Landscape and patch-level factors influence bird communities in an urbanized tropical island

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ABSTRACT

As human population continues to increase and intensification of human land use escalates, it is important to address the role of urban forest patches in supporting bird communities. We related bird species richness and community assemblage to landscape- and patch- level factors in 40 forest patches in the densely populated metropolitan area of San Juan, Puerto Rico. In total, 54 bird species were observed including 26 resident, 10 endemic, 12 migratory, and 6 introduced species. Patch size, level of urbanization in the surrounding matrix, and vertical heterogeneity of forest patches were the most important variables in explaining species richness. Patch size had the highest predictive power in explaining species richness for all groups except migrants, which were best predicted by patch-level factors (vegetation heterogeneity). The degree of matrix urbanization was correlated negatively with endemic species richness, but positively with introduced species. Endemic species were particularly sensitive to landscape factors (patch size, matrix urbanization, and canopy texture). Introduced species richness was not dependent on any patch-level factors. Eight species were relatively unaffected by urbanization, whereas two species were only found in large forest patches, and two species were sensitive to urban development. Seven species demonstrated a preference for small patches. Recommendations for land managers and conservation agencies to maintain a high bird species richness and diversity include: (1) preserve both large and small forest patches, (2) limit urban development near forest patches, (3) manage forest patch structure to maintain vertical heterogeneity, and (4) maintain forest patches with different vegetation types.

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1. Introduction

As metropolitan areas grow worldwide, native vegetation is converted to urban development (Villa et al., 1992; Vitousek et al., 1997; Czech et al., 2000; McKinney, 2002). Due to its persistence on the landscape and its dissimilarity to natural land cover (Marzluff and Ewing, 2001), urban development affects natural communities (Mörtberg, 2001; McKinney, 2002; Lim and Sodhi, 2004; McKinney, 2008) including plants (e.g., Kowarik, 1995; Sax et al., 2005), insects (e.g., McIntyre, 2000; Blair, 2001), birds (e.g., Blair, 2001; Chace and Walsh, 2006), and mammals (e.g., Mackin-Rogalska et al., 1988; Tait et al., 2005), jeopardizing native biodiversity (Shochat et al., 2006; Luck, 2007; Mcdonald et al., 2008; Sodhi, 2008). As human population continues to increase in several tropical countries (United Nations, 2004), and expansion and intensification of human land use escalates, one question that

arises is how critical are urban forest patches to supporting bird communities.

Numerous studies have addressed the effects of urban development on bird communities in temperate regions (e.g., Emlen, 1974; Aldrich and Coffin, 1980; Beissinger and Osborne, 1982; Blair, 1996; Fernández-Juricic, 2000). Many of these studies found that urban development decreased bird diversity, composition, and richness; and increased density and biomass (Chace and Walsh, 2006). However, little is known about the effects of urbanization on avifauna in the tropics, despite the fact that the rich tropical biota is under immense pressure from a rapidly increasing human population (Marzluff et al., 2001). Some studies have been conducted in the tropics, and these have focused on species richness in landscapes of low anthropogenic modification (Lee et al., 2005), for example in different types of habitats in Southeast Asia (Sodhi et al., 2005) or Brazil (Manhães and Loures-Ribeiro, 2005). Some studies have been conducted within human-dominated tropical landscapes (Jones, 1983; Sodhi et al., 1999; Reynaud and Thioulouse, 2000; Koh et al., 2006), and few in the Caribbean (Fonaroff, 1974; de las Pozas and Balát, 1981), but the importance of urban forest patches on bird communities have been little studied in tropical islands, especially in the Caribbean.

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Bird communities are influenced by patch factors (Dunning et al., 1992; Graham and Blake, 2001), and the relation between vegetation complexity and bird species diversity has been well studied (e.g., MacArthur and MacArthur, 1961; Pearson, 1975; Greenberg et al., 1997). Grassland and forest birds respond to vegetation characteristics such as shrub, herbaceous, and litter cover, foliage height diversity, and total foliage volume (Estades, 1997). In addition, the vertical organization of forests influences internal stand microclimates through the characteristics of the canopy and sub-canopy structure (Ambuel and Temple, 1983). In contrast, little is known about the importance of vegetation complexity in urban environments. Some studies have addressed the importance of vegetative cover in urban parks and found that habitat complexity increased bird diversity, for example in Seattle, Washington (Gavareski, 1976), and Madrid, Spain (Fernández-Juricic and Jokimäki, 2001).

Few tropical studies have simultaneously assessed landscape- and patch-level factors (e.g., Graham and Blake, 2001), and little is known about how these factors influence bird communities across a range of urbanization intensity in a tropical island landscape. Puerto Rico has an accelerating and widespread pattern of urban development and deforestation that is causing the loss and fragmentation of its forests (Birdsey and Weaver, 1987; Ramos-González, 2001). Only 1.2% of the lowland moist seasonal evergreen forests of the island are protected (Helmer et al., 2002); generally, these forests occur at the lowest elevations where rates of land-cover conversion to urban and developed areas are highest (López et al., 2001). In addition, Puerto Rico is part of the Caribbean biodiversity hotspot (Myers et al., 2000). The island area is about 8900 km^2 and has approximately 335 bird species, of which 120 species regularly nest, including native species and other birds that have been introduced over the last few centuries (Raffaele, 1989). Urban development is one of the most important factors contributing to the increasing loss of biodiversity in Puerto Rico (Brash, 1987).

The goal of our study was to examine how landscape- and patch-level factors influence the use of urban forest patches by bird communities in a tropical island landscape. We tested the following hypotheses: (1) small patches will support lower bird diversity than larger patches, because some bird species require a minimum area to perform their vital functions (Saunders et al., 1991); (2) fragments with a more convoluted boundary will sustain higher bird diversity than more compact fragments because more edge implies more available habitat types. However, the communities will be different, because more compact patches are less affected by environmental and biotic changes associated with edges (Murcia, 1995); (3) the intensity of land use surrounding a patch will affect bird diversity and community structure because inimical land uses such as urban construction will affect movement of some species among patches (Gascon et al., 1999; Rodewald and Yahner, 2001); (4) isolated patches will have lower species diversity than connected patches because isolation can influence movement between patches and affect occurrence or persistence of species within a patch (Van Dorp and Opdam, 1987; Schmiegelow et al., 1997); (5) patches with high texture, as measured on satellite images, will have greater bird diversity than patches with low texture because texture is correlated with canopy heterogeneity (Lillesand et al., 2004); and (6) a vertically complex patch will support more species than a simply structured patch because complex vertical organization supports more kinds of plants and animals that provide diverse food resources and habitat types (Orians and Wittenberger, 1991). We examined the response of migratory, endemic, resident, and introduced species (i.e., distributional status) and different feeding guilds. Furthermore, we studied individual species responses, because species vary in their ability to respond to urban environments (McKinney, 2002).

2. Methods

2.1. Study area

We conducted this study in the San Juan metropolitan area (between 18° 15′N, 66° 15′W and 18° 30′N, 66° 52′30″W) of northern Puerto Rico (Fig. 1). The metropolitan area covers 541 km^2 of land area, holds 30% of Puerto Rico's residents, has a population density of 2050 people/km^2 (US Census Bureau, 2002), and is composed of commercial, industrial and residential neighborhoods. Despite its urban character, the San Juan area retains scattered remnant and regenerated forest patches in the form of protected areas and privately owned undeveloped parcels, surrounded by different levels of urbanization. San Juan is within the subtropical moist forest life zone (Ewell and Whitmore, 1973) with an annual precipitation of 1752 mm and average monthly temperature ranging from 21 to 31 °C (NOAA, 2008). Elevation ranges from 0 to 238 m above mean sea level.

2.2. Landscape-level factors

We mapped all visible forest patches in the study area by on-screen digitizing of IKONOS satellite images from 2002, degraded to 2 m resolution, in ArcGIS 8.3. From 83 digitized polygons in the study area, we randomly selected 40 forest patches that ranged in size from 1.4 ha to 214.3 ha. The size distribution of the selected patches was similar to that of the whole population of forest patches. We then characterized the surrounding matrix through unsupervised classification with 30 classes, using the ISODATA algorithm in ERDAS Imagine 8.7, with 6 iterations and a threshold of 0.95. We reclassified the image to three major classes: water, forest, and constructed land, and we then generalized the classified image using a 3×3 majority filter. Finally, we created buffers of 1000 m, 500 m, and 100 m around the 40 forest patches to determine the proportion of constructed and forested land in the matrix surrounding each forest patch at different scales.

To characterize the forest patches, we calculated patch size, patch perimeter, boundary configuration index (using the shoreline development index of Lind, 1985), matrix index (percent of constructed land in the matrix surrounding each forest patch), isolation coefficient (Thomlinson, 1995), and texture analysis (measured as the coefficient of variation in normalized difference vegetation index (NDVI; Millward and Kraft, 2004). The maximum radius for isolation coefficient was 2630 m, which was the largest minimum distance between adjacent patches, ensuring that every patch had at least one neighboring patch included. The coefficient of variation in NDVI has been found to discriminate among tropical forest communities in northeastern Puerto Rico better than conventional texture measures (Thomlinson, unpublished data).

2.3. Bird surveys

In each of the 40 forest patches, we censused birds three times: in February–April 2004, May–July 2004, and November 2004–January 2005, to include both dry and wet seasons. Since forest patches varied in size, the absolute sampling effort (number of census points) increased with area to obtain a reasonable count of species present in larger forest patches. Patches from 1 to 2 ha ($n = 2$) had 1 point, 3–4 ha ($n = 6$) 2 points, 5–10 ha ($n = 12$) 3 points, 11–20 ha ($n = 4$) 4 points, 21–30 ha ($n = 9$) 5 points, 40–60 ha 6 points ($n = 4$), and patches > 60 ha ($n = 3$) had 10 points. The census points were selected at random and located in the field with a Trimble XR2 Global Positioning System (GPS), IKONOS images, topographic maps, and compass readings from identifiable landmarks. The
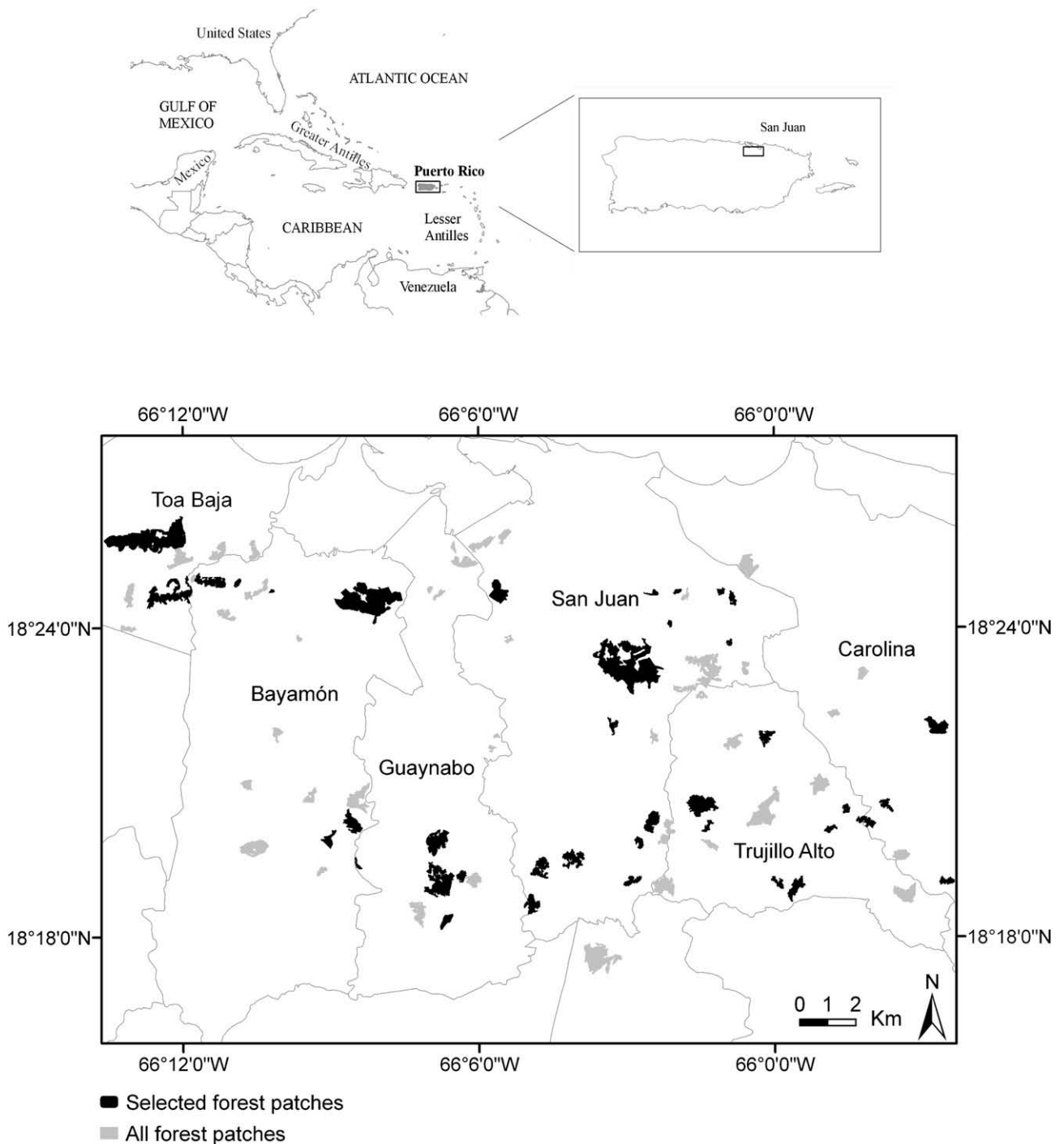
Fig. 1. Map of San Juan metropolitan area, Puerto Rico showing all the forest patches present in the metropolitan area, and the selected forest patches for this study.

birds were surveyed using 20 m fixed-radius point-counts (Hutto et al., 1986), and census points were at least 100 m apart. Each observation point was visited for 15 min during a 4 h period beginning at sunrise on days with little or no wind and no precipitation. All visual/audio observations up to the canopy were recorded, as well as a distance estimate to each bird. Birds flying over the census area were excluded from analyses.

2.4. Patch-level factors

Vegetation was measured in the 20 m radius plots centered at each bird census point. Foliage height profiles were determined at 20 points located at 4 m intervals along the cardinal directions from each census point (Wunderle, 1999). A 3 m pole marked at 0.5 m intervals was placed vertically at each sample point. We recorded the presence or absence of foliage touching the pole within each of the following height classes: < 0.5, 0.5–1, 1–2, 2–3, 3–4, 4–6, 6–8, 8–10, 10–12, 12–15, and >15 m above ground. For height intervals above 3 m, we estimated the height and recorded the presence/absence of foliage in each interval. In addition, we counted and measured stems $\geqslant 10$ cm diameter at breast height (DBH) within the plot, and we estimated the height of the canopy and the percent of canopy and understory coverage at each of the 20 points.

2.5. Analyses

2.5.1. Patch-level factors

We calculated the percent vegetation cover for each height interval by dividing the number of points with foliage present in that interval by the total number of vegetation sample points (Wunderle, 1999). Because higher habitat structural heterogeneity often increases bird species richness due to the presence of more diverse nesting and foraging resources (MacArthur and MacArthur, 1961; Roth, 1976), we calculated the Shannon diversity index of vertical heterogeneity of vegetation using EstimateS 7.5 (Colwell, 2004) by taking the number of vegetation touches to the measuring pole at each height interval as individuals in this class (Sekercioglu, 2002). We performed a Principal Components Analysis (PCA) to analyze the differences in vegetation structure among forest patches. We generated the PCA using a correlation coefficients cross-products matrix and interpreted all factors with eigenvalues > 1. We performed the PCA using PC-ORD 4.10 for Windows (McCune and Grace, 2002).

2.5.2. Bird community

Because the number of census points differed among forest patches, we performed a rarefaction analysis (Gotelli and Colwell, 2001) to compare species richness among patches. We also estimated diversity indexes using EstimateS 7.5 (Colwell, 2004) applying relative abundance values obtained from the bird censuses. To test for spatial autocorrelation between location of forest patches and rarified species richness and diversity, we estimated Moran's *I* using GeoDa (Anselin et al., 2006). In addition, we categorized the bird species according to their distributional status (i.e., migratory, endemic, resident, and introduced), and feeding guild (i.e., insectivore, frugivore, nectarivore, granivore, carnivore, or omnivore) to examine their proportion in relation to the total number of birds recorded per forest patch.

2.5.3. Single-factor associations

We ran simple regressions to examine the relationship between the independent variables and the dependent bird variables and detect significant associations. Dependent variables included were number of bird species, bird species Shannon diversity index, distributional status classes, and feeding guilds.

2.5.4. Community responses to landscape- and patch-level factors

We analyzed differences in bird composition among the forest patches using Non-metric Multi-dimensional Scaling (NMS; McCune and Grace, 2002). Species abundance values were log-transformed, and all landscape and vegetation variables were examined for cross-correlation. We then searched for outliers among forest patches and bird species, using Sørensen (Bray–Curtis) distance with a cutoff of two standard deviations (McCune and Grace, 2002). We ran NMS to ordinate forest patches in species space, using Sørensen distance, with a first approximation run of 6-D solution stepping down to 1-D solution, starting 20 runs from a random configuration and 500 iterations. We selected 3-D as the final solution, using the starting configuration that worked best, and one real-run as suggested by McCune and Grace (2002). Landscape and vegetation variables were correlated with axes of the NMS ordination that represented the highest proportion of variance in species data in the 3-D optimum solution. The Spearman correlation coefficient was used to indicate how well each landscape and vegetation variable explained the position of samples along each ordination axis. For interpretability, landscape and vegetation variables were plotted as vectors on a joint plot to show their relationships with the sample scores (McCune and Grace, 2002). A joint plot of landscape and vegetation variables and species scores (calculated by weighted averaging of the abundances

of each species in each forest patch) was also plotted. We used a multi-response permutation procedure (MRPP) using Sørensen distance to determine statistical differences among the groups formed in the NMS (McCune and Grace, 2002). The outlier analysis, NMS procedure, and MRPP were performed using PC-ORD 4.10 for Windows (McCune and Grace, 2002).

2.5.5. Species prediction models

We created a Generalized Linear Model (GLM; Guisan et al., 2002; Luoto et al., 2004) to identify which landscape and vegetation variables predicted species richness of the different distributional status classes. We used a Poisson-distributed relationship between the number of species and the explanatory variables, because Poisson typically better describes richness data than does a normal distribution (Lobo et al., 2004; Mac Nally and Fleishman, 2004). Statistical inference in the GLM was evaluated by the 'deviance', which has an approximate chi-squared distribution (McCullagh and Nelder, 1989; Palmer et al., 2000). The GLM was created in S-plus 6.1 for Windows.

2.5.6. Individual species response

We conducted an indicator analysis following the method of Dufrêne and Legendre (1997) to find representative species for different landscape and patch variables. The procedure combines a species' relative abundance with its relative frequency of occurrence in each forest patch to provide an indicator value for the particular species for each landscape variable. The indicator value of a given species is independent of other species values. The index ranges from zero to 100, the latter indicating all individuals of a species in a single type of landscape element. We used the Monte Carlo technique with 1000 permutations to test for significance of indicator values (McCune and Mefford, 1999).

3. Results

3.1. Landscape-level factors

Our 40 urban forest patches ranged from 1.4 to 214.3 ha (mean ± s.d.: 28.6 ha ± 46.1), with a perimeter from 0.6 to 19.7 km (3.8 km ± 3.7). Cross-correlation of the landscape variables showed that patch size and patch perimeter were correlated (Pearson $r = 0.94$) and therefore the latter was excluded from further analysis. The boundary configuration index varied from 1.4 to 4.1 (2.2 ± 0.6). The matrix index, indicating the percentage of urban land cover in a 1000 m buffer surrounding each patch, ranged from 11% to 79% (37% ± 23). Although the amount of urbanization changed when considering 500 and 100 m buffers, the species responses were the same as for the 1000 m buffer. For further analysis, therefore, we just considered the 1000 m buffer. The isolation coefficient varied from less than 0.01–71.4 (2.4 ± 11.2; median: 0.46; 95th percentile: 1.99). All forest patches were relatively close to one another (1.3 km ± 0.2), and only two forest patches were considered isolated with higher isolation coefficients than the 95th percentile. Finally, the texture coefficient ranged from 0.18 to 0.32 (0.24 ± 0.03) indicating variation in canopy heterogeneity of the patches.

3.2. Patch-level factors

All height intervals in the vertical foliage structure of the 40 forest patches were represented (Fig. 2). Foliage between 4 and 6 m was the interval with the greatest mean coverage (75% ± 14), while foliage >15 m interval had the smallest mean coverage (8% ± 13). The vertical heterogeneity, measured by the Shannon diversity index, varied from 1.9 to 2.3 (2.2 ± 0.1). The height of the trees
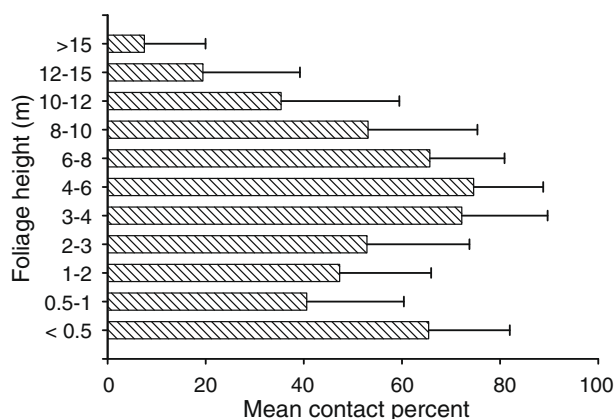
Fig. 2. Foliage height profile of forest patches in San Juan metropolitan area, Puerto Rico. Mean (±SE) percent cover represents the percentage of vegetation touches in a given height class.

Fig. 3. Species accumulation curve based on the forest patch size for birds in San Juan metropolitan area, Puerto Rico.

ranged from 5.5 to 16.1 m (9.6 m ± 2.5). The understory coverage varied from 7% to 95% (33% ± 22) while the canopy coverage ranged from 41% to 96% (83 ± 2). Only six patches (15%) did not have trees ⩾ 10 cm in DBH; the maximum number of large trees in a plot was 21 (4.8 ± 4.2), and their DBH ranged from 14 to 51 cm (28 cm ± 10).

Three axes in the PCA explained 77% of the variation in vegetation structure among the patches. The first principal component (PC1) divided patches primarily on the mean foliage coverage above 8 m, height of the trees, and vertical heterogeneity, explaining 44% of the variance with an eigenvalue of 7.5. The second principal component (PC2) separated the patches on the basis of mean foliage coverage between 2 and 6 m, understory cover, and canopy cover, explaining 23% of the variance with an eigenvalue of 3.9. Finally, the third principal component (PC3) was correlated with mean foliage coverage in the 6–8 m interval, below 0.5 m and above 15 m, and understory cover, explaining 10% of the variance with an eigenvalue of 1.6.

Cross-correlation of vegetation variables showed that some foliage height classes were correlated with each other. Foliage presence in the <0.5 and 0.5–1 m intervals were correlated with foliage presence in the 1–2 m interval (<0.5 m: Pearson $r = 0.75$, 0.5–1 m: Pearson $r = 0.77$), and foliage height classes from 8 to >15 m were correlated with tree height (8–10 m: Pearson $r = 0.83$, 10–12 m: Pearson $r = 0.92$, 12–15 m: Pearson $r = 0.92$; >15 m: Pearson $r = 0.83$), so the classes from <0.5 to 1 m and from 8 to >15 m were removed from further analysis. In addition, understory coverage and canopy coverage were negatively correlated (Pearson $r = -0.71$); therefore we also excluded the latter from further analysis.

3.3. Bird community

We made a total of 2955 observations of 54 bird species including 26 resident (48%), 10 endemic (19%), 12 migratory, (22%) and six introduced species (11%) during the census counts in the forest patches (see Appendix A for list of all observed bird species, English names, and guild classification). Per patch Shannon diversity index ranged from 1.5 to 2.8 with a mean of 2.3 ± 0.3. The bird community was composed of 22 insectivores (41%), eight frugivores (15%), seven granivores (13%), seven omnivores (13%), six carnivores (11%), and four nectarivores (7%; Appendix A). The cumulative species-area curve almost reached saturation (the asymptote) indicating that most species present had been observed (Fig. 3). The most common species were *Coereba flaveola* (23%), *Tyrannus dominicensis* (12%), *Zenaida aurita* (10%), *Melanerpes portoricensis* (7%), and
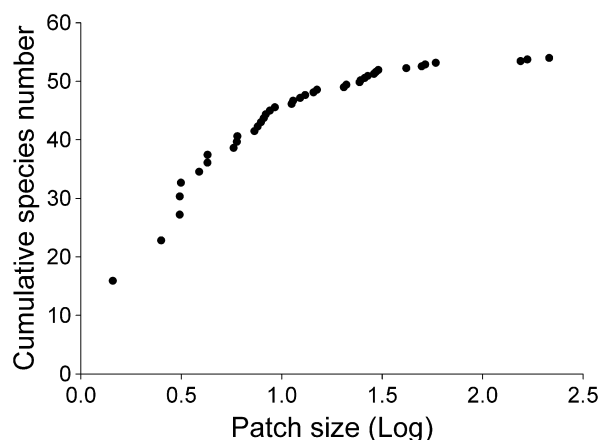
Margarops fuscatus (6%), with all remaining species individually comprising <4% of the total sample (Appendix A). We excluded two species, *Brotogeris versicolurus* and *Bubulcus ibis*, from our analysis because they were flying above the patches and their status in the forest patches was uncertain. Spatial autocorrelation analysis indicated that species richness and diversity of a forest patch were not influenced by surrounding forest patches (species richness: Moran's $I = 0.145$, $p = 0.09$; diversity: Moran's $I = 0.158$, $p = 0.07$).

3.4. Single-factor associations

Larger forest patches supported more bird species than smaller ones. We found a positive relation between both patch size and rarified species richness ($n = 40$, $R^2 = 0.75$, $p < 0.001$), and patch size and bird diversity ($n = 40$, $R^2 = 0.40$, $p < 0.001$). In addition, number of residents ($n = 40$, $R^2 = 0.50$, $p < 0.001$), number of endemics ($n = 40$, $R^2 = 0.40$, $p < 0.001$), and number of introduced species ($n = 40$, $R^2 = 0.20$, $p = 0.003$) increased with patch size. Numbers of species in four of the feeding guilds also significantly increased with patch size: insectivores ($n = 40$, $R^2 = 0.40$, $p < 0.001$), frugivores ($n = 37$, $R^2 = 0.34$, $p < 0.001$), omnivores ($n = 40$, $R^2 = 0.32$, $p < 0.001$), and carnivores ($n = 33$, $R^2 = 0.42$, $p < 0.001$). Forest patches with more convoluted boundary sustained higher rarified species richness ($n = 40$, $R^2 = 0.19$, $p = 0.01$) and bird diversity ($n = 40$, $R^2 = 0.11$, $p = 0.043$). Number of residents ($n = 40$, $R^2 = 0.16$, $p = 0.01$) and number of introduced species ($n = 40$, $R^2 = 0.25$, $p = 0.001$) increased with more convoluted boundaries, as did insectivores ($n = 40$, $R^2 = 0.12$, $p = 0.04$) and omnivores ($n = 40$, $R^2 = 0.21$, $p = 0.003$). The intensity of land use surrounding the forest patches did not affect rarified species richness ($n = 40$, $R^2 = 0.00$, $p = 0.71$), bird diversity ($n = 40$, $R^2 = 0.00$, $p = 0.62$), distributional status classes, or feeding guilds. Additionally, neither isolation nor texture were associated with rarified species richness ($n = 40$, $R^2 = 0.00$, $p = 0.68$; $n = 40$, $R^2 = 0.03$, $p = 0.34$, respectively), bird diversity ($n = 40$, $R^2 = 0.02$, $p = 0.41$; $n = 40$, $R^2 = 0.00$, $p = 0.64$, respectively), distributional status classes, or feeding guilds.

3.5. Community responses to landscape- and patch-level factors

The outlier analysis identified two forest patches as outliers because their average Sørensen (Bray–Curtis) distances were the highest (0.57 and 0.62) compared with the remaining patches (mean ± s.d.: 0.45 ± 0.04); these two forest patches were excluded from further analysis. No bird species was identified as an outlier. NMS analysis produced a final optimum 3-D ordination space, which explained a total of 86% of the variance in the original

Table 1
Summary statistics showing the variance in bird species distribution represented by the final three axes of the Non-metric Multi-dimensional Scaling ordination and Spearman coefficients of landscape- and patch-level factors for 40 urban forest patches in San Juan metropolitan area, Puerto Rico.

	NMS1	NMS2	NMS3
Variance represented (R^2)			
Increment	0.44	0.23	0.19
Cumulative	0.44	0.67	0.86
Correlation with NMS axis (R)			
Patch size	0.76	0.10	−0.45
Vertical heterogeneity	0.62	0.41	0.06
Number of trees > 10 cm DBH	0.51	−0.03	−0.23
Tree height	0.41	0.33	0.00
Mean foliage coverage 6–8 m	0.39	0.03	−0.06
Boundary configuration index	0.35	0.12	−0.13
Mean foliage coverage 4–6 m	0.25	−0.16	−0.37
Mean DBH	0.23	−0.14	0.10
Mean foliage coverage 2–3 m	0.17	−0.11	−0.39
Isolation index	0.04	−0.07	−0.35
Mean foliage coverage 1–2 m	−0.01	−0.42	0.04
Matrix index	−0.11	−0.66	0.03
Texture coefficient	−0.22	0.39	−0.27
Understory coverage	−0.39	−0.31	0.31

species data (Table 1). The vector plots of the landscape and vegetation variables – joined into the ordination – showed that patch size, matrix index, and vertical heterogeneity weighed more than the other landscape and vegetation variables (Fig. 4). The ordination of forest patch scores illustrated that forest patches in the right quadrants of the ordination were positively associated with patch size, those in the lower quadrants were negatively associated with urbanization in the matrix, and patches in the upper right quadrant were positively associated with vertical heterogeneity (Fig. 4a). The ordination of species scores showed that some bird species were associated with larger forest patches (e.g., *Geotrygon montana, Vireo latimeri, Myiarchus antillarum*), others with higher degrees of urbanization in the patch surroundings (e.g., *Lonchura cucullata, Tiaris bicolor, Seiurus motacilla*), and others still with vertical heterogeneity (e.g., *Todus mexicanus, Loxigilla portoricensis, Columba squamosa*; Fig. 4b). There were significant differences in habitat selection among bird species classified by their distributional status (MRPP: $T = -3.981$, $A = 0.027$, $p = 0.001$). Migrants were significantly different from endemics ($T = -5.216$, $A = 0.058$, $p = 0.0008$) and resident species ($T = -3.398$, $A = 0.018$, $p = 0.006$), and endemics were significantly different from introduced species ($T = -2.223$, $A = 0.039$, $p = 0.03$). However, assemblages were not significantly different in terms of feeding guilds, ($T = 0.618$, $A = 0.005$, $p = 0.25$).

3.6. Species prediction models

The significant predictors of species richness for the different distributional classes included both landscape and patch factors (Table 2). Patch size was a significant predictor of all species richness except for migratory species. In addition, species richness was positively predicted by vertical heterogeneity and mean DBH, but negatively correlated with texture and understory coverage. For migratory species, vegetation heterogeneity and the number of trees ⩾ 10 cm DBH were the most significant positive predictors, while texture and the mean DBH of trees were the negative predictors. Endemic species richness was positively predicted by patch size and foliage cover between 6 and 8 m, but negatively predicted by understory coverage, matrix urbanization, and canopy texture. In addition to patch size, resident species richness was positively predicted by foliage cover between 2 and 3 m, and negatively predicted by texture. For introduced species, besides patch area, isolation and matrix urbanization were significant positive predictors.
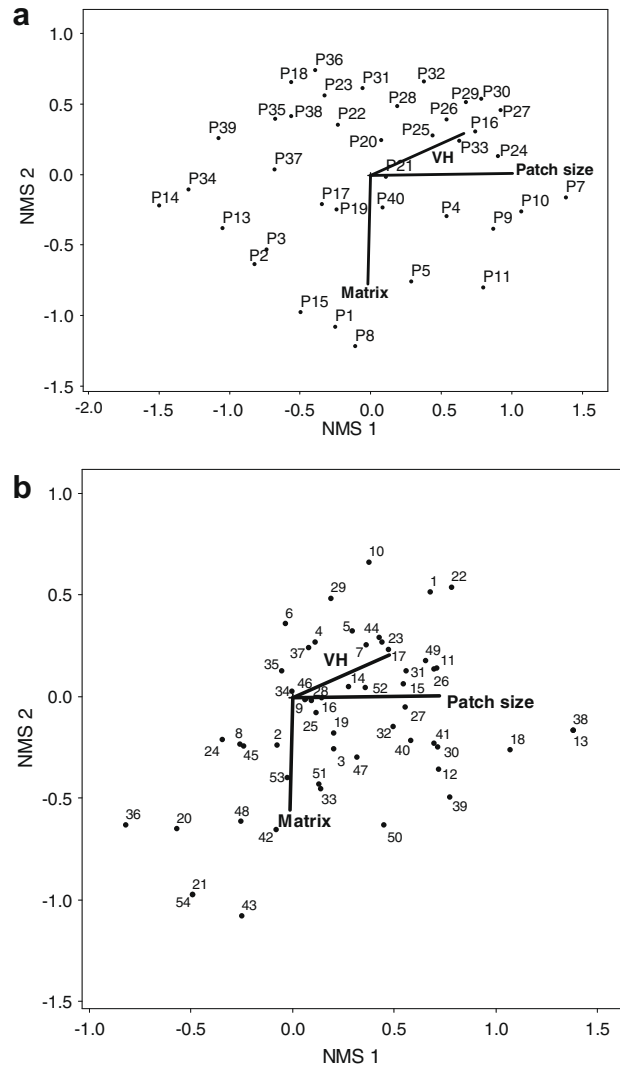
Fig. 4. Joint plot of NMS scores of (a) forest patches and (b) bird species scores with the landscape (i.e., patch size, matrix) and patch-level factors (i.e., vertical heterogeneity: VH) from bird surveys in different habitat patches ($n = 40$) in metropolitan San Juan, Puerto Rico. The first and second NMS axes represent 44% and 23% of the variance, respectively. Species codes are shown in Appendix A.

3.7. Individual species responses

Nine species did not show any patch size preference, 10 species used mainly small or small-medium patches, and 10 used mainly medium or large patches (Table 3). Four species had threshold patch sizes greater than 7 ha, with one (*G. montana*) not found in patches smaller than 26 ha (Table 3). When different levels of urbanization were compared, two species were identified as indicators of low-level urbanization in the matrix (*T. mexicanus, C. squamosa*) while eight species were indicators of high-level urbanization (Table 4). Ten species were identified as indicators of high vertical heterogeneity, and only one species was an indicator of low vertical heterogeneity (*T. bicolor*).

4. Discussion

4.1. Community responses to landscape- and patch-level factors

Most studies of birds in dense urban environments have indicated that these areas are relatively poor in number of species compared to more rural habitats, but rank high in number of indi-

Table 2
Summary of the generalized linear model (GLM) using Poisson distribution as the link showing deviance, degrees of freedom (df), change in deviance, coefficients, and significant predictor variables ($p < 0.05$) for species richness and individual distributional classes (i.e., migrants, residents, endemics, introduced species) for bird distribution in metropolitan San Juan, Puerto Rico.

Variable	Deviance	df	Change in deviance	Coefficient	p
Sp Richness					
Patch size	164.72	38	80.73	0.37	0.00
Texture	12.49	37	68.24	−2.93	0.00
Vertical heterogeneity	11.24	34	54.75	0.74	0.00
Understory percent	7.54	33	47.22	−0.004	0.01
Mean DBH	4.01	32	43.20	0.004	0.05
Migrants					
Vertical heterogeneity	22.43	33	102.20	2.97	0.00
Texture	6.75	35	125.06	−6.99	0.01
Size: boundary	4.74	30	85.30	−0.58	0.03
Number of stems > 10 cm DBH	5.25	32	96.95	0.04	0.02
Mean DBH	6.91	31	90.04	−0.02	0.01
Residents					
Patch size	57.82	38	32.94	0.33	0.00
Foliage 2–3 m	3.09	36	27.85	0.28	0.01
Texture	2.01	37	30.93	−2.14	0.02
Endemics					
Patch size	75.71	38	122.22	0.46	0.00
Understory percent	31.36	32	42.85	−0.02	0.00
Matrix index	24.55	36	89.30	−0.01	0.00
Foliage 6–8 m	11.99	33	74.21	0.90	0.00
Texture	8.37	37	113.85	−7.19	0.00
Introduced					
Patch size	45.52	38	111.34	0.74	0.00
Matrix index	19.45	36	83.77	0.03	0.00
Isolation coefficient	8.11	37	103.23	0.87	0.00

viduals (Emlen, 1974; DeGraaf and Wentworth, 1986), although some studies showed a peak in species richness at intermediate levels of urbanization (e.g., Blair, 1996). The number of species found in metropolitan San Juan is comparable with those found in parks and gardens in French Guyana (Reynaud and Thioulouse, 2000) and abandoned plantations in Singapore (Castelletta et al.,

2005). This is related to the vegetation heterogeneity and the greater variety of food and other resources that these parks and gardens can provide (Tilghman, 1987). In urban environments where large natural forests are distant, urban forest patches pro-

Table 3
Patch size preference of bird species in the San Juan metropolitan area, Puerto Rico.

Species	Patch size preferred	Size threshold (ha)
Vireo latimeri	Large	4.2
Geotrygon montana	Large	25.8
Elaenia martinica	Medium	7.3
Coccyzus minor	Medium	0
Columba inornata	Medium	5.9
Saurothera vieilloti	Medium	6.0
Otus nudipes	Medium	9.2
Todus mexicanus	Medium	6.0
Turdus plumbeus	Medium	0
Columba squamosa	Medium	7.6
Myiarchus antillarum	Small-medium	0
Spindalis portoricensis	Small-medium	0
Melanerpes portoricensis	Small-medium	0
Anthracothorax dominicus	Small	3.1
Tiaris bicolor	Small	3.1
Parula americana	Small	3.1
Columba livia	Small	3.1
Buteo jamaicensis	Small	3.1
Columba leucocephala	Small	0
Zenaida asiatica	Small	0
Zenaida aurita	No pattern	2.5
Crotophaga ani	No pattern	3.1
Vireo altiloquus	No pattern	3.8
Mimus polyglottos	No pattern	0
Myiopsitta monachus	No pattern	0
Coereba flaveola	No pattern	0
Tyrannus dominicensis	No pattern	0
Margarops fuscatus	No pattern	0
Loxigilla portoricensis	No pattern	0

Table 4
Species of birds identified as indicators of matrix urbanization and vertical heterogeneity in the San Juan metropolitan area, Puerto Rico. All indicator values (IV) were significantly larger than random values based on Monte Carlo tests (1000 permutations, $p < 0.05$).

Species by landscape and vegetation variables	Indicator value		SD
	Observed	Random	
Low-level urbanization matrix			
Todus mexicanus	62.2	36.5	6.32
Columba squamosa	58.1	36.3	6.14
High-level urbanization matrix			
Zenaida asiatica	56.8	31.3	6.28
Mimus polyglottos	47.7	23.1	6.41
Myiopsitta monachus	40.2	15.8	5.84
Spindalis portoricensis	49.1	26.1	6.50
Buteo jamaicensis	51.0	30.1	6.25
Dendroica adelaidae	30.4	15.9	5.68
Quiscalus niger	35.4	20.4	6.23
Eulampis holosericeus	21.4	8.7	4.28
High vertical heterogeneity			
Todus mexicanus	56.9	36.4	6.17
Columba squamosa	52.1	36.4	6.03
Myiarchus antillarum	74.9	38.1	6.49
Elaenia martinica	43.0	23.2	6.14
Tyrannus dominicensis	54.7	51.2	1.87
Vireo altiloquus	71.2	37.7	5.94
Coereba flaveola	52.8	50.9	1.75
Saurothera vieilloti	70.2	39.2	6.27
Loxigilla portoricensis	52.5	28.9	6.38
Turdus plumbeus	51.8	35.3	6.19
Low vertical heterogeneity			
Tiaris bicolor	32.3	18.9	5.9

vide habitat for many species that might otherwise only be found in native forests (Tilghman, 1987).

Our multivariate analysis results indicated that bird community or assemblage traits were associated with both landscape- and patch-level factors. Patch size, surrounding matrix, and vertical heterogeneity of forest patches were more important factors determining bird composition than other landscape- and patch-level factors. Many studies of fragmented landscapes have demonstrated that habitat area typically explains most of the variation in the total number of species (e.g., Van Dorp and Opdam, 1987; McIntyre, 1995; Park and Lee, 2000; Fernández-Juricic and Jokimäki, 2001). Bird species in the metropolitan area of San Juan thus appear to show patterns similar to those found in other fragmented environments. This relation may occur because bigger patches have space for more individuals and, thus by chance, more species, or it may be related to resource availability (Sitompul et al., 2004), or habitat heterogeneity (Andrén, 1994; Saunders et al., 1991). As a single variable, patch size explained differences in both the number of bird species and bird diversity. These results support the idea that "habitat islands" in urban settings follow some of the basic concepts of island biogeography (MacArthur and Wilson, 1963), especially the species-area relationship that has been validated in many bird studies in fragmented forests (e.g., MacArthur and Wilson, 1963; Tilghman, 1987; Soulé et al., 1988; Fernández-Juricic and Jokimäki, 2001). The intensity of land use in forest patch surroundings was another important variable driving species composition. This finding is similar to the general trend that urbanization is affecting the distribution, richness and diversity of bird species (e.g., Emlen, 1974; Gascon et al., 1999; Mörtberg, 2001; Parody et al., 2001; Melles et al., 2003).

Vertical heterogeneity was the most important patch-level factor driving bird composition and species richness. Several studies have established a relationship between vertical vegetation complexity and bird species diversity (MacArthur and MacArthur, 1961; Roth, 1976; Greenberg et al., 1997; Walther, 2002). Vertical heterogeneity provides a variety of microhabitats and offers a large number of resources that attract birds from the surrounding areas. Other studies confirm that foliage volume is a critical resource that affects food density and diversity, nest placement, and predator avoidance (Beissinger and Osborne, 1982). In urban environments, the presence of shrub layers influences the variety of bird species in parks (Gavareski, 1976; Fernández-Juricic and Jokimäki, 2001). In our study, the presence of different layers may provide habitats with different types of available resources. While streams were not quantified as part of the analysis, it is likely that the presence of streams flowing through some of the patches also added an attribute to the microhabitats available and thus resulted in influx of additional bird species (e.g., *Ceryle alcyon, S. motacilla, Butorides virescens,* and *Nyctanassa violacea*).

Species richness of the different distributional classes (migratory, endemic, resident, and introduced) was also predicted by a combination of landscape and patch factors. For migratory species, vegetation heterogeneity, and the number of trees $\geqslant 10$ cm DBH were the most significant positive predictors of species richness, whereas migratory species richness was negatively correlated with texture and the mean DBH of trees. Similarly, Wallace et al. (1996) found in Cuba that migrants were more abundant in areas with trees <15 cm DBH and well-developed understory, these features being characteristic of secondary forest or abandoned plantations. This interpretation should be taken with caution because it is not clear if migrants are selecting those habitats for their resources or those are the only habitats available since more suitable habitats elsewhere on the island (or in other urban forest vegetation strata) might already be occupied (Rappole, personal communication). For example, migrants in southern Wisconsin were excluded from small woodlots with supposedly good resource availability by

some forest-edge and farmland species (Ambuel and Temple, 1983). Migrant abundance was related to the interaction between patch size and boundary form, but it was not correlated with patch size. Wunderle and Waide (1993) found similar results in the Caribbean, contrasting with those of Castelletta et al. (2005), who discovered that richness of migrant species in Singapore was only determined by patch area.

Because endemic species are restricted in their range, they are particularly vulnerable to habitat alteration (Abbitt et al., 2000), and in our study we found that endemic species were sensitive to patch size, matrix urbanization, and canopy texture. Endemic species were positively correlated with foliage cover between 6 and 8 m, but negatively with understory coverage, presumably because their distribution is related to specific locations of food sources (Wunderle et al., 1987). In addition to patch size, resident species were positively associated with foliage cover between 2 and 3 m. The presence of midstory provides higher availability of food, shelter and breeding substrates (Fernández-Juricic and Jokimäki, 2001).

For introduced species, besides patch area, isolation and matrix urbanization were significantly predictive. Introduced species were found preferentially in forest patches surrounded by a highly urbanized matrix. They are exploiting urban areas and one of the reasons for their invasion is because they can flourish in urban environments (Vitousek et al., 1997). Introduced species were not dependent on any patch-level factors, probably because vegetation heterogeneity or other patch interior variables are not related to abundance of fruits or seeds used by them (Wunderle, personal communication), or because most introduced species are not inhabitants of forest. Similar results were found in Singapore, where more introduced species were found in areas with open canopy (Castelletta et al., 2005). Texture contributed negatively to all models except introduced species richness. This finding was not expected, since Puerto Rico's forests are subject to frequent wind disturbance (Brokaw and Walker, 1991), and one would expect the avifauna to have adapted to high levels of canopy heterogeneity. However, native tree species often have wind-pruned canopies, which would have less texture than introduced species that may respond differently to wind, and the resident species may simply be expressing a preference for native tree species.

4.2. Individual species responses

Some species did not show patch-size preference because they are generalist species (Oberle, 2000) and are found in different types of habitats around Puerto Rico. For example, *C. flaveola* occurs wherever there are trees, shrubs or flowers, from ground level to the top of the forest canopy. Some species used large forest patches because they require minimum areas to perform their vital functions; for example, *V. latimeri* was only found in patches > 4 ha, and *G. montana* in patches > 26 ha. Both species are considered forest specialists. *G. montana* requires dense forests and is sensitive to openings in the forest canopy (Wauer and Wunderle, 1992). Some edge species used small patches but were not present in patches <3 ha, for example *Anthracothorax dominicus*, which is common in forest edges, especially in the lowlands. The migratory *Parula americana* uses small patches, probably because it is a generalist on the wintering grounds. Wunderle and Waide (1993) observed this species across a wide range of habitats in the Caribbean, particularly in diverse habitats in Puerto Rico.

Some species serve as indicators of high or low levels of urban development in the surrounding matrix. For example, *Mimus polyglottos* is associated with high levels of urbanization (see e.g., Crooks et al., 2004; Parody et al., 2001). Other species associated with relatively high levels of urbanization were *Zenaida asiatica, Myiopsitta monachus,* and *Spindalis portoricensis*. Species indicative

of low urbanization levels were *T. mexicanus* and *C. squamosa*. These are common in dense forest (Raffaele, 1989; Rivera-Milan, 1992), and we found them in patches with <30% of urbanization in the surrounding matrix. Some of the species were indicators of vertical heterogeneity, for example, *T. mexicanus* and *L. portoricensis*. This association might be attributed to food distribution, which is probably related to vegetation structure (Wunderle et al., 1987). *L. portoricensis* is frugivorous and forages in dense vegetation at any level in the forest, but mostly at middle levels (Oberle, 2000). Thus, diverse strata in the forest with some gaps are suitable because the latter may provide fruits, for example of *Urera baccifera* (Family: Urticaceae; Wunderle et al., 1987).

4.3. Conservation implications

Decisions on management of landscape or patch interior structure are very complex, because each species responds differently to landscape and patch characteristics. For example, for the endemic *T. mexicanus* the management of the landscape is crucial because it prefers medium-sized patches with low degrees of urbanization in the surrounding matrix and availability of soil banks for cavity nesting, while the endemic *L. portoricensis* requires complex vegetation within the patch. *P. americana* is a migrant species that uses small patches with a highly textured canopy, where it gleans arthropods from leaf clusters at the ends of branches. This preference for heterogeneous habitats means that it can be found in a variety of forest types across the entire successional spectrum, including primary forests, early second-growth forest, shade coffee plantations, and gardens (Wunderle et al., 1987; Oberle, 2000). Appropriate landscape management will offer the possibility of travel among different types of forest patches in close proximity, complementing the resources available (Dunning et al., 1992). In addition, forest patches provide to humans the opportunity to experience and appreciate nature in an urbanized landscape, as well as to enhance human well-being (e.g., Turner et al., 2004; Miller, 2005). Specific recommendations for land managers and conservation agencies involved in the acquisition, management, and conservation of natural areas within the island include: (1) Large forest patches are necessary to maintain a high bird species richness and diversity, but small remnant fragments should also be preserved because they provide valuable habitats used by several endemic and migrant species, and they can also serve as stepping stones for movement among larger patches. (2) Urban development near forest patches should not increase. More development will eliminate whole patches, reducing population size, and the urban forest patches will not be able to support the levels of diversity we found. Arboreal vegetation should be conserved in the matrix to maintain habitat and connectivity. (3) Forest patches should keep their vertical heterogeneity, because complex layering in the forest provides a larger variety of microhabitats and can provide nesting and feeding sites for a variety of bird species. (4) The maintenance of forest patches with different vegetation types is needed at landscape scale because species have different habitat requirements.

In conclusion, our study shows that there is a rich avifauna in the San Juan metropolitan area despite a very high human population density, and that landscape- and patch-level factors affect the composition of that avifauna. Many of the species present are species of interest (e.g., endemics and neotropical migrants), and these are worthy of conservation. However, given the small area of green space currently protected, the future of this diversity is threatened. Forest patches cannot be expected to continue to attract and support the variety of bird species we found as the land around them is subject to ever-intensified human use and subsequent reductions in patch size. In addition, species supported will depend on the quality of these patches in terms of complex vertical structure. It is essential that existing green space be preserved and, if possible, that new forest patches be created. Complex interactions take place among the factors in an urbanized landscape and species respond in different ways to their effects, further complicating the management of these environments.

Appendix A

Species, distributional class and feeding guilds of the bird community in the metropolitan area of San Juan, Puerto Rico.

Code	Scientific name	English common name	Status	Guild
1	*Butorides virescens*	Green Heron	R	C
2	*Nyctanassa violacea*	Yellow-crowned Night-Heron	R	C
3	*Buteo jamaicensis*	Red-tailed Hawk	R	C
4	*Columba livia*	Rock Dove	I	O
5	*Columba squamosa*	Scaly-naped Pigeon	R	F
6	*Columba leucocephala*	White-crowned Pigeon	R	F
7	*Columba inornata*	Plain Pigeon	R	F
8	*Zenaida asiatica*	White-winged Dove	R	G
9	*Zenaida aurita*	Zenaida Dove	R	G
10	*Columbina passerina*	Common Ground-Dove	R	G
11	*Geotrygon montana*	Ruddy Quail-Dove	R	G
12	*Myiopsitta monachus*	Monk Parakeet	I	O
13	*Ara ararauna*	Blue-and-yellow Macaw	I	F
14	*Coccyzus minor*	Mangrove Cuckoo	R	I
15	*Saurothera vieilloti*	Puerto Rican Lizard-Cuckoo	E	C
16	*Crotophaga ani*	Smooth-billed Ani	R	O
17	*Otus nudipes*	Puerto Rican Screech-Owl	E	C
18	*Cypseloides niger*	Black Swift	R	I
19	*Anthracothorax dominicus*	Antillean Mango	R	I

Appendix A (continued)

Code	Scientific name	English common name	Status	Guild
20	*Eulampis holosericeus*	Green-throated Carib	R	N
21	*Chlorostilbon maugaeus*	Puerto Rican Emerald	E	I
22	*Mellisuga minima*	Vervain Hummingbird	M	N
23	*Todus mexicanus*	Puerto Rican Tody	E	I
24	*Ceryle alcyon*	Belted Kingfisher	M	C
25	*Melanerpes portoricensis*	Puerto Rican Woodpecker	E	I
26	*Elaenia martinica*	Caribbean Elaenia	R	F
27	*Myiarchus antillarum*	Puerto Rican Flycatcher	E	I
28	*Tyrannus dominicensis*	Gray Kingbird	R	I
29	*Tyrannus caudifasciatus*	Loggerhead Kingbird	R	I
30	*Vireo latimeri*	Puerto Rican Vireo	E	I
31	*Vireo altiloquus*	Black-whiskered Vireo	M	I
32	*Turdus plumbeus*	Red-legged Thrush	R	F
33	*Mimus polyglottos*	Northern Mockingbird	R	O
34	*Margarops fuscatus*	Pearly-eyed Thrasher	R	O
35	*Parula americana*	Northern Parula	M	I
36	*Dendroica petechia*	Yellow Warbler	R	I
37	*Dendroica tigrina*	Cape May Warbler	M	N
38	*Dendroica dominica*	Yellow-throated Warbler	M	I
39	*Dendroica adelaidae*	Adelaide's Warbler	E	I
40	*Dendroica discolor*	Prairie Warbler	M	I
41	*Mniotilta varia*	Black-and-white Warbler	M	I
42	*Seiurus motacilla*	Louisiana Waterthrush	M	I
43	*Seiurus aurocapillus*	Ovenbird	M	I
44	*Geothlypis trichas*	Common Yellowthroat	M	I
45	*Wilsonia citrina*	Hooded Warbler	M	I
46	*Coereba flaveola*	Bananaquit	R	N
47	*Spindalis portoricensis*	Puerto Rican Spindalis	E	F
48	*Tiaris bicolor*	Black-faced Grassquit	R	G
49	*Loxigilla portoricensis*	Puerto Rican Bullfinch	E	F
50	*Molothrus bonariensis*	Shiny Cowbird	I	O
51	*Quiscalus niger*	Greater Antillean Grackle	R	O
52	*Icterus dominicensis*	Greater Antillean Oriole	R	I
53	*Estrilda melpoda*	Orange-cheeked Waxbill	I	G
54	*Lonchura cucullata*	Bronze Mannikin	I	G

The distributional class refers to migratory (M), endemic (E), resident (R), and introduced species (I). The feeding guilds are indicated as insectivores (I), frugivores (F), granivores (G), omnivores (O), carnivores (C), and nectarivores (N) following Stotz et al. (1996) classification scheme.

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