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Influence of human population size and the built environment on avian assemblages in urban green spaces

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Abstract While studies of how habitat patch dynamics structures avian communities in urban environments has received some attention, there is considerably less known of how the built environment and human population size may influence the structuring of urban bird communities. We investigated bird populations in Pittsburgh, Pennsylvania (U.S.A.) through replicated point count surveys of breeding birds in 50 parks and cemeteries of varying sizes. We counted 4,435 individual birds in 441 counts. Of the 61 species detected, 27 were rare (detected at <8 points). Migratory species accounted for 46.1 % of all individuals, while 23.2 % of all individuals were of introduced species. Species richness increased significantly with green area size, as did the number of rare species. Species diversity decreased significantly with an increase in the proportion of individuals of introduced species; in particular, cavity nesters were less abundant when introduced species were present. Elements of the built urban environment including commercial development and transportation corridors were associated with significant reductions in park-wide species richness, mean number of species per point, and mean number of individual birds recorded per point. Human population size was positively related to increased numbers of individuals of introduced species, but a lower mean number of species per point. Ours is among the first to identify specific relationships between avian population characteristics and human population size, as few other studies have specifically incorporated human population size into a local, fine grain study design. Our data suggest that human population size is an important

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parameter that can be measured independently of characteristics of the built environment and the physical characteristics of the park itself as a correlate of avian diversity and abundance. Our study points to a variety of trade-offs needed to manage habitat for birds in urban settings.

Keywords Biotic homogenization · Introduced · Exotic · Human population · Breeding birds · Landscape

Introduction

The process of urbanization is pervasive and affects biodiversity worldwide (McKinney 2002; Nelson et al. 2010). Understanding the ecology of urban ecosystems provides important insight into the effects of land development on patterns of species richness, abundance, and biodiversity (Marzluff 2001). Previous studies of the impacts of urbanization on birds have largely focused on reductions or shifts in species compositions resulting from habitat changes. They most often document changes along a gradient of urbanization intensity (McKinney 2002), and generally conclude that bird species richness decreases with urbanization across a wide range of habitats (Marzluff 2001; Chace and Walsh 2006). Groups of birds thought to be most impacted by urbanization include ground-nesters, habitat specialists, and those requiring large areas of intact habitat (Chace and Walsh 2006; McKinney 2006). Species losses have been attributed to habitat fragmentation and the species-area effect, loss of vegetative complexity and the structural simplification of remaining habitat (Savard et al. 2000; Marzluff and Ewing 2001; Luck 2007b; Luck et al. 2010), as well as competition with introduced species (Pimentel et al. 2000). Identifying these and other potential correlates of urban biodiversity loss can yield important information for bird management and conservation (Clergeau et al. 1998; Donnelly and Marzluff 2004).

In urban areas, a major factor influencing the presence or absence of many bird species is habitat destruction through commercial and residential development and forest fragmentation (Marzluff et al. 2001). Public parks and cemeteries thus become the only "green areas" available to birds (Pickett et al. 2001). Ecological theory suggests that with a decrease in habitat patch size there is a decrease in species richness (MacArthur and Wilson 1967). These species-area relationships have been shown for numerous island-type systems including oceanic islands (MacArthur and Wilson 1967), isolated mountaintops (Cook 1974), and patches of fragmented forest (Galli et al. 1976). Similar trends have been observed in urban parks (Donnelly and Marzluff 2004).

Beyond the direct loss and fragmentation of habitat, of particular importance for avian species richness and diversity in urban areas have been studies showing negative impacts on birds resulting from changes to vegetation parameters and the simplification of the habitat (Rebele 1994; Bonier et al. 2007; Chiari et al. 2010). A commonly observed result of urbanization is biotic homogenization, which can include taxonomic homogenization, or the increase in species similarity in space over time, and functional homogenization, or the decrease in functional diversity among species in the community such that specialist species are progressively replaced by generalist species more tolerant of human disturbance (McKinney and Lockwood 1999; Olden and Rooney 2006; Devictor et al. 2008). With biotic homogenization, introduced and synanthropic species, which on the whole have broad environmental tolerances, become more prevalent. Biotic homogenization may be related, in turn, to the number and size of green areas remaining in an urbanized area, as the proportion of introduced and synanthropic species has been shown to correlate negatively with green area size (Donnelly and Marzluff 2004). Cavity nesters, in particular, tend to be negatively affected by introduced species (Ingold 1994), in large part because of increased competition for nest sites from European Starlings (Troetschler 1976; Kerpez and Smith 1990), but also because of a paucity of live trees and dead snags in urban environments (Blewett and Marzluff 2005).

Several recent studies have documented a spatial coincidence of human population density and biodiversity with analyses focused on large sampling grains across nations or regions (Balmford et al. 2001; Araújo 2003; Chown et al. 2003; Pautasso 2007; Luck 2007a; Luck et al. 2010). A positive correlation between human density and avian species richness suggests that regions with high biodiversity coincide with high human population densities. This pattern is seen as a coincidence of humans and wildlife both seeking the most productive ecosystems (Luck 2007a), or as an artifact of sampling bias (McKinney 2010; Barbosa et al. 2010). Studies along urban-rural gradients have found increased species richness at intermediate levels of urbanization resulting from higher levels of habitat heterogeneity, but heavily urbanized areas have the highest density of birds resulting from large numbers of a few synanthropic species (Blair 1996; Chace and Walsh 2006; Grimm et al. 2008).

In this correlative study we focus on potential mechanisms driving urban bird-habitat relationships at a local scale. We employ physical variables, including abiotic and biotic environmental features of the built landscape, as well as human demographics. Research on habitat features that affect bird communities within urban areas is biased towards vegetation cover (Chace and Walsh 2006; Evans et al. 2009; MacGregor-Fors and Schondube 2011), with less attention paid to the quantity or quality of the built environment (MacGregor-Fors and Schondube 2011). We quantified types of built land use including residential areas, industry, commercial developments, and transportation corridors. In addition, while some previous studies of patterns of avian distribution did consider human demography as a factor in avian communities, most studies reported linkages between avian abundance and proxies for density, such as density of housing units (Tratalos et al. 2007; Evans et al. 2009), or used other indicators of human population size (Schlesinger et al. 2008; Sorace and Gustin 2008; Ortega-Álvarez and MacGregor-Fors 2009). We directly link human population size to avian communities by using US Census data in our statistical models. Such an approach has seldom been considered as a factor in characterizing avian communities within the urban context, especially where local studies must consider a fine scale for analysis (Hahs and McDonnell 2006; Fontana et al. 2011).

Here we test the hypothesis that local and landscape variables combine with human population density surrounding urban parks to shape avian assemblages in Pittsburgh, Pennsylvania (USA). Pittsburgh is of particular value for this type of study because of its large number of parks, and especially because of the unusual presence of several very large and many small urban parks in the city. To understand patterns of avian abundance and species richness in this urban setting, we assess the contributions of permanent residents, migratory species, and introduced species to urban breeding bird diversity and species richness. We then use multivariate analyses to test whether urban park size, land use in the surrounding matrix, and human population size are correlated with park-wide species richness, the mean number of species recorded per survey point, the mean number of individuals recorded per point, and the mean number of individuals of introduced species recorded per point. We use these results to make inferences into factors contributing to the structure of avian communities in these parks, and the trade-offs needed to manage birds in an urban setting.

Methods

Study area The city of Pittsburgh, Pennsylvania (40° 26′ 30″ N, 80° 0′ 0″ W) encompasses 151 km^2, and has a human population of just over 300,000. Natural habitats in the area are dominated by deciduous hardwood forests. Dominant species include maple (*Acer* spp.), oak (*Quercus* spp.), tulip poplar (*Liriodendron tulipifers*), cherry (*Prunus* spp.), and American beech (*Fagus grandifolia*). Pittsburgh is noted for its many parks and cemeteries, or "green areas," located throughout the urban landscape (size range 0.6–184 ha). Forested parklands are generally dominated by oak and maple, but many parks also contain athletic fields, mowed savannah-type lawns, shrub and scrubland, ponds, and small lakes or creeks. Many parks also contain paved trails, and occasionally roadways. Cemeteries are generally landscaped with mowed grass and scattered trees, often with a nearly closed canopy. Stands of native or exotic shrubs are also common.

Bird surveys Point counts were conducted at 150 sites placed in 53 parks and cemeteries throughout city green spaces. We used Hawth's Analysis Tools (Beyer 2004), an extension for ESRI's ArcGIS (v. 9.2), to randomly distribute points on maps provided by the Allegheny County GIS Department. No two points were closer than 200 m, and all points were a minimum 25 m from a park edge. The number of points/park varied from 1 to 19 (mean = 2.9).

Fixed-radius point counts (Ralph et al. 1993) were conducted in the breeding season from 2 June to 10 July 2007. The one season of data we collected limits our ability to make interannual conclusions. This is counterbalanced, however, by the large number of replicated point counts that provide a fairly complete picture of avian communities. Each point was counted 3 times (150 points × 3 counts = 450 point counts) with the exceptions of 9 points (1 each in Brighton Heights, St. Peter Cemetery, Les Getz Memorial Park, Highland Park, and Frick Park, and 2 each in Allegheny Cemetery and Shenley Park) which were counted fewer times due to logistical errors or safety concerns. Replicate counts were made in a random order and spread throughout the 6-week study period. Observers counted all perched birds seen or heard within a 50-m radius of the point in a 10-min period. All observations were made after sunrise (approximately 0545) and were completed by 1030. To reduce the incidence of double-counting individuals, observers noted location and movement of birds. Birds detected outside of the 50-m radius were included only in terms of determining park-wide species richness. While this may inflate species richness values, the protocol was standardized by using this approach across all parks, and the results were used only in a comparative manner.

Landscape and population metrics Landscape variables were measured using ArcGIS (ESRI GIS 2007) from ground truthed data provided by Allegheny County GIS Department in 2006, and expressed the area covered (m^2) by a land use category within a 1,000 m radius circle around each bird survey point. The land cover dataset was created by Chester Engineers (Pittsburgh, PA) through combined image processing and GIS analysis of Landsat TM imagery, augmented with existing aerial photography and hardcopy and digital mapping sources. Landscape variables included water bodies, transport corridors, forest, grasslands, low density residential (2–4 housing units/acre), medium density residential (4–8 housing units/acre), high density residential (>8 housing units/acre), malls and commercial developments, and industry. A 1,000 m radius circle (314 ha) was chosen for analysis of landscape impacts on the breeding bird community because it was comparable in size to our largest green area (255 ha), and was large enough that a variety of green areas of a range of sizes were often included in the circle. This resulted in circles that could reflect both the amount of green area in the landscape, as well as the level of isolation of a green area if there were few other parks in the 1,000 m radius circle. This circle size also encompassed the home range or territory size of most songbirds in the region (Poole 2005), and is a distance frequently used in other studies analyzing landscape-level land use impacts on breeding birds (Saab 1999; Melles et al. 2003; Rodewald 2003). Human population size within each 1,000 m radius circle was determined by combining shapefiles of the 140 Pittsburgh census tracts with the year 2000 population data available from the U.S. Census Bureau (http://www.census.gov/) using ArcGIS. When only a portion of a census tract was included in a 1,000 m radius circle, we assumed that human population was evenly distributed within that tract and calculated the corresponding proportion.

Analysis We calculated the mean number of detections of species and individuals of each species at each survey point, and calculated mean values across all survey points within each park or green area. Species richness was defined simply as the number of species detected at a point or in a green area. From these data we then defined for the purposes of this study a "rare species" as any species detected at <8 survey points and we used this to calculate rare species richness and the proportion of rare species at a point or in each green area. Avian diversity (1-D) was calculated using Simpson's index of diversity.

The incidence of introduced species (Rock Pigeon [*Columba livia*], European Starling [*Sturnus vulgaris*], House Finch [*Carpodacus mexicanus*], and House Sparrow [*Passer domesticus*]) was calculated as their proportion of the abundance of the entire avian community recorded at each point and each green area. The incidence of migratory species (see Table 1) and native cavity nesters (American Kestrel [*Falco sparverius*], Red-bellied Woodpecker [*Melanerpes carolinus*], Downy Woodpecker [*Picoides pubescens*], Hairy Woodpecker [*Picoides villosus*], Northern Flicker [*Colaptes auratus*], Pileated Woodpecker [*Dryocopus pileatus*], Northern Rough-winged Swallow [*Stelgidopteryx serripennis*], Carolina Chickadee [*Poecile carolinensis*], Black-capped Chickadee [*Poecile atricapillus*], Tufted Titmouse [*Baeolophus bicolor*], and White-breasted Nuthatch [*Sitta carolinensis*]) were analyzed similarly. A species' status as introduced, migrating or permanent resident, and cavity nesting was determined by reference to American Ornithologists' Union (1998) and Poole (2005).

The size of parks and green areas was determined within ArcGIS. No two parks adjoined one another, but where cemeteries bordered parks these green areas were joined as a single unit for analysis. We did this because two bordering green areas likely function biologically as a single green area. Frick Park was combined with Homewood cemetery to create a total green area of 254.8 ha, Riverview Park was combined with Highwood-Uniondale Cemetery and Uniondale Cemetery to create a total green area of 142.6 ha, and Highland Park was combined with Joe Natoli Playground to create a total green area of 152.0 ha. This resulted in a total of 49 green areas for study. We then determined the amount of edge (i.e. perimeter) of each green area, and calculated edge density of each green area (Howell et al. 2000), defined as the meters of edge per hectare (m/ha).

We did not systematically analyze variation in bird populations within green areas or over time, but pooled samples from different survey points and/or visits for each point or green area to calculate means. Data were tested for normality using normal probability plots and tests of skewness and kurtosis. When data were not normally distributed, we log transformed them to better approximate a normal distribution. A probability of Type I error ≤ 0.05 was accepted as significant, but greater values are shown for descriptive purposes. We tested with regression the association of green area size with the bird community characteristics of species richness, Simpson's diversity, number of individuals per point, number of rare

Table 1 Occurrence of breeding birds in green areas of Pittsburgh, Pennsylvania (U.S.A.) including mean number of individuals/point surveyed, number of survey points where the species was recorded, and the total number of green areas recording each species

Common name (scientific name)	Status[a]	Individuals/point	Points detected	Parks detected
Canada Goose (*Branta canadensis*)	PR	0.00	0	1
Mallard (*Anas platyrhynchos*)	PR	0.22	8	5
Wild Turkey (*Meleagris gallopavo*)	PR	0.02	3	3
Cooper's Hawk (*Accipiter cooperii*)	M	0.01	4	3
Red-shouldered Hawk (*Buteo lineatus*)	M	0.00	2	2
Broad-winged Hawk (*Buteo platypterus*)	M	0.00	1	1
Red-tailed Hawk (*Buteo jamaicensis*)	PR	0.02	5	4
American Kestrel (*Falco sparverius*)	M	0.00	2	1
Ring-billed Gull (*Larus delawarensis*)	PR	0.00	0	1
Rock Pigeon (*Columba livia*)	PR/I	0.08	8	6
Mourning Dove (*Zenaida macroura*)	PR	0.18	37	27
Yellow-billed Cuckoo (*Coccyzus americanus*)	M	0.01	4	3
Ruby-throated Hummingbird (*Archilochus colubris*)	M	0.00	1	1
Belted Kingfisher (*Megaceryle alcyon*)	M	0.00	1	0
Red-bellied Woodpecker (*Melanerpes carolinus*)	PR	0.11	41	18
Downy Woodpecker (*Picoides pubescens*)	PR	0.19	64	27
Hairy Woodpecker (*Picoides villosus*)	PR	0.02	7	6
Northern Flicker (*Colaptes auratus*)	PR	0.19	58	27
Pileated Woodpecker (*Dryocopus pileatus*)	PR	0.00	1	1
Eastern Wood-pewee (*Contopus virens*)	M	0.03	13	5
Acadian Flycatcher (*Empidonax virescens*)	M	0.03	8	4
Eastern Phoebe (*Sayornis phoebe*)	M	0.01	5	4
Yellow-throated Vireo (*Vireo flavifrons*)	M	0.00	1	1
Warbling Vireo (*Vireo gilvus*)	M	0.00	2	2
Red-eyed Vireo (*Vireo olivaceus*)	M	0.22	58	20
Blue Jay (*Cyanocitta cristata*)	PR	0.46	86	30
American Crow (*Corvus brachyrhynchos*)	PR	0.08	19	16
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	M	0.03	5	3
Carolina Chickadee (*Poecile carolinensis*)	PR	0.31	78	36
Black-capped Chickadee (*Poecile atricapillus*)	PR	0.00	2	2
Tufted Titmouse (*Baeolophus bicolor*)	PR	0.16	47	22
Chickadee species (*Poecile sp.*)	PR	0.03	10	10
White-breasted Nuthatch (*Sitta carolinensis*)	PR	0.08	31	16
Carolina Wren (*Thryothorus ludovicianus*)	PR	0.11	34	25
House Wren (*Troglodytes aedon*)	M	0.05	31	16
Blue-gray Gnatcatcher (*Polioptila caerulea*)	M	0.01	4	4
Wood Thrush (*Hylocichla mustelina*)	M	0.06	20	12
American Robin (*Turdus migratorius*)	M	2.23	138	50
Gray Catbird (*Dumetella carolinensis*)	M	0.16	48	31
Northern Mockingbird (*Mimus polyglottos*)	M	0.02	7	7
European Starling (*Sturnus vulgaris*)	PR/I	0.82	46	29

Table 1 (continued)

Common name (scientific name)	Status[a]	Individuals/point	Points detected	Parks detected
Cedar Waxwing (*Bombycilla cedrorum*)	M	0.04	15	6
Yellow Warbler (*Setophaga petechia*)	M	0.03	10	5
Chestnut-sided Warbler (*Setophaga pensylvanica*)	M	0.00	1	1
Black-throated Green Warbler (*Setophaga virens*)	M	0.00	1	1
Hooded Warbler (*Wilsonia citrina*)	M	0.01	3	2
Scarlet Tanager (*Piranga olivacea*)	M	0.11	36	15
Eastern Towhee (*Pipilo erythrophthalmus*)	M	0.07	29	16
Chipping Sparrow (*Spizella passerina*)	M	0.39	74	28
Song Sparrow (*Melospiza melodia*)	M	0.37	76	42
Dark-eyed Junco (*Junco hyemalis*)	M	0.01	5	3
Northern Cardinal (*Cardinalis cardinalis*)	PR	0.62	113	46
Rose-breasted Grosbeak (Pheucticus ludovicianus)	M	0.01	6	3
Indigo Bunting (*Passerina cyanea*)	M	0.04	12	7
Red-winged Blackbird (*Agelaius phoeniceus*)	M	0.03	4	4
Common Grackle (*Quiscalus quiscula*)	M	0.35	53	28
Brown-headed Cowbird (*Molothrus ater*)	M	0.07	21	16
Orchard Oriole (*Icterus spurius*)	M	0.00	1	1
Baltimore Oriole (*Icterus galbula*)	M	0.12	36	20
House Finch (*Carpodacus mexicanus*)	PR/I	0.21	40	26
American Goldfinch (*Carduelis tristis*)	PR	0.21	54	20
House Sparrow (*Passer domesticus*)	PR/I	1.18	93	44

[a] *PR* permanent resident; *M* Neotropical migrant; *I* introduced species

species, proportion of individuals represented by introduced species, and the proportion of individuals represented by migratory species. We also used regression to test the association between the amount of edge per hectare of green area, and the proportion of introduced species with each of these bird community characteristics.

We used a principal components analysis (PCA) on landscape variables (see *Landscape and population metrics*, above) describing 150 survey points in 49 green areas to identify the landscape variables that best distinguish among the avian assemblages recorded at each survey point. Because a Pearson correlation showed correlations >0.60 for only water with commercial lands, and water with industrial developments, all landscape variables were included in our PCA. In addition to our landscape variables, for the PCA we also included park area, edge density, and human population size in the area defined by each 1,000 m radius circle as additional descriptive variables. PCA then transformed the original variables into a linear combination of uncorrelated variables which additively partition the variance for the set of variables. Four components were retained based on the Kaiser criterion (Kaiser 1960) and a scree test. We then used a Varimax rotation (Kaiser 1960) of the components to facilitate interpretation of the resulting factors.

We evaluated the influence of each of the four linear combinations of uncorrelated landscape variables on park-wide species richness, mean number of species per point, mean number of individuals per point, and the mean number of individuals of introduced species recorded per point with a generalized linear mixed model (GLMM; Rencher 2002; Bolker et al. 2009; Zuur et al. 2009). We did not analyze the relationship between the principle components and the number of introduced species because of the limited variation in this variable among green areas. GLMMs combine the properties of linear mixed models (which handle random effects) and generalized linear models (which handle non-normal distributions) by using link functions of exponential families such as Poisson, binomial, and negative binomial (Bolker et al. 2009; Zuur et al. 2009). Using PROC GLIMMIX in SAS (SAS Institute 2008), we assumed a normal distribution and used an identity link function for the two variables that were normally distributed (park-wide species richness and mean number of individuals per point). For the variables of mean number of species per point and the mean number of individuals of introduced species per point, which were not normally distributed, we assumed a negative binomial distribution and used a logarithmic link function. We modeled the explanatory variables as fixed effects. Scatter plots of the factor scores against each landscape variable were used to determine whether the relationship was positive or negative.

Results

Species abundance We counted 4,435 individual birds in 441 counts at 150 points (Table 1). Of the 61 species detected, 27 were rare (detected at <8 points), with 8 of these being recorded only once, and 6 more recorded only 2–3 times. Migratory species accounted for 46.1 % of all individuals recorded, while 23.2 % of all individuals counted were of introduced species (Table 1). The most frequently encountered species, American Robin (*Turdus migratorius*), was recorded in all 49 green areas and at 92 % of points, and represented 22.4 % of all observations (Table 2). Other frequently occurring species in order of abundance included House Sparrow, European Starling, Northern Cardinal (*Cardinalis cardinalis*), and Blue Jay (*Cyanocitta cristata*; Table 2). Numerical dominance was seen in the two most abundant species accounting for 34.4 % of all observations, while the three-most-, four-most-, and five-most common species accounted for 42.8 %, 49.1 % and 53.8 % of all individuals recorded, respectively.

Effects of area and edge Species richness increased significantly with green area size (r^2= 0.77, p<0.001), as did the number of rare species detected (r^2=0.81, p<0.001; Table 3). But the size of the green area was not significantly related with Simpson's diversity, proportion of individuals of introduced species, proportion of migratory individuals, or proportion of cavity nesters (p>0.05).

Table 2 The occurrence and numerical dominance of the most abundant species across 49 green areas surveyed for breeding birds in Pittsburgh, Pennsylvania (U.S.A.), including mean number of individuals recorded/survey point and the proportion of all birds observed represented by each species

Common name	Individuals/point	Proportion
American Robin	2.2	22.4 %
House Sparrow	1.2	12.0 %
European Starling	0.8	8.4 %
Northern Cardinal	0.6	6.3 %
Blue Jay	0.5	4.7 %

Table 3 Number of survey points, area and amount of edge/ha of green areas surveyed for breeding birds in Pittsburgh, Pennsylvania (U.S.A.), along with avian species richness, mean number of species and individual birds recorded per point, and number of rare species recorded in each green area surveyed

Green area	Survey points	Area (ha)	Edge (m)	Edge density (m/ha)	Species richness	Species per point	Individuals per point	Rare species
Armstrong playground	1	0.6	309.2	480.5	5	4.0	16.7	0
Crescent school	1	0.9	430.8	456.9	8	4.0	5.0	0
Glen Hzl playground	1	1.3	528.4	422.6	15	7.7	14.3	0
Homewood North	1	1.3	576.6	434.3	10	6.0	8.5	0
Cliffside	1	1.6	829.1	526.7	15	7.3	10.7	1
Arlington playground	1	1.7	522.2	306.5	7	4.0	10.3	0
Tropical Parklet	1	2.4	622.8	258.2	15	8.7	11.0	1
Vanucci field	1	2.5	681.4	272.9	9	4.3	6.0	0
Monongahela playground	1	2.6	678.0	257.0	12	6.7	9.7	0
German Methodist	1	2.8	891.6	313.5	12	5.0	12.3	0
Fort Pitt playground	1	3.0	808.9	271.6	12	5.5	6.0	1
Moore park	1	4.1	838.8	205.0	8	3.7	9.0	0
Clemente	1	4.1	2893.3	707.1	5	3.3	12.7	2
Hunter park	1	4.5	928.2	0.0	11	5.3	7.3	1
Chartiers playground	1	4.7	918.9	195.1	17	7.3	16.7	0
West End Overlook	2	5.2	2182.6	416.5	18	5.8	10.0	0
St. Martin	1	5.4	1085.5	202.2	17	8.7	12.3	1
Kennard playground	1	5.4	997.7	183.6	9	5.7	22.7	1
St. George's cemetery	2	5.6	1074.0	192.6	19	6.5	12.0	2
Banksville	1	6.7	1474.5	219.0	11	5.3	23.3	0
Southside riverfront	1	6.8	2799.8	413.0	9	5.7	11.0	0
St. Michael's cemetery	1	7.6	1436.1	189.1	11	6.3	11.7	1
Les Getz memorial park	1	8.0	1952.2	242.7	9	7.0	11.5	0
St. Peter cemetery 1	2	8.9	6145.7	690.9	18	6.0	9.7	1
McBride	2	9.2	1343.2	146.0	16	5.0	7.7	1
West Penn park	2	9.4	1434.6	152.4	23	7.8	16.7	1
Phillips	1	9.5	1755.3	185.4	7	3.7	7.7	0
German EUP	2	10.2	1471.4	144.2	17	5.2	8.8	0
Spring Hill playground	1	12.2	2233.2	183.0	12	7.3	11.3	0
St. Peter cemetery 2	2	12.3	5425.6	442.0	18	5.4	8.8	0
Brighton Heights	1	12.5	2322.7	185.6	14	9.0	11.5	2
Grandview park	1	13.9	3091.0	223.0	12	7.3	14.0	1
Chartiers cemetery	2	17.7	2006.5	113.2	19	5.8	13.0	0
West park	2	18.0	2663.9	148.3	20	6.3	24.3	4
St. George ISO	2	18.4	1758.8	95.8	17	6.7	15.0	0
Southside park	3	18.5	2936.5	158.7	21	5.5	8.7	3
Mt. Washington	2	18.5	3464.8	187.1	13	4.7	8.2	0
Southside cemetery	2	18.7	2013.8	107.7	16	5.0	12.5	2
Sheradin	1	20.7	3178.8	153.5	15	8.0	13.7	0

Table 3 (continued)

Green area	Survey points	Area (ha)	Edge (m)	Edge density (m/ha)	Species richness	Species per point	Individuals per point	Rare species
Brookline cemetery	1	20.9	2505.0	119.6	13	6.7	19.3	0
Mckinley	3	31.8	3639.7	114.5	18	5.5	9.3	1
Calvalry cemetery	3	67.3	3833.0	57.0	24	5.5	11.4	2
Allegheney	11	121.7	5841.5	48.0	31	5.2	8.8	5
Riverview + Highwood + Uniondale	19	142.6	10982.1	77.0	35	4.4	10.0	7
Highland Park + Joe Natoli	15	152.0	8767.9	57.7	31	5.7	9.2	5
Shenley	19	167.3	7141.4	42.7	38	4.8	9.7	4
Frick + Homewood	24	254.8	10337.7	40.6	44	4.9	7.2	12

Species richness decreased significantly with the log of the amount of edge per hectare of green area (r^2=0.65, p<0.001), and there was a significant negative relationship between the amount of edge and the number of rare species encountered (r^2=0.58, p<0.001). But the amount of edge per hectare of green area was not significantly related with Simpson's diversity, proportion of individuals of introduced species, proportion of migratory individuals, or proportion of cavity nesters.

Effects of introduced species The proportion of introduced individuals increased significantly as the mean number of individuals per point increased (r^2=0.46, p<0.001). But with an increasing proportion of individuals of introduced species, Simpson's diversity across green areas decreased significantly (r^2=0.58, p<0.001). The abundance of cavity nesting species, in particular, declined significantly as the proportion of introduced species increased (r^2=0.25, p<0.001). But the proportion of introduced individuals was not significantly related with species richness, rare species richness, or proportion of migratory individuals (p>0.05).

Multivariate analysis: Population and landscape effects We used a principal components analysis to identify which linear combination of uncorrelated landscape variables best distinguished variation in avian assemblages among survey points. Within our 1,000 m radius circles, four principal components accounted for 72 % of the variance in avian assemblages (Table 4). Factor 1 had high positive loadings for edge density, water, transportation and commercial land uses, and a high negative loading for park area. This factor separated out smaller parks in the commercial core of the city. Factor 2 had high positive loadings for both human population size and high density housing, and a high negative loading for forest cover, indicating non-forested parks in densely populated areas of the urban environment. Factor 3 separated parks in low density residential areas. Finally, Factor 4 had a high positive loading on industry and grasslands, and a high negative loading for medium density housing, indicating grassy parks or playlots in more industrialized areas of the city.

The four components were then used in a generalized linear mixed model (GLMM; Bolker et al. 2009; Zuur et al. 2009) to evaluate the influence of each of the four linear combinations of uncorrelated landscape variables on park-wide species richness, mean

Table 4 The rotated factor pattern showing the most heavily weighted factors, either positive or negative, for each of the 12 landscape-level measurements

	Factors			
	I	II	III	IV
Eigen root	3.390	2.200	1.590	1.400
Factor contribution to total variance	0.28	0.18	0.13	0.12
Cumulative variance explained	0.28	0.47	0.60	0.72
Landscape characters				
Park area	−0.67			
Edge density	0.73			
Human population		0.74		
Water	0.71			
Transportation	0.70			
Forest		−0.69		
Grasslands				0.53
Low density residential			0.89	
Medium density residential				−0.62
High density residential		0.82		
Malls and commercial	0.65			
Industry				0.61

number of species per survey point, mean number of individuals per survey point, and the mean number of individuals of introduced species recorded per survey point. Park-wide species richness was significantly related to Factor 1 ($F_{1,100}$=5.35, p=0.023), suggesting that smaller parks in the commercial core of the city contained relatively few species. The mean number of species per point was negatively related to Factor 1 ($F_{1,100}$=13.52, $p\leq0.001$) and Factor 2 ($F_{1,100}$=4.89, p=0.029), and was positively associated with Factor 3 ($F_{1,100}$=8.64, p=0.004). This suggests that parks in low density residential areas recorded the highest number of species, while points in smaller, non-forested parks in the urban core, and those in areas with a high human population, recorded significantly fewer species. The mean number of individual birds recorded per point was significantly associated with Factor 1 ($F_{1,100}$= 8.87, p=0.004), suggesting that, as with park-wide species richness, smaller parks in the commercial core of the city contained relatively few birds. Finally, the number of introduced individuals was significantly positively related with Factor 2 ($F_{1,100}$=45.19, $p\leq0.001$) and negatively related with Factor 3 ($F_{1,100}$=6.71, p=0.011). This increase in introduced individuals with human population size was particularly strong, and this pattern was emphasized by the significant negative association between introduced birds and parks in low density residential areas defined by Factor 3.

Discussion

Modern urban bird communities are composed of a mix of naturally-occurring and introduced species. These species are impacted directly by a variety of habitat characteristics including fragmentation and the simplification of the remaining natural environment (Marzluff et al. 2001; Grimm et al. 2008). Our analysis goes beyond characteristics of the natural environment to show how habitat components which may sometimes be unique to the urban environment are correlated with bird diversity. By analyzing habitat attributes not widely studied at this scale of analysis, we show that aspects of the built environment, and especially human population size, may work synergistically with the natural landscape characteristics of habitat area and amount of edge, to influence avian diversity and abundance.

Our detection of 4,435 individuals of 61 species suggests that on the whole Pittsburgh's parks support substantial avian diversity. Comparative quantitative data on species occurrences in southwestern Pennsylvania are rare, but the Pennsylvania breeding bird atlas (Brauning 1992) confirmed 113 breeding species in the Allegheny County region, which includes the city of Pittsburgh, and an average of 57 species per atlas block (24.7 km^2) in this area. Compared with our results, this suggests that Pittsburgh parks and cemeteries provide appropriate habitat for a substantial proportion of the breeding bird species of the region. Rare birds in this study included habitat specialists such as forest interior species (i.e. Hairy Woodpecker, Black-throated Green Warbler [*Setophaga virens*]), and shrubland species (i.e. Chestnut-sided Warbler [*Setophaga pensylvanica*]) which occurred in habitats present only in larger parks. Other rarely occurring birds included raptors and those requiring large territories, and species such as the Orchard Oriole (*Icterus spurius*), Black-capped Chickadee, and Dark-eyed Junco that were near the edge of the species' range.

Introduced species were a large component of the avian community and represented 23.2 % of all individual birds recorded; 20.4 % of individuals were of only two introduced species–House Sparrow and European Starling. Other studies have also shown that in the urban environment a few, generally exotic species dominate, and in North America these are most often the House Sparrow, European Starling, and Rock Pigeon (Emlen 1974; Gavareski 1976; Morneau et al. 1999).

Our data suggest a negative relationship between introduced species and avian diversity because we found Simpson's diversity across green areas decreased significantly with an increasing proportion of individuals of introduced species. Numbers of cavity nesters, in particular, declined in the presence of introduced species. Our study is correlative, so evidence supporting interspecific competition between introduced species and native species is weak, and in fact, rather than interspecific interactions driving these bird populations it is possible that cavity nesters and introduced species are simply responding to other habitat features. For example, urban areas suffer dramatic reductions in numbers of natural cavities for nesting (Sandström et al. 2006), and even though many new cavities are created through urban architecture, in North America these sites are primarily occupied by European Starlings (Cabe 1993) and House Sparrows (Lowther and Cink 1992). However, other studies have found that non-native invasive species can cause declines in biodiversity (Gordon 1998; Manchester and Bullock 2000), and most often this is a result of competition for nest sites with the European Starling (Troetschler 1976; Weitzel 1988; Kerpez and Smith 1990).

The contribution of introduced species to biotic homogenization of the avifauna has been previously reported in other urban areas globally (McKinney and Lockwood 1999; Olden and Rooney 2006; Devictor et al. 2008). In our study, when the introduced House Sparrow and European Starling were combined with the generalist American Robin, Northern Cardinal, and Blue Jay, these five most abundant species accounted for nearly 55 % of all individual birds recorded in our green areas. Yet, of these five species, only two (American Robin, Blue Jay) occur on the list of most frequently recorded breeding birds in Pennsylvania (Brauning 1992). Thus, the biotic homogeneity in Pittsburgh is unlikely representative of the state as a whole.

The landscape characteristics of park size and edge density were important correlates of avian community structure. In our study, species richness and the proportion of rare species increased significantly with the size of the green area, indicating the importance of park size in supporting biodiversity. Not surprisingly since there is an inverse relationship between park size and edge density, we also found a significant relationship between the amount of edge per hectare of park and species richness, and between amount of edge and proportion of rare species in a green area. While our data do not indicate whether birds are responding primarily to park size or the amount of edge, we suggest that the observed patterns in bird occurrence data are the result of increased habitat heterogeneity in larger parks. Most urban parks have a wide variety of land uses and habitats, and seldom include any core habitat, so a decrease in edge resulting in extensive core habitat in larger parks is unlikely. This hypothesis is supported by studies relating declines in avian species richness and diversity primarily to the simplification of vegetation parameters in an urban context (Rebele 1994; Bonier et al. 2007; Chiari et al. 2010).

Our data further suggest a strong relationship between the built environment in the urban matrix and the avian community. Park-wide species richness was significantly lower in smaller parks in the commercial core of the city where transportation corridors and commercial development dominate. Similarly, the mean number of species per point was lowest in smaller, non-forested parks in the urban core, while counts were highest in parks in low density residential areas. These results point to the negative impacts of the built environment on avian species richness. But the impacts are not so clear on the numbers of individual birds. While the mean number of individual birds recorded per point was significantly lower in smaller parks in the commercial core of the city where transportation corridors and commercial development dominate, we found that the number of individuals of introduced species was highest in the urban core and significantly lower in areas with low density residential units. These results suggest that introduced species in particular may be responding positively to elements other than green area characteristics in the urban environment. Exotics such as the House Sparrow (Lowther and Cink 1992) and the European Starling (Cabe 1993) may be more opportunistic than native species in their use of the built environment for nesting, or are better able to take advantage of anthropogenic food sources. These patterns have been seen elsewhere (Sandström et al. 2006; Clergeau et al. 2006; Luck and Smallbone 2011), suggesting that greater numbers of such "urban specialists" may be expected in highly built environments (Luck and Smallbone 2011).

The impact of human population size on urban bird communities at this relatively fine-grain scale of analysis is important. Previous studies of patterns of avian distribution have reported linkages between avian abundance and proxies for human density–housing units (Tratalos et al. 2007; Evans et al. 2009), synanthropic species and the built environment (Blair 1996; Chace and Walsh 2006; Grimm et al. 2008), or other indicators (Schlesinger et al. 2008; Sorace and Gustin 2008; Ortega-Álvarez and MacGregor-Fors 2009). Ours is among the first to explicitly identify specific relationships between avian population characteristics and human population size (but see Hahs and McDonnell 2006; Fontana et al. 2011). Our data suggests human population size as a correlate of avian diversity and abundance that can be measured independently of characteristics of the built environment. A strong positive correlation between human population size and the amount of high density residential areas may be intuitive. But our PCA, which partitions the variance with a linear combination of uncorrelated variables, showed human population size and high density residential areas both contributing independently to the observed pattern of a decreased number of bird species but an increased number of individuals of introduced species. Thus, human population size is contributing to observed patterns in avian distribution that are not reflected only by the built environment.

Because our study was correlative, the question remains as to why species richness might decline while numbers of individuals of introduced species increases in the presence of greater human populations. Beyond the direct loss and fragmentation of habitat, of particular importance for avian species richness and diversity in an urban context has been studies showing negative impacts on birds resulting from changes to vegetation parameters and the simplification of the habitat (Rebele 1994; Bonier et al. 2007; Chiari et al. 2010). In an urban context, even remnant woodlots and forests which provide some natural habitat are likely subjected to high recreation pressure and other impacts from human neighbors and visitors. As the density of human population increases and the intensity of land use increases, habitat likely becomes increasingly disturbed, fragmented and simplified, thus negatively impacting native bird species. But apart from anthropogenic changes in the vegetation characteristics of urban green areas, understanding the contribution of human population size to changes in avian diversity has until now been largely limited to describing the role of the built environment as a driver of species loss. Non-vegetation variables that have been previously implicated in changes in avian diversity and abundance in urban areas include hazards presented by urban infrastructure (MacGregor-Fors and Schondube 2011), anthropogenic feeding of birds (Shochat 2004; Robb et al. 2008), and even dog-walking (Blair 1996; Banks and Bryant 2007).

Some management options are available to city planners desiring to increase avian diversity, especially because the structure of urban avian assemblages has been shown to be more strongly influenced by local habitat features than by factors operating on regional or larger scales (Evans et al. 2009). This is particularly true too because urbanization is typically associated with locally-based planning initiatives and is thus one of the few land uses over which local policy can have direct control of its extent and intensity at fine spatial scales (Fuller and Gaston 2009; Dallimer et al. 2011). Although in most urban settings new parks, or the extension of existing parks to create large habitat patches, are not an option, increasing habitat diversity may be possible. Maximizing area in parks creates green areas with the greatest potential for avian diversity, as does the promotion of vegetative complexity of remaining habitat (Savard et al. 2000; Marzluff and Ewing 2001). Numerous studies have also indicated benefits from domestic gardens (Lepczyk et al. 2004; Loram et al. 2011) and private backyards (Bryant 2006; Goddard et al. 2010) in supporting biodiversity in urban areas.

However, in order to sustain diversity, our study suggests that diverse conservation approaches may be required, perhaps including decreasing the density and influence of non-native introduced species. But reducing the influence of humans and their built environment as attractive nesting and foraging sites for introduced species may be an intractable problem. Conservationists might consider the possibility that only a few synanthropic species or urban specialists are likely to do well in heavily urbanized environments. If accurate, then the best approach for avian conservation may be a triage that minimizes and offsets the consequences of high human population density by encouraging higher densities of development in urban core areas and limiting urbanization and suburbanization of areas which are currently more rural in nature. Sushinsky et al. (2012) recently suggested the ecological impact of urbanization may be minimized by a compact development plan in which the extent of the built up areas is reduced. This forces ecological impacts to be locally intense but spatially constrained. In contrast, sprawling low-intensity development created communities with fewer urban-sensitive species and more introduced species. Notably, large interstitial green spaces and small backyards were important aspects of the compact development plan and contributed significantly to avian diversity. This pattern was seen too in our PCA results, where even small green areas in the city core, including grassy parks and playlots, were important in promoting birdlife. These patterns highlight the ecological impact of high-quality interstitial green spaces in high-density developments, and indicate the potential importance of high-quality "backyard" habitat in urban settings (Bryant 2006; Goddard et al. 2010)

As the world's population continues to increase, competition for land intensifies, especially in urban areas (Nelson et al. 2010). Increased efficiency in land use is therefore critically important in minimizing the global impact of human population growth on biodiversity. Further research and monitoring of impacts on birds should employ a combination of demographic and physical variables, including abiotic and biotic environmental features of the built landscape, rather than focusing solely on environmental features. Such an approach will likely result in a more complete understanding of the factors influencing avian diversity in human-dominated landscapes.

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