frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 11 September 2020
doi: 10.3389/fevo.2020.500791

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

*Juan F. Escobar-Ibáñez[1,2,3], Rafael Rueda-Hernández[1,4] and Ian MacGregor-Fors[1]**

[1] Red de Ambiente y Sustentabilidad, Instituto de Ecología, A.C. (INECOL), Xalapa, Mexico, [2] Gnósis – Naturaleza con Ciencia A.C., Guadalajara, Mexico, [3] Maestría en Biosistemática y Manejo de Recursos Naturales y Agrícolas, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, Mexico, [4] Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

OPEN ACCESS

Edited by:
Christopher Swan, University of Maryland, Baltimore County, United States

Reviewed by:
Marco Moretti, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Switzerland
Paige Warren, University of Massachusetts Amherst, United States

***Correspondence:**
Ian MacGregor-Fors
ian.macgregor@inecol.mx; macgregor.ian@gmail.com

Specialty section:
This article was submitted to Urban Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: *26 September 2019*
Accepted: *13 August 2020*
Published: *11 September 2020*

Citation:
Escobar-Ibáñez JF, Rueda-Hernández R and MacGregor-Fors I (2020) The Greener the Better! Avian Communities Across a Neotropical Gradient of Urbanization Density. Front. Ecol. Evol. 8:500791. doi: 10.3389/fevo.2020.500791

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; Fraterrigo 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).

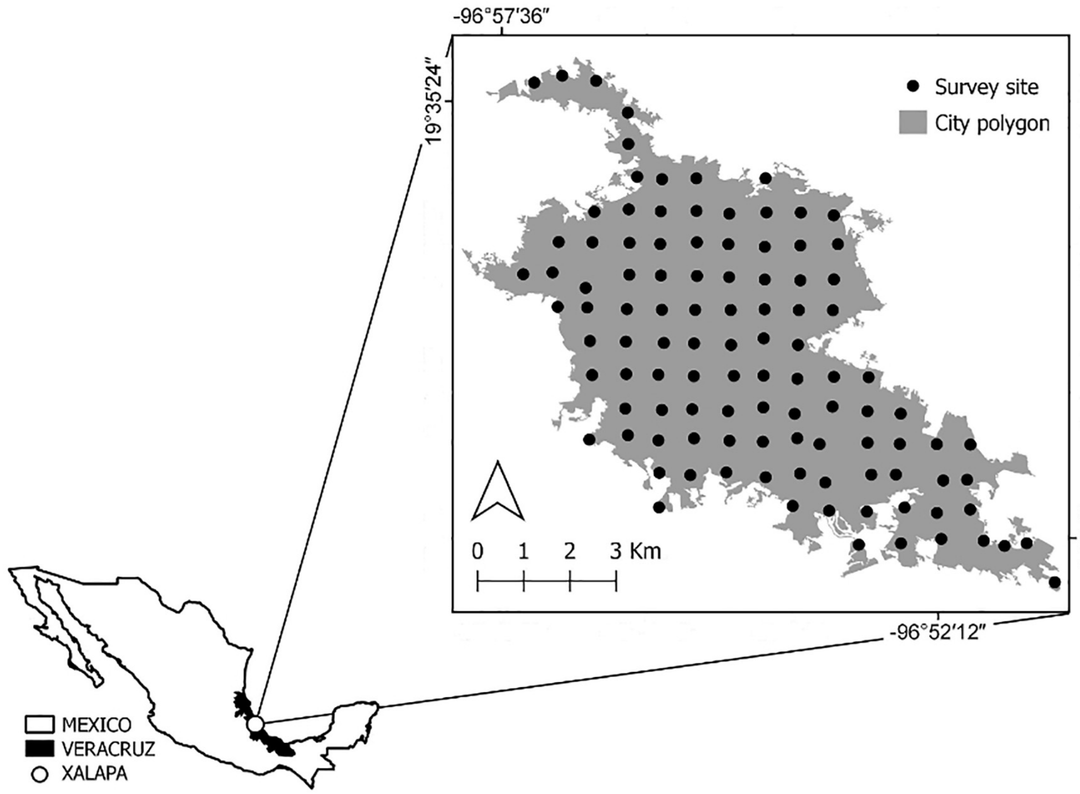

FIGURE 1 | Location of sampling sites within the urban continuum of the city of Xalapa using a citywide grid of 750 m × 750 m. Dots represent survey sites.

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 km^2 (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).

FIGURE 2 | Depiction of the surveyed urbanization density classes. Class I = 0–25% built cover, Class II = 26–50% built cover, Class III = 51–75% built cover, Class IV = 76–100% built cover. Photo credit: Ina Falfán.

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_{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*).

TABLE 1 | List of birds recorded across the city of Xalapa.

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*		•		
	Piaya cayana			•	
Apodidae	*Streptoprocne zonaris*		•	•	
Trochilidae	*Anthracothorax prevostii*				•
	Campylopterus curvipennis	•	•		
	Amazilia cyanocephala	•	•	•	•
	Amazilia beryllina	•	•	•	
Strigidae	*Glaucidium brasilianum*			•	
Picidae	*Melanerpes formicivorus*	•	•		
	Melanerpes aurifrons	•	•	•	•
	Dryobates scalaris		•		
Psittacidae	*Amazona autumnalis*		•		
Furnaridae	*Lepidocolaptes affinis*	•			
Tityridae	*Tityra semifasciata*	•			
Tyrannidae	*Pitangus sulphuratus*			•	
	Megarynchus pitangua			•	
	Myiozetetes similis	•	•	•	•
	Myiodynastes maculatus				•
	Empidonax occidentalis		•		
	Tyrannus melancholicus	•	•	•	•
Vireonidae	*Vireo griseus*				•
	Vireo cassini		•		
	Vireo solitarius	•	•		•
	Vireo gilvus				•
	Vireo leucophrys			•	
Corvidae	*Psilorhinus morio*	•			
Hirundinidae	*Hirundo rustica*	•	•	•	•
	Stelgidopteryx serripennis	•	•	•	•
Troglodytidae	*Troglodytes aedon*			•	•
	Campylorhynchus zonatus	•	•	•	•
Polioptilidae	*Polioptila caerulea*	•	•		•
Regulidae	*Regulus calendula*	•			
Turdidae	*Catharus aurantiirostris*	•			
	Turdus grayi	•	•	•	•
Mimidae	*Melanotis caerulescens*	•			
	Dumetella carolinensis	•	•	•	
Passeridae	*Passer domesticus*	•	•	•	•
Fringillidae	*Euphonia hirundinacea*	•	•	•	
	Euphonia elegantissima	•			
	Haemorhous mexicanus			•	
	Spinus psaltria		•	•	•
Passerellidae	*Melospiza lincolnii*		•		•
	Aimophila rufescens		•	•	
Icteridae	*Icterus graduacauda*			•	
	Icterus galbula				•
	Molothrus aeneus			•	
	Dives dives	•	•	•	•
	Quiscalus mexicanus	•	•	•	•

(Continued)

TABLE 1 | Continued

Family	Scientific name	Class I	Class II	Class III	Class IV
Parulidae	*Mniotilta varia*		•		•
	Leiothlypis celata		•		•
	Leiothlypis ruficapilla				•
	Geothlypis tolmiei		•		
	Setophaga citrina	•			
	Setophaga magnolia	•	•		•
	Setophaga petechia		•	•	
	Setophaga virens	•	•	•	•
	Basileuterus culicivorus	•	•		
	Cardellina pusilla	•	•	•	•
Cardinalidae	*Piranga flava*		•		
	Piranga ludoviciana				•
Thraupidae	*Thraupis abbas*	•	•	•	•
	Sporophila torqueola	•	•	•	

Classification and nomenclature follow the one suggested by the American Ornithologists' Union [AOU] (1998) up to its last supplement (Chesser et al., 2019). Class I = 0–25% built cover, Class II = 26–50% built cover, Class III = 51–75% built cover, Class IV = 76–100% built cover. Dots represent the recording of species in the different urbanization density classes.

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_{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_{est} = 19.0, 84% CIs: 14.2–23.8; Class III: S_{est} = 17.0, 84% CIs: 12.4–21.6; Class IV: S_{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

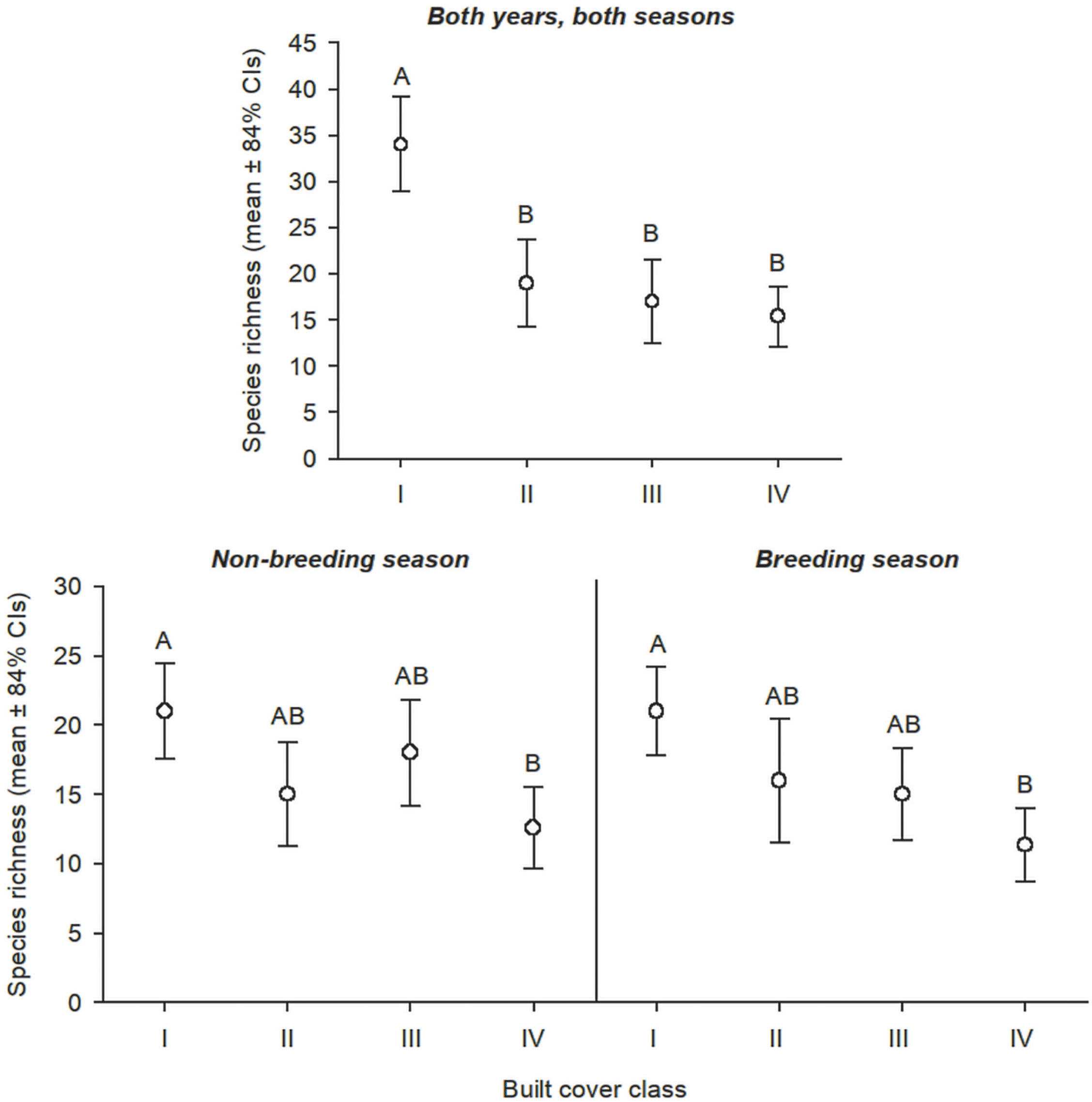

FIGURE 3 | Species richness contrasts among four built cover classes of the city of Xalapa. Class I = 0–25% built cover, Class II = 26–50% built cover, Class III = 51–75% built cover, Class IV = 76–100% built cover. Letters above CI whiskers represent statistical differences based on overlapping 84% CIs.

areas and/or disturbed habitats (e.g., Parulidae, Tyrannidae; Escobar-Ibáñez and MacGregor-Fors, 2016).

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 classess. 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

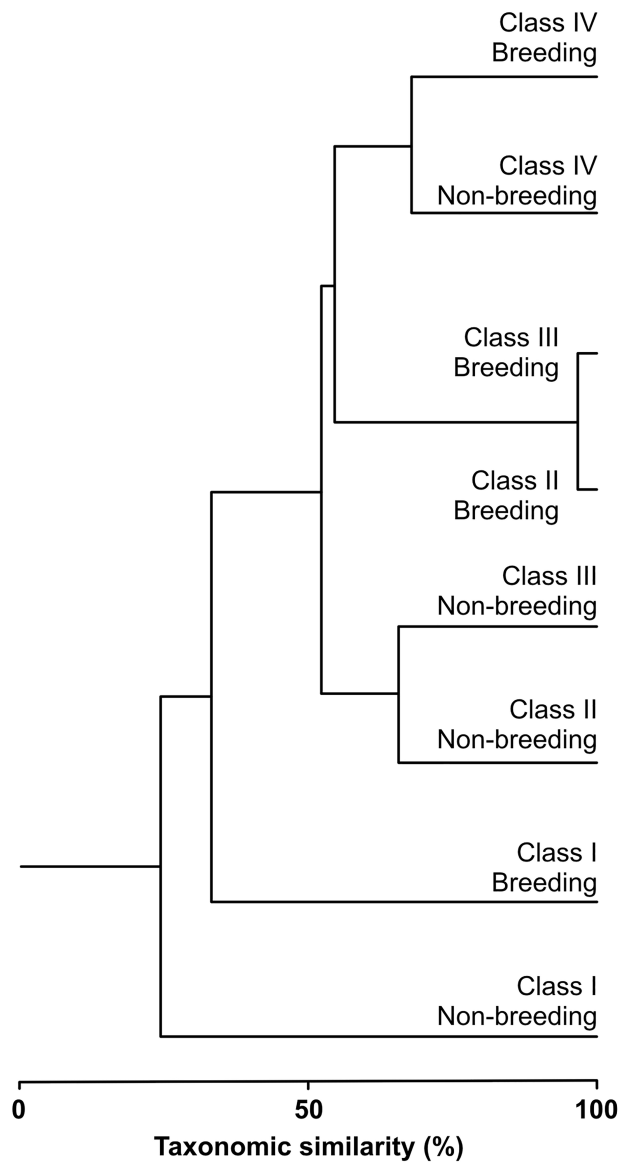

FIGURE 4 | Bray-Curtis abundance-based hierarchical cluster analysis including the four studied built cover classes of the city of Xalapa considering data for both years by season (breeding and non-breeding). Class I = 0–25% built cover, Class II = 26–50% built cover, Class III = 51–75% built cover, Class IV = 76–100% built cover.

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.

FUNDING

JFE-I acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACYT 366146 and 416899, respectively), and the Doctoral Program of the Instituto de Ecología, A.C. (INECOL). RR-H acknowledges the Postdoctoral scholarship provided by the National Council of Science and Technology (CONACYT 171086).

ACKNOWLEDGMENTS

We are most grateful to Eleanor Diamant for her comments and suggestions, which enhanced the clarity and quality of our work. We are also thankful to Ina Falfán, Oscar H. Marín-Gómez, Miguel Á. Gómez-Martínez, Michelle García-Arroyo, Carlos M. Trujillo-Torres, Julián Ávila, Arturo Zavaleta Aguilar, Bruno Florio Lessi, Víctor Piñeros, Salvador González de León, Sonia Morán Rodríguez, Víctor Castelazo Calva, and María Elisa Sandoval Seres for their help in the field.

REFERENCES

Alberti, M., Marzluff, J. M., Shulenberger, E., Bradley, G., Ryan, C., and Zumbrunnen, C. (2003). Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *BioScience* 53, 1169–1179. doi: 10.1641/0006-3568(2003)053[1169:ihieoa]2.0.co;2

American Ornithologists' Union [AOU], (1998). *Check-list of North American Birds*, 7th Edn. Washington, DC: American Ornithologists' Union.

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., et al. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc. R. Soc. B Biol. Sci.* 281:20133330. doi: 10.1098/rspb.2013.3330

Batáry, P., Kurucz, K., Suarez-Rubio, M., and Chamberlain, D. E. (2018). Non-linearities in bird responses across urbanization gradients: a meta-analysis. *Glob. Change Biol.* 24, 1046–1054. doi: 10.1111/gcb.13964

Battisti, C., and Fanelli, G. (2016). Applying indicators of disturbance from plant ecology to vertebrates: the hemeroby of bird species. *Ecol. Indic.* 61, 799–805. doi: 10.1016/j.ecolind.2015.10.032

Benítez, G., Pérez-Vázquez, A., Nava-Tablada, M., Equihua, M., and Álvarez-Palacios, J. L. (2012). Urban expansion and the environmental effects of informal settlements on the outskirts of Xalapa city, Veracruz, Mexico. *Environ. Urban.* 24, 149–166. doi: 10.1177/0956247812437520

Blair, R. (2004). The effects of urban sprawl on birds at multiple levels of biological organization. *Ecol. Soc.* 9:2.

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecol. Appl.* 6, 506–519. doi: 10.2307/2269387

Blair, R. B. (1999). Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecol. Appl.* 9, 164–170. doi: 10.1890/1051-0761(1999)009[0164:babaau]2.0.co;2

Bray, J. R., and Curtis, J. T. (1957). An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27, 325–349. doi: 10.2307/1942268

Chace, J. F., and Walsh, J. J. (2006). Urban effects on native avifauna: a review. *Landsc. Urban Plann.* 74, 46–69.

Chamberlain, D., Kibuule, M., Skeen, R., and Pomeroy, D. (2017). Trends in bird species richness, abundance and biomass along a tropical urbanization gradient. *Urban Ecosyst.* 20, 629–638. doi: 10.1007/s11252-016-0621-6

Chesser, R. T., Burns, K. J., Cicero, C., Dunn, J. L., Kratter, A. W., Lovette, I. J., et al. (2019). Sixtieth supplement to the american ornithological society's check-list of North American birds. *Auk* 136:ukz042.

Clergeau, P., Croci, S., Jokimaki, J., Kaisanlahti-Jokimaki, M. L., and Dinetti, M. (2006). Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biol. Conserv.* 127, 336–344.

Clergeau, P., Jokimaki, J., and Savard, J. P. L. (2001). Are urban bird communities influenced by the bird diversity of adjacent landscapes? *J. Appl. Ecol.* 38, 1122–1134.

Clergeau, P., Savard, J.-P. L., Mennechez, G., and Falardeau, G. (1998). Bird abundance and diversity along an urban-rural gradient: a comparative study between two cities on different continents. *Condor* 100, 413–425. doi: 10.2307/1369707

Clucas, B., and Marzluff, J. M. (2015). A cross-continental look at the patterns of avian species diversity and composition across an urbanisation gradient. *Wildlife Res.* 42:554. doi: 10.1071/wr15007

Coetzee, B. W. T., and Chown, S. L. (2016). Land-use change promotes avian diversity at the expense of species with unique traits. *Ecol. Evol.* 6, 7610–7622. doi: 10.1002/ece3.2389

Colwell, R. K. (2013). *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples Version 7.5*.

Crooks, K. R., Suarez, A. V., and Bolger, D. T. (2004). Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biol. Conserv.* 115, 451–462.

Czech, B., and Krausman, P. R. (1997). Distribution and causation of species endangerment in the United States. *Science* 277, 1116–1117. doi: 10.1126/science.277.5329.1116

Egerer, M. H., Arel, C., Otoshi, M. D., Quistberg, R. D., Bichier, P., and Philpott, S. M. (2017). Urban arthropods respond variably to changes in landscape context and spatial scale. *J. Urban Ecol.* 3, 1–10.

Eldredge, N., and Horenstein, N. (2014). *Concrete Jungle: New York City and Our Last BestHope for a Sustainable Future*. Oakland, CA: University of California Press.

Emlen, J. T. (1974). An urban bird community in Tucson, Arizona: derivation, structure, regulation. *Condor* 76, 184–197. doi: 10.2307/1366729

Escobar-Ibáñez, J. F., and MacGregor-Fors, I. (2016). Peeking into the past to plan the future: assessing bird species richness in a neotropical city. *Urban Ecosyst.* 19, 657–667. doi: 10.1007/s11252-015-0517-x

Escobar-Ibáñez, J. F., and MacGregor-Fors, I. (2017). "What's new? An updated review of avian ecology in Urban Latin America," in *Avian Ecology in Latin American Cityscapes*, eds I. MacGregor-Fors, and J. F. Escobar-Ibáñez, (Cham: Springer), 11–31. doi: 10.1007/978-3-319-63475-3_2

Evans, K. L., Newson, S. E., and Gaston, K. J. (2009). Habitat influences on urban avian assemblages. *Ibis* 151, 19–39. doi: 10.1111/j.1474-919x.2008.00898.x

Falfán, I., and MacGregor-Fors, I. (2016). Woody neotropical streetscapes: a case study of tree and shrub species richness and composition in Xalapa. *Madera Bosques* 22, 95–110.

Falfán, I., Muñoz-Robles, C. A., Bonilla-Moheno, M., and MacGregor-Fors, I. (2018). Can you really see 'green'? Assessing physical and self-reported measurements of urban greenery. *Urban Forest. Urban Green.* 36, 13–21. doi: 10.1016/j.ufug.2018.08.016

Fernández-Juricic, E. (2000). Bird community composition patterns in urban parks of Madrid: the role of age, size and isolation: bird species composition in urban parks. *Ecol. Res.* 15, 373–383. doi: 10.1046/j.1440-1703.2000.00358.x

Fischer, J. D., Schneider, S. C., Ahlers, A. A., and Miller, J. R. (2015). Categorizing wildlife responses to urbanization and conservation implications of terminology: terminology and urban conservation. *Conserv. Biol.* 29, 1246–1248. doi: 10.1111/cobi.12451

Fraterrigo, J. M., and Wiens, J. A. (2005). Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. *Landsc. Urban Plann.* 71, 263–275. doi: 10.1016/s0169-2046(04)00080-5

González-García, F., Straub, R., García, J. A. L., and MacGregor-Fors, I. (2014). Birds of a neotropical green city: an up-to-date review of the avifauna of the city of Xalapa with additional unpublished records. *Urban Ecosyst.* 17, 991–1012. doi: 10.1007/s11252-014-0370-3

González-García, F., Straub, R., Lobato García, J. A., and MacGregor-Fors, I. (2016). Nuevos registros y notas adicionales comentadas sobre la avifauna de la ciudad de Xalapa, Veracruz, México. *Acta Zool. Mexic.* 32, 253–269.

Gonzalez-Oreja, J. A., Bonache Regidor, C., Buzo Franco, D., Diaz Ordaz, A. A. D. L. F., and Hernandez Satin, L. (2007). Ecological characterization of the avifauna of the urban parks of the City of Puebla (Mexico). *Ardeola* 54, 53–67.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., et al. (2008). Global change and the ecology of cities. *Science* 319, 756–760.

Guetté, A., Gaüzère, P., Devictor, V., Jiguet, F., and Godet, L. (2017). Measuring the synanthropy of species and communities to monitor the effects of urbanization on biodiversity. *Ecol. Indic.* 79, 139–154. doi: 10.1016/j.ecolind.2017.04.018

Instituto Nacional de Estadística, Geografía e Informática [INEGI], (2009). *Prontuario de información geográfica municipal de los Estados Unidos Mexicanos-Xalapa, Veracruz de Ignacio de la Llave-Clave geoestadística 30087*. Aguascalientes: INEGI.

Jokimäki, J., and Suhonen, J. (1993). Effects of urbanization on the breeding bird species richness in Finland: a biogeographical comparison. *Ornis Fennica* 70, 71–77.

La Sorte, F. A., and McKinney, M. L. (2007). Compositional changes over space and time along an occurrence-abundance continuum: anthropogenic homogenization of the North American avifauna. *J. Biogeogr.* 34, 2159–2167. doi: 10.1111/j.1365-2699.2007.01761.x

Lepczyk, C. A., Flather, C. H., Radeloff, V. C., Pidgeon, A. M., Hammer, R. B., and Liu, J. (2008). Human impacts on regional avian diversity and abundance: human impacts on diversity. *Conserv. Biol.* 22, 405–416. doi: 10.1111/j.1523-1739.2008.00881.x

Leveau, C. M., and Leveau, L. M. (2005). Avian community response to urbanization in the pampean region, argentina. *Ornitol. Neotrop.* 16, 503–510.

Lim, H. C., and Sodhi, N. S. (2004). Responses of avian guilds to urbanisation in a tropical city. *Landsc. Urban Plann.* 66, 199–215. doi: 10.1016/s0169-2046(03)00111-7

MacGregor-Fors, I. (2011). Misconceptions or misunderstandings? On the standardization of basic terms and definitions in urban ecology. *Landsc. Urban Plann.* 100, 347–349. doi: 10.1016/j.landurbplan.2011.01.013

MacGregor-Fors, I., and Escobar-Ibáñez, J. F. (2017). "Birds fron Urban Latin America, where economic inequality and urbanization meet biodiversity," in *Avian Ecology in Latin American Cityscapes*, eds I. MacGregor-Fors, and J. F. Escobar-Ibáñez, (Cham: Springer International Publishing), 1–10. doi: 10.1007/978-3-319-63475-3_1

MacGregor-Fors, I., and García-Arroyo, M. (2017). "Who is who in the city? Bird species richness and composition in Urban Latin America," in *Avian Ecology in Latin American Cityscapes*, eds I. MacGregor-Fors, and J. F. Escobar-Ibáñez, (Cham: Springer International Publishing), 33–55. doi: 10.1007/978-3-319-63475-3_3

MacGregor-Fors, I., González-García, F., Hernández-Lara, C., and Santiago-Alarcon, D. (2018). Where are the birds in the matrix? Avian diversity in a Neotropical landscape mosaic. *Wilson J. Ornithol.* 130, 81–93. doi: 10.1676/16-087.1

MacGregor-Fors, I., Morales-Pérez, L., and Schondube, J. E. (2011). Does size really matter? Species-area relationships in human settlements: species-area relationships in human settlements. *Divers. Distrib.* 17, 112–121. doi: 10.1111/j.1472-4642.2010.00714.x

MacGregor-Fors, I., and Payton, M. E. (2013). Contrasting diversity values: statistical inferences based on overlapping confidence intervals. *PLoS One* 8:e56794. doi: 10.1371/journal.pone.0056794

MacGregor-Fors, I., and Schondube, J. E. (2012). Urbanizing the wild: shifts in bird communities associated to small human settlements. *Rev. Mexic. Biodivers.* 83, 477–486.

MacGregor-Fors, I., and Vázquez, L.-B. (in press). *Revisiting 'Rural.' Science of the Total Environment*. Available online at: https://linkinghub.elsevier.com/retrieve/pii/S0048969719327068

Machlis, G. E., Force, J. E., and Burch, W. R. (1997). The human ecosystem Part I: the human ecosystem as an organizing concept in ecosystem management. *Soc. Nat. Resour.* 10, 347–367. doi: 10.1080/08941929709381034

Martinson, H. M., and Raupp, M. J. (2013). A meta-analysis of the effects of urbanization on ground beetle communities. *Ecosphere* 4:art60. doi: 10.1890/es12-00262.1

Marzluff, J. M. (2001). "Worldwide urbanization and its effects on birds," in *Avian Ecology and Conservation in an Urbanizing World*, eds J. M. Marzluff, R. Bowman, and R. Donnelly, (New York: Springer), 19–47. doi: 10.1007/978-1-4615-1531-9_2

Marzluff, J. M., Bowman, R., and Donnelly, R. (2001). "A historical perspective on urban bird research: trends, terms, and approaches," in *Avian Ecology and Conservation in an Urbanizing World*, eds J. M. Marzluff, R. Bowman, and R. Donnelly, (New York: Springer), 1–17. doi: 10.1007/978-1-4615-1531-9_1

Marzluff, J. M. (2016). A decadal review of urban ornithology and a prospectus for the future. *Ibis* 159, 1–13. doi: 10.1111/ibi.12430

Maxwell, S. L., Fuller, R. A., Brooks, T. M., and Watson, J. E. M. (2016). The ravages of guns, nets and bulldozers. *Nature* 536, 143–145. doi: 10.1038/536143a

Mcdonald, R. I., Kareiva, P., and Forman, R. T. T. (2008). The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol. Conserv.* 141, 1695–1703. doi: 10.1016/j.biocon.2008.04.025

McDonnell, M. J., and Hahs, A. K. (2008). The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. *Landsc. Ecol.* 23, 1143–1155. doi: 10.1007/s10980-008-9253-4

McDonnell, M. J., and Hahs, A. K. (2015). Adaptation and adaptedness of organisms to urban environments. *Annu. Rev. Ecol. Evol. Syst.* 46, 261–280. doi: 10.1146/annurev-ecolsys-112414-054258

McDonnell, M. J., and MacGregor-Fors, I. (2016). The ecological future of cities. *Science* 352, 936–938. doi: 10.1126/science.aaf3630

McDonnell, M. J., and Pickett, S. T. A. (1990). Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* 71, 1232–1237. doi: 10.2307/1938259

McKinney, M. L. (2008). Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst.* 11, 161–176. doi: 10.1007/s11252-007-0045-4

Meffert, P. J., and Dziock, F. (2013). The influence of urbanisation on diversity and trait composition of birds. *Landsc. Ecol.* 28, 943–957. doi: 10.1007/s10980-013-9867-z

Merenlender, A. M., Heise, K. L., and Research, H. (1998). Effects of subdividing private property on biodiversity in california's north coast oak woodlands. *Trans. West. Sect. Wildlife Soc.* 34, 9–20.

Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Tans, E., Robison, T., et al. (2019). What does urbanization actually mean? A framework for urban metrics in wildlife research. *J. Appl. Ecol.* 56, 1289–1300. doi: 10.1111/1365-2664.13358

Moreno, C. E., Sánchez-Rojas, G., Pineda, E., and Escobar, F. (2007). Shortcuts for biodiversity evaluation: a review of terminology and recommendations for the use of target groups, bioindicators and surrogates. *Int. J. Environ. Health* 1, 71–86. doi: 10.1504/ijenvh.2007.012225

Murgui, E. (2007). Effects of seasonality on the species-area relationship: a case study with birds in urban parks. *Glob. Ecol. Biogeogr.* 16, 319–329. doi: 10.1111/j.1466-8238.2006.00304.x

Murthy, A. C., Fristoe, T. S., and Burger, J. R. (2016). Homogenizing effects of cities on North American winter bird diversity. *Ecosphere* 7:e01216.

Ortega-Álvarez, R., and MacGregor-Fors, I. (2011a). Dusting-off the file: a review of knowledge on urban ornithology in Latin America. *Landsc. Urban Plann.* 101, 1–10. doi: 10.1016/j.landurbplan.2010.12.020

Ortega-Álvarez, R., and MacGregor-Fors, I. (2011b). Spreading the word: the ecology of urban birds outside the United States, Canada, and Western Europe. *Auk* 128, 415–418. doi: 10.1525/auk.2011.10082

Palomino, D., and Carrascal, L. M. (2005). Birds on novel island environments. A case study with the urban avifauna of Tenerife (Canary Islands). *Ecol. Res.* 20, 611–617. doi: 10.1007/s11284-005-0083-4

Payton, M. E., Greenstone, M. H., and Schenker, N. (2003). Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? *J. Insect Sci.* 3, 1–6. doi: 10.1673/031.003.3401

Ralph, C. J., Droege, S., and Sauer, J. R. (1995). *Managing and Monitoring Birds Using Point Counts: Standards and Applications*. Gen. Tech. Rep. PSW-GTR-149. Albany, CA: U.S. Department of Agriculture.

Ruelas-Inzunza, E., and Aguilar-Rodríguez, S. H. (2010). La avifauna urbana del parque ecológico Macuiltépetl en Xalapa, Veracruz, México. *Ornitol. Neotrop.* 21, 87–103.

Seto, K. C., Guneralp, B., and Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. U.S.A.* 109, 16083–16088. doi: 10.1073/pnas.1211658109

Sol, D., Bartomeus, I., González-Lagos, C., and Pavoine, S. (2017). Urbanisation and the loss of phylogenetic diversity in birds. *Ecol. Lett.* 20, 721–729. doi: 10.1111/ele.12769

Sorace, A., and Gustin, M. (2008). Homogenisation processes and local effects on avifaunal composition in Italian towns. *Acta Oecol.* 33, 15–26. doi: 10.1016/j.actao.2007.07.003

Suhonen, J., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Hakkarainen, H., Huhta, E., Inki, K., et al. (2009). Urbanization and stability of a bird community in winter. *Écoscience* 16, 502–507. doi: 10.2980/16-4-3280

United Nations, (2018). *World Urbanization Prospects: The 2018 Revision [key facts]*. New York, NY: United Nations.

Williams Linera, G., Manson, R. H., and Isunza Vera, E. (2002). La fragmentación del bosque mesófilo de montaña y patrones de uso del suelo en la región oeste de Xalapa, Veracruz, México. *Madera y Bosques* 8, 73–89. doi: 10.21829/myb.2002.811307

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., and Jetz, W. (2014). EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals: ecological archives e095-178. *Ecology* 95, 2027–2027. doi: 10.1890/13-1917.1

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer PW declared a past supervisory role with one of the authors JFE-I to the handling editor.