Contributed Paper

Effects of Exurban Development and Temperature on Bird Species in the Southern Appalachians

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Abstract: *Land-use dynamics and climatic gradients have large effects on many terrestrial systems. Exurban development, one of the fastest growing forms of land use in the United States, may affect wildlife through habitat fragmentation and building presence may alter habitat quality. We studied the effects of residential development and temperature gradients on bird species occurrence at 140 study sites in the southern Appalachian Mountains (North Carolina, U.S.A.) that varied with respect to building density and elevation. We used occupancy models to determine 36 bird species' associations with building density, forest canopy cover, average daily mean temperature, and an interaction between building density and mean temperature. Responses varied with habitat requirement, breeding range, and migration distance. Building density and mean temperature were both included in the top occupancy models for 19 of 36 species and a building density by temperature interaction was included in models for 8 bird species. As exurban development expands in the southern Appalachians, interior forest species and Neotropical migrants are likely to decline, but shrubland or edge species are not likely to benefit. Overall, effects of building density were greater than those of forest canopy cover. Exurban development had a greater effect on birds at high elevations due to a greater abundance of sensitive forest-interior species and Neotropical migrants. A warming climate may exacerbate these negative effects.*

Keywords: avian communities, Blue Ridge Mountains, building density, elevation, forest canopy cover, land use, single-season occupancy model

Efectos del Desarrollo Exurbano y de la Temperatura sobre Especies de Aves en las Apalaches del Sur

Resumen: *Las dinámicas de uso de suelo y gradientes climáticos tienen grandes efectos sobre muchos sistemas terrestres. El desarrollo exurbano, una de las formas de uso de suelo con rápido crecimiento en los Estados Unidos, puede afectar a la vida silvestre por medio de la fragmentación de hábitat y la presencia de construcciones puede alterar la calidad del mismo. Estudiamos los efectos del desarrollo residencial y los gradientes de temperatura sobre la ocurrencia de especies de aves en 140 sitios de estudio en la parte sur de las montañas Apalaches (Carolina del Norte, E.U.A.) que variaron con respecto a la densidad de construcciones y a la elevación. Usamos modelos de ocupación para determinar las asociaciones de 36 especies de aves con la densidad de construcciones, cubierta del dosel del bosque, temperatura media promedio diaria y la interacción entre densidad de construcciones y temperatura media. Las respuestas variaron con el requerimiento de hábitat, el territorio de reproducción y distancia de migración. La densidad de construcción y la temperatura media fueron incluidas en los principales modelos de ocupación para 19 de las 36 especies y una densidad de construcciones por interacción con la temperatura fue incluida en modelos para 8 de las especies. Conforme el desarrollo exurbano se expande en el sur de las Apalaches, es probable que especies de bosque interior y migrantes neotropicales disminuyan, pero es probable que no beneficie a las especies de borde o de terreno arbustivo. En general, los efectos de la densidad de construcción fueron mayores a aquellos de la cubierta del dosel del bosque. El desarrollo exurbano tuvo un mayor efecto sobre aves en elevaciones altas debido a una*

mayor abundancia de especies sensibles de bosque interior y migrantes neotropicales. Un clima más cálido puede exacerbar estos efectos negativos.

Palabras Clave: Comunidades aviarias, cubierta del dosel del bosque, densidad de construcciones, elevación, modelo de ocupación de temporada única, montañas Blue Ridge, uso de suelo

Introduction

Human activities have substantially altered land use both globally and within the United States (Vitousek 1997; Theobald 2010). Exurban development, which includes low-density rural residential development and urban fringe development, is one of the fastest growing forms of land use in the United States (Brown et al. 2005; Hansen et al. 2005). Exurban development may alter land cover by fragmenting and reducing the amount of interior forest habitat, and houses may affect the quality of surrounding habitat even when they are beneath continuous forest cover (Theobald et al. 1997; Radeloff et al. 2005). In addition to land-use changes, wildlife is also affected by spatial and temporal variation in climate. Determining the relative importance of land use and climate changes can be challenging (Lemoine et al. 2007). Modeling frameworks that incorporate land use and climate change are emerging (e.g., Hepinstall et al. 2008), but there is a pressing need to develop an empirical understanding of how both land use and climatic gradients affect wildlife occurrence (Opdam & Wascher 2004; McRae et al. 2008).

The southern Appalachian region is among the world's most diverse temperate areas (Stein et al. 2000) and is likely to be sensitive to future land-use change. Temperate forest ecosystems represent the predominant land cover in this region. The abundance of nonforest cover, such as agriculture and developed areas, has changed over time with shifting patterns of human land use (Gragson & Bolstad 2006). The dominant land-use change in recent decades has been a rapid increase in exurban development, especially at higher elevations (Wear & Bolstad 1998; Gragson & Bolstad 2006). Moreover, the number and density of buildings in forests has increased (Turner et al. 2003). In addition, climate in the southeast United States is projected to become warmer and drier (Mearns et al. 2003). Together exurban development and climate change may affect southern Appalachian biota. The avian community can serve as an early indicator of changes that will ultimately affect a wider range of taxa because the mobility of bird species gives them the ability to respond rapidly to habitat changes.

Birds exhibit a wide variety of responses to exurban development (Pidgeon et al. 2007). In general, bird abundance and diversity increase with exurban development (Blair 1996); however, specific groups of birds, such as forest interior and Neotropical migrant species, decrease

with exurban development (Kluza et al. 2000; Fraterrigo & Wiens 2005). Landowners may affect bird abundance and diversity by providing birdfeeders and birdhouses, modifying the structure and species composition of vegetation, and applying fertilizers, pesticides, and herbicides (Lepczyk et al. 2004; Burghardt et al. 2009). Predation rates on birds increase as forest fragmentation increases (Chalfoun et al. 2002; Lampila et al. 2005), and houses are often associated with predation by free-ranging domestic cats (*Felis catus*) (Lepczyk et al. 2003) and an increased abundance of small carnivores (i.e., mesopredator release effect) (Crooks & Soulé 1999). In the southern Appalachians, exurban development results in forest loss and fragmentation. Increasingly, houses are being constructed beneath a relatively continuous forest canopy and have little to no grassy lawn (Turner et al. 2003). These houses reflect the environmental amenities preferred by citizens who choose to live in rural and exurban settings (Cho et al. 2005). Such residential developments are frequently marketed as environmentally friendly to potential home buyers. Therefore, the southern Appalachians present a unique environment in which to observe bird species' separate responses to housing density and forest canopy cover.

Avian responses to exurban development may be complicated by a bird species' response to gradients associated with elevation. In the southern Appalachians, climate and vegetation type vary with elevation (Whittaker 1956; Bolstad et al. 1998), and many bird species with northern latitudinal breeding ranges occur in relatively cool environments at middle to high elevations. In contrast, species with southern breeding ranges occur at warmer, lower elevations. Bird species may be affected by exurban development differently along the elevation gradient at which they occur. Moreover, community-level responses may vary if the proportion of species sensitive to exurbanization changes with respect to elevation.

We sought to determine how bird species occurrence varied with exurban development along a temperature gradient associated with elevation. We used point counts and occupancy modeling to investigate the effects of building density, forest canopy cover, and mean temperature on bird species probability of occurrence in a largely forested landscape. We hypothesized that habitat preferences (forest interior, shrubland or edge, or neither), breeding range, and migratory distance affect the way bird species respond to these factors.

Methods

Study Area and Site Selection

Our study area was in the Southern Blue Ridge Physiographic Province in western North Carolina (U.S.A.). Elevations range from 380 to 2037 m in the region. Higher elevations have cooler temperatures and more precipitation than lower elevations (Bolstad et al. 1998), but these trends are modulated by topographic aspect and surrounding landforms. The region is dominated by well-developed secondary forest, and forest community type varies with elevation, slope, and aspect (Whittaker 1956). Forest types in our study are part of the southern Appalachian Oak-Chestnut region (Braun 1950; Stephenson et al. 1993). Low- to middle-elevation sites were dominated by mixed hardwood forests. Sites at higher elevation were in the transition zone between mixed hardwoods and the high-elevation northern hardwood forests of the southern Appalachians (White et al. 1993).

Study sites ($n = 140$) were located in forested areas that varied in building density (0–4.2 houses/ha) (Table 1). Sites with both high and low building densities were distributed across a gradient of elevation (550–1626 m) (Fig. 1). Our study sites did not extend to the highest elevations of this region because residential development is largely absent above 1700 m. Study sites were circles with radii of 200 m. The center of each study site was located along a tertiary road or residential street. Sites were separated by at least 250 m. We used aerial photographs and field visits to select sites that were stratified by elevation and building density (Lumpkin 2011).

Bird Occurrence

We performed roadside point counts (Ralph et al. 1993) at each study site from 26 May through 25 June 2009 and from 21 May through 24 June 2010. We sampled 70 sites in both 2009 and 2010 and 70 in either 2009 or 2010 ($n = 35$ for both years). We conducted point counts on 3 d, at least 8 d apart, in each year the site was surveyed. All point counts were performed from 06:00 to 10:00 and were 10 min in duration. Three trained observers performed all point counts, and all study sites were surveyed by at least 2 different observers. Singing males detected during the 10-min surveys within 100 m of the center of the study site were used to indicate species presence for each visit.

We assigned each bird species to 1 of 3 habitat groups (forest interior, shrubland or edge, or neither interior nor shrub) and 1 of 3 migration-distance categories (Neotropical migrant, short-distance migrant, or resident species) on the basis of Freemark and Collins (1992), Freemark and Merriam (1986), and Whitcomb et al. (1981) (Table 2). We used a geographic information system to locate the geographic center of each species' breeding range by calculating the centroid of a digital map of the breeding distributions (Ridgely et al. 2007). The latitude of the range's centroid was used to compare the effects of building density, temperature, and forest cover among species with more northern versus southern breeding ranges.

Exurban Development, Forest Canopy Cover, and Climate

We measured building density, forest canopy cover, and average daily mean temperature for each study site. Building density (buildings per hectare) was quantified by counting the number of houses and buildings located within 200 m of the center of each study site visible on 2008 aerial images on Google Earth software (Google 2009). We did not count small barns and storage buildings.

We quantified the structure and cover of the forest canopy from LIDAR (light detection and ranging) data. We measured forest canopy cover by calculating the proportion of LIDAR returns at each study site that were within the subcanopy or canopy layers (i.e., >2.0 m above ground). Discrete-return LIDAR data were collected in 2003 (NCDEM 2004) for Grandfather Mountain and Beech Mountain points and in 2005 (NCDEM 2006) for the remaining study areas during winter. We measured vegetation height from LIDAR first returns by subtracting the elevation of a bare-earth digital terrain model, derived from the same LIDAR data set, from the elevation of each return. Only first returns were used, and the average density was 1215 returns/ha. We excluded returns from roofs of buildings. Although the LIDAR data were collected prior to our field study, we verified the validity of these data with ground-truthing and examination of recent aerial photographs.

We measured air temperature hourly during the breeding season (14 June–21 July 2009 and 29 May–20 July 2010) at each study site with iButton model DS192G temperature data loggers mounted in shade 1.5 m above ground on trees or posts within 5 m of site center and away from buildings. We used these data to calculate the average daily mean temperature for each study site during each year. The average daily mean temperatures for study sites sampled in 2009 and 2010 were highly correlated between years (Spearman rank correlation, $r = 0.98$, $p < 0.001$). However, the average daily mean temperatures were on average 1.78 °C higher in 2010 than in 2009; therefore, we standardized the 2010 values to the 2009 average by subtracting 1.78 from the 2010 average daily mean temperature for each study site. Average daily mean was correlated with average daily high temperature (Spearman rank correlation, $r = 0.93$, $p < 0.001$) and average daily low temperature (Spearman rank correlation, $r = 0.80$, $p < 0.001$).

Table 1. Description and range of values of 9 covariates considered for occupancy modeling of bird species observed at sites varying in elevation and level of exurban development.

Covariate type	Covariate name	Covariate description	Mean (SE)[a]	Range[a]
Survey level	time	time of morning	07:37 (0:03)	06:00–10:00
	day	day in season	17 (<1)	1–34
	cloud	cloud cover and weather (1 = clear, 5 = very light rain)	2 (<1)	1–5
	observer	observer (2 binary covariates required to denote 3 observers)	NA	NA
	year	year of survey (1 binary covariate required to denote 2 years)	NA	NA
Site level	building density	exurban development within 200 m (buildings/ha)	0.8 (0.1)	0–4.2
	mean temperature	average daily mean temperature (°C)	18.3 (0.1)	15.2–21.2
	forest canopy cover	lidar proportion of returns in forest canopy	0.58 (0.01)	0.22–0.90
	easting	UTM easting (m)	390,785 (2,071)	352,650–431,410

[a]*Abbreviation: NA, not available.*
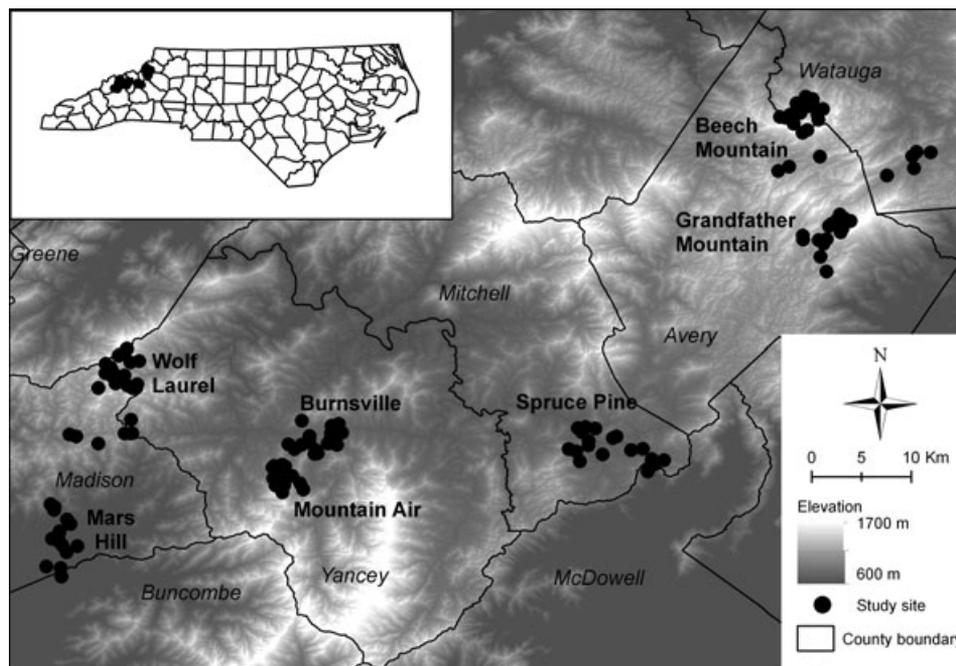
Figure 1. Elevation and location of 140 study sites in the Southern Blue Ridge Province of the southern Appalachian Mountains in North Carolina (inset) (U.S.A.). Names of communities and towns near study sites appear in bold. Names of counties appear in italics.

Data Analyses

We used the program PRESENCE (Hines 2006) to fit a set of single-season occupancy models (MacKenzie et al. 2006) to the data for all bird species detected in at least 10% of study sites. Occupancy modeling is a hierarchical model framework in which the probability of detection (p) and probability of occurrence (ψ) are modeled simultaneously. We used occupancy models to assess the site-level effects of building density, forest canopy cover, and mean temperature on species occurrence (ψ). We used survey-level and site-level covariates, respectively, to model p and ψ. All continuous covariates were standardized by subtracting the mean and dividing by the standard deviation. Survey-level covariates included time, day, cloud cover, and observer (Table 1). We considered combinations of all survey-level covariates and selected the combination resulting in the lowest Akaike's information criterion (AIC) for each species prior to adding site-level covariates for probability of occurrence (ψ).

We analyzed occupancy with a full model that included building density, forest canopy cover, mean temperature, Universal Transverse Mercator (UTM) easting, and a building density × temperature interaction (Table 1) as covariates for probability of occurrence (ψ). The UTM easting was included to account for any biogeographic

Table 2. Beta coefficients used in modeling probability of occurrence (ψ) from best models for each bird species.

Species[a]	Building	Temperature	Interaction	Forest canopy	Easting	Habitat[b]	Migration[c]	Range latitude[d]
Black-throated Blue Warbler	−3.14[e]	−0.74		1.42[e]	1.32[e]	I	N	44.83
Canada Warbler	−2.83[e]	−0.72			1.13[e]	I	N	49.77
Black-throated Green Warbler	−2.31[e]				1.27[e]	I	N	49.10
Scarlet Tanager	−1.89[e]					I	N	41.72
Veery	−0.23	−8.90[e]	3.92[e]	1.58	1.37	I	N	47.15
Blue-headed Vireo	0.78	−1.10[e]		0.50	0.53	I	S	51.01
Acadian Flycatcher	−4.94[e]	1.35[e]		−0.70		I	N	36.53
Ovenbird	−3.25[e]	0.90[e]				I	N	47.18
Black-and-White Warbler	−6.88	3.52	−4.19			I	N	48.05
Hooded Warbler	−1.09[e]	0.77[e]			−0.81[e]	I	N	36.02
Dark-eyed Junco	0.85[e]	−2.37[e]		0.56	0.69[e]		R	53.88
Wood Thrush	−1.52[e]	1.68[e]					N	40.06
Red-eyed Vireo	−0.79[e]				−0.70[e]		N	45.77
Eastern Wood-pewee	−1.20	−0.58			−0.99[e]		N	40.14
Gray Catbird	1.16[e]	−0.33	0.84[e]		−0.58[e]		S	42.60
Red-bellied Woodpecker	−2.63	6.31[e]	5.63				R	36.70
Eastern Phoebe		0.74[e]			−0.46		R	47.33
Blue Jay	−0.43	1.31[e]	0.74				R	42.94
Northern Cardinal		1.81[e]		−0.84[e]			R	34.85
Eastern Towhee				−0.71[e]	−0.89[e]		R	39.15
White-breasted Nuthatch	16.53						R	40.15
Tufted Titmouse		2.57			0.87		R	36.97
Downy Woodpecker		0.76			−0.11		R	48.28
Carolina Wren		1.61[e]			−0.42		R	34.44
Carolina Chickadee		4.02					R	34.90
Chestnut-sided Warbler	−0.85[e]	−2.13[e]		−0.78[e]	−1.68[e]	E	N	47.35
Cedar Waxwing	−0.72			−1.28[e]		E	R	48.07
Song Sparrow	0.86	0.40	0.61	−0.61	−0.46	E	R	48.09
Indigo Bunting	−0.82[e]	−0.67[e]		−0.57	−1.15[e]	E	N	39.11
House Wren	2.33[e]	0.18	0.69		−1.33[e]	E	S	42.38
Chipping Sparrow				−0.64[e]		E	S	46.76
Brown Thrasher		0.98			−1.34[e]	E	S	41.69
American Robin	2.52[e]	0.96	1.55[e]	−0.75	−0.62	E	R	50.70
American Goldfinch	1.25[e]					E	R	44.54
Mourning Dove		0.38		−0.99[e]	−0.70[e]	E	R	39.58
American Crow	1.60	0.59				E	R	45.63

[a]*Scientific names in Supporting Information.*
[b]*Abbreviations: I, forest interior; E, shrubland or edge.*
[c]*Migration distance: N, Neotropical migrant; S, short-distance migrant; R, resident.*
[d]*Latitude of the geographic centroid of the breeding range.*
[e]*Significant coefficients with a 95% CI that does not include zero.*

trends in species occurrences because study sites spanned 100 km from east to west. For each bird species, we used the best combination of survey-level covariates for p while modeling all combinations of the site-level covariates for ψ. When models failed to converge, we varied the order of covariates and their initial starting values.

To measure the effect of each site-level covariate on species' occurrences, we examined the parameter estimates for each species' top-ranked model (i.e., the model with the lowest AIC). We tested these models for goodness of fit, and when goodness of fit was low ($p < 0.3$), we inflated the standard errors of the parameter estimates by the square root of $\hat{c}$ (MacKenzie & Bailey 2004; MacKenzie et al. 2006). Using these standard errors, we calculated 95% confidence intervals for the beta parameter estimate. Confidence intervals including zero indicated no significant effect of the covariate on that bird species.

Functional Group Comparisons and Breeding Ranges

To determine whether groups of bird species responded differently on the basis of habitat or migration distance, an occupancy model of the same structure was fitted for each species. That model included building density, forest canopy cover, mean temperature, and easting. We extracted the beta coefficients for these parameters for each bird species in the group and calculated 95% confidence intervals for the mean beta coefficients for each group of species. Beta coefficients for building density, temperature, and forest canopy cover were tested for a correlation with the latitude of geographic centroid of the species' breeding range.

Results

During 2009 and 2010 surveys, we recorded 4276 detections of 77 species within 100 m of the study site center (Supporting Information). Red-eyed Vireos (*Vireo olivaceus*) and Eastern Towhees (*Pipilo erythrophthalmus*) occurred at more sites (72% of study sites) than any other bird species, and the American Robin (*Turdus migratorius*) was the most commonly detected species (285 detections).

Of the 36 bird species that occurred in at least 10% of the study sites, 28% were in the forest interior habitat group, 42% in the neither forest nor shrub group, and 30% were in the shrubland or edge group. Thirty-nine percent were Neotropical migrants, 14% were short-distance migrants, and 47% were resident species (Table 2). The covariates that affected probability of detection (*p*) varied by species. In the models for 6 bird species, none of the survey-level covariates affected detection (Black-throated Green Warbler [*Dendroica virens*], Dark-eyed Junco [*Junco hyemalis*], Gray Catbird [*Dumetella carolinensis*], Hooded Warbler [*Wilsonia citrina*], Ovenbird [*Seiurus aurocapilla*], and Song Sparrow [*Melospiza melodia*]). Day affected probability of detection for 16 bird species. Time (13 species), observer (12 species), year (12 species), and weather (8 species) were also included as covariates for probability of detection for some bird species (Supporting Information).

Functional groups of bird species responded to building density, forest canopy cover, and mean temperature differently depending on habitat preference and migratory distance (Fig. 2). Increasing building density was negatively associated with the occurrence of forest interior species (−2.54, 95% CI −3.28 to −1.77) and Neotropical migrants (−2.14, 95% CI −2.78 to −1.51). Reponses to building density varied widely among habitat generalists and resident species (Fig. 2a). Forest canopy cover was negatively associated with the occurrence of shrubland or edge species and resident species (Fig. 2b). Mean temperature was positively associated with the occurrence of habitat generalists and resident species; they were more common at low elevations.

For individual species, building density and mean temperature predicted occurrence (Table 2). Mean temperature and building density appeared in the best models for 28 and 26 (respectively) species, followed in importance by easting (22 species) and forest canopy cover (14 species). The best models for 20 species included both building density and mean temperature. Of these models, 8 included an interaction between building density and mean temperature (only significant for 3 species: Veery [*Catharus fuscescens*], American Robin, and Gray Catbird).
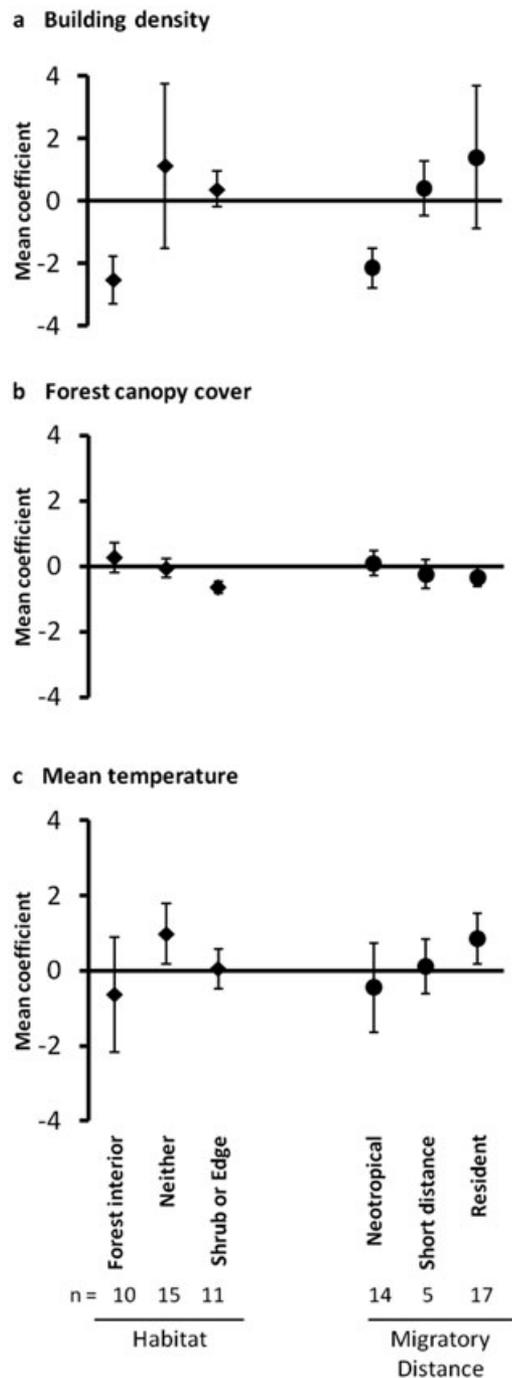

Figure 2. Mean beta coefficients with 95% confidence intervals for (a) building density, (b) forest canopy cover, and (c) mean temperature for functional groups of bird species. Groupings include habitat (forest interior, shrubland or edge, or neither) and migratory distance (Neotropical, short distance, or resident). Beta coefficients are from a full model containing the additive effects of housing density, forest canopy cover, mean temperature, and easting as covariates for occupancy (ψ). The n is number of species included in each group.

Species responses to building density, mean temperature, and forest canopy cover were often related to habitat preference and migration distance, as seen in functional group comparisons (Table 2). Most of the bird species (11 of 16 species) for which building density was significant in the top model responded negatively to increasing building density. These negative responses were mainly observed in birds that prefer interior forest habitat and were Neotropical migrants, but 2 shrubland or edge species that were Neotropical migrants also declined as building density increased (Chestnut-sided Warbler [*Dendroica pensylvanica*] and Indigo Bunting [*Passerina cyanea*]). Only 5 species increased with increasing building density, and all of these were shrubland or edge or generalist species. Responses to mean temperature varied. Of the bird species for which mean temperature was significant in the top model, 5 species declined and 9 species increased with increasing mean temperature. Most species (6 of 7 species) with significant responses to forest canopy cover exhibited negative responses to this factor. These birds were mainly shrubland or edge species and habitat generalists. Only one species, the Black-throated Blue Warbler (*Dendroica caerulescens*), a forest interior species, increased with increasing forest canopy cover.

The latitude of breeding range was negatively correlated with mean temperature (Pearson's $r = -0.51$, $p < 0.01$) (Fig. 3a), which supports the general trend of more northerly species occurring at higher elevations; however, breeding range was not correlated with beta coefficients for building density ($p > 0.10$). If shrubland or edge species are excluded, latitude of breeding range was positively correlated ($r = 0.35$, df $= 23$, $p < 0.04$) with beta coefficients of forest canopy (Fig. 3b). For shrubland or edge species, responses to canopy cover were negatively correlated with latitude of breeding range ($r = -0.41$, df $= 9$, $p = 0.11$). Collectively, these results suggest that northern species were more sensitive to canopy cover, but latitude of breeding range did not affect responses to building density.

Discussion

Our study results show that exurban development and temperature gradients are important when predicting the occurrence of southern Appalachian bird species and that species occurrences vary with habitat preference, migration distance, and breeding range. The importance of temperature indicates that the particular species affected by residential development vary with elevation. Contrary to our initial hypothesis, statistically significant interactions between building density and mean temperature occurred rarely (in only 8 of 36 species). Nevertheless, several bird species responded to both exurban develop-
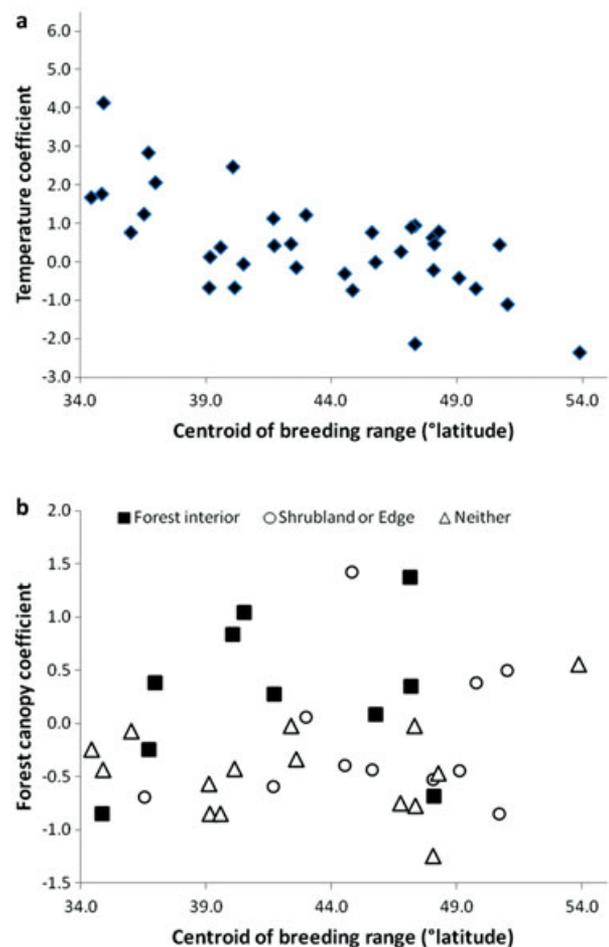
Figure 3. Beta coefficients for (a) temperature and (b) forest canopy cover from a full model plotted against the latitude of the geographic centroid of the breeding range of birds. Habitat (forest interior, shrubland or edge, neither interior nor shrubland) is shown for species responses to forest canopy cover.

ment and temperature, and most of these species showed reduced occurrence as building density increased.

Our results suggest that expanding exurban development in the southern Appalachians will affect the occurrence of many bird species. In our study area, overall forest cover has increased and become less fragmented since the early 20th century (Wear & Bolstad 1998; Turner et al. 2003) due to reduction in agricultural land uses and regrowth of forests (Gragson & Bolstad 2006). Since 1970, forest cover has declined in localized areas near cities and towns, associated with increased human populations and economic development, but continued to increase in rural and exurban zones. Moreover, the building density increased in forested habitats in late 20th century as more residents chose to live in houses built in the forests (Turner et al. 2003). The general trend of increasing forest cover and reduced forest fragmentation should

benefit forest wildlife, but our results suggest that the effects on these species can be complicated. We observed lower occurrences of forest interior and Neotropical migrants with increased building density, which suggests that exurban development without forest loss, could contribute to a decline in sensitive bird species via fragmentation or degradation of habitats in these heavily forested landscapes.

Shrubland or edge species would be expected to benefit from forest openings created by residential development, but that trend was not consistent on the basis of our data. These species were less abundant as forest canopy cover increased, but only 3 of 11 species increased as building density increased. However, responses by species in this group varied widely. Several resident species decreased as canopy cover increased (e.g., Northern Cardinal [*Cardinalis cardinalis*], Eastern Towhee, Cedar Waxwing [*Bombycilla cedrorum*], Chipping Sparrow [*Spizella passerina*], Mourning Dove [*Zenaida macroura*]) (Table 2). The responses by shrubland or edge and generalist species likely depend on the type of nonforest habitat created. Lawns, pastures, and shrub or scrub habitats favor different bird species. For example, Chestnut-sided Warbler and Indigo Bunting, 2 species that occupy dense shrubby areas usually not associated with residential development, declined in occurrence as building density increased, whereas House Wren (*Troglodytes aedon*), American Robin, and American Goldfinch (*Carduelis tristis*) increased (Table 2). These latter 3 species benefited from lawns and ornamental plants associated with buildings. The American Robin responded positively to increases in both building density and canopy cover. Our results are consistent with a growing understanding that forest edges are not optimal habitat for all shrubland birds. Many species require a minimum area of shrub habitat and actively avoid forest edges (Rodewald & Vitz 2005; Schlossberg & King 2008).

The effects of exurban development depend on the specific habitat alterations associated with the construction and maintenance of residential dwellings and roadways. Landowners may modify habitat structure and species composition in forests on their property by removing natural vegetation, altering vegetative structure, and adding new plant species. For example, one practice common to high-elevation areas within the study region is to remove shrub and subcanopy vegetation when it impedes scenic views. This practice will reduce the occurrence of bird species that require well-developed shrub layers for nesting habitat. In our study, forest canopy cover, measured within 200 m of each study site, had a relatively small effect on bird species. It is possible that other vegetation characteristics or scales of measurement are more important for explaining bird occurrence.

Collectively, our results suggest that exurban development accompanied by extensive forest clearing will likely result in an increase in some shrubland or edge and generalist species and a decline in interior forest and Neotropical migrant species. In contrast, buildings constructed within the forest, without extensive clearing, will still cause declines in forest interior and Neotropical migrant species without benefitting shrubland or edge species. This result is consistent with the results of several studies that suggest that building presence degrades the surrounding forest habitat (Friesen et al. 1995; Odell & Knight 2001). It is important to consider building presence in conservation strategies for interior and Neotropical species because the effect of building density was stronger than any other variables we measured. Clustering houses may be a useful strategy for mitigating the effects of exurban development because this housing arrangement reduces the area of forest habitat with building effects (Theobald et al. 1997; Odell et al. 2003).

Changes in the climate of the southern Appalachian Mountains are likely to affect the occurrence of bird species. Although our study included direct measurements of temperature only (not precipitation), our data can inform predictions about the response of birds to changing climates in this region. Worldwide, changing climates are correlated with latitudinal and altitudinal range shifts by a variety of species (Chen et al. 2011). Mean temperature had a positive association with species with a southerly range (Fig. 3); therefore, southern species are likely to increase in occurrence and their ranges may expand into higher elevations if the region warms (Sekercioglu et al. 2008). Northerly species associated with cooler temperatures will likely decline in occurrence or could disappear entirely from the southern Appalachians as their ranges shift northward (Hitch & Leberg 2007). In mountainous terrain, northern species are expected to shift their breeding grounds upslope with a warming climate (Chen et al. 2011). However, the total area of available habitat declines with increasing elevation because mountaintops occupy less area than their slopes and bases. Management strategies for reducing the negative effects of climate change rely on understanding species' responses to climate (Pearce-Higgins et al. 2011) and land cover. Our data show that forest interior and Neotropical species were most sensitive to building density. Therefore, these species, which were more common at higher elevations, will receive the greatest benefits from management strategies aimed at controlling the spatial distribution of exurban development and preserving forest interior habitats.

Predation may be an important mechanism through which exurban development and temperature gradients affect bird species occurrence. Nest predation is the cause of most nest failure (Wilcove 1985), and corvids, including the American Crow and Blue Jay, commonly act as nest predators (Chalfoun et al. 2002; Cox et al. 2012). Our results showed that Blue Jays increased in

occurrence with mean temperature, and American Crows increased with building density and mean temperature (Table 2). Lumpkin et al. (2012) found that nest predation rates increased at warmer, low-elevation sites and as building density increased. They documented predation by corvids and a variety of mammal species. The occurrence of domestic predators, such as house cats (*F. catus*) and dogs (*Canis lupus familiaris*), also increases as the proximity to houses increases (Odell & Knight 2001; Lumpkin et al. 2012). Finally, landowner modifications to vegetation may affect risk of nest predation. For example, Borgmann and Rodewald (2004) found nest predation risk is higher in invasive shrubs than in native shrubs. Thus, expanding exurban development and warming climate may result in an increase in avian nest predators and, in turn, an increase in risk of nest predation.

Projections indicate that both land use and climate will be important drivers of change within the southern Appalachian Mountains (Wear & Bolstad 1998; Mearns et al. 2003), and a better understanding of the joint effects of these changes is needed. In Europe, climate change has become more important in explaining bird populations than land-use change over the last few decades (Lemoine et al. 2007). Increases in exurban development will reduce the occurrence of many interior forest and Neotropical migrant species. Although shrubland or edge species can benefit from forest fragmentation, these birds may not necessarily benefit from increasing building density without extensive clearing. Our results indicate that the negative effects of exurban development will be greater at cooler, higher elevations because sensitive species, including Neotropical migrants and forest-interior birds, are more common at those sites. These species will also be negatively affected by the climate warming projected for the southern Appalachians, and warming may serve to exacerbate the effects of increasing exurban development.

Acknowledgments

Supporting Information

A list of all 77 species detected (Appendix S1) and a list of top models for individual species (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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