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Landscape Patterns Associated with Occupancy of Disturbance-Dependent Birds in the Blackland Prairie Ecoregion of Alabama and Mississippi

Neil A. Gilbert^{1,2,*} and Paige F.B. Ferguson¹

Abstract - The Blackland Prairie Ecoregion of Alabama and Mississippi, formerly a mosaic of prairie, shrubland, and forest, has undergone massive landcover change in the past 2 centuries. Even though the region is now dominated by agriculture and ranchland, disturbance-dependent birds—a guild in decline—continue to inhabit the Blackland Prairie Ecoregion. Therefore, we investigated the relationship between landscape patterns at 4 spatial scales (within 200 m, 600 m, 1000 m, and 3000 m of survey points) and occupancy for 17 species of disturbance-dependent birds. We used a Bayesian occupancy model to relate avian detections to landcover covariates and used stochastic search variable selection to identify covariates that were relevant to occupancy for each species. The amount of canopy cover was the covariate most frequently identified as relevant to occupancy. Grassland and open-country species showed a negative relationship with canopy cover, while shrubland species showed a positive relationship with canopy cover. The association between occupancy and covariates was strongest at the smaller spatial scales, though covariates at the larger spatial scales were still selected as relevant to occupancy. Our results highlight the importance for land managers to consider the landscape context prior to making on-the-ground conservation action; measures aimed to conserve grasslands, for example, will likely be ineffective if they take place in landscapes with high canopy cover.

Introduction

Anthropogenic modification of the environment has allowed small numbers of generalist species to thrive while driving declines of many specialists (McKinney and Lockwood 1999). Among birds, disturbance-dependent species (e.g., shrubland and grassland birds) are some of the fastest-declining specialists in North America (Brennan and Kuvlesky 2005, Hunter et al. 2001). Scientists implicate habitat loss—especially from landcover conversion and alteration of natural disturbance regimes—as the greatest cause of declines (Brennan and Kuvlesky 2005).

Prior to European colonization, eastern North America was not completely forested (Askins 1999). Rather, certain regions contained extensive early-successional vegetation, including grassland and shrubland (Hunter et al. 2001). One such area is the Blackland Prairie Ecoregion of Alabama and Mississippi, a crescent-shaped band stretching 500 km from Russell County, AL to McNairy County, TN (Fig. 1; Griffith et al. 2001, Peacock and Schauwecker 2003). However, most of the grassland and shrubland has been converted to agriculture and ranching

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(Brown 2003); for example, it is estimated that 99% of the native prairie has been lost (Noss et al. 1995). These shifts in land use have produced ecological issues such as woody encroachment and extreme erosion (Schotz and Barbour 2009). Conservation and restoration efforts have been limited (Schotz and Barbour 2009), but in the past decade, landowners, state agencies, and nonprofit organizations have begun collaborating with the goal of restoring prairies and managing working lands to more closely resemble native landscapes (Coggin and Gruchy 2012, Schotz and Barbour 2009). The majority of the Blackland Prairie is privately owned; thus, these efforts have targeted private lands (Burger 2012). Although early results have been encouraging, widespread restoration and conservation has been hindered by low landowner participation (Gruchy et al. 2012) and financial cost (Coggin and Gruchy 2012).

Despite the land-use change in the region, several disturbance-dependent bird species persist in the Blackland Prairie Ecoregion and occupy these modified landscapes (Haggerty 2006). However, the Blackland Prairie Ecoregion has received little research attention from biologists, and studies investigating habitat selection of disturbance-dependent birds in the region have been limited. For example, Farrell (2015) investigated landscape patterns associated with occupancy but studied only 3 species of grassland birds, and Monroe et al. (2016) studied vegetation

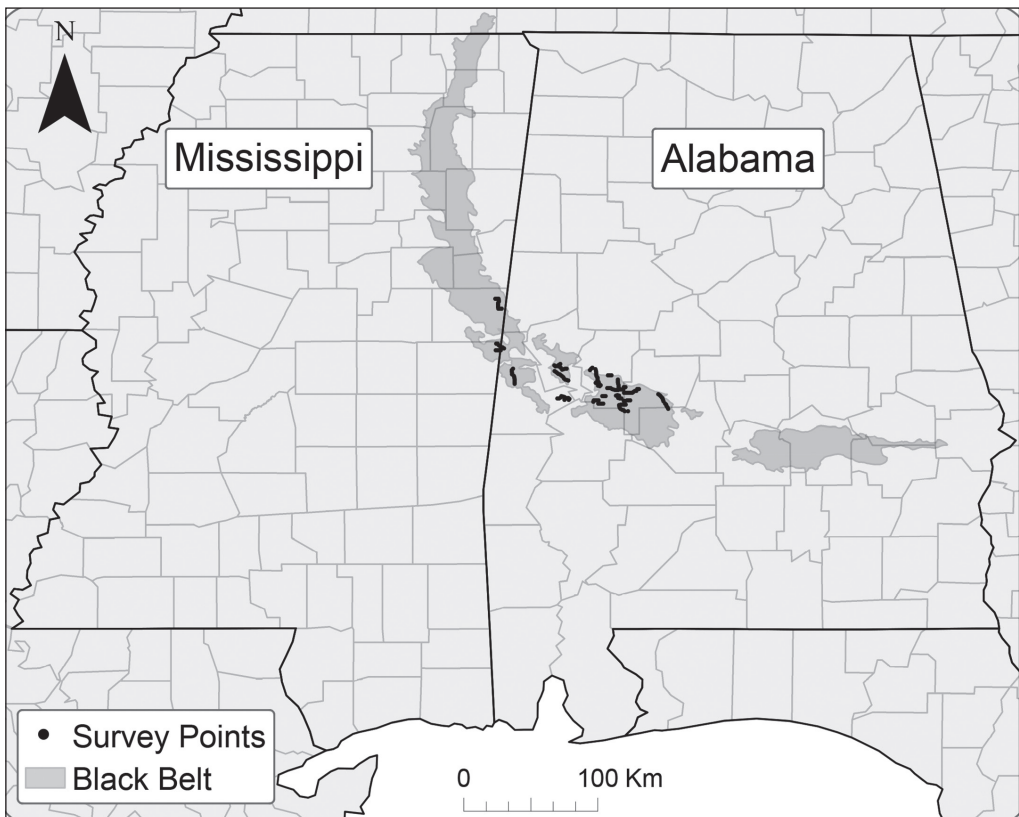


Figure 1. The location of the Blackland Prairie Ecoregion within Alabama, Mississippi, and Tennessee. Point-count locations are shown.

characteristics associated with productivity of just a single grassland species. Therefore, the landscape-scale habitat associations of the region's disturbance-dependent birds are poorly documented. Further, information from other locations cannot necessarily be applied to the Blackland Prairie because habitat preferences and spatial-scale effects vary regionally (Askins et al. 2007). A landscape perspective on habitat preferences is crucial for successful habitat conservation and restoration (McGarigal et al. 2016).

Our objective was to identify landscape patterns associated with occupancy of disturbance-dependent birds in the Blackland Prairie Ecoregion in order to inform additional conservation efforts in the region. We selected 17 disturbance-dependent species known to breed in the region (Haggerty 2006, Post et al. 2009) that represent a successional gradient from species that require open grasslands to species that use shrublands and openings within forests. We predicted the direction of the relationship between occupancy and each landscape pattern we evaluated (Table 1), dividing the selected disturbance-dependent birds into 2 categories: grassland (i.e., preferring grassland or open areas with scattered trees or fencelines) or shrubland (i.e., preferring scrub-shrub, edges, or openings within forests). The grassland species were *Colinus virginianus* L. (Northern Bobwhite; NOBO), *Zenaida macroura* L. (Mourning Dove; MODO), *Tyrannus tyrannus* L. (Eastern Kingbird; EAKI), *Lanius ludovicianus* L. (Loggerhead Shrike; LOSH), *Sialia sialis* L. (Eastern Bluebird; EABL), *Mimus polyglottos* L. (Northern Mockingbird; NOMO), *Sturnella magna* L. (Eastern Meadowlark; EAME), *Icterus spurius* L. (Orchard Oriole; OROR), *Passerina caerulea* L. (Blue Grosbeak; BLGR), and *Spiza americana* (Gmelin) (Dickcissel; DICK). The shrubland species were *Vireo griseus* (Boddaert) (White-eyed Vireo; WEVI), *Toxostoma rufum* L. (Brown Thrasher; BRTH), *Pipilo erythrophthalmus* L. (Eastern Towhee; EATO), *Icteria virens* L. (Yellow-breasted Chat; YBCH), *Piranga rubra* L. (Summer Tanager; SUTA), *Passerina cyanea* L. (Indigo Bunting; INBU), and *Passerina ciris* L. (Painted Bunting; PABU).

Field-Site Description

We focused on the central portion of the Blackland Prairie Ecoregion, conducting surveys in Noxubee and Kemper counties in Mississippi and Sumter, Greene, Hale, Marengo, Perry, and Dallas counties in Alabama (Fig. 1). The topography is flat to undulating and is low (<100 m) in elevation (Griffith et al. 2001). The climate is humid subtropical, with hot summers, mild winters, and abundant (132–142 cm annually) precipitation throughout the year, particularly in the winter months (Griffith et al. 2001). Millions of years ago, the region was covered by a shallow sea, which formed the Blackland Prairie's limestone substrate (Peacock and Schauwecker 2003). Prior to European colonization, the region was a mosaic of prairies interspersed with *Quercus-Carya-Pinus* spp. (oak-hickory-pine) forests and *Juniperus virginiana* L. (Eastern Redcedar) thickets (Barone 2005, Griffith et al. 2001). The prairies were dominated by *Schizachyrium scoparium* (Nees) (Little Bluestem) and *Sorghastrum nutans* (Nash) (Indiangrass), and shared many taxa with the Great Plains (including *Bison bison* L. [American Bison]) but also hosted many

Table 1. Landscape patterns that we hypothesized would be associated with disturbance-dependent bird occupancy. Covariate = the covariate measured; Prediction = the predicted direction of the association (+ for positive, - for negative, +/- for variable by species), with separate predictions provided for grassland/open country species ("Grass") and for shrubland/edge species ("Shrub"); and Justification = our rationale for including the covariate in the analysis. Under the "Covariate" column, AG is the percentage of the landscape that is agriculture, CANOPY is the mean percent canopy cover of the landscape, CONTAG is contagion (a metric of landscape heterogeneity), FALLOW is the percentage of the landscape that is fallow fields, FOREST is the percentage of the landscape that is forested (all forest subcategories aggregated), IMPERV is the mean percent impervious cover of the landscape, PAFRAC is perimeter-area fractal dimension (a metric of patch shapes), PASTURE is the percentage of the landscape that is pasture, and SHRUB is the percentage of the landscape that is shrub. We measured all covariates within 200-m, 600-m, 1000-m, and 3000-m radii of point-count locations

Covariate	Prediction	Justification
AG	Grass +/- Shrub -	Agricultural fields do not provide habitat for grassland birds, but some species use edges within agricultural landscapes (Dechant et al. 1999, Warner 1994). Agricultural edges are associated with decreases in shrubland bird nesting success (Shake et al. 2011).
CANOPY	Grass- Shrub +/-	Landscapes dominated by closed-canopy forests do not provide habitat for grassland or most shrubland birds; however, later-successional shrub or edge species may prefer areas that are more forested (Schlossberg and King 2007, 2008).
CONTAG	Grass + Shrub -	Grassland species favor uniformly open landscapes (high contagion; Ribic and Sample 2001). Shrubbyland species select for heterogeneous landscapes, which are formed by disturbance and contain early-successional vegetation (Swanson et al. 2011).
FALLOW	Grass + Shrub +/-	Fallow fields may provide habitat for certain grassland and edge species but may be too open to host later-successional shrubbyland species (Sample and Mossman 1997).
FOREST	Grass - Shrub +/-	Forested landscapes contain less open space and early-successional vegetation and therefore do not provide habitat for grassland and most shrubbyland species; however, later-successional shrubbyland species may prefer more forested areas (Lumpkin and Pearson 2013).
IMPERV	Grass +/- Shrub +/-	Development is a form of ecological disturbance and may form open space, early-successional vegetation, and heterogeneous landscapes; however, it only benefits urban-adapted species (Schlossberg et al. 2011).
PAFRAC	Grass - Shrub +/-	Many grassland birds prefer grassland patches with simpler edges (Davis 2004); however, complex patch shapes increase the amount of edge, which can be used by some shrubbyland and edge species (Hawrot and Niemi 1996).
PASTURE	Grass + Shrub -	Grassland birds use pastures (Gawlik and Bildstein 1993, Hanauer et al. 2010, Knopf 1994). Landscapes dominated by pasture, however, may be undesirable for shrubbyland birds that require at least some woody vegetation (Schlossberg and King 2007).
SHRUB	Grass +/- Shrub +	Some grassland birds cannot tolerate even small amounts of low woody vegetation (Graves et al. 2010). Shrubbyland bird occurrence should increase with amount of early successional vegetation (Fahrig 2013, Roberts and King 2017).

endemic plant and insect species (Brown 2003). Europeans arrived in the 18th and 19th centuries and converted nearly all of the prairie to agriculture (Brown 2003). Over the ensuing decades, cattle ranching and catfish farming became major forms of land use in addition to agriculture (Peacock and Schauwecker 2003). Currently, the region is a mosaic dominated by ranching, forestry, aquaculture, and agriculture—especially *Zea mays* L. (Corn), *Gossypium hirsutum* L. (Cotton), and Poaceae spp. (hay) (Peacock and Schauwecker 2003). According to the 2011 National Land Cover Database (NLCD), the landcover of our study landscapes (within a 3000-m radius of points) was characterized by pasture (44%), forest (21%), wetland (10%), shrub and agriculture (7% each), open water and development (5% each), and grassland (1%) (Homer et al. 2015). Socioeconomically, the region is characterized by high rates of absentee landowners (Majumdar 2010), while the resident population shows steadily declining densities over the last century and some of the highest poverty rates in the country (USCB 2016).

Methods

Study species

We broadly defined disturbance-dependent birds as species that require some level of ecological disturbance to create habitat (Hunter et al. 2001). Within our set of study species, we aimed to capture a gradient of habitat requirements, from grassland species that require large expanses of open habitat (e.g., Eastern Meadowlark) to late-successional species that occupy open forests or gaps within forests (e.g., Summer Tanager). We used habitat descriptions in Birds of North America Online to determine whether potential study species were disturbance-dependent and then to classify them as either grassland or shrubland species (Rodewald 2015). We analyzed only species that we detected at >10% of study sites because rare detection can be problematic for occupancy modeling (MacKenzie et al. 2006).

Survey protocol

We conducted roadside point-count routes because most of the land in the region was under private ownership and because roadside point-counts do not introduce excessive bias into avian survey data (Lituma and Buehler 2016). Each route was composed of 9–12 points separated by 1-km intervals. We used a stratified random sampling method based on landcover to identify route starting points, and used a systematic method to create subsequent points on the routes (see Supplemental File 1 for more details, available online at <http://www.eaglehill.us/SENAonline/suppl-files/s18-3-S2499-Gilbert-s1>, and for BioOne subscribers, at <https://dx.doi.org/10.1656/S2499.s1>). The total number of points surveyed was 173.

We performed 15-minute, double-observer point counts from 15 May to 5 July 2017. To avoid violating the closure assumption of single-season occupancy models, we designed our survey window to include the breeding season of the study taxa, a period when birds are vocal and relatively sedentary (MacKenzie et al. 2006). Moreover, our survey window was of comparable length to those of many published occupancy studies (e.g., Holubek and Jensen 2015). We conducted

surveys between twilight (i.e., 30 min before sunrise) and 1000 h CST (Ralph et al. 1995). The 2 observers conducted point-counts simultaneously but stood on opposite sides of the field vehicle and did not share information (Farnsworth et al. 2005). During the counting period, the observers recorded all species detected and noted whether each species was <25 m or >25 m from the point. Prior to the point count, the observers paced off 25 m to calibrate their distance estimates. We conducted 3 replicate surveys during the study period, reversing the direction the route was traveled in the second replicate to obtain counts at different times of day.

Covariates quantifying landscape patterns

We measured 9 covariates that we hypothesized would be associated with disturbance-dependent bird occupancy (Table 1). We measured each covariate within radii of 200 m, 600 m, 1000 m, and 3000 m of points. While previous studies have found that landscape patterns within 100–1000 m of points were good predictors of passerine distributions (e.g., Morelli et al. 2013), we included the 3000-m scale because recent studies have identified grassland bird responses to even larger scales (e.g., Dreitz et al. 2017). The points were separated by 1000 m; thus, the landscapes at the larger scales overlapped. While overlapping landscapes can result in higher spatial autocorrelation of predictor variables, they do not impair the independence of model error, which is the critical independence assumption (Zuckerberg et al. 2012).

We measured mean percent canopy cover (CANOPY) at each scale from the NLCD 2011 Tree Canopy cartographic layer using the R package “raster” (Hijmans 2017, Homer et al. 2015). We predicted that grassland species would show a negative association with CANOPY and that most shrubland species would exhibit a positive association with CANOPY (Table 1; Schlossberg and King 2007).

We measured mean percent impervious surface (IMPERV) at each scale from the NLCD 2011 Percent Developed Imperviousness layer using the R package “raster” (Hijmans 2017, Homer et al. 2015). Development is a form of disturbance, but generally only urban-adapted species benefit (Marzluff 2001). Therefore, we predicted a negative relationship between occupancy and IMPERV, though we anticipated exceptions for urban-tolerant species (e.g., Northern Mockingbird; Table 1).

We measured the remaining 7 covariates from the 2016 CropScape data layer (USDA 2016) using FRAGSTATS with the 8-cell neighbor rule (McGarigal et al. 2012). The CropScape layer is based on the NLCD but is updated annually with information about agricultural landcover. Therefore, CropScape shares the NLCD’s 30 m x 30 m resolution and landcover categories with the addition of more detailed agricultural categories. We used CropScape because we were interested in a subset of those agricultural categories and because CropScape provided more recent landcover information (2016) than the latest available NLCD layer (2011).

Of the CropScape covariates, 5 were class-level metrics that quantified the percentage of the landscape (PLAND) comprised of agriculture (AG), fallow fields (FALLOW), forest (FOREST), pasture (PASTURE), or shrubland

(SHRUB). We aggregated CropScape's subcategories for AG and FOREST (e.g., evergreen, mixed, and deciduous for FOREST) because we expected birds to respond to the structure of these landcovers regardless of crop or forest type (Warner 1994). We provide the predicted relationship between each PLAND covariate and occupancy in Table 1.

In addition to the class-level metrics, we calculated 2 landscape-level metrics of landscape configuration: perimeter–area fractal dimension (PAFRAC) and contagion (CONTAG). PAFRAC evaluates the shape of patches; values approaching 1 are associated with landscapes containing patches with simple geometries, while values approaching 2 are associated with landscapes containing patches with convoluted perimeters (McGarigal et al. 2012). We predicted that grassland species, which prefer patches with simple perimeters, would show negative relationships with PAFRAC (Davis 2004), while shrubland species, which use edge habitat, would show positive relationships with PAFRAC (Terraube et al. 2016). CONTAG measures patch aggregation (spatial distribution of 1 landcover class) and interspersion (spatial distribution of all landcover classes relative to each other) (McGarigal et al. 2012). Formally, it is defined as the sum of 2 probabilities: first, the probability that a pixel is of class i , which is equivalent to the proportional representation of that class in the landscape, and second, the probability, given a pixel is of class i , that 1 of the neighboring pixels is of class j (Hargis et al. 1998, McGarigal et al. 2012). CONTAG spans from 0 to 100, with low values describing landscapes having maximally disaggregated and interspersed patch types and high values describing landscapes with patch types maximally aggregated (McGarigal et al. 2012). We predicted that grassland species, which prefer uniformly open landscapes (Ribic and Sample 2001), would show positive relationships with CONTAG, and that shrubland species, which prefer heterogeneous landscapes with early-successional vegetation (Swanson et al. 2011), would show negative relationships with CONTAG (Table 1).

Occupancy model

Occupancy modeling has emerged as a prominent method for analyzing presence/absence (more accurately, detection/nondetection) data in ecology (Bailey et al. 2014). These models account for the imperfect detection inherent to surveys by modeling the probability of detecting the species of interest at site i during survey t , given the species is present (MacKenzie et al. 2006). Occupancy models that also account for false positive detection errors have recently been developed (e.g., Ferguson et al. 2015) to address the fact that false positive detections are pervasive in auditory surveys, and, when unaccounted for, lead to biased inference about occupancy and covariate relationships (Bailey et al. 2014). We used a hierarchical Bayesian occupancy model that estimates occupancy probability ψ_i while accounting for true positive detection probability (p_{1i}) and false positive detection probability (p_{10}) (Ferguson et al. 2015; see Supplemental File 2, available online at <http://www.eaglehill.us/SENAonline/suppl-files/s18-3-S2499-Gilbert-s2>, and for BioOne subscribers, at <https://dx.doi.org/10.1656/S2499.s2>). In order to distinguish between true positive and false positive detections, the model requires

a subset of the detections to be confirmed (i.e., no chance of a false positive detection). We considered detections to be confirmed when both observers detected a species within 25 m (Ferguson et al. 2015).

Across i sites and t surveys, we modeled confirmed detections c_{it} as outcomes of a Bernoulli trial with probability $b * z_i$, where z_i indicates the occupancy state of a site and b is the probability of a confirmed detection (Ferguson et al. 2015). We modeled all detections (i.e., both confirmed and unconfirmed) y_{it} as outcomes of a Bernoulli trial with probabilities dependent upon the states of c_{it} and z_i (Ferguson et al. 2015). We modeled z_i as outcomes of a Bernoulli trial with probability ψ_i , which we modeled as a function of the landcover covariates. We held the detection parameters (i.e., p_{11} , p_{10} , and b) constant across sites and surveys.

Bayesian analysis requires the assignment of prior probability distributions for model parameters. We used *Beta*(4, 4) priors for p_{11} , b , and the intercept of the function relating covariates to ψ_i (Cruz 2019). We used a *Beta*(4, 10) prior for p_{10} , which suggests that if a site is unoccupied, there is a greater chance that an observer will make a true negative detection than a false positive detection (Miller et al. 2012). For the covariate coefficients, we used a mixture of 2 normal prior distributions to perform indicator variable selection (details below).

Stochastic search variable selection

We used stochastic search variable selection (SSVS) to determine which covariates were relevant to occupancy for each species (George and McCulloch 1993, O'Hara and Sillanpää 2009). With this method, indicator variables δ_j are added to the regression model to indicate which of $j = 1, 2, \dots, n$ covariates are important in explaining occupancy (Hooten and Hobbs 2015, O'Hara and Sillanpää 2009).

For each spatial scale, we built a global model containing all standardized (mean = 0, $s = 1$), non-collinear covariates (Pearson's $|r| < 0.7$; Dormann et al. 2013). For the 200-m scale, we omitted PAFRAC from the global model because of missing values, a frequent problem in calculating this metric for small landscapes (McGarigal et al. 2012). For the 600-m scale, we omitted FOREST because of collinearity with CONTAG. Although it is important to consider multiple scales because of the scale dependency of habitat selection (McGarigal et al. 2016), collinearity between the different scales prevented us from constructing a global model containing every covariate measured at all of the scales.

Within the global model at each scale, the regression coefficients β_j were replaced by the product of a binary indicator variable and a regression coefficient, $\delta_j * \beta_j$. We gave the δ_j parameters an uninformative *Bern*(0.5) prior. If the posterior of δ_j approaches 1, the j th covariate is important in the model; conversely, if the posterior of δ_j approaches 0, the effect of the j th covariate is essentially removed from the model. We judged an indicator δ_j with posterior mean > 0.7 to indicate that the j th covariate was important in the model (Weiser et al. 2018). The prior for $\beta_j | \delta_j$ was $\delta_j N(0, c^2 \tau^2) + (1 - \delta_j) N(0, \tau^2)$. Within each Markov Chain Monte Carlo (MCMC) iteration of the model, each β_j is given either a normal prior centered at 0 with a large ($c^2 \tau^2 = 2$) variance when $\delta_j = 1$ or a normal prior centered at 0 with a small

($\tau^2 = 0.02$) variance when $\delta_j = 0$ (Cruz 2019, Hooten and Hobbs 2015). The global models for each scale (200-m, 600-m, 1000-m, and 3000-m scales, respectively) are as follows:

$$\text{logit}(\psi_i) = \beta_0 + \delta_1\beta_1AG_i + \delta_2\beta_2CANOPY_i + \delta_3\beta_3CONTAG_i + \delta_4\beta_4FALLOW_i \\ + \delta_5\beta_5FOREST_i + \delta_6\beta_6IMPERV_i + \delta_7\beta_7PASTURE_i + \delta_8\beta_8SHRUB_i$$

$$\text{logit}(\psi_i) = \beta_0 + \delta_1\beta_1AG_i + \delta_2\beta_2CANOPY_i + \delta_3\beta_3CONTAG_i + \delta_4\beta_4FALLOW_i \\ + \delta_5\beta_5FOREST_i + \delta_6\beta_6IMPERV_i + \delta_7\beta_7PARFAC_i + \delta_8\beta_8PASTURE_i \\ + \delta_9\beta_9SHRUB_i$$

$$\text{logit}(\psi_i) = \beta_0 + \delta_1\beta_1AG_i + \delta_2\beta_2CANOPY_i + \delta_3\beta_3CONTAG_i + \delta_4\beta_4FALLOW_i \\ + \delta_5\beta_5IMPERV_i + \delta_6\beta_6PARFAC_i + \delta_7\beta_7PASTURE_i + \delta_8\beta_8SHRUB_i$$

$$\text{logit}(\psi_i) = \beta_0 + \delta_1\beta_1AG_i + \delta_2\beta_2CANOPY_i + \delta_3\beta_3CONTAG_i + \delta_4\beta_4FALLOW_i \\ + \delta_5\beta_5FOREST_i + \delta_6\beta_6IMPERV_i + \delta_7\beta_7PARFAC_i + \delta_8\beta_8PASTURE_i \\ + \delta_9\beta_9SHRUB_i$$

We fit models in OpenBUGS 3.2.3 using the R2OpenBUGS package and R 3.5.1 (R Core Team 2017, Sturtz et al. 2005). We used 3 MCMC chains with 100,000 iterations, a burn-in of 25,000, and thinning of 5. We assessed convergence via visual inspection of traceplots and the Gelman-Rubin potential scale reduction factor (Rhat); chains with $Rhat \leq 1.1$ were considered converged (Brooks and Gelman 1998).

Model predictive performance

We used the area under the receiver operating characteristic curve (AUROC) to assess the predictive performance of each of the 4 single-scale models after SSVS was performed. In the context of occupancy modeling, models with high predictive performance are expected to correctly classify sites as occupied or unoccupied (Hosmer et al. 2013). The ratio of true positives (i.e., the species occupied the site and the model predicted it) to false positives (i.e., the species did not occupy the site but the model predicted the site was occupied) is plotted using a range of cutoff values (in our case, thresholds in occupancy probabilities that differentiated occupied and unoccupied sites). AUROC ranges from 0 to 1, with 0.5 describing performance no better than random and larger values describing greater discriminatory ability. We used the “plotROC R” package (Sachs 2017) to create AUROC plots for the global model at each spatial scale.

Results

Landscape patterns associated with occupancy

The most frequently selected covariate was CANOPY, which was selected 50 times for 14 species (Table 2, Fig. 2). Grassland species showed consistent negative relationships with CANOPY, while shrubland species exhibited consistent positive relationships with CANOPY (Table 2, Fig. 3). IMPERV, the next most commonly selected covariate, was selected 8 times for 7 species. Five were grassland species, and all but one (Eastern Meadowlark) showed positive associations

Table 2. Covariates associated with disturbance-dependent bird occupancy. For each covariate, we provide the species, ordered by habitat group and then by taxonomy (Chesser et al. 2018), that had the covariate selected. We present the spatial scale at which the covariate was measured. “Mean” reports the mean of the posterior distribution for each parameter. “Lower” and “Upper” are the bounds of the parameter’s 95% credible interval. “Trend 95%” provides the effect direction of each covariate (“+” for positive, “-“ for negative, and “?” for cases in which the 95% credible interval spanned zero). Finally, the “% > 0” column provides the percentage of posterior distribution that was greater than zero. Within the “Species” column, the species are presented with their standard four-letter banding code (USGS 2016). NOBO = Northern Bobwhite, MODO = Mourning Dove, EAKI = Eastern Kingbird, LOSH = Loggerhead Shrike, WEVI = White-eyed Vireo, EABL = Eastern Bluebird, BRTH = Brown Thrasher, NOMO = Northern Mockingbird, EATO = Eastern Towhee, YBCH = Yellow-breasted Chat, EAME = Eastern Meadowlark, OROR = Orchard Oriole, SUTA = Summer Tanager, BLGR = Blue Grosbeak, INBU = Indigo Bunting, PABU = Painted Bunting, and DICK = Dickcissel. [Table continued on following page.]

Species	Group	Covariate	Scale	Mean	Lower	Upper	Trend 95%	% > 0
EAKI	Grass	AG	200	-0.66	-1.44	0.01	?	2.70%
EAME	Grass	AG	600	-0.59	-1.36	0.06	?	5.00%
EAME	Grass	AG	1000	-0.56	-1.13	-0.01	-	2.30%
DICK	Grass	AG	200	0.50	-0.04	1.21	?	95.80%
DICK	Grass	AG	1000	0.52	0.03	1.09	+	98.50%
DICK	Grass	AG	3000	0.72	0.13	1.31	+	99.60%
MODO	Grass	CANOPY	200	-1.20	-2.14	-0.28	-	3.00%
MODO	Grass	CANOPY	600	-1.08	-1.90	-0.23	-	0.40%
MODO	Grass	CANOPY	1000	-0.87	-1.60	-0.10	-	0.90%
EAKI	Grass	CANOPY	200	-1.31	-1.96	-0.76	-	0.00%
EAKI	Grass	CANOPY	600	-1.05	-1.61	-0.55	-	0.00%
EAKI	Grass	CANOPY	1000	-0.86	-1.40	-0.31	-	0.00%
LOSH	Grass	CANOPY	200	-0.9	-1.93	0.01	?	2.90%
LOSH	Grass	CANOPY	600	-1.05	-1.98	-0.07	-	1.20%
LOSH	Grass	CANOPY	1000	-0.65	-1.57	0.08	?	6.30%
EABL	Grass	CANOPY	200	-0.86	-1.53	-0.15	-	0.40%
EABL	Grass	CANOPY	600	-0.79	-1.46	-0.13	-	0.50%
EABL	Grass	CANOPY	1000	-0.7	-1.36	-0.08	-	0.90%
NOMO	Grass	CANOPY	200	-1.52	-2.24	-0.90	-	0.00%
NOMO	Grass	CANOPY	600	-1.51	-2.22	-0.90	-	0.00%
NOMO	Grass	CANOPY	1000	-1.31	-1.90	-0.79	-	0.00%
NOMO	Grass	CANOPY	3000	-0.84	-1.39	-0.27	-	0.00%
EAME	Grass	CANOPY	200	-2.35	-3.05	-1.73	-	0.00%
EAME	Grass	CANOPY	600	-2.77	-3.57	-2.06	-	0.00%
EAME	Grass	CANOPY	1000	-2.39	-3.13	-1.75	-	0.00%
EAME	Grass	CANOPY	3000	-1.50	-2.06	-0.98	-	0.00%
OROR	Grass	CANOPY	200	-1.54	-2.40	-0.83	-	0.00%
OROR	Grass	CANOPY	600	-1.10	-1.79	-0.50	-	0.00%
OROR	Grass	CANOPY	1000	-0.85	-1.51	-0.18	-	0.30%
BLGR	Grass	CANOPY	200	-1.63	-2.44	-0.94	-	0.00%
BLGR	Grass	CANOPY	600	-1.37	-2.13	-0.71	-	0.00%
BLGR	Grass	CANOPY	1000	-1.16	-1.85	-0.56	-	0.00%
DICK	Grass	CANOPY	200	-1.57	-2.32	-0.92	-	0.00%
DICK	Grass	CANOPY	600	-1.48	-2.14	-0.88	-	0.00%
DICK	Grass	CANOPY	1000	-1.29	-1.93	-0.70	-	0.00%
DICK	Grass	CANOPY	3000	-0.91	-1.58	-0.17	-	0.40%
WEVI	Shrub	CANOPY	200	2.20	1.55	2.95	+	100.00%

with IMPERV (Table 2). The other 2 selected were shrubland species; Indigo Bunting showed a negative association, while Eastern Towhee showed a positive association with IMPERV (Table 2). AG was selected 6 times for 3 grassland species; Eastern Kingbird and Eastern Meadowlark showed negative relationships, while Dickcissel showed a positive relationship (Table 2). PAFRAC was selected 4 times for 3 grassland species, all of which showed a positive association (Table 2). CONTAG was selected 3 times for 2 species; Orchard Oriole (a grassland species) showed a negative association, and Painted Bunting (a shrubland species) showed a positive association (Table 2). Finally, PASTURE was selected only for Summer Tanager (a shrubland species) and showed a negative association with occupancy (Table 2).

Table 2, continued

Species	Group	Covariate	Scale	Mean	Lower	Upper	Trend 95%	% >0
WEVI	Shrub	CANOPY	600	2.31	1.66	3.09	+	100.00%
WEVI	Shrub	CANOPY	1000	2.24	1.61	2.98	+	100.00%
WEVI	Shrub	CANOPY	3000	1.91	1.24	2.75	+	100.00%
EATO	Shrub	CANOPY	200	1.66	0.94	2.68	+	100.00%
EATO	Shrub	CANOPY	600	1.61	0.99	2.38	+	100.00%
EATO	Shrub	CANOPY	1000	1.60	0.97	2.37	+	100.00%
EATO	Shrub	CANOPY	3000	1.05	0.31	1.83	+	99.90%
YBCH	Shrub	CANOPY	200	0.70	0.16	1.21	+	99.80%
YBCH	Shrub	CANOPY	600	1.11	0.63	1.66	+	100.00%
YBCH	Shrub	CANOPY	1000	1.03	0.55	1.58	+	100.00%
YBCH	Shrub	CANOPY	3000	0.61	0.07	1.15	+	99.20%
SUTA	Shrub	CANOPY	200	1.51	0.89	2.28	+	100.00%
SUTA	Shrub	CANOPY	600	1.74	0.97	2.69	+	100.00%
SUTA	Shrub	CANOPY	1000	1.40	0.68	2.34	+	100.00%
SUTA	Shrub	CANOPY	3000	1.35	0.62	2.29	+	100.00%
INBU	Shrub	CANOPY	200	1.15	0.51	1.85	+	100.00%
INBU	Shrub	CANOPY	600	1.45	0.82	2.22	+	100.00%
INBU	Shrub	CANOPY	1000	1.30	0.68	2.06	+	100.00%
INBU	Shrub	CANOPY	3000	0.90	0.14	1.66	+	99.50%
OROR	Grass	CONTAG	200	-0.63	-1.57	0.08	?	6.10%
OROR	Grass	CONTAG	3000	-0.65	-1.62	0.09	?	6.40%
PABU	Shrub	CONTAG	1000	0.81	-0.11	1.96	?	92.50%
MODO	Grass	IMPERV	200	1.04	-0.12	2.36	?	92.60%
MODO	Grass	IMPERV	600	1.17	-0.15	2.82	?	90.00%
EABL	Grass	IMPERV	200	0.83	0.11	1.66	+	99.50%
NOMO	Grass	IMPERV	200	1.37	0.09	2.44	+	98.80%
EAME	Grass	IMPERV	3000	-1.23	-2.33	-0.14	-	0.50%
OROR	Grass	IMPERV	200	0.61	-0.02	1.59	?	96.80%
EATO	Shrub	IMPERV	3000	0.69	-0.08	1.92	?	93.20%
INBU	Shrub	IMPERV	200	-0.55	-1.33	0.03	?	3.80%
EAKI	Grass	PAFRAC	600	0.70	0.01	1.41	+	97.60%
EAME	Grass	PAFRAC	600	0.81	-0.02	1.67	?	97.00%
OROR	Grass	PAFRAC	600	1.21	0.20	2.09	+	99.50%
OROR	Grass	PAFRAC	1000	0.83	-0.01	1.67	?	97.10%
SUTA	Shrub	PASTURE	200	-0.59	-1.45	0.08	?	6.30%

In summary, the maximum number of covariates that could possibly be selected was 578 (i.e., if every covariate from all 4 global models had been selected for every species). Across all species, 72 covariates were selected (Table 2, Fig. 2). No covariates were selected for 2 species (Northern Bobwhite and Brown Thrasher). For the other 15 species, 1–8 covariates were selected as important for each species (Table 2). Three covariates (FALLOW, FOREST, and SHRUB) were never selected.

Spatial scale patterns

We assessed spatial scale patterns by comparing the following items: the number of covariates selected per scale, the strength of the relationship between occupancy and the covariates at the different scales, and the predictive performance of the global model at the different scales.

Covariates measured at the smaller spatial scales dominated the selected set of covariates; 23, 19, 18, and 12 covariates were selected for the 200-, 600-, 1000-, and 3000-m scales, respectively (Fig. 2).

CANOPY was the only covariate that was selected frequently enough to evaluate the strength of relationship between occupancy and the covariate at different

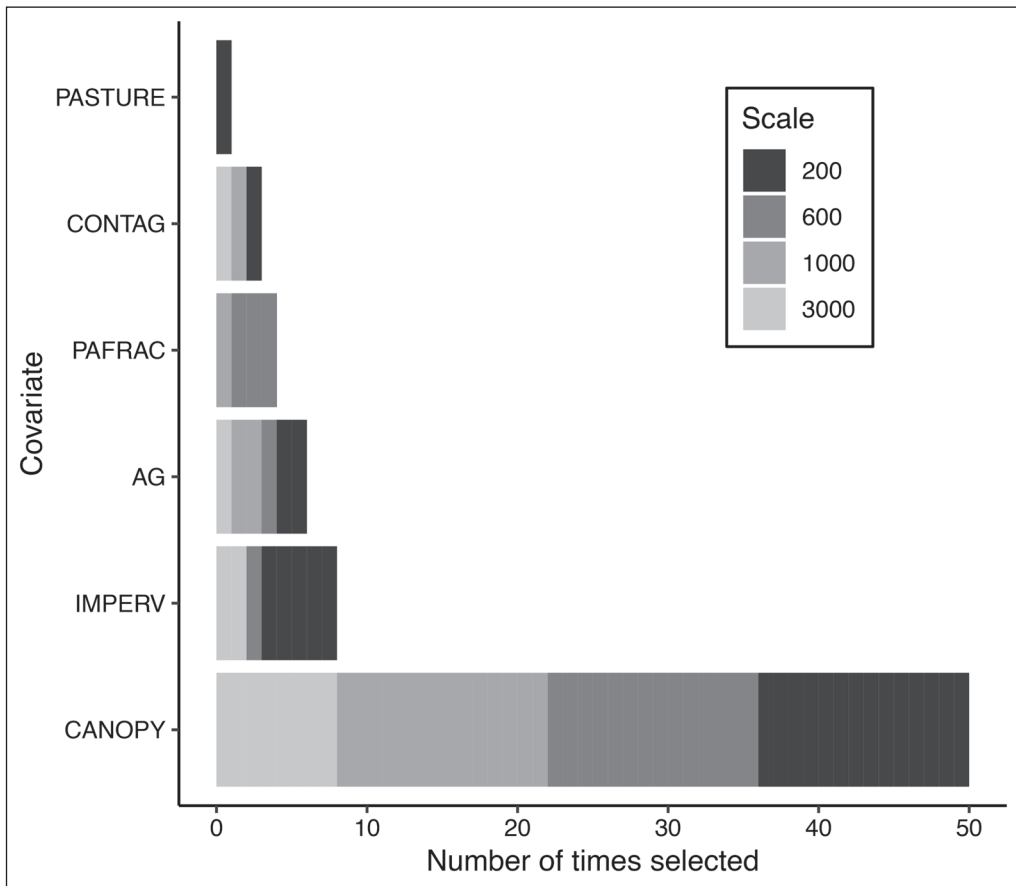


Figure 2. Covariates associated with disturbance-dependent bird occupancy across all species and all spatial scales.

scales for the same species. CANOPY was selected for 14 species; it was selected for all 14 taxa at its 200-, 600-, and 1000-m measures, but for only 8 species at the 3000-m scale. The strongest relationships with occupancy (judged by distance of the coefficient from zero) were seen for the 200-m scale (8 species) and the 600-m scale (6 species; Fig. 3).

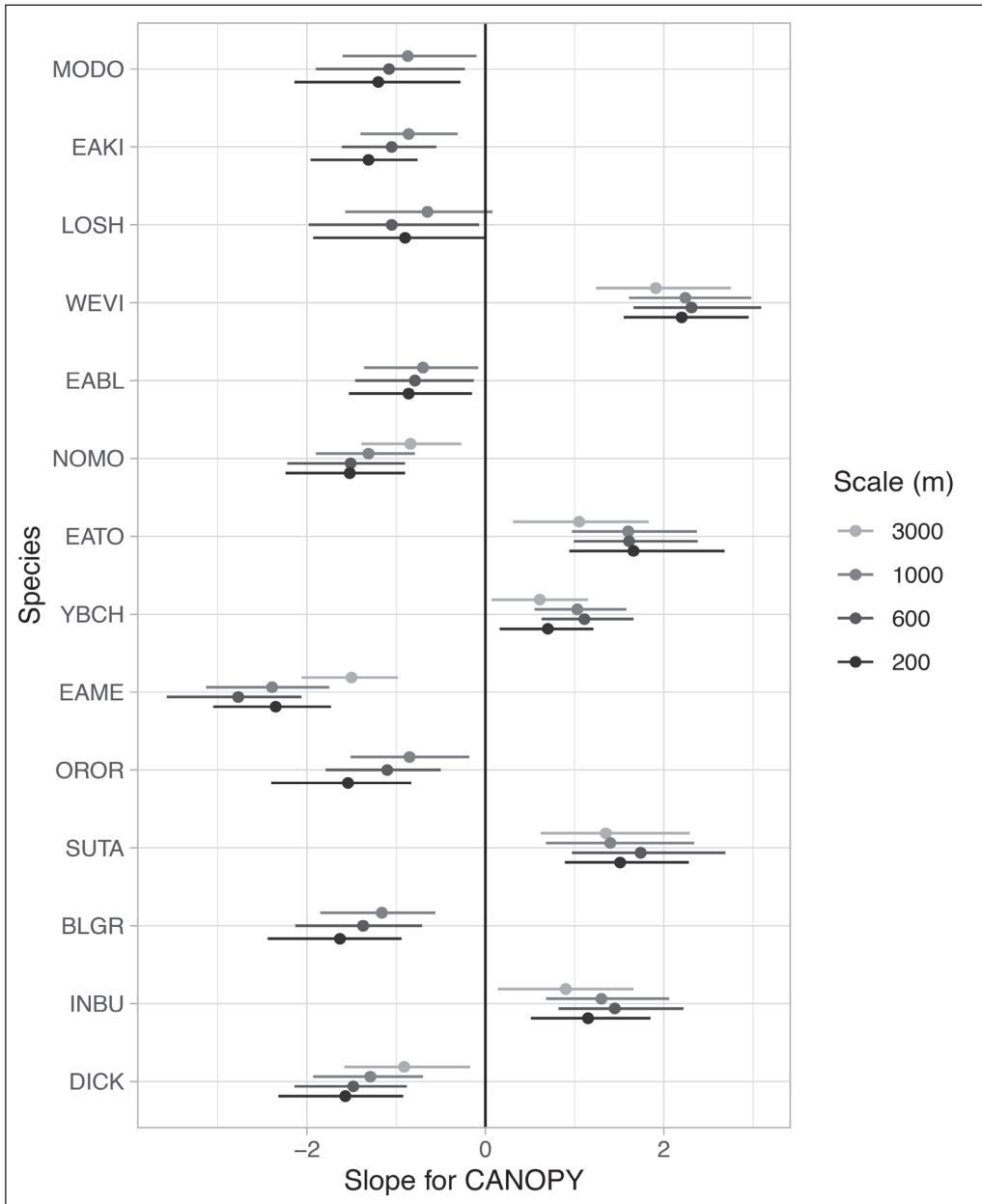


Figure 3. Coefficient estimates for CANOPY for the 14 species for which this covariate was selected. The points represent the mean of the coefficient’s posterior distribution and the bars represent the 95% credible interval.

Model predictive performance was generally good; all but 1 species had AUROC > 0.8 for the best-predicting model (Table 3). The model with the highest predictive performance was the 200-m model for 8 species, the 600-m model for 6 species, the 1000-m model for 1 species, and the 3000-m model for 2 species (Table 3).

Occupancy trends

Occupancy varied between species and oftentimes within species across sites (Fig. 4). The lowest occupancy probabilities (mean and max ψ_i , respectively) were seen for Painted Bunting (0.06 and 0.14), Northern Bobwhite (0.07, 0.19), Loggerhead Shrike (0.10, 0.31), and Brown Thrasher (0.17, 0.56). The highest occupancy rates (mean ψ_i) were seen for Blue Grosbeak (0.74), Mourning Dove (0.70), Northern Mockingbird (0.69), and Indigo Bunting (0.65).

Detection parameters

True positive detection probability (p_{11}) was generally moderate to high, with the lowest mean p_{11} for Brown Thrasher (0.49) and highest for Northern Mockingbird (0.96) (Table 4). False positive detection probability (p_{10}) was usually low (i.e., mean < 0.25 for 13 species; Table 4), though 4 species showed rather high mean values: Mourning Dove (0.64), Northern Mockingbird (0.56), Blue Grosbeak (0.39), and Indigo Bunting (0.32). Observation confirmation probability (b) was generally low (i.e., mean < 0.25 for 16 species), except for Northern Mockingbird, which had a posterior mean of 0.47 (Table 4).

Table 3. Area under the receiver operator characteristic curve (AUROC) for the global models at each spatial scale for all of the study species. Larger values indicate models with better predictive performance.

Species	AUROC200m	AUROC600m	AUROC1000m	AUROC3000m	Highest
NOBO	0.79	0.68	0.78	0.85	3000 m
MODO	0.94	0.92	0.84	0.86	200 m
EAKI	0.85	0.76	0.70	0.60	200 m
LOSH	0.79	0.86	0.78	0.81	600 m
WEVI	0.92	0.93	0.91	0.85	600 m
EABL	0.82	0.78	0.72	0.67	200 m
BRTH	0.62	0.68	0.69	0.68	1000 m
NOMO	0.94	0.93	0.88	0.80	200 m
EATO	0.88	0.88	0.86	0.79	200 m
YBCH	0.77	0.82	0.79	0.68	600 m
EAME	0.92	0.95	0.92	0.83	600 m
OROR	0.92	0.86	0.81	0.77	200 m
SUTA	0.89	0.91	0.89	0.85	600 m
BLGR	0.96	0.92	0.88	0.81	200 m
INBU	0.83	0.84	0.83	0.75	600 m
PABU	0.64	0.90	0.89	0.91	3000 m
DICK	0.85	0.82	0.81	0.78	200 m

Discussion

Landscape patterns associated with occupancy

Canopy cover. CANOPY was the covariate most strongly associated with occupancy (Fig. 2), and this is conceptually fitting. The species we modeled are disturbance-dependent, meaning that they require disturbance followed by varying amounts of succession to create habitat (Hunter et al. 2001). CANOPY provides a measure of the successional stage of the landscape; for example, a landscape at a late-successional stage will have a high value for CANOPY.

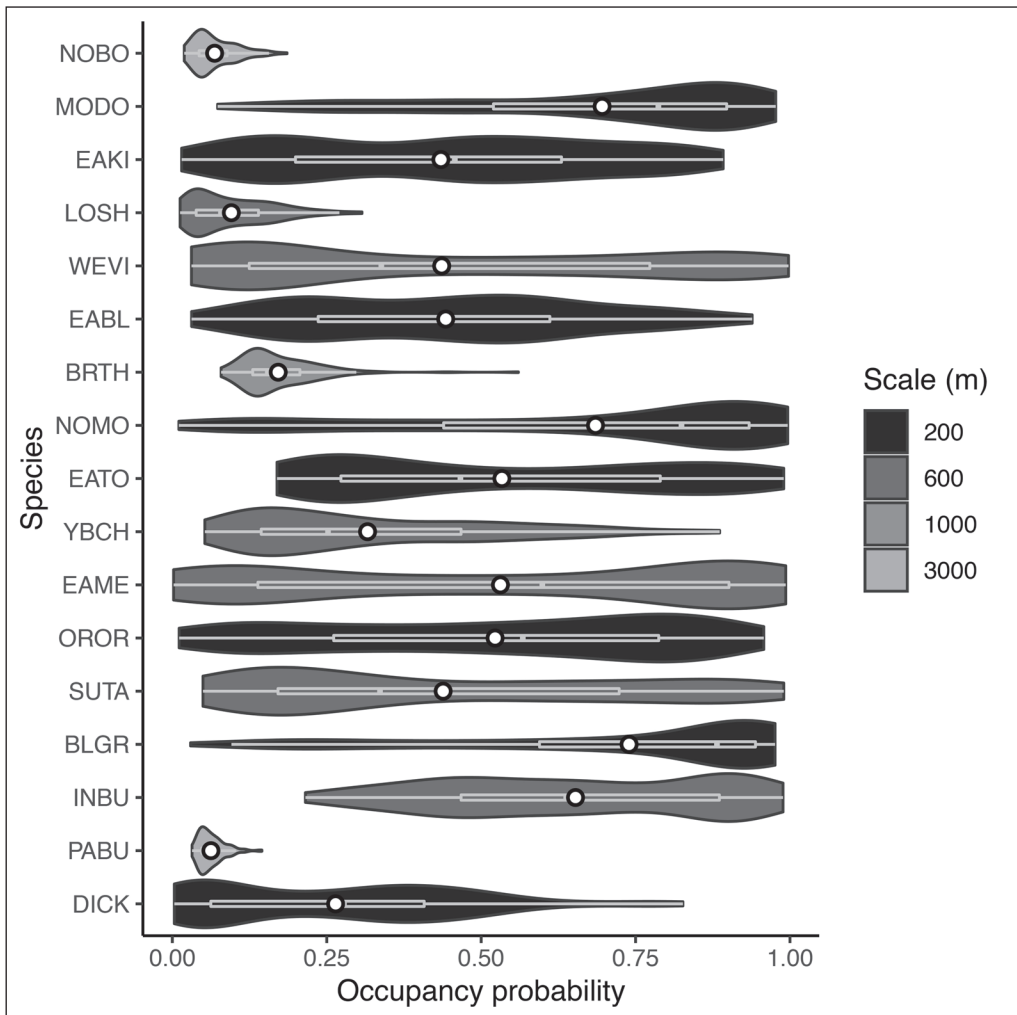


Figure 4. Mean posterior occupancy probabilities across sites from the model with the highest predictive performance (as judged by AUROC) for all species. The violins show the distribution of the posterior means; the boxplots display the medians and quantiles; the white points show the mean (across sites) of the posterior means; and the fill shows the spatial scale of the model used to estimate occupancy. Species codes are provided in the caption for Table 2.

CANOPY's prevalence may also be explained by the nature of the data. Unlike most of the covariates we evaluated, CANOPY comes from a continuous, not a categorical, landcover map. Each pixel within the NLCD canopy layer is assigned a percentage concealed by canopy, whereas with CropScape, each pixel is assigned a categorical landcover class. Although landscape analyses based on categorical landcover maps have a well-founded basis, emerging research suggests that a gradient paradigm (which assigns continuous values to pixels) has greater power in explaining animal distributions (Cushman et al. 2010).

The results supported our prediction that grassland species would show a negative relationship with CANOPY and shrubland species would generally show positive relationships with CANOPY (Table 1). For the grassland species, this negative relationship is consistent with previous literature that indicates that these taxa require open areas (e.g., Harms et al. 2017, Lumpkin and Pearson 2013, Ribic and Sample 2001). For the shrubland species, however, we documented a positive relationship with CANOPY that contradicts other studies. For example, Annand and Thompson (1997), working in southeastern Missouri, found the highest abundance of White-eyed Vireo, Eastern Towhee, Yellow-breasted Chat, and Indigo Bunting in large clearcuts in landscapes with the least amount of canopy cover of those studied. Similarly, in the southern Appalachians, Lumpkin and Pearson (2013) documented a negative relationship between canopy cover and occupancy of Eastern Towhee and Indigo Bunting. Our results demonstrate the importance of

Table 4. Detection statistics and parameters (from the model with the highest predictive performance as judged by AUROC) for each species. "Scale" reports the spatial scale of the model. The "y" column shows the percentage of sites at which each species was detected, while the "c" column shows the percentage of sites at which each species was confirmed. p_{11} , p_{10} , and b are the probabilities for true positive detection, false positive detection, and observation confirmation, respectively. The standard deviations (σ) of the posterior distributions of the parameters are provided.

Species	Scale	y	c	p_{11}	$\sigma_{p_{11}}$	p_{10}	$\sigma_{p_{10}}$	b	σ_b
NOBO	3000	0.19	0.00	0.67	0.13	0.06	0.01	0.13	0.07
MODO	200	0.99	0.17	0.93	0.02	0.64	0.06	0.10	0.02
EAKI	200	0.67	0.13	0.71	0.05	0.17	0.03	0.13	0.03
LOSH	600	0.10	0.02	0.52	0.11	0.02	0.01	0.16	0.07
WEVI	600	0.53	0.18	0.75	0.04	0.08	0.02	0.18	0.03
EABL	200	0.69	0.18	0.62	0.05	0.20	0.03	0.19	0.03
BRTH	1000	0.30	0.03	0.49	0.09	0.08	0.02	0.12	0.05
NOMO	200	0.95	0.53	0.96	0.01	0.56	0.05	0.47	0.03
EATO	200	0.78	0.10	0.82	0.03	0.24	0.04	0.09	0.02
YBCH	600	0.42	0.05	0.71	0.06	0.07	0.02	0.08	0.02
EAME	600	0.66	0.10	0.95	0.02	0.12	0.03	0.12	0.02
OROR	200	0.73	0.10	0.65	0.05	0.19	0.04	0.08	0.02
SUTA	600	0.59	0.08	0.56	0.05	0.14	0.03	0.07	0.02
BLGR	200	0.94	0.24	0.82	0.02	0.39	0.06	0.13	0.02
INBU	600	0.88	0.23	0.86	0.03	0.32	0.06	0.16	0.02
PABU	3000	0.16	0.01	0.50	0.14	0.05	0.01	0.23	0.11
DICK	200	0.33	0.03	0.79	0.05	0.05	0.01	0.10	0.03

landscape context when interpreting habitat associations. The other studies took place in largely forested landscapes; thus, these 2 species showed a negative association with the amount of canopy cover. However, our study took place in a mosaic of open landcover types (e.g., agriculture), and therefore a positive association with canopy cover (which, in this region, likely correlates with amount of early-successional habitat) emerged.

Impervious cover. The next most frequently selected covariate was IMPERV. Like CANOPY, IMPERV comes from a continuous landcover map, which may explain why it was frequently selected (Cushman et al. 2010). We predicted that only urban-tolerant taxa would benefit from the disturbance caused by impervious development (Table 1). Three of the species—Mourning Dove, Eastern Bluebird, and Northern Mockingbird—are documented synanthropes and showed the expected positive association with IMPERV (e.g., Hanauer et al. 2010). Two other species—Eastern Towhee and Orchard Oriole—showed weak positive associations with IMPERV. Orchard Orioles inhabit open, parklike areas (Scharf and Kren 2010), so an association with low-intensity urbanization might be expected. For Eastern Towhee, Greenlaw (2015) suggested a negative effect of urbanization in the upper Midwest. The positive association we documented indicates that this species shows a regionally variable relationship with urbanization. Finally, Eastern Meadowlark and Indigo Bunting showed a negative relationship with IMPERV, which is consistent with previous literature that has documented a negative association with urbanization for these species (Gilbert and Ferguson 2019, Lumpkin and Pearson 2013).

Agriculture. AG was selected for 3 species, all of which were classified as grassland species. The only species to show a positive relationship with AG was Dickcissel. This relationship is surprising because Dickcissel is an obligate grassland species that does not nest in row crops (Pranty et al. 2002, Temple 2002). However, Dickcissels can inhabit small habitat patches such as roadside ditches and field edges, which are common in agriculture-dominated landscapes (Conover et al. 2014, Farrell 2015, McNair 1990). Two species—Eastern Kingbird and Eastern Meadowlark—showed a negative relationship with AG. These species do not use agricultural fields, and the edge habitats within agricultural landscapes may be too small for them to use (Jaster et al. 2012, Murphy and Pyle 2018). Considering that these species decline with increasing canopy cover (Table 2), our results indicate that Eastern Kingbirds and Eastern Meadowlarks require open landscapes that are not dominated by agriculture.

Patch shape. PAFRAC was selected for 3 species, all classified as grassland species. Eastern Meadowlark showed a positive association with PAFRAC, which is surprising because grassland obligates prefer patches with simple geometries (Davis 2004). However, the measure of PAFRAC we used considered the shape of all patches within the landscape rather than the shape of 1 focal grassland patch. Therefore, our results suggest there may be a disconnect between grassland bird response to the shape of individual patches versus the shapes of all of the patches within a landscape. Eastern Kingbird and Orchard Oriole also showed positive

associations with PAFRAC, which is fitting because, while classified as grassland species, these species use edges (Murphy and Pyle 2018, Scharf and Kren 2010).

Contagion. Only Orchard Oriole and Painted Bunting had CONTAG selected as a significant covariate, though the credible interval included zero for both (Table 2). Orchard Oriole showed a negative relationship with CONTAG, which is fitting because it is an edge-associated species and is expected to be associated with landscape heterogeneity (Scharf and Kren 2010). Notably, CONTAG was the only covariate selected for Painted Bunting, though the relationship was not conclusive (Table 2). The sparsity of covariates selected for this species hints that processes other than landcover (e.g., microhabitat characteristics or interactions with other species) may drive occupancy patterns in the region. Given the poorly understood status of this species in the Blackland Prairies (Gilbert et al. 2019, Shipley et al. 2013), further research into the factors driving Painted Bunting occupancy in the region is needed.

Pasture. PASTURE was selected only for Summer Tanager, which showed a weak negative association, as predicted for a shrubland species (Table 2). That PASTURE was not selected for many species is surprising because several of the grassland species included in this study use pastures (Froehly et al. 2018, Gawlik and Bildstein 1993, Hanauer et al. 2010, Jaster et al. 2012, Temple 2002). The nature of the data may drive this result; PASTURE is from a categorical landcover map, and the covariates from continuous landcover maps (i.e., CANOPY and IMPERV) may have provided greater explanatory power, which would lead to the omission of PASTURE from the model. Alternatively, the nature of the pastures themselves may make them unsuitable for grassland birds. Overgrazing is common in the region (P. Ferguson, University of Alabama, Tuscaloosa, AL, unpubl. data), which degrades habitat for grassland species (Brennan and Kuvlesky 2005). Also, many of the pastures are planted with exotic cool-season grasses, which are linked to decreased grassland bird productivity (Monroe et al. 2016).

Spatial scale patterns

We documented that occupancy was most strongly associated with covariates that were measured at smaller spatial scales. Similar scale effects have been documented for passerines in many studies (e.g., Morelli et al. 2013). However, 2 caveats merit mention. First, the covariate that provided the best inference about scale effects was CANOPY, and CANOPY is not a direct measure of habitat for most of the species we evaluated. The amount of habitat for a particular organism is expected to be the primary driver of the distribution of that organism (Fahrig 2013). Therefore, spatial dependencies in habitat selection may operate differently than in the covariates we measured. Second, habitat selection is hierarchical, meaning that territories must be imbedded within suitable landscapes to be selected, and indeed, covariates measured at the larger spatial scales were still selected. These reasons, together with literature that suggests grassland birds respond to broad spatial patterns, implies that scales of up to several kilometers from sites should be considered when managing habitat for disturbance-dependent birds (Dreitz et al. 2017).

Conservation and management

Our study provides landscape context for conservation and management practices in the Blackland Prairie Ecoregion. The region, having undergone significant landcover change, suffers from major ecological challenges such as overgrazing, erosion, and encroachment by *Juniperus virginiana* L. (Eastern Red Cedar), processes that negatively affect disturbance-dependent birds (Brennan and Kuvlesky 2005). Conservation practices to address these issues are costly and therefore must often take place at relatively small spatial scales. For example, for an overgrazed pasture, effective conservation measures might include replanting the pasture from exotic, cool-season grasses—e.g., *Cynodon dactylon* L. (Bermudagrass)—to native warm-season grasses (e.g., Little Bluestem) followed by implementing a grazing system to promote rangeland heterogeneity (Derner et al. 2009). Such practices benefit birds, improve the quality of the land, and ultimately are economically viable, but these actions require startup costs and typically occur 1 pasture at a time (Coggin and Gruchy 2012, Monroe et al. 2016). However, the effectiveness of conservation action (as judged by benefit to wildlife) is influenced by the landscape context. In the case discussed above, if the pasture is imbedded in a forested landscape, benefits to grassland species such as Eastern Meadowlark and Loggerhead Shrike will be minimal. Given the landscape context, shifting pasture management practices to benefit shrubland birds may lead to greater ecological return on the investment. Based on our results, we encourage managers to develop and implement conservation plans with reference to landcover patterns within at least a kilometer of sites.

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