

Article

Range-Wide Assessment of Recent Longleaf Pine (*Pinus palustris* Mill.) Area and Regeneration Trends

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Abstract: Longleaf pine (*Pinus palustris* Mill.) is a conifer historically associated with an open forest ecosystem that extended across much of the coastal plain of the Southeastern United States. It now exists mainly in isolated fragments following the conversion of forests and the long-term disruption of the low-intensity fire regime upon which the species depends. Recent decades have seen efforts to restore longleaf pine forests by government and private landowners. This was reflected in analyses of national forest inventory data during two time periods, ca. 2009–2015 and 2016–2021, that showed increases in the estimated number of longleaf pine trees, the area of the longleaf pine forest type, and the number and area of planted longleaf pine, along with growth in mean plot-level longleaf pine carbon and importance value. At the same time, we found a decrease in the overall forest area containing longleaf pine, manifested across a variety of other forest types. These results point to a dynamic through which forests dominated by longleaf pine are becoming more widespread via restoration, while forests in which the species is a less important component are transitioning to other forest types or land uses. We also detected a decrease over time in the estimated number of longleaf seedlings across most states and forest types and a decline in naturally regenerated longleaf pine. To further assess regeneration trends in longleaf pine, we calculated the estimated proportion of small trees (seedlings and saplings) for the entire species and for seed zone sub-populations. We found a species-wide decrease in the proportion of small trees, from 82.1 percent to 75.1 percent. This reduction was most pronounced along the edges of the species distribution and could indicate less sustainable levels of regeneration in some areas. These results underscore the challenges of facilitating natural regeneration in this important species.

Keywords: forest restoration; regeneration; national forest inventory; seed zone



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1. Introduction

Longleaf pine (*Pinus palustris* Mill.) is strongly associated with a longleaf pine–grassland ecosystem that covered 23.1 million hectares in the Southeastern United States at the time of initial European settlement of the region; it was also an important component in another 14.2 million ha of mixed pine–oak forest [1]. Its distribution spans an arc from southeastern Virginia to east Texas, encompassing parts of the Atlantic Coastal Plain, the Gulf Coastal Plain, the Piedmont, and the Appalachian–Cumberland Highlands [2]. Across that area, it occurs on a wide variety of sites, ranging from poorly drained flatwoods to dry and rocky mountain ridges, and from just above sea level to about 600 m in the mountains of Alabama [3]. The high density of understory plant species in some longleaf pine savanna systems results in remarkably high biodiversity at small scales [4,5].

Only a small fraction of the original longleaf pine forest now remains, mostly in isolated fragments, following the long-term disruption of historical fire regimes, coupled with other anthropogenic factors including land conversion and overharvesting [6,7]. By

the early 2000s, about 1.2 million ha of longleaf pine forests remained [8] along with about 380,000 ha of mixed longleaf pine–oak forests. Longleaf pine ecosystems were considered among the most threatened in North America [9] and the species itself was listed as endangered by the International Union for Conservation of Nature (IUCN) because of its ongoing replacement by other pine species outside protected areas [10]. Animal and plant species associated with the longleaf pine ecosystem have also declined, most notably the endangered red-cockaded woodpecker (*Dryobates* (formerly *Picoides*) *borealis* Vieillot), which nests in and forages on old longleaf pines [11,12].

Restoration and management of degraded longleaf pine woodland and savanna ecosystems has become a priority, particularly at a time of rapid environmental change and loss of habitat [7]. In 2007, several non-profit organizations and government agencies launched America’s Longleaf Restoration Initiative (ALRI) with the goal of increasing the area of longleaf forests while improving the condition of already existing forests and of the habitat for wildlife species associated with them [13]. The conservation plan, initially released in 2009 and recently revised to track progress through to 2040, aims to increase the area of longleaf pine forest types from 1.4 million ha to 3.2 million ha [14,15]. From 2010 to 2022, the ALRI reported the establishment of approximately 701,000 ha of longleaf pine forest in addition to the protection of 147,000 ha and the prescribed burning of 6,923,000 ha [15].

Analyses using Forest Inventory and Analysis (FIA) data from the United States Department of Agriculture (USDA) Forest Service have confirmed that efforts to restore the iconic longleaf pine forest type have been successful: an assessment of FIA data in 2020 [16] showed large increases in the number of longleaf pines in the 27.7 cm and smaller diameter classes and in the area of longleaf pine forest types in the 0–40 year age classes compared to a 2012 report [17]. The results indicate that a wave of ingrowth is heading toward larger size classes following efforts for more than a decade to establish and manage smaller size and age classes [16].

At the same time, evidence exists that forests of longleaf pine continue to be converted to agricultural use, to be replaced by planted stands of short-rotation loblolly pine (*P. taeda* L.), and to be removed from the expanding wildland–urban interface [16,18]. These pressures may be particularly intense in the forest types [3] in which longleaf pine is a minor component, some of which are likely to have been classified as the longleaf pine or the longleaf pine–oak forest types in the past before the suppression of frequent low- to moderate-intensity fires upon which longleaf pine ecosystems depend [6,19]. Such forests may represent important opportunities for longleaf pine restoration, but the extent of these forests and the ecological importance of longleaf pine in these forests may be declining. Areal trends of these other forest types containing longleaf pine have not been quantified recently, nor have trends in the importance of longleaf pine on plots of various forest types.

In addition to continuing efforts to plant longleaf pine on sites to which it is adapted but no longer present or where it is only a minor component, the success of longleaf pine restoration efforts will require adequate levels of natural regeneration by the species. Understanding the regeneration dynamics of longleaf pine, therefore, is essential for the long-term sustainability of longleaf pine forest ecosystems and the ecological services those forests provide, including as habitat for endangered flora and fauna [20]. Populations with a proportion of small trees below a regeneration threshold, that is, having a regeneration deficit [21], may be at risk of losing important adaptive genetic variation based on the idea that sustainable forest ecosystems have a balanced and stable size–structure relationship across broad scales, in which mortality and removals are offset by regeneration and growth [22]. The species currently may be experiencing declining levels of regeneration because of the extensive planting in recent decades of trees that are not yet reproductively mature. This information could form a baseline to assess future longleaf pine regeneration trends.

The objective of this study was to assess recent trends of the longleaf pine resource across the entirety of its distribution in the Southeastern United States. To that end, we

used tree occurrence data from two time periods (generally 2009–2015 and 2016–2021, depending on the state), available through the FIA program, to test four longleaf pine-related hypotheses: (1) The recent emphasis on longleaf pine restoration has translated into an increase in the number of longleaf pine trees across the Southeastern United States in forest types dominated by the species but a decrease in its numbers in other forest types. (2) Forest types in which longleaf pine dominates have increased in area, while those in which it is a minor component have decreased. (3) The ecological importance and carbon content of longleaf pine has increased on plots in longleaf pine-dominant forest types but declined in those in which it is a minor component. (4) The large number of recently planted trees, coupled with the ongoing mortality and removals of large trees, coincides with a decline in natural regeneration across the distribution of the species.

2. Materials and Methods

2.1. Data

Longleaf pine data were collected from an equal-probability sample network of forest plots maintained by the Forest Inventory and Analysis (FIA) program of the USDA Forest Service. Each of these plot locations is selected at random within a 2428 ha hexagon from a national hexagonal sampling framework to ensure spatial balance; field crews visit plot locations in forest land use, defined as having $\geq 10\%$ tree canopy cover (or evidence of previous canopy cover) that is ≥ 0.4 ha in area and at least 37 m wide [23]. Plot locations in the Eastern United States are typically visited every 5–7 years in discrete evaluation periods that differ from state to state. For our study, we analyzed data from two evaluation periods (generally 2009–2015 and 2016–2021, depending on the state) for each of the nine Southeastern states in which longleaf pine naturally occurs (Table 1). The first evaluation period encompassed 1868 plots with longleaf pine, while the second period encompassed 2042 (Figure 1). The difference in the number of plots between measurement periods is attributable to changes in where longleaf pine was growing, differences in which plots were accessible to field crews (some private landowners may allow access to plot locations during one measurement period but not another), and increases in sampling intensity during one measurement period (including an intensification of plot measurements for National Forests in Mississippi during the second measurement period). The statistical design of the plot network accounts for these differences when assigning expansion factors to each plot condition. (See Section 2.2 on count and areal estimates).

Table 1. The first and second evaluation periods, and number of plots containing longleaf pine (*Pinus palustris* Mill.) for each, collected by state by the Forest Inventory and Analysis (FIA) program.

State	First Evaluation		Second Evaluation	
	Years	Plots	Years	Plots
Alabama	2006–2014	345	2015–2022	360
Florida	2009–2013	481	2014–2019	539
Georgia	2010–2014	300	2015–2021	326
Louisiana	2001–2010	133	2011–2019	91
Mississippi	2009–2015	184	2016–2021	289
North Carolina	2009–2015	141	2016–2021	152
South Carolina	2012–2016	246	2017–2021	229
Texas	2004–2014	38	2015–2021	54
Virginia	2012–2016	0	2017–2021	2

FIA plots encompass four 7.32-m radius circular subplots that are arranged at the vertices and center of a triangle [23,24] (Figure 2). On the subplots, field crews record the species, diameter, and height of every live tree with a diameter at breast height (DBH) of ≥ 12.7 cm. Smaller trees are inventoried on a single 2.07-m radius microplot located in each subplot. This includes sapling-sized trees (DBH ≥ 2.54 cm and < 12.7 cm), which are recorded individually, and seedlings (woody stems with a DBH < 2.54 cm and a

height ≥ 30.48 cm if a hardwood, or a height of ≥ 15.24 cm if a conifer), which are tallied by species [23].

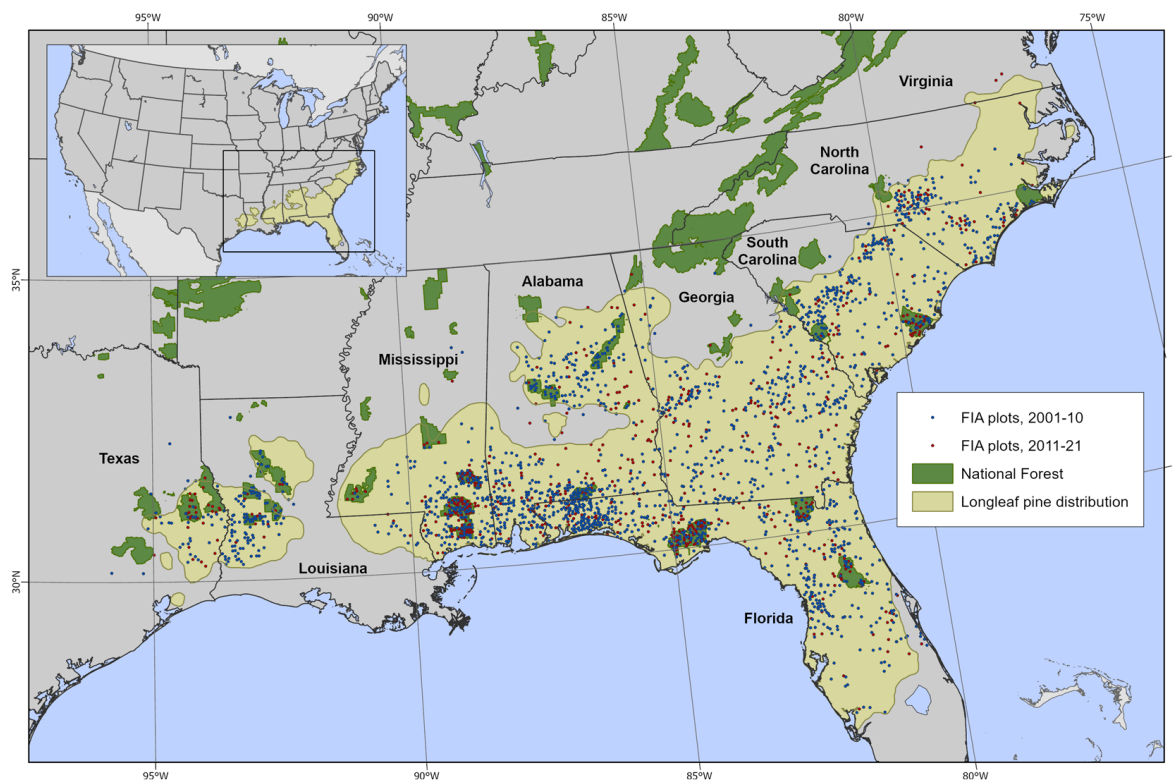


Figure 1. Forest Inventory and Analysis (FIA) plots containing longleaf pine (*Pinus palustris* Mill.) (approximate locations), inventoried from ca. 2009 to 2015 and 2016 to 2021. Also depicted are the species distribution and the boundaries of National Forests within the Southeastern United States.

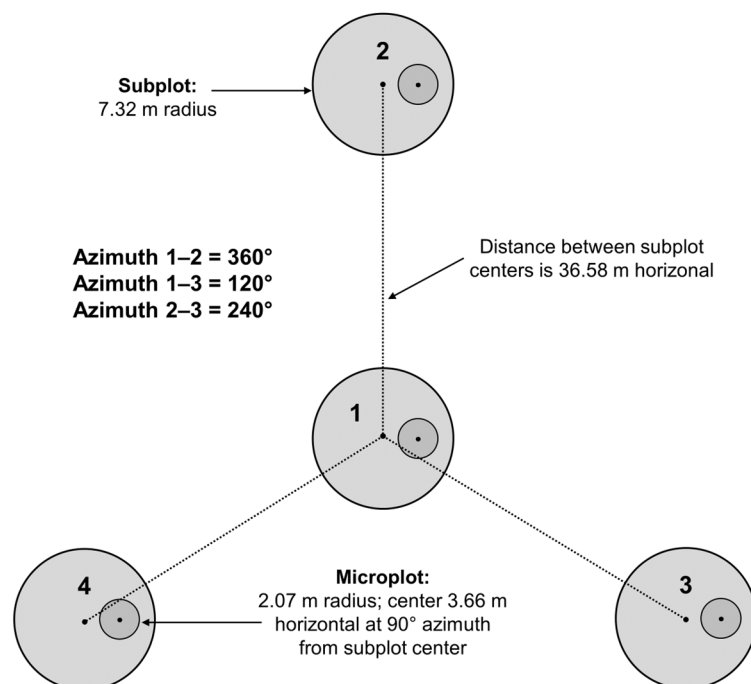


Figure 2. Forest Inventory and Analysis (FIA) plot design, as described in [23].

2.2. Count and Areal Estimates

Population-level estimates of forest area with longleaf pine were possible using “expansion factors” assigned to each condition (e.g., forest type or ownership) on a plot and enabled by the FIA statistical design [23,24]. Summing these scaling factors across all the conditions in a population (such as an ownership group) resulted in an estimate of the total area in that population. We specifically estimated, for our two evaluation periods, (1) the area of forest containing longleaf pine trees and saplings, (2) longleaf pine seedlings, and (3) stems of any size, all by forest type, state, ownership group, and stand origin (natural versus planted). Forest type is a key assessment category because forest types are the focus of many silvicultural, management, and monitoring decisions. The state is important for quantifying geographical differences in longleaf pine extent and importance. The ownership group is important for assessing the outcomes of differing management strategies and approaches. Stand origin is important for quantifying the relative importance of natural versus artificial regeneration.

Similarly, the FIA statistical design allows for estimates of the number of longleaf pine trees in a sampled area by summing the scaling factors associated with each tree within statistical populations. We estimated, again for the two evaluation periods, the number of live and dead trees and saplings as well as live seedlings by forest type, state, ownership group, and stand origin. In both sets of analyses, we focused on two forest types in which longleaf pine is a dominant species (longleaf pine and longleaf pine–oak), two in which it is an associate species (sand pine [*P. clausa* (Chapm. ex Engelm.) Sarg.] and slash pine [*P. elliottii* Engelm.]), and one that frequently develops on areas formerly occupied by longleaf pine (Southern scrub oak) [23].

2.3. Plot-Level Analyses

We tested the null hypothesis that there was no significant difference in longleaf pine plot-level importance value and carbon between the two measurement periods for each forest type, state, ownership group, and stand origin. We used non-parametric Kruskal–Wallis tests using the NPAR1WAY procedure in SAS 9.4 [25], which generated *p*-values via 10,000 Monte Carlo iterations. This set of analyses was limited to the plots on which there was at least one longleaf pine tree with a DBH ≥ 2.54 cm (1754 for the first evaluation period and 1914 for the second) because of the requirements for calculating the importance value (IV) and carbon. The IV is a measure of community dominance that encompasses the number and size of trees of a species of interest (or group of species) within a community [26]. This was calculated in our study for longleaf pine as the mean percentage of the species’ relative abundance and relative basal area on a plot (both scaled to a per-hectare estimate) compared to the per-hectare abundance and basal area of all species on the plot. The per-hectare estimate of longleaf pine C was calculated using FIA’s aboveground dry biomass estimates for each stem with DBH ≥ 2.54 cm [27,28]. We converted pounds of biomass to metric tons per hectare of C. (C is equivalent to 0.5 of biomass).

We additionally tested whether significant correlations existed between county mean plot-level change in longleaf pine IV and C and the county means of a suite of topographic and geographic variables encompassing latitude, longitude, elevation, slope, stand age, and aspect (cosine- and sine-transformed to generate continuous variables that reflect the “northness” and “eastness” of plot aspects, respectively). Each of these was calculated using the plot observations within the county; counties with fewer than five FIA plots were excluded ($n = 120$ counties). We calculated Spearman’s correlation coefficients because of the non-normality of the data.

2.4. Regeneration within Seed Zones

Finally, we applied a regeneration deficit indicator for the two evaluation periods to assess where across the distribution of longleaf pine the species may be experiencing insufficient regeneration [21]. This indicator combines FIA tree occurrence data and cli-

matically and edaphically defined provisional seed zones, geographic areas in which plant materials can be transferred with relatively little risk of being poorly adapted to their new location [29,30]. Because these provisional seed zones are determined using important environmental factors, they may be associated with adaptive genetic differentiation within species and can be used to divide a species into areas with presumably similar adaptive genetic variation. We specifically used a set of provisional seed transfer zones based on minimum temperature and aridity [31] that intersected with USDA Forest Service ecoregions [32] to account for edaphic factors.

For our two evaluation periods, both for the entire longleaf pine distribution and for each provisional seed zone containing at least five FIA longleaf plots, we divided the estimated total number of stems into large (trees ≥ 12.7 cm) and small (saplings and seedlings combined, DBH < 12.7 cm) diameter classes. We then determined the proportion of stems that fall into the small diameter class, with an assumption that populations with less than 75 percent small stems are more vulnerable to the loss of genetic variation [21]. This somewhat arbitrary threshold is informed by the negative exponential or rotated sigmoid diameter distributions expected in balanced uneven-aged forests at the stand level [33,34]. We applied this concept of stand-level balance to aggregated uneven- and even-aged stands at the landscape scale, at which tree diameters are expected to exhibit a negative exponential distribution through the averaging of multiple uneven- and even-age stands of different ages [22,33].

3. Results

3.1. Count and Areal Estimates

The estimated area of any forest containing longleaf pine decreased slightly between the two evaluation periods (~280,000 ha), while the area of the longleaf pine forest type, where longleaf pine is dominant, increased by approximately 275,000 ha (Table 2). The area of all other forest types containing longleaf pine decreased, as did the area of the longleaf pine forest type containing seedlings of the species. As a result, the percentage of forest with longleaf that was specifically in the longleaf pine forest type grew from 32.1 percent to 42.8 percent between the two evaluation periods. Most states (except Georgia, North Carolina, Texas, and Virginia) experienced a decrease in the area of forest with longleaf pine, with the greatest decreases in Louisiana and Florida. Mississippi and Texas were the only states with increases in the area of forest with longleaf pine seedlings. The area of USDA Forest Service ownership of forest containing longleaf pine decreased by about 69,000 ha, while the area in other federal and state/local ownership increased. Privately owned forest with longleaf pine decreased by almost 282,000 ha. At the same time, the share of forest with longleaf pine that was specifically in the longleaf pine forest type increased for each ownership type (Table S1): from 41.1 percent to 48.8 percent for the Forest Service land; from 40.1 percent to 44.3 percent for other federal land; from 41.4 percent to 42.4 percent for state and local land; and from 27.9 percent to 40.0 percent for private property. Meanwhile, the area of forest with longleaf pine seedlings decreased across all ownerships (Table 2). The area of forest with planted longleaf pine grew by approximately 392,000 ha, with the percentage of planted forest nearly doubling from 12.4 percent to 23.9 percent. Meanwhile, the area of forest with naturally regenerated longleaf decreased by about 671,000 ha.

The estimated number of live longleaf pine trees increased by about 227 million between the two evaluation periods, while the number of estimated seedlings decreased by about 111 million (Table 3). The longleaf pine forest type saw a marked increase in the number of stems (~251 million) while the longleaf pine–oak forest type experienced a ~38 million decrease in longleaf trees. Nearly all forest types, except for the sand pine and slash pine types, experienced a decrease in longleaf seedlings. The number of longleaf trees increased in every state except Louisiana, where there were an estimated ~16 million fewer. The largest increases were in South Carolina (~54 million), Alabama (~53 million), and Georgia (~47 million). The number of seedlings increased only in Florida, Mississippi, and Georgia. Longleaf tree numbers increased across ownerships, with the largest increase

on private land (~176 million). Seedling numbers decreased on private and Forest Service land but increased on other federal and state/local ownerships. The number of planted trees grew by ~270 million while the number of planted seedlings grew by ~42 million, while the number of naturally regenerated trees and seedlings both declined over time.

Table 2. Estimates of forest area, in hectares, with longleaf pine (*Pinus palustris* Mill.) trees, longleaf pine seedlings, or any longleaf pine, by forest type, state, ownership group, and natural versus having clear evidence of artificial regeneration for the ca. 2009–2015 and 2016–2021 evaluation periods from Forest Inventory and Analysis (FIA) data.

	Forest w. Longleaf Trees			Forest w. Longleaf Seedlings			Forest w. Any Longleaf		
	2009–2015	2016–2021	Diff.	2009–2015	2016–2021	Diff.	2009–2015	2016–2021	Diff.
Total	3,732,870	3,452,281	(280,590)	1,016,689	790,995	(225,693)	3,989,344	3,710,503	(278,841)
Forest type									
Longleaf pine	1,201,830	1,477,531	275,700	493,504	389,222	(104,282)	1,279,533	1,554,154	274,621
Longleaf pine–oak	358,715	290,847	(67,868)	155,551	104,673	(50,877)	387,048	327,579	(59,468)
Sand pine	41,589	35,039	(6550)	4056	6730	2673	45,645	36,891	(8754)
Slash pine	446,880	360,578	(86,302)	63,842	43,658	(20,184)	459,717	382,643	(77,075)
Southern scrub oak	150,330	87,927	(62,402)	54,219	42,860	(11,358)	160,551	100,488	(60,063)
Other	1,533,526	1,200,359	(333,167)	245,517	203,852	(41,664)	1,656,850	1,308,749	(348,101)
State									
Alabama	681,425	659,739	(21,686)	231,877	161,951	(69,925)	738,019	724,822	(13,197)
Florida	1,008,431	924,504	(83,927)	284,826	234,970	(49,856)	1,069,826	978,683	(91,143)
Georgia	584,017	593,689	9672	155,262	154,966	(296)	636,731	661,444	24,713
Louisiana	296,713	187,512	(109,201)	60,227	16,619	(43,608)	316,838	193,736	(123,102)
Mississippi	389,163	332,238	(56,925)	46,609	57,575	10,966	403,439	343,578	(59,861)
North Carolina	266,733	280,363	13,630	76,442	59,117	(17,325)	284,584	299,732	15,148
South Carolina	427,519	389,986	(37,533)	151,455	91,606	(59,849)	460,403	418,747	(41,655)
Texas	78,868	80,075	1207	9991	14,190	4199	79,504	85,588	6084
Virginia	-	4174	4174	-	-	-	-	4174	4174
Ownership									
US Forest Service	556,980	499,569	(57,410)	132,627	88,180	(44,447)	578,899	509,493	(69,406)
Other federal	325,055	365,413	40,358	121,692	114,445	(7,247)	354,075	379,125	25,051
State/local	314,843	347,940	33,097	98,953	83,973	(14,980)	324,162	371,174	47,013
Private	2,535,992	2,239,358	(296,635)	663,416	504,396	(159,020)	2,732,209	2,450,711	(281,498)
Stand origin									
Planted	372,417	733,348	360,931	265,707	298,007	32,300	495,985	887,675	391,690
Natural	3,360,453	2,718,932	(641,521)	750,982	492,988	(257,994)	3,493,359	2,822,829	(670,530)

Table 3. Estimates of live longleaf pine (*Pinus palustris* Mill.) trees and seedlings, by forest type, state, ownership group, and natural versus having clear evidence of artificial regeneration for the ca. 2009–2015 and 2016–2021 evaluation periods from Forest Inventory and Analysis (FIA) data.

	Longleaf Pine Trees			Longleaf Pine Seedlings		
	2009–2015	2016–2021	Diff.	2009–2015	2016–2021	Diff.
Total	849,365,838	1,076,035,524	226,669,686	873,738,658	762,597,568	(111,141,090)
Forest type						
Longleaf pine	587,763,975	838,628,811	250,864,836	513,204,378	466,011,442	(47,192,936)
Longleaf pine–oak	106,566,711	68,643,383	(37,923,328)	150,363,604	111,686,978	(38,676,626)
Sand pine	3,890,053	6,166,582	2,276,529	894,634	3,545,699	2,651,065
Slash pine	33,980,134	31,035,931	(2,944,203)	51,368,336	51,635,537	267,201
Southern scrub oak	13,900,984	10,055,168	(3,845,816)	35,120,160	29,846,280	(5,273,880)
Other	103,263,982	121,505,650	18,241,668	122,787,546	99,871,632	(22,915,914)

Table 3. Cont.

	Longleaf Pine Trees			Longleaf Pine Seedlings		
	2009–2015	2016–2021	Diff.	2009–2015	2016–2021	Diff.
<u>State</u>						
Alabama	173,281,807	226,563,837	53,282,030	252,174,168	145,826,710	(106,347,458)
Florida	210,628,965	252,874,091	42,245,126	241,042,409	304,188,108	63,145,699
Georgia	128,540,953	175,635,129	47,094,176	94,323,502	114,678,563	20,355,061
Louisiana	46,201,822	30,459,653	(15,742,169)	37,495,017	8,931,903	(28,563,114)
Mississippi	60,265,210	71,499,713	11,234,503	21,044,587	52,919,285	31,874,698
North Carolina	74,856,173	97,142,343	22,286,170	71,913,367	41,093,302	(30,820,065)
South Carolina	143,780,505	197,722,995	53,942,490	139,051,212	87,416,243	(51,634,969)
Texas	12,138,545	20,074,562	7,936,017	16,694,396	7,543,454	(9,150,942)
Virginia	-	4,063,200	4,063,200	-	-	-
<u>Ownership</u>						
US Forest Service	105,633,731	116,763,998	11,130,267	112,043,178	62,706,090	(49,337,088)
Other federal	71,138,687	98,333,275	27,194,588	116,812,765	211,470,053	94,657,288
State/local	89,923,705	102,341,331	12,417,626	99,139,226	133,866,455	34,727,229
Private	582,669,715	758,596,919	175,927,204	545,743,488	354,554,970	(191,188,518)
<u>Stand origin</u>						
Planted	224,744,876	494,323,030	269,578,154	192,371,057	234,457,884	42,086,827
Natural	624,620,963	581,712,493	(42,908,470)	681,367,600	528,139,684	(153,227,916)

3.2. Plot-Level Analyses

We detected a significant increase over time in mean IV (from 30.7 to 38.0) and C content (2.20 to 3.11 metric tons per hectare) on the plots on which the species occurred (Table 4). The increase in longleaf pine importance value extended only to the longleaf pine and the slash pine forest types, and to the “other” forest type category. The longleaf pine C content also increased on “other” forest type plots. Not surprisingly, the longleaf IV on plots in the longleaf pine forest type was at least twice that of any other forest type, followed by the longleaf pine–oak forest type. Longleaf pine C was highest in these two forest types as well. Mean plot-level longleaf IV increased significantly in several states: Florida, Georgia, Mississippi, North Carolina, and South Carolina. The same states, except North Carolina and Louisiana, experienced a significant increase in mean plot-level longleaf C. The IV was highest on plots in South Carolina, Florida, North Carolina, and Georgia. The C was highest in Louisiana, Mississippi, South Carolina, and North Carolina. Private ownership was the only ownership group with a significant increase in IV, while private and Forest Service land experienced significant increases in C. Mean IV and C were highest on Forest Service and other federally managed plots. Both naturally regenerated and planted stands had a significant increase in C but only naturally regenerated plots had a significant IV increase.

We additionally found statistically significant correlations between the county-level mean plot change in longleaf pine IV and the mean plot elevation, and between the county-level mean plot change in C per hectare and the mean plot latitude (Table 5).

3.3. Regeneration within Seed Zones

In the earlier evaluation period (ca. 2009–2015), 82.1 percent of longleaf pine stems across the distribution of the species were small trees (1,414,765,724 seedlings and saplings). This decreased to 75.1 percent in the second evaluation period (1,380,113,624 small trees in ca. 2016–2021). The mean plot-level percent of small trees also decreased over time, from 35.8 percent (SD: 44.2) to 32.3 percent (SD: 42.3). The majority of seed zones (six of nine with five or more plots) in the earlier evaluation period had greater than 80 percent small trees and only one had less than 70 percent but only one (the furthest north) exceeded the 80 percent threshold in the second period while five had less than 70 percent (Figure 3). The mean percent of small trees across seed zones decreased from 81.0 percent (SD: 11.2) to 65.4 percent (SD: 13.4). The seed zones averaged a 13.3-percent decrease in small trees, with one zone occurring in northern Alabama and Georgia and south-central North Carolina

experiencing a 29.2-percent decrease and another in peninsular Florida experiencing a 17.1-percent decrease.

Table 4. Mean and standard errors of Forest Inventory and Analysis (FIA) plot-level measures of longleaf pine (*Pinus palustris* Mill.) importance value (IV) and carbon for the ca. 2009–2015 and 2016–2021 evaluation periods by forest type, state, ownership group, and natural versus having clear evidence of artificial regeneration. Values are in bold when they are significantly different between evaluation periods at $p \leq 0.05$ based on Kruskal–Wallis tests of group differences.

	Plots		Importance Value (IV)				C Tonnes/ha			
			2009–2015		2016–2021		2009–2015		2016–2021	
	2009–2015	2016–2021	Mean	SE	Mean	SE	Mean	SE	Mean	SE
All	1754	1914	30.7	0.7	38.0	0.8	2.20	0.07	3.11	0.08
Forest type										
Longleaf pine	520	745	62.4	1.3	65.9	1.1	4.38	0.17	5.26	0.16
Longleaf pine–oak	151	136	36.4	2.0	33.1	2.0	1.95	0.11	2.29	0.15
Sand pine	18	17	9.4	1.6	13.9	2.7	0.59	0.20	0.70	0.22
Slash pine	209	215	14.9	1.1	17.8	1.1	1.44	0.13	1.83	0.13
Southern scrub oak	65	45	22.0	2.8	22.4	3.5	0.63	0.09	0.98	0.17
Other	791	756	14.0	0.7	18.5	0.8	1.17	0.06	1.68	0.09
State										
Alabama	319	328	27.6	1.6	32.9	1.8	2.28	0.15	2.85	0.18
Florida	476	512	36.7	1.6	42.5	1.5	1.95	0.12	2.57	0.13
Georgia	275	292	31.4	1.9	39.6	2.1	1.96	0.14	2.51	0.17
Louisiana	130	89	26.9	2.7	31.4	3.4	3.08	0.37	4.19	0.53
Mississippi	188	281	19.6	1.8	33.3	1.9	2.01	0.23	4.11	0.26
North Carolina	131	142	32.3	2.8	40.3	2.8	2.83	0.30	3.45	0.33
South Carolina	198	216	33.9	2.2	42.6	2.4	2.22	0.23	3.58	0.26
Texas	37	52	19.1	3.8	26.1	4.0	1.95	0.44	3.31	0.66
Virginia	0	2	-		65.8	34.2	-		0.66	0.34
Ownership group										
US Forest Service	248	477	37.8	2.2	41.3	1.5	3.63	0.26	4.62	0.21
Other federal	144	162	40.2	2.7	44.5	2.6	3.20	0.28	3.37	0.28
State/local	144	157	41.2	2.9	41.2	2.7	2.48	0.21	2.92	0.26
Private	1218	1118	26.8	0.8	35.1	1.0	1.75	0.07	2.54	0.09
Stand origin										
Planted	158	313	64.7	2.6	65.3	1.9	2.28	0.26	3.19	0.20
Natural	1596	1601	27.3	0.7	32.6	0.8	2.19	0.07	3.09	0.09

Table 5. Spearman’s correlations of county mean plot-level changes in longleaf pine (*Pinus palustris* Mill.) importance value (IV) and metric tons of carbon per hectare (C/ha) with county plot mean latitude, longitude, elevation, slope, stand age, and aspect (transformed to generate continuous variables that reflect aspect “northness” and “eastness”). Counties with fewer than five FIA plots were excluded ($n = 120$ counties). p -values ≤ 0.05 are in bold.

	Mean Plot-Level Change	
	IV	C/ha
Latitude	0.144	0.189
Longitude	0.089	0.039
Elevation	0.183	0.103
Slope	0.070	0.135
Aspect (northness)	0.055	0.077
Aspect (eastness)	−0.039	0.125
Stand age	−0.120	0.124

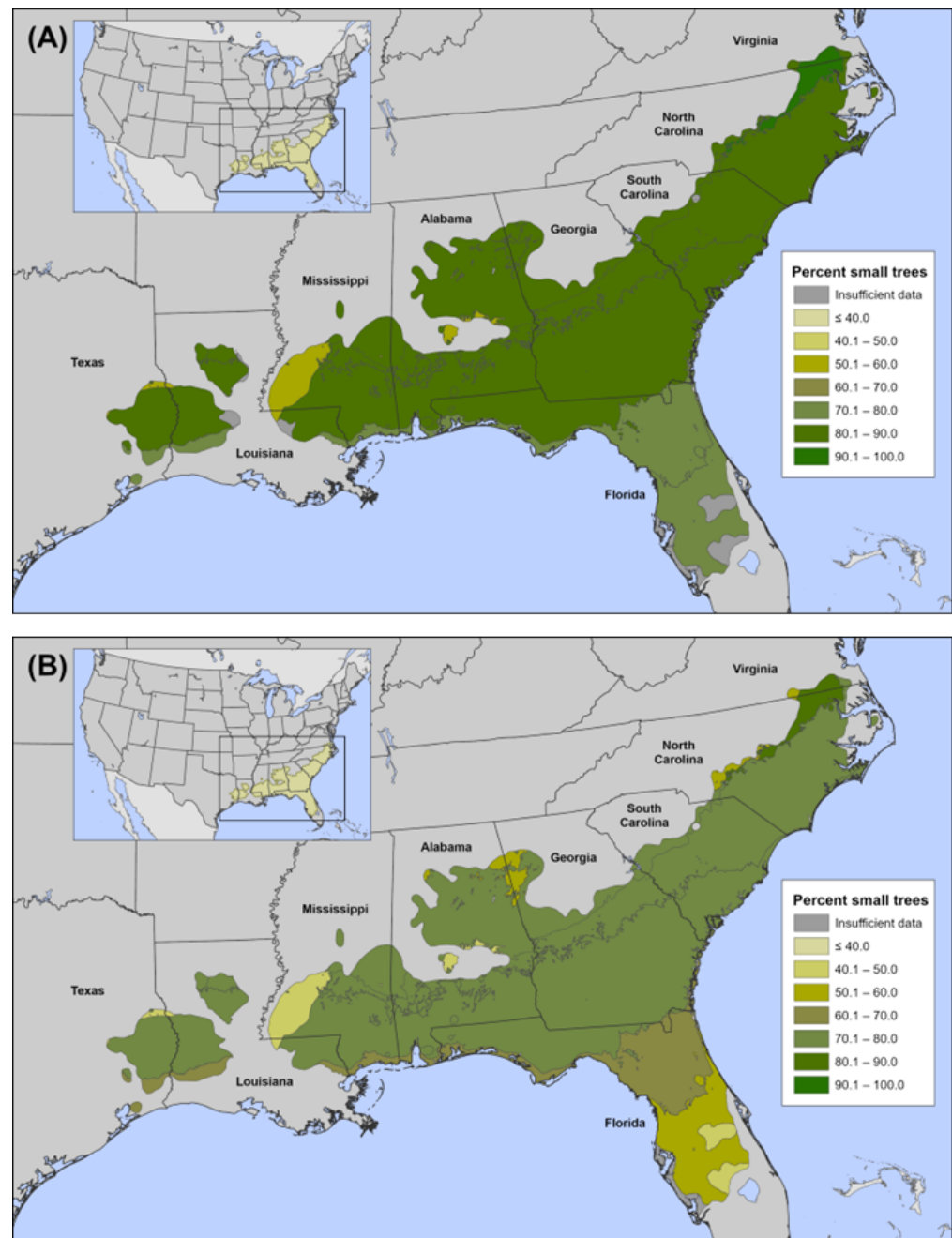


Figure 3. Percent of estimated longleaf pine (*Pinus palustris* Mill.) stems that are small trees (seedlings and saplings, diameter < 12.7 cm), by provisional seed zone, from Forest Inventory and Analysis (FIA) data collected (A) ca. 2009–2015, and (B) ca. 2016–2021.

4. Discussion

Longleaf pine is a species of high conservation concern throughout much of the Southeastern United States, where widespread restoration efforts in recent years have focused on expanding the extent of longleaf pine forest [15]. While recent research has established that these efforts have successfully increased the area of forest types in which longleaf pine dominates, longleaf pine areal trends in other forest types have not been thoroughly investigated. Similarly, we do not have a solid understanding of change over time in longleaf pine numbers and importance across these different forest types. Finally, it is important to monitor regeneration trends across and within the distribution of the species to assess and predict the long-term success of restoration efforts.

Our evaluation of forest inventory data from two time periods (ca. 2009–2015 and 2016–2021) confirms that both the estimated number of longleaf pine trees and the area of the longleaf pine forest type have increased. These trends are consistent with recent analyses of FIA data from slightly different years [16,17]. While the number of trees has increased in recent decades, from approximately 849 million to 1.076 billion by our estimates, the recent estimate is about 14 percent less than the 1.251 billion estimate for 1970 [17]. Still, this is a positive development and suggests the timeliness of updating the IUCN's assessment of longleaf pine as having a decreasing population trend and a continuing decline in mature individuals [10]. The increasing number of planted longleaf pine trees and the growing area of planted longleaf forests are also positive developments.

Meanwhile, the areas of all other major forest types containing longleaf pine have decreased, resulting in an overall decline in the area of forest (of any type) occupied by longleaf pine. The number of longleaf pines has also decreased in several forest types. These results, coupled with the increase in the longleaf pine forest type area, suggest a dynamic through which forests dominated by longleaf pine are becoming more widespread, while the extent declines of forests in which longleaf pine is a less important component. One possible driver of this dynamic is that some forests of the longleaf pine–oak type have been converted to the longleaf pine type through silvicultural tools such as prescribed burning, reproduction cutting or thinning, and release treatments to allow longleaf pine to return to dominance, as described by Guldin [35]. At the same time, other longleaf pine–oak forests have undergone a transition to hardwood dominance as a result of active or passive management that has reduced the longleaf component [16]. Additionally, forests such as those in the longleaf pine–oak type may be more likely than those of the longleaf pine forest type to be converted to either short-rotation loblolly pine plantations or to agricultural use. In at least some cases, these forests were dominated by longleaf pine in the past before changes in land management, especially the suppression of frequent low-intensity fires. As such, they may be preferable sites for longleaf pine reforestation given that America's Longleaf Restoration Initiative conservation plan calls for the restoration of longleaf forests from suitable sites currently in other forest types [14,15]. The decline of longleaf pine in these other forest types suggests that the window of opportunity to expand the longleaf forest type footprint via the restoration of forests with a minor longleaf overstory component may be narrowing.

The importance of longleaf pine has shown statistically significant growth over time on plots across the species' distribution in five of nine states and in the longleaf pine forest type, findings which are in keeping with previous work [36]. This trend was not detected, however, in most other forest types. Again, this result emphasizes the dynamic through which longleaf pine is increasing its dominance in the longleaf pine forest type but not in other forest types. (The importance of longleaf pine in fact declined on plots in the longleaf pine–oak forest type but the change was not statistically significant.)

We additionally detected a decrease in the number of longleaf seedlings across the species distribution and in most states and forest types, as well as declines in the number and area of naturally regenerated longleaf pine. Assessing the proportion of small trees (seedlings and saplings) as a further indicator of regeneration trends, we found a species-wide decrease from 82.1 percent to 75.1 percent, with the decline most pronounced along the edges of the species extent. In other words, both the number of seedlings and the proportion of small trees are decreasing despite the increase in longleaf pine trees and the area of the longleaf pine forest type. The decline in longleaf pine seedlings, as well as a decrease in forest encompassing seedlings, is consistent across forest types, including the longleaf pine forest type. An important factor in the longleaf pine forest type may be the development of stands less than 40 years old [17], in which natural regeneration is likely suppressed during the stem exclusion stage of stand development [37]. Longleaf pine seedling growth is greatly reduced when the stand basal area exceeds 9 m² per ha, and their survival is impacted when it is greater than 17 m² per ha [38].

In other forest types, the declining regeneration we found may reflect longleaf pine's inability to compete in the understory with other species, such as oaks and shrubs, in the absence of fire [38]. Meanwhile, in recently planted stands of the longleaf pine forest type, it is possible that many of the planted trees have not yet reached reproductive maturity, which is estimated at age 20 [39] or 30 [40]. Other factors, such as tree size, stand density, site quality, and genetics also affect the production of cones by individual longleaf pine trees, with the best cone producers being those that are open-grown, dominant trees with large crowns and a DBH of at least 38 inches [40]. At the stand level, seed production for dominant and codominant trees of cone-bearing size reaches its peak at longleaf pine basal areas of 6.9 to 9.2 m² per ha [41]. Recently, an increase in longleaf pine regeneration at broad scales was found to be associated with an increase in the proportion of longleaf basal area on FIA plots [20]. Another factor that may be contributing to the declining regeneration of longleaf pine is the cyclical nature of its cone production [42], with large cone crops typically occurring episodically, with regional synchrony, every five to seven years [39]. The successful regeneration of seed produced by such "bumper crops" may largely depend on the availability of appropriate stand conditions. Croker, for example, found that longleaf pine advanced regeneration benefitted from the interaction between a large longleaf seed crop and the well-timed removal of most of the overstory, similar to a shelterwood harvest following reproduction [43]. For our study, the more recent evaluation period (ca. 2016–2021) may not have corresponded as well as the previous period (ca. 2009–2015) with a longleaf pine masting event. Additionally, little natural regeneration is expected to occur in fully stocked mature stands that exceed basal areas of 9 m² per ha.

Longleaf pine natural regeneration is difficult for several reasons, including poor seed production, slow seedling growth, and low seedling survival [44]. Historically, longleaf pine forests were multi-aged with even-aged cohorts regenerating in small patches formed by the mortality of canopy trees [19], a structure now existing only in the presence of frequent fires [38]. Replicating this structure in planted stands is complicated and takes time. It requires effective competition control and seedbed preparation, which are achieved most efficiently in mixed-aged stands with the use of controlled burning [45]. Silvicultural research indicates that uneven-aged management approaches, including single-tree or group selection and variable density thinning, may establish conditions suitable for natural regeneration and canopy recruitment in longleaf pine stands [46,47]. A three-cut shelterwood system also has been proposed as a way to develop larger longleaf pine crowns and increase seed production [40,48]. Such management strategies that foster and maintain structural heterogeneity in longleaf pine stands have the added benefit of potentially increasing their resilience to disturbance events [36].

Our broad-scale regeneration indicator—changes in the proportion of small trees (seedlings and saplings) compared to all stems of the species—reflects the general relationship that exists between sustainability and small tree density [34,49]. It assumes that the existence of fewer smaller trees is an indication of less successful regeneration and increased vulnerability to the loss of genetic diversity within parts of the species distribution where regeneration has declined the most [21]. While this may not be the case for all tree species, it seems reasonable to expect that those with balanced and stable size–structure relationships are more likely to have sustainable levels of regeneration [21]. For longleaf pine, the existence of a range of stand structures with abundant younger cohorts across broad scales is likely to increase both the sustainability of the species and its associated forest ecosystems [36]. Importantly, the abundant overstory of longleaf pine trees provides opportunities to restore, improve, and expand longleaf pine forests [20], which will contribute to the health, diversity, productivity, and sustainability of southern forest ecosystems [35]. There is considerable uncertainty, however, about the degree to which adequate natural regeneration of the species will occur given the challenges associated with it, including its reliance on the dynamics of periodic large seed crops and overstory conditions [43] as well as fires [38]. Our assessment of the proportion of small trees in longleaf pine included both naturally regenerated and planted seedlings and saplings. It will be important to continue

monitoring the proportion of small trees planted across the distribution of the species, information that will guide our understanding of the degree to which a balanced and stable size–structure relationship across broad scales may depend on human intervention.

5. Conclusions

Using standardized tree occurrence data from two recent evaluation periods across the Southeastern United States, we found that the number of longleaf pine trees has increased in the longleaf pine forest type, while the estimate of the abundance of longleaf trees in other forest types has decreased. Similarly, the area of the longleaf pine forest type has increased as the area of other forest types containing longleaf pine has declined. These findings indicate that restoration efforts have resulted in more forests dominated by longleaf pine, while forest in which the species is a less important component are likely transitioning to other forest types or land uses. At the same time, we found that the mean importance value and carbon content of longleaf pine increased over time across the plots on which the species was inventoried, with significant increases in several states. Finally, we detected a decrease over time in the estimated number of longleaf seedlings across most states and forest types. Our application of a regeneration deficit indicator demonstrated a species-wide decrease in the proportion of small trees (seedlings and saplings together), which was most pronounced along the edges of the species distribution and could indicate less sustainable levels of regeneration in some areas. These findings underscore the challenges associated with facilitating natural regeneration in longleaf pine.

Supplementary Materials: The following supporting information is available online at <https://www.mdpi.com/article/10.3390/f15071255/s1>, Table S1: Estimates of forest area, in hectares, and percentages by forest type within ownership groups, for the ca. 2009–2015 and 2016–2021 evaluation periods, and changes between the evaluation periods, from Forest Inventory and Analysis (FIA) data.

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