# SPECIAL TOPIC A

# Does Habitat Heterogeneity Affect Bird Community Structure in Urban Parks?

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Abstract. We selected 21 green areas in the City of Puebla and its metropolitan area, located in the central region of México, to explore the relationships between habitat heterogeneity and bird communities in urban environments. For each site, tree vegetation heterogeneity was summarized using 14 floristic and six physical descriptors of habitat structure. During May 2004, bird communities at each site were surveyed by means of the Echantillonnage Frécuentiels Progressifs method (355 censuses, from 10 to 30/site), and their structure was described by the number of species (total species, urban exploiters, urban adapters, and urban avoiders), the Shannon diversity of the assemblages, and the nestedness in species composition. A principal components analysis (PCA) was used to find main axes of variation in tree vegetation descriptors. The first principal component described a gradient in the physical diversity of the tree vegetation; the second component described changes in richness, density, and diversity of the native trees; and the third and fourth described gradients in the diversity

and dominance of exotic trees. Although apparent spatial changes in the metrics measuring the structure of bird communities were found in the region, no robust, statistically significant effect of the habitat gradients described by the PCA was found. The relative abundance of seven bird species was correlated to several of the principal component axes, but this relationship was not statistically significant when correcting for multiple comparisons. The structure of bird communities in the urban greenspaces of the City of Puebla and its metropolitan area was not strongly a function of the habitat heterogeneity measures analyzed, but it may depend on variables acting at different scales, or on a combination of both explanations. Bird communities in Puebla did, however, exhibit a strong pattern of nestedness across sites and reflected similar changes in community composition as found in cities in temperate climates.

Key Words: birds, conservation, habitat diversity, management, México, trees, urbanization.

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rbanization, the concentration of human presence in residential and industrial settings and their associated effects, is currently a worldwide concern to biodiversity conservation (McKinney 2002). The continued expansion and growth of cities in the near future could bring about the conversion of large swaths of natural habitats to urban areas (Marzluff et al. 2001a), resulting in general decreases in bird species richness and diversity (for a review, see Chace and Walsh 2006). The negative effects of urbanization on birds could be even worse in biodiversityrich locations, such as developing countries in tropical latitudes (Marzluff et al. 2001b), where the highest growth of human population is expected (Cunningham and Saigo 2001). In fact, urbanization and the ecological footprint of urban centers have been recognized as underlying causes driving deforestation in tropical forests in Latin America (Geist and Lambin 2002). Therefore, it is important to better understand the relationships of birds to urban habitats; research on habitat characteristics is needed for developing landscape planning and management methods to enhance biodiversity in urban environments by creating or maintaining suitable habitats for birds (Jokimäki and Suhonen 1998, Jokimäki 1999). In many cases, urban green areas, such as urban parks, wooded streets, and cemeteries, represent the last remnants of greenery in large cities, providing potential habitat for bird life in urban environments (Miller and Hobbs 2002). While urban green areas differ in many ways from those in the surrounding countryside (McDonnell and Pickett 1990), relatively little is known as to whether management recommendations obtained from natural areas can be applied to urban greenspaces (Fernández-Juricic 2004).

Changes in biological diversity are correlated with several factors, such as productivity, age, size, and spatial heterogeneity of the sample area (Huston 1994). In natural habitats, the more heterogeneous the environment, the more complex the communities and the higher the richness and diversity of species found there (Huston 1994). The number of factors that contribute to habitat heterogeneity is virtually unlimited, but it can be summarized in some measure of the complexity of the vegetation (Huston 1994). Usually the link between habitat heterogeneity and biodiversity is more evident if, instead of plant species richness, plant structural heterogeneity is considered (Begon et al. 1996). If the relationship between habitat heterogeneity

and species richness and diversity holds in urban environments, this could guide urban planners and managers to improve biodiversity conservation in the generally monotonous urban greenspaces (Azerrad and Nilon 2001) by altering the structure and/or the composition of the tree vegetation. On the other hand, if differences exist between natural and urban environments, new management recommendations should be developed and incorporated into conservation planning in urban habitats (Fernández-Juricic 2004).

In this paper, we explore the relationships between habitat complexity and the structure of bird communities inhabiting the urban greenspaces of the City of Puebla (including its metropolitan area), México. The rich biodiversity of México is threatened by a large number of factors, including inadequate models of economic and demographic development in the recent past and a human population above 100 million people, strongly centered on México City (for more details on the natural and social contexts of México, see Sarukhán 2006 and references therein). However, part of this human growth is currently being redirected toward other cities, including Puebla (Garza 2002). Thus, using Puebla as a case study, our objectives were to: (1) reveal the multivariate patterns of variation in the arboreal habitat of urban greenspaces; (2) describe bird community structure in the urban greenspaces; and (3) relate bird community metrics to habitat heterogeneity. Given the large number of features that create habitat heterogeneity (Huston 1994), we focus on a limited set of habitat variables which summarize woody vegetation, taking into account the important ecological roles of trees in urban green areas (Mills et al. 1989, Nilsson et al. 1997, Porter et al. 2003).

### **METHODS**

The City of Puebla (the capital city of the State of Puebla) is located in central México, at ~2,160 m above sea level (asl). The smaller towns of San Andrés Cholula and San Pedro Cholula are in close proximity, and altogether form the Puebla–Cholula Metropolitan Area (PCMA). In 2005 the human population in the PCMA was approximately 1,700,000 inhabitants (INEGI 2007), the fourth most populous metropolitan area in the country.

Geographically, the PCMA is located in the natural region of the Neovolcanic Axis Province, where the Popocatépetl and Iztaccíhuatl volcanoes (>5,000 m asl) and other snow-capped mountains

are found. Mean annual temperature ranges from 15.0 to 17.1°C, and mean annual precipitation varies between 797 and 913 mm (subhumid climate with summer rains). Historically, temperate mixed forests of pine (e.g., Pinus pseudostrobus, P. montezumae, or P. patula) and oak (e.g., Quercus oleoides, Q. excels, and Q. candolleana), along with other tree species such as Abies religiosa and Liquidambar styraciflua, covered great extensions of the landscape (INAFED 2005). However, the natural vegetation has been greatly modified by changes in soil conditions, due to the long history of continuous human settlement, dating from pre-Hispanic times (Rzedowski 1978; see also Flores Villela and Gerez 1994, INAFED 2005).

A total of 21 urban green areas (cemeteries, manicured parklands, "plazas" or "zocalos," and university campuses) were selected in the PCMA, ranging in size from 0.3 to 140.9 ha (mean = 27.0 ha; SE = 8.1 ha). Both tree vegetation and bird community structure were measured at each urban green area. Following Kocian et al. (2003), we analyzed tree vegetation structure in two ways: floristic (taxonomic) composition, and physical (size) characteristics.

#### Structure of Trees

### Floristic Analysis

Within each urban green area we set up between three and seven quadrats (20 m  $\times$  20 m; n = 95 across all urban green areas), depending on size of the greenspace, and counted, identified, and measured the DBH of all trees that were ≥5 cm DBH (Brower et al. 1997; see Barillas-Gómez 2004 and Bonache-Regidor 2005 for results). Mills et al. (1989) found a different role of the volume of native versus exotic vegetation on the structure of breeding bird communities in urban environments (see also Chace and Walsh 2006). Therefore, we described the structure of trees in each urban green area in terms of richness (S: observed number of species), density (D: number of trees/ha), basal area (BA: cm2 of trunks/ha) and canopy cover (CC: m2 of canopy/ha; see Appendix A.1 for procedures about CC), for both native (15 species native to México) and exotic tree species (18 species introduced from other countries). In addition, Shannon diversities ( $H' = -\sum p_i \log p_i$ ; Magurran 2005) were calculated for D, BA, and CC values at each urban green area, for both native and exotic species. Thus, seven descriptors (S, D, BA, CC, diversity of D, diversity of BA and diversity of CC) for two

groups of species (native and exotic) were calculated, yielding 14 parameters describing the structure of trees from a floristic (taxonomic) point of view.

# Physical (Size) Analysis

The floristic analysis was complemented with an analysis of the physical (size) structure of the trees. First, by using DBH values, each tree was assigned to a trunk size class (DBH range was divided into 14 classes at 10-cm intervals). In addition, by taking into account CC data, trees were assigned to a canopy size class (CC range was separated into 10 classes at 25-m² intervals). Then physical structure of the trees at each urban green area was described in terms of the following six parameters: number of DBH classes present, average DBH, diversity of DBH, number of CC classes present, average CC, and diversity of CC.

### **Bird Communities**

The structure of bird communities inhabiting Puebla was described in terms of species richness and diversity of bird assemblages, both descriptors of alpha diversity (Magurran 2005). To minimize seasonal variation in the structure of bird communities, 355 censuses (from 10 to 30 censuses/ urban green area) were conducted during May 2004 by means of the Echantillonnages Frecuentiels Progressifs (EFP) method (Blondel et al. 1970). This method resembles the standard fixed-radius point count since the observer records the identity of all the bird species seen or heard during a limited time span inside an imaginary circle centered on the researcher, but without indicating quantities. Because EFP is a qualitative method, it cannot directly provide density data; however, the frequency of occurrence of each species at each site (i.e., the number of times a species is recorded within the censuses performed in a given study site) can be readily derived from inventory data and be used as an indirect estimator of its local abundance (Tellería 1978, Fonderflick 1998). Given that abundance is not actually measured, the EFP method is less prone to many of the confounding factors that hamper density estimations from fixed-radius point counts as they are often used (Watson 2003). In this study, all the censuses were conducted for 10 minutes between 07:00 and 11:30 CDT, using a 25-m radius and counting only Columbiformes, Cuculiformes, Piciformes, and Passeriformes birds.

Across Puebla, we detected 51 bird species, which, based on a multivariate cluster analysis of their similarity in regional distribution and local abundance, were divided into three groups: urban exploiters, urban adapters, and urban avoiders (see González-Oreja et al. 2007 for details). Thus, we used the total number of bird species richness ( $S_{tot}$ ), the richness of each group (i.e. urban exploiters  $[S_{exp}]$ , urban adapters  $[S_{adp}]$ , and urban avoiders  $[S_{avo}]$ ), the richness of urban exploiters + urban adapters ( $S_{\text{expada}}$ ), and the richness of urban adapters + urban avoiders ( $S_{adpavo}$ ), as descriptors of the bird richness at each urban green area. In order to remove the effect of sample area on species richness, the Chao2 estimator of the number of species expected in 2 ha (equivalent to the minimum number of samples per urban green area, 10 censuses) was obtained for each of the six richness groupings (i.e.,  $S_{tot}$ ,  $S_{exp}$ ,  $S_{\text{adp}}$ ,  $S_{\text{avo}}$ ,  $S_{\text{expada}}$ , and  $S_{\text{adpavo}}$ ) by running EstimateS 6.0b1 (Colwell 2000).

The relative frequencies of appearance of each species at each urban green area were also used to calculate whole community diversity (since summed incidence data for replicated samples converges exactly on relative abundance; R. K. Colwell, pers. comm.). The H' and Shannon evenness (E) measures were calculated, using incidence rather than abundance to calculate proportions (Magurran 2005).

Finally, we examined the possible existence of nested subsets in the composition of the bird communities of Puebla, in which the species comprising a small avifauna represent a proper subset of those on richer assemblages (Patterson 1987, Ganzhorn and Eisenbeib 2000), by taking into account the "temperature" (T) of the maximally packed, species × sites matrix. Matrices can be packed to a condition of maximal nestedness by reordering rows and columns (i.e., changing the overall appearance of the matrix, but not its information content), until unexpectedness is minimized. In nestedness analyses, the temperature of a species × sites matrix is a measure of unexpected species absences and presences on individual sites; system T ranges from 0° to 100°, with colder temperatures equaling a more nested matrix. Monte Carlo simulations (1,000 runs) were used to estimate the probability that the nested structure could be produced at random using the Nestedness Temperature Calculator software package (Atmar and Patterson 1995).

## Statistical Analyses

First, in order to reduce the dimension of the original set of descriptors of habitat heterogeneity, a principal components analysis (PCA) was performed on the variable correlation matrix (see Fernández-Juricic 2004 for a related approach). To maximize the loading factors of the variables on the PCA axes, a varimax raw rotation was employed. The first PCA axes were considered as descriptors of the main patterns of habitat heterogeneity in the urban green areas. Then the relationships between bird community metrics at each urban green area with the position of the same areas on the main PCA axes (as described by their factor scores), was explored by calculating the corresponding Pearson linear correlation coefficients (r; Zar 1996). The possible effect of habitat heterogeneity on the existence of nested subsets in bird communities was assessed by calculating the nonparametric Spearman rank correlation coefficient ( $r_s$ ) between the ordering of sites after the nestedness analyses and their corresponding factor scores on the main PCA axes (Patterson and Atmar 2000).

Finally, the possible existence of linear responses of individual bird species to habitat heterogeneity was evaluated by calculating the Pearson correlation between the abundance of bird species at each site (as described by their relative frequency of appearance) and the position of the sampling sites on the PCA axes, as previously described; only the 19 species recorded in at least 10 urban green areas were considered.

Taking into account the high number of simultaneous tests performed, and the enhanced likelihood of finding "significant" values because of chance, a sequential Bonferroni procedure to correct for *P* values was applied (global  $\alpha = 0.05$ ). The sequential Bonferroni method is a technique developed to increase the statistical power of the simplest, more conservative case of Bonferroni correction for simultaneous inference (Beal and Khamis 1991, Peres-Neto 1999). Following Fernández-Juricic (2002), five groups of related tests were considered between habitat gradients (four principal component axes) and bird responses. The groups of tests, along with the number of P-estimates, were as follows: (1) observed bird community richness (24 estimates), (2) estimated bird community richness (24 estimates), (3) bird community diversity (8 estimates), (4) nestedness (4 estimates), and (5) individual bird species

(76 estimates). All statistical analyses were performed in Statistica version 6.0 (StatSoft, ver. 6).

### **RESULTS**

# Habitat Heterogeneity

A total of 927 trees, comprised of 15 native and 18 exotic species, were identified across the urban green areas. Across the urban green areas, S ranged from 2 to 10 species, with native species varying between 0 and 6 and exotic species varying between 1 and 7. Total D ranged from 55 trees/ha to 405 trees/ha, with the maximum located in the urban green area containing the highest density of Eucalyptus camaldulensis. The mean density was comprised of ~59.4% exotic species. Among the natives, Fraxinus udhei (mean D = 38.6 trees/ha) and Cupressus lindleyi (34.9 trees/ha) had the highest densities, while the remaining natives had mean densities of <5 trees/ha. Among the exotics, E. camaldulensis (37.8 trees/ha) and Ligustrum japonicum (24.9 trees/ha) had the maximum densities, while the rest of the exotics had mean densities of  $\leq$ 7 trees/ha. BA ranged from 0.9 m<sup>2</sup>/ha to 66.9 m<sup>2</sup>/ ha, with exotic species contributing 64.2% to the mean basal area. In terms of BA, the dominant species were F. udhei (mean BA =  $5.47 \text{ m}^2/\text{ha}$ ), E. camaldulensis (5.47 m²/ha), C. lindleyi (2.4 m²/ha), Phoenix canariensis (2.3 m<sup>2</sup>/ha), and L. japonicum (2.2 m<sup>2</sup>/ha). The CC ranged between 1,465 m<sup>2</sup>/ha and 14,065 m<sup>2</sup>/ha, which corresponded to the simplest and highest BA urban green areas, respectively. On average, ~67.1% of the CC was comprised of exotic species. Two species dominated the CC, the exotic E. camaldulensis (mean  $CC = 1,866.7 \text{ m}^2/\text{ha}$ ) and the native F. udhei  $(1,365.9 \text{ m}^2/\text{ha})$ .

According to DBH distributions, the smallest trees (min average DBH: 8.32 cm) were located in the taxonomically poorest urban green area, where only two DBH size classes were found. On the other hand, the largest trees (max average DBH: 57.6 cm) were found in the urban green area with the highest BA and CC. The most homogeneous-sized trees (min diversity of DBH: 0.67) were located at the simplest urban green area, whereas the most heterogeneous-sized trees (max diversity of DBH: 2.14) were located in the urban green area with the highest number of DBH size classes (10). Regarding CC distributions, the smallest trees (min average CC: 10.1 m²) were also located in the simplest urban green area (all the trees belonging

to the same CC size class); the largest trees were seven times larger (max average CC: 74.8 m<sup>2</sup>).

The first four axes of the PCA explained 84.5% of the initial variance in the whole data set of tree structure. The first principal component explained 29.0% of the variance and can be interpreted as a gradient describing an increment in physical (size) diversity of trees, since its positive side was strongly linked to the number of DBH classes, the number of CC classes, the diversity according to DBH data, the diversity according to CC data, and mean DBH (Table A.1). The second principal component explained 23.2% of the variance and can be interpreted as a descriptor of the importance of the native tree vegetation, since its positive end was clearly related to the S, D, and diversity of native trees. The third principal component explained 18.9% of the variance and could be interpreted as a gradient showing an increase in the diversity of exotic trees in the floristic structure of the vegetation (as it was correlated to the S and diversity of exotic trees). Last, the fourth principal component explained 13.4% of the variance and was related to the D and CC of exotic trees (Table A.1).

### **Bird Communities**

Of the 51 birds detected across all the urban green areas, 5 were urban exploiters, 13 were urban adapters, and 33 were urban avoiders (see Table A.2 for the composition and main characteristics of each group).  $S_{tot}$  ranged from 7 to 37 per urban green area (mean = 21.8; CV = 36.0%). The  $S_{\text{exp}}$ was the most homogeneous descriptor of species richness among sites ( $S_{\text{exp}} = 4 \text{ or } 5$ ; mean = 4.9; CV = 6.1%), whereas the  $S_{avo}$  was the most variable ( $S_{avo} = 0$  to 19; mean = 6.8; CV = 87.3%), and the  $S_{ada}$  was intermediate ( $S_{ada} = 2$  to 13; mean = 10.1; CV = 25.8%). Therefore, no further tests for linear relationships between habitat variables and  $S_{\text{exp}}$  were conducted. The Chao2 estimator of  $S_{\text{tot}}$  in 2 ha ranged from 7.2 to 44.3 per site (mean = 21.8; CV = 36.0%). No differences were found between  $S_{\text{exp}}$  and the corresponding Chao2 estimator in 2 ha (min = 4; max = 5.2; mean = 4.9; CV = 6.4%). For  $S_{\text{ada}}$ , Chao2 ranged from 2 to 19.8 (mean = 12.2; CV = 34.4%), and for  $S_{avo}$ , Chao2 ranged from 0 to 22.5 (mean = 9.5; CV = 80.1%).

H' ranged from 1.73 to 3.22 (mean = 2.69), and was a more homogeneous community metric (CV = 13.0%) than  $S_{\text{tot}}$ . H' was highly correlated with all the richness descriptors except  $S_{\text{exp}}$ 

TABLE A.1

Results of the principal components analysis performed on the correlation matrix of the 20 variables describing tree vegetation structure (14 floristic + 6 physical parameters) measured in the 21 Urban Green Areas.

			PC Axes			
		Comm. (%)	1	2	3	4
Number of size classes according to DBH values	DBHk	89.6	0.92			
Number of size classes according to CC values	CCk	87.9	0.92			
Diversity of size classes according to DBH values	DBHH	89.4	0.91			
Diversity of size classes according to CC values	CCH	83.3	0.88			
Mean DBH	meanDBH	61.8	0.77			
Mean CC	meanCC	57.3	0.71			
Richness of native trees	Sn	96.7		0.97		
Diversity according to basal area of native trees	HBAn	96.4		0.97		
Diversity according to canopy cover of native trees	HCCn	95.0		0.96		
Diversity according to density of native trees	HDn	95.0		0.96		
Density of native trees	Dn	78.8		0.80		
Diversity according to canopy cover of exotic trees	HCCx	97.5			0.98	
Diversity according to basal area of exotic trees	HBAx	94.3			0.96	
Diversity according to density of exotic trees	HDx	95.4			0.94	
Richness of exotic trees	Sx	90.8			0.83	
Density of exotic trees	Dx	78.5				-0.84
Canopy cover of exotic trees	CCx	92.3				-0.88
Basal area of native trees	BAn	80.5				
Canopy cover of native trees	CCn	74.9				
Basal area of exotic trees	BAx	54.2				
Eigenvalue			5.8	4.6	3.8	2.7
Expl. Variance			29.0	23.2	18.9	13.4
Summ. Expl. Variance			29.0	52.2	71.1	84.5

NOTE: After varimax raw rotation, only the highly significant loading factors of the variables in the PCA axes are shown (P < 0.001). Comm. (%) is the percentage of the total communality of each variable extracted by the first four PCA axes. Only variables with Comm. (%) > 75 are shown.

(n=21; 0.826 < r < 0.933; P < 0.0001). Among urban green areas there was little variation in E (range: 0.81 to 0.93; mean = 0.89; CV = 3.1%), and no correlation to any of the richness measures (in all cases, P >0.05).

Bird communities clearly exhibited a pattern of nestedness (T =  $16.74^\circ$ ; P < 0.0001). After maximally packing the incidence matrix, 3 out of the 5 urban exploiters were ranked before urban adapters, and 11 out of the 13 urban adapters before urban avoiders. Species order in the packed

matrix was correlated with the group of species (i.e., urban exploiters, urban adapters, urban avoiders) where it was classified ( $r_S = 0.83$ ; n = 51; P < 0.001).

# Relations between Habitat Heterogeneity and Birds

The  $S_{\text{tot}}$  (Fig. A.1a),  $S_{\text{avo}}$  (Fig. A.1c), and  $S_{\text{adaavo}}$  (Fig. A.1e) were negatively correlated with the gradient in the taxonomic diversity of exotic trees described

TABLE A.2

Composition and main characteristics of the birds in the three groups of species considered in this study.

Measure	e Urban exploiters <sup>a</sup> Urban adapters <sup>b</sup>		Urban avoiders <sup>c</sup>	
Number of species	5	13	33	
Regional distribution	98.1	77.7	20.9	
Local abundance	73.5	33.0	9.6	
Body length (cm)	24.19 (4.7)	20.56 (1.69)	18.26 (1.00)	
Body mass (g)	96.2 (46.5)	57.7 (12.2)	34.7 (4.9)	
Main diet	80% granivorous	38.5% granivorous, 38.5% insectivorous	48.5% insectivorous, 33.3% omnivorous	
Main migratory status	100% residents	100% residents	51.5% residents, 30.3% wintering	

SOURCE: Modified from González-Oreja et al. (2007).

NOTE: Regional distribution is expressed as the average percentage of urban green areas (n = 21) where the species of the group are present, whereas local abundance is expressed as the mean relative frequency of occurrence of the species in the censuses performed at the sites where they are present (i.e., their incidence in 10-30 censuses/urban green area). Values in brackets for body length and body mass are standard errors.

- <sup>a</sup> Carpodacus mexicanus Columbina inca Columba livia Passer domesticus Quiscalus mexicanus <sup>b</sup> Molothrus aeneus
- Quiscalus mexicanus

  b Molothrus aeneus
  Pheucticus melanocephalus
  Pipilo fuscus
  Pyrocephalus rubinus
  Spizella passerina
  Sturnus vulgaris
  Thryomanes bewickii
  Toxostoma curvirostre
  Fam. Trochilidae
  Turdus rufopalliatus
  Tyrannus melancholicus
  Zenaida asiatica
  Zenaida macroura
- Agelaius phoeniceus
  Aphelocoma coerulescens
  Campylorhynchus gularis
  Carduelis psaltria
  Colaptes auratus
  Columbina passerina
  Contopus borealis
  Contopus virens
  Crotophaga sulcirostris
  Setophaga coronata
  Setophaga townsendi
  Empidonax sp.
  Icterus bullockii
  Icterus cucullatus

Icterus galbula

Icterus parisorum

Icterus spurius Lanius ludovicianus Melanerpes formicivorus Melospiza melodia Mniotilta varia Passerina caerulea Pheucticus ludovicianus Picoides scalaris Piranga ludoviciana Psaltriparus minimus Sporophila torqueola Turdus migratorius Tyrannus verticalis Tyrannus vociferans Oreothlypsis ruficapilla Cardellina pusilla

by the third principal component. No other bird community descriptor was linearly related to the environmental gradients in habitat heterogeneity described by the PCA (P > 0.05). After applying the sequential Bonferroni correction to this first set of data, none of the abovementioned correlation coefficients were significant (global  $\alpha = 0.05$ ).

The following Chao2 estimates of species richness in 2 ha were correlated to the gradients in habitat heterogeneity:  $S_{\rm tot}$  (Fig. A.1b),  $S_{\rm avo}$  (Fig. A.1d), and  $S_{\rm adaavo}$  (Fig. A.1f). The Chao2 values for  $S_{\rm ada}$  and  $S_{\rm expada}$  were correlated to the first principal component ( $S_{\rm ada}$ : n=21; r=0.45;  $S_{\rm expada}$ : P=0.042; n=21; r=0.44; P=0.048). Nonetheless, these two correlations were strongly influenced by the most speciespoor urban green area (where  $S_{\rm ada}$  was 2, as was the Chao2 estimator of urban adapter species in 2 ha). After removing this outlier, the correlations were

not significant (P>0.05). No other estimated bird community richness descriptor was linearly related to the environmental gradients in habitat heterogeneity described by the PCA (P>0.05). Moreover, after applying the sequential Bonferroni correction to this second set of data, none of the abovementioned correlation coefficients were significant.

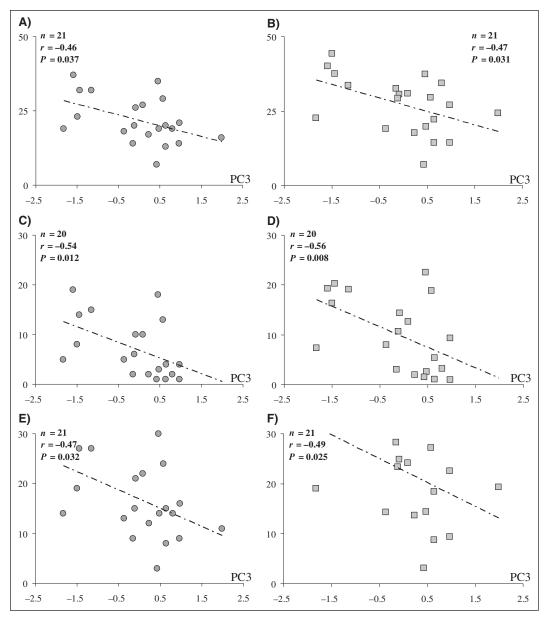


Figure A.1. Scatterplots showing the relationship between species richness and the gradient in the diversity of exotic trees described by the third principal component. Left column, circles: observed species richness per site for: (a) total species, (c) urban avoiders, and (e) urban adapters + urban avoiders. Right column, squares: Chao2 estimator of species richness in 2 ha per site for: (b) total species, (d) urban avoiders, and (f) urban adapters + urban avoiders. No other bird community metric—habitat heterogeneity gradient relationship was statistically significant (P > 0.05).

Fig. A.2c), and Canyon Towhees (*Pipilo fuscus*; Fig. A.2d), all urban adapters, were positively correlated with the second principal component (i.e., the gradient in S, D, and diversity of native trees). The Vermilion Flycatcher was the only species associated with the fourth principal component (i.e., the gradient in D and CC of exotic trees; Fig. A.2b). Three urban exploiters exhibited relationships to the third

principal component. Specifically, the abundance of House Sparrows (*Passer domesticus*; Fig. A.2e) and Rock Pigeons (*Columba livia*; Fig. A.2h) increased in urban green areas with a high diversity of exotic trees (the third principal component), whereas the abundance of the House Finches (*Carpodacus mexicanus*; Fig. A.2f) decreased along the same gradient. Finally, the abundance of Lesser Goldfinches

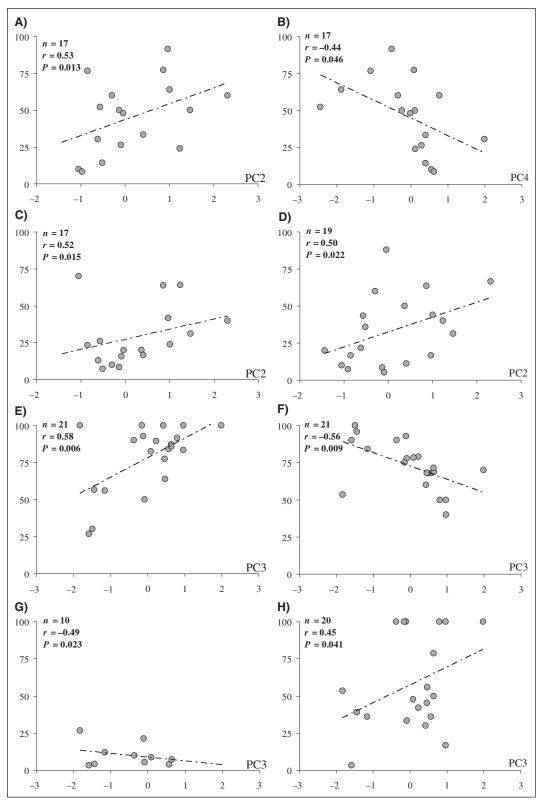


Figure A.2. Scatterplots showing the relationships between the relative abundance of individual bird species (measured as the frequency of occurrence of each species at the sites where it is present, Y axis) and the gradients in habitat heterogeneity described by the PCA (X axis) for (a and b) *Pyrocephalus rubinus*, (c) *Molothrus aeneus*, (d) *Pipilo fuscus*, (e) *Passer domesticus*, (f) *Carpodacus mexicanus*, (g) *Carduelis psaltria*, and (h) *Columba livia*. In all cases, n is the number of sites where the species was registered. See Table A.1 for the meaning of the PCA axes. No other bird species—habitat heterogeneity gradient relationship was statistically significant (P > 0.05).

(*Carduelis psaltria*; Fig. A.2g), an urban avoider, showed a negative relationship to the third principal component. Similar to previous analyses, after applying the sequential Bonferroni correction to this last set of data, none of these correlations were significant.

### DISCUSSION

Most studies of birds in urban environments have concluded that these areas are relatively poor in species richness and diversity when compared to more natural habitats (Chace and Walsh 2006), although clear disparities in the structure of local communities have been described. In fact, bird communities in urban areas could be regarded as being as complex and variable as those in natural habitats (Mills et al. 1989). The main factor implicated in variation in species richness has been patch size (Fernández-Juricic and Jokimäki 2001), following some of the basic patterns previously described by the theory of island biogeography (MacArthur and Wilson 1967). Residual differences in species richness have been linked to other attributes, like the effect of local habitat characteristics on species richness and abundance (Mills et al. 1989, Jokimäki 1999, Clergeau et al. 2001, Crooks et al. 2004, Fernández-Juricic 2004). Unfortunately, the effect of local habitat heterogeneity on bird species richness in urban environments is unclear, since it might have been confounded with that of patch size in several studies (Gavareski 1976, Tilghman 1987). Thus, it could be that larger parks and green areas have greater habitat heterogeneity as well, and therefore could maintain higher bird diversity than smaller and structurally simpler ones (but see Donnelly and Marzluff 2004). However, habitat heterogeneity (as described by the first principal component) was not related to green area size in Puebla (-0.064 <r < +0.105; 0.236 < P < 0.784; in all cases, n = 21). Only the environmental gradient in exotic trees was related to the area of the urban green areas (the fourth principal component: r = -0.556; P = 0.009). Thus, cover and density of exotic trees was larger in larger green areas. Notwithstanding, no bird community metric was related to this gradient in habitat heterogeneity (see Results).

We documented clear spatial differences in tree vegetation heterogeneity among the urban green areas in Puebla, for both native and exotic tree species, and for both the taxonomic and the physical approaches used. In addition, we detected dissimilar bird community structures in terms of richness ( $S_{\text{tot}}$ , but also for the  $S_{\text{exp}}$ ,  $S_{\text{ada}}$ , and  $S_{avo}$ ) and diversity (H' and E). Bird community metrics were only correlated to the gradient in habitat complexity describing changes in the richness and diversity of exotic tree species (the third principal component). The  $S_{\text{tot}}$ ,  $S_{\text{avo}}$ , and  $S_{adaavo}$  all decreased when the diversity of the exotic trees increased. The role of exotic vegetation in shaping the structure of bird communities in urban environments has been previously documented by, among others, Beissinger and Osborne (1982), who concluded that an elevated cover of nonnative trees supports fewer species of insectivorous birds. Similarly, Mills et al. (1989) found that densities of introduced birds correlated best with the volume of exotic vegetation. However, we did not find any effect of D, BA, or CC of exotic trees on bird community measures. In addition, no effect of native vegetation on the structure of bird communities (second principal component) was found. By contrast, Mills et al. (1989) found that native bird species richness, density, and diversity correlated more strongly with native vegetation volume than with any other variable (see also Chace and Walsh 2006). Moreover, if the high number of simultaneous tests performed is taken into account, then the probability of committing a Type I error is inflated. After applying a sequential Bonferroni procedure (Beal and Khamis 1991, Peres-Neto 1999), no statistically significant relationships were found between the structure of bird communities studied and the gradients in habitat complexity previously described (global  $\alpha = 0.05$ ).

Thus, no statistically significant effects of habitat heterogeneity on the richness and diversity of urban bird communities were found. It looks as if the structure of bird communities in the urban greenspaces of Puebla did not depend on the measured portion of local habitat structure. Similarly, Feldman and Krannitz (2002) concluded that differences in richness of bird species across fragments of forests in an urban-to-rural gradient were not related to local habitat characteristics. On the other hand, other studies have documented clear patterns of individual bird species related to habitat variables measuring the effects of urbanization, like human development and fragmentation (Jokimäki 1999, Crooks et al. 2004, Fernández-Juricic 2004). We also found speciesspecific responses to the gradients in tree habitat

complexity. As could be expected (Mills et al. 1989), the abundance of three urban exploiters (House Finch, Rock Dove, and House Sparrow) was linked to changes in the diversity of exotic trees, but only the frequency of occurrence of one urban avoider (Lesser Goldfinch) was correlated to the same gradient. At the species level, the role of native vegetation on bird assemblages was evident, because the abundance of three urban adapters (Vermilion Flycatcher, Bronzed Cowbird, and Canyon Towhee) increased as did the richness, density, and diversity of native trees. However, after correcting probability values for the risk of inflated Type I errors, no globally significant relationship was found.

Habitat complexity did not affect community nestedness either. The nested subset pattern described in some urban bird communities has been linked to other environmental variables, like human disturbance (Fernández-Juricic 2002; but see Platt and Lill 2006 for contrasting results), vegetation structure, and isolation (Fernández-Juricic 2004) or size of the sample area (Ganzhorn and Eisenbeib 2000, Donnelly and Marzluff 2004, Fernández-Juricic 2004). Clearly, the fact that species-poor bird communities in Puebla are nested into rich ones deserves more research, given the possible applications of nestedness to bird conservation (Ganzhorn and Eisenbeib 2000, Patterson and Atmar 2000, Fleishman et al. 2007).

Many other environmental variables, while not measured in our study, could account for the observed changes in bird community structure between habitats (Huston 1994). In fact, we only took into account horizontal changes in tree diversity, but did not consider the vertical structure of tree canopy. One of the classic generalizations of ecology is based on MacArthur and MacArthur's (1961) finding that bird species diversity in natural habitats is positively correlated to the statistic they called foliage height diversity (FHD), a descriptor of the vertical structure of the vegetation. Following this study, similar results have been repeatedly published in the literature (Huston 1994; but see Austin 1999 for a critique). However, the role of FHD as a factor conditioning bird diversity in urban environments is not obvious either. Beissinger and Osborne (1982) described large spatial differences in bird diversity among urban and rural forests, not explained by spatially similar FHD. Likewise, Jokimäki (1999) did not find any effects of FHD on the breeding-bird species richness in urban parks, and suggested that

factors other than "natural" ones (i.e., the amount of green areas, FHD, shrub density, etc.) could be more important for urban birds (like the presence of adjacent buildings, density of human population, or abundance of supplementary food; see also Mills et al. 1989, Jokimäki and Suhonen 1998). Our study shows that the only gradient in physical (size) diversity of the tree vegetation (first principal component) was not related to any measure of bird community structure, or to individual species. Habitat structure was described in our study at a single, local scale, but birds in urban green areas could also depend on factors at larger scale than the individual, immediate habitat (Jokimäki 1999; but see Clergeau et al. 2001 for a different opinion). Moreover, different species probably respond to habitat characteristics at different scales, and single-scale studies may not reflect the proper response of birds to the landscape (Hostetler 2001).

In summary, notwithstanding the exploratory, correlative nature of our study, the structure of bird communities inhabiting urban green areas in Puebla did not show consistent relationships to the habitat heterogeneity measures considered. Thus, (1) the structure of bird communities seems to be a function of other environmental variables not taken into account in this study, (2) it depends on variables acting on different scales, or (3) a combination of both.

### MANAGEMENT IMPLICATIONS

The conservation of birds in urbanized landscapes is important for different reasons. For example, if populations of birds can be established in urban areas, the chances of species extinction at the regional level would decrease (Fernández-Juricic 2004). Also, it would enhance the aesthetic values of urban green areas and promote public awareness about animal life (Savard et al. 2000). Avian ecologists can increase the applicability of their research by working in an interdisciplinary way with urban planners and managers, landscape architects, policy scientists, and so on (Bowman and Marzluff 2001). Considering that most decisions regarding management in urban greenspaces are made at a local scale, and commonly without the benefit of scientific knowledge about their ecological effects (Miller et al. 2001), can management recommendations for increasing the diversity of bird species in the urbanizing Central México be gathered from this study?

Dissimilar recommendations regarding sitespecific actions on habitat heterogeneity have been published in the literature, including the maintenance or increase of native vegetation in the tree and shrub layers, in order to increase the variety of microhabitats and maximize bird species richness and diversity (see, for example, Tilghman 1987, Mills et al. 1989, Clergeau et al. 2001, Kocian et al. 2003). In addition, the minimization of development around the patches and the promotion of ecosystem management at a landscape level have also been suggested (Feldman and Krannitz 2002). Actually, in order to perform a proper management of bird diversity in urban environments, habitat requirements of particular species should be known, since different species could benefit from diverse environmental parameters (Mills et al. 1989, Jokimäki and Suhonen 1998, Crooks et al. 2004, Fernández-Juricic 2004, this study), and probably at a range of different scales (Miller et al. 2001).

City planners and managers are usually constrained by important economic and political realities, like the quantity of area available for greenspaces to be manipulated, and the landscape matrix where it is embedded in (Hostetler 2001, Pickett et al. 2001). Taking into account the rigid models of human and economic development currently implemented in México (Sarukhán 2006), it is probably naïve to think of modifying park size, shape, edge, or other landscape ecology variables for the existing urban green areas. In addition, bearing in mind the statistically ambiguous results of our study, no clear management recommendation can be made regarding how to increase the diversity of bird species in urban parks by managing the structure of trees. At least our study has addressed some of the complexities involved in understanding the structure of bird communities in urban environments. Future research on the species-specific habitat requirements is needed to allow for proper management of species populations.

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### APPENDIX A.1

# Modeling canopy cover.

In plant ecology studies performed in natural forests, it is usually assumed that the canopy cover (CC) of a tree is directly related to the basal area (BA) of its trunk (as estimated by its diameter at the breast height-DBH; see Brower et al. 1997). However, environmental conditions in urban habitats (e.g., soil water stress, prune cutting in the canopy, etc.) can modify the relationship between CC and BA (or DBH) (Rapoport et al. 1983, Hough 1998). To control for this problem, we first developed linear models describing the true relationship between CC and BA for 13 species frequent in the study area (9 angiosperm, 1 palm, and 3 gymnosperm trees), which then were applied to estimate the canopy cover of each species at each site. To this end, we randomly selected 6-28 trees of each of the 13 species and measured both their DBH (using a DBH meter) and the projection on the soil of their canopy cover (measuring with a flex meter the length of the major and minor axes of the canopy, calculating the average value, and using it as the radius of a circle which best estimates the tree cover). For the species with multiple (i) trunks,

we measured DBH for each trunk and obtained its equivalent value as  $DBH_{EO} = 2[\Sigma_i (DBH_i/2)^2]^{1/2}$ . Then, for each species, simple linear regression models (Zar 1996) were obtained relating CC and DBH (or DBH<sub>EO</sub>). CC of some taxa (Acacia sp., Phoenix canariensis, or Salix sp.) was estimated by applying models of closely related species (Acacia retinodes, Washingtonia robusta, and Salix humboldtiana, respectively). Finally, two new models were developed by pooling all the cases from all the species for which significant results were obtained, for both angiosperms and gymnosperms trees as a whole. These two general models were applied as needed for those species with no closely related species. The results of these analyses are summarized in Appendix Table A.1, with the results of the ANOVA (F; in all cases, P < 0.001), and the rest of tree species for which each model was applied (for example, the model for Eucalyptus camaldulensis was used to estimate CC values of E. globulus). General models for angiosperms and gymnosperms are also included. All models have the same structure:  $CC [m^2] = b*DBH [cm].$ 

# APPENDIX TABLE A.1 Modeling canopy cover.

	Model					
Taxa	n	R <sup>2</sup> (%)	F	ь	Other species	
Angiosperms	190	79.3		1.501	Annona cherimola, Casimiroa edulis, Citrum limonicum, Persea americana, Prunus persica, Schinus molle, Senecio praecox, Ulmus sp.	
Acacia retinodes	16	94.8	275.2	1.342	Acacia sp.	
Erythrina americana	6	98.6	355.7	0.564		
Eucaliptus camaldulensis	25	79.9	95.5	1.717	E. globulus	
Ficus indica	25	86.1	148.2	1.812	Ficus sp. pl.	
Fraxinus udhei	28	81.9	122.0	1.467		
Jacaranda mimosifolia	25	91.9	271.8	1.654		
Ligustrum japonicum	25	89.1	197.0	0.813		
Populus alba	25	95.2	477.1	0.765	P. tremula	
Salix humboldtiana	15	84.5	76.5	2.061	Salix sp.	
Palms						
Washingtonia robusta	10	90.4	84.5	0.184	Phoenix canariensis	
Gymnosperms	63	78.6	227.8	1.144	Araucaria heterophylla, Juniperus sp. pl., Taxodium mucronatum	
Cupressus sp.	13	65.1	22.4	0.055	C. lindleyi	
Casuarina equisetifolia	25	83.5	121.1	1.262		
Pinus sp.	25	92.6	301.6	1.219	Pinus sp. pl.	