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Non-native shrubs and calcium availability are important for birds breeding in urban forests

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Abstract

Global increases in urbanization requires us to better understand how species are adapting to novel ecosystems in urbanized environments. We conducted a multi-year study to compare how five bird species with different life history strategies responded to local- and landscape-scale factors within forests in an urbanizing landscape. We modeled the responses of species to factors that have been shown to influence habitat selection for forest breeding birds including soil, vegetation, food quality and availability, and land cover. We found that, within an urbanized landscape, local-scale variables related to Ca prey availability and vegetation cover explained variation in territory density for the five bird species. Specifically, territory density for Carolina Wren (*Thryothorus ludovicianus*), Eastern Towhee (*Pipilo erythrophthalmus*) and Gray Catbird (*Dumetella carolinensis*) were positively related to non-native shrub cover and Carolina Chickadee (*Poecile carolinensis*), Eastern Towhee, and Wood Thrush territory density were positively related to calcium rich prey availability. These results suggest that species-specific responses to vegetation structure and nutrient composition are important factors for habitat selection of birds within urban forests.

Keywords Avian territory · Calcium · Forest · Non-native · Soil, urban

Introduction

Important aspects of breeding bird habitat selection are influenced by scale-dependent characteristics of landscape (i.e., surrounding a habitat patch) and local (i.e., within habitat patch) factors which can affect species differentially depending, to some extent, on species' life history strategies (Wiens 1989). Disentangling how breeding birds in urban forests respond to scale-dependent factors is important for determining best management practices for maximizing benefits to local biodiversity conservation within existing forest habitat remnants. Landscape-scale factors like patch size (Dunning et al. 1992; Graham and Blake 2001; Suarez-Rubio and Thomlinson 2009), road density (Reijnen and Foppen 1995; Shriver et al. 2004), and land cover types (Hinsley et al. 1998; Bennett et al. 2004) surrounding a patch have been shown to influence breeding birds among different landscapes. However, in urbanized and fragmented landscapes where all patches are generally small and the surrounding land cover is human dominated, our understanding of how these factors influence the bird community is less clear. Maseko et al. (2020), found that the breeding bird community metrics they assessed in a fragmented landscape in South Africa were best explained by patch size and habitat area but this study did not compare these landscape-scale factors with local or within patch scale factors. Here, we were specifically interested in determining how within patch factors, like vegetation structure and food availability competed against landscape-scale factors like patch size and the surrounding landscape land cover.

Local factors have been shown to influence breeding bird habitat selection. Specifically, vegetation structure and composition have long been known to influence bird habitat selection (MacArthur and MacArthur 1961; Greenberg et al. 1997), and invasions by non-native plants can alter vegetation and therefore, influence breeding bird habitat selection (Saunders et al. 1991; Remeš 2003; Borgmann and Rodewald 2004; Gleditsch and Carlo 2014). Non-native

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invasive shrubs, such as multiflora rose (*Rosa multiflora*) and Japanese honeysuckle (*Lonicera japonica*) form dense understories in urban forests (Morse and Robinson 1999) which can benefit some breeding birds by providing vegetation structure available for nesting (Rodewald et al. 2009). Additionally, there is some evidence that non-native understory plants may not necessarily be maladaptive choices for nesting substrates (Meyer et al. 2015; Gleditsch 2017), and in some cases, can provide food in the form of fruits for breeding birds (Gleditsch 2017). Alternatively, non-native plants may reduce site fidelity (Ortega et al. 2006), reproductive success (Remeš 2003; Ortega et al. 2006; Rodewald et al. 2009), and territory density (Scheiman et al. 2003) for some breeding bird species (Pickett et al. 2011).

Non-native invasive plants have been shown to influence soil chemistry dynamics including important soil constituents important for breeding birds, such as calcium. Calcium availability can be a limiting factor in forest breeding bird fledging success (Graveland and Drent 1997), range-wide species declines (Hames et al. 2002), and territory densities associated with acidified soils (Pabian and Brittingham 2007, 2011). Calcium is acquired by breeding birds foraging on calcium rich arthropods and snails (Graveland and van Gijzen 1994; Blum et al. 2001), and the availability of calcium rich prey sources varies throughout forested ecosystems (Hames et al. 2002; Pabian and Brittingham 2007, 2011). However, calcium availability has yet to be assessed as a driver of avian community assembly in urban forests.

Food availability for successfully raising offspring in urban environments can also influence breeding birds and may be a factor in habitat selection for some species (Narango et al. 2017). Breeding birds depend on arthropod biomass, especially larval Lepidoptera (Cooper 1988), which varies with vegetation species composition (Tallamy 2004). The conversion from native plant dominated landscapes to non-native dominated landscapes can reduce arthropod biomass and thereby limit food availability for breeding birds (Tallamy 2004). Food availability does not only vary with forest vegetation structure and composition but also with leaf litter volume and the extent of coarse woody debris within the forest patch, which could influence territory density for ground foraging species.

Our primary motivation was to explore the relationships among landscape, local, and food variables and forest breeding bird responses for species with different life-history strategies within an urbanized landscape. We predicted that, in our fragmented study area, within patch factors would be more important in determining our focal breeding bird species territory density than would landscape scale factors. To this end, we tested how territory density (as an indicator of the strength of habitat use) of five breeding bird species was related to a suite of landscape, local, and food availability measures.

Methods

Study area

We randomly selected 30 study sites within 22 discrete forest patches in northern Delaware and Southern Pennsylvania (Fig. 1, Ladin et al. 2016a). Within each site we established a 25 × 25-m grid and used a systematic random sample to select between 10 and 15 sampling points per site, resulting in a total number of sampling points ($n = 428$). Sites were dominated by canopy trees such as tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), American sweetgum (*Liquidambar styraciflua*), red oak (*Quercus rubra*), and white oak (*Quercus alba*). Common native shrub species included spicebush (*Lindera benzoin*), arrowwood viburnum (*Viburnum dentatum*), and coastal sweetpepperbush (*Clethra alnifolia*).

Landscape covariates

To assess factors of the landscape context around each forest patch, we calculated patch size (ha), road density within a 100-m buffer, and the extent of forest and agricultural land cover within a 500-m buffer surrounding the patch. We chose a 500-m buffer around each patch because we were most interested in the landcover of the matrix adjacent to the patch. We calculated forest and agricultural land cover around each patch as the proportion of 30 m resolution raster cells (Fry et al. 2011) within 500 m around each site's perimeter using 2011 National Land Cover Dataset (NLCD) data (Homer et al. 2015), including forest (NLCD classes 41–43, 90) and agricultural land (NLCD classes 81, 82) in ArcGIS 9.0 (Environmental Systems Research Institute Inc. (ESRI), Redlands, CA). We estimated forest patch size (ha) using an 8-neighbor cell rule based on the NLCD 2011 raster to identify patch boundaries. We calculated road density within 100 m of the patch based on 2010 US Census Bureau Tiger/Line® data (https://www.census.gov/geo/maps-data/data/tiger.html).

Local covariates

Within each site, we sampled; soil to estimate exchangeable calcium, litter volume, shrub density, tree basal area, and coarse woody debris (cwd). We estimated exchangeable calcium via the Mehlich-III method from soil samples (Mehlich 1984) collected at each sampling location. At each sampling location, we extracted five soil core samples from the top 10 cm of the soil and mixed the samples to generate a testable homogeneous soil sample ($n = 428$) that were processed at the University of Delaware Soil Laboratory (Newark, DE, USA) where they were oven-dried for 72 h, ground, and sieved to 2-mm partials. We collected all the leaf litter within 0.5 m^2

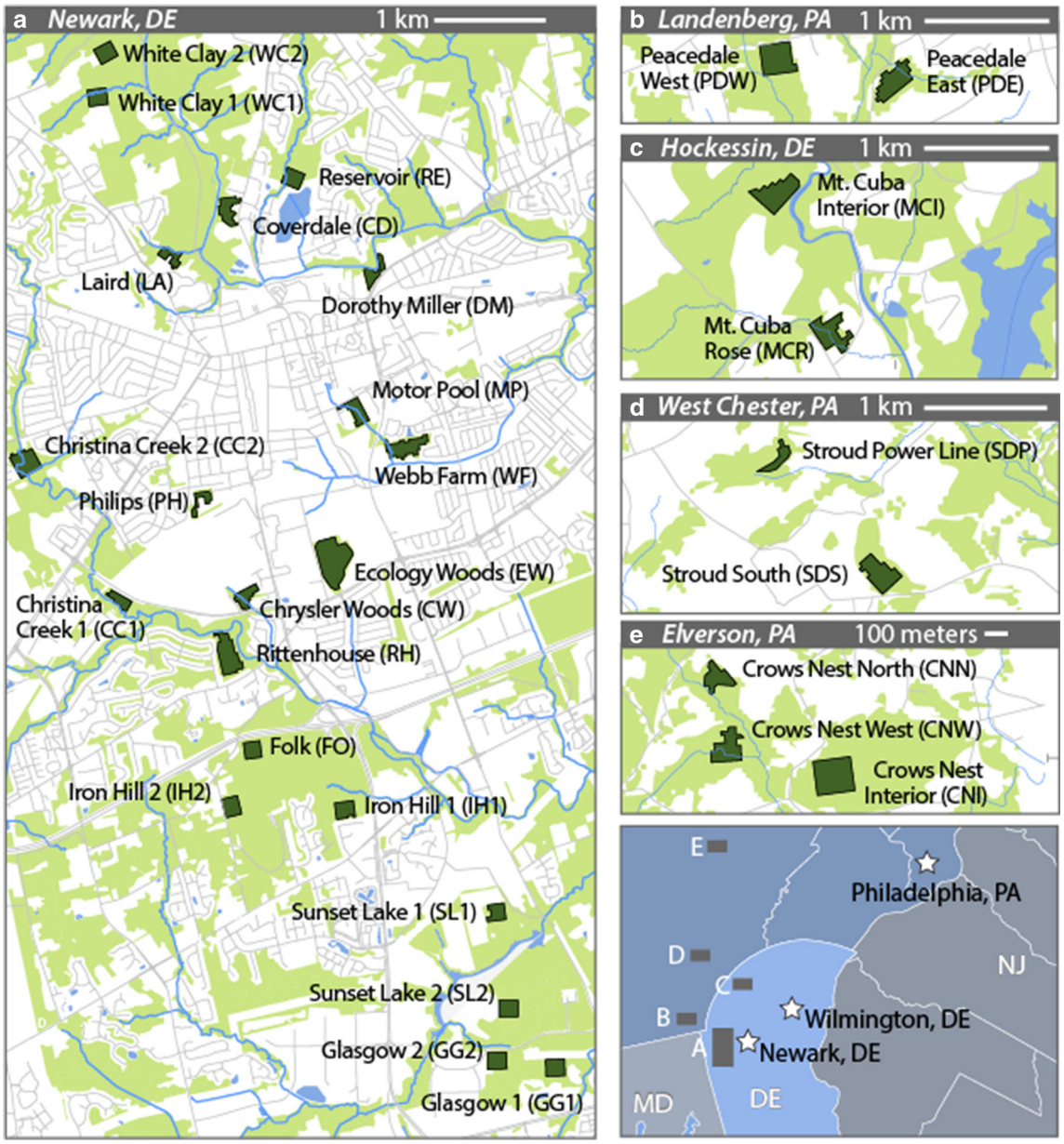

Fig. 1 Map of the 30 sites included in this study. Green polygons represent forested land cover. Black polygons represent sampled areas within the forested land cover. All sites are labeled with their specific names. The enclosed map is the location of the study region within the eastern United States

surrounding the location of the soil core sample to estimate leaf litter volume (m^3) and to extract snails and arthropods (see below). We estimated coarse woody debris volume (m^3) by estimating length and diameter of fallen trees and limbs and calculating the volume (m^3) of material within a 10-m radius. We estimated shrub density, tree basal area, and vertical vegetation density at all sampling points. Within a 2.5 m radius of each sample point, we counted all shrub stems greater than 1 m in height, less than 15 cm in DBH, and identified the shrub to species. We used the U.S. Department of Agriculture PLANTS Database to determine whether a species was native to the study region (USDA 2006). We estimated tree basal area at each sampling point using a factor-10 prism (Mannel et al. 2006) and we used a 2.5 m tall vegetation profile board and measured the percentage of the board obscured by vegetation 15 m from the sampling point flag in each of the four cardinal directions to estimate vertical vegetation density (Nudds 1977). We conducted all sampling during the avian breeding season (May – August).

Food covariates

For our food covariates we sampled calcium rich prey (i.e. land snails, millipedes [Diplopoda], and isopods [Isopoda]), Arachnida, Insecta, and a Lepidopteran Index. We collected snails and arthropods within the leaf litter obtained within a

0.5 m^2 area surrounding the location of the soil core sample and stored the sample in a cold room (4 °C). We sieved the dried litter for individual snails greater than 3 mm. We then placed the litter in a Berlese funnel (Berlese 1905) which removed all remaining arthropods. We also conducted time-constrained searches (5 min) specifically for snails within a 2.5 m radius of the sampling location. We combined the snails collected via the litter sieving and time constrained searches to estimate the total snails and total snail weight for each sampling point. We identified and weighed (g) arthropods into potentially important avian food items; isopod (Class Malacostraca, Order Isopoda), millipede (Class Diplopoda), arachnid (Class Arachnid), and insects (Class Insecta). We combined all arthropod groups to estimate the weight of total arthropods at each site. All snails and arthropods were stored within 95% ethanol until identification. We obtained known calcium concentrations of 73 arthropod families from the literature (Gist and Crossley 1975; Burton and Likens 1975). With these values, we calculated the amount of calcium within each taxa by multiplying the calcium concentration by the weight of each specimen. The total calcium concentration found in these potential food sources were pooled at each sampling location. We calculated a Lepidopteran Index for each patch by multiplying the estimated weight of foliage from dominant forest tree species at a sampling point using iTree software (i-Tree 2013) by the number of lepidopteran species supported by each tree genus (Tallamy and Shropshire 2009). The Lepidopteran Index was used to provide a measure of the relative availability of important prey within each site.

Breeding bird territory density

We selected five bird species that included non-migratory residents: Carolina Chickadee (*Poecile carolinensis*) and Carolina Wren (*Thryothorus ludovicianus*), short-distance migrants: Eastern Towhee (*Pipilo erythrophthalmus*) and Gray Catbird (*Dumetella carolinensis*), and a long-distance migrant: Wood Thrush (*Hylocichla mustelina*). Carolina Chickadee is a cavity nesting resident in mid-Atlantic forests showing slight population declines since 1966 in the New England / Mid-Atlantic coastal plain (Sauer et al. 2017). Narango et al. (2017) showed that breeding Carolina Chickadees in an urban landscape were more likely to breed in areas dominated by native plants compared to areas dominated by non-native plants. The Carolina Wren is a relatively common forest breeding bird with a positive population trend since 1966 in the New England / Mid-Atlantic coastal plain (Sauer et al. 2017). Carolina wrens are year-round residents throughout their range, forage primarily on the ground, and nest in areas of dense vegetation cover (Haggerty and Morton 2014). Identified as an indicator of forest habitat along an urban / exurban gradient (Suarez-Rubio et al. 2011) and indicators of mercury (Hg) in contaminated watersheds (Jackson et al. 2011), however little is known about basic habitat selection for Carolina Wrens (Haggerty and Morton 2014). Eastern Towhees, considered early successional species that select nesting habitat with dense shrub cover (Kellner et al. 2016), have declined by 5.2% annually since 1966 in the New England / Mid-Atlantic coastal plain (Sauer et al. 2017) primarily due to habitat loss and alteration. Eastern Towhee abundance is generally positively related to greater shrub density (Reidy et al. 2014), and habitat management practices that reduce ground and mid-story vegetation cover tend to reduce habitat quality and therefore, Eastern Towhee abundance (Hagan 1993; Greenlaw 1996; Krementz and Powell 2000). Gray Catbirds, a migratory species, have had a stable or increasing population since 1966 in the New England / Mid-Atlantic coastal plain (Sauer et al. 2017) and is considered a shrub nesting species that often occurs in more fragmented and human-dominated landscapes (Canterbury et al. 2000; Keller and Yahner 2007; Parrish and Hepinstall-Cymerman 2012). Wood thrushes are Nearctic-Neotropical migrants breeding in temperate deciduous forests and have declined significantly since 1966 in the New England / Mid-Atlantic coastal plain (Sauer et al. 2017). A well-studied species in our study area (Roth and Johnson 1993; Brown and Roth 2002; Brown and Roth 2004), Ladin et al. (2015) showed that Wood Thrushes preferred calcium- and protein-rich foods, and that metapopulation persistence could be increased by adding forest areas and reducing cowbird parasitism rates (Ladin et al. 2016a).

We used spot-map sampling (Bibby et al. 2000) at each site to estimate breeding bird territory density (number of breeding pair territories per ha). We visited each site ten times during the 2010–2012 breeding seasons (13 May – 20 July) to estimate the territory density of each of five focal species. We spot-mapped sites between 0630 and 1400 h, on days without precipitation or high winds (>15 km/h). All observers received training to identify birds by sight and vocalizations, in addition to the spot mapping method. We created master maps of each species at each site and defined a territory if a bird was recorded in the same relative location during three site visits, with the sightings at least 10 days apart (Bibby et al. 2000). We used the average territory density for each species from 2010 to 2012 at each of the 30 sites as the response variable in our model selection analyses.

Analyses

We first used pairwise correlation analysis among all independent covariates and eliminated one metric from pairs with $r > 0.60$ (Supplemental Fig. 1). Using the remaining covariates, we developed a priori models (Burnham and Anderson 2002) to test hypotheses related to how birds used breeding habitat in response to our landscape, local, and food metrics (Table 1). Our 'Landscape' model included patch size, agricultural land

Table 1 Variables used in model selection procedure to determine how five breeding birds responded to patch and landscape scale covariates at 30 urban forest fragments in Delaware and Pennsylvania, USA, 2010–2012

Model Name	Variables Included in Model
1. Landscape	Patch size (ha) + Ag. cover 500 m + Road density 100 m
2. Local:Soil	Litter vol. + CWD + Exch. Ca
3. Local:Vegetation	% Non-native stems + Basal area
4. Food Availability	LepIndex + Isopoda + Snails + Arthropods
5. Ca Rich Prey	Isopoda + Diplopoda + Snails
6. Total Ca in Invertebrates	Total Ca content from all invertebrates
7. Landscape + Local:Soil	
8. Landscape + Local:Vegetation	
9. Local:Soil + Food Availability	
10. Local:Vegetation + Food Availability	
11. Local:Soil + Ca Prey	
12. Local:Vegetation + Ca Prey	
13. Global	
14. null	

cover (500 m), and road density (100 m) to test the effects of patch size, land cover, and human disturbance around the patch on territory density. Our 'Local:Vegetation' model included our vegetation covariate and our 'Local:Soil' model included litter volume, soil Ca, and course woody debris covariates to determine if these within patch factors influenced territory density. Because we were specifically interested in disentangling the effects of calcium rich prey from total arthropod food availability, we developed three avian food related models; 'Food Availability', 'Ca Rich Prey', and 'Total Ca in Invertebrates' to determine if territory density was influenced by the estimated total available food that included all of the arthropod metrics combined or if territory density was more influenced by the amount of Ca in the prey (Table 1). We also included all univariate models, a 'Global' model (all covariates) and a 'Null' model (no covariates) in our model selection procedure (Table 1). We used 'glm' in R to test for the effects of these covariates on bird territory density for each species independently (R Development Core Team 2016). We used standardized covariates in all models and used the AICcmodavg package (Mazerolle 2017) to compare the models using AICc and selected models with the lowest AICc score that differed from the next best model by at least 2 AIC (Burnham and Anderson 2002).

Results

Our sites represented a range of values for each covariate (Fig. 2, Table 2, Suppl. 1–3) where our focal bird species established territories (Fig. 3). Carolina Chickadees established territories at 29 of the 30 sites with an average territory density of 0.83 (± 0.09 SE, Fig. 3, Suppl. 1). Carolina Wrens established territories at 25 of the 30 sites with an average territory density of 0.43 (± 0.09 SE, Fig. 3, Suppl. 1). Eastern Towhees established territories at 19 of the 30 sites with an average territory density of 0.33 (± 0.16 SE, Fig. 3, Suppl. 1). Gray Catbirds established territories at 20 of the 30 sites with an average territory density of 0.84 (± 0.25 SE, Fig. 3, Suppl. 1). Wood Thrushes established territories at 25 of the 30 sites with an average territory density of 0.83 (± 0.15 SE, Fig. 3, Suppl. 1). The 'Isopoda weight' and 'Ca Rich Prey' were the top models that explained variation in Carolina Chickadee territory density (Table 3) and showed a positive relationship with isopod weight ($\beta = 0.219 \pm 0.080$, $P = 0.011$, $R^2 = 0.258$, Fig. 4a). Carolina wren territory densities were positively related to the percent of non-native stems ($\beta = 0.292 \pm 0.063$, $P < 0.001$, $R^2 = 0.416$, Table 3, Fig. 4b). Gray Catbird territory densities were positively related to the percent of non-native stems ($\beta = 1.244 \pm 0.175$, $P < 0.001$, $R^2 = 0.640$, Table 3, Fig. 4c). Eastern Towhee territory density was positively related to percent of non-native stems ($\beta = 0.408 \pm 0.046$, $P < 0.001$), basal area ($\beta = 0.184 \pm 0.047$, $P < 0.001$), and diplopoda weight ($\beta = 0.085 \pm 0.039$, $P = 0.042$, $R^2 = 0.779$, Table 3, Fig. 4d and e). Wood Thrush territory density was positively related to basal area ($\beta = 0.454 \pm 0.160$, $P = 0.009$) and diplopoda weight ($\beta = 0.341 \pm 0.135$, $P = 0.018$, $R^2 = 0.296$, Table 3, Fig. 4f and g) however, the 'Null' model was in the top model group and the relationship was marginally significant.

Discussion

We found that relationships among species' territory density were driven by local-scale effects rather than landscape-scale effects, with non-native shrub cover and Ca rich prey the primary drivers. These findings provide an increased

Table 2 Summary statistics for local, food, and landscape covariates used to determine which factors influence five breeding bird species at 30 urban forest fragments in DE and PA, 2010–2012

	Measure	Mean	SE	Min	Max	CI 95%
Local	Exchangeable Ca (meq/100)	5.075	0.495	0.673	10.083	1.013
	Coarse Woody Debris (m^3)	1.031	0.158	0.089	4.456	0.323
	Litter Volume (m^3)	4.817	0.369	0.880	9.133	0.754
	Basal area	27.082	0.917	16.77	42.12	1.875
	Non-native stems (%)	12.873	2.787	0.000	51.444	5.700
Food	Snail weight (g)	0.021	0.004	0.000	0.068	0.004
	Isopod weight (g)	0.018	0.004	0.000	0.119	0.009
	Diplopod weight (g)	0.021	0.031	0.000	0.154	0.014
	Arthropod weight (g)	0.100	0.010	0.008	0.238	0.020
	Lepidopteran index	19,886.12	1560.70	7220	41,365	3191.99
	Total Ca invertebrates (g)	0.013	0.002	0.000	0.057	0.005
	Total Ca rich prey (g)	0.060	0.040	0.010	0.176	0.015
Landscape	Patch size (ha)	65.328	10.833	4.618	163.557	22.156
	Agricultural cover (% 500 m)	0.185	0.033	0.000	0.586	0.068
	Road density (100 m)	3.518	0.5361	0.000	9.206	1.101

appreciation for the complex role of non-native invasive plants within urbanized landscapes, and an improved understanding for how local-scale conservation efforts may benefit breeding bird populations more generally. Territory densities for Carolina Wren, Eastern Towhee, and Gray Catbird, were positively related to the percent of non-native stems in the shrub layer. Breeding birds have been shown to have greater occupancy rates and densities in areas with a greater proportion of non-native shrub cover perhaps due to increased access to fruit, earlier leafing out, and more abundant nesting sites (Remeš 2003; Lafleur et al. 2007; Rodewald et al. 2009). In the urban forests included in this study, where there is

Table 3 Model selection for territory density at 30 urban forest fragments in DE and PA, 2010–2012. Top models shown

Species	Models	K	AICc	Delta AICc	AICc Wt
Carolina Chickadee	Isopoda weight	3	39.986	0.000	0.453
	Ca Rich Prey weight	5	41.863	1.877	0.177
	Litter volume	3	43.591	3.604	0.074
	Diplopod	3	44.057	4.071	0.059
Carolina Wren	Local:Veg	4	23.069	0.000	0.596
	Non-native stems	3	25.022	1.954	0.224
	Landscape + Local:Veg	7	26.240	3.171	0.122
	Litter Volume	3	29.529	6.461	0.024
Gray Catbird	Local:Veg	4	80.785	0.000	0.417
	Non-native stems	3	81.377	0.592	0.310
	Landscape + Local:Veg	7	82.536	1.751	0.174
	Local:Veg + Ca Prey	7	83.707	2.921	0.010
Eastern Towhee	Local:Veg	4	0.145	0.000	0.656
	Local:Veg + Ca Prey	7	1.961	1.816	0.264
	Landscape + Local:Veg	7	4.804	4.660	0.064
	Local:Veg + Food Aval.	8	7.785	7.641	0.014
Wood Thrush	Local:Veg	4	75.624	0.000	0.131
	Local:Veg + Ca Prey	7	75.760	0.136	0.122
	Snail weight	3	76.126	0.502	0.102
	Total Ca Inverts	3	76.333	0.709	0.091
	Diplopod	3	76.673	1.049	0.078

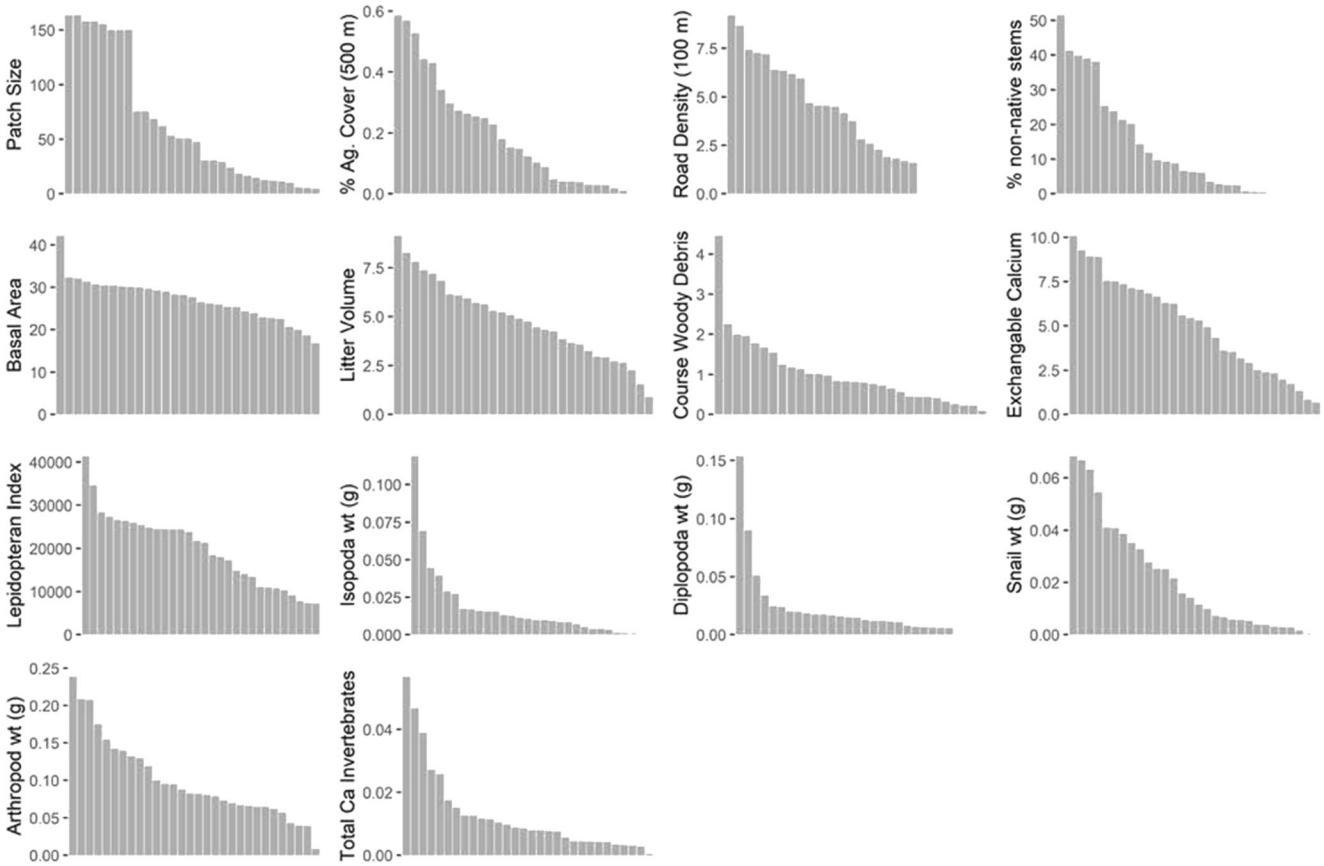

Fig. 2 Site values used to model the effects of landscape (patch size, % Ag. Cover, road density), local (basal area, litter volume, coarse woody debris, exchangeable calcium), and food (lepidopteran index, isopods, diplopods, arthropods, snails, total calcium) covariates on breeding bird territory density at 30 forested sites in DE and PA

vegetation cover in the ground and mid-story layers, the cover is dominated by non-native shrubs. Our study area is also located in an area with relative high deer densities where the only shrub cover is primarily non-native (Tymkiw et al. 2013). Therefore, non-native shrubs, which are dominated by multi-flora rose, are providing the majority of the vegetation structure in the height strata where these species construct nests. Gray Catbirds showed the strongest positive association with non-native stems and this species seems to be well-adapted to urban and suburban environments with demographic parameters increasing with increasing impervious surface cover (Evans et al. 2015). Eastern Towhees also selected urban forests within our study area to establish and defend breeding territory at greater density in areas with more non-native stem density. Eastern Towhee breeding in pine barren ecosystems in New York were more likely to occur and have greater abundance in uninvaded compared to invaded sites (Beachy and Robinson 2008). However, in this system canopy tree species are non-native and the understory is primarily native, unlike the vegetation in our urban forest sites. While our results do link territory density to the extent of non-native shrub cover, territory density may not provide a direct estimate of fecundity or productivity, which might suggest that non-native dominated habitats ecological traps with limited reproductive success (Remeš 2003; Borgmann and Rodewald 2004; Lloyd and Martin 2005; Ortega et al. 2006; Rodewald et al. 2009). For example, despite Gray Catbirds having overall, greater territory densities, in a pair of studies on postfledging survival that were conducted within our study area, Gray Catbirds were found to spend more time in human-dominated land cover types (Ladin et al. 2018) and had lowered survival rates as a function of increased road crossing events (Adalsteinsson et al. 2018). Alternatively, Ausprey and Rodewald (2011) found that Northern Cardinal (*Cardinalis cardinalis*) postfleding survival increased from rural to urban forest patches indicating that some species may be adapting to these urbanizing landscapes. Conversion of native plant communities to those dominated by non-native species can clearly have negative effects on breeding birds and other measures of biodiversity (Burghardt et al. 2009; Aronson et al. 2014; Concepción et al. 2016; Narango et al. 2018).

The relationship between calcium availability in the environment and breeding birds has been shown for a few species (Graveland and Drent 1997; Hames et al. 2002; Pabian and Brittingham 2007; Gosler and Wilkin 2017), however, to our knowledge, this is the first study to show this pattern in urban

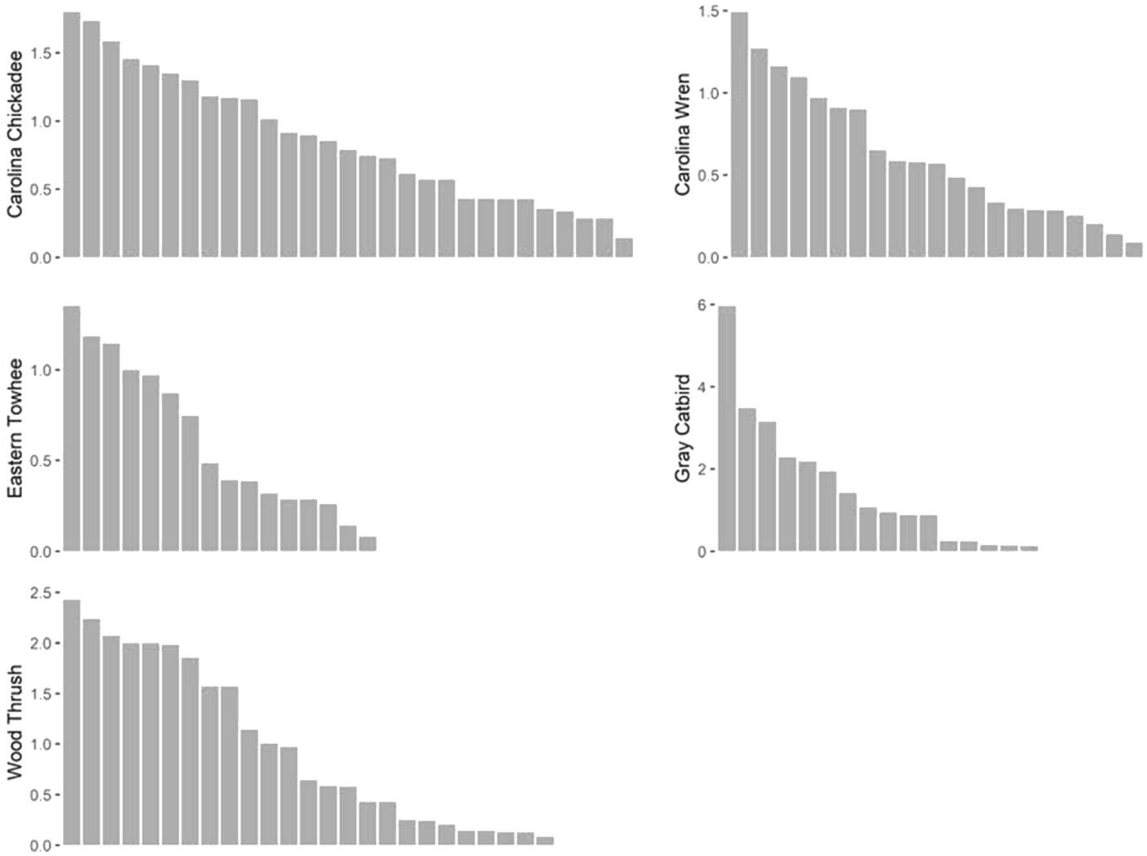

Fig. 3 Territory density (# / ha) for Carolina Chickadee, Carolina Wren, Eastern Towhee, Gray Catbird, and Wood Thrush at 30 forested sites in DE and PA

forests. We found that Carolina Chickadee, Eastern Towhee, and Wood Thrush territory densities were positively related to the abundance of calcium rich prey. Our results within urban forests are consistent with previous studies that have demonstrated negative effects of Calcium depletion on multiple trophic levels in forested ecosystems (Graveland and Drent 1997; Hames et al. 2002; Pabian and Brittingham 2007; Wilkin et al. 2009). Calcium is an essential and limiting nutrient for avian reproduction, specifically for egg formation and skeletal development of the embryo (Graveland and Drent 1997; Klasing 1998). Breeding birds acquire calcium from local food sources during the breeding season (Graveland and van Gijzen 1994; Blum et al. 2001; Ladin et al. 2015), and females cannot acquire enough calcium for egg formation without access to calcium-rich prey such as isopods and snails (Blum et al. 2001, Taliaferro et al. 2001; Graveland and van Gijzen 1994). Wood thrush occupancy was negatively related to soil acidity were calcium availability is low (Hames et al. 2002) and, ovenbirds (*Seiurus aurocapilla*), increased abundance, clutch size, and nest density in large contiguous forest after a calcium application (Pabian and Brittingham 2007, 2011). Within our urban forest system, Wood Thrush nestlings parasitized by Brown-headed Cowbird (*Molothrus ater*) received fewer calcium-rich prey than non-parasitized nestlings (Ladin et al. 2015).

Wood Thrush, as well as many other species, have been shown to be 'area sensitive' (Robbins 1989; Ladin et al. 2018) and negatively affected by forest fragmentation (Robinson and Wilcove 1994; Faaborg et al. 1995; Driscoll and Donovan 2004), but in our urban forest landscape we did not detect a response to the landscape factors we considered. Importantly, our study did not include an urban-rural gradient where patch size has been shown to play a role in forest breeding bird ecology (Robinson and Wilcove 1994; Maseko et al. 2020), but rather we focused solely on urban forest patches. Wood Thrushes clearly breed in small patches (Roth and Johnson 1993) and Friesen et al. (1999) found that Wood Thrush pairing success was high (96%) in small forest patches (3–13 ha) in Ontario, indicating that this species successfully reproduces in fragmented landscapes. Here, we observed Wood Thrushes establishing territories in all but five of our sites, including our smallest (4.62 ha) site, and a positive relationship with basal area. The relatively small forested sites in our study do provide Wood Thrush breeding opportunities however, Ladin et al. (2016a), showed that Wood Thrush fecundity in many of these same sites was 2.5 times lower than in a more forested landscape in Massachusetts (Schlossberg et al. 2018).

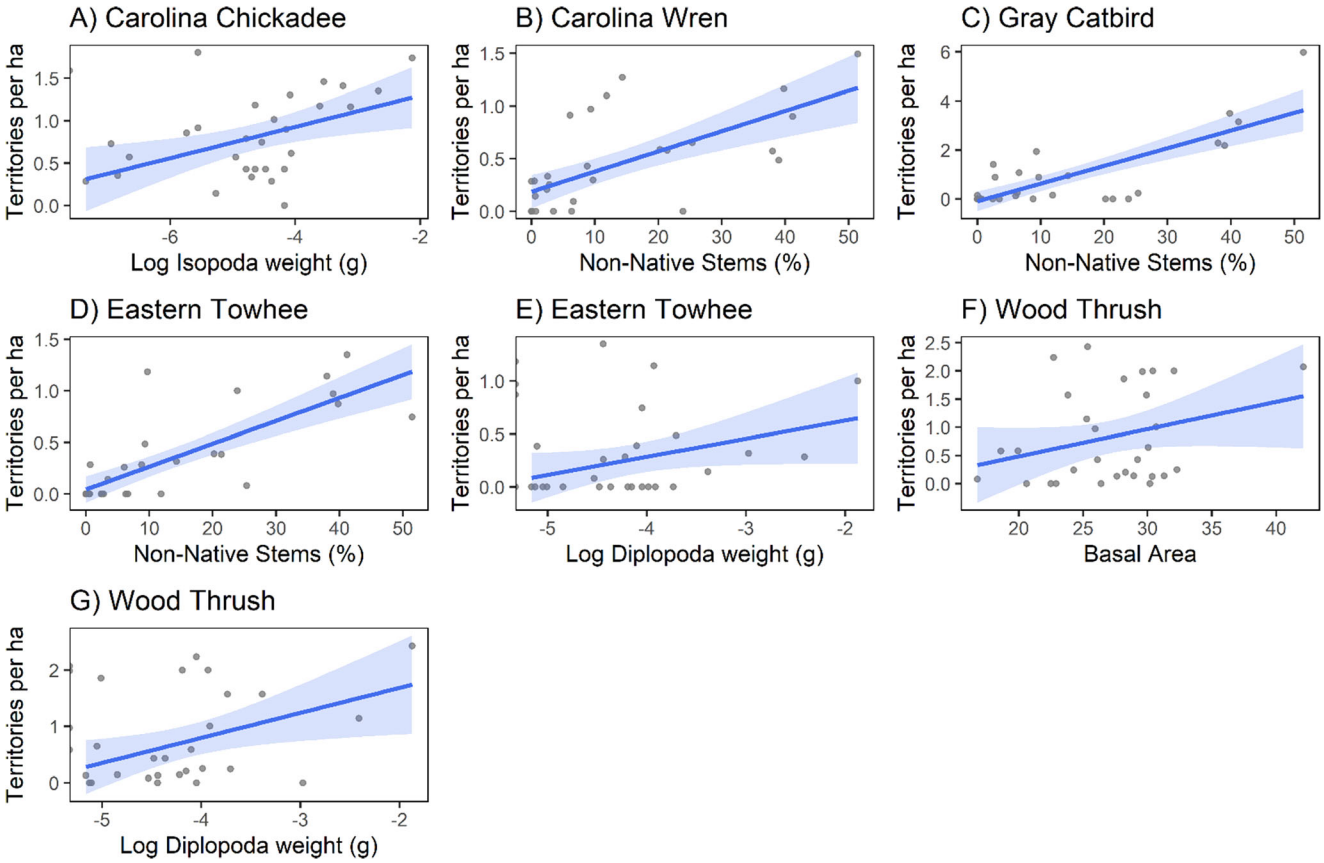

Fig. 4 Relationships among bird territory density and significant covariates. Carolina Chickadee territory density was positively related to isopod weight; Carolina Wren, Eastern Towhee, and Gray Catbird territory density were positively related to non-native stems. Eastern Towhee and Wood Thrush territory density were positively related to diplopoda weight. Wood Thrush territory density was also positively related to basal area

Urbanization changes ecosystem structure and function (Mcdonnell and Pickett 1990; Mckinney 2006) and birds attempting to use modified habitats in urbanized landscapes differ in their responses to these changes (Marzluff et al. 2001; Rodewald et al. 2013). Urban forests also vary in their quality for maintaining biological diversity in general. Some bird species respond positively (Ausprey and Rodewald 2011) while others respond negatively (Ladin et al. 2016a, b) to the availability and condition of forests within urban landscapes. Bird community structure changes along the urban-to-rural gradient (Beissinger and Osborne 1982; Blair 1996; Germaine et al. 1998; Loss et al. 2009; Marzluff et al. 2016), but because species differ in their responses to urbanization, it is important to assess factors that influence species-specific responses. Aspects of habitat selection, territory density, adult survival, juvenile survival, nest survival and fecundity, and metapopulation dynamics vary among species as well, further challenging us to advance our understanding of how birds respond to urbanization (Ryder et al. 2010; Rodewald et al. 2009; Ausprey and Rodewald 2011; Evans et al. 2015; Ladin et al. 2016b). Our urban forest study helps elucidate some of these species-specific responses attributed to changing vegetation and nutrient composition.

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