

Article

Life Stage and Neighborhood-Dependent Survival of Longleaf Pine after Prescribed Fire

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Abstract: Determining mechanisms of plant establishment in ecological communities can be particularly difficult in disturbance-dominated ecosystems. Longleaf pine (*Pinus palustris* Mill.) and its associated plant community exemplify systems that evolved with disturbances, where frequent, widespread fires alter the population dynamics of longleaf pine within distinct life stages. We identified the primary biotic and environmental conditions that influence the survival of longleaf pine in this disturbance-dominated ecosystem. We combined data from recruitment surveys, tree censuses, dense lidar point clouds, and a forest-wide prescribed fire to examine the response of longleaf pine individuals to fire and biotic neighborhoods. We found that fire temperatures increased with increasing longleaf pine neighborhood basal area and decreased with higher oak densities. There was considerable variation in longleaf pine survival across life stages, with lowest survival probabilities occurring during the bolt stage and not in the earlier, more fire-resistant grass stage. Survival of grass-stage, bolt-stage, and sapling longleaf pines was negatively associated with basal area of neighboring longleaf pine and positively related to neighboring heterospecific tree density, primarily oaks (*Quercus* spp.). Our findings highlight the vulnerability of longleaf pine across life stages, which suggests optimal fire management strategies for controlling longleaf pine density, and—more broadly—emphasize the importance of fire in mediating species interactions.

Keywords: longleaf pine; species interactions; prescribed fire; life stages



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1. Introduction

Detecting and quantifying ecological interactions in disturbance-prone systems is challenging because the strength and direction of interactions might shift during periods with and without disturbance [1,2]. Disturbances can function as selective filters, altering competitive hierarchies and promoting species coexistence [3]. The importance, magnitude, and direction of interactions can vary in response to disturbance intensity and frequency [4]. Indirect interactions may also arise during disturbance and stress [5], creating complex spatial and temporal dynamics that influence community structure.

The sandhill longleaf pine (*Pinus palustris* Mill.) forests and savannas of the southeastern United States are an ecosystem shaped by disturbances that mediate community interactions. Once occupying ≈ 37 million hectares across the Southeastern Coastal Plain, longleaf pine now occupies less than 3% of its historic range and is a focal species for restoration efforts [6]. In sandhill ecosystems, frequent fires drive forest structure and ecosystem dynamics through processes regulated by the dominant canopy species, primarily longleaf pine [7,8]. Low-intensity fires are spread by highly flammable longleaf pine needles [9–12]

and fine herbaceous fuels, such as grasses and forbs. As a result, ground fires burn through the understory, reducing encroachment from hardwoods (e.g., oaks; *Quercus* spp.) and competition from the herbaceous community, creating viable environments (i.e., bare soil and reduced competition) for establishing longleaf pine (“pyrogenicity paradigm” *sensu* Platt et al. [10]) and resulting in a range of conditions from nearly grasslands to savanna to closed-canopy forest.

Longleaf pines interact with themselves and individuals of other coexisting species through fire-mediated [13], competitive [14], and facilitative [15] processes. For example, heavy fuel loads clustered near longleaf pines create zones of reduced recruitment potential, resulting in distinct patches of recruitment outside these exclusionary zones, often in canopy gaps [16–19]. Hence, juvenile longleaf pines are known to exhibit strong, fire-induced, conspecific distance-dependent survival [7,13,20]. Interspecific interactions may also influence patterns of longleaf pine survival, growth, and recruitment [15]. Identifying which potential regulating processes structure communities is challenging because longleaf pine dynamics are conditional on the interactions of fuel beds, local biology, and environmental gradients (e.g., light availability) [21]. Hence, understanding the culmination of these effects on longleaf pine is essential to effective management and conservation [22,23].

Identifying interactions pertinent to longleaf pine dynamics is also complicated by the unique transitional life stages. Initial longleaf pine establishment depends on fine-scale habitat conditions (e.g., soil moisture, exposed soil) for successful germination and seedling emergence [24,25]. Following the initial seedling stage, longleaf pines have a characteristic grass stage, whereby a grass-like tuft of needles protects the apical meristem ([26,27]; Figure 1). During the extended grass stage, longleaf pines accumulate carbon reserves which support stem and foliar growth [28]. Individuals reside in the grass stage for 2 to 14 years [29,30] before allocating resources to stem elongation (i.e., “rocket” or “bolt” stage; Figure 1). Individuals in different life-history stages might vary in their sensitivity to disturbances, often resulting in distinct demographic bottlenecks. High mortality in the early grass stage should be a key determinant of juvenile survival [31]. However, the bolt stage has long been regarded as particularly vulnerable to fire because the apical meristem is exposed and not protected by needles [32–34].



Figure 1. Four distinct life stages of longleaf pine: grass stage, bolt stage, sapling, and tree (left to right). Photo Credit: L. Magee.

Grass-, bolt-, and sapling-stage longleaf pines are predicted to display enhanced survival in forest canopy gaps due to reduced competition for above- and belowground resources—namely light and moisture—and lower fuel loads [16,18,24]. Although juvenile pines have been shown to exhibit some degree of leaf plasticity towards shade tolerance [35], and many longleaf pine savannas have considerable understory light availability [20,36,37], juvenile longleaf pine performance typically increases with gap creation and light availability [14,16,38]. Underground competition from longleaf pine fine root tissues may extend beyond gap boundaries [18]. Thus, maximum nutrient uptake and moisture retention may

be highest in gap centers, distant from neighboring trees. However, at least one study documented lower longleaf pine seedling survival probabilities in gap centers, likely due to higher evaporative demands and excess light [39]. Therefore, the cumulative effect of gaps on longleaf seedling dynamics is not fully understood, and the complex interactions of light, moisture, nutrients, and fuel loads could significantly impact individual seedling survival probabilities during fire.

A facilitative relationship may exist between heterospecifics, specifically oaks, and juvenile longleaf pines [14,15,20]. Longleaf saplings aggregated in areas of high oak densities suggest enhanced survival either through increased moisture retention [15] and relative fuel reduction [9] provided by high oak densities, or through spatial segregation from larger longleaf pines [20]. However, the potential facilitative effects of heterospecifics on longleaf pine during fire have not been directly quantified. As juvenile longleaf pine mortality is typically high after fire [13], heterospecific facilitation may have profound effects on patterns of longleaf pine recruitment and population structure [20]. Alternatively, some studies have documented negative or neutral effects of hardwood retention on seedling establishment (e.g., [40]), further underscoring the need to better understand longleaf pine–oak relationships.

We sought to understand the influence of biotic neighborhoods and environmental factors on the survival of longleaf pine in a sandhill ecosystem after a prescribed fire. We incorporated data derived from tree censuses, sampling of early longleaf pine life stages, dense lidar point clouds acquired from a drone, competition indices calculated from fully censused tree data, and fire-intensity metrics to answer the following questions: (1) Is fire temperature related to overstory density, understory density, or ground-level vegetation, as those layers are likely to influence fire fuel loads? (2) What biotic and environmental conditions influence longleaf pine survival after fire, and do these effects vary among life stages?

2. Materials and Methods

2.1. Study Area

This study was conducted at the Ordway-Swisher Forest Dynamics Plot (OSFDP) in Putnam County, Florida, USA [20]. The 23.04 hectare OSFDP is located within the xeric sandhills portion of the Ordway-Swisher Biological Station, a long-term research facility operated by the University of Florida. Mean annual temperature at the OSFDP is 20.5 ± 0.6 °C (mean and standard deviation) and annual total precipitation is 1200 ± 290 mm (mean and standard deviation) over the last twenty years. Beginning in March 2019, surveyors gridded the 480 m \times 480 m plot into 40 m \times 40 m quadrats ($n = 144$). All stems ≥ 1 cm diameter at breast height (1.3 m; DBH) were identified, tagged, mapped, and measured according to standardized ForestGEO protocols [41–43]. Two species, longleaf pine and turkey oak (*Quercus laevis* Walt.), are the dominant trees in the plot, accounting for $> 95\%$ of all censused stems and 97% of the basal area [20]. After a prolonged fire-free period, which ended in 2003, the plot has been burned at regular (2–4 year) intervals, including forest-wide prescribed burns in March 2003, February 2007, May 2010, April 2013, April 2015, and June 2019.

2.2. Longleaf Pine Population Sampling

Prior to the growing season prescribed fire in the OSFDP in June of 2019, a random subset of 40 quadrats (40 m \times 40 m) was selected for thermocouple placement (see description of thermocouples below). All individual longleaf pines were mapped and measured in a random 13 plots of the 40 with thermocouples. For each longleaf pine smaller than 1 cm DBH, we recorded basal diameter and height, or DBH (if ≥ 1 cm DBH) and height, and the crown position of the individual. On 24 and 25 July 2019 (one month after the prescribed fire), all seedlings (< 1 cm DBH) were resurveyed and mortality status of all individuals was recorded. We used a second post-fire survey conducted between September and November 2020 to determine if any lag effects caused further seedling mortality [44].

2.3. Prescribed Fire

The thermocouple sampling points ($n = 40$) were deployed on a non-aligned, systematic sampling frame to ensure coverage of the plot. At each point, a temperature logger was buried below the soil surface and the thermocouple sensor end was placed at 25 cm above the ground prior to the fire. Temperatures were sampled every two seconds for the duration of the fire [45,46]. The prescribed fire occurred on 24 June 2019. The wind was out of the west at 0.45–1.79 m s⁻¹ with gusts up to 1.79 m s⁻¹; RH was 76% at time of ignition (10:00 EST) and fell to 48% by 14:00 EST (<https://fawn.ifas.ufl.edu/data/reports/-PutnamHall> accessed on 20 September 2021). One data logger failed, leaving 39 thermocouple data loggers with usable data.

2.4. Biotic Neighborhoods

To understand the influence of neighboring trees on longleaf pine mortality, we calculated neighborhood crowding indices (NCI) for each individual longleaf pine based on inverse distance weighted basal area of living longleaf pines (≥ 1 cm DBH):

$$\text{Longleaf pine NCI} = \sum_{j=1}^n (BA_j / \text{distance}_{ij})$$

where BA is the basal area of stem j and $distance$ is the distance of stem j to the focal individual i [47,48]. To examine the relative effects of longleaf pines versus other species, we divided overstory neighborhoods into longleaf pines (conspecifics) and oaks (heterospecifics). Based on preliminary analysis, we used density (stems per m²) rather than an oak NCI because it provided better or equal fits in all our models (based on AIC values; Appendix A Table A1). Based on the spatial relationships observed by Johnson et al. [20], we included all stems within 15 m of the focal longleaf pine. We used a proportional correction factor for individuals with spatial buffers extending past the plot boundary.

2.5. Lidar, Canopy Openness, and Topography

UAV Lidar data were collected using the GatorEye Unoccupied Flying Laboratory in June of 2019 prior to the prescribed fire ([20]; see www.gatoreye.org (accessed on 20 September 2021) for detailed information). Lidar point cloud returns (~292 pts/m²) were used to derive a digital elevation model, from which estimates of slope were derived using the terrain functions in the *raster* and *lidR* packages in R [49,50]. The normalized point cloud data were also used to create a canopy height model. Using the normalized point cloud, we calculated canopy openness as gap fraction—a proportional density of returns reaching a specified threshold (in this case, 1.37 m). We also estimated understory (≥ 0.5 and < 1.37 m) and ground vegetation (> 0 and < 0.5 m) densities, based on methods and bin thresholds described by Dell et al. [36], where densities are the ratio of returns above the height threshold to total number of returns [51]. All raster layers were calculated at 0.5 m resolution, and values were derived for each individual longleaf pine using a bilinear extraction method.

2.6. Data Analysis

2.6.1. Life Stage Determination

We fit a segmented regression equation to the pre-fire basal diameter and height data to determine the local break point where grass stage longleaf pine entered the bolt life stage. We found that 3.5 cm basal diameter was the breakpoint between the grass and bolt stages (Appendix A Figure A1). We classified longleaf pine stems 1 to 10 cm DBH as saplings, and trees as all longleaf stems > 10 cm DBH based on previous work at the OSFDP [20], resulting in four life stages used in this study (Figure 1).

2.6.2. Effects on Fire Temperatures

To determine biotic and environmental factors associated with fire temperature (as measured by thermocouple temperature), we constructed linear regression models to predict duration of thermocouple temperatures above 60 °C, maximum temperature, and area under the integrated curve of instantaneous temperatures >60 °C (see Appendix A Table A2 for model equations). Combined, these values represent standard indicators of temperature and fire residence times [52], and have been used in previous studies of fire effects and tree mortality [46,47,53–55]. A temperature of 60 °C constitutes an observed threshold where protein denaturation, tissue death, and often, plant mortality occurs [56,57]. We examined our regression models for violations of assumptions including multicollinearity and, after applying a natural log transformation to time above 60 °C, found all variance inflation factors were less than 2.0, indicating no worrisome multicollinearity.

2.6.3. Longleaf Pine Survival

We analyzed the probability of longleaf pine survival in response to longleaf pine NCI, oak density, understory density, vegetation density, gap fraction, and slope using a generalized linear mixed model with a binomial error distribution and logit link ([58]; Appendix A Table A2). We included each thirteen 1600 m² quadrat as a random effect to account for spatial autocorrelation. All continuous predictors were standardized by subtracting the mean and dividing by one standard deviation. To compare longleaf pine survival across life stages, we ran separate models for each life stage. Finally, to directly test the influence of longleaf pine basal area and oak density on survival across life stages, we included all individuals in a single model with interaction terms between longleaf pine NCI and life stage and oak density and life stage. We included the same ground vegetation density, understory density, gap fraction, and slope covariates in the full, life stage neighborhood interaction models, and covariates were standardized in the same manner as the individual life stage models.

3. Results

3.1. Effects of Local Conditions on Fire Temperatures

Fire temperatures varied greatly across the 39 thermocouple sampling points. The average maximum temperature was 342.6 °C, with the lowest peak temperature at any sensor reaching 52.8 °C and an absolute maximum temperature at any sensor of 836.1 °C. The mean time above 60 °C for a sensor was 488 s, with a minimum of zero seconds and a maximum of 7364 s. The area under the integrated curve for temperatures above 60 °C ranged from 0 to 310.59, with a mean of 17.7 across the 39 thermocouple sampling locations. Although the significance of predictors of fire temperature varied according to each temperature metric (Figure 2), the qualitative effect was mostly consistent. For all three metrics, fire temperature was positively related to longleaf pine basal area and understory density. Oak density was negatively correlated with fire temperature, but parameter estimates were not statistically significant. Observed maximum fire temperatures were negatively correlated with gap fraction, indicating significantly lower temperatures in gaps (Figure 2). Lidar-based estimates of vegetation density had variable (and insignificant) effects on fire temperatures. Predictors in the linear models explained 25.6, 28.2, and 14.7% of the variation in temperature for area under the integrated curve for temperatures >60 °C, maximum temperature (°C), and log-transformed time above 60 °C, respectively.

3.2. Longleaf Pine Survival across Life Stages

Longleaf pine survival varied widely across life stages, with the bolt stage exhibiting the lowest survival probability ($48.9 \pm 10.0\%$; $n = 98$). The tree stage had the greatest survival probability ($94.2 \pm 3.9\%$; $n = 81$). Survival probabilities of the grass stage exceeded the bolt stage by over 16% on average ($65.0\% \pm 10.6\%$; $n = 86$). Survival was dramatically higher for longleaf individuals in the sapling stage ($82.5 \pm 8.1\%$; $n = 139$).

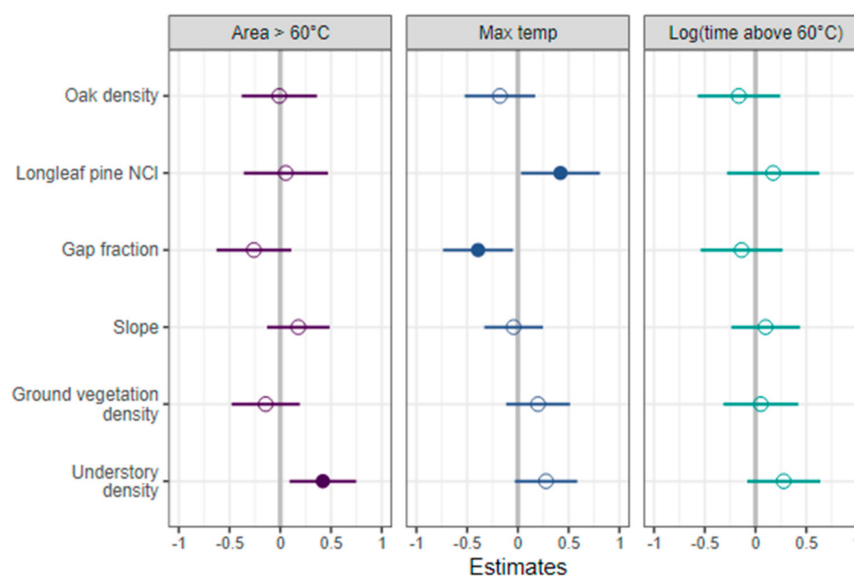


Figure 2. Coefficients from linear models estimating fire temperature metrics: area under the integrated curve for temperatures above 60 °C (**left**), maximum temperature (**center**), and time above 60 °C (log transformed; **right**). Filled circles indicate significant parameter estimates ($p < 0.05$).

3.3. Predictors of Survival across Life Stages

For grass stage and sapling longleaf pines, survival increased with initial size (height for grass stage individuals, DBH for saplings; Figure 3B). A nonlinear relationship between height and survival in bolt stage individuals (Figure 4) likely rendered height non-significant as a predictor. For individuals in the tree stage, which had the maximum survival probability, initial size and neighborhood effects were not significant. Slope was the strongest predictor of longleaf tree survival over our study period (with lower survival on steeper slopes), presumably through an environmental resource or fire behavior associated with slope [59]. Although considered a strong driver of longleaf pine recruitment [18], gap fraction showed mixed results as a predictor of survival. We found a significant, negative effect of gap fraction on bolt stage survival. Understory density, a positive predictor of fire temperature, showed a significant positive association with longleaf sapling survival, and negligible effects on survival of bolt and grass stages. We also found that lidar-based estimates of ground vegetation density were positively related to sapling survival, and marginal for the other life stages.

Survival probability declined significantly with increasing longleaf pine NCI for the three smallest life stages (Figures 3B and 5B). The same covariate positively correlated with all three fire severity metrics (Figure 2), suggesting fire-mediated distance- or density-dependent survival. Longleaf survival probability increased with neighborhood oak density for the three smallest life stages, with a strong significant effect on sapling survival (Figure 3B).

When life stage and neighborhood variables were included as interactions in the full (i.e., all life stages) model, a more specific effect of neighborhood on survival emerged (Figure 5, Appendix A Figures A2 and A3). For areas of low oak density (<0.012 stems/m²), predicted seedling survival (both grass and bolt stage) was higher than that of longleaf pine saplings. However, when a sapling was surrounded by a density of 0.015 or more neighboring oaks per m², survival of saplings exceeded that of both grass and bolt stage individuals, eventually approaching the survival probability of trees for areas of highest oak densities (Figure 5A and Appendix A Figure A2). Oak density had little influence on longleaf pine tree survival and longleaf trees were rarely found in areas of high oak stem density (Figure 5A and Appendix A Figure A3). Overall, oak stem density had varied and dynamic correlations with longleaf pine survival that was life-stage dependent.

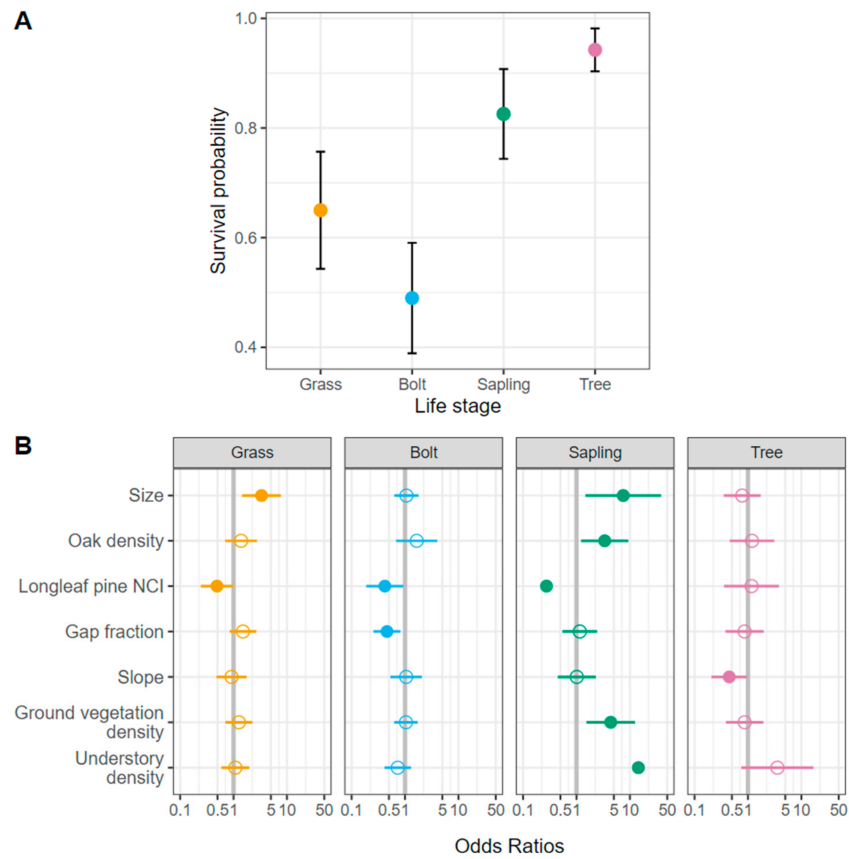


Figure 3. (A) Survival across life stages; error bars represent 95% confidence intervals of survival probabilities for each life stage and colors are unique to life stage and this palette will be used throughout following figures. (B) Plots depicting standardized odds ratio estimates (± 2 SE) from GLMMs assessing correlates of longleaf pine survival across life stages. Filled circles indicate significant parameter estimates ($p < 0.05$).

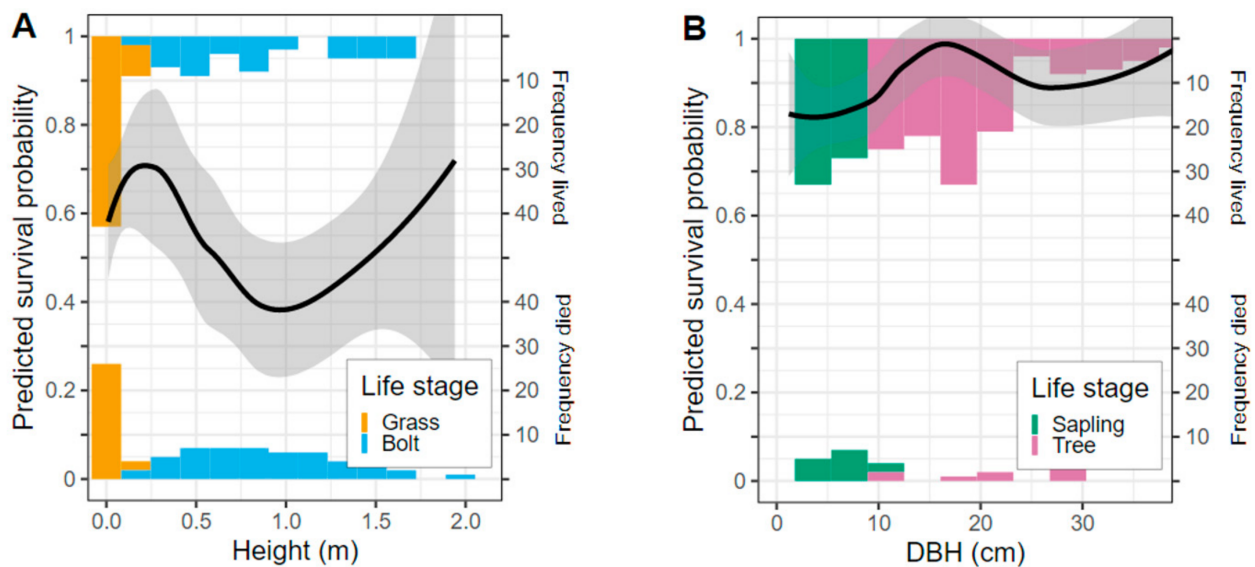


Figure 4. Longleaf pine survival probability as a function of size (height or DBH) for (A) grass stage and bolt stage longleaf pines, and (B) sapling and tree life stages. Regression lines are fit with LOWESS estimation (left axis). Note the frequency histogram axes on the right sides of the cave plots indicating the number of individuals in each size range that survived (top) or died (bottom).

The positive effects of oak density on longleaf pine survival were more pronounced for grass-stage individuals and saplings than for bolt-stage longleaf pines. In contrast to oak density, longleaf pine NCI had negative effects on the three smallest life stages (Figure 5B and Appendix A Figure A3). For longleaf pine NCI values less than 0.06 (m^2/m), predicted bolt stage survival probability was higher than that of grass-stage individuals. When longleaf pine NCI values exceeded 0.125 (m^2/m), predicted survival probabilities of both saplings and bolt-stage longleaf pine were lower than grass-stage individuals, eventually approaching zero for longleaf pine NCI values of 0.25 (m^2/m).

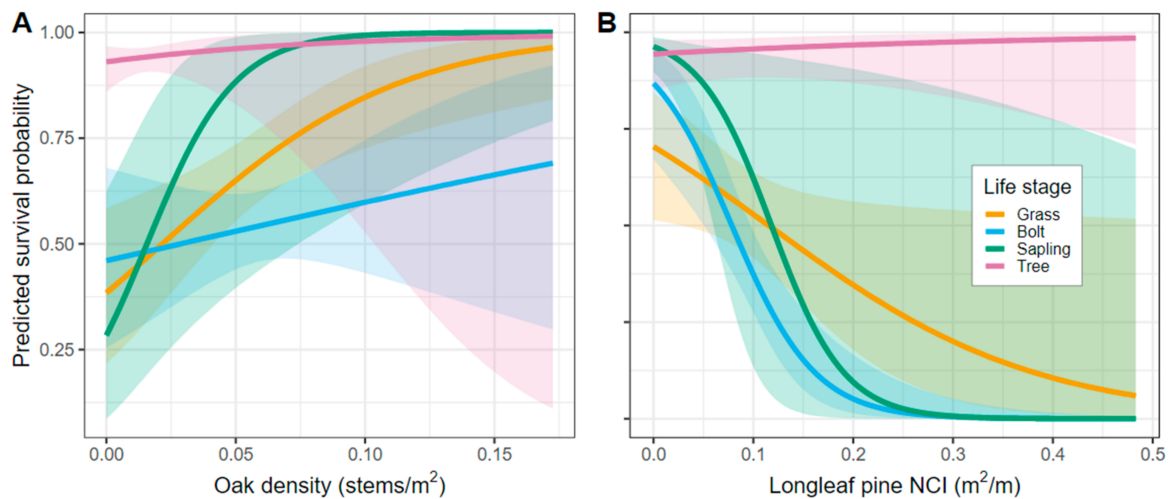


Figure 5. Survival probability as a function of oak (i.e., heterospecific) density (A) and longleaf pine NCI (B), with values partitioned by life stage. Results shown from full GLMM containing interactions between life stage and neighborhood metrics as well covariates for gap fraction, slope, understory density, and ground vegetation density. Shaded ribbons indicate 95% confidence intervals of parameter estimates by life stage. See Appendix A Figures A2 and A3 for individual panels per model.

4. Discussion

We quantified definitive patterns of survival across the life stages of longleaf pines during our study period, which included a warm season prescribed fire. Although scientists and land managers have long regarded the grass stage as highly fire resistant [32,33], data on continuous, size-based longleaf pine survival are sparse. We observed higher survival probabilities for grass-stage individuals compared to bolt-stage longleaf pines in this large area research plot. Longleaf pines in the bolt stage, an interval of prolific vertical growth, exhibit lower survival, likely because unprotected apical buds are susceptible to fire and the bark has not thickened. We found the survival probability of longleaf pines 12.5 cm DBH and larger approached a maximum of 94.2%, a rate which is relatively low for mature undisturbed trees [60,61], thus, highlighting the influence of fire on longleaf pine demography in this sandhill plot. In xeric sandhill forests of the southeastern United States, the influence of fire interacting with biotic plant communities can drive spatial patterns of tree survival [54] and recruitment [17]. Ecological interactions between coexisting species can shift during periods of stress and disturbance [1,62]. Our results indicate that these patterns can arise through positive and negative species interactions, which vary considerably across ontogenetic stages.

Microsite conditions can substantially impact local fuel loads and fire intensity [21,46,63]. We observed mixed results regarding the importance, direction, and magnitude of microsite characteristics' relation to fire temperatures. However, we documented a consistent positive relationship between longleaf pine NCI and all three fire-temperature metrics. Our results strongly agree with those of previous studies which found higher fire temperatures in areas of higher longleaf tree density or basal area [9,12,13,47,64]. Fire temperatures often peak in

areas of high longleaf pine density and basal area [9,10,65] due to increased fuel loads through accumulated pyrogenic needles; coarse woody debris can also add hotspots and heterogeneity to the temperature indices [66,67]. We do not have detailed data on the composition and density of herbaceous and small woody species in the understory that may also influence fire behavior and temperatures, leaving some uncertainty in our characterization of the large-area plot. Considering the variable effects of other parameters across our models, the pervasive pyrogenicity of longleaf pine needles is a critical driver of longleaf pine dynamics.

Quantifying fire severity and intensity across large landscapes remains a challenge [68,69], and different metrics of fire temperature can be driven by different local conditions [47,54]. Although maximum temperature, time above 60 °C, and area under the integrated 60 °C curve were significantly correlated at each thermocouple location (Pearson's correlation, $\rho = 0.43$ to 0.55), local conditions likely affected each metric differently. For example, we observed significantly lower maximum temperatures in areas with higher gap percentage, but gap fraction did not seem to drive duration of temperature intensity (i.e., time >60 °C). Understory density, which accounts for shrubs, tall grasses, and resprouting oaks, was significantly related to time >60 °C, but not to maximum temperature or area under the 60 °C curve, but again we do not currently have detailed information of the species composition of this layer which likely contributes to fire heterogeneity on the OSFDP. The overall predictive power of our models ($R^2 = 0.147$ to 0.282) indicates other unmeasured factors (e.g., soil moisture or fine fuels) are driving fire temperature. Our hottest and longest duration above 60 °C was recorded from a location within a downed oak top indicating the distribution of coarse woody debris can aid in understanding fire effects [70]. Additionally, it is possible our lidar-based understory and ground vegetation estimates did not accurately quantify the heterogeneity in understory- and ground-level vegetation.

Size-dependent survival of trees is a global phenomenon [71]. However, our results indicate that other variables, namely the composition of biotic neighborhoods, including neighboring trees, understory, and ground vegetation density, mediate size-dependent survival. The qualitative effects of neighboring trees on longleaf pine survival were consistent across the three smallest life stages (i.e., grass stage, bolt stage, and saplings). Positive interspecific interactions with oaks appear to promote longleaf survival, at least in earlier life stages. One possible reason might be relative reduction in fuel loading of oak litter compared to longleaf pine. Increased moisture availability in areas of higher oak densities is another plausible mechanism facilitating juvenile longleaf pine survival during fire-free intervals [15,72]. Our results suggest this positive influence applies to periods of recurrent fire as well.

In systems evolved to withstand frequent, widespread abiotic disturbances, ecological interactions (i.e., those affecting per capita dynamics) among and between species may change dramatically over time [69,73–75]. Shifts in growth-survival trade-offs across ontogenetic stages are frequent in many long-lived species (e.g., [76]). We show that population dynamics of longleaf pine are influenced by conspecifics, heterospecific trees (i.e., oaks), and, to a lesser extent, understory and ground vegetation layers. Consistent with previous demographic studies at other longleaf forests (e.g., [7,13]), we document marked decreases in longleaf pine survival in areas of higher longleaf densities. Conspecific distance-dependent survival is a mechanism invoked to explain coexistence in plant communities and has been observed in numerous different forest types [77–80], including frequently disturbed systems [81]. In contrast to those systems, which are driven by intraspecific competition and natural enemies, distance dependence in longleaf pine forests is driven largely by fire, further underscoring fire as a community-regulating ecological process [82].

Longleaf pine demonstrates a distinct demographic bottleneck in the transition from grass to bolt stages. Low survival of bolt-stage longleaf pines during fire can be used to manage longleaf pine populations. Managers should consider timing of stage transition to maximize the effectiveness of fire to control pine densities, particularly in locations where fire is more heavily influenced by local biotic conditions (e.g., areas of high oak or longleaf pine densities). Large, synchronized seed output events across longleaf populations will

result in cohorts of seedlings, which will eventually shift to grass and then bolt stage within similar time periods (i.e., 3–7 years; [7,83]). Further investigations into the cues of life-stage transitions, especially the relevant environmental and biotic predictors of the transition to the bolt stage, could considerably improve longleaf pine management and demographic projections. To maintain the complex mosaic of the longleaf system, management operations should consider biotic neighborhoods and the role of stage transitions in the intensity and timing of fire application.

Author Contributions: D.J.J. conceived the project. L.M., D.J.J. and K.P. carried out the analysis and wrote the initial draft of the manuscript. Materials, mental support, and crucial feedback were provided by S.L.F., R.M.C., S.B., E.N.B., W.D. and G.A.P. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Data available upon request.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

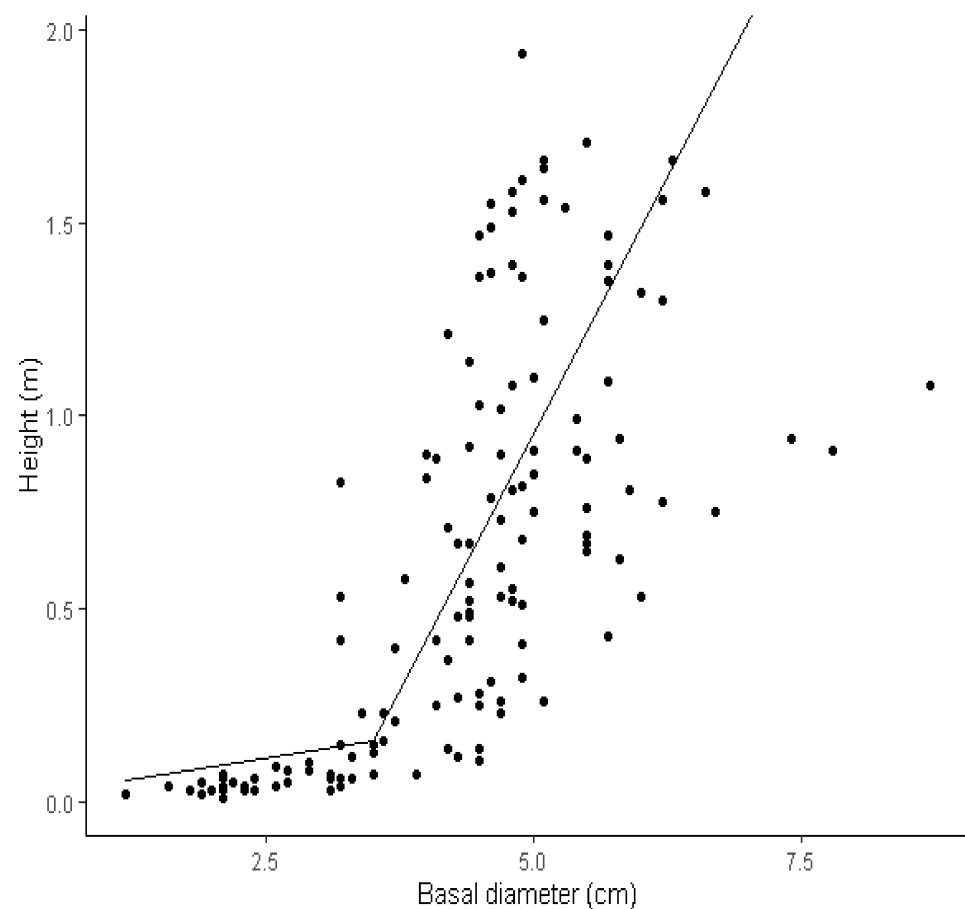


Figure A1. Longleaf pine seedling basal diameter to height relation with segmented regression fit.

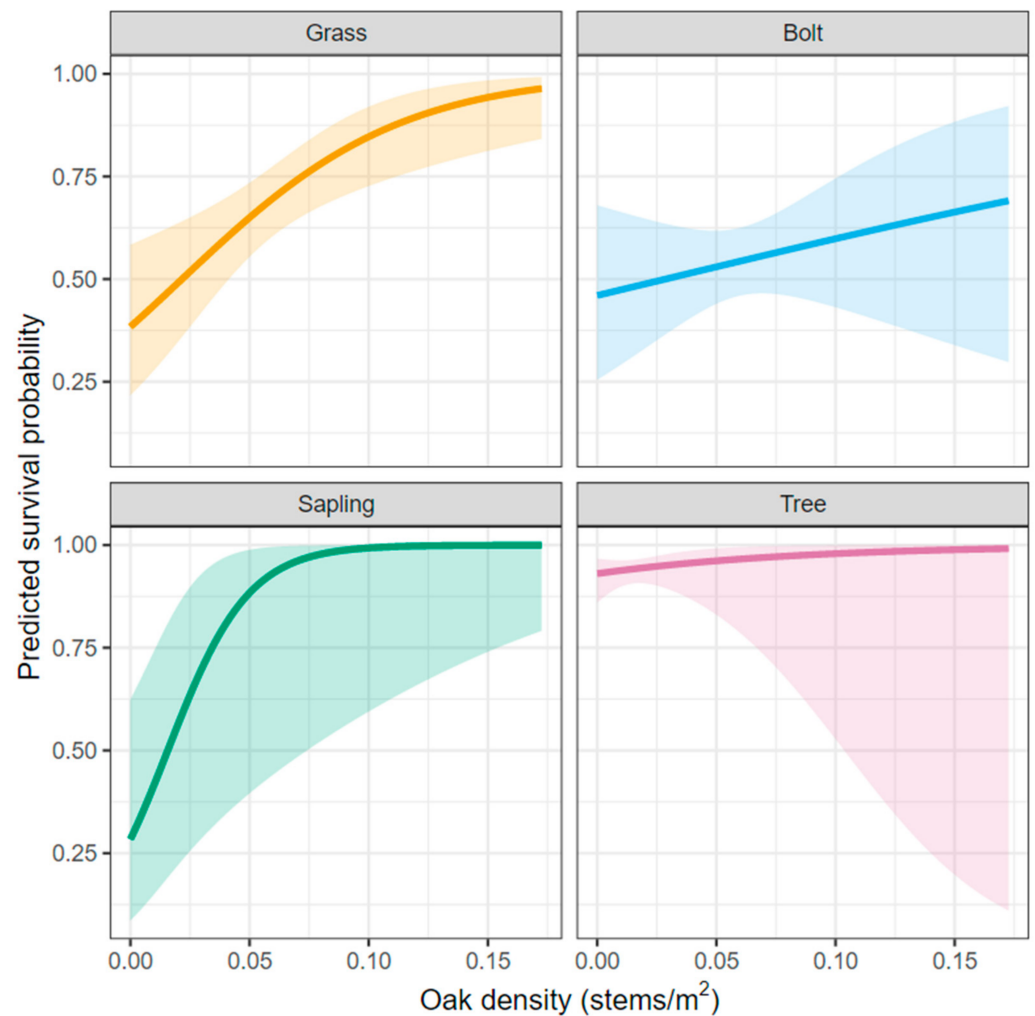


Figure A2. Longleaf pine survival probability as a function of oak (i.e., heterospecific) density with values partitioned by life stage. Results shown from full GLMM containing interactions between life stage and neighborhood metrics as well covariates for gap fraction, slope, understory density, and ground vegetation density. Shaded ribbons indicate 95% confidence intervals of parameter estimates by life stage.

Table A1. Comparison of AIC values for candidate LMs and GLMMs used to assess the response of fire temperature and longleaf pine survival probabilities to biotic neighborhoods and abiotic conditions that included different oak neighborhood metrics. Best fit models are shown in bold. Oak density provided equal (AIC values within 2.0) or better fits in all modeling scenarios.

Model	AIC	
	Inverse Distance Weighted Oak Basal Area	Oak Density
Maximum temperature	536.48	533.48
Area below curve for temperatures >60° C	419.75	419.16
Time above >60° C	158.58	157.51
Grass stage survival	100.28	99.36
Bolt stage survival	79.45	72.95
Sapling survival	131.27	131.17
Tree survival	71.06	71.96

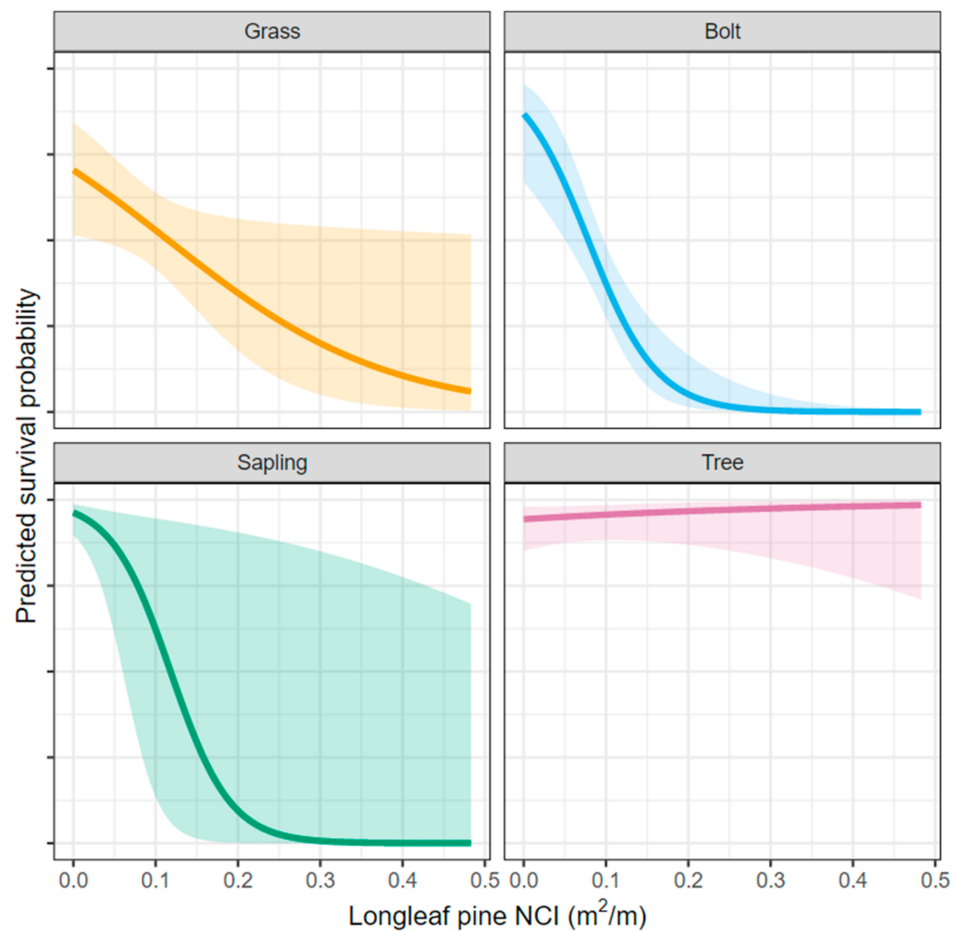


Figure A3. Survival probability as a function of longleaf pine NCI, with values partitioned by life stage. Results shown from full GLMM containing interactions between life stage and neighborhood metrics as well covariates for gap fraction, slope, understory density, and ground vegetation density. Shaded ribbons indicate 95% confidence intervals of parameter estimates by life stage.

Table A2. LM and GLMM model equations used to analyze fire temperature response and individual longleaf pine survival probabilities, for thermocouple *i* and individual *i*, respectively. The γ s are normally distributed random intercept terms for *j* quadrats.

Model	Equation
Thermocouple temperature Maximum temperature, Time above 60 °C, Area under the integrated curve for temperatures >60 °C	$Temperature_i = \alpha + \beta_1 Oak\ density_i + \beta_2 Longleaf\ pine\ NCI_i + \beta_3 Gap\ fraction_i + \beta_4 Slope_i + \beta_5 Ground\ vegetation\ density_i + \beta_6 Understory\ density_i$
Individual survival model (distinct life stages)	$Survival_{ij} = \alpha + \beta_1 Size + \beta_2 Oak\ density_{ij} + \beta_3 Longleaf\ pine\ NCI_{ij} + \beta_4 Gap\ fraction_{ij} + \beta_5 Slope_{ij} + \beta_6 Ground\ vegetation\ density_{ij} + \beta_7 Understory\ density_{ij} + \gamma_{quadrat_j}$
Interaction model	$Survival_{ij} = \alpha + \beta_1 Oak\ density_{ij} * Life\ stage_{ij} + \beta_2 Longleaf\ pine\ NCI_{ij} * Life\ stage_{ij} + \beta_3 Gap\ fraction_{ij} + \beta_4 Slope_{ij} + \beta_5 Ground\ vegetation\ density_{ij} + \beta_6 Understory\ density_{ij} + \gamma_{quadrat_j}$

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