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Cover Photograph: A *Turdus migratorius* (American Robin) with the SUNY New Paltz Campus in the background.Photograph © Kara Loeb Belinsky.

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Bird Communities at the Suburban–Rural Interface: The Role of Low-intensity, Small-scale Urbanization

Kara Loeb Belinsky[1,*], Eric Keeling[1], and Dakota R. Snyder[1]

Abstract - Urbanization is one of the main drivers of biodiversity loss, and birds are an efficient way to assess this threat. Although it is generally less intense than that found in urban centers, development occurring along the suburban–rural interface represents a far larger area of rapid land-use change. In this study, we compared bird species richness, diversity, and community composition at 3 suburban sites on our university campus with that at 3 nearby naturally forested sites to assess whether this level of development results in the same pattern of diversity loss and community changes that have been documented in large cities. We report a significant shift in bird communities, with lower diversity and evenness at the suburban sites, and a positive correlation between bird diversity and tree density. We conclude that even small-scale development significantly alters bird communities in the growing suburban–rural interface, and that more research is needed to identify ways to mitigate its impact.

Introduction

Urban centers, while growing rapidly, currently account for less than 3% of the Earth's land area (Schneider et al. 2010). The majority of land area becoming newly developed is located at the suburban–rural interface (Brown et al. 2005, Picket et al. 2011, Theobald 2005). The suburban–rural interface is the mosaic of urbanizing land outside of cities that includes suburban sprawl and exurban residential developments interspersed with agricultural lands, recreational parks, and preserved or otherwise undeveloped wilderness (Batty 2008, Brown et al. 2005, Picket et al. 2011, Theobald 2005). Understanding the effects of urbanization in the suburban–rural interface is critical to biodiversity both because urbanization there makes up the largest area of land-use change overall and therefore is the largest contributor to habitat loss, and also because of its close proximity to remaining wilderness where much of our vulnerable native wildlife persists (Brown et al. 2005, Destefano and Degraff 2003, Hansen 2005).

Birds are useful indicators of the overall biodiversity of wildlife and their habitats because they are easily detectable and mobile enough to escape poor habitats and quickly repopulate restored habitats. Decades of research has revealed a trend of decreased bird diversity and increased bird abundance in cities as compared to native habitats outside of cities (Chace and Walsh 2006, Evans et al. 2011, Warren and Lepczyk 2012). Cities may also experience biological homogenization, which occurs when populations of many of the same human-associated species increase

[1]Department of Biology, State University of New York – New Paltz, New Paltz, NY, 12561, USA. [*]Corresponding author - belinskk@newpaltz.edu.

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in city centers across the globe at the expense of species unique to each ecological region (Devictor et al. 2007, McKinney 2002, Murthy et al. 2016, Olden 2006). The effects of suburban and exurban development on birds have received less attention. Garaffa et al. (2009) found that larger towns have more depressed avian diversity at their centers than smaller towns and villages in Argentina, and Puga-Caballero et al. (2014) found that different land covers (cropland, grassland, or shrubland) along the rural–suburban interface of Mexico City, had different effects on species richness. In the US, urban–rural gradient studies have described a trend of higher bird diversity in the suburbs as compared to both city centers and rural areas, likely due to the overlap of human-associated species and native species that are both found in the mosaic of suburban habitats (Blair 1996, 1999; Lepczyk et al. 2008; Marzluff and Ewing 2008). However, it is still unclear if the trends of diversity loss and homogenization discovered in cities also apply to bird communities in the lower-intensity, smaller-scale urbanization that characterizes many smaller cities, towns, and villages in the rapidly expanding suburban–rural interface world wide.

Understanding avian diversity in the suburban–rural interface is an important concern, but the composition of avian communities is perhaps even more pressing given the potential homogenization that may be occurring there. Birds that dominate urbanizing communities are described as synurbic when their urban populations outnumber those in their own native habitats (Francis and Chadwick 2012). High abundances of these species likely account for the increase in overall abundance of birds in city centers (Evans et al. 2011, Kark et al. 2007, Rodewald and Bakermans 2006) and may contribute to decreased diversity by outcompeting other species (Gurevitch and Padilla 2004, Kath and Dunn 2009). Alternatively, synurbic species may lead to homogenization through biological filtering (Croci et al 2008), where synurbic species have certain ecological and behavioral traits that are pre-adapted to the conditions found within urban habitats humans create, while other species do not (González-Lagos and Quesada 2017, Sol et al. 2014). Behavioral plasticity, or the ability of many synurbic species, such as *Passer domesticus* (House Sparrow), to quickly adjust their behavior in the face of a changing environment, is likely to be an important component of this filtering process (González-Lagos and Quesada 2017). In addition, urbanization may reduce species richness because urbanized locations have reduced seasonal variability, thus favoring certain species (Leveau 2015). Many synurbic bird species are exotic or invasive species, and most are widespread generalist granivores that are not long-distance migrants (Evans et al. 2011, Lancaster and Rees 1979, Paz Silva et al. 2016). Non-synurbic species typically include specialist insectivores, ground-nesters, and species that migrate across long distances (Blair and Johnson 2008, Sol et al. 2014). Long-distance migrants are particularly vulnerable to extinction because they depend on specialized habitats on their far-flung breeding and wintering grounds, as well as at key stopover points along their migration routes (Faaborg et al. 2010). Very few species of migratory birds worldwide currently have all types of their habitats protected, and many of these species are suffering global or local extinctions or are listed as threatened or endangered species (Runge et al. 2015).

In this study, we explored the effects of low-intensity, small-scale urbanization on avian species diversity and community composition in a region where suburban and exurban development interfaces with extensive preserved lands, at a far edge of one of the most urbanized regions of the world (Greater New York City, NY, USA). We surveyed avian diversity and composition on the suburban campus of the State University of New York (SUNY) at New Paltz and compared them to nearby forested sites separated by exurban development. Specifically, we asked whether bird communities differ between a low-urbanization site (i.e., university campus) and forest sites in terms of diversity, relative abundance, and species composition. We additionally assessed whether any recorded differences were associated with differences in tree community composition and structure. If the low-intensity, small-scale development style of our campus is not problematic for any of the bird species present in the area, then we expect to find similarly diverse bird communities on our campus and in our forest sites. However, if the avian community differs, we hypothesize that tree diversity, composition, size, or density may account for some portion of this difference and direct us towards possibilities for studying how to limit any deleterious effects of urbanization with regard to avian populations on our campus and across the suburban–rural interface.

Methods

Field-site description

We assessed bird and tree diversity, abundance, and community composition at 3 forest sites and 3 suburban sites on or near the campus of the State University of New York (SUNY) - New Paltz in Ulster County, NY, USA (41.74°N, 74.09°W, elevation: 75m; Fig. 1). The forest sites are all undeveloped 50- to 100-year-old secondary growth mixed coniferous and deciduous forests, which is the current native habitat for this historically agricultural region (i.e., the forests were cut and farmed, but have been re-growing undisturbed for >50 years now). The campus is 87 ha in area, with a roughly 20-ha forest fragment at its southern end. The campus houses a student population of 7658 (as of 2015), and is located 2 blocks from the downtown of the small village of New Paltz with a population of 6924 (as of 2013). The village and campus are surrounded by a combination of agricultural lands (apple orchards and small vegetable farms), rural and suburban residential neighborhoods, small conservation lands, and other small nearby towns. However, due west of New Paltz is a large tract of conservation land comprised of Minnewaska State Park and the private, non-profit Mohonk Preserve, which together protect over 12,000 ha of the Shawanagunk Mountain Ridge. New Paltz may be considered suburban due to its location near the far edge of the suburban fringe of one of the largest and most intensely developed urban zones in the United States: the New York City–Newark metropolitan area (Nowak 2005). The campus is also located in a region with high rates of urbanization and exurbanization: the Atlantic Forest region of the US (Nowak and Walton 2005, Seto et al. 2012). On the other hand, since New Paltz is a small campus and village immediately surrounded by low-density development and bordered by a large swath of preserved lands, it can be also be considered an example of exurban development.

The SUNY New Paltz campus includes areas that vary in terms of pedestrian traffic, density of buildings, and types of plantings, but the entire campus contains a relatively high number of trees. Campus sites consisted of the 3 main turf-covered quads that include many large trees in 3 different areas of campus (Fig. 2): (1) the "central campus" quad, a smaller quad (7143 m^2) centrally located amid the largest academic buildings with the heaviest pedestrian traffic (41.74°N, 74.08°W); (2) the "historic campus" quad (13,936 m^2), which is surrounded by older buildings and experiences moderate pedestrian traffic (41.74°N, 74.04°W); and (3) the "residential campus" quad (9048 m^2), a quad with large trees set among dormitories nearer to the edge of campus where pedestrian traffic is lighter (41.73°N, 74.08°W). Our 3 forest sites varied from a small suburban forest fragment to a site at the edge of a large protected forest. The "campus forest" site (20 ha) is adjacent to the campus and bordered by playing fields, abandoned apple orchards, and suburban housing (41.73°N, 74.08°W). The "gatehouse forest" site

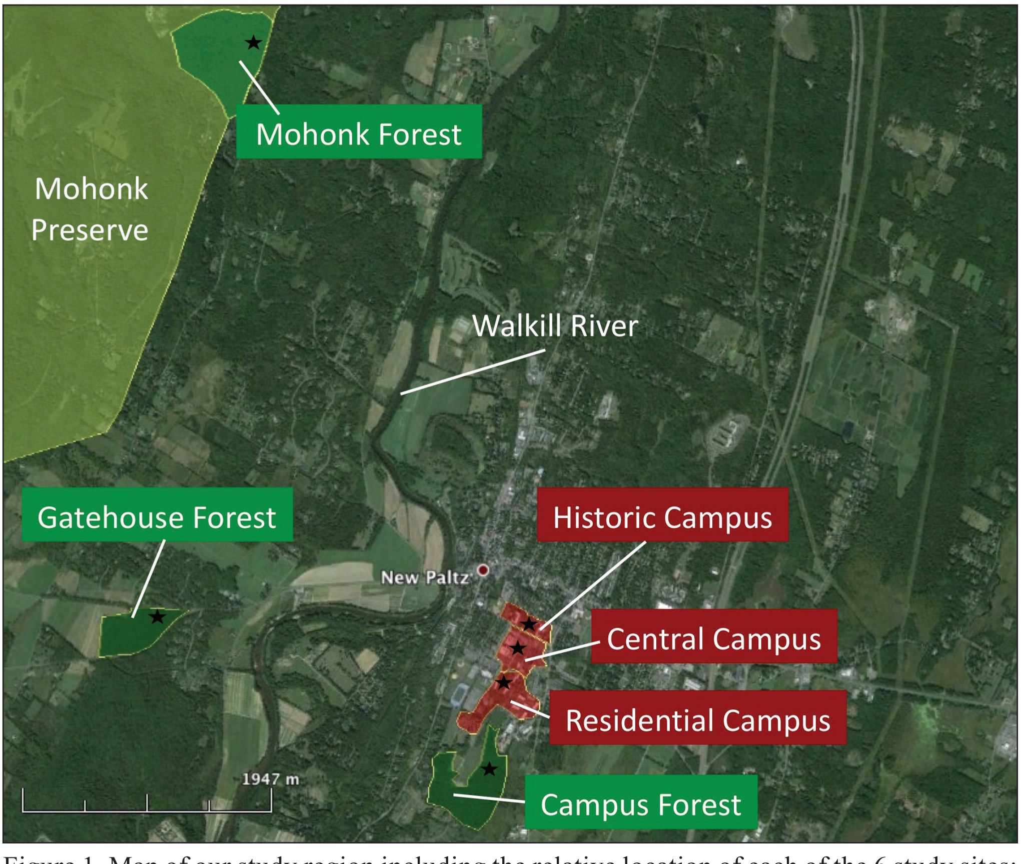

Figure 1. Map of our study region including the relative location of each of the 6 study sites: 3 "campus" sites at SUNY New Paltz shaded in red, and 3 "forest" sites adjacent (campus forest) or near to campus (gatehouse and Mohonk forests are <5 miles from campus) shaded in green. The gatehouse forest is similar in area to the campus forest, while the Mohonk forest is a lowlands forest fragment contiguous with the much larger upland/ridge forests of the Mohonk Preserve (visible portion shaded in yellow).

(15 ha) is a forest fragment 4.5 km from campus and surrounded by agricultural land (hay/corn) and nearby suburban housing (41.74°N, 74.12°W). The "Mohonk forest" site is 4.7 km from campus and 1.8 km from the gatehouse forest (41.78° N, 74.11° W). This site is bordered by the Mohonk Preserve on 3 sides and low-density, rural, exurban, housing on the fourth side.

Bird surveys

We conducted 10-minute point counts at the center of a circle with a 50-m radius within each of 3 forest sites and inside the 3 rectangular campus quads described above (Petit et al. 1995, Ralph et al. 1993) on 4 dates during the height of the breeding season in May and June of 2014. Most birds are singing at this time of year in the temperate zone, which aids in maximizing the detection and identification of species (Ralph et al. 1993). We visited each site in succession on each point-count date beginning just after dawn at 5:00 am and finishing by 10:00 am, when most birds are singing consistently (Ralph et al. 1993). We rotated the order of our visits to the sites to balance the time of day for sites in each category across the dates. Since these are unbanded bird populations, we consider abundance data as the largest number of individuals of each species seen at one time or heard singing from different locations simultaneously. Because of this limitation, the abundances we report here are likely conservative underestimates, especially for the species with large populations. Each point-count sample was completed by K.L. Belinski and 1 additional observer on each date. The second observer was one of a pair of experienced volunteers, each of whom assisted with the complete cycle of sampling on 2 of 4 dates. We calculated bird species richness for each site by tallying all of the species detected across the 4 point counts at that site, relative frequencies of each bird species at each site by dividing the total counts of each species across the 4 point counts by the total number of bird counts within that site, and Simpson's

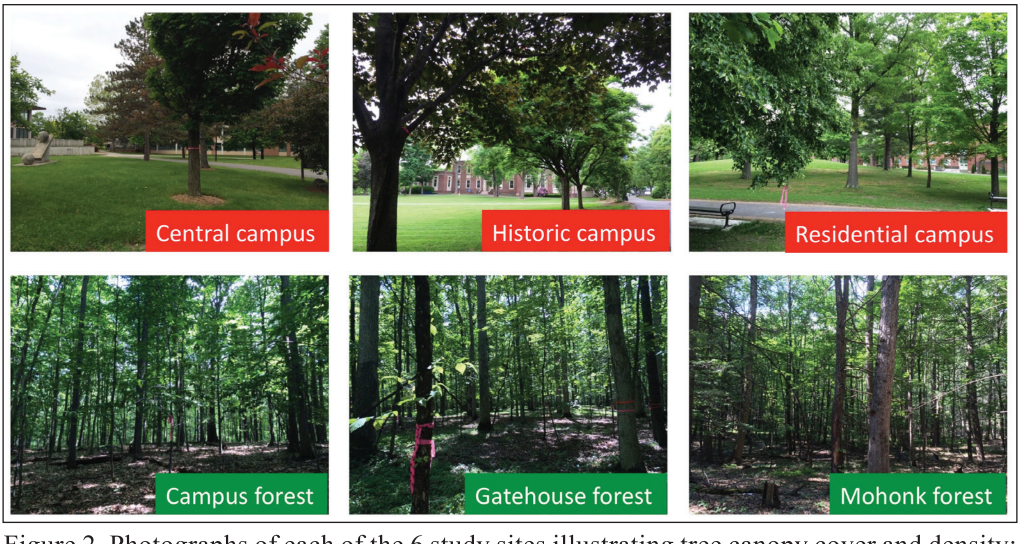

Figure 2. Photographs of each of the 6 study sites illustrating tree canopy cover and density: 3 "campus" sites at SUNY New Paltz, and 3 "forest" sites.

indices (1/D) for each site from relative frequencies of each species (Magurran 1988). We calculated mean species richness and mean Simpsons' index across the 3 sites for each group of sites (forest vs. campus).

Survey sites and habitat variables

Our study was intended to establish if the urbanization of our campus had consequences for the bird community and, if so, to begin exploring how this type of development might cause these effects by assessing the tree community. We chose to begin with the campus trees because trees are fairly plentiful on our campus and are the obvious structural feature used by birds that is common to both forest and campus sites. We measured tree diversity and abundance on various dates from fall 2012 to fall 2014. Tree diversity and abundance was sampled by E.G. Keeling and D.R. Snyder, with help from groups of additional volunteers at some sites. On campus, we identified, counted, and measured diameter at breast height (DBH) for all trees >2.5 cm DBH (Avery and Burkhart 2001) inside the 3 campus quads. Two categories of campus trees that were not identified to species level (ornamental cultivars of apple and rose species; Table 1) were each lumped as a single species group. Within each forested site, we identified, counted and measured DBH of all trees >2.5 cm DBH in three 400-m^2 plots centered on the bird point-count location and running approximately parallel to the nearest road. The 3 plots were separated by at least 20 m, so total area sampled was representative of a larger area (12,000 m^2 per site), similar to the total area assessed in the bird point counts. The forested sites required sub-sampling using these plots due to the much higher densities of trees growing there as compared to the campus plots where all trees were easily measured and counted. We calculated tree densities for each site by dividing the total number of trees counted by the area sampled (this corrects for the difference in areas between the fully sampled campus sites and sub-sampled forest sites), tree species richness for each site as the tally of all tree species observed (pooled from 3 plots for forest sites), and overall relative densities of tree species by dividing the total counts per area of each species by the total number of trees counted across all sites for each type of site (forest vs. campus). Basal areas for each tree were determined from measured DBH's by assuming circular stems. We calculated overall relative basal areas by summing all basal areas for each species and dividing by the total basal area for each type of site. Dead trees (not identified to species) were included in total density and basal area estimates. We calculated relative importance values for each tree species across each type of site (forest vs. campus) as relative density plus relative basal area divided by 2. We compared bird and tree community composition using rank abundance charts categorized into ecologically important groups of species. We categorized birds as "invasive species" (species introduced from outside the region with robust populations), "regional native species" (species native to the region year-round), and "migratory native species" (migratory species native to the region during the breeding season), and tree species were categorized as "regional native" (species native to the region), "non-native" (species originally from outside the region), or "human-associated" (native species that are rare outside of highly managed locations within the region).

Statistical analysis

For statistical analyses, we treated each site as an independent sampling unit, and categorized sites into one of 2 groups: "forest" vs. "campus". We used Student's *t*-tests to test for differences between campus and forest sites in mean bird species richness and mean Simpson's diversity index, Pearson's correlations to test for relationships between bird and tree species richness and tree density across all sites, and multi-response permutation procedures (MRPP; McCune et al. 2002) to test for differences in bird community composition between forest and campus sites. MRPP is a non-parametric test that is applied to a multi-variate response matrix (species abundance values per site) and uses distance measures to generate average matrix distances for each test group. MRPP also generates a within-group agreement statistic, A, which measures effect size. $A = 1$ when all sample units within a group are identical, and $A = 0$ when groups are no more similar than expected by chance. We used a Monte-Carlo test to generate a significance value (p) for differences between groups. Our MRPP analyses used the Sørensen distance measure. We used the software program PC-Ord (McCune et al. 2002) for the MRPP analyses and JMP 10 software for Mac for all other analyses.

Results

We detected a total of 335 birds representing 38 species during our point counts (Table 1). The diversity of the bird communities differed significantly between campus and forest sites. The total avian species richness at our forest sites (32 species) was double the number detected at campus sites (16 species). Mean bird diversity was also significantly higher at forest than campus sites, both in terms of mean species richness (Student's t: $t = 5.14$, $P < 0.01$) and the Simpson's diversity index (Student's t: $t > 4.25$, $P < 0.04$) (Table 2). Bird diversity was similar within forest and within campus categories of sites, with the overall greatest number of species (21) recorded at the gatehouse forest site, which is the intermediate forest site in terms of its size and distance from campus (Table 2). Total bird abundances were similar between campus and forest sites (Student's t: $t = -0.77$, $P = 0.48$) because abundances varied among sites within each category: the residential campus site had a somewhat lower bird abundance than the 2 other campus sites, while the gatehouse forest site had a higher bird abundance than the other 2 forest sites (Table 2) .

In addition to reduced bird diversity, the community composition of birds also differed markedly between campus and forest sites, with campus sites featuring many invasive and synurbic species and few long-distance migrants. Based on MRPP analyses, bird species composition was significantly different between forest and campus communities, with a within-group agreement (A) of 0.43 (Monte-Carlo test: $p = 0.02$), which is considered a "large effect" (Peck 2016). Average Sørensen distance was similar for both groups (0.36 for campus sites, and 0.38 for forest sites), indicating similar within-group heterogeneity. The campus bird community was dominated by invasive species, with 86 of 181 (48%) individual birds observed on campus belonging to 2 invasive species: House

Table 1. Bird and tree species list. Common and scientific bird names follow the American Ornithological Association's Check-list of North American Birds (http://checklist.aou.org/). [Table continued on the following page.]

Common name	Scientific name	Authority
Birds		
American Crow	*Corvus brachyrhynchos*	C.L. Brehm
American Goldfinch	*Spinus tristis*	(L.)
American Robin	*Turdus migratorius*	L.
Black and White Warbler	*Mniotilta varia*	(L.)
Black-capped Chickadee	*Poecile atricapillus*	(L.)
Black-throated Green Warbler	*Setophaga virens*	(J.F. Gmelin)
Blue Jay	*Cyanocitta cristata*	(L.)
Blue-headed Vireo	*Vireo solitarius*	(A. Wilson)
Cedar Waxwing	*Bombycilla cedrorum*	Vieillot
Chimney Swift	*Chaetura pelagica*	(L.)
Chipping Sparrow	*Spizella passerina*	(Bechstein)
Common Grackle	*Quiscalus quiscula*	(L.)
Common Raven	*Corvus corax*	L.
Downy Woodpecker	*Picoides pubescens*	(L.)
Eastern Wood Pewee	*Contopus virens*	(L.)
European Starling	*Sturnus vulgaris*	L.
Gray Catbird	*Dumetella carolinensis*	(L.)
Great Crested Flycatcher	*Myiarchus crinitus*	(L.)
Hairy Woodpecker	*Picoides villosus*	(L.)
House Finch	*Haemorhous mexicanus*	(P.L. Statius Müller)
House Sparrow	*Passer domesticus*	(L.)
Louisiana Waterthrush	*Parkesia motacilla*	(Vieillot)
Mourning Dove	*Zenaida macroura*	(L.)
Northern Cardinal	*Cardinalis cardinalis*	(L.)
Northern Flicker	*Colaptes auratus*	(L.)
Northern Mockingbird	*Mimus polyglottos*	(L.)
Ovenbird	*Seiurus aurocapilla*	(L.)
Pileated Woodpecker	*Dryocopus pileatus*	(L.)
Pine Warbler	*Setophaga pinus*	(L.)
Red-bellied Woodpecker	*Melanerpes carolinus*	(L.)
Red-eyed Vireo	*Vireo olivaceus*	(L.)
Red-tailed Hawk	*Buteo jamaicensis*	(Gmelin)
Red-winged Blackbird	*Agelaius phoeniceus*	(L.)
Scarlet Tanager	*Piranga olivacea*	(J.F. Gmelin)
Song Sparrow	*Melospiza melodia*	(A. Wilson)
Tufted Titmouse	*Baeolophus bicolor*	(L.)
White-breasted Nuthatch	*Sitta carolinensis*	Latham
White-throated Sparrow	*Zonotrichia albicollis*	(J.F. Gmelin)
Wood Thrush	*Hylocichla mustelina*	(Gmelin)
Trees		
American Beech	*Fagus grandifolia*	Ehrh.
American Elm	*Ulmus americana*	L.
Apples	*Malus* spp.	Mill.
Austrian Pine	*Pinus pallasiana*	Lamb.
Basswood	*Tilia americana*	L.
Bigtooth Aspen	*Populus grandidentata*	Michaux

Sparrows (55) and *Sturnus vulgaris* (European Starling; 31) (Fig. 3A). The second most commonly observed species at campus sites was *Turdus migratorius* (American Robin; 45), a synurbic species common to areas with expansive lawns and scattered trees. Regional native species excluding the American Robin accounted for 17.7% of observations, while long-distance migrants accounted for the remaining 9.9% of birds detected on campus. The long-distance migrants were primarily the lawn- and human-associated *Spizella passerina* (Chipping Sparrow; 12) and *Chaetura pelagica* (Chimney Swift; 1), although they also

Table 1, continued.

Common name	Scientific name	Authority
Bitternut Hickory	*Carya codiformis*	(Wangenh.) K. Koch
Black Locust	*Robinia pseudoacacia*	L.
Black Oak	*Quercus velutina*	Lamark
Black Walnut	*Juglans nigra*	L.
Blue Magnolia	*Magnolia acuminata*	(L.) L.
Blue Spruce	*Picea pungens*	Engelm.
Butternut	*Juglans cinerea*	L.
Eastern Hemlock	*Tsuga canadensis*	(L.) Carrière
Eastern Hornbeam	*Ostrya virginiana*	(Mill.) K. Koch
Eastern Red-Cedar	*Juniperus virginiana*	L.
Eastern Redbud	*Cercis canadensis*	L.
Eastern White Pine	*Pinus strobus*	L.
Flowering Dogwood	*Cornus florida*	L.
Honey Locust	*Gleditsia triacanthos*	L.
Ironwood	*Carpinus caroliniana*	Walter
Juneberry	*Amelanchier arborea*	(F. Michx.) Fernald
Kousa Dogwood	*Cornus kousa*	Hance
Nikko Fir	*Abies homolepis*	Siebold & Zucc.
Norway Maple	*Acer plataniodes*	L.
Norway Spruce	*Picea abies*	(L.) Karst.
Pignut Hickory	*Carya glabra*	(Mill.) Sweet
Pin Oak	*Quercus palustris*	Muenchh.
Red Maple	*Acer rubrum*	L.
Red Oak	*Quercus rubra*	L.
Roses	*Rosaceea* spp.	L.
Russian Olive	*Elaeagnus angustifolia*	L.
Shagbark Hickory	*Carya ovata*	(Mill.) K. Koch
Silver Maple	*Acer saccharinum*	L.
Sourgum	*Nyssa sylvatica*	Marsh.
Sugar Maple	*Acer saccharum*	Marsh.
Sweet Birch	*Betula lenta*	L.
Sycamore	*Platanus occidentalis*	L.
Tulip Tree	*Liriodendron tulipifera*	L.
Turkish Hazel	*Corylus colurna*	L.
White Ash	*Fraxinus americana*	L.
White Fir	*Abies concolor*	(Gordon & Glend.) Lindl. ex Hildebr.
White Oak	*Quercus alba*	L.
White Spruce	*Picea glauca*	(Moench) Voss
Witch-hazel	*Hamamelis virginiana*	(L.) Gronov.

included the edge habitat-associated *Dumetella carolinensis* (Gray Catbird; 3) and single observations each of the typically forest-dwelling *Vireo olivaceus* (Red-eyed Vireo) and *Contopus virens* (Eastern Wood Pewee).

Table 2. Bird abundance and diversity across sampling sites.

Site	Mean abundance	Species richness	Simpson's diversity
Historic campus	10.50	9	3.90
Central campus	16.25	11	5.45
Residential campus	11.75	8	5.13
Mean all campus	15.08	16	4.82
Campus forest	18.25	17	9.00
Gatehouse forest	15.00	21	14.62
Mohonk forest	8.00	19	13.07
Mean all forest	12.83	32	12.23

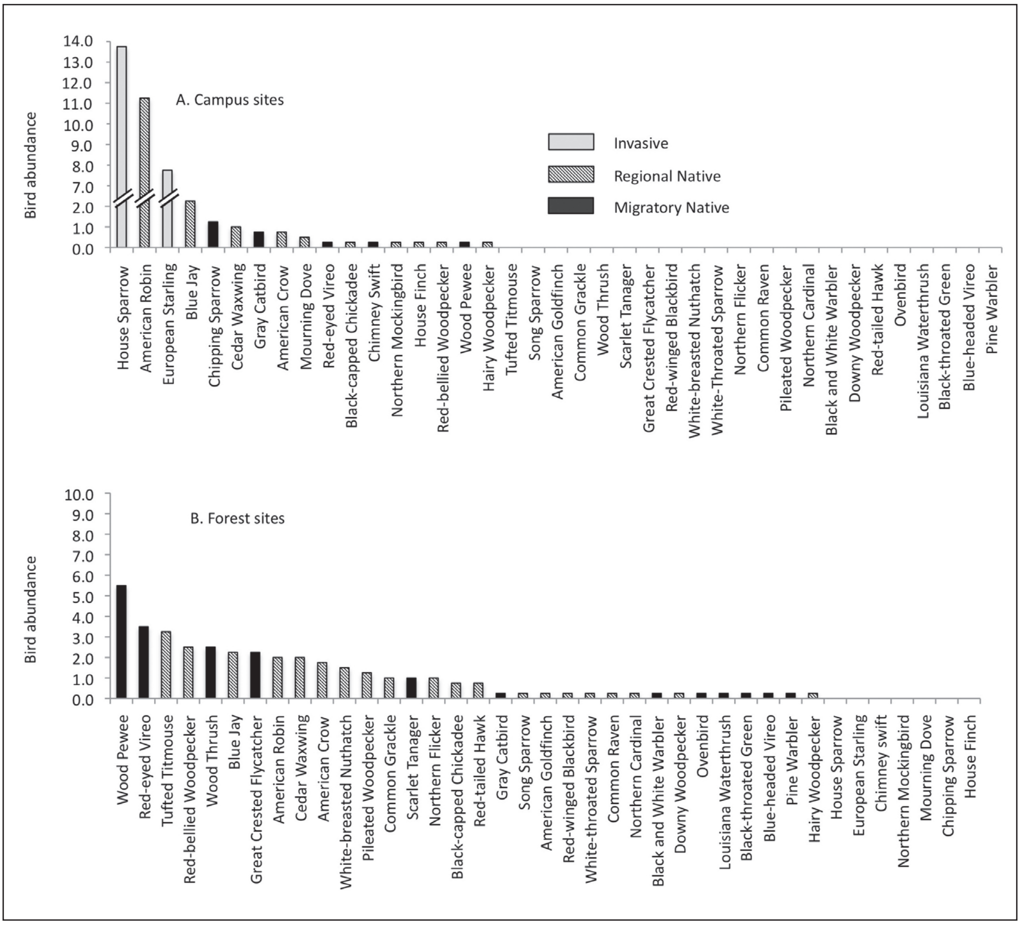

Figure 3. Rank abundance charts for birds using mean abundance per species at (A) campus sites, and (B) forest sites. Note that the Y axis in panel A is broken above 2, to allow for the first 3 bars to be lowered while the rest of the bars are at the same scale as in panel B. Mean abundance of House Sparrow = 13.75, American Robin = 11.25, and European Starling = 7.75.

In the forest sites, no invasive bird species were detected, and the 2 most commonly observed species were long-distance migrants, the Eastern Wood Pewee (22) and the Red-eyed Vireo (14) (Fig. 3B). Fifty-seven percent of the forest birds detected were regional native species, including 8 American Robins and 7 *Corvus brachyrhynchos* (American Crow). The remaining 43% of the birds detected in the forest sites were long-distance migrants, including the aforementioned Eastern Wood Pewee and Red-eyed Vireo, with the final 20% of the migrants represented by 9 other species including *Hylocichla mustelina* (Wood Thrush), *Piranga olivacea* (Scarlet Tanager), and 5 wood warbler species. Rank abundance charts of the bird species (Fig. 3), show that the campus sites not only had lower overall diversity and higher abundances of invasive and synurbic species, but that the evenness of the community was lower than the forest communites, which were more species-rich and native-dominated.

We measured 496 trees representing 43 species and 3 species groups during the study (Table1). Tree species richness was similar between forest and campus sites (Table 3). Bird species richness was not related to tree species richness (r = -0.10, P = 0.85) (Fig.4A). Tree richness was similar among the 3 forest sites, but varied

Table 3. Tree density and diversity across sampling sites.

Site	Density (trees/ha)	Species richness	Shannon diversity
Historic campus	56	21	2.59
Central campus	63	8	1.60
Residential campus	63	12	2.15
Mean all campus	60	14	2.82
Campus forest	1208	15	1.83
Gatehouse forest	967	14	2.07
Mohonk forest	692	12	1.81
Mean all Forest	956	14	2.50

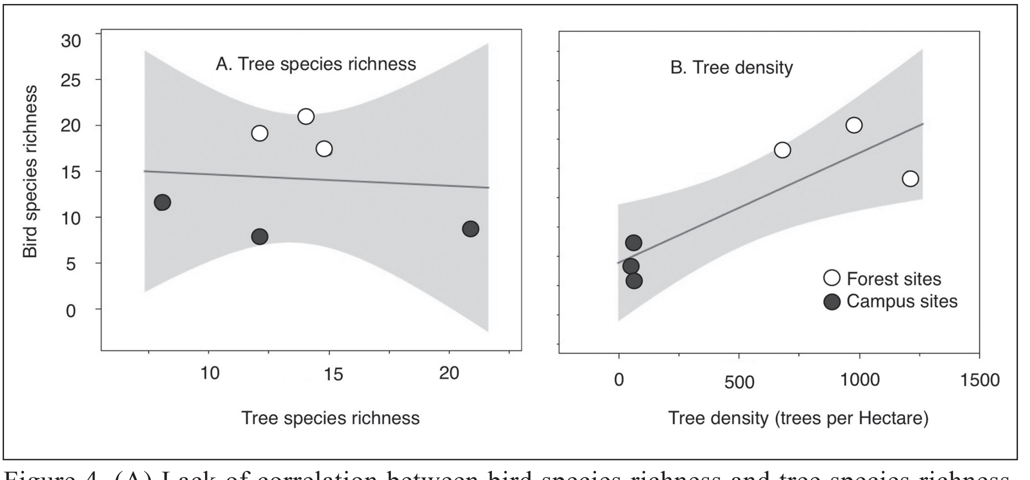

Figure 4. (A) Lack of correlation between bird species richness and tree species richness. (B) Positive correlation between bird species richness and tree density. Trend lines represent linear regressions and the gray shading represents 95% confidence intervals.

among campus sites (historic campus had the highest species richness and central campus had the lowest species richness of all sites). Trees at all 3 campus sites were larger than those at the campus and gatehouse forest sites, but overlapped in DBH with trees at the Mohonk forest site, and so the difference in mean DBH between campus and forest sites overall was not statistically significant (t = -2.46, P = 0.07).

Tree density was significantly lower at campus sites than that at forest sites (t = 6.00, P < 0.01). The trees on the campus sites grew in clumps or rows over areas of bark mulch that were separated from each other by expansive lawns and numerous paved walkways, whereas all forest sites were more or less continuous forest with a closed canopy and natural leaf-litter covering the ground. A few patches of dense ornamental shrubs grew on campus, while the forests had very little undergrowth except at the forest edges, which were outside of our sampling areas. Because there were fewer trees overall on campus, bird species richness was positively correlated with tree density (r = 0.88, P = 0.02; Fig. 4B).

Similarly to the way that bird species composition differed between forest and campus sites, tree species composition also varied in respect to numbers of non-native and human associated species found on campus. Campus trees included a higher overall proportion of non-native and human-associated species (17 out of 28 species), whereas forest sites had only 1 non-native species out of 25 total species (Fig. 5). While the native *Acer saccharum* (Sugar Maple) had the highest importance value on campus, and 2 other native species also had importance scores above 0.05 on campus (*Pinus strobus* [Eastern White Pine], and *Quercus rubra* [Red Oak]), shared species between campus and forest was low overall—only 6 tree species were present in both sampling areas (Fig. 5). Several trees of high importance in the forested sites (e.g., *Tsuga canadensis* [Eastern Hemlock], *Quercus alba* [White Oak], *Ostrya virginiana* [Eastern Hornbeam], *Fagus grandifolia* [American Beech]) were absent from campus sites (Fig. 5).

Discussion

Bird communities differed significantly between the campus and forest sites. Total bird species richness on campus was half that detected in the forests, and bird diversity based on the Simpson's diversity index was also significantly lower at our campus sites than at our forest sites, although overall abundances were similar. Our campus bird community was dominated by 3 synurbic species that comprised 72% of the total bird abundance detected on campus. Two of the 3 are invasive bird species (House Sparrow and European Starling) that are common across the temperate zone worldwide (Jokimäki and Kaisanlahti-Jokimäki 2003, McKinny 2002), and the third is a native species (American Robin) that thrives in anthropogenic habitats with lawns and trees (Aldrich and Coffin 1980). In addition, few species of long-distance migrants were found on campus, but many ecologically sensitive forest-dependent species, including 9 long-distance migrant species were found only in the forest sites. These results indicate that the scope and style of development of our relatively tree-filled suburban campus has significantly shifted the campus bird community. These results echo the general patterns of bird diversity loss and homogenization observed in large cities worldwide (Devictor et al. 2007, Leveau et al. 2015, Murthy et al. 2016, Shanahan et al. 2014, Warren and Lepczyk 2012). Similar results have been reported from other studies where bird diversity was compared to habitat parameters such as the density of roads, buildings, and green spaces across other university campuses including one featuring a similar-sized campus in a small city in coastal northern California, USA (Kalinowski and Johnson 2010) and another near a larger city in the tropics: greater Manila in the Philippines (Vallejo et al. 2008).

In many cases, it is unclear whether invasive or synurbic species cause a reduction in native species diversity directly, or if the diversity loss is due to habitat changes resulting from development that also favor these species (Gurevitch and Padilla 2004). However, at a rapidly urbanizing city (Morelia, Mexico), MacGregor-Fors et al. (2010) found that sites recently invaded by House Sparrows had lower

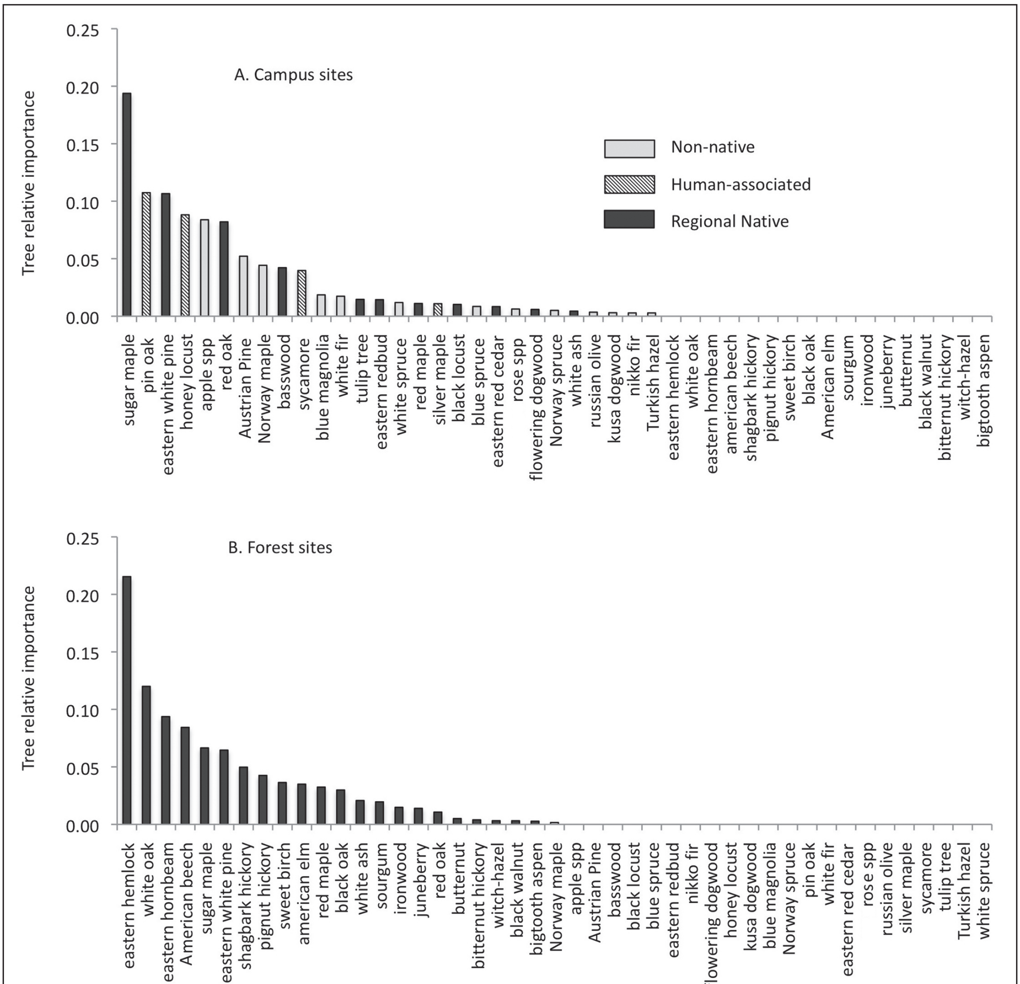

Figure 5. Rank abundance charts for trees using relative importance (relative density plus relative basal area divided by 2) per species at (A) campus sites, and (B) forest sites.

species diversity and evenness, and those with House Sparrows had much higher bird abundances because of the large numbers of this species dominating these communities. They also found that community composition changed after House Sparrow invasion, and that populations of several native species were reduced or lost altogether. In fact, Shochat et al. (2010) propose that dominant urban species, including House Sparrows, have higher foraging efficiency, which may partially explain their dominance in urban centers. Habitat conversion due to urbanization may start a process that changes relationships between the species in a community that result in diversity loss, indicating the need to understand both the broad trends of how urbanization affects biodiversity and also the details of between-species interactions in the wake of that urbanization.

Our study is limited in that we only surveyed 3 sites on 1 campus and 3 sites in nearby forest fragments, and because we sampled on only 4 dates at each site. It is telling that our results are significant even at these low sample sizes, and it is likely that our results are conservative. However, data from a nearby site offers an estimate of species we may have missed at 1 forest site. A Breeding Bird Census (BBC) plot, referred to as the Duck Pond BBC (DPBBC), is located 2 km farther inside the Mohonk Preserve as compared to our Mohonk forest site. The Duck Pond BBC plot is ~30 ha in area and was last surveyed in 2011. Sampling included 11 separate May and June dates using a standard, 2-hour BBC spot-mapping protocol for counting territories of breeding (singing) birds throughout the plot. The DPBBC survey results include a total of 31 species, with 13 of the same species we detected and 18 species that we did not observe, which included 9 species of long-distance migrants, most of which are wood warbler species (Tables 4, 5; Mohonk Preserve, New Paltz, NY, upubl. data). The discrepancy between our results and those gathered at the nearby DPBBC indicate that our estimate of the differences between bird diversity on campus and in the forests is probably an underestimate, and that the actual differences are likely much larger.

Tree species richness was similar at our campus and forest sites. The lack of difference in tree diversity explains why tree diversity was not correlated with bird diversity; however, this lack of relationship also suggests that tree diversity, at least on its own, is not sufficient to support a diverse bird community on our campus.

Table 4. Bird species list for those found at the DPBBC site. but not in our survey of the Mohonk forest site Common and scientific bird names follow the American Ornithological Association's Check-list of North American Birds (http://checklist.aou.org/).

Common name	Scientific name	Authority
American Redstart	*Setophaga ruticilla*	(L.)
Baltimore Oriole	*Icterus galbula*	(L.)
Barred Owl	*Strix varia*	Barton
Blackburnian Warbler	*Setophaga fusca*	(Statius Müller)
Brown-headed Cowbird	*Molothrus ater*	(Boddaert)
Cerulean Warbler	*Setophaga cerulea*	(A. Wilson)
Common Yellowthroat	*Geothlypis trichas*	(L.)
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	(L.)
Wild Turkey	*Meleagris gallopavo*	L.

The campus tree community was characterized by a smaller number of trees that translated into lower tree density on campus. In contrast, the tree communities at the forest sites contained overall higher densities of almost exclusively native tree species. Tree species richness and composition in any urbanized landscape is the consequence of remaining native species and those that were subsequently planted and maintained, and these attributes vary by land-use type (Jim and Lui 2001,

Table 5. Comparison of bird species detected at the Mohonk forest site in the present study and those detected at the nearby Duck Pond BBC plot in 2011. Ten-minute point counts at a single location were completed in the present study while the Duck Pond was surveyed using far more extensive spot-mapping protocols covering a large area. X denotes species presence, while O denotes absence. Long-distance migrants are highlighted by ***.

Bird species	Mohonk forest	Duck Pond BBC
Common Grackle	X	O
Northern Flicker	X	O
Common Raven	X	O
Black-throated Green Warbler***	X	O
Pine Warbler***	X	O
Blue-Headed Vireo***	X	O
Blue Jay	X	X
Tufted Titmouse	X	X
Black-capped Chickadee	X	X
White-breasted Nuthatch	X	X
Red-bellied Woodpecker	X	X
Pileated Woodpecker	X	X
Downy Woodpecker	X	X
Great Crested Flycatcher***	X	X
Red-eyed Vireo***	X	X
Eastern Wood Pewee***	X	X
Louisiana Waterthrush***	X	X
Wood Thrush***	X	X
Scarlet Tanager***	X	X
Hairy Woodpecker	O	X
Northern Cardinal	O	X
Red-winged Blackbird	O	X
Song Sparrow	O	X
American Robin	O	X
Barred Owl	O	X
Wild Turkey	O	X
Brown-headed Cowbird	O	X
Gray Catbird	O	X
Baltimore Oriole***	O	X
Rose-breasted Grosbeak***	O	X
Worm-eating Warbler***	O	X
Black and White Warbler***	O	X
Ovenbird***	O	X
American Redstart***	O	X
Common Yellowthroat***	O	X
Blackburnian Warbler***	O	X
Cerulean Warbler***	O	X
Total number of species	19	31

McPherson 2003, Trentanovi et al. 2013). Non-native plant species are common in urbanizing landscapes world wide, but the need for and effectiveness of removing these species is controversial (D'Antonio and Meyerson 2002). Retaining native vegetation, including large native trees, in particular, has been found to increase bird diversity in urban green spaces, such as parks and residential neighborhoods (Barth et al. 2015, Lessi et al. 2016, and Threlfall et al. 2016), although Chong et al. (2014) recently found that natural vegetation and cultivated (invasive) trees were able to support bird (but not butterfly) diversity in Singapore, and Gray and van Heezik (2016) similarly report that invasive tree species sustain native bird species in some urban woodlands of New Zealand .

We found that bird diversity was correlated with tree density and that both bird and tree community composition shifted from native-dominated communities at forest sites to the appearance of various numbers and abundances of non-native species on campus. These results are concordant with the findings of Donnelly and Marzluff (2006), who report that after the extent of urbanization (a measure of land-cover use), tree density most strongly correlated with overall songbird species richness and the retention of native bird species surveyed in developed areas. In our study, the association between low bird diversity and lower tree density on campus may be an artifact of correlations with other factors we did not measure that separate our campus and forest sites, including human-disturbance levels (pedestrian, vehicular, noise, and light differences), the large extent of lawn and urban (i.e., impervious) land cover interrupting the tree canopy, and the lack of understory or natural ground cover, such as leaf litter (Aronson et al. 2017, Francis et al. 2009, Marzluff 2016, Longcore and Rich 2004, Platt and Lill 2006). However, the presence of the campus trees likely does enhance the diversity and abundance of birds to some degree because many are large trees and are either remnant native or older invasive species, each of which have recently been linked to increases in bird diversity in urban settings (Barth et al. 2015, Chong et al. 2014, Gray and van Heezik 2016, and Threlfall et al. 2016), and on our campus they appear to support arboreal species that we detected, such as Black-capped Chickadee and Red-bellied Woodpecker. Other researchers have reported that tree cover, forest complexity, tree density, or tree size predict the prevalence of native bird species in the residential suburbs (Degraff and Wentworth 1986) and forests (Robbins et al 1989) of the Eastern US.

Aronson et al. (2014) compiled a vast data set for bird and plant diversity in many cities worldwide. They found that while cities are dominated by a few cosmopolitan species and contain vastly reduced densities of both birds and plants, they are still populated mainly by native species, implying that even the world's largest cities provide habitat for wildlife that can be maximized. Sol et al. (2014) assessed the loss or retention of over 800 bird species between urban, suburban, and control (surrounding) sites in a large number of locations scattered across the globe, and found that urban species loss is associated with the narrow life-history strategies of many species that reduce success in urban environments, especially non-communal nesting in open areas or on the ground and having either few broods per year or few lifetime breeding attempts. Understanding how and why urbanization affects various species in exurban, suburban, and urban locations across the planet is critical to helping us decide how we can preserve the wildlife we have and manage the growth and development of our cities and towns into the future. In our study, we report avian diversity loss and increasing dominance of synurbic bird species in response to low-intensity, small-scale urbanization on our campus. We also offer the preliminary finding that while tree diversity per se is likely not a factor, reduced tree density as well as the abundance of human-associated tree species may be among the factors affecting bird communities on our campus. Future research is needed to delineate which types of landscaping and development best support wildlife on our campus and at other sites along the rapidly expanding suburban–rural interface.

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