The Greener the Better! Avian Communities Across a Neotropical Gradient of Urbanization Density

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Urbanization has been recognized as one of the most widespread threats to biodiversity. However, the response of wildlife to urbanization differs among groups, with many species being able to persist, adapt, and even thrive in these novel ecosystems. With the aim of assessing the response of avian communities in a neotropical green city, we evaluated their species richness and composition across a gradient of urbanization density comprised by a citywide survey performed in two consecutive years and considering both breeding and non-breeding seasons. As expected, species richness decreased with urbanization. Species loss was drastic when considering data from both years and both seasons, and gradual when seasons were assessed separately. Avian composition for both years and seasons differed largely between the less urbanized and the more urbanized sites, whereas sites with intermediate built cover showed to be more similar to each other. When evaluating avian composition by season in both years, highest differences were recorded between more urbanized sites and all other studied sites, while less urbanized sites showed high similarity regardless of the surveyed season. Sites with intermediate built cover had higher similarity among seasons, showing that such conditions shelter similar species in both seasons. This study presents findings on one of the first citywide gradients of urbanization density from the urban Neotropics, showing both differences and similarities in relation to previous studies from the Global North. Briefly, our species richness results showed a punctuated decrease when considering both seasons and years, rather than a gradual decrease or humped-shaped relations with higher richness at intermediately urbanized sites. Also, our composition findings stress the high representation of insectivore birds as part of avian communities across a citywide gradient of urbanization density. Undoubtedly, identifying the similarities and differences in the urban ecology patterns across cities, together with the particularities of some urban systems, will allow for increased effectiveness of urban management and planning strategies in the transformation toward more livable, resilient, and biodiverse cities.

Keywords: avian communities, citywide survey, gradient framework, green city, urban ecology
INTRODUCTION

Urbanization has been shown to be one of the main threats to biodiversity (Czech and Krausman, 1997; Mcdonald et al., 2008; Maxwell et al., 2016) and currently represents one of the fastest growing land use change forces worldwide (Seto et al., 2012; Eldredge and Horenstein, 2014). Along its process, preexisting systems are replaced with a set of artificial and natural components that seek to cover modern urban needs, representing long-term modifications at different spatio-temporal scales (Eldredge and Horenstein, 2014). Among the global negative consequences of urbanization, species are lost, biogeochemical cycles are disrupted, biological invasions are promoted, and important sources for climate change occur (Grimm et al., 2008).

Although many of the changes implied in the process of urbanization are focused on human well-being (Alberti et al., 2003), many species have been able to persist, adapt, and even thrive in these novel ecosystems with a peculiar set of conditions, resources, and hazards (McDonnell and Hahs, 2015). It is notable that not only human-commensal species are well represented within cities, but also species with particular conservation relevance (Aronson et al., 2014). Yet, the response of wildlife to urbanization varies across species, environmental conditions, and even locations (McDonnell and Hahs, 2008; McKinney, 2008; Egerer et al., 2017), with population dynamics between urban and non-urban areas determining their fate (Fischer et al., 2015).

One of the essential components of urban systems is that they are spatially heterogeneous, mainly given by the way in which they grow (often without proper planning; Benítez et al., 2012), and how their land-uses are planned (e.g., residential, commercial, industrial, recreational) (Machlis et al., 1997; Alberti et al., 2003). Spatial heterogeneity, together with variations in the physical and social spheres of cities, creates numerous conditions for biodiversity to colonize (Chace and Walsh, 2006; McKinney, 2008; Aronson et al., 2014). In an attempt to understand ecological variations across cities, urban ecologists have used gradients to assess the response of biodiversity to urbanization (McDonnell and Pickett, 1990; McDonnell and Hahs, 2008). In fact, the gradient framework is the one that has enhanced most of our understanding of several wildlife groups’ response to urbanization to date (McDonnell and Hahs, 2008; McKinney, 2008; Martinson and Raupp, 2013).

Together with plants, birds are the most studied wildlife group in urban areas across the globe (McKinney, 2008). Not surprisingly, it is the group that has had the largest amount of studies using gradients of urbanization (McDonnell and Hahs, 2008). Despite the high variability of cities across the globe and the conceptual differences in the establishment of gradients of urbanization, studies have found that avian species richness decreases with urbanization, but also have found hump-shaped patterns, with higher species richness at intermediate levels of urbanization (Marzluff, 2001; Chace and Walsh, 2006; Lepczyk et al., 2008). Studies have also reported important changes in the composition of the species comprising urban bird communities. Briefly, generalist species tend to increase with urbanization, while specialists tend to fade out (Clergeau et al., 2006; La Sorte and McKinney, 2007).

Given that several species richness patterns have been found in relation to urbanization gradients, with no current consensus, we performed a bibliographic search to know if such responses are found in similar proportions. Thus, we performed an exploratory search in the Web of Science platform using the following advanced Boolean operator string: ((avian OR bird*) AND (urban*) AND (gradient)). We retrieved a total of 114 publications after filtering out those outside our research focus. It was evident that the most frequent response to urbanization was negative (84% of publications; e.g., Clergeau et al., 1998; Palomino and Carrascal, 2005; Lepczyk et al., 2008; MacGregor-Fors and Schondube, 2012; Chamberlain et al., 2017; Sol et al., 2017), few studies reported no clear relationships (8% of studies; e.g., Merenlender et al., 1998; Fratterigio and Wiens, 2005; Sorace and Gustin, 2008; Suhonen et al., 2009; Meffert and Dziock, 2013), as well as higher species richness at intermediate levels of urbanization (6%; i.e., Jokimäki and Suhonen, 1993; Blair, 1996, 1999, 2004; Clucas and Marzluff, 2015; Battisti and Fanelli, 2016; Guetté et al., 2017), and even positive responses to urbanization (2%; i.e., Leveau and Leveau, 2005; Coetzee and Chown, 2016).

Despite the fact that the majority of the human population lives in small-to-medium sized urban settlements (<500,000 inhabitants; United Nations, 2018) and that the projected expansion of urban areas is foreseen to occur in tropical areas (Seto et al., 2012), most studies focused on avian diversity in urban gradients have been conducted in large urban areas of temperate developed regions. Fortunately, an increasing number of studies from tropical regions are starting to populate the literature, finding both similar and different responses of bird communities to urbanization when compared with those of temperate regions (see Ortega-Álvarez and MacGregor-Fors, 2011a,b; Escobar-Ibáñez and MacGregor-Fors, 2017; MacGregor-Fors and García-Arroyo, 2017). Such differences have been suggested to be related not only to the particular and diverse tropical avifaunas, but to the nature of tropical urban systems, including their socioeconomic realities (MacGregor-Fors and Escobar-Ibáñez, 2017). Thus, generating information from small-to-medium sized tropical cities is crucial if we aim to understand the response of urbanization on avian diversity, which has shown to be an excellent urban bioindicator (sensu Moreno et al., 2007). Thus, in this study we assessed the relationship between the gradient of urbanization density (considering built cover within a radius of 25 m as the gradually changing variable) of the city of Xalapa de Enríquez, Mexico (referred to as Xalapa hereafter) and bird diversity during the breeding and non-breeding seasons. Given that most of the reviewed studies report a decrease in bird species richness in response to urbanization, we expected to find a negative response of species richness with increasing built cover. Regarding species composition, we expected communities from highly urbanized sites to be different, in general, from moderately and lowly urbanized sites; yet, based on recent evidence for the study region, we expected a less marked pattern during the non-breeding season, when habitat requirements for birds appear to be less strict (MacGregor-Fors et al., 2018).
MATERIALS AND METHODS

Study Area
We carried out this study in the city of Xalapa, located in the highlands of central Veracruz, Mexico (19°32′37″ N, 96°54′37″ W). The city has a territory of ~64 km² (Falfán et al., 2018) that extends through an elevation range of ~600 m (~1,100–1,700 m asl). Given its history, location, and high rainfall (1,100–1,600 mm/year; Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2009), Xalapa is a green city with ~40% of its territory covered by vegetation. Original vegetation associations surrounding Xalapa included cloud forests, tropical dry forests, and temperate forests (Williams Linera et al., 2002).

Survey Design and Bird Sampling
In order to have an overall representation of the physical, ecological, and social components of Xalapa, we performed a citywide survey. After delineating the polygon of the city based on the spatial aggregation and communication of built elements, we set survey sites at quadrant centers of a 750 m × 750 m grid (for further details see Escobar-Ibáñez and MacGregor-Fors, 2016; Falfán and MacGregor-Fors, 2016; Figure 1). Although the resulting grid included 110 survey sites, we removed 4 of them for security reasons. When sampling sites were located within private property, the location was set on the closest public space. It is notable that all survey sites were located within the urban continuum of the city, including its built-up matrix and greenspace network, and excluding surrounding non-urban environments (sensu MacGregor-Fors and Vázquez, in press).

Afterward, we considered the amount of urban greenery at each sampling site in a 25 m radius to classify them in relation to a gradient of urbanization density. For this, we used a previously published spatial classification of urban vegetation for Xalapa (Falfán et al., 2018) and considered the remaining surface as built cover. Finally, we categorized our sampling sites into four classes: (1) Class I: 0–25% built cover (i.e., mainly greenspaces and few very well vegetated residential areas), (2) Class II: 26–50% built cover (i.e., well vegetated residential areas and urbanized greenspaces), (3) Class III: 51–75% built cover (i.e., residential and/or commercial areas with moderate vegetation cover), and (4) Class IV: 76–100% built cover (i.e., residential and/or commercial areas without or with little vegetation cover) (Figure 2). Of the 106 sampled sites, 11 pertain to Class I, 10 to Class II, 19 to Class III, and 66 to Class IV.

We surveyed bird communities using 5 min fixed-radius (25 m) point-counts, recording all birds seen or heard actively using the surveyed area, from sunrise (~07:00 h) up to four subsequent hours (~11:00 h) (Ralph et al., 1995). We surveyed the 106 sites on four occasions, once during the non-breeding season (February–March) and once during the breeding season (June–July) of two subsequent years (i.e., 2014, 2015).
Data Analysis
We approached species richness contrasts in relation to the built cover categories at two different temporal levels: (1) all data for both years (including both seasons) and (2) data for both years by season. For this, we calculated the rarefied statistical expectation of species richness ($S_{\text{est}}$) in EstimateS 9 (Colwell, 2013). Since sampling effort was uneven among built cover classes, we randomly generated subsets from over-represented categories taking into account the class with less samples (i.e., Class II = 10) and performed species richness calculations (i.e., we randomly subtracted 1 sample from Class I and generated 2 and 6 random subsets for Classes III and IV, respectively). We averaged the estimated species richness and corresponding confidence intervals for such categories. To statistically contrast species richness calculations, we used overlapping confidence intervals. Given that inferring results from overlapping 95% intervals have shown to fall into Type I errors, mainly when intervals slightly overlap, we used 84% intervals that have been shown to robustly mimic 0.05 tests. Thus, we assumed statistical differences when intervals did not overlap (Payton et al., 2003; MacGregor-Fors and Payton, 2013). We also evaluated shifts in species composition at the above-mentioned temporal levels by calculating the similarity of bird communities using data for both years (including both seasons) with a Bray-Curtis (Bray and Curtis, 1957) index by randomly selecting subsets from the species richness analyses. Afterward, we performed a similar analysis considering both years by season, using a hierarchical clustering procedure (average grouping).

RESULTS
We recorded a total of 67 bird species of 26 families (Table 1). Most of them ($n = 46$) were resident breeders, 19 migrants or winter residents, and 2 summer residents (i.e., Barn Swallow—Hirundo rustica, Streaked Flycatcher—Myiodynastes maculatus).
| Family       | Scientific name | Class I | Class II | Class III | Class IV |
|--------------|-----------------|---------|----------|-----------|----------|
| Cracidae     | Ortalis vetula  | •       |          |           |          |
| Columbidae   | Columba livia   | •       | •        | •         |          |
|              | Patagioenas flavirostris | •       | •        | •         |          |
|              | Streptopelia decaocto | •       | •        | •         |          |
|              | Columbina inca |  •      |          |           |          |
| Cuculidae    | Crotophaga sulcirostris | •       |          |           |          |
|              | Playa cayana   |  •      |          |           |          |
| Apodidae     | Streptoprocne zonaris | •       | •        | •         |          |
| Trochilidae  | Anthracothorax prevosti | •       |          |           |          |
|              | Campylopterus curvipennis | •       | •        | •         |          |
|              | Amazilia cyancephala | •       | •        | •         |          |
|              | Amazilia beryllina | •       | •        | •         |          |
| Strigidae    | Glaucidium brasilianum | •       |          |           |          |
| Picidae      | Melanerpes formicivorus | •       | •        | •         |          |
|              | Melanerpes aurifrons | •       | •        | •         |          |
|              | Dryobates scalaris |  •      |          |           |          |
| Psittacidae  | Amazona autumnalis | •       |          |           |          |
| Furnariidae  | Lepidocolaptes affinis | •       |          |           |          |
| Tityridae    | Tityra semifasciata | •       |          |           |          |
| Tyrannidae   | Pitangus sulphuratus | •       |          |           |          |
|              | Megarynchus pitangus | •       |          |           |          |
|              | Myiozetetes similis | •       | •        | •         |          |
|              | Myiodynastes maculatus | •       |          |           |          |
|              | Empidonax occidentalis | •       |          |           |          |
|              | Tyrannus melancholicus | •       | •        | •         |          |
| Vireonidae   | Vireo griseus   | •       |          |           |          |
|              | Vireo cassini   |  •      |          |           |          |
|              | Vireo solitarius | •       | •        | •         |          |
|              | Vireo gilvus    |  •      |          |           |          |
|              | Vireo leucophrys |  •      |          |           |          |
| Corvida      | Pseudorhynchus morio | •       |          |           |          |
| Hirundinidae | Hirundo rustica | •       | •        | •         |          |
|              | Stelgidopteryx serripennis | •       | •        | •         |          |
| Trogodytidae | Trogodytes aedon | •       | •        | •         |          |
|              | Campylorhynchus zonatus | •       | •        | •         |          |
| Polioptilidae| Polioptila caerulea | •       | •        | •         |          |
| Regulidae    | Regulus calendula | •       |          |           |          |
| Turdidae     | Catharus aurantirostris | •       |          |           |          |
|              | Turdus grayi    | •       | •        | •         |          |
| Mimidae      | Melanotis caerulescens | •       |          |           |          |
|              | Dumetella carolinensis | •       | •        | •         |          |
| Passeridae   | Passer domesticus | •       | •        | •         |          |
| Fringillidae | Euphonia hirundinacea | •       | •        | •         |          |
|              | Euphonia elegantissima | •       |          |           |          |
|              | Haemorhous mexicanus | •       |          |           |          |
|              | Spinus psaltria |  •      |          |           |          |
| Passerellida | Melospiza lincolnii | •       |          |           |          |
|              | Amophilus rufescens | •       |          |           |          |
| Icteridae    | Icterus graduacauda | •       |          |           |          |
|              | Icterus gabiula |  •      |          |           |          |
|              | Molothrus aeneus |  •      |          |           |          |
|              | Dives dives    |  •      |          |           |          |
|              | Quiscalus mexicanus | •       | •        | •         |          |

(Continued)
The most abundant species across all surveys was the Great-tailed Grackle (Quiscalus mexicanus) with 415 records, followed by the House Sparrow (Passer domesticus) with 175 records, and Rock Dove (Columba livia) with 135 records. Based on species-level foraging attributes of a global bird database (Wilman et al., 2014), the best represented group across the city was the one that feeds majorly on invertebrates (60%), followed by those that mainly consume plant/seeds (mainly granivores; 15%), fruit/nectar (mainly frugivores; 13%), and omnivores (12%).

When assessing both years (considering both seasons), we found statistically higher species richness in Class I ($S_{\text{est}} = 34.0$, 84% CIs: 28.9–39.1) when contrasted to the rest of studied categories, which did not differ statistically among them (Class II: $S_{\text{est}} = 19.0$, 84% CIs: 14.2–23.8; Class III: $S_{\text{est}} = 17.0$, 84% CIs: 12.4–21.6; Class IV: $S_{\text{est}} = 15.4$, 84% CIs: 12.1–18.6; Figure 3). It is notable that the magnitude of the difference of species richness between Class I and Classes II–IV was, on average, 2-fold. When contrasting values by seasons (considering both years), we found a similar pattern of species loss, but more gradual in both seasons, with values in Class I significantly higher when compared with those of Class IV, but values from Classes II and III not showing significant differences with Classes I and IV (Figure 3).

Bray-Curtis index calculations for all data of both years (including both seasons) showed that the most similar classes were II and III (67% similarity). Class I showed ≤ 46% similarity with the rest of studied Classes (Class II = 38%, Class III = 46%, Class IV = 28%). Class IV was the most different (≤ 34% similarity) when contrasted with the other studied classes (Class I = 28%, Class II = 34%, Class III = 34%). Regarding data of both years by season, the hierarchical cluster analysis showed a similar pattern, with both seasons from Classes I and IV differing from the rest, although both seasons for Class IV were more similar (68% similarity) than those of Class I (30% similarity). Classes II and III were grouped by season, with 97% similarity during the breeding season and 65% similarity during the non-breeding season (Figure 4).

**DISCUSSION**

Our 2-year citywide survey allowed us to record ~20% of the bird species historically recorded for Xalapa (González-García et al., 2016). In agreement with previous studies of the avian ecology of Xalapa (e.g., Escobar-Ibáñez and MacGregor-Fors, 2016), it was not surprising to find the Great-tailed Grackle to be the most abundant bird in all built cover classes, except Class IV where the House Sparrow and Rock Pigeon outnumbered it (a common scenario in Mexican urban settlements of differing sizes; MacGregor-Fors et al., 2011). It is notable that the only class in which Neotropical–Nearctic wintering species were among the most abundant species was Class I, represented mainly by the Wilson’s (Cardellina pusilla) and Black-throated Green Warblers (Setophaga virens).

Contrary to what has been synthesized in global reviews (e.g., Chace and Walsh, 2006; Evans et al., 2009; Marzluff, 2016), the avian community recorded in this study was majorly comprised of birds whose main feeding resource is invertebrates (also known as insectivores in the literature; ~67%), followed by granivores, frugivores and nectarivores, and omnivores representing a negligible percentage of the community (~3%). Remarkably, despite the fact that insectivore species richness was higher than that of omnivorous species, the latter were more abundant throughout the studied gradient of urbanization density. The pattern of insectivores representing important proportions of urban bird communities in Latin America has long been reported (see Ortega-Álvarez and MacGregor-Fors, 2011a,b and references therein). The latter seems to be related with the fact that some of the best represented families in urban areas in the region are mainly insectivores, many of which are related with open...
Insectivores were the dominating group in all studied built cover classes (58–65%), frugivores declined with urbanization (12, 5, 4, 6%, respectively), and granivores increased (6, 21, 20, 18%, respectively), with other groups remaining similar along the gradient. The omnivore guild has been widely reported as closely related to urbanization, and while some studies have not found differences in representation by guilds in urbanization gradients (e.g., Clergeau et al., 2001), others have found frugivores (Lim and Sodhi, 2004) and granivores to thrive (Gonzalez-Oreja et al., 2007). This suggests that the composition of urban avifaunas does not only vary depending on the study region, but can also be attributed to the temporal availability of resources (Murthy et al., 2016).

The recorded avian species richness showed a decrease with urbanization, regardless of the temporal levels of analysis. However, our findings show an important difference when contrasting both seasons of both surveyed years: species richness was significantly higher in Class I, with 0–25% built cover, when contrasted with the rest of classes. This shows that the pattern found at this temporal level is punctuated (i.e., an abrupt change in diversity at some point of the gradient of urbanization density, sensu McDonnell and Hahs, 2008). Thus, our results are in agreement with the vast majority of studies that have documented elevated avian diversity in lowly-urbanized conditions, typically represented by greenspaces or disturbed habitats (e.g., Parulidae, Tyrannidae; Escobar-Ibáñez and MacGregor-Fors, 2016).

**FIGURE 3** Species richness contrasts among four built cover classes of the city of Xalapa. Class I = 0–25% built cover, Class II = 26–50% built cover, Class III = 51–75% built cover, Class IV = 76–100% built cover. Letters above CI whiskers represent statistical differences based on overlapping 84% CIs.
highly vegetated residential areas, usually associated with higher income housing (Fernández-Juricic, 2000; Crooks et al., 2004; Chace and Walsh, 2006; Murgui, 2007; Marzluff, 2016). Our results also show that many of the recorded migratory species concentrate in well-vegetated urban sites of Xalapa, which also agrees with previous studies from the region (Ruelas-Inzunza and Aguilar-Rodríguez, 2010; González-García et al., 2014). Yet, of the 67 recorded species, only 28% were Neotropical–Nearctic wintering birds, suggesting that the vast majority of the migrant birds that winter in Xalapa (i.e., over 100 species sensu Ruelas-Inzunza and Aguilar-Rodríguez, 2010) are mainly using large greenspaces that are not well represented in our citywide survey (pers. obs.). Actually, this agrees with Chace and Walsh’s (2006) review, where the authors state that urbanization tends to favor resident over migratory species. When we assessed species richness by season (considering both years), species richness decreased with urbanization density gradually, which is similar to the general findings in most studies that are conducted over a short term (e.g., one season, one year; Marzluff et al., 2001).

Regarding the composition of the recorded bird communities across Xalapa’s gradient of urbanization density, our results show important differences between Classes I and IV, with Classes II and III showing certain similarity with Classes I and IV. Remarkably, Class IV, represented by heavily built environments (>76% built cover), was the most different to the rest of the studied urbanization gradient. Thus, our composition results show a gradual pattern of taxonomic similarity shift along the gradient of urbanization density, with a marked difference in relation with Class IV. This result was given by the depauperization of its bird community. Notably, three species (i.e., House Sparrow, Rock Pigeon, Great-tailed Grackle) added 75% of the total recorded individuals in Class IV. A recent global study indicates that the sparrow and pigeon are among the most common species of cities around the world (Aronson et al., 2014), being majorly generalist (Emlen, 1974; Evans et al., 2009). Thus, our results reinforce the idea that urbanization is related to changes in bird communities, making them less diverse as urbanization density increases and more different in relation to the avifaunas of surrounding ecosystems (Clergeau et al., 2006; Sorace and Gustin, 2008; Guetté et al., 2017).

Our study presents findings on one of the first citywide urbanization density gradients from the urban tropics. Although robust comparisons with previous studies can be tricky and need to be taken cautiously given the variety of gradient types and concepts (MacGregor-Fors, 2011; Batáry et al., 2018; Moll et al., 2019; MacGregor-Fors and Vázquez, in press), we show here both differences and similarities in relation to previous studies from outside the tropics. In a nutshell, our species richness results show a punctuated decrease when considering both seasons and years, rather than a gradual decrease or a humped-shaped distribution of higher richness at intermediately urbanized sites (Marzluff, 2001, 2016; Evans et al., 2009), while our composition findings stress the high representation of insectivore birds as part of avian communities across a citywide gradient of urbanization density. If we aim to understand urban ecosystems globally in order to manage them toward having more livable, resilient, biodiverse cities (McDonnell and MacGregor-Fors, 2016), we need to understand their generalities together with their temporal and spatial particularities, as management and planning actions may derive negative results when generalizing knowledge from well-studied regions.

### DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.
ETHICS STATEMENT

Ethical review and approval was not required because the study was observational.

AUTHOR CONTRIBUTIONS

All authors conceived the study and wrote the manuscript. IM-F developed the study design and acquired funding. JFE-I collected all field data. RR-H and IM-F analyzed the data.

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