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Differentiating Historical Open Forests and Current Closed Forests of the Coastal Plain, Southeastern USA

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Abstract: The southeastern United States was historically characterized by open forests featuring fire-adapted species before land-use change. We compared tree composition and densities of historical tree surveys (1802 to 1841) to contemporary tree surveys, with the application of a similarity metric, in the Coastal Plain ecological province of Mississippi, southeastern USA. We detected the boundary between historical pine and oak-pine open forests and differentiated historical and current forests. In the Coastal Plain, historical open forests converted from fire-tolerant longleaf pine (*Pinus palustris*) dominance, with pines comprising 88% of all trees, to loblolly (*Pinus taeda*) and slash (*P. elliottii*) pines within monocultures (45% of all trees). Wetland and successional tree species increased to 33% of all trees. Contemporary forests have greater tree densities, transitioning from closed woodlands (range of 168 to 268 trees ha^{-1}) to closed forests (336 trees ha^{-1}). In the ecotonal boundary of the northern Coastal Plain between historical pine and pine-oak woodlands, the pine component shifted over space from 88% to 34% of all trees due to a greater oak component. Fire-tolerant shortleaf pine and oak dominance converted to planted loblolly pine (52% of all trees), while successional tree species increased (20% of all trees). Historical tree densities represented woodlands (range of 144 to 204 trees ha^{-1}) but developed into closed forests (400 trees ha^{-1}). Historical Coastal Plain longleaf pine woodlands differed more from historical ecotonal oak-pine woodlands than contemporary forests differed from each other, demonstrating unique historical ecosystems and landscape-scale homogenization of ecosystems through forestation.

Keywords: disturbance; ecotone; fire; forestation; homogenization; land use; longleaf pine; oaks; tension zone

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1. Introduction

Globally, following European colonization, biodiverse grasslands, savannas, and open forests have been converted to agriculture and dense forests to maximize food and forest product yield [1,2]. In addition, exclusion of frequent surface fire, often in combination with replacement of native herbivores by domesticated livestock, has allowed tree encroachment, which eventually leads to forestation through afforestation of grasslands and tree densification within forest stands [2,3]. Herbaceous plants typically support a range of invertebrates, including pollinators, and a variety of wildlife species that require food resources from herbaceous plants or insects and open, 'clutter'-free vegetation structure [4–8]. In addition to habitat and species loss, forestation can decrease resistance and resiliency to severe fires, damaging insect outbreaks, windfall, and die-offs due to drought, along with increasing water use by trees, which may be exacerbated by climate change [9–12]. Open ecosystems supply unique ecosystem services, encompassing wildlife support, food and forage production, pollination, disturbance regulation, water supply, and cultural importance [6,7,10,13].

Before Euro-American settlement and accompanying land use changes, longleaf pine (*Pinus palustris*) open woodlands were the dominant ecosystem across the Coastal Plain ecological region in the southeastern United States (Figure 1; [14–16]. Historical accounts, early forest reports, and limited reconstructions of historical tree surveys characterized the Coastal Plain as longleaf pine savannas and woodlands with interspersed grasslands and wetlands [15–19]. Savannas and woodlands were two-layered, featuring longleaf pine at low densities in the overstory and a species-diverse herbaceous layer, making savannas continuous in structure with grasslands. Equally, longleaf pine is a component of wetlands. Longleaf pine ecosystems with embedded wetlands and grasslands provided conditions, structure, and function to promote biodiversity, including 6000 vascular plant species, of which 1630 were endemic [20–25]. Frequent surface fires at intervals of two to nine years, both from anthropogenic and lightning ignitions, maintained longleaf pine savannas and woodlands, preventing succession to closed forests of broadleaf tree species [26–30]. Indigenous peoples used frequent surface fire to create openings for villages and croplands, manage and hunt animals, and maintain foodways of plants and wildlife supported by open conditions of grasslands, savannas, and woodlands [31,32].

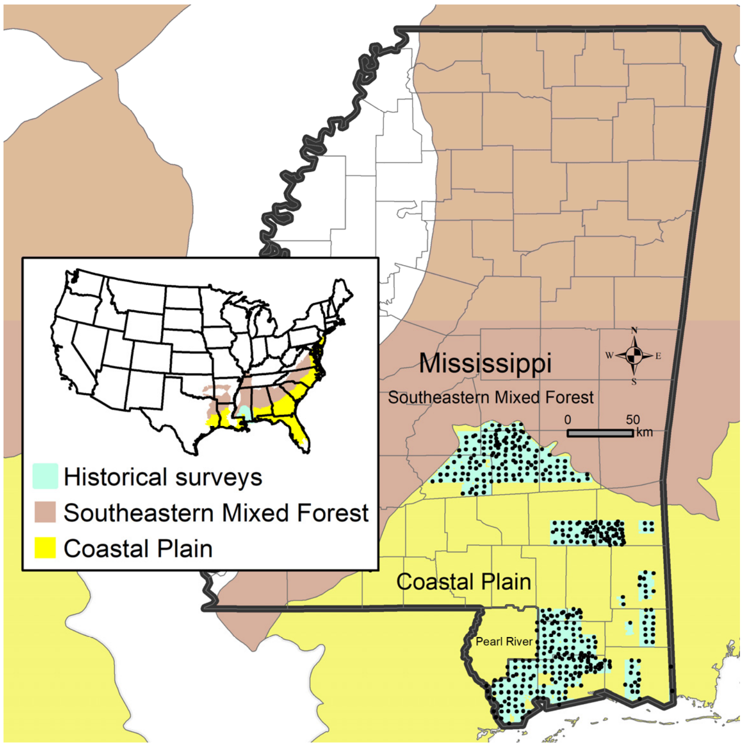

Figure 1. The Coastal Plain ecological province (yellow); [33], which is the southern ecological region of the southeastern U.S., south of the Southeastern Mixed Forest ecological province (brownish pink). The study area included available historical General Land Office surveys (green sections), with intersected plots from current tree surveys (black points), in the Coastal Plain of southern Mississippi, USA. We excluded surveys from Pearl River County to prevent overlap and allow comparison with density estimates from previous research [19].

Euro-Americans cleared historical forests and altered fire regimes before either were well documented [31]. Longleaf pine ecosystems provided pasturelands, lumber, and chemical products such as turpentine [16,34,35]. A general pattern of land use may have occurred where livestock herders first primarily used existing open ecosystems for forage, followed by conversion to row crop agriculture [32,35]. In the Coastal Plain of Mississippi, commercial logging companies first entered the area around 1840 [35]. Steam-powered technology, railroads, and inexpensive land prices coincided to escalate tree removal ('cut-out and get-out') between 1880 and 1920, from which longleaf pine forests did not naturally recover [36]. Land uses of chemical extraction for naval supplies, lumbering, and intensive livestock grazing or agriculture resulted in extensive areas without mature longleaf pines [16]. Longleaf pine regeneration was hindered by lack of mature trees, sporadic cone production, limited seed dispersal, fire exclusion, and seedling depredation by feral livestock, chiefly the hogs that saturated the land [15]. Of the 25-to-30 million ha of longleaf pine woodlands in the Coastal Plain at Euro-American settlements, about 2 million ha exists currently [16,20].

Historical map compilations and a few small studies indicate that longleaf pine frequency decreased along the margins of the Coastal Plain, but boundaries generally remain uncertain due to unavailable or inaccessible records [15,37]. Indeed, the use of longleaf pine for naval supplies and other purposes in early Euro-American settlements before documentation means that northern boundaries in the easternmost states may never be known [15]. Historical maps of longleaf pine distributions were developed based on assessments after Euro-American land use had already removed forests [16]. Several studies have examined longleaf pine forests recorded by historical land surveys conducted generally during the first half of the 1800s to record and sell land, although some eastern states were not surveyed with grid-based methods [16]. However, the historical surveys largely remain in inaccessible formats, resulting in slow research progression. The boundary of longleaf pine dominance (>70% of all trees) has been clearly defined in part of Georgia [37], and Black et al. [38] may have detected the border of decreasing longleaf pine in part of Alabama. North of longleaf pine savannas and woodlands, the dissected northern southeastern U.S. contained distinctive historical oak-pine savannas and woodlands, containing a balanced mixture of shortleaf pine (*Pinus echinata*) and upland oak species [37,39–42]. Longleaf pine occupancy decreased along with surface fire frequency in the smaller fire compartments of the northern southeastern U.S., where rugged topography broke up fire spread (e.g., [25]). According to scattered historical tree studies and accounts, areas where pine comprises 50% to 60% of all trees may represent a zone where longleaf and shortleaf pine frequently co-occurred [17,42]. Meanwhile, the existence of longleaf pine woodlands abutting oak-shortleaf pine woodlands indicates an ecotonal boundary.

Paralleling global accounts of historical ecosystems lost to forestation, open longleaf pine forests prior to Euro-American settlement have become closed forests featuring broadleaf and commercial pine tree species, with frequent overstory removal through harvest or other land uses resulting in successional cycles of clearcuts and young, dense forests (Shafale and Harcombe [43] in southeast Texas; Hanberry et al. [19] in extreme southern Mississippi). Our objective in this study was to characterize how historical forests differed from contemporary forests on the Coastal Plain of Mississippi, particularly strengthening density estimates for historical longleaf pine open forests. Because we limited the extent to the Coastal Plain ecological province that represents the southern southeastern U.S. [33], we expected to find historical open forests of longleaf pine, likely at densities of open to closed woodlands, similar to Predmore et al. [44] and Hanberry et al. [19] We also examined ecological boundaries and similarities based on the composition of historical and contemporary forests to compare spatial and temporal turnovers in tree composition within the Coastal Plain ecological province to that within the northern province of the southeastern U.S. Collectively, this study provides a valuable record of long-term forest development in a region where restoration efforts are extensive but historical evidence to guide these efforts is often lost to land-use changes.

2. Methods

2.1. Study Area

Based on vegetation and soils, among other factors, McNab et al. [33] subdivided the southeastern U.S. into ecological provinces of the Outer Coastal Plain Mixed Forest in the southern extent and Southeastern Mixed Forest in the northern extent. Our study area was the Outer Coastal Plain Mixed Forest ecological province in Mississippi, hereafter referred to as the Coastal Plain province (Figure 1). Soils in the region are generally classified as ultisols, which are highly leached and low in organic matter, with sand derived from oceanic sediments [45]. Climate is Cfa in the Köppen climate classification: humid, featuring mild winters with minimum temperatures ranging from −4 to 15 °C during January and hot summers with maximum temperatures ranging from 29 to 35 °C during July (mean during 1981–2010; [46]). Annual precipitation ranging from 100 to 174 cm (mean during 1981–2010) is partially offset by evapotranspiration, heavy downpours leading to surface run-off, and sandy soils with poor moisture-holding capacity. Abundant rainfall and warm temperatures with long growing seasons combine to make the region one of the most productive for tree growth in North America.

2.2. Surveys, Tree Composition, Historical Boundary, and the Squared Chord Distance

The General Land Office (created year 1812) administered surveys of the Public Land Survey System (created year 1785) based on 1.6 km square sections for the purpose of land sales. Each section, for 36 sections within a township, was surveyed once, with survey points that occurred every 0.8 km at the corners and middle of each section line [47]. Survey points contained information recorded about tree species, diameter, distance, and azimuth of two to four trees. We transcribed 10,984 survey points recorded between 1807 to 1841 in the Coastal Plain ecological province in Mississippi (Figure 1; [33]) from all available scanned field notes [48]; additionally, we examined the northern part of the province to check for changes in forest type to oak-pine forests. We excluded sections from Pearl River County to prevent overlap and allow comparison with density estimates from previous research [19]. The survey points contained 25,555 trees, but only 6940 trees had recorded diameters. Following survey instructions, surveyors selected trees of moderate diameter that were sound rather than the nearest trees [49,50]. Due to lack of information about diameters for most trees, we did not exclude 218 trees, out of 6940 trees with diameter information, which had diameters < 12.7 cm at a 1.37 m height above ground level (DBH). The historical distribution of trees may have contained a greater percentage of larger-diameter trees than the moderate-diameter trees recorded by surveyors due to limited tree harvesting before Euro-American settlement.

The modern Forest Inventory and Analysis (FIA) surveys occur in long-term plots located in forests about every 2500 ha nationally [51,52]. Each plot consists of four 7.31 m radius subplots. We selected 446 plots from the latest complete cycle of surveys from years 2009 to 2015 that intersected the sections with available GLO surveys. These plots contained 7865 trees (DBH $\geq$ 12.7 cm).

For both datasets, we determined composition, as a percentage of all trees. Although pine species (*Pinus*) were not differentiated in historical surveys, most pines were probably longleaf pine based on historical accounts and early forest reports [16,18]. Similarly, hickory species (*Carya*) were not distinguished in historical surveys. Oak species (*Quercus*) and evergreen broadleaf species (*Magnolia* and *Persea*) identification was variable; therefore, we grouped evergreen broadleaf species and oaks. We divided trees recorded as 'gum' proportional to the recorded number of blackgum (*Nyssa sylvatica*) and sweetgum (*Liquidambar styraciflua*).

We inspected the historical tree surveys for changes in the percentage of pine from south to north. The five northern counties were at the margins of the Coastal Plain ecological province, at the ecotone between longleaf pine and oak-pine woodlands (Figure 1). We mapped the fit of boundaries from ecological classification systems [33,51,53,54] for changing historical pine composition.

We differentiated the composition of historical and current forests. We used differences between historical and contemporary tree compositions to delineate current boundaries. In addition, we assigned a value of dissimilarity with the squared chord distance metric, which is the standard metric for comparing how analogous species assemblages are over time [55,56]. Historical and contemporary forests that differ in composition tend to have a squared chord distance $\geq$ 0.15, while values between 0.12 and 0.15 indicate some divergence [55]. We compared species or species groups that had at least moderate presence ($\geq$2% of all trees) in either historical or contemporary surveys for the Coastal Plain or ecotonal forests.

2.3. Historical Density

Density estimates from the plotless method of historical surveys are not as accurate as from plot surveys [57]. Nonetheless, density estimates from the Morisita plotless estimator [58] are relatively accurate if sample sizes are at least 2000 survey points with two trees, with correction factors for the number of trees per survey points, potential spatial pattern, and surveyor bias [57,59]. Clustering of trees will inflate density estimates. Conversely, density is underestimated if recorded trees are not the nearest trees, but adjustments can correct for surveyor bias [59].

We estimated density using the Morisita plotless estimator for two trees per survey point, providing a range of estimates to account for uncertainty and to place density estimates into ecosystem classes for context [60]. For 311 survey points with no trees or 1 tree, we added a distance of 70 m for the missing distances, albeit the small number of survey points has an accordingly small effect on overall density [57]. For 2110 survey points with more than two trees, we retained only the two nearest trees. We decreased the density for points with two trees [57]. We generated low and high density values according to potential clustered and regular spatial patterns [57]. We increased the low and high density values to incorporate uncertainty from surveyor bias [59]. We adjusted for non-random frequencies of quadrant location, quadrant configuration, and azimuth by applying adjustment quotients from regression equations [59]. The final low density value was the adjusted low density estimate, about 0.9 of the value for the Morisita density estimate of survey points with two trees. The moderately low density value was a simple mean of the adjusted low and high densities, about equal to the Morisita density estimate for survey points with two trees. For a moderately high density value, we applied a correction from a rank-based method for a mean tree rank of 1.8 (i.e., surveyors most often selected the second nearest tree; [59], which was about 1.35-fold greater than the Morisita density estimate for survey points with two trees. We calculated a moderate density value as a simple mean of the moderately low and moderately high density estimates, or about 1.2-fold greater than the Morisita density estimate for survey points with two trees.

From modern surveys, we calculated mean densities. We selected plots with at least two trees (i.e., to reduce the potential influence of clearcutting). We summed densities in each plot using the tree expansion factor of 6.018, by which one tree represents the inverse of the plot area.

3. Results

3.1. Identification of the Historical Boundary between Pine and Oak-Pine Open Forests

Although we expected longleaf pine forests within the Coastal Plain, the five northern counties were at the margins of the ecological province (Figures 1 and 2). This location indeed contained the ecotone between longleaf pine woodlands and oak-pine woodlands, albeit comprehensive survey data were not available to cover the entire boundary (Figure 2). From south to north, pine percentages decreased from 88% and 89% in longleaf pine woodlands south of the ecotonal boundary to 56% through the ecotonal boundary that extended within a short distance, covering at most two townships, which is less than 20 km. Within another four townships, pine percentages were at 34% in oak-pine forests. Compared to the Coastal Plain ecological province [33] that encompassed the ecotone, other ecological classification systems shared a similar boundary (East Gulf Coastal Plain; [54]), a more northern boundary (Southeastern Plains; [61], or a southern boundary that matched well with the historical ecotonal boundary (Southeastern Conifer Forests; [53]).

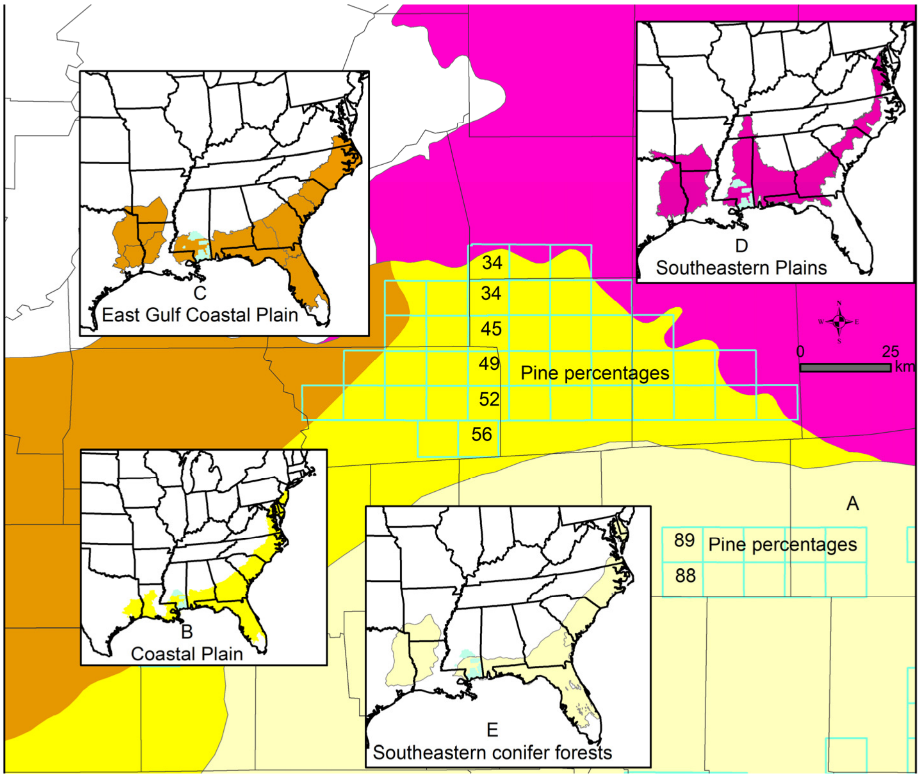

Figure 2. Historical shift in pine percentage from longleaf pine forests (88% and 89% pine) to oak-pine forests (56% pine decreasing to 34%) at the margin of the Coastal Plain ecological province (**A**). Compared to the Coastal Plain ecological province ((**B**); yellow); [33], other ecological classification systems shared a similar encompassing boundary ((**C**); brown); East Gulf Coastal Plain; [54], a more northern boundary ((**D**); pink); Southeastern Plains; [61], or a southern boundary that intersected with the historical ecotonal boundary ((**E**); light yellow); Southeastern Conifer Forests; [53].

3.2. Historical and Current Forests in the Central and Southern Coastal Plains

Within the central and southern Mississippi Coastal Plain province, for 16,105 historical tree records and 5210 contemporary tree records, nine species or species groups had greater than trace presence (≥0.5% of all trees, generally DBH ≥ 12.7 cm) in either the historical (mean year 1824, ranging from 1807 to 1841) GLO surveys or current FIA surveys (Table 1). Pine was the predominant genus in both datasets but decreased over time from 87.5% in historical surveys to 55.5% of all trees in contemporary surveys. Fire-tolerant longleaf pine is documented to be the preponderant historical species and decreased to 10.2% of all trees, which is a high percentage for diminished longleaf pine currently. Plantation species of slash (*Pinus elliottii*) and loblolly pines (*Pinus taeda*) were 23% and 22%, respectively, of all trees in contemporary surveys. Broadleaf evergreen species, of which 'bays' are primarily a wetland species, increased from 4.0% to 9.8% of all species; oaks increased from 2.6% to 9.8% of all species, primarily due to wetland water oak (*Quercus nigra*); and blackgum increased from 1.2% to 8.1% of all species. Trace (≤0.5% of all trees) historical early and mid-successional species of sweetgum, yellow-poplar (*Liriodendron tulipifera*), and red maple (*Acer rubrum*) increased to 2.5%, 2.3%, and 3.2% of all trees, respectively. Swamp tupelo (*Nyssa biflora*) may also have increased, albeit surveyors may have avoided recording trees in swamps.

Table 1. Count and percentage of historical (1807 to 1841) species or species groups compared to contemporary count and percentage of species in the central and southern Coastal Plain ecological province in Mississippi. Uncommon historical and current species (≤0.5%) were excluded.

Historical			Contemporary			
Species Group	**Count**	**%**	**Species**	**Scientific Name**	**Count**	**%**
pine (longleaf pine)	14,085	87.5				55.5
			slash pine (planted)	*Pinus elliottii*	1194	22.9
			loblolly pine (planted)	*Pinus taeda*	1139	21.9
			longleaf pine	*Pinus palustris*	530	10.2
			shortleaf pine	*Pinus echinata*	21	0.4
			spruce pine	*Pinus glabra*	9	0.2
bay (broadleaf evergreen)	638	4.0				9.8
			sweetbay	*Magnolia virginiana*	430	8.3
			southern magnolia	*Magnolia grandiflora*	41	0.8
			redbay	*Persea borbonia*	39	0.7
oak	425	2.6				9.8
			water oak	*Quercus nigra*	259	5.0
			laurel oak	*Quercus laurifolia*	82	1.6
			post oak	*Quercus stellata*	50	1.0
			southern red oak	*Quercus falcata*	46	0.9
			white oak	*Quercus alba*	36	0.7
blackgum	200	1.2	blackgum	*Nyssa sylvatica*	424	8.1
cypress-tupelo	117	0.7				5.5
			swamp tupelo	*Nyssa biflora*	189	3.6
			pondcypress	*Taxodium ascendens*	53	1.0
			baldcypress	*Taxodium distichum*	44	0.8
holly	90	0.6	American holly	*Ilex opaca*	63	1.2
sweetgum	80	0.5	sweetgum	*Liquidambar styraciflua*	128	2.5
maple	65	0.4	red maple	*Acer rubrum*	165	3.2
poplar	16	0.1	yellow-poplar	*Liriodendron tulipifera*	119	2.3
Total	15,716	97.6			5061	97.9

Only about 10% of historical tree records had diameter information, but mean diameter was 42.9 cm historically (simple means rather than quadratic means, and no small trees excluded) and 22.8 cm currently (for DBH ≥ 12.7 cm; Table 2). Historical pines (1041 records and 85% of diameter records) had a mean diameter of 45.8 cm. For contemporary forests, mean slash pine diameters (1194 records) and longleaf pine diameters (539 records) were both 24.6 cm, whereas loblolly pine diameters (1139 records) were 22.4 cm.

Table 2. A range of estimated historical tree densities (trees ha^{-1}) to account for uncertainty, current tree densities, and historical and current mean diameters (cm) for the central and southern Coastal Plain and northern Coastal Plain.

Landscape	Historical Densities					Current Densities			Historical	Current
	Unadjusted	**Low**	**Mod Low**	**Moderate**	**Mod High**	**Mean**	**Low**	**High**	**Diameter (cm)**	
Coastal Plain	197	168	189	228	268	336	308	364	42.9	22.8
Northern Coastal Plain	150	144	162	183	204	400	352	447	38.9	23.2

Historically, estimates of tree density ranged from a low value of 168 trees ha^{-1}, moderately low value of 189 trees ha^{-1}, moderate value of 228 trees ha^{-1}, to a moderately high value of 268 trees ha^{-1} (Table 2). These densities generally indicated the existence of closed woodlands (open woodlands < 175 trees ha^{-1} and closed woodlands < 250 trees ha^{-1}; [60]. In contrast, contemporary mean tree density was 336 trees ha^{-1}, representing a transition to closed forests.

3.3. Historical and Current Forests in the Ecotonal Northern Coastal Plain

Within the northern five counties of the Mississippi Coastal Plain province, for 9450 historical tree records and 2655 current tree records, 17 species or species groups had greater than trace presence (≥0.5% of all trees) in either the historical (mean year 1829, ranging from 1821 to 1833) or contemporary surveys (Table 3). Historically, fire-tolerant pine represented 47% of all trees, and fire-tolerant oaks were 32% of all trees. Fire-tolerant shortleaf pine and longleaf pine were the predominant historical pine species in this ecotone; longleaf pine decreased to 0.5% of all trees, and shortleaf pine decreased to 1.8% of all trees. Currently, pine was 55% of all trees, with primarily planted loblolly pine at 51.6% of all trees. Oaks have decreased to 13.2% of all trees, of which the wetland water oak was 6.2% of all trees. Hickories were historically a moderate component of these forests, at 6% of all trees, but have declined to 1.3% of all trees. Smaller tree species of American holly (*Ilex opaca*) and flowering dogwood (*Cornus florida*) decreased, while 'ironwood' (*Ostrya virginiana*) and sourwood (*Oxydendrum arboreum*) may have increased, although samples were small for both historical and current surveys. American beech (*Fagus grandifolia*) and *Castanea* species were also minor components that decreased over time; indeed, no *Castanea* were present in current surveys, indicating that these species may have been American chestnut (*Castanea dentata*). Early successional species, with low shade tolerances (<2.5 shade tolerance; [62]), increased. Sweetgum increased from 1.5% to 10.8% of all species, while yellow-poplar and black cherry (*Prunus serotina*) increased from few recorded trees to 3.5% and 2.5% of all trees, respectively. Chinese tallowtree (*Triadica sebifera*) is an invasive species.

Table 3. Count and percentage of historical (1821 to 1833) species or species groups compared to contemporary count and percentage of species in the northern part of the Coastal Plain ecological province in Mississippi. Uncommon historical and current species (≤0.5%) were excluded. Chinese tallowtree is a non-native species (N/A).

Historical			**Contemporary**			
Species Group	**Count**	**%**	**Species**	**Scientific Name**	**Count**	**%**
pine (shortleaf pine)	4419	46.7				55.1
			loblolly pine (planted)	*Pinus taeda*	1369	51.6
			shortleaf pine (planted)	*Pinus echinata*	48	1.8
			spruce pine	*Pinus glabra*	28	1.1
			longleaf pine	*Pinus palustris*	13	0.5
			slash pine	*Pinus elliottii*	5	0.2
oak	3029	32.0				13.2
			water oak	*Quercus nigra*	165	6.2
			white oak	*Quercus alba*	78	2.9
			southern red oak	*Quercus falcata*	39	1.5
			post oak	*Quercus stellata*	27	1.0
			cherrybark oak	*Quercus pagoda*	17	0.6
hickory	567	6.0				1.3
			mockernut hickory	*Carya alba*	13	0.5
			pignut hickory	*Carya glabra*	11	0.4
holly	210	2.2	American holly	*Ilex opaca*	5	0.2
blackgum	177	1.9	blackgum	*Nyssa sylvatica*	67	2.5
beech	153	1.6	American beech	*Fagus grandifolia*	10	0.4
sweetgum	140	1.5	sweetgum	*Liquidambar styraciflua*	287	10.8
maple	130	1.4	red maple	*Acer rubrum*	58	2.2
dogwood	105	1.1	flowering dogwood	*Cornus florida*	12	0.5
bay	94	1.0				1.9
(broadleaf evergreen)			sweetbay	*Magnolia virginiana*	41	1.5
chestnut	98	1.0		*Castanea*	0	0.0
ironwood	47	0.5				1.0
			American hornbeam	*Carpinus caroliniana*	24	0.9
			eastern hophornbeam	*Ostrya virginiana*	3	0.1

Table 3. *Cont.*

Historical			Contemporary			
Species Group	**Count**	**%**	**Species**	**Scientific Name**	**Count**	**%**
elm	37	0.4				1.6
			winged elm	*Ulmus alata*	28	1.1
			American elm	*Ulmus americana*	13	0.5
poplar	35	0.4	yellow-poplar	*Liriodendron tulipifera*	92	3.5
sourwood	33	0.3	sourwood	*Oxydendrum arboreum*	20	0.8
cherry	9	0.1	black cherry	*Prunus serotina*	67	2.5
N/A			Chinese tallowtree	*Triadica sebifera*	19	0.7
Total	9283	98.2			2559	98.2

While only about 60% of historical tree records had diameter information, mean diameter was 38.9 cm historically (simple means rather than quadratic means, with no small trees excluded) and 23.2 cm currently (for DBH $\geq$ 12.7 cm; Table 2). Historical pines (2419 records and 42% of diameter records) had a mean diameter of 44.8 cm. In contrast, loblolly pine diameters (1369 records) currently average 23.0 cm. Historical oaks (2070 records and 36% of diameter records) had a mean diameter of 37.9 cm, while currently, white oak (*Quercus alba*), the upland oak species with the most records (78), had a mean diameter of 26.0 cm.

Tree density historically ranged from a low value of 144 trees ha^{-1}, moderately low value of 162 trees ha^{-1}, moderate value of 183 trees ha^{-1}, to a moderately high value of 204 trees ha^{-1} (Table 3). These densities represent open and closed woodlands (open woodlands < 175 trees ha^{-1} and closed woodlands < 250 trees ha^{-1}; [60]). In contrast, current mean tree density was 400 trees ha^{-1}, representing a transition to closed forests.

3.4. Comparison between Historical and Contemporary Forests with the Squared Chord Distance

Pine and oak-pine percentages varied between historical forests of the central and southern Coastal Plain and ecotonal area of the northern margin, that is, 87.5% pine compared to 46.7% pine and 2.6% oak compared to 32% oak, respectively (Figure 3; with species assignments for pine described below). Historical fire-tolerant pine and oak dominance resulted due to species filtering by fire disturbance. Contemporary forests remained relatively comparable in pine percentage to historical forests due to the establishment of pine monocultures, with current pine percentages of about 55%. Current oak percentages were around 10%. Hickory was common only in the historical ecotone of the northern Coastal Plain province, whereas black cherry was common in current forests of the northern Coastal Plain province. Likewise, sweetgum was common in contemporary forests throughout the Coastal Plain province. Red maple and yellow-poplar percentages were relatively similar and increased in both contemporary forest locations compared to their minor presence in historical forests. Although blackgum was common in contemporary forests of the northern Coastal Plain province, wetland species including blackgum, cypress, and bay were more abundant in contemporary forests of the central and southern Coastal Plain province than in historical forests or contemporary forests of the northern Coastal Plain province (Figure 4). According to this distinction of woody wetlands cover, which remains abundant (23% of area; [63]) in the Coastal Plain, we delineated a current boundary for these forests (Figure 5) based on tree species with high ($\geq$3.5) waterlogging tolerance [62], albeit blackgum is only a facultative wetland species, similar to many tree species. We calculated percentage of tree species with high water-logging tolerance by ecological subsections (i.e., smaller landscapes within ecological provinces; [33]) and selected ecological subsections where these species were >5% of all trees [52].

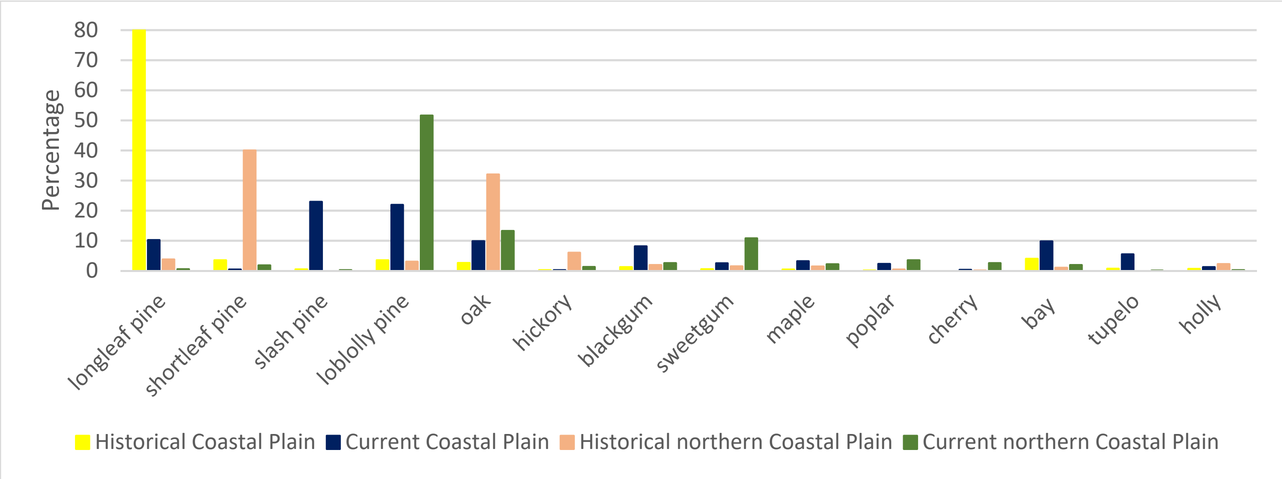

Figure 3. Changes in tree species composition (percentage of all trees) between historical and currrent forests of the central and southern Coastal Plain and northern Coastal Plain.

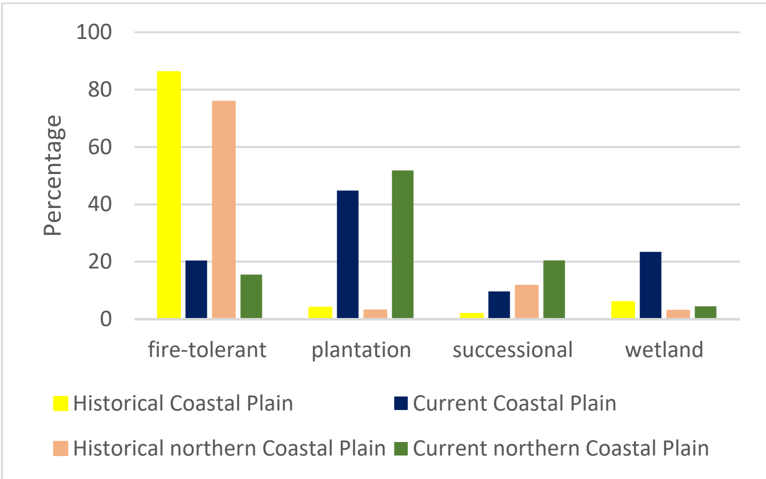

Figure 4. Changes in tree species composition (percentage of all trees) by groupings between historical and currrent forests of the central and southern Coastal Plain and northern Coastal Plain.

We calculated a dissimilarity metric for the more abundant species or species groups of pines, oaks, hickories, blackgum, tupelo, bays, sweetgum, black cherry, holly, maple, and yellow-poplar with pair-wise comparisons of historical and current composition (Figure 3). The squared chord distance was 0.295 between historical longleaf pine forests and historical ecotonal oak-pine forests, 0.162 between historical longleaf pine forests and contemporary forests, 0.151 between historical ecotonal oak-pine forests and contemporary forests, and 0.146 between contemporary forests in the northern Coastal Plain and the central and southern Coastal Plain. Because the pine grouping contained both fire-tolerant historically dominant species and currently dominant plantation species, for a general idea of change, we also used the current pine percentages of loblolly pine, slash pine, longleaf pine, and shortleaf pine and then assigned the majority of pine to the primary species of the historical forests, dividing up the remainder among the other three pine species (Figure 3). For example, we assigned 80% to longleaf pine of the 87.5% total pine for the longleaf pine forests of the central and southern Coastal Plain and 40% to shortleaf pine of the 46.7% total pine for ecotonal forests, while recognizing that these percentages are not known. With these changes, the dissimilarities indicated by squared chord distance values increased to 0.928 between historical forests, 0.713 and 0.720 between both sets of historical and contemporary forests, and 0.464 between contemporary forests.

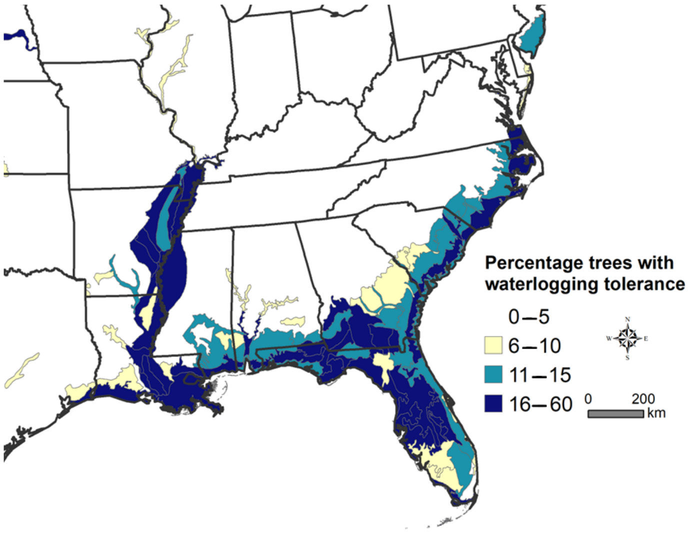

Figure 5. Currently, instead of fire-maintained longleaf pine woodlands, wetland tree species (defined by >5% of all trees with high waterlogging tolerance at landscape scales of ecological subsections; [33,52]) may demarcate Coastal Plain vegetation.

4. Discussion

Historical forest ecosystems in the United States were distinct, with strong ecological boundaries separating ecosystem types, and provided a range of ecosystem services due to a gradient of open structure. Specifically, longleaf pine woodlands dominated the Coastal Plain and oak-pine woodlands occurred in the northern province of the southeastern U.S. [16,42]. In this study, we detected the ecotonal boundary between longleaf pine woodlands and oak-pine woodlands in the northern margin of the Coastal Plain of Mississippi. We strengthened the information about historical longleaf pine forests, supplying an historical density estimate of closed woodlands in Mississippi (similar to [19]), and we provided a density estimate of open to closed woodlands in the ecotonal landscape. We also had the opportunity to contrast historical forest types and the differences between contemporary forests (Figure 6), finding that the greatest compositional difference existed between historical forest types, based on the squared chord distance. Conversely, contemporary forests are not comprised of such differentiated, dominant vegetation types. Instead, in the southeastern U.S., current forests are a homogenized mixture of commercial pines, early and mid-successional broadleaf species, and wetland species, which do not contain the range of open ecosystem structure in woodlands of the past, analogous to other newly developed forests in the U.S. and elsewhere [64]. Nonetheless, the moderate component of wetland tree species in the southern Coastal Plain offers one approach to delineate current forest type boundaries between the Coastal Plain and northern southeastern U.S. Aligning with many regions world-wide, unique open longleaf pine ecosystems that have ecological and cultural importance have been replaced by plantations, dense forests after fire exclusion, and other land uses [1–3,65].

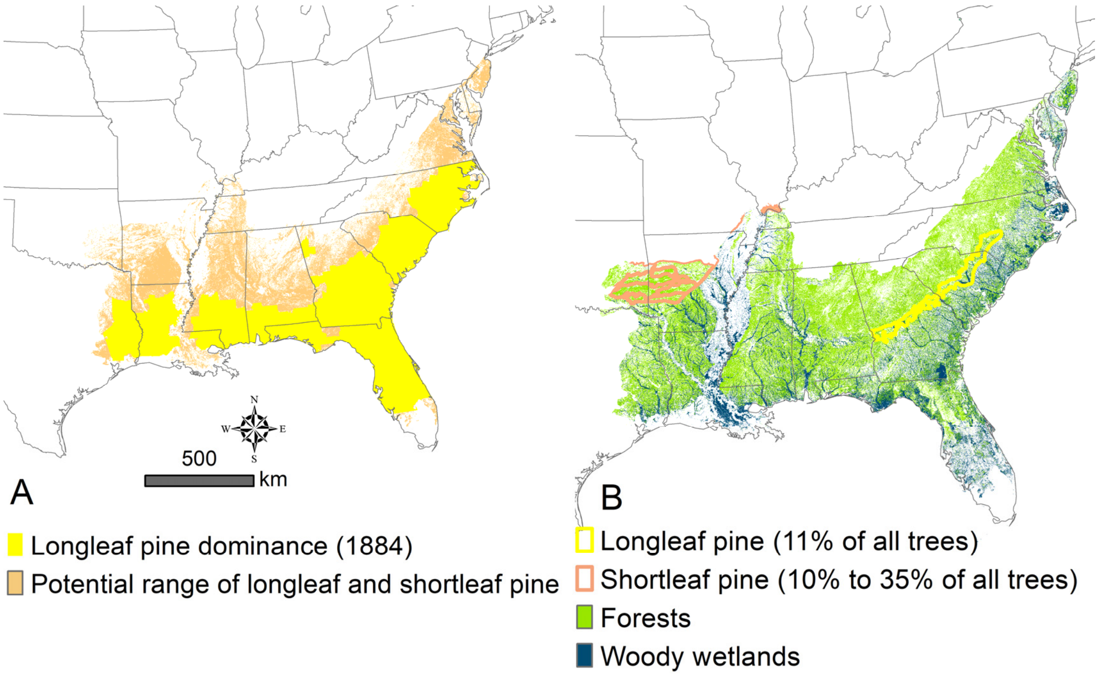

Figure 6. Longleaf pine dominance after onset of harvesting, particularly in the easternmost states where historical composition is unknown (Sargent 1884), and potential historical range of longleaf and shortleaf pine, interspersed with grasslands and wetlands, in the southeastern U.S. and extending along the Coastal Plain ((**A**); [25]). Currently, longleaf pine and shortleaf pine have limited dominance (dominance defined by ≥10% of all trees at landscape scales of ecological subsections; [33,52]), despite an overall forested region, comprised of broadleaf forests, pine plantations, and woody wetlands ((**B**); [63]).

4.1. Longleaf Pine Open Forests in the Coastal Plain

Before Euro-American settlement, forests in the central and southern Coastal Plain of Mississippi were dominated by pines, at 87.5% of all trees. Based on historical accounts and early forest reports by contemporaneous authors, fire-tolerant longleaf pine was the dominant species, with a minor component of loblolly pine and other southern pine species [16,18,66,67]. Indeed, due to the frequent occurrence of surface fire, only the longleaf pine grass stage, which is a rare adaptation among *Pinus* [68] to protect the apical meristem, may have allowed tree species to persist throughout the Coastal Plain. Similarly high historical percentages for pines have been reported for other locations within the Coastal Plain [16,19,37,38,43,44,69,70]. The remainder of the historical forests was comprised primarily of broadleaf tree species, whereas inundated areas were host to cypress and tupelo.

Longleaf pine has been replaced by commercial species of loblolly pine and slash pine and diverse broadleaf tree species, which cycle from clearcuts to dense forests. Following Euro-American settlement, longleaf pine forests have been logged and converted to other land uses, with attendant surface fire exclusion, generally after the historical land surveys in Mississippi [18]. Longleaf pine did not regenerate well following the exploitative logging era, due to factors such as lack of seed trees and presence of feral hogs [15]. Benefitting from the absence of fire and a lack of competition from longleaf pine, tree species increased in abundance as they migrated from firebreaks to adjacent upland areas previously occupied by longleaf pine before clearing and agricultural abandonment. In this study, broadleaf tree species consisting of evergreen species known as ‘bays’, blackgum, sweetgum, red maple, yellow-poplar, and water oak increased. Although loblolly and other pine species also are pioneers on abandoned agricultural land [71], loblolly and slash pine plantations have become progressively more common in the southeastern U.S. since 1950, covering

17 million ha in 2017 [16]. Therefore, slash and loblolly pines now account for about 45% of all tree species.

Historical tree density estimates ranged from 168 to 268 trees ha^{-1}, depending on spatial pattern and bias, in the central and southern Coastal Plain of Mississippi, similar to estimates in an adjacent area [18]. Predmore et al. [44] calculated 105 trees ha^{-1}, a density that indicates open woodlands, in historical pine forests of southern Alabama. For several longleaf pine forests in southeastern Alabama, southern Mississippi, and Southern Louisiana, Schwarz [44] quantified densities from 128 to 230 trees ha^{-1}, but two stands, one of which was 'immature', had densities of 407 and 417 trees ha^{-1}. Taken together, these estimates suggest that across the Coastal Plain, longleaf pine ecosystems may have been a mosaic of open and closed woodlands. As noted by early explorers such as William Bartram in the 1770s [72], savannas and grasslands were present, while some embedded wetlands, including riparian forests, contained closed, dense forests [25].

A mosaic of stand densities is typically the outcome of differences in surface fire regimes, which are influenced by interactions with topography, vegetation, and water bodies. Surface fire is an understory disturbance that preferentially removes small diameter trees, but other forms of disturbance that impact large, canopy trees also occurred on a less frequent basis. Surveyors in Mississippi noted areas destroyed by hurricanes [48]. These would have disturbed a portion of the forest, initiating its regrowth. Nonetheless, tree diameters were historically large, and longleaf pine is a long-lived species capable of reaching more than 450 years [73], which is an advantageous trait where overstory disturbance is rare.

Compared to historical forests, contemporary forests in the Coastal Plain ecological province are closed forests containing a high density of smaller-diameter trees. The structural transition to closed forests has also been reported for other historical longleaf pine open forests [19,28]. In naturally regenerated forests, stand density increased as broadleaf species invaded [14]. Artificially established monocultures also contain high densities of planted pines. Frequent overstory disturbance, including harvest of pine plantations on about 25-year cycles, has contributed to reduced tree diameters [16].

4.2. Oak-Pine Ecotonal Forests in the Northern Coastal Plain

Shifts in space between dominant ecosystem types at landscape scales are different than environmental gradients along the topographic positions from ridges and upper slopes to lowlands within watersheds. Historical forests at the northern edge of the Coastal Plain in Mississippi transitioned into oak-pine woodlands from longleaf pine woodlands in the central and southern Coastal Plain. Pine percentages decreased in space from 89% to 34% of all trees at the margin of the Coastal Plain province. Tree composition changed relatively rapidly; over a distance of at most 20 km, or a gap of two townships, pine decreased from 89% to 56% of all trees, and over the next 40 km, pine decreased from 56% to 34% of all trees (Figure 2). Based on shortleaf pine as the primary pine component of oak-pine forests [39,42], longleaf pine decreased and shortleaf pine increased as pine, overall, decreased; upland, fire-tolerant oaks also increased.

Like longleaf pine woodlands to the south, the combined legacies of overstory disturbance, fire exclusion, and commercial monoculture expansion have changed the composition and structure of the ecotonal forests of the northern Coastal Plain in Mississippi [71]. Currently, loblolly pine is the primary pine species, replacing fire-tolerant shortleaf pine and fire-tolerant oaks, albeit oak reductions are partially disguised by the increase in the wetland water oak species. Water oak has increased by tree encroachment from wetlands to adjacent mesic uplands [74]. Fire-tolerant species depend on fire to reduce competition from other tree species. Indeed, fire-tolerant oaks encourage fire by producing a highly combustible litter [75,76]. Hickories also decreased, and while not particularly fire-tolerant when young, mockernut hickory (*Carya alba*) and pignut hickory (*C. glabra*), like all true hickories, sprout prolifically from stumps and/or root suckers [77,78]. Likely of greater importance than fire to hickories, historical agroforestry favored mast-bearing tree species [70].

Oak and hickory species typically do not grow rapidly while young, and, thus, are overtopped by faster-growing species, such as sweetgum, that are abundant in contemporary forests [79].

Encroachment by shade-intolerant, early successional species such as sweetgum, yellow-poplar, and black cherry is remarkable in this area. Sweetgum and yellow-poplar were the major increasing broadleaf species in other studies for this province, but not black cherry, although black cherry has increased greatly in other locations [16,42]. Sweetgum has several traits that allow it to colonize sites. Besides rapid growth, advantageous invading attributes include physiological traits that alter its chemistry to dissipate heat, structural traits that make it resistant to breaking in high winds, and developmental traits that produce root suckers when lateral roots become exposed to light [80]. Yellow-poplar colonization is enhanced by wind dispersal of its winged carpels [81]. Once seeds become imbedded in the soil seed bank, they are viable for three to seven years [82]. With repeated seed introduction, this species is poised to germinate whenever a gap is formed by a wind-toppled canopy tree and may persist in the absence of fire. In addition, prolific stump-sprouting after being top-killed facilitates yellow-poplar persistence after a high-intensity fire. Black cherry may enter openings especially through animal dispersal. Once established, black cherry seedlings may resprout repeatedly over extended time intervals [83]. Resprouts have been reported to produce fruits as early as their second year, a feature which would enhance encroachment potential [84].

Tree densities have increased, while frequent overstory disturbance has reduced tree diameters. Historical tree densities of the ecotonal oak-pine forests were open to closed woodlands, with lesser tree density estimates than closed woodland estimates for longleaf pine forests in the central and southern Coastal Plain. Although this is just one estimate for forests in transition over space, to our knowledge, it is the first landscape estimate for historical oak-pine forests. Without understory control of fire-sensitive tree species by frequent surface fire, ecosystems have transitioned from open woodlands to closed forests.

4.3. Comparisons among Forests through Boundaries and the Squared Chord Distance

Historical ecosystems had distinct tree composition, dominated by a few foundational species or genera. The greatest squared chord distance, a measure of compositional similarity, among comparisons of historical and current forests was between historical longleaf pine forests and the historical oak-pine and ecotonal pine forests, indicating strong differentiation. Fire regimes filtered the available tree species pool of hundreds of broadleaf tree species throughout most of the eastern U.S., favoring fire-tolerant oak and pine species. Due to greater rugged topography that broke up fire spread in the northern southeastern U.S. (Hanberry and Noss 2022), longleaf pine percentage decreased along with surface fire frequency in the smaller fire compartments north of the flat Coastal Plain, where oaks and shortleaf pine had greatest abundance. Although the McNab et al. [33] and related The Nature Conservancy [54] ecological classifications had boundaries along historical ecotonal forests, the Olson et al. [53] boundary occurred within the ecotone between pine percentages of 89% and 56% (Figure 2).

The least squared chord distance difference was between boundaries of contemporary forests, but the values indicated that contemporary forests of the Coastal Plain were different from those of the northern margin of the Coastal Plain in the ecotone. Pine monocultures have become abundant, and the two contemporary forest landscapes had an equivalent composition of 55% pines, primarily of commercially managed species. The percentage of early successional broadleaf species and wetland species varied among contemporary forests. Many broadleaf species are no longer confined to fire breaks; consequently, early successional tree species have become abundant, particularly in the northern margin of the Coastal Plain.

Nonetheless, as successional status may change over time, wetland tree species may more permanently delineate the Coastal Plain from the northern southeastern U.S. The Coastal Plain currently is comprised of about 28% wetlands in land area excluding water, while the northern southeastern U.S. contains only 8% wetlands [63]. Instead of historical patterns of pine abundance resulting from surface fire regimes that decreased in frequency from the flat Coastal Plain to the more rugged interior, wetlands may provide the current filter on the species pool that differentiates Coastal Plain forests from northern forests. Thus, the description of 'mixed forest' (i.e., Outer Coastal Plain Mixed Forest and Southeastern Mixed Forest ecological provinces) does not represent historical pine or pine-oak forests or differentiate current forests in the Coastal Plain from the northern southeastern U.S. Ecological classification systems are useful constructs but do not necessarily describe current or historical boundaries in vegetation. Boundaries may soften and become even less distinct in the future as species ranges shift under climate change.

5. Conclusions

Similar to other studies conducted internationally, we documented the forestation of historically open forests in the Coastal Plain of the southeastern U.S. Open forests of historically distinctive longleaf pine woodlands and ecotonal oak-pine woodlands transitioned to contemporary closed forests of predominant commercial pine species, successional broadleaf tree species, and wetland tree species. The moderate component of wetland tree species in the abundant wetlands of the Coastal Plain may help delineate contemporary forest boundaries now that forests have developed similar structures and tree species without fire disturbance. In contrast, historically, wetlands were incorporated within dominant longleaf pine forests, and historical pine and oak composition resulted from surface fire regimes, which shifted at regional scales. Ecoregional boundaries have meaning, but both the boundaries and the meaning have changed over time, as contemporary forests have become more similar than unique historical open forests. Forestation, particularly by fire-sensitive tree species, had produced homogenized forests, which do not deliver the same ecosystem services as open gradients in ecosystems of the past.

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