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Timing of Tree Density Increases, Influence of Climate Change, and a Land Use Proxy for Tree Density Increases in the Eastern United States

Brice B. Hanberry 

USDA Forest Service, Rocky Mountain Research Station, Rapid City, SD 57702, USA; brice.hanberry@usda.gov

Abstract: Long-term observations inform relationships among changes in vegetation, climate, and land use. For the eastern United States, I compared the timing of tree change, comprised of density and diversity increases, with the timing of climate change, as measured by change point detection of the Palmer Modified Drought Index (PMDI) that accounts for water balance, in two prairie ecological provinces, four grassland landscapes, and four forest landscapes. Historical evidence supplied documentation of tree density increases between approximately 1860 and 1890 in the two prairie provinces of grasslands bordering eastern forests. Additionally, because timing of tree increases paralleled when land area reached $\geq 25\%$ agricultural use, I categorized grassland and forest landscapes that increased to $\geq 25\%$ agricultural area during 1860, 1880, 1900, and 1920. One change point detection method identified no significant PMDI change points during the 1800s. The other method found the southern prairie province, bordering eastern forests, had change points of 1855 and 1865 during an interval of relative dryness. Only two of four grassland landscapes, and one of four forest landscapes had change points, which occurred during relative dryness or were continuous with historical variation. Inconsistent changes in moisture availability did not provide correlations with comprehensive tree increases, but land use change corresponded with tree changes based on timing, magnitude and direction of change, and mechanism. The agricultural threshold may provide the critical missing component that allows progression in analysis of land use change effects on vegetation.

Keywords: alternative state; drought; fire; moisture; PDSI; PMDI; state change



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1. Introduction

Historical records impart the necessary context to identify general timing and magnitude of vegetation changes, and to separate land use and climate influences on vegetation changes. The degree to which climate and land use contribute to changes in vegetation is not established. Climate has conventionally been used to explain distribution and type of ecosystems, and climate data typically have been more accessible than land use data. However, examination of current trends in tree density or diversity during recent decades, without consideration of comprehensive forest transitions during past centuries, will not discern whether trends are new, or long-standing transitions due to changing baseline conditions. If timing of tree changes in density or diversity is misidentified, a mismatch between tree change and climate change will occur. Depending on the timing of when tree change is first documented to occur, examination of the corresponding climate may be decades or centuries too late. For example, in the eastern United States, precipitation has generally increased during the 1900s, particularly since the 1970s, which can result in confounding climate change with wholesale land use changes since Euro-American settlement [1–3].

Furthermore, a lag interval may occur between when climate changes, which commonly is a 30 year period of sustained change as opposed to typical weather variation, and when tree density and diversity change enough in response to override the inertia of

older trees in forests. Trees are slow-growing, long-lived, and immobile after establishment, resulting in resistance to change under historical range of variation. Saplings sometimes are examined, but most saplings will die regardless of conditions, simply because many more saplings are produced than can become canopy trees; therefore, saplings are indefinite indicators of change because they have not yet succeeded at surviving conditions to adulthood. Unless forests are extensively cleared or trees are scarce or at lower densities, such as in grasslands or savannas, trees that are surveyed during a 30 year interval may better reflect conditions of the previous 30 years or longer, given the mean age of forests.

Even a significant climate change that corresponds with tree change in density or diversity may not necessarily cause consistent changes in tree density or diversity, particularly if the magnitude of change is relatively small or the sign or direction of climate change varies. Significant climate changes may not be ecologically meaningful, if climate change remains within historical variation of when trees did not change in density or diversity [3]. Most tree species are distributed across a range of annual total precipitation and significant precipitation change may not be equivalent to an effect size in tree response. If the same patterns of tree change in density or diversity occur under a variety of different climate conditions, then climate is not a sufficient mechanism for tree change. Indeed, in some cases, trees may have the same response of increased density and diversity under drought as under increased moisture because they are actually responding to other, more immediately influential disturbance changes, such as no longer dying from fire (i.e., drought can reduce the quantity of fuels available to burn trees [4–6]).

Historical tree surveys and pollen records demonstrate that primary tree composition of oaks and pines has remained stable at landscape scales in the eastern United States for at least the past few thousand years throughout a range of moisture and temperature variability, until changing after Euro-American settlement [7,8]. Historical open oak- and pine-dominated forests that were most dominant during the 1800s may have persisted for hundreds of years without replacement due to low severity, non-stand-replacing disturbances [9]. Long-lived oak and pine trees recorded in historical tree surveys during the 1800s or earlier represent a relatively unbroken timeline. That is, 1000 years of climate may represent two to four generations of oak and pine trees because oak and pine trees present during the 1800s may have established during the 1500s to 1600s and were offspring of trees that likely, similarly, lived for hundreds of years and provided the major source of propagules and advance regeneration to the forests.

Since Euro-American settlement in the eastern United States, many tree species have densified where they are present and expanded in range, which has been attributed to both increased precipitation and exclusion of frequent surface fires, in addition to other land use changes [2,8,10]. Current closed successional forests of diverse tree species are novel and not analogous to historical open old-growth fire-dependent oak and pine forests or closed old-growth forests of shade-tolerant tree species [7,10,11]. Most naturally regenerated forests in the eastern U.S. are young due to frequent overstory tree removal, with a mean age of 40 to 80 years [12]. The southeastern U.S. contains even younger loblolly pine (*Pinus taeda*) plantations, harvested in 20 to 30-year rotations, in which broadleaf species typically are controlled with herbicides; thus, intensive forestry products management supplants tree response to other influences.

With a hard boundary of ocean to the east, eastern tree species are concurrently shifting westward in distribution into the central grasslands of the United States (Figure 1) [13], which has been ascribed to slight increases in precipitation [2]. Based on survey records during the 1800s, of trees that were present historically in the tallgrass prairie provinces bordering eastern forests, fire-tolerant oaks may have been about 65% of all trees, along with some representation by upland hickories and also lowland elms and similar mesic, fire-sensitive species (e.g., in wetland prairies and along the Missouri River and numerous tributaries) [6,8,14]. Historically rare or nearly absent fire-sensitive but drought-tolerant eastern redcedar (*Juniperus virginiana*) and a variety of mesic, fire- and drought-sensitive species have increased in Nebraska, Illinois, and Missouri [8,15,16]. In the southern

prairie province of Texas, *Juniperus ashei* and *Prosopis glandulosa* are examples of species that have increased in density and expanded in grasslands [17]. Furthermore, eastern forests as a whole are also expanding and replacing grasslands [13]. Tree advancement and densification in grasslands were well-recognized in historical accounts. Scribner's statistical atlas of the United States during 1883 [18] stated that due to arborescent vegetation: "The prairie region is fast disappearing . . . The result is that that the eastern part of what was, fifty years ago, a prairie region would scarcely be recognized as such today."

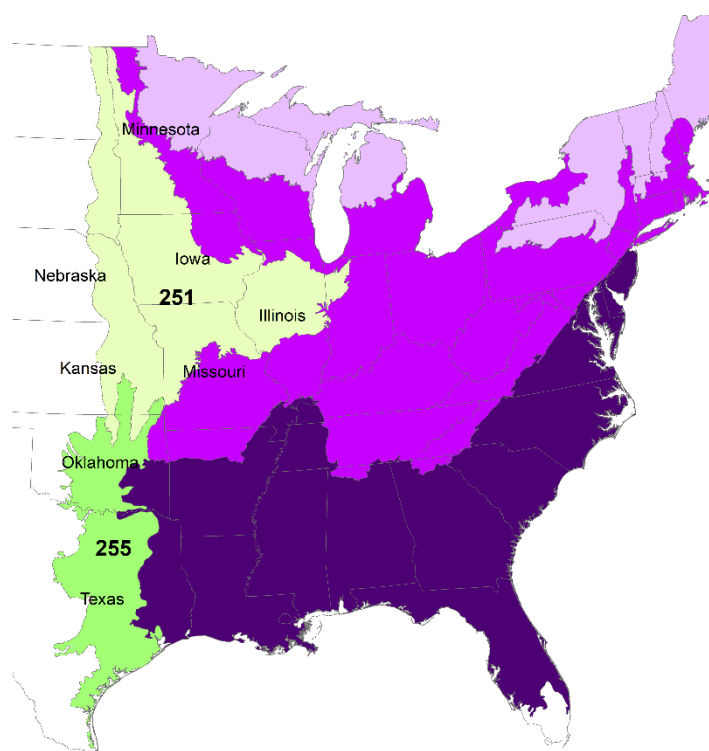


Figure 1. Generalized boundaries of eastern tallgrass prairie grasslands (light green) and forests in the eastern United States (purple colors with variation depicting the southeast region, central east region, and northeast region). The northern (251) and southern (255) prairie ecological provinces are also demarcated.

Here, I applied an approach that included a combination of historical evidence from published accounts to isolate initiation of tree changes in density or diversity, the climate metric of water availability from the Palmer Modified Drought Index (PMDI) modeled from tree-ring chronologies calibrated with instrumental records [19], and statistical change point tests of PMDI to determine if significant change in climate preceded tree expansion from eastern forests into the central grasslands during the period 1860 to 1890 in the United States. I also applied change point detection to grassland and forest landscapes based on an index of land use change, the threshold of 25% land area in agriculture, which appeared to indicate approximate timing of vegetation change throughout the eastern United States, for four grassland and four forest landscapes representing land use change around 1860, 1880, 1900, and 1920 throughout the eastern United States (Figure 2). However, if timing of tree change followed unprecedented land use change after Euro-American settlement, then land use change was determined to be the driving factor and any corresponding and significant climate change points would only be supporting secondary factors. I then discussed whether climate and land use met the following criteria: correspondence in timing with tree change, magnitude beyond historical range of variation, consistent direction of change, and mechanism.

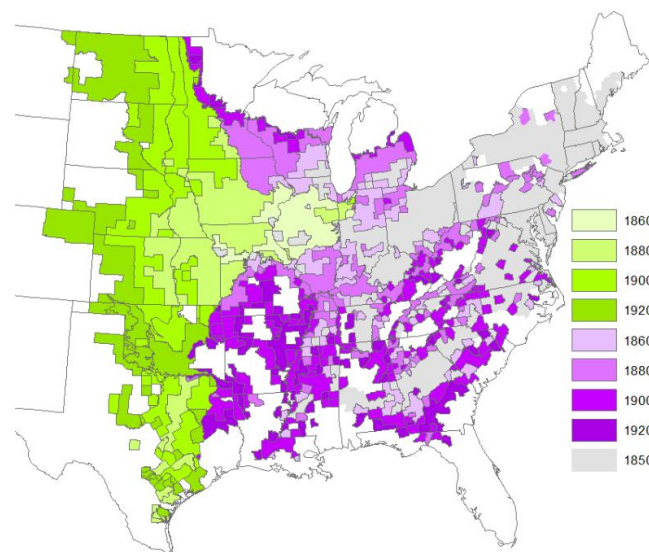


Figure 2. Decade where area in agriculture reached $\geq 25\%$ for four grassland landscapes (green) and four forest landscapes (purple). Gray designates where area in agriculture was $\geq 25\%$ by 1850, at the beginning of the agricultural surveys.

2. Materials and Methods

2.1. Timing of Tree Change from Historical Records

Historical evidence was compiled from published accounts to establish timing, as specifically as possible, of tree expansion from eastern forests into the northern and southern prairie provinces of the central grasslands in the United States. Historical accounts usually are difficult to translate into specific data points for analysis. Additionally, archival literature is obscure and challenging to locate and consequently, fragmentary in nature. Nonetheless, historical records can inform timing of trends when surveys do not supply continuous data in space and time, and in fact, national surveys were suspended during the approximate time of change. Historical land surveys, principally conducted by the General Land Office, recorded trees generally before 1860 in the eastern United States. The oldest available modern and spatiotemporally comprehensive tree surveys began during the 1960s (although surveys commenced after the McSweeney–McNary Forest Research Act of 1928), varying by U.S. state. Well-accepted ecological divisions were used for delineating grasslands and forests [20].

2.2. Decade That Agricultural Area Reached $\geq 25\%$ by County as an Index of Land Use Change

Further context for the issue of climate change and tree change can occur if the timing of tree change is derived from a time series of spatial land use data. This is an improvement to determining tree change by imprecise literature for each ecological province. However, logically, if land use change dictates timing of tree change, then any detection of climate change points will be, at best, supporting secondary factors.

One historical land use dataset is agricultural area since 1850, where area in agriculture $\geq 25\%$ by county provides a rough approximation for tree change (Figure 3) [21]. For example, during 1860, 77% of Illinois, the easternmost state in the northern prairie province where Gleason [22] documented the progressive change to agriculture, with fire exclusion and tree increases, was $\geq 25\%$ agricultural area. During the previous decade, 11% of Illinois was $\geq 25\%$ in agriculture, as Gleason [22] described. Oklahoma did not become a state officially until 1907 but based on agricultural area in Kansas to the north and Texas to the south, a large part of the southern prairie province may have become $\geq 25\%$ in agriculture between 1870 and 1880 (Figure 4). Additionally, the agricultural map captured both western expansion of Euro-American settlement and forested areas that were less suitable for agriculture due to cold temperatures, mountains, or wetlands. Initiation of

tree change in the eastern United States may range from as early as 1620 in the first Euro-American settlements to as late as 1950 in remote forested locations, but these ending and starting points are localized areas rather than larger landscapes, where climate is likely to match in scale [23,24]. As with any threshold for continuous values, values <25% also may indicate initiation of change, particularly given a surrounding matrix of heavily modified land and high road densities. A few areas never reached the 25% agriculture threshold, but as little as 10% anthropogenic land cover may cause a 50% reduction in fire extent, particularly due to linear barriers of trails and roads [25]. Although generalized, the (15% to) 25% agriculture threshold is a proxy for origination of tree change with specific time and locations by county (Figure 2).

2.3. The Palmer Modified Drought Index of Climate Change

Trees are expanding westward along a moisture gradient that decreases from east to west; therefore, precipitation change rather than temperature change is the purported factor for climate change. However, precipitation alone does not represent available water for vegetation. Therefore, many indices have been developed to represent available moisture; the Palmer Drought variants approximate the long-term balance between precipitation and water loss. The Palmer Modified Drought Index (PMDI), modeled from tree-ring chronologies calibrated and validated with instrumental data [19], may be the most accurate and realized proxy of available water for trees over time. Drought intensity is represented by negative numbers. Reconstructions extend PMDI estimates to over 2000 years on a 0.5 degree latitude/longitude grid.

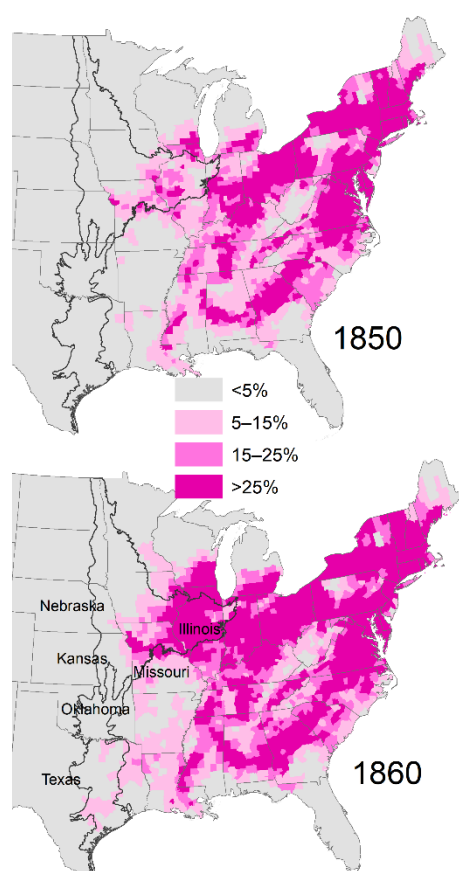


Figure 3. Area in agriculture in 1850 and 1860 (modified from [21]).

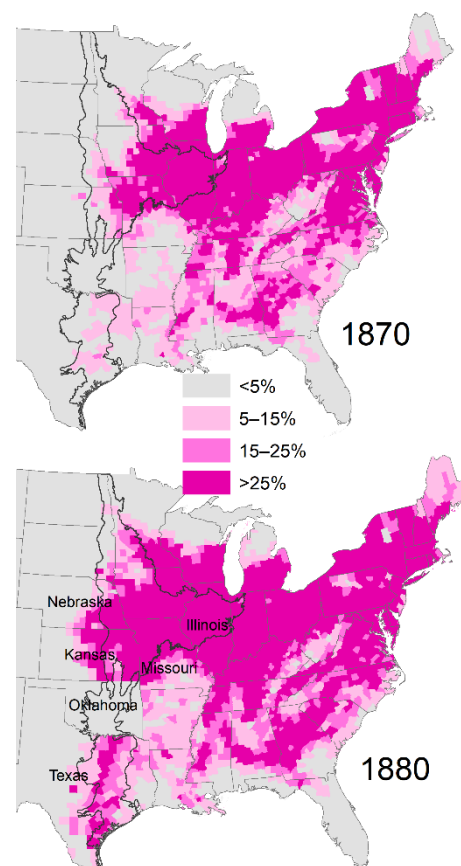


Figure 4. Area in agriculture in 1870 and 1880 (modified from [21]).

2.4. Change Point Detection

Sequential change point detection are tests (e.g., t -test) to identify points at which statistical properties of a time series of observations change. Change point detection does not require separation into time intervals for comparison, particularly appropriate for detecting anomalies. Similarly to drought indices, a variety of different approaches to identify change point detection are available; one method may not identify all major changepoints efficiently [26]. Therefore, to detect all major changepoints, I used two methods for change point detection that applied different algorithms and options (changepoint package with PELT algorithm [27], cpm package with t -test [28,29]).

2.5. Change Point Detection for Historical Records of Tree Change in the Prairie Provinces

In grasslands, tree response is noticeable after a change in conditions and rapid tree change may occur within two decades [22,30–32]. To match documented timing of vegetation change from about 1860 to 1880 in the northern prairie province and a decade later in the southern prairie province, based on historical information, with significant changes in PMDI values, change point detection was applied. Climate change was expected to occur within the preceding 20 years of density or diversity tree changes in grasslands, although other reasonably adjacent change points were considered (Table 1).

Table 1. Approximate decades of tree change in density and diversity and expected preceding Palmer Modified Drought Index (PMDI) change for two prairie provinces based on historical records and for grassland and forest areas after reaching the threshold of 25% agriculture.

Extent	Tree Change	PMDI Change
North prairie	1860–1880	1840–1860
South prairie	1870–1890	1850–1870
Grassland	1860 (1850–1870)	1830–1850
	1880 (1870–1890)	1850–1870
	1900 (1890–1910)	1870–1890
	1920 (1910–1930)	1890–1910
Forest	1860 (1850–1870)	1820–1850
	1880 (1870–1890)	1840–1870
	1900 (1890–1910)	1860–1890
	1920 (1910–1930)	1880–1910

2.6. Change Point Detection for Grassland and Forest Landscapes Based on Land Use Change

Change points for PMDI were identified in four grassland and four forest landscapes that reached $\geq 25\%$ agriculture by 1860, 1880, 1900, and 1920 (i.e., each landscape corresponded with a decade of land use change; Figure 2; Table 1). The date of tree change is relatively fixed, albeit with some uncertainty. For grasslands, with rapid response by trees within 20 years, climate change was expected to occur between 1830 to 1850 for areas $\geq 25\%$ agriculture by 1860, that is, initiation of tree increases in density and diversity from 1850 to 1870 (Table 1). Because forests are resistant to change if larger trees already occupy growing space, long lags may occur. However, as indicated by rapid conversion to agriculture, the majority of eastern forests were cleared in cycles during this time interval, which opened growing space for trees. Additionally, many of these forests were savannas and woodlands, essentially a combination of grasslands and overstory trees. For forests then, the lag before tree change was extended from 20 years to 30 years. For example, climate change was expected to occur between 1820 to 1850 for areas $\geq 25\%$ agriculture by 1860, with tree change initiating between 1850 to 1870.

3. Results

3.1. Timing of Tree Change from Historical Information

According to historical accounts, tree changes commenced from about 1860 to 1880 in the northern prairie province and while not unvarying in onset, perhaps a decade later for the landscape of the southern prairie province (Table 2). Timing and location remained relatively general despite the search for precise information. These changes encompassed both increased tree density and diversity. Moreover, trees have continued to increase in density and diversity since the 1800s.

Table 2. Location and years when tree or shrub encroachment were documented in the two prairie provinces.

Extent	Location	Year	Reference
North prairie	Kansas	before 1867	Taylor 1867
	Illinois, Indiana, Iowa, Wisconsin	after 1860	Gleason 1922
South prairie	Oklahoma	before 1931	Bruner 1931
	Oklahoma and south prairies	before 1844	Grigg 1844
	Texas	before 1878 to 1898	Cook 1908

For the northern prairie province, Taylor [33] documented rapid spread of trees into the grasslands of Kansas: “I first witnessed a phenomenon of which I had often heard—the spontaneous production of forests from prairie land. Hundreds of acres, which the cultivated fields beyond had protected against the annual inundation of fire, were completely covered with young oak and hickory trees, from four to six feet in height.” Gleason [22], who is now regarded as a prominent ecologist, wrote that rapid and noticeable tree advancement into grasslands ensued after fire exclusion, which he determined occurred about 1860 in Illinois: “Settlement of the forested regions of the Middle West began about the opening of the nineteenth century, progressed steadily westward, and reached the Missouri River in fifty years. Actual settlement of the prairies was long avoided, vast areas were still untouched at the time of the Civil War, and prairie fires did not cease being a menace in parts of Illinois until 1860 and in Iowa until somewhat later. As soon as fires ceased, the advance of the forest was renewed, and at a rate probably more rapid than the original, since considerable improvement of climate may have taken place since the first advance was stopped by fires. Early literature contains many accounts of this spread of the forested area, which was rapid enough to attract the attention of travelers. It seems to have progressed in several different ways. The lateral advance of the forest at right angles to the streams and the longitudinal advance along the streams continued as before. Willows, cottonwoods, and some hydrophytic shrubs moved rapidly up the rivers and creeks, and were followed by elms, maples, and ashes. Thirty years after the first prairie settlements were made in Macon and Moultrie counties Illinois, these fringing forests had extended one or two miles up the smaller streams. Isolated colonies of mobile species, especially willow, *Salix humilis*, and wild plum, *Prunus americana*, were established well out on the prairie, grew into thickets, and frequently received further additions of forest species, carried in by the birds which visited them or by wind. Large areas of barrens were converted into forest as by magic, when the fires that had maintained them were stopped and the oak sprouts became trees. The total afforestation during this period was considerable and in some cases almost unbelievable, and may best be indicated by a few examples. Thus the driftless area, of northwestern Illinois and southwestern Wisconsin, which now gives the impression of having been heavily forested, was, 80–90% prairie a century ago . . . A little later we find farmers near St. Louis complaining that the rapid growth of trees had seriously restricted the natural pastures. The Mississippi and Illinois rivers at that time had long strips of prairie in their floodplains, which are now completely forested, except where under cultivation. The dune region at the head of Lake Michigan, which is now well forested with oak, was then “treeless, except for a few stunted pines.” Forested areas in Indiana were developed, within the memory of men now living, from barrens over which a man on horseback had been visible for six miles (personal communication from Mr. C. C. Deam). The rapid development of forests on the sand dunes of the Illinois River has been noted elsewhere.”

For the southern prairie province, Bruner [34] specified for Oklahoma: “Because of the recurrence of prairie fires, forest has not developed, but there is abundant evidence

that forests are replacing the prairie since the settlement of the country and the cessation of fires . . . Prairie fires are assumed to be the main factor in keeping the more moist prairies free from trees and even at this early date pioneers had observed the spread of forests into various grassland areas which were protected from fire.” The cited ‘early date’ refers to Gregg [35], who stated: “We are now witnessing the encroachment of the timber upon the prairies, wherever the devastating conflagrations have ceased their ravages.” For Texas, Cook [36] wrote: “It is a matter of popular knowledge in south Texas that extensive regions which were formerly grassy, open prairies are now covered with a dense growth of mesquite (*Prosopis*), prickly-pear cactus (*Opuntia*), and many other shrubby plants of intermediate size. Testimony to this effect is definite and unanimous. It differs locally only in the number of years since the bushes began to grow—thirty years, or twenty, or ten—subsequent to the establishment of the grazing industry on a large scale, the annual burning of the grass by the cattlemen, and finally the fencing of the land for still more intensive grazing . . . That such fires were evidently the cause of the former treeless condition of the southwestern prairies is also shown by the fact that trees are found in all situations which afford protection against fires . . . Trees of many kinds have thriven well where planted in villages and about homesteads, in addition to the natural spread of the woody vegetation as soon as the fires cease . . . If reforestation were to continue uninterrupted by fires or other forms of human interference the Gulf plains of Texas would again become covered with dense subtropical forests . . . ”

3.2. Climate Change Points Based on Historical Accounts of Timing

As a summary of the PMDI dataset over time, mean values during the period between 1800 and 1899 were -0.16 (standard deviation (SD) of 1.47, coefficient of variation (CV) of -949) for the northern prairie province, and -0.11 (SD of 1.61, CV of -1476) for the southern prairie province (Figure 5). Between 1900 and 1999, mean PMDI values were 0.30 (SD of 1.62, CV of 543) for the northern prairie province, and 0.27 (SD of 1.75, CV of 641) for the southern prairie province. Frequent oscillations from drought to pluvials occurred, such as above-average PMDI during the early 1900s followed by the Dust Bowl drought of the 1930s in the northern prairie province, which created a wide range of deviation.

Because tree changes were initiated from about 1860 to 1880 in the northern prairie province and a decade later in the southern prairie province, the expected change in climate was between 1840 and 1860 in the northern prairie province, and between 1850 and 1870 in the southern prairie province (Table 1) [22,36]. The cpm method produced many more change points than the changepoint method, which had no change points during the 1800s. The southern province had 12 significant change points since 1000, including change points at years 1855 and 1865 and then again at 1952 (Table 3). The interval of 1855 and 1864 marked an extremely dry interval (mean of -2 , SD of 1.46; Figure 5). Removal of the years 1855 to 1864 also removed those change points, leaving a continuous interval of similar dryness between 1494 and 1952. By 1952, tree change already had been noticed and documented in scientific publications.

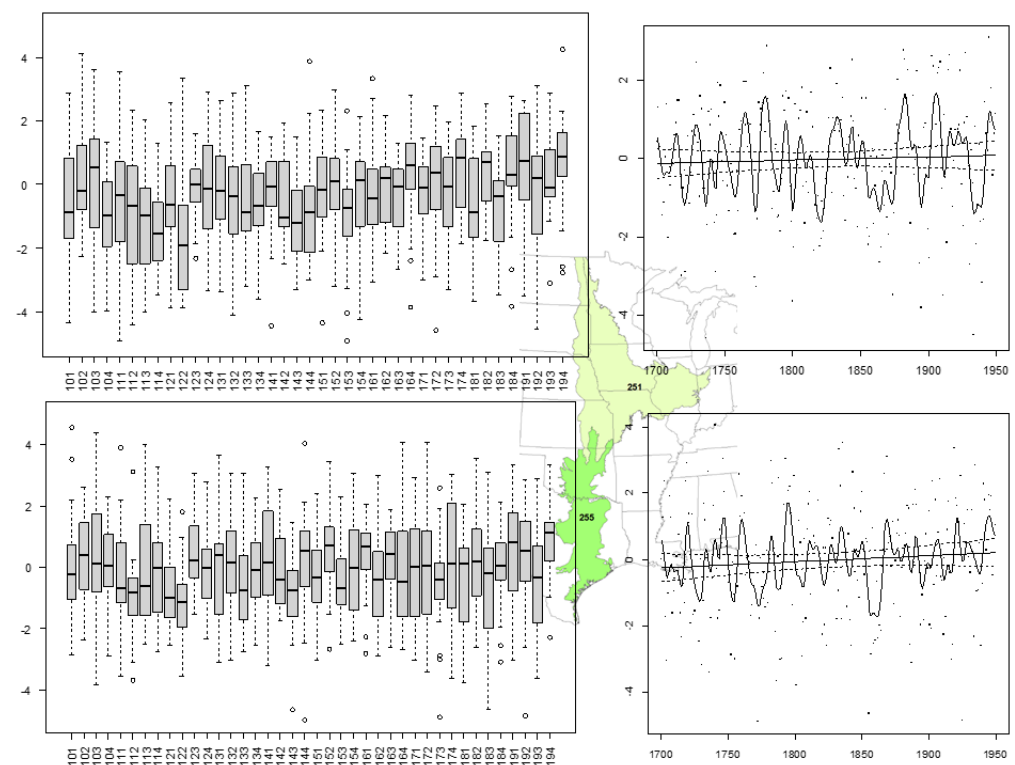


Figure 5. The PMDI values for quarter-century interval box plots during years 1000 to 2000 (101 equals first quarter-century of the 1000s) and all PMDI values during years 1700 to 1950 with a fitted line and 95% confidence intervals for the northern (251) and southern (255) prairie provinces.

Table 3. Approximate decades of tree change in density and diversity and expected preceding change in Palmer Modified Drought Index (PMDI) and sequential change point detection (with two methods) for two prairie provinces and for grassland and forest areas after reaching the threshold of 25% agriculture.

Extent	Tree Change	PMDI Change	Change Point Years
North Prairie	1860–1880	1840–1860	
cpm			1011 1036 1104 1108 1115 1233 1245 1276 1440 1490 1548 1619 1627
changepoint			1636 1664 1672 1697 1700 1903 1931 1942 1953 1973
			1104 1108 1115 1233 1245 1619 1627 1993
South prairie	1870–1890	1850–1870	
cpm			1053 1061 1165 1177 1258 1455 1459 1494 1855 1865 1952 1957
changepoint			1053 1061 1168 1177 1257 1973
Grassland	1860 (1850–1870)	1830–1850	
cpm			1104 1107 1245 1276 1736 1738 1799 1882
changepoint			1104 1107 1619
	1880 (1870–1890)	1850–1870	
cpm			1011 1036 1104 1108 1115 1233 1245 1276 1440 1490 1492 1619 1627
			1636 1664 1672 1697 1700 1736 1855 1876 1894

Table 3. Cont.

Extent	Tree Change	PMDI Change	Change Point Years
changepoint			1104 1108 1115 1233 1245 1440 1490 1492 1973
	1900 (1890–1910)	1870–1890	
cpm			1011 1036 1076 1104 1233 1245 1276 1282 1455 1490 1576 1619 1626
changepoint			1673 1697 1827 1838 1855 1877 1893 1902 1931 1942 1952 1965 1993
	1920 (1910–1930)	1890–1910	1076 1233 1245 1992
cpm			1017 1040 1090 1146 1160 1233 1238 1265 1421 1425 1449 1498 1579
changepoint			1592 1610 none
Forest	1860 (1850–1870)	1820–1850	
cpm			1021 1023 1104 1142 1154 1346 1351 1563 1574 1882
changepoint			none
	1880 (1870–1890)	1840–1870	
cpm			1021 1023 1104 1265 1273 1346 1351 1555 1581 1736 1738
changepoint			none
	1900 (1890–1910)	1860–1890	
cpm			1142 1150 1265 1269 1309 1346 1402 1450 1457 1556 1575 1903
changepoint			none
	1920 (1910–1930)	1880–1910	
cpm			1035 1104 1142 1150 1179 1204 1207 1249 1309 1322 1450 1457 1488
changepoint			1600 1608 1903 1104 1600

The northern province had 23 significant change points since 1000 but no change points during the expected time interval needed to initiate tree change from 1855 to 1880. However, a change point occurred in 1903, which was later than the documented tree change. The time between 1903 and the next change point of 1931 (i.e., the Dust Bowl drought) was less dry (mean of 0.71, SD of 1.61) than the antecedent same length interval of 1875 to 1902 (mean of 0.16, SD of 1.65). If it is plausible that tree changes in the northern prairie province of the grasslands did not occur on average until 1903 or later, then the question is whether a PMDI change between a mean of 0.71 and the antecedent mean of 0.16 is ecologically necessary for change. Comparable fluctuations occurred during the 1600s. Indeed, removal of PMDI values from 1625 to 1899 resulted in continuity until change points in 1930, the Dust Bowl drought, indicating that the early 1900s were similar to the early 1600s. The magnitude of climate change was within historical range and multiple significant climate change points since 1000 were not sufficient to allow eastern redcedar and mesic eastern tree species increases into the grasslands [37,38].

3.3. Climate Change Points Based on Timing of Land Use

All the ecological landscapes (i.e., >1 million ha; Figure 2) had at least eight change points with the cpm method (Table 3). Only two of the grassland landscapes and one of the forest landscapes had PMDI change points that fell within the bounds of expected tree change, with the cpm method. No change points occurred for the changepoint method during the 1800s.

The grassland landscape for land use change by 1880 had change points during the period 1855 to 1876, for which PMDI values decreased from -0.02 (SD of 1.43) during the period 1736 to 1854, to -1.06 (SD of 1.32) during the period 1855 to 1875; therefore, this interval was drier. The PMDI values increased to 0.88 (SD of 1.23) during the period 1876 to 1893, the next change points. Nevertheless, values in 1876 and later were continuous

with historical values during the 1500s. The grassland landscape for land use change by 1900 had change points in 1877 and 1893, for which PMDI increased from -1.23 (SD of 1.40) during the period 1855 to 1876, to 0.83 (SD of 1.32) during the period 1877 to 1892, and decreased back to -1.26 (SD of 1.06) in 1893 and 1902. These short fluctuations from drier to wetter to drier conditions are not unusual in the PMDI record. The forest landscape with change in land use by 1920 had a change point in 1903, with similar PMDI values for change from about -0.30 (SD of 1.06) during the period 1608 to 1902, to 0.01 (SD of 1.46) after 1902. These PMDI values were typical, and the magnitude of change was minimal considering the amount of variation.

4. Discussion

4.1. Influence of Climate Change

Increased moisture did not constitute a consistent correlation for tree density or diversity change in grasslands and forests of the eastern United States. Correlation of climate change with vegetation change was inconsistent. Only one change point method detected changes in PMDI during the 1800s. For this method, less than half of the ecological landscapes (i.e., >1 million ha) had change points in climate that matched with range of expected timing to influence tree density or diversity change in the United States. The magnitude of change was not unusual compared with past climate; oscillations from dry to wet intervals were typical. Moreover, change points included droughts that transpired during 1855, to either 1864 or 1875, resulting in direction of change contradictions. Fye et al. [39] also documented a drought, analogous in magnitude to the Dust Bowl drought, from 1855 to 1865 that extended from the western U.S. into the tallgrass prairie provinces of the North American grasslands.

The mechanism of climate effects on trees is unreliable in temperate grasslands and forests that have moderate precipitation (e.g., 65 cm to 125 cm). Release of tree growth, tree establishment, and woodland expansion within the central grasslands have occurred during dry climate intervals [4–6,40]. Wells [37] noted that there was no range of climate too arid for trees in the Great Plains grasslands. Gleason [41] declared: “In Illinois, where forest species habitually spring up along roadsides and on un-cultivated places on the prairie, it is obvious that the climate favors the forest, and that forest should rapidly succeed the prairie if no other causes were in operation.”

Without long-term records, tree changes that have been ensuing since Euro-American settlement may be ascribed to short-term climate changes that are within historical ranges of variation. In the eastern tallgrass prairie provinces, annual precipitation increased from 82 cm during the period 1951 to 1980, to 89 cm during the period 1981 to 2015, which is a range of precipitation that is tolerable to eastern tree species [37,42]; moreover, precipitation increases alone do not account for concurrent temperature increases that may boost evapotranspiration. Between 1980 and 2015, Fei et al. [2] found 65% of 86 tree species had a significant westward shift in abundance centers. After acknowledging that indirect and non-climatic factors could have influenced westward movement, Fei et al. [2] stated: “we observed clear broad-scale evidence of the impact of climate change on forest tree spatial dynamics, where changes in mean annual precipitation alone explained about 19% of the variability in species abundance change and spatial shift.” Even so, tree changes detected between the earliest and most recent modern tree inventories will not correspond with before and after climate changes if tree changes originated before the tree surveys. Attribution of change to precipitation during the period 1951 to 1980, as compared with the period 1981 to 2015, is a correlation mismatch, because trees increased and expanded west before 1980 at steady and noticeable rates after Euro-American settlement [22]. Indeed, the primary implication of Fei et al.’s [2] research may be that trees increased and expanded during a range of mean annual precipitation.

Nevertheless, climate will become increasingly influential, compared with land use, as climate changes beyond historical variation, at least of the past 20,000 years. In the eastern United States, widely distributed temperate tree species will not face the same

challenges as northern boreal species with genetic commitment to traits of cold and freeze tolerance [43]. However, extreme meteorological events such as flash droughts, flooding, windstorms, heatwaves, and fire weather days are expected to increase with warming, which progressively will test the ability of vegetation to survive, grow, and reproduce [44]. For example, in the United States during the 1980s, 2.8 events occurred per year that cost at least a billion dollars, at USD 12.8 billion per year; the number of events has increased steadily each decade, and during the 2010s, 11.9 $\geq$ billion-dollar events occurred per year, at USD 80.2 billion per year, which surpassed inflation rates [45]. Moreover, extreme events may interact and create more pathways for damage; stressed trees may become susceptible to insect and disease outbreaks. Current standards of healthy trees, which are fast-growing, and healthy forests, which are fully stocked, may be maladaptive under climate change. McNulty et al. [44] recommended forest management such as thinning to curb maximum potential forest growth, creating a “resource availability buffer” as a strategy for extreme climatic conditions and associated secondary impacts. Slower-growing tree species with greater root resources, such as fire-tolerant species with early growth dedicated to roots rather than shoots for survival of frequent surface fire, may be more resistant to catastrophic episodic mortality [44], and grassland vegetation too is likely more resistant and resilient than current forests in the eastern U.S.

Indeed, the tree species that have increased during the past century, along with tree density increases, due to changing land use including agriculture, probably have made eastern U.S. forests less resilient to climate change and extreme events. Historically dominant, widespread oak and pine species are drought- and fire-tolerant, but these species have been replaced by more mesic, drought- and fire-sensitive species, such as maples, ashes, and elms [46–48]. Historically dominant forests occurred as low-density savannas and woodlands, which provide benefits of reduced water demand and also reduced chance of insect outbreaks and spreading crown fires compared with dense forests [44]. Forests of lower tree densities, with tree continuity rather than high contrast edges, comprised of trees that allocate resources to roots (i.e., historical open forests and historically dominant fire-tolerant oak and pines species) are likely to be more windfirm [49].

4.2. Influence of Land Use Change

If increased moisture does not constitute a consistent correlation, with sufficient magnitude and direction, or mechanism for tree change in grasslands and forests of the eastern United States, then an alternative option is that land use was driving tree change in density and diversity. Intensive and extensive agricultural use was unprecedented, resulting in appropriate magnitude and direction for driving tree change along with correlation in timing and a consistent mechanism for tree change. Vegetation changes arose directly from land conversion to land uses, exacerbated by cycles of conversion and abandonment. Clearing removed established vegetation, and plowing damaged propagules of rootstocks and seed banks. Continued severe disturbance created opportunities for a new suite of species with traits for responding to relatively frequent vegetation removal every 20 to 100 years [12]. However, in addition to direct land use change to severe vegetation disturbance, land use change excluded frequent surface fire. Historical accounts described a sequence of advancing western Euro-American settlement, gradually extinguished surface frequent fire regimes, and release of young trees [30].

Surface fire occurred almost annually in eastern tallgrass prairies, which have the greatest amount of precipitation of the central grasslands of North America, allowing growth of plentiful herbaceous vegetation that are fuels for frequent surface fire. Tree propagules attempted to establish in grasslands, but most tree establishment was removed by fire. Trees were limited to firebreak locations of either water and wetlands; rocky outcrops or thin soils; and rough and steep topography of bluffs, escarpments, and ridges [34,37,50–52]. Because the prevailing winds are from the west and drove fire eastward, more trees occurred on the protected east sides of firebreaks [50,51].

Exclusion of fire includes active fire suppression, discontinuation of fire as a management tool with additional restrictions by laws and changing cultural norms, and passive land use changes that prevent fire spread by reducing herbaceous vegetation that provides fine fuels. Roads and other linear vegetation discontinuities specifically act as firebreaks. Indeed, Euro-American settlers in grasslands cleared herbaceous vegetation for some distance around their fields and houses and wore down vegetation with wagon tracks or plowed furrows as fireguards around their holdings to disrupt fire spread and to encourage tree growth into the disturbed soil [50,53]. Tree presence disrupted flammability while protected conditions under trees reduced probability of fire occurrence. Equally, on unburned areas, woody plant cover both increased in density and invaded new locations. A combination of historical tree surveys, aerial photos, and field observations allowed Bragg and Hulbert [32] to quantify that on unburned sites, tree and shrub cover increased 34% from 1937 to 1969 and tree cover alone increased 24% from 1856 to 1969 in Kansas. In contrast, woody plants in regularly burned sites increased by only 2% from 1937 to 1969. These measurements concurred with Kettle et al. [54] for the interval between 1957 and 1997 in Kansas; mowing or burning limited tree cover to <3% compared with >97% tree cover without treatment. Penfound [55] wrote for Oklahoma: “With heavy grazing and fire protection, a continuing increase in arborescent cover has occurred in areas which were formerly occupied by savanna.”

Agricultural activities such as harvested row crops and grazing by cattle also reduce vegetation for fuels and chance of fire occurrence. For example, area in crop is related inversely to fire occurrences. Mean area of cropland was about 23% for the entire United States where no fires occurred during the period 1999 to 2017; conversely, area in crop was <2% where fires recently occurred [56]. Likewise, Gleason [22], in one of his key papers, documented that fire ended when agriculture increased in Illinois to 1860 levels of agriculture compared with 1850. In Illinois, agriculture averaged 36% of total area in 1860, compared with 14% in 1850. The threshold of 25% land in agriculture acts as an indicator of timing for when humans influenced ecosystem change, which will require additional evaluation, and likely lessens to 10% given surrounding land conversion. In contrast, agricultural area initially may need to exceed the 25% threshold to disrupt fire in undeveloped grasslands and forests, with low density of roads and harvested fields in particular, and additionally less area in houses combined with a persistent culture of fire use as a management tool. Although data about population densities are also available for the 1800s, humans at very low densities can affect vegetation and modulate fire regimes (e.g., by increasing ignitions while producing fewer firebreaks of fields and trails), so that a threshold is less apparent. Relatedly, housing densities and not human densities was the influential variable for modeling recent fire occurrences [57]. Housing densities and percent of land converted to agriculture are manifestations of the magnitude of human influence on fire exclusion and vegetation.

Land use change, specifically fire exclusion, satisfies the requirements for timing of tree change in conjunction with land use following Euro-American settlement, exceptional magnitude, unidirectional sign of change, and mechanism. Compared with climate fluctuations around historical ranges of variation during the time of vegetation change, departure of fire from historical frequencies is of a greater magnitude due to fire exclusion. While fire return intervals have varied over time, which may produce significant change points, exclusion was a definitive departure in magnitude. In addition to correlation in time and magnitude, fire exclusion provides a consistent mechanism for change, by allowing fire-sensitive tree species to survive. Surface fire removes small diameter woody vegetation, thereby reducing tree density, particularly of fire-sensitive tree species, and favoring herbaceous vegetation, which is adapted to removal of aboveground growth. Herbaceous vegetation provides fine fuels that ignite more readily than coarse woody fuels, increasing fire frequency. As fire exclusion is prolonged, flammability markedly decreases with replacement of herbaceous vegetation by trees, further reducing the probability of fire occurrence. A moderate range of precipitation (e.g., 65 cm to 125 cm) in temperate climates

supplies both wet periods that produce abundant herbaceous fuels and dry periods that dry herbaceous fuels, which are necessary conditions for fire. Climate changes that increase or decrease moisture and continuity of herbaceous fuels may affect fire frequency.

5. Conclusions

This approach to determine timing of vegetation change in tree density and diversity accounted for both climate (i.e., water balance with PMDI) and land use change. Climate change points were frequent but not consistent with timing of tree changes, and if they corresponded, a range of climate occurred, including drought, indicating a problem with mechanism. Additionally, the magnitude of climate change was within historical ranges. Conversely, novel land use provided the correct timing, mechanism, direction, and magnitude of change. Land use has many components that influence ecosystem change, including the progression from Euro-American settlement to exclusion of frequent surface fires.

The other outcome of this research was the identification of a potential proxy for when humans influenced vegetation change, a threshold of 15% to 25% land area in agriculture that is a direct index of human modification of the landscape. Percent of land in agriculture is available as spatially explicit GIS layers by decade since 1850 for the United States [21]. At landscape scales, fit appeared to be appropriate and an improvement to searching through archival records that cannot provide specific data points. Additional close evaluation and refinement by experts is necessary, with corroboration from multiple lines of historical evidence. Thresholds of agricultural area by county may decrease as surrounding agricultural area increases. In any event, an approximate data layer that indicates timing and location of vegetation change is a major progression in the ability to analyze drivers of change.

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References

1. Kangas, R.S.; Brown, T.J. Characteristics of US drought and pluvials from a high-resolution spatial dataset. *Int. J. Climatol.* **2007**, *27*, 1303–1325. [CrossRef]
2. Fei, S.; Desprez, J.M.; Potter, K.M.; Jo, I.; Knott, J.A.; Oswalt, C.M. Divergence of species responses to climate change. *Sci. Adv.* **2017**, *3*, e1603055. [CrossRef]
3. Hanberry, B.B.; Abrams, M.D.; White, J.D. Is increased precipitation during the 20th century statistically or ecologically significant in the eastern US? *J. Land Use Sci.* **2018**, *13*, 259–265. [CrossRef]
4. Ziegler, S.S.; Larson, E.R.; Rauchfuss, J.; Elliott, G.P. Tree establishment during dry spells at an oak savanna in Minnesota. *Tree-Ring Res.* **2008**, *64*, 47–55. [CrossRef]
5. Shuman, B.; Henderson, A.K.; Plank, C.; Stefanova, I.; Ziegler, S.S. Woodland-to-forest transition during prolonged drought in Minnesota after ca. AD 1300. *Ecology* **2009**, *90*, 2792–2807. [CrossRef]
6. Rogers, T.R.; Russell, F.L. Historical patterns of oak population expansion in the Chautauqua Hills, Kansas. *J. Biogeogr.* **2014**, *41*, 2105–2114. [CrossRef]

7. Delcourt, P.A.; Delcourt, H.R. Late-Quaternary dynamics of temperate forests: Applications of paleoecology to issues of global environmental change. *Quat. Sci. Rev.* **1987**, *6*, 129–146. [\[CrossRef\]](#)
8. Hanberry, B.; Kabrick, J.M.; He, H.S. Changing tree composition by life history strategy in a grassland-forest landscape. *Ecosphere* **2014**, *5*, art34. [\[CrossRef\]](#)
9. Lorimer, C.G. Historical and ecological roles of disturbance in eastern North American forest: 9,000 years of change. *Wildl. Soc. Bull.* **2001**, *29*, 425–439.
10. Hanberry, B.B.; Coursey, K.; Kush, J.S. Structure and composition of historical longleaf pine ecosystems in Mississippi, USA. *Hum. Ecol.* **2018**, *46*, 241–248. [\[CrossRef\]](#)
11. Hanberry, B.B. Baseline to novel ecosystems in Michigan, USA, with a quantitative and qualitative assessment. *Écoscience* **2020**, *27*, 255–268. [\[CrossRef\]](#)
12. Pan, Y.; Chen, J.M.; Birdsey, R.; McCullough, K.; He, L.; Deng, F. Age structure and disturbance legacy of North American forests. *Biogeosciences* **2011**, *8*, 715–732. [\[CrossRef\]](#)
13. Hanberry, B.B.; Hansen, M.H. Advancement of tree species across ecotonal borders into non-forested ecosystems. *Acta Oecologica* **2015**, *68*, 24–36. [\[CrossRef\]](#)
14. Srinath, I.; Millington, A.C. Evaluating the Potential of the Original Texas Land Survey for Mapping Historical Land and Vegetation Cover. *Land* **2016**, *5*, 4. [\[CrossRef\]](#)
15. Rothenberger, S.J. Extent of woody vegetation on the prairie in eastern Nebraska, 1855–1857. In *Prairie Pioneers: Ecology, History and Culture: Proceedings of the Eleventh North American Prairie Conferences*; Bragg, T.B., Stubbendieck, J., Eds.; University of Nebraska: Lincoln, NE, USA, 1989; pp. 15–18.
16. McLachlan, J. Settlement Trees, Illinois Level 0 Ver 0. Environmental Data Initiative. 2020. Available online: <https://portal.edirepository.org/nis/mapbrowse?packageid=msb-paleon.28.0> (accessed on 30 December 2020).
17. Landers, R.Q. Native vegetation of Texas. *Rangel. Arch.* **1987**, *9*, 203–207.
18. Hewes, F.W.; Gannett, H. *Scribner's Statistical Atlas of the United States*. Scribner's Sons: New York, NY, USA, 1883. Available online: <https://www.loc.gov/item/a40001834/> (accessed on 7 January 2021).
19. Cook, E.R.; Seager, R.; Heim, R.R.; Vose, R.S.; Herweijer, C.; Woodhouse, C. Megadroughts in North America: Placing IPCC projections of hydroclimatic change in a long-term paleoclimate context. *J. Quat. Sci.* **2010**, *25*, 48–61. Available online: <https://www.ncdc.noaa.gov/paleo-search/study/19119> (accessed on 1 December 2020). [\[CrossRef\]](#)
20. Keys, J.E.; Cleland, D.T.; McNab, W.H. *Delineation, Peer Review, and Refinement of Subregions of the Conterminous United States*; Gen. Tech. Report WO-76A; Department of Agriculture, Forest Service: Washington, DC, USA, 2007.
21. Maizel, M.; White, R.D.; Root, R.; Gage, S.; Stitt, S.; Osborne, L.; Muehlbach, G. Historical Interrelationships between Population Settlement and Farmland in the Conterminous United States, 1790 to 1992. 1998. Available online: <https://archive.usgs.gov/archive/sites/landcover.usgs.gov/luhna/chap2.html> (accessed on 21 May 2020).
22. Gleason, H.A. The vegetational history of the Middle West. *Ann. Assoc. Am. Geogr.* **1922**, *12*, 39–85. [\[CrossRef\]](#)
23. Day, G.M. The Indian as an ecological factor in the Northeastern forest. *Ecology* **1953**, *34*, 329–346. [\[CrossRef\]](#)
24. DeSantis, R.D.; Hallgren, S.W.; Lynch, T.B.; Burton, J.A.; Palmer, M.W. Long-term directional changes in upland Quercus forests throughout Oklahoma, USA. *J. Veg. Sci.* **2010**, *21*, 606–618. [\[CrossRef\]](#)
25. Duncan, B.W.; Schmalzer, P.A. Anthropogenic influences on potential fire spread in a pyrogenic ecosystem of Florida, USA. *Landsc. Ecol.* **2004**, *19*, 153–165. [\[CrossRef\]](#)
26. Marine Data Science. Comparison of Change Point Detection Methods. 2019. Available online: <https://www.marinedatascience.co/blog/2019/09/28/comparison-of-change-point-detection-methods/> (accessed on 25 September 2021).
27. Killick, R.; Eckley, I. Changepoint: An R package for changepoint analysis. *J. Stat. Softw.* **2014**, *58*, 1–19. [\[CrossRef\]](#)
28. Ross, G.J. Parametric and nonparametric sequential change detection in R: The cpm Package. *J. Stat. Softw.* **2015**, *66*, 1–19. [\[CrossRef\]](#)
29. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020.
30. Davidson, R. An Excursion to the Mammoth Cave and the Barrens of Kentucky. A.T. Silliman and Son: Lexington, Kentucky, 1840. Available online: https://www.google.com/books/edition/An_Excursion_to_the_Mammoth_Cave_and_the/71EVAAYAAJ?hl=en&gbpv=1&printsec=frontcover (accessed on 1 July 2021).
31. Shaler, N.S. Kentucky: A Pioneer Commonwealth. Houghton, Mifflin and Co.: Boston, MA, USA; New York, NY, USA, 1885; Available online: https://www.google.com/books/edition/Kentucky_a_Pioneer_Commonwealth/eIAXAQAAMAAJ?hl=en&gbpv=1&printsec=frontcover (accessed on 2 June 2021).
32. Bragg, T.B.; Hulbert, L.C. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manag.* **1976**, *29*, 19–24. [\[CrossRef\]](#)
33. Taylor, B. Colorado, a Summer Trip. Putman: New York, NY, USA, 1867. Available online: <https://babel.hathitrust.org/cgi/pt?id=hvd.32044072260284&view=1up&seq=9> (accessed on 7 January 2021).
34. Bruner, W.E. The vegetation of Oklahoma. *Ecol. Monogr.* **1931**, *1*, 100–188. [\[CrossRef\]](#)
35. Gregg, J. Commerce of the Prairies. 1844. Available online: <https://atlas.nmhum.org/pdfs/CommerceofthePrairies.pdf> (accessed on 24 September 2021).

36. Cook, O.F. *Change of Vegetation on the South Texas Prairie*; USDA, Bureau of Plant Industry Circular: Washington, DC, USA, 1908; Volume 14. Available online: <https://archive.org/details/changeofvegetati14cook/page/n1/mode/2up> (accessed on 7 January 2021).
37. Wells, P.V. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains region. *Science* **1965**, *148*, 246–249. [[CrossRef](#)]
38. Hall, S.A. Deteriorated pollen grains and the interpretation of Quaternary pollen diagrams. *Rev. Palaeobot. Palynol.* **1981**, *32*, 193–206. [[CrossRef](#)]
39. Fye, F.K.; Stahle, D.W.; Cook, E.R. Paleoclimatic analogs to twentieth-century moisture regimes across the United States. *Bull. Am. Meteorol. Soc.* **2003**, *84*, 901–910. [[CrossRef](#)]
40. Stambaugh, M.C.; Guyette, R.P.; Marschall, J. Fire history in the Cherokee nation of Oklahoma. *Hum. Ecol.* **2013**, *41*, 749–758. [[CrossRef](#)]
41. Gleason, H.A. Further views on the succession-concept. *Ecology* **1927**, *8*, 299–326. [[CrossRef](#)]
42. Prism Climate Group. PRISM Climate Data. 2020. Available online: <https://prism.oregonstate.edu/> (accessed on 30 December 2020).
43. Loehle, C. Height growth rate tradeoffs determine northern and southern range limits for trees. *J. Biogeogr.* **1998**, *25*, 735–742. [[CrossRef](#)]
44. McNulty, S.G.; Boggs, J.L.; Sun, G. The rise of the mediocre forest: Why chronically stressed trees may better survive extreme episodic climate variability. *New For.* **2014**, *4*, 403–415. [[CrossRef](#)]
45. National Oceanic and Atmospheric Administration National Centers for Environmental Information (NCEI). U.S. Billion-Dollar Weather and Climate Disasters. 2020. Available online: <https://www.ncdc.noaa.gov/billions/> (accessed on 25 February 2020).
46. Niinemets, Ü.; Valladares, F. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* **2006**, *76*, 521–547. [[CrossRef](#)]
47. Hanberry, B.B. Recent shifts in shade tolerance and disturbance traits in forests of the eastern United States. *Ecol. Process* **2019**, *8*, 32. [[CrossRef](#)]
48. Hanberry, B.B.; Bragg, D.C.; Hutchinson, T.F. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. *Ecosphere* **2018**, *9*, e02431. [[CrossRef](#)]
49. Gresham, C.A.; Williams, T.M.; Lipscomb, D.J. Hurricane Hugo wind damage to southeastern US coastal forest tree species. *Biotropica* **1991**, *23*, 420–426. [[CrossRef](#)]
50. Christy, M. Why are the prairies treeless? In *Proceedings of the Royal Geographical Society and Monthly Record of Geography*; Duke University Press: Durham, NC, USA, 1892; Volume 14, pp. 78–100.
51. Gleason, H.A. The relation of forest distribution and prairie fires in the Middle West. *Torreyana* **1913**, *13*, 173–181.
52. Davis, A.M. The prairie-deciduous forest ecotone in the upper Middle West. *Ann. Assoc. Am. Geogr.* **1977**, *67*, 204–213. [[CrossRef](#)]
53. Gerhard, F. Illinois as It Is. Keen and Lee: Chicago, IL, USA, 1857. Available online: <https://catalog.hathitrust.org/Record/001268669> (accessed on 10 December 2020).
54. Kettle, W.D.; Rich, P.M.; Kindscher, K.; Pittman, G.L.; Fu, P. Land-use history in ecosystem restoration: A 40-year study in the prairie-forest ecotone. *Restor. Ecol.* **2000**, *8*, 307–317. [[CrossRef](#)]
55. Penfound, W.T. The savanna concept in Oklahoma. *Ecology* **1962**, *43*, 774–775. [[CrossRef](#)]
56. Hanberry, B.B. Classifying large wildfires by land cover in the United States. *Remote Sens.* **2020**, *12*, 2966. [[CrossRef](#)]
57. Hanberry, B.B. Reclassifying the wildland-urban interface using fire occurrences for the United States. *Land* **2020**, *9*, 225. [[CrossRef](#)]