Title: Influence of Landscape- and Stand-scale Factors on Avian Communities to Aid in Open Pine Restoration

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Abstract:

Determining species occurrence in ecosystems of high conservation concern is especially important for recommending habitat management techniques and identifying suitable restoration sites. We investigated 1) how stand- and landscape-scale attributes affect occupancy of priority bird species associated with longleaf pine (*Pinus palustris*) ecosystems, 2) if these priority birds can be used as indicator species for desired open pine forest structure, and 3) if these indicator species are positively correlated with greater avian richness. We compared priority bird occupancy among 12 stand types (habitat types) throughout the historic range of longleaf pine in Mississippi. We found stands resembling the historic longleaf pine ecosystem were positively associated with Red-cockaded Woodpecker (*Picoides borealis*) and Bachman's Sparrow (*Peucaea aestivalis*) occupancy probabilities, but were not significantly correlated with Northern Bobwhite (*Colinus virginianus*) or Brown-headed Nuthatch (*Sitta pusilla*) occupancy. Both of which were too generalized in their occurrence to be useful indicators. Red-cockaded Woodpecker and Bachman's Sparrow occupancy probabilities positively correlated with desired forest structure metrics of longleaf pine ecosystems such as low midstory density (< 10%) and basal area (9.2 – 16.1 m²/ha) and 40-60% canopy cover suggesting they are effective indicators of historic longleaf pine conditions. Co-occurrence of Red-cockaded Woodpecker and Bachman's Sparrow was positively correlated with avian richness, indicating these species can be used in conjunction as effective indicators for desired open pine endpoints used for restoration and management. Inclusion of priority bird species in management efforts provides assurance that restored areas will incorporate desired forest structure endpoints that have been linked to open pine priority bird presence. Correlation between priority bird species and avian species richness ensures restored areas provide suitable habitat for local avian communities.

Key Words: Bachman's Sparrow, indicator species, longleaf pine, occupancy, open pine,
Red-cockaded Woodpecker

Introduction

Longleaf pine (*Pinus palustris* Mill.) ecosystems were once a co-dominant forest type across the southeastern United States from the Atlantic Coastal Plains to the West Gulf Coastal Plains, an area estimated at 37 million hectares (Frost 1993). Today approximately 1.4 million hectares remain (a 96% loss from the original extent), making the longleaf pine ecosystem the third most endangered ecosystem in the United States (Noss & Peters 1995; Van Lear et al. 2005; America's Longleaf 2009). At present, longleaf pine ecosystems are associated with 27 species federally listed as endangered or threatened by the U. S. Fish and Wildlife Service (USFWS), 99 species that are proposed candidates for listing, and over 180 rare plant species (Walker 1993; Noss et al. 1995; Noss & Peters 1995). Much of the remaining area of longleaf pine does not resemble historic conditions that provided suitable habitat for these species (America's Longleaf 2009; Aschenbach et al. 2010; McIntyre 2012; Singleton et al. 2013). Today, estimated historic conditions of gulf coastal plain longleaf pine used as restoration objectives include an open canopy ($\leq 60\%$ cover), low basal area ($9.2\text{--}16.1\text{ m}^2/\text{ha}$ or $40\text{--}70\text{ ft}^2/\text{acre}$), little to no midstory ($< 20\%$ cover), and a dense herbaceous ground cover ($>65\%$) comprised of native graminoids (Hedman et al. 2000; GCPOLCC 2013). These conditions were historically maintained by frequent, low-intensity fires that burned over large areas and helped suppress hardwood understory and midstory, fostering a dense, herbaceous ground cover (Varner et al. 2005; Brudvig & Damschen 2011; Oswalt et al. 2012; Steen et al. 2013).

Decline in the extent and quality of longleaf pine ecosystems is attributed to the suppression of naturally occurring fire, increased urbanization, increased habitat fragmentation, unsustainable harvest, and conversion of old growth forests into timber plantations and agriculture lands (Frost 1993; Noel et al. 1998). Priority bird species associated with longleaf

pine ecosystems have similarly declined through loss of suitable habitat (Noss & Peters 1995; Van Lear et al. 2005; Singleton et al. 2013). A priority species is a species of high conservation concern, usually selected by conservation organizations as a species of focus (e.g. endangered species, game species, or public interest species). An indicator species represents specific habitat characteristics of an ecosystem within an ecoregion (Landres et al. 1988). Several species can serve as an indicator species representing the local habitat conditions in which they occur (Landres et al. 1988; Caro & O'Doherty 1999; Wiens et al. 2008). Selecting appropriate species to serve as indicator species requires knowledge about the species' ecology, and how the presence of these species is tied to local habitat and other wildlife (Landres et al. 1988). Priority species and indicator species are used to inform management decisions regarding wildlife habitat conservation and ecosystem restoration (McIntyre 2012). Miller and Hobbs (2007) suggest the first step in ecosystem restoration is identifying target species that the restoration efforts will benefit and then focusing on the habitat conditions that will allow those target species to persist. This provides a systematic approach to restoration by creating practical management objectives tailored to the specific requirements of target species (Miller and Hobbs 2007).

Federal agencies and their research partners identified priority bird species that are associated with longleaf pine ecosystems, and that have potential for use as indicators (McIntyre 2012). These species, Red-cockaded Woodpecker (*Picoides borealis*), Bachman's Sparrow (*Peucaea aestivalis*), Brown-headed Nuthatch (*Sitta pusilla*), and Northern Bobwhite (*Colinus virginianus*), meet several criteria that make them potentially suitable indicator species, including being practical to monitor, they possess an ability to respond to restoration efforts, have a wide distribution throughout the range of longleaf pine, are perceived to be associated with high quality longleaf pine habitat, and are permanent residents. (McIntyre 2012).

Determining which of these priority bird species to use as indicators of desirable open pine characteristics will aid in restoring longleaf ecosystems as they can be used as a metric to gauge suitable habitat for local wildlife and effectiveness of restoration efforts. Specifically, determining which landscape-scale and stand-scale factors are significantly related to the presence of these priority avian species would provide information to managers deciding what management techniques are important to longleaf restoration (Tirpak et al. 2006; McIntyre 2012).

America's Longleaf Initiative established a 15-year restoration objective to increase the area of longleaf ecosystem coverage from the current 1.4 million to 3.2 million ha (America's Longleaf 2009). Longleaf area in Mississippi was 100,912 ha as of 2009, with an ultimate desired area of 234,459 ha by America's Longleaf Initiative (America's Longleaf 2009). However, increasing land coverage of longleaf pine alone may not translate proportionally to an increased presence of priority wildlife (McIntyre 2012). The East Gulf Joint Venture and the Gulf Coastal Plains and Ozarks Landscape Conservation Cooperative (GCPOLCC) recommend specific forest structure and landscape endpoints to restore open pine habitat so that it will resemble historic conditions and provide habitat for local wildlife (GCPOLCC 2013). Testing these forest structure and landscape endpoints will aid in restoration and management efforts for longleaf pine ecosystems.

Objectives of this study were to: 1) determine which stand- and landscape-scale factors influence priority bird species occupancy in different habitat types, referred to as stand types, in the historic range of longleaf pine in Mississippi, 2) evaluate which priority avian species could serve as indicators of open pine stands that resemble historic longleaf ecosystems, and 3) determine if these indicator species are correlated with greater avian species richness.

Methods

Study Area

Longleaf pine habitat within Mississippi is distributed among National Forest (100,912 ha), U.S. Fish and Wildlife Service (5,252 ha), County and Municipal (2,020 ha) and private lands (46,864 ha), totaling 155,048 ha of longleaf pine habitat (America's Longleaf 2009). We distributed study sites throughout the historic range of longleaf pine ecosystems in southern Mississippi including federal, state, and private lands. We sampled within 13 locations: Bienville National Forest (NF), Desoto NF, Homochitto NF, Grand Bay National Wildlife Refuge (NWR), Sandhill Crane NWR, Marion County Wildlife Management Area (WMA), Copiah County WMA, Theodore Mars WMA, and private lands in Greene, Perry, Marion, Copiah, and Lamar counties (Figure 1). Several of these areas support populations of Red-cockaded Woodpeckers, with larger populations occurring on each of the national forests listed above, and study areas were within a few tens of km of these or other potential source populations, which is on the order of magnitude of documented dispersal distances of Red-cockaded Woodpeckers (*e.g.*, Walters 1991).

Figure 1. Locations within the historic range of longleaf pine in Mississippi, USA used for avian surveys and stand-level structural evaluation during summer 2014. Federal lands within Mississippi are designated with dark gray shading, survey locations are indicated with open triangles, and the historic range of long leaf is indicated by dashed lines. Each of the four largest federal lands in southern Mississippi within the range of longleaf corresponds to national forest that support known populations of Red-cockaded Woodpeckers.

Sampling Design

Stand-scale factors shown to affect occupancy probabilities of priority birds within longleaf systems include forest structure (canopy cover, midstory density, understory density, and basal area), vegetation composition (tree species and ground cover composition), and stand type (predefined habitat type; Table 1) (Willson 1974). Landscape-scale factors addressed in this study were ‘potential source areas’, ‘urban density’, and ‘stewardship’ (public or privately owned) (Grand et al. 2009, Bonnot et al. 2013). A ‘potential source area’ refers to locations near large patches of potential habitat that could sustain priority bird source populations for colonization of smaller patches (Grand et al. 2009). Increased urbanization can decrease the amount of available habitat for local wildlife and impede the implementation of prescribed fire to maintain open pine ecosystems (Grand et al. 2009). We apply the term ‘urban density’ to represent how urbanized an area is based on density maps. ‘Stewardship’ reflects how an area is managed. Specifically, referring to private or public ownership. Public lands can be managed long term to meet varying objectives and the ability to apply prescribed fire is usually more feasible than on private lands (Grand et al. 2009). While conservation on private lands may be necessary for the conservation of some species, private land owners may have less capacity to manage for the appropriate conditions (e.g., via prescribed burning) (Cox & Engstrom 2001). These landscape- and stand-scale attributes should be considered when restoring longleaf pine to ensure restored areas can be maintained to promote priority species presence and avian species richness. The Open Pine Decision Support Tool (OPDST) was developed using an overlay of several GIS layers pertinent to determine the suitability of an area to be restored to open pine (Grand et al. 2009). These GIS layers include priority bird potential source areas, an urban density layer (referred to as ability to burn in tables), density of conservation lands within the

116 range of longleaf pine, and a layer of sites suitable for restoration (Grand et al. 2009). We used
117 the OPDST to select 13 study sites across the historic range of longleaf pine in Mississippi
118 representing high, medium, and low restoration suitability. We selected points by normalizing
119 the habitat suitability output from OPDST to between 0 and 1, and dividing the range into three
120 equal divisions. We then selected forest stands in each of these high, medium, and low suitability
121 categories to maximize the likelihood of sampling across a gradient of suitability at surveyed
122 points. Specific study sites were selected within each category based on accessibility, and to
123 broadly distribute sites among federal, state and private land ownership. Within each study site
124 there were a variety of forest stand types. Stands reflected a range of management history
125 including unmanaged regenerating clear cut pine forest, commercial timber production,
126 unmanaged mixed forest, intensively management for open pine forest, including thinning and
127 controlled burns, and non-forest management, which we included as experimental bounds, and
128 included urbanized areas and agricultural management. Sites averaged $7,831 \pm 18,900$ ha. We
129 randomly distributed the maximum number of survey points within each study site across forest
130 stands, provided survey points were greater than or equal to 250 m apart, resulting in 148 survey
131 points. We classified each survey point according to land use type associated with one of 12
132 types (hereafter “stand types”) identified by a working group consisting of Alabama Cooperative
133 Fish and Wildlife Research Unit, U.S. Fish and Wildlife Service, Nature Serve, and Jones
134 Research Center biologists (Table 1) (McIntyre 2012). These 12 stand types reflect the seral
135 stage of forest habitats, specific forestry management techniques, and current land use. We
136 conducted bird point counts and took forest structure measurements at each survey point.

137 Table 1. Stand type description and typical forest metrics associated with each where they .

	Stand Type	Description	Typical Characteristics	N
1	AGR	Agriculture lands, in row crop.		8
2	OPN	Includes old fields/fallow fields or any pasture type area. Also includes grasslands/savannas.	Basal Area $\leq 6.9 \text{ m}^2/\text{ha}$ or $30 \text{ ft}^2/\text{acre}$	24
3	ESP	Pine stands in early succession, perhaps due to recent clear-cut or disturbance.	Basal Area $0 \text{ m}^2/\text{ha}$ (no mature trees)	10
4	SAP	Stands dominated by young pine trees (saplings) with a DBH $< 4''$ and at least $3'$ in height.	Average DBH $< 4''$	2
5	POL	Stands dominated by intermediate age pine trees.	Average DBH $> 4'' \leq 12''$	10
6	G12	Represents mature pine habitat. Stands that are characterized by pine trees with DBH $> 12''$.	Average DBH $> 12''$ Basal Area $> 16.1 \text{ m}^2/\text{ha}$ or $70 \text{ ft}^2/\text{acre}$	35
7	OPI	Stands that are characterized by an open canopy, low basal area, little to no midstory and dense herbaceous ground cover.	Basal Area $9.2\text{-}16.1 \text{ m}^2/\text{ha}$ or $40\text{-}70 \text{ ft}^2/\text{acre}$ Canopy Cover $\leq 60\%$ Midstory $< 20\%$ Herbaceous $> 65\%$	11
8	2AP	Stands that have usually been managed to have two distinct age classes of trees.		13
9	UAP	Stands that have at least three distinct age classes or diameter classes of trees.		9
10	MXD	Stands that have interspersed pine trees with hardwoods.		17
11	UAH	Hardwood dominated stands. Most hardwood stands are uneven aged.		5
12	DEV	Areas that are developed due to urbanization		4

138 Stand types and some associated forest structure metrics. N/A refers to stand types that were not
139 forest types or were classified by land use or management practices and did not have specific
140 forest structure metrics. The number of points classified column displays how many sample
141 points were classified as each stand type. AGR- agriculture, OPN- open, ESP- early successional
142 pine, SAP- pine sapling stand, POL- pine pole stand, G12- pines greater than $12''$ DBH stand,
143 OPI- open pine stand, 2AP- two-aged pine stand, UAP- uneven-aged pine stand, MXD- mixed
144 pine stand, UAH- uneven-aged hardwood stand, DEV- developed area.

Bird Point Counts

We conducted bird point counts at each survey point from late May–July 2014. We began counts no earlier than 6:00 am and ended counts no later than 10:00 am. Each count was 6 minutes in length divided into three, 2-minute intervals. We recorded all birds detected within 100 m of the observer during counts. All birds detected were used to determine species richness for each point. Counts were not conducted during the rain, or when wind speeds exceeded 24 kph (Huff et al. 2000). This method was replicated three times at each of the 148 points, sampled at approximately three week intervals (22–26 days between surveys) ($148 \text{ points} \times 3 \text{ replicates} = 444 \text{ total surveys}$).

Vegetation Sampling

We measured forest structure metrics once at each point count location from June 2–19, 2014. We used the survey point as a transect center and measured 10 m north and south from this center to create a 20 m transect. We measured canopy cover, midstory density, understory density, herbaceous density, and leaf litter density along the transect at one meter intervals. We walked along the 20 m transect and stopped at each 1 m interval to record a (1) for each metric (midstory, understory, herbaceous, and leaf litter) if it was present at that distance interval, and a (0) if it was not present. We determined presence by projecting each point up to the canopy with a moosehorn (device that uses mirrors to project a point up to the canopy) and observed if any leaf litter, herbaceous, understory, and/or midstory structure intersected each point. These measurements were then individually summed and divided by total observations to create a single percentage value for each metric at each point. We measured canopy cover at the first interval, transect center and last interval along the transect with a convex spherical densiometer and averaged these 3 measurements for each survey point (Lemmon 1956). We measured basal

area with a 10-factor wedge prism (Exact-Factor Cruising Prism, 10 BAF) at transect center for each point. We identified each tree species counted in the basal area measurement, and measured the DBH of these trees. We used these data in conjunction with management history, vegetation growth aspect, and tree species composition to help classify each point as one of twelve stand types according to predefined forest structure classification (Table 1).

Statistical Analysis

We used a pairwise correlation matrix to test for multicollinearity among forest structure variables (basal area, midstory density, understory density, herbaceous density, leaf litter density, and canopy cover). If variable pairs were correlated, identified with a correlation coefficient greater than 0.70, then one of the variables was removed to avoid issues associated with multiple near-linear dependencies among variables (McGarigal et al. 2000).

We used a model-based approach to estimate which variables were statistically relevant to occupancy and detection of each priority species (Red-cockaded Woodpecker, Bachman's Sparrow, Brown-headed Nuthatch, and Northern Bobwhite). We defined occupancy as a binary function where '1' indicates a species was present and detected within 100 m of a survey point and '0' indicates a species was absent or not detected within 100 m of a point. We assumed occupancy and detection varied by species, and stand-scale and landscape-scale factors affected presence/absence of priority bird species at each point (MacKenzie et al. 2006). We developed single-species, single-season occupancy models to determine which landscape-scale (OPDST, feasibility to burn, habitat suitability, proximity to conservation lands and potential source areas) and stand-scale variables (canopy cover, midstory density, understory density, herbaceous density, basal area, and stand type) best predicted priority bird species presence. Stand type was included as a categorical variable classified as "open pine" for stands that met the open pine

endpoints and “other” for all other stand types. This classification system was implemented within occupancy models to test if open pine stands were more strongly correlated with the presence of priority bird occupancy, as opposed to other stand types.

We used a two-stage model selection, first fitting detection covariates for each species and then fitting occupancy covariates (Mackenzie et al. 2006). We developed a global model for each priority bird species that included all forest structure variables for occupancy and hypothesis-based variables for detection (Mackenzie et al. 2006). Observation-level (wind speed and time of day) and stand specific (habitat characteristics) covariates were tested in the detection stage. We then selected the best detection model using Akaike’s Information Criterion corrected for small sample size (AICc). Detection covariates from the best supported detection model were then used in all occupancy models for each respective species during the second stage of model development and selection.

We conducted a chi-square goodness-of-fit test, $\alpha = 0.05$, to compare observed and expected values of global models, associated with each priority species, before selecting among models (Burnham & Anderson 2002; Fiske & Chandler 2011). We developed models for each species, testing variables predicted to affect occupancy based on species-specific hypotheses. We predicted that priority bird occupancy rates would have an intermediate optimal value for the forest structure metrics basal area and canopy cover, and therefore we included a quadratic function in the models that contained these variables allowing the model to express these optima.

We used an information-theoretic approach employing AIC to select the best candidate model for each priority bird species (Burnham & Anderson 2002). We used AICc to correct for small sample sizes and avoid over-fitting the models (Burnham & Anderson 2002; Riffell & Gutzwiller 2012). Using this model-based approach allowed us to select the best model

incorporating forest structure variables, and compare this model to the best candidate model incorporating landscape-scale variables (Burnham & Anderson 2002). We also used model averaging of all candidate occupancy models for each species to generate average parameter estimates and parameter importance values (Burnham & Anderson 2002).

The same detection covariates from the stand-scale models were used in the landscape-scale models for each species. The top stand-scale model and a stand type model were tested with the landscape-scale models to determine if landscape-scale or stand-scale variables influence priority bird species occupancy or if a combination of these variables better indicated priority bird species occupancy. Models with a $\Delta AICc$, reflecting difference in AICc value from the best supported model, of 0–2 were considered competitive models best supported by the data. Models with a $\Delta AICc$ of 4–7 were considered less supported and models with a $\Delta AICc > 10$ were considered not supported by the data (Burnham & Anderson 2002). Parameter estimates are on the logit scale except where noted, model estimates are reported as mean, standard error.

We used generalized linear models to determine if occupancy of priority species associated with open pine metrics were positively correlated with observed species richness. Observed species richness refers to the number of species at each point. We first tested the relationship between priority species occupancy and species richness in all forest stand types by using the top occupancy models from previous analysis. We then tested pine-forest stands independently to determine if priority species occupancy predict species richness solely in pine stand types and not in all forested stands. These occupancy models were used to fit predicted occupancy probabilities at each point location. Fitted predictions were used as independent variables with point-specific observed richness as the dependent variable. Response data were log transformed to meet assumptions of normality as is typical with count data. We also tested

models of univariate response of each priority species and the interaction between priority species. We used model selection to determine the best model of species richness for forested stands and pine-only forest stands independently.

Results

The pairwise correlation matrix indicated that basal area and canopy cover were each were highly correlated ($r > 0.70$) with leaf litter, but not with each other. We removed leaf litter from further analyses because none of our hypotheses included leaf litter as a predictor of priority bird species occurrence. Goodness-of-fit tests indicated that each priority species global model suitably fit the data (each $P \leq 0.05$).

Stand-Scale Models

Model selection for Red-cockaded Woodpecker indicated that detection probability was negatively influenced by understory density ($\bar{x} = -4.28$, $SE = 1.69$) and stand type (other) ($\bar{x} = -4.61$, $SE = 2.04$), suggesting that Red-cockaded Woodpeckers were less likely to be detected in stand types other than open pine. Red-cockaded Woodpecker detection was positively influenced by canopy cover ($\bar{x} = 3.43$, $SE = 1.50$). Observation-level covariates, wind speed and time of day, were also tested but did not significantly affect detection of this species. The best fit detection covariates were subsequently used in the occupancy models. We plotted continuous stand-level covariates supported by the data ($<2 \Delta AICc$ from top model, and ranked above the null model). Competitive occupancy models for Red-cockaded Woodpecker were stand type + midstory density, basal area + basal area² (quadratic function), stand type only, and basal area only (Table 2). Red-cockaded Woodpecker occupancy was negatively influenced by midstory density, with the greatest probability of occupancy in areas with less than 15% midstory density (Figure 2). There was a quadratic relationship between Red-cockaded Woodpecker occupancy

260 and basal area, with the greatest probability of occupancy in areas with a basal area of 13.8 m²/ha
261 or 60 ft²/acre (Figure 3). Occupancy was negatively correlated with stand type (other), indicating
262 Red-cockaded Woodpeckers have a greater probability of occurring in open pine than any other
263 stand type sampled. From the model averaged estimates, the pattern of positive or negative
264 parameter effects were the same as corresponding parameters from the best occupancy model
265 (Table 3). Importance values indicated that stand type was the most important parameter
266 influencing Red-cockaded Woodpecker occupancy followed by midstory, basal area, and basal
267 area² (Table 4).

Figure 2. Predicted probability of Red-cockaded Woodpecker occupancy as a function of midstory density (%). Red-cockaded Woodpecker occupancy is negatively influenced by midstory density, with the greatest probability of occupancy in areas with < 15% midstory density. MLE = -9.78, SE = 80.10. ψ - Occupancy probability.

Figure 3. Predicted probability of Red-cockaded Woodpecker occupancy as a function of basal area (m^2/ha). There is a quadratic relationship between Red-cockaded Woodpecker occupancy and basal area. For basal area: MLE = -3.10, SE = 1.60. For basal area²: MLE = -2.83, SE = 2.10. ψ - Occupancy probability.

Bachman's Sparrow detection probability was negatively influenced by midstory density ($\bar{x} = -1.19$, $SE = 1.16$) and stand type (other) ($\bar{x} = -1.44$, $SE = 0.69$). The best models that predicted Bachman's Sparrow occupancy were canopy cover + canopy cover² (quadratic function) and canopy cover + canopy cover² + stand type (Table 2). Bachman's Sparrow occupancy was best described with a quadratic response to canopy cover, with occupancy probability greatest in areas with 40–60% canopy cover (Figure 4). Model averaged parameter estimates supported the best model parameter estimates with the same quadratic response to canopy cover and negative correlation with stand type, indicating Bachman's Sparrows are more likely to occur in open pine stands (Table 3). Importance values indicated that canopy cover and canopy cover² were the most important parameters that influence Bachman's Sparrow occupancy (Table 4).

Figure 4. Predicted probability of Bachman's Sparrow occupancy as a function of canopy cover (%). There is a quadratic relationship between Bachman's Sparrow occupancy and canopy cover, with greatest probability of occupancy in areas with 40–60% canopy cover. For canopy cover: $MLE = -1.72$, $SE = 1.03$. For canopy cover²: $MLE = -3.30$, $SE = 1.75$. ψ - Occupancy probability.

Detection probability for Brown-headed Nuthatch was negatively influenced by basal area ($\bar{x} = -2.16$, $SE = 0.39$) and stand type (other) ($\bar{x} = -1.25$, $SE = 0.47$). The only competing occupancy model was stand type + basal area (Table 2). Stand type (other) was positively correlated with occupancy, indicating Brown-headed Nuthatches are more likely to occur in stand types other than open pine. In open pine, predicted occupancy probability was 100% in areas with a basal area $\geq 10.3 \text{ m}^2/\text{ha}$ or $45 \text{ ft}^2/\text{acre}$ and 0% in areas with a basal area less than or equal to $5.7 \text{ m}^2/\text{ha}$ or $25 \text{ ft}^2/\text{acre}$ (Figure 5). In “other” stand types, predicted probability approached 100% in areas where basal area was $\geq 4.6 \text{ m}^2/\text{ha}$ or $20 \text{ ft}^2/\text{acre}$ (Figure 6). Although this was typically in forested stand types, the relationship also held in the urban stand type. Model averaged parameter estimates also demonstrated a positive correlation with stand type and basal area (Table 3). Importance values indicated that basal area was the most important parameter that influences Brown-headed Nuthatch occupancy followed by stand type (Table 4).

Figure 5. Predicted probability of Brown-headed Nuthatch occupancy as a function of basal area (ft^2/acre) in open pine. In the open pine stand type predicted occupancy probability is 100% in areas with basal area $\geq 10.3 \text{ m}^2/\text{ha}$ and 0% in areas with basal area $\leq 5.7 \text{ m}^2/\text{ha}$. $MLE = 28.3$, $SE = 18.2$. ψ - Occupancy probability.

Figure 6. Predicted probability of Brown-headed Nuthatch occupancy as a function of basal area (ft²/acre) in other stand types. In other stand types (11 stand types other than open pine) predicted Brown-headed Nuthatch occupancy is 100% in areas with basal area ≥ 4.6 m²/ha. MLE = 28.3, SE = 18.2. ψ - Occupancy probability.

Northern Bobwhite detection probability was negatively influenced by basal area ($\bar{x} = -0.69$, SE = 0.18) and wind speed ($\bar{x} = -0.44$, SE = 0.20). The null model was the best candidate model indicating that no stand-scale variables predicted Northern Bobwhite occupancy (Table 2). Model averaged estimates indicate a small negative effect of stand type on Northern Bobwhite occupancy with a low importance value (Table 3, Table 4).

Table 2. Model selection tables for occupancy probabilities for Red-cockaded Woodpecker, Bachman's Sparrow, Brown-headed Nuthatch, and Northern Bobwhite derived from single season occupancy models, Mississippi, USA, May–July 2014. Only models with $\Delta AIC_c < 10$ presented.

Model	K	logLik	AIC _c	ΔAIC_c	w
<i>Red-cockaded Woodpecker</i>					
Stand Type + Midstory	7	-26.8	68.7	0.00	0.280
Basal Area + Basal Area ²	7	-27.4	69.8	1.12	0.160
Stand Type	6	-28.7	70.2	1.46	0.135
Basal Area	6	-28.9	70.7	2.00	0.103
Understory + Midstory	7	-27.9	70.8	2.13	0.096
Basal Area + Stand Type	7	-27.9	71.0	2.24	0.091
Herbaceous x Basal Area	8	-27.5	72.4	3.71	0.044
Midstory	6	-29.8	72.4	3.72	0.043
Canopy Cover	6	-30.1	73.0	4.31	0.032
Herbaceous x Canopy Cover	8	-28.8	74.9	6.20	0.013
Null	5	-33.9	78.5	9.76	0.002
<i>Bachman's Sparrow</i>					
Canopy Cover + Canopy Cover ²	6	-49.9	112.5	0.00	0.588
Canopy Cover + Canopy Cover ² + Stand Type	7	-49.5	114.0	1.48	0.280
Herbaceous x Canopy Cover	7	-50.3	115.7	3.23	0.117
Stand Type	5	-55.7	122.0	9.49	0.005
<i>Brown-headed Nuthatch</i>					
Basal Area + Stand Type	6	-108.3	229.2	0.00	0.665
Basal Area	5	-110.5	231.5	2.28	0.213
Basal Area + Basal Area ²	6	-109.9	232.6	3.42	0.120
<i>Northern Bobwhite</i>					
Null	4	-198.3	405.0	0.00	0.267
Stand Type	5	-197.4	405.3	0.32	0.227
Understory	5	-198.1	406.6	1.64	0.118
Midstory	5	-198.2	406.7	1.77	0.110
Basal Area	5	-198.2	406.9	1.95	0.100
Canopy Cover	5	-198.3	407.1	2.14	0.091
Midstory + Basal Area	6	-197.9	408.5	3.57	0.045
Canopy Cover + Understory	6	-198.0	408.7	3.73	0.041

K- number of parameters in model, logLik- log likelihood, AIC_c- Akaike Information Criterion adjusted for small sample sizes, ΔAIC_c - reflecting difference in AIC_c value from the best-supported model, w- model weight.

Table 3. Model averaged occupancy models for each priority bird species.

Model	Intercept	Stand Type	Midstory	Basal Area	Basal Area ²	Canopy Cover	Canopy Cover ²
RCWO	-0.85	-1.11	-4.12	-0.83	-0.45	–	–
BACS	9.62	-0.55	0.00	0.00	–	5.70	-2.72
BHNU	19.28	9.32	-0.02	23.8	-1.69	0.00	–
NOBO	1.15	-0.47	-0.09	0.08	–	0.00	–

Single-season, single species occupancy models averaged for each priority bird species. All candidate models averaged for each species. RCWO- Red-cockaded Woodpecker, BACS- Bachman's Sparrow, BHNU- Brown-headed Nuthatch, and NOBO- Northern Bobwhite.

Table 4. Occupancy parameter importance for each priority bird species.

Parameter	RCWO	BACS	BHNU	NOBO
Stand Type	0.51	0.29	0.66	0.23
Midstory	0.42	<0.01	<0.01	0.16
Basal Area	0.40	<0.01	1.00	0.15
Basal Area ²	0.16	–	0.12	–
Canopy Cover	0.05	0.99	<0.01	0.13
Canopy Cover ²	–	0.87	–	–
Understory	0.10	<0.01	<0.01	0.16
Herbaceous	0.06	0.12	–	–
Herbaceous x Canopy Cover	0.01	0.12	–	–
Herbaceous x Basal Area	0.04	–	–	–

RCWO- Red-cockaded Woodpecker, BACS- Bachman's Sparrow, BHNU- Brown-headed Nuthatch, and NOBO- Northern Bobwhite.

Landscape-Scale Models

The top stand-scale model(s) were tested with the landscape-scale models to compare how well stand-scale and landscape-scale models predict priority bird species occupancy. Red-cockaded Woodpecker occupancy was positively influenced by habitat suitability. There were no other competing landscape-scale models for this species (Table 5). The competing models that predicted Bachman's Sparrow occupancy were canopy cover + canopy cover² (quadratic function), potential source area, OPDST, conservation lands, and canopy cover + canopy cover² + stand type (Table 5). The two top competing stand-scale models were also competitive in the

350 landscape-scale model selection process. Bachman's Sparrow occupancy was quadratically
351 related to canopy cover, with the greatest predicted probability of occupancy in stands with 40–
352 60% canopy cover (Figure 4). Landscape-scale variables (potential source area, OPDST, and
353 conservation lands) were positively correlated with Bachman's Sparrow occupancy. Stand type
354 (other) was negatively correlated with Bachman's Sparrow occupancy, indicating they have
355 greater probability of occupancy in open pine stands within the study area. Brown-headed
356 Nuthatch occupancy was positively influenced by conservation lands. There were no other
357 competing models (Table 5). Northern Bobwhite occupancy was positively influenced by
358 potential source area and habitat suitability (Table 5).

Table 5. Landscape-scale model selection table for Red-cockaded Woodpecker, Bachman's Sparrow, Brown-headed Nuthatch and Northern Bobwhite, Mississippi, USA, May–July, 2014. Only models with $\Delta AIC_c < 20$ presented.

Model	K	logLik	AIC _c	ΔAIC_c	w
<i>Red-cockaded Woodpecker</i>					
Suitability	6	-21.8	56.3	0.00	0.726
OPDST + Stand Type	7	-21.8	58.7	2.33	0.227
RCWO potential source area	6	-24.7	62.1	5.80	0.040
OPDST	6	-27.2	67.2	10.84	0.003
Conservation Lands	6	-27.5	67.7	11.40	0.002
Stand Type	6	-28.7	70.2	13.82	0.001
Ability to burn	6	-30.0	72.8	16.47	0.000
<i>Bachman's Sparrow</i>					
Canopy Cover + Canopy Cover ²	6	-49.7	112.2	0.00	0.251
BACS potential source area	5	-51.1	112.7	0.50	0.195
OPDST	5	-51.1	112.8	0.67	0.179
Conservation Land	5	-51.3	113.1	0.92	0.159
Canopy Cover + Canopy Cover ² + Stand Type	7	-49.3	113.7	1.53	0.117
OPDST + Stand Type	6	-50.8	114.4	2.25	0.081
Suitability	5	-53.8	118.2	6.04	0.012
Stand Type	5	-55.2	120.9	8.76	0.003
Null	4	-56.7	121.9	9.71	0.002
Ability to burn	5	-56.6	123.8	11.62	0.001
<i>Brown-headed Nuthatch</i>					
Conservation Land	5	-69.1	148.7	0.00	1
Ability to burn	5	-77.9	166.5	17.76	0
<i>Northern Bobwhite</i>					
NOBO potential source area	4	-136.8	281.9	0.00	0.489
Suitability	4	-137.5	283.3	1.35	0.249
OPDST	4	-138.1	284.6	2.66	0.129
OPDST + Stand Type	5	-137.2	285.0	3.07	0.105
Ability to burn	4	-140.5	289.4	7.49	0.012
Null	3	-142.3	290.8	8.89	0.006
Conservation Land	4	-141.3	291.0	9.02	0.005
Stand Type	4	-141.5	291.3	9.37	0.005

Single-season, single species occupancy model selection table for Red-cockaded Woodpecker. K- number of parameters in model, logLik- log likelihood, AIC_c- Akaike Information Criterion adjusted for small sample sizes, ΔAIC_c - reflecting difference in AIC_c value from the best-supported model, w- model weight. OPDST- Open Pine Decision Support Tool and RCWO- Red-cockaded Woodpecker.

Species Richness Models

Red-cockaded Woodpecker and Bachman's Sparrow were linked with open pine metrics in our previous analysis so these two species were used in subsequent species richness models. The top ranked model linking avian species richness to the presence of priority species within all forested stand types was the null model with the Red-cockaded Woodpecker model competing (Table 6). The Red-cockaded Woodpecker model was positively correlated with species richness ($\bar{x} = 0.24$, $SE = 0.17$) but the confidence interval overlapped zero (95% C.I. = -0.10–0.58) suggesting it is not the best predictor of species richness (Zar 2009). The top model for pine-only forest stands was the Red-cockaded Woodpecker and Bachman's Sparrow interaction model (RCWO x BACS) indicating a relationship between predicted Red-cockaded Woodpecker and Bachman's Sparrow occupancy and observed species richness in areas where both species occur (Table 6) (Figure 7).

Table 6. Model selection table for models of species richness as predicted by potential indicator species' occupancy probabilities within all forested stand types, and within pine forest types only, Mississippi, USA, May–June 2014.

Model	K	logLik	AIC _c	ΔAIC _c	w
<i>All forest types</i>					
Null	2	15.2	-26.2	0.00	0.395
RCWO	3	16.1	-26.0	0.22	0.354
BACS	3	15.2	-24.1	2.10	0.138
RCWO x BACS	5	17.1	-23.7	2.52	0.112
<i>Within Pine forests only</i>					
RCWO x BACS	5	20.3	-29.8	0.00	0.347
Null	2	16.9	-29.6	0.12	0.327
BACS	3	17.4	-28.4	1.34	0.178
RCWO	3	17.2	-28.1	1.70	0.148

RCWO- Red-cockaded Woodpecker, BACS- Bachman's Sparrow. K- number of parameters in model, logLik- log likelihood, AIC_c- Akaike Information Criterion adjusted for small sample sizes, ΔAIC_c- reflecting difference in AIC_c value from the best-supported model, w- model weight.

Figure 7. Observed species richness predicted from modeled Red-cockaded Woodpecker and Bachman's Sparrow occupancy in pine stands. Bachman's Sparrow and Red-cockaded Woodpecker occupancy range from 0–1. BACS- Bachman's Sparrow occupancy, RCWO-Red-cockaded Woodpecker occupancy, richness- mean predicted species richness at each survey point. This figure shows that when BACS and RCWO are both present, species richness significantly increases.

Discussion

Landscape-scale and stand-scale factors, as measured within the historical context of longleaf pine, were statistically significant predictors of Red-cockaded Woodpecker, Bachman's Sparrow, and Brown-headed Nuthatch occupancy. Northern Bobwhite occupancy was only significantly related to landscape-scale factors (potential source area and habitat suitability). Stand- and landscape-scale factors should be taken into consideration when restoring open pine ecosystems, ensuring that suitable wildlife habitat is conserved in areas restored to open pine. Our analyses support the use of Red-cockaded Woodpecker and Bachman's Sparrow as indicator species for longleaf pine/open pine ecosystems because their occupancy rates were correlated with the *a priori* selected metrics used in describing structure of open pine ecosystems and the co-occurrence of both species was positively correlated with observed avian species richness. Northern Bobwhite and Brown-headed Nuthatch occupancies were not predicted by the forest structure metrics we used to define open pine stands. Northern Bobwhite and Brown-headed Nuthatch occupancies were also positively correlated stand types other than open pine, suggesting these species are more likely to occur in the 11 other stand types sampled. For these reasons, we do not recommend the use of Northern Bobwhite or Brown-headed Nuthatch as indicator species for the historic conditions of open pine ecosystems.

The observation-level covariates, wind speed and time of day, did not significantly influence detection for Red-cockaded Woodpeckers, Bachman's Sparrow, or Brown-headed Nuthatch. Wind speed did have a slightly negative affect on Northern Bobwhite detection probability ($\bar{x} = -0.44$, $SE = 0.20$). Bird point count surveys were conducted under a fairly uniform set of environmental conditions (from 6:00 a.m. to 10:00 a.m. and only when wind speed was under 24 kph), so it is not surprising that observation-level covariates did not

significantly affect detection probability. Stand covariates that were associated with the density of each stand (canopy cover, basal area, and midstory) slightly affected detection probability for all of the priority species. Stands that had higher basal area and midstory density may have hindered an observer's ability to detect each species. Canopy cover was positively correlated with Red-cockaded Woodpecker detection probabilities. This may reflect that Red-cockaded Woodpeckers were actively foraging in the forest canopy during the survey periods.

The forest structure endpoints recommended by the GCPOLCC for open pine ecosystems were generally supported by occupancy rates estimated for Red-cockaded Woodpecker and Bachman's Sparrow. However, these endpoints could be altered slightly to better match the forest metrics positively correlated with Red-cockaded Woodpecker and Bachman's Sparrow presence. Red-cockaded Woodpecker occupancy was negatively influenced by midstory, with the greatest probability of occupancy in areas with little to no midstory (<10%) supporting earlier work indicating that Red-cockaded Woodpeckers will abandon clusters if midstory becomes too dense (Conner et al. 1996; Ross et al. 1997; USFWS 2003). Red-cockaded Woodpecker occupancy exhibited a quadratic function relative to basal area with the greatest probability of occupancy in areas with 9.2–16.1 m²/ha or 40–70 ft²/acre basal area, the current recommended endpoint for open pine. However, reducing the current endpoint from <20% midstory to <10% midstory cover may promote higher Red-cockaded Woodpecker occupancy. Red-cockaded Woodpeckers require mature, pine trees, usually infected with heart rot, to excavate cavities (Rudolph et al. 1990; Conner et al. 1996). Many studies have shown that areas where forest and vegetation structure is managed for Red-cockaded Woodpecker positively influence other avian species including Bachman's Sparrow and Northern Bobwhite populations, suggesting that Red-cockaded Woodpecker can be used as an indicator species for open pine habitat (Bowman et al.

1999; Conner et al. 2002; Wood et al. 2004). It should be taken into consideration that Red-cockaded Woodpeckers have historically been translocated to areas managed for their persistence. However, Red-cockaded Woodpeckers will abandon clusters if specific forest structure conditions do not meet their habitat requirements, so they should still be considered as an open pine indicator species (USFWS 2003). Bachman's Sparrow occupancy was a quadratic function with canopy cover, with the greatest probability of occupancy in areas with 40–60% canopy cover. The GCPOLCC recommended open pine endpoint for canopy cover is less than 50%. Our analysis shows that Bachman's Sparrow occupancy is less likely when canopy cover is less than 40% and greater than 60%, suggesting the endpoint could incorporate a lower bound on canopy cover at 40% and an upper bound at 60%. Red-cockaded Woodpecker and Bachman's Sparrow occupancy was associated with stand type, with probability of occupancy greatest in open pine stands when compared to the other 11 stand types sampled suggesting their usefulness as indicators of open pine conditions.

Avian species richness was correlated with the presence of both Red-cockaded Woodpecker and Bachman's Sparrow, but only when these species co-occurred and only in pine stands, relative to the other habitat types evaluated. (Figure 7). The benefits of habitat managed or restored for Red-cockaded Woodpeckers for other wildlife species is well documented (Bowman et al. 1999; Conner et al. 2002; Masters et al. 2002; Wood et al. 2004). Conner et al. (2002) found that areas managed for Red-cockaded Woodpeckers had greater species richness than mature forests that were not managed for Red-cockaded Woodpecker. Masters et al. (2002) found that restoration for Red-cockaded Woodpeckers significantly increased community abundance, species richness, and small mammal and breeding bird diversity. Red-cockaded Woodpeckers require large, mature pine trees to nest and do not tolerate dense midstory (Ross et

al. 1997). Bachman' sparrows require dense, herbaceous ground cover to nest and some woody understory for perching (Dunning & Watts 1990; Tucker et al. 2006). The presence of both of these species indicates the structural and vegetation composition endpoints for open pine ecosystems are present and thus promotes avian species richness. This is supported by James et al. (2001) who found that ground cover was just as important as tree structure and that both should be managed together to reach optimal longleaf pine conditions. There is a wide array of forest stand types in the southeast and the recommended open pine metrics may not increase species richness in all forest types. Within pine stands, Red-cockaded Woodpecker and Bachman's Sparrow occupancy were associated with stands with greater species richness. Stands with low predicted probability of occupancy of both species exhibited a wide range of observed richness; however, mean response was roughly half that of stands that had high probability of occupancy (≈ 1.0) for both species.

Unlike Red-cockaded Woodpecker and Bachman's Sparrow, which can be used to monitor the effectiveness of restoration and on-going management, Brown-headed Nuthatch and Northern Bobwhite occupancy were not associated with open pine endpoints or greater species richness. Our results show that Brown-headed Nuthatches will occupy an area with a minimum threshold of basal area, and occur more frequently in forest types other than open pine especially open pine savannas. Our results suggested that they are associated with a wider host of forest types than necessary to be an open pine indicator. Northern Bobwhite occupancy was predicted by the potential source area GIS layer and the habitat suitability GIS layer and no forest structure metrics. Given these findings, we do not suggest using Brown-headed Nuthatch and Northern Bobwhite as indicator species for longleaf pine/open pine ecosystems. Other studies have found that Northern Bobwhite respond positively to restoration for Red-cockaded Woodpeckers

including midstory and basal area reductions (Wilson et al. 1995, Cram et al. 2002, Burke et al. 2008). Our lack of an association between forest structure metrics and Northern Bobwhite occupancy may be the result of varied species requirements in different habitats, as we sampled across several forested and non-forested habitat types. Intensive management for open-pine conditions may not necessarily increase Northern Bobwhite habitat quality depending on the specific implementation due to potential reductions in brood habitat, nesting cover, visual screening cover and suitable winter habitat conditions (Cram et al. 2002, Burke et al 2008, Jones et al. 2010). Crosby et al. (2015) found that within grasslands and shrublands Northern Bobwhite are correlated with species richness and occurrence and are a significant positive predictor for several species of conservation concern. Northern Bobwhite may be a better indicator in those habitat types than open pine. It should be noted that the results of this study apply to the gulf-coastal plain, and results, such as the lack of an association of Northern Bobwhite with open-pine conditions, may not necessarily hold for longleaf habitat types in other regions.

Naugle et al. (2001) also used a landscape-scale approach to predict habitat suitability for wetland birds (in the Prairie Pothole region of South Dakota), and found that some bird species are influenced by local vegetation structure (stand-scale factors) while other species are affected by landscape-scale factors. They used an overlay of GIS layers, similar to this research, which included a wetlands layer and a land-use layer to determine areas on the landscape that were suitable protected wetlands (Naugle et al. 2001). Using a landscape-scale approach as a coarse filter proved beneficial because many bird species require suitable local habitat structure, but if this suitable habitat is within an unsuitable landscape (highly fragmented, not large enough, near high urban densities, etc.) birds may not be able to persist in the area (Naugle et al. 2001). We

recommend a similar approach to identify areas on the landscape in Mississippi for longleaf pine conservation and restoration.

Today ecosystems and the wildlife they contain face widespread issues such as habitat loss, fragmentation, increased urban density, and climate change. Using a multi-scale approach is the most effective way to conserve and restore ecosystems and wildlife habitat (Tirpak et al. 2009; Bonnot et al. 2013). The multi-scale framework employed in this study was developed as an aid to assist in restoring historic conditions of open pine in areas that contain suitable landscape- and stand-scale endpoints and can be managed to promote priority species presence and benefit bird communities as a whole. Knowledge of how stand-scale factors affect local wildlife can be used to manage habitat characteristics such as forest structure and vegetation composition in these restored areas to promote priority wildlife occupancy and persistence (Tirpak et al. 2009).

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