

Article

Documenting Two Centuries of Change in Longleaf Pine (*Pinus palustris*) Forests of the Coastal Plain Province, Southeastern USA

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Abstract: While many tree species occur across the Coastal Plain of the southeastern United States, longleaf pine (*Pinus palustris* C. Lawson) savannas and woodlands once dominated this region. To quantify longleaf pine's past primacy and trends in the Coastal Plain, we combined seven studies consisting of 255,000 trees from land surveys, conducted between 1810 and 1860 with other descriptions of historical forests, including change to the present day. Our synthesis found support that *Pinus palustris* predominantly constituted 77% of historical Coastal Plain trees and upland oaks (*Quercus*) contributed another 8%. While *Pinus* still dominates these forests today (58% of all trees), most are now either planted loblolly (*Pinus taeda* L.) or slash (*Pinus elliottii* Engelm.) pines. Water oak (*Quercus nigra* L.), live oak (*Quercus virginiana* Mill.), sweetgum (*Liquidambar styraciflua* L.), and red maple (*Acer rubrum* L.) have increased their proportions compared to historical surveys; both longleaf pine and upland oaks have declined to ≤5% of all trees. Our work also supports previous estimates that longleaf pine originally dominated over 25–30 million ha of Coastal Plain forests. As late as the early 1900s, longleaf pine may still have covered 20 million ha, but declined to 7.1 million ha by 1935 and dropped to 4.9 million ha by 1955. Longleaf pine's regression continued into the mid-1990s, reaching a low of about 1.3 million ha; since then, restoration efforts have produced a modest recovery to 2.3 million ha. Two centuries of overcutting, land clearing, turpentine for chemicals, fire exclusion followed by forest densification by fire-sensitive species, and other silvicultural influences, including widespread loblolly and slash pine plantations, have greatly diminished the Coastal Plain's once extensive open longleaf pine forests.

Keywords: European; fire; historical; oak; plantation; savanna



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1. Introduction

Widespread adoption of forest management practices, such as fire exclusion, preferences for quicker-yielding species, and denser stands to increase timber production have transformed North America for centuries [1,2]. For instance, the forests of the Outer Coastal Plain Mixed Forest Province (hereafter, Coastal Plain), an ecological region that covers about 56 million ha of the United States [3] are today different than those formerly dominated by longleaf pine (*Pinus palustris*; [4–7]). Two centuries ago, longleaf pine was the primary tree species across tens of millions of hectares and a prominent component of millions of additional hectares of this province (Figure 1; [4,8–10]). Indeed, most of the earliest explorers to this region marveled at this vast timber resource [11–13], estimated by Mattoon (1922; [14]) to once contain nearly 2.3 billion cubic meters of merchantable longleaf pine. Not surprisingly, then, longleaf pine forests were crucial to the socioeconomic well-being of the United States for many decades [5,15,16].

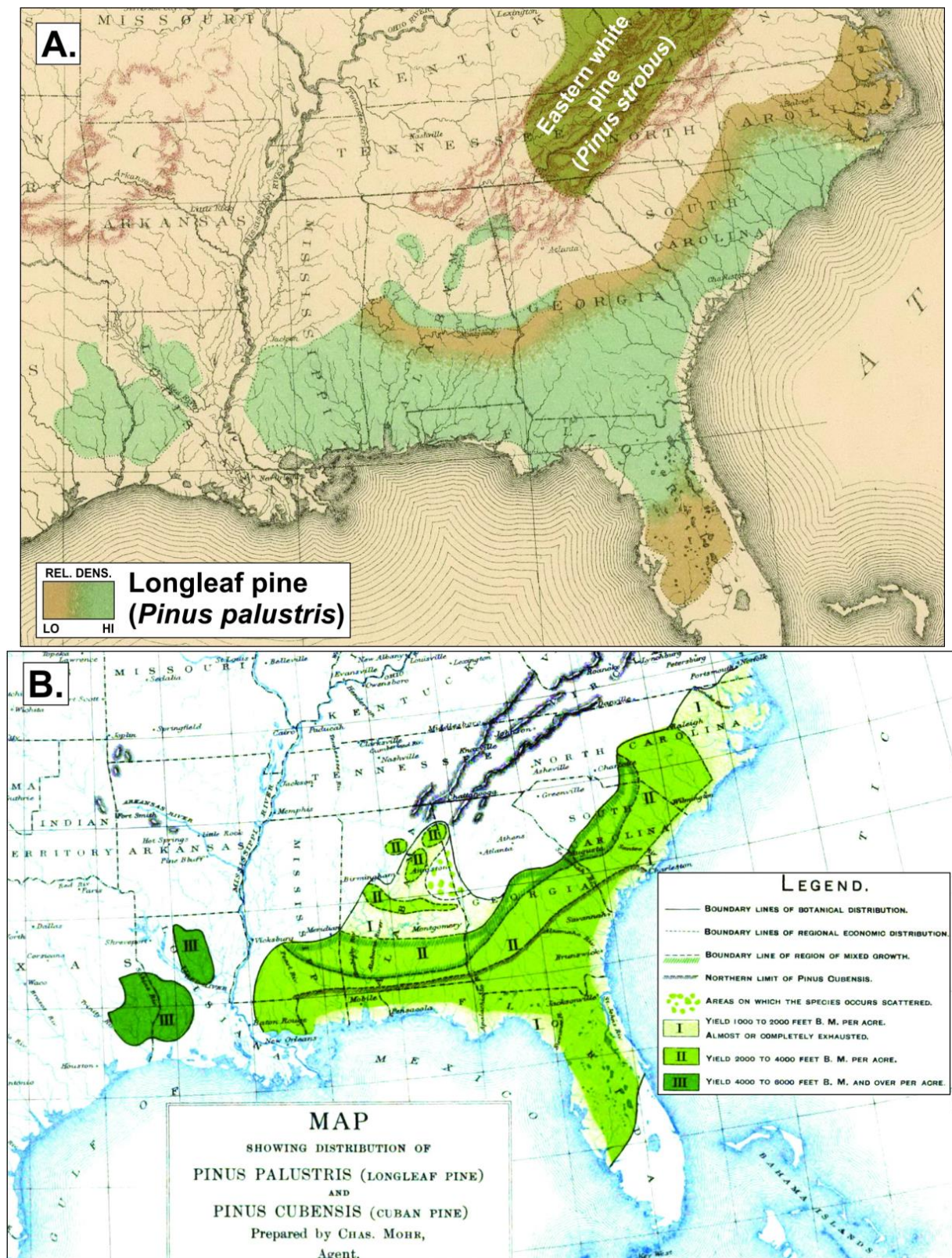


Figure 1. (A) Historical distribution of longleaf pine according to Sargent (1884; legend adapted from [10]) with the darkest green shade representing the “region of greatest development” (relative stem density) and the tan areas of lower longleaf density. (B) Semi-quantitative estimates of standing volume, as adapted from the original Mohr and Roth (1897; [9]) map of longleaf and slash pine distributions across the southeastern U.S.

The longleaf ecosystems of the Coastal Plain in the southeastern U.S. also were ecologically important [5]. The Coastal Plain province is a complex mosaic of landforms arising from a long geological history of marine advances and retreats, and affected by erosion, deposition, and biogeochemical weathering of parent materials [17]. The longleaf pine ecosystems of the Coastal Plain are often interspersed with forested wetlands [8,15,18,19] and biologically diverse, encompassing large numbers of rare and endemic taxa, such as unique fire-specialist amphibians [6,20–25]. Longleaf pine forests are particularly renowned for their floristic richness and endemism, containing at least 6000 vascular plant species including over 1600 endemics [5,26]. The extraordinarily high number of herbaceous species in longleaf pine ecosystems, averaging 25 to 35 species per m² up to 168 species per m², represent some of the greatest floral diversity found in the temperate zone [5,27,28].

This richness was possible because most longleaf pine ecosystems were savannas and woodlands, which coexisted with an understory of wiregrass (*Aristida*), saw palmetto (*Serenoa repens*), bluestem (*Andropogon* and *Schizachyrium*), panicgrasses (*Panicum*), other graminoids (e.g., *Paspalum*), and multitudes of forb species. Given favorable temperatures and precipitation that permit rapid tree growth in the Coastal Plain, which now has the shortest timber rotations and greatest generation of forest products in the U.S., fire was vital to control tree regeneration of diverse tree species and perpetuate expansive longleaf pine ecosystems [29,30]. The open, but structurally complex, nature of longleaf pine savannas and woodlands arose from many centuries of low severity, high frequency (2 to 5-year return interval, [31]) surface fires. Adaptations of longleaf pine allow it to persist and thrive in this fire regime that excludes many other woody shrubs and trees. Consequently, across much of the Coastal Plain, fire-sensitive tree taxa (e.g., loblolly, *Pinus taeda*, and slash, *Pinus elliotii*, pines and broadleaf tree species) were largely restricted to fire refugia, such as wetlands [32–35] or sheltered upland locations [1,36]. Longleaf pine has a lifespan of several centuries and overstory disturbance was rare relative to current overstory disturbance, resulting in old-growth longleaf forest systems rather than current successional forests [1,2].

In addition to abiotic and biotic factors, humans have influenced natural communities of the Coastal Plain for at least 12,000 years [4,6,15,37]. Human-caused ignitions contributed greatly to the surface fire regimes of the Coastal Plain, helping to ensure their frequency and spread across the flat, largely barrier-free region [31,38]. Native Americans used fire to clear vegetation and support their lifeways for millennia [39,40]. Upon their arrival, Euro-American settlers adopted these practices and even increased burning frequencies to keep the fire-adapted longleaf pine communities open for pastoralism and to control pests [6,41–45]. Deliberate and accidental fires were also part of the practice of naval stores (chemicals) extraction, called “turpentineing”, which became one of the first major forest-based industries in the Coastal Plain, until replaced by petroleum-based products [46,47].

The rapidly industrializing nation harvested vast amounts of forest products, ushering in a decades-long period of exploitation of valuable longleaf pine, by prioritizing maximum harvest and immediate economic gains over a sustained flow of goods and services [17,46,48,49]. Early turpentineing, lumbering, and row crop agriculture resulted in the loss of some Coastal Plain longleaf forests. However, most of the ‘cut out and get out’ impacts occurred between 1880 and 1930, supplying forest products and chemical materials to a developing nation in exchange for the longleaf pine ecosystems, concurrently compromising the needs of future generations for natural capital [50].

Additional changes to land management practices in the following decades, including effective fire exclusion starting in the 1930s and then silvicultural preferences for loblolly (*Pinus taeda*) and slash (*Pinus elliotii*) pines, further degraded the once-dominant Coastal Plain longleaf pine forests [16]. While numerous observers recognized both the biological value and the increasing loss of longleaf ecosystems [51–59], the decimation of longleaf-dominated ecosystems continued unabated. It was only in the latter decades of the 20th century that the magnitude of the problem was truly grasped, and by this time, only a small percentage of the longleaf pine forest remained [2,4,6,16,22,60,61]. Following decades of harvest, agricultural cultivation, overgrazing by livestock, exclusion of frequent surface

fires, and stand conversions to plantations of other tree species, scientists and managers have few contemporary examples of functional longleaf pine upon which to develop restoration strategies.

Today, longleaf pine restoration has become a priority for many public land managers and private owners across the Coastal Plain, and providing useful information to guide restoration is critical. However, the change in longleaf pine's dominance over time has been unevenly documented. Hence, our objective for this paper was to synthesize and interpret sources of existing information to document the extent and dominance of longleaf pine ecosystems across the Coastal Plain during the past two centuries. Information from original public land survey reports and modern assessments, when combined with other historical records including traveler and settler narratives, early maps, scientific studies, and forestry reports, offer a means to describe past forest conditions. When compared with contemporary Coastal Plain forests of the southeastern U.S. as measured by the modern large-scale forest surveys of USDA Forest Service's Forest Inventory and Analysis (FIA) program, this synthesis also allows for tracking longleaf pine's decades-long decline. An understanding of the factors that shaped longleaf pine's current Coastal Plain distribution will help provide insight about how an altered environment may affect future ecosystems in this province.

2. Materials and Methods

2.1. Historical Tree Records from Public Land Surveys in the Coastal Plain Province

Public land surveys have been used for a century to quantify past forest composition, structure, and dynamics [62–64]. Comparable to explorer narratives, public land surveys typically occurred before or during Euro-American settlement [65] and the witness trees recorded in these surveys are sometimes the only widely available record of historical forests. Using land surveys to reconstruct past forests and other environmental conditions presents many challenges because public land surveys were designed as a basis for land distribution rather than to quantitatively describe forests. Challenges include an inherently sparse inventory of trees that surveyors may have poorly identified, imprecisely estimated, or selected with biases.

The surveys of the Coastal Plain province also reflect a diverse mixture of surveying systems. Before the passage of the Land Ordinance of 1785, an irregular surveying approach known as “metes and bounds” that used various landmarks to designate property boundaries dictated the approach to land allocation in Virginia, the Carolinas, and the eastern part of Georgia that was part of the original thirteen colonies. The western half of Georgia was surveyed using a gridded survey system similar to the later General Land Office surveys [39,66,67]. Most of the rest of the land surveys of the Coastal Plain province followed the General Land Office system of gridded square longitudinal townships and latitudinal ranges comprising 1.6×1.6 km sections [68]. Surveyors recorded two to four trees at every section corner and halfway along section lines.

Regardless of their origin, survey systems used trees to “witness” the corners and lines established by land surveyors by providing a measured distance and bearing from their referenced property corner or line. For this study, we adapted data from previously published research of witness trees covering approximately 9 million ha of the Coastal Plain province (Figure 2). From these studies, about half of the 255,000 tree records in total were from northern Florida during 1822–1854 [69], 87,000 from southwestern Georgia during the 1820s [39], 10,000 in five counties from central Georgia during 1805–1821 [67,70], 13,000 from southern Alabama during 1820–1846 [71], 8000 from eastern Alabama during the 1830s–1850s [72,73], and 10,000 from southern Mississippi during 1810–1840 [74]. Studies were located in ecological subsections to provide estimates for ecological units and match reporting for current trees. We then averaged species composition weighted by sample size for any subsections that contained more than one compositional table.



Figure 2. Locations of the historical tree studies used for this paper (black) and the Coastal Plain ecological province (gray shading) where longleaf pine was dominant.

To analyze the trends of longleaf pine dominance, we considered the original forest composition of this portion of the Coastal Plain. Surveyors labeled witness trees with common names, sometimes only with genera, and taxonomic imprecision required additional refinement. For instance, the native pine species were all labeled “pine”, and not designated by species. To adjust for lack of specification, we used two different approaches. For pines, we used historical descriptions and early silvicultural accounts to infer that most of the “pine” in the Coastal Plain areas was longleaf pine, with fire-sensitive pines accounting for only a limited fraction of the total (see Results section and sources; e.g., [12,75,76]). For broadleaf species such as “oak” or “gum” that were sometimes labeled only to genera, we proportionally distributed these vaguely identified taxa to the most appropriate species, based on known rates of frequency of species in that genus from survey notes.

2.2. Additional Sources of Information on Composition and Dominance of Longleaf

The first written descriptions of pine-dominated Coastal Plain forests, predating the land survey records, are a limited number of narratives by explorers, soldiers, missionaries, and early Euro-American settlers. Most of their accounts of forest conditions are qualitative and impart only limited insights on species composition, structure, and dynamics; furthermore, many are also imprecise, incomplete, and sometimes subject to inaccuracy and even embellishment. The earliest explorers and botanists who wrote about their travels through this province often marveled at the extensive and nearly pure longleaf pine landscapes they witnessed, but otherwise did not estimate stand attributes (e.g., stocking, biomass, or size class distributions) calculated today to understand forest composition, structure, and function. Nevertheless, these accounts still supply useful and early information on the historical forests of the Coastal Plain province.

More accurate descriptions than early visitor accounts and land surveys of Coastal Plain forests eventually developed. By the end of the 19th century, academics, government agencies, and even some industries began documenting natural communities and forest resources across the region [31,35,54,73,77]. These first reports represent some of the most

coherent ecological community descriptions, but often lacked quantitative details or focused on a specific element or geography. As an example, the forestry-based reports produced by various federal agencies during this period rarely provided the community-level detail of botanical studies but often attempted more quantitative assessments of the tree species, especially the commercially valuable ones. Some of this information was developed from local “experts” or crudely designed questionnaires (self-assessments) distributed to mills or large corporate landowners. The capacity to comprehensively assess using statistically robust means the extent and quantity of longleaf pine across the Coastal Plain was not available until well into the 20th century when the USDA Forest Service first conducted large-scale forest inventories [78].

To quantify current forest composition on the ecological subsections paralleling where the compiled historical land surveys were present, we used the most recent FIA surveys (FIA DataMart, www.fia.fs.fed.us/tools-data, accessed on 31 January 2021; [79]). This resulted in about 120,000 trees for our comparative compositional analysis. The FIA plots occur every 2500 ha and generate landscape-scale estimates.

2.3. Determining Longleaf Pine Extent in the Coastal Plain over the Past 200 Years

The earliest estimates of the original longleaf pine extent (Figure 1) are likely low because they probably did not fully account for decades of prior lumbering and land clearing. Hence, to estimate historical cover of longleaf pine in the Coastal Plain during the first half of the 1800s, we adapted Frost’s [4] approach of upland area and pine percentage of that area as calculated from historical surveys. Cleland et al.’s [3] map of the entire Coastal Plain province (from southern New Jersey into Texas) covers 56 million ha (Figure 3). To determine the Coastal Plain’s upland area, we first removed the northeastern extension of the Coastal Plain province, from part of Virginia to New Jersey, due to unknown longleaf pine distributions before the 1800s (see also 49). This produced an initial estimate of 49.1 million ha of possible longleaf pine distribution in the Coastal Plain province, which is a flat region that allows for the frequent fire spread necessary for longleaf pine dominance. We then applied the 2016 National Land Cover Database [80] to remove areas currently classified as vegetated wetlands and open water, which presumably are sites too wet to support dominance by longleaf pine, to approximate upland area. This was important for describing the potential historical extent of longleaf pine-dominated uplands, as large areas of the Coastal Plain are various types of forested wetlands. For instance, in northern Florida, wetlands comprised 8% of forests that were largely a mixture bay (*Persea borbonia* (L.) Spreng., *Gordonia lasianthus* (L.) Ellis, *Magnolia virginiana* L., *M. grandiflora* L.), cypress (*Taxodium*) and tupelo (*Nyssa*), and other broadleaf-dominated swamps [69].

Between this circa-1820 approximation of the original longleaf extent and the development of formal Forest Service inventories of longleaf pine from the Southern Forest Survey, we gathered the most quantitative and reliable estimates we could locate in the literature associated with a specific time period. These included a number of estimates for the late 1880s and 1890s [9,58,81] and some produced during the 1920s and early 1930s in support of early conservation efforts and other national assessments of potential timber shortages [14,82].

To analyze longleaf spatial extent and trends from 1935 until circa 2020, we used the various Forest Service published data and large-scale forest surveys. Starting in the early 1930s, these inventories followed a scientifically designed transect-based sampling approach applied to geographic areas of approximately 1/3 of a state in size [78]. Underfunded and understaffed, the initial forest surveys of the Coastal Plain took about a decade to finish, with some not completed and analyzed until the 1940s. After this, a more regular fixed plot-based large-scale inventory approach, eventually known as Forest Inventory and Analysis, was adopted, which was roughly decadal until about 2000, when they became “annualized” [79,83]. The forest surveys supplied the most detailed and accurate means to consider regional forest composition and change, especially in a series of monographs and reports featuring the longleaf pine resource over the decades [17,22,84–87].

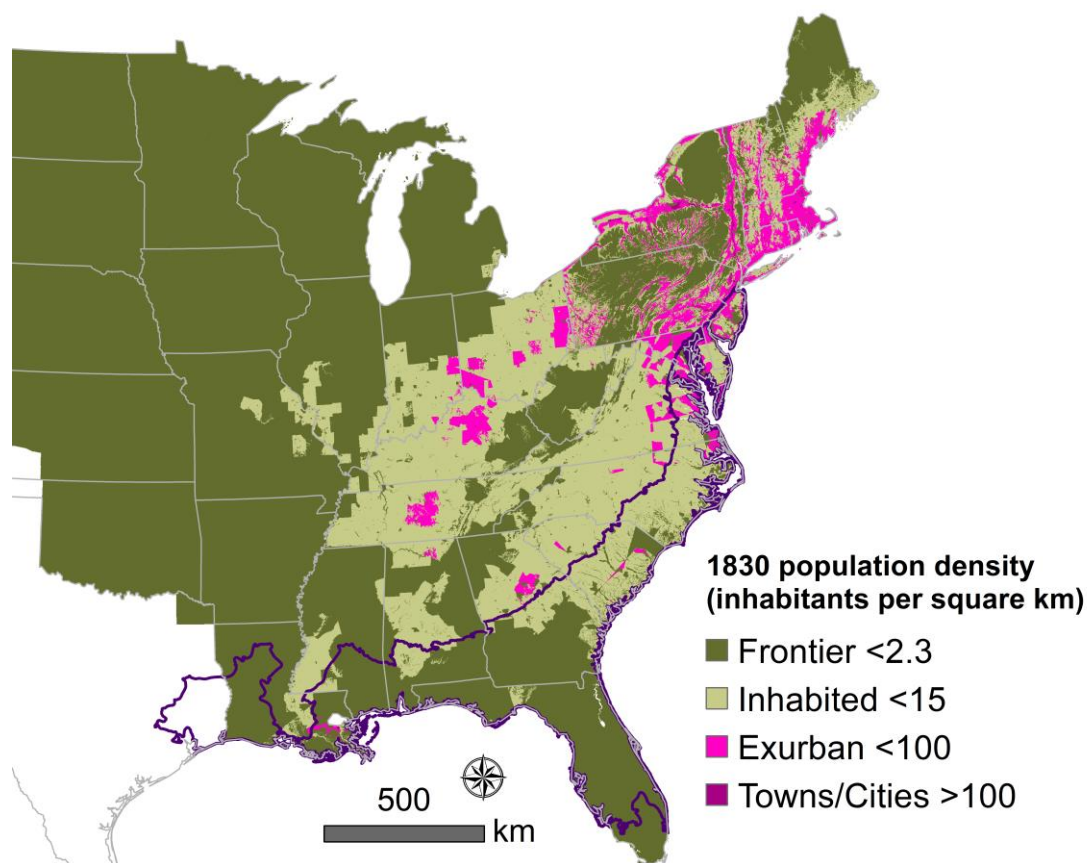


Figure 3. Euro-American settlement during 1830 in the United States (Texas annexed during 1845; Coastal Plain ecological province outlined in purple; adapted from [65]).

3. Results

3.1. Historical Accounts of Longleaf Pine Abundance from North Carolina to Louisiana

Descriptions of the longleaf pine dominance of the Coastal Plain can be found before the beginning of the historical land surveys in the early 19th century. English naturalist Mark Catesby (1731:4; [88]) described three primary types of sites in the Carolinas. According to Catesby, the “worst kind of land” was “pine barren land, the name implying its character. The soil is a light steril [sic] sand, productive of little else but pine-trees. . . One third part of the country is, I believe of this soil”. These pine barrens were interspersed with narrow strips of swamps (stream bottoms and pocosins) with different bottomland broadleaf species and conifers other than longleaf pine. Catesby (1731:23; [88]) commented that “these [longleaf pine] grow usually by themselves, with very few of any other [tree species] intermixed”. Later, Anonymous (1851:107; [89]) observed in North Carolina: “For about 40 miles [64 km] behind the flat country [along the Atlantic Coast] extends. . . a belt of land, of a surface moderately uneven, with a sandy soil, of which pitch-pine [*Pinus palustris*, not *Pinus rigida* Mill.] is the prevailing natural production”. Anonymous (1851:109; [89]) wrote “The pine forests, which cover almost all the district [eastern North Carolina], contribute greatly to the wealth and general prosperity of the state”.

William Bartram traveled extensively across the eastern portion of the Coastal Plain during the 1770s. He described the Sand Hills of the Coastal Plain in the Carolinas and Georgia as “... a vast plain, generally level, which extends west sixty or seventy miles [97–113 km]. . . This plain is mostly a forest of the great long-leaved pine (*P. palustris* Linn.) the earth covered with grass, interspersed with an infinite variety of herbaceous plants, and embellished with extensive savannas. . .” (Harper 1998:20; [12]). Bartram recorded many locations covered by extensive forests of longleaf pine with few other tree species of note, such as the 80 km long route to Mobile, Alabama that was “... one flat grassy savanna and

cane meadows, intersected or variously scrolled over with narrow forests and groves, on the banks of creeks and rivulets, or hommocks and swamps at their sources; with long leaved Pines, scatteringly planted, amongst the grass...” (Harper 1998:255; [12]).

French botanist André Michaux and his son Francis André Michaux spent years in the 1780s and 1790s gathering botanical collections across much of the eastern Coastal Plain. Longleaf pine was “found almost without interruption in the lower part of the Carolinas, Georgia, and the Floridas, over a tract more than 600 miles [966 km] long from north-east to south-west, and more than 100 miles [161 km] broad from the sea towards the mountains of the Carolinas and Georgia”. (Michaux 1819:134; [90]). Michaux also reported longleaf as being most common in stands of mixed composition above the Neuse River in east-central North Carolina but then having “almost exclusive possession” of upland sites, with “not more than one stock in a hundred [being] of another species”. In these pine “barrens”, longleaf could be found mixed with the other southern pines only along the margins of wetlands. Otherwise, longleaf pine formed an “...unbroken mass of woods which covers this extensive country [the Coastal Plain of the Carolinas]” (Michaux 1819:134; [90]).

British officer Captain Basil Hall likewise observed the great expanse of this pinery in his travels from Savannah, Georgia towards Mississippi during the late 1820s. Hall (1830:255–256; [11]) estimated the extent of the longleaf landscape: “For five hundred miles [805 km], at the least, we traveled, in different parts of the South, over a country of this description, almost everywhere consisting of sand, feebly held together by a short wiry grass, shaded by the endless forest. I don’t know exactly what the cause was, but it was a long time before I got quite tired of the scenery of these pine barrens. There was something, I thought, very graceful in the millions upon millions of tall and slender columns, growing up in solitude, not crowded upon one another...”.

Colonel John F.H. Claiborne (1906:523; [91]) reported on his 1840 journey across Mississippi that: “The whole east is thickly planted with an almost unvaried forest of yellow [longleaf] pine. Finer, straighter, loftier trees the world does not produce. For twenty miles [32 km] at a stretch in places you may ride through these ancient woods and see them as they have stood for countless years, untouched by the hand of man and only scratched by lightning or the flying tempest. This growth of giant pines is unbroken on the route we pursued for a hundred miles [161 km] or more, save where rivers or large water courses intervene...”.

Troost (1846:254; [13]) provided a similar description of the extent of longleaf pine: “Stretching through North and South Carolina, Georgia, Alabama and Louisiana, are vast forests of the long yellow pine, of matchless height and straitness [sic]; it is one of the most useful and valuable of the forest trees... It extends over a tract 600 miles [966 km] long and 100 [161 km] in breadth, and grows almost universally over this immense extent of soil”. Physician and scholar Daniel Drake (1850:59; [92]) recounted that the forests near Pensacola, Florida had the “prevailing and characteristic forest tree of this plain, is the long-leaved pine; which, in many parts, as between Pensacola [Florida] and Mobile [Alabama], forms a dense and lofty forest, to the exclusion of almost every other tree”. Featherman (1872:108; [93]) wrote that the pineywoods of southwestern Louisiana were covered with longleaf pine and that these “pine flat forests are without underwood, and the grass grows there as luxuriantly as it does in the sand prairies, and they afford excellent pasture ground for live stock”. Featherman (1872:109; [93]) also observed how this open, grassy ecosystem was sustained by annual burning of the understory that consumed the fallen pine needles and killed off any new pine seedlings, aided by the cattle (*Bos taurus*) that “not only nip the young grass, but also the pine...”.

3.2. Early Scientific Assessments of Longleaf Dominance from North Carolina to Texas

Based on numerous forest experts from early in the period of widespread lumbering between 1880 and the 1920s [9,10,31,33,54,59,73,94–98], most upland Coastal Plain pine forests were dominated by longleaf pine. For instance, Mohr (1882:82; [98]) described an area of over 7.25 million ha between the Chattahoochee River in western Georgia to the

Mississippi River as “...one unbroken forest...[where] the Long-leaved Pine has taken almost entire possession of the soil...”; Mohr (1882:87; [98]) later estimated that longleaf pine forests covered about 14 million ha. In North Carolina, Ashe (1894; [32]) reported that the virgin forests of the North Carolina Coastal Plain were “unanimously” described by the first historians of that state as ubiquitously covered by longleaf pine, with the other major southern pines, primarily loblolly, as only infrequently or locally abundant.

Longleaf dominance continued to be recorded as biogeographers became more detailed in their reports, as in Georgia and Florida. Harper (1905:146; [54]) described one-third of the Georgia Coastal Plain as covered, for at least 90% of the area, by rolling pine wire-grass “barrens” where the dominant tree species was longleaf pine. The much smaller area (less than one-tenth of the landscape) of riparian wetlands and swamps were richer in tree species, dominated by slash pine, pond cypress (*Taxodium ascendens* Brongn.), and swamp tupelo (*Nyssa biflora* Walter). According to Harper [54], the adjoining lime sink (to the north and west of the rolling wire-grass country) and flat pine lands (south and east towards the Atlantic Coast) were both about 90% pine barrens, each prominently longleaf pine with an increasing slash pine admixture near the coast [97]. In a treatise on the development of agriculture in southern Georgia, Harper (1922; [97]) reinforced the accounts of longleaf pine dominance in the lands outside of the wetlands, with few exceptions. For instance, in a small division extending from Florida just into extreme southern Georgia he labeled the “Tallahassee red hills”, the most common trees were live oak (*Quercus virginiana*), sweetgum, and “the short-leaf (rosemary) pine [*Pinus echinata* Mill.] still more so [common]” (Harper 1922:106; [97]). Many of Harper’s (1914; [94]) northern Florida subregions away from the coasts and major wetlands were longleaf dominated, especially outside of local bottoms and wetlands.

Longleaf pine was dominant in the Coastal Plain of Alabama and Mississippi. In the upper reaches of the Coastal Plain in central Alabama, Harper (1913:80; [31]) estimated that in the “original forests about 52% of the trees were evergreen [conifers], most of which figure was made up of long-leaf pine”. Longleaf pine dominance increased markedly in the southern quarter of Alabama, with areas such as Harper’s “Lime-Sink” and “Southwestern Pine Hills” regions containing 77%–91% longleaf of the total pine fraction [31]. Based on Harper’s (1913; [31]) list of tree species for the upper Coastal Plain in central Alabama, longleaf pine may have comprised about two-thirds of the five listed species of pine. Additionally in Alabama, noteworthy areas of “mountain” longleaf pine occurred in the southern Appalachian Highlands. Mohr (1901:59; [34]) described what he called “xerophile forests” along dry rocky ridges up to about 600 m above sea level of overwhelmingly longleaf pine of an open, often stunted nature with virtually no understory or herbaceous groundcover. Similar accounts can be found in L. Harper’s (1857:181; [99]) assessment of the lands of southern Mississippi: “The whole country is overgrown by the long-leaf pine (*Pinus palustris*), which grows there to a very large size...”.

On the western side of the Coastal Plain, across the Mississippi River in Louisiana and Texas, most areas with longleaf contained pronounced longleaf dominance. Foster (1912; [73]) declared that outside of the riparian zones and other wetlands, the longleaf pine regions of southeastern and southwestern Louisiana were “practically” pure longleaf pine. According to Harper (1920a:74; [95]), the extensive “long-leaf pine region” of the Coastal Plain in southern Louisiana had “*Pinus palustris* outnumber[ing] all other trees by a large majority” and on uncut uplands “...it makes a pure stand with no woody undergrowth of any kind”. Harper (1920a; [95]) also noted these Louisiana longleaf stands had several times the average sawtimber volume of this forest type elsewhere in the southeastern U.S. On the far western extreme of the Coastal Plain, Bray (1904:22; [100]) described the extension of the “longleaf pine area” of the Fayette Prairie in southeastern Texas as about 1.3 million ha of longleaf “...characteristically found in heavy forest over large tracts with a practically pure stand” especially in the sandy uplands. Chapman (1909; [101]) and Harper (1920b; [96]) described similar conditions in eastern Texas with stands of open, nearly pure, multi-aged longleaf pine that comprised old trees. Chapman unequivocally stated that “longleaf pine

in the original forests *was always found growing in practically pure stands*". (Chapman 1942:11, his emphasis; [51]).

Longleaf pine thus was described as dominant in the Coastal Plain from North Carolina to Texas, with few localized exceptions. Accounts only rarely mentioned pines other than longleaf in the uplands, although their presence was remarked in wetlands, as in the case of loblolly and slash pines, or in higher, poorer lands with shortleaf pine ([31]; Bartram's account of the Coastal Plain, [12]). This was consistent with later silvicultural accounts noting the dominance of loblolly and slash pines in wetter (moist soil) sites such as those along streams [9,33,51,59,75,102]. As an example, slash pine became the dominant pine species in the southern half of Florida, coastal South Carolina and Georgia, and along coastal wetlands [103]. This is expected for pine species less able to survive frequent surface fires when exposed as seedlings [104,105].

3.3. Historical versus Current Tree Surveys

According to historical land survey notes, pine contributed 77% of all witness trees, or about 197,000 of the 255,000 tree records examined from studies covering 9 million ha of the Coastal Plain province in northern Florida, Georgia, Alabama, and Mississippi, including the 25% of the study area that were wetlands (Table 1). Based on the other historical descriptions and early silvicultural accounts, we interpreted this pine to overwhelmingly be longleaf pine [9,75,102]. Even those few places where localized concentrations of the other southern pines occurred, such as along the margins of the Coastal Plains province, or other unique environmental conditions, were unusual [31]. Upland oaks were another 8.5% of all species; therefore, pines and oaks were 85% of all trees. Combined bays (e.g., *Magnolia*, *Gordonia*, *Persea*) were 3.5% of all trees, followed by cypress (*Taxodium ascendens*, *T. distichum* (L.) Rich.) at about 1.5%, hickories and blackgum (i.e., *Nyssa*) at each about 1%, and all other taxa contributed < 1% of all trees (Table 1). However, these differences varied spatially and by species groups.

Table 1. Count and percentage of trees recorded in historical land surveys for studies in the Coastal Plain.

Group/Common Name	Count	Percent	Most Likely Taxa (Other Possible Taxa)
Pine	197,079	77.18	<i>Pinus palustris</i> (<i>Pinus taeda</i> , <i>Pinus elliottii</i> , <i>Pinus taeda</i> , <i>Pinus echinata</i> , <i>Pinus clausa</i>)
Cypress	4248	1.66	<i>Taxodium ascendens</i> (<i>Taxodium distichum</i>)
Oaks			
Red	8220	3.22	<i>Quercus falcata</i> (<i>Quercus nigra</i> , <i>Quercus pagoda</i>)
Blackjack	7084	2.77	<i>Quercus marilandica</i> (<i>Quercus laevis</i>)
Post	5305	2.08	<i>Quercus stellata</i>
Water	2188	0.86	<i>Quercus nigra</i>
White	1289	0.50	<i>Quercus alba</i>
Live	432	0.17	<i>Quercus virginiana</i> (<i>Quercus laurifolia</i>)
Gums			
Blackgum	2355	0.92	<i>Nyssa sylvatica</i> (<i>Nyssa biflora</i>)
Sweetgum	1964	0.77	<i>Liquidambar styraciflua</i>
Maple	994	0.39	<i>Acer rubrum</i>
Bay	8959	3.51	<i>Magnolia virginiana</i> (<i>Gordonia lasianthus</i> , <i>Persea borbonia</i>)
Others			
Hickories	2795	1.09	<i>Carya</i>
Dogwood	1442	0.56	<i>Cornus florida</i>

Table 1. Cont.

Group/Common Name	Count	Percent	Most Likely Taxa (Other Possible Taxa)
Beech	1123	0.44	<i>Fagus grandifolia</i>
Ash	1012	0.40	<i>Fraxinus pennsylvanica</i>
Poplar	928	0.36	<i>Liriodendron tulipifera</i>
Holly	762	0.30	<i>Ilex opaca</i>
Hornbeam	538	0.21	<i>Carpinus caroliniana</i> (<i>Ostrya virginiana</i>)
Cabbage palmetto	509	0.20	<i>Sabal palmetto</i>
Sourwood	500	0.20	<i>Oxydendrum arboreum</i>

In the modern-day forest composition of this same 9 million ha portion of the Coastal Plains, pines comprised about 58% of all trees (Table 2). Today, longleaf and shortleaf pines contribute only 4.7% and 0.6% of these stems, while loblolly and slash pines, the pines of plantations, constitute just over 30% and 20%, respectively (Table 2). Upland oaks that we interpreted to match recorded historical oaks also decreased to about 2% of all trees, with all upland oaks at 2.5%; therefore, pines and oaks were about 60% of all trees. Besides loblolly and slash pines, other fire-intolerant species, such as water oak, live oak, sweetgum, *Nyssa*, red maple, and *Taxodium*, generally increased. The bays (4%) and hickories (~1%) were similar to their historical levels. However, changes from past to present species abundances are not always as they appear, especially for the less dominant tree species. While *Taxodium* increased in abundance from surveyed witness trees to modern FIA inventories, this is likely more a function of surveyor avoidance of using cypress as witness trees rather than an actual increase in abundance [69]. Other studies have documented greater levels of *Taxodium* in historical forests than modern landscapes [69,94].

Table 2. Count and percentage of trees recorded in current (FIA) surveys for the same extent as historical surveys.

Group and Common Names		Scientific Name	Count	Percent
Pines	Loblolly	<i>Pinus taeda</i>	36,119	30.19
	Slash	<i>Pinus elliottii</i>	24,005	20.07
	Longleaf	<i>Pinus palustris</i>	5623	4.7
	Sand	<i>Pinus clausa</i>	1903	1.59
	Shortleaf	<i>Pinus echinata</i>	737	0.62
Cypress	Pondcypress	<i>Taxodium ascendens</i>	2715	2.27
	Baldcypress	<i>Taxodium distichum</i>	951	0.8
Oaks	Water	<i>Quercus nigra</i>	5444	4.55
	Laurel	<i>Quercus laurifolia</i>	3682	3.08
	Live	<i>Quercus virginiana</i>	879	0.73
	Red	<i>Quercus falcata</i>	815	0.68
	White	<i>Quercus alba</i>	678	0.57
	Blackjack	<i>Quercus marilandica</i> , <i>Quercus laevis</i>	647	0.54
	Post	<i>Quercus stellata</i>	462	0.39
Gums	Swamp blackgum	<i>Nyssa biflora</i>	6698	5.6
	Sweetgum	<i>Liquidambar styraciflua</i>	5767	4.82
	Blackgum	<i>Nyssa sylvatica</i>	1761	1.47
Maples	Red maple	<i>Acer rubrum</i>	3698	3.09
Bays	Sweetbay magnolia	<i>Magnolia virginiana</i>	3381	2.83
	Loblolly bay	<i>Gordonia lasianthus</i>	740	0.62
Others	Red bay	<i>Persea borbonia</i>	408	0.34
	Yellow-poplar	<i>Liriodendron tulipifera</i>	2126	1.78
	Hickory	<i>Carya</i>	913	0.76
	Green ash	<i>Fraxinus pennsylvanica</i>	753	0.63
	Cabbage palmetto	<i>Sabal palmetto</i>	492	0.41

Table 2. Cont.

Group and Common Names	Scientific Name	Count	Percent
Holly	<i>Ilex opaca</i>	479	0.4
Hornbeam	<i>Carpinus caroliniana</i>	385	0.32
Dogwood	<i>Cornus florida</i>	266	0.22
Sourwood	<i>Oxydendrum arboreum</i>	193	0.16
Beech	<i>Fagus grandifolia</i>	104	0.09

3.4. Estimates of Original Longleaf Pine Extent

Our biogeographical approach to the historical (original) cover of longleaf-dominated forests in the Coastal Plain, after removing the northeastern extension and wetlands (particularly forested wetlands at 25% of the land area; see also [55]), provides an extent estimate of 33.5 million ha of upland forests total in the southeastern Coastal Plain. For a potential maximum extent of longleaf pine, if 90% of the upland region of the Coastal Plain was longleaf forest, then this ecosystem covered about 30.1 million ha. If a more conservative 75% of the upland region of the Coastal Plain is applied, although longleaf was this predominant in areas including wetlands, then longleaf forests may have originally covered approximately 25.1 million ha. Even these numbers may prove low, as longleaf pine does occur in some of the forested wetlands [86], which were removed in our estimation process. These estimates are consistent with those made by Frost [8], who calculated 22.9 million ha of pure longleaf and 14.6 million ha of mixed forests; Frost's estimates also include montane longleaf and other longleaf found in wetland communities that we excluded in this analysis.

3.5. Decline of Longleaf Pine Extent over Time

Even before 1900, longleaf pine's prominence had been noticeably diminished by turpentine, lumbering, overgrazing, excessive burning, and agricultural land clearing [73,94,98]. Early published estimates were 20 to 26 million ha of longleaf pine-dominated forests in the Coastal Plain by experts [9,58,81,82]. On the other extreme, Emerson (1919; [106]) placed the extent of the "southern long-leaf pine belt" at over 101 million ha, an estimate so much greater than any others reported that it is either an egregious reporting error or included substantial areas of the Coastal Plain that were never stocked with pine and areas outside of the Coastal Plain.

By the early 1920s, Mattoon (1922; [14]) estimated that less than 20% of the original longleaf pine coverage remained, with millions of hectares of land formerly dominated by longleaf pine "denuded" and "left practically idle". Demmon (1935:323; [82]) used some of the first results of the Forest Service's regional forest surveys and earlier assessments to suggest that all but about 1 million ha of his estimated 20 to 24 million ha of original longleaf pine-dominated forest had been logged. Demmon [82] also noted that most of the second-growth that had arisen following the lumbering of longleaf pine was some mixture of other species and that 3.6 million ha of these lands were "barren" of any forest cover. Wahlenberg (1946:9, his Table 2; [17]) reported that across most of the Coastal Plain (the states of South Carolina, Georgia, Florida, Alabama, Mississippi, and Louisiana) had 7.1 million ha of "pure" longleaf pine forest and an additional 716,000 ha of mixed longleaf and slash pine in 1935. Most (55%) of the pure longleaf was in Florida, which also held the majority (81%) of the nearly 95,000 ha of uncut old growth remaining in 1935 (Wahlenberg 1946, his Table 3; [17]).

According to a series of maps (Figure 4) based on large-scale federal forest surveys [84], by the late 1950s longleaf pine had declined to the third most regionally abundant pine species, less than both loblolly and shortleaf pine. By the next major regional treatment on southern pine distribution and volumes, Sternitzke and Nelson ([87], their Table 1) reported that longleaf had the third most volume of the southern pines, but only slightly ahead of slash pine and only 1/5 the volume of loblolly. Sternitzke and Nelson's ([87], their Figure 4) map of longleaf pine's distribution shows numerous possible range recessions.

Table 3. Timeline of changing area of longleaf pine dominance and extent, with key drivers.

Time Period	LLP Extent; Million ha	Primary Drivers of Dominance and Extent
Pre-1820	>25 * to 30 *	Pre-contact: frequent surface fire and native faunal herbivory; Post-contact: even more frequent fire, agricultural land clearing, livestock (hog, cattle, sheep, etc.) grazing
1820–1860	25 * to 30 *	Very frequent fire, agricultural land clearing, naval stores extraction, livestock grazing
1870–1900	20 * to 26 *	Lumbering, very frequent fire, agricultural land clearing, naval stores extraction, livestock grazing
1920	4 * to 5 *	Lumbering, very frequent fire, agricultural land clearing, naval stores extraction, livestock grazing, regeneration failures (includes needle blight, masting problems, feral hogs)
1935	1 *; 7 **	Lumbering, naval stores extraction, stand conversions (natural regeneration to other forest types), livestock grazing, regeneration failures, fire exclusion
1955	4.9 **	Fire exclusion, stand conversions (natural regeneration), livestock grazing, regeneration failures, naval stores extraction
1965	2.9 **	Fire exclusion, stand conversions (natural regeneration and planted loblolly and slash pine), regeneration failures
1975	1.9 **	Fire exclusion, stand conversions (plantations), regeneration failures
1985	1.5 **	Fire exclusion, stand conversions (plantations), regeneration failures
1995	1.3 **	Fire exclusion, stand conversions (plantations), regeneration failures
2008	1.4 **	Fire exclusion, stand conversions (plantations), regeneration failures, local restorations
2020	2.3 **	Fire exclusion, stand conversions (plantations), regional restoration efforts

* = Original growth estimates only; ** = Mostly second growth with limited amounts of original growth included.

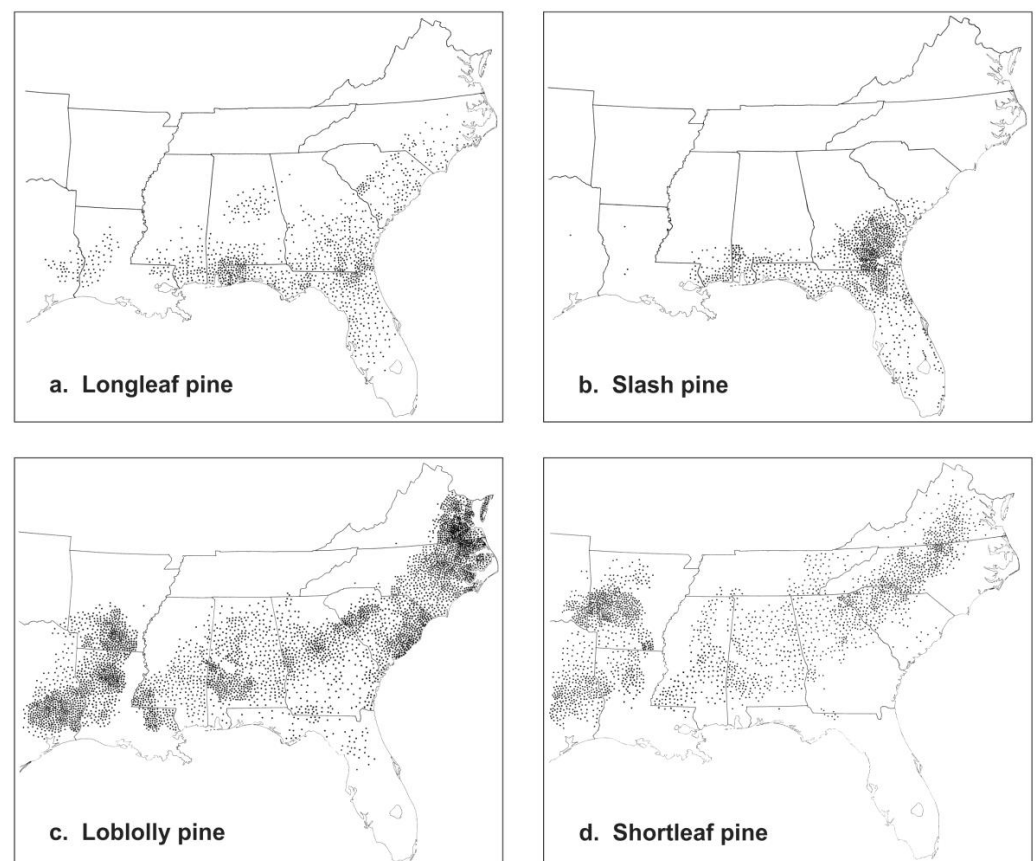


Figure 4. By the early to mid-1950s, the Forest Service regional forest survey information started to show the decreased dominance of longleaf pine (a) in the Coastal Plain, coupled with increases in the other southern pines (b–d). This figure, adapted from [84], used dot maps (at the county level) to describe the abundance of trees in terms of merchantable volumes as determined from forest surveys conducted between 1947–1957. Each dot represents 141,584 m³ of merchantable wood (assuming 1 m³ = 35.3147 ft³ and one dot = 5,000,000 ft³).

Later, more targeted assessments of longleaf pine decline clarified this trend. Kelly and Bechtold [85] used FIA data to show that longleaf pine forests had declined from 4.9 million ha in 1955 to 2.9 million ha in 1965 to 1.9 million ha in 1975 and down to 1.5 million in 1985. By 1995, longleaf coverage had declined to 1.3 million ha [22]. Due to regional conservation efforts, today longleaf pine forests are found only on about 2.3 million ha, mostly in smaller stands [60].

4. Discussion

4.1. Change in Longleaf Pine Forest Composition and Extent

This compilation of historical tree surveys and the literature further imparts evidence of past longleaf pine dominance and decline across the Coastal Plain region of the southeastern United States. According to our samples of historical surveys in a large part of the Coastal Plain, pine was 77% of all witness trees and longleaf pine was the dominant pine taxa from the other documented sources. This evidence clearly shows that the other southern pine species were only abundant in certain localized areas of the Coastal Plain, such as loblolly pine in many riparian zones, shortleaf pine in more rugged uplands on the northern edge of the province, and slash pine in some of the coastal flatwoods of Florida and the Carolinas [8,10,32–34]. Based on quantitative assessments of the Coastal Plain during widespread lumbering [31,94–97], these other southern pines were also interspersed with abundant broadleaf species at levels sufficient to be considered mixed forests (i.e., 25%–75% broadleaf).

The borders of longleaf pine dominance remain unclear, and while identification to pine species is an issue in historical tree records, the sharp decline in pine percentage from >70% of all trees to about equal percentages with oak is strong evidence of taxonomic and fire regime changes across a large region [67,107,108]. Although in some places the dominance transition to other pines was considered “imperceptible”, such as in southwestern and central Louisiana [73], longleaf pine abundance often abruptly lessened at the margins of the Coastal Plain [4,9,10,17,98,109,110]. In the lands north of the Coastal Plain province, which often consisted of about 35% to 45% pine mixed with almost as much upland oak [67,107,108,111], shortleaf pine was the primary pine species of upland forests, with loblolly pine dominating the wetter areas.

Currently, longleaf pine comprises 5% of the FIA-sampled trees in the part of the Coastal Plain with historical land survey studies, while loblolly and slash pines, the pines of plantations, have increased to 30% and 20% of all trees, respectively. For the entire Coastal Plain beyond the study area with historical studies, overall composition and proportion of species is similar, but loblolly pine is more abundant (35% of all trees), whereas slash pine and longleaf pine are less abundant (13% and 3.5% of all trees, respectively). Equally, fire-sensitive broadleaf species have increased, whereas paralleling the decline of fire-tolerant longleaf pine, fire-tolerant shortleaf pine, and oaks have likewise decreased. Upland, fire-tolerant oaks, primarily southern red oak (*Quercus falcata* Michx.), post oak (*Quercus stellata* Wangenh.), turkey oak (*Quercus laevis* Walter), blackjack oak (*Quercus marilandica* Münchh.), and white oak (*Quercus alba* L.), represented about 8.5% of all trees historically. Current FIA data showed that these upland oaks have declined to 2% of all trees in this Coastal Plain study area. Shortleaf pine abundances in the Coastal Plain were highly variable, but likely ranged from a small percentage to perhaps as much as 15% in some subregions [31,94]. Today, shortleaf pine constitutes less than 1% of the overstory in the area with historical land survey studies (Figure 2; Table 2).

Such comprehensive compositional turnover from longleaf pine to other species demonstrated that most of the Coastal Plain had sufficient conditions to support dense, diverse forests. Indeed, this potential was perceived by both Heyward (1939; [55]) and Quarterman and Keever [57], who sampled natural-origin upland forests across the Coastal Plain and noted widespread evidence of conversion of once pine-dominated ecosystems into broadleaf forests. Following the exclusion of frequent fire from remaining woodlands or regenerating cutover forests, loss of grazing or overgrazing in places, and colonization

of abandoned agricultural lands, many fire-sensitive tree species rapidly increased their distribution, typically resulting in more fully stocked and arboreally rich stands [55,57]. Combined with the application of frequent overstory disturbance for different land uses, cycles of community succession in structure and species ensued, as opposed to stable dominance by old-growth longleaf savannas and woodlands [2,112]. However, installation of longleaf and slash pine plantations has regulated community dynamics by intensive management steps of planting commercial pine seedlings, controlling broadleaf tree species with application of chemical and mechanical treatments, thinning tree densities, and harvesting after about 20 to 25 years.

From dominance of the Coastal Plain, longleaf rapidly declined by the 1950s to only a quarter of the original 25 million ha coverage and less than 5% of this extent by the end of the 20th century (Table 3). Although the extent of forest cover of longleaf pine is not fixed in time and depends on a variety of environmental conditions, the standard for determining the decline of this resource is typically held as the extent of longleaf pine-dominated forest at the beginning of widespread use in the 19th century. Applying different approaches, our historical longleaf pine cover estimates of about 25 to 30 million ha during the first half of the 1800s are slightly greater than the estimates of 20 to 26 million ha from the late 1800s [9,58,81,82], but are comparable to Frost [4,8]. Before 1900, longleaf pine's prominence had been noticeably diminished by turpentine, lumbering, overgrazing, excessive burning, and agricultural land clearing [73,94,98]. Citing statistics derived from the 1930s forest surveys, Wahlenberg (1946:1; [17]) stated the “tremendous shrinkage in the area exclusively occupied by [longleaf pine]—a recession that continues to this day”. Perhaps as significantly, longleaf pine forests were altered from contiguous areas of many thousands to even millions of ha in extent to being dominated by small (<40 ha) parcels by the early 1990s [86]. While longleaf pine remained an important component of Coastal Plain pine forests into the mid-20th century, its decline continued to 1.3 million ha in 1995. Conservation efforts, including increasing areas of planted longleaf pine to meet a regional goal of 3.2 million ha of longleaf, have since stemmed this loss, but today, longleaf pine forests are found only on about 2.3 million ha, mostly in small, fragmented stands [60].

4.2. Primary Drivers of Coastal Plain Longleaf Forest Change over Time

Loss of longleaf pine dominance occurred through land clearing, exploitative lumbering and turpentine, fire exclusion, regeneration failures due to foliar disease and feral hogs (*Sus scrofa* L.), and new silvicultural practices for quicker-yielding species and denser stands to increase timber production [17,113]. Although early land clearing and other poor utilization practices resulted in some loss of longleaf pine-dominated forests before 1880, exploitative lumbering and turpentine of this 2.27 billion m³ timber resource [14] between 1880 and 1930 was the primary factor in the depletion of this commercially valuable species across most of the southeastern Coastal Plain. Due to widespread implementation of effective fire exclusion across much of longleaf pine range by the 1930s and 1940s [102], open longleaf pine forests became vulnerable to replacement by high densities of more fire-sensitive tree species, which emerged from fire-protected sites to compete for growing space [9,32,55,102,114]. Not surprisingly, loblolly and some broadleaf species, such as sweetgum, rapidly colonized abandoned agricultural lands across the Coastal Plain that had once been longleaf pine [16,115,116], resulting in extensive pine, broadleaf, and mixedwood forests with very few, if any, longleaf forests [114,117].

Longleaf pine suffered from decades of extensive failures in its natural regeneration due to factors such as lack of seed sources (Figure 5), annual or even biannual burning (Figure 6; [105,118]), infrequent seed production (pronounced masting), and high predation rates of its large seeds [17,32]. Without frequent fire, sudden emergence of an endemic foliar disease (brown spot needle blight; *Lecanosticta acicola* (von Thümen) Sydow) developed, which had previously been held in check by the fires that consumed infected needles. Brown spot needle blight killed longleaf seedlings in the young, grass stage [113,119]. When a longleaf seed managed to germinate, the resultant seedlings were often lost to consumption

by feral hogs (Figure 7; [8,17,32,82,98,113]). Even if seedlings escaped excessive fires and hog rooting, the open, grass- and herbaceous-dominated longleaf pine ecosystem was often used as poorly managed (overgrazed) sheep (*Ovis aries* L.) or cattle pasture (Figure 8), sometimes for decades [12,49,73,118,120].

Likewise, the influence of herbivory by native fauna and then later livestock was consequential in past forests. Research of herbivory as a primary ecological driver of historical forests has been inconclusive, but the influence of large herbivores likely declined following megaherbivore extinctions after human arrival [23,121–124]. White-tailed deer (*Odocoileus virginianus* Zimm.), eastern elk (*Cervus canadensis canadensis* Erxleben), and American bison (*Bison bison* L.) traversed eastern landscapes at various densities and intensities, acting as powerful stabilizers of the open state through their herbivory and other site-impacting activities [125]. Their eventual replacement by the domesticated livestock of Euro-American settlers helped to offset the loss or dramatic reduction of large native herbivores, but only until grazing and related burning practices became too intensive to sustain regeneration of the longleaf pine community (Figure 8).



Figure 5. An example from central Louisiana of how millions of hectares of Coastal Plain landscapes appeared in the mid-20th century following lumbering, annual burning, and heavy grazing by cattle and other livestock; the inability of the handful of potential longleaf pine seed trees in the distance to reforest these areas helped lead to extensive planting of slash and loblolly pines and the resulting conversion of once open longleaf pine forests to denser stands of other species. Photograph is from US Forest Service negative #442959 taken in 1946 by John T. Cassaday.



Figure 6. A more regulated approach to managing open longleaf pine range. The location in this image from the Alapaha Experimental Range of Georgia was entirely grazed by cattle, but only half of the study area (**right** side of picture) was burned annually, resulting in more woody plant encroachment on the unburned (**left**) side. Photograph is from US Forest Service negative #425247 taken in 1942 by H.H. Biswell.

Actions taken to address earlier land management problems often led to further longleaf pine declines. Early work often proved counter-productive in sustaining this resource. In part as a response to the widespread loss of longleaf pine forests, the USDA Forest Service opened its Southern Forest Experiment Station (SOFES) in 1921 [52,126,127]. For decades, prominent SOFES scientists generally thought the benefits of fire and grazing in natural or planted pines did not outweigh the costs, even with some modest exceptions for longleaf pine [55,82]. In dismissing compelling evidence of the benefits of properly applied and suitably frequent fire in longleaf pine, SOFES recommendations were largely consistent with the Forest Service's then-discouragement of fire as a management tool for southern pines in order to ameliorate perceived negative effects of burning on regeneration, stocking, and tree log quality in second-growth Coastal Plain pine stands. These early federal research efforts also produced evidence of better individual tree and stand-level growth and yield of unburned loblolly and slash pines [9,76,101,128,129]. These studies supported later work on southern pine productivity in the first widespread inventories of the Coastal Plain [83] and then, the development of management treatments unfavorable to the previously preferred longleaf pine. While research to improve the success of longleaf pine never disappeared [116,126,130–132], more effort was invested into silvicultural research in the other southern pines that further encouraged their widespread use and sped the demise of longleaf [133]. For example, early reforestation efforts often failed regardless

of species, but SOFES researchers, company foresters, and landowners also quickly realized that extra difficulty of securing longleaf regeneration, coupled with its slower initial growth (due to the grass stage) favored other options [17,51].



Figure 7. Feral hogs have a fondness for the taproots of longleaf pine seedlings and have had major impacts on longleaf's regeneration for many decades. Photograph is from US Forest Service negative #450317 taken in 1947 by Walt Hopkins while on the Kistachie National Forest.



Figure 8. In overgrazed pastures, cattle can inflict serious damage on longleaf pine saplings by consuming their needles. Photograph from US Forest Service negative #443364 was taken in 1947 by Walt Hopkins while on the Kistachie National Forest.

As nursery technology improved and forest genetics/tree improvement programs began in the mid-20th century, difficulties in working with longleaf pine [116] further contributed to its decline. Widespread conversion of natural forests to intensively managed, genetically “improved” southern pine plantations began in earnest by the 1950s [133]. These plantations, which were overwhelmingly loblolly and slash pine, covered only 0.8 million ha south-wide in 1952; this extent increased to 5 million ha of planted pine by the late 1960s, over 12 million ha by 1999, and 16.75 million ha (or about 54%) of all southern pine-dominated forests in 2017 [4,114,134].

The widespread need to restore a foundational species and ecosystem such as longleaf pine is not an easy task. Even with progress to date, many challenges remain; for instance, after years of fire exclusion and other societal constraints, fire alone typically is not enough for restoration of open longleaf pine forests [6,29,133]. Fortunately, there remain some factors favorable for restoration of this charismatic tree species. For instance, and despite current alterations of longleaf pine forests, a cultural awareness still connects humans to longleaf pine forests of the past. This awareness likely results from numerous factors including a continuous written narrative [4] and private landowners who maintained quail (i.e., northern bobwhite; *Colinus virginianus* L.) hunting in open longleaf pine forests through burning [135]. These property owners may have burned 300,000 to 365,000 ha annually during the 1900s when other regions experienced complete fire exclusion [135]. While the cultural abatement of fire as a management tool occurred across the Coastal Plain, the Southeast remains one of the remaining cradles of active prescribed fire management in the U.S.

Under increasingly warm temperatures and precipitation variability, including flash droughts, restoration of fire- and drought-tolerant tree species, such as longleaf pine, at low densities (and their supporting disturbance regimes) may deliver stability to regional biodiversity with many disturbance-dependent plant and animal species identified as conservation concerns. Some researchers have recommended that historical ecosystems are irrelevant due to climate change. However, evidence suggests that historical forests of drought- and fire-tolerant species in low tree densities are more stable, resistant, and resilient to disturbances ranging from fire, wind, drought, and insects [136,137]. Ultimately, restoration of reduced tree density and diversity that provides climate resistance for ecosystems, including biodiversity, may be more beneficial socioeconomically than die-offs of the mesic forests which have largely failed to support much of the biodiversity once offered by open longleaf pine [2]. Hence, restoration and expansion of longleaf forest management across the Coastal Plain is imperative to secure declining native flora and fauna [6,22,138].

Due to the recognition of longleaf pine range-wide decline, concurrent impacts to ecosystem goods and services are also being studied [6,16,22,61,139]. In addition to commodities, or goods with a market price such as timber, longleaf pine ecosystems supply other provisioning services, including livestock forage and water quality and quantity. That is, longleaf pine ecosystems consist of a drought-tolerant tree species at low tree densities, resulting in reduced and efficient water use compared to forests of drought-sensitive species [140]. Longleaf pine ecosystems are a temperate hotspot of biodiversity, a supporting service [5,23,27,28]. Longleaf pine ecosystems offer regulating services of pollination and also disturbance regulation, because open longleaf pine ecosystems are resistant to severe fires, drought, wind, heat, flood, and insect damage, creating protection from climate change, severe fires, hurricane damage, and insect outbreaks [117]. Longleaf pine forests are valued culturally, giving a sense of place, well-being, identity, and connection to heritage for rural people of the South [102,135]. Hunting and other recreational activities are preferred in longleaf pine forests. Economies depend on ecosystem services; consequently, ecosystem service degradation will reduce economic performance [141]. Economic decisions that degrade the environment also degrade society, particularly future generations, and economic capital, which depends on ecosystems. In the Coastal Plain, and the United States in general, people learned there was not much use for a sawmill without a forest [142].

5. Conclusions

To assemble a more comprehensive assessment of two centuries of change to the forests of the Coastal Plain province in the southeastern U.S., we collected information about the extent and dominance of longleaf pine over time based on both historical records and modern reports. Longleaf pine savannas and woodlands once dominated an area of 25–30 million ha of the Coastal Plain but declined to 1.3 million ha in 1995, with modest recovery to 2.3 million ha today. A century-long legacy of fire exclusion is marked by the decline in fire-tolerant longleaf pine and oaks and release of diverse native tree species in

upland areas. Historically, pine constituted 77% of all trees and upland oaks contributed another 8% in the Coastal Plain. Today, longleaf pine currently comprises 5% of all trees and upland oaks represent about 2% of the total, while loblolly and slash pines have increased to 30% and 20% of all trees, respectively. Additionally, fire-sensitive broadleaf species have increased their proportions compared to historical trees surveys. Similar to other forests in North America, this synthesis highlights how the late 21st century composition and structure of dense forests with diverse tree species and pine plantations represent a sharp contrast to fire-tolerant pine savannas and woodlands of the early 1800s, after the exclusion of frequent fires, unsustainable harvest, fragmentation of land use, plantation forestry, and extirpation of herbivores. Under changing climate, restoration of fire- and drought-tolerant longleaf pine at low densities will help secure the ecological and socioeconomic future of the southeastern Coastal Plain.

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References

1. 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*, 1–22. [\[CrossRef\]](#)
2. Hanberry, B.B.; Bragg, D.C.; Alexander, H.D. Open forest ecosystems: An excluded state. *For. Ecol. Manag.* **2020**, *472*, 118256. [\[CrossRef\]](#)
3. Cleland, D.T.; Freeouf, J.A.; Keys, J.E.; Nowacki, G.J.; Carpenter, C.A.; McNab, W.H. *Ecological Subregions: Sections and Subsections for the Coterminous United States*; General Technical Report WO-76D; USDA Forest Service: Washington, DC, USA, 2007.
4. Frost, C.C. History and future of the longleaf pine ecosystem. In *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*; Jose, S., Jokela, E.J., Miller, D.L., Eds.; Springer: New York, NY, USA, 2006; pp. 9–48.
5. Noss, R.F.; Platt, W.J.; Sorrie, B.A.; Weakley, A.S.; Means, D.B.; Costanza, J.; Peet, R.K. How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. *Divers. Distrib.* **2015**, *21*, 236–244. [\[CrossRef\]](#)
6. Van Lear, D.H.; Carroll, W.D.; Kapeluck, P.R.; Johnson, R. History and restoration of the longleaf pine grassland ecosystem: Implications for species at risk. *For. Ecol. Manag.* **2005**, *211*, 15–165. [\[CrossRef\]](#)
7. Wear, D.N.; Greis, J.G. (Eds.) *Southern Forest Resource Assessment*; General Technical Report SRS-53; USDA Forest Service: Asheville, NC, USA, 2002.
8. Frost, C.C. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In *Proceedings, Tall Timbers Fire Ecology Conference 18*; Hermann, S.M., Ed.; Tall Timbers Research Station: Tallahassee, FL, USA, 1993; Volume 18, pp. 17–43.
9. Mohr, C.T.; Roth, F. *The Timber Pines of the Southern U.S.*; US Government Printing Office: Washington, DC, USA, 1897.
10. Sargent, C.S. *Report on the Forests of North America (Exclusive of Mexico)*; 10th US Census Report; U.S. Department of Interior, Census Office: Washington, DC, USA, 1884; Volume 9.
11. Hall, B. *Travels in North America in the Years 1827 and 1828*; Robert Cadell: Edinburgh, Scotland, 1830; Volume III.
12. Harper, F. *The Travels of William Bartram*; Naturalist Edition; University of Georgia Press: Athens, GA, USA, 1998.
13. Troost, L. Military and naval resources and necessities of the south and west. *Debow's Rev. Agric. Commer. Ind. Prog. Resour.* **1846**, *1*, 251–269.
14. Mattoon, W.R. Longleaf pine. In *USDA Bulletin 1061*; Government Printing Office: Washington, DC, USA, 1922.
15. Croker, T.C. The longleaf pine story. *J. For. Hist.* **1979**, *23*, 32–43. [\[CrossRef\]](#)
16. Croker, T.C. *Longleaf Pine: A History of Man and a Forest*; Report R8-FR; USDA Forest Service: Atlanta, GA, USA, 1987.
17. Wahlenberg, W.G. *Longleaf Pine: Its Use, Ecology, Regeneration, Protection, Growth, and Management*; Charles Lathrop Pack Forestry Foundation and the USDA Forest Service: Washington, DC, USA, 1946.

18. Jones, P.D.; Hanberry, B.B.; Demarais, S. Managing the southern pine Forest—Retained wetland Interface for wildlife diversity: Research priorities. *Wetlands* **2010**, *30*, 381–391. [[CrossRef](#)]
19. Webb, T., III. Vegetation change in Eastern North America from 18,000 to 500 Yr B.P. Climate-vegetation interactions. In *Proceedings of a Workshop*; Rep. OIES-2; Rosenzweig, C., Dickinson, R., Eds.; Office for Interdisciplinary Earth Studies and University Corporation for Atmospheric Research: Boulder, CO, USA, 1986; pp. 63–69.
20. Darracq, A.K.; Boone, W.W.; McCleery, R.A. Burn regime matters: A review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. *For. Ecol. Manag.* **2016**, *378*, 214–221. [[CrossRef](#)]
21. Guyer, C.; Bailey, M.A. Amphibians and reptiles of longleaf pine communities. *Proc. Tall Timbers Fire Ecol. Conf.* **1993**, *18*, 139–158.
22. Landers, J.L.; Van Lear, D.H.; Boyer, W.D. The longleaf pine forests of the southeast: Requiem or renaissance? *J. For.* **1995**, *93*, 39–44.
23. Means, D.B. Vertebrate faunal diversity in longleaf pine savannas. In *Longleaf Pine Ecosystems: Ecology, Management, and Restoration*; Jose, S., Jokela, E., Miller, D., Eds.; Springer: New York, NY, USA, 2006; pp. 155–213.
24. Semenova-Nelsen, T.A.; Platt, W.J.; Patterson, T.R.; Huffman, J.; Sikes, B.A. Frequent fire reorganizes fungal communities and slows decomposition across a heterogeneous pine savanna landscape. *New Phytol.* **2019**, *224*, 916–927. [[CrossRef](#)]
25. Walker, J. Rare vascular plant taxa associated with the longleaf pine ecosystems: Patterns in taxonomy and ecology. *Proc. Tall Timbers Fire Ecol. Conf.* **1993**, *18*, 105–126.
26. Peet, R.K. Ecological classification of longleaf pine woodlands. In *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*; Jose, S., Jokela, E.J., Miller, D.L., Eds.; Springer: New York, NY, USA, 2006; pp. 51–93.
27. Noss, R.F. *Forgotten Grasslands of the South: Natural History and Conservation*; Island Press: Washington, DC, USA, 2013.
28. Walker, J.; Peet, R.K. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetation* **1984**, *55*, 163–179. [[CrossRef](#)]
29. Bragg, D.C.; Hanberry, B.B.; Hutchinson, T.F.; Jack, S.B.; Kabrick, J.M. Silvicultural options for open forest management. *For. Ecol. Manag.* **2020**, *474*, 118383. [[CrossRef](#)]
30. Prestemon, J.P.; Abt, R.C. Timber products supply and demand. In *Southern Forest Resource Assessment*; Wear, D.N., Greis, J.G., Eds.; GTR SRS-53; USDA Forest Service, Southern Research Station: Asheville, NC, USA, 2002; pp. 299–324.
31. Harper, R.M. *Economic Botany of Alabama, Part 1, Geographical Report*; Monograph 8; Geological Survey of Alabama, University of Alabama: Tuscaloosa, AL, USA, 1913.
32. Ashe, W.W. The long leaf pine and its struggle for existence. *J. Elisha Mitchell Sci. Soc.* **1894**, *11*, 1–16.
33. Mattoon, W.R. *Life History of Shortleaf Pine*; US Department of Agriculture: Washington, DC, USA, 1915.
34. Mohr, C. Plant life of Alabama. *Contrib. US Natl. Herb.* **1901**, *6*, 921.
35. Wells, B.W. Plant communities of the coastal plain of North Carolina and their successional relations. *Ecology* **1928**, *9*, 230–242. [[CrossRef](#)]
36. Hanberry, B.B.; Noss, R.F. Locating potential historical fire-maintained grasslands of the eastern United States based on topography and wind speed. *Ecosphere* **2022**, *13*, e4098. [[CrossRef](#)]
37. Richardson, D.M.; Rundel, P.W.; Jackson, S.T.; Teskey, R.O.; Aronson, J.; Bytnerowicz, A.; Wingfield, M.J.; Procheş, Ş. Human impacts in pine forests: Past, present, and future. *Annu. Rev. Ecol. Evol. Syst.* **2007**, *38*, 275–297. [[CrossRef](#)]
38. Komarek, E.V. Lightning and Lightning Fires as Ecological Forces. *Proc. 8th Tall Timbers Fire Ecol. Conf.* **1968**, *8*, 169–197.
39. Fern, R.R.; Stober, J.M.; Morris, M.A.; Rutledge, B.T. Native American landscape modification in pre-settlement south-west Georgia. *Landsc. Hist.* **2020**, *41*, 57–68. [[CrossRef](#)]
40. Hudson, C.M. *Knights of Spain, Warriors of the Sun: Hernando de Soto and the South's Ancient Chiefdoms*; University of Georgia Press: Athens, GA, USA, 2018; 561p.
41. Ethridge, R. *From Chicaza to Chickasaw: The European Invasion and the Transformation of the Mississippian World, 1540–1715*; University of North Carolina Press: Chapel Hill, NC, USA, 2013.
42. Fowler, C.; Konopik, E. The History of Fire in the Southern. *U.S. Hum. Ecol. Rev.* **2007**, *14*, 165–176.
43. Guyette, R.P.; Stambaugh, M.C.; Dey, D.C.; Muzika, R.M. Predicting fire frequency with chemistry and climate. *Ecosystems* **2012**, *15*, 322–335. [[CrossRef](#)]
44. Noss, R.F. *Fire Ecology of Florida and the Southeastern Coastal Plain*; University Press of Florida: Gainesville, FL, USA, 2018.
45. Stambaugh, M.C.; Varner, J.M.; Jackson, S.T. Biogeography: An interweave of climate, fire, and humans. In *Ecological Restoration and Management of Longleaf Pine Forests*; Kirkman, K.L., Jack, S.B., Eds.; CRC Press: Boca Raton, FL, USA, 2018; pp. 17–38.
46. Barnett, J.P. *Naval Stores: A History of an Early Industry Created from the South's Forests*; Gen. Tech. Rep. SRS-240; U.S. Department of Agriculture, Forest Service, Southern Research Station: Asheville, NC, USA, 2019.
47. Wyman, L. *Experiments in Naval Stores Practice*; Technical Bulletin 298; USDA Forest Service, Government Printing Office: Washington, DC, USA, 1932.
48. Fernow, B.E. *Economics of Forestry: A Reference Book for Students of Political Economy and Professional and Lay Students of Forestry*; TY Crowell & Company: New York, NY, USA, 1902.
49. Wahlenberg, W.G.; Gemmer, E.W. Southern forest ranges. In *The Western Range—A Great but Neglected Natural Resource*; Separate #16, U.S. Senate Document 199; Government Printing Office: Washington, DC, USA, 1936; pp. 567–580.
50. Williams, M. *Americans and Their Forests: A Historical Geography*; Cambridge University Press: Cambridge, UK, 1992.
51. Chapman, H.H. Management of loblolly pine in the pine-hardwood region in Arkansas and in Louisiana west of the Mississippi River. In *Yale University School of Forestry Bulletin* 49; Yale University: New Haven, CT, USA, 1942.

52. Clapp, E.H. *Forest Experiment Stations*; Circular 183; U.S. Department of Agriculture: Washington, DC, USA, 1921.
53. Greeley, W.B. The relation of geography to timber supply. *Econ. Geogr.* **1925**, *1*, 1–14. [[CrossRef](#)]
54. Harper, R.M. Phytogeographical explorations in the Coastal Plain of Georgia in 1903. *Bull. Torrey Bot. Club* **1905**, *32*, 141–171. [[CrossRef](#)]
55. Heyward, F. The relation of fire to stand composition of longleaf pine forest. *Ecology* **1939**, *20*, 287–304. [[CrossRef](#)]
56. MacCartee, R. The long-leaf pine. *For. Leaves* **1889**, *2*, 73–75.
57. Quarterman, E.; Keever, C. Southern mixed hardwood forest: Climax in the southeastern Coastal Plain, U.S.A. *Ecol. Monogr.* **1962**, *32*, 167–185. [[CrossRef](#)]
58. Sargent, C.S. *The Silva of North America*; Coniferae (*Pinus*); Houghton, Mifflin and Company: New York, NY, USA, 1897; Volume XI.
59. Schwarz, G.F. *The Longleaf Pine in Virgin Forest: A Silvical Study*; John Wiley & Sons: New York, NY, USA, 1907.
60. Matthews, J.M.; Hinchey, J.; Guldin, J.M. Restoration of longleaf pine in the southern region of the U.S. Forest Service: An overview of the million-acre challenge. In *Proceedings of the 20th Biennial Southern Silvicultural Research Conference*; Tech. Rep. SRS-253; Bragg, D.C., Koerth, N.E., Holley, A.G., Eds.; USDA Forest Service: Asheville, NC, USA, 2020; pp. 112–119.
61. Oswalt, C.M.; Cooper, J.A.; Brockway, D.G.; Brooks, H.W.; Walker, J.L.; Connor, K.F.; Oswalt, S.N.; Conner, R.C. *History and Current Condition of Longleaf Pine in the Southern U.S.*; Report No. 166; US Department of Agriculture Forest Service, Southern Research Station: Asheville, NC, USA, 2012.
62. Bourdo, E.A. A review of the General Land Office survey and of its use in quantitative studies of former forests. *Ecology* **1956**, *37*, 754–768. [[CrossRef](#)]
63. Delcourt, H.R. Presettlement vegetation of the North of Red River Land District, Louisiana. *Castanea* **1976**, *41*, 122–139.
64. Sears, P.B. The natural vegetation of Ohio. *Ohio J. Sci.* **1925**, *25*, 139–149.
65. Fang, Y.; Jawitz, J. High-resolution reconstruction of the U.S. human population distribution, 1790 to 2010. *Sci. Data* **2018**, *5*, 180067. [[CrossRef](#)] [[PubMed](#)]
66. Cowell, C.M. Presettlement piedmont forests: Patterns of composition and disturbance in central Georgia. *Ann. Am. Assoc. Geogr.* **1995**, *85*, 65–83.
67. Plummer, G.L. 18th century forests in Georgia. *Bull. Georgia Acad. Sci.* **1975**, *33*, 1–19.
68. White, C.A. *A History of the Rectangular Survey System*; USDI Bureau of Land Management, Government Printing Office: Washington, DC, USA, 1983.
69. Schwartz, M.W. Natural distribution and abundance of forest species and communities in northern Florida. *Ecology* **1994**, *75*, 687–705. [[CrossRef](#)]
70. Merry, K.L. Reconstruction of Early 19th Century Vegetation to Assess Landscape Change in Southwestern Georgia. Master's Thesis, University of Georgia, Athens, GA, USA, 2003.
71. Predmore, S.A.; McDaniel, J.; Kush, J.S. Presettlement forests and fire in southern Alabama. *Can. J. For. Res.* **2007**, *37*, 1723–1736. [[CrossRef](#)]
72. Black, B.A.; Foster, H.T.; Abrams, M.D. Combining environmentally dependent and independent analyses of witness tree data in east-central Alabama. *Can. J. For. Res.* **2002**, *32*, 2060–2075. [[CrossRef](#)]
73. Foster, H.T.; Black, B.; Abrams, M.D. A witness tree analysis of the effects of Native American Indians on the pre-European settlement forests in east-central Alabama. *Hum. Ecol.* **2004**, *32*, 27–47. [[CrossRef](#)]
74. 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](#)]
75. Gano, L. A study in physiographic ecology in northern Florida. *Bot. Gaz.* **1917**, *63*, 337–372. [[CrossRef](#)]
76. Eldredge, I.F. The forest survey in the South. In *Occasional Paper 31*; USDA Forest Service, Southern Forest Experiment Station: New Orleans, LA, USA, 1934.
77. Bechtold, W.A.; Patterson, P.L. (Eds.) *The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures*; Gen. Tech. Rep. SRS-80; U.S. Department of Agriculture, Forest Service, Southern Research Station: Asheville, NC, USA, 2005.
78. Homer, C.; Dewitz, J.; Jin, S.; Xian, G.; Costello, C.; Danielson, P.; Gass, L.; Funk, M.; Wickham, J.; Stehman, S. Conterminous U.S. land cover change patterns 2001–2016 from the 2016 National Land Cover Database. *ISPRS J. Photogramm. Remote Sens.* **2020**, *162*, 184–199. [[CrossRef](#)]
79. Fernow, B.E. Report of the Chief of the Division of Forestry for 1891. In *The Report of the Secretary of Agriculture for 1891*; Government Printing Office: Washington, DC, USA, 1892; pp. 191–229.
80. Demmon, E.L. The silvicultural aspects of the forest fire problem in the longleaf pine region. *J. For.* **1935**, *33*, 323–331.
81. Mesavage, C. Forest Survey estimates of southern forest growth. *South. Lumberm.* **1944**, *169*, 168–170.
82. Janssen, P.L.; Weiland, M.R. Softwood distribution maps for the South. In *Forest Survey Release 83*; USDA Forest Service, Southern Forest Experiment Station: New Orleans, LA, USA, 1960.
83. Kelly, J.F.; Bechtold, W.A. The longleaf pine resources. In *Proceedings of Symposium on the Management of Longleaf Pine*; USDA Forest Service Gen. Tech. Rep. SO-75; Southern Forest Experiment Station: New Orleans, LA, USA, 1990; pp. 11–22.
84. Outcalt, K.W.; Sheffield, R.M. The longleaf pine forest: Trends and current conditions. In *Resource Bulletin SRS-9*; U.S. Department of Agriculture, Forest Service, Southern Research Station: Asheville, NC, USA, 1996.
85. Sternitzke, H.S.; Nelson, T.C. The southern pines of the United States. *Econ. Bot.* **1970**, *24*, 142–150. [[CrossRef](#)]

86. Catesby, M. *The Natural History of Carolina, Florida and the Bahama Islands*; Mark Catesby: London, UK, 1731; Volume I.
87. Anonymous. North Carolina. *De Bow's South. West. Rev.* **1851**, 11, 105–122.
88. Michaux, F.A. *The North American Sylva, or a Description of the Forest Trees, of the U.S., Canada and Nova Scotia*; Thomas Dobson and Solomon Conrad: Philadelphia, PA, USA, 1819; Volume III.
89. Claiborne, J.F.H. A trip through the piney woods. *Publ. Miss. Hist. Soc.* **1906**, 9, 487–538.
90. Drake, D. *A Systematic Treatise, Historical, Etiological, and Practical, on the Principal Diseases of the Interior Valley of North America, as They Appear in the Caucasian, African, Indian, and Esquimaux Varieties of Its Population*; Winthrop, B. Smith & Co.: Cincinnati, OH, USA, 1850.
91. Featherman, A. *Third Annual Report of Botanical Survey of Southwest and Northwest Louisiana, Made during the Year 1871*; The Republican Office: New Orleans, LA, USA, 1872; pp. 101–161.
92. Harper, R.M. Geography and vegetation of northern Florida. In *Florida Geological Survey 6th Annual Report*; Florida Geological Survey: Tallahassee, FL, USA, 1914.
93. Harper, R.M. Southern Louisiana from the car-window. *Torreya* **1920**, 20, 67–76.
94. Harper, R.M. A week in eastern Texas. *Bull. Torrey Bot. Soc.* **1920**, 47, 289–317. [[CrossRef](#)]
95. Harper, R.M. Development of agriculture in lower Georgia from 1850 to 1880. *Ga. Hist. Q.* **1922**, 6, 97–121.
96. Mohr, C. On the distribution of the more important forest trees in the Gulf Region. *Am. J. For.* **1882**, 1, 78–88.
97. Harper, L. *Preliminary Report on the Geology and Agriculture of the State of Mississippi*; Barksdale, E., Ed.; State Printer: Jackson, MS, USA, 1857.
98. Bray, W.L. Forest resources of Texas. *USDA Bur. For. Bull.* **1904**, 47, 71.
99. Chapman, H.H. A method of studying growth and yield of longleaf pine applied in Tyler Co., Texas. *Proc. Soc. Am. For.* **1909**, 4, 207–220.
100. Burns, R.M.; Honkala, B.H. *Tech. Coords. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654*; U.S. Department of Agriculture, Forest Service: Washington, DC, USA, 1990.
101. Stoddard, H.L. Use of fire in pine forests and game lands of the deep Southeast. *Proc. Tall Timbers Fire Ecol. Conf.* **1962**, 1, 31–42.
102. Critchfield, W.B.; Little, E.L., Jr. Geographic distribution of the pines of the world. In *Miscellaneous Publication 991*; USDA Forest Service, Washington Office: Washington, DC, USA, 1966.
103. Glitzenstein, J.S.; Platt, W.J.; Streng, D.R. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. *Ecol. Monogr.* **1995**, 65, 441–476. [[CrossRef](#)]
104. Stambaugh, M.C.; Guyette, R.P.; Marschall, J.M. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. *J. Veg. Sci.* **2011**, 22, 1094–1104. [[CrossRef](#)]
105. Emerson, F.V. The southern long-leaf pine belt. *Geogr. Rev.* **1919**, 7, 81–90. [[CrossRef](#)]
106. Bragg, D.C.; Bragg, H.A. Historical and contemporary environmental context for the Saline-Fifteen site (3BR119). *Ark. Archeol.* **2016**, 55, 1–30.
107. Hanberry, B.B.; Brzuszek, R.F.; Foster, H.T., II; Schauwecker, T.J. Recalling open old growth forests in the Southeastern Mixed Forest province of the U.S. *Ecoscience* **2019**, 26, 11–22. [[CrossRef](#)]
108. Delcourt, H.; Delcourt, P. Pre-Columbian Native American Use of Fire on Southern Appalachian Landscapes. *Conserv. Biol.* **1997**, 11, 1010–1014. [[CrossRef](#)]
109. Schafale, M.P.; Harcombe, P.A. Presettlement vegetation of Hardin County, Texas. *Am. Midl. Nat.* **1983**, 109, 355–366. [[CrossRef](#)]
110. Foster, J.H. Forest conditions in Louisiana. In *USDA Forest Service Bulletin 114*; Government Printing Office: Washington, DC, USA, 1912.
111. Hanberry, B.B.; Thompson, F.R., III. Open forest management for early successional birds. *Wildl. Soc. Bull.* **2019**, 43, 141–151. [[CrossRef](#)]
112. Chapman, H.H. Some further relations of fire to longleaf pine. *J. For.* **1932**, 30, 602–604.
113. Conner, R.C.; Hartsell, A.J. Forest area and conditions. In *Southern Forest Resource Assessment*; GTR SRS-53; Wear, D.N., Greis, J.G., Eds.; USDA Forest Service, Southern Research Station: Asheville, NC, USA, 2002; pp. 357–402.
114. Buttrick, P.L. Forest growth on abandoned agricultural land. *Sci. Mon.* **1917**, 5, 80–91.
115. Snyder, E.B.; Dinus, R.J.; Derr, H.J. *Genetics of Longleaf Pine*; Research Paper WO-33; USDA Forest Service: Washington, DC, USA, 1977.
116. Hanberry, B.B. Transition from fire-dependent open forests: Alternative ecosystem states in the southeastern United States. *Diversity* **2021**, 13, 411. [[CrossRef](#)]
117. White, C.R.; Harley, G.L. Historical fire in longleaf pine (*Pinus palustris*) forests of south Mississippi and its relation to land use and climate. *Ecosphere* **2016**, 7, e01458. [[CrossRef](#)]
118. Siggers, P.V. Observations on the influence of fire on the brownspot needle blight of longleaf pine seedlings. *J. For.* **1934**, 32, 556–562.
119. Grelen, H.E. Forest grazing in the South. *J. Range Manag.* **1978**, 31, 244–250. [[CrossRef](#)]
120. Brockway, D.G.; Lewis, C.E. Influence of deer, cattle grazing and timber harvest on plant species diversity in a longleaf pine bluestem ecosystem. *For. Ecol. Manag.* **2002**, 175, 49–69. [[CrossRef](#)]
121. Gill, J.L.; Williams, J.W.; Jackson, S.T.; Lininger, K.B.; Robinson, G.S. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **2009**, 326, 1100–1103. [[CrossRef](#)]
122. Ripple, W.J.; Newsome, T.M.; Wolf, C.; Dirzo, R.; Everatt, K.T.; Galetti, M.; Hayward, M.W.; Kerley, G.I.; Levi, T.; Lindsey, P.A.; et al. Collapse of the world's largest herbivores. *Sci. Adv.* **2015**, 1, e1400103. [[CrossRef](#)] [[PubMed](#)]

123. Robinson, G.S.; Burney, L.P.; Burney, D.A. Landscape paleoecology and megafaunal extinction in southeastern New York State. *Ecol. Monogr.* **2005**, *75*, 295–315. [\[CrossRef\]](#)
124. Hanberry, B.B.; Faison, E.K. Re-framing deer herbivory as a natural disturbance regime with ecological and socioeconomic outcomes in the eastern United States. *Sci. Total Environ.* **2023**, *868*, 161669. [\[CrossRef\]](#) [\[PubMed\]](#)
125. Gemmer, E.W.; Maki, T.E.; Chapman, R.A. Ecological aspects of longleaf pine regeneration in south Mississippi. *Ecology* **1940**, *21*, 75–86. [\[CrossRef\]](#)
126. Kirkland, B.P. Status and opportunities of private forestry. In *A National Plan for American Forestry [Copeland Report]*; US Senate Document 12; Government Printing Office: Washington, DC, USA, 1933; Volume 1, pp. 891–984.
127. Chapman, H.H. An experiment in logging longleaf pine. *For. Q.* **1909**, *7*, 385–395.
128. Mattoon, W.R. Twenty years of slash pine. *J. For.* **1936**, *34*, 562–570.
129. Mlodziansky, A.K. Rate of growth of loblolly pine. *Gard. For.* **1896**, *9*, 92–93.
130. Chapman, H.H. The initiation and early stages of research on natural reforestation of longleaf pine. *J. For.* **1948**, *46*, 505–510.
131. Derr, H.J.; Cossitt, F.M. Longleaf pine direct seeding. *J. For.* **1955**, *53*, 243–246.
132. Wells, O.O.; Wakeley, P.C. Variation in longleaf pine from several geographic sources. *For. Sci.* **1970**, *16*, 28–42.
133. Croker, T.C. Longleaf pine—Myths and facts. In *Proceedings of the Symposium on the Management of Longleaf Pine*, GTR SO-75; USDA Forest Service, Southern Forest Experiment Station: New Orleans, LA, USA, 1990; pp. 2–10.
134. Oswalt, S.N.; Smith, W.B.; Miles, P.D.; Pugh, S.A. *Forest Resources of the United States, 2017: A Technical Document Supporting the Forest Service 2020 RPA Assessment*; Gen. Tech. Report WO-97; U.S. Department of Agriculture, Forest Service: Washington, DC, USA, 2019.
135. Johnson, A.S.; Hale, P.E. The historical foundations of prescribed burning for wildlife: A southeastern perspective. In *The Role of Fire for Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions*; Gen. Tech. Rep. NE-288; Ford, W., Russell, M., Kevin, R., Moorman, C.E., Eds.; U.S. Department of Agriculture, Forest Service, Northeastern Research Station: Newtown Square, PA, USA, 2002; pp. 11–23.
136. Burkhart, H.E.; Haney, H.L., Jr.; Newberry, J.D.; Leuschner, W.A.; Morris, C.L.; Reed, D.D. Evaluation of thinning for reduction of losses from southern pine beetle attack in loblolly pine stands. *South. J. Appl. For.* **1986**, *10*, 105–108. [\[CrossRef\]](#)
137. 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. [\[CrossRef\]](#)
138. Longleaf Partnership Council. America's Longleaf Restoration Initiative, Strategic Priorities and Actions, 2022–2024. 2021. Available online: https://americaslongleaf.org/media/4tocjgyl/aff_americaslongleaf_strategiesprioritiesactions2021_final.pdf (accessed on 21 August 2023).
139. Kirkman, L.K.; Jack, S.B. (Eds.) *Ecological Restoration and Management of Longleaf Pine Forests*; CRC Press: New York, NY, USA, 2018.
140. Weisman, K.; Lord, L.; Lerner, J. Longleaf Pine: A Tall Drink of Water. 2021. Available online: <https://longleafalliance.org/longleaf-pine-a-tall-drink-of-water/> (accessed on 13 September 2023).
141. Costanza, R.; De Groot, R.; Sutton, P.; Van der Ploeg, S.; Anderson, S.J.; Kubiszewski, I.; Farber, S.; Turner, R.K. Changes in the global value of ecosystem services. *Glob. Environ. Chang.* **2014**, *26*, 152–158. [\[CrossRef\]](#)
142. Daly, H.E. Operationalizing sustainable development by investing. In *Investing in Natural Capital: The Ecological Economics Approach to Sustainability*; Jansson, A.-M., Hammer, M., Folke, C., Costanza, R., Eds.; Island Press: Washington, DC, USA, 1994; pp. 22–37.

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