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Divergent historical and current forest composition in Kentucky, including Daniel Boone National Forest, United States

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Outcomes of European colonization encompass surface fire exclusion followed by the forestation of open ecosystems and tree densification within forests, with concomitant replacement of fire-tolerant tree species, specifically oaks, by fire-sensitive tree species. In Kentucky, a 10.5 million ha area of the eastern United States, I compared tree composition between a historical assessment (1907–1909) and modern surveys (2010–2014), utilizing a divergence metric of squared-chord distance, which revealed a similar progression. Following the time since Euro-American settlement and associated fire exclusion, historically dominant fire-tolerant oaks decreased from 52% of all trees to 21% of all trees in Kentucky, while maples increased from 5 to 19% of all trees, reflecting shared changes across three regions. The Loess Hills region in western Kentucky and the Central Interior, a flat region of historical grasslands, displayed greater tree composition divergence than the Appalachian Mountain region in eastern Kentucky. The least decrease in oaks, at 19 percentage points, and the greatest decrease in fire-tolerant shortleaf pine (*Pinus echinata*), at 5.5 percentage points, occurred in the Daniel Boone National Forest, within the Appalachian region. American chestnut (*Castanea dentata*) decreased by nine percentage points in the Appalachian region, where red maple (*Acer rubrum*), previously of trace abundance, became the most abundant tree species at 14% of all trees, with yellow-poplar (*Liriodendron tulipifera*) at 12% of all trees. American beech (*Fagus grandifolia*) decreased by nine percentage points in the Interior region, where eastern redcedar (*Juniperus virginiana*), also previously of trace abundance, became the most abundant tree species at 12% of all trees. Sweetgum (*Liquidambar styraciflua*) decreased in the Loess region, where green ash (*Fraxinus pennsylvanica*) became the most abundant species, along with a new addition of planted loblolly pine (*Pinus taeda*). Kentucky contains a range of ecosystems, reflecting trends common to the eastern U.S. of decreased fire-tolerant species relative to fire-sensitive species following fire exclusion, as well as trends specific to regions, depending on species distributions.

KEYWORDS
agriculture, Appalachian, ash, eastern redcedar, Land Between the Lakes, maples, oaks, yellow-poplar

1 Introduction

Frequent surface fire controls tree and shrub densities, limiting fire-sensitive woody species and favoring fire-tolerant oak and pine species, whereas fire exclusion, following European colonization, enables increased tree and shrub densities of diverse fire-sensitive species (Tulowiecki et al., 2025). In the eastern United States, current land use has favored prominently fire-sensitive red maple, sweetgum, yellow-poplar, eastern redcedar, and loblolly pine, which have replaced fire-tolerant oak and pine species (Hanberry, 2019; Hanberry et al., 2019; Hanberry et al., 2023). This transition was accelerated by the clearing of overstory trees, historically dominated by fire-tolerant oak and pine species, allowing fire-sensitive species to rapidly colonize harvested forests and abandoned fields (Hanberry et al., 2023). Between approximately 1880 and 1920 in the U. S., forests were cut at perhaps an unprecedented rate, leading to a conservation movement and the protection of forests and future forest products in national forest reserves, now known as National Forests (Fernow, 1902; Williams, 1989; Williams, 2005).

In Kentucky, a 10.5 million ha area of the eastern United States, lumber production peaked from 1899 to 1908, after becoming a major industry by 1870 (Holmes and Bradfield, 1908; Collins, 1975). Before the development of markets for timber products, girdling and burning of trees were practiced to clear land, and most of the cut timber was used locally by private landowners, with limited commercial production of charcoal for the iron industry, crossties for railroads, and other forest products such as tannin, barrels, spokes, and handles (Holmes and Bradfield, 1908). To be profitable, harvesting needed to occur within 16 km of railroads, or within a day's travel, although the best trees growing near the creeks and rivers were harvested first and floated downstream to the larger sawmills (Holmes and Bradfield, 1908). By 1907–1909, when an assessment of forest conditions in Kentucky was conducted by the Forest Service in cooperation with the state of Kentucky (Hall, 1909; Holmes and Hall, 1909), only the inaccessible Appalachian Mountains of eastern Kentucky had avoided extensive clearing of original vegetation. A large percentage of the wood was wasted due to inefficient cutting, or it was never used but simply cleared for agricultural conversion, resulting in concerns about sustainability in forest products for future generations (Shaler, 1888; Holmes and Bradfield, 1908; Hall, 1909).

Fire application to remove small trees was a historical land management practice in the central and southern United States, but management gradually shifted to fire suppression for the purposes of sustained timber production after extensive clearing of vegetation (DeFriese, 1880; Sargent, 1884; Holmes and Bradfield, 1908). Typically, Euro-American settlers used fire to clear young trees and encourage forage for livestock, replicating Indigenous management or European pastoral practices (Sargent, 1884; Holmes and Bradfield, 1908). Sargent (1884) reported 225,300 ha of forestlands burned in 1880 in Kentucky, which covers an area of 10.5 million ha. Without a fire reporting system in place, this first report was incomplete, based on 30,000 total surveys nationally, and was recognized as underestimated and limited to forestlands (Sargent, 1884). However, fire suppression became a national policy, supported by the Weeks Act of 1911, which provided matching funds to states with the provision that forest protection agencies meet federal standards, encouraging legislatures to enact fire protection laws (Hall, 1909; Mastran and Lowerre, 1983). Nevertheless, active fire application in Kentucky may have persisted until the early 1960s, as almost 155,000 ha were reported to burn annually from 1938 to 1964, likely concentrated in the remote, mountainous Appalachians (Mastran and Lowerre, 1983). While fire underreporting continues to this day, approximately 17,000 ha burned annually between 1992 and 2018 in Kentucky (Short, 2022).

Historical accounts provide contemporaneous knowledge about tree species composition, forest structure, and disturbance dynamics, but these accounts are typically qualitative. For Kentucky, Sargent (1884, p. 545–546) described tree composition in three major ecological regions with varying characteristics: mountains on the east side, a flat interior, and a west side influenced by the Mississippi River (Figure 1). In the Appalachian Mountains of eastern Kentucky, original forests of high-quality timber still remained (Sargent, 1884), primarily consisting of white oak (*Quercus alba*), yellow-poplar, black walnut (*Juglans nigra*), and black cherry (*Prunus serotina*). The forests were protected by the cost of moving heavy timber in mountainous terrain, due to limited access by railroads and various obstacles that prevented log transport along rivers at that time (Holmes and Bradfield, 1908). Near the Mississippi River, cypress (baldcypress; *Taxodium distichum*), gum (*Nyssa, Liquidambar styraciflua*), and oaks comprised the floodplain forests of the westernmost counties of Kentucky (Sargent, 1884). Oaks and hickories (*Carya*) were present in the Central Interior region, which had been cleared for agriculture (Sargent, 1884). Most of the Interior region had ideal conditions conducive to the spread of frequent surface fires, due to flat topography and strong winds (Hanberry and Noss, 2022). Therefore, extensive tracts of grasslands, along with annual burning by Indigenous peoples, were documented by historical accounts during the earliest Euro-American settlement (Hanberry and Noss, 2022). Following Euro-American settlement, as Sargent (1884, p. 545–546) wrote, 'trees sprang up and this region is now well covered with a vigorous growth of black oaks of different species. White oaks, however, are not abundant, and other species common to the region, such as the walnuts, the yellow-poplar and the beech, are wanting in these young forests, indicating perhaps the effect of fires in checking the subsequent growth or development of many useful timber trees.' According to agricultural census data, between 1870 and 1880 in Kentucky, excluding the Appalachian region, the agricultural percentage of most counties exceeded 25%, which represents a significant land use change that reduced surface fire spread, typically indicating the onset of gradual fire exclusion (Figure 2; Maizel et al., 1998; Hanberry, 2021). Following the Weeks Act of 1911, a management shift from active fire ignition to active fire suppression steadily diminished the area burned annually, resulting in fire exclusion (Hutchison and Winters, 1953).

Rapid European settlement, along with harvest and fire exclusion, resulted in an information deficit about historical forests in the United States. In the absence of other relevant information, my objective was to provide tree composition data from a historical assessment conducted between 1907 and 1909 (Holmes and Bradfield, 1908; Hall, 1909; Holmes and Hall, 1909) for all of Kentucky, three ecological regions (i.e., eastern, central, and western Kentucky), and the Daniel Boone National Forest in eastern Kentucky and the Land Between the Lakes National Recreation Area in central Kentucky (Figures 1–3). This was contrasted with current tree composition, including the application of a divergence index, to answer the research question: What were the spatiotemporal compositional changes? Tree composition during 1907–1909 was likely to reflect the original forests of the Appalachian region in eastern Kentucky, given the limited change in land use and disturbance compared to more accessible regions (Figures 1, 2). In the Loess Hills region of western Kentucky, fire

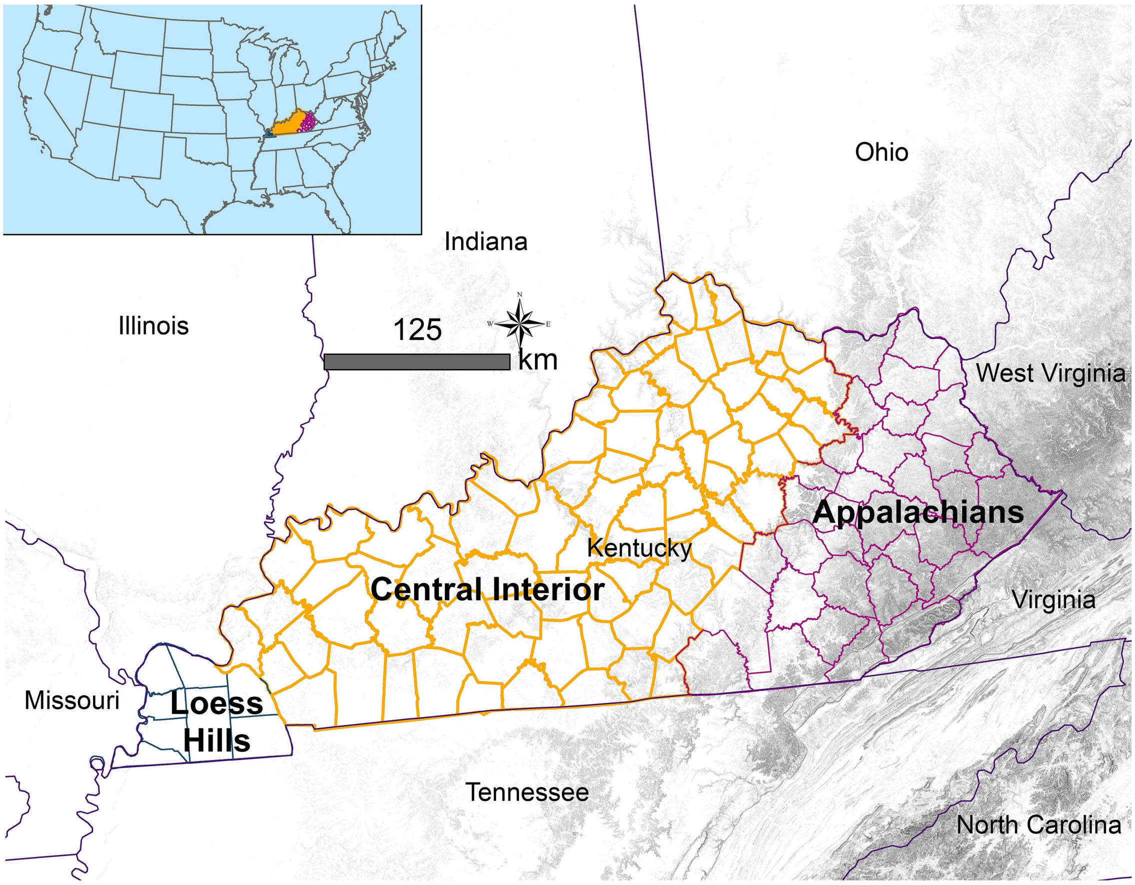

FIGURE 1
Three regions in Kentucky, United States, with topography (darker shading indicates greater ruggedness) and counties (outlined).

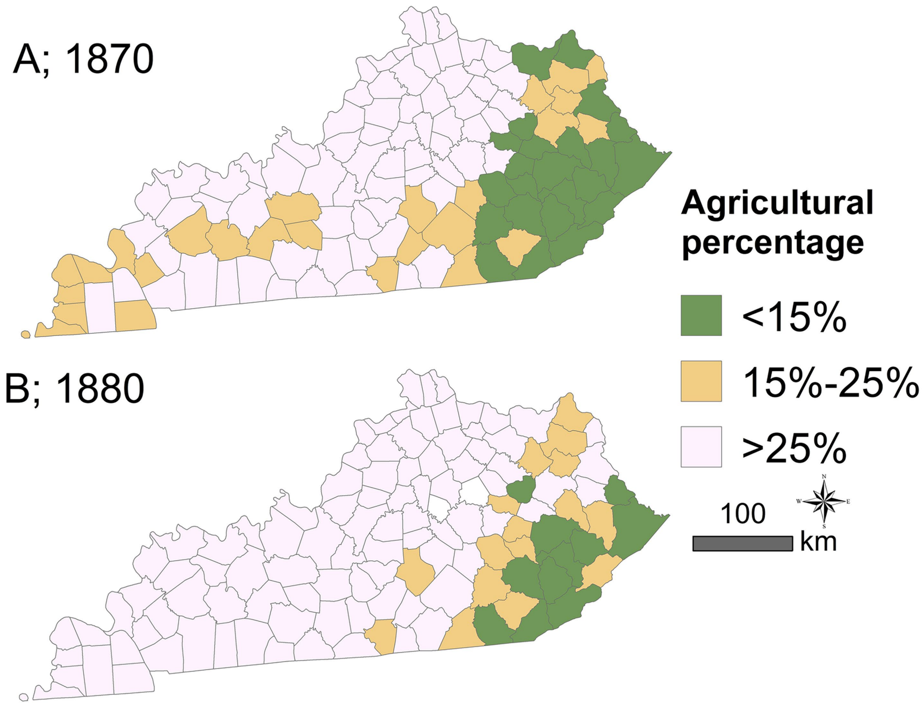

FIGURE 2
Percentage of agricultural area during 1870 and 1880.

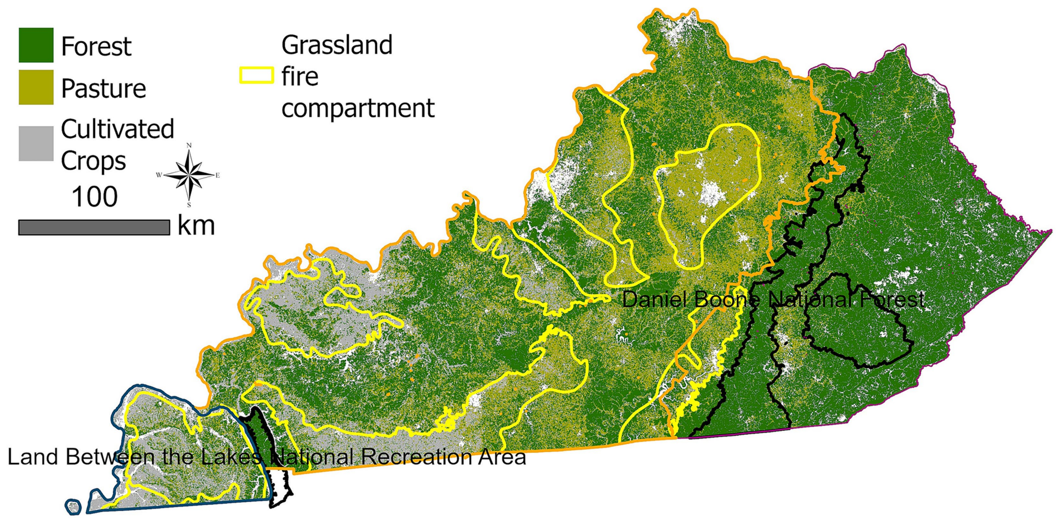

FIGURE 3
Grassland fire compartments (Hanberry and Noss, 2022) and current land use in Kentucky, with Daniel Boone national forest and land between the lakes (outlined).

exclusion and subsequent changes may have started between 1850 and 1860, with substantial changes occurring by 1880 due to agricultural cultivation (> 25% of county area; Figures 1, 2) and the cessation of intentional burning in parts (DeFriese, 1880; Loughridge, 1888). Moreover, some counties in the Central Interior region were under Euro-American land use by 1790, allowing a century for colonizing tree species to establish by the time of the 1907–1909 assessment (Shaler, 1888). Additionally, it is important to note that few current tree samples are available for the Loess region and the Land Between the Lakes National Recreation Area, and the historical assessment likely overlooked less commercial, smaller diameter tree species in the understory (e.g., sourwood, *Oxydendrum arboreum*).

2 Methods

For historical tree composition in Kentucky, I used a 1907–1909 assessment of standing volume for trees ≥ 30.5 cm across 119 counties (Holmes and Bradfield, 1908; Hall, 1909; Holmes and Hall, 1909), which I converted to percentages by tree species or genera. I used total values compiled in Barton (1919) to identify errors. I determined the area-weighted mean of tree composition for ecological units of analysis, which included all of Kentucky, three ecological regions, and the Daniel Boone National Forest and Land Between the Lakes National Recreation Area. For the ecological regions of the Appalachians, Central Interior, and Loess Hills above the Mississippi River, I assigned counties to the three ecological units because the administrative boundaries closely followed the ecological boundaries. This approach allowed the text of the historical assessment to remain relevant. However, for the Daniel Boone National Forest and the Land Between the Lakes National Recreation Area, I clipped the counties by the federal land boundaries and then calculated mean tree percentages weighted by the clipped county area.

Tree percentages from the 1907–1909 assessment of standing volume for trees ≥ 30.5 cm may generally reflect the dominant tree percentages of the past, supported by comparisons to historical tree surveys. To help validate this approach, I compared tree percentages from standing volume estimates in the 1907–1909 assessment in two counties of the Appalachian region to witness trees from land parcel surveys beginning around 1800 (Frost and Harrold, 2013) and to surveys conducted in the Loess region during 1820 by the state of Kentucky (Bryant and Martin, 1988). For witness tree percentages from original land ownership surveys beginning around 1800 (Frost and Harrold, 2013), I used data from the combined Wayne and Whitley Counties, which had only 22 and 9% agricultural area by 1850, with an active fire culture in Kentucky's forestlands during the 1800s (Sargent, 1884). As another validation in the Loess region, 10,330 trees were surveyed during 1820 (Bryant and Martin, 1988). In the Loess region, the county agricultural area ranged from 7 to 19% by 1850, and fire was still applied, according to historical accounts (DeFriese, 1880; Loughridge, 1888).

The USDA Forest Service Forest Inventory and Analysis (FIA; USDA Forest Inventory and Analysis FIA DataMart, 2021; Bechtold and Patterson, 2005) quantifies current forest conditions. The FIA plots occur every 2,500 ha, supplying landscape-scale estimates, and are reported by counties as well as National Forest boundaries. For surveys conducted during 2010–2014 in Kentucky, approximately 38,050 trees ≥ 12.7 cm in diameter at 1.37 m height were recorded: 19,200 trees in the Appalachian region, 17,985 trees in the Interior region, and 880 trees in the Loess Hills region. Within the Appalachian region, 2,600 trees were found in Daniel Boone National Forest. Within the Interior region, 500 trees were found in the Land Between the Lakes National Recreation Area.

To compare similarity, I calculated the squared-chord distance metric between surveys. Divergence in composition is indicated by squared-chord distance ≥ 0.15, and to account for thresholds for continuous data, values between 0.12 and 0.15 suggest initial divergence (nonparametric measure with bounds from 0 to 2, reaching high values when species are not the same; squared-chord distance = $\sum(\sqrt{Pi} - \sqrt{Qi})^2$; where i is the ith percentage of tree groups in the two different sources, Q and P; package philentropy; Overpeck et al., 1985; Ewing, 2002; Drost, 2018; R Core Team, 2024). Comparisons included (1) land parcel surveys for two counties in the

Appalachian region during the early 1800s, (2) Kentucky land surveys for the Loess region during 1820, and (3) modern surveys for Kentucky's three ecological regions, the Daniel Boone National Forest, and Land Between the Lakes National Recreation Area. Typical problems arose when comparing historical trees, including the grouping of species and likely incomplete surveys of smaller-statured species (see tables for groupings). For comparison of oaks, I grouped all 19 oak species recorded in modern surveys, including the rarer lowland oak species (e.g., *Quercus pagoda* and *Quercus shumardii*), given that multiple oak species were included in 'black oak' for the historical assessment. For comparison of 'gum', I grouped sweetgum and blackgum (*Nyssa sylvatica*) in modern surveys. Because small tree species and uncommon tree species (e.g., red maple) were not specifically estimated in the historical assessment (grouped as 'scattered'), to make comparisons as equal as possible, I removed small tree species (*Oxydendrum arboreum*; *Sassafras albidum*). I presented squared-chord distance values with and without American chestnut, which was primarily a species of the Appalachians but was extirpated a few years after 1920, when chestnut blight (*Cryphonectria parasitica*) entered the Appalachian region (Cruikshank, 1943).

3 Results

As validation for this approach of applying standing volume estimates to represent historical forests, I calculated squared-chord distance values of the tree percentages from the assessment of standing volume during 1907–1909 to witness tree percentages from original land parcel surveys during the early 1800s, as well as tree surveys conducted during the early 1800s in the Loess region. The squared-chord distance values were 0.05 and 0.09, indicating similar forests, respectively, for the two comparisons. For example, the oak percentage was the same, at 41% of all trees, for both the assessment and the land parcel surveys in two Appalachian counties. In comparison to the Loess region, Kentucky land surveys during 1820 showed a greater percentage of oaks, at 61% of all trees compared to 49% of all trees in the 1907–1909 assessment, and hickories, at 11% of all trees compared to 6% of all trees in the assessment, as may be expected according to oak decreases over time.

Regarding the squared-chord distance metric between tree percentages in the assessment and modern surveys, overall in Kentucky, divergence was 0.19 excluding American chestnut and 0.24 including chestnut between the historical forests of the assessment and current forests from modern surveys. Daniel Boone National Forest, located within the Appalachians, and the Appalachian region had values of 0.16 and 0.17, respectively; however, with the inclusion of chestnut, these values increased to 0.24 and 0.26, respectively. The Land Between the Lakes National Recreation Area, in the Interior region adjacent to the Loess Hills, displayed the least divergence, with a squared-chord distance of 0.14, as chestnut historically was not an important component of these forests. The Loess Hills region had a squared-chord distance of 0.28, and chestnut was not a component of the forests; the Interior region had squared-chord distances of 0.30 with chestnut and 0.33 without chestnut. Values between 0.12 and 0.15 suggest some divergence, whereas divergence is indicated by a squared-chord distance ≥ 0.15.

In terms of changing composition between the historical assessment and modern surveys, the greatest decreases were in oaks, American chestnut, and American beech (Tables 1–4; Figure 4). Changes in Kentucky largely reflected the greater area and number of trees in the Appalachian and Interior regions. For example, chestnut and beech made up at most 1% of all trees in the Loess region. Oaks overall diminished by 31 percentage points, from 52% of all trees to 21% of all trees in Kentucky. The greatest decrease occurred in the Interior region, where oaks decreased by 34 percentage points. Oaks decreased by 29 to 30 percentage points within the Appalachian and Loess regions. The least decrease in oaks occurred in the Daniel Boone National Forest, at 19 percentage points. Within the Interior region, the Land Between the Lakes National Recreation Area had the greatest oak percentage both historically and currently, at 74.2 and 50.4% of all trees, respectively, with a 24

TABLE 1 Comparison of tree percentage (> 2% of all trees) in the historical assessment and current surveys, including up to two species within genera, for all of Kentucky.

Species/genus	Scientific name	Historical	Current		
Oaks	*Quercus alba, Q. montana, Q. rubra, Q. velutina, Q. coccinea, Q. muehlenbergii*	52.1	20.9	*Q. alba*	6.5
				Q. montana	4.9
American beech	*Fagus grandifolia*	9.9	3.6		
				C. glabra	3.9
Hickories	*Carya glabra, C. alba*	7.0	9.5	*C. alba*	2.4
Gum	*Liquidambar styraciflua, Nyssa sylvatica*	5.2	4.0	*N. sylvatica*	2.4
				A. rubrum	9.1
Maples	*Acer saccharum, A. rubrum*	4.9	18.9	*A. saccharum*	8.6
American chestnut	*Castanea dentata*	4.7	0.0		
Yellow-poplar	*Liriodendron tulipifera*	3.5	8.9		
Ashes	*Fraxinus americana, F. pennsylvanica*	2.1	4.4	*F. americana*	2.4
Pines	*Pinus echinata, P. virginiana, P. taeda*	1.4	3.2		
Elms	*Ulmus americana, U. rubra, U. alata*	1.3	2.8		
Eastern redcedar	*Juniperus virginiana*	0.2	6.1		
Sourwood	*Oxydendrum arboreum*	trace	2.4		

TABLE 2 Comparison of tree percentage (> 2% of all trees) in the historical assessment and current surveys, including up to two species within genera, for the Appalachian Mountain region and Daniel Boone National Forest.

Species/Genus	Scientific name	Historical	Current		
Appalachian region					
		52.5	23.8	*Q. alba*	8.0
Oaks	*Quercus alba, Q. montana, Q. rubra, Q. velutina, Q. coccinea*			*Q. montana*	7.5
American beech	*Fagus grandifolia*	9.4	5.0		
American chestnut	*Castanea dentata*	9.0	0.0		
				A. rubrum	14.3
Maples	*Acer saccharum, A. rubrum*	5.7	20.8	*A. saccharum*	6.2
				C. glabra	4.0
Hickories	*Carya glabra, C. alba*	5.4	8.9	*C. alba*	2.8
Yellow-poplar	*Liriodendron tulipifera*	5.3	12.0		
Shortleaf pine	*Pinus echinata*	3.6	0.5		
Gum	*Liquidambar styraciflua, Nyssa sylvatica*	2.1	3.6	*N. sylvatica*	2.8
Eastern hemlock	*Tsuga canadensis*	1.6	2.6		
Ashes	*Fraxinus americana, F. pennsylvanica*	0.6	2.1	*F. americana*	1.5
Sourwood	*Oxydendrum arboreum*	Trace	4.1		
Virginia pine	*Pinus virginiana*	Trace	2.1		
Daniel Boone					
				Q. alba	13.6
Oaks	*Quercus alba, Q. montana, Q. rubra, Q. velutina, Q. coccinea*	51.1	32.4	*Q. montana*	8.3
American chestnut	*Castanea dentata*	8.9	0.0		
American beech	*Fagus grandifolia*	7.0	3.0		
				C. glabra	3.2
Hickories	*Carya glabra, C. alba*	6.0	6.6	*C. alba*	2.4
Shortleaf pine	*Pinus echinata*	5.9	0.4		
Yellow-poplar	*Liriodendron tulipifera*	5.8	9.3		
				A. rubrum	18.0
Maples	*Acer saccharum, A. rubrum*	4.2	21.6	*A. saccharum*	3.7
Gum	*Liquidambar styraciflua, Nyssa sylvatica*	2.8	2.7	*N. sylvatica*	2.4
Eastern hemlock	*Tsuga canadensis*	2.6	8.8		
American basswood	*Tilia americana*	2.1	0.7		
Sourwood	*Oxydendrum arboreum*	trace	5.3		

percentage point decrease in oaks. American chestnut experienced complete extirpation due to an introduced disease. Overall in Kentucky, American chestnut loss was almost five percentage points, but the historical distribution of chestnut was concentrated in the Appalachian Mountains, including Daniel Boone National Forest, where chestnut decreased by nine percentage points. American beech decreased by six percentage points throughout Kentucky, with the greatest decrease of nine percentage points occurring in the Interior region.

The greatest increase overall was in maples, which increased by 14 percentage points in Kentucky (Tables 1–4). In the assessment, sugar maple (*Acer saccharum*) was the species referred to as maple, whereas red maple was noted in an appended list of species (Holmes and Bradfield, 1908). Red maple increased from a trace species to become the most abundant species, at 9.1% of all trees, along with yellow-poplar at 8.9% of all trees, in Kentucky. Red maple is currently the most abundant species in the Appalachian region, which increased by 15 percentage points in maples. Daniel Boone National Forest had the greatest increase in maples, at 17 percentage points. The smallest increase in maples, by 7.5 percentage points, occurred in the Land Between the Lakes National Recreation Area, within the Interior region that increased by 12 percentage points in maples. Sugar maple is currently more abundant than red maple in the Interior region.

Yellow-poplar increased by 5.5 percentage points in Kentucky. Yellow-poplar was a moderate component of the historical assessment, at 3.5% of all historical trees. Yellow-poplar has become the second most abundant species, at 8.9% of all trees, similar to red maple in current abundance. Yellow-poplar increased the most in the Appalachians, with increases in Daniel Boone National Forest and the Interior region, and declines in the Land Between the Lakes National Recreation Area and the Loess region.

TABLE 3 Comparison of tree percentage (> 2% of all trees) in the historical assessment and current surveys, including up to two species within genera, for the Central Interior region and Land Between the Lakes National Recreation Area.

Species/Genus	Scientific name	Historical	Current		
Interior					
Oaks	*Q. alba, Q. montana, Q. rubra, Q. velutina, Q. coccinea, Q. muehlenbergii*	52.2	17.8	*Q. alba*	5.2
				Q. muehlenbergii	2.6
American beech	*Fagus grandifolia*	11.0	2.4		
Hickories	*Carya glabra, C. alba, C. ovata*	7.9	10.2	*C. glabra*	3.9
Gum	*Liquidambar styraciflua, Nyssa sylvatica*	5.4	4.3	*L. styraciflua*	2.4
Maples	*Acer saccharum, A. rubrum*	4.9	17.2	*A. saccharum*	11.5
				A. rubrum	3.8
Ashes	*Fraxinus americana, F. pennsylvanica*	3.0	6.5	*F. americana*	3.3
				F. pennsylvanica	3.0
American chestnut	*Castanea dentata*	3.0	0.0		
Yellow-poplar	*Liriodendron tulipifera*	2.6	5.8		
American sycamore	*Platanus occidentalis*	2.2	1.3		
Black walnut	*Juglans nigra*	2.1	2.2		
Elms	*Ulmus americana, U. rubra, U. alata*	1.4	4.5	*U. americana*	1.6
Eastern redcedar	*Juniperus virginiana*	0.3	11.7		
Pines	*Pinus virginiana, P. taeda*	0.3	2.5	*P. virginiana*	1.3
Celtis	*Celtis laevigata, C. occidentalis*	0.1	2.4	*C. occidentalis*	2.3
Black cherry	*Prunus serotina*	trace	2.2		
Walnut	*Juglans nigra*	2.1	2.2		
Land Between the Lakes					
Oaks	*Q. alba, Q. montana, Q. rubra, Q. velutina, Q. coccinea, Q. stellata, Q. falcata*	74.2	50.4	*Q. alba*	28.2
				Q. montana	8.9
Hickories	*Carya glabra, C. alba*	9.0	10.5	*C. glabra*	6.5
				C. alba	2.4
Gum	*Liquidambar styraciflua, Nyssa sylvatica*	8.6	7.3	*L. styraciflua*	4.8
Yellow-poplar	*Liriodendron tulipifera*	3.7	0.8		
Maples	*Acer saccharum, A. rubrum*	2.0	9.5	*A. saccharum*	5.8
				A. rubrum	3.4
Elms	*Ulmus americana, U. rubra, U. alata*	0.8	3.4	*U. alata*	3.2
Eastern redcedar	*Juniperus virginiana*	Trace	4.6		
Loblolly pine	*Pinus taeda*	0.0	2.6		
Sourwood	*Oxydendrum arboreum*	Trace	3.0		

Eastern redcedar increased by almost six percentage points in Kentucky. Eastern redcedar had a trace presence in the historical assessment and has become the fifth most abundant tree species, at 6.1% of all current trees. In the Interior region, eastern redcedar increased from trace presence (0.3% of all trees) to the most abundant tree species, at 11.7% of all current trees.

The ecological regions and federal lands exhibited unique differences, which were suggested but not fully captured for the state of

TABLE 4 Comparison of tree percentage (> 2% of all trees) in the historical assessment and current surveys, including up to two species within genera, for the Loess Hills region.

Species/Genus	Scientific name	Historical	Current		
Oaks	*Q. alba, Q. coccinea, Q. montana, Q. rubra, Q. stellata, Q. velutina, Q. falcata, Q. pagoda*	48.7	19.1	*Q. falcata*	4.7
				Q. pagoda	2.8
Gum	*Liquidambar styraciflua, Nyssa sylvatica*	19.7	7.5	*L. styraciflua*	5.7
Elms	*Ulmus americana, U. rubra, U. alata*	6.3	10.2	*U. alata*	5.0
				U. americana	3.3
Hickories	*Carya glabra, C. alba, C. ovata*	5.8	10.1	*C. ovata*	4.1
				C. glabra	3.1
Baldcypress	*Taxodium distichum*	4.1	3.5		
Yellow-poplar	*Liriodendron tulipifera*	3.4	2.5		
American sycamore	*Platanus occidentalis*	3.0	1.1		
Maples	*Acer saccharum, A. rubrum, A. saccharinum*	1.9	12.2	*A. rubrum*	4.6
				A. saccharinum	4.3
Ashes	*Fraxinus americana, F. pennsylvanica*	1.2	9.2	*F. pennsylvanica*	7.3
Eastern cottonwood	*Populus deltoides*	1.1	2.2		
Loblolly pine	*Pinus taeda*	0.0	3.1		
Celtis	*Celtis laevigata, C. occidentalis*	Trace	2.8	*C. laevigata*	2.2
Sassafras	*Sassafras albidum*	Trace	2.2		
Black cherry	*Prunus serotina*	Trace	2.1		

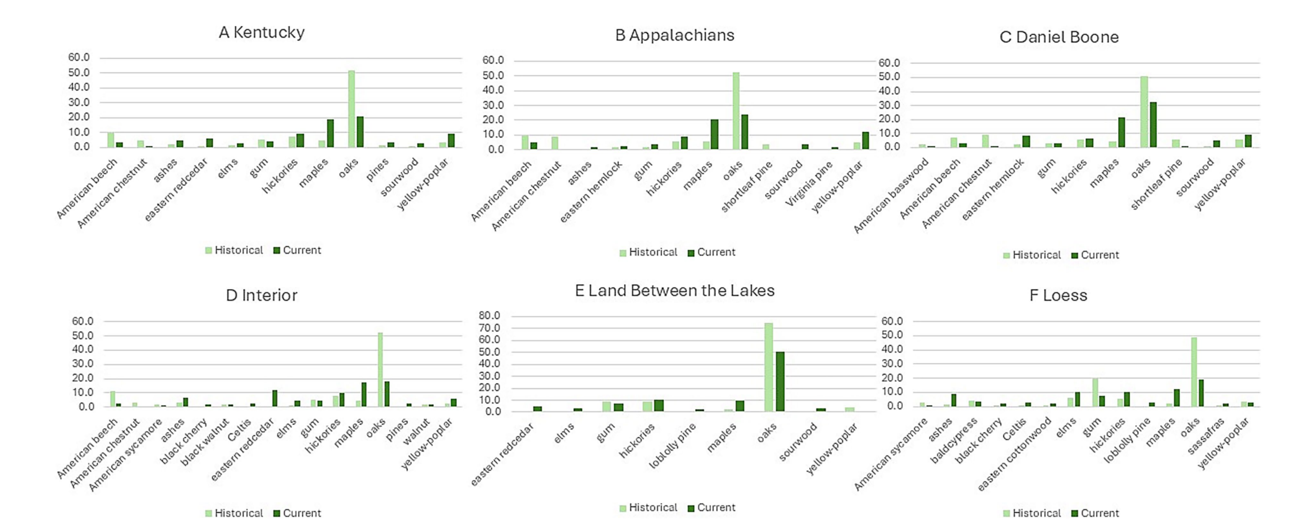

FIGURE 4
Changes in tree species or genera percentages (of all trees) between the historical assessment (1907–1909) and current surveys for **(A)** Kentucky, **(B)** Appalachian Mountains, **(C)** Daniel Boone National Forest, **(D)** Central Interior, **(E)** Land Between the Lakes National Recreation Area, and **(F)** Loess Hills.

Kentucky. In the Appalachian region, sourwood, a small tree species, increased from trace ('scattered') presence in the historical assessment to 4.1% of all trees, with a concentration of 5.3% of all trees in Daniel Boone National Forest. Sourwood also increased in the Land Between the Lakes National Recreation Area. Hickories increased by 3.5 to 4 percentage points in the Loess and Appalachian regions. Eastern hemlock (*Tsuga canadensis*) increased in Daniel Boone National Forest from 2.6 to 8.8% of all trees. Both elms and ashes increased in the Interior region and the Loess region, where green ash became the most abundant species. Sweetgum decreased in the Loess region.

Pine species have increased in Kentucky due to increases in Virginia pine (*Pinus virginiana*) in the Appalachians and loblolly pine in the Loess region, with both species also increasing in the Interior region. Pines overall were a minor historical component (1.4% of all trees) in Kentucky, with moderate abundance in the Appalachian region at 3.6% of all trees, particularly concentrated at 5.9% of all trees in Daniel Boone National Forest. Historically, pines primarily consisted of shortleaf pine, with some pitch pine (*P. rigida*) and Virginia pine (Holmes and Bradfield, 1908). Currently, shortleaf pine has decreased by more than three percentage points to a trace presence (≤ 0.5% of all trees) in the Appalachians and Daniel Boone National Forest. Virginia pine has increased to 2.1% of all trees in the Appalachian region, whereas loblolly pine has been added as a species, particularly in the Loess region and Land Between the Lakes.

4 Discussion

4.1 Overall findings

Concurrent with increased tree densities after surface fire exclusion due to Euro-American settlement, the historical dominance of fire-tolerant oak and pine species was replaced by a diverse array of fire-sensitive, early- and mid-successional tree species in the eastern United States (Hanberry et al., 2019; Hanberry et al., 2023). A comparison between tree composition in a historical assessment (1907 to 1909; Holmes and Bradfield, 1908; Hall, 1909; Holmes and Hall, 1909) and modern surveys (2010 to 2014) in Kentucky revealed similar trends of oak declines relative to gains in red maple. Historically dominant, fire-tolerant oaks decreased from 52% of all trees to 21%, while maples increased from 5 to 19%, with similar trends observed in each region. The historically dominant maple species was primarily the shade-tolerant, late-successional sugar maple, which was evaluated as a species in the assessment (i.e., the species description of maple referred only to sugar maple), whereas red maple was included in the appendix list of trees and shrubs due to its historical limitation to swamps and other wetlands (Holmes and Bradfield, 1908; Hall, 1909; Holmes and Hall, 1909). Currently, red maple is the dominant species in Kentucky, comprising 9.1% of all trees, albeit just slightly more abundant than yellow-poplar and sugar maple, which constitute 8.9 and 8.6% of all trees, respectively. The state transition from grasslands and open oak or pine forests to denser forests of diverse species, including red maple, is well-documented for the eastern U. S. (e.g., Shaler, 1888; Maxwell, 1910; Harrod et al., 1998; Frost and Harrold, 2013; Tulowiecki et al., 2025). Shaler (1888:27) described the vegetation of Kentucky as primarily continuous old-growth forests that were 'singularly open, so that the early track-ways and wagon roads were easily made through them.' The departure in tree composition aligns with changes based on historical land surveys compared to modern tree surveys in part of the Appalachians in Kentucky (Frost and Harrold, 2013), and bordering Kentucky in West Virginia (Thomas-Van Gundy and Morin, 2021), southern Ohio (Deines et al., 2016), Indiana (Hanberry, 2019), and Missouri (Hanberry et al., 2012a, 2012b) within the historically oak-dominated central eastern United States.

In Kentucky, the three ecological regions influenced species distributions. Yellow-poplar increased from 3.5 to 9% of all trees in Kentucky, but it was concentrated in the Appalachian Mountains region, where its proportion rose from 5 to 12% of all species, similar to southern Ohio (Deines et al., 2016) and Indiana (Hanberry, 2019). In the Appalachians, American chestnut and shortleaf pine decreased, along with oaks. Eastern redcedar increased from <1 to 6% of all trees state-wide, but this change occurred in the Interior region, where eastern redcedar increased from a trace presence (0.3% of all trees) to the most abundant tree species at 11.7% of all trees, similar to Missouri (Hanberry et al., 2012a) and Indiana (Hanberry, 2019). Eastern redcedar has been the most successful tree species at colonizing non-forested areas such as the Interior region, where grasslands have historically been converted to pastures and crops (Hanberry et al., 2012a; Hanberry, 2019). Although sweetgum has increased in the uplands of the southeastern U. S., south of Kentucky (Hanberry, 2019; Hanberry et al., 2019; Hanberry et al., 2023), it has decreased in the historical floodplains of the Lower Mississippi Alluvial Valley (Hanberry et al., 2012b), which also occurred in the Loess Hills region of Kentucky, bordering the Mississippi River. Instead, elms, ashes, and hickories increased, similar to changes in Missouri (Hanberry et al., 2012a, 2012b), along with the addition of planted loblolly pine in the Loess region.

These changes in tree species resulted in divergent historical and current forests, as measured by the squared-chord distance, in Kentucky. Following Euro-American settlement and the associated exclusion of fire, the greatest divergence occurred in the Interior region, with the least divergence in the Appalachian region. The Appalachian region as a whole had more divergent forests than the Daniel Boone National Forest within it, perhaps due to management efforts in the Daniel Boone National Forest aimed at maintaining and restoring oak forests. However, the Appalachians and Daniel Boone National Forest were almost as divergent as the other regions from historical forests when American chestnut was included in the divergence analysis. American chestnut was extirpated by an introduced fungal disease (chestnut blight; Cruikshank, 1943). Nonetheless, the Land Between the Lakes National Recreation Area, within the Interior region where chestnut was not as abundant as in the Appalachian region, had the lowest squared-chord distance value (0.14), within the borderline range between similarity and divergence.

Although these results are credible and align with reported ecosystem transitions, I used county assessments of standing volume for trees ≥ 30.5 cm due to the absence of accessible data sources about historical forests in Kentucky. Volume measurements from that time may not directly translate to relative tree proportions. However, the similarity to historical land surveys from the early 1800s in an overlapping part of the Appalachians (Frost and Harrold, 2013) and the Loess region (Bryant and Martin, 1988) indicates that standing volume was generally representative of historical forests. The historical assessment reflected the older trees of the forests, which may have helped in representing tree surveys from the early 1800s. Indeed, representativeness was indicated by (1) tree species/genera percentages from the assessment conducted during 1907–1909 being similar to overlapping historical records from the early 1800s, (2) the surveyors conducted the assessment to represent forests during 1907–1909 in Kentucky, not unrepresentative forests (Holmes and Bradfield, 1908; Hall, 1909), (3) older, larger diameter trees were characteristic of historical forests (Defebaugh, 1906; Holmes and Bradfield, 1908), and (4) the tree species and genera percentages from the assessment during 1907–1909 were consistent with oak-dominated historical forests from surrounding studies, with no evident discrepancies (Frost and Harrold, 2013; Hanberry et al., 2012a, 2012b; Deines et al., 2016; Hanberry, 2019; Thomas-Van Gundy and Morin, 2021). Agricultural cultivation had already occurred by the time of the assessment, affecting the abundance of American beech, sugar maple, chestnut, hickories, and the red oak group, even though these tree species had not been harvested for timber, and commercial supply remained excellent at the time of the assessment (Holmes and Bradfield, 1908:91). Harvesting had exhausted accessible sources of large diameter yellow-poplar, and the more limited black walnut and black cherry, followed by white oak and the commercially similar chestnut oak (*Q. montana*) by the time of this assessment (1907–1909; Holmes and Bradfield, 1908). Nonetheless, trees less than 46 cm in diameter were 'usually too small to be cut with much profit', resulting in relative abundance of most species (Holmes and Bradfield, 1908, p. 67). As with many tree surveys, smaller-statured trees were not measured as carefully as larger species in the historical assessment. For example, while sourwood is a component of Appalachian forests, this species was grouped in the assessment with other undistinguished species (i.e., 'scattered' grouping; Holmes and Bradfield, 1908; Hall, 1909; Holmes and Hall, 1909). As an additional caveat, small samples of modern survey plots were conducted in the Loess Hills and the Land Between the Lakes National Recreation Area.

4.2 Appalachian Mountain region and Daniel Boone National Forest

In the historical assessment, the Appalachian region of eastern Kentucky was dominated by fire-tolerant species, with a significant component of late-successional species. Fire-tolerant oaks, American chestnut, and shortleaf pine comprised 65% of all trees, and when including the hickories, fire-tolerant species represented 70% of all trees. The late-successional species, primarily American beech, along with eastern hemlock and sugar maple, accounted for another 17% of all trees. Tree species were distributed along strong topographic gradients based on fire exposure and protection (Frost and Harrold, 2013; Lafon et al., 2017). The most fire-tolerant species, such as shortleaf pine, were found on the most exposed sites of south-facing upper slopes and upland flats, while the late-successional species were located in the lower elevations, in valleys along aquatic barriers to fire, and on high-elevation rocky ridges and outcrops with limited fine fuels, which reduced the chance of ignition (Frost and Harrold, 2013).

The Appalachians were frequently exposed to surface fires (Ayres and Ashe, 1905; Lafon et al., 2017). The Appalachian region was bordered on the west side by a large extent of relatively flat topography, creating a compartment ideal for the spread of fire, resulting in grasslands (Figure 3; see the Interior region below). Historical accounts and models of fire compartments described grasslands extending into the southeastern counties of the Appalachian region (Frost and Harrold, 2013; Hanberry and Noss, 2022). In addition, fire occurred within the smaller compartments of the Appalachian Mountains, with evidence of surface fires covering 80% of the 2.2 million ha examined during 1900 and 1901 (Ayres and Ashe, 1905; Lafon et al., 2017). Fire compartments encompassed entire mountainsides, and only the most protected sites avoided fire exposure, particularly given fire as a management tool used by both native humans and Euro-American settlers (Ayres and Ashe, 1905; Lafon et al., 2017; Colenbaugh and Hagan, 2023). Frequent surface fire removed small-diameter tree and shrub species, historically producing savannas and woodlands in the Appalachians (Frost and Harrold, 2013). Although historical photographs may show continuous or nearly continuous tree cover, fire histories and descriptions of the understory indicated that beneath the overstory canopy, small-diameter tree species were removed, resulting in closed woodlands with closed overstories and open under- and midstories, relatively free of tree growth (Ayres and Ashe, 1905). The forage available in the open understory of woodlands supported livestock until fire protection led to dense tree growth (Cruikshank, 1943).

Fire exclusion has occurred slowly over time in the Appalachian region, with greater tree establishment beginning during the 1930s–1960s (Harrod et al., 1998; Hutchinson et al., 2019; Stambaugh et al., 2020). Typically during fire exclusion, the historically dominant species first establish more densely, followed by a gradual expansion of fire-sensitive species and a loss of spatial differentiation in species distributions, which is then followed by the replacement of fire-tolerant tree species by fire-sensitive species in the uplands (Harrod et al., 1998; Frost and Harrold, 2013; Flatley et al., 2015). Specifically, species such as beech, sugar maple, hemlock, and eastern white pine (*Pinus strobus*) expanded upslope from fire-sheltered lowlands or downslope from ridges, intermixing into upper slopes and upland flats, thereby blurring the sharp zonation by elevation (Frost and Harrold, 2013). After the initial increase in establishment by historically abundant species, invasion by colonizing, early- and mid-successional species, such as red maple, yellow-poplar, and Virginia pine, was accelerated by the clearing of historical trees. Eventually, oaks and shortleaf pine diminished in abundance relative to fire-sensitive species.

4.3 Central Interior region and the Land Between the Lakes

Large but disrupted fire compartments with conditions suitable for frequent surface fires, potentially supporting grasslands, occurred throughout the Interior region (Frost and Harrold, 2013). The relatively flat Interior region of Kentucky was documented as grasslands and oak savannas ('barrens'), specifically with tree development where hills broke flat topography, and contained large native herbivores such as bison (*Bison bison*) and elk (*Cervus canadensis*), which interacted with surface fire regimes and the open ecosystems of herbaceous vegetation (Michaux, 1805; Engelmann, 1863; Shaler, 1888; Frost and Harrold, 2013). Grassland fire compartments experienced limited topographic disruption of fires spread by strong westerly winds and were fueled by herbaceous vegetation, which thrived due to precipitation in the humid eastern U. S. (Figure 3; Hanberry and Noss, 2022). Frequent surface fires in grassland fire compartments exposed surrounding areas, which had greater topographic resistance, to fire. Ignitions were encouraged by Native Americans, who burned for various purposes, including to support foodways and travelways by removing woody undergrowth and promoting pasturage (Michaux, 1805; Davidson, 1840; Shaler, 1888; Frost and Harrold, 2013). The 'Great Trail', a network of trails, including those used during bison migration, was burned annually from Indiana to Tennessee (Shaler, 1888; Jakle, 1969). Grasslands and open forest ecosystems of the eastern U. S. contained a significant component of cane (*Arundinaria gigantea*), a perennial bamboo favored by bison (and livestock; Campbell, 2015). Fires could extend for several kilometers, moving rapidly due to westerly winds; however, for surface fires spreading through herbaceous fuels, safe spaces for humans could be created by removing herbaceous vegetation, such as by burning it in advance of the main fire or encouraging tree growth (Michaux, 1805). Similarly, vegetation discontinuities protected trees. Grasslands included a tree component, although sometimes stunted to a brushy, shrubby form due to repeated damage to their aboveground parts. Land management through fire played an integral role in maintaining the historical and paleo-ecosystems of grasslands and woodlands (Frost and Harrold, 2013).

Nonetheless, grasslands in Kentucky were not monolithic like the adjacent Prairie Peninsula extension of the Great Plains grasslands in Illinois, northwest of Kentucky, but were more similar to the grasslands and savannas of Indiana and Ohio, north of Kentucky (Sears, 1926; Hanberry and Noss, 2022). The Interior region of Kentucky did not consist solely of grassland fire compartments; particularly, rivers and other areas that offered protection from fire, such as ravines, valleys, and rugged hills, contained fire-sensitive species and denser forests intermixed with grasslands and oak-dominated savannas and woodlands (Hussey, 1876; Shaler, 1888). Grassland landscapes may contain a smaller oak component than woodland landscapes because uplands in grasslands burn too frequently (i.e., nearly annually) for fire-tolerant tree species to establish, and by definition, only at low densities in grasslands. In protected locations, a range of conditions may support a variety of species. Historical assessments noted a lack of trees and the presence of limited tree species, specifically oaks, but accounts described diverse species and a mosaic of ecosystems, often depicting protected locations near watercourses or along steep valleys for forests of fire-sensitive species (Owen, 1856; Hussey, 1876; Sargent, 1884; Shaler, 1888; Campbell, 1989; Campbell, 2014, 2015). Grasslands and grassland compartments in the eastern U. S., including the eastern Prairie Peninsula merging into eastern woodlands and forests, were intermixed with a range of tree densities and species in fine-textured landscapes (Hanberry et al., 2025).

However, oaks constituted 52% of all trees, and fire-tolerant species reached 63% of all trees when including relatively fire-tolerant chestnut and hickories, in the Interior region during the 1907–1909 assessment, which occurred about a century in some counties after fire exclusion and the transition to increased tree establishment, including fire-sensitive tree species. The fire exclusion process was evidenced by diminished oak percentages in current surveys. Fire-tolerant oak species were more dominant before decades of fire exclusion allowed encroachment by other tree species into uplands, which historically were exposed to fire. Beech, at 9.4% of all trees, ranked second in abundance after oaks in the Interior for the historical assessment, which was similar to Indiana and Ohio, where beech was intermingled with oaks historically, suggesting some tolerance to fire by beech (Sears, 1926; Hanberry, 2019). The relative magnitude of fire-tolerant species to fire-sensitive species indicated that historically, more area than not was exposed to frequent fires and in open ecosystem states, rather than closed forests (Hanberry et al., 2025).

Rapid tree growth occurred after fire exclusion. The initiation of fire exclusion was dated as early as 1790 (Shaler, 1888), extending to 1850 or later, corresponding to Euro-American settlement and land use expansion across the Interior region (Frost and Harrold, 2013). By the first agricultural census in 1850, agricultural area exceeded 95% in three counties within the grasslands centered in the northeastern Interior region, or 'Bluegrass' area, indicating the location of the earliest fire exclusion. In contrast, agricultural area remained less than 15% in most counties in the northwestern Interior region during 1850 (Maizel et al., 1998). Grasslands were plowed into fields that were harvested annually, road density increased, native large herbivores were extirpated, and domestic livestock reached saturation to oversaturation by 1840 to 1850, eliminating grass fuel connectivity, while deliberate annual burning ceased (Shaler, 1888; Frost and Harrold, 2013). In addition, overgrazing of herbaceous plants and the direct clearing of herbaceous vegetation for agricultural use, followed by field abandonment, opened up growing space for trees. Oaks were observed to increase in density, extent, and diameter during the initial few decades of release from fire exclusion (Davidson, 1840; Hussey, 1876; Sargent, 1884). Late-successional sugar maple also increased, likely in locations protected from land use, while American beech decreased. Shaler (1888, p. 30) wrote, 'The germs of the small-seeded trees, maples, etc., were rapidly transported by the wind from the nearest remaining trees which clung about the entrances to the canons that abound in this district and other damp places, and quickly repossessed the ground in forest'. Following increases in the historically dominant species, eastern redcedar expanded throughout the uplands, along with ashes, elms, and red maple, ultimately increasing relative to oak species. Hussey (1876, p. 37) documented, 'the very numerous ravines, valleys, and hillsides become covered with tree growth first. The large tulip trees, hemlocks, sugar maples, beeches, and chestnuts found in these less exposed localities, prove that generations of tree growth have passed since their seeds were scattered here; but the uplands show, that long since the deep valleys and hillsides were covered with forest growth, these were almost or entirely bare.' Land Between the Lakes National Recreation Area contained the greatest oak percentage during the historical assessment, at 74% of all trees, and while oaks have decreased by 24 percentage points in current surveys, oak composition remains significant relative to encroaching tree species. Land Between the Lakes National Recreation Area may represent changes that occurred in parts of the Interior region between Euro-American settlement and the historical assessment during the early 1900s.

4.4 Loess Hills region

The Loess Hills region is the smallest of the regions, located in western Kentucky. Historical vegetation comprised localized floodplain ecosystems on the very western margin and upland forested ecosystems, dominated by grasslands, oak savannas, and woodlands, with extensive areas of cane (*Arundinaria gigantea*; Bryant and Martin, 1988; Bryant, 1993). Monotypic stands of cane, a perennial grass, were known as canebrakes, and the Loess Hills region was historically called the Cane Hills (Shull, 1921). Loess, or wind-blown soil, hills of 30 to 60 m in height stretch along the east side of the Mississippi River floodplain from Louisiana to Kentucky, confined to the western quarter of the region (Bryant, 1993). The loess hills thin and flatten on the eastern side of the Loess Hills region (Bryant, 1993). Therefore, the majority of the region had conditions that favored fire spread and the maintenance of grasslands and savannas, similar to the adjacent Interior region (Bryant, 1993).

By the time of the historical assessment during 1907–1909, oaks represented 49% of all trees, and oaks and hickories together accounted for 55% of all trees, indicating the initiation of fire exclusion and the replacement of fire-tolerant oaks by fire-sensitive tree species, compared to the land survey of 1820 (Bryant and Martin, 1988). Oaks made up 61% of all trees, and oaks and hickories collectively comprised 72% of all trees during the Kentucky land survey of 1820. Agricultural area ranged from 7 to 19% in all counties of the Loess region during 1850, but by 1880, it ranged from 25 to 50% in all counties. Over the 30 years between approximately 1850 and 1880, grasslands and savannas maintained by annual fires became covered by the dominant oak species as burning ceased with Euro-American settlement (DeFriese, 1880; Loughridge, 1888). Oaks were likely released throughout the region, but with disproportionate increases by colonizing sweetgum and elms, which were a more moderate component of forests during the 1820 survey. The eponymous canes of the Cane Hills were replaced by other vegetation, as occurred throughout the southeastern U. S., accelerated by excessive disturbances from livestock (Shull, 1921).

Current forests were reminiscent of floodplain and upland forests and agriculturally disturbed areas of the adjacent Lower Mississippi River Alluvial Valley, rather than the historically dominant oak open ecosystems of this region. The current forests are comprised of abundant elms, ashes, and maples, many of which were species that historically displayed spatial separation in protected lowlands and then expanded into upland old fields after fire exclusion, due to their colonizing traits of rapid early growth and abundant seed production (Defebaugh, 1906; Hanberry et al., 2012b). Specifically, the most abundant current species are green ash (a colonizing species associated with wetlands), sweetgum (a colonizing species historically associated with coastal and floodplain forests, particularly in the Lower Mississippi Alluvial Valley), winged elm (*Ulmus alata*; a colonizing species in old fields and agricultural areas), southern red oak (*Quercus falcata*), red maple (a colonizing species from wetlands into disturbed areas), silver maple (*Acer saccharinum*; a colonizing species in floodplains), shagbark hickory (*Carya ovata*; a colonizing species in old fields), baldcypress (found in floodplains), and American elm (*U. americana*; found in floodplains). Sweetgum, combined with blackgum, was most abundant during the 1907–1909 assessment compared to the 1820 survey or modern surveys. Given about a century between each survey, sweetgum may have increased first, particularly due to colonization from the Lower Mississippi River Alluvial Valley and other rivers bordering the Loess region (Hanberry et al., 2012b), and then, in turn, sweetgum was disproportionately displaced by ashes, elms, and maples. Loblolly pine was a new species in current surveys, arising from plantations; however, loblolly pine is also a colonizing species, historically confined to wetlands, that expanded into upland old fields following fire exclusion (Hanberry et al., 2023). Although all the current forests in the three regions differ from historical forests in different ways, the change from fire-tolerant species and ecosystems to floodplain species in upland forests for this region may exhibit the greatest departure in terms of turnover in species traits, which historically were restricted to zones encompassing a gradient from fire exposure to flood exposure.

5 Conclusion

European colonization resulted in surface fire exclusion, followed by the forestation of open ecosystems and tree densification within woodlands and forests, along with the replacement of fire-tolerant oak and pine species by fire-sensitive tree species. A historical assessment (1907–1909) and modern surveys (2010–2014) of Kentucky revealed the progression from oaks to a diversity of fire-sensitive tree species, with unique differences by region and different initiation dates for fire exclusion, as early as 1790 in the Bluegrass part of the Interior region and as late as the 1930s–1960s in the Appalachian region. In current surveys compared to the historical assessment, red maple increased in all three regions, with regional increases particularly in yellow-poplar, eastern redcedar, green ash, and the new addition of planted loblolly pine. The replacement of fire-tolerant oaks by fire-sensitive species, alongside contemporaneous assessments of rapid tree growth in densities and spatial extent, and the loss of understory disturbance mechanisms (fire, native large herbivores) to control small-diameter tree densities, indicated that forestation and densification ensued after fire exclusion.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

BH: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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References

Ayres, H. B., and Ashe, W. W. (1905). *The southern Appalachian forests*. Washington, DC: Department of the Interior US Geological Survey.

Barton, J. E. (1919). *The amount of standing timber in Kentucky*. Washington, DC: Northeastern Forest Experiment Station, US Department of Agriculture, 25I–284I.

Bechtold, W. A., and Patterson, P. L. (2005). *The enhanced forest inventory and analysis program—National sampling design and estimation procedures*. Asheville, NC: USDA Forest Service, Southern Research Station.

Bryant, W. S. (1993). "Vegetation of loess bluff ravines in the Jackson purchase region of Kentucky" in *Proceedings of the 9th central hardwood Forest conference*. eds. A. R. Gillespie, G. R. Parker, P. E. Pope and G. Rink (St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station), 281–288.

Bryant, W. S., and Martin, W. H. (1988). "Vegetation of the Jackson purchase of Kentucky based on the 1820 general land office survey" in *Proc. of the first annual symposium on the natural history of lower Tennessee and Cumberland River valleys*. ed. D. H. Snyder (Clarksville, TN: The Center for Field Biology. Austin Peay State University), 264–276.

Campbell, J. J. N. (1989). "Historical evidence of forest composition in the bluegrass region of Kentucky," in *Proceedings of the central Hardwood Forest Conference 7*, 231–246.

Campbell, J. J. N. (2014). Summary statement. Available online at: https://bluegrass-woodland.com/uploads/Summary_Statement.pdf

Campbell, J. J. N. (2015). Historical notes on the big barrens in Kentucky. Available online at: https://bluegrasswoodland.com/uploads/Historical_Notes_on_the_Big_Barrens.pdf (accessed May 31, 2025).

Colenbaugh, C., and Hagan, D. L. (2023). After the fire: potential impacts of fire exclusion policies on historical Cherokee culture in the southern Appalachian Mountains, USA. *Hum. Ecol.* 51, 291–301. doi: 10.1007/s10745-023-00395-z

Collins, R. F. (1975). *A history of the Daniel Boone national forest*. Winchester, KY: USDA Forest Service, Southern Region.

Cruikshank, J. W. (1943). *North Carolina forest resources and industries*. Washington, DC: US Department of Agriculture Forest Service, Government Printing Office.

Davidson, R. (1840). *An excursion to the mammoth cave and the barrens of Kentucky*. Lexington, KY: A.T. Silliman and Son.

Defebaugh, J. E. (1906). *History of the lumber industry of America*. IL: American Lumberman.

DeFriese, L. H. (1880). Report on the timbers of the district west of the Tennessee River, commonly known as the Purchase District. *Geol. Surv. Kentucky* 5, 125–158.

Deines, J. M., Williams, D., Hamlin, Q., and McLachlan, J. S. (2016). Changes in forest composition in Ohio between euro-American settlement and the present. *Am. Midl. Nat.* 176, 247–271. doi: 10.1674/0003-0031-176.2.247

Drost, H. G. (2018). Philentropy: information theory and distance quantification with R. *J. Open Source Softw.* 3:765. doi: 10.21105/joss.00765

Engelmann, H. A. (1863). Remarks upon the causes producing the different characters of vegetation known as prairies, flats, and barrens in southern Illinois with specific reference to observation made in Perry and Jackson counties. *Am. J. Sci. Arts Series* 2, 84–396.

Ewing, H. A. (2002). The influence of substrate on vegetation history and ecosystem development. *Ecology* 83, 2766–2781. doi: 10.1890/0012-9658(2002)083[2766:TIOSOV]2.0.CO;2

Fernow, B. E. (1902). *Economics of forestry: A reference book for students of political economy and professional and lay students of forestry*. New York, NY: Crowell.

Flatley, W. T., Lafon, C. W., Grissino-Mayer, H. D., and LaForest, L. B. (2015). Changing fire regimes and old-growth forest succession along a topographic gradient in the Great Smoky Mountains. *Forest Ecology and Management*, 350, 96–106.

Frost, C. C., and Harrold, C. (2013). *Historic fire regimes and presettlement vegetation of big south fork National Recreation Area, Tennessee & Kentucky*. Oneida, TN: Report for the National Park Service.

Hall, R. C. (1909). *Study of forest conditions in Kentucky*. Frankfort, KY: State Board of Agriculture, Forestry and Immigration.

Hanberry, B. B. (2019). Trajectory from beech and oak forests to eastern broadleaf forests in Indiana, USA. *Ecol. Process.* 8, 1–8. doi: 10.1186/s13717-018-0155-3

Hanberry, B. B. (2021). Timing of tree density increases, influence of climate change, and a land use proxy for tree density increases in the eastern United States. *Land* 10:1121. doi: 10.3390/land10111121

Hanberry, B. B., Brzuszek, R. F., Foster, H. T., and Schauwecker, T. J. (2019). Recalling open old growth forests in the southeastern mixed Forest province of the United States. *Écoscience* 26, 11–22. doi: 10.1080/11956860.2018.1499282

Hanberry, B. B., Dey, D. C., and He, H. S. (2012a). Regime shifts and weakened environmental gradients in open oak and pine ecosystems. *PLoS One* 7:e41337. doi: 10.1371/journal.pone.0041337

Hanberry, B. B., Kabrick, J. M., He, H. S., and Palik, B. J. (2012b). Historical trajectories and restoration strategies for the Mississippi River Alluvial Valley. *For. Ecol. Manag.* 280, 103–111. doi: 10.1016/j.foreco.2012.05.033

Hanberry, B. B., and Noss, R. F. (2022). Locating potential historical fire-maintained grasslands of the eastern United States based on topography and wind speed. *Ecosphere* 13:e4098. doi: 10.1002/ecs2.4098

Hanberry, B. B., Ruffner, C. M., and Tatina, R. (2025). Contextualizing estimated tree densities and expert-classified ecosystems in the historical Midwestern United States, a region with exposure to frequent fires. *Forests* 16:748. doi: 10.3390/f16050748

Hanberry, B. B., Stober, J. M., and Bragg, D. C. (2023). Documenting two centuries of change in longleaf pine (*Pinus palustris*) forests of the coastal Plain Province, southeastern USA. *Forests* 14:1938. doi: 10.3390/f14101938

Harrod, J., White, P. S., and Harmon, M. E. (1998). Changes in xeric forests in western Great Smoky Mountains National Park, 1936-1995. *Castanea* 63, 346–360.

Holmes, J. S., and Bradfield, W. (1908). First report on a study of forest conditions of Kentucky. 17th biennial report of Bureau of Agriculture, labor, and statistics. Frankfort, Kentucky, USA: State Board of Agriculture, Forestry and Immigration.

Holmes, J. S., and Hall, R. C. (1909). Study of forest conditions in Kentucky. 18th biennial report of Bureau of Agriculture, labor, and statistics, Frankfort, Kentucky. Frankfort, Kentucky, USA: State Board of Agriculture, Forestry and Immigration.

Hussey, J. (1876). Report on the botany of barren and Edmonson counties. Kentucky geological survey part II, Vol. I, second series. Frankfort, Kentucky, USA: State Board of Agriculture, Forestry and Immigration.

Hutchinson, T. F., Stambaugh, M. C., Marschall, J. M., and Guyette, R. P. (2019). Historical fire in the Appalachian plateau of Ohio and Kentucky, USA, from remnant yellow pines. *Fire Ecol.* 15, 1–12. doi: 10.1186/s42408-019-0052-x

Hutchison, O. K., and Winters, R. K. (1953). *Kentucky's forest resources and industries*. Washington, DC: US Department of Agriculture Forest Service, Government Printing Office.

Jakle, J. A. (1969). Salt on the Ohio Valley frontier, 1770–18201. *Ann. Assoc. Am. Geogr.* 59, 687–709. doi: 10.1111/j.1467-8306.1969.tb01807.x

Lafon, C. W., Naito, A. T., Grissino-Mayer, H. D., Horn, S. P., and Waldrop, T. A. (2017). *Fire history of the Appalachian region: A review and synthesis*. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station.

Loughridge, R. N. (1888). *Report on the geological and economic features of the Jackson purchase region*. Frankfort, KY: Kentucky Geological Survey.

Maizel, M., White, R. D., Root, R., Gage, S., Stitt, S., Osborne, L., et al. (1998). "Historical interrelationships between population settlement and farmland in the conterminous United States, 1790 to 1992" in *Perspectives on the land use history of North America: A context for understanding our changing environment*. ed. T. D. Sisk (Washington, DC: U.S. Geological Survey, Biological Resources Division, Biological Science Report).

Mastran, S. S., and Lowerre, N. (1983). *Mountaineers and rangers: A history of federal forest management in the southern Appalachians, 1900–1981*. Washington, DC: U.S. Department of Agriculture, Forest Service.

Maxwell, H. (1910). The use and abuse of forests by the Virginia Indians. *William Mary Q.* 19, 73–103. doi: 10.2307/1921261

Michaux, F. A. (1805). *Travels to the west of the Allegheny Mountains*. London: Shury.

Overpeck, J. T., Webb, T. I., and Prentice, I. C. (1985). Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quat. Res.* 23, 87–108. doi: 10.1016/0033-5894(85)90074-2

Owen, D. D. (1856). *Report of the geological survey of Kentucky, made during the years 1854 and 1855*. Frankfort, KY: A.G. Hodges.

R Core Team (2024). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Sargent, C. S. (1884). *Report on the forests of North America (exclusive of Mexico)*. Washington, DC: US Government Printing Office.

Sears, P. B. (1926). The natural vegetation of Ohio. II. The prairies. *Ohio J. Sci.* 26, 128–146.

Shaler, N. S. (1888). *Kentucky: A pioneer commonwealth*. Boston, MA: Houghton, Mifflin and Co.

Short, K. C. (2022). *Spatial wildfire occurrence data for the United States, 1992–2020 [FPA_FOD_20221014]*. Fort Collins, CO: Forest Service Research Data Archive.

Shull, C. A. (1921). Some changes in the vegetation of western Kentucky. *Ecology* 2, 120–124.

Stambaugh, M. C., Marschall, J. M., and Abadir, E. R. (2020). Revealing historical fire regimes of the Cumberland plateau, USA, through remnant fire-scarred shortleaf pines (*Pinus echinata* mill.). *Fire Ecol.* 16, 1–15. doi: 10.1186/s42408-020-00084-y

Thomas-Van Gundy, M., and Morin, R. (2021). Change in montane forests of east-Central West Virginia over 250 years. *For. Ecol. Manag.* 479:118604. doi: 10.1016/j.foreco.2020.118604

Tulowiecki, S. J., Hanberry, B. B., and Abrams, M. D. (2025). Spatial and temporal pervasiveness of indigenous settlement in oak landscapes of southern New England, US, during the late Holocene. *Land* 14:525. doi: 10.3390/land14030525

USDA Forest Inventory and Analysis FIA DataMart. (2021). Available online: https://www.fia.fs.usda.gov/tools-data/ (accessed October 18, 2023).

Williams, M. (1989). *Americans and their forests: A historical geography*. Cambridge: Cambridge University Press.

Williams, G. (2005). *The USDA Forest Service – The first century*. Washington, DC: U.S. Department of Agriculture.