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Tradeoffs between timber and wildlife habitat quality increase with density in longleaf pine (*Pinus palustris*) plantations

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ABSTRACT

Longleaf pine (*Pinus palustris*), a historically abundant tree species in the southeastern United States, is often planted to restore the ecologically and culturally important longleaf pine ecosystem that once covered vast acreages in the southeastern United States. Government cost-share programs that support establishment of these plantations place restrictions on planting rates to promote wildlife habitat, as greater tree planting density may reduce canopy openness and herbaceous plant cover that are critical components of habitat for priority species, including gopher tortoise (*Gopherus polyphemus)* and Bachman's sparrow (*Peucaea aestivalis*). However, there is expressed concern among some forest managers that more open grown trees in the plantations will be of inferior timber quality with more and larger horizontal branches and associated knots. We examined how density affects dynamics and tradeoffs among understory vegetation structure and composition, longleaf pine stem form (branch density and straightness), and longleaf pine survival by sampling 73 plantations of various ages (5–25 years) and planting rates (653–2445 trees per hectare (TPH)/264–990 trees per acre (TPA)) throughout the southeastern United States. We documented a relationship between planting rate and longleaf pine stand density at time of sampling ($r = 0.69$, $p = 0.0001$) and relationships between stand density and habitat and timber quality metrics. Greater stand density resulted in lower tree diameters but greater stand basal area than lower stand density. Higher planting rates led to lower branch density and lower straightness grades than lower planting rates. Canopy openness decreased with greater stand density, and bare ground cover and herbaceous cover decreased as density and stand age at time of sampling increased. Based on our results, we suggest that lower maximum planting rates are appropriate when wildlife habitat is a program objective because lower rates result in fewer tradeoffs, as reducing planting rates slows degradation of wildlife habitat when compared with higher maximum planting rates that have only mixed benefits on timber quality.

1. Introduction

Longleaf pine *(Pinus palustris)* ecosystems once covered over 37 million hectares in the southeastern United States (Frost, 1993) and are central to the designation of the North American Coastal Plain as the world's 36th biodiversity hotspot (Noss et al., 2015). Due to declines in fire occurrence because of fire suppression and lack of human ignition, intensive logging, and conversion to other land uses (e.g., agriculture, forest plantations), longleaf pine forests declined to only 3–5 % of the pre-colonial range (Frost, 1993, Guldin et al., 2016). Many plant and animal species associated with longleaf pine communities are now declining or rare (VanLear et al., 2005, Mitchell et al., 2006).

Longleaf pine conservation efforts are often focused on using plantation forestry to restore the longleaf pine ecosystem, but densely stocked plantations may fail to provide many ecosystem services (Oswalt et al., 2012). Conservation partners, including non-industrial private landowners, non-governmental organizations, and government agencies, typically manage longleaf pine forests for diverse objectives, including producing forest products, providing wildlife habitat, yielding aesthetics, offering recreational opportunity, and conserving biodiversity. However, plantations may not adequately mimic the characteristics of the historical longleaf pine ecosystem, including the provision of habitat for important flora and fauna (Greene et al., 2019). Densely stocked pine plantations transition quickly to the stem exclusion stage of

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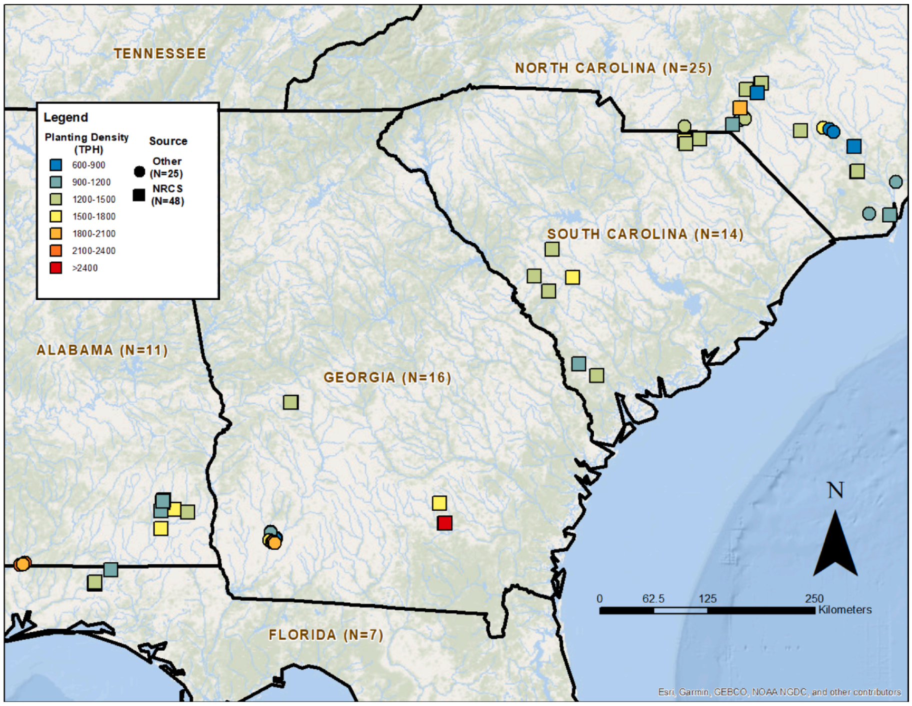

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Fig. 1. Map showing all stands sampled. Square points are NRCS cooperator sites, and circular points are all other sites. Symbol color represents planting rate.

stand development, at which point crown closure casts heavy shade on the understory. This rapid canopy closure results in an understory with low herbaceous cover and biomass, which results in lower habitat quality for many species of wildlife (Harrington et al., 2013).

Longleaf pine is also recognized for its value as timber or other related forest products, but timber quality can be affected by planting density. Longleaf pine is resistant to fusiform rust (*Cronartium fusiforme*) and the southern pine bark beetle (*Dendroctonus frontalis*) and has been proven to be less vulnerable to wind damage than other pines (Van Lear et al., 2005; Oswalt et al., 2012; Samuelson et al., 2014). Common silvicultural recommendations for timber-focused stands are to plant 1236–1853 trees per hectare (TPH) and manage for early thinnings to promote pole or sawtimber quality stems (Dickens et al., 2012). Recommendations for planting in old fields suggest using 1483–2223 TPH to foster an earlier first thinning and to produce fuels to support prescribed burning earlier in the rotation (Albritton, 2012). Proponents of higher planting rates indicate it will maximize options for managing for multiple forest products. High stocking rates promote rapid canopy closure, which leads to self-pruning, smaller branches and knots, and higher quality wood products from crop trees (Kellomäki, 1984, Ballard and Long, 1998, Dean, 1999, Harrington, 2011, Albritton, 2012, McGuire et al., 2021). Early recommendations for planting rates in longleaf pine plantations were as high as 3459 TPH and may reflect rates proposed to provide protection from high seedling mortality associated with low quality bareroot stock (Wahlenberg, 1946). Despite the important implications of branching and knots on lumber strength, little information is available on the relationship between planting rates and tree form for plantation grown longleaf pine (South, 2006).

Initial planting rate affects light dynamics and thus vegetation composition and structure in young plantations. In fact, previous studies documented an inverse relationship between planting rate and biodiversity, and between planting rate and herbaceous cover (Brockerhoff et al., 2003, Carnus et al., 2006, Newmaster et al., 2006). Lower planting rates, in the range of 618 to 1236 TPH, have been recommended when managing for wildlife to prolong the onset of crown closure and maintain conditions for open forest species (e.g., gopher tortoise *(Gopherus polyphemus)*, Bachman's sparrow (*Peucaea aestivalis*)). Wider spacing reduces the costs associated with establishment because it requires fewer seedlings and less site preparation, unless survival is low and replanting is necessary. The need for pre-commercial thinning is often reduced, though management of competing vegetation may be necessary.

More than half (58 %) of forested land within the southeastern US is owned by private non-corporate landowners (Oswalt et al., 2019), making it critical to include these properties if conservation programs are to be effective across at a broad scale. Government incentive programs encourage private landowners to restore longleaf pine communities by providing financial and technical assistance. Two primary incentives programs are the Longleaf Pine Initiative (LLPI) and the Working Lands for Wildlife Gopher Tortoise Partnership (WLFW) administered by the Natural Resource Conservation Service (NRCS). The LLPI provides resources in nine states to support establishment of longleaf pine forest and implement conservation practices to maintain ecosystem function. The WLFW program is concentrated on the southern portion of the longleaf pine range, specifically targeting longleaf pine community restoration to provide habitat for gopher tortoise. Moreover, the NRCS has different recommendations for wildlife-focused plantations (1122–1495 TPH or 400–600 TPA) and timber-focused plantations (1483–2223 TPH or 600–800 TPA). Gopher tortoise habitat is characterized by sparse woody understory cover, abundant herbaceous cover, open canopy, and bare sandy soil (Wilson et al., 1997, McIntyre et al., 2019). This vegetation condition may support other longleaf pine associate species, including the Bachman's sparrow (McIntyre et al., 2019; Fish et al., 2020; Choi et al., 2021). These attributes of gopher tortoise habitat are not associated with densely stocked plantations, and active management is required to maintain openness in the canopy and herbaceous groundcover. Thinning can be used to slow canopy closure, but prescribed fire or other vegetation control is necessary to limit woody plant cover and favor forbs and grasses (Harrington et al., 2013).

Research on longleaf pine planting regimes is limited (Harrington, 2011) and only more recently explored for relationships with wildlife habitat quality (Wheeler et al., 2020). South (2006) suggested the decision to use a planting rate less than 1235 seedlings per ha is straightforward if the landowner is primarily interested in maximizing the stand's net present value. However, it is not clear if there is an optimal range of planting densities where both wildlife and timber are enhanced. We quantified the relationships among planting density, timber quality, and vegetation composition and structure in longleaf pine plantations across the southeastern US. We evaluated privately owned and publicly managed properties with a range of site histories and management objectives. We were interested primarily in evaluating how planting rate affects longleaf pine survival, habitat quality metrics such as canopy openness and understory composition and structure, and treeform metrics that affect economic return such as branchiness and straightness. We sought to examine if longleaf pine quality is positively correlated with planting rates and if important herbaceous groundcover is negatively correlated with planting rates as has been widely speculated. We designed our study to encompass a broad range of planting densities, and a mix of ages and ownerships, so that we could document survivorship and growth patterns of seedlings across a large portion of the longleaf pine range. By including a wide range of planting rates, we were able to evaluate the direction and shape of relationships to determine if there is an optimal rate or range where both timber and wildlife objectives are enhanced.

2. Methods

2.1. Study area

We sampled longleaf pine plantations in 2019 and 2021, with sampling locations ranging from North Carolina westward to Alabama and south to Florida (latitude range from 30.84° N to 34.74° N; longitude range from −87.09° W to −79.97° W) (Fig. 1). The geographic range included the Piedmont and Coastal Plain physiographic regions and incorporated a wide variation in soil type and moisture levels. The most common soil series were Waukegan, Onteora, Talbott, and Lackawanna. Prior land use varied among sites, with some plantings occurring on previously forested sites and others on old-field or pasture sites.

2.2. Study design

Initial selection criteria in 2019 included plantations that: (1) had not been thinned or raked, (2) were at least 2 ha, and (3) were between 5 and 20 years since planting. In 2021, we increased the minimum age to 8 years to avoid younger plantations that had limited canopy formation. A random subset of projects fitting these criteria was identified in the NRCS database, and landowners were contacted to request participation in the project. We selected sites to have a wide geographic range, but to maximize sampling efficiency sites were clustered by county, based on which counties had the most NRCS cooperators. We prioritized sampling on properties of NRCS cooperators, but we sampled plantations on other properties to supplement the NRCS sites.

In 2019, we measured 27 plantations; 14 were on properties managed by the North Carolina Wildlife Resource Commission (referred to as NCWRC gamelands), 13 were privately owned plantations from the NRCS database, and 2 were privately owned plantations not from the NRCS database. In 2021, we measured 46 plantations; 33 were privately owned NRCS program properties, 10 were affiliated with a privately-owned research forest, and 3 were affiliated with a US Forest Service property. We measured sites from June to October in 2019 (North Carolina and South Carolina) and 2021 (South Carolina, Georgia, Alabama, Florida).

2.3. Data collection

Within each stand, a minimum of 3 0.02-ha (0.05-ac) plots were measured, with additional plots based on stand size; plot size was expanded up to 0.04 ha (0.10ac) in sparse stands to sample a minimum of 10 planted longleaf per plot. For every longleaf pine in a plot, we recorded basic timber measurements, and for a subset of the 5 longleaf pines closest to plot center, we recorded more detailed quality metrics. Timber measurements were diameter at breast height (DBH), total height, height to live crown, forks/ramicorn branches (noted on a presence absence basis), status (living, dead, grass, or bottlebrush), and crown class (the crown's position relative to the canopy). Grass and bottlebrush refer to early stages of longleaf pine development, grass being the earliest stage before any vertical growth, and bottlebrush being the second stage, prior to branch development. For a subset of 5 trees, we additionally measured branch density and straightness. Branch density was measured by recording all branches within a meter surrounding breast height by size class (<2.54 cm, 2.54 cm-7.62 cm, >7.62 cm) and categorized as being living or dead; later we used these data to calculate weighted branch density, which was the sum of branches weighted by the midpoint of their size class. The straightness of the main stem was graded using a visual stem assessment scale adapted from MacDonald et al. (2001) (Table S1). Stems were graded based on the length and number of straight stretches of main bole within the first 5 m; a 1 (the lowest grade) indicated no stretches of straight stem within the first 5 m. A score of 7 (the highest grade) indicated a straight stretch of 5 m along the bole. We estimated initial planting rate by measuring the average distances between trees within planted rows; however, for stands with less of an apparent pattern in the placement of planted trees, we used the reported target planting rate from landowner documents.

We measured understory vegetation using a modified version of the Wiens pole or point-contact method (Wiens, 1969, Wiens and Rotenberry, 1981, Moorman and Guynn, 2001). A graduated pole was held vertically and placed at points along transects across the plot, and any intersection of vegetation with the pole was recorded by cover class and height. The pole used was 2 m long and graduated at 0.1-m intervals for the first 0.5 m, and at 0.5-m intervals for the upper 1.5 m of the pole. Transects originated at plot center and extended for 5 m in each cardinal direction, with an additional point at plot center, for a total of 21 points. We recorded contacts with the pole into the following cover classes – wiregrass (*Aristida stricta)*, broomsedge (*Andropogon virginicus*), other grass (including non-natives), legume (in 2021 only), other forb, longleaf pine, other pine, and other woody. We measured ground cover under the pole as litter, bare ground, or a vegetation cover class when applicable. Simplified contact cover classes were created to summarize total grass cover (combined broomsedge, wiregrass, and other grass), total forb cover (forbs and legumes in 2021), and total herbaceous cover (total grass and forb cover).

We measured canopy cover using a spherical densiometer with readings recorded at the ends of each vegetation transect and plot center (for a total of 5 readings per plot) in 2019. In 2021, we collected hemispherical photos using a Nikon D700 with a fisheye lens mounted and leveled pointing directly up from 1 m above the ground at plot center, and later analyzed using Gap Light Analyzer (Frazer, 1999). The two methods were calibrated using the method described in Beeles et al. (2022).

Several site characteristics were compiled from either the NRCS database or communication with the landowners. We obtained site history information from landowners, and when that was not possible, by using satellite imagery. The percent sand, silt, clay, organic content, bulk density, soil type, and site index for each site were extracted from Web Soil Survey using plot geographic coordinates (Soil Survey Staff, n.d).

2.4. Statistical analyses

All plot level tree measurements were averaged for each stand, including basal area, current stand density, total height, live crown ratio, quadratic mean diameter, straightness, branch density, and canopy cover. We calculated longleaf pine survival by dividing the density at the time of measurement by the initial planting rate by plot and averaged for each stand. We evaluated treeform characteristics in plantations with trees meeting a minimum criterion of 4.9 m (based on 16-foot log) to exclude stands with trees still in the bottlebrush and grass stages. This reduced the timber quality analysis to 60 stands.

We summarized Wiens pole data in multiple ways: (1) horizontal percent cover for each cover class, defined as the percentage of the 21 transect points containing that cover class, at any height along the pole, (2) vertical vegetation density, defined as the average number of vegetation contacts along the pole across all transect points, (3) average vegetation height, defined as the average of the max contact height along the pole across the 21 transect points, and (4) vegetation heterogeneity index (VHI), defined as the variation in vertical density within a plot, as described in Wiens (1969). Plot-level values for each Wiens pole metric were averaged for each stand.

Given the potential correlation among the soil variables, we used a collinearity test to identify potential covariates to be used in analyses relating planting rates and quality trends. As expected, soil texture components (the percentage of sand, silt, and clay in the soil) were highly correlated ($r_{sand,silt} = 0.84$, $r_{sand,clay} = 0.87$, $r_{clay,silt} = 0.48$). To eliminate this multicollinearity, we elected to retain only the percentage of sand in the model selection, as percentage of sand had the widest and most variable spread of data. Longitude and latitude were highly correlated, limiting the inclusion of only one of the variables for modeling purposes. Longitude was selected because it had a more even distribution than latitude.

To evaluate the relationships between planting rate and timber and habitat quality characteristics, we first evaluated simple correlations between planting rate and stand density and each characteristic (PROC CORR, SAS). We then used best fit regression modeling selection procedures to evaluate if the relationship with stand density remained important when other covariates were included. Models were selected using a backwards general linear model selection process where models were ranked based on the Akaike information criterion (AIC), with goodness of fit determined by comparing the AIC to the full model AIC (PROC GLMSELECT). Input parameters included percent sand, site index, bulk density, organic content, longitude, stand density (however, we instead used planting rate when modeling survival and stand density), height, plantation age, and interaction terms between density and plantation age. Bulk density and percentage of organic content in soil were never selected, and therefore removed from further consideration. We used a T-test to evaluate the effect of stand density on the presence of wiregrass, broomsedge, and legumes (continuous variables were converted to presence/absence due to low occurrence) (PROC TTEST). We also used a T-test to compare differences in response variables between previously agricultural and forested sites. We performed all analyses using SAS software, version 9.4 (SAS, 2013).

To summarize the relative value for timber and wildlife objectives, we calculated the overall benefit score using methods from Bradford and D'Amato (2011). Each individual characteristic was relativized on a scale of 0–1, and detrimental characteristics (weighted branch density, large branches, and woody understory cover) were inverted to scale so that lower values of detrimental characteristics represented higher benefit values. Average timber benefit was based on straightness, weighted branch density, number of large (>3 in.) branches, and live crown ratio. Average wildlife benefit was based on canopy openness, percent bare ground cover, percent herbaceous cover, and percent woody understory cover. The overall benefit was calculated by averaging individual benefits including both management objectives. To evaluate tradeoffs between planting rates associated with each management goal (timber and wildlife), we calculated the root mean squared error (RMSE) of individual benefits compared to the overall benefit. A high RMSE indicates greater differences (trade-offs) among individual benefits.

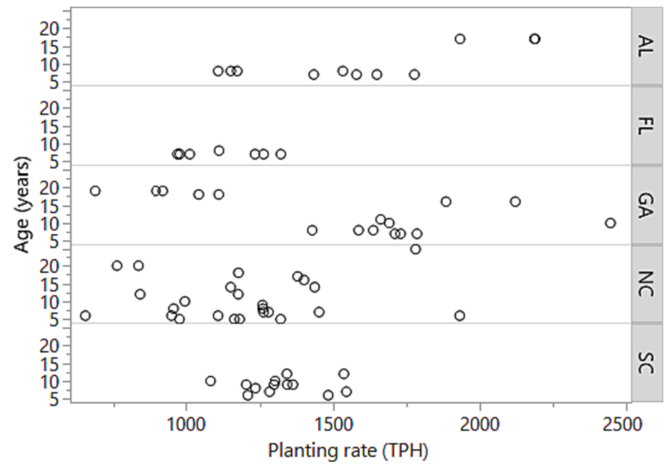

Fig. 2. Age of longleaf pine plantations established across a range of planting rates (trees per hectare) displayed by state.

Table 1
Summary statistics for variables characterizing the vegetation structure and composition of longleaf pine plantations across the southeastern US (n = 73).

Variable	Mean	Std. Deviation	Minimum	Maximum
Stand Summary				
Age	10	4.7	5	25
Planting Density (TPH)	1,344	364	654	2,445
Basal Area (m^2/ha)	8.5	6.0	0.1	27.0
Density (TPH)	860	361	199	2,319
Average Height (m)	7.3	3.1	2.2	15.8
Quadratic Mean Diameter (cm)	4.5	1.7	0.7	9.1
Survival (%)	60	22	17	100+
Soils				
Sand (%)	86.3	10.9	42.6	97
Site Index	68	7	53	80
Quality				
Straightness	5	1	1	7
Branch Density	3.96	1.84	0	9.15
Live Crown Ratio	0.73	0.12	0.37	1
Habitat				
Canopy Openness (%)	50	22	6	98
Broomsedge Cover (%)	12	15	0	58
Wiregrass Cover (%)	3	7	0	31
Legume Cover (%)	0	1	0	2
Herbaceous Cover (%)	53	25	0	99
Shrub Cover (%)	27	17	0	59
Mean Understory Height (m)	0.62	0.27	0	1.50
Bare Ground Cover (%)	24	18	0	68

3. Results

3.1. Plantation Summary

Longleaf pine plantations ranged from 654 to 2445 TPH planting rate and were 5 to 25 years of age (Fig. 2, Table 1), with current stand density (in 2019 or 2021) from 81 to 2319 TPH. Average survival was 60 %, with a median of 61 % and ranging from 17 % to 100 %. Survivorship did not differ based on previous land use (mean and SD for agriculture and continuously forested was 53 % ± 18 % with a median of 52 %, and 61 % ± 22 % with a median of 65 %, respectively; p = 0.4). Canopy openness averaged 43 % ± 14 %, ranging from 6 % to 66 %. We

Table 2
Correlation coefficients and associated p-values for relationships between planting rate and stand density, and habitat and timber quality indicators. Significant p–values (α = 0.10) are shown in bold.

	Stand Density (TPH)	*p*	Planting rate (TPH)	*p*
Stand Density (TPH)	.		0.69	**<0.0001**
Planting rate (TPH)	0.69	**<0.0001**	.	
Diameter (cm)	−0.21	**0.07**	−0.2	0.1
Basal Area (m^2/ha)	0.38	**<0.001**	0.19	0.11
Straightness Grade	−0.29	**0.02**	−0.17	0.16
Weighted Branch Density	−0.51	**<0.0001**	−0.31	**0.01**
Canopy Openness (%)	−0.28	**0.01**	−0.32	**0.01**
Bare Ground (%)	−0.14	0.24	−0.31	**0.01**
Herbaceous Understory Cover (%)	0.15	0.22	0.01	0.94
Forb Cover (%)	0.22	**0.06**	0.05	0.68
Grass Cover (%)	0.03	0.77	−0.05	0.69
Vegetation Heterogeneity Index	−0.24	**0.04**	−0.23	**0.05**

observed a wide range in understory vegetation conditions across the plantations, with herbaceous cover averaging 54 % ± 25 %, and woody cover averaging 34 % ± 21 %. Bare ground cover averaged 25 % ± 18 %, ranging from 0 to 68 %.

3.2. Effects of planting rate and stand density

Planting rate was related to stand density, and to timber and habitat quality metrics. Independently, planting rate was strongly correlated with stand density (r = 0.69, p < 0.0001). Understory woody cover increased with greater planting rates, and weighted branch, canopy openness, and understory vegetation heterogeneity decreased with greater planting rates (Table 2). As stand density increased, basal area

Table 4
Selected best fit models for survival and density. Models were selected via backwards selection based on AIC. Model goodness of fit statistics are displayed in Table 2.

Response	Parameter	Estimate	Std. Error	Pr > |t|
Survival	Intercept	−3.25	0.60	<0.0001
	Planting Rate	−2.65E-4	1.41E-4	0.06
	Age	−0.03	1.4E-4	0.02
	Planting Rate (TPH)*Age	2.02E-5	1.0E-5	0.05
	% Sand	0.003	0.002	0.15
	Longitude	−0.5	0.007	<0.0001
Density	Intercept	−5007.1	780.69	<0.0001
	Planting Rate*Age	0.045	0.005	<0.0001
	Age	−63.09	8.80	<0.0001
	% Sand	4.57	2.34	0.051
	Longitude	−66.35	8.74	<0.0001

Table 3
Best fit models were selected using a backwards selection procedure, based on the Akaike's information criteria (AIC). All parameters were included in the full model. Symbols represent the direction of the effect for parameters included in alternative models. K indicates the number of parameters and ΔAIC indicates the change from the full to the selected model. TPH represents planting rate in models for survival and density, but stand density (at time of sampling) for all other models. Age is included as a continuous variable but displayed as categorical in associated figures to highlight relationships with planting rate and stand density.

Model	TPH	Age	TPH* Age	SI	%Sand	Long.	K	ΔAIC	R^2
Full							6		
Survival	–	–	+		+	–	5	−1.83	0.50
Density		–	+		+	–	4	−3.18	0.73
QMD		+	–				2	4.65	0.32
Basal Area	+	+					2	−2.78	0.34
Straightness	–				+		2	−3.07	0.14
Branch Density			–			+	2	−4.41	0.31
Bare Ground			–			–	2	−5.73	0.24
Canopy Openness	–	–		–		–	4	−3.62	0.30
Herbaceous Cover			–		–	–	3	−3.49	0.26

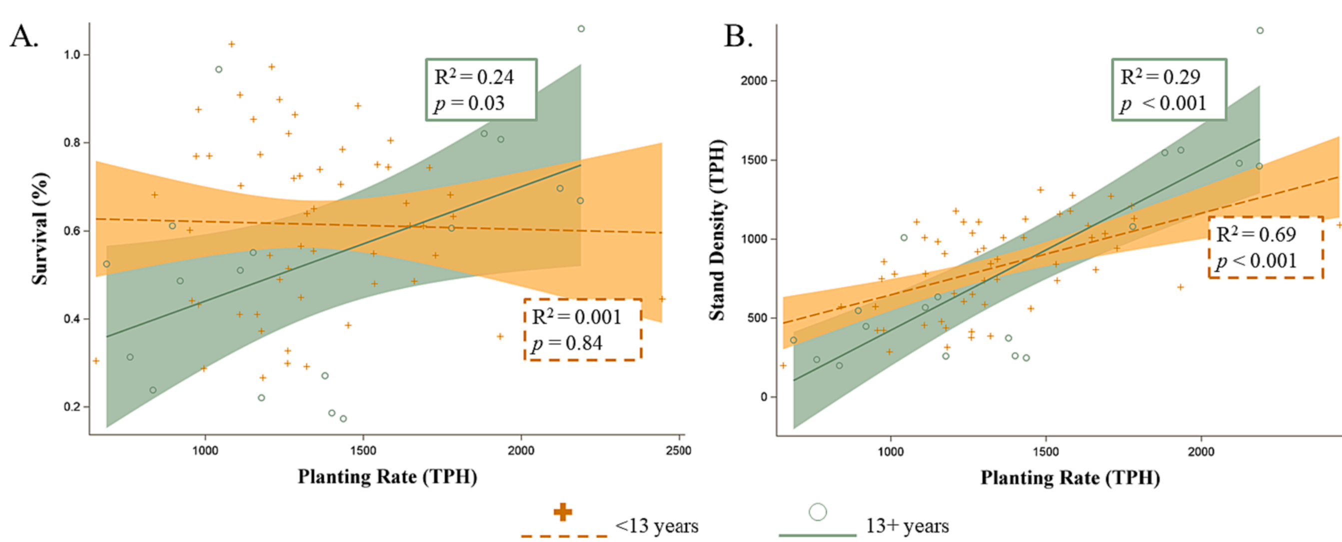

Fig. 3. Planted longleaf pine survival (A) and stand density (B) plotted against planting rate. Sites were divided into two age classes, which is reflected by symbology (Table 3). Boxes indicate R^2 and p-values for each regression, and the outline of the box (solid or dashed) corresponds to the age class.

Table 5
Selected best fit models for timber and habitat quality indicators. Diameter and basal area were modeled using only stands reaching a minimum average height requirement of 1.35 m; straightness and branch density were modeled using only stands reaching a minimum average height requirement of 4.88 m. Habitat indicators were measured in all stands. Models were selected via backwards selection based on AIC. Model goodness of fit statistics are displayed in Table 2.

Response	Parameter	Estimate	Std. Error	Pr > |t|
Timber indicators				
Branch Density (branches/m)	Intercept	23.41	5.54	<0.0001
	Density (TPH)*Age	−8.24E-5	2.89E-5	0.006
	Longitude	0.23	0.07	0.0014
Straightness Grade	Intercept	4.05	1.02	2.00E-04
	Density (TPH)	−8.00E-04	3.00E-04	0.01
	% Sand	2.10E-02	0.01	0.07
Quadratic Mean Diameter (cm)	Intercept	−6.62	1.04	<0.0001
	Age	0.60	0.11	<0.0001
	Density (TPH)*Age	−1.78E-4	7.77E-05	0.02
Basal Area (m^2/ha)	Intercept	−2.13	1.85	0.25
	Density (TPH)	5.85E-3	7.79E-05	1.00E-04
	Age	0.56	0.12	<0.0001
Habitat indicators				
Canopy Openness (%)	Intercept	−28.76	47.25	0.54
	Density (TPH)	−1.65E-02	4.63E-03	0.00
	Age	−0.98	0.30	0.00
	SI	−0.53	0.24	0.03
	Longitude	−1.59	0.64	0.02
Bare Ground (%)	Intercept	−1.41	0.55	0.01
	Density (TPH)*Age	−1.42E-05	3.16E-06	<0.0001
	Longitude	−2.15E-02	6.89E-03	0.001
Herbaceous Cover (%)	Intercept	−1.98	0.87	0.03
	Density (TPH)*Age	−9.21E-06	4.48E-06	0.04
	% Sand	−5.50E-03	2.47E-03	0.03
	Longitude	−3.75E-02	9.92E-03	0.003

and woody understory cover increased and weighted branch density, stem straightness, canopy openness, and understory vegetation heterogeneity decreased (Table 2). Within the wiregrass range (N = 70), stands planted below 1495 TPH, as recommended for wildlife use, were on average 3 % higher in wiregrass cover than stands planted above 1495 TPH, as recommended to promote timber quality ($p = 0.08$).

Best fit modeling procedures indicated that planting rate was a predictor in the presence of biotic and abiotic covariates (Table 3). Survivorship was best explained as a function of age at time of sampling, planting rate, percent sand in soil, and geographic range. Survival was positively related to planting rate in older stands and was not affected by planting rate in younger stands (Fig. 3A, Table 4). Survivorship increased as the percentage of sand in the soil composition increased. Longitude described a significant portion (34 %) of the variation in survivorship, indicating that survivorship was lower in the 2 eastern most states relative to the 3 more western oriented states (FL, GA, AL). Because planting rate was strongly related to the density at the time of sampling, we substituted stand density for planting rate in all subsequent analyses to minimize the influence of early mortality that

Table 6
Selected best fit models canopy openness, bare ground cover, and herbaceous cover. Model goodness of fit statistics are displayed in Table 2. Models were selected via backwards selection based on AIC.

Response	Parameter	Estimate	Standard Error	Pr > |t|
Canopy Openness (%)	Intercept	−28.76	47.25	0.54
	Density (TPH)	−1.65E-02	4.63E-03	0.00
	Age	−0.98	0.30	0.00
	SI	−0.53	0.24	0.03
	Longitude	−1.59	0.64	0.02
Bare Ground (%)	Intercept	−1.41	0.55	0.01
	Density (TPH) *Age	−1.42E-05	3.16E-06	<0.0001
	Longitude	−2.15E-02	6.89E-03	0.001
Herbaceous Cover (%)	Intercept	−1.98	0.87	0.03
	Density (TPH) *Age	−9.21E-06	4.48E-06	0.04
	% Sand	−5.50E-03	2.47E-03	0.03
	Longitude	−3.75E-02	9.92E-03	0.003

occurred at several sites. Tables 5 and 6.

Stand density was an important predictor for several of the timber and habitat quality variables, though it often interacted with other covariates (Table 2). The effect of stand density generally differed with the age of the plantation (TPH*Age in Table 3). Weighted branch density and QMD were lowest in the older stands established with higher stand densities (Fig. 4A and C, Table 1). Similarly, the cover of bare ground decreased with age for higher density stands (Fig. 5A, Table 2). The best model indicated that herbaceous cover decreased with greater stand density as stand age increased; however, herbaceous cover was highly variable and without incorporating additional factors, such as geographic location and soil qualities, there was no relationship. Herbaceous cover was strongly positively related to canopy openness ($r = 0.62$, $p < 0.0001$) and strongly negatively related to basal area ($r = -0.51$, $p < 0.0001$). Indicators of site quality explained additional variation in basal area (increased with site index), canopy openness (decreased with site index), and herbaceous cover (decreased with increased percentage of sand in soil). Covariates added little to explain the variation in straightness grade beyond stand density, though the increased percentage of sand in soil led to a slightly higher grade. Straightness was weakly negatively related to stand density (Fig. 4D, Table 2, $R^2 = 0.14$). Diameter decreased with stand density in older stands, but stand density had no effect on diameter in younger stands (Fig. 4A, Table 3, $R^2 = 0.32$). Basal area increased with stand density and age (Fig. 4B, Table 3, $R^2 = 0.34$). A number of these relationships, including between stand density and bare ground, canopy openness, and herbaceous cover, showed variation across the geographic range (Fig. 5). Relationships with longitude and soil quality overshadowed the weak relationship between stand density and the habitat quality variables, including woody cover, total grass cover, total forb cover, and understory heterogeneity.

3.3. Benefits and tradeoffs

The average timber benefits varied minimally based on age or initial planting rate (Fig. 6A). The average wildlife benefits declined with plantation age across planting rates, but with greater magnitude in plantations established with higher planting rates (Fig. 6B). The overall benefit (average of all timber and wildlife benefits) decreased with age in both planting rate recommendation ranges but more so for the higher planting rates (Fig. 6C). The relationship between tradeoffs and stand age (Fig. 6D) differed greatly between the two sets of planting rates, with

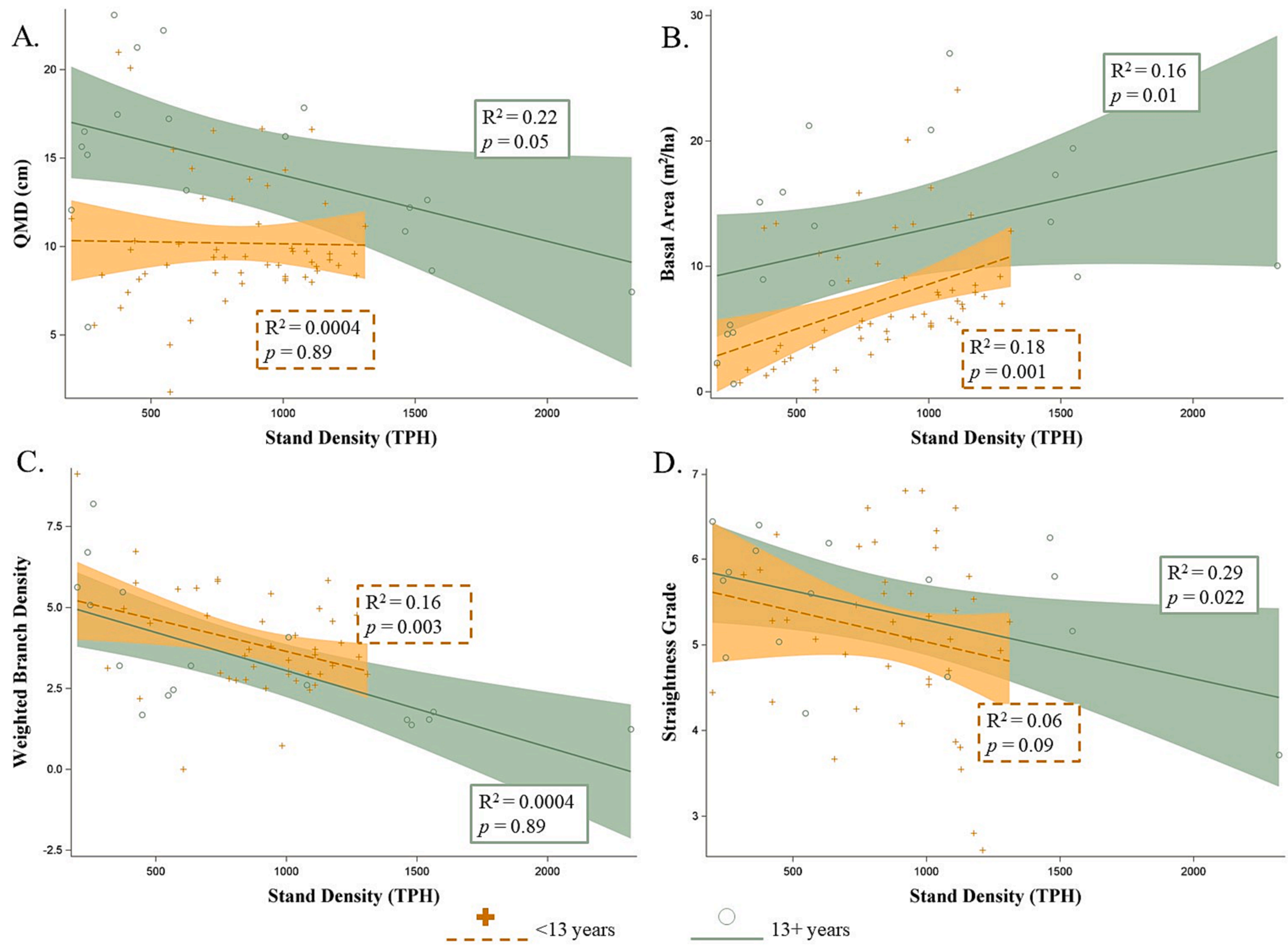

Fig. 4. Planted longleaf pine Quadratic Mean Diameter (A) and basal area (B) plotted against planting rate. Only plots with an average tree height greater than 1.35 m were included in modeling BA and QMD (N = 70). Weighted branch density (C) and straightness (D) plotted against density. Only plots with an average height greater than 4.88 m were included in modeling weighted branch density and straightness (1 log, N = 65). Sites were divided into two age classes, which is reflected by symbology. Boxes indicate R^2 and p-values for each regression, and the outline of the box (solid or dashed) corresponds to the age class.

tradeoffs decreasing with age for plantations established at lower wildlife-oriented planting density while tradeoffs increased with age for plantations established with higher timber-oriented planting rates.

4. Discussion

Our analyses illustrate how planting rate and stand density influenced indicators of timber quality and wildlife habitat quality in longleaf pine plantations. Within our inventory, 53 stands were established within the planting range recommended for providing wildlife habitat (988–1483 TPH/400–605 TPA), and 20 were within the higher range recommended for timber (1483–2223 TPH/600–900 TPA). In many cases, planting rate exerted a stronger influence on stand characteristics in older stands. Plantations with lower initial planting rate had larger average tree diameters, lower basal area, and stems with more branches than stands of similar ages with higher initial planting rates. Plantations with lower initial planting rate had more open canopies, more bare ground cover, and less woody cover than stands of similar ages with higher initial planting rates. Herbaceous cover was variable among stands; although results indicated lower herbaceous cover as stand density increased in older plantations, there was no relationship between stand density and herbaceous cover for all stands combined. However, there was a strong relationship between herbaceous cover and canopy openness, which declined as planting rate increased. Additional management actions, including prescribed fire and herbicide use, could have confounded the relationship between stand density and herbaceous cover, especially in younger stands. Despite these potentially confounding factors, an inverse relationship between planting rate and wildlife habitat indicators was present. The effects of planting rates on timber quality were mixed. At higher planting rates, branch density declined but stem straightness also declined.

The results of the tradeoffs analysis indicate that the effects of planting rate on wildlife and timber benefits differed among stand ages. Stands planted below 1495 TPH had a constant relationship between average timber benefit and stand age, and average wildlife benefits declined less rapidly as stands aged in lower density plantations than in higher density plantations. Tradeoffs increased with age in more densely (>1495 TPH) stocked stands, as wildlife benefits declined more rapidly than timber benefits in these stands than in lower density stands.

4.1. Timber quality indicators

Longleaf pine diameters decreased with higher planting rates, indicating that individual trees grow more quickly in widely spaced stands relative to tighter spacings (Kush et al., 2006). As higher value forest products have larger diameters, lower planting rates could reduce the time until plantations are merchantable. Multiple growth and yield models predict that longleaf pine stands planted at 625–1111 TPH will

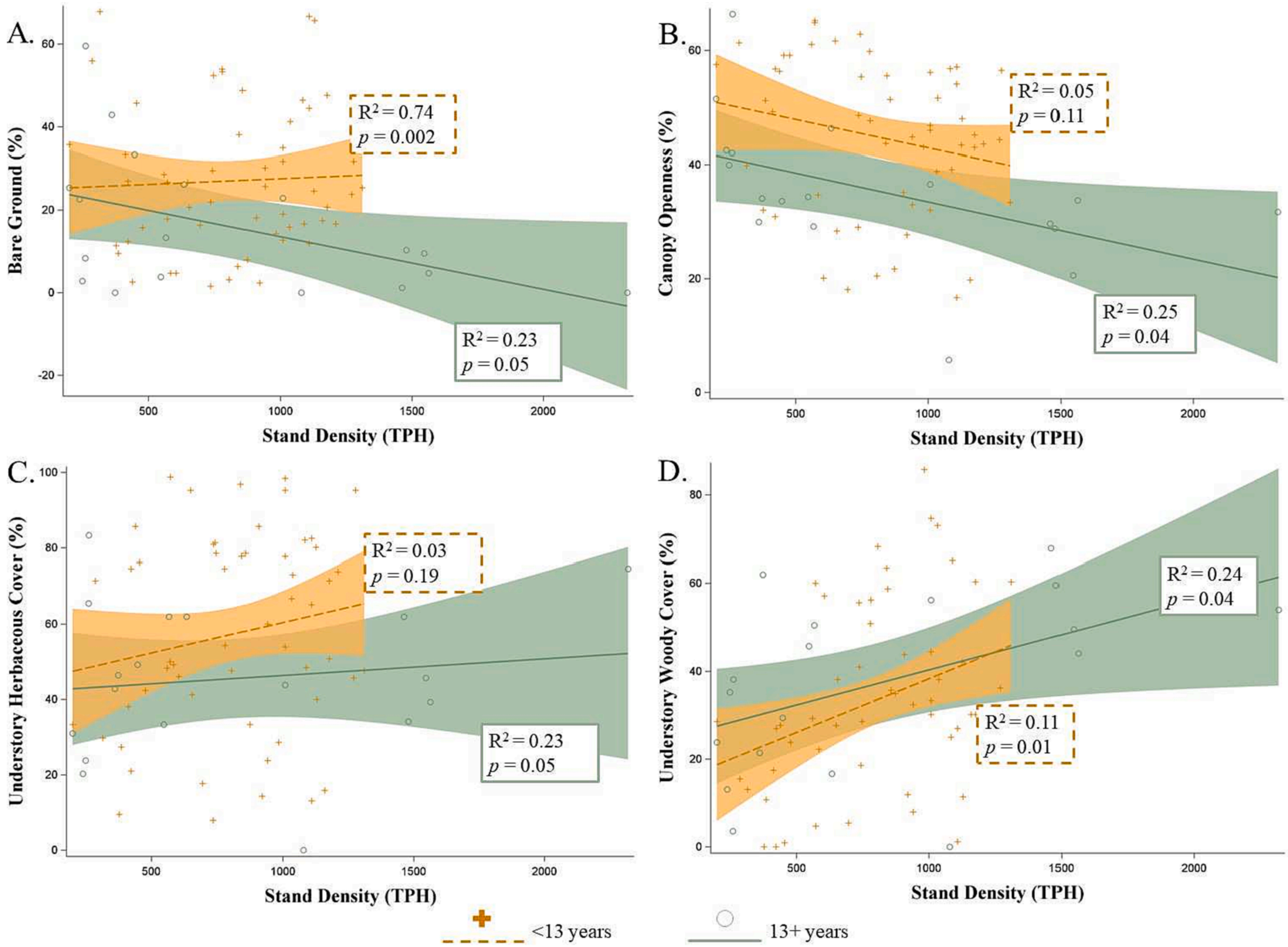

Fig. 5. Bare ground percent cover (A), canopy openness (B), herbaceous plant percent cover (C), and woody percent cover (D) of all stands plotted against density. Sites were divided into two age classes, which is reflected by symbology. Boxes indicate R^2 and p-values for each regression, and the outline of the box (solid or dashed) corresponds to the age class.

outperform stands planted at 1600–2066 TPH in terms of sawtimber produced (Hepp, 2019, South, 2006, ForesTech International, 2009), although timber quality is often not included in these models. As lower planting rates promote higher individual tree growth, and higher planting rates promote higher stand growth, these objectives cannot be simultaneously maximized.

We hypothesized that higher planting rates would lead to more positive timber quality benefits, including lower branch density and higher straightness grades. Our results only partially supported this hypothesis as both stem straightness and branch density declined with increased planting rate. Paul (1938) similarly reported that more densely stocked longleaf pine stands had stems with fewer knots in the first log when compared to lower stocked stands, and Ballard and Long (1988) reported that knot size decreased with stand density in lodgepole pine (*Pinus contorta*). Our finding that straightness grade declined as planting density increased contradicted previous studies. Malinauskas (2003) reported that increased planting rate increased stem straightness in 20- and 25-year-old Scots pine (*Pinus sylvestris*), and that a 500 TPH stand would have only 13 % grade A butt logs, and an 8000 TPH stand would have 82 % grade A butt logs. Ståhl et al. (1990) documented less extreme, but similar patterns in slightly more mature (27–29-year-old) Scots pine, reporting on average 5 % more stems with minimal crookedness in 6410 TPH stands than 2500 TPH stands. It is possible we did not document this relationship because the maximum planting rate in our study (2445 TPH) was lower than in Malinauskas (2003) and Ståhl et al. (1990), which were 8000 TPH and 6410 TPH, respectively. The relatively young age of plantations (average of 10 years) of longleaf pines in our study also may have masked some of the relationships.

4.2. *Habitat quality indicators*

Planting density influenced understory vegetation, and in turn likely influenced habitat quality for gopher tortoise and other longleaf pine community wildlife associates. Open canopy longleaf pine stands with extensive herbaceous and bare ground cover and limited woody understory cover offer high quality habitat for the gopher tortoise (McIntyre et al., 2019). Canopies were more closed in stands with higher planting rates, and dense canopies cast heavy shade and may limit the development of the herbaceous layer. We documented this negative relationship between canopy closure and herbaceous cover, as well as between basal area and herbaceous cover, though there was high variability in the relationship between stand density and herbaceous cover because of variation in management history and abiotic factors. Woody understory vegetation cover increased with stand density, which was surprising given decreased light penetration through denser canopy would be expected to have restricted woody understory (Kush and Meldahl, 2006). It could be that as canopies began to close, shade tolerant woody plants remained and were able to become well established in the understory particularly in the absence of fire, as found by Lewis and Harshbarger (1976). The target ranges for gopher tortoise

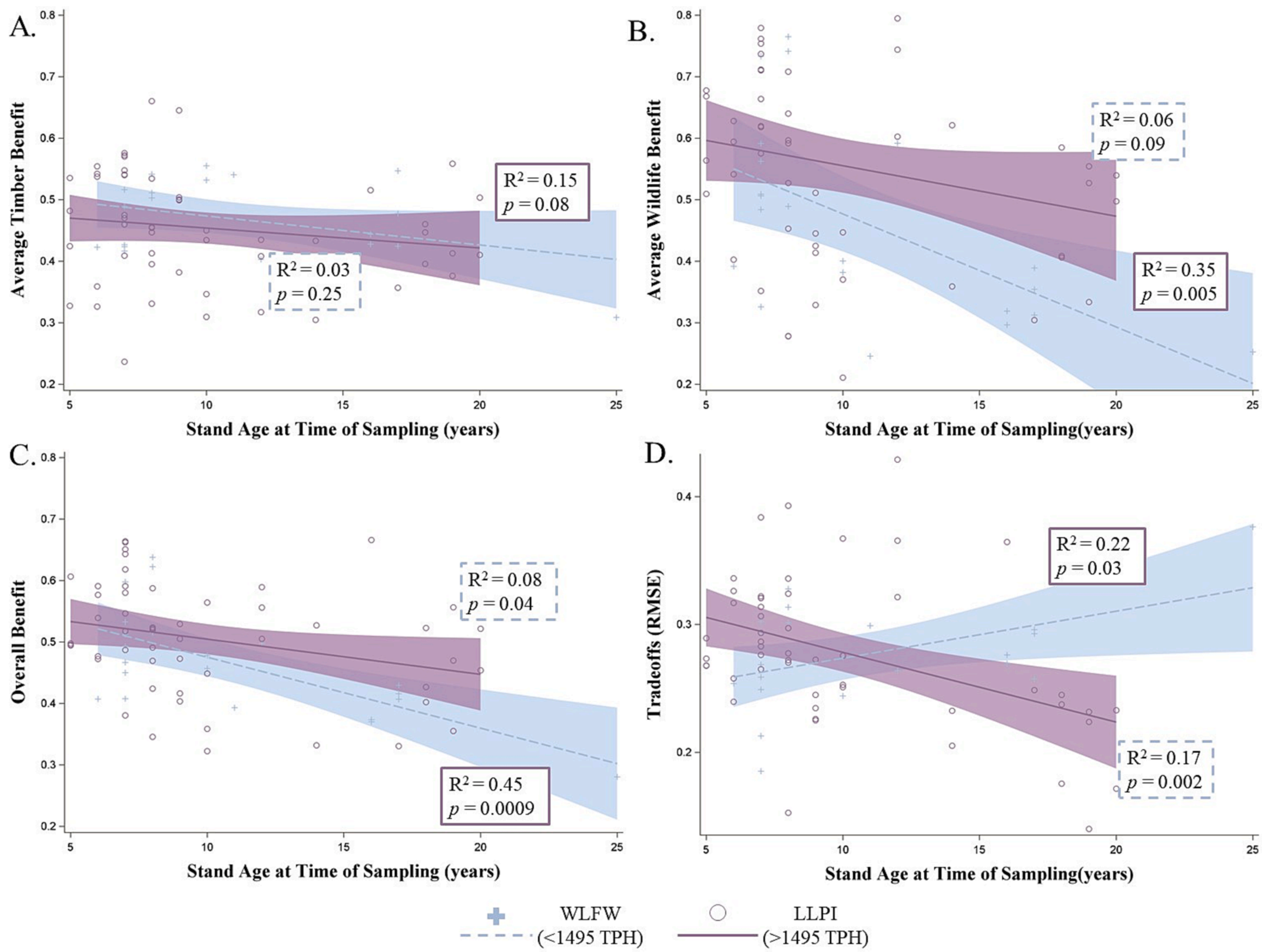

Fig. 6. Average timber benefit (A), average wildlife benefit (B), overall (combined timber and wildlife) benefit (C) and tradeoffs (D) between individual benefits (calculated as RMSE). Plots are grouped by whether they fall into the recommended planting rate range for the Longleaf Pine Initiative (timber objective) or the Working Lands for Wildlife Gopher Tortoise Initiative (wildlife objective). Boxes indicate R^2 and p-values for each regression, and the outline of the box (solid or dashed) corresponds to the planting rate class.

habitat are 24–53 % canopy openness, 9–41 % bare ground cover, <24 % woody understory cover, and 33–67 % herbaceous cover (Wilson et al., 1997). Only 7 % of stands met all characteristics, 37 % met 3 standards, 34 % met 2 standards, 23 % met 1 standard, and 5 % met no standards.

Canopy closure drives changes in understory dynamics. Planting at lower rates can slow the rate of canopy closure, but not stop it. Previous studies have reported that mid-rotation management options, like prescribed fire, can delay canopy closure and increase habitat quality in older plantations (Noss, 1989). We were not able to include the history of herbicide use or prescribed fire in analyses, but doing so would likely better isolate the effect of planting rate and would be useful to include in future studies.

4.3. Importance of abiotic factors

Relationships among planting density, tree form, and vegetation structure and composition likely are confounded by numerous site characteristics, including prior land use, site quality, and the history of prescribed burning. Prior agricultural usage alters the soil profile and reduces the seed bank, requiring more effort and cost in the establishment of an herbaceous layer in the conversion process. In comparison, following clearcut harvests, legacy forbs and grasses establish readily from the seed bank, especially after prescribed fire (Guldin, 2019). Agricultural sites have lower longleaf seeding survival when compared to previously forested sites, but our findings did not support this result (Hainds, 2004). Additionally, stand growth increases with the quality and quantity of soil nutrients and water. Thus, although the choice of initial planting density is critical in plantation management, stand growth can appear independent of initial stocking due to the quality of the site. Although we did not have access to detailed fire history data, we knew whether prescribed burning had occurred at least once for 48 of 73 stands. For these stands, those previously burned had on average 15 % greater longleaf pine seedling mortality than stands that had not burned since planting ($p = 0.03$). Similarly, Willis et al. (2021) reported 16–21 % mortality in stands burned biennially.

Although we focused on how planting rate influenced longleaf pine stands, we also observed effects of other abiotic factors on timber quality and vegetation characteristics. Basal area increased and canopy openness decreased as site index increased. Longleaf pine, like other trees species, grows more quickly on more productive sites, resulting in earlier canopy closure and faster basal area accumulation. The percentage of sand in soil also had a positive effect on seedling survival, which could be due to less competition from other tree species on sandy soils where longleaf pine is most competitive (Gilliam et al., 1993).

Along with effects of site characteristics, we observed geographic patterns (correlations with longitude) in branch density, herbaceous cover, bare ground cover, and canopy openness. All these relationships likely represent differences in plantation ownership across the range of sample sites. A greater number of plantations managed to promote wildlife use were measured in North Carolina (NCWRC gamelands, n = 12). Survivorship (mean ± SD; 40±15 %) was lower for sites in North Carolina than in stands measured in the other states to the south and west (71±15 %; $t = -8.5$, $p < 0.0001$), which could be partially due to regional differences in management, longleaf pine seed source, or local weather.

4.4. Conservation and management implications

We demonstrated that longleaf pine plantations established at lower planting rates were more beneficial for wildlife later in stand development than plantations with higher planting rates. Tradeoffs between timber and wildlife objectives decreased with age in low density stands and increased with age in high density stands. More specifically, we documented a more rapid decrease in wildlife benefits in stands with higher planting rates than in stands with lower planting rates; timber benefits differed less dramatically with changing planting rate. Planting at higher rates decreased light availability, which degrades understory conditions for the gopher tortoise and other longleaf pine wildlife associates (Harrington et al., 2013). Although higher planting rates may buffer the effects of post-planting seedling mortality, the higher rate appears to have mixed effects on tree form and inhibits diameter growth, therefore increasing the time needed to harvest larger diameter (and more valuable) forest products. The increased bare ground cover and canopy openness (and therefore greater herbaceous cover) as planting rates declined validate lower planting rates to target conservation of wildlife habitat, but the mixed relationships between planting rate and treeform attributes (e.g., branchiness, stem straightness) do not support higher planting rates (1483 TPH/600 TPA) to definitively improve timber quality.

Although the lower planting rates improved understory conditions for longleaf pine wildlife associates, stand structure eventually became unfavorable for these species regardless of planting density. For many of the stand qualities we evaluated, including herbaceous cover, bare ground cover, and canopy openness, conditions also degraded as stands aged. Hence, early and frequent thinnings and/or frequent use of prescribed fire are critical to maintain an open canopy, high herbaceous and bare ground cover, and low woody understory cover, regardless of initial planting rate.

CRediT authorship contribution statement

J.M.T. Hausle: Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **J.A. Forrester:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Visualization, Supervision. **C.E. Moorman:** Methodology, Writing – review & editing, Supervision. **M.R. Martin:** Conceptualization, Resources, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121497.

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