



Oaks enhance early life stage longleaf pine growth and density in a subtropical xeric savanna

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Abstract

The interplay of positive and negative species interactions controls species assembly in communities. Dryland plant communities, such as savannas, are important to global biodiversity and ecosystem functioning. Sandhill oaks in xeric savannas of the southeastern United States can facilitate longleaf pine by enhancing seedling survival, but the effects of oaks on recruitment and growth of longleaf pine have not been examined. We censused, mapped, and monitored nine contiguous hectares of longleaf pine in a xeric savanna to quantify oak-pine facilitation, and to examine other factors impacting recruitment, such as vegetation cover and longleaf pine tree density. We found that newly recruited seedlings and grass stage longleaf pines were more abundant in oak-dominated areas where densities were 230% (newly recruited seedlings) and 360% (grass stage) greater from lowest to highest oak neighborhood densities. Longleaf pine also grew faster under higher oak density. Longleaf pine recruitment was lowest under longleaf pine canopies. Mortality of grass stage and bolt stage longleaf pine was low ($\sim 1.0\% \text{ yr}^{-1}$) in the census interval without fire. Overall, our findings highlight the complex interactions between pines and oaks—two economically and ecologically important genera globally. Xeric oaks should be incorporated as a management option for conservation and restoration of longleaf pine ecosystems.

Keywords Positive species interactions · Savanna · Dryland plant communities · Longleaf pine · Oaks

Introduction

Community assembly reflects the accumulation of positive (facilitative) and negative interactions within and among trophic levels. Facilitation can balance negative species interactions and prevent competitive exclusion (Callaway and Walker 1997; Bruno et al. 2003). The importance of facilitative interactions is thought to increase under stress, variable environmental conditions, and possibly disturbances (Bertness and Callaway 1994). For instance, nurse plants in xeric systems provide refuge for many plant species by reducing evaporative stress and enhancing recruitment (Tewksbury and Lloyd 2001; Filazzola and Lortie 2014). Xeric longleaf pine (*Pinus palustris* Mill.) savannas of the southeastern United States are shaped by both stress (e.g., excessively drained soils) and widespread disturbances—fires and hurricanes (Myers and Van Lear 1998; Gilliam and Platt 1999; Provencher et al. 2001; Zampieri et al. 2020), suggesting a potential role for facilitation in this system.

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Most studies of species interactions in longleaf pine systems have focused on the interplay between fire and negative species interactions, including aboveground (e.g., light) and belowground (e.g., water and nutrients) competition (Grace and Platt 1995a; McGuire et al. 2001; Jose et al. 2003). Much less attention has been given to positive species interactions in longleaf pine systems. However, analyses of spatial patterns, which find that longleaf pine densities are higher where oak density is high, suggest that positive interactions are happening in some xeric savannas (Johnson et al. 2021; Magee et al. 2022; Loudermilk et al. 2016). This implies a potentially important knowledge gap because forecasting population dynamics and species coexistence relies on understanding both positive and negative ecological interactions across species' life stages and for various vital rates.

The xeric sandhill savannas dominated by longleaf pine provide an excellent system to explore both intra- and inter-specific interactions. In addition to providing an excellent system for looking at interactions, the results of these interactions have important consequences for management and restoration of the longleaf pine ecosystem, whose coverage in the SE US has been reduced 95% from its original range (Frost 2006). Longleaf pine savannas are characterized by a diverse herbaceous understory, a scattered midstory of hardwood species (mainly oaks; *Quercus* spp.), and a canopy dominated by sparse longleaf pine trees (Landers et al. 1995). Frequent fires (2–7 years) maintain savanna conditions, reducing southern mixed-hardwood species encroachment (e.g., *Liquidambar styraciflua*, *Quercus nigra*, *Quercus hemisphaerica*, *Carpinus caroliniana*; Hartnett and Krofta 1989), or preventing conversion to sand pine scrub (Myers 1985; McCay 2001). Fires enhance longleaf pine seedling recruitment (Ford et al. 2010) by top-killing individuals of competing species (Glitzenstein et al. 1995). Juvenile longleaf pine are thought to capitalize on the high light availability typical of savanna ecosystems to acquire carbon reserves, then initiate rapid growth (“bolt”) to reach a fire-resistant size and thus escape recurrent fires (O’Brien et al. 2008). High light availability enhances juvenile longleaf pine survival and growth (Pessin 1944; Palik et al. 1997; Pecot et al. 2007; Pope et al. 2023), potentially leading to aggregations in canopy gaps (Brockway and Outcalt 1998). Thus, longleaf pine has often been described as a “light-demanding” or “gap-demanding” species, particularly early in the history of longleaf pine science and management (Chapman 1936).

Given the high-light conditions of savannas, longleaf pine seedlings might associate with canopy gaps due to mechanisms unrelated to light availability, such as reduced underground resource competition in gaps (Brockway and Outcalt 1998; McGuire et al. 2001; Rodríguez-Trejo et al. 2003; Palik et al. 2003). A variety of experiments—including trenching and greenhouse experiments—have been

used to separate above versus belowground competitive effects on longleaf pine seedlings revealing positive seedling growth and survival responses to increased availability of belowground resources, particularly water and nitrogen (McGuire et al. 2001; Jose et al. 2003; Palik et al. 2003; Harrington 2006; Pecot et al. 2007). Thus, gap dynamics in these high-light environments likely depend on belowground processes, which produces distance-dependent longleaf pine recruitment patterns during non-fire intervals (Grace and Platt 1995b). Spatially heterogeneous fuel loading and fire severity (Platt et al. 1991; Thaxton and Platt 2006; Wenk et al. 2011; Loudermilk et al. 2014; Whelan et al. 2021) may further reinforce conspecific distance-dependence due to the fire-sensitivity of some longleaf pine life stages, leading to the ‘patchiness’ commonly observed in longleaf pine savannas (Platt et al. 1988; Robertson et al. 2019).

Competition, distance-dependency, and patchiness have been considered the dominant drivers of longleaf pine dynamics for decades (Boyer 1963; Grace and Platt 1995a) with studies almost exclusively focused on negative effects of both adult pines and hardwoods on longleaf pine recruitment. Recently though, more attention has been given to the hypothesis of Wahlenberg (1946, pg 106) that oak canopies ‘favor survival and growth [of longleaf pines] in early life stages’, with recent studies discussing the importance of oaks to wildlife and forest structure (Greenberg and Simons 1999; Hiers et al. 2014). Consistent with the oak-facilitation hypothesis, recent studies have shown positive associations of oaks on longleaf pine sapling abundance (Johnson et al. 2021) and seedling survival during both during fire (Magee et al. 2022) and non-fire intervals (Loudermilk et al. 2016).

Several important questions remain about oak facilitation of longleaf pine recruitment (hereafter oak-pine facilitation). To our knowledge, no previous studies have examined oak-pine facilitation of seedling growth. Longleaf pine has drastic and ecologically distinct life stage transitions that are growth-dependent, particularly at its earliest life stages. After an initial non-woody, fire sensitive, seedling stage (typically the first year only), longleaf pines transition to a fire-resistant grass stage (typically 2–7 years; Pessin 1934; Boyer 1993). Individuals persist in the grass stage—during which a dense bundle of needles and the ground surface boundary conditions provide protection from fire—until enough carbon reserves have accumulated to enter the bolt stage of rapid stem elongation (Aubrey 2021). Bolt longleaf pine can grow more than 1 m yr⁻¹ in height but are vulnerable to fire mortality for several years until the apical meristem grows beyond the flame length of fires (Magee et al. 2022). Thus, longleaf pine juveniles trade high survivorship (grass stage) for rapid growth but low survivorship (bolt stage) (Heyward 1939). This so-called intra-individual trade-off confers an advantage in fire-frequented systems, although these traits did not necessarily evolve with fire, nor evolve

to promote fire (Mutch 1970; Bowman et al. 2014; Freeman et al. 2017).

The overall demographic importance of oak-pine facilitation depends on how this relation influences various longleaf pine vital rates and how the effects vary across gradients of light, forest structure, and community composition. Interspecific (oak) effects may help offset the negative intraspecific (pine) effects (Grace and Platt 1995a, b; Johnson et al. 2021); however, oak-pine facilitation may be a transient effect that shifts abruptly across longleaf pine life stages (Soliveres et al. 2010). As longleaf pine seedlings shift from a survival to a growth strategy, neighborhood effects might shift as well. Neighbors could function as benefactors during one individual life stage and compete during others (Miriti 2006). Thus, understanding oak-pine facilitation requires a demographic assessment across multiple life stages.

To better understand the positive and negative species interactions controlling longleaf pine demography across early life stages, we mapped all living longleaf pine individuals one-year-old and older in 8.96 ha of xeric sandhill longleaf pine savanna and followed individuals for one year, during a non-fire interval. We modeled longleaf pine density and growth rates as a function of pine and oak densities as well as canopy openness. We tested the following hypotheses: first, we hypothesized that juvenile longleaf pine density, growth, and new recruitment would increase with oak density, as predicted by the oak-pine facilitation hypothesis. Second, we hypothesized that canopy openness would positively affect juvenile longleaf pine growth, but new recruitment and occurrence would be influenced more through positive and negative effects from neighboring oaks and pines, respectively. Third, we hypothesized that all vital rates and occurrence would decline with increasing longleaf pine tree density due to intraspecific competition. We examined each hypothesis at three different early longleaf pine life stages to better understand how positive and negative species interactions shift across different stages of longleaf pine regeneration. Finally, we discuss the implications of the oak and pine interactions for management and restoration of longleaf pine ecosystems.

Methods

Site description

This study was conducted in the 23.04-ha Forest Dynamics Plot (FDP) at the University of Florida Ordway-Swisher Biological Station in Putnam County, FL, USA (Johnson et al. 2021), located on the ancestral homelands of the Potano Tribe of the Timucua peoples (Johnson 1991; Hann 1996, Ch. 1). Beginning in 2019, all stems ≥ 1 cm diameter at breast height (DBH) were tagged and mapped, and

the health status was recorded according to standardized ForestGEO protocols (Condit 1998; Anderson-Teixeira et al. 2015; Davies et al. 2021). The 480 \times 480 m plot was gridded and subdivided into 40 \times 40 m quadrats monumented with corner and center posts. We conducted mortality censuses of stems ≥ 1 cm DBH between September–November 2020 and again between September–October 2021. Mortality data were screened for quality assurance, particularly in the second census, where data were continuously integrated with quality assurance coding scripts (sensu Kim et al. 2022). The FDP is characterized by Entisolic soils, with a mean elevation of 47.5 m.a.s.l and 14.9 m of relief across the plot. Precipitation is seasonal with 60–70% of the average annual 1290 mm of rain occurring between May and September. Mean annual temperature is 20 °C. The site has been pine savanna since at least the 1930s with little, if any, timber harvesting occurring in that time, and limited turpentine collection. There was a 37 year interval of fire suppression that ended in 2000 (Varner et al. 2005). Since April 2000, prescribed burns have been conducted at 2–4-year intervals in the area that includes the FDP (Magee et al. 2022).

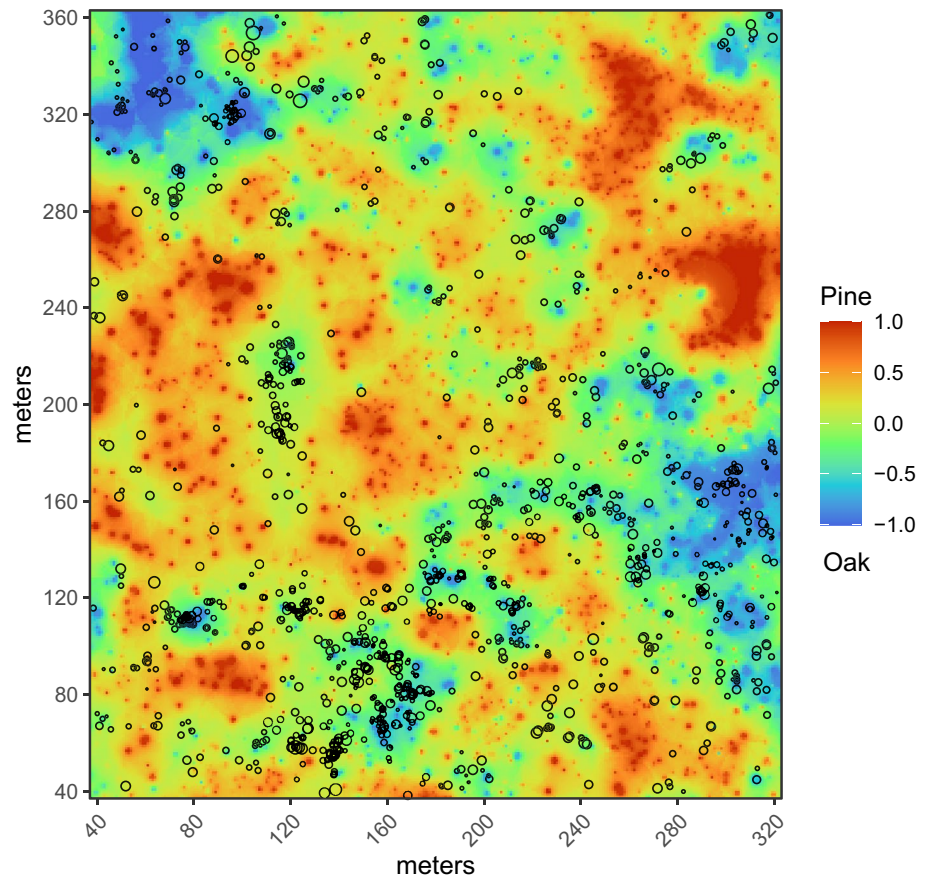
Longleaf pine recruitment data collection

To measure longleaf pine seedling demographics, we mapped, tagged, and measured all longleaf pines older than one year (i.e., not germinated in the current calendar year) and < 1 cm DBH (i.e., not in the main census described above) between February and May 2021 and again in 2022. During the 2021 census, we did not tally seedlings < 1 year old, which were distinguished from older seedlings by the lack of a woody stem. We used a strategic gridded search to locate seedlings. Utilizing the established grid of the FDP (40 \times 40 m), we further divided our searches into four 20 \times 20 m sub-quadrats to sample a 280 \times 320 m (8.96 ha) core area of the plot that was representative of the variation in longleaf pine and oak densities across the 23-ha area. The sampling area included a 40 m buffer of mapped trees to provide data on neighborhood effects (Fig. 1). Proceeding from the center of sub-quadrat, we searched in a clockwise direction, mapping and measuring all individuals. All sub-quadrats were searched at least twice, and all longleaf pines were mapped and measured for height and basal diameter. We conducted a second follow-up survey in January–April 2022, recording any mortality, measuring living individuals for height and basal diameter, and mapping and measuring all newly recruited seedlings.

Life stage delineation

All longleaf pines tallied during the first census (2021) were classified as grass stage or bolt stage. We distinguished bolt stage from grass stage longleaf pines by quantitatively examining size-dependent growth behavior.

Fig. 1 Longleaf pine seedling census region in the forest dynamics plot with the background colors representing relative neighborhood competition index dominance by longleaf pine or oak species at the 1-m resolution. Red tones indicate pine dominance, and blue tones indicate oak dominance. All mapped longleaf pine seedlings are shown in black circles and scaled by regeneration basal diameter



We first estimated seedling height growth (cm yr^{-1}) as a function of basal diameter (cm) by fitting a logistic curve (Fig. S1a). We then identified the inflection point of the curve's derivative, where height growth is accelerating most rapidly (Fig. S1b–c; see Supplement for methods details). We used this inflection point, 3.51 cm basal diameter, to define the breakpoint between the grass and bolt stages. Newly recruited seedlings that entered the census in 2022 were treated as a separate, pre-grass (recruitment) life stage.

Oak and longleaf pine neighborhoods

We leveraged the spatially explicit main tree census (i.e., stems ≥ 1 cm DBH) to calculate size and distance-weighted oak and pine tree neighborhoods, which were used as explanatory variables in models of longleaf pine density (in a 1×1 m grid cells) and individual seedling growth. We calculated the simplified form of a commonly used neighborhood crowding index (NCI; Hegyi and Fries 1974; Canham et al. 2004; Uriarte et al. 2004) for every individual or grid cell (1 m^2), i :

$$\text{NCI}_i = \sum_{j=1}^n \text{basal area}_j / \text{distance}_{ij} \quad (1)$$

where n is the number of oak or pine trees in the neighborhood of grid cell or seedling i , basal area_j is the basal area (m^2) of the j th neighbor, and distance_{ij} is the distance from the j th tree to the center of grid cell i or to seedling i . We used a 15 m neighborhood radius, because 15 m is the approximate distance over which interactions occur at this study site (Johnson et al. 2021; Magee et al. 2022). A previous longleaf pine neighborhood study used an exponential decay functional form (Bigelow and Whelan 2019); however, another study found the inverse-distance-weighted formula to be more effective at our study site (Magee et al. 2022).

Lidar data collection and processing

Lidar data were obtained from the NEON aerial observatory fixed-wing platform collected on September 30, 2021. The sensor platform flew at 54 m s^{-1} at approximately 1000 m aboveground. Successive flight passes had approximately 37% overlap. Lidar data are freely available for download

through the NEON data portal (NEON 2022; <https://www.neonscience.org/data>).

The original average point density was 53.3 points m^{-2} . Point cloud processing was conducted in the R environment (R Core Team 2023) using the *lidR* package (Roussel and Auty 2019; Roussel et al. 2020). The preprocessing stage included filtering out points having scan angles higher than 15° off-nadir, noise removal, ground point classification and interpolation, and point cloud height normalization (i.e., scaling point altitude values to aboveground height values). Post-processed average point density of the normalized point cloud was 35 points m^{-2} .

Previous studies focusing on plot-level estimates have shown that LAI and light availability strongly correlate with lidar-based canopy or vegetation cover, albeit in different forest types (Solberg et al. 2009; Korhonen et al. 2011). We used the lidar-based vegetation cover index metric (Eq. 2 below) to quantify the effects of light availability, with lower values of Eq. 1 indicating more available light. Following Solberg's Cover Index (SCI), we calculated:

$$\text{SCI} = 1 - \frac{[\text{Single}_{\text{ground}} + 0.5(\text{First}_{\text{ground}} + \text{Last}_{\text{ground}})]}{[\text{Single}_{\text{All}} + 0.5(\text{First}_{\text{All}} + \text{Last}_{\text{All}})]} \quad (2)$$

where “Single,” “First,” and “Last” refer to the number of single, first, and last returns from one lidar emitted pulse; and the subscripts All and ground specify if all or only ground returns were considered (i.e., $\text{Single}_{\text{ground}}$ is the number of points that were single returns from a lidar pulse and were classified as ground). We set the bottom return profile equal to 0.5 m, as this value combines returns that would be intercepted by canopy, midstory, and understory vegetation. We calculated SCI at a 5 m resolution (Fig. S3).

Seedling density analysis

We used a spatial inhomogeneous Poisson point process model to examine the influence of canopy openness and oak and longleaf pine neighborhoods on the spatial density of grass stage, bolt stage, and newly recruited longleaf pine individuals. The sampling units for this analysis were 1×1 m grid cells, spanning the 8.96 ha seedling monitoring area. We chose 1×1 because it matched the grid cell size for oak and pine NCI values. We calculated longleaf pine and oak NCIs (Eq. 1) from the center of every meter across a 1×1 m grid cell. Grid cells whose centers were very near (e.g., < 1 cm) a mapped stem had greatly inflated the NCI values. These were assigned the 99th quantile NCI value to avoid extreme data outliers. We used a 5×5 m raster of vegetation cover (i.e., Solberg's Cover Index). All raster data were transformed into spatial pixel images using the *spatstat* library in R (Baddeley and Turner 2005, 2014).

We modeled longleaf pine seedling point intensity (λ) of the three juvenile life stages: newly recruited seedlings, existing grass-stage individuals, and bolt stage individuals as defined by their log-linear relationship with the canopy cover index (SCI), and oak and pine NCI.

$$\lambda(l) = \exp(\beta_0 + \beta_1 * \text{pine NCI}(l) + \beta_2 * \text{oak NCI}(l) + \beta_3 * \text{SCI}(l)) \quad (3)$$

where λ is equal to the seedlings point intensity (expected number of seedlings m^{-2}) at the 1 m^2 grid cell the individual was located l ; $\text{SCI}(l)$ is the value from the 5-m SCI raster that includes grid cell l ; and oak $\text{NCI}(l)$ and pine $\text{NCI}(l)$ are the NCI values (Eq. 1) at location l .

We implemented our point process model (Eq. 3) using the ‘ppm’ function in *spatstat* (Baddeley et al. 2015, Ch. 9, Renner et al. 2015), which uses maximum pseudo-likelihood estimation to obtain parameter estimates for the point process model (Baddeley and Turner 2000). We specified in *spatstat* a Berman-Turner quadrature scheme and a 5 m Ripley's boundary correction (Berman and Turner 1992; Baddeley et al. 2015, Ch. 9). The assumption of independent observations was evaluated by simulating 999 realizations of fitted models with the ‘Kinhom’ function in *spatstat* (Ripley 1977; Baddeley et al. 2015, Ch. 11; Renner et al. 2015), which allowed us to evaluate the potential for interpoint spatial interactions (Fig S4). We added scaled x and y Cartesian coordinates as covariates to one model with spatial independence violations because grass stage longleaf pine densities gradually decreased from west to east and decreased from south to north. To better understand the marginal response to each covariate, we interpreted each covariate independently by multiplying the associated parameter estimate by a 10% increase in the covariate and holding other variables constant (Table S1). We further quantified the marginal effects of NCI parameters by adding a single neighboring tree of a standardized size, at a specified distance (Supplementary Methods).

Growth analysis

We modeled the volume growth rate ($\text{cm}^3 \text{y}^{-1}$) of longleaf pine as a function of oak and pine NCI (Eq. 2) and vegetation cover (i.e., SCI, Eq. 3), assuming a Gaussian error distribution. We first derived a local allometric equation to approximate seedling volume based on seedling height and diameter data from 32 randomly selected juvenile longleaf pines (see Fig. S2 and Supplemental Methods). We then applied our derived allometry to calculate volume for all the established seedlings ($n = 892$).

We modeled the volume growth rate ($\text{cm}^3 \text{y}^{-1}$) of seedling i as a linear combination of four predictor variables:

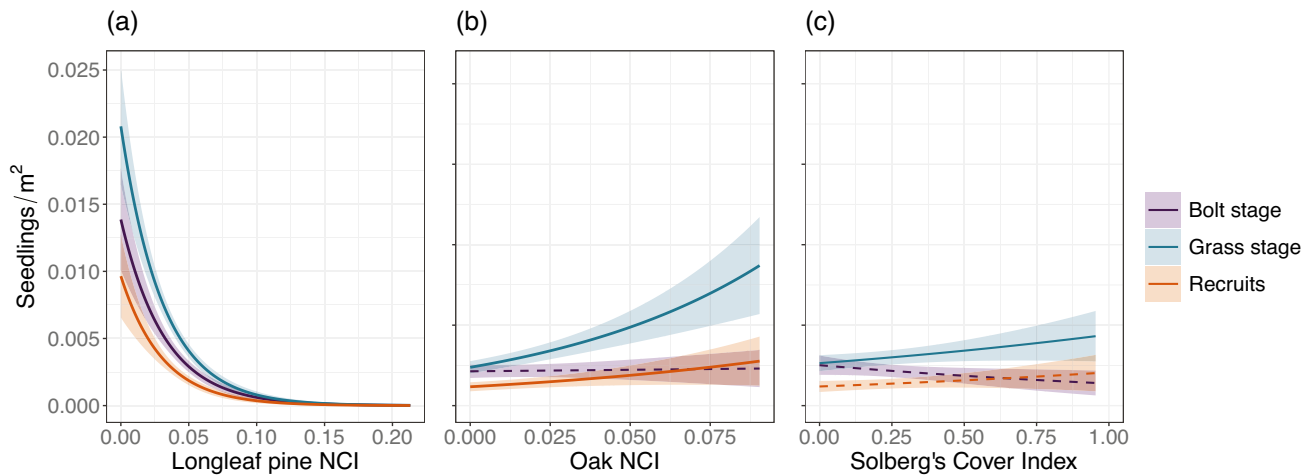


Fig. 2 Predicted seedling density (seedlings m⁻²) as a function of **a** longleaf pine neighborhood crowding indices, **b** oak neighborhood crowding indices, and **c** canopy cover. Separate models were run for each life stage: newly recruited seedlings, grass stage longleaf pines,

and bolt stage longleaf pines. Solid lines indicate significant effects ($p < 0.05$). See Supplemental Tables S2–S4 for parameters and associated statistics

$$E[\text{growth rate}_i] = \beta_0 + \beta_1 \times \text{volume}_i + \beta_2 \times \text{pinNCI}_i + \beta_3 \times \text{oakNCI}_i + \beta_4 \times \text{SCI}_i + \epsilon_i \quad (4)$$

where growth rate was calculated as the change in volume divided by the remeasurement interval (0.72–1.05 years), volume_i is the volume (cm³) of the individual in the first census (2021), SCI_i is the SCI (Eq. 2) 5-m raster value interpolated to the location of the seedling i (see details below), and oak and pine NCIs are the neighborhood crowding indices (Eq. 1). Initial volume (cm³) was included as a covariate because growth is a size-dependent process. We used a bilinear extraction method in the raster R package to associate the 5-m SCI raster to individual longleaf pine based on the average of the four nearest cells to the individual (Hijmans 2021). We fit Eq. 4 using the ‘lm’ function in R. We used Moran’s I to test model residuals for spatial autocorrelation (Crane et al. 2012); there was no significant autocorrelation, which justifies treating each seedling as an independent sample. We report model parameters in the results as partial effects the same as in the seedling density models (Tables S2, S3).

Results

In 2021, we mapped and measured 892 longleaf pine individuals (553 grass stage and 339 bolt stage) within the 8.96 ha study area. In spring 2022, we observed 1209 longleaf pines, including 881 seedlings tallied in 2021, 235 newly recruited seedlings (~1 year old), and 88 that may have been missed during the previous year (established

grass stage individuals >2 cm basal diameter) or were newly recruited individuals. Of the 892 juvenile longleaf pine tallied in 2021, five were found dead, and another four were not relocated. If the four missing individuals died, the juvenile longleaf pine annual mortality rate was approximately 1.01% (Sheil et al. 1995; Eq. 6). If the four seedlings survived, this equals a 0.55% annual mortality rate. For reference, within the same 8.96-ha study area, between October 2020 and October 2021 (also a non-fire interval), oaks (>96% *Quercus laevis*) and longleaf pine ≥ 1 cm DBH had annual mortality rates of 9.1 and 1.3%, respectively (Magee and Johnson unpublished data).

Seedling densities

Longleaf pine densities varied considerably across the plot (Fig. 1, Fig S3). The density models revealed mostly consistent effects of longleaf pine and oak neighbor indices on juvenile longleaf pine densities across three longleaf pine stages. Specifically, we observed significant and strong negative effects of longleaf pine neighbors and positive effects of increasing oak neighbor index. Vegetation cover (lidar-based SCI) varied in its relationship with longleaf pine seedling density depending on life stage but positively affected grass stage density (Fig. 2, Table S4–S6).

The average density ($\lambda_{\text{recruits}}$) of newly recruited longleaf pine seedlings ($n = 235$) was 0.00263 seedlings per m² (26 seedlings ha⁻¹). Of the measured covariates (SCI, oak NCI, and pine NCI), pine NCI had the strongest effect; in areas with 10% greater pine NCI ($Z\text{-stat} = -9.12$, $P < 0.001$), the expected number of new recruits was 49% lower (Table S4, Fig. 2). For reference, assuming Eq. 1, a 10%

increase in longleaf pine NCI corresponds to adding, one 50 cm DBH tree 9.34 m from the focal individual (or grid point) or two 20 cm DBH trees at 3.0 m. Oak neighborhood density positively affected recruitment: with 10% higher oak NCI, the expected number of longleaf seedlings was 9% lower (Z -stat = 2.87, $P < 0.001$; Table S4, Fig. 2). A 10% increase in oak density corresponds to adding two 20 cm DBH trees at 7 m from the focal individual. The density of new recruits was not significantly related to the vegetation cover (SCI).

Mean grass stage density was 0.006 seedlings per m^2 (60 per hectare, $n = 553$). For a 10% increase in longleaf pine NCI, we found a 49% decrease in grass stage density (Z -stat = -13.57, $P < 0.001$), but a 10% increase in oak NCI resulted in a 13.7% increase in grass stage density (Z -stat = 6.91, $P < 0.001$; Table S5, Fig. 2). For a 10% increase in canopy coverage (SCI), grass stage seedling abundance was 5.01% lower (Z -stat = 2.21, $P < 0.05$).

Bolt stage seedlings ($n = 339$) had an average density of $0.0037\ m^{-2}$ (37 seedlings per hectare), and patterns differed from the earlier two life stages in that the oak effect was nonsignificant (Fig. 2, Table S6). Across the range of oak NCI values, bolt stage density was 7.7% higher from lowest to highest longleaf pine NCI locations (Z -stat = -10.4, $P < 0.001$). Spatial association with SCI was nonsignificant at this seedling stage.

Seedling growth

For the 339 bolt stage longleaf pine, mean height, basal diameter, and volume growth rates were equal to $12.2\ cm\ yr^{-1}$ ($sd = \pm 11.6$), $0.43\ cm\ yr^{-1}$ ($sd = \pm 0.81$), and $238.4\ cm^3\ yr^{-1}$ ($sd = \pm 355.3$), respectively. As evidence for the potential prolific growth of bolting seedlings, one seedling grew 97.0 cm in one year. For the 553 grass stage individuals, mean grass stage height, basal diameter, and volumetric growth were $1.4\ cm\ yr^{-1}$ ($sd = \pm 0.41$), $0.48\ cm\ yr^{-1}$ ($sd = \pm 0.41$), and $13.24\ cm^3\ yr^{-1}$ ($sd = \pm 20.5$). Initial seedling volume, tree neighborhoods, and SCI values explained 56.7 and 42.8% of the variation in volumetric growth for bolt stage and grass stage seedlings, respectively. There was no evidence of multicollinearity as all variance inflation factors fell below 2.0.

For bolt stage seedlings, the most important growth predictor was the individual's volume in the previous year (Fig. 3, Table S8). Holding other variables constant, bolt stage seedling volumetric growth increased by $0.40\ cm^3\ yr^{-1}$ for every additional $1\ cm^3$ of seedling volume (t -stat = 20.93, $P < 0.001$; Table S8). Grass stage seedling growth was also size-dependent; predicted volumetric growth increased by $0.71\ cm^3\ yr^{-1}$ for a $1\ cm^3$ increase in initial volume (t -stat = 19.78, $P < 0.001$). Oak NCI positively affected grass stage growth rate. For a 10% increase in oak NCI, grass

stage volume was predicted to increase by $0.68\ cm^3\ yr^{-1}$ (t -stat = 1.98, $P < 0.05$; Fig. 3, Table S9). In contrast, bolt stage growth rate was unaffected by oak NCI. Neighboring longleaf pines had stronger negative effects on bolt stage seedlings than grass stage seedlings, but this effect was not significant at either life stage. Vegetation coverage (SCI) had a significant negative effect on grass stage growth but was not significantly related to bolt stage growth. For a 10% increase in SCI, the growth of grass stage seedlings decreased by $1.12\ cm^3\ yr^{-1}$ (t -stat = -2.83, $P < 0.01$).

Discussion

As we hypothesized, oaks positively affected juvenile longleaf pine density, particularly for new recruits and grass stage individuals. Contrary to our hypothesis, the SCI, an index of vegetation cover, negatively correlated with grass stage seedling growth, suggesting that grass stage volumetric growth was lower under increasing canopy cover. In addition, longleaf pine neighbors negatively affected seedling occurrence for all life stages, but longleaf pine neighbors only weakly reduced the growth of their recruits when they were able to establish during a census interval without fire. Mortality rates among juvenile longleaf pines were spatially variable but low over two annual censuses. We discuss the demographic consequences of oak-pine interactions in sandhill communities below, management implications, and recommend research to expand scientific understanding of this phenomenon.

Oak-pine facilitation

Oaks have been described as obstacles to longleaf pine recruitment because they compete with seedlings and occlude canopy gaps (Provencher et al. 2001; Pecot et al. 2007), which have been considered the best conditions for longleaf pine recruitment. Yet, we found increased longleaf pine recruitment, abundance, and growth in areas of higher oak density. Oak effects on longleaf pine abundance and dynamics were consistently positive across three early life stages. Oak-pine facilitation has been shown at other longleaf pine life stages. For example, Loudermilk et al. (2016) found increased longleaf pine seedling survival under oak mid-stories during the earlier, pre-grass seedling stage. Longleaf pine trees have also been shown to grow faster in oak-dominated areas (Bigelow et al. 2023). Our findings of increased abundance and recruitment near oaks also agree with spatial point-patterns analyses of longleaf pine that found longleaf pine saplings to be clustered near pyrophytic oaks (Johnson et al. 2021). With the addition of our study, oak-pine facilitation has now been shown to influence recruitment, growth, or survival of longleaf pine across five distinct life stages.

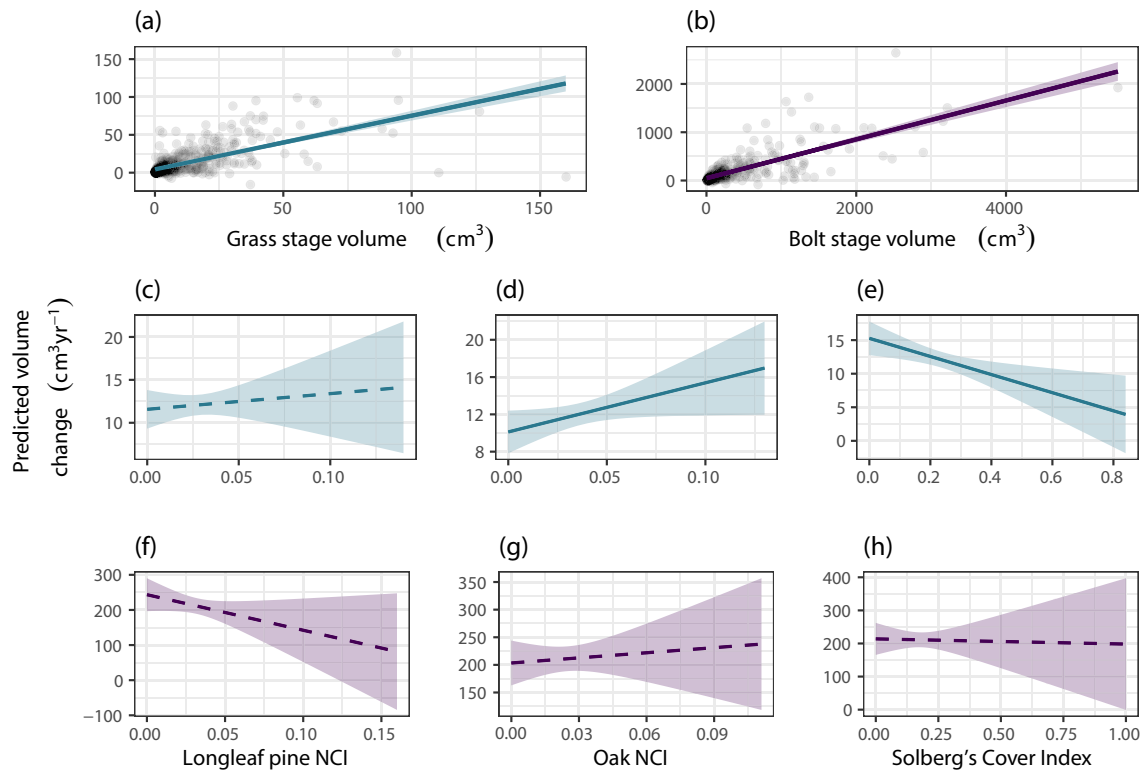


Fig. 3 Predicted seedling volumetric growth as a function of initial seedling volume, longleaf pine and oak crowding indices, and canopy vegetation cover. Predicted volume change relative to initial size for **a** bolt (purple) and **b** grass (blue) stage longleaf pines. Predictions of grass stage volume change from each of the neighborhood variables: **c** longleaf pine NCI, **d** oak NCI, and **e** canopy cover. Predictions of

bolt stage volume change from each of the neighborhood variables: **f** longleaf pine NCI, **g** oak NCI, and **h** canopy cover. Estimated effects are linear regression model predictions. Solid lines indicate significant effects ($p < 0.05$), and bands indicate 95% confidence intervals. See Supplemental Table S8–S9 for parameters and associated statistics

We documented apparent oak-pine facilitation operating during a non-fire interval. This complex process is also prevalent during fire as indicated by a previous analysis at this site that observed the highest survival probabilities during fires in areas of high oak densities (Magee et al. 2022). In our study, mortality was so low ($\sim 1.0\% \text{ yr}^{-1}$) that we could not test for differences in neighborhood effects on seedling survival. The low longleaf pine seedling mortality observed in this study further emphasizes fire's role on mortality, where mortality rates of grass and bolt stage seedlings appear to be 10–70% higher during fire years (Magee et al. 2022).

Reduced fire severity in areas of high oak density acts as a facilitation mechanism by allowing seedlings to escape the fire trap (Williamson and Black 1981; Bigelow and Whelan 2019; Hoffmann et al. 2020). Although pyrophytic oak species (e.g., turkey oak) might have leaf litter properties 'similar' to longleaf pine (Kane et al. 2008), oaks provide a fire rescue effect via a reduction in litter quantity, differences in flammability, or both, which decreases longleaf pine seedling mortality during fires (Whelan et al. 2021). Longleaf pine litter flammability may have intraspecific

variation, as measured in another pine species, and may also contribute to fire heterogeneity (Kane et al. 2022). We also did not distinguish between different species of oaks in making neighborhood calculations because more than 95% of oak individuals were turkey oak (*Q. leavis*). Variation in litter and combustion surrounding other, less pyrophytic oaks (e.g., *Q. geminata*) might create larger fire rescue effects (Varner et al. 2016), which feedback to promote oak islands (Guerin 1993) and longleaf pine seedling refugia.

Canopy openness on longleaf pine recruitment

We found mixed results regarding canopy cover effects on longleaf pine seedling dynamics. The vegetation cover index (SCI) negatively affected grass stage longleaf pine growth, but not the growth of bolt stage individuals. Our findings contrast with some previous accounts of longleaf pine regeneration being strongly enhanced by light (Chapman 1936; Boyer 1963; Jose et al. 2003), given that we found increased abundance of grass stage longleaf pine seedlings under higher vegetation cover. A potential explanation for this observation is that intact, fire-maintained xeric savannas

are typically not light-limited (Dell et al. 2017; Atkins et al. 2018). Therefore, facilitation by oaks, including hydraulic lift and fire rescue, may overcome light disadvantages under oak canopies. Our measurements of canopy cover were derived from lidar measurements taken when oak leaves were fully emerged. Turkey oak, by far the dominant oak in the study plot, is deciduous such that canopy cover measured at different times of the year would have different spatial patterns.

Longleaf pine tree effects on seedling recruitment

We found that longleaf pine NCI had negative effects on the densities of existing (grass stage and bolt stage) and newly recruited seedlings, as well as the growth rate of bolt stage individuals. This negative intraspecific effect is consistent with previous accounts of longleaf pine growth dynamics. For example, spatial pattern analyses that examine the locations of longleaf pine recruitment in relationship to oaks and longleaf pine trees typically document longleaf bolt stage and sapling overdispersion relative to longleaf pine trees (Johnson et al. 2021; Phillips et al. 2022; Fan et al. 2022). Similarly, Rebertus et al. (1989a, b) documented *Q. laevis* tree overdispersion from longleaf pines. Dynamic assessments of longleaf pine seedlings also show reduced survival near longleaf pine trees (Grace and Platt 1995b; Knapp et al. 2018), likely driven by increased fire intensity under longleaf pine canopies (Whelan et al. 2021).

Our study found lower early-life-stage longleaf pine densities in areas of higher longleaf pine abundance. Newly recruited seedlings had not yet experienced fire effects; therefore, other mechanisms likely drove non-random relations between neighboring longleaf pine and new recruits. As seedlings progressed to the subsequent grass stage and then bolt stage, the overdispersion from longleaf pine trees became stronger. This pattern is thought to emerge into patches of the uneven-aged mosaic typical of longleaf pine savannas (Robertson et al. 2019).

Restoration implications for xeric savannas

Identifying longleaf pine population bottlenecks and conditions (or species) that allow individuals to escape demographic constraints is a priority restoration objective.

Oaks, which enhanced longleaf pine seedling recruitment in our study, have long been viewed as a barrier to longleaf pine regeneration. Our study, in contrast, shows that in a xeric setting, pyrophytic oaks can promote regeneration. There are several distinct longleaf pine communities (Zampieri and Pau 2022), such as mountainous (upland) longleaf pine, mesic flatwoods, and scrub flatwoods that all vary according to climate, fire, and herbaceous communities. Oak-pine facilitation appears to operate more in xeric

savannas. We have not found reports of oak-pine facilitation in sandhill savannas with Ultisol soils that have higher water-holding capacity. Hardwood species in these sandhills (e.g., *Quercus falcata*, *Carya tomentosa*) may not enhance longleaf pine recruitment. Our results support the suggestions by Loudermilk et al. (2016) that oak retention should be considered in longleaf pine restoration on xeric sites, as long as the savanna remains sufficiently open. To gain a deeper understanding of the demographic processes and mechanisms controlling oak-pine facilitation, more research across different longleaf pine communities is warranted. Results from this research and others (e.g., Hiers et al. 2014) support planting or retaining certain oak species in savanna restoration.

Applications and conclusions

In the southeastern United States, ecologically and economically important longleaf pine savannas have received attention due to their significant range reduction (~2.2% of original range; Frost 2006). However, restoration efforts are challenged by a lack of understanding of the biophysical factors influencing natural regeneration dynamics, among other reasons. Our findings suggest that if management goals include maximizing longleaf pine demographic performance, xeric oaks should be maintained on the landscape. We have not quantified the optimal oak density, basal area, and spacing for longleaf pine individual and population growth, and it seems likely that excessive oak abundance, particularly mesophytic oaks, would have negative consequences for longleaf pine. However, in a xeric savanna, we have documented strong and consistent effects of oak presence on longleaf pine seedling recruitment. Evidence suggests that oak-pine facilitation operates during intervals with and without fire, but the largest benefit may be gleaned during fires when oak neighborhoods promote heterogeneous fires, increasing the survival of longleaf pines. At our study site, recent mortality rates for oak trees (DBH > 1 cm) were 9% yr⁻¹ (2020–21) and 12% yr⁻¹ (2021–22), including mortality of large (>30 cm DBH) *Q. laevis*, which exhibit an inverse DBH-resprouting probability (Rebertus et al. 1989b). The high mortality rates suggest that the oak population at our study site may be in decline. In addition to understanding mechanisms of oak-pine facilitation, successful management and restoration of longleaf pine ecosystems may also require a better understanding of the mechanisms that control oak population dynamics. Positive and negative species interactions influence community dynamics, and both should be considered integral components of the complex ecological processes that maintain xeric savanna ecosystems.

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Author contribution statement This study was conceived by DJJ and LM. Data were collected by LM, DJJ, SL, DTC, SM, DW, BT, KP, NM, RB, and CC. Analysis were conducted by LM, DJJ, JM, DTC, and DNC. RL assisted with data processing. LM wrote the original draft with feedback from DJJ, JL, RMC, SB, DTC, and DV. All authors provided feedback and approval of the final version of the manuscript.

Data availability Forest plot data are freely available online through the ForestGEO data portal (<http://ctfs.si.edu/datarequest/>). Code and seedling data are available from the corresponding author upon request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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