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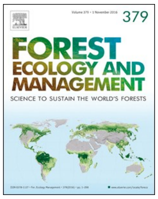

The relationship between upland hardwood distribution and avian occupancy in fire-maintained longleaf pine forests

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ABSTRACT

Prescribed fire and other forest management practices aimed at restoring longleaf pine (*Pinus palustris*) communities often focus on the reduction, or removal, of upland hardwoods with the goal of providing habitat for threatened and endangered plant and animal species, including the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis*), and restoring forests to pre-settlement conditions. Although contemporary restoration and management practices benefit species dependent on the resulting conditions, recent research has called attention to the ecological value of retaining upland hardwoods, especially for mast-dependent wildlife (e.g., fox squirrels [*Sciurus niger*]). Moreover, retention of indigenous hardwoods in upland longleaf pine communities may benefit a variety of birds. We used fixed-radius, breeding season point counts to sample the presence-absence of 15 avian species and assessed forest composition and structure around each point. We developed single-season single-species occupancy models with an emphasis on the influence of overstory hardwood cover on occupancy. Due to issues with model fit, we were unable to model occupancy for 3 of the 15 focal species. Occupancy probabilities for 6 out of the 12 focal species were positively influenced by overstory hardwood cover or stem density, whereas occupancy probabilities of 4 out of 12 of the focal species was negatively influenced by hardwood cover or stem density. Overstory hardwood cover between 5 and 15% resulted in high occupancy probabilities for the species that were positively influenced but did not result in substantially low occupancy probabilities for the species that were negatively influenced. Longleaf pine uplands with lower and upper bounds of 5% to 15% hardwood overstory cover with hardwood stem densities of ≤250 stems/ha could be targeted to provide habitat for the greatest diversity of birds while avoiding negative impact to species associated with upland longleaf pine communities.

1. Introduction

The longleaf pine (*Pinus palustris*) ecosystem is globally endangered and critically important to biodiversity conservation in the southeastern United States (Noss et al., 1995). Throughout the 20th century, longleaf pine communities declined dramatically, due in part to fire exclusion (Frost, 1993). Near the end of the 20th century, the need to conserve longleaf pine communities through fire management became widely recognized (Noss, 1989; USFWS, 2003; Brockway et al., 2005), and extensive restoration efforts have been underway since; however, remnant longleaf pine forests still occupy a small fraction of the original extent of this ecosystem (Oswalt et al., 2012). With consideration of the marked decline in range, disruptions to essential disturbance regimes, and the system's contribution to biodiversity in the Atlantic coastal plain (Noss et al., 2015), the need for widespread conservation of longleaf pine communities is now widely accepted.

Where conservation of longleaf pine communities is the focus, managers use frequent prescribed fire to create or maintain longleaf pine dominated overstories with understories of grasses, forbs, and longleaf pine regeneration (USFWS, 2003; Brockway et al., 2005). Because fire exclusion typically results in hardwood encroachment in upland areas, reducing the stature and abundance of midstory and overstory hardwoods in longleaf pine uplands is a common motive driving prescribed fire management (Gilliam and Platt, 1999; Hiers et al., 2014; Hoffmann et al., 2020). Hiers et al. (2014), describes the ecological value of retaining pyrophytic oaks in longleaf pine ecosystems, however, variations in edaphic conditions among longleaf pine community types (e.g., xeric sandhills, mesic flatwoods, and wet flatwoods) are accompanied by differences in the hardwood species component, the degree to which the hardwood component degrades the

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function of the community, and the hardwood response to fire management. Although hardwood control is a key component of longleaf pine ecosystem restoration, long-term management requires a more complex understanding regarding the role of upland hardwoods – especially with respect to their influence on ecological diversity, including faunal community dynamics.

Prescribed fire management typically aims to achieve reduction or removal of upland hardwood cover with the goal of restoring pre-settlement forest conditions (Noss et al., 2015), promoting diverse herbaceous cover (Glitzenstein et al., 2003), and providing habitat for rare plants and animals such as the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis*) (Garabedian et al., 2017). Although removal or substantial reduction of hardwood canopy and midstory cover benefits those species dependent on the resulting conditions, recent research has called attention to the ecological value of retaining upland hardwoods (Perkins et al., 2008; Hiers et al., 2014; Lashley et al., 2014). Hence, the appropriate amount of upland hardwood cover in restored longleaf pine communities is debated, as more hardwood cover can provide vegetative structure (Hiers et al., 2014), escape cover or wildlife refugia (Conner and Godbois, 2003), valuable invertebrate production as food for vertebrate wildlife (Wagner, 2005; Tallamy and Shropshire, 2009), and mast as food for wildlife (e.g., fox squirrels [*Sciurus niger;* Perkins et al., 2008], white-tailed deer [*Odocoileus virginianus;* Lashley et al., 2015]), while less hardwood cover is important to for maintaining habitat for red-cockaded woodpecker (Garabedian et al., 2014, 2017). Although the ecological importance of upland hardwoods in longleaf pine communities has long been recognized (Landres et al., 1990; Greenberg and Simons, 1999; Hiers et al., 2014; Loudermilk et al., 2016), management efforts are often based on precise goals of forest structure and composition.

Although abundant hardwood cover is an indicator of fire exclusion and has been suggested to negatively influence a subset of avian species in longleaf pine uplands (Allen et al., 2006), variable amounts of mature hardwoods certainly persist in uplands managed with long-term frequent fire (Greenberg and Simons, 1999; Jacqmain et al., 1999; Hiers et al., 2014; Hoffmann et al., 2020). Previous studies evaluated the habitat associations of conservation priority birds in longleaf pine communities (Cox et al., 2012; Taillie et al., 2015; Hannah et al., 2017; Fish et al., 2018), or examined avian community response to restoration practices (Conner et al., 2002; Provencher et al., 2003; Allen et al., 2006; Steen et al., 2013), but few directly modeled the role (positive and negative) of mature hardwood cover on avian dynamics in longleaf pine communities managed with frequent fire (Cox et al., 2012). Although the negative association between dense hardwood midstory cover and red-cockaded woodpecker habitat use is well documented (James et al., 1997, 2001; Walters et al., 2002; Macey et al., 2016; Garabedian et al., 2017), the contribution of upland hardwoods to sustaining avian diversity may be underappreciated. Specifically, the effects of hardwoods on other avian species of conservation concern in the longleaf pine ecosystem, including Bachman's sparrow (*Peucaea aestivalis*), brown-headed nuthatch (*Sitta pusilla*), and northern bobwhite (*Colinus virginianus*), are poorly understood. Additionally, upland longleaf pine forests interspersed with low to moderate amounts hardwood cover may support many species of breeding, wintering, resident, or migrating birds associated with mixed forests (e.g., blue-gray gnatcatcher [*Polioptila caerulea*], blue-headed vireo [*Vireo solitaries*], red-eyed vireo [*Vireo olivaceus*], summer tanager [*Piranga rubra*], yellow-throated vireo [*Vireo flavifrons*]), without reducing habitat quality for longleaf pine community specialists. Although Allen et al. (2006) classified breeding bird assemblages in fire-maintained longleaf pine forests, their analysis did not consider how overstory hardwoods in longleaf pine uplands influenced the avian community. Moreover, a subset of bird species studied by Allen et al. (2006) did not demonstrate clear agreement with their *a priori* assemblage categories; we believed this could be due to the lack of consideration for the role of upland hardwoods Therefore, we sought to resolve this knowledge gap by directly modeling avian distributions using continuous metrics of overstory hardwood cover.

We investigated the role of tree-sized and mature hardwood cover in driving avian occupancy in a landscape managed with long-term frequent fire. We used fixed-radius point count surveys with repeat visits to sample the presence-absence of 15 focal species (Bachman's sparrow, blue-gray gnatcatcher, brown-headed nuthatch, blue-headed vireo, Carolina chickadee [*Poecile carolinensis*], eastern wood-pewee [*Contopus virens*], great crested flycatcher [*Myiarchus crinitus*], northern bobwhite, pine warbler [*Setophaga pinus*], prairie warbler [*Setophaga discolor*], summer tanager, tufted titmouse [*Baeolophus bicolor*], red-eyed vireo, red-headed woodpecker [*Melanerpes erythrocephalus*], yellow-throated vireo) that we expected to display a range of responses to hardwood midstory and canopy cover. We assessed forest composition around each point count location using field-based and remote sensing methods to capture information about hardwood cover, which typically is sparse and patchily distributed in longleaf pine uplands on the study area. We developed models of occupancy with the goal of identifying avian species for which hardwood cover is an important predictor of occupancy, negative or positive, in longleaf pine uplands. We sought to identify specific thresholds of hardwood cover for individual bird species, in turn informing efforts aimed at balancing the goals of endangered species management and biodiversity conservation.

2. Materials and methods

2.1. Study area

We conducted the study at Fort Bragg Military Installation (hereafter Fort Bragg) in the Sandhills physiographic region of south-central North Carolina, USA (35.1°N, −79.2°W; Fig. 1). Fort Bragg is a 625-km^2 active military installation that is among the largest contiguous landscapes of the longleaf pine-wiregrass (*Aristida strica*) ecosystem. Management of longleaf pine-wiregrass communities on Fort Bragg is focused on conservation of rare, threatened, and endangered species (e.g., red-cockaded woodpecker) and maintenance of troop training facilities and infrastructure (FBMI, 2018). To achieve management goals, Fort Bragg implements a 3-year rotation of early, growing season fire wherein one-third of the base is targeted to be burned each year (Cantrell et al., 1995; Lashley et al., 2014; FBMI, 2018). Since 1990, frequent growing season fire has been the dominant management strategy, but land managers also incorporate dormant season prescribed fire to reduce fuel loads that increase the likelihood of catastrophic fire. In addition, managers use thinning and herbicides to control hardwood encroachment and maintain open stand structures with overstory pine basal area of ~11.5 m^2/ha and understories dominated by grasses, forbs, and longleaf pine regeneration (Lashley et al., 2014; FBMI, 2018).

The landscape is comprised of rolling sandhills heavily dissected by streams, bottomlands, and stream-head pocosins (Sorrie et al., 2006; FBMI, 2018). The elevation ranges from 36 m to 183 m above sea level, and uplands typically are composed of deep, well-drained sandy soils (Sorrie et al., 2006; FBMI, 2018). The lower slope areas usually are composed of loamy sands, while loam soils typically predominate the lowland areas (Cantrell et al., 1995; Sorrie et al., 2006; FBMI, 2018). The climate is characterized as sub-tropical with long, hot summers and short, mild winters (FBMI, 2018). Much of the base is composed of pine/scrub oak sandhill community in which longleaf pine, wiregrass, and oaks (*Quercus* spp.) are the dominant plant species (Cantrell et al., 1995; Sorrie et al., 2006). Other vegetative communities include upland hardwood, bottomland hardwood, and managed grasslands used for military training (Sorrie et al., 2006; Lashley et al., 2014). Common hardwood species include turkey oak (*Quercus laevis)*, blackjack oak (*Quercus marilandica*), sweetgum (*Liquidambar styraciflua*), sand post oak (*Quercus stellata*), and blackgum (*Nyssa sylvatica*) (Sorrie et al., 2006; Lashley et al., 2014).

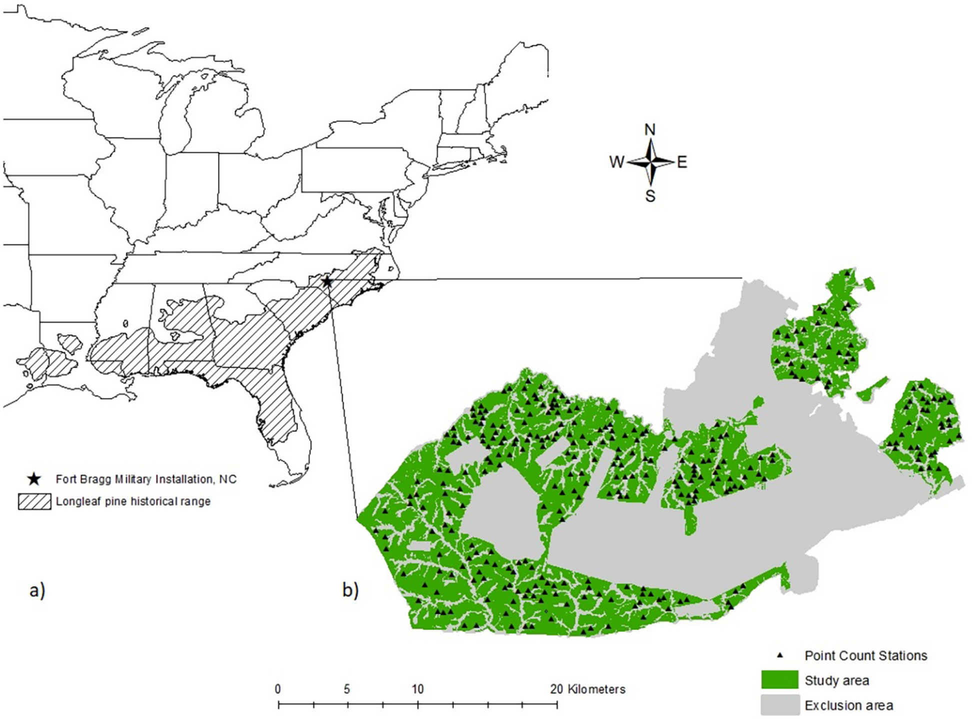

Fig. 1. Fort Bragg Military Installation in relation to the historic range of longleaf pine ecosystem (a); avian point count study area and exclusion areas on Fort Bragg Military Installation, North Carolina, 2018.

2.2. Site selection and avian surveys

We used ArcGIS (Arcmap v. 10.5; ESRI, Redlands, CA, USA) to eliminate from the study area all locations within 50 m of streams, classified wetlands, and bottomland hardwood communities. We randomly located 305 points in upland longleaf pine communities with a minimum point spacing of 300 m using ArcGIS. Each random location served as the center point of a 150-m fixed-radius point count station. Prior to the first round of surveys, each observer was trained to identify the distance cut-off of 150 m using both Garmin handheld GPS, and Nikon rangefinders; these tools were used on each survey to ensure that only birds detected within the sampling unit were recorded as present.

We visited each point between one-half hour before sunrise and 1000 h on four occasions between 27 April 2018 and 15 July 2018. Each of the two observers surveyed every point on two of the four occasions, and the order of points surveyed and the path of visitation was changed on subsequent rounds to survey each point across the range of time during the survey window. Generally, surveys were conducted when precipitation was absent, but occasionally, we continued surveys in light drizzle conditions. We did not survey when wind exceeded a three on the Beaufort wind scale (e.g., ~19 kph [Sauer et al., 2011; Cox et al., 2012]). During each visit, we identified all focal species by sight and sound for a 10-min period and recorded the presence and absence of each focal species.

2.3. Forest structure and composition

We quantified forest structure and composition at each point using both field-based and remote sensing methods. At each point location, we established a 0.04-ha (11.4-m radius) plot wherein we counted and identified all stems $\geq$5-cm diameter at breast height (DBH), and we summarized the number of hardwood trees and pine trees at each plot. We used a 10-factor prism to quantify total basal area (m^2/ha) and basal area of hardwoods and pines separately. Additionally, we quantified grass cover at 21 points, with one point at plot center and five points located at 2-m intervals along 10-m transects in each cardinal direction from plot center. At each transect point, we recorded whether a 2-m vertical pole intersected grass (Moorman and Guynn, 2001). Percent grass cover for each plot was calculated by dividing the number of points with grass stems by the total number of points (21).

We developed a fine-scale land cover layer using 4-band aerial imagery and LiDAR-derived models of canopy height and canopy intensity (all raster datasets were in a 1- x 1-m resolution). Fort Bragg collected the leaf-off aerial imagery, taken with a Leica ADS80-SH82 sensor, during the winter of 2015, and the LiDAR point cloud was collected during the growing season of 2014. Specifically, we used ArcGIS to transform a full-return LiDAR point cloud with 0.4-m point spacing into raster layers of canopy height and canopy intensity. We calculated a normalized difference vegetation index (NDVI) using the red and near-infrared band of the aerial imagery. The four bands of aerial imagery, NDVI, and LiDAR-derived canopy models (all 1- x 1-m resolution) served as predictive layers in a pixel-based supervised classification using a RandomForest algorithm (Breiman, 2001). We used R statistical software, package RandomForest (Liaw & Wiener, 2002; R Core Team, 2018) to extract raster values to the training data, fit the RandomForest model, and develop the classified map. The final classified map used in analysis included four classes: pine, upland hardwood, bottomland hardwood, and other, although the original classification contained 12 classes. To improve accuracy in classifying mature hardwood cover, we reclassified the canopy height model into two categories including ≥ 5 m and < 5 m, and all hardwood cover < 5 m was reclassified as “other.” Additionally, we sieved the land cover classification using a majority filter algorithm and a boundary cleaning algorithm using ArcGIS (ArcMap v. 10.5; ESRI, Redlands, CA). We assessed the accuracy of the final map by extracting the raster value of the classified map at the center point of the 305 randomly located point count locations and manually categorizing the land cover at each point; these data were analyzed using a confusion matrix, and the overall accuracy, user’s accuracy, and producer’s accuracy were assessed according to Olofsson et al. (2013). We summarized the proportion of upland hardwood canopy cover and pine canopy cover within each sampling unit by generating a 150-m circular buffer around each point, calculating the area covered (m^2) by each class, and dividing by the total area of the buffer.

2.4. Statistical analysis

In R statistical software, we used package "Corrplot" to assess all pair-wise correlations for all independent variables, and package "Usdm" to assess multi-collinearity among independent variables with variance inflation factors (VIF [Naimi et al., 2014; Wei and Simko, 2017; R Core Team, 2018]). If two variables were highly correlated ($R > |0.6|$), we used the variable with a lower VIF. After eliminating highly correlated pairs of independent variables, we excluded any variable with VIF > 3. We used R statistical software package "Unmarked" to develop single-season, single-species occupancy models for each focal species (Fiske and Chandler, 2011; R Core Team, 2018). We first fit a global model for each species and assessed goodness-of-fit as per MacKenzie and Bailey (2004). If a species' global model indicated lack of fit ($\hat{c} \geq 4.0$), we did not make inferences regarding the relationship between site covariates and occupancy. Because we expected species' models to exhibit varying degrees of overdispersion, and to keep model ranking uniform across species, we ranked all models using quasi-Akiake information criteria (QAIC) with c-hat ($\hat{c}$) specified using package "AICcmodavg" (Mazerolle, 2017). When $\hat{c} = 1.0$, QAIC is equivalent to AIC ranking; however, when $> 1\hat{c}.0$, QAIC represents a model selection criterion that both accounts for overdispersion, and favors more parsimonious models due to an additional estimated parameter ($\hat{c}$) included in the "penalty" term (2 k) of the AIC/QAIC equation (Burnham and Anderson, 2002).

The model selection process was initiated by fitting a series of *a priori* models in which detection probability (*p*) was predicted by observation-level covariates, including linear effects of observer, date, and visit as well as a quadratic effect for date (Taillie et al., 2015). We chose the top model of detection probability for each species by lowest QAIC (Burnham and Anderson, 2002; Cox et al., 2012). Each species' top model of detection probability was used in all subsequent efforts to model species occupancy (Taillie et al., 2015). Next, we fit a series of *a priori* models in which species occupancy (ψ) was predicted by linear, quadratic, and interacting effects of field measured vegetation metrics (e.g., hardwood stem counts, pine basal area, grass cover [Table 1]). We ranked field measured vegetation models with QAIC, and all models with ΔQAIC < 2 were considered competitive unless they were more complex versions of the top model and contained uninformative parameters (Arnold, 2010). We repeated this process on the *a priori* set of remotely sensed metrics including linear, quadratic, and interacting effects of upland hardwood canopy cover and pine canopy cover within a 150-m radius of each point (Table 1). We then developed a set of models where occupancy was predicted by all combinations of competitive models from both scales. Finally, we ranked all models (e.g., *a priori* models, combined models) using QAIC, and selected the top model based on the lowest QAIC (Burnham and Anderson, 2002). Again, all models with ΔQAIC < 2 were considered competitive unless they were more complex versions of the top model and contained uninformative parameters (Arnold, 2010), and our top model of occupancy for each species was the most parsimonious model among the final set of competitive models.

Table 1
Mean, standard deviation, and range of independent variables used in a priori models of occupancy for 15 bird species. Fort Bragg Military Installation, North Carolina, 2018.

Variable	Mean	SD	Range
Field measured			
Grass cover (%)	54.3	32.4	0–100
Hardwood stem density (trees/ha)	151	187	0–985
Pine basal area (m^2/ha)	13.4	7.9	0–39.0
Remotely sensed			
Hardwood canopy cover (%)	6.3	4.4	0.0–37.0
Pine canopy cover (%)	44.9	13.2	9.0–81.0

2.5. Model inference

To investigate the support for covariate effects on occupancy, we calculated both 95% confidence intervals (CI) and 85% CI for all parameters in the top model of occupancy for each species on the logistic scale. In an effort to further account for overdispersion ($\hat{c} > 1.0$), we inflated the standard error of each parameter by multiplying by $\sqrt{\hat{c}}$ prior to calculating all CIs. If neither CI crossed zero, we considered this strong support for a covariate effect for a given parameter. If the 95% CI crossed zero, but the 85% CI did not, we considered this weak support of a covariate effect, and if both the 95% CI, and 85% CI overlapped zero, we concluded there was no support for a covariate effect on occupancy for a given parameter. Moreover, all CIs presented in fitted occupancy predictions were inflated by multiplying the standard error by $\sqrt{\hat{c}}$ prior to calculating all CIs.

3. Results

We documented high pairwise correlation coefficients ($|R| > 0.6$) and multicollinearity (VIF > 3) between pine basal area and total basal area, pine stem counts, and total stem count, and thus selected pine basal area as a metric of pine cover for *a priori* model development. Although hardwood basal area and hardwood stem counts were highly correlated ($|R| = 0.68$), we wanted to maintain as much information about hardwood stem density as possible, and thus we selected hardwood stem counts for all *a priori* model development. There was no collinearity between upland hardwood canopy cover and pine canopy cover, so *a priori* models containing remotely sensed metrics included linear, quadratic, and interacting effects of these two covariates (Appendix A, Table A.1). The independent variables used in occupancy models included hardwood stem density (151. 4 ± 187.3), pine basal area (13.4 ± 7.9), percent grass cover (54.3 ± 32.4), hardwood canopy cover within 150 m (6.3 ± 4.4), and pine canopy cover within 150 m (44.9 ± 13.2 [Table 1]). From the independent accuracy assessment of the land cover classification of Fort Bragg, the overall accuracy was 79.67% (Appendix A, Table A.2), and user's accuracies of 80.60%, 78.79%, and 79.00% for pine, hardwood, and other, respectively (Table 3), with producer's accuracies of 83.10%, 72.22%, and 78.42% for pine, upland hardwood, and other, respectively (Table 3).

The number of sites occupied by the species we surveyed ranged from a low of 51 of the 305 sampling sites for yellow-throated vireo (16.72%) to a high of 299 of the 305 sampling sites for pine warbler (98.03%, Table 2). On average, yellow-throated vireo had the lowest detection probability, and blue-gray gnatcatcher had the greatest detection probability (0.11 ± 0.03, 0.71 ± 0.02, respectively, Table 2). With exception of yellow-throated vireo, the results from goodness-of-fit tests on the global models for all species indicated varying levels of overdispersion across the species we sampled. For species models that indicated overdispersion, the global model for blue-headed vireo had the lowest level of overdispersion, and the model for pine warbler had the highest level of overdispersion ($\hat{c} = 1.10$, $\hat{c} = 20.83$, respectively, Table 2). Great crested flycatcher, pine warbler, and prairie warbler had levels of overdispersion where model fit is considered questionable ($\hat{c} = 8.08$, $\hat{c} = 20.83$, $\hat{c} = 5.00$, respectively, Table 2); hence, we did not rank models or make inferences regarding great crested flycatcher, pine warbler, and prairie warbler due to the lack-of-fit indicated by their respective global models. Northern bobwhite was the only species for which the top model of occupancy did not contain either hardwood stem density or hardwood cover within 150 m.

The top model for occupancy probability of Bachman's sparrow included linear effects of hardwood stem density and grass cover

Table 2
Species, alpha code, overdispersion parameter ($\hat{c}$), naïve occupancy (ψ), mean detection probability (p), and top model of detection probability for 15 bird species. Fort Bragg Military Installation, North Carolina, 2018. Shaded cells indicate lack-of-fit ($\hat{c} \geq 4.00$) and species that were not modeled.

Species	Code	$\hat{c}$	Naïve ψ	p	Top detection model
Bachman's sparrow	BACS	2.27	0.50	0.36 ± 0.02	p(.) psi(.)[a]
Blue-gray gnatcatcher	BGGN	3.68	0.71	0.71 ± 0.02	p(.) psi(.)
Blue-headed vireo	BHVI	1.10	0.23	0.29 ± 0.03	p(Date + visit) psi(.)
Brown-headed nuthatch	BHNU	2.48	0.68	0.36 ± 0.02	p(.) psi(.)
Carolina chickadee	CACH	1.92	0.61	0.40 ± 0.03	p(Observer + Visit) psi(.)
Eastern wood-pewee	EWPE	1.99	0.65	0.50 ± 0.02	p(.) psi(.)
Great crested flycatcher	GCFL	8.08	0.91	0.58 ± 0.02	–
Northern bobwhite	NOBO	3.27	0.21	0.13 ± 0.03	p(.) psi(.)
Pine warbler	PIWA	20.83	0.98	0.66 ± 0.01	–
Prairie warbler	PRWA	5.00	0.42	0.53 ± 0.03	–
Red-eyed vireo	REVI	2.46	0.25	0.28 ± 0.03	p(.) psi(.)
Red-headed woodpecker	RHWO	3.34	0.60	0.36 ± 0.02	p(.) psi(.)
Summer tanager	SUTA	1.87	0.88	0.57 ± 0.02	p(Date + Date^2) psi(.)
Tufted titmouse	TUTI	2.50	0.75	0.58 ± 0.02	p(Date + Date^2) psi(.)
Yellow-throated vireo	YTVI	0.70	0.17	0.11 ± 0.03	p(.) psi(.)

[a] Null model – detection probability constant.

(Table 3). The effects of hardwood stem density were negative, with neither CI overlapping zero (Table 4), and thus we concluded there was strong support for hardwood stem density as a negative predictor of Bachman's sparrow occupancy. Specifically, sites with hardwood stem densities greater than 300 trees/ha had an occupancy probability less than 0.50 (Fig. 2a). The effect of grass cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Specifically, sites with grass cover comprising at least 75% of the plot had an occupancy probability greater than 0.75 (Fig. 2b).

The top occupancy model for blue-headed vireo and brown-headed nuthatch contained linear effects of hardwood stem density and pine cover within 150 m (Table 4). For blue-headed vireo, the effect of hardwood stem density was positive, and though the 95% CI slightly overlapped zero, the 85% CI did not (Table 4); hence there was weak support for hardwood stem density as a positive predictor of blue-headed vireo occupancy. Sites with at least 1120 hardwood stems/ha had an occupancy probability greater than 0.75 (Fig. 3a). The effect of pine cover within 150 m on blue-headed vireo occupancy was positive, and though the 95% CI slightly overlapped zero, the 85% CI did not (Table 4). Sites with greater than 60% pine cover had an occupancy probability greater than 0.50 (Fig. 3b). For brown-headed nuthatch, the effect of hardwood stem density was negative, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Sites with at least 685 hardwood stems/ha had an occupancy probability greater than 0.50 (Fig. 4a). The effect of pine cover within 150 m was negative for brown-headed nuthatch, and though the 95% CI slightly overlapped zero, the 85% CI did not (Table 4). As pine cover within a 150-m radius around sampling points increased, brown-headed nuthatch occupancy probability decreased; however, brown-headed nuthatch occupancy probability only dropped below 0.50 when pine cover within 150 m surpassed 75% (Fig. 4b).

The top occupancy model for eastern wood-pewee and red-eyed vireo included linear effects of hardwood cover within 150 m and pine cover within 150 m (Table 4). For eastern wood-pewee, the effect of upland hardwood cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Sites with at least 7% hardwood cover had an occupancy probability greater than 0.75 (Fig. 5a). The effect of pine cover within 150 m was positive for eastern wood-pewee, and though the 95% CI slightly overlapped zero, the 85% CI did not (Table 4). Occupancy probability was greater than 0.75 when pine cover within 150 m surpassed 50% (Fig. 5b). For red-eyed vireo, the effect of upland hardwood cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Sites with at least 15% hardwood cover had an occupancy probability greater than 0.75 (Fig. 6a). The effect of pine cover within 150 m was positive for red-eyed vireo, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Occupancy probability was greater than 0.75 when pine cover within 150 m of sites surpassed 75% (Fig. 6b).

The top occupancy model for blue-gray gnatcatcher, tufted titmouse, and yellow-throated vireo included the linear effect of hardwood cover within 150 m (Table 4). For blue-gray gnatcatcher, the effect of hardwood cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Sites with upland hardwood cover comprising at least 5% of the surrounding 150-m buffer had an occupancy probability greater than 0.75 (Fig. 7). For tufted titmouse, the effect of upland hardwood cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Specifically, as hardwood cover increased from $\sim$1% to $\sim$4%, tufted titmouse occupancy probability increased from 0.50 to 0.75, respectively (Fig. 8). For yellow-throated vireo, the effect of upland hardwood cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Specifically, at sites with greater than 12% upland hardwood cover within 150 m, yellow-throated vireo occupancy probability was greater than 0.75 (Fig. 9).

The top model of occupancy probability for Carolina chickadee included a linear effect of hardwood stem density (Table 4). Although the effect of hardwood stem density was positive, both the 95% CI and 85% CI overlapped zero (Table 4); hence there was no support for a covariate effect. Moreover, both the 95% CI and the 85% CI overlapped zero for every parameter in all competitive models, and thus we did not make inferences regarding any covariate effects on Carolina chickadee occupancy.

The top model of occupancy for red-headed woodpecker and summer tanager contained a linear effect of hardwood stem density and pine basal area and an interaction between these two variables (Table 4). Although the top AIC model of summer tanager occupancy included a linear effect of hardwood stem density, we chose a model that included linear effects of hardwood stem density and pine basal area as the top model because we considered the additional parameter informative (Table 4). For red-headed woodpecker, the effect of hardwood stem density was negative, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). Sites with more than 250 hardwoods/ha had an occupancy probability less than 0.50 (Fig. 10a). The effect of pine basal area was negative for red-headed woodpecker, and neither the 95% CI nor the 85% CI overlapped zero (Table 4). As pine basal area increased, red-headed woodpecker occupancy decreased, and sites with pine basal area above 18 m^2/ha had occupancy probability less than 0.50 (Fig. 10b). The interaction of hardwood stem density and pine basal area was negative for red-headed woodpecker, and the 95% CI overlapped zero, but the 85% CI did not (Table 4). Specifically, red-

Table 3
The number of parameters (K), QAIC, ΔQAIC, and model weight (ω) for models ≤ 2 ΔQAIC with combinations of grass cover, hardwood (HW) stem density, hardwood cover, pine basal area (BA), and pine cover as covariates of occupancy for 12 bird species. Fort Bragg Military Installation, North Carolina, 2018.

Species	Model	K	QAIC	ΔQAIC	ω
BACS	Grass cover + HW stems[a]	5	524.59	0.00	0.32
	Grass cover + HW stems + Pine BA	6	525.80	1.21	0.18
	Grass cover + HW cover + HW stems	6	525.81	1.22	0.18
	Grass cover * HW stems	6	526.57	1.98	0.12
BGGN	HW cover[a]	4	309.67	0.00	0.36
	HW cover + HW stems	5	311.01	1.34	0.19
	HW cover^2	5	311.59	1.92	0.14
	HW cover + Pine cover	5	311.66	1.98	0.14
BHVI	HW stems + Pine cover[a]	9	620.34	0.00	0.18
	HW cover + Pine cover	9	620.93	0.59	0.14
	HW cover + HW stems + Pine cover	10	621.33	0.99	0.11
	Pine cover	8	621.51	1.17	0.10
	HW cover * Pine cover	10	621.88	1.54	0.09
	HW stems	8	622.12	1.77	0.08
BHNU	HW stems + Pine cover[a]	5	594.24	0.00	0.26
	HW cover + HW stems + Pine cover	6	595.51	1.27	0.14
	HW cover + Pine cover	5	595.66	1.42	0.13
CACH	HW stems[a]	7	579.79	0.00	0.10
	HW cover	7	579.96	0.17	0.09
	HW stems + Pine BA^2	9	581.27	1.48	0.05
	Pine cover^2	8	581.51	1.72	0.04
	HW cover + Pine BA^2	9	581.54581.64	1.751.85	0.04
	Pine BA^2	8	581.64	1.85	0.04
EWPE	HW cover + Pine cover[a]	5	738.73	0.00	0.33
	HW cover * Pine cover	6	739.32	0.59	0.24
	HW cover	4	739.82	1.09	0.19
GCFL	–	–	–	–	–
NOBO	Pine cover[a]	4	194.37	0.00	0.24
	HW cover + Pine cover	5	195.19	0.82	0.16
	Pine cover^2	5	196.03	1.66	0.11
	Null	3	196.08	1.71	0.10
PIWA	–	–	–	–	–
PRWA	–	–	–	–	–
REVI	HW cover + Pine cover[a]	5	281.50	0.00	0.24
	HW cover * Pine cover	6	281.57	0.07	0.24
	HW cover + HW stems + Pine cover	6	282.31	0.81	0.16
	HW stems + HW cover * Pine cover	7	282.49	0.99	0.15
	Grass cover + HW cover + Pine cover	6	283.40	1.91	0.09
	Grass cover + HW cover * Pine cover	7	283.43	1.94	0.09
RHWO	HW stems * Pine BA[a]	6	407.34	0.00	0.24
	HW cover + Pine cover	5	408.39	1.05	0.14
	HW stems * Pine BA + HW cover + Pine cover	8	408.75	1.41	0.12
SUTA	HW stems	6	670.50	0.00	0.17
	Grass cover + HW stems	7	670.85	0.35	0.14
	HW stems + Pine BA^2[a]	8	670.89	0.38	0.14
	HW stems * Pine BA	8	671.95	1.45	0.08
	Grass cover + HW stems + Pine BA	8	672.30	1.79	0.07
TUTI	HW cover[a]	6	480.78	0.00	0.39
	HW cover^2	7	482.06	1.29	0.21
	HW cover + HW stems	7	482.36	1.59	0.18
	HW cover + Pine cover	7	482.70	1.93	0.15
YTVI	HW cover[a]	3	468.12	0.00	0.36
	HW cover + Pine cover	4	468.92	0.79	0.24
	HW cover^2	4	469.27	1.15	0.20
	HW cover * Pine cover	5	469.95	1.82	0.15

[a] Best model of species occupancy.

Table 4
Parameters, estimates (logit scale), standard error, and confidence intervals (95% and 85%) for covariates in the best models of occupancy for 12 bird species. Fort Bragg Military Installation, North Carolina, 2018. Shaded cells indicate that the interval(s) overlapped zero.

Species	Parameter	Estimate	SE[a]	95% CI[b]		5% CI[c]	
BACS	HW stems	−0.65	0.29	−0.08	−1.21	−1.06	−0.23
	Grass cover	0.90	0.30	1.50	0.31	0.47	1.34
BGGN	HW cover	1.52	0.74	0.07	2.97	0.51	2.53
BHVI	HW stems	0.31	0.18	−0.05	0.67	0.05	0.57
	Pine cover	0.36	0.19	−0.01	0.73	0.08	0.63
BHNU	HW stems	−0.63	0.31	−1.24	−0.03	−1.07	−0.19
	Pine cover	−0.78	0.44	−1.64	0.08	−1.41	−0.15
CACH	HW stems	0.58	0.55	−0.50	1.66	−0.21	1.38
EWPE	Pine cover	0.37	0.22	−0.05	0.80	0.06	0.68
	HW cover	0.95	0.40	0.17	1.73	0.38	1.52
NOBO	Pine cover	−0.68	0.40	−1.47	0.11	−0.10	−1.26
REVI	Pine cover	0.85	0.31	0.23	1.46	0.40	1.30
	HW cover	1.11	0.48	0.18	2.05	0.43	1.80
RHWO	HW stems	−1.12	0.44	−1.98	−0.25	−0.48	−1.75
	Pine BA	−0.89	0.41	−1.70	−0.08	−0.30	−1.49
	HW stems * Pine BA	−0.83	0.49	−1.79	0.14	−0.12	−1.53
SUTA	Pine BA	0.37	0.89	−1.38	2.11	−0.91	1.65
	Pine BA ^{2}	−0.82	0.53	−1.86	0.22	−1.59	−0.06
	HW stems	−1.33	0.77	−2.85	0.18	−2.45	−0.22
TUTI	HW cover	1.78	0.68	0.44	3.12	0.79	2.76
YTVI	HW cover	1.12	0.44	0.25	1.99	0.48	1.76

[a] Standard errors multiplied by $\sqrt{\hat{c}}$ prior to calculating confidence intervals.

[b] Strong support for a covariates effect - zero was not overlapped at a 95% confidence level.

[c] Weak support for a covariates effect - zero was not overlapped at a 85% confidence level.

headed woodpecker occupancy probability was lowest in areas with high pine basal area and dense hardwood stems. For summer tanager, the effect of hardwood stem density was negative, and the 95% CI overlapped zero, but the 85% CI did not (Table 4). Although we documented weak support for hardwood stem density as a negative predictor of summer tanager occupancy, occupancy probability was greater than 0.50 across the entire range of hardwood densities we observed (Fig. 11a). The quadratic trend between summer tanager occupancy and pine basal area was negative, and the 95% CI overlapped zero, but the 85% CI did not (Table 4). Summer tanager occupancy increased as pine basal area increased from 0 to 25 m^2/ha, but then declined (Fig. 11b). However, summer tanager occupancy probability fell below 0.50 only as pine basal area approached 37.5 m^2/ha, which was at the high end of the range of pine basal area that we observed (Fig. 11b).

The top model of occupancy for northern bobwhite contained a linear effect of pine cover within 150 m (Table 4). The effect of pine cover within 150 m was negative, and the 95% CI overlapped zero, but the 85% CI did not (Table 4). As pine cover within a 150-m radius around sampling points increased, occupancy probability decreased, and occupancy probability was less than 0.50 when pine cover within 150 m of sites surpassed 40% (Fig. 12).

4. Discussion

Our results demonstrate the importance of mature hardwood composition in determining the distribution of avian species within upland longleaf pine forest. Of the 12 bird species we modeled, 10 were influenced either by hardwood stem density measured in the field, or hardwood canopy cover measured remotely. Although occupancy probability for three species commonly associated with open pine conditions responded negatively to high hardwood stem densities, occupancy probability for 6 of the 12 species was positively influenced by hardwood composition. These results further support the importance of

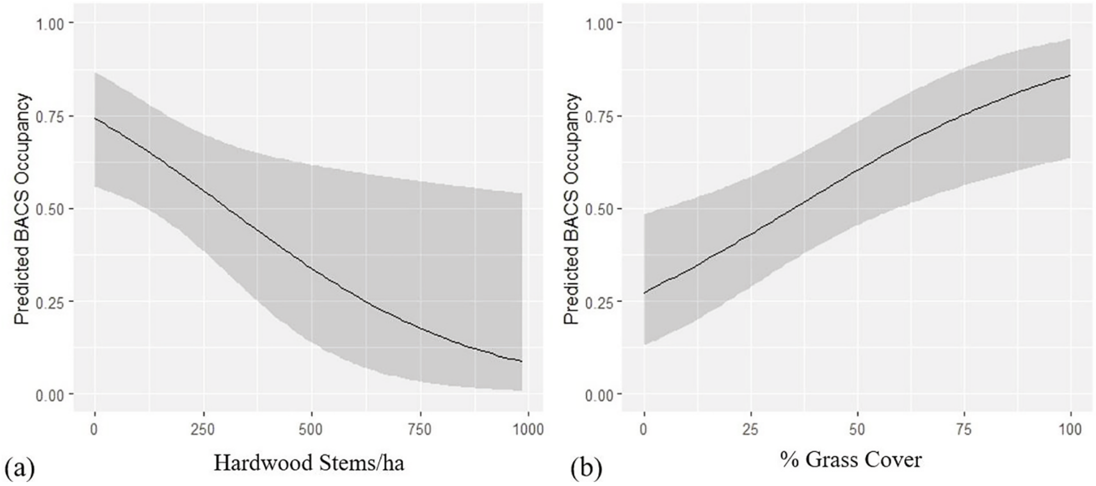

Fig. 2. The predicted occupancy probability for Bachman's Sparrows estimated across the range of hardwood stem density (a) and grass cover (b) using the top model, Fort Bragg Military Installation, North Carolina, 2018.

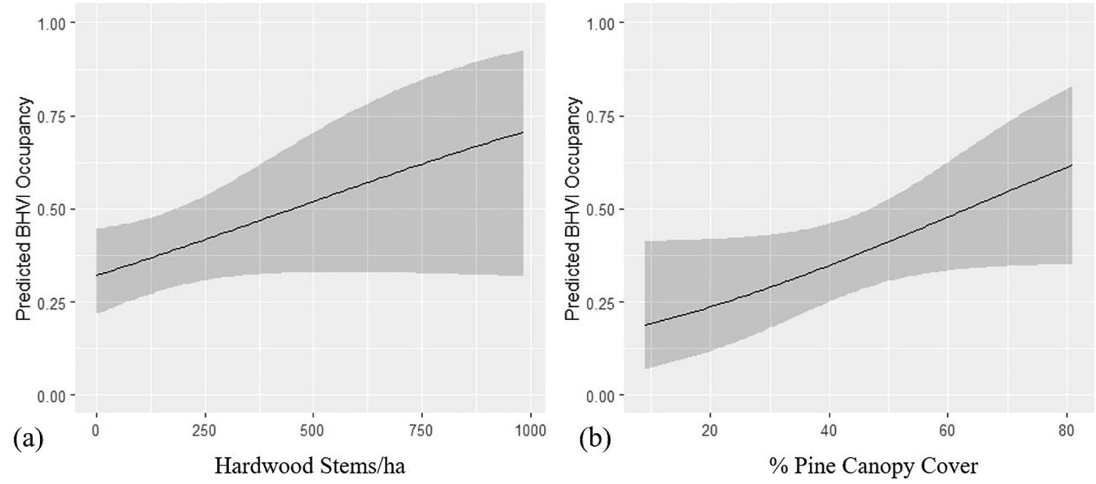

Fig. 3. The predicted occupancy probability for blue-headed vireo estimated across the range of hardwood stem density (a) and pine canopy cover (b) using the top model. Fort Bragg Military Installation, North Carolina, 2018.

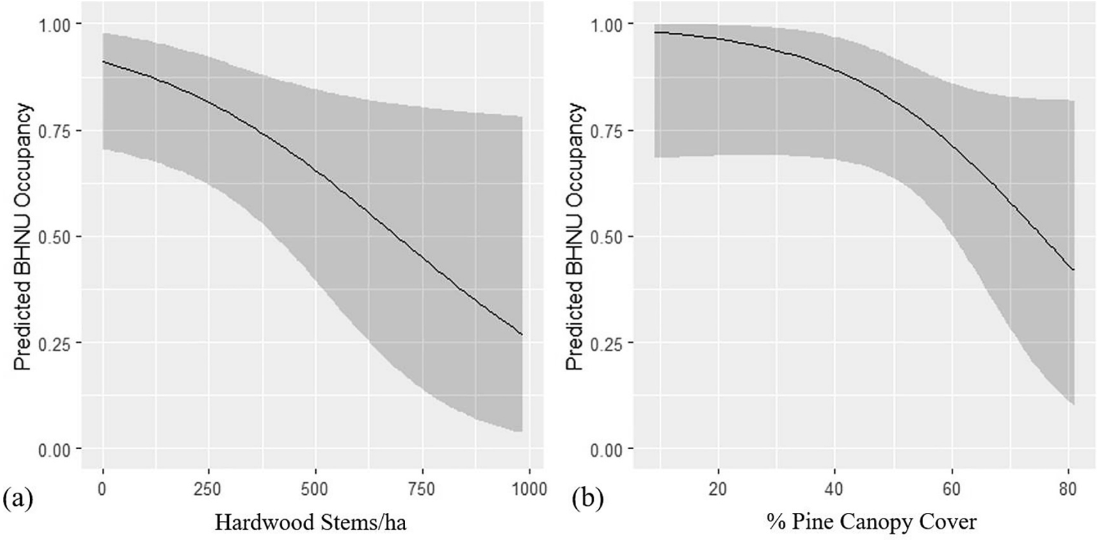

Fig. 4. The predicted occupancy probability for brown-headed nuthatch estimated across the range of hardwood stem density (a) and pine canopy cover (b) using the top model. Fort Bragg Military Installation, North Carolina, 2018.

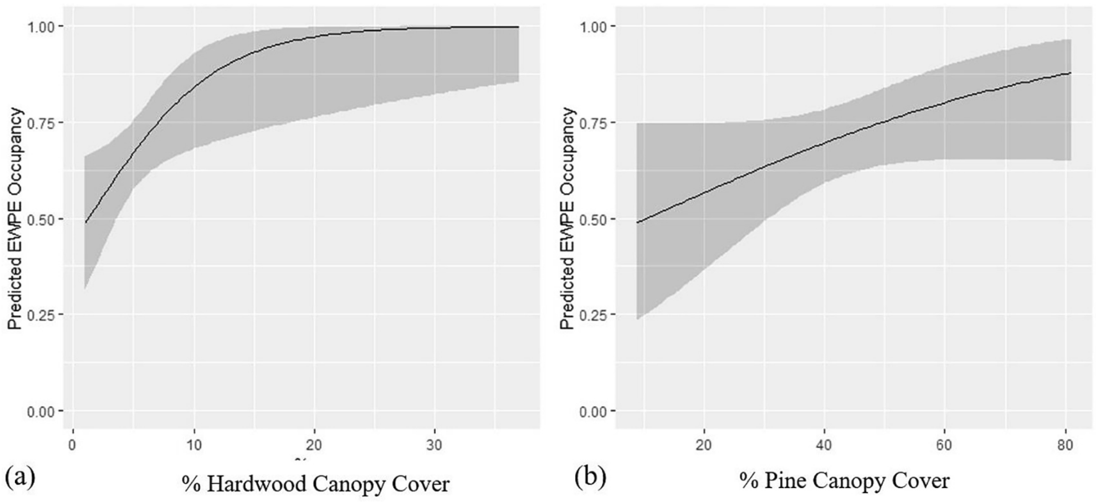

Fig. 5. The predicted occupancy probability of eastern wood-pewee estimated across the range of upland hardwood canopy cover (a) and pine canopy cover (b) using the top model. Fort Bragg Military Installation, North Carolina, 2018.

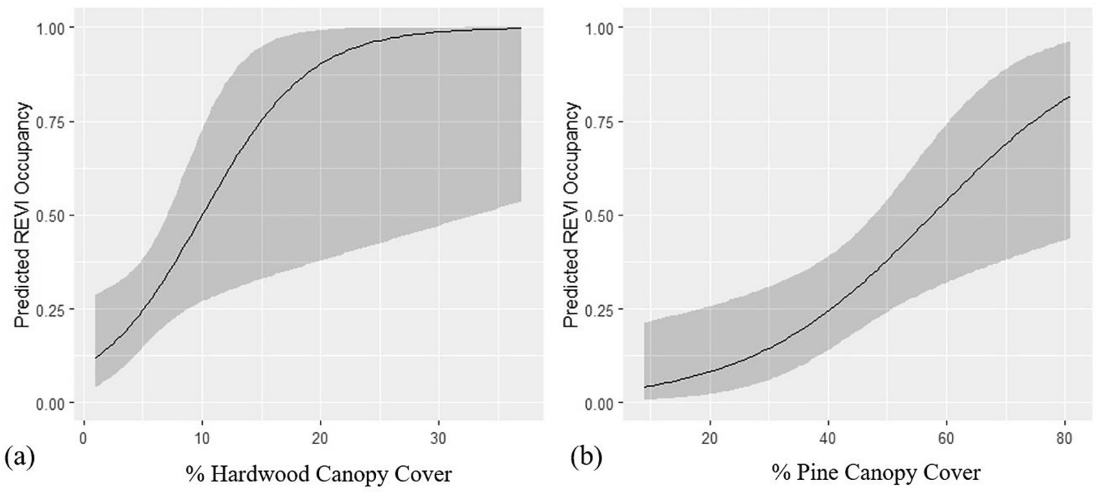

Fig. 6. The predicted occupancy probability for red-eyed vireo estimated across the range of upland hardwood canopy cover (a) and pine canopy cover (b) using the top model. Fort Bragg Military Installation, North Carolina, 2018.

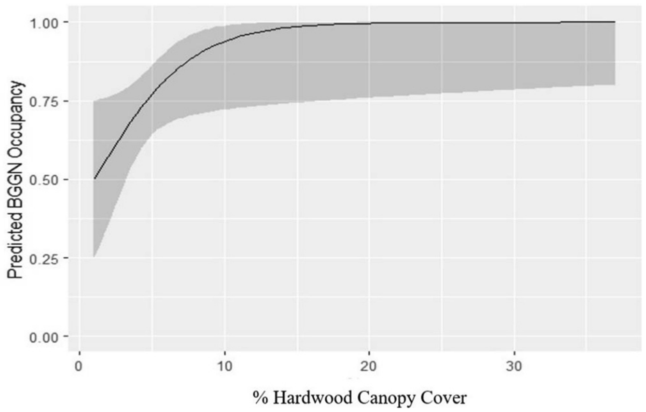

Fig. 7. The predicted occupancy probability for blue-gray gnatcatcher estimated across the range of upland hardwood canopy cover using the top model. Fort Bragg Military Installation, North Carolina, 2018.

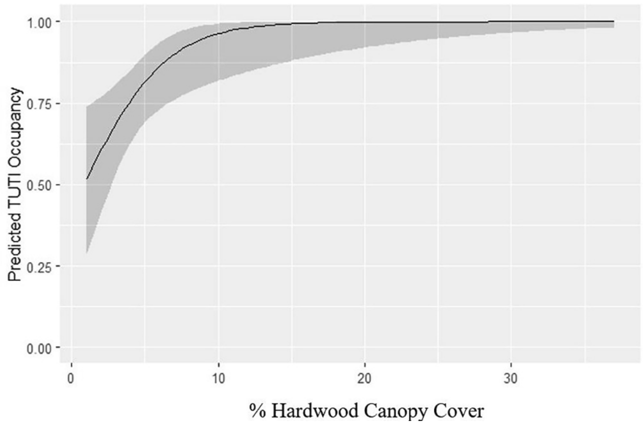

Fig. 8. The predicted occupancy probability for tufted titmouse estimated across the range of upland hardwood canopy cover using our top model. Fort Bragg Military Installation, North Carolina, 2018.

limiting hardwood densities for open pine species (Steen et al., 2013; Allen et al., 2006; Conner et al., 2002), but our results also demonstrate that retention of lower densities of hardwood midstory and overstory stems is important when the management objective includes avian diversity.

Although other researchers have inferred that hardwood reduction positively influences Bachman's sparrows, brown-headed nuthatch, and

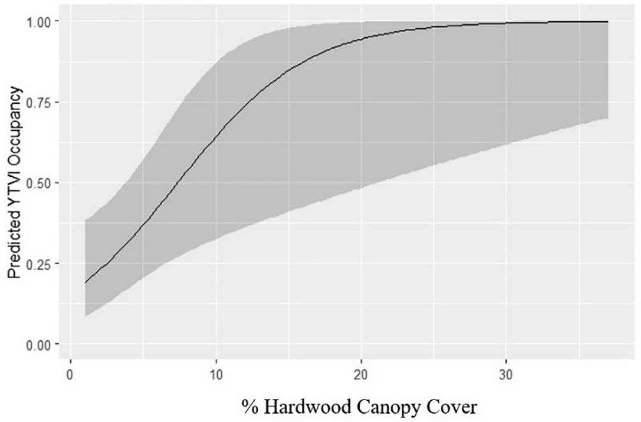

Fig. 9. The predicted occupancy probability for yellow-throated vireo estimated across the range of upland hardwood canopy cover using our top model. Fort Bragg Military Installation, North Carolina, 2018.

red-headed woodpeckers (Steen et al., 2013; Allen et al., 2006; Conner et al., 2002; Provencher et al., 2003; Wilson and Watts1999), our study demonstrated this relationship over a continuous gradient of hardwood cover. Previous studies have made inferences about the negative effects of hardwoods on these species based on categorical classes of forest type (e.g., open pine), and conditions resulting from experimental treatments (Steen et al., 2013; Allen et al., 2006; Conner et al., 2002; Provencher et al., 2003; Wilson and Watts, 1999), but we were able to demonstrate thresholds related to hardwood composition. Of the five species for which hardwood stem density was an important predictor of occupancy, Bachman's sparrow, brown-headed nuthatch, red-headed woodpecker, and summer tanager were negatively influenced by high densities of hardwood stems, while blue-headed vireo was positively influenced. Because hardwood stem density was a more important predictor of occupancy than was hardwood canopy cover, hardwood-sensitive bird species may be more adversely affected by midstory hardwoods in large, dense patches rather than high hardwood canopy cover which can be provided by a few large canopy trees. Moreover, our results indicated that occupancy probability for hardwood-sensitive species can remain above 0.50 in areas where hardwood density is ≤250 stems/ha.

Upland hardwood canopy cover positively influenced occupancy probability of blue-gray gnatcatcher, eastern wood-pewee, red-eyed vireo, tufted titmouse, and yellow-throated vireo, most of which are known to be hardwood associates or generalist species (Allen et al., 2006). Of the five species with positive influences of hardwood canopy cover, blue-gray gnatcatcher, eastern wood-pewee, and tufted titmouse had a similar threshold with the greatest occupancy probability occurring when hardwood cover exceeded 10%. Red-eyed vireo and yellow-throated vireo occupancy probability peaked at approximately 20% hardwood cover. The positive association between hardwood composition and occupancy of these species is not surprising due to the known associations between these species and mixed forest conditions (Cimprich et al., 2018; Ritchison et al., 2015; Kershner and Ellison, 2012; Rodewald and James, 2011). Although, Allen et al. (2006) classified red-eyed vireo, tufted titmouse, and yellow-throated vireo as members of the fire-suppressed songbird assemblage in the longleaf pine-wiregrass ecosystem, eastern wood-pewee were classified as members of an “open longleaf” assemblage, and they were unable to classify the assemblage of blue-gray gnatcatcher. We demonstrated that hardwood cover was an important predictor of occupancy for these species regardless of their previous assemblage classification, and that in open, upland longleaf pine communities managed with frequent fire, these species can thrive as long as low levels of hardwood cover between ~5% and 15% are present. Although we excluded bottomlands from the study, and these areas likely provide habitat for some of the species we determined were positively associated with upland hardwood cover, the importance of upland hardwoods should not be overlooked for species such as blue-gray gnatcatcher, blue-headed vireo, and eastern wood-pewee, particularly in lands such as the Fort Bragg Sandhills where uplands constitute > 44,000 ha and > 90% of the landscape.

Our results contradict previous research regarding eastern wood-pewee habitat associations in that both hardwood canopy cover and pine canopy cover had a positive influence on eastern wood-pewee occupancy (Allen et al., 2006; Conner et al., 2002). Although eastern wood-pewee occupy a wide range of forest types throughout their breeding range (Watt et al., 2017), this species was classified by Allen et al. (2006) as a member of the open longleaf assemblage, and Conner et al. (2002) reported greater eastern wood-pewee abundance in areas managed for red-cockaded woodpeckers which included extensive reductions in hardwood cover when compared to areas that did not receive hardwood reduction treatments. Allen et al. (2006) suggested links between open stand structure and eastern wood-pewee abundance, and Conner et al. (2002) suggested a negative relationship between hardwood cover and eastern wood-pewee abundance, but our results indicate there may be a lower limit of hardwood cover and pine

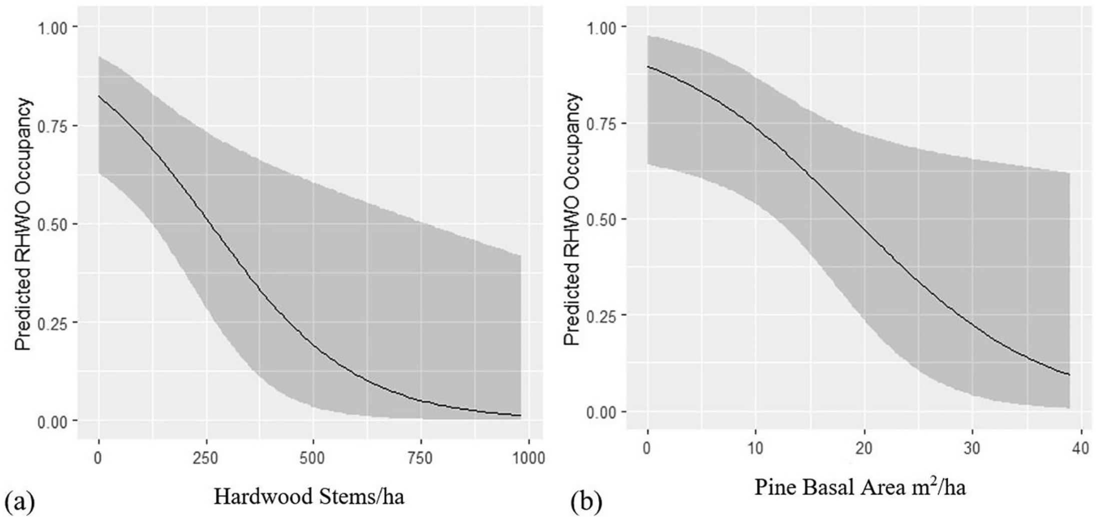

Fig. 10. The predicted occupancy probability for red-headed woodpecker estimated across the range of hardwood stem density (a) and pine basal area (b) using the top model. Fort Bragg Military Installation, North Carolina, 2018.

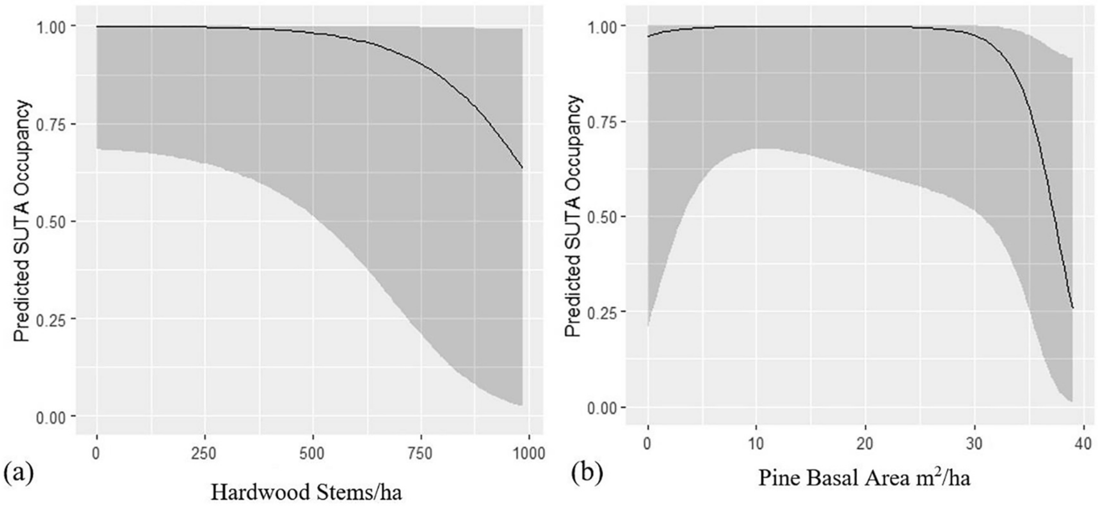

Fig. 11. The predicted occupancy probability for summer tanager estimated across the range of hardwood stem density (a) and pine basal area (b) using the top model. Fort Bragg Military Installation, North Carolina, 2018.

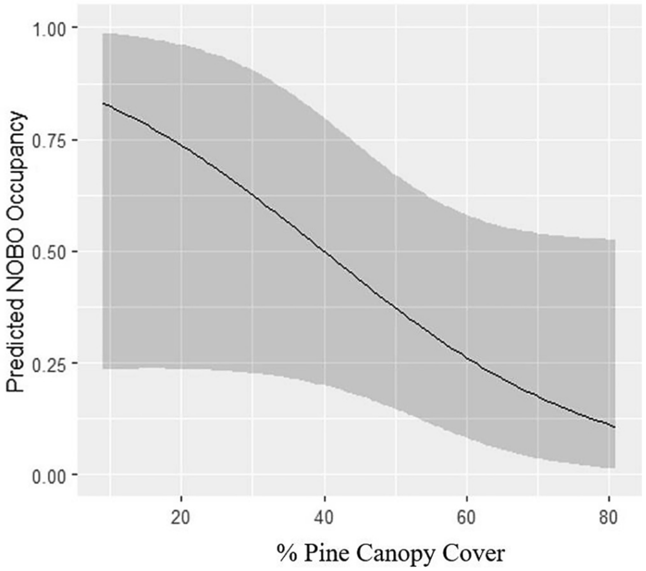

Fig. 12. The predicted occupancy probability of northern bobwhite estimated across the range of pine canopy cover using the top model. Fort Bragg Military Installation, North Carolina, 2018.

cover tolerated by this species.

Of the 12 avian species we studied, northern bobwhite was the sole species for which we did not document an association between hardwoods and occupancy. Although Kroeger et al. (2020) reported that non-breeding bobwhite selected sites with 3–6 m^2/ha hardwood basal area on Fort Bragg, Rosche et al. (2019) showed that breeding bobwhite selected sites with combined basal area of pines and hardwoods < 9.2 m^2/ha. These seasonal differences in northern bobwhite selection of hardwoods indicate that hardwood mast is seasonally important to bobwhite, and therefore, our results should not be used to discount the importance of hardwoods for northern bobwhite during the non-breeding season. Moreover, the lack of a negative association between northern bobwhite occupancy and hardwood cover or stem density, and the weak negative relationship between pine tree cover and bobwhite occupancy, indicate that pine tree cover can be equally or more important than hardwood cover in determining breeding season occupancy of northern bobwhite.

For some bird species, pine canopy cover was as important as hardwood cover as a predictor of occupancy. Pine canopy cover or basal area were important predictors of occupancy probability for 7 of the species we modeled, including negative relationships between pine composition and occupancy of brown-headed nuthatch, northern bobwhite, and red-headed woodpecker, and a quadratic relationship between pine basal area and summer tanager occupancy. Cox et al. (2012) similarly reported a negative relationship between brown-headed nuthatch occupancy and pine basal area. Areas with high levels of pine canopy cover or basal area are less likely to have the dense understory strata required for northern bobwhite to remain present (Cram et al., 2002; Rosche et al., 2019), especially on lower site index soils (Landers and Mueller, 1986). Similarly, high pine basal area likely has negative effects on the foraging strategy of red-headed woodpecker (Vierling et al., 2009), and the grass component required for Bachman's sparrow (McIntyre et al., 2019). Our results indicate that forest thinning is needed to maintain appropriate conditions for these bird species. Where red-cockaded woodpecker is a focal species, managers can target mature pine stands with hardwood basal areas at the lower end of the recovery standard to maintain habitat for the full suite of open-pine species (~9 m^2/ha).

With consideration to the relative rarity of the avian species we monitored, 5 species are experiencing range-wide population declines: Bachman's sparrow, brown-headed nuthatch, eastern wood-pewee, northern bobwhite, and red-headed woodpecker (Sauer et al., 2017). Of these declining species, 3 were negatively influenced by hardwood stem density and 4 were negatively influenced by pine canopy cover or pine basal area. Conversely, 5 of the 6 species positively influenced by hardwood composition are experiencing range-wide population increases (Sauer et al., 2017). Our results indicate that maintaining low to moderate levels of hardwoods on the landscape can increase overall avian diversity with limited negative effects to the aforementioned species experiencing population declines, especially when ~5% to 15% hardwood cover can be achieved with stem densities below ~250 stems/ha. However, coupling hardwood reductions with reductions in pine canopy cover or pine basal area may be equally important for providing habitat for the species of high conservation concern, especially where northern bobwhite management is a focus for managers.

5. Conclusions

We recognize that maximizing avian diversity may not be a priority on many properties managed to conserve and restore fire-maintained longleaf pine communities and the rare species therein. However, when and where maximizing avian diversity is an objective, we suggest maintaining upland hardwood overstory cover between a lower

Table A1

A priori models of field measured (grass cover, hardwood stem density, and pine basal area) and remotely sensed (upland hardwood canopy cover and pine canopy cover) used to rank models of occupancy probability for 15 bird species. Fort Bragg Military Installation, North Carolina, 2018.

Model	K[a]
Null	
psi(.)	2
Field	
psi(Grass cover[b])	3
psi(Hardwood Stems[c])	3
psi(Pine basal area[d])	3
psi(Grass cover + Hardwood stems)	4
psi(Grass cover * Hardwood stems)	5
psi(Grass cover + Pine basal area)	4
psi(Grass cover * Pine basal area)	5
psi(Hardwood stems + Pine basal area)	4
psi(Hardwood stems * Pine basal area)	5
psi(Pine basal area + Pine basal area^2)	4
psi(Hardwood stems + Pine basal area + Pine basal area ^{2})	5
psi(Grass cover + Hardwood stems + Pine basal area)	5
Remotely sensed	
psi(Hardwood cover[e])	3
psi(Pine cover[f])	3
psi(Hardwood cover + Hardwood cover^2)	4
psi(Hardwood cover + Pine cover)	4
psi(Hardwood cover * Pine cover)	5
psi(Pine cover + Pine cover^2)	4

[a] K – number of parameters in model including intercept, covariate(s), and $\hat{c}$.

[b] Percent grass cover measured at 0.04-ha plots.

[c] Hardwood stem density measured at 0.04-ha plots.

[d] Pine basal area measured with 10-factor prism.

[e] Upland hardwood canopy cover with a 150-m radius of point.

[f] Pine canopy cover within a 150-m radius of point.

Table A2

Confusion matrix resulting from the independent accuracy assessment at 305 randomly located point count locations, with the overall accuracy, producer's accuracy, and user's accuracy for each class present at the point count locations. Fort Bragg Military Installation, North Carolina, 2018.

Class	Pine	Hardwood	Other	User's (%)	Producer's (%)	Overall (%)
Pine	108	2	24	80.60	83.08	79.67
Hardwood	1	26	6	78.79	72.22	–
Other[a]	21	8	109	79.00	78.42	–

[a] Other includes water, herbaceous, road, and developed collapsed into one class.

threshold of $\sim$5% and an upper threshold of 15% cover, with hardwood densities < 250 stems/ha. The lower threshold likely is comparable to the recommendations by Perkins et al. (2008), who advised retaining at least $\sim$2.7 m^2/ha of hardwood basal area comprised of scattered overstory trees and small patches of midstory hardwoods. Although patches of midstory hardwoods with diverse floral species and structural composition are important, retaining large overstory hardwoods can meet the upper limit of the threshold with fewer stems, potentially mitigating effects to the species negatively influenced by dense hardwood stems. Additionally, patches of midstory hardwoods are more readily replaced than are large overstory hardwoods, and thus the retention of overstory hardwoods is desirable in that the structure, cover, and mast they provide is difficult to replace on the landscape. Moreover, for managers seeking to promote northern bobwhite, we suggest thinning pines to achieve pine canopy cover levels of $\leq$40%. Also, reducing pine canopy cover would promote herbaceous cover beneficial for increasing Bachman's sparrow habitat, as well as ground cover biodiversity and rare plant conservation, important characteristics of open pine systems in the southeastern United States. Moreover, we recognize that xeric longleaf pine communities, such as in the sandhills and on microsites located within longleaf pine flatwood communities, support different suites of hardwood species and distinct forms of community structure, and thus represent different paradigms of hardwood management as compared to mesic and wet pine flatwood sites; these differences constitute a caveat to applying our management recommendations outside of sandhill sites and xeric microsites within flatwood longleaf pine communities. Finally, we suggest viewing hardwoods as an important source of landscape heterogeneity similar to what was suggested by Fill et al. (2015), who described longleaf pine ecosystems as a dynamic mosaic of longleaf pine dominated savanna, woodland, and forest interspersed with hardwood patches of variable extents and age distributions. We demonstrated that managing longleaf pine communities with lower and upper thresholds of hardwood cover can provide habitat to the greatest number of avian species while maintaining habitat for species sensitive to hardwood encroachment.

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.

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Appendix A

See Tables A.1 and A.2.

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