

Avian distribution along a gradient of urbanization in northeastern Puerto Rico

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We studied avian distribution along an urban to forest gradient in northeastern Puerto Rico to document how different species, species groups, and diet guilds respond to urbanization. Mean avian abundance and species richness sampled at 181 point count sites increased with urbanization and was associated with measures of developed habitat, pasture and elevation. Endemic species were sensitive to urbanization as evidenced by their negative association with an urbanization index, positive association with forest cover, and their rarity in urban habitat in contrast to their abundance and species richness in forest. Exotic species showed the opposite pattern by a positive association with an urbanization index and highest abundance and species-richness in suburban/urban habitats and absence from forest. Resident (non-endemic) species were found throughout the gradient, although species differed in the locations of peak abundance along the gradient. Resident species also displayed a positive association with the urbanization index and their abundance and species richness increased with urbanization. The increased avian abundance and species richness with urbanization was attributed to exotic granivores and omnivores and resident insectivores, granivores and omnivores. We hypothesize that availability of nearby undeveloped habitats may be critical for maintaining avian abundance and species richness in Puerto Rico's urban areas, but emphasize that research is needed to test this hypothesis.

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Urbanization has complex direct and indirect effects on native biota (Marzluff 2001). For birds, urbanization can affect species abundance, diversity, richness, distribution, biomass and community composition (Blair 1996, 2004, Clergeau et al. 1998, Crooks et al. 2004, White et al. 2005). In addition, urbanization also increases local rates of extinction and loss of native species, and is a major cause of biotic homogenization (McKinney and Lockwood 1999, McKinney 2002, 2006). However, urbanization provides research opportunities to study the effects of habitat modification on ecological communities. A useful research approach has been to study avian community composition along a gradient of urbanization (Blair 1996, Clergeau et al. 1998, Crooks et al. 2004). Studies across urban-rural gradients suggest that species richness and diversity peak at intermediate levels of urbanization (Lancaster and Rees 1979, Blair 1996, 2004, Crooks et al. 2004, van Rensburg et al. 2009) and that avian biomass increases with urbanization (Chace and Walsh 2006).

The Caribbean island of Puerto Rico is attractive for urban studies because it is densely populated, has a high degree of urban sprawl (Martinuzzi et al. 2007), and the landscape is in rapid transformation due to urban expansion and forest recovery (Thomlinson et al. 1996, Thomlinson and Rivera 2000, López et al. 2001, Grau et al. 2003), as typical of other tropical regions (Aide and Grau 2004). In recent decades Puerto Rico has become predominantly urban with about 84% of its 3.9 million inhabitants living in cities (USBC 2000). At present about 11% of Puerto Rico is covered by urban/built-up surfaces (Martinuzzi et al. 2007). Within this setting, the island's terrestrial avifauna provides ample diversity in which the effects of urbanization can be compared among endemic, resident and exotic species. The island is notable in having 36 naturalized exotic bird species (12.7% of the recorded bird species; Wege and Anadón-Irizarry 2008). Together with 16 endemic species and 142 breeding species the island provides an ideal situation in which the effects of

urbanization can be compared between introduced and native species, both endemic and residents with wider geographic distributions.

Changes in Puerto Rico's land use and land cover are believed to have been major factors contributing to a large-scale reorganization (i.e. extinctions, colonization by exotics and range shifts) of the island's biota (Lugo et al. 2012) including bird assemblages (Acevedo and Restrepo 2008). Although this latter study indicated that endemic and exotic species occurred throughout the island, the abundance of exotics was found to be highest in open lowland habitats in contrast to the endemics, which were most abundant in cloud forests. At a smaller scale, within the urban zone, Puerto Rico's, endemic species decline with the degree of urbanization and are especially sensitive to landscape features (patch size, matrix urbanization, canopy texture) in contrast to exotic species that increase with the degree of urbanization (Suárez-Rubio and Thomlinson 2009). Similar distribution patterns have been documented at least for endemic species elsewhere in the Caribbean (Cox and Ricklefs 1977, Ricklefs and Cox 1978), where terrestrial species tend to be habitat generalists, often with high population densities, as a result of ecological release (MacArthur and Wilson 1967, Terborgh and Faaborg 1973). Ecological release occurs as species colonize islands and use a wide range of resources that several species might use under the competitive conditions of species-rich continental communities (MacArthur and Wilson 1967). In addition, the high incidence of tropical cyclones in the Caribbean may further select for habitat generalists (Walker et al. 1991, Wiley and Wunderle 1993).

In this study, we examine the relationship between urbanization and the abundance, distribution and species composition of bird communities along an urbanization gradient including a rain forest reserve and nearby exurban, suburban, and urban habitats of towns in northeastern Puerto Rico. Here, given ecological release characteristics of the avifauna of the West Indies (Cox and Ricklefs 1977), we predict that many island species are less sensitive to the effects of urbanization because they are able to occupy a broader range of habitats than mainland species. Also we expect that urbanization increases the within habitat abundance of some resident species, and that endemic species are most sensitive to the effects of urbanization. Most Caribbean endemic birds evolved in forest habitats (Ricklefs and Cox 1978), and therefore we expect them to be less tolerant of the environmental conditions present in urban habitats. The decrease of endemic and native bird species with urbanization has been reported in other studies on islands (Douglas 2001, Palomino and Carrascal 2005). To test these hypotheses we examined patterns of species abundance, composition, richness, and diversity as well as foraging guilds, in four land use types along a gradient of urbanization in northeastern Puerto Rico.

Methods

Study site

Field work was conducted in El Yunque National Forest, also known as the Luquillo Experimental Forest and previously the Caribbean National Forest (henceforth LEF) and the nearby rural and urban areas in northeastern Puerto Rico (Fig. 1). The study area spanned a gradient of urbanization from the LEF to highly urbanized landscapes and reflected the typical urban-suburban matrix that results from urban sprawl and the low density exurban development that surrounds the LEF. The LEF is a 11 332 ha subtropical rain forest reserve, with elevation ranging from 100 to 1075 m and mean temperature ranges from 18.5°C to 25.5°C depending on elevation (for site description see Scatena, <<http://luq.lternet.edu>>). The reserve hosts 99 bird species including 25 breeding species (13 of which are endemic) and 74 non-breeding transients or rare visitors, which include 34 native species and 5 naturalized exotic species that breed elsewhere on the island, and 35 migrant species that breed off island (Wunderle and Arendt 2011). The lands surrounding the LEF were designated as a special zoning area by the Puerto Rican government with emphasis on the protection of natural resources (JPPR 1983). However, changes in land use zoning at the LEF's periphery have resulted in urban sprawl that is presently encroaching on the reserve (Lugo et al. 2004).

Land cover and gradient of urbanization

In this study we used land cover and density of structures as measures of urbanization. We used the 2004 digital aerial photographs of the study area to characterize land cover at 181 point count sites (henceforth designated as sites). Each site was selected randomly by placement of a grid over the aerial photographs of the study area with the constraint in the forest that sites had to be accessible by trails or roads. At each site, we calculated the area covered by developed land (i.e. constructed land), trees, exposed land and pasture in a 500 m radius from its center and converted the areas into percentage of site covered. Also, we determined the density of structures in the 500 m plot, and the elevation at each site center. These data were transformed to meet assumptions of normality and used in a Canonical Discriminant Analysis (CDA) to rank point count sites from relatively undisturbed to highly developed across the gradient of urbanization.

Ground cover and vegetation

Ground cover and vegetation characteristics were measured in 10 m radius plots (0.03 ha) centered on each

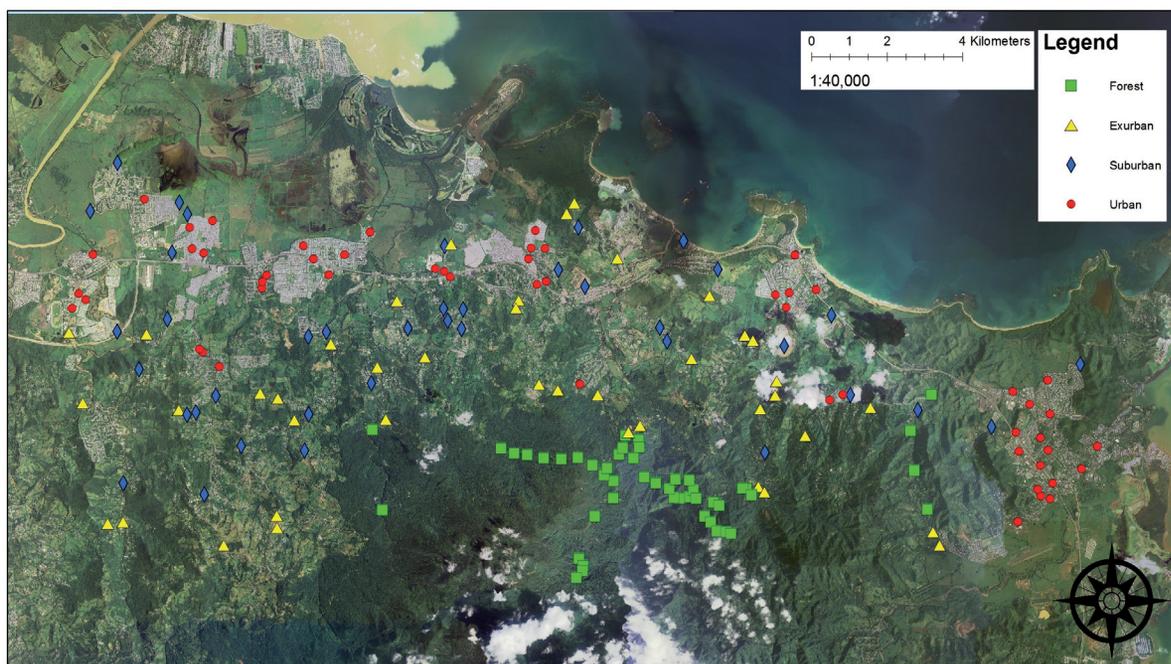


Figure 1. Satellite image of northeastern Puerto Rico where 181 sites were used to census birds in 25 m fixed-radius point counts along an urbanization gradient including forest, exurban, suburban and urban habitats. See methods for descriptions of the four habitats.

point count site. Within each plot we measured the diameter at breast height (DBH) for all trees ≥ 8 cm and recorded diameters into the following categories: 8–15, 16–20, 21–25, 26–38, and > 39 cm. DBH classes were combined to calculate total basal area per plot. Several different measurements were taken at 2 m intervals along the cardinal directions of each 10 m plot (20 points total). For example, ground cover was evaluated by sighting vertically downward through a 4.5 cm diameter tube at each of the 20 points along the four radii of the circular plot and recording the percent cover of pavement, dead wood, dead leaves, rocks, roots, live broadleaf vegetation, lawn, ferns and water. The mean percentage ground cover of each cover category was calculated by taking the average value for 20 points in the plot. Also, canopy cover at each of the 20 points was determined by sighting vertically upwards through a 4.5 cm diameter plastic tube. Presence or absence of broadleaf canopy cover observed by sighting upwards with the plastic tube was recorded at each of the 20 points within a plot and mean percent canopy cover for the plot determined by adding the number of individual points in which canopy was detected and dividing by the total number of sample points in a plot ($n = 20$).

Foliage height profiles were also determined for each 10 m radius plot following Schemske and Brokaw (1991). Foliage height distribution at each point was determined using a 3-m long \times 2.5 cm diameter pole marked at 0.5 m intervals placed vertically at each sample point along the four radii. The presence/absence of foliage touching the

pole within each height class was recorded for each half meter height interval. For height intervals between 3 and 10 m we sighted along the upright pole and recorded the presence/absence of foliage in each of the following height intervals: 3–4, 4–6, 6–8, and 8–10 m. For height intervals above 10 m we used a laser rangefinder. Percent cover for each height interval was calculated by adding the number of individual points in which foliage was present in the specified height interval and dividing by the total number of sample points in a plot ($n = 20$).

Bird surveys

Birds were censused in each of the 181 point count sites by the first author during the breeding and post-breeding season (March–August 2005) following the methods of Hutto et al. (1986). At each site, censuses were conducted for 10 min between 07:00 to 11:00 h and each site was visited on three occasions in randomized sequence. No counts were conducted during rainy or windy conditions. Point count sites were at least 150 m apart and those located in the forest were a minimum of 50 m from the habitat edge. In urban areas, census sites were located on existing roads, parks, industrial and residential areas, and downtown sections of cities. Census sites ranged in elevation from 0 to 500 m, but most (89%) were < 300 m.

At each site we recorded species, sex, and number of individuals detected within a 25 m radius from the observer.

The distance between individual birds and observer was measured with a laser rangefinder and distance to birds heard, but not seen was estimated. Bird species were identified using visual or aural cues and classified into three distribution categories (i.e. endemic, resident, and exotic). Species names and alpha codes follow the AOU checklist (2011) and Pyle and DeSante (2003) respectively and classification into feeding guilds follows Faaborg (1985), Raffaele (1989), and Waide (1996). Migrants and nocturnal species, as well as birds flying over the census sites were excluded from analyses.

Data analysis

Ground and land cover variables

We used analysis of variance (ANOVA) to test for differences in land cover variables among habitat types, and to assess differences between bird species distribution groups or guilds and the number of habitats occupied. We performed Kruskal–Wallis tests to assess differences in ground cover of point count sites among habitat types. In addition, forward stepwise multiple regressions were used to assess which ground cover and land cover variables were significant predictors of bird abundance.

The urban gradient

We performed a Canonical Discriminant Analysis (CDA) in TANAGRA 1.4 (Rakotomalala 2005) to rank point counts across the gradient of urbanization. The scores from the first axis of the CDA were used as an index of the level of urbanization present at each point count site, based on the percentage of land cover types within a 500 m radius of the individual points. CDA was used because it produces maximum separation of a priori designated groups of categorical variables (Wiley 1981). The index of urbanization was used to classify individual points into four types of land use/habitat (i.e. forest, exurban, suburban and urban) as described in Marzluff (2001). Habitats were defined on the basis of the percent of built land surface within a 500 m radius of each point, and classified according to Marzluff's (2001, Table 1.1) definitions for wildland or forest (0–2%), exurban (5–20%), suburban (30–50%), and urban (> 50%) habitats.

Bird community

We used one-way ANOVA to test for differences in mean bird abundance and to assess differences among distribution categories of bird species (endemic, resident and exotic) and the number of habitats occupied and mean abundance per habitat. For those species with non-normal distributions of abundance we used Kruskal–Wallis and Mann–Whitney tests to evaluate differences among habi-

tats in median number of birds per point count. Logistic regression was used to relate the abundance of endemic, resident, and exotic birds with the number of habitats occupied. In addition, we used linear regressions to relate total bird abundance and the abundance of endemic, exotic, and resident birds with the urbanization index. Mean and total species richness, Shannon Diversity Index (H' , Pielou 1966) and Simpson's evenness index (Krebs 1989) were calculated per point count site and tested for differences among habitats with ANOVA.

Bird community response to urbanization

We used Non-metric Multidimensional Scaling (NMS) to generate an ordination of bird species with land cover variables (McCune and Grace 2002). Species abundance values and landscape variables were log-transformed and tested for cross correlations. We ran NMS to ordinate bird species in land cover space using Sørensen distance and selected 3-D as the final solution as suggested by McCune and Grace (2002). The NMS procedure was conducted using the 'slow and thorough' autopilot mode in PC-ORD 5.0 with a maximum of 500 iterations and 250 runs of real data. Bird species and land cover variables were correlated with axes of the NMS ordination that represented the highest proportion of variation in species data in the 3-D solution.

Individual species response to urbanization

To contrast the distribution of individual species along the urban gradient we used an Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997). This method combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group (i.e. four habitat types: forest, exurban, suburban, urban). The indicator values range from 0 (no indication) to 100 (perfect indication). Perfect indication means that presence of a species indicates a particular group without error, at least with the specified data set. Indicator values are tested for statistical significance using a Monte Carlo randomization with 1000 permutations. A Multi-response permutation procedure (MRPP) was used to test for differences in species indicator values among habitats. MRPP provides a nonparametric multivariate test of differences between two or more groups, based on analysis of a distance matrix.

Data were corrected for outliers and some were transformed to meet normality assumptions, which allowed use of parametric tests. Non-parametric tests were used for data that could not be transformed to meet assumptions of normality. Statistical analyses were conducted using MINITAB software package. Multivariate analyses were conducted using PC-ORD 5.0 (McCune and Grace 2002) and TANAGRA (Rakotomalala 2005). Diversity

statistics were calculated using PAST 1.35 (Hammer et al. 2001) and EstimateS 7.5 (Colwell 2005).

We were interested in population-level response of individual species and species groups to the four habitat types. Therefore we interpret results without application of Bonferroni Sequential Adjustments (BSA). Such adjustments can be misleading in some instances because they are very conservative and therefore inappropriate for exploratory studies using multivariate approaches (Moran 2003, Ro-back and Askins 2005). Here we report p values without application of BSA and accept as significant all values of $p \leq 0.05$ and also show marginally significant values for descriptive purposes.

Results

Land cover and gradient of urbanization

Land cover variables measured at 181 point count sites were ordinated using a CDA to determine a gradient of urbanization. The first three axes accounted for 100% of the total variance in land cover, with axis 1 accounting for 89% of the variation (Table 1). Scores from axis 1 were used as an index of urbanization for each site, which were directly related to the level of urbanization per habitat type. Percent developed land had the highest score on axis 1 whereas percent of exposed land had the lowest value. In contrast, percent pasture had the highest positive value on axis 2 and housing density had the lowest negative value. Only a small proportion of the variation in land cover was explained by axis 3 which ranged from developed land (highest value) to percent pasture cover (lowest value). Among habitats, exurban sites had the greatest within habitat variation followed by suburban sites (Fig. 2) as indicated by the coefficient of variation of the CDA-1 scores (CV: exurban -110.98; suburban 94.20; urban 32.32; forest -12.33).

Table 1. Canonical Discriminant Analysis scores, eigenvalues, and proportion of the variance explained for the first three axes for the percentage of land cover of various types and housing density at 181 point count sites situated across a gradient from forest to urban development in northeastern Puerto Rico.

	CDA-1	CDA-2	CDA-3
% Developed land	1.090	0.416	0.256
% Tree cover	0.240	0.692	-0.409
% Pasture cover	0.636	1.445	-0.225
% Exposed land	0.168	0.537	-0.818
Housing density	0.203	-0.238	-0.838
Eigenvalue	11.71	1.388	0.019
Cumulative proportion	0.892	0.998	1.000

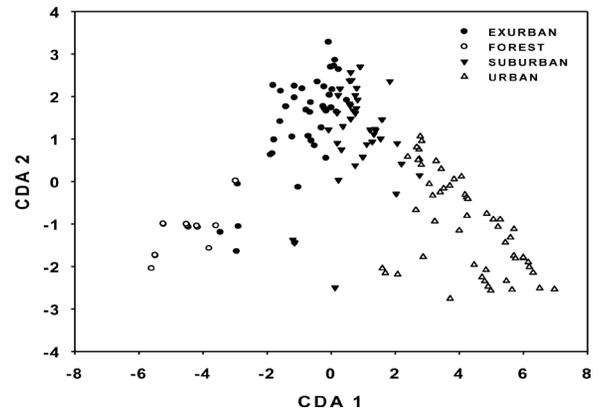


Figure 2. Graph of the Canonical Discriminant Analysis axis 1 vs axis 2 for landscape variables (percentages of land cover of developed land, trees, pasture, exposed land and housing development) measured at 181 point count sites across four habitat types along a gradient of urbanization in northeastern Puerto Rico. The weights of the landscape variables for the two CDA axes are shown in Table 1.

The landscape within 500 m radius of point count sites differed significantly among habitats in land cover, rainfall, and elevation among habitat types (Table 2). Point counts in the forest had the highest percentage of tree cover. Exurban points had higher pasture cover, whereas, suburban points had the highest percentage of exposed land (i.e. bare ground). In contrast, urban points had the highest percentage of developed land and housing density. As expected, forest point count sites were located at a higher elevation and received more rainfall compared with other habitats.

Ground cover within a 10 m radius of point count centers also differed significantly among habitats (Table 3). Within a 10 m radius, forest point count sites had the highest percentage ground cover of broadleaf, dead leaves, dead wood, exposed soil, ferns and rocks. Forest point count sites also had the highest canopy cover, canopy height and basal area. Suburban points had the highest ground cover percentage of pasture cover (i.e. overgrown grassy areas), whereas urban points had the highest percentages of pavement and lawn cover. Exurban point counts had percentage values for each ground cover category that fell within the range of values found in the other habitats.

Avian abundance, species richness and diversity

Forty-seven bird species were recorded during this study (28 resident, 11 endemic, and 8 exotic) distributed among six foraging guilds (see Appendix 1 for common and scientific names, status, and guild classification). The six most abundant species composed 68% of the total abundance, but represented only 13% of the bird species. Overall, mean bird abundance (all species) per point count varied

Table 2. Distribution of mean (\pm SE) percentage of cover types (developed land, tree cover, pasture cover and exposed land), housing density, annual rainfall and elevation among forest, exurban, suburban and urban habitats in northeastern Puerto Rico. Significance levels (p) are shown for one-way ANOVA results. All variables were measured at point count center (rainfall, elevation) or within a 500 m radius of the center of 181 point count sites distributed across the four habitats as shown in Fig. 1 (N indicates the number of point counts sampled per habitat).

N	(Mean \pm SE)				p
	Forest 42	Exurban 46	Suburban 40	Urban 53	
% cover of					
Developed land	0.9 \pm 0.2	15.8 \pm 0.9	32.8 \pm 1.4	77.9 \pm 2.1	0.01
Trees	97.9 \pm 0.5	46.8 \pm 3.6	29.6 \pm 3.0	11.1 \pm 1.5	0.01
Pasture	0.1 \pm 0.1	33.4 \pm 3.2	2.6 \pm 3.5	10.3 \pm 1.6	0.01
Exposed land	0	2.7 \pm 1.1	4.2 \pm 1.7	0.8 \pm 0.3	0.01
Housing density (ha)	0.01 \pm 0.0	0.3 \pm 0.02	0.8 \pm 0.1	2.3 \pm 0.1	0.01
Rainfall (cm)	786.5 \pm 37.7	588.3 \pm 35.4	491.5 \pm 17.3	512.5 \pm 11.0	0.01
Elevation (m)	252.0 \pm 19.5	96.4 \pm 15.0	67.0 \pm 10.6	30.1 \pm 3.3	0.01
CDA-1	-4.80 \pm 0.1	-0.9 \pm 0.1	0.8 \pm 0.1	4.2 \pm 0.2	0.001

significantly among habitats. Mean bird abundance per point was highest in urban and lowest in forest (Table 4). Mean abundance of endemic, resident, and exotic birds per point count also differed among habitats (Table 5). Endemic birds were most abundant in the forest, whereas resident and exotic birds were most abundant in urban sites.

Mean bird abundance per point count site was best predicted by landscape measures (i.e. < 500 m radius) of percent cover of developed land, pasture and elevation ($R^2 = 0.54$, $p < 0.001$). For measures within the 10 m radius of

the point count site the percentage of canopy cover, broad-leaf and dead leaf cover and elevation were significant predictors of total bird abundance ($R^2 = 0.53$, $p < 0.01$). The urbanization index was a positive predictor of resident ($R^2 = 0.54$, $p < 0.001$), exotic ($R^2 = 0.51$, $p < 0.001$) and mean bird abundance ($R^2 = 0.61$, $p < 0.001$) per point count. In contrast, the urbanization index was a negative predictor for endemic abundance ($R^2 = 0.49$, $p < 0.001$).

Differences among the four habitats in mean number of individuals per point count site were detected in 21

Table 3. Mean (\pm SE) percentage cover, mean canopy height (m), and basal area (m) in 0.03 ha plots at 181 point count sites in four habitat types in northeastern Puerto Rico. See Table 2 for number of point count sites per habitat. Significance levels (p) are indicated for comparison of median values (Kruskal–Wallis test) for comparisons among habitats.

	Forest	Exurban	Suburban	Urban	p
Broadleaf	25.0 \pm 1.7	3.2 \pm 1.9	0.5 \pm 0.5	1.5 \pm 0.9	0.01
Canopy cover	57.7 \pm 2.3	7.3 \pm 2.3	3.4 \pm 1.6	1.6 \pm 0.7	0.01
Dead leaves	34.9 \pm 2.0	12.8 \pm 1.7	8.1 \pm 1.6	3.1 \pm 0.9	0.01
Dead wood	9.0 \pm 1.0	1.6 \pm 0.8	0.3 \pm 0.3	0.2 \pm 0.2	0.01
Exposed soil	13.8 \pm 1.4	12.9 \pm 2.6	12.2 \pm 3.0	8.0 \pm 2.2	0.01
Fern	17.3 \pm 2.1	0	0	0	0.01
Lawn	0	3.4 \pm 1.7	0.2 \pm 0.2	12.6 \pm 3.1	0.01
Pasture	17.4 \pm 2.0	45.4 \pm 4.0	50.1 \pm 4.0	19.9 \pm 3.5	0.01
Pavement	0.4 \pm 0.4	20.1 \pm 3.1	21.9 \pm 3.9	48.6 \pm 4.2	0.01
Rock	9.3 \pm 1.7	2.8 \pm 1.1	5.1 \pm 2.4	1.4 \pm 0.8	0.01
Roots	1.7 \pm 0.7	0	0	0	0.01
Water	0.1 \pm 0.1	1.5 \pm 0.6	0.3 \pm 0.3	0	0.04
Canopy height (m)	14.2 \pm 0.7	8.3 \pm 0.9	4.1 \pm 0.9	2.6 \pm 0.7	0.01
Basal area (m)	0.4 \pm 0.05	0.03 \pm 0.01	0.02 \pm 0.01	0.05 \pm 0.02	0.01

Table 4. Mean number of birds (\pm SE) \times 100 per 25 m fixed-radius point count in four habitat types in northeastern Puerto Rico. Scientific names are provided in Appendix 1. Symbol x indicates habitats in which the species was not detected. See Table 2 for number of point counts per habitat. The p value indicates significance level for comparison of point counts based on one-way ANOVA (Kruskal–Wallis test *, Mann–Whitney **).

Bird species	Forest	Exurban	Suburban	Urban	p
Cattle egret	x	2.4 \pm 0.02	5.0 \pm 0.08	1.9 \pm 0.02	x
Green-backed heron	x	2.4 \pm 0.02	5.0 \pm 0.03	1.9 \pm 0.02	x
Red-tailed hawk	2.1 \pm 0.02	x	2.5 \pm 0.02	x	x
American kestrel	x	2.4 \pm 0.02	7.5 \pm 0.07	x	x
Kildeer	x	x	7.5 \pm 0.07	x	x
Rock dove **	x	2.4 \pm 0.02	153.0 \pm 1.02	438.0 \pm 1.07	< 0.01
Scaly-naped pigeon *	69.6 \pm 0.17	16.6 \pm 0.06	x	7.5 \pm 0.07	< 0.01
Common ground dove	x	42.9 \pm 0.15	32.5 \pm 0.14	35.8 \pm 0.13	0.87
Ruddy quail-dove.	2.4 \pm 0.02	x	x	x	x
White-winged dove	2.1 \pm 0.02	104.8 \pm 0.25	210.0 \pm 0.44	326.4 \pm 0.61	< 0.01
Zenaida dove	8.7 \pm 0.05	97.6 \pm 0.20	152.5 \pm 0.25	203.8 \pm 0.36	< 0.01
Orange-fronted parakeet	x	2.4 \pm 0.02	x	x	x
White-winged parakeet	x	7.1 \pm 0.07	x	x	x
Mangrove cuckoo	x	4.7 \pm 0.05	x	x	x
Smooth-billed ani	x	73.8 \pm 0.21	35.0 \pm 0.11	13.2 \pm 0.11	< 0.01
Puerto Rican lizard-cuckoo *	21.7 \pm 0.07	2.4 \pm 0.02	5.0 \pm 0.05	x	< 0.01
Antillean mango	13.0 \pm 0.05	7.0 \pm 0.05	12.0 \pm 0.06	2.0 \pm 0.06	0.46
Green mango	x	x	2.5 \pm 0.02	x	x
Puerto Rican emerald	21.7 \pm 0.07	7.1 \pm 0.04	2.5 \pm 0.02	1.9 \pm 0.02	x
Green-throated carib	x	x	x	1.9 \pm 0.02	x
Puerto Rican tody **	74.5 \pm 0.14	9.7 \pm 0.06	x	x	< 0.01
Puerto Rican woodpecker	19.6 \pm 0.11	54.8 \pm 0.15	47.5 \pm 0.15	22.6 \pm 0.07	< 0.01
Puerto Rican flycatcher	8.5 \pm 0.05	2.4 \pm 0.02	2.5 \pm 0.02	x	x
Gray kingbird	41.3 \pm 0.16	500.0 \pm 0.35	580.0 \pm 0.41	475.5 \pm 0.37	< 0.01
Loggerhead kingbird	x	21.7 \pm 0.22	x	x	x
Cave swallow	x	7.3 \pm 0.05	42.5 \pm 0.33	17.0 \pm 0.17	0.80
Caribbean martin *	x	7.1 \pm 0.05	12.5 \pm 0.06	9.43 \pm 0.07	0.44
Red-legged thrush *	17.4 \pm 0.07	35.7 \pm 0.11	7.5 \pm 0.04	1.9 \pm 0.02	< 0.01
Pearly-eyed thrasher	39.1 \pm 0.07	142.9 \pm 0.23	80.0 \pm 0.22	47.2 \pm 0.10	< 0.01
Northern mockingbird	6.5 \pm 0.04	82.8 \pm 0.17	142.5 \pm 0.26	66.0 \pm 0.12	< 0.01
Black-whiskered vireo *	106.5 \pm 0.18	9.5 \pm 0.04	5.0 \pm 0.05	1.9 \pm 0.02	< 0.01
Bananaquit	569.0 \pm 0.28	435.7 \pm 0.31	270.0 \pm 0.34	326.0 \pm 0.33	< 0.01
Antillean euphonia**	6.3 \pm 0.06	2.4 \pm 0.02	x	x	x
Puerto Rican spindalis *	21.7 \pm 0.07	21.4 \pm 0.08	10.0 \pm 0.06	16.9 \pm 0.06	0.48
Puerto Rican tanager	123.9 \pm 0.16	4.7 \pm 0.03	x	5.6 \pm 0.04	< 0.01
Black-faced grassquit	6.5 \pm 0.04	42.8 \pm 0.09	47.5 \pm 0.13	96.2 \pm 0.20	< 0.01
Yellow-faced grassquit *	x	26.2 \pm 0.11	10.0 \pm 0.06	3.7 \pm 0.03	0.15
Puerto Rican bullfinch **	78.3 \pm 0.19	2.8 \pm 0.02	x	x	< 0.01
Greater antillean grackle	x	97.6 \pm 0.22	327.5 \pm 0.72	786.8 \pm 0.89	< 0.01
Shiny cowbird *	4.3 \pm 0.04	33.3 \pm 0.13	32.5 \pm 0.11	3.7 \pm 0.03	< 0.01
Puerto Rican oriole *	4.2 \pm 0.03	17.0 \pm 0.06	15.0 \pm 0.07	x	0.15
House sparrow	x	16.7 \pm 0.11	152.5 \pm 0.39	352.8 \pm 0.49	< 0.01
Orange-cheeked waxbill *	x	107.1 \pm 0.51	45.0 \pm 0.17	5.6 \pm 0.05	< 0.01
Bronze mannikin	x	26.8 \pm 0.37	27.9 \pm 0.40	23.7 \pm 0.41	0.69
Nutmeg mannikin *	x	35.7 \pm 0.14	85.0 \pm 0.26	30.2 \pm 0.10	0.06
Pin-tailed wydah *	x	9.5 \pm 0.06	32.5 \pm 0.16	22.6 \pm 0.12	0.44

Table 5. Mean (\pm SE) abundance, species richness, and species diversity for endemic, resident and exotic birds per 25 m fixed-radius point count conducted in forest, exurban, suburban and urban habitats in northeastern Puerto Rico. See Table 2 for number of point counts per habitat. The p value indicates significance level for comparison of point counts based on one-way ANOVA.

Index Distribution status	Forest	Exurban	Suburban	Urban	p
Mean abundance per point	8.9 \pm 0.5	11.6 \pm 1.0	14.3 \pm 1.5	15.0 \pm 0.1	< 0.001
Endemic	2.5 \pm 0.3	0.7 \pm 0.2	0.5 \pm 0.2	0.3 \pm 0.1	< 0.001
Resident	6.5 \pm 0.3	8.5 \pm 0.5	9.3 \pm 0.7	10.7 \pm 0.7	< 0.001
Exotic	0.0	2.5 \pm 0.8	4.5 \pm 1.0	4.0 \pm 0.5	< 0.009
Mean species richness per point	3.8 \pm 0.2	5.1 \pm 0.3	5.5 \pm 0.3	6.0 \pm 0.3	< 0.001
Endemic	1.6 \pm 0.1	0.6 \pm 0.2	0.4 \pm 0.1	0.2 \pm 0.07	< 0.001
Resident	2.1 \pm 0.2	3.8 \pm 0.2	4.0 \pm 0.2	4.2 \pm 0.2	< 0.001
Exotic	0.0	0.6 \pm 0.1	1.1 \pm 0.2	1.2 \pm 0.1	< 0.001
Mean diversity (H') per point	2.76 \pm 0.00	2.71 \pm 0.02	2.65 \pm 0.03	2.71 \pm 0.03	< 0.05
Endemic	2.11 \pm 0.01	2.03 \pm 0.03	1.96 \pm 0.05	2.06 \pm 0.02	< 0.01
Resident	2.46 \pm 0.00	2.41 \pm 0.17	2.36 \pm 0.03	2.41 \pm 0.02	< 0.05
Exotic	0.0	1.21 \pm 0.03	1.44 \pm 0.00	1.48 \pm 0.00	< 0.001

bird species (Table 4). A decrease in mean abundance with urbanization was detected in five endemic species (Puerto Rican woodpecker, Puerto Rican bullfinch, Puerto Rican tody, Puerto Rican tanager, Puerto Rican lizard-cuckoo), six resident species (scaly-naped pigeon, smooth-billed ani, red-legged thrush, pearly-eyed thrasher, bananaquit, shiny cowbird), a migrant breeder (black-whiskered vireo; treated as a resident), and an exotic species (orange-cheeked waxbill). In contrast, an increase in mean abundance with urbanization occurred in six resident species (greater antillean grackle, gray kingbird, white-winged dove, zenaida dove, northern mockingbird, black-faced grassquit) and two exotic species (rock pigeon, house sparrow).

Mean species richness per point count site differed among habitats with the highest mean richness occurring in urban and the lowest in forest habitat (Table 5). Breaking mean species richness per point count site down by distributional status (i.e. endemic, resident, exotic) also indicated that mean species richness differed significantly among habitats, although the differences were not concordant among the status categories (Table 5). For example, forest point counts had the highest richness of endemic species, whereas urban points had the highest richness of resident species and exotic species. Mean evenness values varied significantly ($F_{3, 172} = 3.41$, $p = 0.019$) among the habitats with mean evenness highest in exurban (mean = 0.80 ± 0.01 SE) and forest (mean = 0.78 ± 0.01 SE) and lowest in the more developed habitats (suburban mean = 0.75 ± 0.01 SE; urban mean = 0.75 ± 0.01 SE). Mean diversity (H') per point count site differed significantly among habitats (Table 5) with highest values in forest and the lowest in suburban habitat.

Bird-habitat relationships

The Indicator Species Analysis (ISA) showed that 24 bird species had significant Indicator Values (IV), which suggests preference of individual species for particular habitats. Eight species (62.5% endemics) showed significant IVs for forest habitat (Puerto Rican tanager, 66.2, $p = 0.001$; black-whiskered vireo, 47.2, $p = 0.001$; Puerto Rican tody, 46.4, $p = 0.001$; Puerto Rican bullfinch, 44.3, $p = 0.001$; bananaquit, 34.2, $p = 0.001$; scaly-napped pigeon, 25.8, $p = 0.001$; Puerto Rican lizard-cuckoo, 14.6, $p = 0.001$; and Puerto Rican emerald, 11.4, $p = 0.007$).

Species in exurban habitat with high IVs included pearly-eyed thrasher (27.6, $p = 0.003$), orange-cheeked waxbill (14.5, $p = 0.009$) and red-legged thrush (13.6, $p = 0.006$). In suburban habitat the high IV species included gray kingbird (36.3, $p = 0.001$), northern mockingbird (29.8, $p = 0.001$), nutmeg mannikin (19.4, $p = 0.002$) and ground dove (13.9, $p = 0.003$), whereas urban habitat high IV species included greater antillean grackle (57.4, $p = 0.001$), house sparrow (48.5, $p = 0.001$), rock dove (46.8, $p = 0.001$), white-winged dove (39.2, $p = 0.001$), zenaida dove (27.4, $p = 0.003$) and black-faced grassquit (20.7, $p = 0.006$). Results from the Multi-Response Permutation Procedure (MRPP) confirmed differences in species composition among habitats ($T = -62.082$, $p < 0.001$).

Bird species and land cover variables were plotted against the axes of the NMS plot to visualize their relationship with bird community composition (Fig. 3). The two-axis solution recommended by NMS was stronger than expected by chance, based on a Monte Carlo randomization test ($p = 0.024$). The best solution yielded a stress value of 15.5. Cumulatively, these two axes represented 79.3% of the community variation for which axis 1 accounted

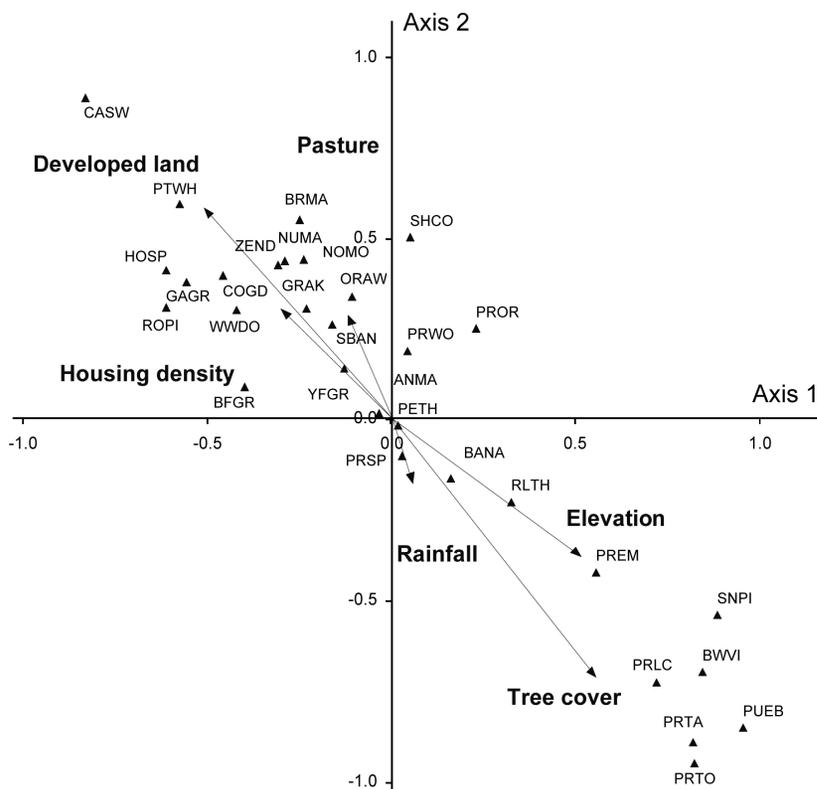


Figure 3. Non-Metric Multidimensional Scaling ordination of bird species versus land cover variables measured at 181 point count sites (with 25 m fixed-radius) across an urbanization gradient in northeastern Puerto Rico as shown in Fig. 1. See Appendix 1 for bird species four letter alpha codes.

for 64% of the variance. The species with the strongest association with axis 1 were: bananaquit ($r = 0.65$), Puerto Rican tanager ($r = 0.62$), black-whiskered vireo ($r = 0.56$), Puerto Rican tody ($r = 0.53$) and Puerto Rican bullfinch ($r = 0.50$). Also positively associated with axis 1 was percent tree cover ($r = 0.28$) and rainfall ($r = 0.24$). Conversely, ordered by decreasing strength of the relationship, greater antillean grackle ($r = -0.74$), gray kingbird ($r = -0.67$), house sparrow ($r = -0.59$), white-winged dove ($r = -0.55$), rock pigeon ($r = -0.43$) and zenaida dove ($r = -0.42$) were all negatively related to axis 1. Cover of pasture land ($r = -0.31$), developed land ($r = -0.21$) and housing density ($r = -0.11$) were also negatively correlated with this axis.

The second NMS axis represented 15.3% of community variation. The birds most strongly associated with the axis 2 were gray kingbird ($r = 0.75$), zenaida dove ($r = 0.55$), northern mockingbird ($r = 0.50$) and bronze mannikin ($r = 0.48$). Land cover variables positively associated with axis 2 were tree cover ($r = 0.31$), elevation ($r = 0.25$) and rainfall ($r = 0.14$). Overall, half of the bird species were positively correlated with axis 2, although most showed only weak associations. In contrast, the bananaquit ($r = -0.59$), Puerto Rican tanager ($r = -0.59$) and Puerto Rican tody ($r = -0.54$) were all negatively correlated with

axis 2. Among land cover variables associated with axis 2, percent tree cover ($r = 0.31$), developed land ($r = -0.33$) and housing density ($r = -0.23$) had the highest correlation with bird community structure. Because bananaquits and gray kingbirds were especially abundant we conducted a second NMS ordination excluding both species to test for skewness in the ordination related to superabundant species and found no changes in the overall pattern as reported in Fig. 3.

Ecological release parameters (i.e. number of habitats occupied per species and increase in within-habitat abundance) were tested as possible factors in the response of individual species to urbanization with inconsistent results. For example, the mean number of habitats occupied by a species did not vary significantly ($p > 0.05$) among endemic (mean = 2.88 ± 0.35 SE), resident (mean = 2.92 ± 0.19 SE) and exotic species (mean = 2.62 ± 0.37 SE). For resident species, however, we found a weak, but significant correlation ($r = 0.40$; $p < 0.03$) between the number of islands in the Caribbean occupied by a species and the number of habitats it occupied. Overall, the mean bird abundance per point count site was a significant positive predictor of the number of habitats occupied by resident birds (logistic regression, $R^2 = 0.72$; $p < 0.001$).

Diet guilds

The mean numbers of birds per point count for certain diet guilds varied significantly among habitats (Table 6). For example, nectarivores (e.g. bananaquits) were most abundant in forest. In contrast, insectivores were most abundant in suburban habitat, whereas omnivores and granivores were most abundant in urban sites. Abundance of frugivores and carnivores did not vary significantly among the habitats. Mean species richness per point was highest for insectivores in suburbs, and granivores in urban habitat (Table 6). No significant differences were found among habitats in the mean number of species per point for frugivores, carnivores, nectarivores or omnivores.

Discussion

By spanning a diversity of habitats from closed canopy rain forest to lightly developed exurban habitat, through suburban housing developments into urban habitats, our bird surveys included a wider range of suburban-urban habitats than previous surveys of avian distribution on Puerto Rico. Although, the analysis by Acevedo and Restrepo (2008) of breeding bird surveys based on point counts along highways, coupled with landscape traits, covered a greater geographic extent on the island and variety of habitats than our study, relatively few urban surveys were available. In contrast, Suárez-Rubio and Thomlinson (2009) restricted their point counts to forest patches in metropolitan San Juan where they related avian distribution to patch-level and landscape traits in the urban zone. Our study differed

from the latter by sampling across a greater range of elevation and ignored forest patch size in our sampling design, and with the exception of the rainforest, we sampled the matrix of the developed habitats. Despite differences in design, our findings are mostly consistent with these previous studies.

A difficulty for evaluating the effects of urbanization on birds in Puerto Rico is that the greatest habitat disturbance and most urbanization is found in the lowlands and most remnant forest patches or second growth forests occurs in the uplands (Thomlinson and Rivera 2000, Grau et al. 2003, Martinuzzi et al. 2007). Moreover, forest age increases with elevation, protection, distance from roads and slope and decreases with amount of surrounding pasture (Helmer et al. 2008); urbanization shows the opposite relationship (Helmer 2004). The elevation gradient in disturbance is especially evident in the NE portion of the island as shown in our habitat gradient that corresponded with mean elevation, with forest at the highest elevation and urban habitat at the lowest elevation. Average annual rainfall was also positively correlated with elevation. Therefore, caution is needed in interpretation of the urbanization effects given that our urbanization gradient varied inversely with elevation and rainfall and because the island's endemics were most common in montane forests (Acevedo and Restrepo 2008). In addition, fruit abundance is greater in the island's mountains than lowlands (Carlo et al. 2003) and fruit-tracking by frugivores could contribute to an increase in frugivore abundance with elevation. Thus it may be argued that low abundance or absence of endemics from the urban habitat is as much a function of low eleva-

Table 6. Mean abundance and mean species richness for avian frugivores, nectarivores, insectivores, carnivores and omnivores per 25 m fixed-radius point counts conducted in forest, exurban, suburban and urban habitats in northeastern Puerto Rico. See Table 2 for number of point counts per habitat. The p value indicates significance level for comparison of point counts based on one-way ANOVA and NS indicates absence of statistical significance.

Foraging guild	Forest	Exurban	Suburban	Urban	p
Mean abundance per point					
Frugivores	0.3 ± 0.1	0.2 ± 0.1	0.10 ± 0.1	0.2 ± 0.1	NS
Nectarivores	5.3 ± 0.3	3.6 ± 0.3	2.2 ± 0.3	2.6 ± 0.3	< 0.001
Insectivores	1.5 ± 0.2	2.8 ± 0.3	4.0 ± 0.5	2.1 ± 0.3	< 0.001
Carnivores	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	NS
Omnivores	1.6 ± 0.2	1.3 ± 0.2	2.8 ± 1.0	3.8 ± 0.6	< 0.002
Granivores	0.1 ± 0.03	3.8 ± 1.0	5.3 ± 1.0	6.2 ± 1.0	< 0.001
Mean species richness per point					
Frugivores	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	NS
Nectarivores	1.3 ± 0.1	1.0 ± 0.1	1.0 ± 0.1	1.0 ± 0.1	NS
Insectivores	1.0 ± 0.1	1.4 ± 0.1	1.5 ± 0.2	1.0 ± 0.1	< 0.002
Carnivores	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	NS
Omnivores	1.0 ± 0.1	0.7 ± 0.1	1.0 ± 0.1	1.2 ± 0.1	NS
Granivores	0.1 ± 0.0	1.5 ± 0.2	2.0 ± 0.2	2.4 ± 0.2	< 0.001

tion or its correlates, as it is due to urbanization. However, we note that most endemics that were more abundant in forest than urban habitat (Puerto Rican bullfinch, Puerto Rican tody, Puerto Rican lizard-cuckoo, and Puerto Rican flycatcher) are common in the lowland Guánica dry forest reserve of the south coast (Kepler and Kepler 1970). Although the endemic Puerto Rican tanager, a forest species in our study, is absent from Guánica and elsewhere in the lowlands it is also absent from mountain towns, despite its abundance in nearby montane forest (e.g. Cayey, Wunderle unpubl.).

The urban gradient we studied included a range of habitats that retained sufficient tree cover and heterogeneity to support some urbanization-sensitive species, but also had enough modified habitat to attract native and exotic birds. The gradient ranged from lowland rain forest, to high density urbanization and reflected the contrasts in land use on the island. The urban areas of northeastern Puerto Rico are highly developed compared with other urban systems studied either on continents (Clergeau et al. 1998, Blair 2001) or islands (Lim and Sodhi 2004, Palomino and Carrascal 2005), although these studies used different methods to estimate intensity of urbanization.

Responses by distributional status to urbanization

As predicted, the abundance and richness of endemic birds decreased with urbanization. Of the eight forest indicator species, five were endemics and no endemic species occurred as an indicator species in the other habitats. Only the endemic Puerto Rican woodpecker was most abundant outside the forest in exurban and suburban habitats. The progressive loss of endemic birds corresponded with the transition from forest to urban landscape reflecting the reliance of these species on structurally diverse forest. The importance of tree cover to endemics was evident in the NMDS ordination, which separated the endemics to the positive side of the axis 1 and showed an association with tree cover and less strongly with elevation and rainfall. The ordination clearly shows the separation of endemics from the more developed or urbanized areas with exotic species. Previous studies have reported a high proportion of endemic birds in the forests of the LEF (Wiley and Bauer 1985, Wunderle and Arendt 2011). The sensitivity of island endemic birds to urbanization has also been reported in Jamaica (Douglas 2001), Taiwan (Lee et al. 2004), Tenerife (Palomino and Carrascal 2005), Singapore (Lim and Sodhi 2004) and recently in Puerto Rico (Suárez-Rubio and Thomlinson 2009).

Resident species as a group showed an inconsistent response to urbanization and were spread widely across the gradient, as evident in the NMDS ordination. Some resident species increased with urbanization, whereas others decreased. The inconsistency was evident in the distribution of resident species as indicator species spread across

all habitats: two species in forest, three in exurban, four in suburban and four in urban habitat. Some residents common in forest (bananaquit, black-whiskered vireo) or exurban (pearly-eyed thrasher) habitat were sensitive to urbanization. Overall, however, abundance and species richness of resident birds increased across the gradient from forest to urban habitat where residents were most abundant overall and proportionally. The abundance of doves, greater antillean grackle, gray kingbird, and northern mockingbird increased with urbanization and these species predominated in suburban and urban habitats. For example, the two most abundant species in point counts in suburban and urban habitats were resident species (greater antillean grackle and gray kingbird) indicating that some island resident species may readily adapt to novel habitats.

As expected, naturalized exotic species as a group showed progressive increases in species richness, diversity, and abundance across the urbanization gradient from exurban, suburban and urban habitats. In the latter two habitats, exotic species accounted for 35% of the avian abundance. Not all exotic species, however, were evenly distributed across the gradient as evident in distribution of exotics as indicator species including orange-cheeked waxbill in exurban habitat, nutmeg mannikin in suburban habitat and house sparrow and rock pigeon in urban habitats. The bronze mannikin, rock pigeon and house sparrow were the most abundant exotic species in urban habitat, which for the latter two species has been documented widely (Clergeau et al. 1998, Crooks et al. 2004, Palomino and Carrascal 2005, van Rensburg et al. 2009). Exotic species responded positively to developed land, housing density and pastures as evident in the NMDS ordination where exotics were loosely clustered in the upper left quadrant with positive values on axis 1 and negative values on axis 2. Our findings of exotic species limited to anthropogenically disturbed habitats is consistent with conclusions of Raffaele (1989) that Puerto Rico's exotic bird species have been successful as a result of the creation of novel habitats, especially grasslands and urban habitats with exotic plant species.

Distribution of diet guilds along the gradient

Analyses based on diet guilds indicated guild distribution differences across the urban gradient. Diet requirements undoubtedly play an important role in determining avian distribution across the urban gradient. For example, the nectarivore guild was most abundant in the exurban and forest habitats and least abundant in the more developed habitats where flowers may have been less abundant. However, mean species richness of the nectarivore guild did not vary among habitats and we believe that ornamental flowers (e.g. *Hibiscus* spp., *Russelia* spp., *Tecoma stans*) popular with urban and suburban dwellers may provide a food source for some nectarivores as found in other tropical cit-

ies (Lim and Sodhi 2004). Although fruit appears to be relatively rare in urban areas (Vázquez-Plass and Wunderle unpubl.), the mean abundance and species richness of the frugivore guild did not vary significantly among the habitats. However, two species of frugivores did show significant sensitivity to urbanization (scaly-naped pigeon, Puerto Rican bullfinch). In contrast, the frugivorous Puerto Rican spindalis was abundant throughout the gradient, including developed areas, perhaps because consumption of leaves aids the species' use of human-modified habitats (Carlo et al. 2012).

The granivore guild was the most abundant along the urban gradient accounting for 30% of total guild abundance (all guilds combined) and granivore abundance increased consistently with urbanization as found elsewhere (Lancaster and Rees 1979, Chace and Walsh 2006), although some species-specific differences occurred. No endemic granivores are known from the island, although some endemic species occasionally include seeds in their diet. Resident species of granivores (e.g. doves and *Tiaris* spp.) accounted for 51% of the observations and were most abundant in urban and suburban habitats. Exotic species (mostly finches) accounted for 49% of granivore guild abundance and predominated in urban habitat. Although some exotic granivores have widespread distributions and are abundant on the island, none have colonized forests (Raffaele 1989), including the LEF (Wunderle and Arendt 2011). The absence of exotic granivores in the forest is undoubtedly due to their dependence on grass seeds, which are rare or absent in the forest.

As expected from previous studies (Emlen 1974, Beissinger and Osborne 1982), most omnivores increased in abundance with urbanization. In general, omnivores showed a strong positive association with urban variables (e.g. percent developed land and house density), and some were superabundant in urban habitat accounting for approximately 26% of the total guild abundance, although species richness of omnivores did not increase with urbanization. Numerically, the omnivore guild was dominated by resident species, especially the greater antillean grackle and pearly-eyed thrasher. The Puerto Rican tanager and Puerto Rican woodpecker were the only endemic omnivores detected and both were sensitive to urbanization. Thus even with an omnivorous diet, endemic species were unable to colonize the urban zone in contrast to exotic and resident omnivores.

Contrary to previous tropical studies (Canaday 1996, Lim and Sodhi 2004) we found that intermediate levels of urbanization increased the abundance and richness of insectivores, although insectivore abundance and richness decreased in urban habitat. Insectivores also had intra-guild differences in their response to urbanization. For example, the gray kingbird, an aerial-sallying insectivore especially in developed areas (Vázquez-Plass and Wunderle unpubl.), frequently consumes fruit in non-urban areas (Carlo and Yang 2011), and was most abundant in subur-

ban and urban habitats, where it may benefit from insects attracted to outdoor lights and safe nest sites provided by utility structures. In contrast, foliage-gleaning insectivores were rare or absent in urban habitats, possibly due to the absence of appropriate foliage substrate for foraging and/or inadequate arthropod prey. Thus the insectivore guild did not exhibit a consistent response to urbanization, likely reflecting variation in their foraging modes. Overall, resident species dominated the insectivore guild accounting for 96% of the total abundance and their numbers peaked in the suburbs. The Puerto Rican tody and Puerto Rican flycatcher were the only endemic insectivores encountered and both were rare outside the forest. In both instances, absence of appropriate foraging substrates and their cavity-nesting requirements may limit them to forest.

The carnivore guild was small (about 2% of total observations) and did not show significant variation in abundance or species richness among the habitats, although abundance of one species within the guild varied significantly among the habitats. For instance, abundance of the endemic Puerto Rican lizard-cuckoo varied significantly among the habitats and appeared to be sensitive to urbanization. Given that *Anolis* lizards and *Eleutherodactylus* frogs constitute a sizeable proportion of the prey of the lizard-cuckoo and prey of other avian carnivores (Waide 1996), we suspect that much of the guild's distribution is explained by lizard and frog availability.

Changes in diversity measures along the gradient

The different measures of diversity per point count site varied along the urban gradient, but not always in manner consistent with expectations. For instance, species richness was expected to decline with urbanization (Chace and Walsh 2006), however, we found an increase in mean species richness per point with urbanization. This pattern was mostly attributable to the increased abundance of a variety of exotic species in the urban areas, which were absent from the forest as well as the greater abundance of resident species in urban habitat. Both the Shannon diversity index (H') and Simpson's evenness index per point varied in a manner that was mostly consistent with expectations that a few very abundant species would predominate in urban bird communities (Chace and Walsh 2006). Mean species diversity (H') per point count site was highest in the forest as expected and lowest in the suburban habitat with intermediate levels in exurban and urban habitat. Diversity (H') was relatively lower in suburban and urban habitats due in part to exceptional abundance of the resident gray kingbirds, greater antillean grackles, and white-winged doves as well as exotic house sparrows in both habitats. Although variation in evenness index values among the habitats was not expected to fully coincide with the H' index variation, because Simpson's index weights the common species and the H' weights the rare species more heavily (Krebs 1989),

the variation in the two indexes mostly coincided. Evenness values were lower in the urban and suburban habitats relative to exurban and forest habitats. Thus our findings are consistent with previous studies in showing that urbanization results in avian communities with reduced equitability in species' abundances, but our results differ from previous studies in demonstrating increased abundance of a few resident species in the urban habitat.

Ecological release and distribution along the gradient

Our ecological release predictions related to distribution across the gradient were only weakly supported. For instance, resident species showed a non-significant trend in occupying a higher number of habitats and having higher within-habitat abundance relative to endemic and exotic species. Most resident species were abundant along the urban gradient and showed broad habitat preferences, and some attained high densities in suburban and urban habitats. Resident species showed a weak positive correlation of number of habitats occupied along the gradient with number of islands colonized. This was consistent with expectations that species that utilize a wide breadth of habitats are pre-adapted for colonizing islands and likely pre-adapted for colonizing novel habitats. Conversely, most endemic species (except the woodpecker and spindalis) showed narrow habitat preferences, were most abundant in forest habitat, and were sensitive to urbanization. Our results indicate that some resident species (e.g. bananaquits) are able to occupy a range of different habitats and increase their abundances within those habitats as consistent with other Caribbean ecological release studies (Terborgh and Faborg 1973, Cox and Ricklefs 1977, Wunderle 1985).

The need for further studies

The urban habitat showed a surprising abundance and richness of species mostly due to exotic granivores and omnivores and some resident insectivores, granivores and omnivores, whereas most endemic species avoided the urban habitat. Some resident species appeared to be especially adaptable in their use of urban areas. However, it is not evident that the urban zone provides sufficient resources for all species that were abundant there during our March–August censuses. Our observations suggest that breeding greater antillean grackles, white-winged doves, zenaida doves, and the two mannikin species routinely leave the urban areas to forage in nearby grasslands, second growth woodlands, and mangroves (Vázquez-Plass and Wunderle unpubl.). In addition, in the nonbreeding period (October–January), greater antillean grackles, white-winged doves, gray kingbirds, and some exotic finches leave the urban areas for less developed habitats (Vázquez-Plass and

Wunderle unpubl.). These observations, however, need to be quantified. In addition, research is needed to determine if urban bird populations have adequate reproductive success for their own maintenance rather than being 'rescued' by dispersal from populations with excess production of offspring from undeveloped habitats nearby (i.e. source-sink dynamics, Pulliam 1988). Although availability of nearby undeveloped habitats may be critical for maintaining avian abundance and species richness in Puerto Rico's urban areas, research is needed to substantiate this hypothesis.

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Appendix 1

Bird species recorded in four habitat types in northeastern Puerto Rico. Species names according to AOU (2011), alpha codes follows Pyle and De Sante (2003), distribution (Raffaele et al. 1998), and guild classification (Faaborg 1985, Raffaele 1989, Waide 1996). Black-whiskered vireo is a migrant that breeds in Puerto Rico, but treated here as a resident.

Common name	Scientific name	Alpha code	Distribution	Guild
Great egret	<i>Ardea alba</i>	GREG	Resident	Carnivore
Cattle egret	<i>Bubulcus ibis</i>	CAEG	Resident	Omnivore
Green-backed heron	<i>Butorides striatus</i>	GRHE	Resident	Carnivore
Red-tailed hawk	<i>Buteo jamaicensis</i>	RTHA	Resident	Carnivore
American kestrel	<i>Falco sparverius</i>	AMKE	Resident	Carnivore
Killdeer	<i>Charadrius vociferous</i>	KILL	Resident	Carnivore
Rock dove	<i>Columba livia</i>	ROPI	Exotic	Omnivore
Scaly-naped pigeon	<i>Columba squamosa</i>	SNPI	Resident	Frugivore
Common ground-dove	<i>Columbina passerina</i>	COGD	Resident	Granivore
Ruddy quail-dove	<i>Geotrygon montana</i>	RUDQ	Resident	Granivore
White-winged dove	<i>Zenaidura asiatica</i>	WWDO	Resident	Granivore
Zenaida dove	<i>Zenaida aurita</i>	ZEND	Resident	Granivore
Orange-fronted parakeet	<i>Aratinga canicularis</i>	ORAW	Exotic	Granivore
White-winged parakeet	<i>Brotogeris versicolorus</i>	WWPA	Exotic	Granivore
Mangrove cuckoo	<i>Coccyzus minor</i>	MACU	Resident	Carnivore
Smooth-billed ani	<i>Crotophaga ani</i>	SBAN	Resident	Omnivore
Puerto Rican lizard-cuckoo	<i>Saurothera vieillot</i>	PRLC	Endemic	Carnivore
Antillean mango	<i>Anthrocothorax dominicus</i>	ANMA	Resident	Nectarivore
Green mango	<i>Anthrocothorax viridis</i>	GMAG	Endemic	Nectarivore
Puerto Rican emerald	<i>Chlorostilbon maugaeus</i>	PREM	Endemic	Nectarivore
Green-throated carib	<i>Eulampis holocericeus</i>	GTCA	Resident	Nectarivore
Puerto Rican tody	<i>Todus mexicanus</i>	PRTO	Endemic	Insectivore
Puerto Rican woodpecker	<i>Melanerpes portoricensis</i>	PRWO	Endemic	Omnivore
Puerto Rican flycatcher	<i>Myiarchus antillarum</i>	PRFL	Endemic	Insectivore
Gray kingbird	<i>Tyrannus dominicensis</i>	GRAK	Resident	Insectivore
Loggerhead kingbird	<i>Tyrannus caudifasciatus</i>	LOKI	Resident	Insectivore
Cave swallow	<i>Hirundo fulva</i>	CASW	Resident	Insectivore
Caribbean martin	<i>Progne dominicensis</i>	CAMA	Resident	Insectivore
Red-legged thrush	<i>Turdus plumbeus</i>	RLTH	Resident	Omnivore
Pearly-eyed thrasher	<i>Margarops fuscatus</i>	PETH	Resident	Omnivore
Northern mockingbird	<i>Mimus polyglottos</i>	NOMO	Resident	Insectivore
Black-whiskered vireo	<i>Vireo altiloquus</i>	BWVI	Resident	Insectivore
Bananaquit	<i>Coereba flaveola</i>	BANA	Resident	Nectarivore
Antillean euphonia	<i>Euphonia musica</i>	ANEU	Resident	Frugivore
Puerto Rican spindalis	<i>Spindalis portoricensis</i>	PRSP	Endemic	Frugivore
Puerto Rican tanager	<i>Nesospingus speculiferus</i>	PRTA	Endemic	Omnivore
Yellow-faced grassquit	<i>Tiaris olivacea</i>	YFGQ	Resident	Granivore
Black-faced grassquit	<i>Tiaris bicolor</i>	BFGQ	Resident	Granivore
Puerto Rican bullfinch	<i>Loxigilla portoricensis</i>	PUEB	Endemic	Omnivore
Greater antillean grackle	<i>Quiscalus niger</i>	GAGR	Resident	Omnivore
Shiny cowbird	<i>Molothrus bonariensis</i>	SHCO	Resident	Insectivore
Puerto Rican oriole	<i>Icterus portoricensis</i>	PROR	Endemic	Insectivore
House sparrow	<i>Passer domesticus</i>	HOSP	Exotic	Granivore
Orange-cheeked waxbill	<i>Estrilda melpoda</i>	ORAW	Exotic	Granivore
Bronze mannikin	<i>Lonchura cucullata</i>	BRMA	Exotic	Granivore
Nutmeg mannikin	<i>Lonchura punctulata</i>	NUMA	Exotic	Granivore
Pin-tailed whydah	<i>Vidua macroura</i>	PTWH	Exotic	Granivore