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REVIEW

Shortleaf Pine (*Pinus echinata*): Management Challenges, Knowledge Gaps, and Opportunities for an Unsung Species

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Abstract

Shortleaf pine has the broadest range of the southern pine species, occurring in 22 states and extending north into New Jersey, Pennsylvania, and New York (Staten Island). Shortleaf pine has been understudied compared to loblolly pine and longleaf pine, typically favored for timber production and conservation value, respectively. The extensive range of shortleaf pine contributes to a high degree of variability within and among its ecosystems and contributes to the need to understand regional context in considering its ecology and management. The goal of this paper is to review and synthesize the state-of-knowledge on shortleaf pine ecosystems, emphasizing the importance of variation across its range in identifying management challenges and opportunities. We discuss the variation in growing conditions that occur across the geographic range, shortleaf pine natural community groups, and contemporary shortleaf pine forest types that occur on the landscape. We provide a review of the state-of-knowledge for topics related to shortleaf pine management, including its fire ecology, genetic considerations, economics, and others. Finally, we synthesize these into key considerations and highlight regionally specific management challenges and opportunities.

Keywords Conservation · Ecosystem management · Natural communities · Prescribed fire · Southern pine

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Introduction

Shortleaf pine (*Pinus echinata* Mill.) occurs across a large geographic extent encompassing broad variation in environmental conditions and associated plant species within the United States (US). Its native range is commonly referenced as covering 22 states (Little 1971; Lawson 1990), although some sources have noted it in 23 (Mohr and Roth 1987), from New York to Florida, west to Texas and Missouri. Shortleaf pine has the most northern extent of the major southern pine species (subsection Australes), and its large geographic range has notable variation in climate, topo-edaphic conditions, species associations, and disturbance patterns. Historically, shortleaf pine was estimated to occur as the dominant pine species in pure pine or mixed pine-oak (*Quercus* spp.) stands across 28.3 to 32.4 million ha (Anderson et al. 2016; Guldin 2019). In 2010, shortleaf pine remained on only 2.5 million ha (Oswalt 2012) in the 'shortleaf pine' and 'shortleaf pine-oak' forest types (those dominated by shortleaf pine) according to the USDA Forest Service Forest Inventory and Analysis (FIA). Since then, these shortleaf pine-dominated forest types have further reduced to current estimates of 2.3 million ha, an approximately 92% reduction in its former extent (FIA EVALIDATOR data, accessed March 1, 2025). Similar to other fire-adapted pines, the reduction in shortleaf pine abundance and extent is associated with legacies of timber exploitation, land conversion, and fire exclusion.

However, shortleaf pine remains widespread across the eastern US; in 2010, at least one shortleaf pine tree was present on 10% of FIA plots across the 22 state range (Oswalt 2012), usually occurring at low relative abundance and in mixture with other species (Fig. 1). Moser et al. (2007) reported that 59.9% of all shortleaf pine trees occurred within the 'shortleaf pine' and 'shortleaf pine-oak' forest type

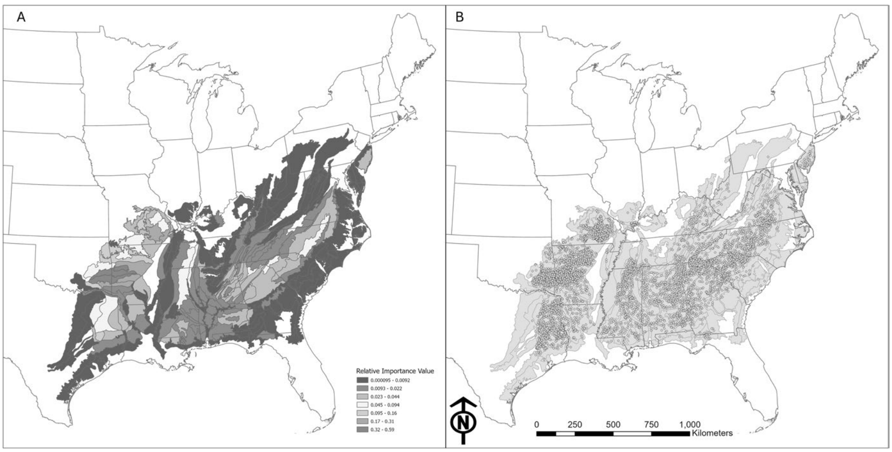

Fig. 1 **A** Relative importance value of shortleaf pine throughout its range (Little 1971). Mapping units are ecological subsections. Relative importance is calculated as a sum of the relative proportion (number of trees) and relative dominance (basal area) of overstory (≥ 12.7 cm DBH) shortleaf pine using Forest Inventory and Analysis (FIA) data. **B** Approximate locations of FIA plots with at least one shortleaf pine tree present, with ecological subsections in the background

classifications of FIA, while 17.3% occurred within the ‘loblolly pine’ (*Pinus taeda* L.) forest type and the remainder occurred across other forest types. Current FIA estimates show similar patterns, with 64.5% of all shortleaf pine trees > 2.54 cm diameter at breast height (DBH) occurring within ‘shortleaf pine’ and ‘shortleaf pine-oak’ forest types, while 16.8% of shortleaf pine trees occur within the ‘loblolly pine’ forest type (Supplemental Table 1). Shortleaf pine currently occurs across an additional 42 FIA forest types. Areas with shortleaf pine occurring in low abundance in other forest types likely represent, in part, the broader historical extent of shortleaf pine-dominated ecosystems.

Shortleaf pine has received less attention from both scientists and managers than other southern pines (Fig. 2) and associated hardwood species. Although the specific gravity and wood quality of shortleaf pine are high, timber production is dominated by loblolly pine in the southeastern region (Schultz 1999; Bragg 2016) and by oaks and other hardwood species in the Central Hardwoods region (Luppold and Bumgardner 2018). Management for conservation objectives and restoration of frequent-fire ecosystems have focused for the last few decades on longleaf pine (*P. palustris* Mill.), although more recent efforts have been directed to similar restoration and conservation goals in shortleaf pine ecosystems (e.g., Anderson et al. 2016; Guldin 2019; Bragg et al. 2020). More attention on shortleaf pine provides potential opportunities for expanding management objectives and targets across the eastern US, yet

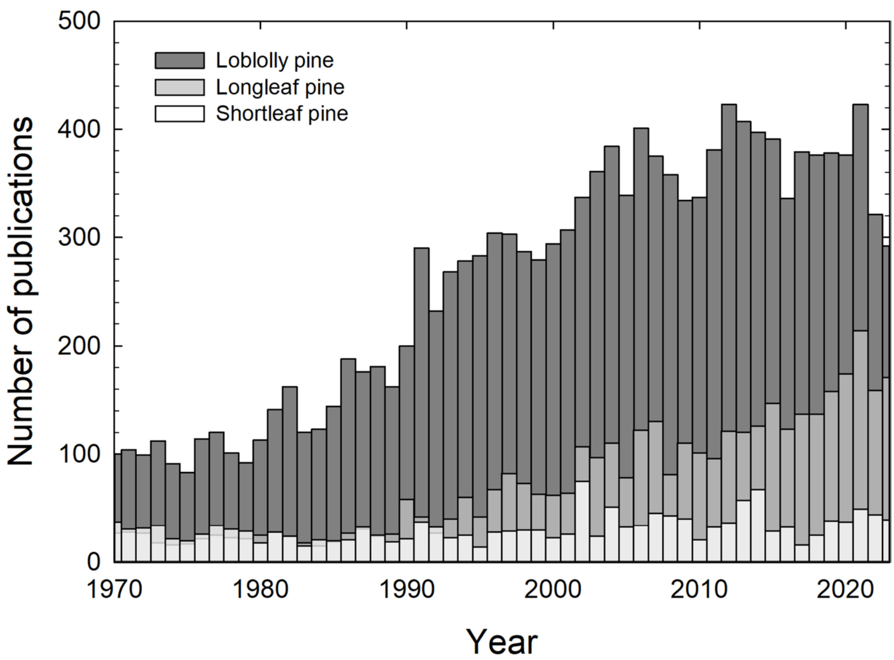

Fig. 2 Number of publications discovered through Web of Science search for loblolly pine, longleaf pine, and shortleaf pine since 1970. Search criteria included all databases within Web of Science and the search terms “common name OR Latin name” for each of the species (results from web access February 4, 2025)

there remain many challenges to realizing actionable shifts in management focus toward shortleaf pine ecosystems across its range.

The goal of this review and synthesis is to evaluate the state-of-knowledge on shortleaf pine ecosystems, highlighting opportunities to expand shortleaf pine management, describing major challenges impeding management progress, and identifying knowledge gaps requiring further research. We consider shortleaf pine ecosystems to include not only the 'shortleaf pine' and 'shortleaf pine-oak' forest types of FIA, which represent current shortleaf pine dominance, but more generally to extend throughout the shortleaf pine range and consider areas where shortleaf pine has likely declined from historical abundance. Throughout, we consider the variability associated with shortleaf pine ecosystems to be an important theme for understanding and attempting to generalize shortleaf pine ecosystems and management needs. Toward that end, our first objective is to describe the variation in: 1) growing conditions and disturbance regimes within the shortleaf pine range; 2) classification of shortleaf pine natural communities; and 3) types of shortleaf pine stands (structure and composition) that are common across the contemporary landscape. Our second objective is to describe important considerations that affect shortleaf pine management across the range. Finally, our third objective is to synthesize these into action-oriented summary points and provide a regional assessment of opportunities and challenges relevant to the scientific and management communities. This paper brings attention to a species often underappreciated despite its common occurrence, highlighting management uncertainties and research priorities needed to fill gaps in our understanding of shortleaf pine ecosystems.

Objective 1: Variation Across Shortleaf Pine Ecosystems

Diverse Environments

Shortleaf pine occurs across a broad range of growing conditions (Fig. 3). Across its range, mean annual temperature ranges from 6.8 °C in West Virginia to 21.4 °C in Texas, with an overall mean of 15.9 °C (Fig. 3A). The coolest portion of the range is generally the central and southern Appalachian Mountains in West Virginia, Virginia, and North Carolina, where shortleaf pine abundance is relatively low. Mean annual precipitation ranges from 890 mm in western West Virginia to 2491 mm at high elevations along the border between Tennessee and North Carolina, with a mean of 1334 mm (Fig. 3B). Although shortleaf pine can occur across a variety of soil conditions, its native range generally aligns with spatial patterns of soil acidity (Fig. 3C) and soil drainage class (Fig. 3D). Its best growth occurs on deep, well-drained soils with loamy or coarse texture (Lawson 1990). However, in natural stands, shortleaf pine is most abundant on dry sites where soils are acidic and relatively infertile, explaining its prominence on dry, rocky soils that limit the occurrence of less stress-tolerant species (Fletcher and McDermott 1957; Lawson 1990). Local variation in soil conditions or topography can affect shortleaf pine abundance, including greater association with higher slope positions and more exposed aspects (Fig. 3E).

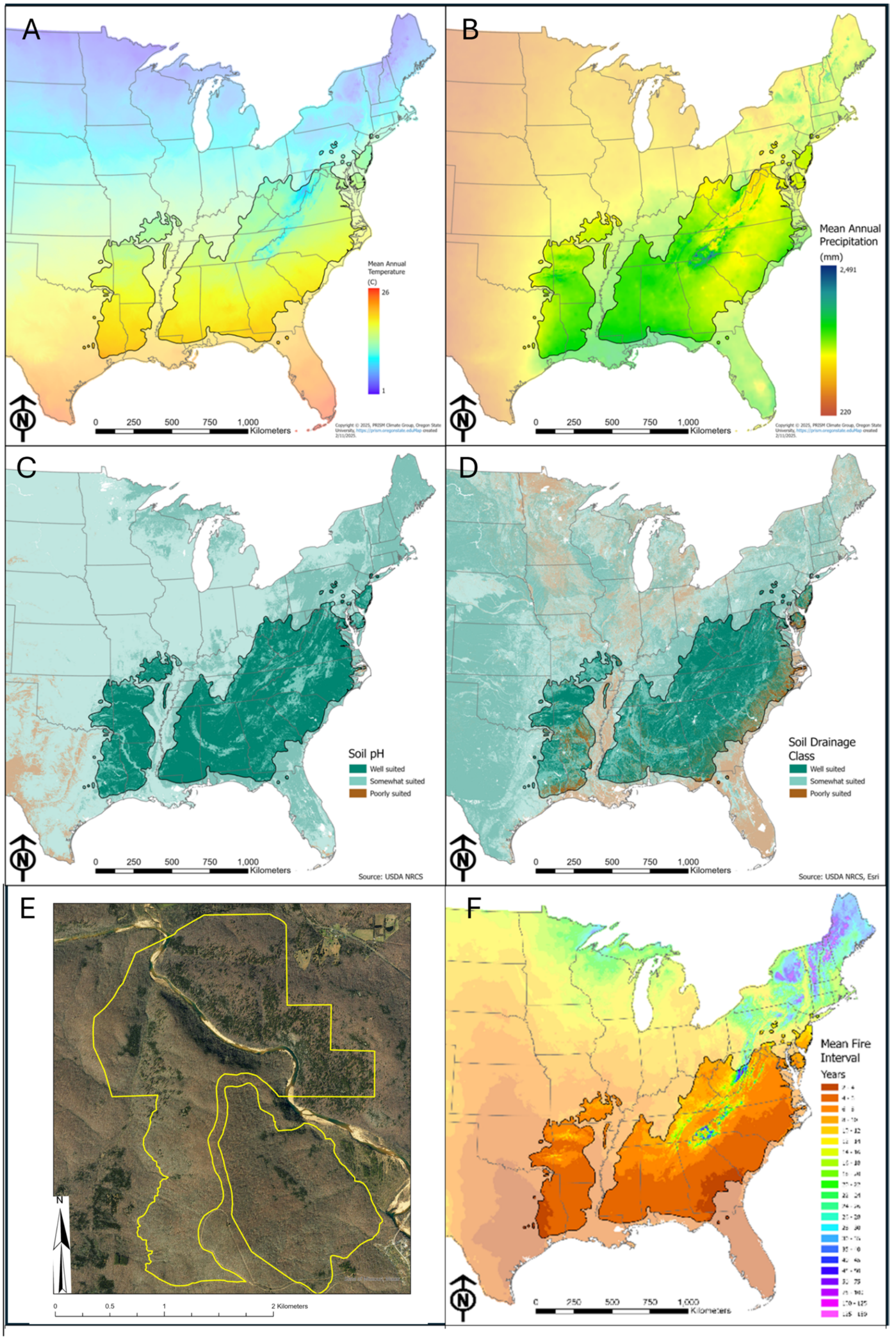

Fig. 3 Spatial variation in growing conditions across the shortleaf pine range, showing: **A** mean annual temperature; **B** mean annual precipitation; **C** soil pH categories; **D** soil drainage class; **F** mean fire return interval from PC2FM model. Panel **E** shows that the distribution of shortleaf pine is partitioned toward exposed slopes (south and west facing) at the old-growth Mudlick Mountain Natural Area (outlined in yellow) in Wayne County, Missouri

Shortleaf pine ecosystems experience a variety of disturbance regimes, with variation in type, frequency, and severity occurring across their range. Disturbance models of frequent-fire, open structured longleaf pine ecosystems have been described as an interplay of canopy disturbance from broad-scale (e.g., hurricane) to local-scale (e.g., lightning, local wind) events and frequent low-intensity surface fire (Gilliam et al. 2006). A similar disturbance model for shortleaf pine would need to encompass a wider range of disturbances. Damage from wind can occur as high-severity, large-extent events such as tornados and derechos, occurring with greater frequency in western and southern portions of the range (Peterson 2000), or as hurricanes with greater impacts in the Coastal Plain regions (Cannon et al. 2023). Intermediate-severity disturbances from wind events or ice damage are important drivers of forest dynamics within the central portion of shortleaf pine's range (Hart and Cox 2017; Goode et al. 2021), where damaging ice storms occur several times per century (Irland 2000; Bragg et al. 2003). Fire is critical to shortleaf pine ecosystems; across the range, frequent fire regimes predominate (Guyette et al. 2012), with greater frequencies in the southern and western portions of the range and lower frequencies in portions of the Appalachians (Fig. 3F). Fire regimes vary in other ways across the range, with shortleaf pine co-occurring with species adapted to intermediate- or high-severity fires (e.g., Table Mountain pine [*P. pungens* Lamb.], pitch pine [*P. rigida* Mill.], Virginia pine [*P. virginiana* Mill.]) as well as low-severity surface fires (e.g., longleaf pine). Likewise, constraints to conducting prescribed burns vary across the region, affecting the operational burn regimes that may be feasible within shortleaf pine ecosystems (Wonkka et al. 2015; Chiodi et al. 2018).

Natural Community Classification

Shortleaf pine is commonly associated with open ecosystems, which are characterized by tree densities lower than site potential based on productivity, canopy openings that provide substantial light transmittance to the floor, absence of a midstory or multi-layer vertical structure, and an understory layer dominated by perennial grasses and forbs or ericaceous shrubs (Dey et al. 2017; Hanberry et al. 2018). Open ecosystems include savannas and woodlands that, with increasing tree density and lack of disturbance, grade to closed-canopy forests. In the eastern US, most open ecosystems are maintained by frequent surface fire, the absence of which results in increased abundance of woody stems that develop into closed-canopy forests and can lead to the loss of shortleaf pine and increases in mesophytic species (Nowacki and Abrams 2008; Hanberry et al. 2014, 2020).

A recent classification based on the US National Vegetation Classification System identifies six shortleaf pine natural community groups (Nordman et al. 2021a; 2021b) (Table 1; Fig. 4A). All six are characterized by relatively open overstory conditions, generally dominated by shortleaf pine or shortleaf pine in mixture with other pine and fire-tolerant hardwood species. Across all the natural community groups, the target basal area of fire-intolerant tree species is low (≤ 2.3 m^2/ha), midstory tree and shrub cover is relatively low, and herbaceous ground cover is moderate to high, although the specific conditions identified as desired targets vary across

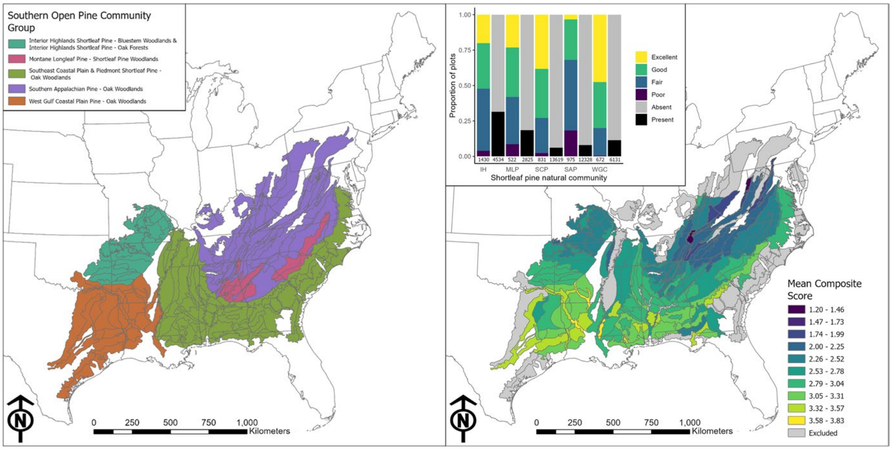

Fig. 4 **A** Shortleaf pine natural community groups as identified in Nordman et al. (2021a) mapped to the ecological subsection classification hierarchy described in Cleland et al. (2007). **B** The mean composite rating of open woodland shortleaf pine overstory metrics applied to Forest Inventory and Analysis (Westfall et al. 2022) plots within ecological subsection. For each inventory plot, overstory metrics that met the criteria of excellent were assigned a numeric score of 4, good were assigned a score of 3, fair were assigned a score of 2, and poor were assigned a score of 1. The mean composite score of each plot was calculated and the mean score for each ecological subsection was calculated from the scores of plots within its boundaries. Ecological subsections that had five or fewer FIA plots with occurrence of shortleaf pine were excluded

the groups (see Supplemental Table 2 for values rated as Excellent for each of these metrics).

We crosswalked the distribution of the six shortleaf pine natural community classifications with the ecological subsections of Cleland et al. (2007) (Fig. 4A; Supplemental Table 3). In the western portion of the range, the Interior Highlands region includes two shortleaf pine natural community groups: the *Interior Highlands Shortleaf Pine-Oak Forests and Woodlands* and the *Interior Highlands Shortleaf Pine-Bluestem (Andropogon spp.; Schizachyrium scoparium (Michx.) Nash) Woodlands*. These two natural community classifications occur within the same geographic region, with differences largely driven by local topo-edaphic conditions and disturbance history. We consider these two natural community groups together in discussing geographic differences across the shortleaf pine range in this paper. The *Montane Longleaf Pine-Shortleaf Pine Woodlands* is the smallest geographic area, overlaying 10 ecological subsections and occurring across dry sites within northern Alabama, Georgia, North Carolina, and South Carolina. The *Southern Appalachian Pine-Oak Woodlands* occupy the eastern and northern portions of the shortleaf pine range, occurring with other pines such as pitch pine, Table Mountain pine, and Virginia pine, often on rugged slopes with south to west aspects and shallow soils. These natural communities commonly have lower abundance of herbaceous vegetation and greater density of ericaceous shrubs. The *Southeastern Coastal Plain and Piedmont Shortleaf Pine-Oak Woodlands* occupy the greatest extent, overlaying 41 ecological subsections that occur east of the Mississippi River. Finally, the *West*

Table 1 Summarized description of open shortleaf pine natural community types, from Nordman et al. (2021a)

	Geographic region	Common topo-edaphic conditions	Overstory species composition	Midstory	Ground layer vegetation
Interior Highlands Shortleaf Pine-Oak Forests and Woodlands	Ozark-Ouachita Highlands (MO, AR, OK)	Dry, dry-mesic, or mesic	*Pinus echinata*; *Quercus* spp.; *Carya* spp.	Tall shrub layer sparse; short shrubs patchy to dense	*Schizachyrium scoparium; Danthonia* spp.*; Chasmanthium* spp.*; Carex pensylvanica; Solidago ulmifolia; Echinacea pallida*
Interior Highlands Shortleaf Pine-Bluestem Woodlands	Ozark-Ouachita Highlands (MO, AR, OK)	Dry or dry-mesic; ridgetops	*Pinus echinata*; *Quercus* spp.; *Carya* spp.	Tall shrubs mostly absent; short shrub layer very open	*Andropogon gerardii; Schizachyrium scoparium;* mixture of graminoids, legumes, and other forbs
Montane Longleaf Pine-Shortleaf Pine Woodlands	Appalachian/Piedmont (AL, GA, NC, SC)	Dry sites and ridges	*Pinus echinata; Pinus palustris; Quercus* spp.; *Carya* spp.	Tall shrub layer open or absent; short shrub layer open	*Andropogon gyrans*; *Andropogon ternarius*; *Andropogon gerardii*; *Schizachyrium scoparium*; *Danthonia* spp.; *Sorghastrum nutans*; *Coreopsis major*; *Desmodium* spp.; *Lespedeza* spp.
Southeastern Coastal Plain and Piedmont Shortleaf Pine-Oak Woodlands	Southeastern Coastal Plain (east of Mississippi River; MS, TN, AL, GA, SC, NC, VA)	Upland sites	*Pinus echinata*; *Quercus* spp.; *Carya* spp.; *Acer rubrum; Oxydendrum arboreum; Ostrya virginiana*	Tall shrub layer is open; short shrub layer is open	Graminoid cover can range from open to dense; *Piptochaetium avenaceum*; *Danthonia spicata*; *Chasmanthium* spp.; *Dichanthelium sphaerocarpon*; *Schizachyrium scoparium*

Table 1 (continued)

	Geographic region	Common topo-edaphic conditions	Overstory species composition	Midstory	Ground layer vegetation
Southern Appalachian Pine-Oak Woodlands	Southern Appalachian Mountains/Cumberland Mountains (AL, GA, NC, TN, KY, WV, VA, NJ, PA)	Steep slopes and ridges; dry sites with short-statured trees	*Pinus echinata*; *Pinus rigida*; *Pinus pungens*; *Quercus* spp.	Tall shrub layer open; shrub layer can be dense with heath species	Sparse herbaceous cover mixed with Ericaceae shrubs
West Gulf Coastal Plain Shortleaf Pine-Oak Woodlands	West Gulf Coastal Plain (AR, LA, TX)	Upland sites	*Pinus echinata*; *Pinus taeda*; *Quercus* spp.; *Carya* spp.; *Cratageus* spp.; *Ostrya virginiana*	Tall shrub layer is open; short shrub layer is open	Graminoid cover can range from open to dense; *Chasmanthium* spp.; *Dichanthelium sphaerocarpon*; *Schizachyrium scoparium*

Gulf Coastal Plain Shortleaf Pine-Oak Woodlands occurs west of the Mississippi River, from southern Arkansas and Oklahoma through east and southeast Texas. In these communities, shortleaf pine may be co-dominant with loblolly pine, longleaf pine, or both, and the herbaceous layer is comprised of a mixture of warm season and cool season grasses as well as shrubs such as American beautyberry (*Callicarpa americana* L.). The classification system does not address the Outer Coastal Plain of southern New Jersey (e.g., the Pine Barrens region), where shortleaf pine is also abundant (see Figs. 1 and 4). This region has relatively flat topography, with soils derived from deep, unconsolidated marine deposits and with pitch pine as a common dominant species.

Contemporary Shortleaf Pine Forest Types

The target conditions of the natural community groups can generally be described as open ecosystems (relatively low stand density, open midstory) composed of shortleaf pine either as the dominant species or in mixture with other pines or fire-tolerant hardwoods such as oaks (Supplemental Table 2). However, the conditions of contemporary shortleaf pine stands commonly diverge from the desired conditions of the natural communities. We used FIA data to assess the overstory condition of all plots with at least one shortleaf pine tree (> 2.54 cm DBH), according to the rating system of Nordman et al. (2021a). The two natural communities in the Interior Highlands were combined for the analyses, using criteria for the Interior Highlands Shortleaf Pine-Oak Forests and Woodlands for our analysis. We rated each canopy metric and averaged them to calculate a composite score for each FIA plot, with a greater score indicating greater similarity to the natural community target metrics. We then summarized statistics of all FIA plots within an ecological subsection or shortleaf pine natural community group. The analysis was based on only the canopy metrics (see Supplemental Table 2 for definitions of Excellent ratings for each metric), because data were not available through FIA to assess the midstory or ground cover metrics. Data were summarized only for ecological subsections with at least five FIA plots in which shortleaf pine occurs. Consequently, the assessment is useful for considering general overstory structure and composition for areas where shortleaf pine occurs but does not provide a full assessment of the condition of these ecosystems. This is especially relevant given the critical importance of the midstory and understory in defining open woodland ecosystems (Bragg et al. 2020).

The West Gulf Coastal Plain group had the highest composite mean score from the assessment of overstory metrics, followed by the Southeastern Coastal Plain and Piedmont group (Table 2; Fig. 4B). Both community groups scored well for the ‘fire-tolerant hardwood basal area’ metric and had the lowest assessment scores for the ‘southern yellow pine basal area’ and ‘southern yellow pine stand size structure’ metrics (Table 2). The Interior Highlands and Montane Longleaf Pine-Shortleaf Pine groups had similar mean composite scores (Table 2). The Interior Highlands group scored well for the ‘fire-intolerant hardwood basal area’ category, reflecting the lower abundance of mesic competitors within this region. Similar to the West Gulf Coastal Plain and Southeastern Coastal Plain groups, the Interior Highlands

Table 2 Mean condition scores for each overstory metric and open pine natural community group

	Interior Highlands Shortleaf Pine-Oak Forests and Woodlands $n=1430$	Montane Longleaf Pine-Shortleaf Pine Woodlands $n=522$	Southeastern Coastal Plain and Piedmont Shortleaf Pine-Oak Woodlands $n=847$	Southern Appalachian Pine-Oak Woodlands $n=990$	West Gulf Coastal Plain Shortleaf Pine-Oak Woodlands $n=698$
Southern Yellow Pine Basal Area	2.30	2.44	2.87	1.80	2.90
Southern Yellow Pine Canopy Cover	3.02	2.72	3.01	2.77	3.06
Southern Yellow Pine Stand Size Structure	2.29	2.44	2.63	1.81	2.88
Fire-Tolerant Hardwood Basal Area	2.38	3.25	3.36	2.72	3.53
Fire-Intolerant Tree Basal Area	3.71	2.66	2.98	2.13	3.41
Stand Density Index	2.37	2.64	2.97	N/A	3.06
Mean	2.68	2.69	2.97	2.25	3.14

For each inventory plot (n = number of FIA plots per natural community group), scores were assigned based on meeting criteria for each metric rating (1 = poor, 2 = fair, 3 = good, 4 = excellent) and the Montane Longleaf Pine-Shortleaf Pine groups scored low for 'southern yellow pine basal area' and 'southern yellow pine stand size structure', indicating stands of high density but with a lack of large pines. The Southern Appalachian group had the lowest mean composite score among the natural community groups, with 50% of plots with mean composite scores rated as 'fair' (between 1.75 and 2.5) and 18% with a mean composite score rated as 'poor' (< 1.75) (Fig. 4B). These results suggest challenges with attaining the desired density of pine, a lack of large pines, and high density of fire-intolerant hardwood species in the Southern Appalachian region (Table 2).

The results of the FIA assessment reflect the variety of structures and compositions in which shortleaf pine ecosystems occur across the contemporary landscape. Throughout the shortleaf pine range, historical fire frequencies aligned with anthropogenic events that included periods of frequent fire before the fire exclusion policies of the early 1900s (Guyette et al. 2002; Stambaugh et al. 2018, 2020; Flatley et al. 2023), a consequence of which has been increased density of forests over the past century (Hanberry et al. 2014). Recent efforts to restore open pine ecosystems or to establish new shortleaf pine stands, in combination with historical legacy conditions of shortleaf pine across the landscape, have resulted in some common forest types based on similarities in composition and structure. Compositionally, shortleaf pine may occur in pure stands (either pure shortleaf pine stands, as in portions of its range that lack other native pine species [e.g., Missouri], or within pure pine stands that include other pine species) or in mixture with hardwood species, also referred to as mixedwoods. Pure stands differ from mixedwoods in their ecology and in their management challenges, with mixedwoods having greater complexity due to the contrasting silvics of the co-occurring species (Kabrick et al. 2017; Kenefic et al. 2021). Structurally, the desired conditions of shortleaf pine ecosystems are those characteristic of woodlands (Guldin 2019; Bragg et al. 2020; Nordman et al. 2021b), although the current condition of many shortleaf pine ecosystems more closely resembles fully stocked, closed-canopy forests.

These compositional and structural conditions result in four contemporary shortleaf pine forest types (Fig. 5). In *pure pine forests and woodlands* (Fig. 5A), shortleaf pine may occur as the canopy dominant or mixed with other southern pines. This forest type is associated with open structure and diverse herbaceous understory composition, although variable across the range. Prescribed fire is critical for sustaining this forest type, although the appropriate fire regime may also vary across the range. Similar in its open structure, the *shortleaf pine-oak mixed woodlands* (Fig. 5B) forest type also requires frequent surface fire but has the additional complexity of managing mixedwood composition, deliberately maintaining species that have different life histories and fire adaptations. While these two forest types most closely represent the target conditions for the shortleaf pine natural community groups, contemporary stands commonly diverge from these conditions. Across much of the range, land use legacies that include fire exclusion have resulted in *mature shortleaf pine-hardwood mixedwood forests* (Fig. 5C). This forest type often occurs on sites that historically had greater proportions of shortleaf pine but experienced compositional changes due to timber extraction followed by shortleaf pine regeneration

Fig. 5 Examples of common shortleaf pine forest types, based on composition and structure. **A** pure pine forests and woodlands; Mark Twain National Forest, Missouri; **B** shortleaf pine-oak mixed woodlands; Boggy Slough Conservation Area, Texas; **C** mature shortleaf pine-hardwood mixedwood forest; Big Spring Conservation Area, Missouri; **D** three-year-old planted shortleaf pine on cutover site, Putnam County, Georgia. Photo credit: Ben Knapp (panels A-C), David Clabo (panel D)

failures associated with fire exclusion (Stambaugh et al. 2020). In these forests, shortleaf pine trees may be of an older cohort than associated hardwoods, and shortleaf pine regeneration remains challenging; the persistence of this forest type on the contemporary landscape is largely due to retention of existing mature shortleaf pine rather than replacement through regeneration. This condition is likely common on many of the FIA forest types in which shortleaf pine is not a dominant species (Supplemental Table 1). Without management, this forest type is transitional to hardwood forests. Finally, *planted shortleaf pine forests* (Fig. 5D) often represent more recently established shortleaf pine stands. These stands are commonly established for conservation or restoration goals and may also meet timber production objectives. These stands differ from the others in their stage of stand development and offer opportunities for intermediate silvicultural treatments to create alternative trajectories (e.g., Puhlick et al. 2024) depending on management goals. However, planted stands made up a low percentage of the extent of FIA forest types 'shortleaf pine' (10%) and 'shortleaf pine-oak' (2%) in 2010 that, combined with a lack of small diameter shortleaf pine across the landscape, suggests long-term sustainability issues associated with an aging resource (Oswalt 2012).

Objective 2: Management Considerations and Knowledge Gaps

We provide an overview of the state-of-knowledge of important topics for shortleaf pine ecosystem management. While these topics are not exhaustive, they highlight important contemporary considerations relevant to shortleaf pine management and identify knowledge gaps that warrant research attention.

Ecosystem Services

The recognition and management priority given to shortleaf pine for its contribution to ecosystem services vary across its range. Shortleaf pine ecosystems provide benefits associated with open ecosystems, such as high diversity of understory vegetation (e.g., Hanberry et al. 2020) and habitat for wildlife species (e.g., Reidy et al. 2014; Starbuck et al. 2015). In the southeastern Coastal Plain, conservation action has focused mostly on longleaf pine for conserving open ecosystems (Landers et al. 1995; Mitchell et al. 2006; Kirkman and Jack 2017), with shortleaf pine described as functionally similar and not commonly prioritized (Willis et al. 2024a). In other ecoregions, however, shortleaf pine is the only occurring pine species (e.g., Missouri) or co-occurs with other pines (e.g., Table Mountain pine, pitch pine, and Virginia pine) in open stands within a largely closed-canopy deciduous hardwood matrix where there are no functional surrogates (e.g., central and southern Appalachians). In these regions, shortleaf pine fills unique functional roles that have resulted in its prioritization for management of open ecosystems (Pile Knapp et al. 2024). Shortleaf pine also occurs as mixedwood forests throughout much of its range. These forests provide a different suite of ecosystem services and have recently gained increased attention in the region (Kabrick et al. 2017; Willis et al. 2019; Kenefic et al. 2021).

Shortleaf pine plant communities managed with frequent fire contain significant biodiversity, especially in the understory layer. An analysis of vegetation plot data (N = 1371) from shortleaf pine stands indicates that at least 1727 plant species are affiliated with these ecosystems (Palmquist and Saladyga in review). Shortleaf pine vegetation is represented by 53 Associations of the International Vegetation Classification system, 79% of which are ranked as critically imperiled (G1), imperiled (G2) or vulnerable (G3) by NatureServe (USNVC 2025). The compositional and structural variation in plant communities across the shortleaf pine range (Nordman et al. 2021a) creates substantial spatial heterogeneity, which directly influences ecosystem function, fuel properties, and fire behavior (Sparks et al. 1998; Vander Yacht et al. 2019). The feedbacks among vegetation, fuels, and fire behavior have profound effects on overstory-understory dynamics, including shortleaf pine recruitment, herbaceous diversity, and stand structure (South and Harper 2016; Vander Yacht et al.

2019, 2020; Adhikari et al. 2021). These interactions have been more thoroughly studied in other frequent-fire pine species such as longleaf pine (e.g., Dell et al. 2017; Jensen et al. 2025), and more research on this topic specific to shortleaf pine ecosystems is needed.

Although no wildlife species are known to exclusively depend on shortleaf pine, many require a pine component in their habitats (Masters 2007). Shortleaf pine differs from other pines in several traits that have implications for wildlife (Willis et al. 2024a). Shortleaf pine produces less resin, facilitating cavity excavation by red-cockaded woodpeckers (*Leuconotopicus borealis* Vieillot), while increasing susceptibility to mortality by southern pine beetles (*Dendroctonus frontalis* Zimmermann) (Conner and Rudolph 1995). Relative to loblolly pine, shortleaf pine snags persist longer on the landscape, affecting dynamics of coarse woody debris, an important resource for many wildlife species (Conner et al. 2001; Jones et al. 2009). Open ecosystems maintained by frequent fire support greater species diversity and richness (Masters et al. 1998; Adams et al. 2022) with some species obligates that exhibit strong affinities to the resources available in these systems (Hanberry and Thompson 2019). The regional importance of shortleaf pine ecosystems is exemplified by a recent reintroduction of the Brown-headed Nuthatch (*Sitta pusilla* Latham) within a shortleaf pine woodland restoration project in Missouri (Pile Knapp et al. 2024). Beyond traditional taxonomic metrics, predators in open ecosystem food webs also have greater functional and trophic redundancy (Adams et al. 2022, 2024). Open ecosystems maintained by frequent disturbance can exhibit greater resilience through these diverse, yet redundant, assemblages of predators (Sanders et al. 2018).

Fire Ecology

Fire scar studies provide detailed fire regime information spanning the last 500 years and suggest that shortleaf pine was a much more important species prior to the "Great Cutover" of forests in the early industrial era (Cunningham and Hauser 1989; Bragg 2016). Fire regimes associated with shortleaf pine were spatially and temporally dynamic but can be generalized as consisting of frequent, low-severity, and dormant season fires (Carey 1992; Guyette et al. 2002; Hutchinson et al. 2019; Stambaugh et al. 2020). Regardless of the region, historical fire frequencies associated with shortleaf pine ecosystems are relatively similar. Some historical fire events deviated from generalization including occurrence in the growing season, extensive in area, and of high severity (Guyette et al. 2006, Center for Tree-Ring Science unpublished data). These deviations may have produced outcomes that differed from typical conditions and further promoted shortleaf pine. For example, fires occurring prior to pine seedfall, which typically occurs in October-December, may promote shortleaf pine establishment compared to those occurring after seedfall (Fillingim et al. 2023). Higher severity fires may have favored shortleaf pine based on its relative tolerance of severe fires and effectiveness at colonizing in post-fire conditions (Gnehm and Hadley 2007). Many historical fire regime conditions are unrepresented in the modern era and fall outside of typical desired prescribed fire conditions but nonetheless are important to recognize in relation to shortleaf pine's fire ecology.

Shortleaf pine has numerous adaptive traits that enable it to survive a variety of fire regimes. Shortleaf pine casts flammable litter and cones that, combined with cured herbaceous vegetation in open stands, fuel surface fires with sufficient intensity to kill competitors (Varner et al. 2022; Willis et al. 2024b). As with most pines, seedling establishment is greatest in exposed mineral soil, as occurs following surface fires. Small shortleaf pine seedlings and saplings are capable of vigorous resprouting from their basal crook, a rare adaptation that allows them to persist (Clabo and Clatterbuck 2019). As they develop, juvenile shortleaf pines accrue rugose, thick bark that can withstand surface fire heat and protect underlying vascular tissues, enabling saplings to survive frequent surface fires (Shearman and Varner 2021). Resprouts following top-kill from fire can grow vigorously in open conditions, enabling them to reach sizes resistant to top-kill from subsequent fires relatively quickly (Robertson et al. 2021; Bohannon et al. 2025). Shortleaf pine self-prunes along its bole, which increases the height of the live crown and reduces crown injury from surface fires. Following crown damage, its ability to refoliate heavily scorched or consumed crowns enables large trees to survive more intense fires (Lawson 1990). In spite of this long list of fire adaptations, the fire ecology literature rarely classifies shortleaf pine alongside more classic fire-adapted pines [e.g., longleaf, slash (*P. elliottii* Engelm.), or ponderosa (*P. ponderosa* Lawson & C. Lawson) pines (McCune 1988; Lawson 1990; Landers 1991; Keeley and Zedler 2000)], further establishing shortleaf as either an understudied, misunderstood, or enigmatic pine with need for more research into its fire adaptations.

Genetics

The contiguous, extensive range of shortleaf pine and its adaptability to a wide variety of environmental conditions suggest that the species has considerable genetic diversity (Mattoon 1915; Lawson 1990). As a long-lived, wind-pollinated conifer, shortleaf pine exhibits widespread gene flow and prolific outcrossing that has been confirmed by genetic markers (Stewart et al. 2016). However, no clear genetic structure has been observed in relation to geography, suggesting greater levels of genetic variation within than among populations (Hendrickson et al. 2018). A study based on shortleaf pine isoenzymes confirmed low (9%) interpopulation genetic variation, indicating that the vast remainder (91%) of the genetic variation occurred within populations (Raja et al. 1997). The lack of interpopulation diversity suggests that seed compartmentalization may not be necessary for reintroducing the species across its range (Xu et al. 2008b; Hendrickson et al. 2018). Nonetheless, taking into account shortleaf pine's high local genetic variation may improve restoration success. Provenance tests have shown better adaptation of local seed sources compared to their distant counterparts, ostensibly due to adaptive genes in local sources (Wells and Wakeley 1970; Stewart et al. 2016). Some studies (e.g., Raja et al. 1997) have also reported greater genetic diversity of western populations than their eastern counterparts, with provenance tests showing western sources had significantly better survival and eastern gall rust (caused by *Cronartium quercuum*) resistance than eastern sources (Posey and McCullough 1969).

Hybridization between shortleaf and loblolly pines presents a risk to genetic integrity of both species (Zobel 1953; Hicks et al. 1972; Xu et al. 2008a; Stewart et al. 2010, 2017). Historically, fire has had an important role in determining the abundance and distribution of these species and their hybrids, with fire exclusion increasing the dominance of loblolly pine (Tauer et al. 2012). Shortleaf × loblolly hybrid seedlings do not produce pronounced basal crooks and consequently suffer higher mortality following fire, thereby maintaining shortleaf pine genetic integrity where frequent fires are persistent (Bradley et al. 2016). Additional research to improve understanding of the threat of introgression could focus on developing standardized genomic assays to identify hybrid seedlings and the direction and extent (F1, F2, BC) of introgression rapidly, inexpensively, and reliably, as well as regional variation in hybridization due to different species interactions or other geographic factors.

Although programs for genetic improvement of shortleaf pine were established widely in the 1950s and 1960s (Kitchens 1986), shortleaf pine has been largely understudied in more recent tree genetics work, due largely to the dominance of loblolly pine for production and the susceptibility of shortleaf pine to littleleaf disease (caused by *Phytophthora cinnamomi* Rands) in the Southern Appalachians, Montane Longleaf Pine-Shortleaf Pine, and Piedmont portion of the Southeastern Coastal Plain and Piedmont natural community groups (Fig. 4A) (Sites 1975). Older tree improvement programs focused on establishing seed orchards for reforestation and restoration, but these activities have slowed or been abandoned altogether in recent years (Stewart et al. 2016; Hossain et al. 2021). Still, seed from genetically improved, first- and second-generation seed orchards remains available through nurseries in 12 southeastern states (Shortleaf Pine Initiative 2025). Breeding programs and provenance trials focused on genetic improvement for cold hardiness, disease resistance, and the development of an understanding of potential mal- and pre-adaptation due to hybridization with loblolly pine are important research topics to inform shortleaf pine restoration and management.

Stand Development Pathways

Patterns of stand development can guide management and provide the basis for silvicultural systems (Oliver and Larson 1996; Palik et al. 2020). In addition to variation in structure and composition (Fig. 5), contemporary shortleaf pine ecosystems vary in age structure. Across much of the range, shortleaf pines occur as large, older trees but are often absent in smaller size classes (Shelton and Murphy 1991; Moser et al. 2007; Olson et al. 2017). Given the role of fire in shortleaf pine regeneration ecology, widespread fire exclusion over the past century has disrupted critical stand development processes for shortleaf pine and limited our understanding of shortleaf pine stand dynamics. However, the silvics of shortleaf pine, including its fire adaptations, and the disturbance regimes within its range suggest that shortleaf pine ecosystems can be maintained through multiple stand development pathways (Baker et al. 1996; Hart et al. 2024).

Intermediate-severity disturbances are common throughout the shortleaf pine range, creating opportunities for establishment of even-aged stands at patch- to stand-scales (Goode et al. 2021, 2022). Exposed mineral soil can promote abundant seedling establishment if seed trees are available, because seed dispersal is typically limited to within 100 m of adult trees (Baker 1992). Disturbance from wind events, which may be combined with surface fire, or from higher severity fires may create these conditions, resulting in even-aged shortleaf pine stands intermixed with scattered remnant trees. Tornados have been documented to initiate even-aged stands of shortleaf pine in the Interior Highlands region of Missouri, Arkansas, and Oklahoma (Mattoon 1915). This pattern of stand development is also demonstrated in Shannon County, MO, near an old-growth shortleaf pine stand located on land owned by Pioneer Forest (L-A-D Foundation). In 1953, a wildfire burned through an area adjacent to the old-growth stand that had been harvested in 1947. Scattered overstory shortleaf pine seeded the burned area, resulting in a pure, even-aged shortleaf pine stand today (harvest records and personnel communication, J. Green, Pioneer Forest staff).

Stand reconstruction studies also support shortleaf pine stand development through local gap dynamics. Studies from old-growth shortleaf pine forests in Missouri and Arkansas document continual recruitment of shortleaf pine within canopy gaps, maintaining an uneven-aged structure during past periods of frequent surface fire (Stambaugh et al. 2002; Flatley et al. 2023). Similar patterns were observed in shortleaf pine-oak mixedwoods in Tennessee, where overstory shortleaf pine trees were clustered in spatial patterns linked to past disturbances (Goode et al. 2021). Given shortleaf pine's shade intolerance and mineral soil seedbed requirements, maintaining stands through gap dynamics may be feasible in open woodlands managed with frequent fire, but is unlikely to be successful in closed-canopy forests without hardwood control by herbicides and stand density management (Baker et al. 1996). Additional research is needed to develop target structure and age distributions and the management approaches that sustain them.

Major Management Challenges

There are widespread challenges with regenerating and recruiting shortleaf pine, although specific management goals and the composition of competing species may vary regionally. Competition from faster growing pine species, such as pitch pine in the mid-Atlantic or loblolly pine in the Southeast, can be problematic, as can competition from co-occurring hardwood species in mixedwood forests or woodlands of the Central Hardwoods region. Legacies of fire exclusion include the accumulation of hardwood (e.g., red maple (*Acer rubrum* L.) or shrub (e.g., mountain laurel (*Kalmia latifolia* L.)) competitors (e.g., Elliott and Vose 2005), many of which have established rootstocks capable of resprouting vigorously after reintroduction of surface fire. Site productivity can moderate these competitive interactions, typically disadvantaging shortleaf pine as site productivity increases. While it is understood that shortleaf pine regeneration requires reduction in accumulated litter layer and its recruitment requires competition control (e.g., Shelton and Cain 2000; Kabrick et al.

2015; Clabo and Clatterbuck 2020), effective silvicultural prescriptions need to be developed to address site-specific conditions and different management objectives.

Prescribed fire is a critical tool for shortleaf pine management, yet there are many questions regarding its use. Across most of the shortleaf pine range, frequent surface fire is necessary to maintain open woodland and savanna conditions (Hanberry et al. 2018). Prescribed fire can also be used to improve shortleaf pine seedling establishment by reducing litter and exposing mineral soil (Grano 1949; Yocom and Lawson 1977; Fillingim et al. 2023) and can reduce the abundance of fire-sensitive competitors (Robertson et al. 2021). However, there is uncertainty about the best use of fire to control competition around recruiting shortleaf pine and to maintain or promote herbaceous cover. While shortleaf pine persists following fire due to resprouting, recruitment requires stems to become large enough to survive typical surface fire intensity, suggesting the need for a fire-free period to allow recruitment. Research from Missouri reported 0.5 probability of resisting top-kill once shortleaf pine basal diameter reaches 2–3 cm (Dey and Hartman 2005; Fillingim et al. 2026). The appropriate fire-free interval may vary regionally due to differences in growth rates from site productivity and growing season length. Stambaugh et al. (2007) reported that shortleaf pine needed an 8–15 year fire-free period to recruit in Missouri, while Kabrick et al. (2015) projected planted shortleaf pine seedlings in Missouri reached 3 cm basal diameter after 5 years with no canopy but up to 10 years under residual overstory. In Tennessee, Clabo and Clatterbuck (2019) found that 3-year old planted shortleaf pine seedlings usually survived fire without top-kill, and Robertson et al. (2021) reported that 1–2 year fire return intervals maintained over decades enabled shortleaf pine recruitment in Florida. Other factors related to the burn regime (e.g., fire seasonality or fire intensity) or stand conditions (e.g., shade level, understory cover or composition) can affect the responses of shortleaf pine and its competitors to fire (Willis et al. 2025). Implementing the minimum fire-free period to allow suitable shortleaf pine recruitment would help maintain the herbaceous understory plant community. Because of the diversity in shortleaf pine stand conditions locally and across its wide range, fire prescriptions to meet varied objectives are similarly diverse. The prescribed burning window (i.e., the occurrence of weather conditions suitable for burning) also varies across the shortleaf pine range, further affecting ability to use fire for shortleaf pine management (Chiodi et al. 2018).

Economic Considerations

Another widespread challenge to shortleaf pine management is the general absence of timber markets. Mills in the US Coastal Plain and Piedmont are often associated with loblolly pine production, and shortleaf pine is a relatively minor southern pine component within pulpwood procurement zones. In regions where papermills exist and shortleaf pine is common, fiber needs are often met from sawmill residues, providing few markets for shortleaf pine pulpwood. Due to sourcing of sawtimber from plantation-grown loblolly pine, many mills are not currently equipped for large diameter shortleaf pine trees that commonly occur growing in mixture with other species. In regions outside the Southeast, hardwoods drive the market and development of shortleaf pine markets has been difficult, to the point that shortleaf pine removal may be avoided during harvests of mixedwood stands. However, shortleaf pine may prove valuable for emerging mass timber products such as cross-laminated timber. The narrower growth rings and lower proportion of juvenile wood make slower grown pine ideal for these applications and high-quality lumber (Bragg 2016).

Shortleaf pine can provide financial opportunities while maintaining longer rotations than conventional production approaches. Shortleaf pine has been shown to respond to thinning from above (Gingrich et al. 1965). An economic simulation study found that in the absence of a pulpwood or other small wood market, thinning from above yielded the best economic returns with rotation ages from 44 to 72 years and outperformed thinning from below with shorter rotations (Pelkki 1997, 2005). This approach resulted in an average stand basal area of 18.6 m^2/ha at rotation, which would be suitable for conversion to woodland management. Shortleaf pine may also be well-suited to take advantage of carbon markets and the annualized returns from holding trees longer than "business as usual" practices.

Open shortleaf pine ecosystems offer economic opportunities through management of game and non-game wildlife. Management of northern bobwhite quail (*Colinus virginianus* L.) is an excellent example. Quail-managed lands approximate reference conditions of open pine woodlands in east Alabama, northern Florida, southwest Georgia, and other areas of the overlapping shortleaf pine range. These sites attract tremendous hunting-related tourism and generate substantial revenues without necessitating timber revenues (Nimlos et al. 2023). Other game (e.g., white-tailed deer [*Odocoileus virginianus* Zimmermann] and wild turkey [*Meleagris gallopovo* L.]) and non-game wildlife recreation (e.g., wildlife watching) provide substantial economic returns to landowners and communities in the region (e.g., Poudel et al. 2017).

Adaptability to Future Conditions

Shortleaf pine is well-adapted to expected future changes in climate and growing conditions. Its large geographic range provides opportunity to track changing environmental conditions (Aitken et al. 2008) and provides pathways for adaptation to future conditions (Alberto et al. 2013). Shortleaf pine's importance value based on abundance in FIA plots is projected to increase by a factor of 2.86 in a moderate emissions scenario (RCP 4.5) and by a factor of 3.77 in a high emissions scenario (RCP 8.5) (Peters et al. 2020), with the greatest projected increases occurring in the Southern Appalachians and Interior Highlands (Peters et al. 2020). However, factors other than climate (e.g., soils, topography, disturbances, and competition) impact shortleaf pine's potential for establishment (Lafleur et al. 2010). In the future, the most limiting factor for shortleaf pine migration may be the lack of dry sites that provide it a competitive advantage. It is uncertain how changing conditions, including drought patterns, will influence relative competitiveness of shortleaf pine compared to its co-occurring tree species, some of which are also expected to respond positively to future change.

Risks from both abiotic and biotic disturbances are likely to increase in the coming decades (Seidl et al. 2017; Crimmins et al. 2023). Drought, wildfires, hurricanes, and other extreme weather events are expected to increase in frequency and severity (Dale et al. 2001; Gao et al. 2021; Fortuin et al. 2022). Shortleaf pine is well-adapted to many of these changes, as it is considered relatively tolerant to drought, fire, and ice damage (Lawson 1990; Bragg et al. 2003; Stewart et al. 2016). Similarly, insect and disease activity are likely to intensify, including agents to which shortleaf pine is both highly susceptible (e.g., southern pine beetle) and relatively resistant (e.g., spongy moth [*Lymantria dispar dispar* L.] and brown-spot needle blight [caused by *Lecanosticta acicula* (von Thumen) Sydow]) (Duerr and Mistretta 2013; Weed et al. 2013; An and Gan 2022). Pest interactions with drought and other extreme weather events can reduce tree vigor and promote high-severity outbreaks in the future.

Stand structure and composition strongly influence forest ecosystem responses to biotic and abiotic disturbances, meaning management plays an important role in facilitating adaptation (DeRose and Long 2014). Two characteristics in particular – open stand structure and mixedwood composition – confer general resistance and resilience to a variety of disturbances (Kabrick et al. 2017; Maclean and Clark 2021; Asaro et al. 2023). For example, open ecosystems are less susceptible to damage from drought and wildfires (DeRose and Long 2014; Clark et al. 2016), and managing for low-density, mixedwood stands is a recommended tactic for reducing southern pine beetle activity (Belanger and Malac 1980; McNulty et al. 2014). However, open woodlands may be less resistant to wind damage and suffer increased damage from ice storms due to larger individual crown sizes (Beach et al. 2010). Ultimately, the risk from different disturbances varies across shortleaf pine's range, requiring forest managers to develop site-specific prescriptions that increase shortleaf pine's capacity to adapt to future change.

Objective 3: Regional Assessment of Opportunities and Challenges

Shortleaf pine occurs across diverse and complex ecosystems, and this range-wide variation is an important theme that underscores the need for understanding local and regional context and makes generalization of management issues difficult. We synthesized our state-of-knowledge review of key topics relevant to shortleaf pine ecology and management into 10 practical overarching points relevant to its management:

1. *The large range of shortleaf pine encompasses broad variation in biotic and abiotic conditions.* Shortleaf pine occurs across wide temperature, precipitation, soil, and disturbance gradients. Differences in site productivity and growing season length modify its growth potential, and variation in co-occurring species create different competitive environments across its range. The outcomes of specific management practices may not be transferrable across different portions of the range.

2. *Shortleaf pine ecosystems have changed dramatically from historical conditions.* Changes in fire regimes have been well-documented in the eastern US. Across many portions of its range, shortleaf pine occurs in low abundance in other forest types (Supplemental Table 1), often as mature, remnant trees, with contemporary ecological functions differing from those during their establishment and an absence of regenerating seedlings and saplings. Active management using prescribed fire or other methods to control competition and reduce stand density are important to sustain shortleaf pine.
3. *Shortleaf pine occurs in contemporary ecosystems that often differ from natural community classifications.* Natural shortleaf pine communities are classified as open ecosystems maintained by frequent fire. Shortleaf pine stands occurring in other structural conditions (e.g., closed-canopy forests) can fulfill other management objectives but still require management for long-term sustainability. The magnitude of divergence from target conditions varies regionally, with the Southern Appalachian and Piedmont regions showing the greatest challenge and likely the greatest need for management.
4. *Shortleaf pine contributes to valuable ecosystem services, but its functional role varies across the range.* The apparent functional redundancy of shortleaf pine with other pine species has deemphasized its management in the southeastern portion of its range. In contrast, it is recognized for high conservation value in western and northern portions of its range, providing potential to leverage its unique functional role in those regions into greater conservation investment.
5. *Fire is critical for shortleaf pine ecosystems, but its fire ecology is variable.* Shortleaf pine has numerous fire adaptations and occurs in association with variable fire regimes across its range. Although it is commonly managed with frequent, low-intensity, dormant-season surface fires, it is likely that historical fire regimes across its large geographic range included periods with longer fire-free periods, greater severity fires, and wider variation in fire season.
6. *Basic and applied genetic information is underdeveloped for shortleaf pine.* Restoration and conservation practices often use artificial regeneration, providing opportunities for selecting genetic material to improve outcomes. This is particularly important given shortleaf pine's extensive range and variety of growing conditions in which it occurs, including the risk of hybridization within portions of the range overlapping with loblolly pine. Expanding shortleaf pine restoration would require greater nursery production to supply seedlings for artificial regeneration.
7. *The establishment and recruitment of new shortleaf pine cohorts is a major management challenge.* Limited shortleaf pine regeneration and recruitment is a consistent issue across its range, despite variation in the composition of competing tree and shrub species. Specific management approaches to address this challenge will vary, but active management, including releasing young shortleaf pine from competition, is important for regeneration success.
8. *Market opportunities enhance or constrain shortleaf pine management.* The availability of markets for forest products or other financial opportunities make management possible, especially for private landowners. Regions without markets for small diameter products have greater difficulty incentivizing release

treatments, and regions without strong markets for pine have lower general priority for shortleaf pine management. Developing forest products or alternative markets in these regions may facilitate scaling up of shortleaf pine management.

9. *Land ownership and landowner objectives will drive shortleaf pine management outcomes.* Forestland across the shortleaf pine range is predominantly under private ownership. Despite examples of restoration and conservation of shortleaf pine ecosystems on public lands, motivating private landowners to increase shortleaf pine management is difficult where timber revenues are the primary objective. Loblolly pine is the conventional species in the southern portion of the range and shortleaf pine markets are limited in the northern portions. Increasing availability of cost-share or other incentive programs for shortleaf pine could address this challenge.
10. *Shortleaf pine is well-adapted to expected future conditions.* As a southern pine species that already extends relatively far to the north, shortleaf pine is expected to be an optimal choice for enhancing forest resistance and resilience to address uncertainty in future conditions. Although susceptible to pests and diseases such as southern pine beetle and littleleaf disease, shortleaf pine's tolerance to drought and ice offer potentially better balance in response to multiple disturbances than other pines.

Building on these overarching points, we highlight specific management challenges and opportunities across the shortleaf pine natural community groups based on seven factors that we expect to be important for shortleaf pine management success (Table 3). Each of our 20 co-authors independently scored the factors in Table 3 for each open shortleaf pine natural community group using a qualitative rating scale (e.g., 1 = poor, 2 = marginal, 3 = fair, 4 = good, 5 = excellent), with scores indicating the favorability of current conditions for shortleaf pine management for each respective factor and region. We combined the two Interior Highlands natural community groups, such that the groups followed the geographic range in Fig. 4A. The qualitative scoring represents our collective experience with shortleaf pine ecosystems, and we use it to identify and highlight specific regional management challenges and opportunities.

Overall, the Interior Highlands was rated as having conditions most favorable for shortleaf pine management, followed by the West Gulf Coastal Plain and then the Southeastern Coastal Plain and Piedmont natural community groups (Fig. 6). The lowest score was for the Southern Appalachians, followed by the Montane natural community group. There was general agreement in the independent scores provided by co-authors. For each co-author, we ranked the shortleaf pine natural community groups by their mean scores across all seven factors, with the community group ranked 1 being the highest mean score and 5 being the lowest mean score. All co-authors had the Interior Highlands ranked as either 1 or 2 among the community groups, with a mean ranking of 1.2 (Supplemental Fig. 1), and the rankings ordered the shortleaf pine natural community groups the same as the mean scores (Fig. 6 and Supplemental Fig. 1).

Among the factors we considered in the assessment, there was a relatively broad range of scores among the natural community groups for the following

Table 3 Factors scored in the qualitative regional assessment to identify management challenges and opportunities for each shortleaf pine natural community group. Qualitative scores were assigned independently by all co-authors based on a rating scale (1 = poor, 2 = marginal, 3 = fair, 4 = good, 5 = excellent) and summarized as means and rankings by shortleaf pine natural community group

Factor	Description
1. Low barriers for effective prescribed fire management	Weather conditions provide adequate burn windows; vegetation and stand conditions allow safe and effective prescribed burning; social acceptance of prescribed fire; operational support for resources, labor, and training
2. Growing conditions that favor shortleaf pine regeneration and recruitment	Site and stand factors that inherently favor shortleaf pine and its regeneration, such as: acidic soils with low water holding capacity; relatively low site productivity; low abundance of fast-growing competitors. These factors are independent of management activities (e.g., prescribed burning, harvest) promoting shortleaf pine
3. Resilience to forest health concerns and suitability to future conditions	Expected future biotic and abiotic conditions favorable for shortleaf pine, recognizing climate shifts, extreme events (drought, wind, ice, etc.), and forest health (pest, pathogens) concerns may vary regionally
4. Market opportunities for shortleaf pine	Accessible market opportunities for small and large diameter shortleaf pine trees; market opportunities for small diameter hardwoods to support release treatments; opportunities for non-timber economic return from shortleaf pine ecosystems
5. Management of shortleaf pine prioritized for conservation value	Recognized importance of shortleaf pine for meeting conservation objectives, including its deliberate management rather than incidental management when associated with other species; availability of incentive programs to promote conservation management on private lands
6. Genetics and hybridization	Adequate information on genetic variation, genetic basis of adaptation to the environment, and implications of hybridization with congeners to aid tree improvement and management
7. Availability of science-based information on shortleaf pine ecosystems	Adequate information on shortleaf pine ecology and management. Available research on shortleaf pine varies across range, with uncertainty if results from studies are transferrable to other regions

Qualitative scores were assigned independently by all co-authors based on a rating scale (1 = poor, 2 = marginal, 3 = fair, 4 = good, 5 = excellent) and summarized as means and rankings by shortleaf pine natural community group

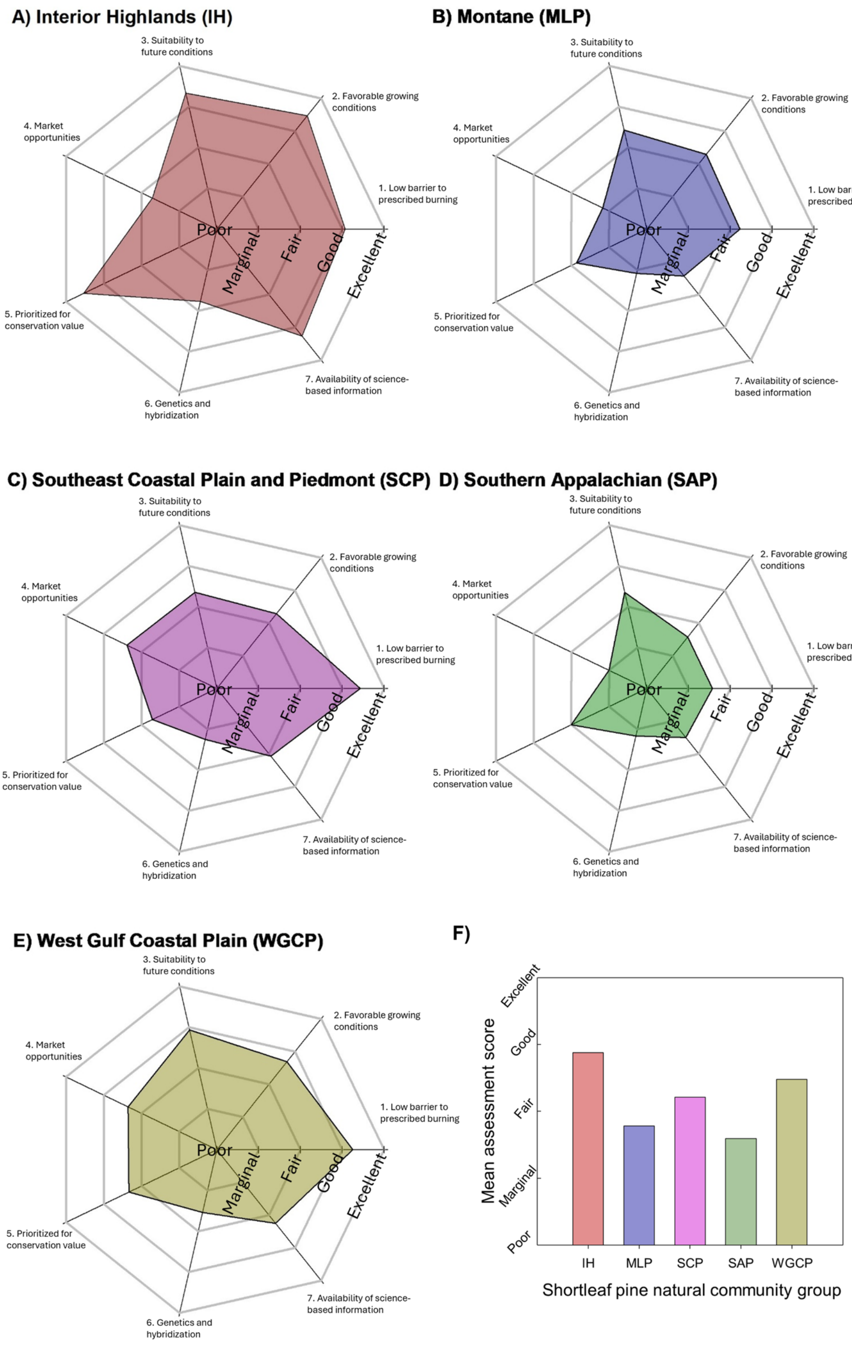

Fig. 6 Assessment of major factors important to shortleaf pine management (Table 3) by shortleaf pine natural community group (**A-E**). Each factor was scored (1 = poor; 2 = marginal; 3 = fair; 4 = good; 5 = excellent) independently by all co-authors and mean scores are shown. Panel **F** shows mean scores across all factors for the shortleaf pine natural community groups

factors: low barriers to prescribed burning (2.6–4.4), growing conditions that favor shortleaf pine (2.6–4.5), recognized importance for conservation value (2.7–4.5), and availability of science-based information (2.4–4.2). The other factors had relatively low ranges for their scores: suitability to future conditions (3.4–4.3), market opportunities (2.0–3.4), and genetic considerations (2.1–2.8). Suitability to future conditions was considered generally good across all the natural community groups, and information on genetics/concerns with hybridization scored consistently low across all the natural community groups in the shortleaf pine range.

Interior Highlands Shortleaf Pine-Oak Communities

The Interior Highlands Shortleaf Pine-Oak natural communities scored highly (> 4, indicating scores of 'good' or 'excellent') for all factors other than available markets and genetics (Fig. 6A). The region currently has high abundance of shortleaf pine, occurring primarily in shortleaf pine-dominated forests rather than dispersed at low abundance in other forest types (Fig. 1, Supplemental Table 1).

Challenges: The lack of market opportunities for shortleaf pine management is a challenge, particularly in the northern portion of the region (i.e., Missouri), where hardwood sawtimber dominates the market. In the southern portion of this region, hybridization with loblolly pine can present a challenge and underscores the importance of regular prescribed burning.

Opportunities: Overall, conditions within this region are favorable for shortleaf pine management. Developing markets for shortleaf pine or for small diameter pine and hardwood material would allow for more management. Across the northern portion of this region, shortleaf pine is the only native pine species, and its conservation value has been prioritized for restoration of open ecosystems. Efforts to restore shortleaf pine include artificial regeneration, which could benefit from increased tree improvement and nursery production efforts.

Montane Longleaf Pine-Shortleaf Pine Woodlands

The Montane Longleaf Pine-Shortleaf Pine Woodlands natural community group scored relatively low across all factors, with its highest score for suitability to future conditions (3.4). It ranked 4th among the five natural community groups (Fig. 6B). Based on FIA data, nearly half (47.3%) of shortleaf pine trees on timberland in this natural community group occur with the FIA 'loblolly pine' forest types (Supplemental Table 1).

Challenges: The availability of science-based information on shortleaf pine scored lowest for this region among all the natural community groups, indicating uncertainty in our understanding of shortleaf pine ecosystems and best management practices in this region. The abundance of fast-growing competing species and challenges with the use of prescribed burning make regenerating shortleaf pine challenging.

Opportunities: The co-occurrence with longleaf pine may provide opportunities to extend prescribed fire management into areas with shortleaf pine. Efforts to increase the recognition of the conservation value of shortleaf pine, often providing similar functions as longleaf pine, may justify greater interest in shortleaf pine management.

Southeastern Coastal Plain and Piedmont Shortleaf Pine-Oak Woodlands

The Southeastern Coastal Plain and Piedmont natural community group ranked 3rd among the natural community groups, with considerable variation in scores among the factors considered (Fig. 6C).

Challenges: In this region, the conservation of open ecosystems is generally focused on longleaf pine and timber objectives promote loblolly pine. Co-occurrence with loblolly pine results in the possibility of hybridization across the region. High abundance of fast-growing competing species can challenge shortleaf pine regeneration, and susceptibility to littleleaf disease can be problematic, particularly on poorly drained soils.

Opportunities: This region has the greatest use of prescribed burning, often associated with longleaf pine management, and shortleaf pine can benefit from this co-occurrence. Efforts to increase longleaf pine management, including through cost-share or other incentive programs, could expand to shortleaf pine to increase its deliberate management and serve as a model for other regions to incentivize shortleaf pine management.

Southern Appalachian Pine-Oak Woodlands

The Southern Appalachian Pine-Oak Woodland natural community group scored lowest across most factors and ranked last in the regional assessment (Fig. 6D). This large region has relatively low abundance of shortleaf pine (Fig. 1), with only 35% of the shortleaf pine trees occurring with FIA 'shortleaf pine' and 'shortleaf pine-oak' forest types (Supplemental Table 1). Contemporary conditions where shortleaf pine occurs is the most divergent from the target conditions of the natural community group (Table 2; Fig. 4).

Challenges: Shortleaf pine management in this region is challenged by the abundance of fast-growing competitors, barriers to prescribed fire use, a lack of market opportunities for shortleaf pine, and a lack of science-based information on shortleaf pine ecology and management.

Opportunities: Shortleaf pine is recognized to provide conservation value in this region. Despite challenges with prescribed fire management in the region, the conservation value and unique habitats provided by shortleaf pine natural communities create opportunity to increase social awareness of frequent-fire ecosystems through shortleaf pine restoration and management.

West Gulf Coastal Plain Shortleaf Pine-Oak Woodlands

The West Gulf Coastal Plain Shortleaf Pine-Oak Woodlands natural community group scored highly and ranked 2nd among the natural community groups (Fig. 6E). The region also has relatively abundant shortleaf pine on the landscape (Fig. 1), although the plurality (39.9%) of the shortleaf pine trees in the region occur within the FIA ‘loblolly pine’ forest type (Supplemental Table 1). Among the natural community groups, conditions of stands with shortleaf pine most aligned with the target overstory metrics for the natural community (Table 2; Fig. 4).

Challenges: Shortleaf pine management in this region can be challenged by fast-growing competitors, including co-occurring hardwood species in mixed-wood stands, that create problems with regeneration. Shortleaf pine co-occurs with loblolly pine and longleaf pine in the region, species which commonly receive greater priority for timber production or conservation management, respectively.

Opportunities: The abundance of shortleaf pine and the use of prescribed burning in the region create opportunities to expand management of the species. The relative importance of shortleaf pine for conservation value is greater in this region than in the Southeastern Coastal Plain and Piedmont due to lower abundance of longleaf pine, offering opportunity to develop incentive programs and focus conservation efforts on shortleaf pine.

Overall, the regional assessment demonstrates that management constraints vary across the shortleaf pine range. Regions where shortleaf pine currently occurs in greater abundance generally have fewer management challenges (Figs. 1 and 6); however, questions regarding best management practices specific for shortleaf pine are common across all portions of the range, highlighting the need for basic and applied research on shortleaf pine ecosystems.

Conclusion

Shortleaf pine is a common tree species that eludes simple characterization, having been understudied and largely underappreciated relative to other southern pine species. Its range encompasses considerable variation and extends north to include associations with a broad range of species, including central and northern pine and hardwood species. Interest in managing shortleaf pine is primarily driven by conservation objectives, particularly in portions of its range where it provides unique ecosystem functions, although there are also viable financial opportunities for shortleaf pine. Variability in the recognition of shortleaf pine’s conservation value and in market opportunities contribute to regional context for shortleaf pine management. In northern portions of its range, where greater barriers to prescribed burning exist, conservation value of shortleaf pine ecosystems may serve as a model to increase awareness and implementation of prescribed burning. Across its range, it is considered well-suited for future conditions and likely a good choice for enhancing adaptive capacity to changing growing conditions.

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Authors Contributions

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JB – conceptualization, methodology, writing – original draft preparation, writing – reviewing and editing.
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Data Availability Data and materials used in this manuscript are available by request.

Declarations

Competing Interests The authors do not declare any competing interests.

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