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Microhabitat Factors Associated with Occupancy of Songbirds in Suburban Forest Fragments in the Eastern United States

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ABSTRACT.—Forests in the eastern United States have become fragmented by urban development and agriculture, creating a landscape of remnant forest patches. Many bird species rely on these fragments for breeding habitat, but habitat selection in these patches is not well-understood. Our objective was to examine the effects of forest structure, native plants, and invertebrate biomass on the occupancy of an assemblage of common Eastern songbird species in suburban forest fragments. We collected data at 98 plots in remnant forest patches in Delaware and Maryland. Avian point counts were conducted three times per season between 15 May–7 August 2009–2010. We estimated occupancy probability, while accounting for imperfect detection, for nine common songbird species in order to understand how they are influenced by invertebrate biomass and vegetation characteristics. We ranked competing models using Akaike Information Criteria (AIC). Occupancy of six of our 10 candidate species was affected by forest structure, native plant density, or invertebrate biomass. Species we identified to have occupancy relationships with forest structure variables in suburban forest fragments appear to align well with habitat relationships that have been previously identified for the species in more forested areas. This supports that managing for structural characteristics associated with these species in more heavily forested areas could improve habitat quality for these species in suburban forest fragments as well. Occupancy of only one species we examined was related to native plants, suggesting vegetation structure, rather than composition, was a more important factor in occupancy.

INTRODUCTION

Forest cover in the eastern United States has been fragmented by suburban development and agriculture (Zhou *et al.,* 2011), creating a landscape of remnant forest patches surrounded by a matrix of varying land uses (Saunders *et al.*, 1991). The structural characteristics of remnant forest patches are different from those of nonfragmented patches (Saunders *et al.,* 1991; Harper *et al.,* 2005). The impacts of fragmentation on forest structure can extend up to 75 m into a patch and can include decreased canopy coverage, increased understory tree density, increased shrub abundance, and increased herbaceous cover (Harper *et al.,* 2005). In addition to these impacts, suburban development at forest edges may decrease understory vegetation through increased mowing or habitat alteration (De Chant *et al.,* 2010).

Fragmentation, which results in an increase in the amount of edge, typically causes remnant forest patches to have high levels of invasion by nonnative plants. Densities of nonnative invasive plants are often highest along forest edges (Yates and Levia, 2004; Harper *et al.,* 2005), and this effect may be exacerbated along edges of suburban habitat that can act as sources of invasive plants via horticultural plantings (Lussier *et al.,* 2006). As nonnative

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plants have been shown to be unpalatable to many invertebrate herbivores, a dominance of nonnative plants could cause a decrease in native arthropod biomass (Tallamy *et al.,* 2010). Therefore, the replacement of native plants with nonnative invasives may trigger a trophic cascade (Paine, 1980) and lead to reduced availability of invertebrate prey for higher trophic levels in forest fragments (Cripps *et al.,* 2006; Gerber *et al.,* 2008; Wu *et al.,* 2009; Yoshioka *et al.,* 2010).

Many Eastern forest bird species rely on remnant forest patches as the only breeding habitat available in the landscape (Tilghman, 1987; Melles *et al.,* 2003). Populations of many Eastern forest birds have declined steadily over the last 40 y (Sauer *et al.,* 2014), and efforts to reverse these trends likely need to include management of remnant forest patches as breeding habitat for forest birds. However, effective management of remnant forest patches requires an understanding of how birds occurring in suburban forest fragments are affected by microhabitat factors such as forest structure, nonnative plants, and invertebrate biomass. While there are known differences in microhabitat factors in remnant forest patches such as forest structure (Saunders *et al.,* 1991; Harper *et al.,* 2005), nonnative plant densities (Yates and Levia, 2004; Harper *et al.,* 2005), and invertebrate biomass (Burke and Nol, 1998; Zanette *et al.,* 2000; Doyle 2008) it is not known how these factors influence occupancy of birds in suburban forest fragments. Therefore, our objective was to examine the effects of these factors on nine species of common songbirds. Results may be used to guide habitat management and restoration of remnant forest fragments.

STUDY AREA

Our study was conducted in Delaware and Maryland, U.S.A. in upland and riparian mature forest patches located in White Clay Creek State Park (39°43′19.40″, 75°45′41.77″), Fair Hill Natural Resources Management Area (39°41′51.35″, 75°50′08.82″), University of Delaware Ecology Woods (39°39′49.09″, 75°44′47.73″), Iron Hill Park (39°37′58.7742″, 75°45′25.3362″), St. Andrew's School (39°25′56.67″, 75°41′13.56″), Mount Cuba Center (39°47′18.19″, 75°38′56.97″), Red Clay Creek within Brandywine State Park (39°48′21.57″, 75°34′22.66″), and Ashland Nature Center (39°47′50.99″, 75°39′32.54″) (Fig. 1). Sampling plots were randomly placed within these seven natural area complexes using the Hawths Tools extension for ArcGIS 9.2 (Beyer, 2004). The tool was used to generate the maximum possible number of sampling locations within each natural area that were located in mature forest 25 m from a forest edge and separated from another point by at least 250 m. There were 30 sampling plots within White Clay Creek State Park, 39 within Fair Hill Natural Resources Management Area, four within University of Delaware Ecology Woods, five at St. Andrew's School, five at Iron Hill Park, and 15 points within the complex consisting of Mount Cuba Center, Red Clay Creek State Park, and Ashland Nature Center. Patches were highly linear and often interconnected making it difficult to determine number of sampling locations per forest patch. Across all natural area complexes, forest patches containing sampling plots varied in width from 52 m to 1388 m with an average width of 415.75 m (SE = 31.13 m).

The native land cover of the area is a mix of hardwood species including northern red oak (*Quercus rubra*), white oak (*Q. alba*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sycamore (*Platanus occidentalis*), and yellow poplar (*Liriodendron tulipifera*) (Heckscher, 2004). The land use in the surrounding landscape includes both agricultural and residential properties (Conover, 2011). Nonnative plants present in the study areas include, but are not limited to: autumn olive (*Elaeagnus umbellate*), garlic mustard (*Alliaria petiolata*), Japanese barberry (*Berberis thunbergii*), Japanese honeysuckle (*Lonicera japonica*), Japanese stilt grass (*Microstegium vimineum*), Norway maple (*Acer platenoides*), oriental

FIG. 1.—Map of study area in Maryland and Delaware, U.S.A. Shaded areas indicate forested patches within study areas. Black circles denote study plots where point counts for birds, vegetation sampling, and vacuum sampling for invertebrates were conducted from 15 May–7 August 2009–2010

TABLE 1.—Nine forest songbird species selected for occupancy analysis using data collected during point count surveys in Delaware and Maryland, U.S.A., from 15 May–7 August 2009–2010

Species	Scientific Name
Wood Thrush	*Hylocichla mustelina*
Ovenbird	*Seiurus aurocapilla*
Eastern Towhee	*Pipilo erythrophthalmus*
Carolina Wren	*Thryothorus ludovicanus*
Northern Cardinal	*Cardinalis cardinalis*
Gray Catbird	*Dumetella carolinensis*
American Robin	*Turdus migratorius*
Red-eyed Vireo	*Vireo olivaceus*
Carolina Chickadee	*Poecile carolinensis*

bittersweet (*Celastrus oriculatus*), multiflora rose (*Rosa multiflora*), and wineberry (*Rubus phoenicolasius*).

METHODS

AVIAN SURVEYS

We sampled 98 plots in seven natural area complexes for the presence of forest songbirds (Fig. 1). Sample plots were located in mature forest 25 m from a forest edge and were randomly placed within selected forest patches using the Hawths Tools extension for ArcGIS 9.2 (Beyer, 2004). We separated plots by 250 m to minimize the likelihood that individual birds would be double counted between sample plots (Bibby and Burgess, 2000). At each of the 98 sampling plots, we conducted 25 m radius avian point counts to estimate occupancy (Bibby and Burgess, 2000). The use of small radius plots allowed for the measurement of vegetation characteristics in close physical proximity to locations of birds, increasing the accuracy of resulting bird-habitat relationships (Ralph *et al.,* 1995). This sampling method does not account for landscape-scale factors such as percent forest cover. However, as these factors were not the focus of this study, the natural area complexes containing our sampling plots were selected to have high overlap at a landscape scale to limit difference between sampling plots at a landscape level.

We conducted point counts three times per summer between 15 May–7 August in 2009 and 2010. Each point was visited on a randomly selected day between 15 May–15 June, 16 June–15 July, and 16 July–7 August. A single observer (AMD) was trained to identify Eastern forest bird species by sight and sound and conducted all point counts across both seasons.

We selected an assemblage of Eastern songbird species that commonly forage on invertebrates, including within our surveyed vegetation zone of $\leq$2 m above the ground (De Graaf *et al.,* 1985; Table 1). We conducted point counts between 15 min before sunrise and 5 h after sunrise, with >96% of the surveys taking place between sunrise and 4 h after sunrise. Surveys were only conducted on precipitation-free days when the wind speed was <6.5 km/hr. At each plot, we recorded the date, time, and temperature, and estimated percent cloud cover. Time, date, percent cloud cover, and temperature were recorded for use as detection covariates, as these factors influence the probability that a bird was detected during a survey if it was present at a site (MacKenzie *et al.,* 2006). A 1 min acclimation period of minimal observer movement preceded each survey to minimize effects from observer disturbance (Buckland *et al.,* 2001; Rosenstock *et al.,* 2002). Following the acclimation period, we

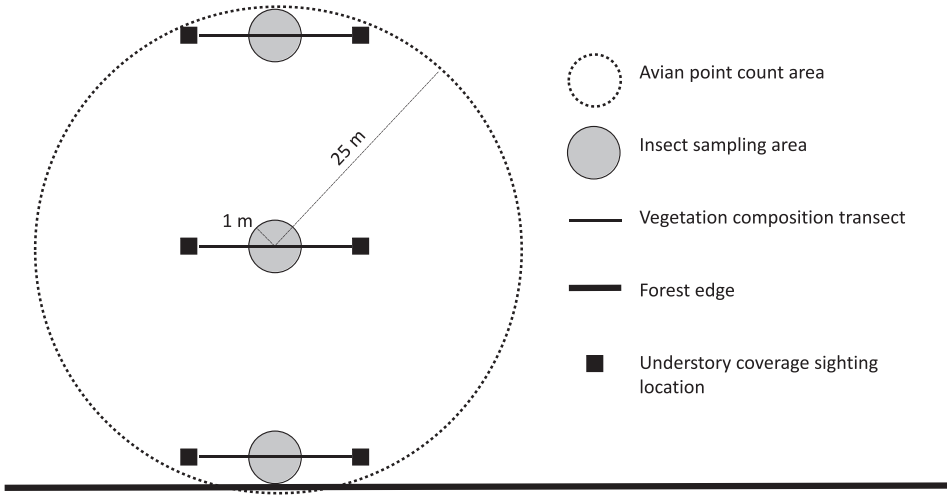

FIG. 2.—Design of study site for avian and vegetation surveys and invertebrate sampling within Delaware and Maryland, U.S.A., forest fragments, 15 May–7 August 2009–2010

recorded all birds seen or heard within the survey area during a 5 min period of passive observation.

VEGETATION CHARACTERISTICS

Within each 25 m radius plot, we measured a number of environmental variables for use as site covariates. We assumed vegetation structure and composition were constant across sampling years and sampled vegetation only in 2009. We sub-sampled vegetation at distances of 0 m, 25 m, and 50 m from the forest edge (Fig. 2). At each distance we measured understory coverage via a Vegetation Profile Board (Nudds, 1977). The board is marked in alternate colors (red/white) and set in the ground and viewed from two cardinal directions (parallel to the forest edge) from a distance of 10 m. The proportion of each ½ m interval covered by vegetation is recorded as single digit between one and five, allowing for the calculation of an average density for each vertical layer of vegetation. We also measured basal area with a 10 factor prism and canopy coverage with a densiometer (Strickler, 1959). We recorded vegetation composition along a transect 5 m in length and 15 mm in width running parallel to the forest edge at 0 m, 25 m, and 50 m from the forest edge. We identified all understory vegetation $\leq$ 2 m in height intersecting each transect (where focal avian species commonly forage on invertebrates; De Graaf *et al.,* 1985; Williamson, 1971). We identified plants to species (plants from the genera *Rubus* and *Trifolum* were only identified to genus) and as native or nonnative species. Due to difficulty in identification, the terms "ferns" and "grasses" were used to indicate all species within these groups, which were excluded from calculations of native species proportion. The proportion of native plants at each site was calculated by dividing the number of decimeter sections of the 5 m transects that contained at least one native plant by the number of sections that contained any vegetation, either native or nonnative. The proportions calculated for the transects at the forest edge, 25 m from the forest edge, and 50 m from the forest edge at each point were averaged to obtain a value of native plant proportion for each sample plot. Nonvegetated

ground at each site was calculated by dividing the number of decimeter sections of the 5 m transects that did not contain any vegetation by the total number of decimeter sections of the transect (50). The proportions calculated for the transects at the forest edge, 25 m from the forest edge and 50 m from the forest edge at each point, were averaged to obtain a value of nonvegetated ground for each sample plot.

Invertebrate sample collection

We collected 588 vacuum samples for invertebrates within the 98 plots at three points per site each year during June and July, for a total of six samples over the 2 y. We sampled for invertebrates within three 1 m radius circles at the center of the same transects used for the vegetation surveys, totaling 6.28 m^3 per plot. We vacuum sampled vegetation for invertebrates using a leaf blower (Craftsman 25cc Gas Blower/Vac Model #358794740) in the vacuum setting and fitted with a nylon mesh paint strainer bag. A single technician performed all vacuum sampling to minimize the effects of sampling technique. Following sampling, we searched the vegetation for any remaining Lepidoptera larvae. Specimens were frozen at –10 C in plastic zip-top bags before being sorted to retain invertebrate taxa known to be preferred breeding songbird foods (Martin *et al.,* 1951). These taxa include the orders Orthoptera, Hemiptera, Coleoptera, Lepidoptera, Araneae, Opiliones, Hymenoptera, Diptera, and Isopoda, and the classes Gastropoda and Diplopoda. To determine biomass, we dried samples at 55 C for $\geq$48 h and weighed them to the nearest 0.0001 g.

Statistical analysis

We used the single season habitat occupancy modeling approach of MacKenzie *et al.,* (2006) for the nine songbird species to examine bird habitat selection. This approach predicts the probability of a site being occupied and at least one individual being detected during the survey using site and survey specific variables (MacKenzie *et al.,* 2006). Our models included the site covariates native plant proportion (native), understory coverage (uc), canopy coverage (canopy), basal area (basal), and invertebrate biomass (inverts), which were consistent over the duration of the season. A $\log_{10}$ transformation was applied to insect biomass data and a square-root transformation was applied to basal area and nonvegetated ground data to meet the assumptions of normality and homoscedasticity. All means and 95% confidence intervals are reported as back-transformed values. Survey covariates, which changed between repeat visits, included time since sunrise (time), number of days since start of survey period (day), temperature (temp), and cloud cover (clouds) for each avian survey.

We used the 'unmarked' package in program R (Fiske and Chandler, 2011; R Development Core Team, 2010) to model single-season occupancy for candidate species. The models were evaluated using Akaike Information Criterion (AIC) to determine the most parsimonious model (MacKenzie *et al.,* 2006). We first modeled detection of each individual species using the survey covariates (date, temperature, minutes since sunrise, and cloud cover) and constant occupancy to determine the variables influencing detection of the species. For each species, every single-variable detection model was considered, as well as a null model where detection was constant, and a global model containing all detection variables. Detection models with ΔAIC values > 2 were rejected due to a lack of empirical support (Burnham and Anderson, 2002). If multiple detection models had ΔAIC

TABLE 2.—Covariate models used to analyze occupancy of 9 forest songbird species in Delaware and Maryland, U.S.A., from 15 May–7 August 2009–2010

Model	Covariate(s)
null	None
global	All
native	Native Plant Proportion
canopy	Canopy Cover
basal	Basal Area
inverts	Invertebrate Biomass
non-veg	Nonvegetated Ground
uc	Understory Coverage
native+uc	Native Plant Proportion, Understory Coverage
native+inverts	Native Plant Proportion, Invertebrate Biomass
native+non-veg	Native Plant Proportion, Nonvegetated Ground
canopy+non-veg	Canopy Coverage, Nonvegetated Ground
canopy+uc	Canopy Coverage, Understory Coverage
basal+uc	Basal Area, Understory Coverage
non-veg+uc	Nonvegetated Ground, Understory Coverage

values ≤ 2, the higher ranked model of either the null or global model was selected for the species.

To reduce our model set, we incorporated the best supported model(s) of detection for each species into an *a priori* set of occupancy models, including single-variable models of all site covariates, a selected set of two-variable models representing biologically meaningful interactions, a null model where occupancy was considered constant, and a global model with all site covariates (Table 2). Again, models with a $\Delta AIC > 2$ were rejected (Burnham and Anderson, 2002). Variance-covariance matrix or model convergence errors, were resolved by providing different initial values or fixing the beta value for certain parameters. The beta value for each variable was used to assess whether a variable was significantly related to the occupancy of a species, and whether the variable was positively or negatively related to species occupancy. The relationship was considered nonsignificant if the 95% confidence interval for the beta value contained zero.

RESULTS

Naïve occupancy estimates for the candidate species at our study plots ranged from 45.9% to 81.6%. Naïve occupancy rates were calculated simply as the percentage of plots where each species was detected during at least one visit and do not account for imperfect detection. Modeled occupancy rates accounted for factors which affected the probability of detecting a species during a visit if it is present at the site. The modeled occupancy rates of the candidate species at study plots based on the best-supported model of detection for each species ranged from 65.8% to 96.7% (Table 3).

We observed 94 species of plants during vegetation surveys (Conover, 2011), with 78.7% considered native to the study region (U.S. Department of Agriculture, 2011). Vegetation composition and forest structure measurements varied across study points (Table 4).

Invertebrate sampling yielded 12,108 individuals and 18.69 g of preferred breeding songbird foods. Total invertebrate biomass collected from each invertebrate sampling point in 2009 ranged from 0.018 g/m^3 to 0.12 g/m^3 (mean = 0.049, 95% CI [0.046, 0.052]). In

TABLE 3.—Occupancy rates of nine forest songbird species during point count surveys at 98 sites in Delaware and Maryland, U.S.A., from 15 May–7 August 2009–2010. Naive occupancy estimates calculated as the percentage of study sites where the species was detected. Predicted occupancy estimates and associated standard errors (SE) incorporate imperfect detection using the best-supported detection model for each species

Species	Number of plots with species detected	Naive occupancy estimate (%)	Predicted occupancy estimate (%) ± SE	
Red-eyed Vireo	80	81.6	96.7	0.06
Gray Catbird	80	81.6	82	0.04
Northern Cardinal	73	74.5	88.3	0.06
Wood Thrush	72	73.5	87	0.06
Eastern Towhee	70	71.4	79.6	0.05
Carolina Chickadee	57	58.2	84.2	0.1
American Robin	52	53.1	65.2	0.07
Carolina Wren	49	50	84.3	0.14
Ovenbird	42	42.9	65.8	0.1

2010 total invertebrate biomass collected from each invertebrate sampling point ranged from 0.022 g/m^3 to 0.18 g/m^3 (mean = 0.053, 95% CI [0.050, 0.056]).

Time of day was a significant factor influencing detection of six of the songbird species (Table 5). Of the 13 models included in our *a priori* set to model occupancy, nine were top-ranked models for at least one of the songbird species (Table 6). Null models were included in the top models of occupancy for six species, ovenbird (*Seiurus aurocapilla*), Northern cardinal (*Cardinalis cardinalis*), Eastern towhee (*Pipilo erythrophthalmus*), Carolina chickadee (*Poecile carolinensis*), red-eyed vireo (*Vireo olivaceus*), and Carolina wren (*Thryothorus ludovicanus*). Of these species Eastern towhee, ovenbird, and Carolina chickadee did not show significant relationships between occupancy and any variables we examined.

Nonvegetated ground appeared in the top models for four species, more than any other variable. It was positively related to occupancy in Northern cardinal and American robin (*Turdus migratorius*) and negatively related to gray catbird (*Dumetella carolinensis*) occupancy. Proportion of native plants was the next most common variable, appearing in the top-ranked models for three species. However, the only significant relationship was in the occupancy of Carolina wren, which was positively related to the variable. Basal area also appeared in the top-ranked models for three species and had a significant positive relationship with only one species, wood thrush (*Hylocichla mustelina*).

TABLE 4.—Vegetation composition and forest structure covariates measured at study sites in June 2009 for use in developing occupancy models of nine forest songbird species in Delaware and Maryland, U.S.A. Means and 95% confidence intervals of the means are reported as back-transformed values

Variable	Minimum value	Maximum value	Mean (95% CI)
Native Plant Proportion	0	1	0.616 (0.613, 0.619)
Basal Density (m/ha)	0.82	11.08	5.25 (4.85, 5.66)
Canopy coverage	66.02%	97.57%	87.54% (87.47%, 87.61%)
Non-vegetated ground	0%	62.66%	16.70% (13.69%, 20.25%)
Understory coverage	4.17%	75.69%	40.34% (40.16%, 40.52%)

TABLE 5.—Top ranked models of variables affecting detection of nine forest songbird species during point count surveys in Delaware and Maryland, U.S.A, from 15 May–7 August 2009–2010. Table presents the difference in Akaike's Information Criterion value compared to the top-ranked model (ΔAICc), the AIC model weight (W), and the number of parameters in the model (K). Global models contain all detection covariates. Models selected for use in modeling occupancy shown in bold

Species	Model	ΔAICc	W	K
Gray Catbird	**time**	0	0.6524	3
Northern Cardinal	time	0	0.3286	3
	null	0.76	0.2247	2
Wood Thrush	**temp, time**	0	0.3306	4
	time	0.67	0.2365	3
Eastern Towhee	clouds, temp	0	0.3796	4
	temp	0.54	0.2898	3
	global	1.78	0.1559	5
Carolina Chickadee	Time	0	0.7229	3
	global	1.92	0.2768	5
American Robin	**null**	0	0.2604	2
	clouds	0.37	0.2164	3
	temp	1.1	0.1502	3
	time	1.85	0.1032	3
Carolina Wren	**null**	0	0.3978	2
Red-eyed Vireo	time	0	0.3999	3
	global	0.31	0.3416	5
	temp	1.22	0.2172	3
Ovenbird	**time**	0	0.2168	3
	temp	1.05	0.1283	3

time: time since sunrise; temp: air temperature; clouds: cloud cover

AIC model weight (W) indicates the strength of evidence of each model relative to other models in the set of models considered

Canopy coverage and invertebrate biomass each appeared in the top-ranked models for one species, American robin and Carolina wren respectively, and each were positively related to the occupancy of that species. Understory coverage did not appear in the top-ranked models for any of the songbird species.

DISCUSSION

Occupancy of six of our nine songbird species in suburban forest fragments was affected by forest structure, native plant density, or invertebrate biomass. Percentage of nonvegetated ground had a significant relationship with the occupancy of more of our songbird species than any other variable, including gray catbird, Northern cardinal, and American robin. Gray catbird was the only species that had a negative relationship with the variable, indicating the species prefers sites with increased ground coverage. Occupancy of American robin and Northern cardinal were positively related to percentage of bare ground, indicating these species prefer sites with a more open understory. However, none of the species showed a relationship with understory coverage, suggesting they are responding to the presence of vegetation cover closest to the ground (measured by percentage of nonvegetated ground), rather than vegetation density within the entire understory up to 2 m (measured by understory composition). A relationship between abundance and vegetation

TABLE 6.—Models of variables affecting probability of occupancy of 8 forest songbird species during point count surveys in Delaware and Maryland from 15 May–7 August 2009–2010. Table presents the difference in corrected Akaike's Information Criterion value compared to the top-ranked model (ΔAICc), the AIC model weight (W), the number of parameters in the model (K), and the slope and standard error of the relationship between the variable and occupancy (β (SE))

Species	Model	ΔAICc	W	K	β (SE)
Gray Catbird	non-veg	0	0.7995	11	−5.92 (1.84)
Northern Cardinal	null	0	0.3877	8	
	non-veg	1.08	0.2258	11	3.84 (2.63)
	native	1.53	0.1806	11	4.44 (5.06)
Wood Thrush	basal	0	9.80E−01	11	3.16 (1.59)
Eastern Towhee	null	0	5.30E−01	8	
Carolina Chickadee	null	0	0.49892	8	
American Robin	canopy	0	0.50354	11	11.10 (5.43)
	canopy+non-veg	0.35	0.42281	14	10.93 (5.90), 3.25 (1.83)
Red-eyed Vireo	inverts	0	4.20E−01	11	2.49 (1.59)
	null	1.47	2.00E−01	8	
Carolina Wren	native	0	0.2341	11	2.193 (2.08)
	null	0.25	0.20667	8	
	inverts	0.31	0.20084	11	62.2 (87.5)
	basal	0.38	0.19325	11	14.2 (34.9)
Ovenbird	basal	0	2.90E−01	11	1.81 (3.10)
	native	0.36	2.40E−01	11	−0.024 (1.96)
	non-veg	0.63	2.10E−01	11	1.57 (2.06)
	null	1.96	1.10E−01	8	

native: native plant proportion; inverts: invertebrate biomass; canopy: canopy coverage; basal: basal area; non-veg: non-vegetated ground; time: time since sunrise; temp: air temperature; clouds: cloud cover

density has been identified in previous studies for gray catbirds (Lent, 1990), American robins (Blake and Karr, 1987), and northern cardinals (Leston and Rodewald, 2006), although our results distinguish the importance of cover specifically in lowest part of the understory for these species in suburban forest fragments.

We found basal area to be the most significant factor influencing occupancy of wood thrush in suburban forest fragments. Wood thrush occupancy was positively associated with basal area, a relationship that has also been well documented for this species in contiguously forested areas (Wang *et al.,* 2006**,** Sargent *et al.,* 2003**,** Annand and Thompson III, 1997). Our results provide support that occupancy relationships with forest structure for wood thrush within suburban forest fragments align with those in areas of more contiguous forest cover.

Two foliage gleaning species, red-eyed vireo and Carolina wren were the only species found to have positive associations with either native plants or invertebrate biomass. Given the implications of the replacement of native plants by nonnative invasive species on the availability of invertebrate prey for avian insectivores in forest fragments, a positive relationship between the occupancy of foliage gleaning species and native plants may indicate selection of habitats offering a greater abundance of invertebrate prey. If native plants are providing a greater abundance of invertebrate prey for foliage gleaners, a positive relationship would then be expected between the occupancy of these species and invertebrate biomass at a site. Results of a study of bird occupancy along a gradient of urban development in California recorded increasing numbers of foliage gleaning species as

the level of urbanization decreased, a relationship the author attributed to low insect densities in the urban areas dominated by nonnative plants (Rottenborn, 1999).

While a positive correlation between invertebrate biomass and occupancy of all insectivorous species would be expected, this finding for only one species in our study is likely due to an alignment between the primary foraging substrate of the red-eyed vireo and the most effective range of our invertebrate sampling method. Red-eyed vireos forage most commonly among live leaves and twigs near branch ends (Barrow, 1990), from which invertebrates would have been effectively sampled using our vacuum sampling technique (Doxon *et al.,* 2011). However, we did not sample the leaf litter, soil, or air column for invertebrates. If birds were responding to invertebrates that were not sampled, vacuum-sampled invertebrate biomass values may not be an accurate measure of the entire avian food supply within sampling plots. In future studies litter collection and a wider variety of insect sampling techniques may provide a more accurate assessment of the availability of invertebrate biomass at our sites for species with varying foraging strategies.

Eastern towhee, ovenbird, and Carolina chickadee occupancy did not show significant relationships with any variables we examined. The null model was well-supported for each of these species, suggesting they were responding to variables outside the scope of this study. The occupancy of all our songbird species was likely influenced by unmeasured factors in the suburban landscape, including surrounding land use and forest patch size. Previous work examining factors influencing avian species richness in remnant habitat patches within suburban development has found while forest structural characteristics contribute to determining bird species richness, landscape-scale factors, including patch size, were also significant determinants of avian species richness (Palmer *et al.,* 2008; Melles *et al.,* 2003).

Overall, the occupancy relationships with forest structure variables we identified for our songbird species in suburban forest fragments aligned well with those previously identified in studies examining habitat use in more forested areas. This supports management activities encouraging forest structural characteristics associated with these species in more heavily forested areas could improve habitat quality for these species in suburban forest fragments as well. However, our study was a micro-scale analysis of the habitat factors influencing bird occupancy at the site level, and some of our selected species appeared to be responding primarily to factors outside the scope of this analysis. With this in mind, it is important to also consider the role of landscape-scale factors before planning the management of suburban forest fragments.

Only one species had a significant relationship with native plants, suggesting for the species we examined, vegetation structure, rather than composition is a more important factor in occupancy. However, if the replacement of native plants with nonnative invasives does lead to reduced availability of invertebrate prey, the impacts of this trophic breakdown may not be easily detected using occupancy analysis. Species may be selecting for the vegetation structure offered by native plants, while suffering fitness impacts from a lack of invertebrates in these patches. Further study of fitness impacts such as nest success is needed to fully understand how best to manage suburban forest fragments as habitat for songbirds.

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