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Research Paper

Using a birdfeeder network to explore the effects of suburban design on invasive and native birds

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ABSTRACT. Studying the effects of urbanization on native wildlife presents an opportunity for us to learn how to design anthropogenic habitats that can best support wildlife and humans alike. In order to explore which types of suburban development best support bird diversity, a network of 16 bird feeders was installed across a university campus to compare bird diversity and community composition at locations varying in land covers such as natural forest, lawn, plantings, pavement, and buildings. Birds were observed at all feeder stations over three seasons and mist-nets were used to capture and band birds during the summer. Bird species richness, diversity, and invasive species dominance varied significantly across the feeder station sites, with higher diversity in less urbanized locations with larger areas of natural forest. Invasive House Sparrows (*Passer domesticus*) dominated the most urban sites and were associated with larger areas of buildings and herbaceous plantings. However, when sites with natural forest were removed from the analysis, the area of trees planted over lawn was associated with higher diversity, indicating that an increase in tree cover can support diversity in a completely developed landscape. Midscale suburban developments typically feature lawns, pavement, and landscaped plantings, but our results indicate that replacing lawns with trees, or better yet, restored forest patches, may allow us to preserve and even increase the biodiversity of our rapidly multiplying suburban landscapes.

Exploration des effets de l'aménagement périurbain sur les oiseaux envahissants ou indigènes au moyen d'un réseau de mangeoires

RÉSUMÉ. L'examen des effets de l'urbanisation sur la faune indigène nous permet de concevoir des aménagements anthropiques meilleurs pour la cohabitation de la faune et de l'homme. Afin d'explorer quel type de milieu périurbain contribuait le plus à la diversité des oiseaux, nous avons installé un réseau de seize mangeoires d'oiseaux sur un campus universitaire pour comparer la diversité et la composition des communautés aviaires dans des lieux d'affectation diverse, comme la forêt naturelle, les pelouses, les plantations, les zones pavées ou bâties. Nous avons observé des oiseaux à toutes les stations d'alimentation durant trois saisons, et avons utilisé des filets japonais pour leur capture et leur baguage pendant l'été. Le nombre et la diversité des espèces d'oiseaux et la prédominance des espèces envahissantes ont varié significativement selon le lieu des stations : la diversité la plus élevée a été observée dans les lieux moins urbanisés, là où les zones de forêt naturelle étaient plus grandes. Les Moineaux domestiques (Passer domesticus), espèce envahissante, dominaient dans les sites les plus urbanisés et étaient associés avec les zones bâties et de plantations d'herbacées les plus grandes. Toutefois, lorsque nous retirions des analyses les sites comportant des forêts naturelles, les parterres de plantation d'arbres sur pelouse présentaient des diversités plus élevées, indiquant qu'une hausse du couvert forestier permet d'obtenir une diversité d'oiseaux dans un paysage entièrement aménagé. Les aménagements périurbains de taille moyenne comportent typiquement des pelouses, des zones pavées et des aménagements paysagers; or, nos résultats indiquent que le remplacement des pelouses par des arbres, ou encore mieux, la restauration des îlots de forêt, nous permet de conserver et même d'augmenter la biodiversité dans nos paysages périurbains qui se multiplient rapidement.

Key Words: bird diversity; birdfeeder; invasive species; suburban development; urbanization

INTRODUCTION

Urbanization is the process of replacing natural habitats such as vegetation, landforms, and waterways with anthropogenic habitats featuring ornamental landscaping, pavement, and buildings (Gaston 2010). Urbanization is known to reduce the abundance and diversity of native wildlife, and is one of the major drivers of biodiversity loss across the globe (Grimm et al. 2008, Gaston 2010, Pickett et al. 2011, Seto et al. 2012). However, because even the largest urban areas still contain a significant number and diversity of wildlife (Aronson et al. 2014), urbanization also presents an opportunity for us to learn how to

design anthropogenic habitats that are better for wildlife and and humans (Fuller et al. 2007). Birds are useful indicators of the effects of urbanization because they are plentiful in urban, suburban, and rural habitats, and because they are mobile, allowing them to respond quickly to habitat changes by vacating degraded habitats and repopulating restored habitats. Decades of research has revealed a trend of decreased diversity and increased abundance of birds in urban centers as compared to native habitats outside of cities (Warren and Lepczyk 2012, Shanahan et al. 2013). Many researchers are increasingly focusing on the resiliency provided by urban green spaces, such as public parks and private yards/gardens (Sandström et al. 2006, Mason et al. 2007, MacGregor-Fors et al. 2010, Lerman and Warren 2011, Yang et al. 2015), as well as how to make recommendations for better design of urban developments to retain and perhaps increase biodiversity in urbanizing landscapes (Shanahan et al. 2011, Sushinsky et al. 2013, Aronson et al. 2017).

Most research on urbanization is focused on large cities; however, the largest area of land undergoing urbanization is the construction of suburban developments surrounding cities and exurban developments in rural areas (Hanson et al. 2005). Suburban towns and neighborhoods often contain invasive birds along with adaptable native species that thrive in less-intensely urbanized areas, but they often lose specialists such as ground nesting, migratory, and insectivorous birds (Aldrich and Coffin 1980, Clergeau et al. 2001, Jokimäki and Kaisanlahti-Jokimäki 2003). Even the smallest exurban developments, such as additions of single homes in a forest, can repel the most sensitive native species (Kluza et al. 2000, Glennon and Kretser 2013). Few empirical studies have been published about how the design and landscaping of suburban developments at the local scale can better support diverse bird communities.

Bird feeders concentrate birds in specific areas for easy identification and counting, which makes them a potential tool for assessing foraging habitat preferences or tolerances for songbirds that use feeders (Jones and Reynolds 2008). Supplementary bird feeding is a common recreational activity that is increasing in popularity (Jones and Reynolds 2008, Robb et al. 2008, Amrhein 2013). A number of researchers have studied how and why people feed birds, and how bird feeders may be affecting the birds themselves (Robb et al. 2008, Amrhein 2013). but fewer researchers have used bird feeders as a method of studying the ecology of birds more generally. A network of bird feeders may be used to measure habitat suitability across variable habitats, such as those in urbanizing landscapes. For example, Cox et al. (2016) used bird feeder networks to assess how songbirds respond to varying levels of habitat fragmentation among residential gardens in the UK. Here, a network of bird feeders is used to compare bird diversity, abundance, and community composition with specific features of urbanization across a suburban university campus in New York State, U.S. Prior work using point counts to compare the bird community on our campus with nearby forest fragments demonstrated that the campus bird community has lower species richness and evenness as compared to the forest communities, and few insectivorous neotropical migrants; the campus community is also dominated by invasive House Sparrows (Passer domesticus; Belinsky et al. 2019).

In this study, the details of suburban design on our campus are examined at the habitat level. The specific features that affect the birds are identified by comparing bird communities among habitats using GIS-based land cover measurements at each bird feeder station in our network. Feeders in areas with more retained native habitats such as natural forest and more highly structured landscaping that includes trees and other plantings were predicted to have higher diversity. Additionally, feeders surrounded by buildings were predicted to be dominated by invasive House Sparrows. How time of year affects the communities of birds using feeders in each habitat type was also explored, because the distinctive demands of breeding and overwintering may affect how birds respond to the design of suburban habitats (Cox et al. 2016). The goal of the study is to make recommendations for how to improve our campus and other midsized suburban developments as habitats for native birds. Understanding the effects of subtle differences in suburban design at small scales is necessary to seize the opportunity presented by urbanization to improve the design of our growing suburbs to better support wildlife.

METHODS

Study site

This study was conducted on the suburban campus of the State University of New York at New Paltz (SUNY New Paltz) in New Paltz, New York (41°44'37"N 74°05'02"W). The Village of New Paltz has population of 7221 people (U.S. Census Bureau 2018), and is surrounded by smaller residential towns, forest fragments, apple orchards, vegetable farms, and hayfields with the closest city of Poughkeepsie 15 km to the east, across the Hudson River. New York City is only 137 km to the south, positioning New Paltz on the edge of one of the most intense urban expanses in the United States (Nowak and Walton 2005). However, several large protected forests (including the 9000 ha Minnewaska State Park and 3000 ha Mohonk Preserve) are located on the western border of New Paltz. The SUNY New Paltz campus itself serves 7628 students (Fall 2016 Student Profile), and consists of 87 ha of almost entirely developed land that span a range of urbanization intensities. The campus includes a central core of high-traffic academic and administrative buildings, suburban residential areas, groomed turf fields, and remnant 50-year-old secondary forest fragments along the southern and western edges of campus.

Bird feeder network

A network of 16 feeder stations were installed across the campus, with four stations in each of four urbanization categories referred to as Forest Edge, Residential Campus, Turf, and Central Campus. Forest Edge feeder stations were placed in close proximity to natural forest fragments (undisturbed secondary growth forest with closed tree canopy and natural leaf-litter ground cover) located along the edges of campus in areas with low amounts of pedestrian traffic and little development (pavement and buildings). Residential Campus feeder stations were placed near dormitories in areas with low levels of pedestrian traffic. Turf feeder stations were located near athletic fields and parking lots, with large open expanses of lawn and few pedestrians. Central Campus feeder stations were placed among academic and administrative buildings with the highest levels of pedestrian traffic. Each bird feeder station consisted of an iron double-armed shepherd's hook style pole, with each hook holding one high-capacity tube style birdfeeder with six feeding perches/ ports, enclosed in caging to exclude squirrels (Duncraft Squirrel-Proof Avian Bird Feeder). The squirrel-proof caging also prevented larger bird species such as Mourning Doves (Zenaida macroura) and medium-sized species such as European Starlings (Sturnus vulgaris), Red-bellied Woodpeckers (Melanerpes carolinus), and Common Grackles (Quiscalus quiscula) from feeding at the feeder ports. However, small numbers of these species were counted as they still foraged on the ground below the feeders, and occasionally perched on the sides of the feeders to eat seed that spilled out of the ports. Each feeder was filled with sunflower seed hearts during the study periods, and all feeders were emptied, washed, sterilized with a bleach solution, refilled and returned each time mold was detected and three times during the year, at the start of May, August, and January.

Three-season feeder observations

The birds visiting each feeder station were identified and counted during 10-minute observations on 16 dates between 18 February and 20 November of 2016. All feeder stations were observed on each sampling date between 10am and 4pm, with the order of the observations varied systematically to reduce any bias from time of day. All observations were conducted by T.E. using binoculars while standing at a distance of 15 m from the feeder station. Observations were conducted during three study periods; six observations were completed at least one week apart from February to May, and 10 observations were completed at least one week apart from June to August, and from September to November. During each observation, bird abundances were estimated by counting the maximum number of each species visible at any one time. Counts included any bird on any part of the feeder, or directly below the feeder eating spilled seed, within a 0.5 m radius of the feeder pole.

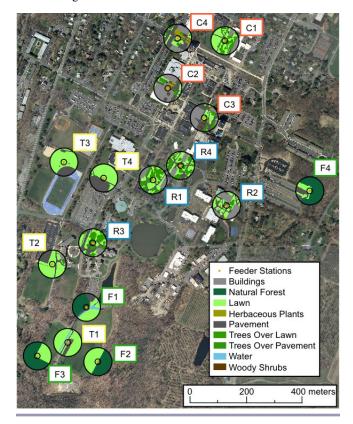
Summer mist-netting and banding

To more accurately determine abundances of each species, mist nets were used to capture and band birds at each feeder station during the summer (Dunn and Ralph 2004). All birds were caught and banded on two dates at each feeder station between 20 May and 22 July, with each session lasting 3 hours and occurring between 7am and 12pm, resulting in 0.096 hours per net m² at each feeder station. For each mist-netting session, two 12 m nylon mist nets (all-purpose, 36 mm mesh size) were set up in a V-shaped formation around a feeder station, using three conduit poles with the two nets connected by a central pole. A banding station was set up \sim 30 m away from the nets and nets were monitored using binoculars so that no bird remained in the net for more than 15 min. All banding was completed by K.L.B., T.E., and two additional technicians, using United States Geological Survey aluminum bands. Captured birds were identified to species, age, and sex (Pyle 1997), and then released. Each banded bird was counted once for relative abundance data used to calculate Shannon's diversity index.

GIS land cover measurements

The bird feeder network was mapped and land cover area was measured at two scales around each bird feeder station using GIS. First, a Garmin Montana 650t GPS handheld device was used to record the exact location of each feeder station, and these points were added to a base map of orthophotos of the campus in ArcGIS. Aerial photos, which were taken in 2013, were downloaded from the New York State Clearinghouse GIS database. Once the base map and GPS locations were combined, 10 m and 50 m buffers were created around each feeder station. Each buffer was used as a reference to create a layer of polygons delineating the borders of each parcel of distinct land cover type apparent on the aerial photos. Each polygon was designated as one of the following land cover types: (1) natural forest (with closed canopy and leaf litter ground cover), (2) lawn, (3) herbaceous plants (flower beds and ground cover vegetation lacking woody stems), (4) woody shrubs (primarily pruned evergreen bushes), (5) trees growing over lawn, (6) trees growing over pavement, (7) water (a stream), (8) pavement (paved walkways and parking lots), or (9) buildings. Next, the polygons were ground-truthed by visiting the site to adjust land-cover designations and borders based on details that were not apparent on the images or the few landscaping and construction changes made to the campus since aerial photos were taken. ArcGIS was then used to calculate total areas of each land cover type in the 10 m and 50 m areas around each bird feeder station (Fig. 1).

Fig. 1. Aerial photo of the study site depicting the location of all 16 feeder stations, the urbanization category of each (Forest Edge site labels are highlighted in green, Residential Campus in blue, Turf in yellow, and Central Campus in orange), and the land cover polygons within the 50 m and 10 m circles surrounding each station.



Statistical analyses

Shannon's diversity indices were calculated following Magurran (1988). ANOVA was used to test for differences in bird species richness and Shannon's Diversity Index among our four bird feeder habitat designations (Central, Residential, Turf, and Forest Edge categories), and Tukey's honest significant difference posthoc tests were run for all ANOVAs. Pearson's correlations were used to screen the land cover variables for collinearity and collinear variables were excluded from further analysis. The variables were examined for normality, and all were found to be skewed because of large numbers of zero values (for example, Forest Edge locations were the only ones with natural forest and

had very little pavement and no buildings while Central Campus locations had high areas of buildings and pavement but no forest). Large differences in magnitude between land cover variables were also found (very small areas of shrubs but large areas of trees over lawn, for example). To correct for this, the land cover variables were standardized by subtracting the mean from each value and dividing by the standard deviation. The dependent variable, the percentage of House Sparrows, was centered by subtracting the mean. The explanatory power of our land cover area variables were evaluated by testing for correlations between each land cover variable and each diversity variable. Any land cover variables that were significantly correlated with a diversity variable (all with r> 0.5), were retained, except those that were collinear. All significant candidate variables were then entered into a linear model (using the standard statistics package in R), to explore which variables best explain bird diversity when combined. Any nonsignificant variables were then removed (threshold where $\alpha < \alpha$ 0.05), to identify the final suite of variables explaining each diversity metric.

A mixed model approach was used to determine whether the feeder use of our four most common bird species changed with time of year, and whether their habitat use varies by season. A generalized linear model was used to fit feeder observations for each species and included the season, the area of buildings within 50 m of the feeder as fixed effects, and the feeder identity as a random effect to account for the dependence structure of repeated observations over time. Akaike information criterion (AIC) was used to evaluate Poisson versus Negative Binomial likelihood distribution fits for each species. The bird feeder observations were then divided into three season categories: Winter (November, February, and March), Summer (June, July, and August), and Transition (mix of spring and fall: April, September, and October). These seasons were chosen because these three seasons are biologically important to birds in New York (most breeding/feeding of young occurs in summer, cold temperatures stress birds and many flock in winter, and intermediate temperatures and the breakup/reforming of flocks occur in spring/fall). Note that these models were also run by splitting the Transition season into fall and spring, and the results were similar but it did not improve the AIC. The area of buildings within 50 m was chosen as our habitat variable, because this variable was an important predictor of House Sparrow dominance in our initial analysis, and it is inversely correlated with the area of forest within 50 m, which was our strongest predictor of species richness and diversity overall.

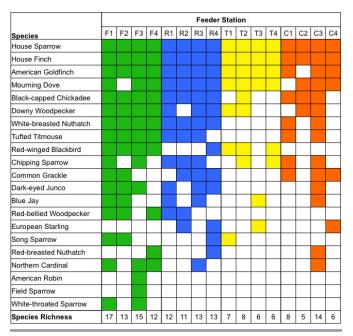
Exploratory analyses were conducted using JMP 2011 for Mac, while regression models were conducted using the R Statistical Software (R Core Team 2018). Mixed effects models used the LME4 (Bates et al. 2015) package to account for repeated measures and results for significant effects are presented as effect size with standard error, z-score, and p-value.

RESULTS

Differences among urbanization categories

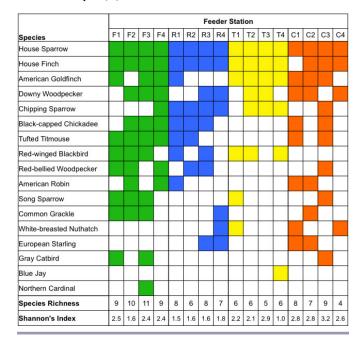
A total of 21 species of birds were observed across the 26, 10minute observations completed through the year at each of the 16 feeder stations (Fig. 2). Two species, the House Sparrow and House Finch (*Haemorhous mexicanus*), were observed at all feeder stations, while three species were observed only at one or two Forest Edge feeder stations (American Robin, Turdus migratorius, Field Sparrow, Spizella pusilla, and White-throated Sparrow, Zonotrichia albicollis). Five species were detected during observations that were not captured during summer banding, including one species that was too large for the net size we used (Mourning Dove), and one species that only appears on campus during the winter months (Dark-eyed Junco, Junco hyemalis). During the summer, a total of 667 birds of 17 different species were mist-netted and banded, including one species that was not detected during our visual observations (Gray Catbird, Dumetella carolinensis), because it does not typically forage at feeders, but was captured at two stations near berry-bearing shrubs (Fig. 3). Only one species, the House Sparrow, was captured at every feeder station. The Northern Cardinal (Cardinalis cardinalis), was captured only at one Forest Edge station, and another species, the Blue Jay (Cyanocitta cristata), was captured only at one turf station; both of these species are too large to enter the caging around our bird feeders, but were observed at, on, or under several feeders stations nonetheless.

Fig. 2. Total species richness and community composition for each feeder station based on data obtained through visual observations over three seasons. Colored blocks indicate the presence of a species at a feeder stations in each of the urbanization categories: Green = Forest Edge (F), blue = Residential Campus (R), yellow = Turf (T), and orange = Central Campus (C).



Significant differences in bird diversity were detected across our birdfeeder network based on our urbanization categories (Fig. 4). Species richness based on observations was significantly different between categories, with the highest richness observed at Forest Edge sites, lower richness at Residential Campus and Central Campus sites, and significantly lower richness at Turf sites (ANOVA: $F_{3,12} = 8.39$, P = 0.003). Similar patterns of differences in species richness and Shannon's index of diversity were found

Fig. 3. Total species richness and community composition for each feeder station based on data obtained through mist-netting and banding during the summer. Colored blocks indicate the presence of a species at a feeder stations in each of the urbanization categories: Green = Forest Edge (F), blue = Residential Campus (R), yellow = Turf (T), and orange = Central Campus (C).

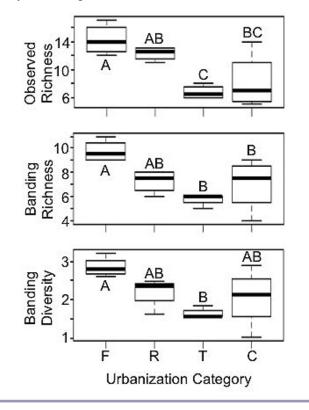


based on our banding data. Species richness differed significantly between categories with the highest richness found at Forest Edge sites, lower richness at Residential sites, and significantly lower richness at both Central Campus and Turf sites (ANOVA: $F_{3,12} =$ 6.65, P = 0.007). Shannon's index of diversity also differed significantly between categories with the highest diversity found again at Forest Edge sites, similarly lower diversity at Residential and Central Campus sites, and significantly lower diversity at Turf sites (ANOVA: $F_{3,12} = 4.92$, P = 0.018). The percentage of invasive House Sparrows that were banded also differed significantly among urbanization categories, with a nearly opposite pattern to that of diversity (Fig. 5). Significantly higher percentages of House Sparrows were banded at Central Campus sites, and significantly lower percentages at Forest Edge sites, with Residential and Turf sites falling in between (ANOVA: $F_{3,12} = 11.24$, P = 0.0008).

Land cover and diversity

The final model for species richness based on year-round feeder observations is the univariate model including only the area of forest within 50 m of the feeders station as the positive predictor of species richness ($F_{1,14} = 6.38$, P = 0.024). The model for species richness from summer banding describes a similar pattern, but it provides a final model with two significant parameters: the area of forest within 50 m as a positive predictor and the area of pavement within 50 m as a negative predictor ($F_{2,13} = 12.73$, P = 0.001). The model for Shannon's index of diversity yielded another univariate model with the area of forest within 50 m being

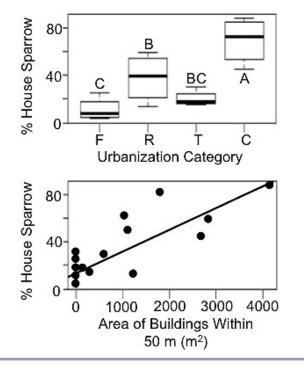
Fig. 4. Differences in mean bird diversity between feeder stations in each urbanization category: Forest Edge (F), Residential Campus (R), Turf (T), and Central Campus (C). The top panel displays species richness from visual observations, the middle panel displays species richness from mist-netting and banding, and the bottom panel displays Shannon's index of diversity from mist-netting and banding. The box plots display the median as the bold central line, with the top and bottom lines of the boxes indicating the first and third quartiles, and the whiskers extending to the maximum and minimum data points. Different letters above or below each box plot indicates statistically different means based on the Tukey's honest significant difference results.



the lone positive predictor. ($F_{1,14} = 10.14$, P = 0.007). Whether any land cover variables predict bird diversity on campus when we removed the Forest Edge sites from our analysis was then explored. This allowed for a test of the effects of land cover variables aside from natural forest because only the Forest Edge sites contained any natural forest. A single land cover, trees growing over lawn, provided the strongest model for species richness from observed data ($F_{1,10} = 8.627$, P = 0.015), and species richness from banding data ($F_{1,10} = 6.886$, P = 0.025). No variables were significant in any model for Shannon's diversity index from banding data.

Land cover and invasive dominance

House sparrows were the most common species observed (at least one House Sparrow was detected during 206 of the 256 ten-minute observations completed) and 225 of 667 birds we banded on campus were House Sparrows. The final linear model of House **Fig. 5.** House Sparrow (*Passer domesticus*) dominance. The top panel illustrates differences in House Sparrow percentage between feeder stations in each urbanization category: Forest Edge (F), Residential Campus (R), Turf (T), and Central Campus (C). The box plots display the median as the bold central line, with the top and bottom lines of the boxes indicating the first and third quartiles, and the whiskers extending to the maximum and minimum data points. Different letters above or below each box plot indicates statistically different means based on the Tukey honest significant difference results. The bottom panel displays the scatterplot and regression line of the relationship between House Sparrow percentage and the area of buildings within 50 m of each feeder station.



Sparrow percentage included the area of buildings within 50 m and the area of herbaceous plantings within 50 m, which were both positive predictors, although the area of buildings explained more of the variance (Fig. 4; $F_{2,13} = 22.03$, P = 0.0001).

Seasonality and species-specific habitat use

Season had significant effects on each of the four most common species observed using the feeders: House Sparrows, House Finches, American Goldfinches (*Spinus tristis*), and Black-capped Chickadees (*Poecile atricapillus*). The AIC values for the negative binomial models were consistently lower (< 100) than for models with Poisson likelihoods across all species except for Black-capped chickadees, where there was no difference. House sparrows were more abundant in summer than either winter (β = -1.40, se = 0.22, Z = -6.32, p < 0.001) or the transition (β = -1.51, se = 0.24, Z = -6.44, p < 0.001) season. Although building cover was a positive predictor of House Sparrow abundance overall, it had the greatest influence during the transition season (β = 0.79,

se = 0.21, Z = 3.92, p < 0.001), followed by winter (β = 0.48, se = 0.18, Z = 2.61, p = 0.009). The next most common species was the House Finch, which also used the feeders in higher numbers in the summer as compared to either transition ($\beta = -0.71$, se = 0.24, Z = -2.97, p < 0.003) or winter ($\beta = -1.18, se = 0.26, Z = -4.52$, p < 0.001) and they used feeders with lower areas of buildings within 50 m at all times of year ($\beta = -0.68$, se = 0.24, Z = -2.80, p < 0.005). In contrast, the two next most common species, the native American Goldfinches and Black-capped Chickadees used the feeders in higher numbers during the winter. American Goldfinches were most commonly observed using feeders in the winter ($\beta = 0.83$, se = 0.26, Z = -1.91, p = 0.001) and feeder use was negatively associated with areas of buildings within 50 m (β = -0.74, se = 0.27, Z = -2.73, p = 0.006). Black-capped chickadees used feeders more in both winter ($\beta = 1.11$, se = 0.27, Z = 4.17, p < 0.001) and transition ($\beta = 0.84$, se = 0.28, Z = 3.03, p = 0.002), and were not significantly associated with building area during any season ($\beta = -0.07$, se = 0.40, Z = -0.17, p = 0.87).

DISCUSSION

Significant differences in bird diversity and community composition were detected across a suburban landscape using a network of birdfeeders. Larger areas of natural forest increased avian diversity and larger areas of pavement decreased diversity, while larger areas of buildings increased invasive House Sparrow dominance. Also, invasive and native birds were found to use feeders differently depending on the season, with invasive species using the feeders more during the summer, and native species using them more during the winter. These results support the hypothesis that the area of natural forest with a closed canopy and leaf-litter covering the ground is the strongest predictor of suburban bird species richness and diversity that was measured. Forest is the native habitat at our study location, so the results confirm that natural forested habitat is still important to a variety of species that are fairly well adapted to urbanized landscapes. Many other researchers have reached similar conclusions about the value of preserving native habitats in urbanizing locations at the landscape level (reviewed by Marzluff and Rodewald 2008 and Gagne et al. 2015). In addition, White et al. (2005) found that older, native vegetated streetscapes had higher bird diversity than exotic or unvegetated roadways in Melbourne, AU, indicating that native vegetation is important at the local level as well. Our study adds that preserving or recreating patches of native habitat helps support native birds at the local level on our campus, and that small landscaping changes may improve suburban habitat for birds.

Forests increase bird diversity because trees and snags provide food, foraging or caching substrates (bark, foliage), and branches or cavities for nesting, while the closed canopy provides continuous cover. The leaf-litter on the ground, in particular, provides a foraging substrate and nesting location that is replaced with pavement or lawn in most anthropogenic habitats (Sharpe et al. 1986, Nowak and Walton 2005, Ignatieva et al. 2015). In this study, several species associated with trees and forest cover were found more frequently at birdfeeder station sites with forest (Figs. 2 and 3), including Tufted Titmice (*Baeolophus bicolor*), Red-bellied Woodpeckers, Northern Cardinals, and Red-breasted Nuthatches (*Sitta canadensis*). Other species found in these locations may have been there to utilize the shrubby understory where the forest edge meets the lawns at these sites (Song Sparrow, Melospiza melodia, and White-Throated Sparrow). The result that natural forest best supports bird diversity seems to indicate that fewer species choose to forage in areas lacking their preferred habitat (or that fewer species forage far from it). The result that pavement may reduce diversity could indicate that some species avoid paved areas. Although, it seems more likely that paved areas are simply areas with a smaller amount of preferred habitat because other attributes of urbanization, such as the area of buildings, had no discernable effect on diversity. However, the birdfeeder stations with less forest and more pavement in our study are also more altered in ways aside from land cover, such as having more pedestrian and vehicular traffic, and more noise and nighttime lighting, and these aspects of urbanization are known to affect birds as well (Fernández-Juricic 2000, Platt and Lill 2006, Patón et al. 2012).

Interestingly, when the sites containing natural forest were removed from our analysis, the area of trees growing over lawn predicted increased bird species richness, although other attributes of habitat complexity such as the area of shrubs or herbaceous plants still had no measurable effect. This result has useful management implications for landscapes where forest restoration is not preferred or not feasible, and indicates that planting more trees, even over manicured lawns, may increase bird diversity. The addition of trees may represent an addition of some aspects of the habitat provided by natural forest, especially cover from predators, which is important during foraging. The results of many larger scale studies have reported that the amount and configuration of tree cover affects bird diversity (Hostetler and Holling 2000, Melles et al. 2003, Donnelly and Marzluff 2006, Mason et al. 2007), but few studies have directly compared natural forest to tree cover created by trees planted over managed lawns (Paker et al. 2014), although several other studies have reported results from studies of varying housing age or density in relation to forest or tree cover (DeGraaf and Wentworth 1986, Kluza et al. 2000).

House Sparrows are well-known urban invaders in cities and towns across the planet; they are omnivorous generalists that nest in cavities, often on or in human-made structures. In this study, House Sparrow dominance was associated with the area of buildings, as expected, and also with the area of herbaceous plantings instead of the woody shrubs that were predicted. Campus buildings provide nesting habitat (active nests have been observed in Central campus, and many hatch year juvenile birds were banded during the study), as well as food in the form of scraps because the areas of campus with the largest areas of buildings also contain the most litter and trash receptacles. Buildings are associated with House Sparrows in several other studies (Wilkinson 2006, MacGregor-Fors et al. 2010, Nath et al. 2016). In addition, Shochat et al. (2010) argue that House Sparrows may outcompete other species in urbanized areas because of their aggressive and efficient foraging, and note that they observed House Sparrows actively excluding a smaller granivore, the Lesser Goldfinch (Spinus psaltria) from feeders during an experiment in Phoenix, AZ. The herbaceous plants in our study seem unlikely to provide direct resources for House Sparrows, but they occur in very small amounts except for at two sites with the highest House Sparrow percentages. These sites also have large areas of tall buildings (4-12 floors), few trees, and high pedestrian and vehicular traffic due to a nearby road. Building height may also be a factor here, as it has been positively linked to House Sparrow abundances in urban Los Angeles (Lee 2016). However, in Europe, where many House Sparrow populations are mysteriously declining, Chamberlain et al. (2007) found that House Sparrows thrive in residential urbanized areas with gardens, which often feature herbaceous plantings, and not denser housing developments without gardens.

Of the four most common species observed at our feeders, season affected all species' use of the feeders. House Sparrows used the feeders more in the summer, and their preference for feeders in locations with large areas of buildings nearby was weaker in the summer, possibly because their population became so large that some dispersed outward looking for additional food sources. This idea is supported by our banding data, because 50% of the House Sparrows we banded during the summer were hatch year birds, whereas only 33% of all other species combined were hatch year birds. House Finches also used the feeders in higher numbers during the summer, although they chose feeders with lower areas of buildings nearby at all times of year. House Finches may be considered invasive to the eastern U.S. because they are native to the southwestern U.S., and spread to the northeast because of releases from the pet trade. In contrast to the invasive species, fewer American Goldfinches and Black-capped Chickadees used the feeders in summer, and American Goldfinches preferred feeders with lower areas of buildings nearby year-round, while Black-capped Chickadees had no preference for or against the amount of buildings nearby. American Goldfinches are known to favor eating and feeding their young crop milk from weed seeds, including thistle, that are abundant in areas of our campus in the summer. Black-capped Chickadees use insects as a summer food source and to feed their young. Both species may reduce their feeder use in the summer because they switch to natural food sources at this time of year. Cox at al. (2016) found that season also affected two native Paridae species; they found that Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*), made more trips between feeders at urban sites with low and medium fragmentation in winter, and more trips between feeders sites with high fragmentation in spring. In addition, Galbraith et al. (2017) found that urban bird feeders in Auckland, NZ were dominated by invasive species, including House Sparrows, and that House Sparrows used the feeders more in summer, while the only native species to use the feeders, the Silvereye (Zosterops lateralis), used them mostly in the winter. Our results along with those from these two other recent studies imply that supplementary bird feeding with seeds may benefit invasive species more than native species, particularly during the summer months.

In conclusion, our study provides empirical data suggesting changes in suburban landscaping and development practices at the local level can better support bird diversity. Our results confirm the importance of retaining remnants of natural habitat (Marzluff and Rodewald 2008, Gagne et al. 2015, Aronson et al. 2017), and indicate that replacing lawns or pavement with vegetation that best replicates native structures (tree cover, in this case), may be a feasible alternative where conservation or restoration of unaltered habitat is not possible. Bouma et al. (2013) reported encouraging results of a reforestation project at a small suburban college, where small habitat patches reforested with native trees and shrubs had greater biodiversity (plants, insects, birds, and mammals) than lawns, trees over lawns, and even forest remnants just four years later. Midsized suburban developments, such as university, commercial, and industrial campuses are viable conservation targets that could help remedy the problem of the mismatch of scales between the needs of wildlife and people (Borgström et al. 2006). Unfortunately, most property owners do not recognize the importance of native features; in fact, most people think of lawns as the default "natural" green space (Ignatieva et al. 2015). Moreover, most people view native habitat, such as forest, unmowed meadows, shrub/scrub edges, and swamps as distastefully untidy (Nassauer 1995). However, in addition to effectively increasing suburban biodiversity, the conservation and restoration of native habitats may actually improve local people's lives. Fuller et al. (2007) report that interviews with urban citizens in the UK reveal that people reap increased psychological benefits from urban green spaces with higher species richness of plants and birds, and so habitat conservation, restoration, and remediation may be worthwhile for birds and humans alike.

Responses to this article can be read online at: http://www.ace-eco.org/issues/responses.php/1408

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