

ABSTRACT

HANNON, DANIEL RICHARD. Predictors of Upland Hardwood Distribution and the Relationship Between Hardwood Distribution and Avian Occupancy in Fire maintained Longleaf Pine Forests. (Under the direction of Christopher E. Moorman and Christopher S. DePerno).

The longleaf pine (*Pinus palustris*) ecosystem has been reduced to a fraction of its original extent, and restoration of longleaf pine communities is a focus of managers across the southeastern United States. The reduction of hardwood tree cover is often a desirable longleaf pine community restoration outcome, although hardwood midstory and overstory trees have been recognized as a natural component of the communities. Moreover, the appropriate amount of hardwood tree cover in a restored longleaf pine community is debated, as more hardwood tree cover can benefit mast-dependent wildlife (e.g., fox squirrels [*Sciurus niger*], white-tailed deer [*Odocoileus virginianus*]) and less hardwood tree cover is critical to the federally endangered red-cockaded woodpecker [*Leuconotopicus borealis*]. To inform the debate, we assessed the environmental and management factors that influenced abundance of mature upland hardwood trees in xeric longleaf pine communities and how hardwood distribution influenced the occupancy probability of 15 avian species on a site where frequent growing-season fire has been ongoing since 1991. We counted upland hardwoods ≥ 5 cm diameter at breast height (DBH) at 307 random field plots (0.04 ha) and categorized all hardwood trees as belonging to either a guild of fire-tolerant oaks or a guild of fire-sensitive hardwood species. We used generalized linear models (GLM) to determine the most important predictors of abundance for both guilds. The predictors of abundance differed between the two hardwood guilds, with fire-tolerant oak abundance increasing with greater slope and proximity to ignition sources and decreasing with greater pine basal area. Fire-sensitive hardwood abundance increased with mesic site conditions and decreased with the number of growing-season fires and greater pine basal area. Although

seasonality in fire history was an important predictor of fire-sensitive hardwood abundance, variables related to long-term fire-history were not important predictors of fire-tolerant oak abundance in longleaf pine communities. Hardwood abundance could be increased by reducing pine basal area, though extensive hardwood encroachment could occur without frequent prescribed fire. We used fixed-radius point counts to sample the presence-absence of 15 avian species at 305 points and assessed forest composition and structure around each point using field-based and remote sensing techniques. We developed single-season single-species occupancy models with an emphasis on the influence of hardwood overstory cover on occupancy. Due to issues with model fit, we were unable to model occupancy for 3 of the 15 focal species. Occupancy probability for 3 of the 12 species was positively influenced by pine overstory cover and occupancy probability for 2 of the 12 species was negatively influenced by pine overstory cover, including 1 species for which pine overstory cover was the sole variable in the top model. Occupancy probabilities for 7 out of the 12 focal species were positively influenced by hardwood overstory 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. Hardwood overstory cover levels of 5-15% 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. We suggest that managing longleaf pine uplands with lower and upper bounds of 5% to 15% hardwood overstory cover with stem densities of ≤ 250 stems/ha will provide habitat for the greatest diversity of birds while avoiding negative effects to species associated with upland longleaf pine communities.

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Predictors of Upland Hardwood Distribution and the Relationship Between Hardwood
Distribution and Avian Occupancy in Fire maintained Longleaf Pine Forests

by
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DEDICATION

To my wife Lauren, my mother Elaine, and Father Rick, thank you for all your support and sacrifice over the years. You always believed in me and encouraged me to succeed in all my endeavors.

BIOGRAPHY

Dan was born and raised in Middletown, New York. He grew up in the woods behind his childhood home searching for crayfish, frogs, and salamanders. Dan was heavily involved in sports from an early age, and among other pursuits, these activities led Dan away from the outdoors during adolescence. Knowing little about potential careers in conservation, he went on to get an Associate's in Electrical Construction in 2008 after which he went to work for his father and was accepted into the local electrical union. Following an epiphany in 2009, he decided to leave his job and the electrical union to pursue a degree in the conservation field. He completed a Bachelor's degree in Wildlife Management at the State University of New York at Cobleskill in the spring of 2015. By the summer after completing his undergraduate education, he had completed 3 internships with United States Fish and Wildlife Service and 1 seasonal job with the University of Maine. He then spent 2 years working as a wildlife technician for the New York State Department of Environmental Conservation – always working towards and hoping for an opportunity to conduct graduate research. In the fall of 2017, he was accepted into NC State University to pursue a Master's degree in Fisheries, Wildlife, and Conservation Biology. He is currently working for the North Carolina Natural Heritage Program.

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CHAPTER 1

PREDICTORS OF FIRE-TOLERANT OAK AND FIRE-SENSITIVE HARDWOOD DISTRIBUTION IN A FIRE-MAINTAIN LONGLEAF PINE ECOSYSTEM

ABSTRACT

The longleaf pine (*Pinus palustris*) ecosystem has been reduced to a fraction of its original extent, and restoration of longleaf pine communities is a focus of managers across the southeastern United States. The reduction of hardwood tree cover is often a desirable longleaf pine community restoration outcome, although hardwood midstory and overstory trees have been recognized as a natural component of the communities. Moreover, the appropriate amount of hardwood tree cover in a restored longleaf pine community is debated, as more hardwood tree cover can benefit mast-dependent wildlife (e.g., fox squirrels [*Sciurus niger*], white-tailed deer [*Odocoileus virginianus*]), and less hardwood tree cover is critical to the federally endangered red-cockaded woodpecker [*Leuconotopicus borealis*]. To inform the debate, we assessed the environmental (e.g., topography, edaphic conditions, and pine basal area) and management (e.g., distance to firebreaks, prescribed fire history) factors that influenced abundance of mature upland hardwood trees in xeric longleaf pine communities on a site where frequent growing-season fire has been ongoing since 1991. We counted upland hardwoods ≥ 5 cm diameter at breast height (DBH) at 307 random field plots (0.04 ha) and categorized all hardwood trees as belonging to either a guild of fire-tolerant oaks or a guild of fire-sensitive hardwood species. We used generalized linear models (GLM) to determine the most important predictors of abundance for both guilds. The predictors of abundance differed between the two guilds, with fire-tolerant oak abundance increasing with greater slope and proximity to ignition sources and decreasing with greater pine basal area. Fire-sensitive hardwood abundance increased with mesic site conditions and decreased with the number of growing-season fires and greater pine basal area.

Although seasonality in fire history was an important predictor of fire-sensitive hardwood abundance, variables related to long-term fire-history were not important predictors of fire-tolerant oak abundance in longleaf pine communities. Hardwood abundance could be increased by reducing pine basal area, though extensive hardwood encroachment could occur in the absence of frequent prescribed fire.

INTRODUCTION

The floral and faunal communities of the fire-dependent longleaf pine (*Pinus palustris*) ecosystem are integral contributors to the biodiversity hotspot associated with the southeastern United States (Noss et al. 1995). In the absence of frequent fire, upland longleaf pine communities become susceptible to hardwood encroachment, which can have deleterious effects on longleaf pine regeneration and herbaceous community composition. Prescribed fire often is used during restoration and management aimed at creating longleaf pine dominated overstory and an understory dominated by grasses and forbs (USFWS 2003, Brockway et al. 2005). Moreover, reducing the stature and abundance of midstory and overstory hardwood trees in longleaf pine uplands is a common motive driving prescribed fire management (Gilliam and Platt 1999, Hiers et al. 2014). Although hardwood tree reduction is an integral component of longleaf pine restoration, long-term management will require a complex understanding regarding the ecological role of upland hardwoods in the ecosystem.

Within the longleaf pine ecosystem, hardwood tree species have complex relationships with fire, edaphic conditions, topography, and local canopy composition and structure (Gilliam et al. 1993, Jacqmain et al. 1999, Addington et al. 2015b, Whelan et al. 2018). For example, research indicates that some oak species present in longleaf pine uplands are fire-tolerant (Rebertus et al. 1989, Greenberg and Simons 1999, Cavender-Bares et al. 2004, Hiers et al. 2014). Thick bark, ability to re-sprout after fire, and reproduction at small sizes have been implicated as evolutionary adaptations to frequent fire (Jackson et al. 1999, Greenberg and Simons 1999, Cavender-Bares et al. 2004, Hiers et al. 2014). Conversely, sensitivity to frequent fire has been reported for a different subset of hardwoods present in upland longleaf pine communities (Boyer 1990, Haywood et al. 2001, Addington et al. 2015b). In addition to fire

frequency, the effect of fire seasonality has been the focus of numerous investigations into hardwood tree dynamics (Glitzenstein 1995, Brockway and Lewis 1997, Haywood et al. 2001, Glitzenstein et al. 2012, Addington et al. 2015a, b, Whelan et al. 2018). Although the reported influence of fire season varies in the literature, researchers have shown that fire conducted during the dormant season is less likely to cause mortality or top-kill of hardwoods than growing-season fires, and repeated dormant-season burning results in greater hardwood abundance than with repeated growing-season burning (Boyer 1990, Streng et al. 1993, Glitzenstein et al. 1995).

Edaphic conditions and topographic characteristics influence forest composition and structure, including hardwood tree abundance, directly through species-site associations and indirectly by influencing fire behavior (Gilliam et al 1993, Jacqumain et al. 1999, Addington et al. 2015b). Slope, aspect, elevation, and topographic position are intrinsically linked to soil properties such as texture, moisture, and associated nutrient availability (Jenny 1994). The effects of topography and soil conditions act either individually, or in combination, to influence forest microclimate, and determine hardwood tree species composition and abundance. Importantly, complex vegetation-fire feedback mechanisms operate throughout longleaf pine ecosystems, wherein environmental conditions influence fire behavior and the composition and density of trees (Fill et al. 2015). Environmental conditions and the resulting plant communities influence fire spread and intensity by affecting the type, continuity, and moisture of fuels (Kane et al. 2008, Wenk et al. 2011, Crandall and Platt 2012, Wiggers et al. 2013, Addington et al. 2015b, Fill et al. 2015). Topography can influence fire behavior by increasing fire intensity associated with upslope head fires and decreasing intensity associated with downslope backing fires (Rothermel 1983, Addington et al. 2015a).

Hardwood tree abundance in upland longleaf pine communities can vary depending on site conditions and fire management, and thus the abundance of mature hardwood trees is an appropriate indicator of how hardwood communities are responding to long-term fire management and ecological gradients. For example, an assemblage of oaks in longleaf pine sandhills are more abundant in xeric conditions (e.g., *Quercus incana* [bluejack oak], *Q. laevis* [turkey oak], *Q. margarettae* [sand post oak], *Q. marilandica* [blackjack oak], *Q. stellata* [post oak]) and on upper slopes and ridges with sandy well-drained soils (Gilliam et al. 1993, Peet and Allard 1993, Jacqmain et al. 1999, Cavender-Bares et al. 2004, Sorrie et al. 2006, Hiers et al. 2014). Conversely, other hardwood trees favor mesic conditions (e.g., *Acer rubrum* [red maple], *Liquidambar styraciflua* [sweetgum], *Nyssa sylvatica* [blackgum], *Prunus serotina* [black cherry]) and are more prevalent on lower slope areas with fine-textured soils (Gilliam et al. 1993, Jacqmain et al. 1999, Carr et al. 2010, Addington et al. 2015b). Further, other hardwood tree species may have less specific associations with edaphic conditions or topography (e.g., *Carya* sp. [hickory], *Cornus florida* [flowering dogwood], *Diospyros virginiana* [common persimmon], *Quercus falcata* [southern red oak], *Q. nigra* [water oak], *Q. velutina* [black oak]) and their presence or abundance is affected by the interaction between fire, edaphic conditions, and topography (Gilliam et al. 1993, Jacqmain et al. 1999).

In addition to edaphic conditions and topography, hardwood tree distributions are related to overstory pine basal area and proximity to firebreaks (Lashley et al. 2014, Addington et al. 2015 a, b). As overstory pine basal area decreases, the likelihood of hardwood release into the mid-story and over-story increases, which may be attributed to less competition for light, space, water, or nutrients (Knapp et al. 2014, Addington et al. 2015 b). Moreover, areas with sparse overstory pine result in less litter composed of flammable pine needles, and decreased fuel

continuity when compared to areas with dense overstory pine which can cause patchy burns and reduced hardwood mortality (Jacqmain et al. 1999, Addington et al. 2015 a,b, Whelan et al. 2018). Also, distance from firebreaks has been cited as a predictor of hardwood tree abundance, with increased densities of hardwood trees in close proximity to firebreaks because fire intensity is lower near the source of ignition (Jacqmain et al. 1999, Lashley et al. 2014).

Previous research has explored predictors of understory and midstory hardwood distribution in longleaf pine communities (Streng et al. 1993, Provencher et al. 2001, Knapp et al. 2014, Addington et al. 2015 a, b, Whelan et al. 2018), but the predictors of mature hardwood tree abundance in the fire-maintained longleaf pine ecosystem has been less studied (but see Glitzenstein et al. 1995, Jacqmain et al. 1999, Addington et al. 2015 b). Studies that have investigated mature hardwoods in the longleaf pine ecosystem have either lacked long-term fire history data (Jacqmain et al. 1999), or combined all hardwood species as a single response variable rather than model the distribution of individual species or guilds (Boyer 1990, Boyer 1993, Streng et al. 1993, Glitzenstein et al. 1995). We intended to address this gap by modeling the distributions of two guilds of mature hardwood trees on a landscape that has been managed with long-term frequent fire.

Our objective was to examine the role of long-term frequent fire and environmental conditions in predicting abundance of two guilds of hardwood species present in upland longleaf pine communities: fire-tolerant oaks (FTO) and fire-sensitive hardwoods (FSH). Hence, our goal was to identify predictors of FTO and FSH abundance resulting from 28 years of frequent prescribed fire. We expected abundance of FTO to be predicted best by xeric conditions such as steep slopes, ridges, and sandy soils regardless of fire history. We expected abundance of FSH to be predicted best by fire history and mesic site conditions such as those present on lower

elevation sites and sandy loam soils. Our goal was not to challenge the importance of frequent fire and hardwood stem reduction for restoring longleaf pine communities, but to identify aspects of long-term fire management and site conditions that influence FTO and FSH persistence following decades of prescribed burning.

STUDY AREA

We conducted the study on Fort Bragg Military Installation, located in the Sandhills physiographic region of south-central North Carolina, USA (35.1°N, -79.2° W; Figure 1). Fort Bragg is a 625-km² military base that is among the most important remnant areas of the longleaf pine-wiregrass (*Aristida stricta*) ecosystem in the southeastern United States. Management of longleaf pine-wiregrass communities on Fort Bragg is focused on conserving endangered species (i.e., the federally endangered red-cockaded woodpecker [*Leuconotopicus borealis*]), 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 approximately one-third of the base is burned each year (Cantrell et al. 1995, Lashley et al. 2014, FBMI 2018). Frequent growing-season fire has been used as the dominant management strategy since 1990; however, land managers also incorporate dormant-season prescribed fire to meet burn quotas not achieved with growing-season burning (Lashley et al. 2014, FBMI 2018).

The landscape is characterized by rolling hills heavily dissected by streams, bottomlands, and stream-head pocosins (Sorrie et al. 2006, FBMI 2018). The elevation ranges from 36m to 183m above sea level. The uplands typically are composed of deep, well-drained sandy soils with the most common soil series being Candor sand and Lakeland sand (Sorrie et al. 2006, Soil Survey Staff, NRCS, 2018, FBMI 2018). The lower slopes are comprised of loamy sands (e.g., Blaney loamy sand, Gilead loamy sand), and loam soils (e.g., Johnston loam)

comprise the bottomland areas (Cantrell et al. 1995, Sorrie et al. 2006, Soil Survey Staff, NRCS, 2018, FBMI 2018). The climate is characterized as sub-tropical with long, hot summers and short mild winters. The average maximum daily temperature and the average monthly precipitation peak in July at 33°C and 150 mm, respectively, whereas the average maximum daily temperature is lowest during January (12°C; [FBMI 2018]). The average annual precipitation is approximately 1129 mm/year, and the average annual temperature is 16°C (FBMI 2018). The majority of Fort Bragg is comprised 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 (Sorrie et al. 2006, Lashley et al. 2014). Common hardwood tree species include turkey oak, blackjack oak, sweetgum, sand post oak, and blackgum (Lashley et al. 2014, Sorrie et al. 2006).

METHODS

Data collection

To strengthen our ability to make inferences about upland hardwood tree abundance, we eliminated all areas within 50m of streams, classified wetlands, bottomland hardwood communities, and areas managed for early successional plant communities. We counted and identified all trees \geq 5-cm diameter at breast height (DBH) at 307 randomly located 0.04-ha circular inventory plots (\sim 11.4-m radius, \sim 408.3 m²) in upland longleaf pine communities. We used 5-cm DBH as a cut-off to define tree-sized hardwoods (hereafter mature hardwoods) based on previous research on the minimum size at maturity of common hardwoods in upland longleaf pine communities (Greenberg and Simon 1999, Cavender-Bares et al. 2004). We categorized all hardwood trees as fire-tolerant oaks (FTO) or fire-sensitive hardwoods (FSH; Table 1) and

summarized the stem count of trees in both categories at each plot (Table 2). The number (count) of FTO and FSH present within the bounds of 0.04-ha plots served as the response variables. In addition, we used 10-factor prisms to quantify pine basal area at each plot. With the exception of pine basal area, all independent variables were collected using ArcGIS (Arcmap v. 10.5; ESRI, Redlands, CA, USA; Table 2).

We used a LiDAR-derived digital elevation model (DEM) to calculate elevation (m), slope (%), and aspect (0-360°) in ArcGIS (Arcmap v. 10.5; ESRI, Redlands, CA, USA); aspect was transformed using a cosine transformation (Beers et al. 1966, Addington et al. 2015 b). We used the Land Facet Tools ArcMap extension (Arcmap v. 10.5; ESRI, Redlands, CA, USA, Jenness et al. 2013) to categorize the DEM into a 3-category topographic position index (upper, mid, and lower). Soil texture was obtained from the SSURGO database (Soil Survey Staff, NRCS, 2018). Rather than using specific soil series, we categorized all soils into broader texture categories of “sand” or “loamy sand” (Gilliam et al. 1993, Addington et al. 2015 b). We used Fort Bragg’s prescribed fire records from 1991 to 2018 to determine number of total fires, dormant-season fires, and growing-season fires at each plot location. The cut-off date used by Fort Bragg to distinguish between growing-season and dormant-season fires varied by year depending on leaf-out and flowering dates observed for dominant trees and shrubs at the time of each fire, but dormant-season fires typically occurred early-January to mid-March, and growing-season fires typically occurred between mid-March and late-June. The number of years elapsed since the beginning of Fort Bragg’s current fire management program (28 yr) was divided by the total number of fires to calculate the average fire return interval at each plot location. We used Fort Bragg’s shapefile of roads and firebreaks to calculate the proximity to firebreaks at the center of each plot; we log-transformed distance to firebreaks to control for skewedness caused

by extreme values. We scaled and standardized all other continuous covariates by subtracting the mean and dividing by the standard deviation.

We assessed pairwise correlations between all continuous independent variables using Pearson's correlation coefficients with a conservative cut-off of $\pm | 0.6 |$. We then used variance inflation factors with a cut-off of 3 to assess multi-collinearity among all variables. If a pairwise correlation coefficient exceeded the cut-off threshold, it was not included in a model with the variable with which it was correlated, and if one or more independent variables demonstrated high multi-collinearity by exceeding the cut-off threshold, we eliminated the variable with the highest VIF until no multi-collinearity was observed.

Analysis

We used generalized linear models (GLM) to assess the important predictors of abundance for FTO and FSH abundance. A preliminary analysis using Poisson GLMs indicated a significant amount of overdispersion in models, so we used negative binomial GLMs using the 'MASS' package in R (Venables and Ripley 2002, R Core Team 2018). Negative binomial GLM routines are widely understood to handle overdispersed count data that are not normally distributed (Burnham and Anderson 2002, Zurr et al. 2009, Miyamoto et al. 2018). We used chi-square goodness-of-fit to calculate dispersion statistics for the global models of both FTO and FSH (Zurr et al. 2009, Hilbe and Robinson 2013). A dispersion statistic (ϕ) > 1 is a sign of overdispersion and may indicate lack-of-fit (Burnham and Anderson 2002, Zurr et al. 2009, Hilbe and Robinson 2013). In models with over-dispersion, we dealt with the potential lack-of-fit by multiplying the standard error by the variance inflation factor ($\sqrt{\phi}$; Anderson et al. 1994, Lindsey 1999, Burnham and Anderson 2002, Zurr et al. 2009). We developed 19 a priori models and ranked them according to Akaike information criteria (AIC). If over-dispersion was detected,

we re-ranked the candidate set with quasi Akaike information criteria (QAIC [Burnham and Anderson 2002]).

A preliminary analysis indicated the number of growing-season fires was correlated with fire return interval and the number of dormant-season fires ($R = -0.76$, $R = -0.53$, respectively); therefore, we did not use the number of dormant-season fires in any models, and no models containing fire return interval contained the number of growing-season fires. First, we fit null models where abundance of FTO and FSH was constant at all sites (Table 3, Model 17). Next, we developed 11 hypothetical models for abundance of FTO and FSH which included combinations of independent variables we expected to influence abundance (e.g., distance from firebreaks, elevation, fire return interval, growing-season fires, pine basal area, slope, soil, and topographic positions; Table 3). All combinatory models contained distance from firebreaks and pine basal area because of their reported importance in predicting hardwood abundance throughout the longleaf pine range (Jacqmain et al. 1999, Addington et al. 2015 a, b) and on Fort Bragg (Lashley et al. 2014). Also, we included one model containing only topographic variables, one containing only environmental conditions, and two sub-global models – one with all variables except the number of growing season fires, and one with all variables except the fire return interval (Table 3, Models 15 and 16, respectively).

We used AIC/QAIC to rank the a priori model set, and we chose the top model for FTO and FSO abundance based on the lowest AIC/QAIC (Burnham and Anderson 2002). We considered any model within $2\Delta\text{AIC/QAIC}$ of the model with the lowest AIC/QAIC and assessed all competitive models for uninformative parameters and parsimony (Burnham and Anderson 2002, Arnold 2010). If a more parsimonious model was within $2\Delta\text{AIC/QAIC}$ of the AIC-best model, it was selected as the final model. If a more complex model was within

$2\Delta\text{AIC}/\text{QAIC}$ of the AIC-best model, we calculated 85% confidence intervals for each coefficient (Arnold 2010); if the confidence intervals of additional parameters overlapped zero, we categorized the parameter as uninformative and selected the AIC-best model as our final model. After selecting the final models of both FTO and FSO, we calculated 85% and 95% confidence intervals to examine the statistical support for evidence of a strong covariate effect for every coefficient in the final model. If neither 95% confidence intervals nor 85% confidence intervals overlapped zero, we considered this strong evidence of a covariate effect. If the 95% confidence interval overlapped zero, but the 85% confidence interval did not, we considered this weak evidence of a covariate effect. Finally, if both the 95% and 85% confidence intervals crossed zero, we considered that covariate effect to have no statistical support and refrained from making inferences related to that parameter.

RESULTS

Fire-tolerant oaks

Fire-tolerant oaks were present at 196 of the 307 plots (63.8%), and stem counts ranged from 1 to 40 stems (Table 2). Across all plots, we counted 1566 stems of FTO species, which accounted for 83.2% of the total number of hardwood stems counted (i.e., 1882), and plots averaged 5.10 ± 6.94 stems (Table 2). Turkey oak, blackjack oak, and sand post oak were the most abundant FTO detected, with 746 (39.7%), 463 (24.6%), and 193 (10.3%) total stems, respectively (Table 1). Bluejack oak and post oak were the least common FTO species across sites, with 50 (2.7%) and 44 (2.3%) total stems, respectively (Table 1). We did not identify over-dispersion in the negative binomial FTO model ($\phi = 0.96$, $X^2 = 283.31$, $df = 295$), and we ranked models using AIC.

The top model for FTO abundance included linear effects of distance from firebreaks, percent slope, pine basal area, and the fire return interval (Table 4). Two models were within $2\Delta\text{AIC}$ of the top model; however, one model was a more complex version of the AIC-best model, with added complexity comprised of uninformative parameters. The second model differed from the AIC-best model only by 1 parameter (e.g., fire return interval, number of growing-season fires) both of which were deemed uninformative, and thus we used the AIC-best model to make inferences about FTO abundance. For distance from firebreaks, neither the 95% confidence interval, nor the 85% confidence interval overlapped zero, and we concluded there was strong statistical support for effect of distance from firebreaks (Table 5). FTO abundance decreased as distance from firebreaks increased (Figure 2a). Additionally, there was weak evidence for the effect of slope on FTO abundance as the 95% confidence interval overlapped zero, but the 85% confidence interval did not (Table 5). FTO abundance was greater on steeper slopes (Figure 2b). There was strong support for pine basal area as a negative predictor of FTO abundance as neither confidence interval overlapped zero (Table 5), and FTO abundance decreased as pine basal area increased (Figure 2c). Although fire return interval was present in the top model, both the 95% and 85% confidence intervals overlapped zero (Table 5); we concluded there was no support for the fire return interval as a predictor of FTO abundance, and we did not make inferences regarding the effect of fire return interval on FTO abundance.

Fire-sensitive hardwoods

Fire-sensitive hardwoods were present at 76 of the 307 plots (24.8%), and at plots where FSH were present, stem counts ranged from 1 to 30 stems (Table 2). Across all plots, we counted 316 stems of FSH species, which accounted for 16.8% of the total number of stems counted (i.e., 1882). Plots averaged 1.03 ± 3.09 FSH stems (Table 2). Hickories, sweetgum, and flowering

dogwood were the FSH species that occurred most frequently across all plots, with 73 (3.88%), 65 (3.46%), and 52 (2.8%) total stems, respectively (Table 1). Butternut, red maple, and black cherry were the least common FSH species, with 2 (0.2%), 1 (0.1%), and 1 (0.1%) total stems, respectively (Table 1). There was over-dispersion in the FSH model ($\phi = 1.59$, $X^2 = 467.378$, $df = 295$), and we ranked models using QAIC and inflated the standard errors prior to calculating confidence intervals and making predictions.

The top model for FSH abundance included linear effects of distance from firebreaks, the number of growing-season fires, elevation, pine basal area, and soil texture (Table 6). There were two models within $2\Delta\text{QAIC}$ of the top model (Table 6). The second ranked model differed from the AIC-best model with the inclusion the fire return interval, but we deemed this parameter uninformative. Moreover, the third ranked model was more parsimonious than the QAIC-best model, but the additional parameter in the AIC-best model (e.g., elevation) was deemed informative, and thus we used the AIC-best model to make inferences about FSH abundance. For distance from firebreaks, the 85% and 95% confidence intervals crossed zero, and thus we concluded that there was no statistical support for the covariate effect (Table 7). Initially, there was strong evidence for the effect of the number of growing-season fires on FSH abundance, but after inflating the standard error by the variance inflation factor ($\sqrt{\Phi}$), the 95% confidence interval overlapped zero, and we concluded there was weak evidence to suggest that the number of growing-season fires influenced FSH abundance (Table 7). The number of FSH decreased with a greater number of growing-season fires (Figure 3a). Furthermore, there was weak evidence in support of elevation as a predictor of FSH abundance (Table 7). FSH abundance decreased as elevation increased (Figure 3b). There was strong support for pine basal area as a predictor of FSH abundance (Table 7). FSH abundance decreased with greater pine basal area

(Figure 3c). Finally, there was evidence of a strong covariate effect of soil texture (Table 7).

Plots that were in areas of loamy sand soils had more FSH trees than plots on sandy soils (Figure 3d).

DISCUSSION

The two guilds of hardwoods demonstrated mostly differing relationships with the variables related to site conditions and fire history. Fire-tolerant oaks were most abundant on xeric sites, and no aspects of fire history were important for predicting abundance for this guild. Fire-sensitive hardwoods were most abundant on mesic sites, and fire seasonality was important for predicting abundance for these species. Abundance of FSH was negatively influenced by the number of burns conducted during the growing-season, which is interesting because this is a relationship that has been investigated previously; however, results have been mixed, with some reporting that growing season burning can either negatively influence hardwoods, or be more likely to result in fire-related mortality than dormant season fires (Waldrop et al. 1992, Boyer 1993, Streng et al. 1993, Glitzenstein et al. 1995), whereas other studies have reported little effect of fire season on hardwoods (Addington et al. 2015 a, b, Whelan et al. 2018). Pine basal area was present in the best models of abundance for both FTO and FSH guilds, which highlights the importance of pine basal area management as a predictor of upland hardwood abundance and distribution in frequently burned, longleaf pine communities.

Our results indicate that FTOs are more likely to be present on xeric sites, and that percent slope is a more important predictor of FTO abundance than soil characteristics and other aspects of topography associated with xeric conditions (e.g., aspect, elevation, and topographic position). Fire-tolerant oak species (e.g., turkey oak, blackjack oak, and sand post oak) have well-documented affinities for xeric and sub-xeric site conditions and accounted for the majority

(89.53%) of the hardwood tree species we encountered (Peet and Allard 1993, Jacqmain et al. 1999, Sorrie et al. 2006, Carr et al. 2010). Many of the FTO species, especially turkey oak, are common on xeric sites in the Sandhills (Peet and Allard 1993, Greenberg and Simons 1999, Sorrie et al. 2006, Carr et al. 2010). Xeric conditions occur frequently on steeper slopes because of decreased soil moisture caused by greater amounts of run-off and the low water holding capacity of the coarser soil textures present (Jenny 1994, Addington et al. 2015 b).

The influence of topography-driven xeric conditions and proximity to ignition points on fire behavior is another plausible explanation for finding slope and distance to firebreaks important for predicting FTO abundance. Although FTO species commonly are associated with xeric conditions, steep slopes could further promote the persistence of mature FTO stems by decreasing fire-induced mortality through increased rates of fire spread, decreased residence times, and increased patchiness due to sparser fuels – depending on ignition conditions, firing techniques, and fuel characteristics (Rothermel 1983, Glitzenstein et al. 1995, Jacqmain et al. 1999, Addington et al. 2015 b). Additionally, areas near firebreaks allow FTO species to achieve greater densities because fires burn with less intensity proximal to ignition sources (Lashley et al. 2014). It is likely that over long time scales, xeric conditions act independently and in concert with proximity to firebreaks to influence fire behavior such that steep slope areas proximal to firebreaks are less likely to experience intense fires capable of damaging FTO species. Our results indicate that managers concerned with retaining upland hardwood inclusions likely would achieve success on steep slopes and areas adjacent to firebreaks; conversely, these areas can be targeted by managers seeking to remove upland hardwoods.

Fire-sensitive hardwood species were more abundant on sandy loam soils and at lower elevations due to how local fire behavior is affected by edaphic conditions. In our study area,

lower elevations and sandy loam soils typically were associated with mesic ecotones adjacent to riparian corridors (Sorrie et al. 2006, Just et al. 2016), and the conditions in these mesic ecotones interact with fire behavior to drive FSH abundance. For example, riparian zones act as natural firebreaks (Just et al. 2016), creating heterogeneity in fire behavior (e.g., patchiness and intensity) that may positively affect FSH abundance. Although we did not document support for fire return interval as predictor of FSH abundance, the number of growing-season fire was an important predictor. Previous research has shown that growing-season burning causes more hardwood mortality than dormant-season fires (Boyer 1990, Streng et al. 1993, Glitzenstein et al. 1995). We suggest the mesic conditions associated with low lying areas and sandy loam soils within our study area experience more intense fires that burn more continuously during the growing season due to higher ambient temperatures and decreased fuel moisture during the late-spring and early-summer; when these factors are combined with the increased vulnerability to fire-induced mortality during the growing season, there is decreased survival and abundance of FSH species in these areas.

Pine basal area was an important predictor of abundance for both guilds of hardwoods, a relationship previously documented (McGuire et al. 2001, Knapp et al. 2014, Addington et al. 2015 a, b, Whelan et al. 2018). Researchers have suggested two mechanisms by which areas with greater pine basal area or canopy cover may negatively influence hardwood tree abundance. Hardwoods may be less abundant in areas with high levels of pine canopy cover because of decreased light availability and greater competition for space and water (McGuire et al. 2001, Knapp et al. 2014, Addington et al. 2015b). Also, areas high in pine canopy cover result in greater amounts of litter composed of flammable pine needles that can increase fuel loads and continuity, which results in more intense fires that burn more contiguously (Platt et al. 2016), and

thus increase fire-related mortality (Addington et al. 2015 b, Whelan et al. 2018). Although we showed the number of growing-season fires was an important positive predictor of FSH abundance, we did not detect support for fire history variables as predictors of FTO abundance. These results indicate that pine-mediated fire behavior potentially influences FSH abundance, but competition for light and other resources, rather than fire history, drive the relationship between pine basal area and FTO abundance. Hence, following thinning to reduce pine overstory, FSH species may be less susceptible to fire due to decreased fire intensity related to less fuel composed of pine needles, and FTO may be released to achieve fire-resistant sizes by increasing light, water, and space availability associated with less pine competition.

There are a couple of explanations for why we did not detect support for fire return interval as an important predictor of hardwood tree abundance. Most importantly, landscape-level homogeneity in fire return interval across Fort Bragg may have limited our ability to test fire return interval as a predictor of FTO and FSH abundance. On Fort Bragg, there was little variation in fire return interval ($\bar{x} = 3.66 \pm 1.02$ years), and the majority of sample plots had intervals between 2 and 4.5 years (83.1 %). Another explanation may be related to the possibility that fire return interval exerted its influence on community structure early in the course of fire reintroduction. Over the long-term, managing with frequent, recurrent fire likely caused plant communities to segregate into the respective landscape positions that enable them to persist in the presence of frequent fire, and thus more fire-sensitive hardwood species become restricted to mesic areas that are prone to burning less intensely and with more heterogeneity; more fire-tolerant species may be able to occupy steep slopes, ridges, and areas near firebreaks because of the ways in which these areas influence fire behavior.

Although we did not determine that fire return interval was an important predictor of FTO and FSH abundance, season of burn had an influence on FSH abundance. The reported effects of fire season on mature hardwood dynamics vary, with some studies reporting greater hardwood stem mortality or decreased abundance in response to growing-season fire (Boyer 1990, Streng et al. 1993, Glitzenstein et al. 1995), increased hardwood stem densities in response to dormant-season burning (Boyer 1993), or no effect of fire season (Waldrop et al. 1992, Brockway and Lewis 1997, Addington et al. 2015 a, b). Although the results of our FTO analysis are inconsistent with Boyer et al. (1990), their grouping of all oaks as a single response variable makes comparisons difficult regarding the effects of repeated growing-season burning. Furthermore, our results contradict those reported by Streng et al. (1993) and Glitzenstein et al. (1995), who reported that trees we categorized as FTO experienced reduced survival, recruitment, and density in response to growing-season fire; however, the relationships in FSH species were similar in that FSH abundance was negatively influenced by the number of growing-season burns.

The differences we observed between important predictors of FTO and FSH highlight the need to consider species or species guilds independently when constructing management plans. FSH species, whether mesophytic or tolerant of a broader range of site conditions, become relegated to mesic areas where fires burn more heterogeneously and with less intensity. Fire return interval was not an important predictor of tree abundance for FTO and FSH species, which may indicate that coarse fire history metrics may be less important than individual fire behavior, or that the observable effects of fire return interval on hardwood distribution are exerted early in a fire restoration program. We suggest that future investigations should account for both the

influence of individual fires, and long-term trends in fire history when studying the effects of fire on hardwood distributions in upland longleaf pine communities.

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Table 1. Species categorized as fire-tolerant oaks and fire-sensitive hardwoods, number of plots where present, occurrence (% of plots), and total number of stems counted at 307 inventory plots (0.04 ha) at Fort Bragg, North Carolina, USA, 2018.

Species	Plots	Occurrence (%)	Total
<i>Fire-tolerant oaks</i>			
Bluejack oak (<i>Quercus incana</i> Bartr.)	20	2.66	50
Blackjack oak (<i>Quercus marilandica</i> Muenchh)	72	24.60	463
Post oak (<i>Quercus stellata</i> Wang.)	17	2.34	44
Sand post oak (<i>Quercus margaretta</i> Ashe.)	46	10.26	193
Southern red oak (<i>Quercus falcata</i> Michx.)	28	3.72	70
Turkey oak (<i>Quercus laevis</i> Walt.)	105	39.64	746
<i>Fire-sensitive hardwoods</i>			
Black cherry (<i>Prunus serotina</i> Ehrh.)	1	0.05	1
Blackgum (<i>Nyssa sylvatica</i> Marsh.)	10	0.96	18
Black oak (<i>Quercus velutina</i> Lam.)	13	2.66	50
Butternut (<i>Juglan cinerea</i> L.)	2	0.16	3
Flowering dogwood (<i>Cornus florida</i> L.)	15	2.76	52
Hickory (<i>Carya sp.</i>)	27	3.88	73
Persimmon (<i>Diospyros virginiana</i> L.)	6	0.32	6
Red maple (<i>Acer rubrum</i> L.)	1	0.05	1
Sweetgum (<i>Liquidambar styraciflua</i> L.)	13	3.45	65
Water oak (<i>Quercus nigra</i> L.)	8	2.50	47

Table 2. Summary (mean, standard deviation, and range) of response and explanatory variables used to model abundance of fire-tolerant oaks and fire-sensitive hardwoods counted at 307 inventory plots (0.04 ha) at Fort Bragg, North Carolina, USA, 2018. Type distinguishes between numerical and categorical variables.

	Type	$\bar{X} \pm \text{SD}$	Range
<i>Response variable</i>			
Fire-tolerant oak (stems)	N	5.10 ± 6.94	0 - 40
Fire-sensitive hardwood (stems)	N	1.03 ± 3.09	0 - 30
<i>Explanatory variable</i>			
Aspect (°)	N	169.35 ± 106.06	0 - 360
Distance to firebreak (m)	N	69.34 ± 50.51	11.74 - 257.54
Dormant fires (count)	N	1.26 ± 1.20	0.00 – 6.00
Elevation (m)	N	92.26 ± 18.47	52.73 - 140.81
Fire return interval (years)	N	3.66 ± 1.02	2.15 - 9.33
Growing fires (count)	N	6.85 ± 2.09	1.00 - 13.00
Pine basal area (m ² /ha)	N	13.40 ± 7.90	0.00 – 39.00
Slope (%)	N	5.72 ± 3.21	0.54 - 16.11
Soil texture	C	-	sand
		-	loamy sand
Topographic Position Index	C	-	lower
		-	middle
		-	upper

Table 3. Names and formulas of a priori models used to predict abundance of fire-tolerant oaks and fire-sensitive hardwoods counted at 307 inventory plots (0.04 ha) at Fort Bragg, North Carolina, USA, 2018. Type distinguishes between numerical and categorical variables.

Model	Formula
M1	Dist. firebreak + FRI + Pine BA + Slope + Soil text.
M2	Dist. firebreak + FRI + Elevation + Pine BA + Soil text.
M3	Dist. firebreak + FRI + Pine BA + Slope
M4	Dist. firebreak + FRI + Pine BA + TPI
M5	Dist. firebreak + FRI + Pine BA + Slope + TPI
M6	Dist. firebreak + Growing fire + Pine BA + Slope + Soil text.
M7	Dist. firebreak + Growing fire + Elevation + Pine BA + Soil text.
M8	Dist. firebreak + Growing fire + Pine BA + Soil text.
M9	Dist. firebreak + Growing fire + Pine BA + Slope + TPI
M10	Dist. firebreak + Growing fire + Pine BA + TPI
M11	Dist. firebreak + Growing fire + Pine BA + Slope
M12	Aspect + Elevation + Slope + TPI
M13	Aspect + Elevation + Slope + Soil text. + Pine BA + TPI
M17	Null
M18	Aspect + Dist. firebreak + Elevation + FRI + Slope + Soil text. + Pine BA + TPI
M19	Aspect + Dist. firebreak + Elevation + Growing fire + Slope + Soil text. + Pine BA + TPI

Table 4. The number of parameters (K), AIC, Δ AIC, model weight (ω), and negative loglikelihood (-LogLik) for all models of fire-tolerant oak abundance at Fort Bragg, North Carolina, USA, 2018.

Model	K	AIC	Δ AIC	ω	-LogLik
FB + FRI + Pine + Slope	6	1530.6	0.0	0.3	-759.3
FB + Grow + Pine + Slope	6	1531.1	0.5	0.2	-759.6
FB + FRI + Pine + Slope + Soil	7	1532.6	2.0	0.1	-759.3
FB + Grow + Pine + Slope + Soil	7	1533.1	2.5	0.1	-759.6
FB + Grow + Pine + Soil	6	1533.6	3.0	0.1	-760.8
FB + FRI + Pine + Slope + TPI	8	1534.4	3.8	0.0	-759.2
FB + FRI + Pine + TPI	7	1534.9	4.3	0.0	-760.5
FB + Grow + Pine + Slope + TPI	8	1534.9	4.3	0.0	-759.5
FB + FRI + Elevation + Pine + Soil	7	1535.0	4.3	0.0	-760.5
FB + Grow + Pine + TPI	7	1535.3	4.7	0.0	-760.7
FB + Grow + Elevation + Pine + Soil	7	1535.4	4.8	0.0	-760.7
Sub-Global: FRI	11	1540.0	9.4	0.0	-759.0
Sub-Global: Grow	11	1540.6	10.0	0.0	-759.3
Environmental	9	1540.9	10.3	0.0	-761.5
Null	2	1585.1	54.5	0.0	-790.5

FB – Distance to firebreaks, Pine – pine basal area, Soil – soil type, Grow – number of growing-season fires, FRI – fire return interval, Slope – percent slope, TPI – topographic position index

Table 5. Coefficients, 85% confidence interval, and 95% confidence interval of parameter estimates for covariates in the top-ranked model of fire-tolerant oak abundance at Fort Bragg, North Carolina, 2018.

Parameter	β	SE	85% CI		95% CI	
Intercept	2.23	0.40	1.65	2.81	1.45	3.02
Dist. Firebreak ^a	-0.22	0.10	-0.36	-0.07	-0.41	-0.02
Pine BA ^a	-0.72	0.09	-0.85	-0.59	-0.89	-0.54
FRI ^b	0.06	0.08	-0.06	0.18	-0.10	0.22
Slope ^c	0.14	0.08	0.03	0.26	-0.02	0.30

^a Parameters with strong statistical support

^b Parameters without statistical support

^c Parameters with weak statistical support

Table 6. The number of parameters (K), QAIC, Δ QAIC, model weight (ω), and negative log-likelihood (-LogLik) for all models of fire-sensitive hardwood abundance at Ft. Bragg, North Carolina, USA, 2018.

Model	K	QAIC	Δ QAIC	ω	-LogLik
FB + Grow + Elevation + Pine + Soil	7	394.9	0	0.5	-302.8
FB + FRI + Elevation + Pine + Soil	7	396.6	1.7	0.2	-304.2
FB + Grow + Pine + Soil	6	396.8	1.9	0.2	-305.9
FB + Grow + Pine + Slope + Soil	7	398.8	3.9	0.1	-305.9
Environmental	9	399.5	4.6	0.0	-303.3
Sub-Global: Grow	11	400.7	5.8	0.0	-301.0
FB + FRI + Pine + Slope + Soil	7	402.6	7.7	0.0	-308.9
Sub-Global: FRI	11	402.7	7.8	0.0	-302.7
FB + Grow + Pine + TPI	7	412.3	17.4	0.0	-316.7
FB + Grow + Pine + Slope	6	413.9	19	0.0	-319.5
FB + Grow + Pine + Slope + TPI	8	414.3	19.4	0.0	-316.6
FB + FRI + Pine + TPI	7	415.5	20.6	0.0	-319.2
FB + FRI + Pine + Slope	6	415.8	20.9	0.0	-321.0
FB + FRI + Pine + Slope + TPI	7	415.8	20.9	0.0	-319.4
Topography	7	426.2	31.4	0.0	-327.7
Null	2	431.1	36.2	0.0	-339.5

FB – Distance to firebreaks, Pine – pine basal area, Soil – soil type, Grow – number of growing-season fires, FRI – fire return interval, Slope – percent slope, TPI – topographic position index

Table 7. Coefficients, 85% confidence interval, and 95% confidence interval of parameter estimates for covariates in the top-ranked model of fire-sensitive hardwood abundance at Fort Bragg Military Installation, North Carolina, 2018. Overdispersion corrected for by inflating standard error by $\sqrt{1.59}$.

Parameter	β	SE	85% CI		95% CI	
Intercept	0.60	0.93	-0.74	1.94	-1.22	2.42
Dist. firebreak ^a	-0.44	0.52	-1.19	0.31	-1.46	0.58
Growing fires ^b	-0.27	0.19	-0.54	-0.01	-0.64	0.10
Elevation ^b	-0.36	0.20	-0.64	-0.07	-0.75	0.03
Pine BA ^c	-0.93	0.23	-1.26	-0.60	-1.38	-0.48
Soil (sand) ^c	-1.98	0.46	-2.64	-1.32	-2.88	-1.09

^a Parameters without statistical support

^b Parameters with weak statistical support

^c Parameters strong statistical support

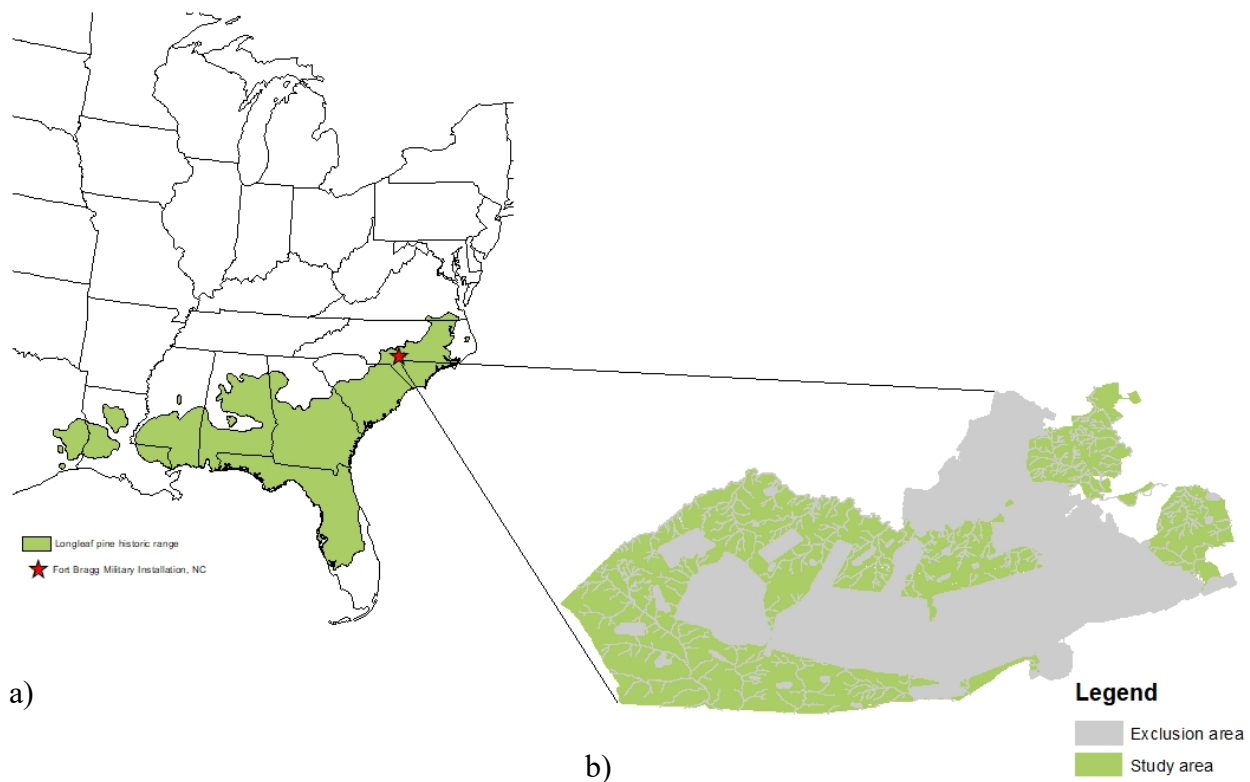


Figure 1. Study area (a) in relation to the historical range of the longleaf pine ecosystem, and (b) the upland study area and exclusion areas at Fort Bragg Military Installation, North Carolina, 2018.

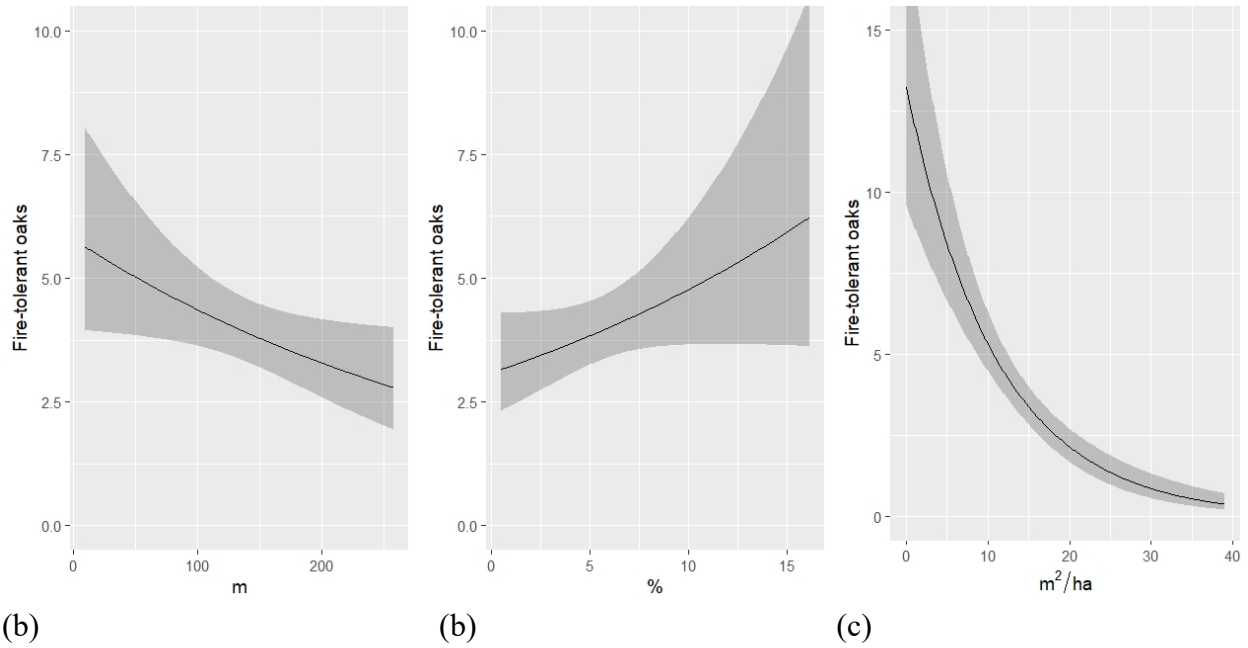


Figure 2. Fire-tolerant oak abundance in relation to predictors in the top model (a) distance to firebreaks, (b) slope, and (c) pine basal area at Fort Bragg, North Carolina, 2018.

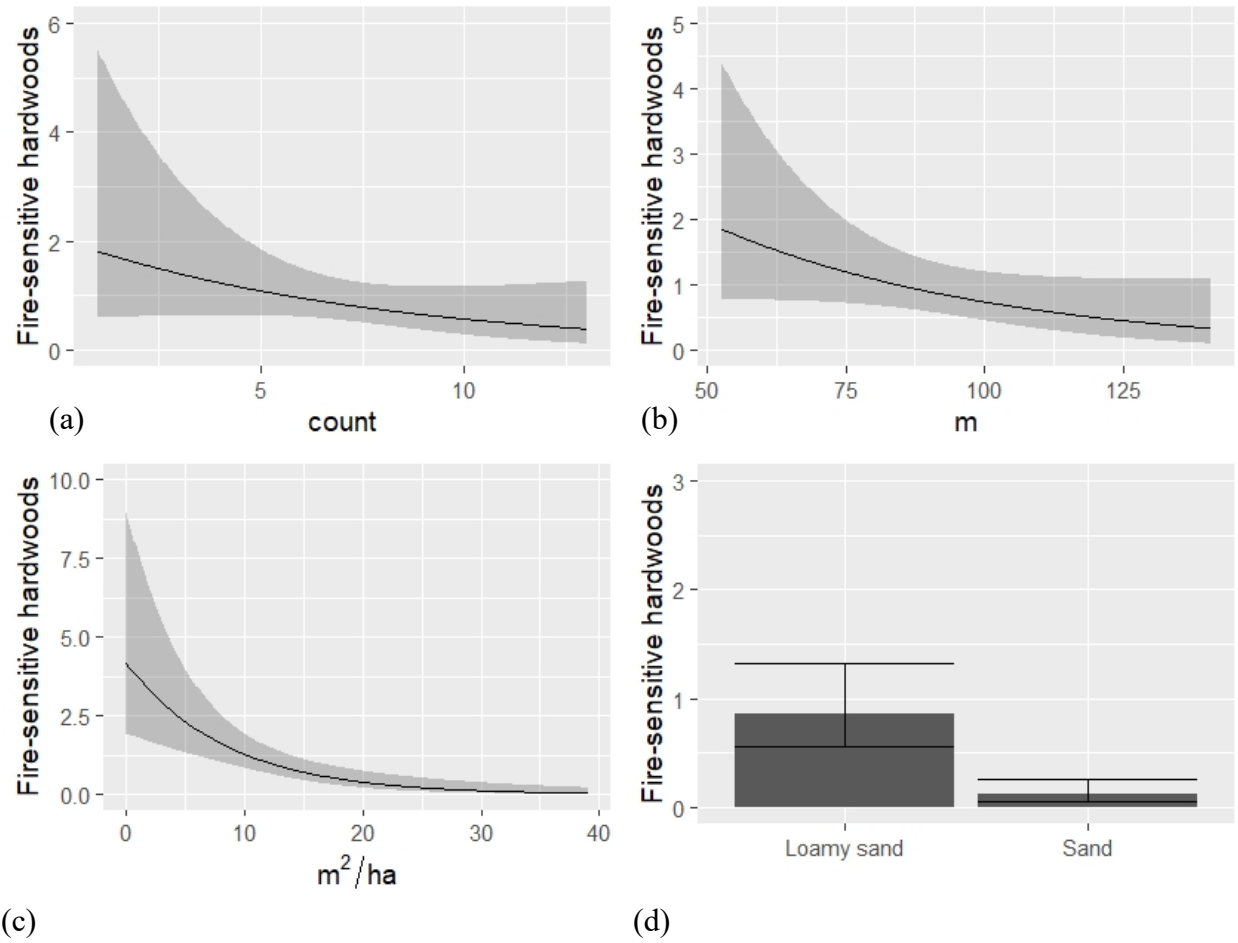


Figure 3. Fire-sensitive hardwood abundance in relation to predictors in the top model (a) number of growing-season fires, (b) elevation, (c) pine basal area, and (d) soil texture at Fort Bragg, North Carolina, 2018.

CHAPTER 2

THE RELATIONSHIP BETWEEN UPLAND HARDWOOD DISTRIBUTION AND AVIAN OCCUPANCY IN FIRE-MAINTAINED LONGLEAF PINE FORESTS

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*). 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 some overstory hardwoods in upland longleaf pine communities may benefit a variety of birds. We used fixed-radius 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 hardwood overstory cover on occupancy. Due to issues with model fit, we were unable to model occupancy for 3 of the 15 focal species. Occupancy probability for 3 of the 12 species was positively influenced by pine overstory cover and occupancy probability for 2 of the 12 species was negatively influenced by pine overstory cover, including 1 species for which pine overstory cover was the sole variable in the top model. Occupancy probabilities for 7 out of the 12 focal species were positively influenced by hardwood overstory 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. Hardwood overstory cover levels of 5-15% 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. We suggest that managing longleaf pine uplands with lower and upper bounds of 5% to 15% hardwood overstory cover with stem densities of ≤ 250 stems/ha will provide habitat for the greatest diversity of birds while avoiding negative impact to species associated with upland longleaf pine communities.

INTRODUCTION

The longleaf pine (*Pinus palustris*) ecosystem is globally endangered and important to biodiversity conservation in the southeastern United States (Noss et al. 1995). Throughout the 20th century, longleaf pine communities declined due in large 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 critical management and restoration efforts have been underway since that time; however, remnant longleaf pine forests still occupy a small fraction of 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. 2014), the need for widespread conservation of longleaf pine landscapes 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 dominated by grasses, forbs, and longleaf pine regeneration (USFWS 2003, Brockway et al. 2005). Because fire exclusion 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). 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 faunal community dynamics.

Prescribed fire management typically aims to achieve reduction or removal of upland hardwood cover with the goal of providing habitat for the federally endangered red-cockaded

woodpecker (Garabedian et al 2017). Although removal or substantial reduction of hardwood canopy and midstory cover benefits 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 benefit mast-dependent wildlife (e.g., fox squirrels [*Sciurus niger*; Perkins et al. 2008], white-tailed deer [*Odocoileus virginianus*; Lashley et al. 2015]), and less hardwood cover is important to for maintaining red-cockaded woodpecker habitat (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 narrowly precise goals of forest structure and composition (i.e., single species management).

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). 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. 2002, 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 hardwood cover 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 of hardwood cover may support species 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 specialists. Although Allen et al. (2006) classified breeding bird assemblages in fire-maintained longleaf pine communities, their analysis did not consider how overstory hardwoods in longleaf pine uplands influence 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, possibly because measures of hardwood cover were not included as independent variables in analyses. 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 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.

METHODS

Study area

We conducted the study at Fort Bragg Military Installation in the Sandhills physiographic region of south-central North Carolina, USA (35.1°N, -79.2° W; Figure 1). Fort Bragg is a 625-km² 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 approximately one-third of the base is 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 meet burn quotas. In addition, managers using thinning and herbicides to control hardwood encroachment and maintain open stand structures with overstory pine basal area of ~

11.5 m²/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 36m to 183m 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 comprised of loamy sands, while loam soils typically predominate the bottomland 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 comprised 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).

Site selection and bird surveys

We used ArcGIS (Arcmap v. 10.5; ESRI, Redlands, CA, USA) to eliminate from the study area all locations within 50m of streams, classified wetlands, and bottomland hardwood communities. We randomly located 305 points in upland longleaf pine communities with a minimum nearest neighbor distance of 300m 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 150m 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 hr 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 conditions 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.

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 ≥ 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) 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 $\geq 5\text{m}$ and $< 5\text{m}$, and all hardwood cover $< 5\text{m}$ 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.

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]). 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). 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-Akaike information criteria (QAIC) with $c\text{-hat}$ (\hat{c}) specified using package “AICcmodavg” (Mazerolle 2017). When $\hat{c} = 1.0$, QAIC is equivalent to AIC ranking; however, when $\hat{c} > 1.0$, 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 ($2k$) 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 via 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 2]). We ranked field measured vegetation models with QAIC, and all models with $\Delta\text{QAIC} < 2$ were considered competitive unless they were more complex versions of the top model and contained uninformative parameters (Arnold et al. 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 2). 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 $\Delta\text{QAIC} < 2$ were considered competitive unless they were more complex versions of the top model and contained uninformative parameters (Arnold et al. 2010), and our top model of occupancy for each species was the most parsimonious model among the final set of competitive models.

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.

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 (Table 1). The independent variables used in occupancy models included hardwood stems density (151.4 ± 187.3), pine basal area (13.4 ± 7.9), percent grass cover (54.3 ± 32.4), hardwood canopy cover within 150m (6.3 ± 4.4), and pine canopy cover within 150m (44.9 ± 13.2 [Table 2]). From the independent accuracy assessment of the land cover classification of Fort Bragg, the overall accuracy was 79.67% (Table 3), 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 to a high of 299 of the 305 sampling sites for pine warbler (16.72, 98.03%, respectively, Table 4). On average, yellow-throated vireo had the lowest detection probability, and blue-gray gnatcatcher had the highest detection probability (0.11 ± 0.03 , 0.71 ± 0.02 , respectively, Table 4). 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 4). 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 4). 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 150m.

The top model for occupancy probability of Bachman's sparrow included linear effects of hardwood stem density and grass cover (Table 5). The effects of hardwood stem density were negative, with neither CI overlapping zero (Table 6), and thus we concluded there was strong support for hardwood stem density as a negative predictor of Bachman's sparrow. Specifically, sites with hardwood stem densities greater than 375 trees/ha had an occupancy probability less than 0.50 (Figure 2a). The effect of grass cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 6). Specifically, sites with grass cover comprising at least 75% of the plot had an occupancy probability greater than 0.75 (Figure 2b).

The top occupancy model for blue-headed vireo and brown-headed nuthatch contained linear effects of hardwood stem density and pine cover within 150m (Table 5). 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 6); 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 (Figure 3a). The effect of pine cover within 150m on blue-headed vireo occupancy was positive, and though the 95% CI slightly overlapped zero, the 85% CI did not (Table 6). Sites with greater than 60% pine cover had an occupancy probability greater than 0.50 (Figure 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 6). Sites with at least 685 hardwood stems/ha had an occupancy probability less than 0.50 (Figure 4a). The effect of pine cover within 150m was negative for brown-headed nuthatch, and though the 95% CI slightly overlapped zero, the 85% CI did not (Table 6). 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 150m surpassed 75% (Figure 4b).

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

(Figure 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 6). Sites with at least 15% hardwood cover had an occupancy probability greater than 0.75 (Figure 6a). The effect of pine cover within 150m was positive for red-eyed vireo, and neither the 95% CI nor the 85% CI overlapped zero (Table 6). Occupancy probability was greater than 0.75 when pine cover within 150m of sites surpassed 75% (Figure 6b).

The top occupancy model for blue-gray gnatcatcher, tufted titmouse, and yellow-throated vireo included the linear effect of hardwood cover within 150m (Table 5). For blue-gray gnatcatcher, the effect of hardwood cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 6). Sites with upland hardwood cover comprising at least 5% of the surrounding 150-m buffer had an occupancy probability greater than 0.75 (Figure 7). For tufted titmouse, the effect of upland hardwood cover was positive, and neither the 95% CI nor the 85% CI overlapped zero (Table 6). Specifically, as hardwood cover increased from ~ 1% to ~ 4%, tufted titmouse occupancy probability increased from 0.50 to 0.75, respectively (Figure 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 6). Specifically, at sites with greater than 12% upland hardwood cover within 150m, yellow-throated vireo occupancy probability was greater than 0.75 (Figure 9).

The top model of occupancy probability for Carolina chickadee included a linear effect of hardwood stem density (Table 5). Although the effect of hardwood stem density was positive, both the 95% CI and 85% CI overlapped zero (Table 6); 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 5). 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 6). For red-headed woodpecker, the effect of hardwood stem density was negative, and neither the 95% CI nor the 85% CI overlapped zero (Table 6). Sites with more than 250 hardwoods/ha had an occupancy probability less than 0.50 (Figure 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 6). As pine basal area increased, red-headed woodpecker occupancy decreased, and sites with pine basal area above 18 m²/ha had occupancy probability less than 0.50 (Figure 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 6). Specifically, red-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 6). 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 (Figure 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 6). Summer tanager occupancy increased as pine basal area increased from 0 to 25 m²/ha, but then

declined (Figure 11b). However, summer tanager occupancy probability fell below 0.50 only as pine basal area approached 37.5 m²/ha, which was at the high end of the range of pine basal area that we observed (Figure 11b).

The top model of occupancy for northern bobwhite contained a linear effect of pine cover within 150m (Table 5). The effect of pine cover within 150m was negative, and the 95% CI overlapped zero, but the 85% CI did not (Table 6). 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 150m of sites surpassed 40% (Figure 12).

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, 11 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 hardwood density or canopy cover, occupancy probability for 7 of the 12 species was positively influenced by hardwood composition. These results further support the importance of 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 low densities of hardwood midstory and overstory stems is important when the management objective is to maximize avian diversity.

Although other researchers have inferred that hardwood reduction positively influences Bachman's sparrows, brown-headed nuthatch, and red-headed woodpeckers (Steen et al. 2013, Allen et al. 2006, Conner et al. 2002, Provencher et al. 2002, Wilson and Watts 1999), 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. 2002, Wilson and Watts 1999), but we were able to demonstrate thresholds related to hardwood composition. Of the six 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. Interestingly, our results indicated that hardwood stem density was a more important predictor of occupancy than was hardwood canopy cover. This stronger connection to stem density than to overall canopy cover implies these bird species may be more adversely affected by high numbers of midstory hardwoods than by fewer overstory trees with large canopies. However, our results indicated that occupancy probability for these species can remain above 0.50 in areas where hardwood density was ≤ 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. Of these five species, 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 (or abundance) of these species is not surprising due 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, which typically are associated with dense hardwood cover, 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 upland longleaf pine communities managed with frequent fire, low levels of hardwood cover between ~5% and 15% are needed for these species to remain present in upland longleaf pine communities. Although we excluded bottomlands from our 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.

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 than in areas that did not receive hardwood reduction treatments. Whereas 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, our results indicate there may be a lower limit of hardwood cover and pine cover tolerated by this species. Management aimed at creating and maintaining uplands as open

longleaf pine-wiregrass woodlands with low levels of hardwood midstory and overstory at Fort Bragg has been ongoing for 28yr., and thus hardwood cover availability is limited on the landscape. If eastern wood-pewee occupancy is positively affected by low to moderate levels of hardwood cover, then directly measuring hardwood cover and stem density on a continuous scale may be required to detect this relationship, and this may explain our results from previous research.

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. Our results support those reported by Cox et al. (2012), who 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), and likely have negative effects on foraging strategy of red-headed woodpecker (Vierling et al. 2009). 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 hardwood basal areas at the lower end of the recovery standard to maintain habitat for the full suite of open-pine species ($\sim 9\text{m}^2/\text{ha}$).

We suggest maintaining hardwood overstory cover between a lower threshold of $\sim 5\%$ and an upper threshold of 15% hardwood canopy cover, with hardwood densities < 250 stems/ha, to maximize avian diversity on the landscape. The lower threshold likely is comparable to the recommendations by Perkins et al. (2008), who recommended retaining at least $\sim 2.7\text{ m}^2/\text{ha}$ of

hardwood basal area comprised of scattered overstory trees and small patches of midstory hardwoods. Although patches of midstory hardwoods are important, retaining large overstory hardwoods should be the priority because the upper limit of the threshold can be met with fewer stems; hence this would mitigate effects to the species negatively influenced by dense hardwood stems. Moreover, for managers seeking to promote northern bobwhite, we suggest thinning pines to achieve pine canopy cover levels of $\leq 40\%$. Reducing pine canopy cover would also benefit other species negatively influenced by pine canopy cover or basal area, but it would also promote herbaceous cover which would be beneficial for increasing Bachman's sparrow habitat. 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 grasslands interspersed with hardwood patches of variable extents and age distributions. We believe 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.

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Table 1. 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 on Fort Bragg Military Installation, North Carolina, 2018.

Model	K ^a
<i>Null</i>	
psi(.)	2
<i>Field</i>	
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
<i>Remotely sensed</i>	
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 2. Mean, standard deviation, and range of independent variables used in a priori models of occupancy for 15 bird species on Fort Bragg Military Installation, North Carolina, 2018.

Variable	Mean	SD	Range
<i>Field measured</i>			
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
<i>Remotely sensed</i>			
Hardwood canopy cover (%)	6.3	4.4	0.0 - 37.0
Pine canopy cover (%)	44.9	13.2	9.0 - 81.0

Table 3. 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 on 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.

Table 4. Species, alpha code, overdispersion parameter (\hat{c}), naïve occupancy (ψ), mean detection probability (p), and top model of detection probability for 15 bird species on 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	$p(.) \text{ psi}(.)^a$
Blue-gray gnatcatcher	BGGN	3.68	0.71	0.71 ± 0.02	$p(.) \text{ psi}(.)$
Blue-headed vireo	BHVI	1.10	0.23	0.29 ± 0.03	$p(\text{Date} + \text{visit}) \text{ psi}(.)$
Brown-headed nuthatch	BHNU	2.48	0.68	0.36 ± 0.02	$p(.) \text{ psi}(.)$
Carolina chickadee	CACH	1.92	0.61	0.40 ± 0.03	$p(\text{Observer} + \text{Visit}) \text{ psi}(.)$
Eastern wood-pewee	EWPE	1.99	0.65	0.50 ± 0.02	$p(.) \text{ psi}(.)$
Great crested flycatcher	GCFL	8.08	0.91	0.58 ± 0.02	-
Northern bobwhite	NOBO	3.27	0.21	0.13 ± 0.03	$p(.) \text{ psi}(.)$
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	$p(.) \text{ psi}(.)$
Red-headed woodpecker	RHWO	3.34	0.60	0.36 ± 0.02	$p(.) \text{ psi}(.)$
Summer tanager	SUTA	1.87	0.88	0.57 ± 0.02	$p(\text{Date} + \text{Date}^2) \text{ psi}(.)$
Tufted titmouse	TUTI	2.50	0.75	0.58 ± 0.02	$p(\text{Date} + \text{Date}^2) \text{ psi}(.)$
Yellow-throated vireo	YTVI	0.70	0.17	0.11 ± 0.03	$p(.) \text{ psi}(.)$

^a Null model – detection probability constant.

Table 5. The number of parameters (K), QAIC, Δ QAIC, and model weight (ω) for models ≤ 2 Δ QAIC with combinations of grass cover, hardwood (HW) stem density, hardwood cover, pine basal area (BA), and pine cover as covariates of occupancy for 15 bird species on Fort Bragg Military Installation, North Carolina, 2018.

Species	Model	K	QAIC	Δ QAIC	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	581.54	1.75	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

Table 5. Continued

Species	Model	K	QAIC	Δ QAIC	ω
RHW0	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 6. Parameters, estimates (logit scale), standard error, and confidence intervals (95% and 85%) for covariates in the best models of occupancy for 12 bird species on Fort Bragg Military Installation, North Carolina, 2018. Shaded cells indicate that the interval(s) overlap zero.

Species	Parameter	Estimate	SE ^a	95% CI ^b		85% 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.

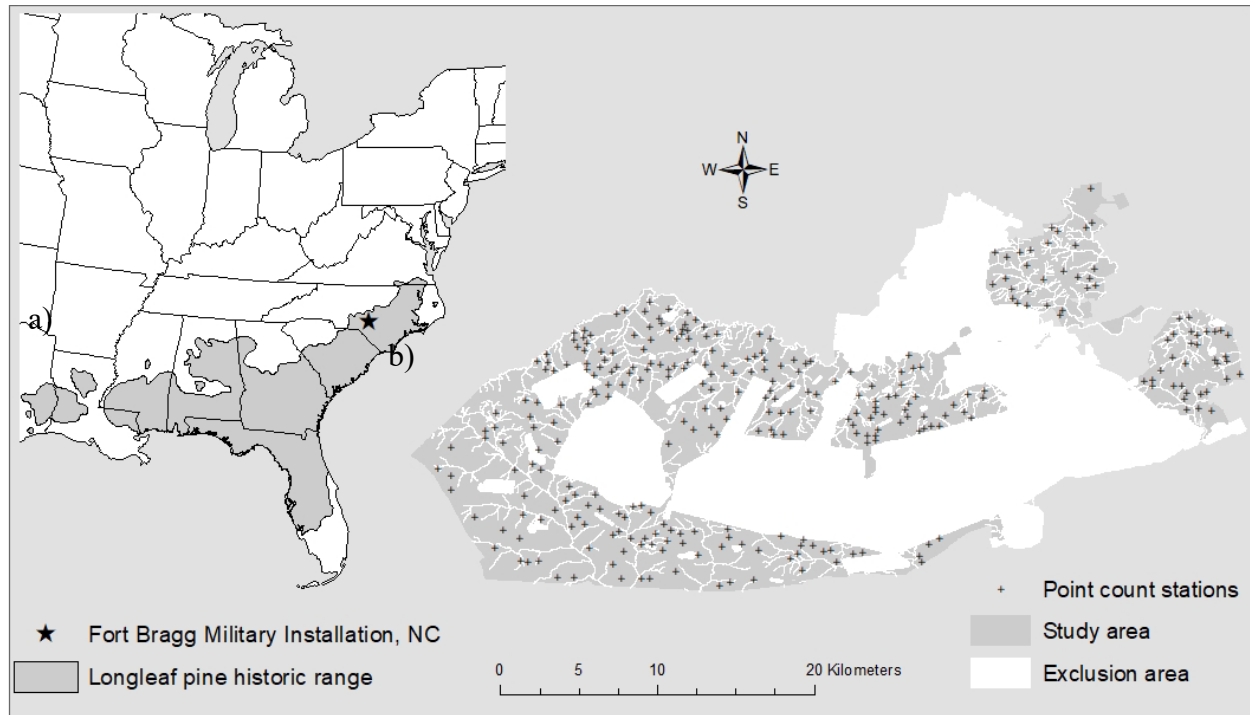


Figure 1. Fort Bragg Military Installation in relation to the historic range of longleaf pine ecosystem (a); avian point count study area and exclusion areas on Fort Bragg Military Installation, North Carolina, 2018.

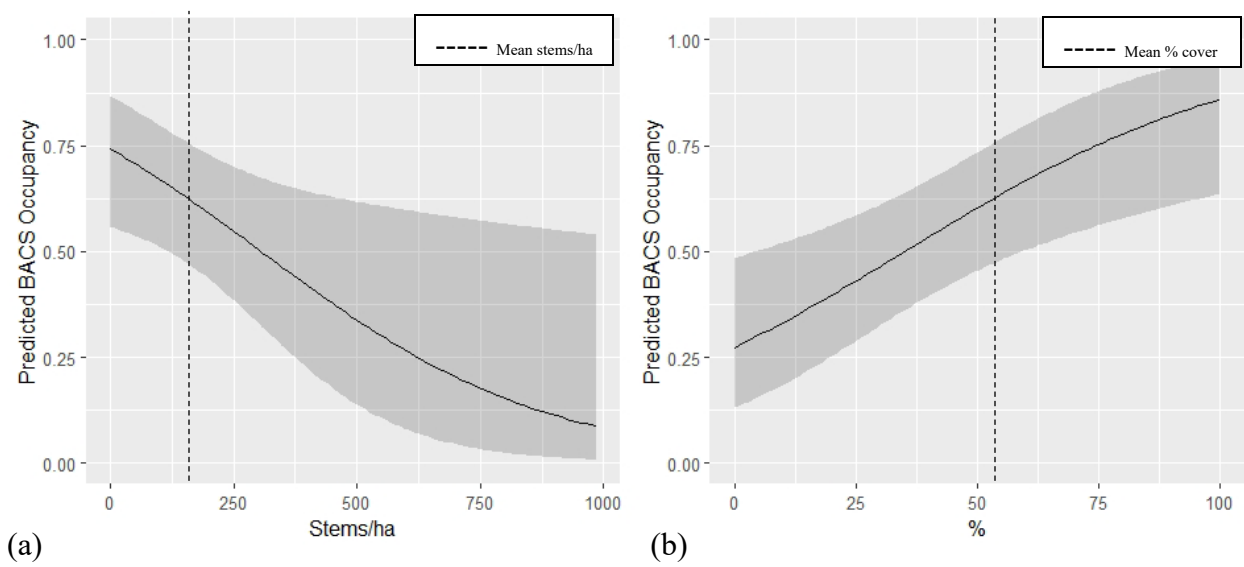


Figure 2. The predicted occupancy probability for Bachman's Sparrows estimated across the range of hardwood stem density (a) and grass cover (b) using the top model, Fort Bragg Military Installation, North Carolina, 2018.

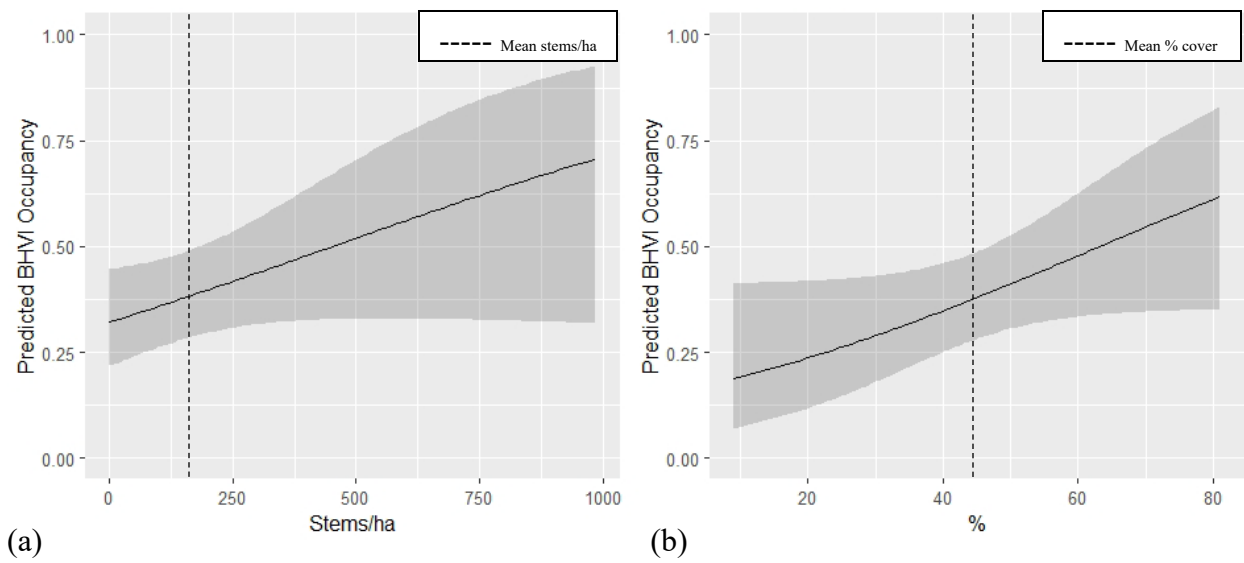


Figure 3. The predicted occupancy probability for blue-headed vireo estimated across the range of hardwood stem density (a) and pine canopy cover (b) using the top model, Fort Bragg Military Installation, North Carolina, 2018.

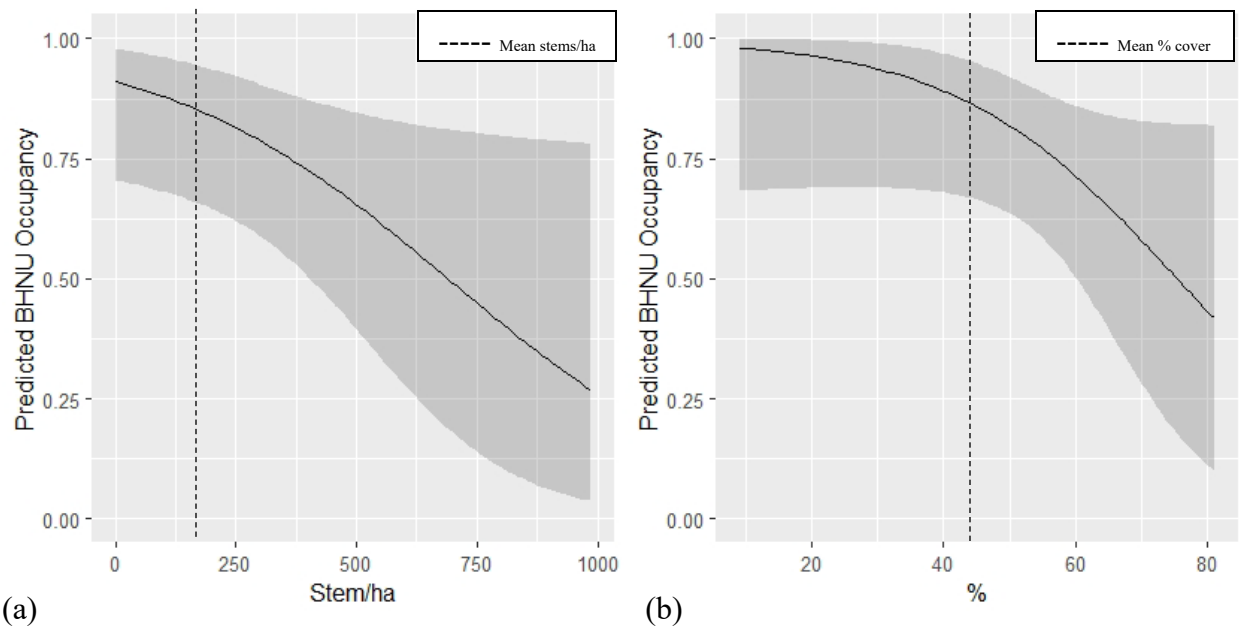


Figure 4. The predicted occupancy probability for brown-headed nuthatch estimated across the range of hardwood stem density (a) and pine canopy cover (b) using the top model, Fort Bragg Military Installation, North Carolina, 2018.

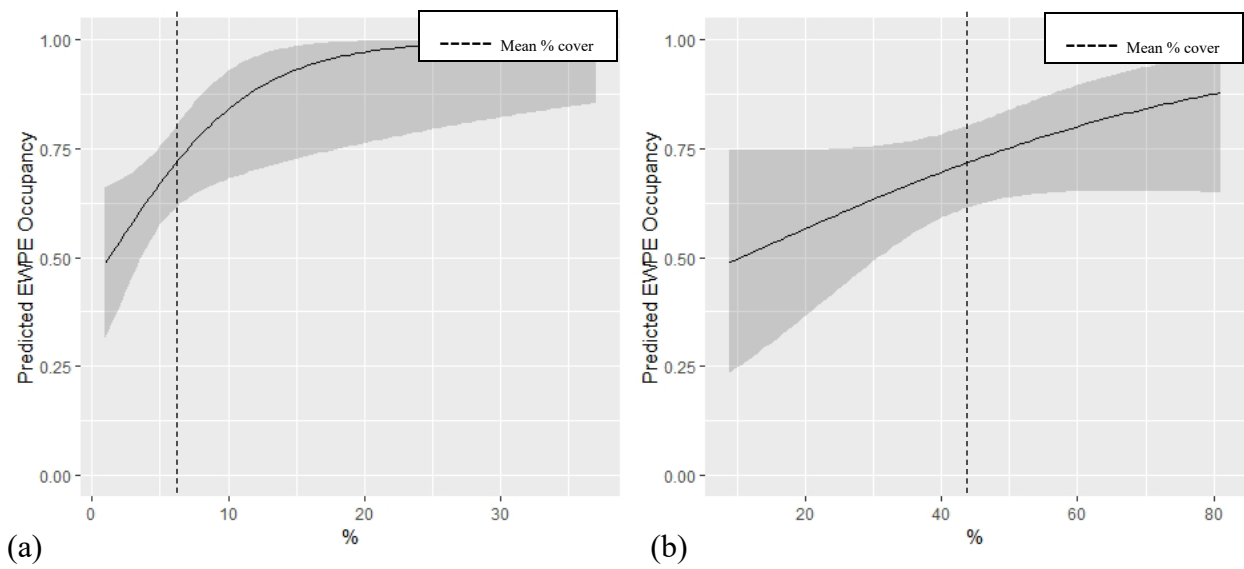


Figure 5. The predicted occupancy probability of eastern wood-pewee estimated across the range of upland hardwood canopy cover (a) and pine canopy cover (b) using the top model, Fort Bragg Military Installation, North Carolina, 2018.

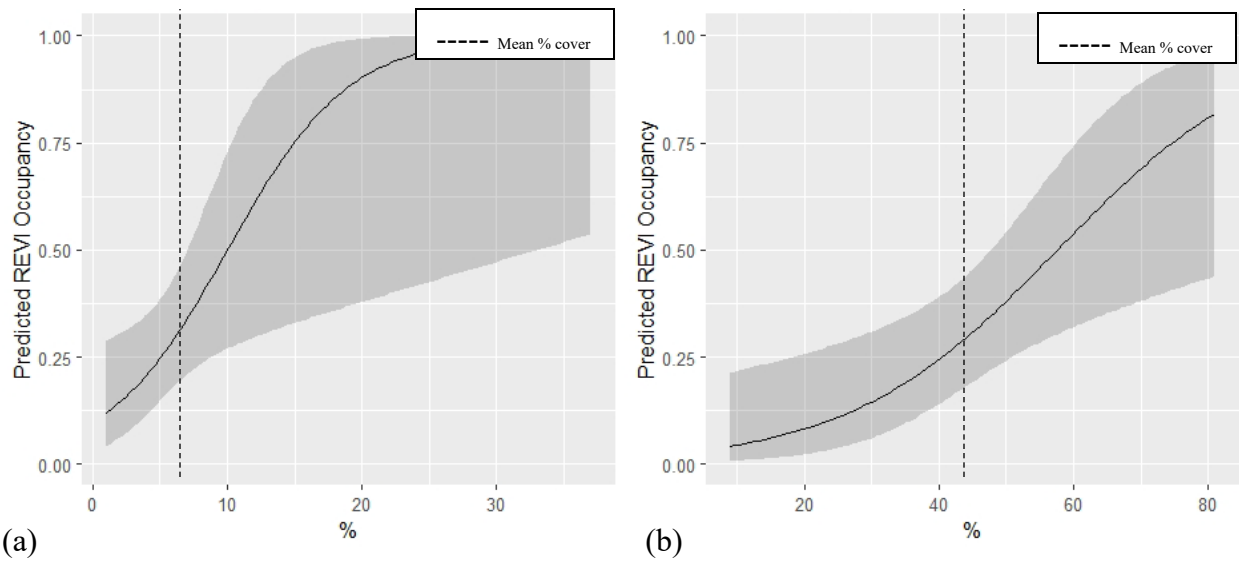


Figure 6. The predicted occupancy probability for red-eyed vireo estimated across the range of upland hardwood canopy cover (a) and pine canopy cover (b) using the top model, Fort Bragg Military Installation, North Carolina, 2018.

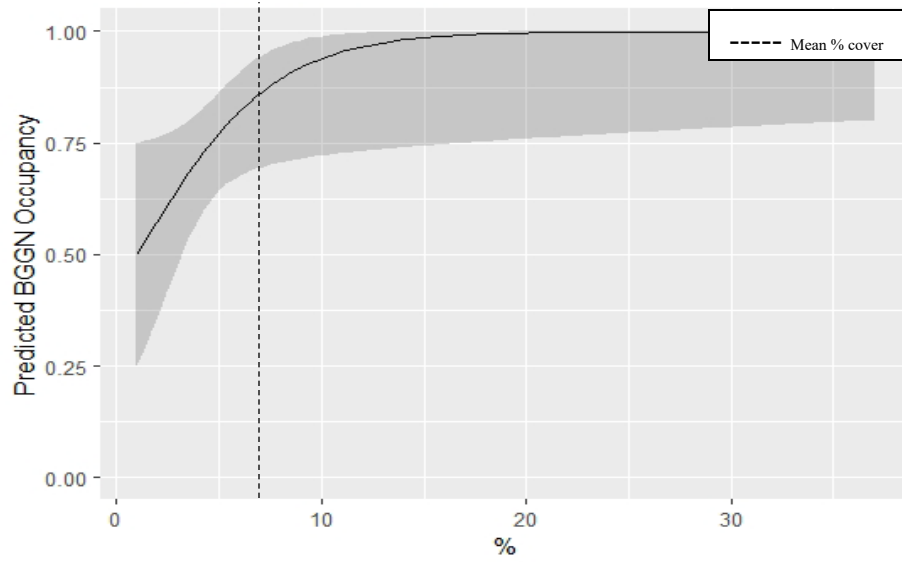


Figure 7. The predicted occupancy probability for blue-gray gnatcatcher estimated across the range of upland hardwood canopy cover using the top model, Fort Bragg Military Installation, North Carolina, 2018.

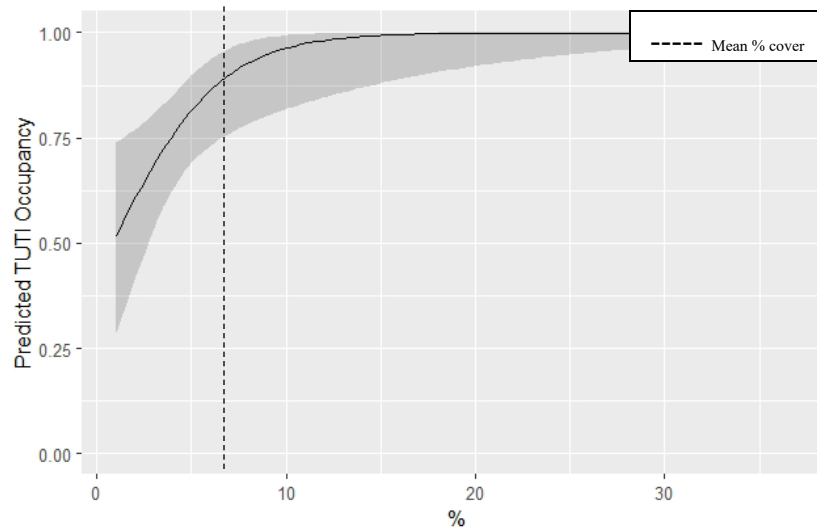


Figure 8. The predicted occupancy probability for tufted titmouse estimated across the range of upland hardwood canopy cover using our top model, Fort Bragg Military Installation, North Carolina, 2018.

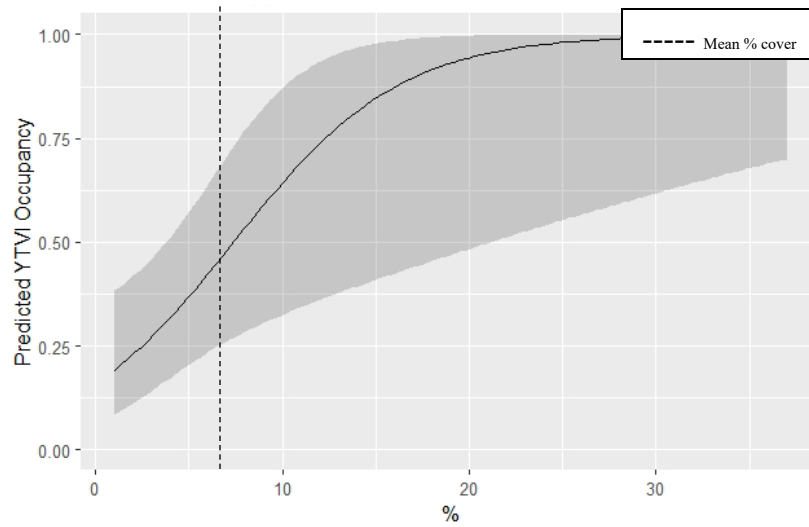


Figure 9. The predicted occupancy probability for yellow-throated vireo estimated across the range of upland hardwood canopy cover using our top model, Fort Bragg Military Installation, North Carolina, 2018.

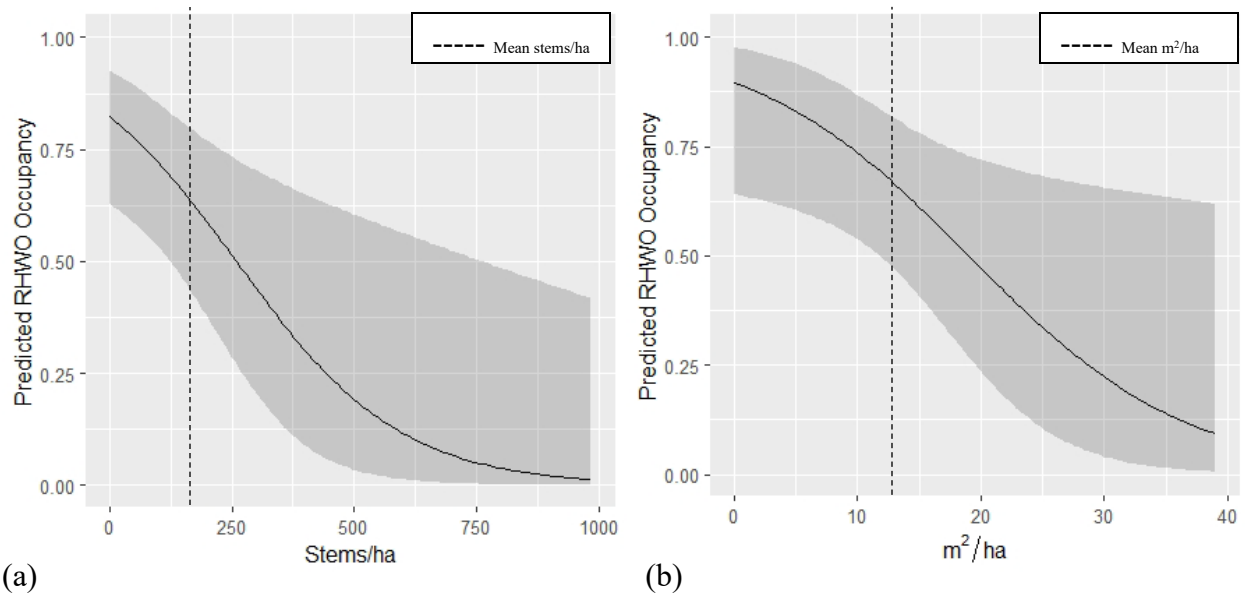


Figure 10. The predicted occupancy probability for red-headed woodpecker estimated across the range of hardwood stem density (a) and pine basal area (b) using the top model, Fort Bragg Military Installation, North Carolina, 2018.

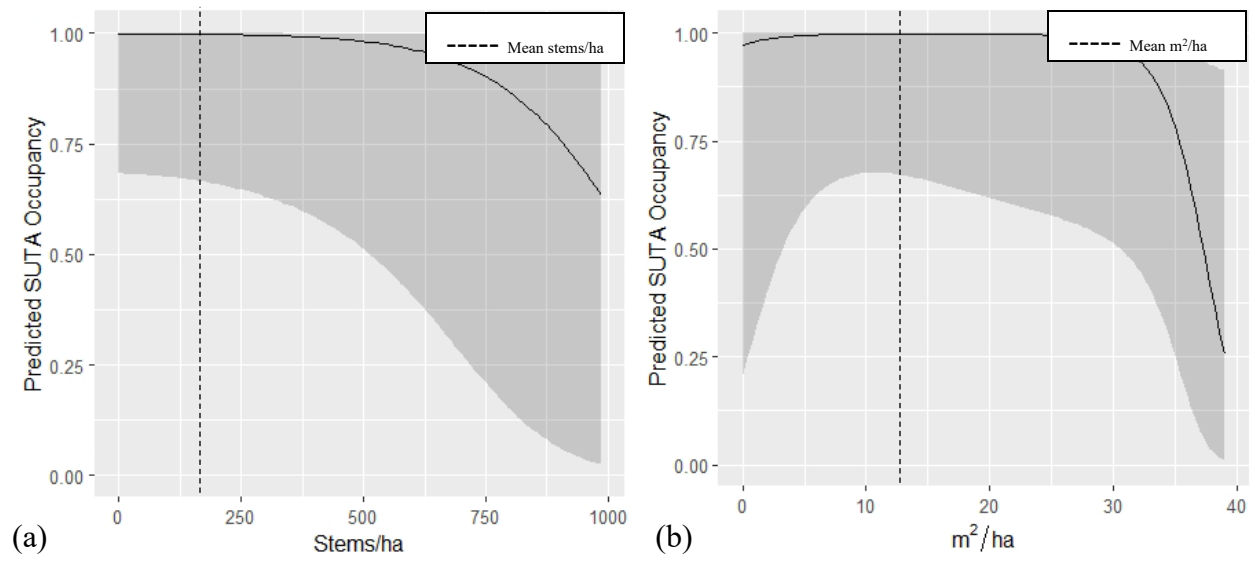


Figure 11. The predicted occupancy probability for summer tanager estimated across the range of hardwood stem density (a) and pine basal area (b) using the top model, Fort Bragg Military Installation, North Carolina, 2018.

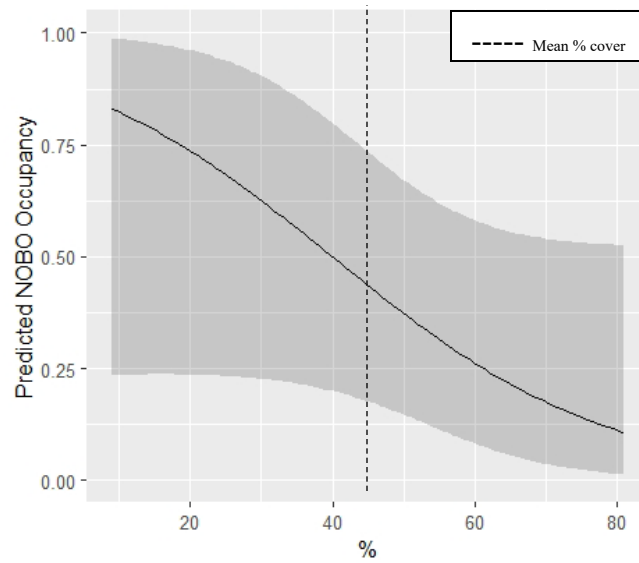


Figure 12. The predicted occupancy probability of northern bobwhite estimated across the range of pine canopy cover using the top model, Fort Bragg Military Installation, North Carolina, 2018.