ABSTRACT

IGLECIA, MONICA N. Occupancy Models and Strategic Habitat Conservation for Avian Species in the Southeastern Coastal Plain of the United States. (Under the direction of Jaime A. Collazo).

Rapidly expanding lists of priority species has increased the need for a framework that can utilize existing datasets to inform landscape-scale conservation strategies. This is evident in the South Atlantic Coastal Plain of the United States where no fewer than 91 avian species are considered high priority for conservation. It is believed that the process of urbanization is a contributing factor. This process transforms natural habitats into impervious surfaces and semi-permanent structures, threatening many avian species. We used single-season occupancy models, coupled with regional land cover and Breeding Bird Survey data from 2001, to address two objectives aimed at informing conservation planning in the region. The first objective addressed two questions: (1) do occupancy patterns correspond with purported species-habitat associations at two thematic resolutions of habitat classification, and if so, which of two thematic resolutions of habitat classification provided the best support? and (2) does the composition of the matrix of habitat surrounding a sampling unit influence species occurrence? The second objective addressed whether: (1) species richness differed between sampling units containing high and low levels of urban habitat, and (2) a species' response conformed with expected sensitivity to urbanization.

To address the first objective, we focused on three priority species: brown-headed nuthatch, red-headed woodpecker and eastern wood-pewee. Model results supported knowledge-based hypotheses for the nuthatch and wood-pewee; occupancy probabilities were strongly associated with predicted vegetation classes ranked as optimal habitat. This was not so for the woodpecker; vegetation regarded as marginal habitat received greater

support. Results affirmed the woodpecker's designation as a generalist. The influence of landscape-matrix composition on occupancy was consistent with species-habitat relationships at the BBS route-segment scale. Generally, the influence of amount of habitat on occupancy was inversely related to distance.

To address the second objective, we used three groupings to categorize species according to their observed sensitivity to urban habitats: exploiters, adapters, and avoiders. We used occupancy models and gauged the sensitivity of 16 focal species based on the direction and strength (95%CIs did not overlap estimates) of the beta parameter relating percent urban habitat along BBS route-segments to occupancy probability. We expected the relationship to be positive and strong for exploiters, and negative and strong for avoiders. As predicted, species richness was higher in low-urban route-segments than in high-urban segments. Also as predicted, 2 of 3 urban exploiters were positively and strongly associated with increasing urbanized landscapes. In contrast, there was no support for a strong, negative relationship for urban avoiders. Results suggest that urban adapters and avoiders are adept at using the low-levels of urbanized habitat characterizing BBS routes. Options to relocate BBS routes will diminish with increasing urbanization. Thus BBS routes provide opportunities in the future to assess responses of urban avoiders, a sensitivity group that contains many species of conservation concern in most states.

Our data-driven models can be used to test knowledge-based models and estimate the consequences of conservation actions in a structured-decision framework. Breeding bird surveys will continue to be a source of landscape scale data to assess changes in species composition and their relative sensitivities to habitat alteration. The potential to inform conservation design could benefit from estimating patterns of local extinction and local colonization rates. However, spatio-temporal inferences derived from the application of such modeling frameworks will require the availability of land cover data over short time intervals, which is not presently available.

Occupancy Modeling and Strategic Habitat Conservation for Avian Species in the Southeastern Coastal Plain of the United States

by
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BIOGRAPHY

Monica Iglecia grew up in Moorpark, California where she completed high school at the High School at Moorpark College. She then headed north and received a Bachelor of Arts in Environmental Studies at the University of California at Santa Cruz in 2005. While in Santa Cruz, she participated in two programs, the Natural History Field Quarter and Sierra Institute, which reaffirmed her commitment to the conservation of biodiversity and natural resources. In these field-based programs she obtained the influential mentorship of Dr. Steve Gliessman, Breck Tyler, and Walker Abel, in natural history and nature philosophy.

An internship with the Ventana Wilderness Society California condor program in Big Sur, CA materialized her passion for conservation ecology. She spent the next few years mapping the seafloor, exploring the United States and Canada by van, providing legal assistance, rehabilitating wildlife, and waiting tables. Her interests in landscapes, birds, and conservation ecology led her to join the Biodiversity and Spatial Information Center and pursue graduate study under the advisorship of Jaime Collazo in 2007.

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CHAPTER 1

AVIAN OCCUPANCY MODELS AND HABITAT CONSERVATION IN SOUTHEASTERN UNITED STATES

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ABSTRACT.-- Rapidly expanding lists of priority species in the South Atlantic Coastal Plain of the United States and elsewhere has increased the need to formulate landscape-scale conservation strategies. Avian distribution and abundance are influenced by the amount and spatial configuration of habitat, and a basis to quantify trade-offs among conservation alternatives is needed. We used single-season occupancy models, coupled with land cover and Breeding Bird Survey data to meet this need. We asked: 1) do occupancy patterns conform to purported species-habitat associations at two thematic resolutions of habitat classification, and if so, which of two thematic resolutions of habitat classification provided the best support?, and 2) does the composition of the matrix of habitat surrounding a sampling unit influence species occurrence? We then constructed conservation design models to illustrate and facilitate the application of results. We focused on three priority species, two of which are considered surrogate species: eastern wood-pewee, brown-headed nuthatch, and red-headed woodpecker. Results supported predicted associations for the nuthatch and wood-pewee; occupancy probability was strongly associated with predicted vegetation classes ranked as optimal habitat. This was not so for woodpeckers; vegetation regarded as marginal habitat received greater support. Results affirmed the woodpecker's designation as a generalist. The influence of landscape-matrix composition on occupancy was consistent with species-habitat relationships at the BBS route-segment scale. Generally, the influence of amount of habitat on occupancy was inversely related to distance. Our data-driven models serve to validate expert/knowledge-based models and provide a quantitative basis to link objectives to alternative actions in a strategic habitat conservation framework.

KEYWORDS: breeding bird survey, brown-headed nuthatch, eastern wood-pewee, red-headed woodpecker, South Atlantic Coastal Plain, occupancy models.

INTRODUCTION

Landscape-scale habitat conservation is concerned with how amount of habitat and its spatial configuration influence biological processes, and ultimately, a species' abundance and distribution (Wiens et al., 1993). For example, species-specific attributes, such as dispersal distances, influence population structure, recruitment, and genetic diversity, and these can be mediated by the amount and spatial configuration of habitat (Greenwood and Harvey, 1982; Greenwood, 1987; Sinclair, 1992; Hansen and Urban, 1992). A variety of habitat characteristics are often used as conservation design elements because species perceive habitats and landscapes differently (Cody, 1981; Lima and Zollner, 1996). Examples include habitat composition, amount and structure (Cody, 1981; Whitcomb et al., 1981; Wiens and Rotenberry, 1981; Askins et al., 1987; Robbins et al., 1989). Others highlight the importance of scale-dependent characteristics of the landscape such as patch area, distance, and the composition of the intervening habitat matrix (Ewers and Didham, 2006). Certainly, the interplay between biological processes and landscape habitat characteristics points at the vulnerability of a species' abundance and distribution to habitat loss, fragmentation, and eventually, to potential impacts from climate change (Vitousek et al., 1997; Wilcove et al., 1998; Franklin et al., 2002, Parmesan and Yohe, 2003).

The South Atlantic Coastal Plain of the United States harbors high biological diversity of birds and reptiles (Ricketts et al., 1999), but their conservation faces many challenges. Approximately 40% of the region's natural vegetation communities have been fragmented or altered by human use (Hunter et al., 2001). Ninety-one avian species are considered of high priority for conservation due to declining population trends, sensitivity to habitat fragmentation, and shifting distributions (Watson and McWilliams, 2005; Valiela and Martinetto, 2007). Rapidly expanding lists of priority species across taxa has placed increasing pressure on limited conservation resources, and consequently, on the need to formulate landscape-scale conservation strategies (Baker et al., 2008).

In this work we coupled recent statistical advances in occupancy estimation with land cover and avian data sets to model patterns of species occurrence in the South Atlantic Coastal Plain as a means to inform conservation planning (MacKenzie et al., 2006; USFWS, 2006; USGS, 2008, Hines et al., 2009). Specifically, we asked: 1) do occupancy patterns conform to purported species-habitat associations at two thematic resolutions of habitat classification?, and 2) does the composition of the habitat matrix surrounding a sampling unit influence species occupancy? Occupancy is defined as the probability that a site is occupied, given the probability of detecting an individual when it is present at the site (MacKenzie et al., 2006). Birds are suitable biological models for this work's goal because they are good indicators of ecosystem function, and are sensitive to changes in vegetation structure and landscape composition (Hutto, 1998; O'Connell, 2000; Savard, 2000; Sekercioglu, 2006; Veech, 2006; Sauer et al., 2008). Results from the aforementioned objectives were used to construct conservation design or user's models to illustrate and facilitate the application of results from our work. These were constructed using spatial covariates commonly used in conservation planning (e.g., patch size, amount of habitat, distance to habitat). Models were built for three species: the brown-headed nuthatch (*Sitta pusilla*), the eastern wood-pewee

(*Contopus virens*), and the red-headed woodpecker (*Melanerpes erythrocephalus*). These are priority species in the coastal plain (NCWRC, 2005), and two of them, the nuthatch and woodpecker, are considered surrogate species (Moody and Grand, in prep). As such they are viewed and serve as focal species for conservation planning because their habitat requirements are representative of other species (Lambeck, 1997). We discuss how our work augments our understanding about species-habitat associations and its applicability to conservation planning in the southeast and elsewhere in the United States.

METHODS

Study Area

Our study area was the South Atlantic Coastal Plain, specifically the South Atlantic Migratory Bird Initiative region, a physiographic area of high avian species diversity (SAMBI; Watson and McWilliams, 2005). The region intersects portions of the Middle Atlantic Coastal Plain, Southeastern Plains, and the Southern Coastal Plain ecoregions (Omernik, 1987), and spans across the states of Virginia, North Carolina, South Carolina, Georgia and Florida (latitudes 29° - 37° North; Figure 1). The northern edge of the SAMBI is in southern Virginia at the watershed boundary between the Chowan River and Lower James River basins (Watson and McWilliams, 2005). The northern region is dominated by longleaf pine (*Pinus palustris*) and loblolly pine (*Pinus taeda*). The SAMBI is bound on its western edge at the Fall Line where alluvial and marine sediment meet the exposed continental bedrock of the Piedmont region (Hupp, 2000), and on the eastern edge by the Atlantic Ocean. The southern SAMBI is in a transitional zone of northeastern Florida where tropical mangroves meet coastal plain plant communities; this region is dominated by pond pine (*Pinus erotina*) and Atlantic white cedar (*Chamaecyparis thyoides*; Watson and McWilliams, 2005). We buffered the SAMBI boundary by 30 km to avoid edge effects and to encompass the habitats surrounding BBS routes that straddle the limits of the region. The total area of the buffered SAMBI is 29, 073,338 ha with 2,606,020 ha of water and elevation ranges from 0 m to 219 m.

Focal Species

Below we describe the ecological characteristics and habitat requirements of each of the focal species. The brown-headed nuthatch (hereafter nuthatch) is an endemic, resident species in the southeastern United States. The species ranges from eastern Texas to Florida and northward to the southern tip of Delaware (Withgott and Smith, 1998). Nuthatch are commonly found in southeastern pine forests with open understories, especially open longleaf pine savannas in the coastal plain (Bent, 1948; Potter et al., 1980). Increased fire suppression increases growth of deciduous trees and shrubs, and in turn fills open understories which may make forests unsuitable for the species (Meyers and Johnson, 1978; Smith and Smith, 1994). This common passerine excavates nests in the cavities of snags, dead pine trees, and some deciduous trees (McNair, 1984; Kaufman, 1996). The nuthatch has limited dispersal abilities across long distances (Withgott and Smith, 1998) and observed natal dispersal distances are short in northern Florida (1.2 km; Cox and Slater, 2007).

The red-headed woodpecker (hereafter woodpecker) is a short-distance migrant found in many forested habitat types in the eastern United States. This species uses a diverse range of habitats including grassland, shrubs, and deciduous, hardwood, and pine forests. In the southeastern United States the species inhabits coniferous forests more often than in other portions of its range (Smith and Withgott, 2000). The woodpecker is an omnivore, but population densities and migration are closely related to acorn mast abundance (Forbush, 1927). The woodpecker is a primary cavity nester, creating tree cavities that are beneficial to multiple other vertebrate species (Venables and Collopy, 1989). The species begins nesting later in the breeding season than any other eastern woodpecker (Nicholson, 1997).

The eastern wood-pewee (hereafter wood-pewee) is a forest-interior, neotropical migrant (Robbins et al., 1989). The breeding distribution for this species ranges from southern Canada to central Texas and northern Florida (McCarty, 1996). While the species most often inhabits deciduous forests, the species increasingly inhabits evergreen forest types in the southern United States (McCarty, 1966). Wood-pewee are insectivorous aerial feeders, and open understories with feeding perches in the canopy provide ideal foraging conditions for the species (Via, 1979).

Breeding Bird and Land Cover Data

We used North American Breeding Bird Survey data from 2001 to assess the evidence of support for predicted species-habitat relationships. The North American Breeding Bird Survey (BBS) is a national, standardized, volunteer-based survey, with over 4000 routes sampling breeding birds across North America each year (Flather and Sauer, 1996). Each survey is a ~39.4 km long route composed of fifty stops spaced ~0.8 km apart. Observers conduct three-minute point counts at each stop, recording all birds seen and heard within a 400 m radius. We included routes in the analyses if: 1) the routes were actively run (between 1992 - 2002); 2) the digital route map did not differ from hardcopy maps; 3) route lengths were within 10% of the standard 39.4 km length; and 4) routes did not overlap themselves or other active routes. We acquired and individually assessed the paper maps that were given to the volunteers conducting the surveys. BBS routes can be longer than 39.4 km when it is not conducive to stop safely or the route crosses a body of water. This screening yielded 120 out of 130 possible routes in the SAMBI.

We split each route into four segments composed of eight stops each. The resulting route segments were ~6.4 km long, and ~4.8 km from the adjacent route segment (Appendix 1). The average area covered by the buffered segments was 513 ha (SE = 2 ha). Restructuring BBS data minimized habitat heterogeneity within route segments. On average, route segments had fewer habitat classes (14.20, SE = 0.37) than entire BBS routes (16.15, SE 0.45; Z_{20}= 14.92, $P<0.05$). We converted counts per stop to presence (1) and absence (0) data; species were considered present at a stop if at least one individual was detected. Spatial replication within route segments, the primary sampling units, allowed the estimation of probability of detection (MacKenzie et al., 2002). While temporal replication provides information on presence at a specific location, spatial replication can support greater certainty of the species-habitat relationship (Goodinson, 2000).

We used two land cover datasets that differed in their specificity of thematic-habitat classifications to model species-habitat relationships. The first dataset was the 2001 National Land Cover Dataset; the second was the 2001 Southeast Gap Analysis Program land cover (SEGAP; MRLC, 2001; USGS, 2008). Both datasets are 30 m x 30 m resolution, derived from Landsat-7 imagery using normalized tassel-cap transformations for spring, summer and fall images, digital elevation maps, and a set of decision tree classification rules (Homer et al., 2007; USGS, 2008). The National Land Cover Dataset is composed of 29 general habitat classes including evergreen, deciduous and mixed forests, and has a national thematic accuracy of 78.7% (Wickham et al., 2010). SEGAP further developed the National Land Cover Dataset using aerial photos and the National Vegetation Classification System from NatureServe to map the southeastern United States at the alliance level, delineating 118 habitat classes in the SAMBI region (Appendix 2; USGS, 2008). All data were processed in the North American Datum 1983 Albers, an equal area projection. All spatial analyses were performed with ArcMAP 9.2 and Arc Macro Language (ESRI Inc. 1999).

Data Analysis

We used single-season, single-species occupancy models with and without adjustment for spatial dependency to estimate the probability of occupancy (ψ) and detection (p) using program PRESENCE (Hines, 2006). Before running models all continuous covariates were normalized. We ranked models using Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). We considered models with ΔAIC ≤ 2 to have strong support (Burnham and Anderson, 2002). We considered an effect (i.e., covariate beta coefficient) to be strongly supported if the 95% confidence intervals did not overlap zero. Model fit for models without spatial dependence was assessed using the Goodness of Fit (GOF) option in program PRESENCE based on 5,000 parametric bootstraps (Mackenzie and Bailey, 2004). A GOF is not yet available for spatial dependence models (Hines et al., 2009). We assumed that adjusting for spatial dependence, when evidence supported it, was an improvement over the alternative because unadjusted estimates tend to be biased-low (Hines et al., 2009).

We followed the rationale and steps outlined by Franklin et al., (2004) and Anthony et al., (2006) to construct candidate model sets for each species. We first assessed the need to adjust for spatial dependence and for changes in detection probability with three model structures for occupancy and two model structures for detection: (1) no spatial dependence [$\psi(.)$, $p(.)$ and $\psi(.)$, $p(\mathrm{S})$]; (2) generalized spatial dependence [$\psi(.)$, $\theta = \theta`$, $p(.)$; $\psi(.)$, $\theta = \theta`$, $p(\mathrm{S})$]; and (3) spatial dependence for all stops except the first one [$\psi(.)$, $\theta \neq \theta`$, $p(.)$; $\psi(.)$, $\theta \neq \theta`$, $p(\mathrm{S})$]. The rationale for considering these model structures follows. BBS surveys were conducted between 15 May and 15 July in 2001. We arbitrarily created two survey periods (15 May – 15 June and 16 June – 15 July), using 15 June as its mid-point. This setup provided a contrast between peak (S) and late spring because variation in species detection has been known to vary seasonally for some southeastern breeding bird species (Farnsworth et al., 2002). Because stops along BBS routes are sampled sequentially, it is possible that the probability of occupancy is influenced by the state (occupied or not) of the previous survey stop or segment (Hines et al., 2009). We assessed support in the data for spatial dependency using two spatial models in program PRESENCE (Hines, 2006). The first can be viewed as a generalized spatial dependence model. It assumes that all stops are equally influenced by the state of the preceding stop or habitat (model notation is $\theta = \theta`$; Hines et al., 2009). The alternative model assumes that the occupancy of the first stop is not influenced by the preceding habitat or state. Thus, the first stop and the rest of the stops in the segment are not equally subject to spatial dependence ($\theta \neq \theta`$; Hines et al., 2009). The former model was of particular interest to us because it provided a framework to account for the possible influence of adjacent route segments along a BBS route.

We used the model structure with the lowest AIC to create model sets to evaluate the influence of landscape covariates (Franklin et al., 2004; Anthony et al., 2006). One set, hereafter Hamel-NLCD models, addressed the first objective of the study, that is, an assessment of species-habitat relationships at two thematic levels of land cover resolution. Another set, hereafter Matrix models, addressed the second objective, or influence of matrix composition on occupancy probability. A third set, hereafter Conservation Design models, modeled occupancy probability as a function of landscape spatial characteristics often used in conservation planning and design. We included latitude as a covariate in all models because the SAMBI spans five states and nine degrees of latitude and thus occurrence might vary as a function of the location sampled within the species' range. We expected that occupancy probabilities would vary along the SAMBI's latitudinal gradient with higher occupancy towards the core of a species range (Brown, 1984; Lawton, 1993). To model this factor, we arbitrarily stratified the SAMBI into three regions: southern (LatS = 29 to 31 °N), central (Lat C = 32 to 34 °N), and northern (Lat N = 35 to 37 °N). This partitioning split the SAMBI into roughly equal sections, containing similar numbers of route segments (southern = 168, central = 204, northern =108). The relationship between the probability of occupancy and covariates was established using a logistic model (logit link) in program PRESENCE (Mackenzie and Nichols, 2004).

Hamel-NLCD Models

We evaluated the support in the data for hypothesized species-habitat associations with land cover data at two thematic resolutions (Table 1). We used higher resolution thematic data (SEGAP) to assess support for species-habitat associations advanced by Hamel (1992). Hamel ranked southeastern-specific forest types in decreasing order of quality for terrestrial land birds using three categories: optimal, suitable, and marginal. Optimal habitat was defined as forest types that supported the highest frequency or abundance of a species. Suitable and marginal habitats were defined as those that supported species in successively lower frequency or abundance. Accordingly, we expected support in the data for each species to be greater for optimal habitat, followed by suitable and marginal (i.e., O>S>M). To assess these predictions we cross-walked 118 SEGAP habitat classes to correspond to the forest types described by Hamel (1992; Appendix 2). We summarized the percentage of the new land cover types within the BBS route-segments and pooled habitat classes into the species-specific definitions of optimal, suitable, and marginal habitat. These categories were directly applicable to the nuthatch and wood-pewee. However, Hamel's report did not include open-habitat types that have been highlighted as important for the woodpecker in models and field observations (Venables and Collopy, 1989; Kale and Maehr, 1990; Stevenson and Anderson, 1994; Belson, 1998; Thogmartin, 2007). Thus, we included grassland and shrub habitats in our definition of optimal habitat for the woodpecker.

We included competing models featuring habitat associations at a coarser level of thematic resolution using the National Land Cover Dataset to determine whether support in the data was greater for more parsimonious classifications. We also hypothesized that support for greater parsimony in thematic resolution would be expected for species classified as generalists in the avian scientific literature (e.g., Red-headed woodpecker). Under the coarse thematic resolution, we predicted that the nuthatch occupancy would be best explained by the amount of the evergreen forest class, followed by deciduous and mixed forest classes (NCWRC, 2005; Withgott and Smith, 1998). For the woodpecker, occupancy probabilities were predicted to be higher in deciduous forests. Competing models included evergreen and mixed forest types as well as shrub and grassland habitats (NCWRC, 2005; Smith and Withgott, 2000). Finally, we predicted that the wood-pewee would have highest occupancy probabilities in mixed forests. Competing models included evergreen and deciduous forest types (NCWRC, 2005; McCarty, 1996).

Matrix Models

We used two natal dispersal distances to define the space within which we assessed the influence of the habitat matrix surrounding BBS route-segments on species occupancy. Specifically, occupancy was allowed to vary as a function of: 1) the land cover type at the thematic resolution that received the most support in the Hamel-NLCD models, 2) the percentage of all other forest cover types, and 3) the amount of urbanized habitat and other impervious surfaces. We expected habitat within a species' natal dispersal distance to influence occupancy, and expected habitat closest to route segments to have stronger effects than habitat at greater distances (Moilanen and Nieminen, 2002; Fagan and Calabrese, 2006). Rates of natal dispersal are species-specific and data requirements for empirical estimates are rarely acquired in the field (Swingland, 1982). Therefore, we used allometric equations based on mean body mass and the diet of avian guilds to estimate natal dispersal distances

(Dunning, 1993, 2007; Sutherland et al., 2000). These estimates are approximate natal dispersal distances, so we calculated a generalized value (average) based on thirteen southeastern species within the same taxa (Appendix 3). We used estimates of the median (50%) and 90% dispersal distances in our models. The former was 1.47 km (i.e., 50 % probability that an individual will disperse farther) and the latter was 4.73 km (i.e., 10% probability that an individual will disperse farther).

Conservation Design Models

We modeled occupancy as a function of: 1) the number of patches (N), 2) size of the largest patch (Max), 3) distance to patches (D), and 4) the interaction between number of patches and distance (N x D) within the two natal dispersal distances. Other spatial covariates were considered but not modeled because they were highly correlated with the aforementioned covariates (Appendix 3, Cooper and Walters, 2002). We defined habitat patches as contiguous habitat (pixels of land cover connected using the Regiongroup 4 function in ArcGIS) with a minimum patch-size reflective of observed breeding territories (nuthatch = 2.8 ha, Norris, 1959; woodpecker = 3.1 ha, Venables and Collopy, 1989; wood-pewee = 2.2 ha, Best and Stauffer, 1986). The distance between BBS route-segments and habitat patches was defined as the average Euclidean distance to all patches within each dispersal distance. Euclidean distance should be a good measure of patch distance because elevation variation in the SAMBI is minimal. We reported the median number of patches, size of largest patches, and distance to patches (± 90% confidence intervals) for each species. We summarized data for two arbitrarily selected occupancy probability levels, namely, ≥

0.50 and ≥ 0.75. We used PROC UNIVARIATE CIQUANTDF (does not assume normality) to generate confidence intervals (SAS 2002).

Model Assumptions

Careful consideration of model assumptions is important to interpret results. Single-season occupancy models assume that: 1) the system was closed to changes in occupancy during the sampling period; 2) the species was not falsely detected; and 3) species detections were independent. The first two assumptions were likely met given that surveys were conducted in one morning by qualified bird observers. We assessed the third assumption using a candidate model set that included two spatial dependence model structures and one that did not, as described above. We adopted the appropriate modeling framework based on the evidence from the data. We also assumed that both the grain (i.e., 30 x 30 m pixels) and the thematic resolution (habitat classes) are reasonable for developing avian species-habitat models. We believe that the "grain" assumption was met as all species have territory sizes larger than 20 pixels. We assumed that the land cover is an adequate representation of the available habitat on the ground (see Wickham et al., 2010). Finally, we assumed the species responses to their environment are homogeneous within species. We acknowledge that intra- and inter-specific interactions influence occupancy patterns, but these were not assessed in this study.

RESULTS

We found evidence for within-route spatial dependence for the nuthatch and the wood-pewee (Tables 2 and 3). Evidence was equivocal for the woodpecker; a constant model was a plausible alternative (ΔAIC ≤ 2, Table 4). Woodpecker data supported models accounting for seasonal detection ($\beta = -0.57$; 95%CI= -1.15 – -0.01). The probability of detection was significantly lower during peak breeding season ($p = 0.05$, SE = 0.01) than later in the season ($p = 0.08$, SE = 0.02; Z = 7.34, P < 0.01). We found evidence for variation in occupancy across SAMBI's latitudinal gradient. Occupancy was highest for the nuthatch in the central region of the SAMBI, in the southern and central region for the woodpecker, and in the northern region for the wood-pewee (Figures 2 - 4). A regional average estimate of occupancy (i.e., not constrained by latitude) for the nuthatch was 0.58 (SE = 0.24), 0.44 (SE = 0.11) for the wood-pewee, and 0.46 (SE = 0.15) for the woodpecker.

Optimal habitat accounted for most of the variation in occupancy probability for the nuthatch and wood-pewee in the Hamel-NLCD models (Tables 2 and 3). For the woodpecker, marginal habitat received most of the support in the data but models with evergreen forest or shrub/ scrub habitat were competitive (Table 4). Model assumptions for the woodpecker model were met (GOF $\chi^2 = 147.98$, P = 0.20). High estimates of occupancy for all three focal species overlapped throughout South Carolina (Figure 5).

Results from the Matrix models indicated that occupancy probability for the three focal species was influenced by the amount of habitat within 1.47 km of route-segments (Table 5). Specifically, nearest optimal habitat strongly influenced wood-pewee and the nuthatch occurrence. The amount of other forested habitat within 1.47 km was a competitive alternative for the wood-pewee. Much of the variation in occupancy for woodpeckers was explained by marginal habitat within both natal dispersal distances (AIC weight = 0.53), but a model featuring urban habitat within 1.47 km was a plausible alternative (AIC weight =

0.15, ΔAIC ≤ 2). Neither covariate had a strong influence of occupancy (95%CIs overlapped zero; Table 5).

Model selection for Conservation Design models indicated that most of the variation in occupancy probability for the nuthatch was explained by location of the species within its range in the SAMBI (Lat 32°-34°), the number of patches of optimal habitat, the distance to habitat patches, and a negative interaction between the two terms within 1.47 km (AIC w_i = 0.98, Table 2). These same factors influenced occupancy for the wood-pewee, but a model featuring large patches within 4.73 km received slightly higher support from the data (Table 3). Model selection results for the woodpecker indicated that any of the two measures of amount of habitat, number of patches or largest patch size, was the predominant factor influencing occupancy probability (Table 4), but virtually similar support for each alternative made it unclear to ascertain which covariate exerted the strongest influence and at what dispersal distance. Table 6 summarizes the median number of patches, size of largest patches, and distance to patches (± 90% CI) for each species for two arbitrary occupancy probability levels (i.e., ≥ 0.50 and ≥ 0.75).

DISCUSSION

We assessed the strength of evidence for predicted habitat associations and the influence of habitats surrounding BBS route-segments for three species of land birds in the South Atlantic Coastal Plain of the United States using two land cover datasets of different thematic resolutions and static, spatially explicit, occupancy models. Findings augmented our understanding of the species' ecology and provided a data-driven framework to inform conservation planning in the region and elsewhere in the United States in several important ways. For instance, expert-based models are used extensively to make conservation recommendations, but are rarely tested (Schlossberg and King, 2009). This work was a step towards addressing this need. We validated 2/3 of Hamel's (1992) purported species-habitat associations. As predicted, the nuthatch and wood-pewee were positively and strongly associated with optimal habitat. Composition of optimal habitat for the nuthatch consisted of loblolly, shortleaf (*Pinus echinata*), longleaf and slash pine forests (Bent 1948; Potter et al., 1980; Hamel 1992). In contrast, model selection results indicated that variation in woodpecker occupancy was best explained by marginal habitat, a combination of bay-swamp-pocosin, live oak (*Quercus virginiana*), elm-ash-cottonwood, loblolly and shortleaf pine, and mixed-pine-hardwood habitats (see Hamel, 1992 for description of forest types). Composition of the purported optimal habitat was sandhills-longleaf pine, longleaf pine, and slash pine forests. We suggest that accounting for detection probability helped highlight the importance of the purported marginal habitat for the species (MacKenzie et al., 2006). The conservation implications of this finding are important, particularly because the woodpecker is considered a surrogate species in the coastal plain (Moody and Grand, in prep.). It follows that a conservation strategy for the red-headed woodpecker, and those under its surrogate role, would be deficient by failing to consider important forest types on the landscape (Lambert, 1997).

The value of higher thematic resolution to model species-habitat associations was underscored in this study. Habitat selection is a multi-scale, hierarchical process (Johnson, 1980; Hutto, 1985). As such one would expect, for example, an association between the nuthatch and evergreen forest types. This is evidenced by how the NLCD models ranked against each other in the NLCD-Hamel models. However, BBS surveys are conducted in May-June in the SAMBI, and by this time avian species are about to start or are fully engaged in reproduction. Thus one would also expect that species have completed the process of the fine-scale level of habitat selection, and where available, species have occupied optimal and suitable habitat (e.g., Fretwell and Lucas, 1970; Johnson, 1980; Block and Brennen, 1993). Stronger support for higher resolution land cover classes is consistent with this process, allowing the formulation of competing models that reflect greater knowledge about a species' specific habitat requirements at this critical stage in their annual cycle. This leads to stronger inferences about occupancy patterns at landscape levels, and by implication, benefits conservation planning. The possibility of using more parsimonious thematic land cover classes (e.g., NLCD) was stronger for the red-headed woodpecker (AIC ≤ 2). We suggest that this was consistent with a habitat generalist. Indeed, the lack of strong predictive covariates in all of our model types was consistent with previous studies of other habitat generalists that fail to identify strong habitat predictors of abundance or occurrence (Dettmers et al., 2001; Manel et al., 2001; Kadmon et al., 2003; Thogmartin et al., 2007).

Matrix models were insightful in two ways. First, they affirmed results from the NLCD-Hamel models but at larger scales where other important biological processes occur (e.g., natal dispersal, Wiens et al., 1993). Second, impervious surfaces and urbanized habitat did not exert a strong influence on occupancy along BBS route-segments. These results benefited the user's or conservation design models by providing a basis to focus on habitat classes of importance for the species, and consequently, a simpler modeling framework to better isolate the influence of patch size, distance and amount of habitat on occupancy probabilities. At the broadest level, conservation design models highlighted the geographic extent where the three focal species overlapped, providing a data-driven basis to assess trade-offs among alternatives in a multi-species context. At finer scales, specifics for conservation design arose. For example, route-segments with a $\psi \geq 0.50$ for the nuthatch were associated with 25 patches (median) of optimal habitat within 1.47 km, the largest patch being of 58 ha. The strong association between route-segment occupancy and proximity to optimal habitat was likely related to the species' limited dispersal abilities (e.g., 1.2 km; Withgott and Smith, 1998; Cox and Slater, 2007). Models for the wood-pewee raised the prospect of considering habitat features not emphasized in the scientific literature. The wood-pewee is considered a forest interior species; however, prior studies suggested that the species is not sensitive to forest area (Robbins et al., 1989; Friesen et al., 1995). In contrast, our models featured large patches in the top competing models (AIC ≤ 2), which underscored a positive relationship between large patches and species occupancy probability. Finally, specific habitat associations and their spatial arrangement were not clearly discernable for the woodpecker. This may have been due to the species' generalist habits. This situation may create difficulties to formulate habitat conservation strategies. In this case, we suggest that emphasis be given first to the amount of habitat within 1.47 km as most model results indicated that habitat within that distance exerted a stronger influence on occupancy probability than those farther away (4.73 km). The basis for this recommendation is also supported by other studies assessing the interplay between habitat and natal dispersal distances (Moilanen and Nieminen, 2002; Fagan and Calabrese, 2006).

The application of occupancy models to inform conservation planning is relatively new (e.g., DeWan et al., 2009). Some of its appeal stems from being able to adjust occupancy by detection probability, essential when making inferences about the strength of species-habitat relationships (Pollock et al., 2002; MacKenzie et al., 2006; Simons et al., 2007; Hines et al., 2009; Schlossberg and King, 2009; Riddle et al., 2010). Another is that it is a flexible framework. For example, a multi-season framework permits asking ecological questions in a dynamic context, gauging responses with vital rates such as patch extinction and colonization rates (MacKenzie et al., 2006). This dynamic framework has the potential of informing conservation in the advent of climate change by sorting out the effects of the transient nature of habitat change (i.e., land use-land cover) from those of changes in temperature and precipitation. Our results point at the prospect of gaining meaningful insights in this regard. Latitude had a strong influence on occupancy probability and highlighted the center of each species' latitudinal distribution. For example, nuthatch occupancy was higher in the central SAMBI (32-34° N), the latitudinal center of the species' distribution (Withgott and Smith, 1998). This is coincident with observations of a unimodal distribution of occupancy and abundance reaching their peaks at the core of a species' range (Lawton, 1993). The wood-pewee has the widest latitudinal range of our focal species and occupancy probabilities were highest at higher latitudes (35 – 37° N), corresponding with the latitudinal center of the species range (McCarty, 1996).

We suggest that predictions about the potential effects of climate change can be formulated using this biogeographical covariate. For example, some species are limited along their northern boundaries by winter freezing temperatures (Root et al., 1988; Newton, 1998). This information, coupled with hypotheses of northward shifts in species ranges (Parmesan et al., 2003; Hitch and Leberg, 2006), could be assessed with a multi-season framework and aid in long-term conservation planning in the SAMBI. If the southeast continues its warming trajectory (Karl et al., 2009), we would expect increases in local colonization rates along the species' northern range in the SAMBI provided that habitat also becomes available. Conversely, higher extinction rates might be expected in the southern portions of the SAMBI due to increasing frequency and intensity of droughts. Models can be further constrained by other covariates, such as fire frequency, which will be influenced by climate change and is an important determinant of habitat suitability for species like the nuthatch and wood-pewee (Meyers and Johnson, 1978; Wilson et al., 1995).

In a strategic habitat conservation framework, models link conservation objectives and alternatives by providing an estimate of the system's response to a management action (Williams et al., 2007; USFWS, 2008). Models can also highlight the degree of confidence or uncertainty inherent in natural systems and their processes, and thus help guide research and monitoring activities to enhance management effectiveness (Nichols and Williams, 2006; Williams et al., 2007). Some of this uncertainty reflects the state of knowledge of the systems we are modeling, but database and methodological limitations are also restricting factors (Zimmerman et al., 2003). We point at two areas where additional work or adjustments could lead to improved model inferences. For example, our definition of habitat does not include characteristics of vegetation-structure, and models do not include the possible effects of biological interactions, such as competition (Pulliam, 2000). The former would be benefitted by national-scale development of Light Detection and Ranging data (e.g.

Arcaro, 2008); the latter could be incorporated using multi-species occupancy models (MacKenzie et al., 2006). Likewise, Pollock et al., (2002) suggested that double-sampling methods might improve inferences made from data such as that collected by BBS. Ultimately, it is appropriate to consider engaging in model validation in the field to avoid the misallocation of valued conservation dollars (Schlossberg and King, 2009).

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TABLES

Table 1. Environmental variables and associated *a priori* hypotheses evaluated in single-season occupancy models for avian species in the South Atlantic Migratory Bird Initiative region, USA, 2001. Hamel-NLCD Model hypotheses were developed using the species habitat relationships defined by NCWRC (2005) and Hamel (1992), and included the percentage of each habitat type within 400 m of the sampled units. Matrix and Conservation Design Models derived covariates within two distances: 1.47 and 4.73 km.

Model Set	Variable (in model)	Species and hypotheses		
		Brown-headed nuthatch	Red-headed woodpecker	Eastern wood-pewee
Hamel-NLCD Models				
	Optimal (O)	longleaf pine-scrub oak, Sandhills longleaf pine, longleaf pine-slash pine, loblolly pine-short leaf pine	sandhills longleaf pine, longleaf pine-slash pine (with and without grassland/shrub)	sandhills longleaf pine, southern mixed mesic hardwoods, longleaf pine-slash pine, loblolly pine-shortleaf pine, mixed pine-hardwood, oak-hickory
	Suitable (S)	pine savanna, pond pine pocosin	pine savanna, longleaf pine- scrub oak, pond pine pocosin, oak-gum-cypress, oak-hickory	longleaf pine-scrub oak, bayswamp-pocosin, elm-ash-cottonwood
	Marginal (M)	mixed pine-hardwood	bayswamp-pocosin, live oak maritime, elm-ash-cottonwood, loblolly pine- shortleaf pine, mixed pine-hardwood	pine savanna, pond pine pocosin, oak-gum-cypress, live oak maritime
	Deciduous Forest (Deciduous)		+	+
	Evergreen Forest (Evergreen)	+	+	+
	Mixed Forest (Mixed)	+	+	+
	Shrubland (Shrub)		+	
	Grassland (Grass)		+	
Matrix Models	Optimal within 1.47 or 4.73 km (Optimal)	+	+	+
	Forest within 1.47 or 4.73 km (Forest)	+	+	+
	Urban within 1.47 or 4.73 km (Urban)	-	-	-
Conservation Design Models	Average number of patches (N 1.47, 4.73)	+	+	+
	Average distance to patches (D 1.47, 4.73)	-	-	-
	Interaction of number of patches and average distance to patches (NxD 1.47, 4.73)	-	-	-
	Largest patch size (Max 1.47, 4.73)	+	+	+

Table 2. AIC model selection results from brown-headed nuthatch (*Sitta pusilla*) species-habitat occupancy models in the South Atlantic Migratory Bird region of the United States, 2001. Occupancy (ψ) was modeled as constant (.), or as a function of latitude (LatS = 29-31°, LatC = 32-34° N, LatN = 35-37° N), general habitat types, southeastern-specific hypotheses of optimal (O), suitable (S) and marginal (M) habitat types proposed by Hamel (1992), matrix content, number of patches (N), distance to patches (D), their interaction (NxD), and the size of the largest patch (Max) within two dispersal distances. Data are assessed for spatial dependence under two assumption frameworks (θ=θ' and θ≠θ'). Detection probability (p) was modeled as constant, or as a function of an indicator variable for seasonal detection. N=480.

Model Set	Model	Brown-headed nuthatch					
		AIC	Δ AIC	AIC wgt	Model Likelihood	K	(-2*LogLike)
Hamel-NLCD Models (400 m)	Ψ(Optimal + LatC),(θ≠θ'),p (.)	841.96	0.00	1.00	1.00	6	829.96
	Ψ(Evergreen + LatC),(θ≠θ'),p (.)	854.79	12.83	0.00	0.00	6	842.79
	Ψ(Marginal + LatC),(θ≠θ'),p (.)	859.66	17.70	0.00	0.00	6	847.66
	Ψ(Suitable + LatC),(θ≠θ'),p (.)	859.88	17.92	0.00	0.00	6	847.88
	Ψ(Deciduous + LatC),(θ≠θ'),p (.)	859.95	17.99	0.00	0.00	6	847.95
	Ψ(Mixed + LatC),(θ≠θ'),p (.)	862.29	20.33	0.00	0.00	6	850.29
	ψ(·),(θ≠θ'),p (.)	885.47	43.51	0.00	0.00	4	877.47
	ψ(·),(θ=θ'),p (.)	886.21	44.25	0.00	0.00	4	878.21
	ψ(·),(θ≠θ'),p (Season)	886.65	44.69	0.00	0.00	5	876.65
	ψ(·),(θ=θ'),p (Season)	887.44	45.48	0.00	0.00	5	877.44
	Ψ(.),p (.)	890.96	49.00	0.00	0.00	2	886.96
	Ψ(.),p (Season)	892.01	50.05	0.00	0.00	3	886.01
Matrix Models (1.47 and 4.73 km)	Ψ(Optimal 1.47 + LatC),(θ≠θ'),p (.)	846.00	0.00	0.92	1.00	6	834.00
	Ψ(Forest 1.47 + LatC),(θ≠θ'),p (.)	851.13	5.13	0.07	0.08	6	839.13
	Ψ(Forest 4.73 + LatC),(θ≠θ'),p (.)	855.55	9.55	0.01	0.01	6	843.55
	Ψ(Optimal 4.73 + LatC),(θ≠θ'),p (.)	856.31	10.31	0.01	0.01	6	844.31
	Ψ(Urban 1.47 + LatC),(θ≠θ'),p (.)	863.79	17.79	0.00	0.00	6	851.79
	Ψ(Urban 4.73 + LatC),(θ≠θ'),p (.)	863.82	17.82	0.00	0.00	6	851.82
	ψ(·),(θ≠θ'),p (.)	885.47	39.47	0.00	0.00	4	877.47
	ψ(·),(θ=θ'),p (.)	886.21	40.21	0.00	0.00	4	878.21
	ψ(·),(θ≠θ'),p (Season)	886.65	40.65	0.00	0.00	5	876.65
	ψ(·),(θ=θ'),p (Season)	887.44	41.44	0.00	0.00	5	877.44
	Ψ(.),p (.)	890.96	44.96	0.00	0.00	2	886.96
	Ψ(.),p (Season)	892.01	46.01	0.00	0.00	3	886.01
Conservation Design Models (1.47 and 4. 73 km)	Ψ(NxD1.47 + Lat C),(θ≠θ'),p (.)	841.40	0.00	0.98	1.00	8	825.40
	Ψ(NxD4.73 + Lat C),(θ≠θ'),p (.)	850.46	9.06	0.01	0.01	8	834.46
	Ψ(N 1.47 + Lat C),(θ≠θ'),p (.)	851.00	9.60	0.01	0.01	6	839.00
	Ψ(N 4.73 + Lat C),(θ≠θ'),p (.)	855.18	13.78	0.00	0.00	6	843.18
	Ψ(Max 1.47 + Lat C),(θ≠θ'),p (.)	856.37	14.97	0.00	0.00	6	844.37
	Ψ(Max 4.73 + Lat C),(θ≠θ'),p (.)	858.45	17.05	0.00	0.00	6	846.45
	Ψ(.),(θ≠θ'),p (.)	885.47	44.07	0.00	0.00	4	877.47
	ψ(·),(θ=θ'),p (.)	886.21	44.81	0.00	0.00	4	878.21
	Ψ,(θ≠θ'),p (Season)	886.65	45.25	0.00	0.00	5	876.65
	ψ(·),(θ=θ'),p (Season)	887.44	46.04	0.00	0.00	5	877.44
	Ψ(.),p (.)	890.96	49.56	0.00	0.00	2	886.96
	Ψ(.),p (Season)	892.01	50.61	0.00	0.00	3	886.01

Table 3. AIC model selection results from eastern wood-pewee (*Contopus virens*) species-habitat occupancy models in the South Atlantic Migratory Bird region of the United States, 2001. Occupancy (ψ) was modeled as constant (.), or as a function of latitude (LatS = 29-31°, LatC = 32-34° N, LatN = 35-37° N), general habitat types, southeastern-specific hypotheses of optimal (O), suitable (S) and marginal (M) habitat types proposed by Hamel (1992), matrix content, number of patches (N), distance to patches (D), their interaction (NxD), and the size of the largest patch (Max) within two dispersal distances. Data are assessed for spatial dependence under two assumption frameworks ($\theta=\theta'$ and $\theta\neq\theta'$). Detection probability (*p*) was modeled as constant, or as a function of an indicator variable for seasonal detection. N=480.

Model Set	Model	Eastern wood-pewee					
Hamel-NLCD Models		AIC	Δ AIC	AIC wgt	Model Likelihood	K	(-2*LogLike)
(400 m)	Ψ(Optimal + LatC + LatS),($\theta\neq\theta'$),p(.)	1519.96	0.00	0.97	1.00	7	1505.96
	Ψ(Evergreen + LatC + LatS),($\theta\neq\theta'$),p(.)	1527.22	7.26	0.03	0.03	7	1513.22
	Ψ(Mixed + LatC + LatS),($\theta\neq\theta'$),p(.)	1529.87	9.91	0.01	0.01	7	1515.87
	Ψ(Deciduous + LatC + LatS),($\theta\neq\theta'$),p(.)	1535.84	15.88	0.00	0.00	7	1521.84
	Ψ(Suitable + LatC + LatS),($\theta\neq\theta'$),p(.)	1536.96	17.00	0.00	0.00	7	1522.96
	Ψ(Marginal + LatC + LatS),($\theta\neq\theta'$),p(.)	1537.56	17.60	0.00	0.00	7	1523.56
	Ψ(.),($\theta\neq\theta'$),p(.)	1606.93	86.97	0.00	0.00	4	1598.93
	Ψ(.),*p* (.)	1608.16	88.20	0.00	0.00	2	1604.16
	$\psi(\cdot)$,($\theta=\theta'$),*p* (.)	1608.60	88.64	0.00	0.00	4	1600.6
	Ψ,($\theta\neq\theta'$),*p* (.)	1608.93	88.97	0.00	0.00	5	1598.93
	Ψ,($\theta\neq\theta'$),*p* (Season)	1610.52	90.56	0.00	0.00	5	1600.52
Matrix Models							
(1.47 and 4.73 km)	Ψ(Optimal 1.47 + LatC + LatS),($\theta\neq\theta'$),p(.)	1521.54	0.00	0.49	1.00	7	1507.54
	Ψ(Forest 1.47 + LatC + LatS),($\theta\neq\theta'$),p(.)	1521.98	0.44	0.39	0.80	7	1507.98
	Ψ(Optimal 4.73 + LatC + LatS),($\theta\neq\theta'$),p(.)	1525.46	3.92	0.07	0.14	7	1511.46
	Ψ(Forest 4.73 + LatC + LatS),($\theta\neq\theta'$),p(.)	1526.49	4.95	0.04	0.08	7	1512.49
	Ψ(Urban 1.47 + LatC + LatS),($\theta\neq\theta'$),p(.)	1532.57	11.03	0.00	0.00	7	1518.57
	Ψ(Urban 4.73 + LatC + LatS),($\theta\neq\theta'$),p(.)	1534.39	12.85	0.00	0.00	7	1520.39
	Ψ,($\theta\neq\theta'$),*p* (.)	1606.93	85.39	0.00	0.00	4	1598.93
	Ψ(.),*p* (.)	1608.16	86.62	0.00	0.00	2	1604.16
	$\psi(\cdot)$,($\theta=\theta'$),*p* (.)	1608.6	87.06	0.00	0.00	4	1600.6
	Ψ,($\theta\neq\theta'$),*p* (Season)	1608.93	87.39	0.00	0.00	5	1598.93
	$\psi(\cdot)$,($\theta=\theta'$),*p* (Season)	1610.52	88.98	0.00	0.00	5	1600.52
Conservation Design							
Models	Ψ(Max 4.73 + LatC + LatS),($\theta\neq\theta'$),p(.)	1527.95	0.00	0.41	1.00	7.00	1513.95
(1.47 and 4. 73 km)	Ψ(NxD1.47 + LatC + LatS),($\theta\neq\theta'$),p(.)	1528.23	0.28	0.35	0.87	9.00	1510.23
	Ψ(Max 1.47 + LatC + LatS),($\theta\neq\theta'$),p(.)	1530.31	2.36	0.13	0.31	7.00	1516.31
	Ψ(N 1.47 + LatC + LatS),($\theta\neq\theta'$),p(.)	1531.76	3.81	0.06	0.15	7.00	1517.76
	Ψ(NxD 4.73 + LatC + LatS),($\theta\neq\theta'$),p(.)	1533.32	5.37	0.03	0.07	9.00	1515.32
	Ψ(N 4.73 + LatC + LatS),($\theta\neq\theta'$),p(.)	1533.49	5.54	0.03	0.06	7.00	1519.49
	Ψ,($\theta\neq\theta'$),*p* (.)	1606.93	78.98	0.00	0.00	4.00	1598.93
	Ψ(.),*p* (.)	1608.16	80.21	0.00	0.00	2.00	1604.16
	$\psi(\cdot)$,($\theta=\theta'$),*p* (.)	1608.60	80.65	0.00	0.00	4.00	1600.60
	Ψ,($\theta\neq\theta'$),*p* (Season)	1608.93	80.98	0.00	0.00	5.00	1598.93
	$\psi(\cdot)$,($\theta=\theta'$),*p* (Season)	1610.52	82.57	0.00	0.00	5.00	1600.52

Table 4. AIC model selection results from red-headed woodpecker (*Melanerpes erythrocephalus*) species-habitat occupancy models in the South Atlantic Migratory Bird region of the United States, 2001. Occupancy (ψ) was modeled as constant (.), or as a function of latitude (LatS = 29-31°, LatC = 32-34° N, LatN = 35-37° N), general habitat types, southeastern-specific hypotheses of optimal (O), suitable (S) and marginal (M) habitat types proposed by Hamel (1992), matrix content, number of patches (N), distance to patches (D), their interaction (NxD), and the size of the largest patch (Max) within two dispersal distances. Data are assessed for spatial dependence under two assumption frameworks (θ=θ' and θ≠θ'). Detection probability (*p*) was modeled as constant, or as a function of an indicator variable for seasonal detection. N=480.

Model Set	Model	Red-headed woodpecker					
Hamel-NLCD Models		AIC	Δ AIC	AIC wgt	Model Likelihood	K	(-2*LogLike)
(400 m)	Ψ(Marginal + LatN),*p* (Season)	653.21	0.00	0.33	1.00	5	643.21
	Ψ(Evergreen + LatN),*p* (Season)	654.78	1.57	0.15	0.46	5	644.78
	Ψ(Shrub/ Scrub + LatN),*p* (Season)	655.08	1.87	0.13	0.39	5	645.08
	Ψ(Mixed + LatN),*p* (Season)	655.55	2.34	0.10	0.31	5	645.55
	Ψ(Deciduous + LatN),*p* (Season)	655.69	2.48	0.09	0.29	5	645.69
	Ψ(Suitable + LatN),*p* (Season)	656.32	3.11	0.07	0.21	5	646.32
	Ψ(Grassland + LatN),*p* (Season)	656.47	3.26	0.06	0.20	5	646.47
	Ψ(Optimal + LatN),*p* (Season)	656.53	3.32	0.06	0.19	5	646.53
	Ψ(.),*p* (Season)	663.55	10.34	0.00	0.01	3	657.55
	Ψ(.),*p* (.)	665.06	11.85	0.00	0.00	2	661.06
	ψ(·),(θ=θ'),*p* (Season)	666.28	13.07	0.00	0.00	5	656.28
	ψ(·),(θ≠θ'),*p* (Season)	667.48	14.27	0.00	0.00	5	657.48
	ψ(·),(θ=θ'),*p* (.)	667.74	14.53	0.00	0.00	4	659.74
	ψ(·),(θ≠θ'),*p* (.)	668.99	15.78	0.00	0.00	4	660.99
Matrix Models							
(1.47 and 4.73 km)	Ψ(Marginal 1.47 + LatN),*p* (Season)	653.89	0	0.315	1	5	643.89
	Ψ(Marginal 4.73 + LatN),*p* (Season)	654.57	0.68	0.2242	0.7118	5	644.57
	Ψ(Urban 1.47 + LatN),*p* (Season)	655.34	1.45	0.1526	0.4843	5	645.34
	Ψ(Forest 1.47 + LatN),*p* (Season)	655.96	2.07	0.1119	0.3552	5	645.96
	Ψ(Urban 4.73 + LatN),*p* (Season)	655.98	2.09	0.1108	0.3517	5	645.98
	Ψ(Forest 4.73 + LatN),*p* (Season)	656.62	2.73	0.0804	0.2554	5	646.62
	Ψ(.),*p* (Season)	663.55	9.66	0.0025	0.008	3	657.55
	Ψ(.),*p* (.)	665.06	11.17	0.0012	0.0038	2	661.06
	ψ(·),(θ=θ'),*p* (Season)	666.28	12.39	0.0006	0.002	5	656.28
	ψ(·),(θ≠θ'),*p* (Season)	667.48	13.59	0.0004	0.0011	5	657.48
	ψ(·),(θ=θ'),*p* (.)	667.74	13.85	0.0003	0.001	4	659.74
	ψ(·),(θ≠θ'),*p* (.)	668.99	15.1	0.0002	0.0005	4	660.99
Conservation Design							
Models	Ψ(N 4.73 + Lat N),*p* (Season)	655.34	0	0.329	1	5	645.34
(1.47 and 4. 73 km)	Ψ(N 1.47 + Lat N),*p* (Season)	655.4	0.06	0.3193	0.9704	5	645.4
	Ψ(Max 4.73 + Lat N),*p* (Season)	656.32	0.98	0.2016	0.6126	5	646.32
	Ψ(NxD1.47 + Lat N),*p* (Season)	658.13	2.79	0.0815	0.2478	7	644.13
	Ψ(NxD4.73 + Lat N),*p* (Season)	658.83	3.49	0.0575	0.1746	7	644.83
	Ψ(.),*p* (Season)	663.55	8.21	0.0054	0.0165	3	657.55
	Ψ(.),*p* (.)	665.06	9.72	0.0025	0.0078	2	661.06
	ψ(·),(θ=θ'),*p* (Season)	666.28	10.94	0.0014	0.0042	5	656.28
	ψ(·),(θ≠θ'),*p* (Season)	667.48	12.14	0.0008	0.0023	5	657.48
	ψ(·),(θ=θ'),*p* (.)	667.74	12.4	0.0007	0.002	4	659.74
	ψ(·),(θ≠θ'),*p* (.)	668.99	13.65	0.0004	0.0011	4	660.99

Table 5. Parameter estimates and standard errors (β and SE) estimates using single season occupancy models for three focal species of conservation concern in the South Atlantic Migratory Bird region of the United States, 2001.

Hamel-NLCD		Brown-headed nuthatch		Red-headed woodpecker		Eastern wood-pewee	
Models	Covariate	β	SE	β	SE	β	SE
(400 m)	LatS	-	-	-	-	-1.82[a]	0.29
	LatC	0.65[a]	0.17	-	-	-0.82	0.22
	LatN	-	-	-2.07[a]	0.80	-	-
	O	0.33[a]	0.09	-	-	0.34[a]	0.09
	S	-	-	-	-	-	-
	M	-	-	5.34	4.12	-	-

Matrix Models		Brown-headed nuthatch		Red-headed woodpecker		Eastern wood-pewee	
(1.47 and 4.73 km)	Covariate	β	SE	β	SE	β	SE
	LatS	-	-	-	-	-1.64[a]	0.24
	LatC	0.69[a]	0.17	-	-	-0.68[a]	0.19
	LatN	-	-	-2.29	1.45	-	-
	Optimal 1.47	0.31[a]	0.07	-	-	2.27[a]	0.65
	Marginal 1.47	-	-	0.58	0.78	-	-
	Season	-	-	-0.57	0.28	-	-

Conservation Design		Brown-headed nuthatch		Red-headed woodpecker		Eastern wood-pewee	
Models	Covariate	β	SE	β	SE	β	SE
(1.47 and 4. 73 km)	LatS	-	-	-	-	-1.78[a]	0.27
	LatC	0.67[a]	0.18	-	-	-0.71[a]	0.21
	LatN	-	-	-2.47[a]	0.35	-	-
	N(1.47 km)	1.53[a]	0.39	-	-	-	-
	N(4.73 km)	-	-	0.33	0.34	-	-
	D(1.47 km)	0.08	0.13	-	-	-	-
	DxN(1.47 km)	-1.32[a]	0.41	-	-	-	-
	Max(4.73 km)	-	-	-	-	0.42[a]	0.19
	Season	-	-	-0.63[a]	0.29	-	-

[a] denotes that the 95% confidence intervals did not overlap zero.

Table 6. Patch-based medians and 90% confidence intervals for supported landscape covariates within multiple distances (400m, 1.47 km and 4.73 km) of primary sampling units. Occupancy models were developed for three species in the southeastern United States, 2001. Occupancy estimates were reported from top models that allowed occupancy to vary with the amount of optimal or marginal (red-headed woodpecker) habitat after accounting for species detection and spatial dependence. Patches are composed of the Hamel-defined habitat classes that received the most support in previous modeling efforts (i.e. marginal habitat for the red-headed woodpecker). All patches have a species-specific minimum patch size reflecting the size of species' breeding territories.

Species	Target Probability of Occupancy	n	% Optimal (400m)	# of patches (1.47km)	Largest Patch Size (1.47km)	Average Distance (1.47km)	# of patches (4.73km)	Largest Patch (4.73km)	Average Distance (4.73km)
Brown-headed nuthatch	Overall	480	12.24 (10.99 - 13.07)	17 (16 - 19)	26.87 (23.58 - 30.78)	0.68 (0.66 - 0.69)	79 (75 - 86)	47.84 (42.39 - 52.92)	2.54 (2.52 - 2.56)
	0.50	233	18.34 (16.38 - 20.68)	25 (23 - 28)	58.05 (50.13 - 64.53)	0.68 (0.66 - 0.69	108 (103 - 115)	87.0 (79.11 - 103.68)	2.56 (2.53 - 2.61)
	0.75	16	48.33 (43.86 - 62.29)	27 (23-44)	725.9 (349.38 - 1797.48)	0.65 (0.56 - 0.72)	120 (103 - 160)	725.89 (349.38 - 1797.48)	2.57 (2.52 - 2.71)
Red-headed woodpecker	Overall	387	8.83 (7.86 - 10.35)	12 (11 - 13)	211.05 (176.49 - 265.05)	-	46 (42 - 49)	296.10 (249.84 - 344.97)	-
	0.50	268	12.37 (11.41 - 13.16)	14 (13 - 15)	275.63 (220.23 - 318.69)	-	53 (50 - 57)	325.22 (293.49 - 399.33)	-
	0.75	26	31.78 (28.86 - 33.46)	25 (17 - 31)	699.12 (387.0 - 924.74)	-	84 (62-109)	731.07 (453.51 - 924.75)	-
Eastern wood-pewee	Overall	480	18.33 (16.89 - 19.80)	35 (33 - 36)	-	0.70 (0.69 -0.71)	151 (144 - 158)	-	2.60 (2.58 - 2.62)
	0.50	334	24.27 (21.96 - 25.23)	39 (37 -41)	-	0.68 (0.67 - 0.69)	164 (159- 168)	-	2.59 (2.57 -2.61)
	0.75	147	26.69 (24.53 - 30.03)	39 (36 - 41)	-	0.68 (0.67 - 0.69)	159 (152 - 167)	-	2.59 (2.56 - 2.61)

FIGURES

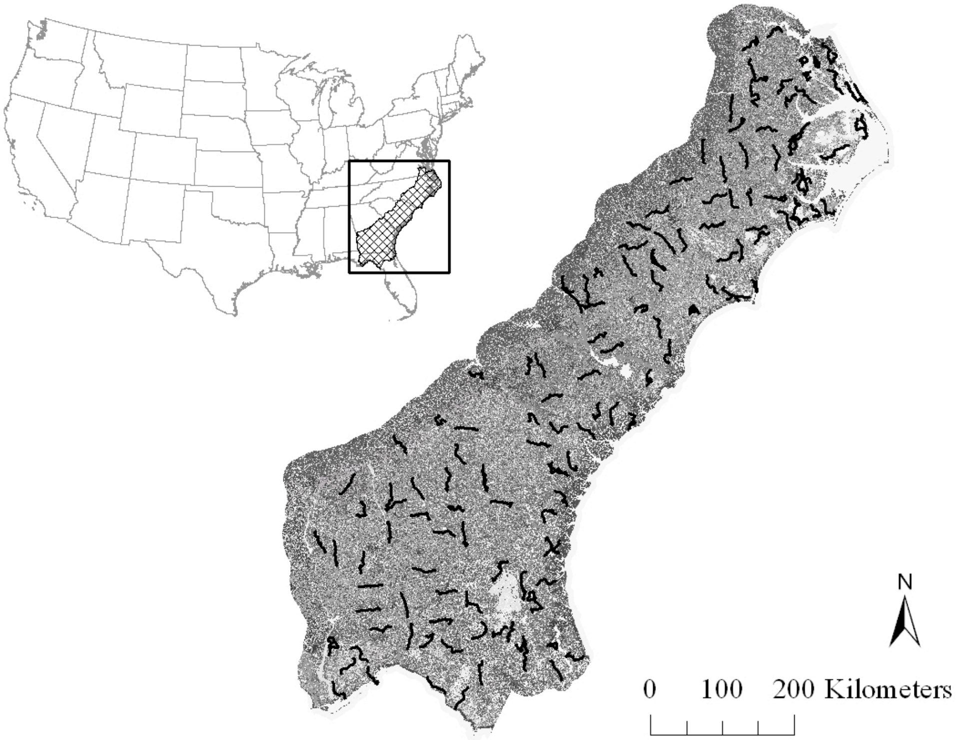


Figure 1. The locations of 120 North American Breeding Bird Survey routes used in occupancy modeling for three avian species in the South Atlantic Coastal Plain region of the United States, 2001.

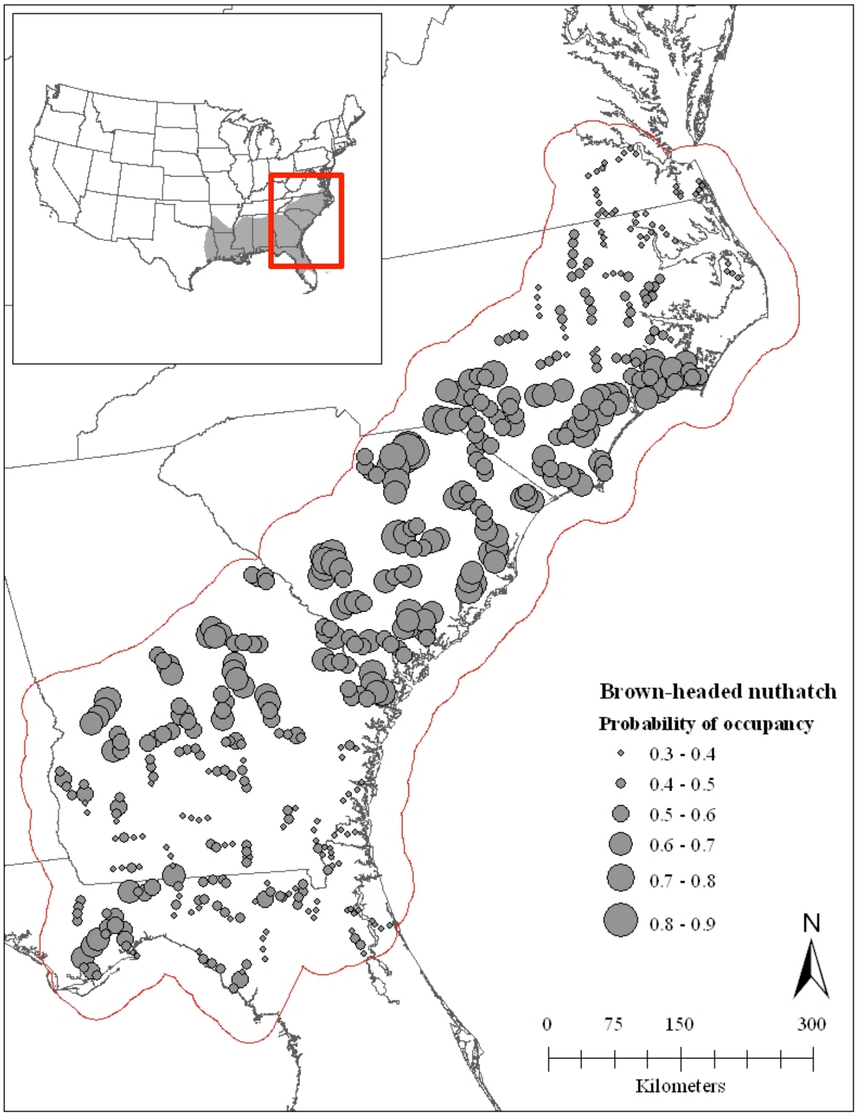


Figure 2. Brown-headed nuthatch estimated occurrence as a function of amount of optimal habitat within 400 m of North American Breeding Bird Survey route segments and latitude in the South Atlantic Migratory Bird region of the United States, 2001. Models account for the probability of detection and spatial correlation of route segments. The species' breeding distribution is shaded grey in the inset (NatureServe, Ridgely et al. 2007).

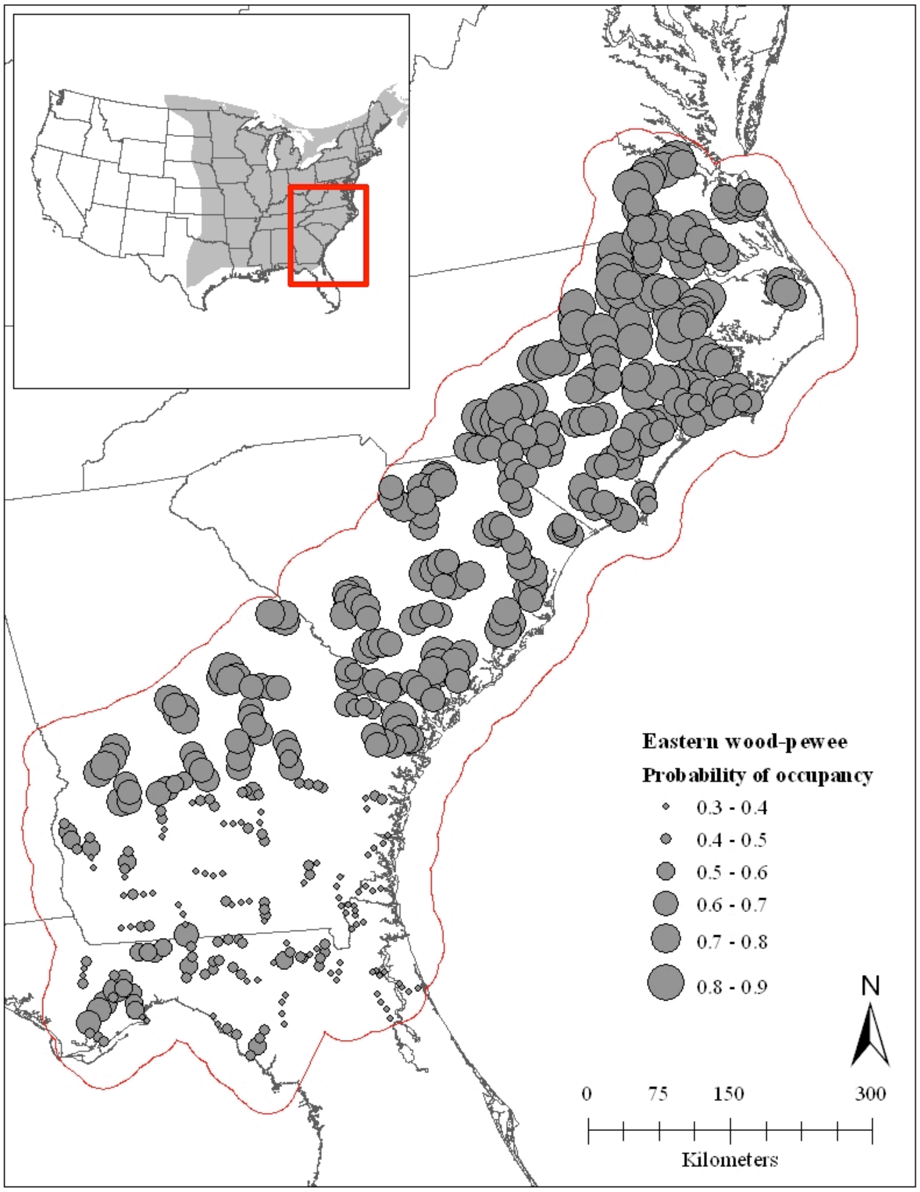


Figure 3. Eastern wood-pewee estimated occurrence as a function of amount of optimal habitat within 400 m of North American Breeding Bird Survey route segments and latitude in the South Atlantic Migratory Bird region of the United States, 2001. Models account for the probability of detection and spatial correlation of route segments. The species' breeding distribution is shaded grey in the inset (NatureServe, Ridgely et al. 2007).

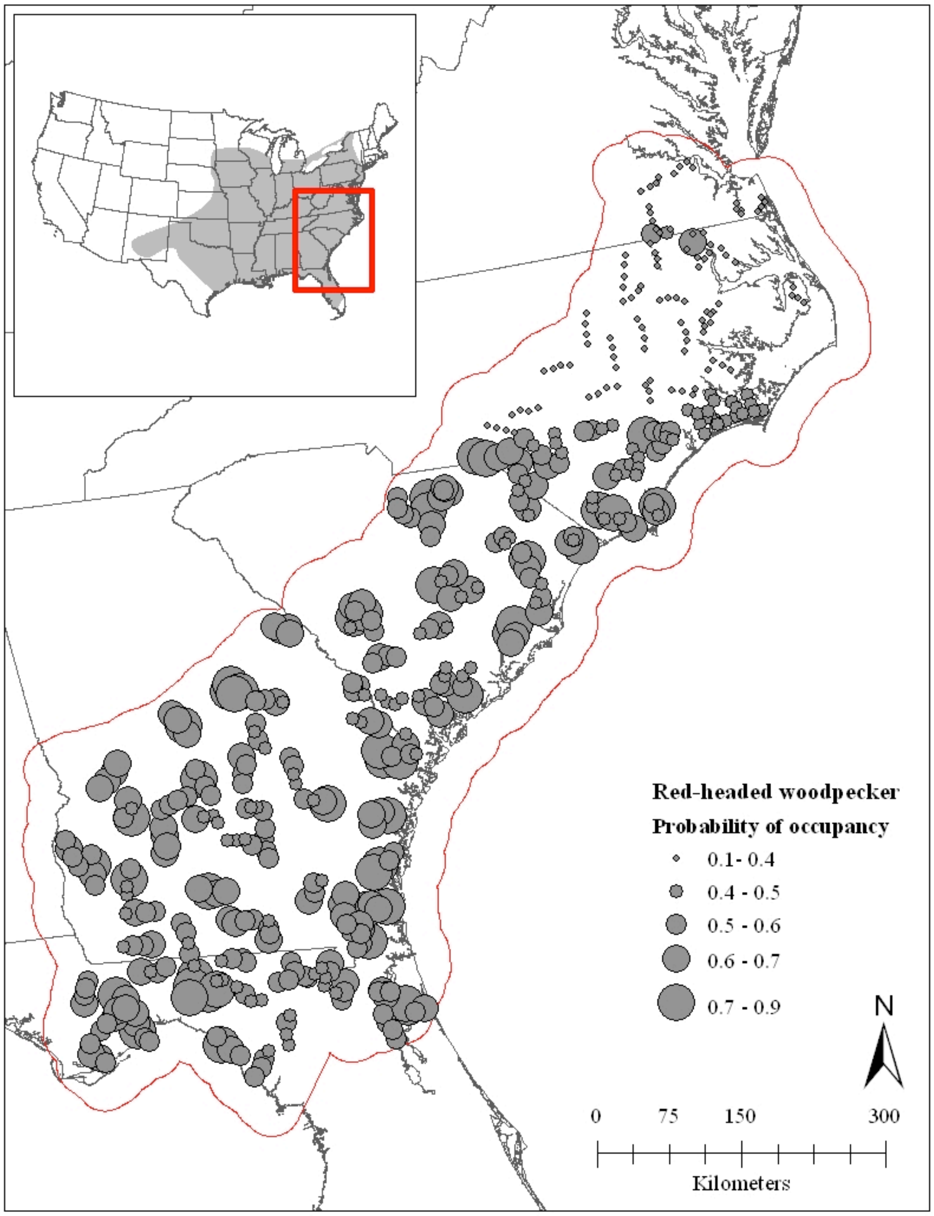


Figure 4. Red-headed woodpecker estimated occurrence as a function of amount of marginal habitat within 400 m of North American Breeding Bird Survey route segments and latitude in the South Atlantic Migratory Bird region of the United States, 2001. Models account for the probability of detection and spatial correlation of route segments. The species' breeding distribution is shaded grey in the inset (NatureServe, Ridgely et al. 2007).

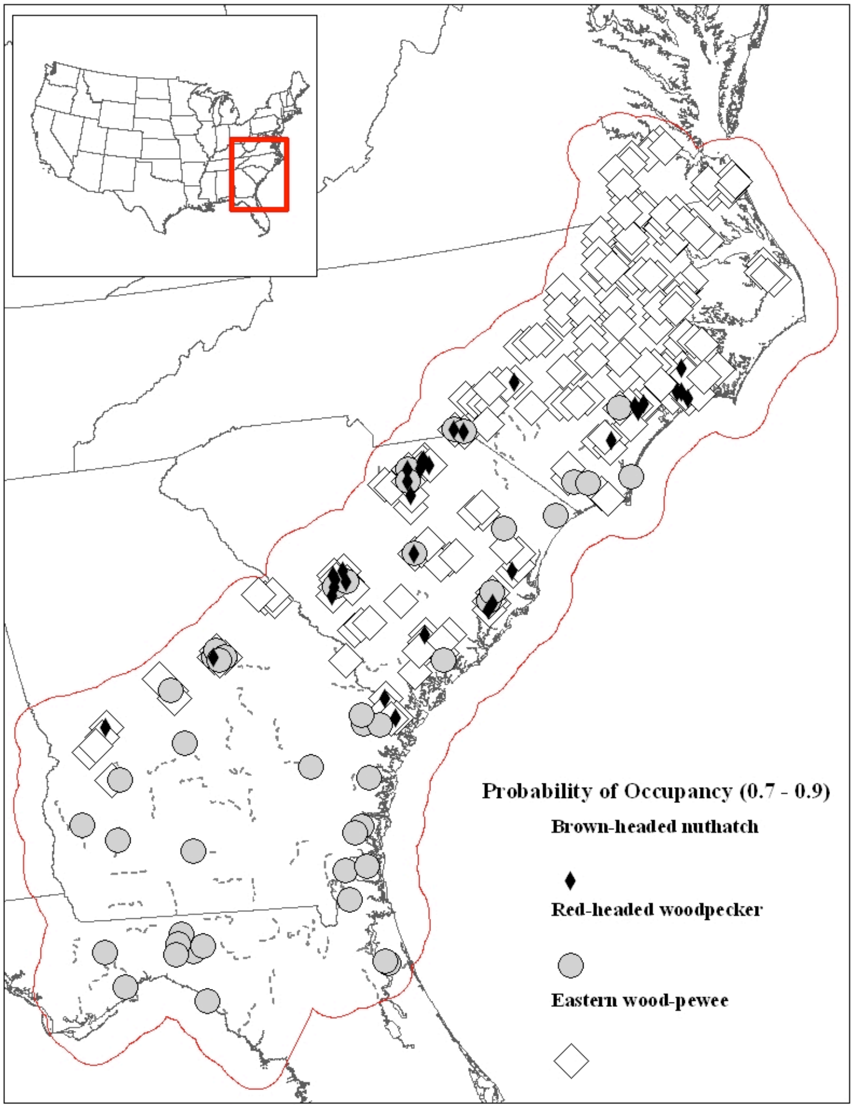
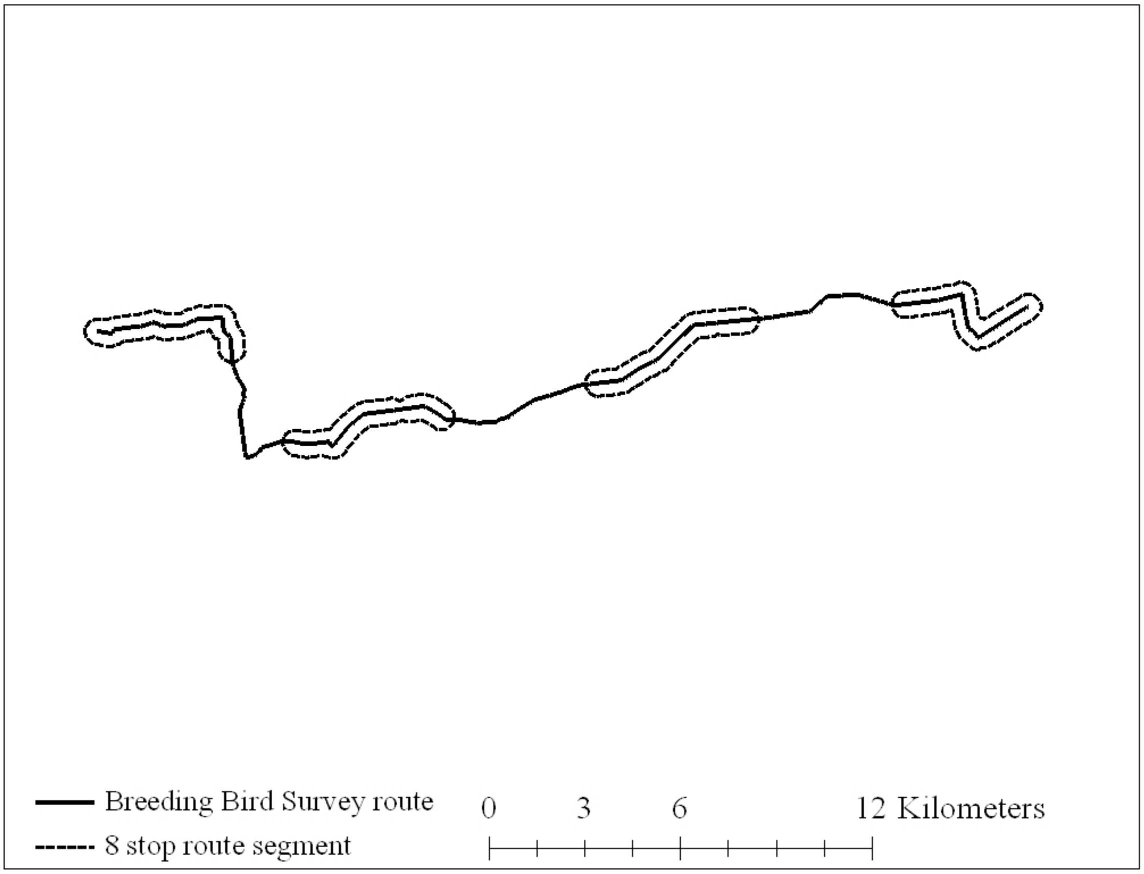


Figure 5. Sampling units with high probabilities of occupancy for three species of conservation concern in the South Atlantic Migratory Bird region of the United States, 2001. Species occurrence was modeled as a function of the amount of optimal habitat (or marginal for the red-headed woodpecker) within 400 m of sampling units, and latitude. Models account for probability of species detection and spatial correlation of route segments.

APPENDIX

Appendix 1. North American Breeding Bird Survey routes were separated into four, eight-stop segments. Count data of avian species were converted to presence and absence. The eight stops were spatial replicates used to estimate the probability of species detection in an occupancy modeling framework assessing species-habitat dynamics. Route segments are ~4.8 km apart.



Appendix 2. Southeast Gap Analysis Program land cover classes crosswalked to correspond with habitat types defined by Hamel (1992).

GAP Code	All Code	Southeast GAP 2001 Class	Hamel-GAP reclass	Hamel code
1	SEGAP111	Open Water (Fresh)	Water	1
2	SEGAP112	Open Water (Brackish/Salt)	Water	1
16	SEGAP311	Bare Sand	Barren	2
17	SEGAP312	Bare Soil	Barren	2
18	SEGAP313	Quarry/Strip Mine/Gravel Pit	Barren	2
20	CES202.297	Southern Appalachian Granitic Dome	Barren	2
30	CES202.386	Southern Piedmont Cliff	Barren	2
33	CES202.329	Southern Piedmont Granite Flatrock	Barren	2
10	CES203.383	Atlantic Coastal Plain Sea Island Beach	Beach/shore	3
11	CES203.535	Atlantic Coastal Plain Southern Beach	Beach/shore	3
35	SEGAP321	Unconsolidated Shore (Lake/River/Pond)	Beach/shore	3
36	SEGAP322	Unconsolidated Shore (Beach/Dune)	Beach/shore	3
4	SEGAP211	Developed Open Space	Developed Open Space	4
5	SEGAP220	Low Intensity Developed	Low Intensity Developed	5
6	SEGAP230	Medium Intensity Developed	Medium Intensity Developed	6
7	SEGAP240	High Intensity Developed	High Intensity Developed	7
37	SEGAP410	Deciduous Plantations	Orchards	8
148	SEGAP810	Pasture/Hay	Pasture/Hay	9
149	SEGAP820	Row Crop	Row Crop	10
12	CES203.266	Florida Panhandle Beach Vegetation	Grassland / Shrubland	11
56	CES202.886	Southern and Central Appalachian Oak Forest	Grassland / Shrubland	11
125	SEGAP511	Successional Shrub/Scrub (Clear Cut)	Grassland / Shrubland	11
126	SEGAP512	Successional Shrub/Scrub (Utility Swath)	Grassland / Shrubland	11
127	SEGAP513	Successional Shrub/Scrub (Other)	Grassland / Shrubland	11
136	CES203.380	Florida Dry Prairie	Grassland / Shrubland	11
141	CES203.264	Atlantic Coastal Plain Northern Dune and Maritime Grassland	Grassland / Shrubland	11
142	CES203.273	Atlantic Coastal Plain Southern Dune and Maritime Grassland	Grassland / Shrubland	11
143	CES203.500	East Gulf Coastal Plain Dune and Coastal Grassland	Grassland / Shrubland	11
145	SEGAP710	Clearcut - Grassland/Herbaceous	Grassland / Shrubland	11
146	SEGAP720	Other - Herbaceous	Grassland / Shrubland	11
147	SEGAP730	Utility Swath - Herbaceous	Grassland / Shrubland	11
178	CES203.384e	Southern Coastal Plain Nonriverine Basin Swamp - Okefenokee Clethra Modifier	Grassland / Shrubland	11
71	SEGAP420	Evergreen Plantations or Managed Pine (can include dense successional regrowth)	Evergreen Plantations or Managed Pine	12
86	CES202.339b	Southern Piedmont Dry Oak-(Pine) Forest - Loblolly Pine Modifier	Loblolly pine / Short leaf pine / Dense pine	13
90	CES203.254c	Atlantic Coastal Plain Fall-Line Sandhills Longleaf Pine Woodland - Loblolly Modifier	Loblolly pine / Short leaf pine / Dense pine	13
94	CES203.496c	East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland - Loblolly Modifier	Loblolly pine / Short leaf pine / Dense pine	13
151	CES203.247a	Atlantic Coastal Plain Blackwater Stream Floodplain Forest - Forest Modifier	Elm / Ash / Cottonwood	14
152	CES203.248	Atlantic Coastal Plain Brownwater Stream Floodplain Forest	Elm / Ash / Cottonwood	14
153	CES203.249	Atlantic Coastal Plain Small Blackwater River Floodplain Forest	Elm / Ash / Cottonwood	14
154	CES203.250	Atlantic Coastal Plain Small Brownwater River Floodplain Forest	Elm / Ash / Cottonwood	14
158	CES203.559	East Gulf Coastal Plain Small Stream and River Floodplain Forest	Elm / Ash / Cottonwood	14
163	CES203.493	Southern Coastal Plain Blackwater River Floodplain Forest	Elm / Ash / Cottonwood	14
165	CES202.323	Southern Piedmont Small Floodplain and Riparian Forest	Elm / Ash / Cottonwood	14
40	CES203.242	Atlantic Coastal Plain Mesic Hardwood and Mixed Forest	Mixed Pine Hardwood	15
61	CES203.254d	Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland - Offsite Hardwood Modifier	Mixed Pine Hardwood	15
62	CES203.496d	East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland - Offsite Hardwood Modifier	Mixed Pine Hardwood	15
107	CES202.592c	Northeastern Interior Dry Oak Forest - Mixed Modifier	Mixed Pine Hardwood	15
108	CES202.339c	Southern Piedmont Dry Oak-(Pine) Forest - Mixed Modifier	Mixed Pine Hardwood	15
119	CES202.328	Southern Piedmont Glade and Barrens	Mixed Pine Hardwood	15
186	CES203.375c	East Gulf Coastal Plain Near-Coast Pine Flatwoods - Offsite Hardwood Modifier	Mixed Pine Hardwood	15
157	CES203.489a	East Gulf Coastal Plain Large River Floodplain Forest - Forest Modifier	Oak-Gum Cypress	16
164	CES202.324a	Southern Piedmont Large Floodplain Forest - Forest Modifier	Oak-Gum Cypress	16
166	CES203.190	Mississippi River Riparian Forest	Oak-Gum Cypress	16
167	CES203.304b	Atlantic Coastal Plain Nonriverine Swamp and Wet Hardwood Forest - Taxodium/Nyssa Modifier	Oak-Gum Cypress	16
168	CES203.304a	Atlantic Coastal Plain Nonriverine Swamp and Wet Hardwood Forest - Oak Dominated Modifier	Oak-Gum Cypress	16
169	CES203.384a	Southern Coastal Plain Nonriverine Basin Swamp - Okefenokee Taxodium Modifier	Oak-Gum Cypress	16
170	CES203.384b	Southern Coastal Plain Nonriverine Basin Swamp - Okefenokee Bay/Gum Modifier	Oak-Gum Cypress	16
173	CES203.245a	Atlantic Coastal Plain Clay-Based Carolina Bay Forested Wetland	Oak-Gum Cypress	16
195	CES203.251	Southern Coastal Plain Nonriverine Cypress Dome	Oak-Gum Cypress	16
204	CES203.282	Atlantic Coastal Plain Northern Tidal Wooded Swamp	Oak-Gum Cypress	16
205	CES203.240	Atlantic Coastal Plain Southern Tidal Wooded Swamp	Oak-Gum Cypress	16
206	CES203.299	East Gulf Coastal Plain Tidal Wooded Swamp	Oak-Gum Cypress	16
39	CES203.241	Atlantic Coastal Plain Dry and Dry-Mesic Oak Forest	Oak-Hickory	17
45	CES203.502	East Gulf Coastal Plain Limestone Forest	Oak-Hickory	17
57	CES203.560	Southern Coastal Plain Dry Upland Hardwood Forest	Oak-Hickory	17
66	CES202.339a	Southern Piedmont Dry Oak-(Pine) Forest - Hardwood Modifier	Oak-Hickory	17
118	CES202.024	Ridge and Valley Calcareous Valley Bottom Glade and Woodland	Oak-Hickory	17
183	CES203.265	Central Atlantic Coastal Plain Wet Longleaf Pine Savanna and Flatwoods	Pine savanna	18
184	CES203.536	Atlantic Coastal Plain Southern Wet Pine Savanna and Flatwoods	Pine savanna	18
185	CES203.382	Central Florida Pine Flatwoods	Pine savanna	18
192	CES203.480	South-Central Interior/Upper Coastal Plain Wet Flatwoods	Pine savanna	18
124	CES203.057	Florida Peninsula Inland Scrub	Sand Pine Southern Scrub Oak	19

Appendix 2 (continued)

93	CES203.281	Atlantic Coastal Plain Upland Longleaf Pine Woodland	Longleaf pine / Slash pine	20
95	CES203.496a	East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland - Open Understory Modifier	Longleaf pine / Slash pine	20
100	CES202.319	Southeastern Interior Longleaf Pine Woodland	Longleaf pine / Slash pine	20
187	CES203.375a	East Gulf Coastal Plain Near-Coast Pine Flatwoods - Open Understory Modifier	Longleaf pine / Slash pine	20
64	CES203.497	Atlantic Coastal Plain Xeric River Dune	Longleaf pine / Scrub oak	21
77	CES203.284b	Florida Longleaf Pine Sandhill - Scrub/Shrub Understory Modifier	Longleaf pine / Scrub oak	21
92	CES203.254b	Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland - Scrub/Shrub Understory Modifier	Longleaf pine / Scrub oak	21
96	CES203.496b	East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland - Scrub/Shrub Modifier	Longleaf pine / Scrub oak	21
188	CES203.375b	East Gulf Coastal Plain Near-Coast Pine Flatwoods - Scrub/Shrub Understory Modifier	Longleaf pine / Scrub oak	21
76	CES203.284a	Florida Longleaf Pine Sandhill- Open Understory Modifier	Sandhills Longleaf Pine	22
91	CES203.254a	Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland - Open Understory Modifier	Sandhills Longleaf Pine	22
49	CES203.477	East Gulf Coastal Plain Northern Mesic Hardwood Forest	Southern Mixed Mesic Hardwoods	23
51	CES203.476	East Gulf Coastal Plain Southern Mesic Slope Forest	Southern Mixed Mesic Hardwoods	23
68	CES202.342	Southern Piedmont Mesic Forest	Southern Mixed Mesic Hardwoods	23
72	CES203.261	Atlantic Coastal Plain Central Maritime Forest	Live Oak Maritime	24
73	CES203.302	Atlantic Coastal Plain Northern Maritime Forest	Live Oak Maritime	24
74	CES203.537	Atlantic Coastal Plain Southern Maritime Forest	Live Oak Maritime	24
79	CES203.503	East Gulf Coastal Plain Maritime Forest	Live Oak Maritime	24
99	CES203.494	Southern Coastal Plain Oak Dome and Hammock	Live Oak Maritime	24
194	CES203.501	Southern Coastal Plain Hydric Hammock	Live Oak Maritime	24
174	CES203.520	Atlantic Coastal Plain Northern Basin Swamp and Wet Hardwood Forest	Bayswamp-Pocosin	25
176	CES203.252	Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, and Baygall	Bayswamp-Pocosin	25
180	CES203.505	Southern Coastal Plain Seepage Swamp and Baygall	Bayswamp-Pocosin	25
207	CES411.289	South Florida Mangrove Swamp	Mangroves	26
171	CES203.384c	Southern Coastal Plain Nonriverine Basin Swamp - Okefenokee Pine Modifier	Pond pine pocosin	27
175	CES203.267	Atlantic Coastal Plain Peatland Pocosin	Pond pine pocosin	27
179	CES203.384	Southern Coastal Plain Nonriverine Basin Swamp	Pond pine pocosin	27
177	CES203.384d	Southern Coastal Plain Nonriverine Basin Swamp - Okefenokee Nupea Modifier	Emergent wetland	28
213	CES203.376	Atlantic Coastal Plain Central Fresh-Oligohaline Tidal Marsh	Emergent wetland	28
214	CES203.259	Atlantic Coastal Plain Embayed Region Tidal Freshwater Marsh	Emergent wetland	28
215	CES203.516	Atlantic Coastal Plain Northern Fresh and Oligohaline Tidal Marsh	Emergent wetland	28
216	CES203.507	Florida Big Bend Fresh-Oligohaline Tidal Marsh	Emergent wetland	28
217	CES203.258	Atlantic and Gulf Coastal Plain Interdunal Wetland	Emergent wetland	28
218	CES203.262	Atlantic Coastal Plain Depression Pondshore	Emergent wetland	28
219	CES203.044	Atlantic Coastal Plain Large Natural Lakeshore	Emergent wetland	28
223	CES203.504	East Gulf Coastal Plain Southern Depression Pondshore	Emergent wetland	28
225	CES203.245b	Atlantic Coastal Plain Clay-Based Carolina Bay Herbaceous Wetland	Emergent wetland	28
228	CES203.077	Floridian Highlands Freshwater Marsh	Emergent wetland	28
231	CES203.078	Southern Coastal Plain Herbaceous Seepage Bog	Emergent wetland	28
233	CES203.192	East Gulf Coastal Plain Treeless Savanna and Wet Prairie	Emergent wetland	28
238	CES203.489b	East Gulf Coastal Plain Large River Floodplain Forest - Herbaceous Modifier	Emergent wetland	28
245	CES203.270	Atlantic Coastal Plain Central Salt and Brackish Tidal Marsh	Emergent wetland	28
246	CES203.260	Atlantic Coastal Plain Embayed Region Tidal Salt and Brackish Marsh	Emergent wetland	28
248	CES203.519	Atlantic Coastal Plain Northern Tidal Salt Marsh	Emergent wetland	28
249	CES203.508	Florida Big Bend Salt-Brackish Tidal Marsh	Emergent wetland	28
250	CES203.303	Mississippi Sound Salt and Brackish Tidal Marsh	Emergent wetland	28

Appendix 3. Correlation matrix of landscape covariates included in models of avian species occurrence in the South Atlantic Migratory Bird Region of the United States, 2001. Spatial Configuration Models included the proportion of optimal (O) or marginal (M) habitat within 400 m of the sampled routes, the average distance to patches (D), number of patches (N) and an interaction term for distance and number of patches (NxD) within two potential dispersal distances (1.47 km and 4.73 km). Matrix Models included the proportion of total forested habitat (Forest), urban, or optimal (marginal for the red-headed woodpecker) habitats within 1.47 km of the sampled routes.

Brown-headed nuthatch and **Eastern wood-pewee**

	Spatial Configuration Models					Matrix Models		
	D (1.47)	N (1.47)	O	N (4.73)	D (4.73)	Forest	Urban	Optimal
D 1.47	1.00	0.27	0.13					
N 1.47	**0.01**	1.00	0.72					
O	**-0.19**	**0.60**	1.00	0.73	0.30			
N 4.73			**0.58**	1.00	0.43			
D 4.73			**-0.14**	**-0.03**	1.00			
Forest						1.00	-0.37	0.50
Urban						**-0.37**	1.00	-0.12
Optimal						**0.49**	**-0.18**	1.00

Red-headed woodpecker

	D (1.47)	N (1.47)	M	N (4.73)	D (4.73)	Forest	Urban	Marginal
D 1.47	1.00	0.10	-0.14					
N 1.47		1.00	0.61					
M			1.00	0.59	-0.02			
N 4.73				1.00	0.11			
D 4.73					1.00			
Forest						1.00	-0.37	0.23
Urban							1.00	-0.07

CHAPTER 2

AVIAN RICHNESS AND SPECIES SENSITIVITY TO URBAN LANDSCAPES

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ABSTRACT.--The process of urbanization transforms natural habitats into impervious surfaces, threatening many avian species. A greater understanding about how these changes influence species richness, composition, and occurrence could inform conservation planning. We integrated the North American Breeding Bird Survey and the National Land Cover Dataset to assess species responses to varying levels of urbanized habitat in the South Atlantic Coastal Plain of the United States. We asked whether: (1) species richness differed between sampling units containing high and low levels of urban habitat, and (2) a species' response conformed with expected sensitivity to urbanization. Species were categorized according to their sensitivity to urban habitats as exploiters, adapters, or avoiders. We used occupancy models to gauge responses of 16 focal species based on the direction (positive/negative) and strength (95%CIs did not overlap zero) of the beta parameter relating percent urban habitat to occupancy probability. We expected the relationship to be positive and strong for exploiters, and negative and strong for avoiders. As predicted, species richness was higher in low-urban route-segments than in high-urban segments. Also as predicted, 2 of 3 urban exploiters were positively and strongly associated with increasingly urban landscapes. In contrast, there was no support for a strong, negative relationship for urban avoiders. Results suggest that urban adapters and avoiders are adept at using the low-levels of urbanized habitat characterizing survey routes. Options to relocate survey routes will diminish with increasing urbanization. Thus survey routes provide future opportunities to assess responses of urban avoiders, a group that contains many species of conservation concern in most states.

KEYWORDS: breeding bird survey, urbanization, occupancy models, species richness

INTRODUCTION

Urbanization and habitat loss threatens more avian species than any other human activity in the United States (Wilcove et al. 1998, Czech et al. 2000). Urbanized habitats affect multiple vital processes for avian species including fecundity, dispersal, mortality, and nest success (Marzluff et al. 2001, Chace and Walsh 2006, Shochat et al. 2006). Urbanization is a process where natural habitats are transformed by human presence, often in the form of "relatively permanent" residences, industry, and roads (Marzluff et al. 2001). This process is evident in the landscape as a gradient of varying human density and settlement, from undeveloped sites to city centers (McDonnell et al. 1993). The rate of conversion of natural habitat to urban landscapes continues to increase in the United States and worldwide (Marzluff et al. 2001). In 2000, 1.6 % of the United States was considered urban or suburban, and 11.8 % was considered low density developed, or exurban (Theobald 2005). Regionally, the southeastern United States has experienced the greatest percentage of population growth and urban development in the country, with the highest rates of habitat change occurring in the southern coastal plains (EPA 2000, Brown et al. 2005). However, in a review of 101 studies, Marzluff et al. (2001) found that the southeastern United States also stood out as a region with a low number of studies assessing the effects of urbanization on avian species.

The need to anticipate the impacts of urbanization on avian species is placing increased pressure on those who must allocate conservation resources (Baker et al. 2008). Detecting patterns of species occurrence and abundance, particularly in response to landscape changes, can be useful to inform planning and conservation. In this study, we integrated the

North American Breeding Bird Survey and the National Land Cover Dataset to assess species responses to varying levels of urbanized habitat in the South Atlantic Coastal Plain of the United States. We asked whether: (1) species richness differed between sampling units containing high and low levels of urban habitat, and (2) a species' response conformed with expected sensitivity to urbanization. We compared estimates of species richness derived from a pool of 70 potential species, after adjusting for detection probability (Boulinier et al. 1998, Hines 1999). We assessed the response of 16 species to varying levels of urbanization using occupancy models. Occupancy (ψ) is defined as the probability that a site is occupied, given the probability of detecting an individual (p) when it is present at the site (MacKenzie et al. 2006). We gauged the response or sensitivity of a species to urban habitats by the direction (positive/negative) and strength (95% CIs did not overlap slope estimates) of the beta parameter relating the urban-habitat covariate to occupancy. Species were categorized according to their sensitivity to urban habitats as exploiters, adapters, or avoiders. Urban avoiders are sensitive to human-induced habitat changes and do not breed in urban or developed areas (McKinney 2006). Urban exploiters thrive in developed environs and can become dependent exclusively on urban resources. Exploiters are expected to maintain populations in urban habitats, can tolerate urban constraints, and reach their highest abundance in urban centers (Blair 1996, McKinney 2006, Croci et al. 2008). An intermediate grouping, urban adapters, are those that can adapt to urban environments but also use the resources in natural habitats. Adapters are expected to peak in suburban environments and use the matrix between human land uses (McKinney 2006). Because there are no established thresholds for these sensitivity groupings, we reasoned that an appropriate framework to draw inferences from our work was from a generalized set of predictions for the groups with sharpest contrasts, the exploiters and avoiders. We expected that occupancy of urban exploiters would be positively and strongly influenced by urban habitat. Conversely, urban avoiders were expected to have a strong and negative relationship. We discuss the conservation implications of the results and their potential to inform conservation actions within the South Atlantic Coastal Plain and across the United States.

METHODS

Study Area

We worked within the South Atlantic Coastal Plain ecoregion, specifically the Migratory Bird Initiative region (SAMBI; Watson et al. 2005). This region is bound on its western edge at the Fall Line, where alluvial and marine sediments meet exposed continental bedrock (Hupp 2000), and on the eastern edge by the Atlantic Ocean. The region spans across the states of Virginia, North Carolina, South Carolina, Georgia and Florida (latitude 29° - 37° North; Figure 1). The study area, buffered by 30 km to incorporate ecoregional edge effects, is approximately 29,073,338 ha of which 2,606,020 ha is water. The SAMBI region comprises many ecological communities including dunes, grasslands, sandhills, marsh, swamp and estuarine systems, and forests dominated by evergreen and deciduous trees (Schafale and Weakley 1990). Longleaf pine forests (*Pinus palustris*) were once the most prevalent vegetative community in the southeastern coastal plain, occupying over 60 million acres from Virginia to Texas. By 1995, the range of longleaf pine had been reduced to ~29 million acres (Outcalt and Sheffield 1996), and the SAMBI now contains some of the largest remnants of these ecosystems (Hunter et al. 2001). The conversion of land for human use, such as agriculture and urban development, accounts for 40% of the natural vegetation loss in the region (Hunter et al. 2001). In addition, the SAMBI region has high avian species diversity, ranking among the top ten regions in North America for its diversity of birds, trees, and reptiles (Ricketts et al.1999, NCWRC 2005).

Avian and Land Cover Databases

We integrated two spatially and temporally extensive datasets: the North American Breeding Bird Survey (BBS; Sauer et al. 2008) and the National Land Cover Dataset (NLCD; Homer et al. 2007). Tabular and spatial BBS data for 2001 were downloaded from the Patuxent Wildlife Research Center BBS website (http://www.pwrc.usgs.gov/bbs/RawData). BBS routes are randomly distributed on secondary roads across North America. Each BBS route is 39.4 km long and composed of fifty stops, spaced 0.8 km apart. At each stop, a volunteer conducts a three-minute point count and records all birds seen or heard within a 400 m radius. We converted all counts per stop to presence (1) and non-presence (0) data. BBS routes were used in this work if the routes were actively run between 1992 and 2002, the digital route map did not differ from the hardcopy map, route lengths were within 10% of the standard 39.4 km length, and routes did not overlap themselves or other active routes. This screening yielded 120 out of 130 possible routes in the SAMBI.

We separated each route into four segments composed of eight stops each (120 routes * four segments). Each of the 480 resulting route segments was ~6.4 km long separated by ~4.8 km (Figure 2). Route segments represented ~1% of the total SAMBI area. Restructuring BBS routes minimized habitat heterogeneity per segment and likely increased our ability to associate habitat data with probability of species occupancy. On average, route segments had fewer habitat classes than entire BBS routes ($Z_{20} = 14.92$, $P < 0.05$). The number of habitat classes within routes averaged 16.15 (SE = 0.45) whereas in route segments it was 14.20 (SE = 0.37).

We used land cover characterizations available in the 2001 NLCD to estimate the amount of urban and forested habitat within 400 m of the route segments (Homer et al. 2007). We created a composite urban covariate to assess a species' sensitivity to any urban-related alteration of natural habitat along routes (Marzluff et al. 2001). This covariate was defined as the percentage of total urban habitat (the sum of the four developed land cover classes / the total area of the buffered route segment) within the 400 m sampling distance of each BBS route segment. The area of each buffered segment was an average of 513 ha (SE = 2). NLCD discerns four types of urbanization and three types of forested habitats in its land cover map at a 30 m x 30 m pixel resolution using impervious-surface data (Homer et al. 2007). Developed open space, where < 20% of the total cover is impervious surface, includes a mixture of constructed materials, lawn grasses, golf courses, parks, or lawns of single-family housing units. Low intensity developed areas have 20-49% impervious surfaces. This class is most commonly rural and suburban single-family housing areas (MRLC 2001). Medium intensity developed has 50-79% impervious surface, whereas high intensity developed areas are composed of ≥ 80% total impervious surfaces (MRLC 2001). Areas with high amounts of impervious surfaces can still have the capacity to support certain species if they contain critical habitat structures, such as large diameter nesting trees (Savard et al. 2000). Forested habitat was defined as the sum of evergreen, deciduous and mixed forest land cover classes.

We stratified the SAMBI into three sections by latitude: southern (Lat S = 29-31° N), central (Lat C = 32-34° N) and northern (Lat N = 35-37° N). These were roughly equal sections, containing similar numbers of route segments (Lat S = 168, Lat C = 204, Lat N =108). We reported the amount of urban habitat within each latitudinal region using the median percentage of urban habitat and the associated 90% confidence intervals. We used PROC UNIVARIATE CIQUANTDF (does not assume normality) to generate confidence intervals (SAS 2002). We used pair-wise, two-sample, Kolmogorov-Smirnoff tests for differences in the amount of within-segment urban habitat by latitudinal region (SAS 2002). All spatial data were processed in the North American Datum 1983 Albers, an equal area projection. All geographic analyses were performed in ArcMAP 9.2 (ESRI Inc. 1999).

Occupancy Models

We used single-season, single-species occupancy models to assess a species' sensitivity to urbanized environments. We developed models for 16 of a pool of 70 species that had been categorized as urban exploiters, urban adapters, or urban avoiders based on expert opinion, field studies in North Carolina (C. Moorman unpubl. data), diet, and nesting habitat (Mason et al. 2007). This framework provided the basis for expected responses or sensitivity to varying levels of urbanization. Species were modeled if they breed in the South Atlantic Coastal Plain and were well-sampled using BBS protocol (i.e., marsh, coastal and nocturnal birds were excluded). The final suite of species included three hypothesized urban exploiters, six adapters and seven avoiders (Table 1).

Encounter histories were derived from the eight stops sampled within a route segment. An example encounter history would be h:10110000, where a species was encountered at the first stop, not encountered at the second stop, encountered at the third and fourth stop, and not encountered at the fifth through eighth stops. While temporal replication provides information on presence at a specific location, spatial replication, as in the case of BBS route segments, can support greater certainty of the species-habitat relationship (Goodinson 2000). Because stops along BBS routes are sampled sequentially, it is possible that the probability of occupancy is influenced by the state (occupied or not) of the previous survey stop or segment (Hines et al. 2009). We assessed support in the data for spatial dependency using two model structures in program PRESENCE (Franklin et al. 2004, Hines 2006). The first can be viewed as a generalized spatial dependence model. It assumes that all stops are equally influenced by the state of the preceding stop or habitat (model notation is $\theta = \theta`$; Hines et al. 2009). The alternative model assumes that the occupancy of the first stop is not influenced by the preceding habitat or state. Thus, the first stop and the rest of the stops in the segment are not equally subject to spatial dependence ($\theta \neq \theta`$; Hines et al. 2009). The former model was of particular interest to us because it provided a framework to account for the possible influence of adjacent route segments along a BBS route.

The response of each species to urbanized habitat was evaluated using a generalized model set, which was constructed as follows. We first assessed evidence for spatial dependence along route segments and the need for adjusting detection by the time during the breeding season that the surveys were conducted (Franklin et al. 2004, Anthony et al. 2006). BBS surveys were conducted between 15 May and 15 July in 2001. We arbitrarily created two survey periods (15 May – 15 June and 16 June – 15 July), using 15 June as its mid-point. This setup provided a contrast between peak (S) and late spring because variation in species detection has been known to vary seasonally for some southeastern breeding bird species (Farnsworth et al. 2002). Six model structures were assessed in this process. The model structures were: (1) no spatial dependence [$\psi(.)$, $p(.)$ and $\psi(.)$, $p(S)$]; (2) generalized spatial dependence [$\psi(.)$, $\theta = \theta`$, $p(.)$ and $\psi(.)$, $\theta = \theta`$, $p(S)$]; and (3) spatial dependence for all stops except the first one [$\psi(.)$, $\theta \neq \theta`$, $p(.)$ and $\psi(.)$, $\theta \neq \theta`$, $p(S)$]. Next, we used the model structure with the lowest AIC to assess the influence of landscape covariates: latitude (Lat), urbanization (%Urb), forested habitat (Forest), and the interaction between latitude and urbanization (Lat x %Urb; Franklin et al. 2004, Anthony et al. 2006). We included regional latitude because the SAMBI spans five states and nine degrees of latitude and species occurrence might vary as a function of their range. The relationship between the probability of occupancy (ψ) and covariates was established using a logistic model (logit link) in program PRESENCE (Mackenzie and Nichols 2004).

We ranked models based on parsimony between model fit and number of parameters using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We considered models with ΔAIC $\leq$2 to have strong support (Burnham and Anderson 2002). If model selection supported multiple competing models (ΔAIC $\leq$2), we model-averaged to acknowledge the uncertainty associated with parameter estimates (White and Burnham 1999, Burnham and Anderson 2002). The influence of a covariate (strength) was considered strong if the urban covariate (%Urb) was featured in a model(s) with ΔAIC $\leq$2 and the 95% confidence intervals of its beta (slope) did not overlap zero (95%CI = beta estimate ± 1.96 * standard error). Beta parameter direction (positive or negative) and strength was an estimate of the species occurrence probability along a gradient of urbanized habitat and taken as an indicator of a species' ability to dwell and utilize such habitats.

Single season models assume that: (1) the system is closed to changes in site - occupancy during sampling, (2) a species is not falsely detected, and (3) a species' detection at a site is independent of detection at other sites. The first two assumptions were likely met given that the data were collected in one morning by qualified birders. We tested for violations of the third assumption using spatial dependence models and adopted models that adjusted for spatial dependence if evidence supported it (Hines 2006, Hines et al. 2009).

We also evaluated the effect of land cover characterization errors on estimates of occupancy. The reported accuracy for the land cover maps used in this study is 78% (Wickham et al. 2010). Specifically, we calculated segment-level minimum amounts of within-segment urban habitat (commission errors) and maximum amounts of urban habitat (omission errors) using Wickham et al.'s (2010) assessment of NLCD thematic accuracy (Appendix 3). Results suggested that the direction (positive/negative) of the beta parameter for %Urb did not change, but as expected, the strength (slope) of the relationship did. The results of these analyses were not included here because the fundamental inferences of our work were not changed. However, inferences made from data adjusted for commission errors will likely be more conservative and perhaps should be favored in conservation planning. We recommend that final determinations be made only after considering the uncertainty in the data and the intended application of results.

Species Richness

We assessed differences in species richness using a pool of 70 species (Appendix 1). Although urbanized habitats constitute a continuous gradient, we created two distinct classes representing extreme opposites of the urban gradient to compare species richness. The contrast was made using 30 segments classified based on the percentage of urban habitat as high-urban (median = 33.99%; 90%CI 29.96 – 37.24%) and low-urban (median = 0.93%; 90%CI 0.69 – 1.51%). Species richness is a widely used measure of biodiversity. However, estimates of species richness can be extremely biased if the probability of species detection is not taken into account (Boulinier et al. 1998). Therefore, we estimated species richness with program SPECRICH2 (White et al. 1978, Rexstad and Burnham 1991). This program uses a jackknife estimator and assumes heterogeneity in species detection (model M_h; Hines et al. 1999). Model M_h has been an appropriate estimator of species richness using BBS data (Boulinier et al. 1998). Estimates of species richness (± SE) were compared using a *Z*-test.

RESULTS

Ninety percent of the route segments had $\leq$ 18.47 % urbanized habitat (Figure 3). The median was 8.38% (range: 0 – 75.90%). Thus, most segments in the SAMBI consisted of the developed open space class. The median amount of urban habitat at northern latitudes was 5.80% (90%CIs: 5.30 – 6.68%; N = 108), 7.36% (90% CIs: 6.78 – 8.42%; N = 204) at central latitudes, and 10.40% (90% CIs: 9.94 - 10.93%; N = 168) at southern latitudes (29 to 31° N). Differences among latitudinal regions were significant ($P < 0.001$; Figure 3).

Occupancy probabilities varied by latitude for most species (Table 1, Appendix 2). For example, house finches had higher probabilities of occupancy in the northern portions of the SAMBI and lower probabilities in the southern and central latitudes (Figure 4). Those segments had the highest amounts of urban habitat (median = 10.71%; 90%CIs: 10.10 – 11.18%).

The amount of urban habitat strongly and positively influenced the occupancy of six species (95%CIs did not overlap zero; Table 1). These included two urban exploiters (European starling *Sturnus vulgaris* and house sparrow *Passer domesticus*) and four urban adapters (brown-headed cowbird *Molothrus ater,* house finch, northern cardinal *Cardinalis cardinalis*, and northern mockingbird *Mimus polyglottos*). None of the purported urban avoiders exhibited a strong and negative relationship to varying levels of urban habitat, however the direction of the relationship was negative for 4/7 avoiders.

The species richness estimate at high-urban segments was 61 (SE 5.41) and 72 (SE 7.04) in the low-urban route segments. The difference between estimates was significant ($Z_{30} = 7.04$, $P < 0.05$). Fifty-four species were shared between low and high-urban segments. Eight species were recorded only in the low-urban route segments, three species only in high-urban route segments and two species were absent from both groups (Figure 5, Appendix 1).

DISCUSSION

We used an occupancy framework to evaluate the hypothesized urban-sensitivity of 16 species of birds in the South Atlantic Coastal Plain. We expected that species at the opposite ends of the purported sensitivity spectrum would exhibit strong responses, positive for exploiters and negative for avoiders (Blair 1996, McKinney 2006). Results supported expectations for exploiters, but not for avoiders. In the case of urban exploiters, 2 of 3 species modeled exhibited a strong positive response to increasing urbanized habitats. The rock pigeon, the third member of this group, did not. We speculate that a BBS sampling artifact may account for the positive yet weak influence of urban habitat on occupancy probability. Most urban exploiters, especially non-native species, are regarded as habitat-generalists (Owens and Bennett 2000, Fernandez-Juricic and Jokimaki 2001, Cassey 2002) . However, Croci et al. (2008) hypothesized that many are actually habitat specialists. These attributes presumably allow species like the rock pigeon, a cliff specialist (Johnston 1992), to thrive in high-urban areas where tall buildings are commonplace. Clearly, this level of urbanized habitat was not sampled by BBS routes in the South Atlantic Coastal Plain.

None of the purported urban avoiders exhibited a strong, negative response to urbanized habitat. We inferred that species under consideration occurred and presumably utilized the gradient of urbanized habitats along BBS routes, which is arguably low density (median impervious surfaces = 8%). Species like the loggerhead shrike may be particularly adept at exploiting opportunities in these novel habitats as they create open and useable habitats features (e.g., perches, Smith and Kruse 1992). The lack of strong, negative responses to urbanized habitat points to the possibility that even so-called high-urban route segments in this work were contextually similar to Marzluff et al.'s (2001) definition of rural-exurban habitats, which are composed of 5 – 20 % built structures. In contrast, and not surprisingly, the intermediate group, the urban adapters, exhibited stronger responses to urbanized habitats. Occupancy of 4/6 species was strongly and positively influenced by urbanized habitats. Consistent with Blair (1996) and McKinney (2002), we speculate that these species were more adept at using urbanized habitats.

The assessment of species richness and composition was consistent with our occupancy results and with findings from previous studies where species richness was significantly higher in areas with low levels of urban habitats (Beissinger and Osborne 1982, Friesen et al. 1995, Melles et al. 2003, Clergeau et al. 2006). Moreover, the majority of the species present only in the low-urban route segments were hypothesized urban avoiders. Two species were missing from both urban habitat groups, the song sparrow (*Melospiza melodia*) and the black-throated green warbler (*Dendroica virens*). Possible explanations accounting for their absence include the sparrow's aversion to urban habitats (Melles et al. 2003) and low detection rates of the warbler (subspecies *Waynei*) in the SAMBI (Watson et al. 2005). It is also worth noting that there were two urban avoiders present only in high-urban route segments, the loggerhead shrike and the horned lark (*Eremophila alpestris*). Both are open habitat dwellers in the Atlantic Coastal Plain (Watts 1999, Watson et al. 2005), but it is worth noting that most routes had ≤ 18% urban habitat. This may explain why route segments on the high end of this range of urbanized habitat were not dominated by just a few species as reported by Clergeau et al. (2006). Indeed, 77 % of the species pool was present in both high- and low- urban route segments.

With urban development on the rise (Marzluff et al. 2001), the need to evaluate the potential consequences on biodiversity has gained importance in the past decade (McKinney 2002, Croci et al. 2008). The impetus to develop landscape-level conservation strategies places a premium on datasets that can allow critical evaluation of existing knowledge while also serving as a benchmark to augment our ability to predict consequences. Our work contributes towards those goals by tapping BBS data to gain insights about species responses to urbanized habitats with an occupancy modeling framework (McKenzie et al. 2006). This framework allowed us to model the influence of percent urban habitat with and without the influence of other factors such as forested habitat and latitude. The importance of including other factors was illustrated by our inclusion of latitude as a covariate and the habitat models for the house finch. This species exhibited a strong, positive response to urbanize habitat. However, occupancy probabilities were higher on the northern portions of the SAMBI as compared to southern latitudes despite the fact that the percent of impervious surfaces were higher on those southern latitudes. This apparent discrepancy does not invalidate our finding, which is consistent with Blair (1996) and McKinney (2006), but rather suggests that other factors, such as history and range dynamics, should be considered during interpretation of results. The house finch is an introduced species, expanding southward from points north of our study area (Hill et al. 1993). It is plausible; therefore, that higher occupancy on northern latitudes reflects that expansion history without negating the species' strong association with urban habitats.

Admittedly, BBS routes are not suited to assess hypothesized sensitivities to urbanized landscapes for all species, as illustrated by the rock pigeon. By design, BBS routes sample landscapes with low amounts of impervious surfaces (K. Pardieck, USFWS, pers. comm.). Because urban-tolerance thresholds are not available, assessments are better off by following carefully designed studies that span the full range of urbanized habitats (e.g., Blair 1996). Such a setting, for example, would have helped us discern the level of urbanized habitat that better discriminates between adapters and exploiters. By the same token, BBS routes seem appropriate to gain a greater understanding of responses by urban avoiders, particularly because over time it is likely that options to relocate BBS routes will diminish and routes will inevitably sample greater proportions of urbanized habitats. This potential has great conservation implications because the hypothesized urban avoiders tend to be comprised of species in greater need of habitat protection, such as those highlighted in State Wildlife Conservation Action Plans (e.g. NCWRC 2005). Our models were spatially-explicit and insightful, but static. We suggest that greater insights about the sensitivity of avian species to dynamic urban landscapes could be obtained if evaluated using a multi-season occupancy framework (MacKenzie et al. 2006). This framework would allow the expression of responses in terms of vital parameters such as local extinction probabilities, and thus, would be more informative for conservation planning.

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TABLES

Table 1. Hypotheses (x) of species sensitivities to urban habitats and model averaged beta coefficients of urbanization effects on the occupancy of 16 southeastern U.S. avian species. Occupancy (ψ) was modeled as constant (.) or as a function of urban habitat (%Urb) within 400 m of the sampling segment, latitude in the northern (Lat N), central (Lat C) or southern (Lat S) regions of the South Atlantic Coastal Plain, forested habitat, or the interaction of urban and latitude (Lat x %Urb). Spatial correlation was modeled under two assumption frameworks (θ=θ' or θ≠θ', see text). Detection probability (*p*) was constant or varied within-season (Season). Models with the lowest AIC score (Top Models), the difference between the first model with urban and the model with the lowest AIC score (ΔAIC (% Urb)), and the relative weight of the urban covariate (w_i) is reported. Estimates and standard errors are on the logit scale.

Common Name	Scientific Name	Urban Exploiter	Urban Adapter	Urban Avoider	Top Model	ΔAIC(%Urb)	w_i	β (%Urb)	SE(%Urb)
House sparrow	*Passer domesticus*	x			ψ(%Urb + LatS + Forest), θ=θ',*p*(Season)	0.00	0.94	0.24[a]	0.10
European starling	*Sturnus vulgaris*	x			ψ(%Urb + LatN + Forest) θ≠θ', *p*(Season)	0.00	0.94	0.16[a]	0.07
Rock pigeon	*Columba livia*	x			ψ(%Urb + LatS + LatS x %Urb), θ=θ', *p*(Season)	0.00	0.58	0.24	0.29
House finch	*Carpodacus mexicanus*		x		ψ(%Urb + LatN), θ≠θ', *p*(.)	0.00	0.99	0.38[a]	0.08
Northern cardinal	*Cardinalis cardinalis*		x		ψ(%Urb + Lat S + LatS x %Urb), θ≠θ', *p*(Season)	0.00	0.99	0.25[a]	0.11
Northern mockingbird	*Mimus polyglottos*		x		ψ(%Urb + LatS + Forest + LatS x %Urb), θ≠θ, *p*(Season)	0.00	0.99	0.31[a]	0.14
Brown-headed nuthatch	*Sitta pusilla*		x		ψ(LatC + Forest), θ≠θ', *p*(.)	1.82	0.51	-0.23	0.53
Brown-headed cowbird	*Molothrus ater*		x		ψ(%Urb + LatN), θ≠θ, *p*(Season)	0.00	0.93	2.33[a]	1.03
Tufted titmouse	*Baeolophus bicolor*		x		ψ(LatC + Forest), θ=θ', *p*(Season)	0.25	0.56	0.05	0.08
Wood thrush	*Hylocichla mustelina*			x	ψ(%Urb + LatS) *p*(.)	0.00	0.76	-0.30	0.23
Great-crested flycatcher	*Myiarchus crinitus*			x	ψ(%Urb + LatS), θ≠θ', *p*(Season)	0.00	0.58	-0.30	0.48
Red-eyed vireo	*Vireo olivaceus*			x	ψ(LatN + Forest), θ=θ', *p*(.)	1.98	0.42	0.00	0.03
Loggerhead shrike	*Lanius ludovicianus*			x	ψ(LatS + Forest) *p*(.)	1.76	0.45	1.93	3.44
Red-headed woodpecker	*Melanerpes erythrocephalus*			x	ψ(LatN + Forest) *p*(Season)	1.42	0.48	-0.11	0.20
Eastern wood-pewee	*Contopus virens*			x	ψ(LatS + Forest), θ≠θ', *p*(.)	1.68	0.41	-0.05	0.09
Summer tanager	*Piranga rubra*			x	ψ(%Urb + LatS + Forest), θ=θ', *p*(Season)	0.00	0.71	0.10	0.09

[a] denotes that the 95% confidence intervals do not overlap zero.

FIGURES

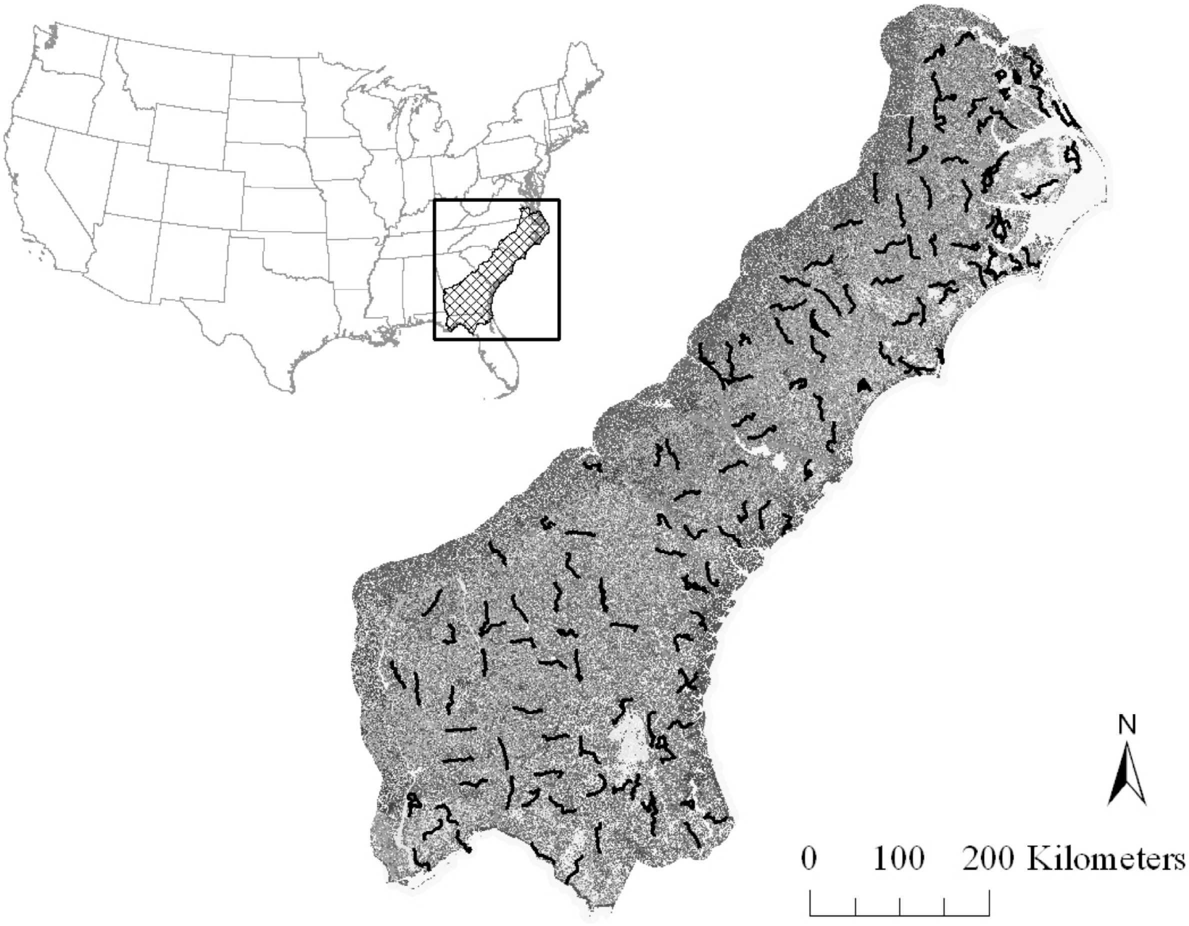


Figure 1. The locations of 120 North American Breeding Bird Survey routes used in the analyses of avian species sensitivities to urban habitats in the South Atlantic Coastal Plain region of the United States, 2001.

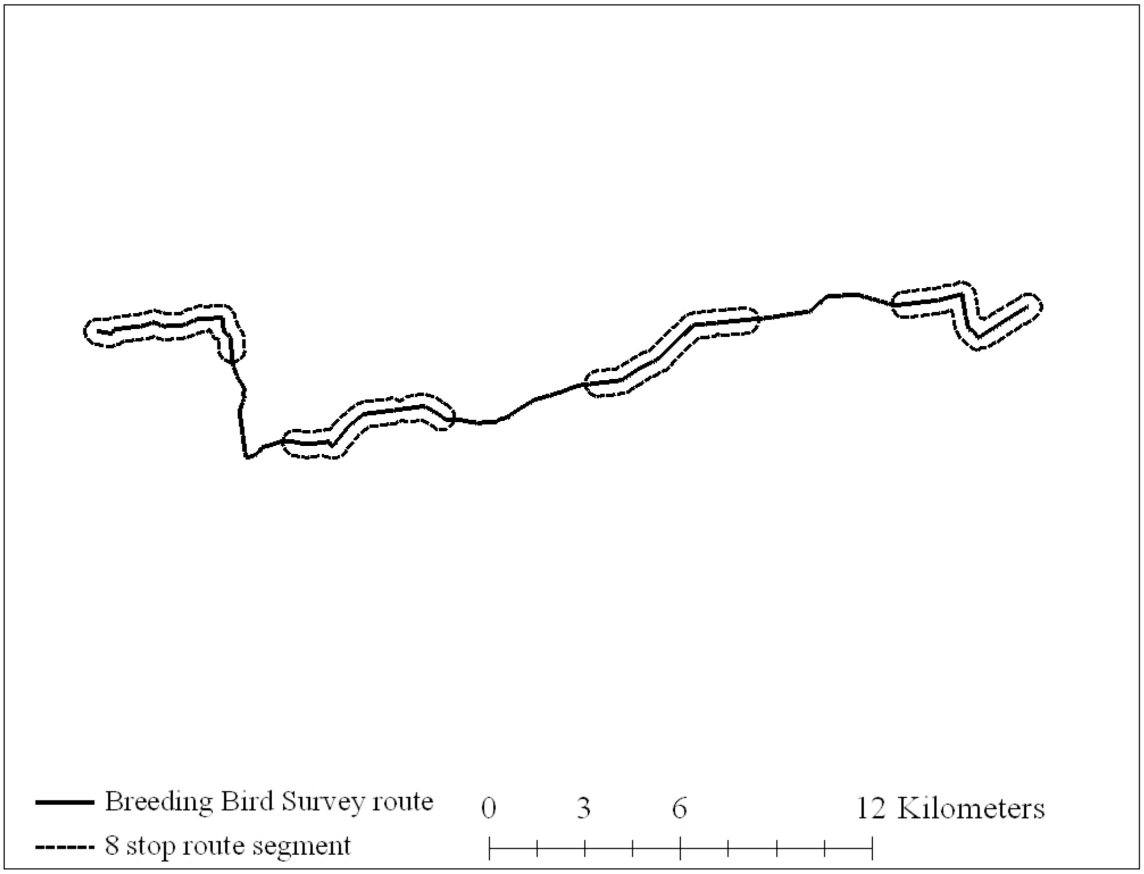


Figure 2. North American Breeding Bird Survey routes were separated into four, eight-stop segments. The eight stops were used as spatial replicates to estimate probability of species detection in occupancy modeling of species-habitat dynamics. Route segments are ~4.8 km apart.

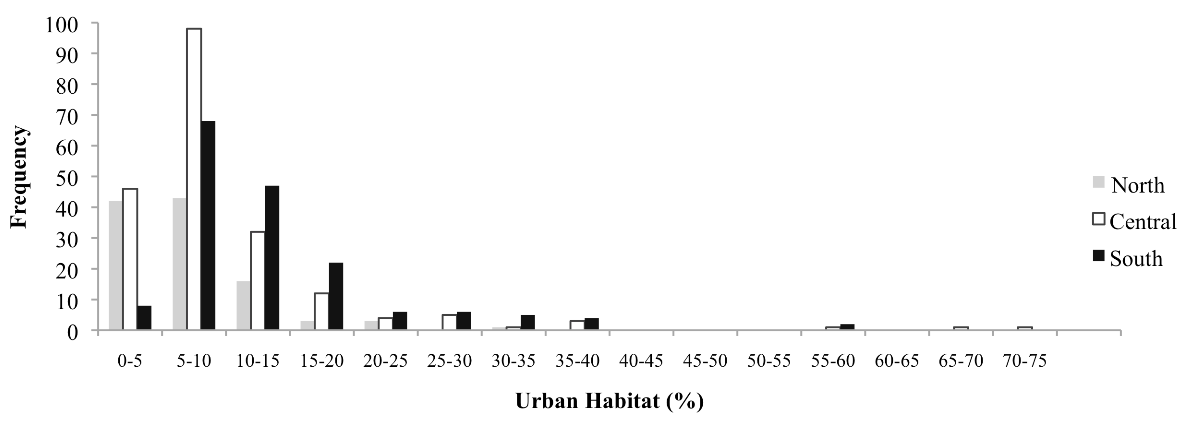


Figure 3. The distributions of the percent of urban habitat by latitudinal region within 400 m of Breeding Bird Surveys in the South Atantic Coastal Plain of the United States using the 2001 National Land Cover Dataset were different (South_{168} = 29 - 31˚ N, Central_{204} = 32 -34˚ N and North_{108} = 35- 37˚ N; Kolmogorov-Smirnov tests for pair-wise differences: North-South D = 0.43, P <0.001; Central-South D = 0.28, P < 0.001; North-Central D = 0.27 P < 0.001).

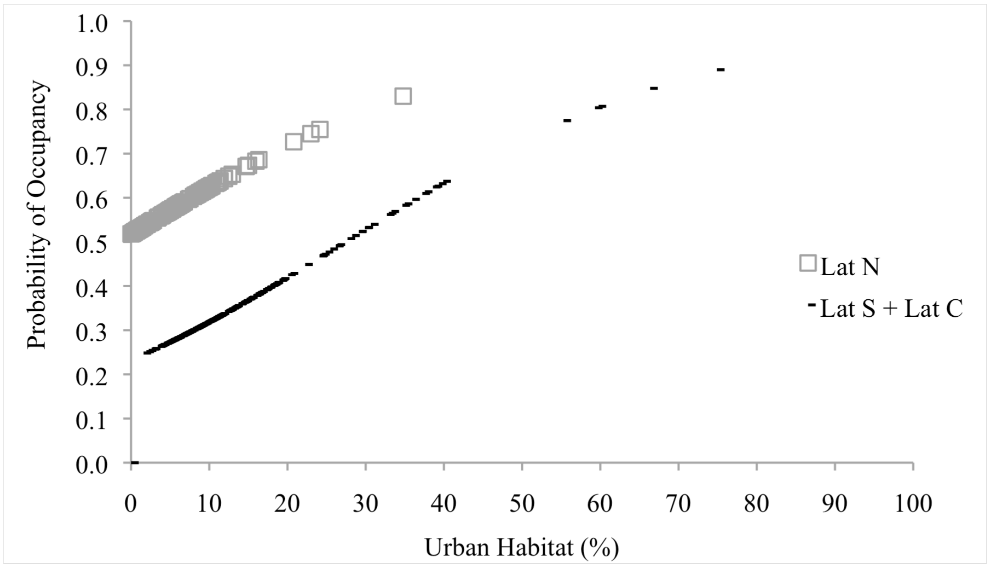


Figure 4. Estimated occupancy of house finch by latitude relative to the percent of urban habitat present within 400 m of North American Breeding Bird Survey route segments in the South Atlantic Coastal Plain of the United States, 2001. The study region was separated into three groups based on the degree of latitude of survey routes (LatS = 29 - 31˚ N, Lat C = 32 - 34˚ N and Lat N = 35- 37˚ N). Estimates are given from the following model: House finch ψ(%Urb + LatN), $\theta \neq \theta'$, p(.).

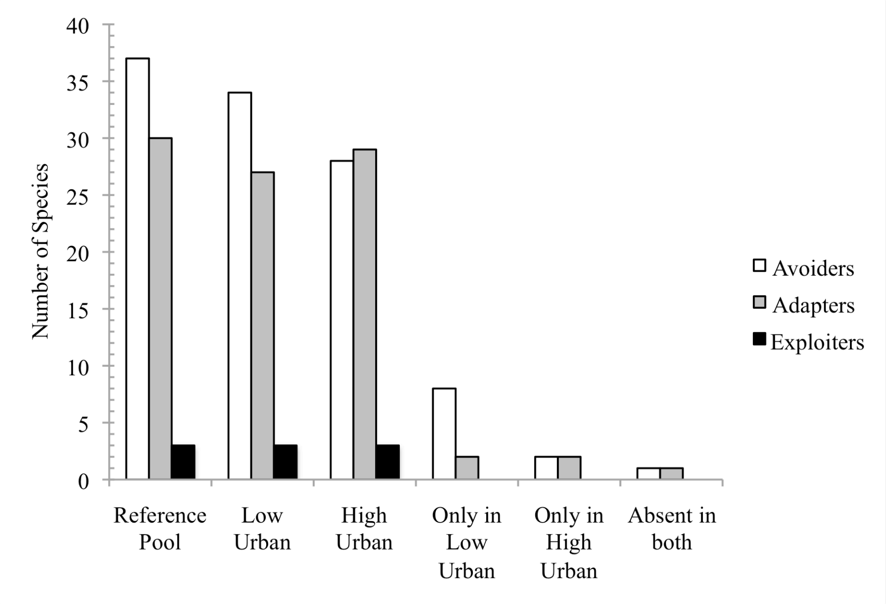


Figure 5. Seventy avian species were included in a species richness analysis in the South Atlantic Coastal Plain of the United States using North American Breeding Bird Survey data for 2001. Species were grouped as urban avoiders, urban adapters, and urban exploiters (Mason et al. 2007; C. Moorman unpubl. data). The representativeness of species-groupings was compared between high-urban (N= 30) and low-urban (N=30) units.

APPENDIX

Appendix 1. Seventy species included in a species richness analysis in the South Atlantic Coastal Plain of the United States, 2001. Hypotheses regarding species sensitivity to urban habitats (Mason et al. 2007; C. Moorman unpubl. data) and results from a community composition comparison of presence and apparent absence between high-urban (N= 30) and low-urban (N=30) sampled units are included. 16 species (*) were selected for occupancy-model development to assess species sensitivity to urban habitats.

		Urban Hypotheses			Community Composition Comparison			
Species	Scientific Name	Urban Exploiter	Urban Adapter	Urban Avoider	Present in Both	Present in High Urban Only	Present in Low Urban Only	Absent in Both
Rock pigeon*	*Columba livia*	x			x			
House sparrow*	*Passer domesticus*	x			x			
European starling*	*Sturnus vulgaris*	x			x			
House finch*	*Carpodacus mexicanus*		x		x			
Northern mockingbird*	*Mimus polyglottos*		x		x			
Mourning dove	*Zenaida macoura*		x		x			
American robin	*Turdus migratorius*		x		x			
American crow	*Corvus brachyrhynchos*		x		x			
Common grackle	*Quiscalus quiscula*		x		x			
Brown-headed cowbird*	*Molothrus ater*		x		x			
Blue jay	*Cyanocita cristata*		x		x			
Carolina chickadee	*Poecile carolinensis*		x		x			
Tufted titmouse*	*Baeolophus bicolor*		x		x			
Chimney swift	*Chaetura pelagica*		x		x			
Northern cardinal*	*Cardinalis cardinalis*		x		x			
Carolina wren	*Thryothorus ludovicianus*		x		x			
Brown thrasher	*Toxostoma rufum*		x		x			
Pine warbler	*Dendroica pinus*		x		x			
American goldfinch	*Carduelis tristis*		x		x			
Downy woodpecker	*Picoides pubescens*		x		x			
Red-bellied woodpecker	*Melanerpes carolinensis*		x		x			
White-breasted nuthatch	*Sitta carolinensis*		x		x			
Gray catbird	*Dumtella carolinensis*		x		x			
Eastern towhee	*Pipilo erythrophthalmus*		x		x			
Eastern phoebe	*Sayornis phoebe*		x				x	
Song sparrow	*Melospiza melodia*		x					x
Eastern bluebird	*Sialia sialis*		x		x			
Chipping sparrow	*Spizella passerina*		x		x			
Purple martin	*Progne subis*		x		x			
Brown-headed nuthatch*	*Sitta pusilla*		x			x		
Ruby-throated hummingbird	*Archilochus colubris*		x			x		
Red-winged blackbird	*Agelaius phoeniceus*		x		x			
Hairy woodpecker	*Picoides villosus*		x				x	
Field sparrow	*Spizella pusilla*			x	x			
Red-headed woodpecker*	*Melanerpes erythrocephalus*			x	x			

Appendix 1 (continued)

		Urban Hypotheses			Community Composition Comparison			
Species	Scientific Name	Urban Exploiter	Urban Adapter	Urban Avoider	Present in Both	Present in High Urban Only	Present in Low Urban Only	Absent in Both
Great-crested flycatcher*	*Myiarchus crinitus*			x	x			
Wood thrush*	*Hylocichla mustelina*			x	x			
Red-eyed vireo*	*Vireo olivaceus*			x	x			
Orchard oriole	*Icterus spurius*			x	x			
Summer tanager*	*Piranga rubra*			x	x			
Blue-gray gnatcatcher	*Polioptila caerulea*			x	x			
Pileated woodpecker	*Dryocopus pileatus*			x	x			
Eastern kingbird	*Tyrannus tyrannus*			x	x			
Eastern wood-pewee*	*Contopus virens*			x	x			
Northern parula	*Parula americana*			x	x			
Scarlet tanager	*Piranga olivacea*			x			x	
Yellow-throated warbler	*Dendroica dominica*			x	x			
Indigo bunting	*Passerina cyanea*			x	x			
White-eyed vireo	*Vireo griseus*			x	x			
Ovenbird	*Seiurus aurocapilla*			x	x			
Black-and-white warbler	*Mniotilta varia*			x			x	
Common yellowthroat	*Geothlypis trichas*			x	x			
Acadian flycatcher	*Empidonax virescens*			x	x			
Yellow-throated vireo	*Vireo flavifrons*			x	x			
Yellow-billed cuckoo	*Coccyzus americanus*			x	x			
American redstart	*Setophaga ruticilla*			x			x	
Yellow warbler - migrant	*Dendroica petechia*			x			x	
Hooded warbler	*Wilsonia citrina*			x	x			
Blue grosbeak	*Buiraca caerulea*			x	x			
Louisiana waterthrush	*Seiurus motacilla*			x			x	
Kentucky warbler	*Oporonis formosus*			x			x	
Yellow-breasted chat	*Icteria virens*			x	x			
Grasshopper sparrow	*Ammodramus savannarum*			x	x			
Loggerhead shrike*	*Lanius ludovicianus*			x		x		
Horned lark	*Eremophila alpestris*			x		x		
Black-throated green warbler	*Dendroica virens*			x				x
Northern bobwhite	*Colinus virginianus*			x	x			
Prothonotary warbler	*Protonotaria citrea*			x	x			
Prairie warbler	*Dendroica discolor*			x			x	
Swainson's warbler	*Limnothlypis swainsonii*			x			x	

Appendix 2. Model averaged beta coefficients of covariate effects on occupancy for 16 southeastern U.S. avian species on Breeding Bird Survey route segments. Occupancy (ψ) is modeled as constant (.), as a function of urban habitat (%Urb) or forested habitat within 400 m of the sampling segment, latitude in the northern (Lat N), central (Lat C) or southern (Lat S) regions of the South Atlantic Coastal Plain, or the interaction of urban and latitude (Lat x %Urb). Detection probability (*p*) was modeled as constant or varied by season (Season). Beta coefficients (β), and standard errors are model averaged across all competitive models (ΔAIC ≤ 2). Estimates and standard errors are on the logit scale.

Common Name	Scientific Name	β(intercept)	SE(intercept)	β(θ)	SE(θ)	β(θ')	SE(θ')	β(LatS)	SE(LatS)	β(LatC)	SE(LatC)	β(LatN)	SE(LatN)	β(%Urb)	SE(%Urb)	β(LatSx%Urb)	SE(LatSx%Urb)	β(LatN x %Urb)	SE(LatN x %Urb)	β(Forest)	SE(Forest)
House sparrow	*Passer domesticus*	0.54	0.68	-2.44	0.37	-0.62	0.57	-0.85	0.41	-	-	-	-	0.24	0.10	-0.13	0.19	-	-	-0.28	0.09
European starling	*Sturnus vulgaris*	0.81	0.94	-2.52	0.48	0.49	0.44	-	-	-	-	0.98	0.22	0.16	0.07	-	-	0.05	0.09	-0.32	0.07
Rock pigeon	*Columba livia*	-0.41	3.91	-2.99	2.50	-0.05	0.98	-0.45	0.50	-	-	-	-	0.24	0.29	-0.08	0.19	-	-	-0.19	0.23
House finch	*Carpodacus mexicanus*	-0.46	0.60	-2.54	0.46	-0.42	0.61	-	-	-	-	0.50	0.09	0.38	0.08	-	-	0.02	0.05	0.00	0.02
Northern cardinal	*Cardinalis cardinalis*	3.59	0.47	-0.27	0.18	1.08	0.43	0.98	0.26	-	-	-	-	0.25	0.11	-0.46	0.16	-	-	0.00	0.02
Northern mockingbird	*Mimus polyglottos*	2.15	0.36	-0.90	0.25	1.42	0.40	0.29	0.24	-	-	-	-	0.31	0.14	-0.14	0.17	-	-	-0.25	0.06
Brown-headed nuthatch	*Sitta pusilla*	-0.40	0.76	-2.75	0.54	-0.75	0.98	-	-	0.78	0.16	-	-	-0.23	0.53	-	-	-	-	0.40	0.47
Brown-headed cowbird	*Molothrus ater*	0.52	0.37	-1.22	0.34	0.53	0.51	-	-	-	-	0.41	0.21	2.33	1.03	-	-	0.59	1.50	0.05	0.13
Tufted titmouse	*Baeolophus bicolor*	1.91	0.22	0.56	0.41	1.54	0.77	-	-	-0.20	0.17	-	-	0.05	0.08	-	-	-	-	0.35	0.13
Wood thrush	*Hylocichla mustelina*	0.46	0.22	-	-	-	-	-2.76	0.51	-	-	-	-	-0.30	0.23	0.08	0.17	-	-	0.09	0.13
Great-crested flycatcher	*Myiarchus crinitus*	2.82	0.78	-0.97	0.23	0.03	0.84	0.68	0.16	-	-	-	-	-0.30	0.48	-0.01	0.02	-	-	0.01	0.03
Red-eyed vireo	*Vireo olivaceus*	-0.28	0.17	-1.47	0.35	-0.93	0.57	-	-	-	-	1.31	0.18	0.00	0.03	-	-	-	-	0.30	0.07
Loggerhead shrike	*Lanius ludovicianus*	0.19	3.02	-	-	-	-	0.15	2.69	-	-	-	-	1.93	3.44	0.63	2.96	-	-	-0.41	0.31
Red-headed woodpecker	*Melanerpes erythrocephalus*	0.16	0.57	-	-	-	-	-	-	-	-	-1.85	0.65	-0.11	0.20	-	-	-	-	0.25	0.31
Eastern wood-pewee	*Contopus virens*	2.11	5.86	-2.13	2.03	2.38	1.07	-1.39	0.35	-	-	-	-	-0.05	0.09	0.06	0.11	-	-	0.22	0.07
Summer tanager	*Piranga rubra*	1.23	0.28	-1.01	0.69	-0.36	0.93	-0.88	0.20	-	-	-	-	0.10	0.09	0.02	0.05	-	-	0.14	0.06

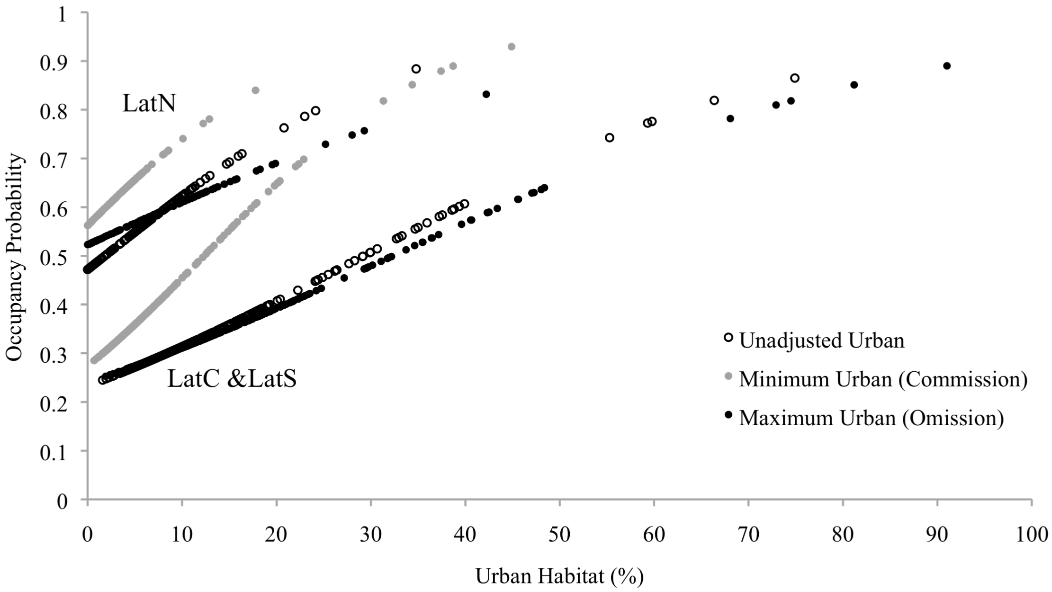
Appendix 3. Assessment of Land Cover Characterization Errors.

We evaluated the effect of land cover characterization errors on estimates of occupancy. We calculated segment-level minimum amounts of within-segment urban habitat (commission errors) and maximum amounts of urban habitat (omission errors) using Wickham et al.'s (2010) assessment of NLCD thematic accuracy. Omission errors were defined as the probability of omitting urban habitat from the urban classification and were calculated as 100 minus the regional producer's accuracy per habitat type (Story and Congalton 1986, Wickham et al. 2010). Commission errors were defined as the probability of classifying a non-urban habitat type as urban and are calculated as 100 – regional user's accuracy per habitat type. The minimum percentage of urban habitat per route segment was calculated as the sum of the differences between the number of urban pixels per urban habitat class and the product of the number of urban pixels and the regional commission error rate for the four urban land cover classes, divided by the total number of urban pixels. The maximum percentage of urban habitat per route segment was calculated as the sum of the differences between the number of urban pixels per urban habitat class and the product of the number of urban pixels and the omission error rate for the four urban land cover classes, divided by the total number of urban pixels.

We assessed and illustrated the implications of land cover characterization errors using house finch (*Carpodacus mexicanus*) data. The candidate set of models was similar to those described above except that the urban covariate was replaced with adjusted estimates of urban habitat based on rates of omission or commission errors.

The median percentage of urban habitat adjusted for rates of thematic commission error was 3.97% (90%CIs: 3.74 – 4.18%) and the median adjusted for rates of omission error was 10.09% (90% CIs: 9.59 – 10.59%). Adjusting for commission and omission errors did not change the direction of estimates of occupancy for the house finch, but did change of the slope of the relationship (Appendix 4). The slope of the occupancy-urban habitat relationship was lessened when occupancy varied with the amount of urban adjusted for omission errors. In contrast, slope increased when occupancy was modeled by the amount of urban habitat adjusted for commission errors.

The slope of the occurrence–urban habitat relationship for the house finch was steeper when urban habitat was adjusted for commission errors. Estimates of commission errors are considered measurements of map ‘reliability’, also known as user’s accuracy (Story and Congalton 1986). This adjustment process should increase our confidence in the claim that urban habitat on the map was indeed urban habitat on the ground. In contrast, model results using rates of omission errors yielded a shallower slope, interpreted as a lessening of the influence of urban on occupancy. Species-habitat models are generally developed using land cover data that is unadjusted for classification errors. Thus, inferences made from data adjusted for commission errors will likely be more conservative and perhaps should be favored in conservation planning. We recommend that final determinations be made only after considering the uncertainty in the data and the intended application of results.



Appendix 4. Estimated occupancy as a function of the amount of urban after adjusting for commission error rates, unadjusted urban, and the amount of urban after adjusted for omission error rates within 400 m within of 480 North American Breeding Bird Survey route segments in the South Atlantic Coastal Plain of the United States, 2001. These models incorporate uncertainty associated with urban land cover classification in the 2001 National Land Cover Dataset. The study region was separated into three regions based on the degree of latitude of survey routes (LatS = 29 - 31˚ N, Lat C = 32 -34˚ N and Lat N = 35- 37˚ N).