A Bird's-Eye View of Young Longleaf Pine

by

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A thesis submitted to the Graduate Faculty of
Auburn University
In partial fulfillment of the
Requirements for the Degree of
Master of Science

Auburn, Alabama
May 1, 2021

Keywords: Occupancy, Mississippi, Partners for Fish and Wildlife,
Bachman's Sparrow, Prairie Warbler, Northern Bobwhite

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Abstract

Longleaf pine (*Pinus palustris*) forests are an endangered ecosystem and a primary focus for restoration in the US. Through the cost-share program Partners for Fish and Wildlife (PFW), the U.S. Fish and Wildlife Service (USFWS) assists private landowners in the southeastern US with longleaf pine planting. We evaluated stands enrolled in the Mississippi PFW program during the breeding seasons of 2018–2019 to determine whether landowners achieved USFWS avian conservation objectives. We detected very few focal songbirds (6 Bachman's Sparrows; *Peucaea aestivalis*), likely due to inadequate application of prescribed fire. In order to provide habitat for declining focal species, we recommend the program shift focus from stand establishment to stand maintenance. We also explored the effects of foraging behavior, nesting behavior, and average species weight on species occupancy probability at multiple spatial scales. Utilizing AICc model selection, we found differential occupancy probability for species could not be explained by these attributes.

Acknowledgments

I want to thank my professors for an amazing opportunity; the U.S Fish and Wildlife Service, Mississippi Department of Fish and Wildlife, and Auburn University School of Forestry and Wildlife Sciences for the funding and support to make this project possible, and my family and friends, without whom I would not have made it through.

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Abstract

The success or failure of habitat restoration programs to meet objectives is not often assessed. One such program, administered by the U.S. Fish and Wildlife Service through their cost-share program Partners for Fish and Wildlife (PFW), assists private landowners in the southeastern US with longleaf pine (*Pinus palustris*) planting. One objective of this program is to provide habitat for species like the Bachman's Sparrow (*Peucaea aestivalis*), which is reliant on fire-maintained longleaf pine forests. To assess this program's success, we conducted avian point counts and vegetation surveys in young longleaf pine stands enrolled in the Mississippi PFW program during the breeding seasons of 2018–2019. We surveyed 51 stands ($\geq$16 ha; $\leq$16 years) and conducted 194 point count surveys, observing >8,000 birds and 47 species. We detected only 6 Bachman's Sparrows in 3 stands at 4 points (5.8% of stands, 2.1% of points), indicating the stands are not providing habitat for this focal species, likely due to inadequate application of prescribed fire. Specifically, coverage of woody vegetation averaged 38%, herbaceous cover 39%, and canopy closure 70%. However, we detected Prairie Warblers (*Setophaga discolor*) in 37 stands (72%) and at 94 points (48%), and Northern Bobwhites (*Colinus virginianus*) in 43 stands (83%) and at 101 points (52%), indicating PFW are providing habitat for declining shrubland species. If providing habitat for grassland birds like Bachman's Sparrow continues to be a high-ranking objective for PFW stands in the Southeast, we recommend stricter requirements for landowner enrollment in the PFW program (e.g., agreements to maintain a burn interval of $\leq$2 years), as well as more assistance in meeting those requirements.

Introduction

Longleaf pine (*Pinus palustris*) dominated over 30 million ha of land across the pre-settlement southeastern United States, with an additional 7 million ha of longleaf pine present in mixed species stands (Frost 1993). These forests spanned from Virginia to eastern Texas (Kozlowski 2012). Today, longleaf pine only exists within 3% of its original range (Frost 1993), and longleaf pine ecosystems are classified as the third most endangered ecosystem in the U.S. (Noss and Scott 1995).

The decline in coverage of longleaf pine is largely due to conversion of land to other cover types (e.g., loblolly pine (*Pinus taeda*), agriculture) and fire suppression (Van Lear et al. 2005; Frost 2006). Without frequent, low-intensity fire, longleaf pine is quickly outcompeted by hardwood species or more aggressive southern pines, such as loblolly, slash (*P. elliotti*), and sand (*P. clausa*) pine (Glitzenstein et al. 1995; Brockway and Outcalt 2000). Low-intensity fire every 1–3 years has the added benefit of creating or enhancing an understory composed of native, fire-dependent grass and forb species, and minimizing the woody mid-story component (Peet and Allard 1993; Van Lear et al. 2005). The dominant grass species in this system are wiregrass (*Aristida stricta*) and bluestem grasses (*Andropogon* and *Schizachyrium* spp.). These species, along with longleaf pine needle litter in the understory, create a nearly continuous fuel bed that facilitates the spread of fire throughout the stand even in relatively moist, humid conditions, like those commonly present in the Southeast during the growing season.

Longleaf ecosystems provide habitat for about 100 bird species, 36 mammal species, and 170 species of reptiles and amphibians (NRCS 2020). Of these species, at least 29 are listed as either threatened or endangered by the United States Fish and Wildlife Service (USFWS). Notable species of conservation concern include the Red-cockaded Woodpecker (*Dryobates*

borealis), gopher tortoise (*Gopherus polyphemus*), and the eastern indigo snake (*Dymarchon couperi*). In order to conserve declining species within the longleaf pine ecosystem, many government recovery programs, that include both government agencies and the public, were established (NRCS 2020).

One such program, established by the USFWS in 1987, is Partners for Fish and Wildlife (PFW), which originally focused on wetland restoration on private lands (U.S. Fish and Wildlife Service 2020). More recently, this program has expanded to include other ecosystems that provide critical habitat for Federal Trust Species, including longleaf pine forests. The PFW program is implemented by state and federal biologists, and provides technical and financial assistance to private landowners interested in ecosystem restoration. To be eligible for participation, projects must meet local habitat and geographic focus area priorities. Specifically, projects must provide habitat for focal species, reduce fragmentation, complement activities on National Wildlife Refuge System lands, and/or create naturally self-sustaining systems (U.S Fish and Wildlife Service 2020).

Over the past 17 years, the PFW program has focused on restoring longleaf pine within the coastal plain region of Mississippi (U.S. Fish and Wildlife Service 2020) to provide habitat for declining longleaf pine-obligate songbird species, among others. The program provides the necessary technical and financial assistance for landowners to establish longleaf pine; however, landowners are responsible for any subsequent management. Research focused on other cost-share programs provides evidence cost-share programs benefit avian species (Riffell et al. 2008; Sieges et al. 2014; Kaminski and Davis 2014; Natural Resources Conservation Service 2015; Osborne et al. 2012; Schroeder and Vander Haegen 2011), but others found that their effectiveness was unclear or not fully understood (Haufler et al. 2005; Shackelford et al. 2019,

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others). Longleaf pine stands planted under the PFW program have not been evaluated for their ability to provide habitat for declining avian species.

While replanting vegetation is sometimes the first step in ecosystem restoration, further management actions are often required, particularly in disturbance dependent systems. However, like many cost-share programs, the PFW program is not responsible for stand management after planting; it is the landowner's responsibility to actively manage for restoration objectives. As a consequence, there is some evidence to suggest that landowners participating in cost-share programs rarely adhere to management guidelines (Lee et al. 2020; Yeiser et al. 2020), and therefore are not likely meeting cost-share program objectives. Overall, our goal was to evaluate the efficacy of privately owned and managed restoration areas at providing habitat for breeding birds. There are many plants and animals that declined alongside longleaf pine in the 1800s. Longleaf pine dependent species, many of which require a grass-dominated understory perpetuated by frequent fire, are of particular interest to biologists because their presence is indicative of desired ecological conditions. Utilizing a suite of longleaf pine associated species, including Bachman's Sparrow (*Peucaea aestivalis*), Prairie Warbler (*Setophaga discolor*), and Northern Bobwhite (*Colinus virginianus*), we evaluated the success of longleaf pine restoration within the PFW cost-share program. We also conducted vegetation surveys within each stand to identify vegetative conditions associated with the presence/absence of our focal species.

Methods

Breeding Season Point Counts

We used stratified random sampling to select study stands from a list of 144 PFW stands ≥16 ha in area. We selected stands ≥16 ha as this was the smallest stand size that could fit four point count survey locations with the desired buffer distance between them (200 m). Standard

point-count protocol is 250 m (Ralph et al. 1995); however, we chose to use 200 m because of stand size limitations in our oldest age class. We stratified stands into three age classes (2–6, 7–13, and 14–17 years) to account for potential differences in vegetation among age classes related to canopy closure, burn history, and time since site preparation. We sampled a similar number of stands in each age category to the extent feasible given the number of available stands per age class; we sampled 17 stands 2–6 years old, 22 stands 7–13 years old, and 12 stands 14–17 years old. Average stand size was 46 ha (range 20–166 ha). Due to irregular shape of stands, we manually placed potential points within each stand using ArcMap 10.4.1, utilizing property boundaries as denoted by the USFWS. We randomly selected a subset of 4 points for stands of adequate size to contain >4 points. In instances where we arrived at the sampling point and found that the point was unsuitable (i.e., not longleaf pine), we dropped the point and randomly selected a replacement point, if available. Therefore, some stands contained 1–4 point count locations. We completed 194 total point counts during 2018–2019 breeding seasons (141 points in 2018; 165 points in 2019).

Based on the breeding season in the southeastern U.S., we conducted point counts between 10 May and 9 July 2018, and 2 May and 9 July 2019. Each year we sampled points twice during the field season, once in the first half of the field season (Days 1–30) and once during the second half of the field season (Days 30–60) to account for potential temporal variation in breeding among species. We conducted point counts from sunrise to 10:00 AM. We identified species by sight, sound, or both. We conducted 10 min point counts at each point, recording each individual or group detected to species for initial detections, and re-sighting individuals or groups every 2 minutes. We did not conduct point counts if there was rain in the area or if wind was higher than a 4 on the Beaufort scale (Beaufort 1805).

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Vegetation Surveys

We sampled vegetation at all point count locations using the center of the point as the mid-point on a 20-m transect (Tucker et al. 2004). We randomly established the azimuth of each transect using a random number generator. Along each transect we placed a 4-m pole at 1-m intervals and recorded the height of all vegetation that touched the pole at 0.05-m height intervals. Specifically, we recorded the height at which 80% of each plant's biomass reached (e.g., if 80% of a plant's biomass reached to 1 m, but a single stem extended to 1.5 m, the height was recorded as 1 m). We identified each plant intercepted to growth form (e.g., grass, forb, or shrub). We also used a spherical densitometer to measure canopy closure at 5-m increments along each transect. We utilized a 10-factor wedge prism to determine pine and hardwood basal area at each transect mid-point.

Study Area

We conducted our research in privately owned longleaf pine stands within the Lower Coastal Plain and Coastal Flatwoods of Mississippi in the following counties: Lamar, Forrest, Franklin, Greene, Hancock, Lawrence, Marion, Pearl River, Perry, Rankin, Simpson, Smith, George, Jones and Stone (Figure 1.1). Soils on our study areas were predominantly sandy and wet with low native fertility, although some were on sand hills/ridges (Kushla and Oldham 2017). Average annual rainfall was 127–178 cm and mean average temperature was 18–20 °C (PRISM Climate Group 2015). All stands were planted using containerized longleaf pine seedlings at a density of 1,363 seedlings/ha from 2002–2018 with the assistance of PFW. We sampled 51 stands that met our criteria, 39 during 2018 and 43 during 2019. We sampled 31 of the stands during both years. Sixteen stands were 2–6 years old, 22 were 7–11 years old, and 13

were 12–16 years old. Average stand size was 47.08 ha. Pine basal area averaged 6.74 m^2/ha and

hardwood basal area 1.50 m^2/ha. Average canopy closure within the stands was 70%.
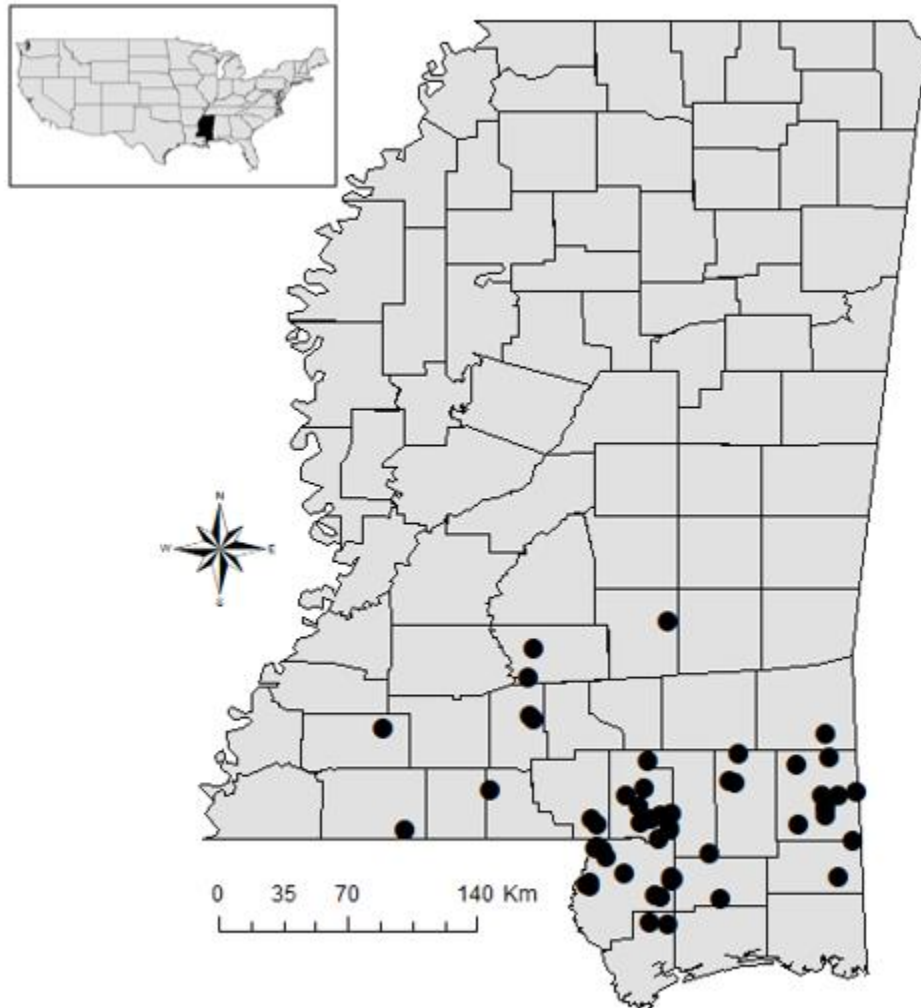
Figure 1.1. PFW longleaf pine stand locations in southern Mississippi where we conducted avian

point count and habitat surveys during 2018-2019.

Analysis

Due to very low detection of Bachman's Sparrows (6 individuals), we summarized observed occurrences at the stand (# of stands with detections) and point (# of points occupied across all stands) levels across both 2018 and 2019. For each point count location, we calculated percent cover of herbaceous and woody vegetation by dividing the number of recorded hits of each growth form by the total number of hits along the intercept. We calculated average woody vegetation height by summing the heights of all woody vegetation along the transect and dividing by the number of woody vegetation hits along the transect. We calculated stand-level averages by averaging across point-level values within the stand.

Results

We completed 194 total point counts during 2018–2019 and detected only 6 individual Bachman's Sparrows (5.8% of stands, 2.1% of points) in 3 PFW longleaf pine stands. We detected Prairie Warblers in 37 stands (72%) and at 94 points (48%). We detected Northern Bobwhites in 43 stands (83%) and at 101 points (52%). Stands in which we detected Bachman's Sparrows had lower average woody vegetation height and coverage, as well as greater average herbaceous coverage, compared to the average stand (Figure 1.2, A&C). Average stand hardwood basal area was 1.50 m^2/ha, whereas stands with Bachman's Sparrows present contained no hardwood understory component (Figure 1.2, B)

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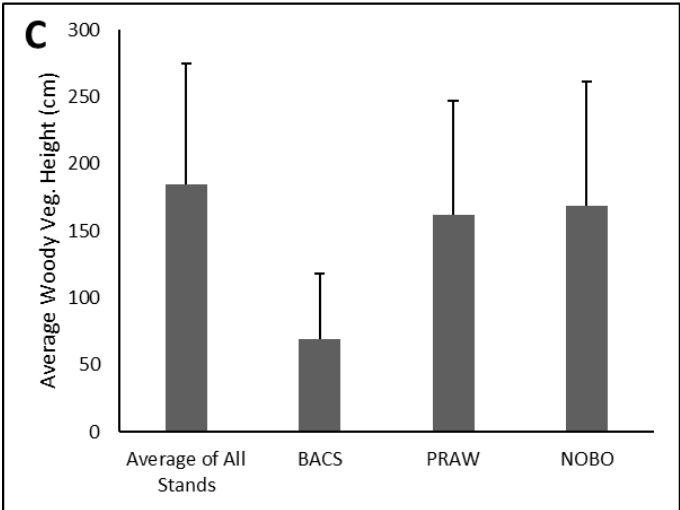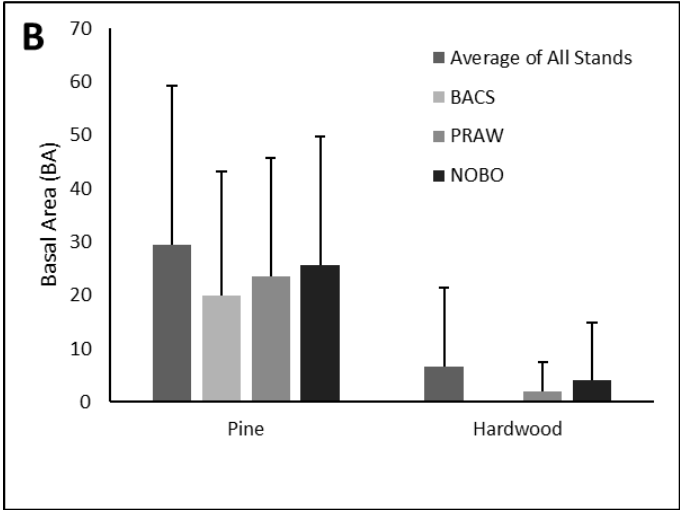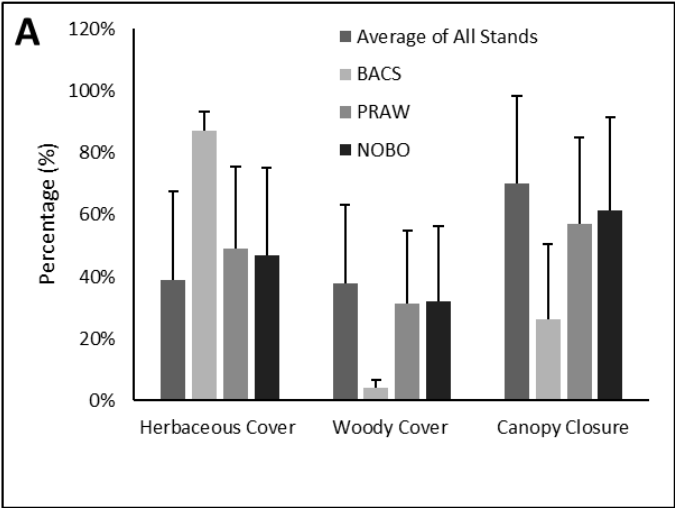
Figure 1.2. Percent herbaceous and woody cover and canopy closure (A), basal area (m^2/ha; B), and average woody vegetation height (C) for stands containing Bachman's Sparrows (*Peucaea aestivalis*; BACS), Prairie Warblers (*Setophaga discolor*; PRAW), and Northern Bobwhites (*Colinus virginianus*; NOBO) in 51 longleaf pine (*Pinus palustris*) stands in Mississippi during the 2018–2019 avian breeding seasons. Error bars represent standard errors.

Discussion

We detected few Bachman's Sparrows or other grassland species during our study, indicating that PFW forests may not have been restored to the desired ecological conditions. Given that most of our stands were characterized by extensive coverage of relatively tall woody plants and low coverage of herbaceous plants, this was not surprising. Previous research indicates Bachman's Sparrows prefer nesting in areas with greater forb and grass cover and lower densities of trees, shrubs, and mid-story vegetation (Haggerty 1998; Plentovich et al. 1998), which describes the stands where Bachman's Sparrows were present in our study. Nonetheless, we detected declining shrub/scrub species, specifically Northern Bobwhite and Prairie Warblers, in a number of the stands we sampled (>70% of stands surveyed). Greene et al. (2019) reported that Bachman's Sparrows prefer midstory shrub coverage of 0–20% and herbaceous plant coverage of 40–80%, Northern Bobwhites prefer midstory shrub coverage of 10–40% and herbaceous plant coverage of 20–80%, and Prairie Warblers prefer midstory shrub coverage of 10–50% and herbaceous plant coverage of 25–50%; our results fell within these established patterns.

Although we were unable to obtain accurate prescribed fire histories for our stands, presence of shrub/scrub species indicates they were not treated with prescribed fire at the regular 1–2 year intervals required to promote grassland conditions (Glitzenstein et al. 2003). Fire is also

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important to Northern Bobwhites, which prefer burn rotations of 2–3 years (Snyder 1991; Burger 2009), and Prairie Warblers colonize stands 2 years after an area is burned (Nolan 1978; Engstrom et al. 1984). Engstrom et al. (1984) also noted that Prairie Warblers would leave an area a few years after shrub layer development. Without continued disturbance at the proper intervals, habitat suitability is highly ephemeral for pine-grassland and shrub/scrub species (Conner and Dickson 1997; Greene et al. 2019), and a difference of only 1–2 years in fire return interval can shift bird species assemblages.

While the almost complete absence of Bachman's Sparrows in our stands was likely the result of stand burn history, other potential explanations exist. One is the lack of available source populations. We did not attempt to locate source populations near our study areas, so we cannot be sure of their presence or absence. However, preferred vegetation characteristics for Bachman's Sparrows are well established (Wilson et al. 1995; Haggerty 1998; Plentovich et al. 1998; Tucker et al. 1998, 2004, 2006; Provencher et al. 2002; Allen et al. 2006; Cox and Jones 2007, 2009; Jones et al. 2013; Winiarski et al. 2017; Fish et al. 2018), and based on the average vegetation characteristics of our sampled stands, it is apparent that the majority of stands in our study were unlikely to support Bachman's Sparrows even if colonization were possible.

Considering the importance of private land in connecting fragmented habitat for breeding populations and facilitating dispersal (Jones et al. 2017), and the fact that most of the United States is privately owned, successful restoration of wildlife habitat on private lands is critical. Specifically, when it comes to longleaf pine, it is estimated that 80% of the targeted increase in longleaf pine forest coverage will need to occur on private land (NRCS 2020).

The Partners for Fish and Wildlife program is not the only government-funded program focused on longleaf pine restoration on private lands. For example, America's Longleaf

Restoration Initiative coordinates partnerships among private landowners, forest industry, state and federal agencies, conservation groups, and researchers. Since 2005, the combined efforts of these groups have increased coverage of longleaf pine forests from 1.4 to nearly 1.9 million ha (NRCS 2020). Unfortunately, in spite of this success, grassland birds are continuing to decline in North America, and Rosenberg et al. (2019) estimated these species have declined by 53% since 1970.

Evaluations of several restoration programs provide some potential insight. A study conducted on young longleaf pine planted under the Longleaf Pine Initiative noted that stands were rarely managed as required by the program, leading to potentially higher levels of non-native vegetation (Lee et al. 2020). Additionally, agricultural fields enrolled in a grassland conservation program found that approximately 30% of landowners participating in the cost-share program did not adhere to management guidelines (Yeiser et al. 2020). Another study in the Central Hardwoods Bird Conservation Region did not find beneficial effects of cost-share conservation efforts on focal grassland songbird species (Lituma and Buehler 2020). Therefore, while there may be 1.9 million ha of longleaf pine planted in the U.S. since 2005, the stands are not necessarily managed to meet planting program conservation objectives. Accordingly, Yeiser et al. (2020) recommended that agencies administering private land conservation need to dedicate significant resources to ensuring landowners are following best management practices for wildlife.

There are many other cost-share programs available to landowners, including the Conservation Reserve Program (CRP), Environmental Quality Incentives Program, Wetland Reserve Program, Wildlife Habitat Incentives Program, and Working Lands for Wildlife, to name a few. While there is evidence these cost-share programs benefit avian species (Riffell et

al. 2008; Sieges et al. 2014; Kaminski and Davis 2014; Natural Resources Conservation Service 2015; Osborne et al. 2012; Schroeder and Vander Haegen 2011), some studies found that their effectiveness is unclear or not fully understood (Haufler et al. 2005; Shackelford et al. 2019, others). For example, many studies have shown a positive relationship between CRP land and wildlife species occupancy, including birds (Johnson and Schwartz 1993; Riffell et al. 2008). However, a positive relationship is not surprising given that CRP lands are often planted for general purposes, without focal wildlife species in mind, and later assessed for their benefits to wildlife. Defining such programs as successes or failures is difficult when objectives are so broadly defined (Wood 2018). In contrast, it is easier to assess efficacy of programs like PFW that focus on a single or small number of wildlife species at the outset, highlighting the importance of establishing explicit management goals and monitoring programs based on focal species habitat requirements prior to program implementation. Additionally, with mid-rotation management so important for disturbance-dependent species, it is imperative that evaluations of cost-share programs are conducted regularly.

While the PFW stands we examined are providing habitat for declining songbirds such as Prairie Warblers and Northern Bobwhites, these species have different habitat requirements and greater tolerance for shrub/scrub cover than Bachman's Sparrows. The low number of Bachman's Sparrow detections within our stands and the relatively high number of Northern Bobwhite and Prairie Warbler detections emphasizes the importance of implementing precise, ongoing management when trying to restore disturbance-dependent ecosystems where 1-2 year differences in fire frequency can shift species assemblages. Post-planting monitoring and management may be more important than strict stand establishment criteria when it comes to successfully restoring longleaf pine forests and the associated wildlife habitat (Wheeler et al.

2020). Our research provides insight for biologists, wildlife managers, and private landowners alike by highlighting the existing conditions within these stands. For state and federal biologists, our research should impact the execution of the program; we recommend revising contract conditions to include agreements to adhere to necessary post-establishment management practices (e.g., prescribed fire), as well as working with previously enrolled landowners to provide additional assistance. Our evaluation of the PFW cost-share program highlights an issue common to many ecosystems, for which initial site preparation and planting operations are not enough; continuous management is necessary for restoration.

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Chapter 2. Multi-scale occupancy of avian species within young longleaf pine forests

Abstract

Understanding the effects of scale on species occupancy is critical for wildlife conservation. For example, low-intensity prescribed fire in longleaf pine (*Pinus palustris*) forests affects plant community composition and structure at different spatial scales, and it is important for avian ecologists to understand what drives species occupancy at these scales. However, longleaf pine systems are not well-represented in previous multi-scale occupancy studies. Therefore, we examined breeding bird occupancy at two scales in young longleaf pine stands in Mississippi during the breeding seasons of 2018–2019. We estimated occupancy using Bayesian hierarchical single-species dynamic models, with occupancy and occupancy dynamics modeled at the stand and point scales. We utilized AICc model selection to distinguish among a set of possible models describing the relationship between species occupancy probability (ψ and θ), foraging behavior, nesting behavior, average species weight, and any interaction between foraging and nesting behavior. Expecting to observe differing patterns of occupancy at the local (point) and landscape (stand) scale, we surveyed 51 stands ($\geq$16 ha; $\leq$16 years) and conducted 194 point count surveys, observing $\geq$8,000 birds and 47 species. Contrary to our expectations, differential occupancy probability for avian species in young longleaf pine stands could not be explained by nesting and foraging behaviors or average species home range size. Analyses of stand vegetation characteristics revealed that stands were fairly homogeneous. The lack of identifiable patterns in foraging and nesting guilds may be a product of stand homogeneity or guild assignment; however, we believe that our analyses should be repeated to determine if our explanatory

variables could account for variance in occupancy probability within other longleaf pine forests or systems.

Introduction

Wildlife space use and resource selection are multi-scale processes, ranging from the broad-scale geographical range of a species to the fine-scale foraging and movement decisions of an individual (Wiens 1973; Johnson 1980). These multi-scale patterns of selection and occurrence are probably most frequently documented for avian species; both highly detectable and mobile, avian species allow for research at great spatial scales. Starting with Wiens (1973), numerous studies document scale-dependent resource selection by birds (e.g., Saab 1999, Hennings and Edge 2003, Perkins et al. 2003, Pavlacky et al. 2012, Lipsey et al. 2017, McGrath et al. 2017, Gilbert and Ferguson 2019, Stevens and Conway 2020, and many others), demonstrating the importance of hierarchical approaches when developing conservation plans for avian species.

Patterns of occurrence at different scales has long been of interest to ecologists: traditionally, ecologists often assumed that processes occurring at local spatial scales were the most important and, therefore, determined overall distribution and occupancy patterns (Saab 1999). Various studies indicate that local features can affect avian guilds and species within those guilds (Perkins et al. 2003; Lee and Carroll 2014; Hannah et al. 2017; Lipsey et al. 2017), but many find that broader scale landscape features are the best predictors of avian species distribution and frequency of occurrence (Saab 1999; Dreitz et al. 2017; Hagen et al. 2020). However, there are many studies that indicate both scales are important to species occupancy. For example, Hannah et al. (2017) found that only landscape-scale factors affected Northern Bobwhite (NOBO; *Colinus virginianus*) occupancy, while both local- and landscape-scale

factors were significant predictors of Red-cockaded Woodpecker (RCW; *Dryobates borealis*), Bachman's Sparrow (BACS; *Peucaea aestivalis*), and Brown-headed Nuthatch (BHNU; *Sitta pusilla*) occupancy. Northern Bobwhite are shrubland birds, while RCW, BACS, and BHNU are open woodland species (Cornell University 2019), possibly indicating that Hannah et al. (2017) observed drivers of different patterns of occurrence between habitat association guilds. Another study, conducted by Lee and Carroll (2014), found that while forest interior species responded only to landscape-scale features, pine-grassland species occupancy was driven by local-scale features; indicating that, depending on ecological traits such as habitat guild association, observations at particular spatial scales can be differentially insightful. Regardless of the determined scale of importance, the results of the aforementioned studies indicate that occupancy models assessing hierarchical spatial scales could improve our understanding of the complex interactions among guilds and species (Pavlacky et al. 2012; Lipsey et al. 2017).

Multi-scale patterns are especially relevant to fragmented landscapes, such as many forested systems, where fragmentation can result in major losses in bird diversity (Robinson et al. 1995; Hermosilla et al. 2019; Liu et al. 2019; Bryan-Brown et al. 2020; Rolstad 1991). In the southeastern United States longleaf pine (*Pinus palustris*) forests, a fire-maintained, disturbance-based ecosystem of great conservation concern, is a prime example of fragmented habitat. However, large multi-scale occupancy studies on birds are rare in fire-maintained systems: we only found two studies that addressed the entire avian community (e.g., Russell et al. 2009, ponderosa pine (*Pinus ponderosa*); Dreitz et al. 2017, prairie). Further, few multi-scale occupancy studies in longleaf pine forests have included species other than Red-cockaded Woodpeckers (*Picoides borealis*) and Northern Bobwhites (*Colinus virinianus*). While Lee et al. (2020) did evaluate the effects of two restoration programs, the Longleaf Pine Initiative (NRCS

2020) and the Bobwhite Quail Initiative (NBCI 2020), on taxonomic and functional diversity of grassland and scrub/shrub species, they were unable to identify patterns in abundance among grassland and scrub/shrub species in young longleaf pine stands at local and landscape scales. However, they found a positive relationship between functional divergence and the amount of shrub vegetation at the landscape scale, which indicated some degree of niche differentiation as amount of shrub cover increased. Further research is necessary in order to identify potential spatial patterns of occupancy among avian species.

Our objective was to determine if occupancy probability among avian species differed at hierarchical spatial scales (stand ~20-166 ha; point = 3.14 ha), and if so, determine if species belonging to the same functional guilds exhibit similar spatial occupancy patterns. Information on patterns among avian functional guilds could inform management decisions for species under-represented within research and provide insight on the effects of management decisions on species with shared characteristics.

We predicted that different bird species would exhibit distinct patterns of occupancy at the point and stand scales and, utilizing ratios of occupancy probabilities at each scale, we could summarize a species or guild's usage of space. We expected functional guilds, such as foraging and nesting guilds, to have explanatory power, as previous studies found that functional guilds had different responses to changes in land-use, vegetation structure, and management (Goijman et al. 2015; Azeria et al. 2011; Raynor et al. 2017; Newbold et al. 2013; Bregman et al. 2014; Wells et al. 2012; Kroll et al. 2017; Ding et al. 2019 and many others). For example, we predicted that some species, such as declining grassland species (e.g. BACS, EAME, etc.), would exhibit greater point-level than stand-level occupancy probability because of variation in stand-level management. Additionally, we predicted that average species weight would account for

some variation in occupancy probabilities due to the relationship between survey unit size, home

range size (Jenkins 1981; Ottaviani et al. 2006; Wells et al. 2012), and accuracy of occupancy

estimates (Hayes and Monfils 2015; Rota et al. 2009; Ramsey et al. 2015). Understanding the

relationship between species occupancy probability estimates and the spatial scale at which it is

assessed could inform future avian survey methodology, with the potential for more accurate

species occupancy estimates. Therefore, because multi-scale occupancy studies can provide

information on avian distribution relevant to conservation, and because longleaf pine forests are

not well-represented in previous work, we examined breeding bird occupancy at two spatial

scales in young, planted longleaf pine stands in Mississippi.

Study Area

We conducted our study across privately owned longleaf pine stands within the Lower

Coastal Plain and Coastal Flatwoods of Mississippi in the following counties: Lamar, Forrest,

Franklin, Greene, Hancock, Lawrence, Marion, Pearl River, Perry, Rankin, Simpson, Smith,

George, Jones and Stone (Fig. 2.1). Soils on our study areas were predominantly sandy and wet

with low native fertility, although some were on sand hills/ridges (Kushla and Oldham 2017).

Average annual rainfall was 127–178 cm and mean average temperature was 18–20 °C (PRISM

Climate Group 2015). All stands were planted using containerized longleaf pine seedlings at a

density of 1,363 seedlings/ha from 2002– 2018 with the assistance of PFW. We used stratified

random sampling to select study stands from a list of 144 PFW stands ≥16 ha in area. We

selected stands ≥16 ha as this was the smallest stand size that could fit four point count survey

locations with the desired buffer distance between them (200 m). Standard point-count protocol

is 250 m (Ralph et al. 1995); however, we chose to use 200 m because of stand size limitations in

our oldest age class. We stratified stands into three age classes (2–6 years, 7–13 years, and 14–17

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years) to account for potential differences among age classes related to stand development (e.g., canopy closure). We sampled 51 stands that met our criteria, 39 during 2018 and 43 during 2019. We sampled 31 of the stands during both years. Sixteen stands were 2–6 years old, 22 were 7–11 years old, and 13 were 12–16 years old. Average stand size was 47.08 ha. Pine basal area averaged 6.74 m^2/ha and hardwood basal area 1.50 m^2/ha. Average canopy closure within the stands was 70%.
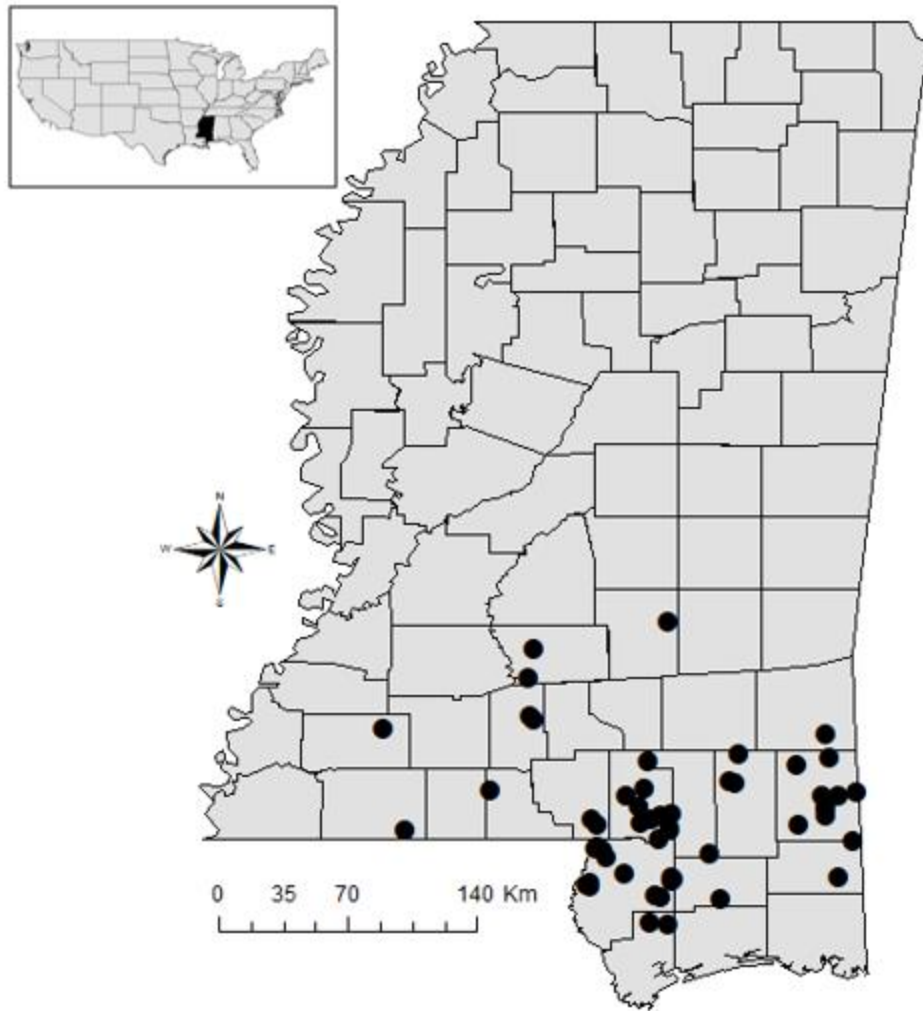
Figure 2.1. Privately owned longleaf pine (*Pinus palustri*s) stand locations in southern

Mississippi where we conducted avian point count surveys during the breeding seasons (May–

July) of 2018–2019.

Methods

Breeding Season Point Counts

We established 1–4 point count locations in each stand. All points were placed ≥200-m

apart and ≥100-m from the stand edge. Due to irregular shape of stands, we manually placed

potential points within each stand in ArcGIS 10.3.1 (ESRI 2017). If a stand was large enough to

accommodate >4 points, we randomly selected 4 of those points. When initial survey visits

indicated that a selected point was not in longleaf pine cover (e.g., riparian, loblolly pine, or

flooded), we dropped the point and selected a replacement point during that sampling year or the

following. We surveyed 39 stands (141 points) in 2018 and 43 stands (165 points) in 2019.

Overall, we surveyed 51 stands (31 stands both years) and 195 points.

We determined occupancy of avian species using breeding season point counts (Ralph et

al. 1995) during a 60 day period each spring/summer (10 May–9 July 2018, 2 May–9 July 2019).

We sampled most points twice during the field season, approximately 30 days apart, to account

for potential temporal variation in breeding among species. Some points could only be sampled

once due to difficulties with weather or access. We conducted point counts from dawn until 10

AM. Specifically, we conducted 10-min point counts divided into five, 2-min intervals (bin). We

recorded each bird in the time bin when it was initially detected, as well as any subsequent time

bins during which it was re-sighted. We did not conduct point counts when it was raining or if

wind was >4 on the Beaufort scale due to noise interference with song or call identification

(Beaufort 1805).

Vegetation Surveys

We sampled vegetation at all point count locations using the center of the point as the

mid-point on a 20-m transect (Tucker et al. 2004). We randomly established the azimuth of each

transect using a random number generator. Along each transect we placed a 4-m pole at 1-m intervals and recorded the height of all vegetation that touched the pole at 0.05-m height intervals. Specifically, we recorded the height at which 80% of each plant's biomass reached (e.g., if 80% of a plant's biomass reached to 1 m, but a single stem extended to 1.5 m, the height was recorded as 1 m). We identified each plant intercepted to growth form (e.g., grass, forb, tree, shrub, etc.). We used a spherical densitometer to measure canopy closure at 5-m increments along each transect.

Analysis

We estimated occupancy using Bayesian hierarchical single-species dynamic occupancy models, with occupancy and occupancy dynamics modeled at the stand and point scales (Pavlacky et al. 2012, MacKenzie et al. 2002, Green et al. 2019). We treated each 2-minute bin within a single point count as a replicate survey within a visit. We summarized species detection status (i.e., detected, not detected) for each two-minute interval per point-visit, producing a 5-digit encounter history for each 10-minute point count for each species. For occupancy and subsequent analyses, we included species with ≥ 5 detections across all visits, omitting species with life history characteristics that make occupancy probability difficult to estimate with our point count protocol, such as currently migrating, nocturnal, or raptor species.

Consistent with previous multi-scale studies, we modeled stand-level occupancy (ψ) and point-scale occupancy conditional on stand-scale occupancy (θ) (Nichols et al. 2008). In addition, we examined ratios of point:stand scale occupancies, as ratios of occupancy at these scales can provide information on species distributions useful to managers. For example, if a species is common across the landscape and in occupied stands, the estimated local occupancy probability divided by the landscape occupancy probability would be close to or equal to 1 (θ / ψ

= 1). However, $\theta / \psi = 1$ can also occur when a species is rare or absent across the landscape and, when found, locally isolated and rare. When a species is common across the landscape but isolated where found, we see the pattern $\theta / \psi < 1$. Finally, when a species is regionally rare but locally abundant, we would see the pattern $\theta / \psi > 1$.

To examine multi-scale occupancy, we used a $\psi_1()\theta_1()\gamma()\varepsilon()$ parameterization (Pavlacky et al. 2012), with closure assumed only within individual point-count visits. We modeled stand and conditional point occupancy probabilities explicitly for the first visit in 2018, with initial stand occupancy probability modeled as homogeneous across stands. We modeled initial conditional point occupancy probability as a function of an intercept plus a random effect of stand.

We modeled stand and conditional point-scale extinction and colonization probabilities for the subsequent 3 intervals (first to second 2018 visits; second 2018 visit to first 2019 visit, and first to second 2019 visits). Each dynamic parameter (extinction, colonization) was assumed constant for the two within-year intervals but different for the between-year interval. Based on the short-term nature of the study, we did not model variability in these dynamic parameters.

Variability in detection probability was modeled as a function of fixed effects of observer (for species with >30 detections) visit (for species with >35 detections), and height of woody vegetation at a point count location (for species with ≥20 detections), a within-point-visit "recapture" fixed effect (for species with ≥10 detections), and a random effect of stand x year (for species with >35 detections). Thus, with decreasing sample size and decreasing information for modeling detectability, the detectability model was simplified by progressively dropping variables that appeared less important based on results from species with greater sample sizes. All occupancy and detectability parameters were modeled on the logit scale.

We conducted analyses with software JAGS through R package rjags (Plummer et al. 2019), using Markov chain Monte Carlo (MCMC) to estimate posterior distributions for model parameters. For each analysis, 3 MCMC chains were run, and convergence evaluated with the Gelman-Rubin statistic. The MCMC analyses included an adaptive phase of 10,000-50,000 iterations, an updating phase of 20,000 to 200,000+ iterations, and post-convergence sampling of 20,000 to 50,000+ iterations, with data sparsity and ease of convergence affecting the number of iterations at each phase as we monitored convergence for each species. Prior distributions included non-informative [Uniform(0,1)] intercept parameters on the probability scale and half-normal (positive only) distributions for random effects logit-scale variance parameters with scale parameters specified to be weakly informative so as to avoid sampling extremely high values in the prior distributions. We formed posterior distributions for derived variables of interest for each species, including overall average stand occupancy (estimated as the average of the finite-sample visit-specific estimated stand occupancy proportions), average conditional point occupancy (estimated as the average conditional finite-sample conditional point occupancy proportion), and the ratio of the two averages (point:stand). We report the posterior median and 95% credible interval based on the sampled posterior distributions.

To examine cross-species patterns, we report the average of the species-specific medians by nesting and foraging guilds. We based our nesting and foraging guilds assignments on Cornell University's bird guide (Cornell University 2019). To determine if there was any relationship between species home range size and occupancy probability at either scale, we utilized average species weight (Dunning 2007) as a proximate metric, since there is a positive relationship between average home range size and species weight (Jenkins 1981).

We used species-specific medians as response variables for linear analysis of covariance. Specifically, we utilized AICc model selection (Burnham and Anderson 2002) to distinguish among a set of possible models describing the relationship between species occupancy probability (ψ and θ), foraging behavior, nesting behavior, average species weight, and any interaction between foraging and nesting behavior (Mazerolle 2020; Barton 2011). We pooled some guilds to eliminate guilds with low numbers of species. Specifically, hovering and fly-catching guilds were pooled in the aerial forager guild, and the human structure nesting guild was pooled with the cavity nesting guild.

To examine whether patterns of variation in selected vegetation structure variables could aid interpretation of occupancy patterns, we used linear mixed-effects models (R package lme4) to analyze variation in herbaceous cover, woody cover, and woody height (Bates et al. 2015). For each variable, we had year-specific estimates of point-level values. We fit a model with no fixed-effects other than the intercept, and included a year:stand random effect, thus partitioning total variability between among-stand variation and other sources of variation (largely within-stand spatial and measurement variation).

Results

We detected 8,055 birds of 47 species during 2018–2019 (Appendix 1). Of those species, 22 were ground foraging, 15 foliage gleaning, 5 aerial foraging, and 5 bark foraging. By nesting guilds, 16 were tree nesting, 13 shrub nesting, 11 cavity nesting, and 7 ground nesting. Yellow-breasted Chat (*Icteria virens*), a foliage-gleaning, shrub-nesting bird, was the species most often observed, comprising 10.5% (846 of 8,055) of total observations.

Several species, including Northern Cardinal (*Cardinalis cardinalis*), Common Yellowthroat (*Geothlypis trichas*), Eastern Towhee (*Pipilo erythrophthalmus*), and Yellow-

breasted Chat had high stand occupancy (Figures 2.2–2.3), where $\psi > 0.9$. Northern Cardinals (θ = 0.86) and Yellow-breasted Chats (θ = 0.83) were the species closest to exhibiting the occupancy pattern $\theta/\psi = 1$ (Figures 2.4–2.5). All other species exhibited the occupancy pattern $\theta/\psi < 1$. We found no species that exhibited the occupancy pattern $\theta/\psi > 1$.

Variance caused by differences in vegetation structure within stands was greater than variance in vegetation structure among stands (Figure 2.6). The best-fit models for our AICc model selection indicated that variation in stand, point, and point:stand occupancy among species could not be explained by guild or species weight (Figures 2.2–2.5, 2.7–2.9). At all occupancy scales the intercept only (null) models were the best fit (Table 2.1). However, for stand level occupancy variation the "Foraging" model ($\Delta AICc = 0.84$) was included in the confidence set of models and for point:stand occupancy variation the "Nesting" model ($\Delta AICc = 1.34$) was included in the confidence set of models.

Figure 2.2. Stand level (ψ) occupancy probabilities for avian species, by nesting guild, in young longleaf pine stands in Mississippi during the 2018–2019 avian breeding seasons. Species are indicated by banding code (see Appendix 1) and are ordered from left to right by increasing average weight.

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Figure 2.3. Stand level (ψ) occupancy probabilities for avian species, by foraging guild, in young longleaf pine stands in Mississippi during the 2018–2019 avian breeding seasons. Species are indicated by banding code (see Appendix 1) and are ordered from left to right by increasing average weight.

Figure 2.4. Point level (θ) occupancy probabilities for avian species by nesting guild in young longleaf pine stands in Mississippi during the 2018–2019 avian breeding seasons. Species are indicated by banding code (see Appendix 1) and are ordered from left to right by increasing average weight.

Figure 2.5. Point level (θ) occupancy probabilities for avian species by foraging guild in young longleaf pine stands in Mississippi during the 2018–2019 avian breeding seasons. Species are indicated by banding code (see Appendix 1) and are ordered from left to right by increasing average weight.

Figure 2.6. Variance in vegetation measurements in young longleaf pine stands in Mississippi surveyed during the 2018–2019 avian breeding seasons. The dark grey represents among-stand variance and the light grey is other sources of variance (mostly within stand variance).
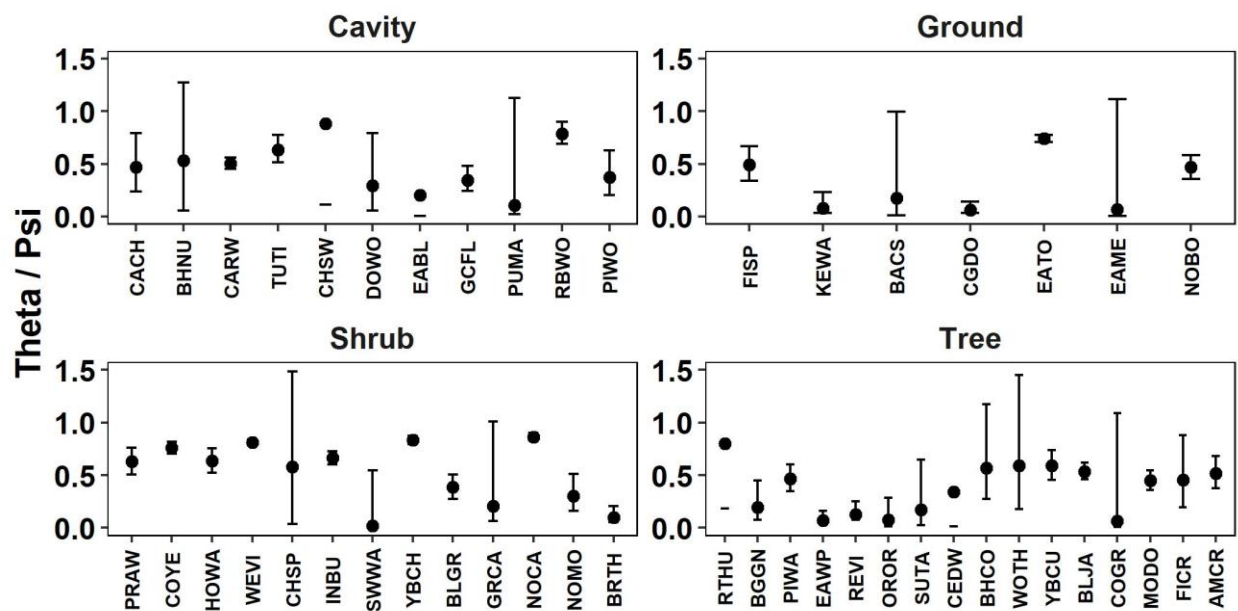
Figure 2.7. Multi-scale occupancy probability ratios for avian species by nesting guild in young longleaf pine stands in Mississippi during the 2018–2019 avian breeding seasons. Psi (ψ) represents stand level occupancy probability, and Theta (θ) represents point level occupancy probability. Species are indicated by banding code (see Appendix 1) and are ordered from left to right by increasing average weight.
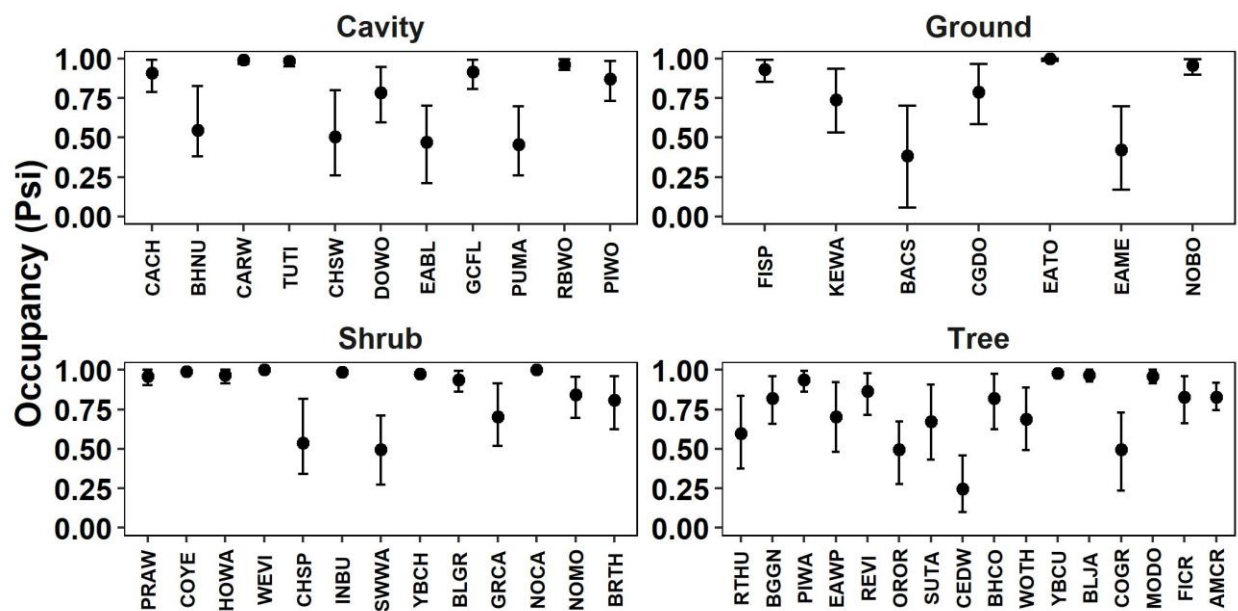
Figure 2.8. Multi-scale occupancy probability ratios for avian species by foraging guild in young longleaf pine stands in Mississippi during the 2018–2019 avian breeding seasons. Psi (ψ) represents stand level occupancy probability, and Theta (θ) represents point level occupancy probability. Species are indicated by banding code (see Appendix 1) and are ordered from left to right by increasing average weight.
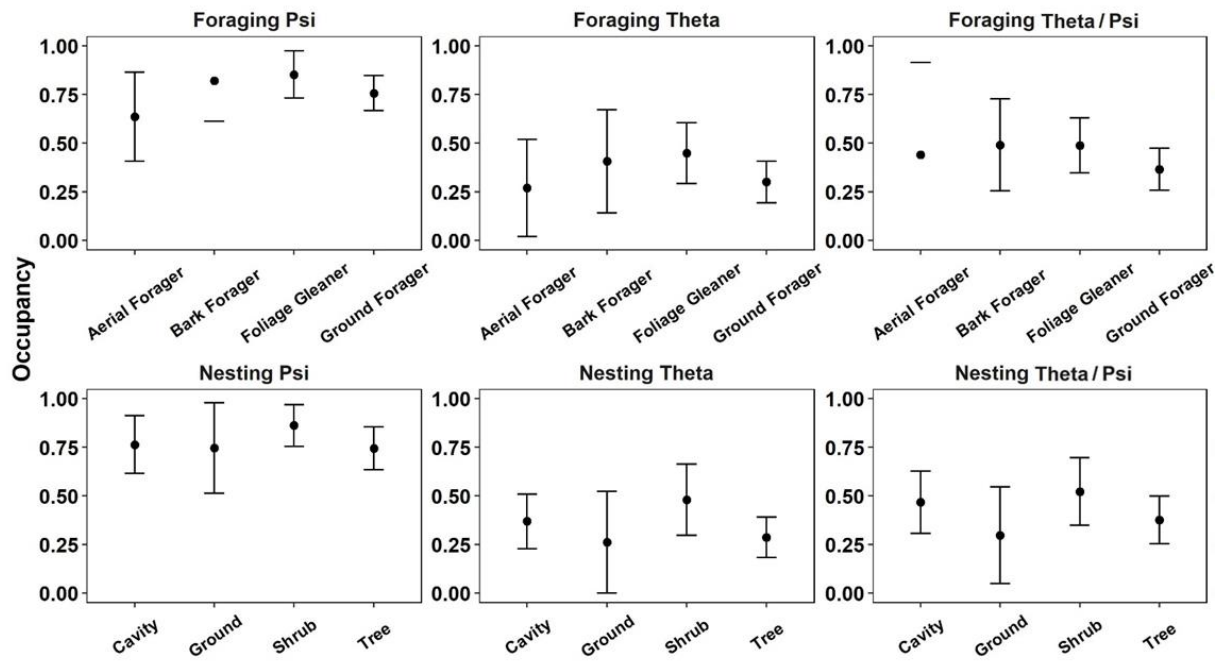
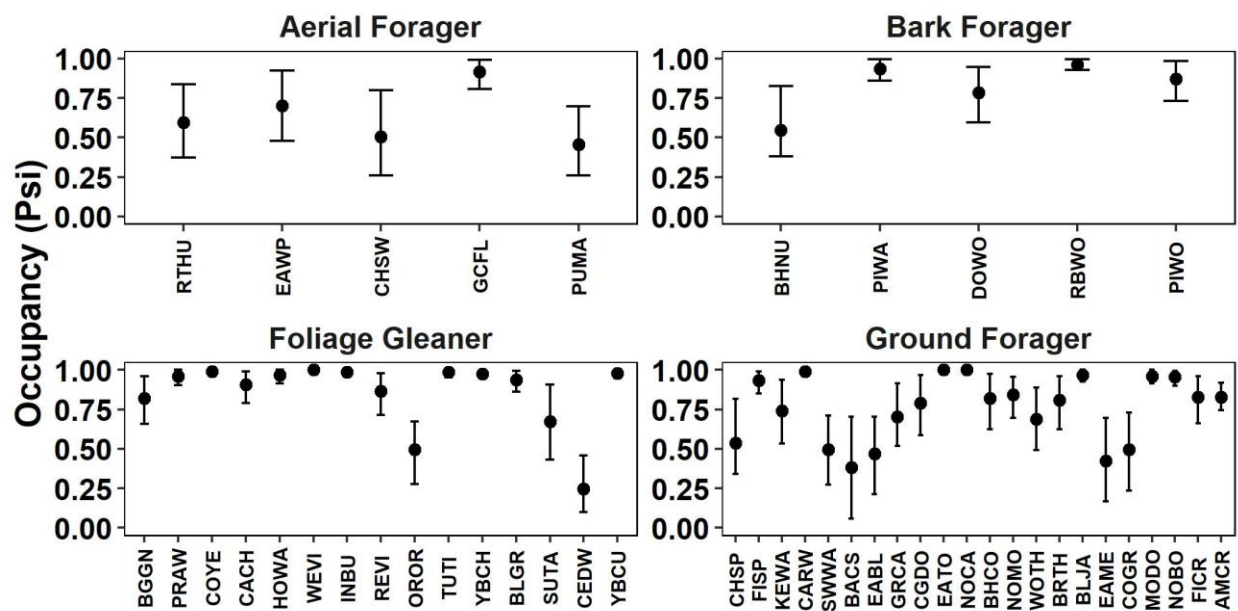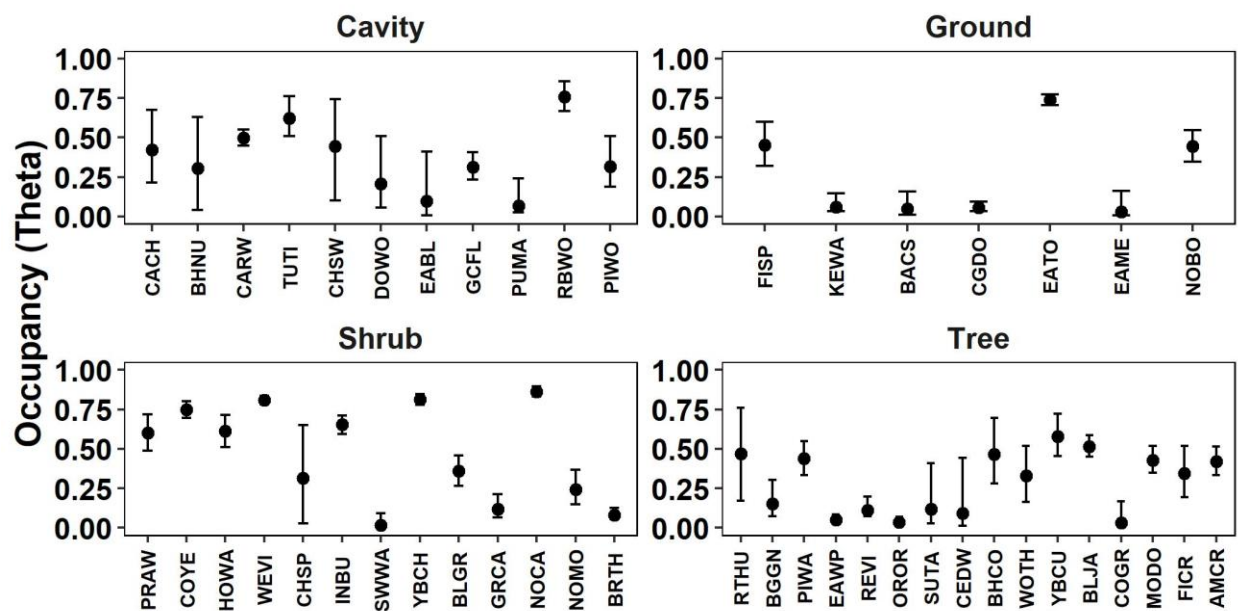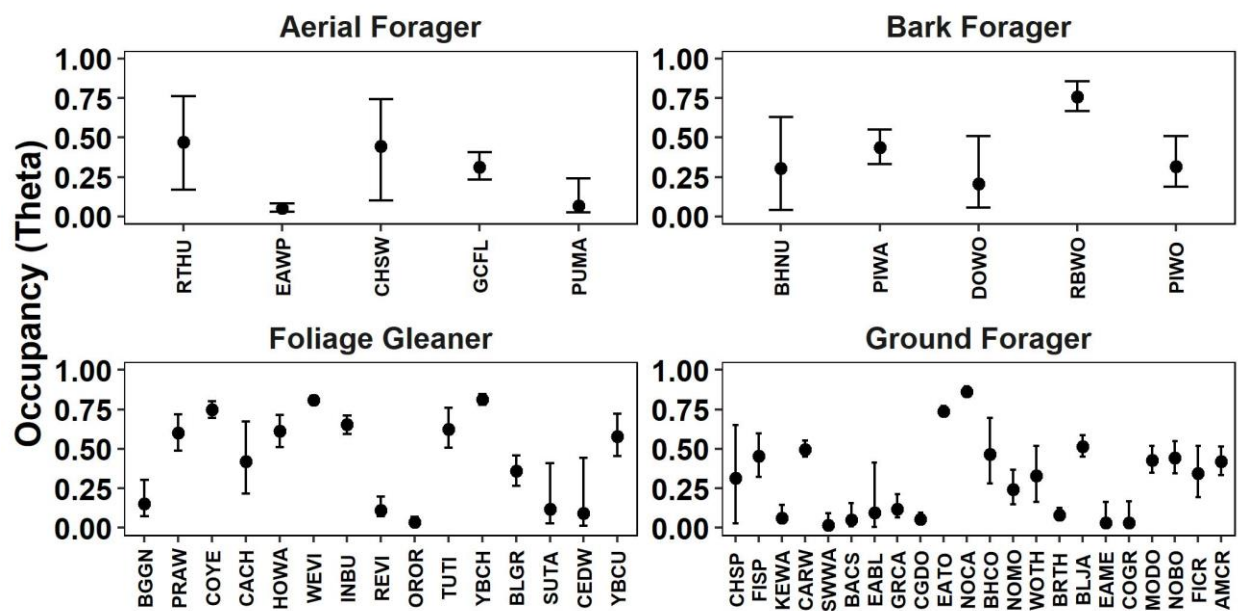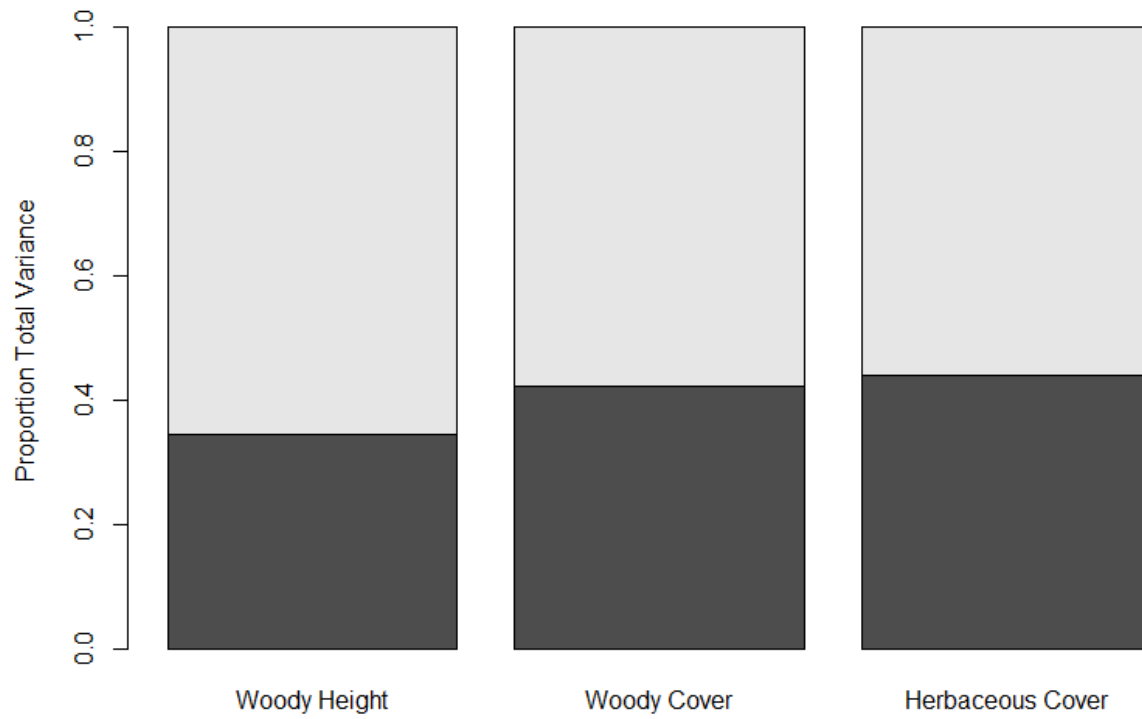Figure 2.9. Multi-scale occupancy probabilities and probability ratios for foraging (top) and nesting (bottom) guilds for avian species in young longleaf pine stands in Mississippi during the 2018–2019 avian breeding seasons.

Table 2.1. Number of parameters (*k*), log likelihood (*logLik),* Akaike's Information Criterion (*AICc*), difference from lowest AICc (*ΔAICc*), and model weights (*w*) for models used to predict the effects of foraging behavior, nesting behavior, interactions between foraging and nesting behavior, and average weight of species on stand (*ψ*) and point (*θ*) lev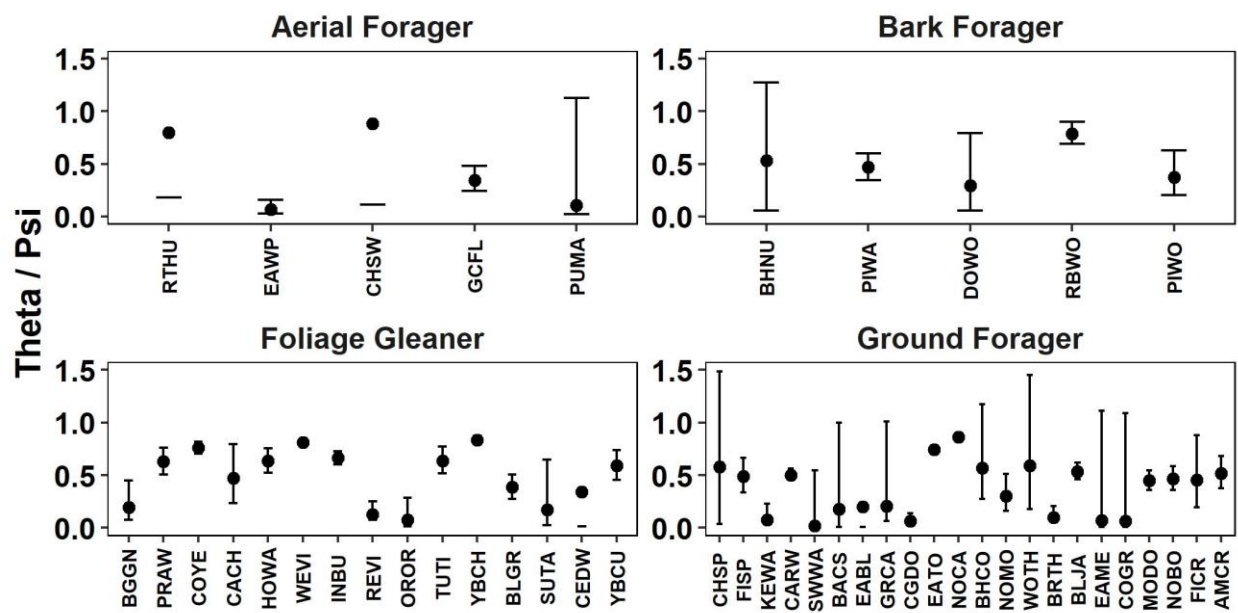el occupancy probability for avian species in young longleaf pine (*Pinus palustris*) stands in Mississippi during the 2018–2019 breeding seasons. Sample size n = 47 species for each analysis.

Model	*k*	*logLik*	*AICc*	*ΔAICc*	*w*
ψ					
Intercept (Null)	2	-7.248	18.8	0.00	0.403
Foraging	5	-4.073	19.6	0.84	0.265
Weight	3	-7.113	20.8	2.01	0.147
Weight + Foraging	6	-3.645	21.4	2.62	0.109
Nesting	6	-4.413	22.9	4.16	0.050
Weight + Nesting	7	-3.924	24.7	5.95	0.021
Foraging + Nesting	9	-2.609	28.1	9.32	0.004
Weight + Foraging + Nesting	10	-1.595	29.3	10.53	0.002
Foraging × Nesting	13	1.523	34.0	15.22	0.000
Weight + Foraging × Nesting	14	2.073	37.0	18.21	0.000
θ					
Intercept (Null)	2	-1.426	7.1	0.00	0.555
Weight	3	-1.425	9.4	2.28	0.177
Foraging	5	0.641	10.2	3.06	0.120
Nesting	6	1.539	11.0	3.90	0.079
Weight + Foraging	6	0.743	12.6	5.49	0.036
Weight + Nesting	7	1.722	13.4	6.30	0.024
Foraging + Nesting	9	3.067	16.7	9.61	0.005
Foraging + Nesting + Foraging × Nesting	13	9.356	18.3	11.19	0.002
Weight + Foraging + Nesting	10	3.577	19.0	11.83	0.001
Weight + Foraging + Nesting + Foraging × Nesting	14	9.417	22.3	15.17	0.000
(θ / ψ)					
Intercept (Null)	2	-2.318	8.9	0.00	0.465
Nesting	6	1.908	10.3	1.38	0.234
Weight	3	-2.307	11.2	2.26	0.150
Weight + Nesting	7	1.997	12.9	3.97	0.064
Foraging	5	-0.800	13.1	4.15	0.058
Weight + Foraging	6	-0.0739	15.6	6.67	0.017
Nesting + Foraging	9	2.967	16.9	8.02	0.008

Weight + Foraging + Nesting	10	3.245	19.6	10.71	0.002
Foraging + Nesting + Foraging × Nesting	13	8.268	20.5	11.59	0.001
Weight + Foraging + Nesting + Foraging × Nesting	14	8.273	24.6	15.67	0.000

Discussion

Unexpectedly, different species did not exhibit distinct patterns of occupancy at the local and landscape scales. Several species were widespread at the landscape scale (i.e., $\psi = 0.75–1.0$) and point scale, but no species had occupancy probability ratios greater than 1.0, meaning that while these species may be ubiquitous at the landscape scale, they are not at the local scale. Many of the species widespread at the landscape scale were foliage gleaning and/or shrub nesting species; however, each functional guild contained species with high stand-level occupancy. Most of the species found commonly across our stands were of low conservation concern. However, Prairie Warblers ($\psi = 0.96$) are currently in decline, and Northern Bobwhite ($\psi = 0.96$) and Yellow-billed Cuckoo (*Coccyzus americanus*) ($\psi = 0.98$) are considered common but in steep decline (Cornell University 2019).

We were surprised to find that no species were uncommon across the landscape but locally prevalent. We predicted that certain species, such as declining grassland species (e.g., BACS), would exhibit greater point-level occupancy than stand-level occupancy because of variation in stand management, however, these species were almost entirely absent from our stands. It is difficult to compare our results to work in other systems because occupancy ratios are rarely explicitly assessed; research concerning grassland songbirds more often addresses drivers of site occupancy by local and landscape attributes (Herse et al. 2017; Shahan et al. 2017; Lituma and Buehler 2020, etc.).

Contrary to our predictions, differential occupancy probability for avian species in young longleaf pine stands was not explained by nesting or foraging guild. We expected guilds to have explanatory power because previous studies found that functional guilds had different responses

to changes in land-use, vegetation structure, and management (Goijman et al. 2015; Azeria et al. 2011; Raynor et al. 2017; Newbold et al. 2013; Bregman et al. 2014; Wells et al. 2012; Kroll et al. 2017; Ding et al. 2019 and many others). With documented divergent responses to environmental changes, we expected functional guilds to exhibit diverse occupancy patterns at the local and landscape scale, however this was not the case in our study.

We expected species weight to have explanatory power because of the relationship between survey unit size, home range size, and accuracy of occupancy estimates (Hayes and Monfils 2015; Rota et al. 2009; Ramsey et al. 2015). With our fixed survey unit size (point) of 3.14 ha, we would expect to observe different patterns of occupancy based on species weight since weight was highly variable, ranging from 7.7g (PRAW) to 506g (AMCR; *Corvus brachyrhynchos*) (Appendix 1). However, point level occupancy probability appears to be the most informative for a majority of species; we observed heterogeneity in point-level occupancy and homogeneity in stand-level occupancy for most species regardless of species attributes.

There are a few explanations for this observed pattern of homogeneity and heterogeneity at different scales: vegetation characteristics of our stands and/or avian guild assignment. We expected variation in stand age (2–17 years), and independent ownership and management of stands would result in enough variation in resources to elicit a measurable response for different guilds. However, homogeneity was greater between stands than within stands, indicating that variation among stands was insufficient to drive diversity gradients. While stands were independently owned and managed, they were all prepared and planted in longleaf pine in the same manner, likely resulting in the homogeneity we observed. Additionally, we observed that many landowners did not burn their stands at regular intervals, favoring high coverage of

aggressive woody species (e.g., loblolly pine; *Pinus taeda*) (Glitzenstein et al. 1995; Brockway and Outcalt 2000), and contributing to homogeneity among stands.

Our choice in guild assignment may also have contributed to the lack of observed patterns among guilds. Theoretically, guilds based on ecological traits are more likely to respond to a common subset of environmental variables than those based on taxonomy or species assemblage (Mac Nally et al. 2008; Simberloff and Dayan 1991). However, a guild assignment may not be useful in a system where stands consistently provide habitat for some members of a guild and not others. For example, BACS and NOBO belong to the same ground foraging and ground nesting guilds; however, these species have contrasting tolerances for shrub cover that would affect their probability of occupancy. Specifically, our stands had an average of 38% woody vegetation coverage (Harris Chapter 1) which is unsuitably high for BACS and suitable for NOBO (Greene et al. 2019). Accordingly, NOBO stand occupancy was high ($\psi = 0.96$) and BACS stand occupancy was low ($\psi = 0.38$). The PFW stands should be managed with prescribed fire every 2–3 years in order to produce the target vegetation structure and support the program's target avian species (i.e., BACS) (Harris Chapter 1). However, homogenously poor stand management is not likely to show distinct occupancy patterns among guilds when stands are differentially suitable for species within guilds.

Prior to our study, few studies conducted multi-scale occupancy analyses in longleaf pine, and those that have assessed the effects of landscape- and local-scale variables on taxonomic and functional diversity of birds, not specific dynamics of foraging or nesting guilds (Lee et al. 2020), or occupancy dynamics for limited species (McGrath et al. 2017; Trager et al. 2018). Studies conducted in other fire-maintained systems using hierarchical assessments similar to our own focused on the effects of fire disturbance at the species level (Russell et al. 2009).

They found prescribed fire resulted in increased occupancy rates for several bark gleaning/cavity nesting species, while occupancy declined for several foliage gleaning species, suggesting prescribed fire can have differential effects on species in different foraging and nesting guilds. A study focused on the spatial scale dependency in avian responses for two habitat obligate guilds (grassland and sagebrush) found that while habitat associations influencing the probability of occupancy varied at the species level, a few general patterns emerged when looking at broader guilds (Dreitz et al. 2017). They found that grassland guild species utilized a broader range of vegetative associations, as opposed to sagebrush guild birds, which were more directly associated with sagebrush habitats. Both of these studies indicate that guild associations can be a meaningful lens through which to view fire-maintained disturbance based ecosystems. Our contrasting results may have a few explanations. Unlike the studies conducted by Dreitz et al. (2017) and Russel et al. (2009), we did not test the direct effects of vegetative conditions or management on species or guild occupancy. Additionally, all three studies consist of study areas with different habitat managers. While our study stands were privately managed, the study by Dreitz et al. (2017) consisted of both private and government managed land, and the study conducted by Russel et al. (2009) was conducted within a National Forest. Therefore, it is possible that fire-maintained ecosystems managed by government agencies do not share the same characteristics that cause guild associations to be seemingly meaningless within our stands.

While most studies that utilize multi-species hierarchical models are focused on occupancy responses to particular management actions (Russell et al. 2009; Magee et al. 2019; Wells et al. 2012), vegetation characteristics, or particular species (Green et al. 2019; Lipsey et al. 2017), we believe revealing potential baseline occupancy patterns for species in a system is critical to understanding both the species and the system. Spatially hierarchical models can offer

a deeper, more integrated understanding of multi-scale occupancy of many species, as nested relationships allow for adjusted responses to local conditions according to broader landscape contexts (Lipsey et al. 2017). Although we tested our predictions of multi-scale occupancy patterns on avian species within the longleaf pine ecosystem, understanding the relative importance of different spatial scales could be a useful tool in other ecosystems, as well as for the management and conservation of other taxa.

Our study stands are only representative of PFW stands <17 years old in the southeastern US, however, our approach considering two nested spatial scales can be applied in different systems. The potential impact of local- and landscape-scale processes on various species is critical, especially when working to restore habitat for threatened species on privately owned land. Our explanatory variables were unable to account for variance in occupancy probability at our two scales; however, across stands or systems with more heterogeneity, occupancy patterns useful to local land managers might be identified. The results of our study imply that all species within our study system exhibit similar occupancy patterns, regardless of size, foraging behavior, or nesting behavior. However, taking into account the observed homogeneity between our stands, our approach should be tested in a system with greater heterogeneity; variation in occupancy probability ratios (if they are present) would likely be easier to detect. We believe further research is needed in order to determine if the lack of identifiable patterns in foraging and nesting guilds in our study is a product of the study area in which we conducted these analyses. Additionally, we suggest future analyses, regardless of study system, utilize more distinctive spatial scales. Despite the uncertainty within our results, we believe that spatially hierarchical models can be a powerful tool for understanding drivers of species occupancy and the conservation of ecosystems.

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Appendices

Appendix 1. Species identified during study, the number of times that species detected, banding codes, average species weight (Dunning 2007), foraging guild, and nesting guild (Cornell University 2019).

Species	Banding Code	Nesting Guild	Foraging Guild	Average Weight (g)	Number of Detections
Yellow-breasted Chat	YBCH	Shrub	Foliage Gleaner	24.9	846
Northern Cardinal	NOCA	Shrub	Ground Forager	42.65	792
White-eyed Vireo	WEVI	Shrub	Foliage Gleaner	11.4	791
Eastern Towhee	EATO	Ground	Ground Forager	40.05	595
Common Yellowthroat	COYE	Shrub	Foliage Gleaner	9.45	506
Indigo Bunting	INBU	Shrub	Foliage Gleaner	14.7	435
Blue Jay	BLJA	Tree	Ground Forager	88	386
Red-bellied Woodpecker	RBWO	Cavity	Bark Forager	69.6	333
American Crow	AMCR	Tree	Ground Forager	506	322
Carolina Wren	CARW	Cavity	Ground Forager	17.2	311
Hooded Warbler	HOWA	Shrub	Foliage Gleaner	10.55	255

Prairie Warbler	PRAW	Shrub	Foliage Gleaner	7.65	231
Northern Bobwhite	NOBO	Ground	Ground Forager	178	198
Tufted Titmouse	TUTI	Cavity	Foliage Gleaner	21.6	197
Mourning Dove	MODO	Tree	Ground Forager	119	194
Yellow-billed Cuckoo	YBCU	Tree	Foliage Gleaner	64	191
Pine Warbler	PIWA	Tree	Bark Forager	12.3	156
Pileated Woodpecker	PIWO	Cavity	Bark Forager	287	109
Blue Grosbeak	BLGR	Shrub	Foliage Gleaner	27.4	108
Field Sparrow	FISP	Ground	Ground Forager	12.5	102
Great Crested Flycatcher	GCFL	Cavity	Aerial Forager	32.1	92
Carolina Chickadee	CACH	Cavity	Foliage Gleaner	10	79
Brown-headed Cowbird	BHCO	Tree	Ground Forager	43.4	57
Wood Thrush	WOTH	Tree	Ground Forager	50.15	54
Northern Mockingbird	NOMO	Shrub	Ground Forager	48.5	51
Red-eyed Vireo	REVI	Tree	Foliage Gleaner	16.8	44
Fish Crow	FICR	Tree	Ground Forager	285	35

Gray Catbird	GRCA	Shrub	Ground Forager	35.3	35
Brown Thrasher	BRTH	Shrub	Ground Forager	68.8	34
Blue-gray Gnatcatcher	BGGN	Tree	Foliage Gleaner	5.8	31
Downy Woodpecker	DOWO	Cavity	Bark Forager	26.7	27
Kentucky Warbler	KEWA	Ground	Ground Forager	14	25
Purple Martin	PUMA	Cavity	Aerial Forager	53.8	25
Common Ground Dove	CGDO	Ground	Ground Forager	35.4	22
Eastern Wood-pewee	EAWP	Tree	Aerial Forager	13.9	21
Cedar Waxwing	CEDW	Tree	Foliage Gleaner	31.6	20
Brown-headed Nuthatch	BHNU	Cavity	Bark Forager	10.2	19
Summer Tanager	SUTA	Tree	Foliage Gleaner	28.2	15
Chimney Swallow	CHSW	Cavity	Aerial Forager	23.6	14
Chipping Sparrow	CHSP	Shrub	Ground Forager	12.2	10
Bachman's Sparrow	BACS	Ground	Ground Forager	20.8	9
Orchard Oriole	OROR	Tree	Foliage Gleaner	19.9	9
Swainson's Warbler	SWWA	Shrub	Ground Forager	18.9	9
Common Grackle	COGR	Tree	Ground Forager	106.1	8

Eastern Meadowlark	EAME	Ground	Ground Forager	101.15	7
Eastern Bluebird	EABL	Cavity	Ground Forager	27.5	6
Ruby-throated Hummingbird	RTHU	Tree	Aerial Forager	3.1	6