and beech, *Fagus grandifolia*, savannas of 80 trees/ha). Because the Indiana land cover map did not identify vegetation phases or states beyond composition, we excluded the southern portion of Indiana, which was composed of oak and beech. We also excluded one small subsection that was likely grasslands (Northern Bluegrass subsection) but not classified as such in the land cover map, in southern Ohio.

We estimated historical density by ecological subsection using the Morisita estimator for point-center quarter sampling (tree diameters ≥ 12.7 cm and 2000 to 40,000 trees per subsection; Hanberry et al. 2012). We made adjustments for spatial patterns and surveyor bias (that increased unadjusted density estimates because surveyors did not select the nearest trees) for Missouri, Minnesota, and Wisconsin (Hanberry et al. 2012). We also calculated mean density by subsection of current USDA Forest Inventory and Analysis plots (FIA DataMart, www.fia.fs.fed.us/tools-data; tree diameters ≥ 12.7 cm).

We compared historical and current density estimates by subsection (beanplot package, Kampstra 2008; R Core Team 2017, R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria). We used an approximate guide (Hanberry et al. 2014a) to classify historical forests at the subsection scale: open forests in the range of 50–250 trees/ha, grasslands at < 50 trees/ha, and closed forests at > 250 trees/ha. Overlap in classes is possible based on density estimates alone.

## Results

Historical boundaries between grasslands and open forests may appear sharp (Fig. 2), but in practice, boundaries were gradual because savannas are continuous with grasslands. In GLO surveys, surveyors were able to locate trees almost continuously throughout Missouri and Wisconsin. Northern Missouri, although part of the Prairie Peninsula, contained numerous drainages to the Missouri and Mississippi Rivers, which resulted in greater tree cover. In western Minnesota prairies, recorded trees were restricted to riparian corridors.

Closed forests bordered rivers or northern mixed forests of the upper Great Lake states or were beech-dominated forests (Fig. 2). Closed forests in Illinois occurred along the Mississippi and Wabash Rivers. Indeed, the Wabash Valley supported some of the greatest diameter trees in the eastern USA historically. Beech-dominated forests, which were abundant in Michigan and Ohio, tend to represent closed old growth forests. We do not have density estimates to determine if oak forests of southern Michigan and Ohio were closed.

Historically, grasslands were 35% (31 million hectares) of the region, while open forests were 38% (33 million hectares) and closed forests were 25% (22 million hectares) of the region, with 2.5% wetlands (Fig. 3). Currently, 86% (76 million hectares) of the region is in land use and 14% (12 million hectares) is closed forests. Wetlands no longer are present at a landscape scale.

All of the grasslands, 75% of open forests, and 83% of closed forests were converted to land uses (Fig. 3). However, 25% of open forests densified to closed forests. Therefore, although all of the grasslands and open forests were lost, closed forests still represented about 15% of the region.

Comparison of densities for 33 ecological subsections in Missouri, Minnesota, and Wisconsin that historically were open forests showed the shift in range and mean of densities to current forests (Fig. 3). Historical open forests ranged in density from 50 to 210 trees/ha, with a mean of about

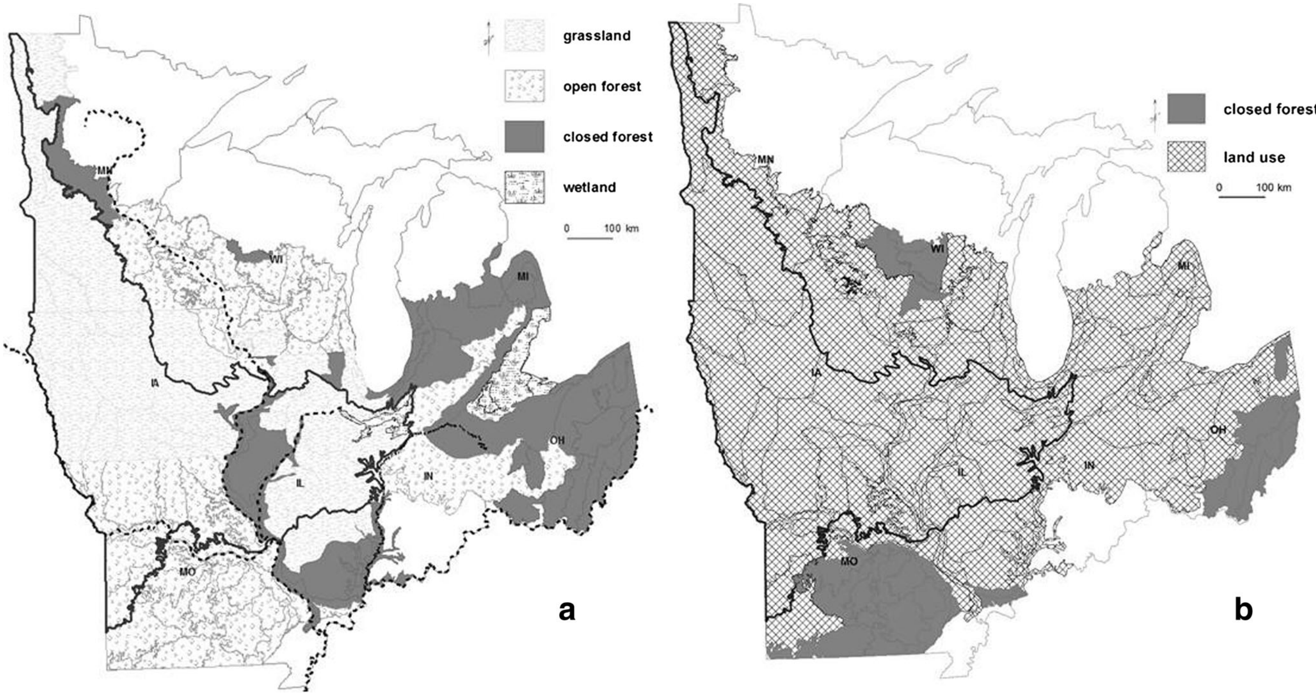


**Fig. 2** Historical land cover (**a**) and current land use (**b**) by ecological subsection (light outlines, the smallest spatial unit of the Ecomap 2007 classification system), in the Prairie and Eastern Broadleaf Forest ecological divisions (separated by dark outline) of Minnesota (MN), Wisconsin (WI), Michigan (MI), Iowa (IA), Illinois (IL), Indiana (IN), Ohio (OH), and Missouri (MO). Dotted black lines are major rivers, which sometimes act as state boundaries

130 trees/ha. These forests currently are dense at 200 to 375 trees/ha, with a mean of 300 trees/ha.

## Discussion

### Loss of open forests, grasslands, and closed old growth forests

Historically there was a wide distribution of grasslands, open forests, and closed forests at landscape (i.e., ecological subsection) scales, with a small component of wetlands (Figs. 2 and 3). We estimated about 31 million hectares of grasslands using land cover maps, whereas Whitney (1996) estimated about 34.9 million hectares of grasslands based on literature review. We estimated 33 million hectares of open forests historically, whereas Nuzzo (1986) estimated 11 million to 13 million hectares of historical oak savannas. This estimate excluded 12.3 million hectares of woodlands in the southern half of Missouri (i.e., the Ozarks ecological section). Currently, there are only closed forest ecosystems at a landscape scale, in a matrix of land use. Ecosystems changed from a gradient of canopy cover to either land use or clearcuts and closed forest end points.

The historical extent of open forests may have been greater than our estimates because open forests also can be classified as either prairie or closed forest. It is difficult to discern a density threshold between savannas and prairies that contain riparian and wetland forests, clumped oak groves, and scattered trees and oak shrubs top-killed by fire. The prairie definition in historical land cover maps included low density oak tree and shrub savanna and wetland woodlands in Illinois (Kaminski and Jackson 1978) and Iowa (Thomson 1987, also see Ecomap prairie/forest border in Fig. 2). For example, the central Sangamon River Basin in Illinois had tree densities of 42 trees/ha on slopes (King and Johnson 1977), which if adjusted for surveyor bias, may cross the threshold from prairie to savanna. Although prairies and savannas may be indistinguishable in the eastern USA where prairies and forests interact, the difference between open and closed forests is more clear based on whether the midstory is open (literally, whether it is possible to see between trees), which will affect whether the understory is similar to grasslands or contains mostly woody vegetation. Nonetheless, surveyors may not have differentiated woodlands and forests. Thus, closed forests in Ohio and Michigan may have been closed oak woodlands. Conversely, the extent of open forests may be less than we estimated. Open forests in northwestern Missouri may have been primarily grasslands with a dense riparian network that protected gallery forests projecting into otherwise open ecosystems, while atypically open beech forests may not have extended the entire subsection into central Indiana.

In northern Indiana, based on extremely low oak tree density (30 trees/ha but mean diameter of 42.5 cm; Lindsey 1961), oak shrubs also may have occurred due to fire continuously top killing trees, similarly to coppicing. This area in

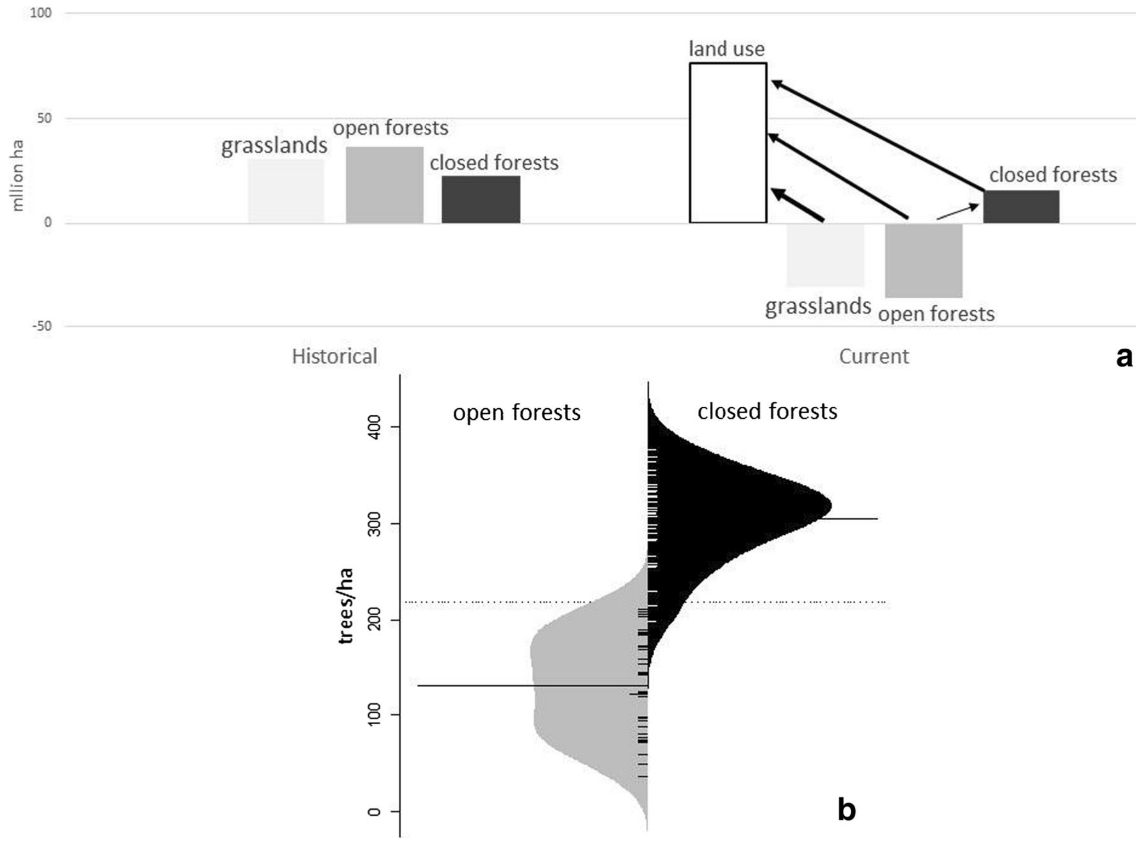


**Fig. 3** Grassland, open forest, and closed forest composition in historical landscapes (**a**). All grasslands have been converted to land use, 75% of open forests have converted to land use and 25% of open forests to closed forests, and 83% of closed forests have converted to land use. The second panel (**b**) illustrates densification of historical open forests to current closed forests (trees ≥ 12.7 cm diameter; long lines represent current and historical density means and an overall mean)

Indiana probably resembled savannas in southern Wisconsin, where oak shrubs were described along with sparse oaks in a tree form (Cottam 1949). Beeches also were present and dominant in northern and central Indiana, but at atypically low densities (80 trees/ha; Lindsey 1961). However, beeches do re-sprout (including root suckers) in coppice systems of Europe and form beech thickets currently in the eastern USA due to beech bark disease. Given that there may have been a small pool of tree species present in the Prairie division, beech apparently was competitive under unusual environmental conditions. Beech tree density probably increased at least to the central eastern part of Indiana, away from grasslands, but we maintained the Indiana land cover map designation, which contained one large expanse of beech cover that overlapped with low density estimates by Lindsey (1961).

Most of the Midwestern USA now is in intensive land use of agricultural crops, with lesser amounts of urbanization and grazing. Based on estimates of localized remnants, loss of eastern tallgrass prairie and oak savannas is perhaps > 99% of historical extent (Nuzzo 1986; Noss et al. 1995). Whitney (1996) estimated about 63,000 ha of prairie remained in these eight states, while Nuzzo (1986) documented 2600 ha of undegraded oak savannas in these eight states during the 1980s.

In localized areas that are not in agricultural land use, a history of tilling and heavy soil disturbance by overgrazing has removed native rootstocks and seedbanks, so that qualitative losses by degradation occur even in remnant prairies and open forests. Grazing during the 1900s occurred at greater intensity than historically, resulting in ecosystem degradation compared to the past (McGranahan et al. 2013). Grazing may be too uniform across grasslands, reducing heterogeneity in species composition and plant height (Fuhlendorf and Engle 2001). Intensification of land use also has removed features that may represent proxies for open forests, such as hedgerows and scattered or residual trees (Manning et al. 2009). In addition to loss and degradation by overuse, fragmented ecosystems embedded in intensively used landscapes contain fewer species and do not maintain diversity, due to local extinctions of smaller populations.

Open forests that did not convert to agriculture (25%) in the study region instead densified to closed forests due to loss of low severity disturbance (Fig. 3). Historical open forests ranged in density from 50 to 210 trees/ha, with a mean of

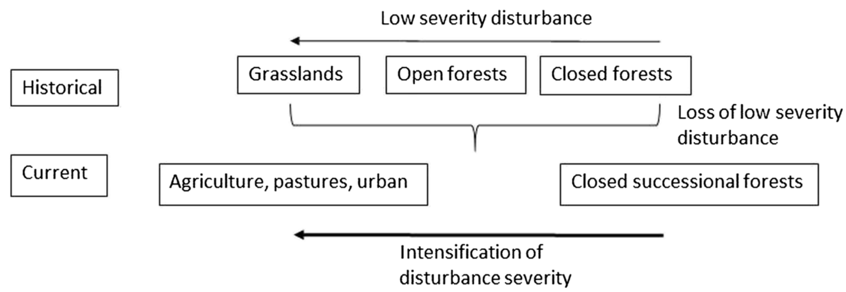


**Fig. 4** A conceptualized model of changes in state from historical grasslands, open forests, and closed old growth forests to current dense forests and land use classes of land cover. Low severity disturbance typically involves fire in grasslands and open forests

about 130 trees/ha. Historical forests provided a range of canopy closure that is missing currently after densification to closed forests, which are 200 to 375 trees/ha. Open grass and forest ecosystems are unstable states without a frequent surface fire regime in mesic regions (see expanded discussion below). Mesic regions can support both open and closed ecosystems as potential states, depending on whether disturbance is present to remove woody growth. Without understory removal of small diameter trees by fire, open forests transitioned in state to closed forests. A potential outcome for grasslands also is to transition to forests, for example, by eastern redcedar encroachment (Briggs et al. 2002; Fig. 4). However, in this region, the land was too productive to escape crop production. Grasslands, once widely distributed, have become rowcrops and cities.

Although there was not as great a quantitative loss in the closed forest state as open ecosystem states, there still was a qualitative loss (see Fig. 4). Just as there are open forest phases of savannas, open woodlands, and closed woodlands depending on time after understory removal, there are the well-described stages in closed forest development after overstory removal, and the oldest forest stage is missing. Closed forests converted from old growth forests to younger successional forests of present day. Current forests have small diameter distributions, while large (and massive) trees are uncommon. Continued overstory tree disturbance by clearing for different land uses, short rotation harvest, cycles of agricultural cultivation and abandonment, or even deliberate management for young forests will keep many eastern forests in a dense, self-thinning state with little light transmittance to the forest floor. Dense, recalcitrant understory layers also reduce diversity (Royo and Carson 2006). If given time without cutting, current successional forests will develop closed old growth characteristics of gaps and light enough to sustain forest plants but will not become open forests without disturbance of the understory.

Current forests represent the density extremes of clearings and closed forests, rather than containing the full representation in structure of historical landscapes (Fig. 4). Current forests are diverse in tree species, each stand containing a rich and evenly distributed subset of all tree species that do not tolerate stress from fire or flooding or compete well for extreme shade. But despite great variation in species composition, homogenization in forest structure punctuated by clearings for different land uses does not contribute to landscape diversity in canopy closure. Current closed forests contain high contrast edges, due to fragmentation by land use that occurs even in heavily forested landscapes (e.g., Hanberry et al. 2013).

## Similarity to Europe, grazing animals, and fire exclusion

Open ecosystems and oak forests with an herbaceous understory in Europe also have converted to either intensive agricultural land uses or closed forests, similarly to this study (Vera 2000; Lindbladh et al. 2003; DeCocq et al. 2004; Hédl et al. 2010; Bobiec et al. 2011; Buse 2012; Plue et al. 2013; Mölder et al. 2014). Oak forests that remain in Europe probably were maintained by labor-intensive practices of coppicing and pollarding, and there is some evidence of fire use (Lindbladh et al. 2003; Hédl et al. 2010). Oak-dominated wood-pastures in Europe occur with livestock grazing (Hanberry et al. 2017). Without continued silvicultural intervention, oaks and other tree species probably will not regenerate under grazing pressure > 0.50 animal units/ha (Hanberry et al. 2017).

Vera (2000) proposed that in Europe and analogously in the eastern USA, large herbivores maintained grasslands. Groves developed within inedible scrub, which subsequently returned to grassland through various disturbances ("cyclical turnover of vegetation", Vera 2000). Bison (*Bison bison*) were present in most, but not all of the eastern USA (Vera 2000). However, historical records demonstrate that the eastern USA was largely forested, rather than grasslands with patchy groves (see results from forested region of this study). In southern New England and the Atlantic Coastal Plain, where bison were not present, open oak and pine woodlands occurred historically and did not appear to have any ecological demarcation from adjacent western areas with bison. Bison feed on grass, not on tree seedlings. Therefore, loss of bison is not likely to be a major driver for increased tree density in eastern forests. Elk (*Cervus canadensis*) also are grazers. Although their extirpation from the eastern USA coincides with tree densification, high elk densities in the western USA only are reported to reduce riparian vegetation (Beschta and Ripple 2016). Also, bison and elk were replaced by cattle, which were free-ranging initially.

Deer are browsers, which provide a better mechanism to reduce tree densities through consumption of seedlings. Near elimination of white-tailed deer (*Odocoileus virginianus*) during the late 1800s to around 1920 to 1930 may have allowed increased tree recruitment (Russell et al. 2001; Côté et al. 2004). Subsequently, deer reached historically high populations in the absence of natural predators (Russell et al. 2001; Côté et al. 2004) while tree densities also have increased. Only in a few localized areas does it appear that deer are able to reduce tree recruitment. Given widespread tree density increases in the understory, midstory, and overstory of Midwestern US forests (see results in this study, for example), herbivores do not appear able to control tree densities systematically at landscape scales.

Deer may be able to decrease tree density, but another driver, which we suggest is fire exclusion, superseded high deer density to allow increased tree density. Historical fires provide a mechanism to favor fire-tolerant tree species, while fire exclusion allows any tree species to survive. Variations in plant response to browse make reports of palatability conflicting even within a region; nevertheless, in eastern forests with high deer densities, both decreasing oak and increasing tree species are favored by deer (Russell et al. 2001; Côté et al. 2004).

Most loss of historical ecosystems was due to land use conversion during the late 1800s and 1900s after Euro-American settlement occurred. All of the grassland landscapes became dominated by agriculture, grazing, or urban or residential development. Likewise, 75% of open forests and 83% of closed forests converted to land use. Nevertheless, the remaining 25% of open forests converted to closed forests, so that 15% of the region remains in closed forest. Therefore, within existing ecosystems, effective fire exclusion, which started about the 1930s, may have produced changes that have more lasting effects than other land uses (Fig. 4). Frequent surface fires removed all but the oak species that have adaptations to frequent fire regimes, reducing tree establishment, which resulted in open forests of savannas and woodlands. In turn, open oak ecosystems were flammable and unfragmented, allowing surface fires to spread, which further stabilized open oak ecosystems.

There is difference of opinion about the extent and effect of historical fire regimes as the major driver of vegetation change (McEwan et al. 2011; Pederson et al. 2015; Abrams and Nowacki 2015). Nonetheless, historical fire regimes have been well-documented by fire scars and charcoal in sediments throughout much of the eastern USA (e.g., McEwan et al. 2007; Varner et al. 2016). Fire return intervals typically were about 10 years and no longer than about 50 years in the central eastern USA (e.g., Wade et al. 2000; Fralish and McArdle 2009). Historical closed forests in this region appeared to be related generally to protection from fire by major rivers or were continuous with closed forests in more northern forests or beech forests that had a different, severe fire regime.

Native Americans used fire for grassland and forest management (Abrams and Nowacki 2008). Indeed, despite ambivalence about use of fire by pre-industrial societies and the influence of fire on vegetation, societies throughout the world used fire (Pausas and Keeley 2009). Fire is a tool that requires relatively little time or energy, and without metal tools or engines, there are numerous reasons for fire, including clearing of woody layers for easier movement, gathering resources, supporting deer, other wildlife, and light-demanding vegetation, such as cultivated crops, edible plants, and cane as a source of fiber and building supplies. It appears that where Native Americans were agrarian, which includes most of the eastern USA excluding northern areas of the Great Lakes and New England and mountains, forests primarily were dominated by oak and pine species at landscape scales and there is evidence of fire disturbance (Wade et al. 2000; Hanberry and Nowacki 2016; Varner et al. 2016). Fire history is not as well documented in the mountainous eastern and northern regions (Wade et al. 2000), where climate is less conducive to fire and growing crops. Areas protected from fire supported well-described closed old growth forests, which in eastern forests predominantly consisted of American beech, sugar maple, and eastern hemlock.

## Consequences of open forest loss and old growth forest convergence

Old growth forests, both open and closed, historically were dominant when frequency of overstory disturbance was rare, occurring on rotations of hundreds to thousands of years (Lorimer 2001). Open forest ecosystem types are not a sere in a stage-based progression; instead, these forests have been stable in many temperate regions for millennia, anchored by long-lived oak and pine species. Current successional forests are missing both the open forest phases of savannas, open woodlands, and closed woodlands and also characteristics and continuity of closed old growth forests. Because species are adapted to a range of environmental conditions that are unavailable compared to the past, there are consequences to considering current forests as normal and ecologically typical.

Groundlayer species in grasslands, open forests, and closed forests are declining due to landscape divergence into the two extremes of croplands and dense forests. Open ecosystems have great diversity in groundlayer plants reliant on light and, in some cases, fire for germination (Gilliam 2007). Understory vegetation is determined by the environment created by the overstory. When very little light reaches the forest floor due to dense woody vegetation, herbaceous vegetation is suppressed and composition converts from light-demanding species to shade-tolerant species, including woody shrubs and vines, resulting in reduced abundance and diversity of herbaceous forbs and grasses (Noss et al. 1995; Rooney et al. 2004). Moreover, agriculture and grazing at landscape scales have thoroughly removed vegetation and the seedbank, so that many herbaceous species became limited to remnant patches of open forest ecosystems and prairies (Leach and Givnish 1999; Rogers et al. 2009). Small, isolated vegetation patches are more likely to lose species without replacement (Rogers et al. 2009). In addition, at more localized scales, low light conditions and current high levels of deer herbivory along with invasive species prevent recovery and interact to further reduce herbaceous plants (Royo and Carson 2006).

Without the open structure and herbaceous plant diversity, other species decline, from fungi (Foltz et al. 2013), insects (Campbell et al. 2007), and mammals (McShea et al. 2007). Over 100 species of birds, many of which are declining and a few are extinct (e.g., heath hen, *Tympanuchus cupido cupido*; passenger pigeon, *Ectopistes migratorius*), rely on open ecosystems (Hunter et al. 2001; Reidy et al. 2014). Buffalo and elk historically ranged throughout the eastern USA, but there is little grassland and open forest to support these species now.

Creation of more early successional forest through transient clearcuts probably is not a necessary forest restoration or wildlife management goal in the central eastern and southern USA. Overstory disturbance will not create old growth forests, either open or closed, or remain open as grasslands without understory tree control. Indeed, clearcuts create fragmentation effects that disrupt ecosystems, produce high contrast edges, and reduce connectivity. Conversely, tree retention during harvest or restoration of open forest ecosystems will soften these effects. Furthermore, public opposition to clearcuts may prevent landowners and governmental agencies from management for "early successional" wildlife by clearcutting. In contrast, tree retention or open forest restoration will produce more esthetic and historically natural landscaping, reducing negative public perceptions.

## Conclusions

Open ecosystems of grasslands and open forest ecosystems that historically provided a range of canopy cover across landscapes have declined to remnants at local scales, as demonstrated in our study region. Grasslands were converted completely to agricultural and urban land uses, while open forests have been converted to either land uses in flat landscapes or densified into closed forests in more rugged landscapes. Closed forests contain extremes of very dense tree layers and transient clearings, which do not supply the historically wide gradient in canopy closure or even the oldest stage of closed forests. It is important to distinguish forest ecosystems with high conservation value and unique attributes from closed successional forests that form over short timescales in response to anthropogenic overstory disturbance (Veldman et al. 2015). There may be substantial extinction debt associated with regime shifts from historical to novel ecosystems (Rogers et al. 2009).

Grasslands are recognized as rare ecosystems that are endangered by loss to land uses or eastern recedar encroachment, which has helped with conservation and restoration. However, grassland recognition without regulation is not preventing continued conversion to agriculture. Lack of recognition of open forest ecosystems, in which both the forest and grassland layers are critical for biodiversity, is an additional challenge where closed forests now are common and considered as normal. Loss of species dependent on open forests due to woody expansion and densification is relevant worldwide (e.g., Archer et al. 2001; Niklasson and Drakenberg 2001; Buse 2012; Plue et al. 2013; Horak et al. 2014; Miklín and Čížek 2014; Mölder et al. 2014). Not all species dependent on open conditions, such as were those documented in our study region, will persist unless the extent of open forest and grassland ecosystems increases.

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