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Disturbance, but not the right kind: Exurban development does not create habitat for shrubland birds

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ABSTRACT—Exurban development (i.e., low-density residential housing) comprises at least 25% of the contiguous United States and disturbs the natural landscape, typically impairing habitat for forest interior songbirds and creating habitat for urban-adapted species. However, it is poorly known how exurban development affects shrubland birds, which require disturbance to create habitat (i.e., early successional vegetation). Therefore, our objective was to explore landscape patterns associated with shrubland bird occupancy in a forested region undergoing extensive exurban development. To address this objective, we conducted point counts across a natural–exurban gradient in Macon County, North Carolina, USA, and measured 8 land-cover covariates within 200 m and 1,000 m of survey sites. The covariates were percent canopy cover (CANOPY), contagion (CONTAG), percent of the landscape (PLAND) that was developed (DEV), elevation (ELEV), PLAND forest (FOREST), forest edge density (ED_DF), Simpson's landscape diversity index (SIDI), and PLAND shrub (SHRUB). We modeled occupancy for 12 shrubland species using a hierarchical occupancy model that accounts for false-positive detections. We fit a global model that incorporated all non-collinear covariates and used stochastic search variable selection to determine which covariates showed a relationship with occupancy. The most frequently selected covariate was CANOPY (8 species), followed by ELEV (5 species), DEV (4 species), SIDI (3 species), and CONTAG (2 species). CANOPY and DEV were negatively associated with occupancy. SIDI and CONTAG are both metrics of landscape heterogeneity; heterogeneity was positively associated with occupancy. Additionally, of the study species, generalists showed the highest occupancy rates, while specialists showed the lowest occupancy rates. We suggest that the associations between occupancy and canopy cover and landscape heterogeneity are logical because natural disturbance, in addition to creating early successional habitat, decreases canopy cover and increases landscape heterogeneity. Furthermore, we suggest that exurban development can drive these patterns, but, given the negative (or neutral) relationship between DEV and shrubland bird occupancy, we hypothesize that exurban development as a form of disturbance does not generate early successional habitat. We conclude that exurban development will benefit only a small subset of urban-adapted shrubland species without creating habitat for most shrubland birds, despite exerting considerable disturbance to forested landscapes. *Received 9 February 2018. Accepted 15 December 2018.*

Key words: Bayesian, disturbance, habitat selection, landscape, occupancy model, southern Appalachian, urbanization

Perturbación, mas no del tipo adecuado: el desarrollo exurbano no crea hábitat para aves de matorral

RESUMEN (Spanish)—El desarrollo exurbano (i.e., desarrollo residencial de baja densidad) se extiende por al menos en el 25% de los estados contiguos de los Estados Unidos. Perturba el paisaje natural, típicamente impidiendo el hábitat de aves de interior de bosque y creando hábitat para especies adaptadas al ambiente urbano. Sin embargo, se sabe poco sobre cómo el desarrollo exurbano afecta a las aves de matorral que requieren de perturbación para crear su hábitat (i.e., vegetación sucesional temprana). Nuestro objetivo fue explorar los patrones del paisaje asociados con la ocupación en una región de bosque que se encuentra en un proceso extensivo de desarrollo exurbano. Para atender este objetivo, llevamos a cabo conteos por puntos a lo largo de un gradiente natural-exurbano en el condado de Macon, North Carolina, EUA, e hicimos mediciones de ocho covariables de cobertura del suelo dentro de 200 y 1000 m de los sitios visitados. Las covariables fueron el porcentaje de cobertura del dosel (CANOPY), contagio (CONTAG), porcentaje del paisaje (PLAND) que ha sido desarrollado (DEV), elevación (ELEV), PLAND de bosque (FOREST), densidad del borde del bosque (ED_DF), el índice de diversidad del paisaje de Simpson (SIDI) y PLAND de matorral (SHRUB). Modelamos la ocupación de 12 especies de matorral usando un modelo jerárquico de ocupación que cuantifica detecciones de falsos positivos. Los ajustamos a un modelo global que incorpora todas las covariables no-colineares y usamos la búsqueda estocástica de selección de variables para determinar qué covariables mostraban una relación con la ocupación. La variable más frecuentemente seleccionada fue CANOPY (ocho especies), seguida por ELEV (cinco especies), DEV (cuatro especies), SIDI (tres especies) y CONTAG (dos especies). CANOPY y DEV fueron negativamente asociadas con la ocupación. Ambas, SIDI y CONTAG, son métricas de heterogeneidad del paisaje. La heterogeneidad estuvo positivamente asociada con la ocupación. Adicionalmente, entre las especies estudiadas las generalistas mostraron las tasas de ocupación más altas, mientras que los especialistas mostraron las tasas de ocupación más bajas. Sugerimos que las asociaciones entre la ocupación, y la cobertura del dosel y la heterogeneidad del paisaje son lógicas debido a la perturbación natural, además de crear hábitat sucesional temprano, disminuyen la cobertura del dosel e incrementan la heterogeneidad del paisaje. Además, sugerimos que el desarrollo exurbano puede ser el responsable de esos patrones, pero, dada la relación negativa (o neutral) entre DEV y la ocupación de aves de matorral, nuestra hipótesis es que el desarrollo exurbano como forma de perturbación no genera hábitat sucesional temprano. Concluimos que, si bien el desarrollo exurbano ejerce una perturbación considerable en paisajes boscosos, éste beneficiara solamente a un pequeño subconjunto de especies de matorral adaptadas a hábitat urbano sin crear hábitat para la mayoría de las especies.

Palabras clave: Apalaches del sur, bayesiano, modelo de ocupación, paisaje, perturbación, selección de hábitat, urbanización

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Humans affect birds profoundly via habitat loss and degradation from land use change (Vitousek et al. 1997, Devictor et al. 2008). Urbanization—a form of land use change—is expanding as cities decentralize (Meyer and Turner 1992, Chen et al. 1996). The effects of urbanization on birds are not uniform across taxa. Rather, urbanization excludes specialist species while creating opportunity for urban-adapted generalists. The resulting community may have higher species richness than that of the original natural landscape despite the loss of specialist species (Connell 1978, Blair 1996, Chace and Walsh 2006).

Urbanization's effects also depend on the type of development. Exurban development, defined as low-density development with each residence occupying at least 0.5 ha of land, is ubiquitous and poorly understood ecologically (Hansen et al. 2005, Theobald 2005). Exurban development is the fastest growing form of land use in the United States and represents at least 25% of the area of the contiguous states (Hansen et al. 2005). Often, exurban development does not dramatically change the dominant land cover (Irwin and Bockstael 2007, Clark et al. 2009). Unlike high-intensity urbanization, which fragments landscapes into discrete patches of natural vegetation surrounded by a developed matrix, exurban development perforates landscapes, leaving a largely natural matrix (Odell and Knight 2001, Bock and Bock 2009). Additionally, exurban development is no longer restricted to the periphery of cities; rather, people are settling landscapes that provide access to open areas and recreation opportunities, often adjacent to protected wildland sites (Marcouiller et al. 2002, Brown et al. 2005).

While previous studies of urban–natural gradients indicate that avian species richness peaks in exurban landscapes, this trend masks the loss of urban-intolerant taxa (Blair 1996, Fraterrigo and Wiens 2005, Glennon and Kretser 2013). New species colonize developments, but other species cannot persist in the altered landscape. The disappearing species are often of conservation interest, while the colonizing species are typically widespread, common, and urban-adapted (Johnston 2001, Odell and Knight 2001, McKinney 2002). Previous research has focused on the disappearing species (often insectivorous Neotropical migrants) in forested landscapes undergoing development (Friesen et al. 1995, Phillips et al. 2005, Rodewald and Shustack 2008, Wood et al. 2014). Fewer studies have focused on non-forest taxa. Consequently, many taxa, including shrubland birds, have poorly understood responses to exurban development (Hansen et al. 2005, Merenlender et al. 2009).

Shrubland birds depend on ecological disturbance to create habitat, which we will consider generally as early successional vegetation. As natural disturbance regimes (e.g., fire) have been altered over the past 2 centuries, many shrubland birds have declined (Brawn et al. 2001, Hunter et al. 2001). Previous research on shrubland birds and exurban development has yielded ambiguous results. For example, Lumpkin and Pearson (2013) found that occupancy of many shrubland species declined with increasing building density, suggesting that shrubland birds do not benefit from the disturbance associated with exurban development. Schlossberg et al. (2011), on the other hand, found that the abundance of most shrubland species was unaffected by low-intensity exurban development, leading them to conclude that exurban development has neutral or positive effects on shrubland species. Additionally, most previous research on shrubland birds has focused on patch-level metrics (e.g., size of shrubland habitat patch; Rodewald and Vitz 2005, Lehnen and Rodewald 2009, Schlossberg et al. 2010), while studies considering landscape-level metrics (i.e., metrics that consider all cover types, not just the habitat class of interest) have focused primarily on forest taxa (e.g., Mitchell et al. 2001). Consequently, the landscape ecology of shrubland birds is poorly understood (Schlossberg and King 2007, Roberts and King 2017a).

In this study, we investigated whether exurban development could create habitat for shrubland birds by exploring landscape patterns associated with shrubland bird occupancy across a natural–exurban gradient in North Carolina, USA. We included 12 shrubland bird species, considering their migratory (temperate/Neotropical) and dietary (omnivorous/insectivorous) guilds as contextual information (Table 1). We modeled their occupancy relative to landscape patterns that we hypothesized would be associated with their occurrence and influenced by exurbanization.

Table 1. The 12 species modeled in this study to investigate the relationship between shrubland bird occupancy and covariates in an exurban landscape in Macon County, North Carolina, USA. The common name, banding code (USGS 2016), family, and scientific names are presented in taxonomic order according to the 7th edition (with changes through the 58th supplement) of the American Ornithological Society Check-list of North and Middle American Birds (Chesser et al. 2018). The migratory and dietary guilds are also presented. Species were classified in their respective guilds based on information available from Birds of North America (Rodewald 2015) and Hamel (1992).

Common name	Code	Family	Scientific name	Migration	Diet
White-eyed Vireo	WEVI	Vireonidae	*Vireo griseus*	Neotropical	Insectivore
Eastern Bluebird	EABL	Turdidae	*Sialia sialis*	Temperate	Omnivore
Gray Catbird	GRCA	Mimidae	*Dumetella carolinensis*	Neotropical	Omnivore
Brown Thrasher	BRTH	Mimidae	*Toxostoma rufum*	Temperate	Omnivore
Cedar Waxwing	CEDW	Bombycillidae	*Bombycilla cedrorum*	Temperate	Omnivore
Field Sparrow	FISP	Passerellidae	*Spizella pusilla*	Temperate	Omnivore
Song Sparrow	SOSP	Passerellidae	*Melospia melodia*	Temperate	Omnivore
Eastern Towhee	EATO	Passerellidae	*Pipilo erythrophthalmus*	Temperate	Omnivore
Yellow-breasted Chat	YBCH	Icteriidae	*Icteria virens*	Neotropical	Insectivore
Chestnut-sided Warbler	CSWA	Parulidae	*Setophaga pensylvanica*	Neotropical	Insectivore
Prairie Warbler	PRAW	Parulidae	*Setophaga discolor*	Neotropical	Insectivore
Indigo Bunting	INBU	Cardinalidae	*Passerina cyanea*	Neotropical	Omnivore

Methods

Study area

We conducted point counts throughout Macon County, North Carolina (centroid 35.15°N, 83.42°W; Fig. 1). Macon County lies within the Blue Ridge Province of the Southern Appalachian Mountains, one of the world's most biodiverse temperate regions (Pickering et al. 2003). The climate is humid with precipitation evenly distributed throughout the year, averaging 180 cm annually at low (i.e., 680 m) elevations and increasing by roughly 5% per 100 m increase in elevation (Laseter et al. 2012). Elevation at our field sites varied from 580 m to 1,500 m. The dominant natural land cover of the region is

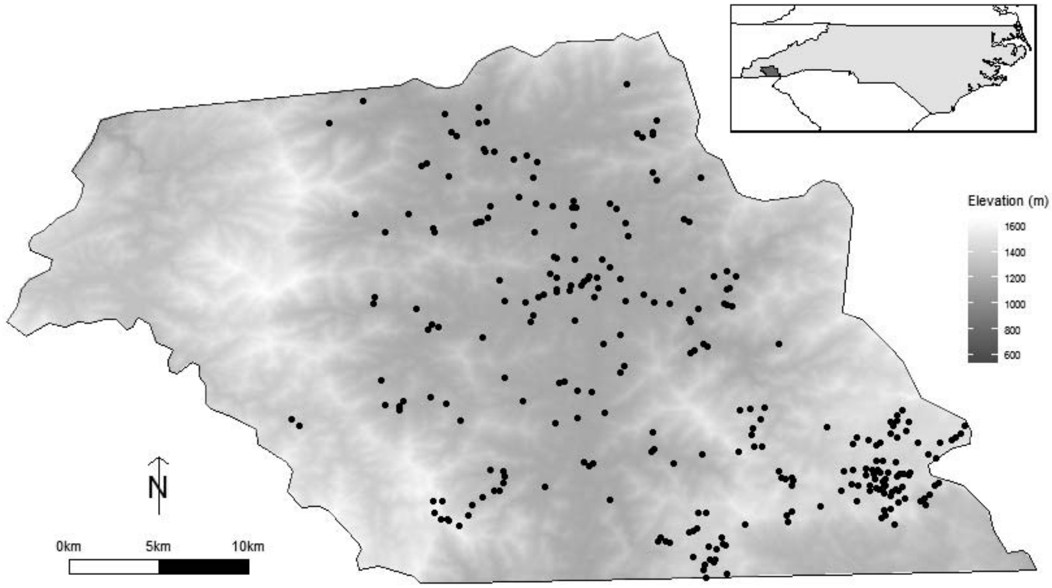

Figure 1. The locations of point counts conducted in Macon County, North Carolina. Elevation is displayed with a grayscale color ramp. The inset map shows the location of Macon County (dark gray) within North Carolina (light gray).

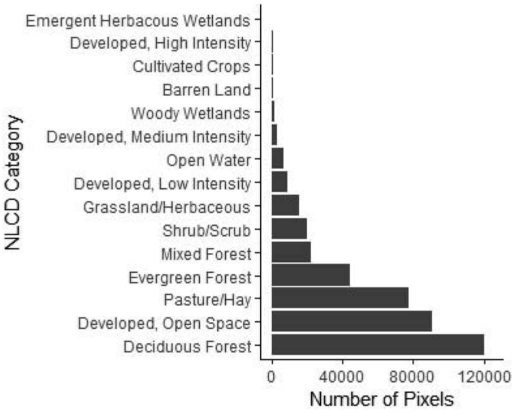

Figure 2. Summary of land cover in Macon County, North Carolina, as classified by the 2011 NLCD layer (Homer et al. 2015).

deciduous forest, although evergreen and mixed forest also comprise a major percentage of the land cover, particularly at high elevations (Fig. 2; Peters et al. 2013). Since European colonization, land use in the region was first dominated by subsistence agriculture, then by resource extraction in the 19th and 20th centuries, and currently by exurban development (Gragson and Bolstad 2006).

Study species

We selected 12 species of shrubland birds for which we recorded detections in at least 20 point counts (Table 1). We defined a "shrubland bird" as a species that requires some form of early successional vegetation for habitat and evaluated habitat preferences of potential study species based on habitat descriptions on Birds of North America Online (BNA; Rodewald 2015). We classified each species into binary migratory (temperate/Neotropical) and dietary (omnivorous/insectivorous) guilds based on Hamel (1992) and BNA (Rodewald 2015). For species without obvious classifications, particularly for the dietary guild, we tried to distinguish opportunism from consistent behavior from the BNA species accounts (e.g., for Yellow-breasted Chat [*Icteria virens*], "Adults feed on small invertebrates. . .and take fruits and berries when available" resulted in an insectivorous classification; Eckerle and Thompson 2001). We recognize that guild classification is challenging (Simberloff and Dayan 1991, Sauer et al. 1996) but argue that defining guilds provides an ecological milieu that helps researchers synthesize results from individual species.

Site selection

We used a stratified random sampling strategy based on land cover, elevation, and development characteristics to identify sites at which to perform avian point counts. First, we generated 10,000 random points (separated by at least 200 m) within Macon County. Next, we used these points to sample a Macon County parcel layer and the 2006 National Land Cover Database (NLCD) layer (Appendix Table A5; Ferguson et al. 2017). From the parcel layer, we extracted the structure age and whether or not the property was part of a subdivision (Appendix Table A5). With the NLCD layer, we used FRAGSTATS to calculate the percentage of the landscape (PLAND) within a radius of 1,000 m of each point that was composed of agriculture, forest (all classes aggregated), and development (all classes aggregated; McGarigal et al. 2012; Appendix Table A5). We defined strata as all possible combinations of the elevation (3 levels), structure age (3 levels), and subdivision (2 levels) variables with 4 combinations of the land cover variables for a total of 64 strata (Appendix Table A5). We randomly selected sites from each stratum and visited the properties to request access from landowners. For a small number of cases in which we had difficulty meeting landowners, we selected adjacent properties opportunistically (see Ferguson et al. 2017 for complete details).

Point count protocol

We performed 8-minute, double-observer point counts from 16 May to 6 July 2010 at 111 sites and from 8 May to 29 June 2011 at 161 sites for a total of 272 sites surveyed (Fig. 1). Surveys were conducted between 30 min before sunrise and 1000 h EST (Ralph et al. 1995). Two individuals performed a point count simultaneously but faced opposite directions and did not share information with each other (Farnsworth et al. 2005). One individual performed surveys in both years, while the role of the second observer was filled with different individuals in 2010 and 2011. Each observer recorded all birds detected and estimated whether the distance to each bird was $\leq$25 m or 25–100 m. We surveyed each site 3 times over the

Table 2. Landscape patterns that we hypothesized would be associated with shrubland bird occupancy. In this table, "Covariate" is the covariate we measured (see key in footnote), "Pred" is the predicted direction of the association (+ for positive, – for negative, +/– for variable across species), and "Justification" is a brief description of our rationale for including the covariate in the analysis.

Covariate[a]	Pred	Justification
CANOPY	–	As the canopy closes, there is a decline in early successional vegetation (Schlossberg and King 2007).
CONTAG	–	Heterogeneous landscapes (low contagion) are formed by disturbance, which creates early successional vegetation (Swanson et al. 2011).
DEV	+/–	Development is a form of disturbance, but shrubland bird response to it is poorly understood (Schlossberg et al. 2011).
ED_DF	+	Shrubland birds are not edge specialists (Schlossberg and King 2008), yet forest edge may provide the only habitat in some landscapes.
ELEV	+/–	Elevation covaries with many bioclimatic and land cover patterns in the region (Laseter et al. 2012).
FOREST	–	Landscapes with more forest should have less early successional vegetation and fewer shrubland birds (Lumpkin and Pearson 2013).
SHRUB	+	Shrubland bird occurrence should increase with amount of early successional vegetation (Fahrig 2013, Roberts and King 2017a).
SIDI	+	Heterogeneous landscapes (high diversity) are formed by disturbance, which creates early successional vegetation (Swanson et al. 2011).

[a] Under the "Covariate" column, CANOPY is the mean percent canopy cover of the landscape surrounding survey points, CONTAG is contagion (a metric of landscape heterogeneity), DEV is the percentage of the landscape that is developed (all NLCD subclasses aggregated), ED_DF is edge density of the deciduous forest class, ELEV is elevation in meters, FOREST is the percentage of the landscape that is forested (all NLCD subclasses aggregated), SHRUB is the percentage of the landscape that is shrub, and SIDI is the Simpson's landscape diversity index. All covariates were measured within 200 m and 1,000 m radii of survey points.

course of a field season; replicate surveys were separated by an average of 16 d.

Covariates quantifying landscape patterns

We measured 8 covariates that we hypothesized would be associated with shrubland bird occupancy and influenced by exurbanization (Table 2). We measured each covariate at 2 spatial scales: within 200 m and 1,000 m radii of survey points, respectively. We used the 200 m scale because this area is several (3–5) times larger than the home range of many passerines (Barg et al. 2004) and therefore represents the local context for the establishment of a home range. We used the 1,000 m scale because this area is expected to characterize the broader landscape that influences the establishment of home ranges at smaller scales (Holland and Yang 2016). These spatial scales are consistent with other studies that suggest that landscape patterns within 100–1,000 m of points are good predictors of passerine distributions (e.g., Söderström and Pärt 2000, Mitchell et al. 2006, Morelli et al. 2013, Schindler et al. 2013).

We calculated the mean percent canopy cover (CANOPY) from the NLCD 2011 USFS Tree Canopy cartographic layer using the R package raster (Homer et al. 2015, Hijmans 2017). We predicted a negative association between CANOPY and shrubland bird occupancy, expecting that landscapes dominated by closed-canopy forest do not contain much early successional vegetation and therefore host few shrubland birds (Askins 1994, Schlossberg and King 2007; Table 2).

Next, we calculated the mean elevation (ELEV) from Shuttle Radar Topography Mission data in the raster package (Hijmans 2017). Given the high variation in elevation in the region and its covariance with climatic and land-cover factors (Laseter et al. 2012), we thought it important to include ELEV as a covariate, although we did not expect consistent relationships with ELEV across species (Table 2).

Next, we calculated 6 class- or landscape-level metrics from the NLCD 2011 Land Cover layer (Homer et al. 2015) using FRAGSTATS 4 with the 8-cell neighbor rule (McGarigal et al. 2012). Three were class-level covariates quantifying the percentage of the landscape (PLAND) composed of developed areas (DEV), forest (FOREST), or shrub (SHRUB).

We included FOREST as a representation of the amount of unsuitable habitat for shrubland birds in the landscape. We predicted a negative relationship between FOREST and shrubland bird occupancy (Table 2). We aggregated the NLCD's 3 forest categories, namely deciduous, mixed, and evergreen forest, because we expected shrubland birds to respond to forest structure regardless of the forest type.

We included DEV as a representation of the amount of exurban development in the landscape. We considered DEV as the aggregation of the NLCD development categories Open Space, Low Intensity, Medium Intensity, and High Intensity (the categories are defined by amount of impervious surface). Most exurban development would be classified as Open Space or Low Intensity (Open Space includes "large-lot single-family housing units" and Low Intensity "most commonly includes single-family housing units"; Homer et al. 2015). However, we believe aggregating all of the categories is justified. First, pixels classified as Medium or High Intensity development were extremely rare in Macon County (Fig. 2). Second, Medium and High Intensity categories can represent features such as roads that are part of exurban development. We predicted variable (by species) relationships between DEV and occupancy (Table 2). Estimating these relationships was of key interest in this study of how exurbanization contributes to habitat for shrubland birds.

We included SHRUB as a measure of the amount of early successional vegetation in the landscape. We expected a positive association with shrubland bird occupancy, since occupancy should increase with increasing amounts of habitat available (Fahrig 2013; Table 2).

In addition to the PLAND covariates, we calculated 3 metrics of landscape heterogeneity: edge density of the deciduous forest class (ED_DF), contagion (CONTAG), and Simpson's landscape diversity index (SIDI). We predicted that shrubland bird occupancy would be positively associated with landscape heterogeneity, since disturbed landscapes are generally more heterogeneous than undisturbed ones (Swanson et al. 2011; Table 2).

For edge density (i.e., ED_DF), we chose to focus on the deciduous forest class because it was the dominant land-cover class (Fig. 2) and because, while shrubland birds do not specialize in edge habitats, forest edge may provide the only habitat available to shrubland birds in some landscapes (Schlossberg and King 2008). We therefore predicted a positive relationship between ED_DF and occupancy (Table 2). CONTAG (a landscape-level metric) measures the dispersion (spatial distribution of one patch type) and interspersion (spatial intermingling of multiple patch types; McGarigal et al. 2012). CONTAG ranges from 0 to 100, with low values representing heterogeneous landscapes and high values representing uniform landscapes. We therefore predicted a negative relationship between occupancy and CONTAG (Table 2). Finally, SIDI (a landscape-level metric) characterizes landscape diversity and is the probability that randomly drawn pixels represent different patch types (McGarigal et al. 2012). We therefore predicted a positive relationship between occupancy and SIDI, since disturbance typically increases the diversity of land cover types (Swanson et al. 2011; Table 2).

Occupancy model

We used a multiple detection state occupancy model that estimates probabilities for occupancy (ψ), true positive detection (p_{11}), false positive detection (p_{10}), and observation confirmation (b) (MacKenzie et al. 2002, Miller et al. 2011, Ferguson et al. 2015; see Supplemental File S1). False positive detections are pervasive in acoustic surveys, and modeling them requires having a subset of confirmed detections (i.e., zero chance of an erroneous detection) to distinguish true positive and false positive detections (Miller et al. 2011).

Essentially, p_{11} is the probability that one or both observers record a species as present when the site is occupied, p_{10} is the probability that one or both observers record a species as present when the site is actually unoccupied, and b is the probability that both observers make a true positive detection when misidentification cannot occur (i.e., a confirmed detection). In our application, we classified detections as confirmed when both observers detected a species within 25 m (Ferguson et al. 2015). Across i sites and t temporal replicates, we modeled confirmed detections c_{it} as the realization of a Bernoulli trial with probability $b*z_i$, where z_i indicates the occupancy state (1 or 0) of a site (Table 3). We modeled all detections y_{it} as the realization of a Bernoulli trial with probabilities dependent upon the states of c_{it} and z_i (Table 3; Ferguson et al. 2015). We modeled z_i as the realization of a Bernoulli trial with probability ψ_i, which we modeled as a function of land cover covariates. Finally, we modeled the

Table 3. Probabilities of detection given occupancy (z_i) and confirmation (c_{ij}) states across *i* sites and *j* replicate surveys used in our "confirmed presences" formulation of the Ferguson et al. (2015) false-positives occupancy model. For example, at an unoccupied site ($z_i = 0$), the probability of recording a detection ($y_{ij} = 1$) is p_{10} and it is impossible to have a confirmed detection ($c_{ij} = 1$). Adapted from figure 1 in Ferguson et al. (2015).

	$z_i = 0$	$z_i = 1$
$c_{ij} = 0$	p_{10}	p_{11}
$c_{ij} = 1$	Undefined	1

detection parameters (i.e., p_{11}, p_{10}, and *b*) as constant across sites and surveys.

We used *Beta(4, 4)* priors for p_{11}, *b*, and the intercept of the function relating covariates to ψ_i (Cruz 2018). 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 (Ferguson et al. 2015). For the covariate coefficients, we used slab/spike priors (see details under "Stochastic search variable selection").

Stochastic search variable selection

We used stochastic search variable selection (SSVS) to evaluate a global model and assess which covariates were relevant to occupancy for each species (George and McCulloch 1993, O'Hara and Sillanpää 2009, Hooten and Hobbs 2015). With SSVS, indicator variables δ_j are added to the regression model to indicate which of $j = 1, 2, \ldots, n$ covariates are informative (O'Hara and Sillanpää 2009, Hooten and Hobbs 2015).

We built a global model containing all standardized ($\bar{x} = 0$, $s = 1$), non-collinear covariates (Pearson's $|r| < 0.7$; Dormann et al. 2013) in which the basic regression coefficients β_j were replaced by the product of a binary indicator variable and a regression coefficient, $\delta_j{*}\beta_j$. We assigned the δ_j parameters a vague *Bern(0.5)* prior. A posterior of δ_j approaching one indicates that the *j*th covariate is important in the model, while a posterior approaching zero essentially removes the effect of the *j*th covariate from the model. The prior for $\beta_j \mid \delta_j$ is $\delta_j N(0, c^2\tau^2) + (1 - \delta_j)N(0, \tau^2)$. Consequently, within each Markov Chain Monte Carlo (MCMC) iteration of the model, each β_j is given either a "slab" prior centered at zero with a large ($c^2\tau^2 = 2$) variance when $\delta_j = 1$ or a "spike" prior centered at zero with a small ($\tau^2 = 0.02$) variance when $\delta_j = 0$ (Hooten and Hobbs 2015, Cruz 2018). 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 global model (shown below) contained 13 non-collinear covariates (for statistical summaries of each covariate, see Appendix Table A6).

$$
\begin{aligned}
logit(\Psi_i) = {} & \beta_0 + \delta_1\beta_1 CANOPY\_200m_i \\
& + \delta_2\beta_2 CONTAG\_200m_i \\
& + \delta_3\beta_3 DEV\_200m_i \\
& + \delta_4\beta_4 ED\_DF\_200m_i \\
& + \delta_5\beta_5 ELEV\_200m_i \\
& + \delta_6\beta_6 FOREST\_200m_i \\
& + \delta_7\beta_7 SHRUB\_200m_i \\
& + \delta_8\beta_8 SIDI\_200m_i \\
& + \delta_9\beta_9 CONTAG\_100m_i \\
& + \delta_{10}\beta_{10} DEV\_100m_i \\
& + \delta_{11}\beta_{11} ED\_DF\_100m_i \\
& + \delta_{12}\beta_{12} FOREST\_100m_i \\
& + \delta_{13}\beta_{13} SHRUB\_100m_i
\end{aligned}
$$

We fit the global model to each species in OpenBUGS 3.2.3 using the R2OpenBUGS package and R 3.5.1 (Sturtz et al. 2005, Lunn et al. 2012, R Core Team 2018). We used 3 MCMC chains with 100,000 iterations, a burn-in of 50,000, and thinning of 5. We assessed convergence via visual inspection of traceplots and the Gelman-Rubin potential scale reduction factor (Rhat); chains with Rhat ≤ 1.1 were considered converged (Brooks and Gelman 1998).

Results

Landscape patterns associated with occupancy

Considering that the global model with 13 covariates was fit for 12 species, it was possible for covariates to be selected 156 times (i.e., if all 13 covariates were important for all 12 species). Across all species, 24 covariates were selected as relevant to occupancy (Table 4). No covariates were selected for 2 species (White-eyed Vireo [*Vireo griseus*] and Yellow-breasted Chat). Of the remaining species, 1–4 covariates were selected for each species (Table 4). The most frequently selected covariate was CANOPY, selected for 8

Table 4. Covariates associated with shrubland bird occupancy. All covariates were selected via stochastic search variable selection from a global model such that covariates that had an indicator variable (δ_j) with posterior mean >0.7 were considered important in the model. For each species (codes provided in Table 1), the important covariates are presented (for an explanation of the covariates, see Table 2), along with the spatial scale at which the covariates were measured. The "Dir" column provides the effect direction for each covariate ("+" for positive, "–" for negative, and "?" for cases in which the coeffecient's 95% credible interval included zero). The coefficient's mean and bounds of the 95% credible interval (Lower, Upper) are provided. Finally, the Gelman-Rubin potential scale reduction factor (Rhat) is provided, which assesses convergence (i.e., Rhat < 1.1). For White-eyed Vireo (WEVI) and Yellow-breasted Chat (YBCH), no covariates were indicated as important.

Species	Covariate	Scale	Dir	Mean	Lower	Upper	Rhat
WEVI	*NA*						
EABL	CANOPY	200	–	−2.21	−3.22	−1.36	1.001
	ELEV	200	–	−1.05	−1.69	−0.42	1.001
	DEV	1000	–	−1.34	−2.24	−0.49	1.001
GRCA	CANOPY	200	–	−1.01	−1.67	−0.25	1.001
	ELEV	200	+	1.44	0.91	2.03	1.001
	CONTAG	1000	?	−0.62	−1.59	0.11	1.001
BRTH	CANOPY	200	–	−2.16	−3.46	−1.09	1.001
CEDW	CANOPY	200	–	−1.33	−2.22	−0.59	1.001
	SIDI	200	?	0.91	−0.06	2.09	1.001
	DEV	1000	–	−1.33	−2.30	−0.58	1.002
FISP	CANOPY	200	–	−1.81	−2.60	−1.54	1.001
	DEV	200	?	−0.81	−2.03	0.03	1.001
	DEV	1000	–	−0.92	−1.81	−0.05	1.001
	SHRUB	1000	+	0.63	0.05	1.22	1.001
SOSP	CANOPY	200	–	−2.40	−3.26	−1.63	1.001
	SIDI	200	+	1.38	0.45	2.43	1.001
EATO	ELEV	200	+	1.41	0.89	1.99	1.001
	SIDI	200	?	0.62	−0.03	1.38	1.001
	CONTAG	1000	?	−0.66	−1.53	0.09	1.001
YBCH	*NA*						
CSWA	ELEV	200	+	1.52	0.79	2.48	1.001
PRAW	CANOPY	200	–	−0.88	−1.71	−0.01	1.001
INBU	CANOPY	200	–	−1.90	−2.76	−1.10	1.001
	ELEV	200	–	−0.76	−1.28	−0.19	1.001
	DEV	1000	–	−2.09	−2.89	−1.36	1.001

species, followed by DEV and ELEV, each selected 5 times (Table 4, Fig. 3). Two covariates (FOREST and ED_DF) were never selected.

Most of the selected covariates showed consistent relationships with occupancy across species. CANOPY had a negative relationship (95% credible interval excluded zero) with occupancy for the 8 species for which it was selected (Table 4, Fig. 4). DEV also showed a negative relationship with occupancy (95% credible interval excluded zero) for 4 species (Table 4). For one of those species (Field Sparrow [*Spizella pusilla*]), DEV was selected at both the 200 m and 1,000 m scales, although for the smaller scale, the coefficient's 95% credible interval included zero. SIDI was selected for 3 species and showed a positive relationship with occupancy, although for only one species (Song Sparrow [*Melospiza melodia*]) did the 95% credible interval exclude zero (Table 4). CONTAG was selected twice (Gray Catbird [*Dumetella carolinensis*] and Eastern Towhee [*Pipilo erythrophthalmus*]) and showed a negative relationship with occupancy, but for both species, the 95% credible interval failed to exclude zero (Table 4). Finally, ELEV was selected for 5 species and was the only covariate to show variable (by species) relationships with occupancy, with 3 species showing a positive relationship (Chestnut-sided Warbler [*Setophaga pensylvanica*], Eastern Towhee, Gray Catbird) and 2 species showing a negative relationship (Eastern Bluebird [*Sialia sialis*], Indigo Bunting [*Passerina cyanea*]; Table 4).

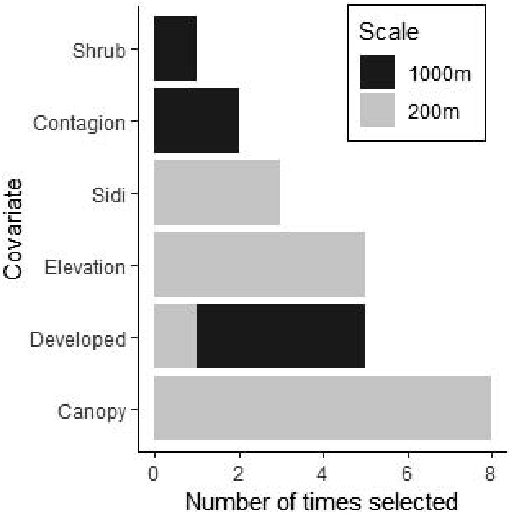

Figure 3. Covariates that stochastic search variable selection indicated were important for occupancy of 12 shrubland bird species. The bars display the number of times each covariate was selected. The fill of the bars denotes the scale at which the covariate was measured.

Spatial scale patterns

Of the 24 covariates selected, 17 (71%) were measured at the smaller (i.e., 200 m) spatial scale. However, CANOPY, ELEV, and SIDI were only included at the 200 m scale in the global model because of extreme collinearity with their 1,000 m counterparts.

General occupancy trends

Occupancy was variable both among species and across sites within species. Three species—all insectivorous Neotropical migrants—had extremely low occupancy probabilities (mean $\psi = 0.1$–0.2): White-eyed Vireo (max $\psi = 0.14$), Yellow-breasted Chat (max $\psi = 0.35$), and Prairie Warbler (*Setophaga discolor*; max $\psi = 0.4$; Fig. 5). The 2 species with the highest occupancy probabilities were both omnivorous temperate migrants—Song Sparrow (mean $\psi = 0.54$) and Eastern Towhee (mean $\psi = 0.64$; Fig. 5). The remaining species showed variable occupancy probabilities across sites but had moderate mean occupancy probabilities (roughly 0.3; Fig. 5).

Detection parameters

True positive detection probability p_{11} was generally high and was lowest for White-eyed Vireo (mean = 0.24) and Brown Thrasher (*Toxostoma rufum*; mean = 0.27; Appendix Table A7). False positive detection probability p_{10} was low—always lower than p_{11}—and was highest for Eastern Towhee (mean = 0.27) and Song Sparrow (mean = 0.18; Appendix Table A7). Observation confirmation probability b was low (posterior means ranged from 0.05 to 0.25) but was high enough to distinguish false positive and false negative detections (Appendix Table A7; Ferguson et al. 2015).

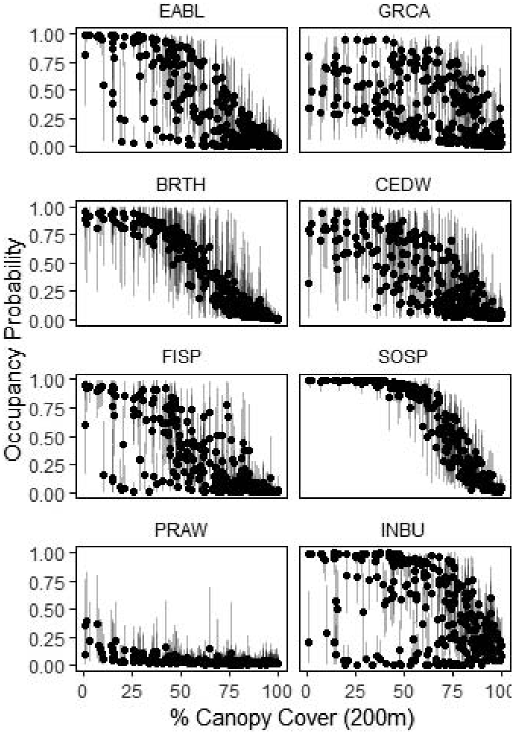

Figure 4. Shrubland bird occupancy is negatively associated with percent canopy cover. CANOPY was an important covariate for 8 species, more than any other covariate we evaluated. Inference for occupancy probability at each site is shown (point = posterior mean, bar = 95% Bayesian credible interval). Species codes provided in Table 1.

Discussion

Landscape patterns associated with occupancy

Canopy cover—CANOPY was selected for more species (8) than any other covariate and, as we predicted, all species showed a negative relationship with it. Such a relationship is intuitive;

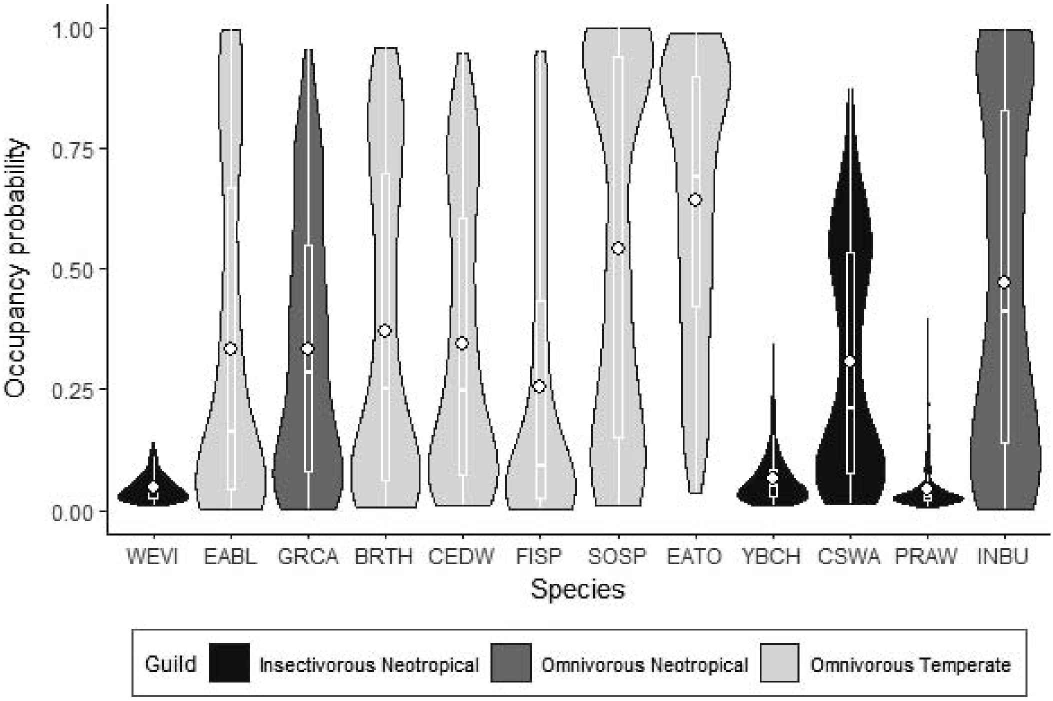

Figure 5. Posterior means of occupancy probability at all sites for all species. The violins show the frequency of the posterior means across sites, the white points show the mean across sites of the posterior means, and the boxplots show the median and quantiles. The fill of the violins indicates the guild of each species. Species codes provided in Table 1.

shrubland birds do not inhabit closed-canopy forests, instead requiring some form of disturbance to break the canopy and permit the growth of early successional vegetation (Askins 1994). However, CANOPY is not a direct measure of shrubland bird habitat (i.e., early successional vegetation), which is difficult to quantify for 2 reasons. First, early successional vegetation is difficult to distinguish from forest using satellite imagery (Cooley et al. 2016). Second, the NLCD layer has a resolution of 30 × 30 m, which means that small patches of early successional vegetation—such as those created by treefall—will go unidentified, and yet such small gaps can create habitat for shrubland birds (Roberts and King 2017b). Therefore, we suggest that canopy cover, while not a direct measure of early successional vegetation, is perhaps the best quantification of habitat suitability for shrubland birds over large spatial extents.

Landscape heterogeneity—Two covariates quantifying landscape heterogeneity—CONTAG and SIDI—were selected for 2 and 3 species, respectively. Occupancy increased with increasing landscape heterogeneity (i.e., lower values of CONTAG and higher values of SIDI; Table 4). In our system, heterogeneous landscapes were mosaics of forest patches, lawn, and pasture, with roads and structures interspersed throughout. Homogeneous landscapes, on the other hand, were unbroken tracts of forest (Fig. 6). Generally, disturbance increases both the amount of early successional vegetation and the heterogeneity of a landscape (Turner 2010). Therefore, metrics of landscape heterogeneity, while again not direct measures of early successional vegetation, may be useful for characterizing shrubland bird habitat.

Elevation—We included ELEV in the global model but regarded it as a nuisance variable, since elevation covaries with climatic and land cover factors that drive avian habitat selection (Laseter et al. 2012). Indeed, ELEV covaried with several patterns we linked to shrubland bird occupancy. First, it showed a positive correlation with CANOPY (Pearson's $r = 0.37$ and 0.38 for the 200 m and 1,000 m measures of CANOPY, respectively). Second, ELEV showed a negative

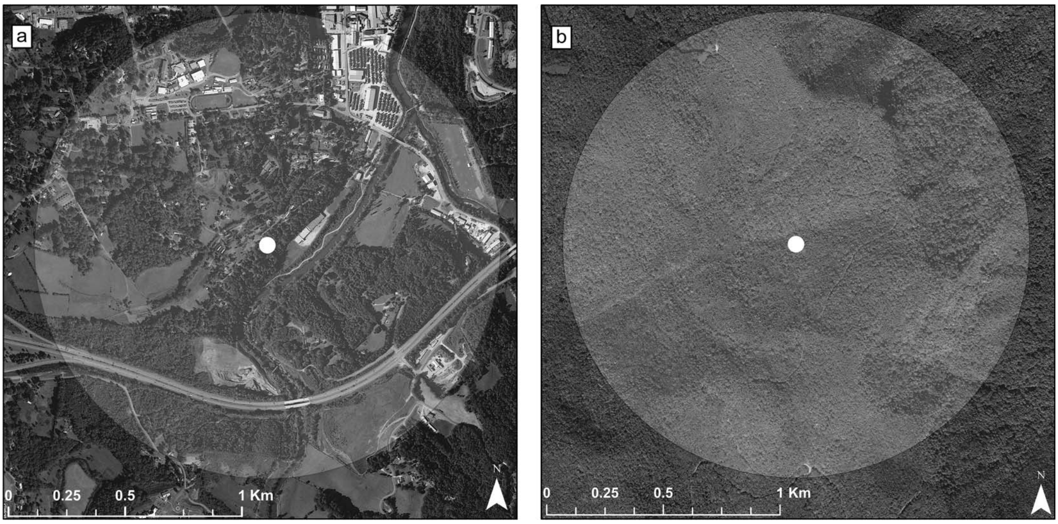

Figure 6. Two example landscapes from our study area. Landscape (a) displays low percent canopy cover (CANOPY), high landscape diversity (SIDI), and low contagion (CONTAG), patterns that were associated with heightened shrubland bird occupancy, while landscape (b) displays high CANOPY, low SIDI, and high CONTAG. Occupancy was higher for 10 out of 12 species in landscape (a) than landscape (b). Paradoxically, landscape (a) also shows extensive development (DEV), which we found to have a negative association with occupancy. Therefore, while landscapes such as (a) may result in higher occupancy for some species, these species will likely mostly be generalist shrubland species (e.g., Song Sparrow); indeed, the 2 species to have higher occupancy in (b) were both insectivorous Neotropical migrants, which are thought to be particulary sensitive to development. Landscape (b) shows little development, but also high CANOPY, low SIDI, and high CONTAG. Landscapes such as these—essentially unbroken forests—do not generally provide habitat for shrubland birds.

correlation with landscape heterogeneity (Pearson's $r = -0.28$ for SIDI and $r = 0.29$ for CONTAG; recall that larger values of CONTAG describe more uniform landscapes). Additionally, ELEV showed no apparent correlation with DEV (Pearson's $r = 0.02$ and 0.10 for the 200 m and 1,000 m measures, respectively), indicating that there was no confounding effect of differing amounts of development at different elevations.

Notably, ELEV was the only covariate to show variable (across species) relationships with occupancy. Of the 5 species for which it was selected, 3 showed a positive relationship with ELEV. Two of these species (Chestnut-sided Warbler and Eastern Towhee) did not have CANOPY selected, and the third (Gray Catbird) showed a weaker negative relationship with CANOPY than other species (coefficient = –1.01, versus –2.21 for Eastern Bluebird, for example). Previous research suggests that these 3 species can inhabit small forest gaps and edges, which may allow them to occupy high-elevation landscapes that have experienced limited disturbance (Smith et al. 2011, Byers et al. 2013, Greenlaw 2015). The 2 species that showed a negative relationship with ELEV (Eastern Bluebird and Indigo Bunting) also showed strong negative relationships with CANOPY and DEV (Table 4), indicating that these species require disturbed landscapes (which are less common at high elevation) but are also averse to development.

Amount of development—We included DEV in our analysis to represent the amount of exurban development in the study landscapes. DEV was selected for only 4 species, all of which showed a negative relationship with it. This suggests that exurban development has either negative or neutral (since it was not selected for 8 species) effects on shrubland bird occupancy (see more details under "Response to exurban development").

Amount of shrubland—SHRUB was selected only for Field Sparrow. Since SHRUB was our only covariate that directly quantified the amount of early successional vegetation, it is surprising that it was selected only once. That SHRUB was selected for Field Sparrow is perhaps unsurprising, since this species—more so than the others we studied—requires large expanses of shrubland habitat, which are more likely to be identified by the NLCD (Rodewald and Vitz 2005, Carey et al. 2008). Therefore, while SHRUB is conceptually the most compelling predictor of occupancy that we evaluated, we suggest that, in practice, indirect measures of early successional habitat such as canopy cover and landscape heterogeneity better characterize habitat suitability for shrubland birds.

Spatial scale patterns—CONTAG, DEV, and SHRUB were included at the 200 m and 1,000 m scales in the global model, while CANOPY, ELEV, and SIDI were included only at the 200 m scale due to collinearity. Notably, of the 3 covariates included at both scales, the 1,000 m scale was always selected as important and the 200 m scale was either not selected or did not show a clear relationship with occupancy probability (Table 4). For CONTAG, this suggests that heterogeneity of the broader matrix is important for shrubland bird occupancy (i.e., a patch of early successional vegetation in an otherwise unbroken forest will be less desirable than a similar patch imbedded in a heterogeneous matrix). For DEV, this suggests that increasing amounts of exurban development in the broader landscape may preclude shrubland birds from colonizing a habitat patch even when there is no development at smaller distances from the patch.

Response to exurban development

We documented that shrubland birds display negative or neutral responses to exurban development. DEV was selected for only 4 species (Eastern Bluebird, Cedar Waxwing [*Bombycilla cedrorum*], Field Sparrow, Indigo Bunting), all of which showed an unequivocal negative association with it. The other 8 species showed no relationship with DEV, which indicates a neutral relationship with exurban development. However, by comparing the occupancy rates of the study species, 2 additional patterns stand out. First, the species with the highest occupancy rates were Song Sparrow and Eastern Towhee (Fig. 5), both of which are omnivorous temperate migrants and could be considered generalists. They could, for example, inhabit features of developed landscapes such as gardens or hedges (Arcese et al. 2002, Greenlaw 2015). Second, the lowest occupancy rates were seen for several of the Neotropical migrants, which could be considered specialists. Therefore, we suggest that shrubland birds follow trends documented in other taxa, with generalists thriving in urbanizing areas and specialists failing to adapt to urbanizing areas (Marzluff 2001, Devictor et al. 2007, 2008). Specifically, we suggest that shrubland birds show a response continuum to exurban development, ranging from avoiders that receive no benefit from exurban development (e.g., Field Sparrow, which had a strong negative association with DEV), to species that may receive marginal benefit (e.g., Brown Thrasher, which did not show any association with DEV but showed moderate occupancy rates in exurban landscapes), to adapters that can thrive in exurban landscapes (e.g., Song Sparrow, which did not show any association with DEV but showed high occupancy rates in exurban landscapes; Marzluff 2001).

Exurban development is a form of disturbance. As such, it increases landscape heterogeneity and decreases canopy cover, patterns that we have shown to be positively associated with shrubland bird occupancy. Therefore, while exurban development would seem to create habitat for shrubland birds, we hypothesize that it does not, for 2 reasons. First, the construction of low-density housing is a one-time disturbance event. Canopy cover may initially be reduced, but in exurban areas, canopy cover increases over time because of the suppression of natural disturbance regimes and the positive attitudes toward trees by residents (Turner et al. 2003, Gragston and Bolstad 2006, Cadieux and Taylor 2013). Second, while exurban development is a form of disturbance, we suggest that it does not actually create early successional vegetation (i.e., shrubland bird habitat). Even though it may drive patterns (e.g., decreasing canopy cover, increasing heterogeneity) that are positively associated with occupancy, exurban development creates lawns, gardens, and forest edges that are not desirable to most shrubland birds (Schlossberg and King 2008). Therefore, we hypothesize that exurban development as a form of disturbance is decoupled from the generation of early successional vegetation and, therefore, shrubland bird habitat.

Conclusion

Our results indicate that exurban development will generally have negative or neutral effects on shrubland bird occupancy. This conclusion is supported by previous work. Lumpkin and Pearson (2013), also working in the Appalachians, found that 2 shrubland species (Chestnut-sided Warbler and Indigo Bunting) were negatively associated with building density, while 5 shrubland species (all generalists) showed a weak positive association with building density. Schlossberg et al. (2011), working in western Massachusetts, suggested that low-density exurban development would have neutral or positive effects on shrubland species. However, the landscapes they analyzed contained lower intensities of exurban development than the landscapes in this study (e.g., the mean percentage of the landscape that was developed was 4.2% for 1 km buffers versus 12.7% for ours; see table 2 of Schlossberg et al. 2011; Appendix Table A6). The negative effects of exurban development that we describe likely weaken with decreasing intensities of development, which would explain the slightly different conclusion of Schlossberg et al. (2011). The trends we document, then, are likely generalizable to forested landscapes undergoing exurban development, at least in the eastern United States. We conclude that exurban development will benefit only certain urban-adapted shrubland birds without creating habitat for most shrubland species despite the fact that it exerts considerable disturbance to forested landscapes.

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Appendix

Appendix Table A5. Landscape and development variables used to define strata for stratified random sampling of point counts across Macon County, North Carolina, USA.

Variable	Level
Elevation	< 800 m
	800–100 m
	> 1,000 m
Structure Age	No structures
	Before 1980
	After 1980
Subdivision	Yes
	No
% Forest (1,000 m)	< 50%
	> 80 %
% Agriculture (1,000 m)	< 10%
	> 25%
% Development (1,000 m)	< 10%
	> 25%

We combined all levels of the elevation, structure age, and subdivision variables with 4 combinations of the land-cover variables for a total of 64 strata. The combinations of land-cover variables were (1) high % Forest, low % Agriculture, low % Development; (2) low % Forest, high % Agriculture, low % Development; (3) low % Forest, low % Agriculture, high % Development; and (4) low % Forest, high % Agriculture, high % Development.

Appendix Table A6. Summary statistics (across the 272 sites) of the covariates that were included in the global model.

	CANOPY	CONTAG$_{200}$	CONTAG$_{1000}$	DEV$_{200}$	DEV$_{1000}$	ED_DF$_{200}$	ED_DF$_{1000}$	ELEV	FOREST$_{200}$	FOREST$_{1000}$	SHRUB$_{200}$	SHRUB$_{1000}$	SIDI
Min	1.2	0.0	33.3	0.0	0.0	0.0	11.5	586.4	0.0	0.0	0.0	0.0	0.0
1st Q	47.4	32.7	50.3	0.0	0.0	44.2	60.4	664.4	0.0	39.0	0.0	0.4	0.3
Med	71.1	41.9	59.4	0.0	0.0	85.5	76.5	795.5	0.0	60.3	0.0	1.3	0.5
Mean	65.1	45.0	60.3	4.4	12.7	82.5	75.7	908.1	7.9	56.8	1.6	1.7	0.5
3rd Q	85.6	56.8	70.5	0.0	18.9	118.0	94.6	1,161.4	0.0	80.3	0.0	2.6	0.6
Max	99.7	98.9	92.3	100.0	77.0	265.5	134.4	1,451.4	100.0	100.0	28.3	8.1	0.8

The $_{200}$ and $_{1000}$ subscripts refer to the spatial scale at which the covariate was measured (in meters from the survey points). Covariates that do not carry a subscript were included only at the 200 m scale because of extreme collinearity with 1,000 m measures of the same covariate. CANOPY is the mean percent canopy cover of the landscape surrounding survey points, CONTAG is contagion (a metric of landscape heterogeneity), DEV is the percentage of the landscape that is developed (all NLCD subclasses aggregated), ED_DF is edge density of the deciduous forest class, ELEV is elevation in meters, FOREST is the percentage of the landscape that is forested (all NLCD subclasses aggregated), SHRUB is the percentage of the landscape that is shrub, and SIDI is the Simpson's landscape diversity index.

Appendix Table A7. Summary statistics for detection parameters' posterior distributions for the 12 study species. For an explanation of the species codes, see Table 1. Under the "Parameter" column, p_{11} is true positive detection probability (i.e., the probability of detecting a species if it occupies a site), p_{10} is false positive detection probability (i.e., the probability of recording a species as present if it does not occupy a site), and b is observation confirmation probability (i.e., the probability that both observers detect a species within 25 m).

Species	Parameter	Mean	SD	Rhat
WEVI	p_{11}	0.24	0.12	1.001
WEVI	p_{10}	0.01	0.00	1.001
WEVI	b	0.25	0.14	1.001
EABL	p_{11}	0.53	0.04	1.001
EABL	p_{10}	0.04	0.01	1.001
EABL	b	0.09	0.02	1.001
GRCA	p_{11}	0.54	0.04	1.002
GRCA	p_{10}	0.06	0.01	1.001
GRCA	b	0.21	0.03	1.001
BRTH	p_{11}	0.27	0.04	1.001
BRTH	p_{10}	0.03	0.01	1.001
BRTH	b	0.06	0.02	1.001
CEDW	p_{11}	0.49	0.05	1.001
CEDW	p_{10}	0.12	0.02	1.001
CEDW	b	0.10	0.02	1.001
FISP	p_{11}	0.62	0.05	1.001
FISP	p_{10}	0.03	0.01	1.001
FISP	b	0.05	0.02	1.001
SOSP	p_{11}	0.90	0.02	1.001
SOSP	p_{10}	0.18	0.03	1.001
SOSP	b	0.36	0.02	1.001
EATO	p_{11}	0.87	0.02	1.001
EATO	p_{10}	0.27	0.04	1.001
EATO	b	0.21	0.02	1.001
YBCH	p_{11}	0.50	0.11	1.001
YBCH	p_{10}	0.01	0.01	1.001
YBCH	b	0.13	0.06	1.001
CSWA	p_{11}	0.58	0.07	1.001
CSWA	p_{10}	0.09	0.02	1.001
CSWA	b	0.09	0.03	1.001
PRAW	p_{11}	0.54	0.12	1.001
PRAW	p_{10}	0.02	0.01	1.001
PRAW	b	0.14	0.07	1.001
INBU	p_{11}	0.77	0.03	1.001
INBU	p_{10}	0.09	0.02	1.001
INBU	b	0.12	0.02	1.001