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RESEARCH ARTICLE

The relative importance of multiscale factors in the distribution of Bachman's Sparrow and the implications for ecosystem conservation

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ABSTRACT

Recent research has shown that landscape-level changes, namely habitat loss and fragmentation, can play an important role in determining the distribution of species across a variety of ecological systems. However, the influence of these large-scale factors in relation to small-scale factors, such as local vegetation structure or composition, is poorly understood. We used Bachman's Sparrow (*Peucaea aestivalis*) as a surrogate species to measure the relative importance of local vegetation and large-scale habitat distribution in the Onslow Bight region of North Carolina, USA. We conducted repeated point counts at 232 points within 111 habitat patches between April 10 and July 20, 2011. We then fit a series of single-season occupancy models, including both local and landscape-level predictors, to identify those that best explained the distribution of Bachman's Sparrows. We documented a strong response to vegetation characteristics best maintained via prescribed fire, but the most influential predictor of Bachman's Sparrow occupancy was the amount of habitat within 3 km. Specifically, the probability of Bachman's Sparrow occurrence was close to zero in landscapes comprised of $<$10% habitat, regardless of local vegetation conditions. Our results illustrate the strong influence of habitat loss on Bachman's Sparrow and likely on other members of this community, many of which are of high conservation concern.

Keywords: Bachman's Sparrow, dispersal, fire, fragmentation, herbaceous cover, landscape, patch

Importancia relativa de los factores a múltiples escalas en la distribución de *Peucaea aestivalis* y las implicancias para la conservación de los ecosistemas

RESUMEN

Las investigaciones recientes han demostrado que los cambios a nivel de paisaje, como la pérdida de hábitat y la fragmentación, pueden jugar un rol importante en determinar la distribución de las especies a través de una variedad de sistemas ecológicos. Sin embargo, poco es lo que se sabe sobre la influencia de estos factores de gran escala en relación con los factores de pequeña escala, como la estructura local de la vegetación o su composición. Empleamos a la especie *Peucaea aestivalis* como un modelo para medir la importancia relativa de la vegetación local y de la distribución del hábitat a gran escala en la región de Onslow Bight en Carolina del Norte. Realizamos conteos repetidos en 232 puntos al interior de 111 parches de hábitat entre el 10 de abril y el 20 de julio de 2011. Luego, ajustamos una serie de modelos de ocupación para una estación única incluyendo predicciones a nivel local y a nivel de paisaje para identificar aquellos modelos que mejor explicasen la distribución de *P. aestivalis*. Documentamos una fuerte respuesta a las características de la vegetación mantenidas adecuadamente por medio de los fuegos prescriptos, pero el predictor más influyente de la ocupación de *P. aestivalis* fue la cantidad de bosque de pino de dosel abierto dentro de los 3 km. Específicamente, la probabilidad de ocurrencia de *P. aestivalis* fue cercana a cero en los paisajes que incluyen $<$10% de bosque de pino de dosel abierto, sin importar las condiciones locales de la vegetación. Nuestros resultados muestran la fuerte influencia de la pérdida de hábitat sobre *P. aestivalis* y probablemente sobre otros miembros de esta comunidad, muchos de los cuales son de alta preocupación en términos de conservación.

Palabras clave: cobertura herbácea, dispersión, fragmentación, fuego, paisaje, parche, *Peucaea aestivalis*

INTRODUCTION

The flora and fauna associated with longleaf pine (*Pinus palustris*) forests are one of the most diverse communities in North America (Peet and Allard 1993, Simberloff 1993, Van Lear et al. 2005). Currently, this ecosystem is also one of the most endangered in North America, occupying a mere 3–5% of its historical range (Frost 1993, 2006, Landers et al. 1995). In addition to the loss in total area, the distribution of this ecosystem across its range has fundamentally changed. Historically, longleaf pine forests dominated the Atlantic and Gulf coastal plains in the

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southeastern United States, interrupted only by rivers and scattered swamps, whereas today these forests persist as isolated patches within a matrix of row-crop agriculture, fire-suppressed pine plantations, and urban development. This fundamental shift in landscape context has important implications for the many plant and animal species that evolved in vast, contiguous tracts of open-canopy longleaf pine forest.

In recent years, attempts to restore functioning landscapes of longleaf pine forest have gained momentum, but the importance of landscape-scale factors to restoration outcomes is not well documented. Developed by a variety of federal, state, and private organizations, the Range-wide Conservation Plan for Longleaf Pine calls for the restoration of 1.9 million ha of longleaf pine forest (Lopez et al. 2013). These efforts include both restoration of previously degraded habitat on public and private lands and acquisition of new lands for conservation. However, information on how site-level factors, landscape characteristics, and land-use history interact to influence restoration outcomes is limited (Brudvig and Damschen 2011). Informed decisions on how best to conserve this ecosystem can be made only after the factors and scales that contribute most to the distribution of species associated with the system have been identified.

We used Bachman's Sparrow (*Peucaea aestivalis*) as a surrogate species to quantify the influence of habitat distribution across various spatial scales on wildlife species associated with the longleaf pine ecosystem. Bachman's Sparrow is appropriate for this purpose because it selects specific vegetation conditions that reflect fire-maintained longleaf pine stands, in particular the presence of a diverse herbaceous groundcover. In fact, Bachman's Sparrow is one of the 6 species used by the U.S. Fish and Wildlife Service for strategic habitat conservation at the landscape scale (Shelton 2014). The range of preferred conditions of Bachman's Sparrows is so narrow that they abandon habitat patches after as little as 3 yr without fire, when grasses begin to form a dense thatch that can restrict movement along the ground (Brooks and Stouffer 2010, Jones et al. 2013) and less fire-tolerant woody species begin to replace existing herbaceous vegetation (Engstrom et al. 1984, Dunning and Watts 1990, Rutledge and Conner 2002, Tucker et al. 2004). In addition, birds may abandon habitat patches when they are burned (Brown 2012) and then likely disperse to other habitat patches. Successful dispersal to new patches will be facilitated by a permeable and connected landscape (Dunning et al. 1995).

Our study expands on previous research which suggested that patch isolation affects colonization of habitat patches by Bachman's Sparrow, possibly because of poor dispersal through the matrix of non–longleaf pine land-cover types (Dunning et al. 1995, Dunning and Kilgo 2000). By modeling Bachman's Sparrow occupancy across a variety of local vegetation characteristics, patch sizes, and degrees of isolation, we quantitatively describe the relative effects of patch-level conditions and larger-scale spatial characteristics on patch occupancy. Our results, along with studies on other species of concern, should help guide restoration of longleaf pine and other rare and declining ecosystems.

METHODS

Study Area

Our study took place in the Onslow Bight region of southeastern North Carolina, USA (Figure 1), which is identified as a "Significant Geographical Area" for longleaf pine conservation by the Longleaf Alliance (Lopez et al. 2013). Three large public properties contained the majority of fire-maintained longleaf pine forest in the region: Croatan National Forest, Marine Corps Base Camp Lejeune, and Holly Shelter Game Lands. In addition to other small public landholdings, a few scattered private properties were managed for longleaf pine forest conservation. Otherwise, the landscape was dominated primarily by loblolly pine (*Pinus taeda*) plantation, row-crop agriculture, and urban development.

Site Selection and Sparrow Surveys

We stratified the study area into 2 categories: (1) open-canopy, pine-dominated forest with a sparse middle story (hereafter referred to simply as "habitat"); and (2) all other areas ("nonhabitat"). Although Bachman's Sparrows have been observed using other habitat types maintained by disturbance, such as clear-cuts and fallow fields, use of these vegetation types is exceedingly rare in North Carolina (J. Carpenter personal communication). To delineate habitat and nonhabitat, we created an index of Bachman's Sparrow habitat suitability by combining remotely sensed data of vegetation cover type and structure in a geographic information system (GIS) using ArcGIS version 10 (ESRI, Redlands, California, USA). First, land-cover data from the National Land Cover Database (2006) and LANDFIRE (2008) were weighted according to Bachman's Sparrow habitat requirements described in the current literature (Table 1). Specifically, each cell (all datasets were in raster format with 30×30 m resolution) was reclassified with a value of 2 for the most suitable cover types, a value of 1 for areas that were marginal, and a value of 0 for areas that were unsuitable. Using a similar approach, we then reclassified layers of vertical habitat structure (canopy height, canopy cover, middle story cover, and understory cover) derived from full-return light detection and ranging (LiDAR) data collected for the North Carolina Floodplain Mapping Program (2001). Again, each cell was reclassified as most suitable (2), marginal (1), or unsuitable (0) in each of the 4 layers of

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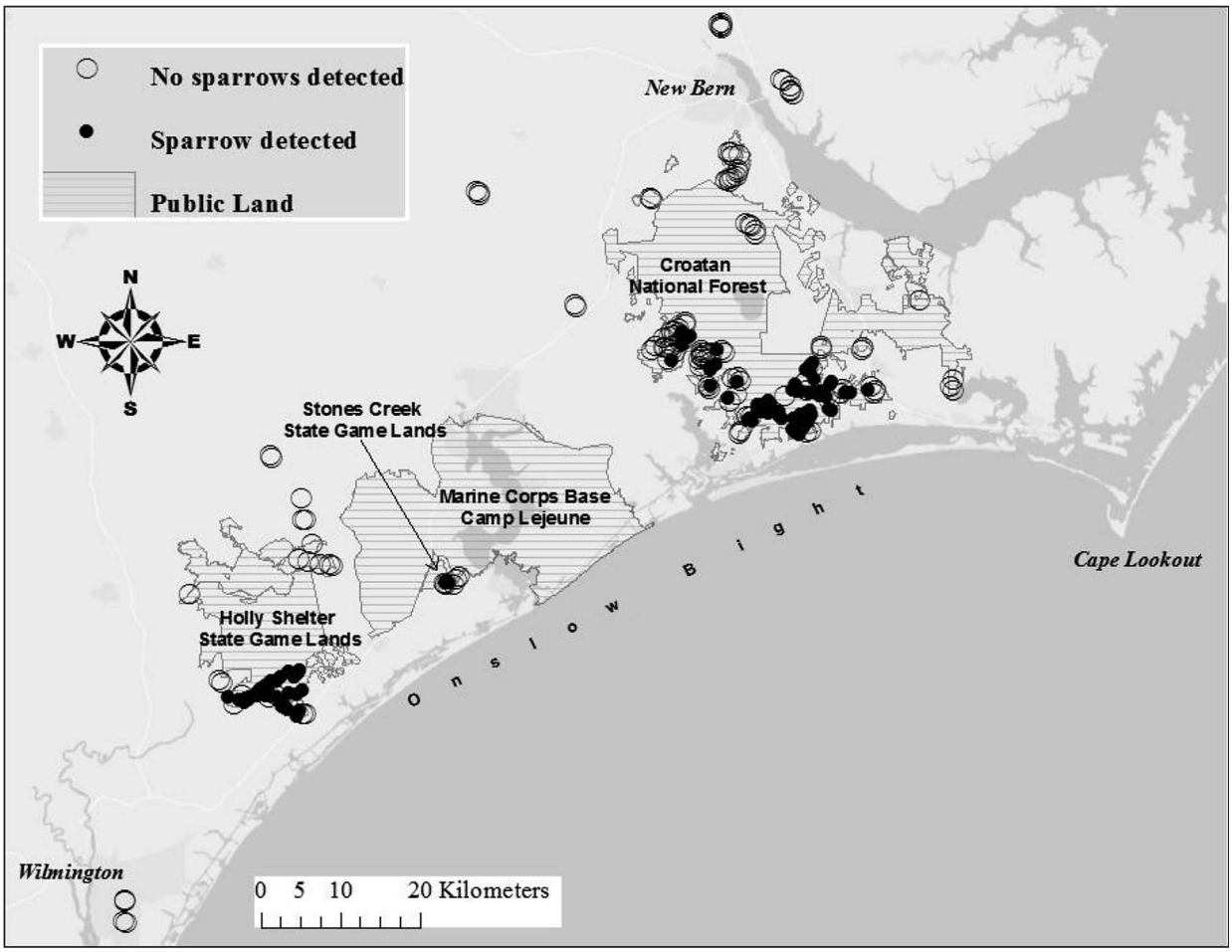


FIGURE 1. Map of Bachman's Sparrow survey locations in the Onslow Bight region of southeastern North Carolina, USA, 2011.

vertical habitat structure (Table 1). Finally, we conducted a series of summations of the 6 total layers, resulting in an index of habitat suitability ranging from 0 to 12. We classified cells of at least 75% of the total possible points ($\geq$9 out of 12) as habitat and areas with values $<$9 as nonhabitat. The resulting layer was a binary grid of 30×30 m cells, in which each cell had a value of either 1 (habitat) or 0 (nonhabitat). We aggregated habitat cells into patches using 8-cell adjacency (i.e. if any of the 4 adjacent or 4 diagonal cells had the same value, they were considered part of the same patch).

We attempted to access as many patches as possible to conduct Bachman's Sparrow and vegetation surveys. First, we contacted local experts to identify properties thought to support longleaf pine community types. We also identified the largest patches of habitat on private land using our GIS model and contacted landowners of the associated properties to solicit access. We were able to access 111 patches of various sizes and degrees of isolation. Patch area ranged from 0.1 ha to 211 ha; isolation, quantified using the proximity index (see below), ranged from 1.4 to 884.

TABLE 1. Criteria used to define the suitability of Bachman's Sparrow habitat patches in southeastern North Carolina, USA, 2011.

		LiDAR				Land cover	
Suitability	Score	Canopy height	Canopy cover	Midstory cover [a]	Understory cover [b]	SEGAP	LANDFIRE
Unsuitable	0	$<$7 m	$<$1%	$>$10%	$>$25%	Non-pine	Non-pine
Marginal	1	7–13 m	$>$30%	5–10%	10–25%	"Other" pine	"Other" pine
Suitable	2	$>$13 m	1–30%	$<$5%	$<$10%	Longleaf pine	Longleaf pine

[a] Vegetation 3–7 m tall.
[b] Vegetation 1–3 m tall.

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To choose locations within these patches to survey for Bachman's Sparrows, we randomly selected the maximum number of survey points within each patch, while maintaining a minimum of 250 m between survey points and 50 m from the patch boundary. After excluding 21 points because of inaccessibility, we surveyed 232 points (Figure 1). Of those 232 points, 94 were visited 5 times, 89 were visited 4 times, 37 were visited 3 times, 11 were visited twice, and 1 was visited once. Some sites were sampled less because of logistical constraints such as hunting season or restrictions on private land; however, by sharing the detection histories from all sites, our analysis accommodates an unbalanced sampling design (Fiske and Chandler 2011). Between April 8 and July 25, 2011, we randomly selected 1 of 4 observers to conduct each visit within 4 hr of sunrise. For the first 3 min of each survey (hereafter "passive survey period"), we recorded all visual and aural Bachman's Sparrow detections, along with the estimated distance at the time of detection. We then broadcast a 30-s recording of a singing Bachman's Sparrow, followed by 5 s of call notes, using an mp3 player and portable speakers. Immediately following the broadcast, we surveyed Bachman's Sparrows for an additional 3 min (hereafter "active survey period"). We recorded detections for all individuals during the passive and active survey periods independently, and only detections at $<$200 m were used in the analysis.

Vegetation

Although fire has been shown repeatedly to be an important factor in Bachman's Sparrow habitat use, obtaining accurate and complete fire-history data (i.e. time since last burned, burn season, fire frequency, fire intensity) was not possible at the scale of our study. Instead, we measured the vegetation characteristics most affected by fire, namely groundcover structure and composition. We quantified groundcover vegetation during each visit, using an index of vegetation density calculated by recording the number of 0.1-m intervals, or "scores," containing vegetation within 1 cm of a vertical 1-m pole (Mills et al. 1989, Dunning and Watts 1990, Plentovich et al. 1998, Moorman and Guynn 2001, Tucker et al. 2004). We categorized each score by grass, forb–fern, woody vine–shrub (hereafter "shrubs"), switchcane (*Arundinaria gigantea*), or dead vegetation. We repeated this measurement every 10 m along a 100-m transect radiating away from the survey point at a random compass bearing. At successive visits, the procedure was repeated with a new random bearing. Understory vegetation height, also recorded by vegetation type using the same categories described above, was obtained by recording the tallest "score" on the 1-m pole, effectively rounding up to the nearest 0.1 m. Using a 10-factor prism, we also measured basal area at the survey location during the first visit, and 50 m away from the survey point at a random bearing during successive visits. We averaged measurements of vegetation score, height, and basal area across visits to obtain 1 value for each survey point.

Landscape

We calculated landscape metrics for the habitat patches delineated in our GIS analysis using the software package FRAGSTATS (McGarigal et al. 2002). For each patch, we calculated the area of the patch and the proximity of neighboring patches (hereafter "proximity"), a commonly used metric of patch isolation (greater proximity = less isolated). This metric incorporates both the distance and the area of all neighboring patches within a specified search distance, or "neighborhood" (McGarigal and McComb 1995). To define this search distance, we used an estimated dispersal distance derived from the proportional relationship between territory size and juvenile dispersal described by Bowman (2003). Using this relationship, the largest Bachman's Sparrow home ranges reported by Cox and Jones (2007) correspond to an estimated dispersal distance of $\sim$3 km. Use of this scale was supported by a study of radio-tagged Bachman's Sparrows in which individuals were occasionally observed moving 3–4 km in a day (Brown 2012). As such, the calculation of proximity for a given patch incorporated all other patches within 3 km of the focal patch.

We calculated the amount of habitat within a given distance from each survey point ("percent habitat"), a metric of habitat contiguity that has proved more reliable and consistent than other metrics and is more easily interpreted (Trzcinski et al. 1999, Cunningham and Johnson 2011, Fahrig 2013). We calculated the percent habitat within the estimated dispersal distance discussed above (3 km), and also within a distance of 1 km, which is intermediate between the 3-km scale and the local scale of the measured vegetation characteristics. Because the minimum distance between survey points was 250 m, these 1-km and 3-km buffers sometimes overlapped for adjacent points, which violated the assumption of independence between sites. However, this lack of independence does not influence model selection (Pan 2001, Cunningham and Johnson 2006), and we took measures to account for the resulting spatial autocorrelation in our parameter estimation procedure (described below). In summary, our analysis incorporated variables at 4 scales: (1) within 100 m of the sampling location (groundcover score, groundcover height, and tree basal area), (2) the patch in which the sampling location was located (patch area), (3) the landscape within 1 km of the site (percent habitat), and (4) the landscape within 3 km of the site (proximity and percent habitat).

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Model Selection

Using the package "Unmarked" in program R (R Core Team 2013), we fit a set of single-season, single-species hierarchical occupancy models (Fiske and Chandler 2011). This software allows for easy comparison of large model sets for occupancy and detection and, thus, was ideal for comparing different combinations of multiple variables. We incorporated both the passive and the active survey data by including a binary indicator variable of survey type in all models, with a "1" corresponding to the active survey. Specifically, 1 visit consisted of 2 consecutive, yet distinct, survey periods; the first passive survey period was assigned a value of 0 for the covariate "survey type," and the second survey using playback was assigned a value of 1 for survey type. To account for imperfect detection, we first fit a series of models containing all possible combinations (including the null model) of a linear effect of observer and both linear and quadratic effects of date as covariates on detection probability (p). In addition to these observation covariates, Unmarked allows for the incorporation of site covariates on detection. We anticipated that vegetation conditions would influence detection, so we fit models containing all combinations of the site covariates "basal area" and "shrub height" as well. We selected the best detection model according to the lowest value of Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and used this model for the detection component of all successive models.

We then modeled site-level occupancy (ψ) at each site. We used grass score as a site-level covariate for occupancy, because previous research has shown this to be an important predictor of Bachman's Sparrow habitat selection (Plentovich et al. 1998). In addition, we added a quadratic effect of grass score because we expected Bachman's Sparrow occurrence to increase with grass score, but then to decline if dense grass impeded the birds' movement (Brooks and Stouffer 2010). We also included basal area and shrub height as site-level covariates because these are directly affected by management, particularly prescribed fire (Tucker et al. 2004, Cox and Jones 2009). For the larger-scale effects, we included linear effects of all landscape metrics previously described. However, a preliminary analysis revealed that percent habitat at 1 km and at 3 km were correlated ($r > 0.5$) with each other and with both patch area and proximity; thus, all models containing percent habitat did not contain either patch area or proximity. We standardized all continuous covariates by subtracting the mean and dividing by the standard deviation. As with detection, we fit all possible models and selected the best model according to the lowest AIC value (Burnham and Anderson 2002). If >1 model had ΔAIC < 2 and differed only by noninformative parameters, we chose the more parsimonious model as the best model (Arnold 2010).

Model Inference

To further investigate the strength of covariate relationships, we refit the best model in a Bayesian framework using the "R2WinBUGS" package in R. In addition to the inherent advantages of Bayesian inference regarding interpretation of uncertainty (Kéry 2012), this approach allowed us to incorporate random effects. Specifically, we included a random effect of the patch in which the site was located, because some patches contained >1 sampling location. This allowed us to separate variability in the response due to a site being in a different patch from the variability in the characteristics of that site (Saracco et al. 2011). To determine the relative strength of covariate relationships, we defined a significance threshold using the 95% credible interval (CRI) of posterior distributions. We further illustrated covariate relationships by predicting occupancy probability across the range of the covariates at each Markov chain Monte Carlo iteration and plotting the means and 95% CRIs of the posterior distributions.

RESULTS

We detected Bachman's Sparrows at 101 of the 232 total points and at 48 of the 111 patches. The best detection model included all the covariates we modeled (Table 2). The average probability of detection ranged from 0.40 to 0.68 for the 4 different observers across all surveys. Because we included data from both passive and active surveys in all models, we did not use model selection to evaluate the importance of this covariate. However, the 95% CRI of the posterior mean was positive and did not overlap zero, which suggests that the use of playback significantly increased detection probability (Table 3). All other covariates (date, shrub height, and basal area) had a negative relationship with detection, though the quadratic effect of date was positive, reflecting an increase in detection toward the end of the season.

Among the sites we surveyed, patches on state or federally owned lands were typically larger, and the associated landscapes were more connected than those on private or municipal properties (Table 4). However, vegetation conditions were comparable across ownership types, though state-owned sites had higher grass scores than other ownership types, and privately owned sites had lower basal areas. The majority of the sites we surveyed were on federally owned properties, but these sites had highly variable vegetation conditions (Table 4).

The best occupancy model included effects of shrub height, percent habitat within 3 km, and both linear and quadratic effects of grass score (Table 3). The next-best model was also competitive (ΔAIC < 2; Table 3), though it differed from the top model only by the inclusion of basal area. The top 7 models contained effects of both grass score and percent habitat within 3 km, suggesting a strong

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TABLE 2. Number of parameters (*K*), Akaike's Information Criterion (AIC), difference in AIC (ΔAIC), model weight (ω), and negative log likelihood (–LogLike) for the top-ranked models of Bachman's Sparrow detection and occupancy in the Onslow Bight, North Carolina, USA, 2011.

Model	*K*	ΔAIC [a]	ω	–LogLike
Detection (*p*)				
type [b] + date + date^2 + observer + BA [c] + shrub [d]	10	0.00	1.00	666.00
Occupancy (ψ)				
shrub + PC3 [e] + grass [f] + grass^2	14	0.00	0.46	623.39
shrub + PC3 + grass + grass^2 + BA	15	1.42	0.23	623.10
shrub + PC3 + grass	13	2.30	0.15	625.54
shrub + PC3 + grass + BA	14	3.82	0.07	625.30

[a] Values of AIC for the top-ranked models for detection and occupancy were 1,351.99 and 1,274.78, respectively.
[b] Survey type (i.e. active or passive).
[c] Basal area.
[d] Shrub height.
[e] Percent habitat within 3 km.
[f] Grass score.

relationship between these variables and Bachman's Sparrow occupancy probability. All models containing one of the landscape variables ranked higher than their analogous models without these variables; models containing percent habitat within 3 km performed best (Table 2).

Analysis of the covariate relationships of the best model provided further support for the importance of percent habitat within 3 km, grass score, and shrub height. Of these covariates, the posterior mean of percent habitat within 3 km was greatest and, thus, had the strongest relationship with occupancy. However, the 95% CRIs for percent habitat within 3 km and grass score overlapped each other (Table 3). As more of the surrounding landscape consisted of Bachman's Sparrow habitat, occupancy probability increased. Specifically, sites with at least 20% (~560 ha) habitat in the surrounding landscape had an occupancy probability >0.75, whereas sites with only 10% (~280 ha) habitat within 3 km had an occupancy probability close to zero (Figure 2). Also, occupancy probability increased with increasing grass score; however, the best model included a negative quadratic effect of grass score as well. Thus, as the average grass score exceeded 2.2, the occupancy probability began to decrease. There was only weak statistical support for this trend (95% CRI slightly overlapped zero; Table 3). Lastly, occupancy probability decreased sharply with increasing shrub height, such that the likelihood of Bachman's Sparrow occurrence at sites with shrubs taller than 0.5 m was close to zero (Figure 2).

TABLE 3. Posterior means and 95% credible intervals of parameter estimates for continuous covariates of detection and occupancy probability for our top-ranked occupancy model of Bachman's Sparrow in southeastern North Carolina, USA, 2011.

Covariate	Mean	2.5%	97.5%
Detection (*p*)			
Type [a]	0.90	0.61	1.20
Date [b]	−0.17	−0.31	−0.02
Date^2	0.37	0.21	0.54
Shrub	−0.72	−0.96	−0.48
BA	−0.37	−0.54	−0.19
Occupancy (ψ)			
Grass	1.73	0.72	3.02
Grass^2	−0.51	−1.21	0.19
Shrub	−1.04	−2.11	−0.17
PC3 [c]	2.28	1.13	3.93

[a] Indicator variable for surveys after call-playback.
[b] Date of survey.
[c] Percent habitat within 3 km.

DISCUSSION

Our findings suggest that large-scale patterns play an important role in the distribution of Bachman's Sparrows. Although local vegetation conditions, particularly herbaceous groundcover, are often emphasized as the most critical aspects of Bachman's Sparrow habitat (Dunning and Watts 1990, Haggerty 1998), we found that Bachman's Sparrow occurrence was also strongly influenced by the percent habitat in the surrounding landscape. As shown by others, consideration of the roles of both local vegetation conditions and the distribution of habitat at larger scales is important to directing habitat conservation for many species (Lichstein et al. 2002, Cunningham and Johnson 2006). Thus, a regional perspective will help ensure that local-scale longleaf pine restoration efforts successfully accommodate Bachman's Sparrow and other species that depend on habitat contiguity.

The sensitivity of Bachman's Sparrows to habitat contiguity is potentially related to dispersal, which has been identified as one of the primary mechanisms

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TABLE 4. Summary statistics (means ± SD) by land ownership for all covariates used to model Bachman's Sparrow occupancy in the Onslow Bight, North Carolina, USA, 2011.

	Ownership				
	Municipal ($n = 4$)	Private ($n = 17$)	State ($n = 60$)	Federal ($n = 151$)	All ($n = 232$)
Area (ha)	41.6 ± 51.4	23.0 ± 13.3	54.0 ± 61.3	84.3 ± 60.1	71.2 ± 61.1
Proximity index	59.6 ± 34.9	62.8 ± 72.8	73.9 ± 77.8	152.9 ± 132.8	124.3 ± 122.2
Habitat within 3 km (%)	8.2 ± 0.7	12.2 ± 6.5	13.8 ± 5.5	18.0 ± 5.1	16.3 ± 5.8
Habitat within 1 km (%)	10.2 ± 2.3	18.6 ± 6.7	23.5 ± 12.5	31.2 ± 9.0	27.9 ± 10.9
Grass score	0.4 ± 0.2	0.8 ± 0.6	1.3 ± 0.7	0.9 ± 0.8	1.0 ± 0.8
Shrub height (m)	1.5 ± 0.5	2.0 ± 1.4	1.8 ± 1.2	2.4 ± 1.6	2.2 ± 1.5
Basal area (m^2 ha^{-1})	10.3 ± 3.9	6.4 ± 4.6	9.6 ± 4.1	13.1 ± 3.7	11.8 ± 4.4

explaining the effects of fragmentation on birds (Lampila et al. 2005) and has been suggested to be related to Bachman's Sparrow habitat use (Dunning et al. 1995). Individuals may abandon a patch either because it burned recently (Seaman and Krementz 2001) or because the lack of fire permitted unsuitable vegetation conditions to develop (Engstrom et al. 1984, Tucker et al. 2004), potentially requiring multiple dispersal events in a lifetime (Cox and Jones 2010). Isolation of a habitat patch can then amplify the challenges associated with each of these dispersal events (Lampila et al. 2005). Increased landscape connectivity will facilitate successful dispersal to previously unoccupied habitat (Dunning et al. 1995). However, a recent study observed little genetic distinction among Bachman's Sparrow populations separated by large natural and anthropogenic barriers, suggesting that individuals may readily traverse such barriers and that dispersal may not be as limiting as previously thought (Cerame et al. 2014). More research is needed to better understand the mechanisms driving the observed sensitivity to the distribution of habitat at large scales. For example, monitoring habitat use over multiple years may better elucidate patterns of occupancy dynamics and the underlying mechanisms.

Dependence on landscape contiguity in longleaf pine ecosystems is not unique to Bachman's Sparrows. Several studies have shown that habitat fragmentation negatively affects Red-cockaded Woodpeckers (*Picoides borealis*), possibly by limiting dispersal of juvenile birds (Rudolph and Conner 1994, Thomlinson 1995, Azevedo et al. 2000, Kesler and Walters 2012). More recently, research on seasonal migrations of gopher frogs (*Lithobates capito*) in North Carolina revealed that individuals moved 0.5–3.5 km between breeding ponds and summer refugia; hence, the amount of contiguous, managed longleaf pine forest required for population persistence (i.e. 3,739 ha around breeding ponds) is far greater than previously thought (Humphries and Sisson 2012). Similarly, our findings suggest that patches are suitable for Bachman's Sparrows only when there is ≥560 ha of habitat within 3 km. This consistent pattern of connectivity dependence among longleaf pine–associated species likely reflects the histor-

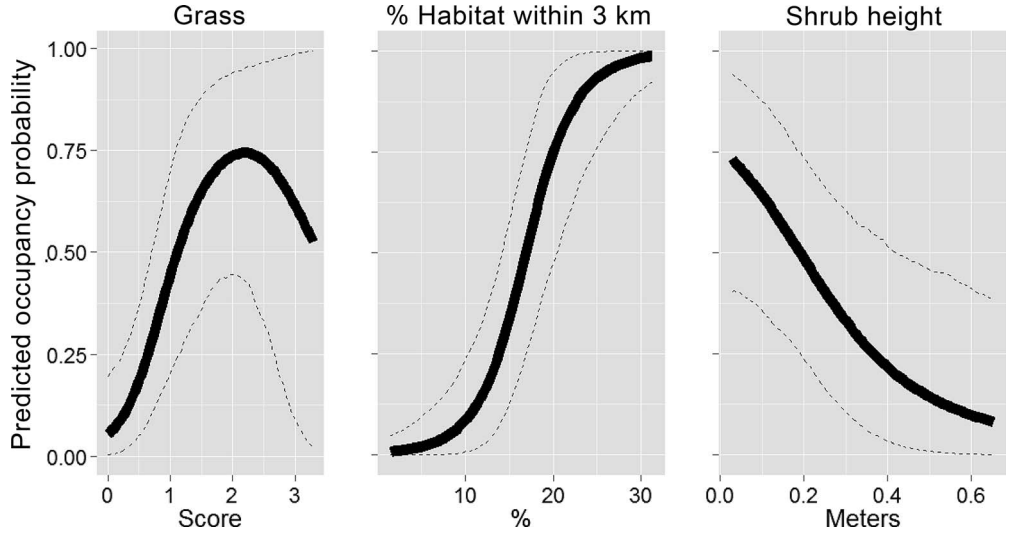


FIGURE 2. Posterior means (solid lines) and 95% credible intervals (dashed lines) of Bachman's Sparrow occupancy probability across the range of each occupancy covariate using our best model.

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ically contiguous distribution of this forest type. As such, restoration of isolated patches may have limited benefits for some species associated with the longleaf pine community, irrespective of whether vegetation conditions in the patches are ideal. This does not imply that we advocate against the continued management of patches with high ecological integrity but less habitat in the surrounding landscape. The longleaf pine community is diverse and contains species that are exceedingly rare or that have complex habitat associations that may benefit greatly from localized conservation efforts. Nonetheless, future restoration efforts targeting areas with high habitat connectivity will likely be most effective in accommodating the entire suite of species associated with longleaf pine forest.

Although we did not incorporate the effect of fire directly, the vegetation characteristics shown to be most important to the distribution of Bachman's Sparrows closely reflect conditions resulting from frequent, low-severity fire (Tucker et al. 2004, Cox and Jones 2009). Although earlier studies have reported greater Bachman's Sparrow occupancy in areas with high grass density (Dunning and Watts 1990, Plentovich et al. 1998), we documented evidence of decreasing occupancy beyond a threshold of grass score, consistent with more recent work by Brooks and Stouffer (2010). Dense grass may reduce bare groundcover, which is an important characteristic of nest-site locations (Jones et al. 2013). In the absence of fire, the formation of a dense grass thatch may restrict movement of Bachman's Sparrows, rendering the site less suitable. As more time elapses without fire, less fire-tolerant woody species can outcompete herbaceous vegetation (Engstrom et al. 1984, Glitzenstein et al. 2003). Although alternative methods are available to control fire-intolerant woody vegetation, such as mechanical thinning and the use of herbicides, prescribed fire best mimics natural disturbance processes and maintains a diverse herbaceous layer (Barnett 1999, Frost 2006). Furthermore, frequent fire, used either exclusively or in addition to other treatment methods, has proved beneficial for a variety of wildlife in longleaf pine systems (Wilson et al. 1995, Russell et al. 1999, Litt et al. 2001, Karmacharya et al. 2012).

Efforts to restore the longleaf pine ecosystem should involve efforts to both establish and maintain the vegetation conditions that characterized historical longleaf pine forest, and should also include larger-scale coordinated efforts focused on landscapes comprising $\geq$20% habitat. This is particularly important as restoration efforts continue to shift to private lands that typically are more fragmented than public lands (Riitters et al. 2012). Specifically, private lands adjacent to large patches of forest managed for longleaf pine, such as those on many public lands, may serve to more efficiently conserve some species, given that such properties could still be functionally connected from the perspective of dispersing wildlife. Additionally, the use of prescribed fire should be promoted as an essential management tool for both public and private landowners (Heuberger and Putz 2003). Our data support previous research that demonstrated the necessity of frequent burning to maintain a diverse groundcover layer and prevent the encroachment of woody vegetation (Glitzenstein et al. 2003, Heuberger and Putz 2003). Unfortunately, the logistical and financial resources associated with prescribed fire currently restrict the widespread and frequent use of prescribed fire by private landowners across the historical range of the longleaf pine ecosystem (Alavalapati et al. 2002, Moorman et al. 2002). Overcoming these logistical hurdles will be essential for conserving biodiversity dependent on functional longleaf pine ecosystems.

As habitat loss and fragmentation continue to transform previously connected landscapes into smaller, more isolated patches, an understanding of the relative effects of factors across multiple scales will become increasingly critical. Our results demonstrate the important role of large-scale factors in the longleaf pine ecosystem and the need for regional, coordinated conservation efforts. Future research addressing similar relationships in other systems and the mechanisms responsible will help mitigate the detrimental effects of habitat loss and fragmentation.

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