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LOCAL AND LANDSCAPE DRIVERS OF BIRD COMMUNITY SHIFTS IN URBAN PARKS IN A NEOTROPICAL CITY

Impulsores locales y paisajísticos de los cambios en la comunidad de aves en parques urbanos de una ciudad neotropical

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ABSTRACT

Urban growth affects bird community composition and diversity. However, these effects may vary based on urbanization level and season. We explored how local and landscape variables influenced urban avoiders, exploiters, and adapters birds during two seasons in urban and peri-urban parks in a neotropical city in southern Mexico. Between 2017 and 2018, we performed bird sampling during non-breeding (August–September) and breeding (February–March) seasons. We compared urban bird diversity between parks using Hill numbers. 67 bird species were recorded—38 adapters, 24 avoiders, and five urban exploiters. Overall, peri-urban parks had the highest bird diversity in both seasons compared to urban parks. Urban exploiters were associated with urbanization at the local and landscape levels in both seasons, while urban avoiders preferred parks with structurally complex vegetation in the non-breeding season. Adapters used urban and peri-urban parks interchangeably. Our findings suggest that densely urbanized parks increase the dominance of exploiter bird species while drastically decreasing the presence of native birds. The findings also highlight the role of peri-urban parks in the conservation and planning of neotropical urban centers, reducing the effects of urbanization.

Keywords: bird diversity, greenspaces, non-native birds, urban settlement, vegetation complexity.

RESUMEN

El crecimiento urbano afecta la composición y diversidad de las comunidades de aves. Sin embargo, estos efectos pueden variar según el nivel de urbanización y la temporada del año. Exploramos cómo variables locales y paisajísticas influyeron en las aves urbanas evasoras, explotadoras y adaptadoras durante dos temporadas en parques urbanos y periurbanos de una ciudad neotropical en el sur de México. Entre 2017 y 2018, realizamos muestreos de aves durante las temporadas no reproductiva (agosto-septiembre) y reproductiva (febrero-marzo). Comparamos la diversidad de aves urbanas entre parques utilizando los números de Hill. Se registraron un total de 67 especies de aves urbanas: 38 adaptadoras, 24 evasoras y cinco explotadoras. En general, los parques periurbanos tuvieron la mayor diversidad de aves en ambas temporadas en comparación con los parques urbanos. Las aves explotadoras urbanas se asociaron con la urbanización a nivel local y paisajístico en ambas temporadas, mientras que las evasoras urbanas prefirieron parques con vegetación estructuralmente compleja en la temporada no reproductiva. Las aves adaptadoras utilizaron parques urbanos y periurbanos indistintamente. Nuestros hallazgos sugieren que los parques densamente urbanizados aumentan la dominancia de especies de aves explotadoras al tiempo que disminuyen drásticamente la presencia de aves nativas. Los hallazgos también destacan el papel de los parques periurbanos en la conservación y planificación de los centros urbanos neotropicales, reduciendo los efectos de la urbanización.

Palabras clave: asentamiento humano, aves no nativas, complejidad de la vegetación, diversidad de aves.

INTRODUCTION

Urbanization is a primary driver of the current global biodiversity crisis (Elmqvist *et al.*, 2021). The annual human population growth rate is approximately 1.5 % (7.7 billion people), with an expected increase of 2.3 % by 2100 (10.9 billion people; United Nations, 2019). This exponential growth has led to the modification and loss of natural habitats, resulting in decreased quality of ecosystem services, such as water availability and food production (Seto and Ramankutty, 2016). Furthermore, alterations to natural environments have contributed to a decline in native species and an increase in non-native species, promoting biotic homogenization in urban areas (Clergeau *et al.*, 2006).

Latin America is one of the world's most biodiverse and urbanized regions, with over 80 % of the population residing in metropolises (United Nations, 2019). High population density has significantly impacted Latin American tropical ecosystems, reducing their functions and dynamics (Dobbs *et al.*, 2019). In Mexico, one of the most densely populated countries in the Neotropics, urban development has been constant and disorderly (United Nations, 2019; INEGI, 2020). Rapid human population growth has also triggered an increase in urban greenspaces, which replace forest areas and affect biodiversity (Puga-Caballero *et al.*, 2014; MacGregor-Fors *et al.*, 2021). However, evidence suggests that urban parks can play a crucial role in supporting bird species diversity if structural vegetation elements that provide feeding, reproduction, and shelter sites are maintained (Zúñiga-Palacios *et al.*, 2020).

The level of urbanization differentially affects the distribution of urban birds. Urban avoider birds (i.e., species sensitive to human-induced changes) and certain species that have adapted to moderate levels of urbanization may be influenced by urban traits such as noise levels, the number of buildings, human population density, and the presence of non-native bird species (Ortega-Álvarez and MacGregor-Fors, 2009; Carral-Murrieta *et al.*, 2020). Increased urbanization generally leads to decreased species richness. Typically, avoider birds benefit from greenspaces such as recreational parks, vacant lots, and gardens that provide natural microhabitats (Puga-Caballero *et al.*, 2014; Zúñiga-Palacios *et al.*, 2020). Conversely, urbanization mainly favors some urban adapters (i.e., species that tolerate moderately developed urban areas) and exploiter bird species (i.e., species entirely dependent on human activities). An increase in the number of birds in these groups in human settlements has been linked to their ability to exploit anthropogenic resources, such as food and artificial nesting sites, as well as their environmental tolerance to urbanized areas (Fischer *et al.*, 2015). Thus, urban adapter and exploiter populations are increasing yearly, promoting biotic homogenization in urban landscapes (Clergeau *et al.*, 2006).

Bird communities can also be seasonally affected by the degree of urbanization (Zhou and Chu, 2014). During the breeding season (February to June), birds tend to be negatively impacted by buildings that replace vegetation cover, reducing the availability of natural sites for nesting, reproduction, and feeding (Leveau and Leveau, 2016). In contrast, during the non-breeding season, the arrival of migratory birds increases the richness and abundance of bird species in neotropical urban parks. Urban ecology studies that evaluate the spatial-temporal relationships of bird communities with different urban traits support the development of conservation and planning strategies for biodiversity in urban parks (MacGregor-Fors *et al.*, 2020).

The primary aim of this study was to evaluate the influence of vegetation and urbanization-related local and landscape characteristics on bird communities in urban and peri-urban parks in a city in southern Mexico during both breeding and non-breeding seasons. We hypothesized that bird diversity decreases in urban parks due to higher human disturbance (e.g., people, noise, buildings) and increases in peri-urban areas, which are adjacent to vacant lots and forest areas. However, we also considered that the vegetation structure and landscape features of each park affect bird diversity (Campos-Silva and Piratelli, 2021), regardless of its location. Thus, urban parks with structurally complex vegetation could support greater diversity, even when surrounded by a densely urbanized matrix.

Additionally, due to the variation in resources available in urban and peri-urban parks and the food, reproduction, and shelter requirements of bird species, we predict that the structure and composition of the bird community would differ between urban and peri-urban parks and between breeding and non-breeding seasons. Since urban avoider birds are less tolerant of urbanization and their habitat preferences are positively associated with vegetation complexity, we expect this bird group to be related to greater vegetation complexity at the local level and areas of greater forest coverage at the landscape level. Conversely, we expect urban exploiters and adapters to be more associated with urbanization variables at both the local and landscape levels, as they have more general habitat requirements and can utilize the urban matrix. Our findings can guide future decisions regarding urban planning and urban park management in cities that are continuously growing but lack orderly urban development practices, a common scenario throughout the Neotropics.

MATERIALS AND METHODS

Study area and sampling sites

This study was conducted in the city of Chilpancingo, the capital of Guerrero state in southern Mexico (17°33′05″N –99°30′03″ W; Fig. 1a). Chilpancingo has an average elevation of 1 250 m. a. s. l. The predominant climates are semi-warm subhumid and humid with mean annual temperatures ranging from 15 to 24 °C. Predominant vegetation surrounding Chilpancingo is tropical dry forest under different land-use covers, such as crops and livestock areas. Other vegetation types include oak and pine forests. Chilpancingo is located within the biogeographical province of the Sierra Madre del Sur, one of Mexico's most important biodiversity hotspots (Luna-Vega *et al.*, 2016).

The city has accelerated demographic growth and disorderly urban development—in the last ten years, its population increased by 2.5 %, about 225,700 inhabitants (INEGI, 2020). This increase places it one of the fastest-growing cities in the country. (Pisanty *et al.*, 2009). Despite this population increase, it occupies 26th position out of the 32 state capitals in the country in terms of population size (INEGI, 2020), so it can still be considered a small to medium-sized city, despite its recent and constant growth.

Six sampling sites were selected within urban greenspaces in Chilpancingo city, separated by an average distance of 1 km to avoid pseudoreplication and ensure data independence. Three of these parks—Margarita Maza (PMM), Alameda (ALA), and Jardín Botánico (JBO)—are located in the city's interior, the most densely urbanized area (hereafter urban parks; Fig. 1b). These parks are surrounded by buildings, residential houses, streets, and avenues that facilitate a greater flow of people and vehicular traffic. Urban parks include management activities such as gardening or tree pruning, as well as human activities like walking, jogging, and picnicking, which peak on weekends. These parks are, on average, 2.1 km from forested areas surrounding the city. The dominant plant species found there include *Bursera linanoe*, *B. submoniliformis*, *B. suntui*, *B. aptera*, *Jacaranda mimosifolia*, *Pithecellobium dulce*, *Casuarina equisetifolia*, *Eucalyptus globulus*, *Tabebuia rosea*, *Ficus* spp., and *Tecoma* spp.

The other three sites are located on the city periphery (hereafter peri-urban parks; Figs. 1a y 1b): Club Deportivo Mitsumaru (CDM), Universidad Sentimientos de la Nación (USN), and Parque Ecológico los Manantiales (PEM). Peri-urban parks have greater vegetation cover and less urban infrastructure. These parks are situated near vacant lots with low levels of human activity. The dominant plant species in these parks include *Guazuma ulmifolia*, *Ipomoea murucoides*, *Jacaranda mimosifolia*, *Pithecellobium dulce*, *Tabebuia* spp., *Ficus* spp., and *Salix* spp. Peri-urban parks are located close to surrounding forest areas (average 0.8 km), allowing for the presence of some native plant species such as *Taxodium mucronatum*, *Cascabela thevetioides*, *Plumeria rubra*, *B. fagaroides*, and *I. murucoides.* The surface area of each urban and peri-urban park was measured using Google Earth© satellite images and geographic information systems (ArcGIS 10.5; Fig. 1b).

Local and landscape-level variables

We associated the presence of urban bird species with vegetation and urbanization variables at two spatial scales—local and landscape. The local scale refers to the entire park, while the landscape scale refers to a radius of 200 m from the boundaries of each park. At the local level, we measured vegetation structure and composition variables in a 30 m radius plot; at the landscape level, we measured the land-use area covered by each urban and peri-urban park.

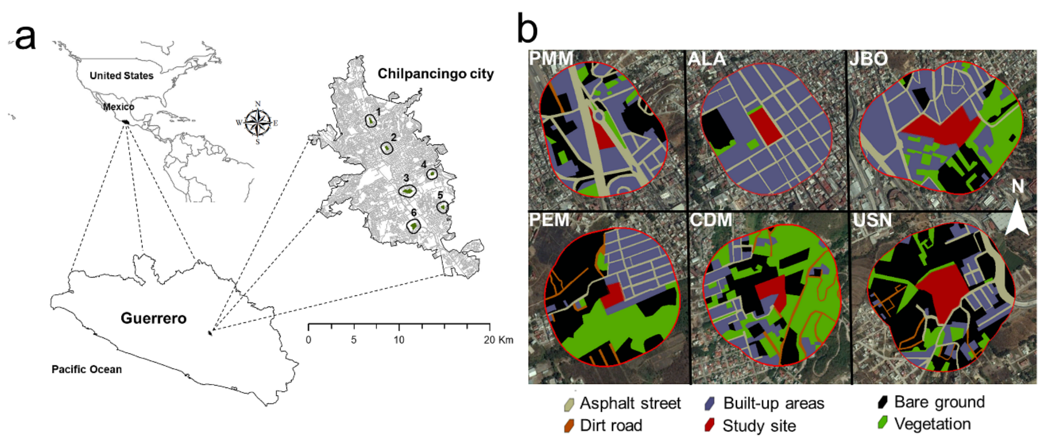

Figure 1. Location of Chilpancingo City in the state of Guerrero, southern Mexico. (a) urban (1-3) and peri-urban parks (4-6): 1) Parque Margarita Maza (PMM), 2) Alameda (ALA), 3) Jardín Botánico (JBO), 4) Parque Ecológico Manantiales (PEM), 5) Club Deportivo Mitsumaru (CDM), 6) Universidad Sentimientos de la Nación (USN). (b) Land-cover classes in the urban and peri-urban parks were delimited by 200 m buffer areas.

In parks smaller than 1.5 ha (PMM, ALA, CDM, and PEM), three circular plots were established, while four circular plots were established in parks larger than 3 ha (JBO and USN). The number of plots varied among parks according to their size. Each plot had a 30 m radius (0.28 ha). To measure vegetation structure and composition variables, two 30 m perpendicular lines were demarcated in each park, oriented toward the four cardinal points. All tree and shrub individuals with a diameter at breast height (DBH ≥ 15 cm) whose branches intersected the rope were measured and identified. Vegetation cover was estimated for each tree and shrub using the ellipse formula based on maximum and minimum diameter lengths (Muller-Dombois and Ellenberg, 1974). Foliage stratification was estimated using an optical square marked with two perpendicular axes, allowing the height of objects above to be assessed when viewed horizontally through the device. In each plot, foliage heights and contacts at the point of intersection were recorded 60 times, at 50 cm intervals along the two axes. Recorded heights were grouped into 1 m intervals. Foliage height diversity was evaluated using the Shannon-Wiener index. Finally, the number of trees and shrubs per unit area (density) of each plot was estimated. The structure and composition variables obtained in the plots at each park included: 1) plant richness, 2) plant abundance, 3) plant dominance (Simpson index; D'), 4) vegetation cover (m^{2-1}), 5) diameter at breast height (cm), 6) foliage height diversity (H'), 7) mean plant height (m), and 8) plant density (ind*ha^{-1}). Additionally, during each bird survey, several urbanization variables in each plot were measured: 1) noise level (expressed in dB), using a sound level digital device to measure noise pollution twice, 5 min apart, in each plot; 2) the number of people per minute, considering only those who crossed within each plot; 3) the number of pets (i.e., dogs and cats) observed per minute; 4) the number of electric wires; and 5) the number of electric poles.

At the landscape level, we delimited buffer areas with a radius of 200 m from the limits of each park (Fig. 1b). This 200-m buffer area was used to assess the effect of urban landscape composition on urban bird communities in each urban and peri-urban park. We considered that this radius would capture the main urban characteristics surrounding the parks that could influence the bird communities. Additionally, the city is small to medium-sized, which limits the use of larger buffer sizes that would cause overlap between them. Other studies have also employed a similar buffer size, demonstrating a favorable response to the effects of urban variables on bird diversity (De Castro *et al.*, 2017). We mapped five land-cover classes: 1) asphalt streets, 2) dirt roads, 3) buildings, 4) bare ground (including areas with herbaceous vegetation), and 5) shrub and tree vegetation (this category included both native and non-native plants, as they were generally combined in the parks; Fig. 1b). The area of each urban and peri-urban park ranged from 0.5 ha (PEM) to 3.36 ha (JBO; Fig. 1b). Overall, because the city is medium-sized, recreational parks are typically not very large.

Urban bird surveys

Urban bird surveys were conducted over two seasons—non-breeding (August–September 2017) and breeding (February–March 2018). A total of 42 days of fieldwork were spread across 21 days in each season. Three to four sampling points were designated within each park. Bird observations were conducted at intervals of one and a half hours during peak bird activity: mornings (between 07:00 and 08:30 am) and afternoons (between 05:00 and 6:30 pm). Each park received 14 visits (84 visits in total), with seven during each season. The 50-m radius point count method was used to record bird species. This distance was chosen because generally allowed for good visibility of birds within each park's specific vegetation and urbanization conditions. Point counts were situated in the same circular plots where vegetation and urbanization variables were measured. To ensure data independence, these plots were separated by at least 200 m (Reynolds *et al.*, 1980). Only bird species that actively used the urban habitat (resting, foraging, or nesting) during the surveys were recorded. Species that did not interact with park vegetation or urban structures were excluded from the study. Additionally, bird observations from weekends were omitted due to the potential influence of higher human activity in some urban parks compared to peri-urban parks, which could compromise data comparability and consistency. Each point received 10 minutes of observation, a timeframe deemed sufficient to count most urban bird species while minimizing the chance of double-counting individuals (Reynolds *et al.*, 1980). Bird identification relied on binoculars (8 × 42 and 10 × 50) and field guides (e.g., Howell and Webb, 1995).

Finally, each recorded bird species was categorized according to its behavior in urban environments. This classification was based on direct field observations and Blair's proposal (1996). 1) urban exploiters, species that can exploit available urban resources (e.g., food, buildings, artificial nests) and are almost entirely dependent on human activities, reaching high population densities in urban environments; 2) urban adapters, species that rely on natural vegetation but can utilize human subsidies in moderately developed urban areas; and 3) urban avoiders, species that disappear with increasing urbanization due to their high sensitivity to human-induced changes (Blair, 1996). The scientific nomenclature and systematic arrangement of urban bird species followed the guidelines of the American Ornithological Society (Chesser *et al.*, 2024).

Data analysis

All analyses, except for the sampling effort evaluation and canonical correspondence analysis, were performed using the *iNEXT*, *MASS*, and *vegan* libraries (Hsieh *et al.*, 2016; Oksanen *et al.*, 2022; Ripley *et al.*, 2022) in R 4.0.3 (R Development Core Team, 2020).

Vegetation variables at the local and landscape levels

Mean ± standard error (SE) values for the thirteen vegetation and urbanization variables at the local and landscape levels were obtained.

Sampling effort

The potential number of urban bird species in each urban and peri-urban park was estimated using the Chao 2 richness estimator in EstimateS 9.1 (Colwell, 2013). Chao 2 is reliable for relatively small sampling units (i.e., point counts; 0.25 km²) and is less dependent on sampling effort than other estimators (Hortal *et al.*, 2006).

Urban bird species richness and diversity

Urban bird diversity in both urban and peri-urban parks was estimated across two seasons (breeding and non-breeding) using the effective number of species, or Hill numbers (Jost, 2006). Diversity was assessed at three levels: first-order diversity, measured as urban bird species richness (q = 0), second-order diversity, or the exponential of Shannon entropy, which accounted for species' proportional abundance (q = 1), and third-order diversity, or the inverse Simpson concentration, which reflected the effective number of dominant bird species in the community (q = 2; Jost, 2006). We compared all diversity values using 84 % confidence intervals (CI), as they robustly mimic $P < 0.05$ statistical tests for both symmetric and asymmetric CI (MacGregor-Fors and Payton, 2013). If the 84 % CI for the three diversity values does not overlap, differences between the urban and peri-urban groups are interpreted as significant.

Structure of urban bird communities

To compare bird community structure (dominance/evenness) between urban and peri-urban parks during the breeding and non-breeding seasons, we employed species rank-abundance plots. Steep curves indicate low evenness and high dominance, while less pronounced curves indicate increasing uniformity and decreasing dominance (Magurran, 2004). We compared the slopes of the rank/abundance plot regression lines using a covariance analysis (ANCOVA) to test whether the proportion of dominant and rare urban bird species varied between urban and peri-urban parks during the two seasons. Urban bird abundance data were log-transformed (log10) as recommended by Magurran (2004).

Influence of habitat at the local and landscape levels

A principal component analysis (PCA) was performed to synthesize the thirteen vegetation and urbanization variables at the local level through varimax rotation to redistribute the variance of factors. To fulfill the assumptions of normality and homogeneity of data variance, vegetation and urbanization variables at the local and landscape levels were standardized to zero means with unit standard deviation and $\sqrt{arcsine\ (x/100)}$, respectively. A canonical correspondence analysis (CCA) was then conducted to analyze the relationship between urban bird species and transformed variables at the local and landscape levels during the breeding and non-breeding seasons (Ter Braak and Verdonschot, 1995). The factors obtained in the vegetation and urbanization PCAs were used in the CCAs and plotted as local-level vectors. The five land-cover classes—asphalt streets, dirt roads, buildings, bare ground, and shrub and tree vegetation—were used in the CCAs as landscape-level vectors. Urban bird species with fewer than three individuals were excluded from the CCAs, as low individual numbers may result from random observations in urban and peri-urban parks. We performed Monte Carlo permutations (999 simulations, $p < 0.05$) to assess the relationship between urban bird species and vegetation and urbanization variables at the local and landscape levels. Two statistical tests were used, one based on the first ordination axis and the other on all canonical axes (Ter Braak and Verdonschot, 1995). These analyses were conducted using CANOCO 4.5 and CANODRAW 4.0 software (Ter Braak and Šmilauer, 2002).

RESULTS

Description of the parks at the local and landscape levels

At the local level, JBO urban park had the most diverse tree species (10 ± 3.47; mean ± standard error). Plant abundance and density were similar across all parks. PEM and CDM parks had the largest trees and the most varied foliage heights. These two parks, along with JBO, had the most vegetation cover. PMM and ALA parks exhibited the highest levels of noise, human and pet presence, as well as electric poles and wires.

At the landscape level, PMM and JBO parks had the most asphalt streets and buildings, respectively. USN and CDM parks had the barest ground and vegetation cover, respectively. USN also had the most dirt roads (Table S1 for details).

During the breeding season, vegetation and urbanization variables were synthesized into three principal components (PCs) that explained 89 % of the variance at the local level. PC1 represented urbanization variables (52.7 % of the explained variance). PC2 and PC3 explained 20.8 % and 15 % of the variance (73.6 % and 89 % of the cumulative variance, respectively), representing vegetation composition and structure variables. In the non-breeding season, the three PCs explained 88 % of the variance. PC1 accounted for 56.3 % of the variance, grouping urbanization variables, while PC2 and PC3 explained 18.7 % and 12.7 % of the variance

(75.1 % and 88 % of the cumulative variance, respectively). Both components represented vegetation composition and structure variables (Table S2).

Urban bird composition, richness, and diversity

We recorded 67 urban bird species belonging to 23 families across the six parks (Table S3). The peri-urban and JBO urban parks exhibited the highest urban bird species richness (Table 1). Based on the Chao 2 estimator, 73 %–92 % of the expected urban bird species were recorded in the urban and peri-urban parks. Further, 38 urban bird species were classified as urban adapters, 24 as avoiders, and five as exploiters. The number of urban exploiters increased slightly in the peri-urban parks. The peri-urban and JBO urban parks had the highest number of urban adapters and avoiders (Table 1). The USN and CDM peri-urban parks had the highest urban bird species richness (q0) and diversity (q1 and q2) during both breeding and non-breeding seasons (Fig. 2).

Table 1. Observed (Robs), estimated (Chao 2) species richness, and urban bird types in urban and peri-urban parks in a Neotropical Mexican city. Urban and peri-urban parks are named in Fig. 1.

	Urban parks			Peri-urban parks		
	PMM	ALA	JBO	PEM	CDM	USN
Robs	26	24	47	41	46	46
% Chao 2	76	92	73	87	90	90
Urban exploiter birds	5	6	6	7	7	7
Urban adapter birds	20	18	30	23	28	29
Urban avoider birds	1	-	11	11	11	10

Structure of urban bird communities

Bird community structure significantly differed between urban and peri-urban parks during the breeding and non-breeding seasons (ANCOVA: both seasons $p < 0.05$; Fig. 3). The House Sparrow (*Passer domesticus*) was dominant in two urban parks (PMM and ALA) in both seasons and during the breeding season in the PEM peri-urban park. The Great-tailed Grackle (*Quiscalus mexicanus*) was dominant in the JBO urban park and the CDM peri-urban park during both seasons, as well as in the PEM peri-urban park during the non-breeding season. While the Rufous-backed Robin (*Turdus rufopalliatus*) was dominant in USN during the breeding season, the Cinnamon-rumped Seedeater (*Sporophila torqueola*) was dominant in this peri-urban park during non-breeding seasons (Fig. 3).

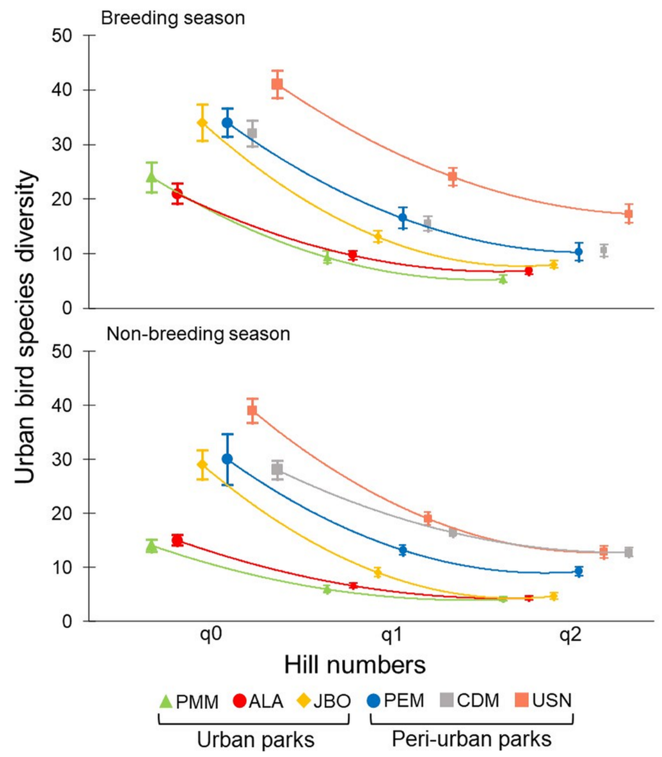

Figure 2. Mean values of richness (q0) and diversity (q1 and q2) of urban bird species in urban and periurban parks during the breeding and non-breeding seasons in a Neotropical Mexican city. Error bars represent 84 % IC. Urban and peri-urban parks are named in Fig. 1.

Distribution of urban bird community at the local and landscape levels

At the local level, the first two axes of the CCA accounted for 82 % (axis 1 = 51 %, axis 2 = 82 %) and 94 % of the cumulative variance (axis 1 = 66 %, axis 2 = 94 %) for breeding and non-breeding seasons, respectively. Only the first axis was significant for both breeding (Monte Carlo: F-ratio = 1.57, p = 0.02) and non-breeding seasons (Monte Carlo: F-ratio = 1.61, p = 0.01). Urbanization variables positively influenced urban exploiters, while some adapters and avoiders were positively associated with vegetation structure and composition during both seasons (4a and 4b).

At the landscape level, two main axes of the CCA explained 68 % (axis 1 = 43 %, axis 2 = 68 %) and 82 % of the cumulative variance (axis 1 = 53 %, axis 2 = 82 %) for breeding and non-breeding seasons, respectively. The Monte Carlo tests for all canonical axes were significant for both breeding (F-ratio = 1.53, p = 0.04) and non-breeding seasons (F-ratio = 1.72, p = 0.01). Most urban avoider species were positively associated with vegetation cover, while urban exploiters were primarily related to buildings, and adapter species were associated with vegetation and urbanization covers throughout the survey periods (Figs. 4c and 4d).

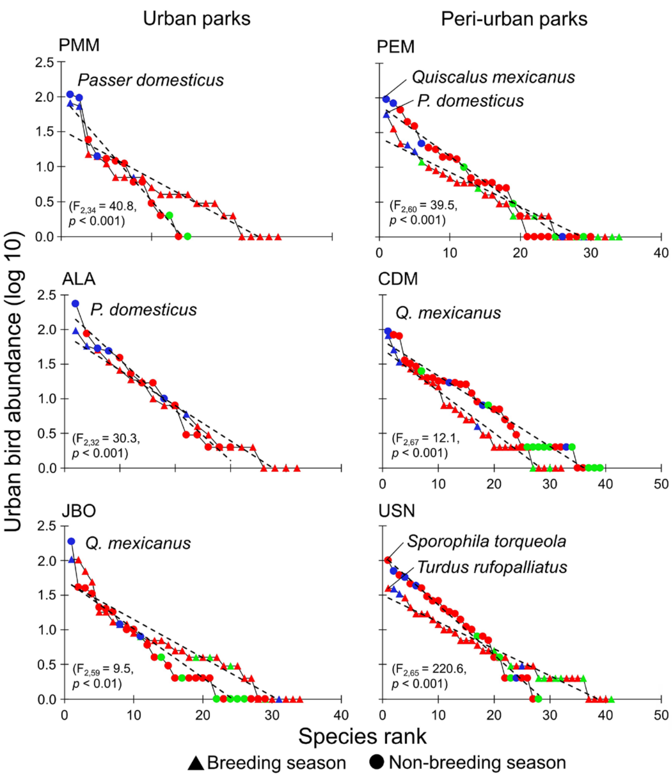

Figure 3. Rank-abundance curves for urban bird species in urban and peri-urban parks during the breeding and non-breeding seasons in a Neotropical city in a Neotropical Mexican city. Urban bird groups: exploiters (blue), adapters (red), avoiders (green). Urban and peri-urban parks are named in (Fig. 1).

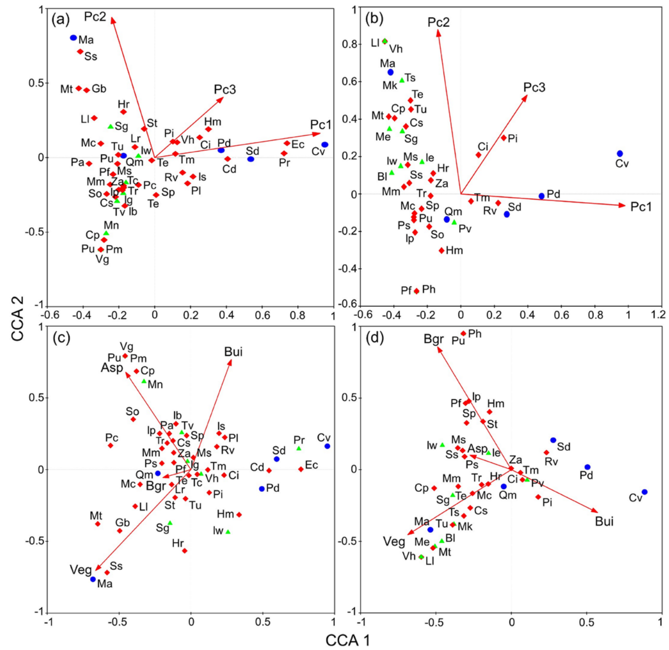

Figure 4. Canonical ordination of exploiter (blue circles), adapter (red diamonds), and avoider birds (green triangles) at the local (upper panels) and landscape level (lower panels) during the breeding (a and c) and non-breeding seasons (b and d) in a Neotropical Mexican city. Urban bird codes are shown in Table S3. Landscape-scale variables: asphalt streets (ASP), dirt road, build-up areas (BUI), bare ground (BGR), vegetation (VEG).

DISCUSSION

Bird diversity among urban parks

As hypothesized, bird species diversity decreased in parks with the greatest influence of urbanization during both breeding and non-breeding seasons. This lower species diversity in urban parks can be attributed to the scarcity of resources and inadequate conditions for the survival of native birds that are intolerant of urbanization (Blair, 2004). Another contributing factor is that two urban parks (ALA and PMM) are public spaces adjacent to schools and commercial centers, characterized by high levels of human presence, buildings, and noise pollution. Previous studies have shown that these factors associated with densely urbanized areas significantly decrease bird species diversity (Carral-Murrieta *et al.*, 2020; Escobar-Ibáñez *et al.*, 2020; Schrimpf *et al.*, 2021). Therefore, parks situated within a densely urbanized matrix pose threats to sensitive bird species due to anthropogenic disturbances (Amaya-Espinel *et al.*, 2019).

However, we also found that vegetation structure, regardless of the park's urban or peri-urban location, appears to be a critical factor in enhancing species diversity. For instance, the JBO urban park exhibited species diversity comparable to that obtained in the peri-urban parks. This urban park, while surrounded by an urban matrix, has greater vegetation cover and plant richness, positively influencing the presence of certain bird species typical of less urbanized areas (e.g., Northern Beardless-Tyrannulet [*Camptostoma imberbe*], White-tipped Dove [*Leptotila verreauxi*], and Summer Tanager [*Piranga rubra*]). This finding aligns with other studies highlighting the importance of local conditions for maintaining bird species diversity in neotropical urban greenspaces (Puga-Caballero *et al.*, 2014; Zúñiga-Palacios *et al.*, 2020). Notably, the JBO park, located within the Guerrero Autonomous University, represents a space characterized by the native flora of southern Mexico. Even though this park is situated within the densely urbanized matrix, the native flora promotes the visitation and permanence of bird species seeking food, shelter, and breeding sites (Castro-Torreblanca and Blancas-Calva, 2014). Latin American university campuses are considered potential refuges for biodiversity, as they maintain greenspaces with native woody plants that provide resources for birds within densely urbanized matrices (Lessi *et al.*, 2016). In the JBO, some native plant species, such as *Bursera linanoe*, *B. submoniliformis*, and *B. aptera,* provide fruits for the Tyrannidae, Turdidae, and Vireonidae families. It has been shown that fruits of *Bursera* spp. contain lipids that constitute a valuable nutrient source for both resident and migratory bird species (Almazán-Núñez *et al.*, 2016).

In contrast to the patterns observed in most urban parks, peri-urban parks exhibited the most diverse bird species diversity during the breeding and non-breeding seasons. As previously documented, this is due to greater vegetation cover and lower human density compared to urban parks (Canedoli *et al.*, 2018). Additionally, these parks, located peripherally in Chilpancingo city, are closer to forest areas, allowing birds tomove toward these peri-urban parks (Puga-Caballero *et al.*, 2014). Some bird groups typical of forest areas, such as the urban avoiders White-tipped Dove, Rusty-crowned Ground-Sparrow (*Melozone kieneri*), and Banded Wren (*Thryophilus pleurostictus*), were primarily observed in peri-urban parks. This highlights the biological and ecological importance of these parks as alternative refuges and biological corridors for avian maintenance and conservation in highly urbanized areas (Lessi *et al.*, 2016; Canedoli *et al.*, 2018).

Urban bird community structure among urban parks

Bird community structure varied significantly between parks during both breeding and non-breeding seasons. These differences are primarily related to the presence of urban exploiter birds, such as the House Sparrow and Great-tailed Grackle. Both species dominated in nearly all parks during both seasons, demonstrating their adaptability to different anthropogenic environments (García-Arroyo *et al.*, 2020). The House Sparrow and Great-tailed Grackle are generalist species associated with human disturbance, utilizing building facades and roofs as resting and nesting sites (MacGregor-Fors and Schondube, 2011; Faggi and Caula, 2017). Additionally, in urban parks, human activities indirectly provide these birds with food and other waste necessary for their survival, increasing their dominance. Conversely, because food and nesting resources derived from natural vegetation are more abundant in peri-urban parks, and human activity is considerably reduced, bird communities tend to be more equitably distributed in these areas (Puga-Caballero *et al.*, 2014; Lessi *et al.*, 2016).

Although House Sparrows and Great-tailed Grackles were abundant in two peri-urban parks (PEM and CDM), their dominance was not as pronounced as in urban parks. This indicates that local conditions within these parks and the matrix of adjacent habitats are not entirely favorable for the settlement of these species (MacGregor-Fors and Schondube, 2011). However, as the populations of these two urban exploiters increase, native birds become less adapted to urbanization, leading to their replacement (García-Arroyo *et al.*, 2020) and avian homogenization in the urban parks of Chilpancingo City, as documented globally (Clergeau *et al.*, 2006).

Distribution of urban bird community at the local and landscape levels

As expected, urban avoider birds were positively related to vegetation complexity, while exploiters and some urban adapters were primarily associated with urbanization at both the local and landscape levels. The biological traits, life histories, and habitat preferences of each urban species drive these associations between urban bird groups and different environmental characteristics. For instance, urban exploiters and adapters are generalist species. These species tend to be larger with broad diets, increasing their probability of adaptation and survival across a wide range of environmental conditions (Palacio, 2020). Our results indicated that these species are predominantly distributed in densely urbanized parks. Most urban exploiters, such as the House Sparrow, Rock Pigeon (*Columba livia*), and Eurasian Collared-Dove (*Streptopelia decaocto*), are invasive birds, while others, such as the Great-tailed Grackle, are native but exhibit invasive behavior. This finding supports the urban tolerance hypothesis, which states that urbanization favors species based on their biological traits, enabling them to utilize resources and adapt to the adverse conditions posed by urban landscapes (Sol *et al.*, 2014).

Urban exploiters and several urban adapters are both granivorous scavenger species, with a vast food spectrum (i.e., euryphagic species; Møller, 2014). Consequently, such species can successfully use anthropogenic resources in urban areas (Blair, 1996; Fischer *et al.*, 2015), explaining the positive association of these species with urbanization. Particularly, urban exploiters were favored by urban variables at the local (number of people, electric poles, and wires) and landscape level (buildings and bare ground), which is explained by their remarkable physiological plasticity and behavior. This plasticity allows urban exploiters to use any resource (e.g., bare ground, buildings, electric poles, and wires) to carry out different functions in their life cycle in densely urbanized matrices (Palacio, 2020). It has been shown, for example, that these species use electric poles and wires as perching places and sites for reproduction (Mikami *et al.*, 2022). This pattern coincides with previous studies describing how urban exploiters and some adapter species are primarily associated with urbanization due to their general behavior in urban landscapes (Ortega-Álvarez and MacGregor-Fors, 2009; MacGregor-Fors and Schondube, 2011).

By contrast, greater vegetation complexity favored urban avoiders at both the local and landscape levels. Blue Mockingbird (*Melanotis caerulescens*), Cinnamon-bellied Saltator (*Saltator grandis*), and Golden Vireo (*Vireo hypochryseus*) were associated with parks exhibiting more complex vegetation during both breeding and non-breeding seasons, preferring peripheral sites adjacent to the urban matrix (Blair, 1996; Fischer *et al.*, 2015). This bird group is associated with wooded areas that provide food, nesting sites, shelter, and reproduction opportunities, situated further away from noise, vehicular traffic, buildings, and the continuous flow of people (Polak *et al.*, 2013). Continuous human activity poses a threat to urban avoider species (Palacio, 2020). Recently, Schrimpf *et al.* (2021) demonstrated that decreased human mobility due to the COVID-19 pandemic increased the abundance of some bird species compared to pre-pandemic levels in urban habitats in North America. This underscores how accelerated and uncontrolled urban growth, particularly in Latin American countries, could jeopardize the survival of native bird species sensitive to anthropogenic disturbance.

CONCLUSIONS

This study provides evidence of the effects of urbanization on the structure and composition of bird communities. Parks that are densely urbanized at the local and landscape levels show an increase in the abundance of exploiters (primarily non-native invasive species) and some urban adapters. Conversely, peripheral parks with a greater supply of resources can retain the local character of their native birds, resulting in a better representation of urban avoiders in these sites. Under certain structural vegetation conditions, parks located on the periphery of cities can serve as connectors for birds found in parks situated within the urban matrix and are essential components of conservation and planning in Neotropical urban centers. This is particularly important for the Latin American region, which contains countries with the greatest biodiversity and some of the highest urbanization rates in the world. Moreover, we demonstrate that seasonality affects differentiation in urban bird community structure, even though general trends in bird diversity patterns were maintained across the different parks.

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CONFLICT OF INTEREST

The authors declared no potential conflicts of interest concerning the research, authorship, and/or publication of this article.

AUTHORS CONTRIBUTIONS

RCA-N: Conceptualization, Methodology, Formal analysis, Writing–Original Draft, Supervision, Project administration. EAA-A: Conceptualization, Methodology, Formal analysis, Writing–Review & Editing. DKP-L: Conceptualization, Writing–Review & Editing. RR-G: Conceptualization, Writing–Review & Editing. PS-M: Conceptualization, Writing–Review & Editing.

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MATERIAL SUPLEMENTARIO / SUPPLEMENTARY MATERIAL

Supplementary Material

Table S1. Local and landscape variables in urban and peri-urban parks in a Neotropical Mexican city. Urban and peri-urban parks are named in (Fig. 1).

Variables	Urban parks			Peri-urban parks		
	PMM	ALA	JBO	PEM	CDM	USN
Local-level						
Vegetation traits						
Plant richness	6 ± 3.54	7 ± 1.42	10 ± 3.47	6.± 0.71	4 ± 1.42	5 ± 0.58
Plant abundance	16 ± 3.54	16 ± 4.25	15 ± 5.04	16 ± 4.95	12 ± 0.71	16 ± 4.51
Plant dominance (D')	0.45 ± 0.40	0.25 ± 0.1	0.15 ± 0.07	0.34 ± 0.07	0.43 ± 0.24	0.30 ± 0.10
Cover (m^{2-1})	2834.21 ±	3321.07 ±	6269.27 ±	5389.40 ±	6800.79 ±	4235.67 ±
	525.92	2459.22	409.87	333.59	5714.3	1347.17
Density (m^2)	0.13 ± 0.03	0.13 ± 0.04	0.12 ± 0.04	0.13 ± 0.04	0.10 ± 0.01	0.13 ± 0.04
Height (m)	8.03 ± 1.89	5.39 ± 0.24	5.64 ± 0.84	6.76 ± 0.36	7.67 ± 2.23	5.78 ± 0.81
Diameter at breast height (cm)	71.13 ± 10.36	71.63 ± 15.35	67.35 ± 18.29	95.88 ± 14.79	128.61 ± 99.81	47.24 ± 10.36
Foliage height diversity (H')	1.63 ± 0.09	1.61 ± 0.10	1.58 ± 0.28	1.73 ± 0.11	1.65 ± 0.08	1.23 ± 0.14
Urbanization traits						
Noise (db)	55.78 ± 1.04	50.57 ± 1.28	25 ± 21.66	36.07 ± 1.33	34 ± 2.07	42.31 ± 1.22
N° people	5.89 ± 0.21	33.07 ± 2.8	0.6 ± 0	2.36 ± 0.51	1.82 ± 0.38	1.74 ± 0.42
N° pets	4 ± 1.41	1.36 ± 0.14	0 ± 0	1.75 ± 0.37	0.46 ± 0.14	0.45 ± 0.11
N° wires	9 ± 4.24	22 ± 4.24	6.33 ± 3.21	11.50 ± 0.71	7.5 ± 2.12	9 ± 4.58
N° light posts	7.5 ± 4.94	9.5 ± 2.12	3.33 ± 1.52	6.50 ± 2.13	6.5 ± 2.12	1.66 ± 0.57
Landscape-level						
Asphalt streets	38.7	22.5	32.5	11.6	28	28.9
Dirt road	0.8	-	-	2.1	1.7	2,6
Built-up areas	37	67.3	69.9	17.2	12	16.8
Bare ground	16.7	6.5	15	31.9	21.7	60.4
Vegetation	6.7	1.1	9.5	21	33.6	8.2

Table S2. Ordination values of the principal components (PC) of the 11 vegetation and urbanization variables in the urban and peri-urban parks during breeding and non-breeding seasons in a Neotropical Mexican city. Significant correlations are as follows: $p \leq 0.05$ (*), $p \leq 0.01$ (**), $p \leq 0.001$ (***).

Variables	Breeding season			Non-breeding season		
	PC1	PC2	PC3	PC1	PC2	PC3
Species richness	-0.15	0.08	-0.89**	0.13	-0.01	-0.9***
Plant abundance	0.38	-0.75	-0.25	0.36	0.81**	-0.06

Variables	Breeding season			Non-breeding season		
	PC1	PC2	PC3	PC1	PC2	PC3
Plant dominance	0.69	-0.48	0.49	0.5	0.41	0.7
Cover (m^{2-1})	-0.53	0.8**	-0.26	-0.45	-0.74	-0.49
Height (m)	-0.19	0.13	0.95***	0.4	-0.1	0.77*
Foliage height diversity (H')	-0.32	0.74*	-0.12	-0.4	-0.59	-0.30
Diameter at breast height (cm)	0.18	0.95***	0.2	0.07	-0.98***	0.11
Noise (db)	0.58	-0.71	0.22	0.75	0.62	0.05
N° people	0.91***	-0.32	-0.2	0.91***	0.37	-0.002
N° wires	0.9***	-0.33	-0.13	0.89**	0.33	0.15
N° light posts	0.96***	0.004	0.15	0.88**	-0.08	0.37
Eigenvalues	5.8	2.29	1.67	6.2	2.05	1.4
Explained variance (%)	52.73	20.86	15.2	56.36	18.77	12.7
Cumulative variance (%)	52.73	73.6	89	56.36	75.13	88

Table S3. Composition and relative abundance of urban bird species in urban and peri-urban parks during breeding and non-breeding seasons in a Neotropical Mexican city. Urban and peri-urban parks are named in (Fig. 1). Urban classification (UC): urban exploiters (UrEx), urban adapters (UrAd), urban avoiders (UrAv). Urban and peri-urban parks are named in (Fig. 1).

Taxon	UC	Code	Breeding season						Non-breeding season					
			PMM	ALA	JBO	PEM	CDM	USN	PMM	ALA	JBO	PEM	CDM	USN
Columbidae														
Columba livia	UrEx	Cv		0.018						0.017				
Streptopelia decaocto	UrEx	Sd	0.047	0.096	0.018	0.044	0.003	0.068	0.027	0.164	0.024	0.066		0.008
Columbina inca	UrAd	Ci	0.037	0.158	0.023	0.092	0.131	0.073	0.011	0.144	0.018	0.023	0.069	0.059
Columbina passerina	UrAd	Cp					0.015	0.006			0.008			0.003
Leptotila verreauxi	UrAv	-					0.002				0.002			
Zenaida asiatica	UrAd	Za			0.002	0.012			0.015		0.024	0.027	0.008	0.028
Cuculidae														
Crotophaga sulcirostris	UrAd	Cs			0.014	0.029	0.029				0.012	0.015	0.003	0.034
Piaya cayana	UrAd	Pc					0.003				0.006		0.005	
Trochilidae														
Cynanthus doubledayi	UrAd	Cd				0.002		0.002		0.006		0.004		0.003
Basilinna leucotis	UrAv	Bl	0.007	0.004		0.002	0.002	0.003						
Ramosomyia violiceps	UrAd	Rv			0.005		0.003		0.004	0.023	0.01	0.008	0.005	0.02
Strigidae														
Glaucidium brasilianum	UrAd	Gb			0.005								0.005	0.003

Taxon	UC	Code	Breeding season						Non-breeding season					
			PMM	ALA	JBO	PEM	CDM	USN	PMM	ALA	JBO	PEM	CDM	USN
Momotidae														
Momotus mexicanus	UrAd	Mm			0.023	0.012	0.02	0.011			0.008	0.008	0.005	0.02
Picidae														
Melanerpes chrysogenys	UrAd	Mc	0.02		0.075	0.029	0.033	0.017	0.004		0.026	0.023	0.046	0.028
Psittacidae														
Eupsittula canicularis	UrAd	Ec			0.002				0.015	0.023				
Tyrannidae														
Camptostoma imberbe	UrAv	-			0.002									
Myarchus nuttingi	UrAv	Mn									0.008			0.006
Myiarchus tyrannulus	UrAd	-	0.007											
Pitangus sulphuratus	UrAd	Ps		0.005	0.046	0.01	0.028	0.041		0.006	0.014	0.012	0.02	0.039
Megarynchus pitangua	UrAv	-					0.003							
Myiozetetes similis	UrAd	Ms				0.002	0.003	0.003				0.004		0.011
Tyrannus melancholicus	UrAd	Tm	0.044	0.042	0.041	0.027	0.03	0.032	0.054	0.073	0.037	0.035	0.043	0.048
Tyrannus vociferans	UrAv	Tv												0.014
Tyrannus crassirostris	UrAv	Tc					0.002					0.004		0.006
Tyrannus verticalis	UrAd	Te				0.014	0.011		0.027		0.006		0.005	0.008
Empidonax minimus	UrAv	-												0.006
Pyrocephalus rubinus	UrAd	Pu						0.027	0.011	0.096				0.02
Vireonidae														
Vireo hypochryseus	UrAv	Vh					0.013		0.004	0.003	0.002		0.003	
Vireo gilvus	UrAd	Vg									0.01			
Laniidae														
Lanius ludovicianus	UrAd	Ll					0.005						0.005	0.006
Hirundinidae														
Stelgidopteryx serripennis	UrAd	Ss			0.005	0.01	0.011	0.013				0.023	0.13	0.006
Hirundo rustica	UrAd	Hr	0.081	0.031	0.091	0.137	0.136	0.063	0.027			0.139	0.064	0.017
Ptiliogonatidae														
Ptiliogonys cinereus	UrAd	Pi	0.02	0.071	0.002		0.052	0.016	0.057	0.011	0.002		0.015	0.025
Polioptilidae														
Polioptila caerulea	UrAd	Pa							0.042	0.054	0.142	0.039	0.054	0.048

Taxon	UC	Code	Breeding season						Non-breeding season					
			PMM	ALA	JBO	PEM	CDM	USN	PMM	ALA	JBO	PEM	CDM	USN
Troglodytidae														
Catherpes mexicanus	UrAd	-				0.002	0.002							
Thryophilus sinaloa	UrAv	Ts				0.002	0.003					0.008		
Thryophilus pleurostictus	UrAv	-										0.004		
Mimidae														
Melanotis caerulescens	UrAv	Me			0.002		0.003					0.008		
Toxostoma curvirostre	UrAd	Tu		0.004	0.007	0.002	0.026	0.003				0.008	0.003	0.008
Mimus polyglottos	UrAv	-												0.003
Turdidae														
Turdus rufopalliatus	UrAd	Tr		0.031	0.094	0.037	0.059	0.041	0.011	0.051	0.209	0.085	0.084	0.11
Passeridae														
Passer domesticus	UrEx	Pd	0.359	0.427	0.027	0.17	0.013	0.09	0.31	0.274	0.002	0.224	0.01	0.11
Fringillidae														
Haemorhous mexicanus	UrAd	Hm	0.003	0.005	0.009	0.002	0.003	0.022	0.027	0.003			0.003	
Spinus psaltria	UrAd	Sp							0.008		0.004			
Passerellidae														
Peucaea ruficauda	UrAd	Pf			0.002	0.039	0.033	0.097				0.012	0.013	0.082
Peucaea humeralis	UrAv	Ph						0.006						
Melozone kieneri	UrAv	Mk				0.002	0.003							0.006
Icteridae														
Icterus wagleri	UrAv	Iw					0.003	0.003				0.046		0.008
Icterus spurius	UrAd	Is								0.028	0.014	0.004	0.005	0.014
Icterus pustulatus	UrAd	Ip			0.005	0.012	0.007	0.028	0.008	0.003	0.037	0.031	0.013	0.048
Icterus bullockii	UrAd	Ib							0.004		0.004			0.014
Icterus pectoralis	UrAv	Ie				0.006	0.002	0.002						
Icterus gularis	UrAv	-			0.002									
Icterus galbula	UrAv	Ig									0.008	0.019		0.006
Molothrus aeneus	UrEx	Ma				0.002	0.028	0.003				0.004	0.087	
Molothrus ater	UrAd	Mt			0.005		0.008				0.002		0.008	
Quiscalus mexicanus	UrEx	Qm	0.322	0.089	0.429	0.194	0.154	0.111	0.28		0.211	0.081	0.209	0.093

Taxon	UC	Code	Breeding season						Non-breeding season					
			PMM	ALA	JBO	PEM	CDM	USN	PMM	ALA	JBO	PEM	CDM	USN
Parulidae														
Mniotilta varia	UrAv	Mn										0.004		
Leiothlypis ruficapilla	UrAd	Lr							0.015	0.006	0.014	0.015	0.018	0.006
Setophaga coronata	UrAd	So							0.019	0.003	0.099	0.004	0.038	0.011
Cardellina pusilla	UrAd	-									0.002	0.004		
Cardinalidae														
Piranga rubra	UrAv	Pr									0.006			
Piranga ludoviciana	UrAd	Pl							0.004	0.006	0.002			0.008
Pheucticus melanocephalus	UrAv	Pm									0.016			
Passerina versicolor	UrAv	Pv	0.003		0.002	0.004								
Thraupidae														
Sporophila torqueola	UrAd	St	0.04	0.015	0.048	0.08	0.048	0.158	0.015	0.008	0.008	0.008	0.02	0.006
Saltator grandis	UrAv	Sg			0.009	0.02	0.041	0.013				0.004	0.003	0.003