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Restoration of the Montane Longleaf Pine Forest Can Increase Understory Plant Species at Bankhead National Forest in Alabama, USA

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Abstract

Longleaf pine (*Pinus palustris* Mill.) forests are well known for their high-quality timber and biodiversity. However, it is unclear whether restoring montane longleaf pine forests from mixed pine–hardwood forests increases understory plant species richness. This study documented understory plant species in 16 stands across three stages (Early: ≤25 years, Late: 25–75 years, and Mature: >75 years) of restored montane longleaf pine forest and in nearby mixed pine–hardwood forests (Control) in Bankhead National Forest, Alabama, USA. Ground LiDAR was used to capture the forest structure, yielding 14 derived parameters. These data were statistically analyzed using ANOVA and Correlation. Results indicated higher understory plant species richness in the montane longleaf pine forest, with the highest richness observed at the Mature stage, particularly for shrub and grass species. While the average understory plant species richness did not differ significantly between the Early and Late stages across categories, their community similarity index was only 0.53. The percentage of shade-tolerant species was 71% at Control sites, 51% at Early sites, 60% at Late sites, and 62% at Mature sites. Understory plant species richness was negatively correlated with total crown area and basal area. These findings imply that forest management practices (e.g., harvesting, thinning, and prescribed burning) could create forest structures suitable for a great diversity of understory plant species. Forest structure can be quantitatively described by 3D structure indices derived from LiDAR and other tools.

Keywords: basal area; biodiversity conservation; crown area; forest structure; LiDAR; *Pinus palustris* Mill.

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1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests were historically a vital ecosystem, offering social, economic and ecological value across the coastal areas of the southeastern United States [1]. These forests provide economic resources such as high-quality timber, pine straw and related chemical products (e.g., historical naval stores including turpentine, rosin, pitch and tar) [2]. Forest management also creates job opportunities for local communities [3]. Longleaf pine forests protect regional watersheds and host high levels of biodiversity, including endemic species like the red-cockaded woodpecker (*Picoides borealis*), gopher tortoise (*Gopherus polyphemus*) and black pine snake (*Pituophis melanoleucus*) [4]. Under current land-use practices, longleaf pine forests support more diverse groundcover plant communities than other southern pine forests [5,6]. Furthermore, due to their long lifespan (up to 450 years) and belowground carbon storage, longleaf pine forests may serve as long-term carbon sinks [7]. However, the area of longleaf pine forests declined dramatically from

approximately 37 million hectares to 1.02 million hectares after European settlement, largely due to timber overharvesting, land-use change (e.g., agricultural and urban development) and fire suppression [8–11]. The longleaf pine found in the Blue Ridge, Ridge and Valley, and Cumberland Plateau in northern Alabama and Georgia, a physiographically and climatically distinct region [12,13], is also known as montane (or mountain) longleaf pine [14–16]. The high understory diversity in montane longleaf pine forests is attributed to the range overlap among Appalachian, Coastal Plain and Piedmont species [17,18]. As of 1996, less than 4000 hectares of montane longleaf pine forest remained, representing about 0.0001% of the entire longleaf pine's range [19]. Currently, the longleaf pine ecosystem is classified as endangered and is recognized as an important refuge for biodiversity [20]. With financial aid from government agencies, restoration efforts have helped maintain and increase longleaf pine acreage in the region [21].

Longleaf pine restoration efforts often involve planting, harvesting and prescribed burning, depending on habitat conditions [21,22]. A key approach is replanting in areas where longleaf pine is heavily degraded or nonexistent. This typically includes clear-cutting undesirable vegetation, planting longleaf pine and establishing a frequent, low-intensity prescribed fire regime to eliminate unwanted broadleaved trees [23,24]. The goal of forest management is to maintain natural diversity and species composition [25]. While varied plant responses to mechanical soil disturbance in longleaf pine communities on the coastal plain have been analyzed [26], changes in understory plant species during montane longleaf pine restoration under current management practices remain poorly understood.

Succession in forest plantations can alter understory plant species diversity and the physical environment [27]. In the early successional stage after a clear-cut, light-demanding species may dominate the understory due to abundant sunlight. Plant traits, such as dispersal ability and life history, can also impact recovery [5,28]. As planted trees grow, sunlight becomes increasingly scarce in the understory, leading to the dominance of shade-tolerant species in the late successional stage. During mid-succession, plant diversity may peak when both shade-tolerant and shade-intolerant species coexist. Many studies have indicated a theoretical U-shaped dynamic in understory plant communities of non-longleaf pine forests [29,30]. However, some researchers contend that diversity is highest in the early successional stages [31–33], while others suggest it should be equal in the early successional and climax stages [34]. Still others have shown a pattern of initial increase followed by a decrease during succession [35,36]. These patterns are primarily observed in closed-canopy, not fire-maintained, forests. Additionally, forest plantations established to replace natural ecosystems may not contribute to biodiversity, with some even being considered "green deserts" [37]. Understory plant cover (herbs, grasses, shrubs, vines and small trees) has been observed to increase after ten years of restoration management in an old-growth montane longleaf pine forest [38]. Previous surveys have also documented plant community conditions in montane longleaf pine forests at various locations and times for different purposes [39,40]. Prescribed burning has been shown to increase grass and herbaceous ground cover [41,42]. However, the pattern of plant species diversity during succession in montane longleaf pine forests in the southeastern US remains unclear. These forests are restored by replacing native mixed pine–hardwood forests through harvesting and prescribed burning (e.g., a 3–5 year cycle), and the ecosystem may be in a state of nonequilibrium [43].

Forest structure influences understory plant species richness by altering the spatial distribution of physical factors, such as sunlight availability, microclimate and nutrient availability, as well as their heterogeneity [44–48]. It may also be a dominant factor in controlling understory plant species through gap dynamics [29,49]. At the mature stage (e.g., more than 75 years), forest structure is thought to facilitate species coexistence through

canopy gaps and tree mortality [46]. Generally, opening the forest canopy, reducing hardwood tree abundance, and conducting prescribed burning could restore montane longleaf pine forests in about 8–10 years. However, specific information regarding the relationship between forest structure and understory plant species richness is lacking [38]. Previously, forest structure was primarily characterized by species composition and basal area (the total area of tree stems at breast height) due to technological limitations. Now, various structural indices can be used to quantify and compare forest stand complexity [50,51], such as multidimensional functional diversity and the Gini index [51,52], which will be helpful for forest management practices.

This study aims to compare understory plant species, including species richness, composition, similarity, and spatial change, in local montane longleaf pine forest stands restored from mixed pine–hardwood forests at different successional stages, under regular management practices, and to examine their relationship with forest structure. Three successional stages of longleaf pine forest were defined: Early (forest age ≤ 25 years), Late (25–75 years) and Mature (>75 years). The hypotheses are: (a) longleaf pine forest stands exhibit greater understory plant species richness, and (b) forest structure is related to understory plant species richness. The specific objectives are to: (i) document understory plant species across different successional stages of planted longleaf pine forest; (ii) compare understory plant species richness among different successional stages and with local mixed pine–hardwood forests; (iii) examine the relationship between understory plant species richness and various forest structural indices; and (iv) provide implications for local longleaf pine restoration and forest management. The findings of this study are expected to contribute new knowledge to local longleaf pine restoration and forest management efforts.

2. Methods

2.1. Study Area

The study area is located in the William B. Bankhead National Forest (hereafter Bankhead National Forest) in Alabama (Figure 1). Bankhead National Forest comprises over 73,000 hectares of public land, protecting regional watersheds and streams. Forests currently cover more than 97% of this area. The major forest communities include upland hardwood and mixed pine–hardwood forests. Loblolly and montane longleaf are the main pine species, while oaks and hickory are the primary hardwoods in this area [53]. According to the USDA soil survey, the soil type in this region is sandy loam (FAO symbol: SL). The study sites were selected in relatively flat areas at elevations of 200–250 m. Based on weather station data from the nearby town of Double Springs (average about 15 km map distance from study sites) over the past 10 years, the average monthly air temperature ranges from 6 °C to 26 °C, and the annual precipitation is about 1420 mm.

2.2. Forest Types, Stages and Categories

Most montane longleaf pine forests in Bankhead National Forest were planted within the last 30 years, though some sites contain naturally regenerated longleaf pine trees. Prescribed burns have been conducted every 2–3 years since the 1990s, with the most recent burns in these stands occurring in 2024 and 2025, according to records. Thinning and logging were carried out more than 20 years ago, before the stands reached maturity. Understory plants were defined as those whose canopies were not part of the forest stand's overstory, mainly including tree seedlings or saplings, shrubs and herbs. In this study, the land-use history, which can also affect understory plant species [54], is similar across all sites because they are part of a national forest. All stands were selected in relatively flat areas to minimize the influence of social and physical factors on the results. Mature longleaf pine stands typically resemble a savanna, with a sparse overstory and an understory dominated

by low-stature groundcover species, such as longleaf pine seedlings and saplings, shrubs, and herbs. For comparison (control), mature mixed pine–hardwood forest stands (over 75 years old) that had no prescribed burning or harvesting were used. This study includes four categories, representing different stages of longleaf pine forests: Control (C), Early (E, age < 25 years), Late (L, age 25–75 years) and Mature (M, age > 75 years). Each category had four replications, with each replication covering approximately 1–3 hectares, totaling 16 stands (4 categories × 4 replications). These stands were separated, randomly distributed, and all located in the southern part of Bankhead National Forest (Figure 1, Table 1). The map distances among these sites varied from approximately 0.5 km to 40 km. Detailed soil information is indicated in [55]. The coordinates and other information for each stand are listed in Table 1. To record understory plant species in each stand, a random 20-m line-intercept approach (sampling at 1-m intervals) was used 2–3 times between May and September 2025. This method was chosen for its efficiency, as previous studies revealed low abundance and diversity of herbs and grasses [56]. This method is a classic approach for plant surveys [57], especially for plant communities with mixed grasses, shrubs and trees [58]. The identification of plant species was based on experience, field guides, suggestions from local botanists and the iNaturalist App. To account for the different light tolerances of species, each species was classified as either shade-tolerant (including partial shade tolerant) or shade-intolerant (light-loving) based on information from the USDA Plant Database, the USDA Forest Service and botanical garden management.

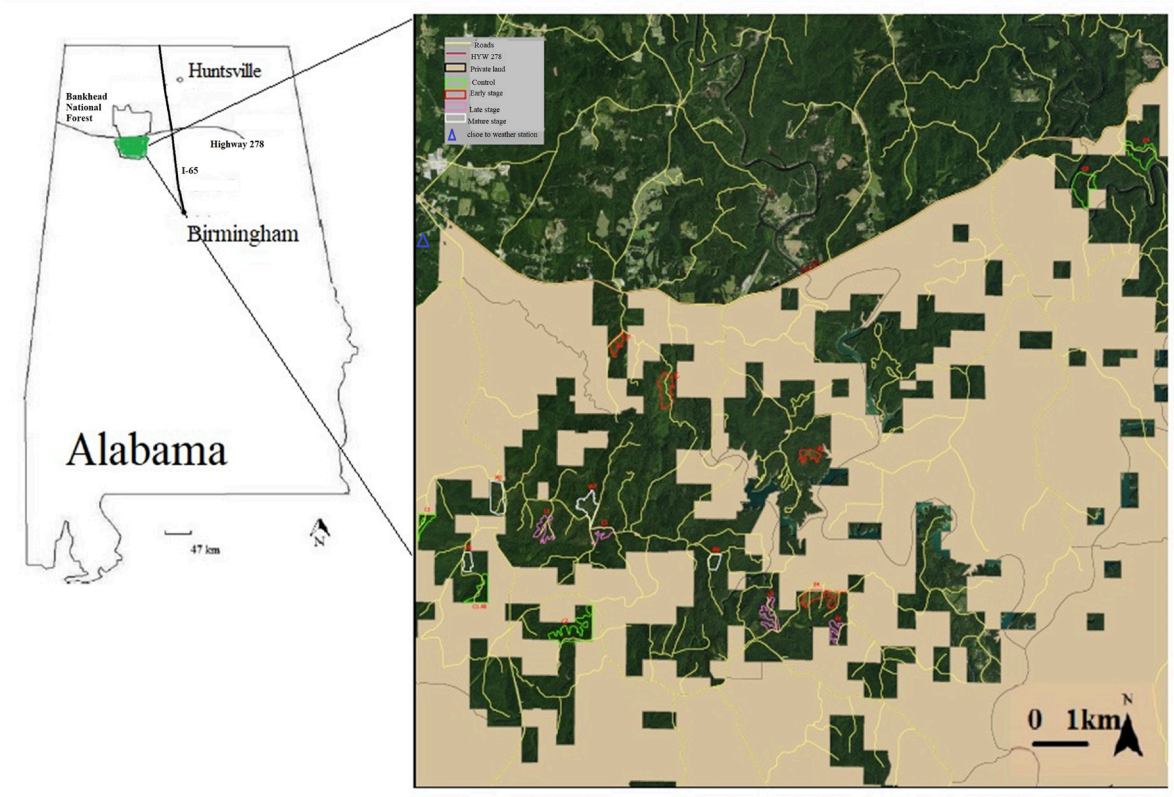


Figure 1. General location of the study area (in green color) in the southern part of Bankhead National Forest in Alabama (**left**) and 16 study sites (**right**). Study sites are delineated by red lines for the Early stage, pink lines for the Late stage, white lines for the Mature stage, and bright green lines for the Control sites. The weather station is outside the map, but a close nearby point is indicated by a blue triangle) (courtesy of William Sutton for the base map).

Table 1. Location and other information for each site in four categories (C: Control sites of mixed pine-mixed hardwood forest, E: Early stage of longleaf pine, L: Late stage of longleaf pine, M: Mature stage of longleaf pine).

Sites	Category	Latitude (N)	Longitude (W)	Elevation (m)	Soil Type	Succession Stage
C1	Control (pine and mixed hardwood forest)	34.0823°	87.3990°	201	Sandy loam	Mature
C2		34.0695°	87.3709°	246		
C3		34.1621°	87.2425°	197		
C4		34.1700°	87.2283°	222		
E1	Early stage (montane longleaf pine forest)	34.1280°	87.3639°	204	Sandy loam	Early
E2		34.1208°	87.3504°	202		
E3		34.1071°	87.3131°	205		
E4		34.0776°	87.3129°	229		
L1	Late stage (montane longleaf pine forest)	34.0902°	87.3791°	230	Sandy loam	Late
L2		34.0924°	87.3634°	229		
L3		34.0712°	87.3212°	240		
L4		34.0692°	87.3068°	250		
M1	Mature stage (montane longleaf pine forest)	34.0833°	87.4029°	214	Sandy loam	Mature
M2		34.0959°	87.3935°	228		
M3		34.0968°	87.3699°	237		
M4		34.0861°	87.3386°	229		

2.3. Forest Structure

A ground-based LiDAR (Light Detection and Ranging) system (LiBackPack, Green Valley International, Berkeley, CA, USA) was used to scan forest structure within a 40 × 40 m^2 plot near the center of each stand. Due to challenges with road access and equipment delivery, three stands per category were scanned. The acquired data were then analyzed and processed using Lidar360 software (v9.1.0). Finally, detailed information for each tree within the plots, including coordinates, DBH, height, canopy diameter, crown area, crown volume and base branch height, was extracted. Based on individual plant data, the following forest structure indices were calculated:

(i) Stem structure index: Stem structural diversity (SSD), based on the distance-based multidimensional index of functional dispersion [52,59], measures the mean distance of every individual tree to the centroid point in the plot within a two-dimensional space of diameter at breast height. This index was applied to DBH, tree height and canopy diameter in this study. For tree height, the approach was applied across three dimensions (x, y, z), with the z-coordinate of the centroid point in the plot set to 0. For DBH and canopy diameter, the distance was measured from the centroid to the tree bark or canopy boundary, assuming tree stems and canopies are perfect circles.

(ii) Gini index: The Gini index measures the inequality of tree size attributes, such as DBH or height, ranging from 0 (perfect uniformity) to 1 (maximum inequality). It offers a distance-independent metric for evaluating forest structural complexity [51]. The formula used in this study was: Gini index = $\Sigma\ (2i - n - 1)\ x_i/n\ \Sigma\ x_{i,}$ where x is the observed value, n is the number of trees measured in the plot, and i is the rank of the observed value in ascending order.

(iii) Fractal dimension: Fractal dimension is frequently employed to characterize complexity. In this study, the two-dimensional tree canopy cover derived from LiDAR data was analyzed using the box-counting method with varying box sizes (e.g., 10 m, 5 m and 2 m). A box was counted if it contained any part of a tree canopy; otherwise, it was not. The fractal dimension was then determined by the slope of the fitted line from a scatter plot of log(box length) versus log(box number) [60].

(iv) Gap fraction: This is the percentage of the plot area that contains no tree canopy or components (e.g., stem) on the ground surface. The average DBH, average crown diameter

and total basal area of individual trees were overlaid to characterize the forest structure within the plot.

2.4. Understory Plant Species Richness

Understory plant species richness can characterize plant species diversity in this study. Two indices were used to assess the spatial variation in plant species within and among categories:

- Sørensen similarity index:

This index measures the species similarity between two categories, ranging from 0 (no similarity) to 1 (complete identity). It was estimated as follows [61,62]:

$$S = 2C/(A + B)$$

where C is the number of species common to both categories, and A and B are the numbers of species in the respective categories.

- Species accumulation curve [63]:

This curve illustrates the cumulative number of unique plant species as distance increases (every 1 m) along a 20 m line, showing how species richness changes with distance.

2.5. Statistical Analysis

This study comprised four categories (C, E, L and M), each with four samples (stands), totaling 16 samples for understory plant species. A one-way ANOVA was used to test for differences in average plant species richness among the four categories, followed by a post hoc multiple-comparison test. For forest structure, each category included three LiDAR-scanned stand replicates. The average and standard deviation of forest structure indices were calculated and statistically compared among categories. Pearson correlation was used to assess the relationship between plant species richness and forest structure indices at the stand level. All analyses were conducted using SAS software (version 9.3, Cary, NC, USA), with statistical significance set at $p < 0.05$.

3. Results

3.1. Plant Species Richness Among Categories

A total of 127 plant species were identified across all categories. The mature stage of the montane longleaf pine forest stand exhibited the highest understory plant species richness (30.5) (Figure 2). Average plant species richness did not differ significantly between the Early (25.4) and Late stages (25.8) at the stand level. Control sites had the lowest plant species richness (16.0).

3.2. Plant Species Composition Among Categories

Common and unique plant species for each category are presented in Table 2. The percentage of shade-tolerant species was 73% at Control sites, increasing from 51% in the Early stage to 60% in the Late stage and 62% in the Mature stage. The Sørensen similarity index was 0.36 between Control sites and Early stages, 0.53 between Early and Late stages (despite similar species richness), and 0.62 between Late and Mature stages (Figure 3). This indicates a high similarity in understory plant species between the Late and Mature stages. At the category level, both the Early stage (73 species) and the Mature stage (67 species) exhibited higher species richness than the Late stage (55 species). Several species were present across all categories, including muscadine (*Vitis rotundifolia* Michx.), poison ivy (*Toxicodendron radicans* (L.)), sourwood (*Oxydendrum arboretum* (L.) DC.), tulip poplar (*Liriodendron tulipifera* L.) and sand hickory (*Carya pallida* (Ashe) Engelm. & Graebn.). Control sites had a greater abundance of tree seedlings, such as

oaks, beech, maple and sweetgum, whereas longleaf sites featured more shrub, flower and grass species. Shrub species included sparkleberry, deerberry, American beautyberry and common dewberry. Grass species included variable witch grass, Heller's Rosette grass (*Dichanthelium oligosanthes* (Schult.) Gould), Bosc's witch grass (*Dichanthelium boscii* (Poir.) Gould & C.A. Clark), woolly beard grass (*Erianthus alopecuroides* Michx.) and narrowleaf silkgrass (*Pityopsis graminifolia* (Michx.) Nutt.). There were approximately 8, 31, 12, and 21 unique species in the C, E, L and M categories, respectively (Table 2). Some unique species at control sites included American beech (*Fagus* Ehrh.), American hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), Carolina buckthorn (*Frangula caroliniana* (Walter) A. Gray), willow oak (*Quercus phellos* L.), winged elm (*Ulmus alata* Michx.) and strawberry bush (*Euonymus americanus* L.). Some unique species at the Early stage sites included shortleaf pine (*Pinus echinata* Mill.), birdsfoot violet (*Viola pedate* L.), common rageweed (*Ambrosia artemisiifolia* L.), horseweed (*Erigeron canadensis* L.), little-leaf tick-clover (*Desmodium ciliare* (Muhl. Ex Willd.), narrowleaf mountainmint (*Pycnanthemum tenuifolium* Schrad.), round-leaved trailing tick-trefoil (*Desmodium rotundifolium* Desv.), slender yellow woodsorrel (*Oxalis dillenii* Jacq.), woolly beardgrass (*Erianthus alopecuroides* Michx.) and yellow crownbeard (*Verbesina occidentalis* L. (Walter)). Unique species at the Late stage included common sweetleaf (*Symplocos tinctorial* (L.) L'Her.), hairy lettuce (*Lactuca hirsute* Muhl. ex Nutt.), one-flower bedstraw (*Galium uniflorum* Michx.), spiked hoarypea (*Tephrosia spicata* (Walter) Torr. & A. Gray), St. Andrew's cross (*Hypericum hypericoides* (L.) Crantz), white boneset (*Eupatorium album* L.), whiteleaf mountainmint (*Pycnanthemum albescens* Michx.) and others. Unique species at the Mature stage sites included Carolina laurelcherry (*Prunus caroliniana* (Mill.) Aiton), Carolina rose (*Rosa carolina* L.), Eastern milkpea (*Galactia regularis* (L.) Britton, Sterns & Poggenburg), false flowering spurge (*Euphorbia pubentissima* Michx.), lanceleaf greenbriar (*Smilax smallii* Morongo), southern spicebush (*Lindera melissifolia* (Walter) Blume), American pokeweed (*Phytolacca Americana* L.), Catesby's false bindweed (*Calystegia catesbeiana* ssp.), pale lobelia (*Lobelia appendiculata* A. DC.), small white aster (*Symphyotrichum racemosum* (Elliott) G.L. Nesom), spurge nettle (*Cnidoscolus stimulosus* (Michx.) Engelm. & Gray), velvet panicum (*Dichanthelium scoparium* (Lam.) Gould) and others. The average accumulated number of plant species increased faster with distance in the longleaf pine forest (Early, Late, and Mature stages) compared to the mixed pine–hardwood forest (Control sites) (Figure 4). High standard deviations were observed at the Mature stage.

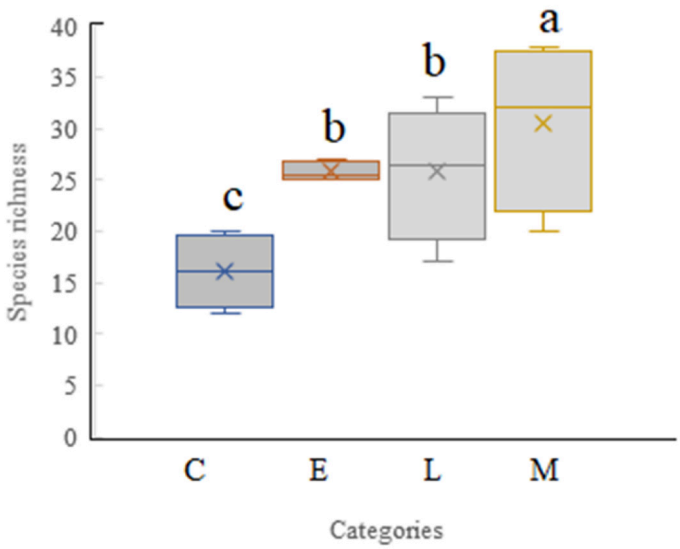


Figure 2. Box plot of average understory plant species richness at three stages of restored longleaf pine forests and Control sites in Bankhead National Forest (C: Control, E: Early stage, L: Late stage, M: Mature stage. Different letters above the boxes indicate statistical significance at $p < 0.05$ by ANOVA).

Table 2. Plant species occurring in restored longleaf pine forest stands at three stages and Control sites in Bankhead National Forest (n = 4, C: Control, E: Early stage, L: Late stage, M: Mature stage, ST: Shade tolerant).

Plant Groups	Common Names	Latin Names	C	E	L	M	ST
Trees	American beech	*Fagus* Ehrh.	×				×
	American hophornbeam	*Ostrya virginiana* (Mill.) K. Koch	×				×
	American persimmon	*Diospyros virginiana* L.	×	×	×		×
	American sweetgum	*Liquidambar styraciflua* L.	×		×	×	
	bigleaf magnolia	*Magnolia macrophylla* Michx.		×			×
	black cherry	*Prunus serotine* Ehrh.	×	×	×		
	black oak	*Quercus velutina* Lam.			×	×	×
	black tupelo	*Nyssa sylvatica* Marshall	×		×	×	×
	chestnut oak	*Quercus montana* Willd.	×	×			×
	Carolina buckthorn	*Frangula caroliniana* (Walter) A. Gray	×				×
	loblolly pine	*Pinus taeda* L.	×	×			
	longleaf pine	*Pinus palustris* Mill.		×	×	×	
	red maple	*Acer rubrum* L.	×	×	×	×	×
	sand hickory	*Carya pallida* (Ashe) Engelm. & Graebn.)	×	×	×	×	
	sassafras	*Sassafras albidum* (Nutt.) Nees	×			×	
	shortleaf pine	*Pinus echinata* Mill.		×			
	smooth sumac	*Rhus glabra* L.			×	×	
	sourwood	*Oxydendrum arboretum* (L.) DC.	×	×	×	×	×
	southern red oak	*Quercus falcata* Michx.	×	×		×	×
	tulip poplar	*Liriodendron tulipifera* L.	×	×	×	×	
	Virginia pine	*Pinus virginiana* Mill.				×	
	water oak	*Quercus nigra* L.	×	×	×	×	
	white oak	*Quercus alba* L.	×	×	×		×
	willow oak	*Quercus phellos* L.	×				×
	winged elm	*Ulmus alata* Michx.	×				×
	winged sumac	*Rhus copallinum* L.		×	×	×	
Shrubs, berries, and vines	American beautyberry	*Callicarpa americana* L.		×	×		×
	bigleaf snowbell	*Styrax grandifolius* Aiton.	×				×
	Carolina laurelcherry	*Prunus caroliniana* (Mill.) Aiton				×	×
	Carolina rose	*Rosa carolina* L.				×	×
	climbing dogbane	*Thyrsanthella difformis* (Walter) Pichon			×	×	×
	common dewberry	*Rubus flagellaris* Willd.		×	×	×	×
	common sweetleaf	*Symplocos tinctoria* (L.) L'Her.			×		×
	deerberry	*Vaccinium stamineum* L.	×				×
	Eastern milkpea	*Galactia regularis* (L.) Britton, Sterns & Poggenburg				×	×
	false flowering spurge	*Euphorbia pubentissima* Michx.				×	×
	Georgia holly	*Ilex longipes* Chapm. ex Trel.			×		×
	lanceleaf greenbriar	*Smilax smallii* Morongo				×	×
	muscadine	*Vitis rotundifolia* Michx.	×	×	×	×	
	New Jersey tea	*Ceanothus americanus* L.		×		×	×
	oakleaf hydrangea	*Hydrangea quercifolia* Bartram		×	×	×	×
	Pennsylvania blackberry	*Rubus pensilvanicus* Poir.		×			×
	poison ivy	*Toxicodendron radicans* (L.)	×	×	×	×	×
	possumhaw	*Ilex decidua* Walter				×	×
	roundleaf greenbrier	*Smilax rotundifolia* L.	×	×	×	×	×
	sawbriar	*Smilax glauca* Walter	×	×		×	×
	saw greenbrier	*Smilax bona-nox* L.		×	×	×	×
	shrub lespedeza	*Lespedeza bicolor* Turcz.				×	×
	smallflower pawpaw	*Asimina parviflora* (Michx.) Dunal				×	×
	southern spicebush	*Lindera melissifolia* (Walter) Blume				×	
	sparkleberry	*Vaccinium arboretum* Marshall		×	×	×	×
	strawberry bush	*Euonymus americanus* L.	×				×
	summer grape	*Vitis aestivalis* Michx.			×	×	
	Virginia creeper	*Parthenocissus quinquefolia* (L.) Planch.	×	×			×
	Virginia sweetspire	*Itea virginica* L.			×		×
	wild yam	*Dioscorea villosa* L.			×	×	×
	yellow jessamine	*Gelsemium sempervirens* (L.) J. St.-Hil.				×	×

Table 2. *Cont.*

Plant Groups	Common Names	Latin Names	C	E	L	M	ST
Grasses, ferns and others	American burnweed	*Erechtites hieraciifolius* (L.) Raf. ex DC.		×			
	American pokeweed	*Phytolacca Americana* L.				×	
	beaked hawkweed	*Hieracium gronovii* L.				×	
	birdsfoot violet	*Viola pedate* L.		×			
	black-stemmed spleenwort	*Asplenium resiliens* Kunze		×			×
	Bosc's witchgrass	*Dichanthelium boscii* (Poir.) Gould & C.A. Clark		×		×	×
	bracken fern	*Pteridium aquilinum* (L.) Kuhn	×	×	×	×	×
	broad-leaved panic grass	*Dicanthelium latifolium* (Lam.) Gould				×	×
	bushy aster	*Symphyotrichum dumosum* (L.) G.L. Nesom		×	×	×	×
	Catesby's false bindweed	*Calystegia catesbeiana* ssp.				×	
	Chinese bushclover	*Lespedeza cuneata* (Dum. Cours.) G. Don		×			
	Christmas fern	*Polystichum acrostichoides* Michx.	×				×
	common ragweed	*Ambrosia artemisiifolia* L.		×			
	Creeping lespedeza	*Lespedeza repens* (L.) W.P.C. Barton				×	×
	dogfennel	*Eupatorium capillifolium* (Lam.) Small		×			
	eastern silver aster	*Symphyotrichum concolor* (L.) G.L. Nesom			×		
	false flowering spurge	*Euphorbia pubentissima* Michx.		×			
	globe flatsedge	*Cyperus echinatus* (L.) Alpha. Wood			×		
	greater tickseed	*Coreopsis major* Walter		×	×	×	×
	hairy angelica	*Angelica venenosa* (Greenway) Fernald				×	×
	hairy lettuce	*Lactuca hirsute* Muhl. ex Nutt.			×		
	Heller's Rosette grass	*Dichanthelium oligosanthes* (Schult.) Gould		×			
	horseweed	*Erigeron canadensis* L.		×			
	hyssopleaf thoroughwort	*Eupatorium hyssopifolium* L.		×			×
	late boneset	*Eupatorium serotinum* Michx.		×			
	late purple aster	*Symphyhotrichum patens* (Aiton) G.L. Nesom			×	×	×
	littleleaf sensitive-briar	*Mimosa microphylla* Dryand.			×	×	
	little-leaf tick-clover	*Desmodium ciliare* (Muhl. Ex Willd.)		×			
	longleaf wood oats	*Chasmanthium sessiliflorum* L.G. Clark	×				×
	Maryland tick-trefoil	*Desmodium marilandicum* (L.) DC.		×	×	×	×
	narrowleaf mountainmint	*Pycnanthemum tenuifolium* Schrad.		×			
	narrowleaf silkgrass	*Pityopsis graminifolia* (Michx.) Nutt.		×			
	one-flower bedstraw	*Galium uniflorum* Michx.			×		×
	open-flower witchgrass	*Dichanthelium laxiflorum* (Lam.) Gould		×			×
	pale lobelia	*Lobelia appendiculata* A. DC.				×	×
	panicled-leaf ticktrefoil	*Desmodium paniculatum* (L.) DC.		×			×
	pigeonwings	*Clitoria mariana* L.		×	×	×	×
	pincushion moss	*Leucobryum glaucum* (Hedw.) Angstr.		×			
	purple crownvetch	*Securigera varia* (L.) Lassen			×		
	purplestem beggarticks	*Bidens connata* Muhl. ex Willd.		×			
	roundleaf thoroughwort	*Eupatorium rotundifolium* L.		×	×	×	×
	round-fruited rosette-panic grass	*Dichanthelium sphaerocarpon* (Elliott) Gould		×			×
	round-leaved trailing tick-trefoil	*Desmodium rotundifolium* Desv.		×			×
	sensitive partridge pea	*Chamaecrista nictitans* (L.) Moench		×	×	×	
	slender bush clover	*Lespedeza virginica* (L.) Britton		×			
	slender goldenrod	*Solidago erecta* Banks ex Pursh		×			
	slender three-seeded mercury	*Acalypha gracilens* A. Gray		×			
	slender yellow woodsorrel	*Oxalis dillenii* Jacq.		×			
	small-leaved white snakeroot	*Ageratina aromatica* (L.) Spach			×	×	×
	small white aster	*Symphyotrichum racemosum* (Elliott) G.L. Nesom				×	
	small woodland sunflower	*Helianthus microcephalus* Torr. & Gray		×		×	
	smooth yellow false foxglove	*Aureolaria flava* (L.) Farw.				×	
	southern dawnflower	*Stylisma humistrata* (Walter) Chapm.				×	
	spiked hoarypea	*Tephrosia spicata* (Walter) Torr. & A. Gray			×		
	spurge nettle	*Cnidoscolus stimulosus* (Michx.) Engelm. & Gray				×	
	St. Andrew's cross	*Hypericum hypericoides* (L.) Crantz			×		
	stiff-hair sunflower	*Helianthus hirsutus* Raf.				×	
	sugarcane plumegrass	*Erianthus giganteus* Michx.		×			
	sweet goldenrod	*Solidago odora* Aiton		×	×	×	×
	tall tick-trefoil	*Desmodium glabellum* (Michx.) DC.		×			

Table 2. *Cont.*

Plant Groups	Common Names	Latin Names	C	E	L	M	ST
Grasses, ferns and others	toothed white-topped aster	*Sericocarpus asteroids* Nees		×			×
	trailing lespedeza	*Lespedeza procumbens* Michx.		×	×	×	×
	variable witchgrass	*Dichanthelium commutatum* (Schult.) Gould		×	×	×	×
	velvetleaf ticktrefoil	*Desmodium viridiflorum* (L.) DC.			×	×	×
	velvet panicum	*Dichanthelium scoparium* (Lam.) Gould				×	
	violet bush clover	*Lespedeza violacea* (L.) Pers.		×		×	
	white boneset	*Eupatorium album* L.			×		
	whiteleaf mountainmint	*Pycnanthemum albescens* Michx.			×		
	woolly beardgrass	*Erianthus alopecuroides* Michx.		×			
	yellow crownbeard	*Verbesina occidentalis* L. (Walter)		×			

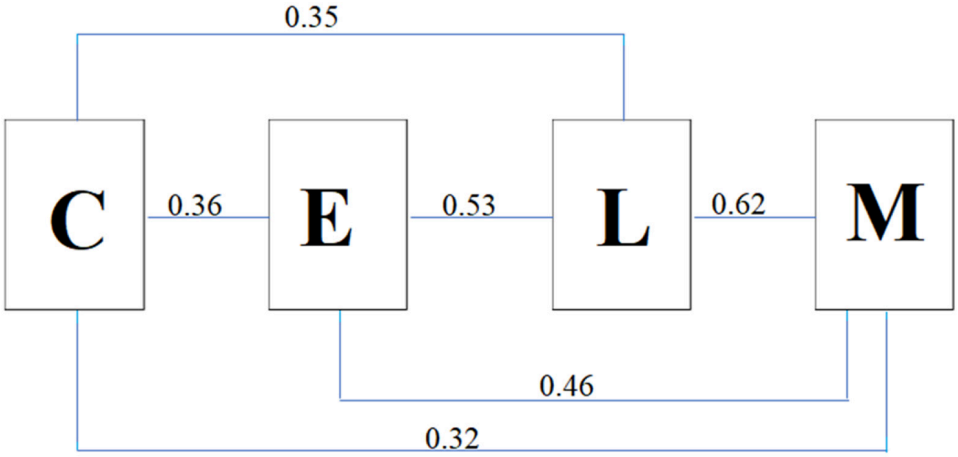


Figure 3. Comparison of the similarity index of understory plant species between any two categories (connected by a solid line) among stages of restored longleaf pine forests and Control sites in Bankhead National Forest (C: Control, E: Early stage, L: Late stage, M: Mature stage).

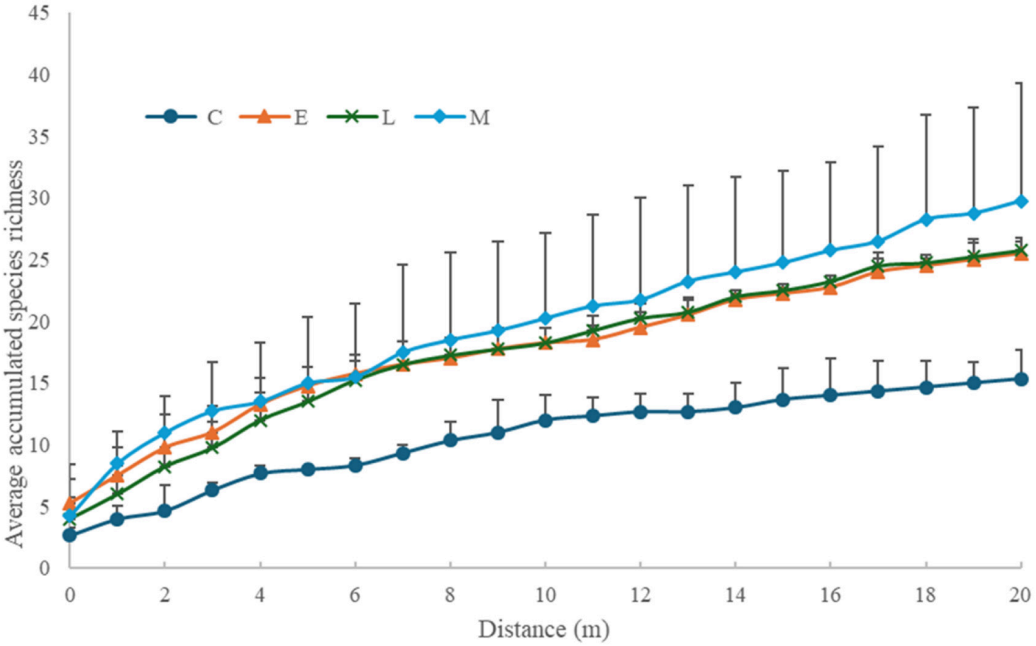


Figure 4. The average accumulated species richness changed with distance at three stages of restored longleaf pine forests and Control sites in Bankhead National Forest (C: Control, E: Early stage, L: Late stage, M: Mature stage. Error bars represent standard deviations).

3.3. Forest Structure Among Categories

Control sites had a higher average tree abundance and fractal dimension (Table 3). In the longleaf pine forest, tree abundance and fractal dimension decreased with succession, while total crown area, total crown volume, average height, average DBH, average canopy base height and gap fraction increased. Multi-dimensional distances in DBH, height and canopy diameter were relatively high in longleaf pine stands at the Late stage. Mature longleaf pine stands also appeared to have a greater total crown area and volume than Control sites.

Table 3. Comparison of average forest stand structure in restored longleaf pine forest stands at three stages and Control sites in the Bankhead National Forest (numbers in parentheses are standard deviations; plot size: 40 m × 40 m; n = 3).

Indices	Control	Early Stage	Late Stage	Mature Stage
Tree abundance	324 (±39)	179 (±54)	193 (±23)	38 (±35)
Total crown area (m^2)	7292 (±943)	2264 (±675)	4014 (±64)	16,580 (±19,850)
Total crown volume (m^3)	24,505 (±945)	7607 (±1472)	14,639 (±7896)	46,572 (±643,864)
Crown diameter (m)	4.4 (±3.8)	4.0 (±0.5)	6.0 (±2.2)	6.8 (±3.2)
Tree height (m)	6.5 (±3.4)	6.8 (±2.3)	12.7 (±0.9)	15.6 (±5.9)
DBH (cm)	12.5 (±6.5)	9.8 (±2.7)	18.9 (±3.9)	37.5 (±23.7)
CBH * (m)	3.5 (±3.4)	2.6 (±0.5)	5.6 (±1.3)	11.4 (±7.5)
Basal area (m^2ha^{-1})	54.4 (±7.5)	10.6 (±2.5)	40.1 (±2.4)	20.7 (±1.9)
FD *	2.1 (±0.1)	1.9 (±0.1)	1.9 (±0.1)	1.6 (±0.3)
ADDBH * (m)	15.2 (±3.4)	12.8 (±1.2)	19.8 (±7.1)	19.0 (±4.7)
ADTH * (m)	17	15.0 (±2.4)	25.1 (±6.0)	26.3 (±7.1)
ADCD * (m)	12.9 (±1.1)	10.9 (±0.9)	17.2 (±6.6)	12.6 (±0.4)
Gap fraction (%)	2.8 (±4.1)	31 (±20)	4.3 (±5.0)	54 (±40)
Gini index	0.15 (0.1)	0.23 (±0.08)	0.43 (±0.04)	0.17 (±1.0)

* CBH: Canopy base height, FD: Fractal dimension, ADDBH: average distance on DBH, ADTH: Average distance on tree height, ADCD: Average distance on canopy diameter.

3.4. Relationship Between Forest Structure and Understory Plant Species Richness

The correlations between understory plant species richness and average stand tree height, average DBH, gap fraction and multi-dimensional distance were not statistically significant. However, understory plant species richness was significantly correlated with total crown area and basal area (Figure 5a,b).

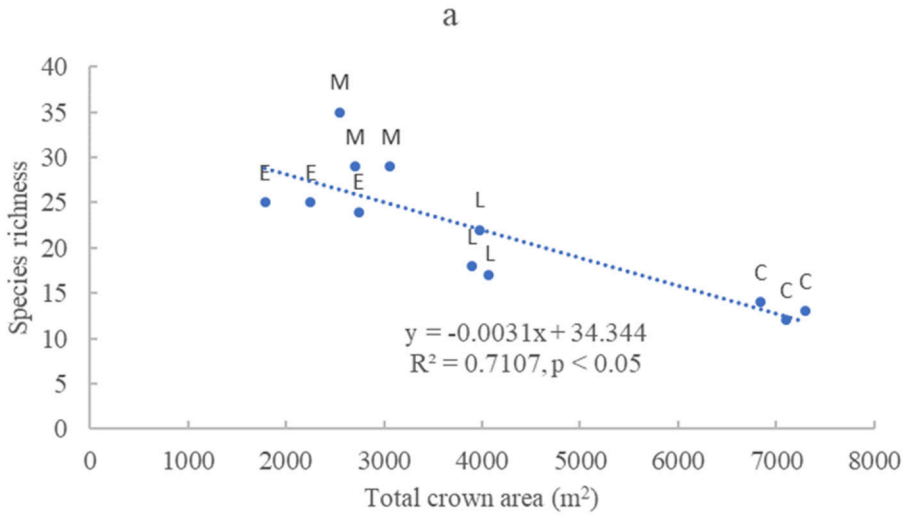


Figure 5. *Cont.*

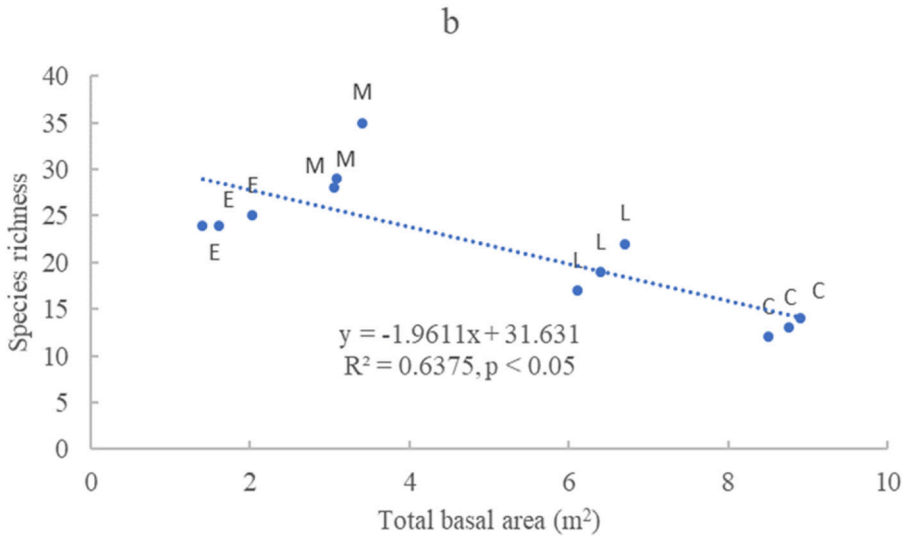


Figure 5. The correlation between (**a**) total crown area or (**b**) total basal area in plots (40 m × 40 m) and species richness across three stages of restored longleaf pine forests and Control sites in Bankhead National Forest (C: Control, E: Early stage, L: Late stage, M: Mature stage; n = 3).

4. Discussion

Approximately 127 species were identified across four categories, which is more than the 100 species reported in frequently burned montane longleaf pine [15,18]. However, this covers only half the number reported for the coastal longleaf pine forest [64], where some forests can achieve 50 species per square meter [64,65]. Although the montane longleaf pine forest typically forms an overstory monoculture due to planting and burning, its understory plant species richness is approximately twice that of local mixed pine- hardwood forests (Control sites). This holds true despite our use of the line-intercept survey method, which may miss some species. Therefore, restoring montane longleaf pine in this region could increase plant species richness at the plot level. The restoration and conservation of longleaf pine ecosystems are crucial for maintaining high levels of endemic species in this global biodiversity hotspot [20].

Although the exact mechanisms remain unclear, frequent prescribed fire is the primary driver of high understory plant species richness in longleaf pine stands [28]. Variation in fire intensity, related to fuel types [66], is considered an important driver of high plant species diversity [67–69]. The combination of fuel and fire intensity contributes to understory plant species richness [70]. Burning can help release long-dormant seed banks by reducing the litter layer [66]. Prescribed fires can also reduce fuel accumulation, release nutrients, enhance aeration and increase heterogeneity in the soil environment. For example, while the average species richness was similar in the Early and Late stages, the similarity index for the understory plant communities was only 0.53, indicating a substantial difference in species composition. However, biological sources, such as seeds, must be dispersed from the surrounding environment by wind, water flow, or animal movement. Frequent prescribed burning allows only fire-resilient species to persist in the longleaf pine forest. Further investigation into these ecological mechanisms is needed.

The dynamics of understory plant species richness in longleaf pine forest stands did not align with the reported U-shaped pattern. This discrepancy might be partly attributed to seed bank and dispersal limitations in some plants [28]. High plant species richness was observed in the early stage, as abundant light from open canopies likely created favorable conditions for light-demanding species, enabling them to quickly exploit resources [71]. As succession progresses and longleaf pine trees grow, their canopies close, limiting sunlight

on the forest floor. Subsequently, the richness of shade-tolerant species may increase in the late stage. With logging, harvesting, or mortality at the mature stage, forest canopies reopen, leading to an increase in plant species richness due to the coexistence of both shade-tolerant and light-demanding species [29]. In this context, the percentage of shade-tolerant species increased slightly from the Early (51%) to the Late (60%) and Mature (62%) stages. Montane longleaf pine forests provide an environment conducive to the coexistence of both shade-tolerant and shade-intolerant species. Some plant species (or families) may serve as environmental indicators [72], such as shade-tolerant species (e.g., ferns) or shade-intolerant species (e.g., horseweed). The greater number of plant species accumulated with increasing distance could indicate spatial heterogeneity in dispersal and environmental conditions. Longleaf pine forests at different successional stages might exhibit more heterogeneous environments than those at the Control sites, providing suitable habitats for shrubs and grasses. The natural openness at the Mature stage facilitates the coexistence of shade-tolerant and shade-intolerant species.

The forest structure differed markedly between the mixed pine–hardwood forest and the montane longleaf pine forest. The mixed pine–hardwood forest exhibited higher tree density, greater basal area, and higher fractal dimension, but a lower Gini index for DBH. Conversely, in the montane longleaf pine forest, the average canopy base height increased with succession, likely due to thermo thinning from frequent prescribed fire [73]. Multiple forest structure indices in this study efficiently characterized distinct aspects of forest structure, particularly across different successional stages. Variations in forest structure can influence understory plant species by altering resource availability and spatial heterogeneity [46,74]. Among various forest indices, understory plant species richness in the montane longleaf pine forest was negatively correlated with total crown area and basal area at the plot level. Since both total crown area and basal area were related to leaf area and tree density, this suggests that understory plant species may be associated with sunlight conditions (e.g., intensity, duration) at the plot level. Maintaining suitable total crown area and tree basal area through logging may therefore stimulate the growth of shrubs and grasses in the montane longleaf pine forest. The lower understory plant species richness at the plot level in the mixed pine–hardwood forest may be linked to light conditions and soil resources. Consequently, logging or partial harvesting could potentially improve its plant species richness. Less sunlight penetrates a mature oak tree canopy than a pine tree due to species differences in canopy structure and leaf area. In this study, the average intensity of solar radiation, measured every 20 min during August 2024 at the Mature site (M3) and the Control site (C3), was approximately 772 lux and 99 lux, respectively, with the maximum readings of 28,743 lux and 8848 lux (Figure 6). Despite the short measurement period, these data may reflect solar radiation patterns among different categories. Although numerous factors influence understory plant species in forests, in this specific case, limited solar radiation appeared to constrain understory plant growth. High heterogeneity in the understory environment, such as light conditions, can promote high plant species richness by supporting both light-demanding and shade-tolerant species. This may partially explain the increased percentage of shade-tolerant species in the Mature sites. Furthermore, there are high bird species in well-managed, fire-maintained longleaf pine forests compared to commercial timber stands [75]. Some birds can transport seeds over long distances [76], especially for shrub species with berries, which birds may consume. It would be interesting to confirm the relationship between birds and plant species.

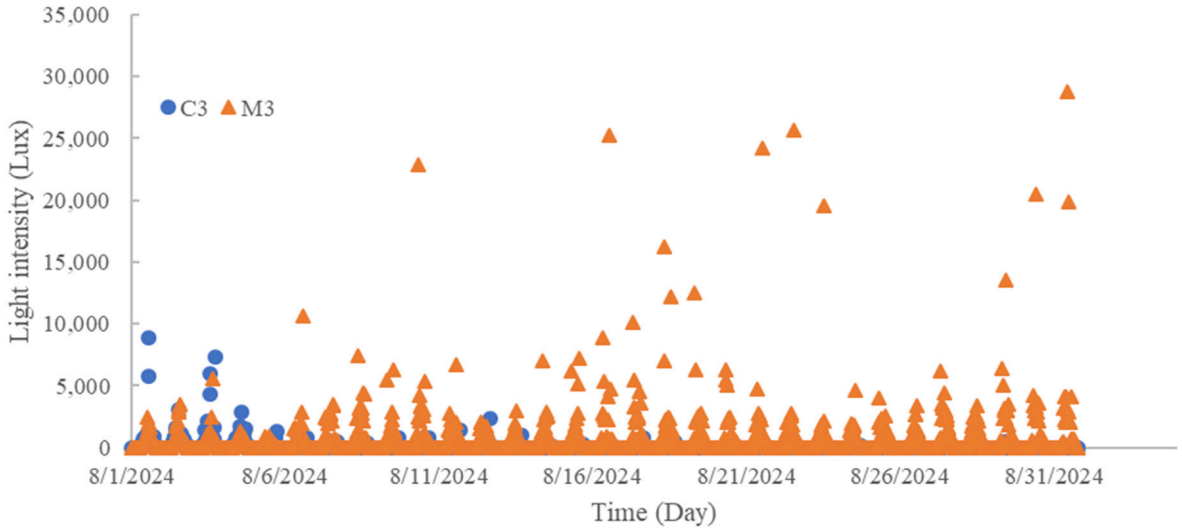


Figure 6. Comparison of solar radiation intensity at a Control site (C3) and a mature longleaf pine stand (M3) in the Bankhead National Forest every twenty minutes during August 2024 (C: Control, M: Mature stage).

This study has several limitations. First, poor trail conditions made it difficult to transport equipment, such as LiDAR, to some sites. Future studies should aim to characterize forest structure at all sites. Second, regarding the methodology for investigating understory plant species, a line-intercept approach was used for efficiency. However, more effort should be made to document and compare understory plant species occurrence using other approaches, such as various-sized squares or circles. Long-term monitoring data, spanning perhaps 10 years of understory plant species, would be beneficial. Third, the study should include more sites with diverse topographic conditions (e.g., slope, aspect). Additionally, if possible, control sites should include both early and late stages of mixed pine–hardwood forest. Furthermore, prescribed burning should be conducted on schedule on each site, though practical delays due to weather conditions and human resources are acknowledged. This study was conducted over a short period under average conditions.

Our results may have implications for forest management in this region, which has traditionally emphasized timber production. First, longleaf pine forest communities exhibit greater understory plant species richness than mixed pine–hardwood forest communities, even though the function of these understory plants (e.g., shrubs and grasses) is unclear. Second, new quantitative indices (such as those used in this study) could be employed to characterize forest 3D structure using LiDAR and other tools. Both horizontal and vertical dimensions should be considered when managing plants and animals [77], and management decisions should be based on these metrics. Prescribed burning could be used not only to decrease fuel accumulation but also to increase pyro-diversity (difference in fire resistance) and create desirable forest structure. Additionally, if understory plant diversity is a high conservation objective for local foresters [78], then restoring montane longleaf pine forest from mixed pine–hardwood forests should be continued. Although more detailed studies are needed, maintaining spatial and temporal heterogeneity in montane longleaf pine forests, such as total crown area and basal area at the stand level, through logging and prescribed burning may be a practical approach. If both understory plant species and timber production are important, then proper thinning, such as shelterwood cutting [79] and prescribed burning may be introduced to create patches of light and soil resources [80]. The frequency of prescribed burning should be adapted to specific objectives. A spatially explicit, integrated management plan should be developed for multi-objective forest management (e.g., timber, biodiversity, carbon, water). Further research should be

conducted to determine whether longleaf pine forests exhibit greater plant species richness at the landscape level and to elucidate the underlying mechanisms. However, frequent prescribed burning in a region could affect local air and water quality [81].

5. Conclusions

The existence of montane longleaf pine forests necessitates specific management practices such as harvesting, prescribed burning and thinning. Restoring the longleaf pine ecosystem from mixed pine–hardwood forests can enhance local understory plant species richness in Bankhead National Forest, even in areas where longleaf pine trees dominate the overstory. Both the percentage of shade-tolerant species and the similarity index of understory plant species increased with the succession of montane longleaf pine forest (Early, Late and Mature stages), though each stage harbored unique species. The average accumulated number of plant species increased faster with distance in montane longleaf pine forests than in mixed pine–hardwood forests. More research sites are needed to comprehensively study understory plant species across the historical range of the montane longleaf pine forest, particularly to understand their function and role within these ecosystems. Forest structure, specifically its three-dimensional composition, can influence understory plant species. In this study, understory plant species richness showed a significantly negative correlation with total crown area and basal area at the plot level. High understory plant species richness in montane longleaf pine forests may be underpinned by mechanisms such as local heterogeneity of sunlight distribution across different forest structures. However, the large-scale implementation of montane longleaf pine restoration in mixed pine–hardwood forests requires further consideration from various perspectives, including timber production, biodiversity conservation, and watershed protection. Future research should focus on montane longleaf pine forests, prescribed burning and landscape-level species richness to clarify the underlying ecological processes.

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