Understory Composition and Structure Influences Deer and Turkey Habitat in Southern Pine Stands

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Abstract- *Pinus* spp. (pine) forests are common throughout the southeastern US, and many of these forests are managed to improve habitat for *Odocoileus virginianus* (White-tailed Deer) and *Meleagris gallopavo* (Wild Turkey). Previous studies have investigated the influence of forest management on deer and turkey habitat, but several aspects of understory vegetation response to management are not well understood. We measured understory composition and structure, overstory basal area, and deer-forage availability at 8 sites in summer 2020. Previous history of dormant-season fire increased grass and decreased vine coverage, but forb and understory tree coverage were not influenced. Vegetation providing visual obstruction for turkey nesting and deer fawning was correlated with increased coverage of semiwoody and woody plants. Forb coverage averaged 14% and was positively correlated with deer nutritional carrying capacity (NCC) using a 14% protein constraint. Conversely, NCC with a 6% protein constraint correlated with shrub and vine coverage. Sunlight available to the understory was most strongly influenced by hardwood overstory and midstory trees. Our results indicate that understory composition strongly influences forage and cover and that pine stands that are not intensively managed generally provided limited resources for deer and turkeys.

Introduction

Pinus taeda L. (Loblolly Pine) and *Pinus echinata* Mill. (Shortleaf Pine) forests cover ~25 million ha of the southeastern US (Oswalt et al. 2019). The most common management practice in southerneastern *Pinus* spp. (pine) forests is commercial thinning, which increases sunlight into the stand by reducing overstory basal area to increase tree growth and fiber production of remaining trees (Feltrin et al. 2016, Grayson et al. 2012). Increased sunlight also stimulates the understory, which typically is dominated by woody and semiwoody species (Amateis 2000, Peitz et al. 1999, Wigley et al. 1989). Despite widespread recommendation for prescribed fire in pine systems throughout the southeastern US (Darracq et al. 2016, Mitchell et al. 2006, Ryan et al. 2013, Weber et al. 2022), the use of fire is relatively infrequent and conducted primarily during the dormant season, which may top-kill trees in the understory and midstory that resprout later (Knapp et al. 2009, Leenhouts 1998, Resop et al. 2023, Ryan et al. 2013).

Odocoileus virginianus (Zimmerman) (White-tailed Deer; hereafter, Deer) and *Meleagris gallopavo* L. (Wild Turkey; hereafter, Turkey) are the 2 most pursued game species in the eastern US (US Department of the Interior et al. 2017), with high occupancy in landscapes dominated by pine forests throughout the South.

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Nutritional and structural conditions for Deer and Turkeys in many of these forests are relatively poor, and Deer morphometrics and Turkey abundance often are reduced in landscapes dominated by pine forests (Iglay et al. 2010, Nelson et al. 2023, Nichols et al. 2021, Yeldell et al. 2017). For example, it is well documented that Deer body and antler size are smaller in areas where nutrition is limited (Hefley et al. 2013, Jones et al. 2018, Lashley et al. 2015a, Strickland and Demarais 2008). Turkey populations have declined in many areas throughout the southeastern US, and low nest and brood survival have been documented to limit population growth (Byrne et al. 2015, Chamberlain et al. 2022, Johnson et al. 2022).

Vegetation composition and structure influence availability of food and cover resources for Deer and Turkeys. Management for Deer often concentrates on improving nutrition during the growing season, as antler size, body weight, and productivity increase with improved nutrition (French et al. 1956, Harmel et al 1989, Michel et al. 2016, Verme 1969). Increasing forb coverage often is a management objective, as forbs provide high-quality forage which meet the 14% crude-protein minimum required by Deer to maximize productivity and antler growth (Lashley et al. 2011, Nanney et al. 2018, National Research Council 2007, Nichols et al. 2021). Understory composition and structure also are important considerations for Turkeys, as nesting and brooding success are critical factors for population productivity (Crawford et al. 2021, Johnson et al. 2022, Wood et al. 2019). Forb-dominated plant communities providing cover and insect resources for broods are selected by Turkeys (Campo et al. 1989, Healy 1985, Speake et al. 1985, Nelson et al. 2022, Wood et al. 2019). Conversely, stands with greater coverage of understory woody species and/or more visual obstruction are selected by Deer during fawning and lactation and by nesting Turkeys (Cherry et al. 2017, Johnson et al. 2022, Kilburg et al. 2014, Lashley et al. 2015b, Little et al. 2016). Given the importance of Deer and Turkeys to many landowners and managers in the Southeast and the expectation that open, thinned stands provide sufficient resources for these species, there is great interest in how pine-forest management might influence understory vegetation.

Extensive research has investigated management practices that influence understory conditions in pine forests for Deer and Turkeys. For example, thinning allows more sunlight to the understory, which can improve Deer forage availability and structure for Turkey nesting and brooding (Blair 1967, Keene et al. 2020, Peitz et al. 2001). Selective herbicide application following thinning shifts vegetation species composition from woody-dominated communities to herbaceous-dominated communities, which benefit Deer and Turkeys (Edwards et al. 2004, Iglay et al. 2014, Mixon et al. 2009). Prescribed fire is one of the most important tools used to maintain and improve habitat for Deer and Turkeys in pine forests, as it can be used to increase Deer forage availability and improve plant-community structure and composition for Turkeys (Chance et al. 2020, Kilburg et al. 2014, Mixon et al. 2009, Wann et al. 2020). Additionally, fire frequency and seasonality can be strategically implemented to provide conditions that meet various life-history requirements of wildlife (Cherry et al. 2017, Nichols et al. 2021, Turner et al. 2024). Despite the availability of information on improving pine forests for wildlife, there is limited information on the current conditions and factors influencing stands managed with wildlife as a primary or secondary objective.

Given the extensive coverage of southern pine forests managed primarily with thinning, evaluating conditions across a variety of sites should provide land managers with important information that may influence their expectations regarding Deer and Turkey productivity and management. We collected data across 8 sites in 4 states to evaluate vegetation composition and structure in a variety of southern pine forests on sites with improvement of habitat for Deer and Turkeys as a primary or competing objective. We did not choose sites to evaluate the full range of conditions in pine forests, but rather to determine if various plant types correlated with either cover or forage availability across a variety of sites with different management histories. Our objectives were to (1) assess the relationship between understory composition and availability of forage for Deer, (2) determine which plant types contributed to nesting cover for Turkeys and fawning cover for Deer, (3) evaluate whether dormant-season fire influenced vegetation composition, and (4) evaluate factors influencing understory sunlight. We predicted lactation-level nutritional carrying capacity would be positively correlated to forb coverage, which is the plant type with the greatest average crude protein (Harper 2019, Harper et al. 2021). Conversely, we expected maintenance-level nutritional carrying capacity would positively correlate with vine, shrub, and understory tree coverage, which are lower-quality forages on average than forbs (Nanney et al. 2018). We predicted woody plants, semiwoody plants, and midstory stems would correlate to visual obstruction from 1 to 2 m. We predicted sites with a history of dormant-season fire would have greater grass coverage and less coverage of trees, shrubs, vines, and brambles than those that had not been burned (Mixon et al. 2009, Turner et al. 2020). Finally, we predicted overstory hardwood and midstory trees would more strongly influence sunlight than overstory pines across all our sites regardless of varying pine basal areas (Harrington and Edwards 1999, Whelan et al. 2018).

Field-site Description

We selected 8 Loblolly and Shortleaf Pine stands (Fig. 1, Table 1) based on geographic distribution to collect data from locations with different soils, seedbank response, and physiographic regions. All sites were 8–21 ha. Additionally, all sites had been thinned in the previous 6 years, allowing >30% sunlight entering the canopy, with a primary or competing objective of improving understory vegetation for Deer or Turkeys based on common management recommendations and practices in the South (Davis et al. 2017, Keene et al. 2020, Turner et al. 2020). Thinning intensity was not uniform across sites, but the variability allowed us to evaluate the influence of different sunlight conditions. Variation in conditions across stands allowed us to better assess factors influencing understory composition and structure, which is typical across the landscape.

Two of our sites were located in South Carolina with management of habitat for Deer and Turkeys as primary objectives. One site was on Belfast Wildlife Management Area, which was owned and managed by the South Carolina

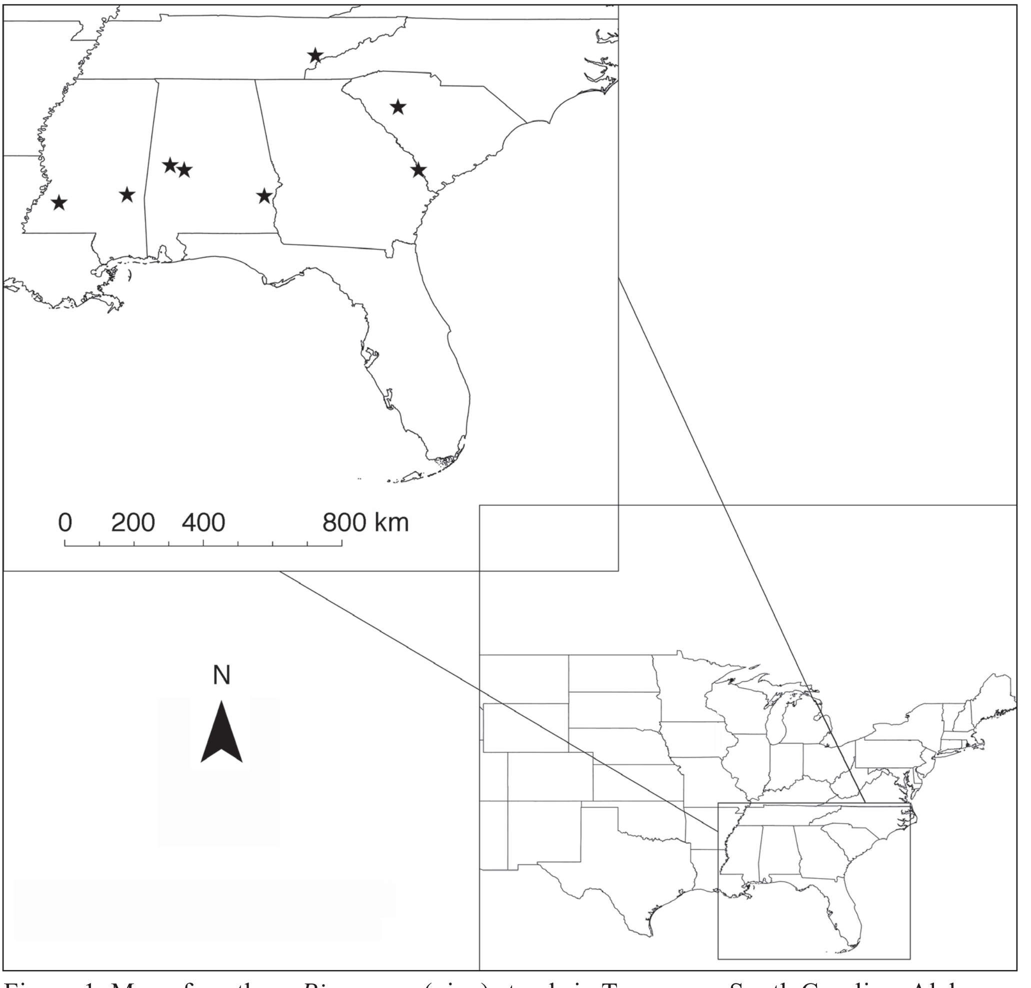

Figure 1. Map of southern *Pinus* spp. (pine) stands in Tennessee, South Carolina, Alabama, and Mississippi where *Odocoileus virginianus* (White-tailed Deer) and *Meleagris gallopavo* (Wild Turkey) forage and cover was assessed, June–July 2020.

Table 1. Location, establishment date, establishment method, and the date of last thin and burn of eight southern *Pinus* spp. (pine) forests across Tennessee, South Carolina, Alabama, and Mississippi evaluated for vegetation composition and structure, June–July 2020.

Site	State	Date established	Establishment method	Last thin	Last burn
Barbour	AL	1998	Planted	2018	None
Belfast	SC	1995	Planted	2019	None
Copiah	MS	~1960	Natural	2014	2017
Folsom	AL	2005	Planted	2020	None
Foothills	TN	~1940	Natural	2014	2017
Mason Bend	AL	2002	Planted	2018	None
Pachuta	MS	1998	Planted	2017	2018
Webb	SC	1992	Planted	2015	2017

Department of Natural Resources (SCDNR). This twice-thinned Loblolly Pine stand was planted in 1995, and soils were Cecil sandy clay loam (NRCS 2022). No fire had occurred in the life of the stand (T. Bennett, SCDNR, Kinards, SC, pers. comm.). Dominant understory plants, listed in order of coverage from greatest to least, included *Rubus* spp. (blackberry), *Vitis rotundifolia* Michx. (Muscadine), *Dichanthelium* spp. (panicgrass), *Chasmanthium laxum* (L.) H.O. Yates (Slender Woodoats), and *Lonicera japonica* Thunb. (Japanese Honeysuckle). The other site in South Carolina was on Webb Wildlife Center, which was owned and managed by the South Carolina Department of Natural Resources. This Loblolly Pine stand was planted in 1992, had been thinned twice, and had been burned on a 3–5-year fire-return interval during the dormant season since the second thinning, but no fire had occurred within 3 years prior to data collection (A. Atkinson, SCDNR, Garnett, SC, pers. comm.). Soils were predominately Eulonia fine sandy loam (NRCS 2022). Dominant understory plants included Slender Woodoats, panicgrass, *Ampelopsis arborea* (L.) Koehne (Peppervine), Muscadine, *Liquidambar styraciflua* L. (Sweetgum), and blackberry.

Three sites were located in Alabama. One was on the Barbour Wildlife Management Area, which was owned and managed by Alabama Department Conservation and Natural Resources (ADCNR) with Deer and Turkey management as a primary objective. This Loblolly Pine stand was planted in 1998 and had been thinned once; no fire had occurred in the life of the stand (C. Childree, ADCNR, Midway, AL pers. comm.). Soils were predominately Luverne–Springhill complex (NRCS 2022). Dominant understory species included panicgrass, Muscadine, *Callicarpa americana* L. (American Beautyberry), Sweetgum, Slender Woodoats, and *Eupatorium serotinum* Michx. (Late-flowering Thoroughwort). Mason Bend was located on private property near Demopolis, AL, and had Deer and Turkey management as a primary objective. This Loblolly Pine stand was planted in 2002, thinned once, and had not been burned (S. Basinger, Demopolis, AL, pers. comm.). Soils were predominately Cahaba fine sandy loam (NRCS 2022). Dominant understory species included blackberry, Slender Woodoats, Muscadine, Sweetgum, *Parthenocissus quinquefolia* (L.) Planch. (Virginia Creeper), and American Beautyberry. Folsom was located on private property near Marion, AL, and had Deer and Turkey management and timber production as objectives. This Loblolly Pine stand was planted in 2005, thinned once, and had not been burned (E. Glass, Marion, AL, pers. comm.). Soils were predominately Smithdale sandy loam (NRCS 2022). Dominant understory plants included Muscadine, blackberry, panicgrass, *Erechtites hieraciifolius* (L.) Raf. ex DC. (American Burnweed), and Japanese Honeysuckle.

Two sites were located in Mississippi. One site was on the Copiah Wildlife Management Area, which was owned and managed by Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) and had Deer and Turkey management as a primary objective. This Loblolly Pine stand was naturally regenerated in 1960 and had been thinned twice; Copiah previously had been burned on a 3–5-year fire-return interval during the dormant season, but no fire had occurred within 3 years prior to data collection (M. Palmer, MDWFP, Hazlehurst, MS, pers. comm.). Soils were predominately Loring silt loam and Lorman–Smithdale association

(NRCS 2022). Dominant understory species included Slender Woodoats, *Andropogon virginicus* L. (Broomsedge Bluestem), blackberry, panicgrass, and American Beautyberry. Triple Creek was located on private property near Pachuta, MS, and had Deer and Turkey habitat management as a competing objective with timber production. This Loblolly Pine stand was planted in 1998, had been thinned twice, and burned once in the dormant season in 2018 after the second thinning (D. Hall, Pachuta, MS, pers. comm.). Soils were predominately Savannah fine sandy loam (NRCS 2022). Dominant understory vegetation included blackberry, panicgrass, Slender Woodoats, American Beautyberry, and *Bidens aristosa* (Michx.) Britton (Beggarsticks).

One site located in Tennessee on the Foothills Wildlife Management Area, owned and managed by the Tennessee Wildlife Resources Agency (TWRA), had Deer and Turkey management as a primary objective. This mixed hardwood–pine stand was naturally regenerated in 1940, and had been thinned once in 2014, removing most hardwood trees in the overstory and retaining the Shortleaf Pine to restore a Shortleaf Pine woodland; Foothills had been burned once after thinning in 2017 during the dormant season (B. Smith, TWRA, Maryville, TN, pers. comm.). Soils were predominately Ramsey stony fine sandy loam (NRCS 2022). Dominant understory vegetation included Broomsedge Bluestem, *Vaccinium* spp. (blueberry), Shortleaf Pine, *Nyssa sylvatica* Marshall (Blackgum), panicgrass, and *Acer rubrum* L. (Red Maple). Average annual temperature across all sites varied from 13.3 °C to 18.2 °C, and elevation varied from 15 m to 658 m above sea level (NOAA 2022).

Methods

Understory, midstory, and overstory data collection

We collected data from 20 points that were >30 m apart and randomly distributed using ArcGIS Pro version 2.6 (Esri, Redlands, CA) at each site during June–July 2020. We placed a 50-m point–intercept transect centered on each point and recorded all plants by species overlapping each meter mark below 1.4 m in height along the transect (Floyd and Anderson 1987). We used a random-number generator to determine transect direction at each point, but ensured transects did not overlap transects from another point. Following data collection, we calculated average coverage of forbs, grasses, vines, brambles (including blackberry and *Smilax* spp. [greenbriar]), shrubs, and trees at each site based on our transect data. We collected overstory composition and basal area of all trees at least 10.6 cm in diameter and 1.4 m in height at a 0.04-ha plot centered on the point. We counted midstory stems at least 1.4 m in height and less than 10.6 cm in diameter within a 0.008-ha plot centered on each point.

We collected vegetation measurements using a vegetation profile board with four 0.5-m strata (Nudds 1977). The board was 2.0 m tall and 0.5 m wide and was read by a kneeling observer at plot center with the board placed 10 m away in 2 directions along the transect line. The lowest stratum was 0.0 to 0.5 m and represented obstruction important for Turkey poults (Campo et al. 1989). Conversely, greater visual obstruction from 0.5 to 1.5 m may be selected by nesting Turkeys (Badyaev

1995, Kilburg et al. 2014). Greater visual obstruction from 0.5 to 2.0 m is important for neonate and adult Deer cover (DePerno et al. 2003, Huegel et al. 1986, Kroeger et al. 2020).

We measured infiltration of photosynthetically active radiation (PAR) along a 20-m transect centered on each point with the same orientation as the vegetation transect. We recorded readings on an AccuPAR® LP-80 ceptometer (Decagon, Inc., Pullman, WA) every 1 m at 1.4 m above ground and paired these measurements with simultaneous measurements taken nearby in a location that allowed full sunlight to determine percent sunlight reaching the understory.

Nutritional carrying capacity

We quantified Deer forage availability at each point. We placed two 0.5-m^2 forage-collection frames systematically along each transect at the 15- and 35-m marks. We collected species up to 1.4 m in height that were documented in the literature as moderately or highly selected by Deer (Table 2; Harper 2019, Miller and Miller 2005), and collected young and old leaves of each species separately because nutrient content may vary based on age (Lashley et al. 2014, Turner et al. 2021). We considered smaller leaves near the tips of stems as younger tissue and larger leaves farther down the stem as older tissue based on Lashley et al. (2014). We dried all samples in a forced-air dryer at 50 °C for 72 hours and weighed in grams using a digital scale.

Following weighing, we sent at least 5 grams of each species and age from each site to the Agricultural Service Laboratory at Clemson University where wet-chemistry methods were used to determine nitrogen content, which we multiplied by 6.25 to estimate the percent crude protein of each forage (Robbins et al. 1987). We used a mixed-diet approach to estimate nutritional carrying capacity (NCC) to determine Deer days per hectare at both maintenance and lactation-level crude-protein demands (Hobbs and Swift 1985). We used a 2.4-kg/day intake rate to represent the intake of a 50-kg doe (Hewitt 2011, National Research Council 2007). Our peak lactation constraint was 14% crude protein, and our maintenance constraint was 6% crude protein (Hewitt 2011, Nanney et al. 2018, National Research Council 2007). After we determined NCC along each transect, we calculated the average site-level NCC at lactation and maintenance levels.

Analyses

We calculated the average percent coverage of grasses, forbs, brambles, vines, shrubs, and trees at each site. To determine whether past dormant-season fire influenced understory composition, we analyzed coverage of each plant class in a mixed-effects model using analysis of variance (ANOVA) in the 'nlme' package-version 3.1-131 (Pinheiro et al. 2017) in Program R v. 4.2.0 (R Core Team 2022) with occurrence/absence of previous fire as a fixed effect and site as a random effect. We used Tukey's test to compare means at $\alpha = 0.05$.

We wanted to determine whether understory woody vegetation (shrubs and trees), understory semiwoody vegetation (vines and brambles), or midstory stem density influenced visual obstruction from 1.0 to 1.5 m or from 1.5 to 2.0 m. Obstruction from 1.0 to 1.5 m may be selected by nesting Turkeys, and obstruction from 1.5 to 2.0 m may be selected by female Deer during fawning. Therefore, we created mixed-effects models for the 1.0–1.5-m and 1.5–2.0-m strata with woody, semiwoody, and midstory stem density as fixed effects and site as a random effect. Additionally, we wanted to determine the influence of forb coverage on lactation-level NCC estimates for Deer, as well as the influence of tree, shrub, and vine coverage on maintenance-level NCC estimates. Thus, we created a mixed-effects

Table 2. Plant species collected in 8 southern *Pinus* spp. (pine) stands across Tennessee, South Carolina, Alabama, and Mississippi for *Odocoileus virginianus* (White-tailed Deer) nutritional carrying capacity (NCC) calculation, June–July 2020.

Species	Scientific name
American Beautyberry	*Callicarpa americana* L.
Beggarsticks	*Bidens* spp.
Blackberry	*Rubus* spp.
Blackgum	*Nyssa sylvatica* Marshall
Blueberry	*Vaccinium* spp.
Bushy Aster	*Aster dumosus* L
Canadian Horseweed	*Conyza canadensis* L.
Chinese Privet	*Ligustrum sinense* Lour.
Common Persimmon	*Diospyros virginiana* L.
Common Ragweed	*Ambrosia artemisiifolia* L.
Crossvine	*Bignonia capreolata* L.
Elm	*Ulmus* spp.
Flowering Dogwood	*Cornus florida* L.
Goldenrod	*Solidago* spp.
Grape	*Vitis* spp.
Greenbriar	*Smilax* spp.
Hickory	*Carya* spp.
Japanese Honeysuckle	*Lonicera japonica* Thunb.
Lateflowering Thoroughwort	*Eupatorium serotinum* Michx
Lespedeza	*Lespedeza* spp.
Narrowleaf Mountainmint	*Pycnanthemum tenuifolium* Schrad
Oak	*Quercus* spp.
Partridge Pea	*Chamaecrista fasciculata* (Michx.) Greene
Peppervine	*Ampelopsis arborea* (L.) Koehne
Red Maple	*Acer rubrum* L
Sassafras	*Sassafras albidum* (Nutt.) Nees
Slender Three-seeded Mercury	*Acalypha virginica* L
Spurred Butterfly Pea	*Centrosema virginianum* L.
Sumac	*Rhus* spp.
Ticktrefoil	*Desmodium* spp. Desv.
Vervain	*Verbena* spp.
Violet	*Viola* spp.
Virginia Creeper	*Parthenocissus quinquefolia* (L.) Planch.
Whorled Tickseed	*Coreopsis verticillata* L.
Virginia Creeper	*Parthenocissus quinquefolia* (L.) Planch.
Yellow Jessamine	*Gelsemium sempervirens* (L.) J. St.-Hil.
Yellow-poplar	*Liriodendron tulipifera* L.

model regressing forb coverage against lactation-level NCC, as well as a model regressing tree, shrub, and vine coverage against maintenance-level NCC, with site as a random effect in both.

Finally, we were interested in determining factors affecting sunlight available to the understory in these systems. Nearly all midstory stems in our forests were hardwoods, but we grouped all hardwood and softwood midstory stems to simplify our analysis. We used understory sunlight as our response variable, with pine basal area, hardwood basal area, and midstory stem density as fixed effects. We also included site as a random effect to model understory sunlight in a mixed-effects ANOVA.

Results

Coverage of grasses, brambles, and vines varied widely among sites, whereas forb coverage was consistently limited (Fig. 2). Grasses were most prevalent in the understory, with an average of 53% coverage (min–max: 10.4–88.1%). Brambles and vines each averaged ~23% coverage (min–max: 4.2–50.2% and 0.2–48.3%, respectively). Understory trees averaged 16% coverage (min–max: 3.3–62.5%), which were followed in relative abundance by forbs, which averaged 14% coverage (min–max: 9.2–18.3%). Understory shrubs had the least relative abundance, and coverage averaged 12% (min–max: 1.7–28.5%). Previous fire treatments did not influence coverage of forbs ($F_{1,6}$ = 0.56, P = 0.48), brambles ($F_{1,6}$ = 0.55, P = 0.48), shrubs ($F_{1,6}$ = 0.33, P = 0.58), or trees ($F_{1,6}$ = 0.63, P = 0.46). Sites with previous fire averaged 74% grass coverage, whereas unburned sites had only 31.8% grass coverage ($F_{1,6}$ = 7.37, P = 0.03). Conversely, burned sites had 8% vine coverage, whereas unburned sites averaged 35% vine coverage ($F_{1,6}$ =13.65, P = 0.01).

Lactation-level NCC estimates with a 14% crude-protein constraint averaged 10.2 Deer days/ha (Table 3), and increased by 1 (± 0.4, $F_{1,151}$ = 5.56, P = 0.02) Deer day/ha for every 2% increase in forb coverage. Maintenance-level NCC estimates were much greater, averaging 213 Deer days/ha (Table 3), and increased by 4.3

Table 3. Average nutritional carrying capacity estimates (Deer days/ha) at 2 crude protein (CP) constraints, pine basal area (m^2/ha), hardwood basal area (m^2/ha), midstory stems per ha, and percent photosynthetically active radiation (PAR) in the understory across southern *Pinus* spp. (pine) forests across Tennessee, South Carolina, Alabama, and Mississippi, June–July 2020. Numbers in parentheses represent standard error.

			Basal area			
Site	6% CP	14% CP	Pine	Hardwood	Midstory	PAR
Barbour	353.8 (± 69.9)	35.9 (± 22.6)	7.9 (± 4.3)	1.4 (± 3.4)	380.5 (± 95.0)	57.5% (± 6.9)
Belfast	179.2 (± 42.5)	3.4 (± 2.7)	11.5 (± 2.9)	0.3 (± 0.4)	612.8 (± 119.8)	49.6% (± 4.8)
Copiah	127.8 (± 31.6)	9.1 (± 4.6)	6.5 (± 7.8)	0.8 (± 1.4)	311.3 (± 151.4)	44.7% (± 4.5)
Folsom	93.4 (± 34.6)	10.7 (± 7.8)	11.6 (± 7.4)	0.2 (± 0.4)	360.8 (± 99.7)	53.0% (± 3.1)
Foothills	418.6 (± 113.1)	3.3 (± 2.6)	4.5 (± 2.9)	2.9 (± 3.2)	2985.0 (± 1009.7)	65.8% (± 5.7)
Mason Bend	188.4 (± 48.8)	14.1 (± 12.8)	8.1 (± 2.3)	1.4 (± 2.3)	1522.1 (± 253.1)	16.5% (± 3.4)
Triple Creek	205.8 (± 80.1)	1.6 (± 2.1)	9.7 (± 3.6)	0 0 (± 0.0)	187.8 (± 77.6)	51.9% (± 4.4)
Webb	136.9 (± 48.3)	3.3 (± 2.4)	10.0 (± 6.4)	0.1 (± 0.2)	879.7 (± 253.5)	56.2% (± 4.0)

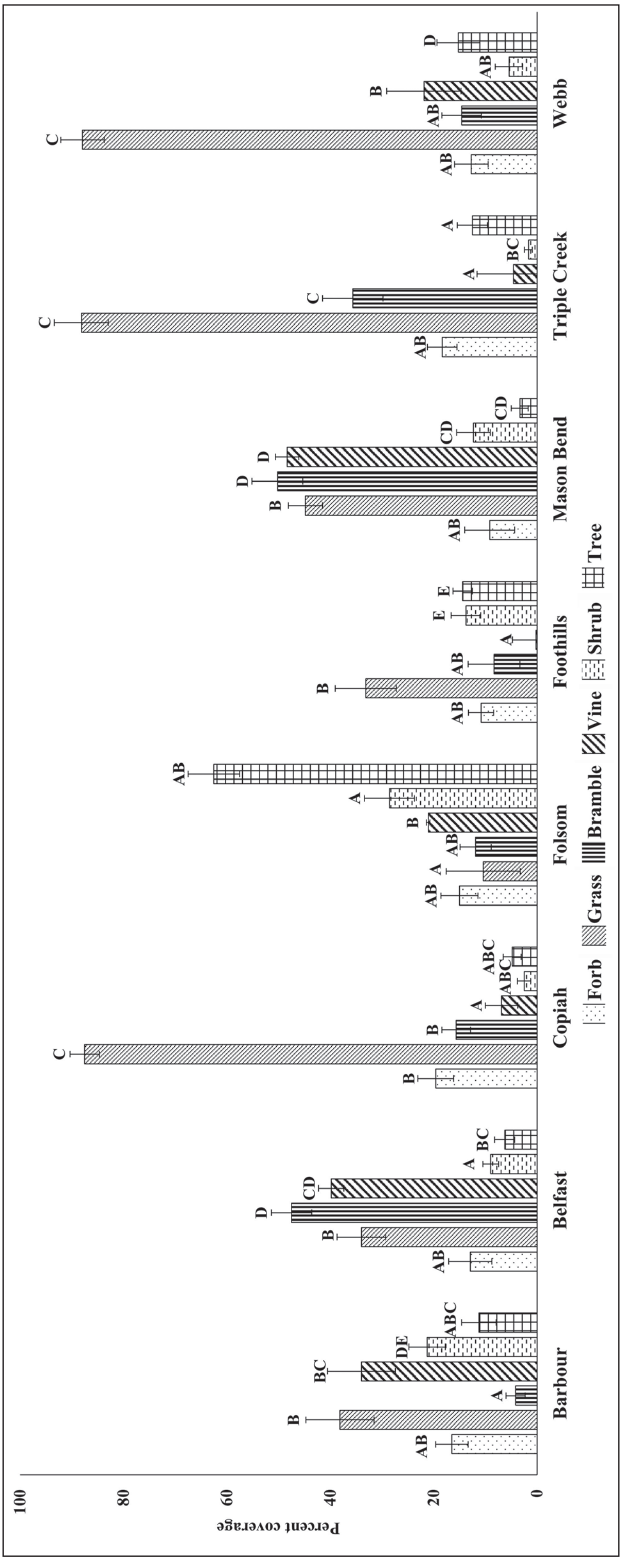

Figure 2. Average understory composition across 8 southern *Pinus* spp. (pine) stands in Tennessee, South Carolina, Alabama, and Mississippi, June–July 2020. Different letters between sites for each understory component represent significantly different coverage.

(± 1.6) Deer days/ha for every 1% increase in shrub coverage ($F_{1, 149}$ = 9.87, P = 0.006) and by 2.0 (± 0.9) Deer days/ha for every 1% increase in vine coverage ($F_{1, 149}$ = 5.08, P = 0.031). Understory trees also were marginally significantly correlated with maintenance-level NCC, with an increase of 2.1 (± 1.1) Deer days/ha for every 1% increase in coverage of understory trees ($F_{1, 149}$ = 3.32, P = 0.075).

Visual obstruction from 1.0–1.5 m increased by 1.2% (± 0.3 standard error, $F_{1, 149}$ = 20.69, P < 0.001) for every 2% increase in understory woody coverage, increased by 0.8% (± 0.2, $F_{1, 149}$ = 17.98, P < 0.001) for every 2% increase in understory semiwoody coverage, and was marginally increased by 0.6% (± 0.2, $F_{1, 149}$ = 3.61, P = 0.059) for every 200 additional midstory stems per ha. Visual obstruction from 1.5–2.0 m increased by 1.1% (± 0.3, $F_{1, 149}$ = 23.00, P < 0.001) for every 2% increase in understory woody coverage, by 0.9% (± 0.3, $F_{1, 149}$ = 19.77, P < 0.001) for every 2% increase in understory semiwoody coverage (P < 0.001), and by 1% (± 0.2, $F_{1, 149}$ = 9.59, P = 0.002) for every 200 additional midstory stems per ha.

Understory sunlight was negatively influenced by hardwood basal area and midstory stems. For every 1 m^2/ha increase in hardwood basal area, sunlight decreased by 2% (± 0.6, $F_{1, 149}$ = 8.43, P = 0.002). For every 1000 additional midstory stems per ha, sunlight decreased by 2% (± 0.001, $F_{1, 149}$ = 6.47, P = 0.01). Pine basal area also was marginally negatively correlated with sunlight, with a decrease of 0.8% (± 0.4, $F_{1, 149}$ = 1.58, P = 0.078) sunlight for every 2 m^2/ha increase in pine basal area.

Discussion

Our study documented relationships between composition, structure, forage availability, and previous management across pine stands. Previous history of dormant-season fire resulted in more grass and less vine coverage, but no changes to other plant types. Coverage of semiwoody and woody plants, along with midstory saplings, provided structure at many sites consistent with that described in the literature as selected nesting cover for Turkeys as well as cover for Deer during lactation and fawning. Relatively low levels of forb coverage at all sites limited high-quality Deer forage, but maintenance-level Deer NCC estimates were moderate and correlated to transect-level coverage of shrubs and vines. Sunlight available to the understory was influenced most by hardwood basal area and midstory saplings, which demonstrated the importance of managing hardwoods in pine-dominated forests following thinning.

Dormant-season prescribed fire influenced only grass and vine coverage on our study sites. Managers often apply fire during the dormant season because of favorable weather conditions and culture but may see limited desired shifts in vegetation composition (Knapp et al. 2009). We documented 100% greater grass coverage at sites where fire was implemented, but grass is not a limiting factor when managing vegetation for Deer and Turkeys (Harper et al. 2021, Powell et al. 2022). Although the reduction in vine coverage may be beneficial if vines are outcompeting forbs, understory trees often are the most important vegetation competing with herbaceous plants (Harrington and Edwards 1999, Whelan et al. 2018). Dormant-season fire tends to be less effective at reducing tree coverage compared to fire during various portions of the growing season (Bond and Parr 2010, Resop et al. 2023, Robertson and Hmielowski 2014). Thus, managers may consider using fire during other seasons if shifts in plant composition are desired.

Managers frequently consider structure and composition separately, but they may interact to influence the wildlife value of an area. Deer and Turkey habitat selection may be more strongly related to cover than food (Chance et al. 2020), yet the type of plants providing structure often is overlooked. Consideration should be given to composition when managing structure for specific life-history events, as composition and structure may interact to influence food availability, selection, and/or survival (Chitwood et al. 2015, Johnson et al. 2022, Kilburg et al. 2014, Nelson et al. 2022). Our results demonstrated the positive influence of semiwoody and woody plant coverage on obstruction at 1.0–2.0 m, which provided cover for Turkey nests and Deer fawns. Turkeys select for overhead cover and greater visual obstruction from 0.5–1.5 m during nesting (Kilberg et al. 2014, Little et al. 2016, Johnson et al. 2022), and cover around nests may influence survival (Badyaev 1995, Johnson et al. 2022). Similar structure is selected by fawns (Huegel et al. 1986), and lactating females select for denser cover during fawning while avoiding more open areas (Cherry et al. 2017, Kroeger et al. 2020, Lashley et al. 2015b). Disturbance every 3–5 years is likely needed to maintain this structure (Yeldell et al. 2017), but our data indicate thinning with or without occasional prescribed fire provides sufficient visual obstruction for Turkey nesting and Deer fawning in many pine forests for at least 3 years after thinning.

Limited forb coverage reduced NCC for lactating does. Most of our sites had similar maintenance-level NCC estimates relative to what others have documented without frequent disturbance, likely a result of the extensive coverage of vines, shrubs, and trees (Iglay et al. 2010, Nichols et al. 2021). However, forb coverage averaged only 14% despite our sites having relatively open canopies. Forbs typically have greater nutrient concentrations than woody and semiwoody species (Harper 2019, Harper et al. 2021), but their availability often is limited (Lashley et al. 2011, Nanney et al. 2018). Given the relationship between forbs and lactation-level NCC estimates we measured, it is clear that a lack of forbs is limiting Deer forage quality and morphometrics in landscapes dominated by infrequently disturbed pine forests. Although we did not use exclusion cages to prevent Deer access to forage, it is unlikely foraging pressure was sufficient at our sites to significantly change our estimates of forage availability (Lashley et al. 2011, 2015c). Relatively abundant maintenance-level forages may allow Deer to exist at the high densities observed in many locations throughout the South where pine forests dominate the landscape, but morphometrics are not optimized with the current nutritional availability (Jones et al. 2018, Kissell et al. 2002, Lashley et al. 2015a, Strickland and Demarais 2000).

Sunlight available to the understory was influenced most strongly by midstory stems and overstory hardwoods across the variety of overstory pine basal areas we sampled. Numerous studies have documented understory responses to additional sunlight following overstory thinning (Blair and Enghardt 1976, Masters et al.

1993), but on sites with reduced pine basal area, retained hardwoods may play an important role in canopy closure. Although management for understory vegetation often focuses on reducing basal area through thinning, reducing midstory stems using herbicide applications and prescribed fire often is necessary to allow sufficient sunlight to stimulate understory vegetation (Edwards et al. 2004, Harrington and Edwards 1999, Iglay et al. 2014, Lashley et al. 2011). Retention of mast-producing overstory hardwoods may be desirable when managing for Deer and Turkey in pine stands, but hardwoods capturing additional sunlight may decrease understory response (Blair 1971, Kroeger et al. 2020, Peitz et al. 2001). Identifying dominant mast producers for retention and removing poor producers would be an effective strategy to manage overstory hardwoods in pine systems (Brooke et al. 2019).

Despite being managed with Deer and Turkey habitat as a primary or competing objective, our study stands generally provided poor resources for Deer and Turkeys during specific life-history periods. Specifically, high-quality Deer forage availability and Turkey brooding cover were limited across our sites. All our sites had lactation-level NCC estimates ≤20% of those reported previously in pine forests managed intensively with fire and/or selective herbicides to increase forage availability (min–max: 202–318 deer days/ha; Edwards et al. 2004, Iglay et al. 2010, Nichols et al. 2021). Although our sites provided structure similar to what the literature describes as Turkey nesting cover (Johnson et al. 2022, Kilberg et al. 2014, Little et al. 2016), brooding cover was relatively poor. Greater than 50% visual obstruction from 1.0–2.0 m at 5 of the 8 sites reduced brooding cover quality (Fig. 3), as brooding hens generally select for herbaceous vegetation ~0.5 m in height with more open structure above (Nelson et al. 2022, Wood et al. 2018). Areas with greater coverage of herbaceous vegetation, especially forbs, are consistently

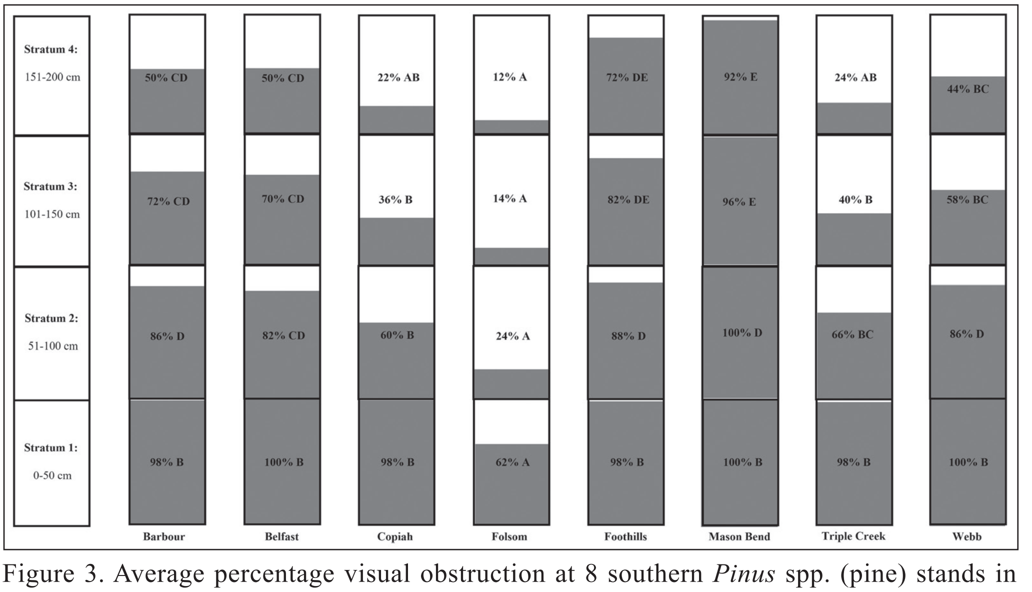

Figure 3. Average percentage visual obstruction at 8 southern *Pinus* spp. (pine) stands in Tennessee, South Carolina, Alabama, and Mississippi, June–July 2020. Different letters at the same stratum represent significant differences in visual obstruction between sites.

selected for brooding (Campo et al. 1989, Johnson 2019, Nelson et al. 2022), yet our stands averaged only 14% forb coverage. Thus, thinning with or without infrequent dormant-season fire failed to promote vegetation for important life-history periods in stands with relatively open canopies. Our results indicate management practices that increase understory sunlight should be paired with frequent disturbance to provide vegetation communities which benefit Deer and Turkeys.

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