

NEOTROPICAL PUZZLES: ASSESSING THE ROLE OF SPATIAL ARRANGEMENT AND HUMAN INDUCED DISTURBANCES ON THE AVIAN DIVERSITY OF LOCAL PATCHES

Melissa Ardila-Villamizar^{1*}, Daniel Sánchez², Laurence H. De Clippele¹, Davide M. Dominoni¹

¹School of Biodiversity, One Health & Veterinary Medicine, Graham Kerr Building, University of Glasgow, Glasgow, UK.

²Facultad de Ciencia y Tecnología, Universidad Pedagógica de Colombia, Bogotá, Colombia.

* **CORRESPONDENCE:** l.ardila-villamizar.1@research.gla.ac.uk

Abstract

Urbanization expansion poses significant challenges to biodiversity. Studies of urban ecology in the Global North abound, but there is an urgent need to understand the drivers of biodiversity decline in highly diverse, yet vulnerable and understudied ecosystems such as Neotropical cities. Specifically, while the influence of environmental, anthropogenic, and ecological factors on biodiversity is well documented, empirical evidence on how specific urban design features such as the spatial arrangement of patches and sources of anthropogenic disturbance contribute to these patterns remains limited. Here, we conducted visual surveys (i.e., point counts) across five cities in the Colombian Andes to assess how the spatial arrangement of urban features relative to vegetation, urban infrastructure and human disturbances such as pedestrian and pet density influenced avian diversity. Patches closer to vegetation, with lower pedestrian density and higher pet density, supported greater species richness and abundance. Interestingly, evolutionary distinctiveness was not affected by the ecological variables considered, whereas functional diversity was highest in patches near urban infrastructure with elevated pedestrian density. Overall, our findings highlight the importance of (1) preserving larger green areas with lower human disturbance to maintain biodiversity within urban ecosystems, (2) habitat edges to promote functional diversity in urban ecosystems and (3) incorporating taxonomic, phylogenetic, and functional dimensions when assessing ecological

dynamics. Thus, this study contributes to the understanding of urban biodiversity patterns in an understudied region by identifying key landscape features that support diverse avian communities, offering insights for biodiversity informed urban planning in rapidly expanding tropical cities.

Resumen

La expansión urbana impone desafíos significativos para la biodiversidad. Por lo tanto, es urgente comprender los factores que promueven su pérdida en ecosistemas altamente diversos como las ciudades neotropicales. Si bien los efectos de factores ambientales, antrópicos y ecológicos sobre la biodiversidad han sido ampliamente documentados, hay poca evidencia empírica sobre cómo la disposición espacial y fuentes de disturbios antropogénicos contribuyen a estos patrones. Realizamos censos visuales en cinco ciudades de los Andes colombianos para evaluar cómo la disposición espacial en relación con la vegetación y la infraestructura urbana y, perturbaciones humanas como la densidad de peatones y mascotas, influye en la diversidad de aves. Encontramos que parches con vegetación cercana, menor densidad peatonal y mayor densidad de mascotas, presentaron una mayor riqueza y abundancia de especies. Interesantemente, la distintividad evolutiva no se vio afectada por las variables ecológicas consideradas, mientras que la diversidad funcional fue mayor en parches cercanos a infraestructura urbana con alta densidad peatonal. En conjunto, nuestros hallazgos destacan la importancia de (1) conservar áreas verdes con menor perturbación humana para mantener la biodiversidad de los ecosistemas urbanos, (2) los bordes de hábitat para promover la diversidad funcional e (3) incorporar dimensiones taxonómicas, filogenéticas y funcionales al evaluar dinámicas ecológicas. Así, este estudio contribuye a la comprensión de los patrones de biodiversidad urbana en una región poco estudiada, al identificar características clave del paisaje que promueven comunidades de aves diversas, ofreciendo información valiosa para una planeación urbana sensible a la biodiversidad en ciudades tropicales en rápida expansión.

KEYWORDS: Biodiversity, Birds, Habitat fragmentation, Neotropics, Point counts, Urbanization

INTRODUCTION

Urbanization is considered one of the main threats for wildlife and its conservation as it introduces novel components such as chemical, visual and auditive pollution that create ecological pressures that only some species can overcome (Aronson et al. 2014). Broadly, urbanization tends to reduce, taxonomically homogenize, and reshape the composition of animal communities (McKinney 2008). However, the impact of urbanization on wildlife can vary regionally and affect species differently (Müller et al. 2013; Kondratyeva et al. 2020; Sun et al. 2025). Moreover, most of this research has focused on temperate ecosystems (but see Leveau and Leveau 2005; Leveau 2019 for studies conducted in the neotropics), limiting our understanding of how urbanization affects biodiverse but vulnerable areas, affected by rapid and often unregulated urban expansion, such as the neotropics (Smit 2021). Therefore, studies assessing the impact of urbanization on tropical ecosystems whilst considering the traits of involved species are needed to provide a comprehensive understanding of the response of biological communities to this process to then inform wildlife management plans aiming to protect diversity in urban ecosystems.

Species diversity can be influenced by an interplay between environmental factors such as primary productivity, vegetation diversity, presence of water bodies and anthropogenic factors such as noise, light and air pollution (review by Hughes et al. 2022). However, the diversity of certain vertebrate groups, such as birds, can be particularly susceptible to changes in these environmental and anthropogenic factors, due to their reliance on vegetation resources for nesting and foraging (Narango et al. 2017), and their high sensitivity to stressors such as light and noise pollution, which can induce behavioral and physiological responses (Dominoni et al. 2020). Indeed, previous studies have reported that factors associated with a higher habitat quality such as a greater primary productivity, vegetation diversity (Leveau 2019), presence of water bodies (Xie et al. 2022) and a reduction in light and noise pollution (Perillo et al. 2017; Morelli et al. 2023) promote avian diversity in urban ecosystems. However, this effect might vary according to the trophic guild of the birds (e.g., Morelli et al. 2023).

Other environmental factors such as domestic animal presence and pedestrian density can also affect the diversity of urban niches however, its study remains largely limited to rural and natural ecosystems (as noted by Forrest and St. Clair 2006). However, some studies showed avian diversity tending to decrease as human population density and dog presence increased (Banks and Bryant 2007; Fontana et al. 2011). Moreover, the impact of urbanization can vary among species as some life-history traits might facilitate the colonization of urban niches and thus, their diversity (McKinney 2008). For example, birds that are smaller, less territorial, generalist, long-lived, with high dispersal distance, that have larger clutches and occupy lower elevations, tend to be more successful under urban conditions when compared to those that do not exhibit these life-history traits (Neate-Clegg et al. 2023).

Although the interplay of environmental, anthropogenic, and ecological factors in shaping biodiversity is well documented, empirical evidence on how urban design features such as the spatial arrangement of local patches in relation to vegetation and urban infrastructure contributes to these patterns remains limited. The proximity of patches to vegetation and urban infrastructure can influence their capacity to support biodiversity, as these features are indicators of habitat connectivity and resource availability (as reported by Qi et al. 2021). Hence, well-connected patches that have proximate vegetation and further urban infrastructure, are expected to provide resources, shelter, and enhance animal movement, supporting greater diversity than fragmented patches with further vegetation and closer urban infrastructure (Qi et al. 2021). Indeed, some studies have shown that patches proximate to native vegetation (Muñoz-Pacheco and Villaseñor 2023) and high levels of woody cover (Muñoz-Pedreros et al. 2018) were associated with higher avian diversity. However, these studies mainly focused on patch distance to vegetation cover and have only focused on one city, overlooking the potential influence of proximity to urban infrastructure, a key indicator of habitat fragmentation, on biodiversity, as well as whether these patterns maintain across regional scales. Therefore, studies that simultaneously assess the effects of both distance to vegetation cover and urban infrastructure on a regional scale are needed to provide a more comprehensive understanding of how spatial

arrangement influences the diversity of patches and to inform the development of biodiversity-friendly urban landscapes.

Here, we conducted visual surveys (i.e., point counts) in five cities in the Colombian Andes to assess how the spatial arrangement of urban features and levels of human disturbance influenced avian diversity on a regional scale. We choose birds as our study model as they offer an interesting opportunity to study this due to their conspicuousness, ease to survey, presence in areas with different human-intervention levels and being ecological indicators of the presence of other taxa such as invertebrates (Fraixedas et al. 2020). We specifically aimed to understand how the distance of patches to urban infrastructure and vegetation cover, as well as pedestrian and domestic animal density, influenced the species richness, relative abundance, functional diversity, and evolutionary distinctiveness of avian communities. We expected species richness and relative abundance to decline and communities to homogenize as distance to vegetation, pedestrian density, domestic animal density increase and, distance to urban infrastructure decrease as less fragmented and disturbed areas tend to support greater biodiversity. Overall, this study aims to provide insights regarding how specific urban design and human-induced disturbances shape bird communities across tropical cities with the goal of informing more biodiversity-sensitive urban planning.

METHODS

Study area

This study was conducted in five cities located in the Colombian Andes (Figure 1). Cities were selected based on accessibility and aiming to ensure a broad representation of the Andean region, allowing us to evaluate whether the observed avian diversity patterns maintain across a regional gradient formed by cities with varying levels of impervious surface (Table 1). Impervious surfaces reflect the degree of human development of a given site, as they consist of built infrastructure such as roads, rooftops, and sidewalks that limit water infiltration. Therefore, we used the extent of impervious surface as a proxy

for urbanization level (as suggested by Hanh Nguyen et al. 2023). The impervious surface for each selected city and study site was calculated using the Zonal Statistics tool in QGIS (QGIS Development Team 2018) on the 2024 Global Artificial Impervious Area (GAIA) raster covering the study region (Gong et al. 2020).

Study sites within each city were selected to represent a local urbanization gradient ranging from natural sites, parks to residential areas (Figure 2) based on the extent of their impervious surface (IS) and patterns of human use (following Ardila-Villamizar et al. 2022). Natural sites consisted of areas with a low percentage of impervious surface where recreational activities are prohibited, resulting in a lower intensity of human-induced disturbances. Parks were sites with a medium percentage of impervious surface, higher than natural sites but lower than residential areas, that have infrastructure for recreational use, leading to a higher intensity of disturbances. Lastly, residential areas had a high percentage of impervious surface, with heavy vehicular traffic and pedestrian density, and consequently, experienced the highest level of human-induced disturbances within categories. We selected two sites per category in each city, thus, there were six study sites per city and 30 in total (Figure 2).

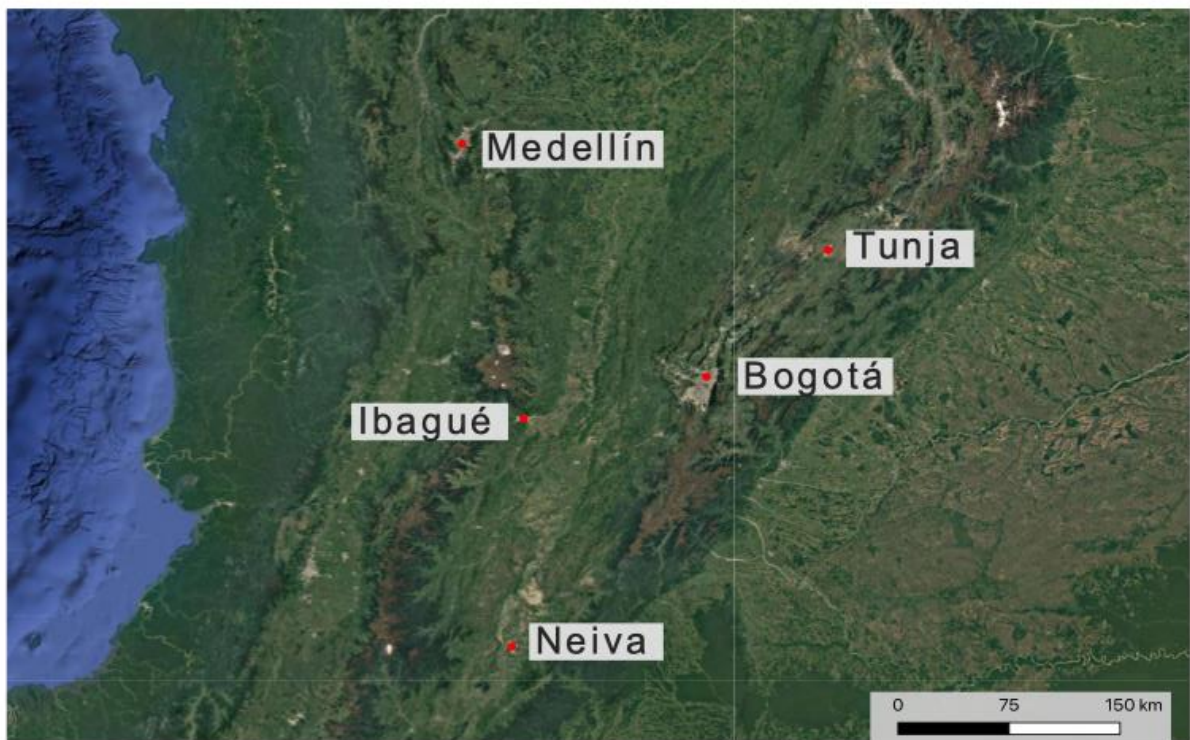


Figure 1. Map highlighting the five Colombian Andes cities selected for this study. Cities (Bogotá, Medellín, Ibagué, Neiva and Tunja) are represented by a yellow bubble. This image was recovered from Google Earth.

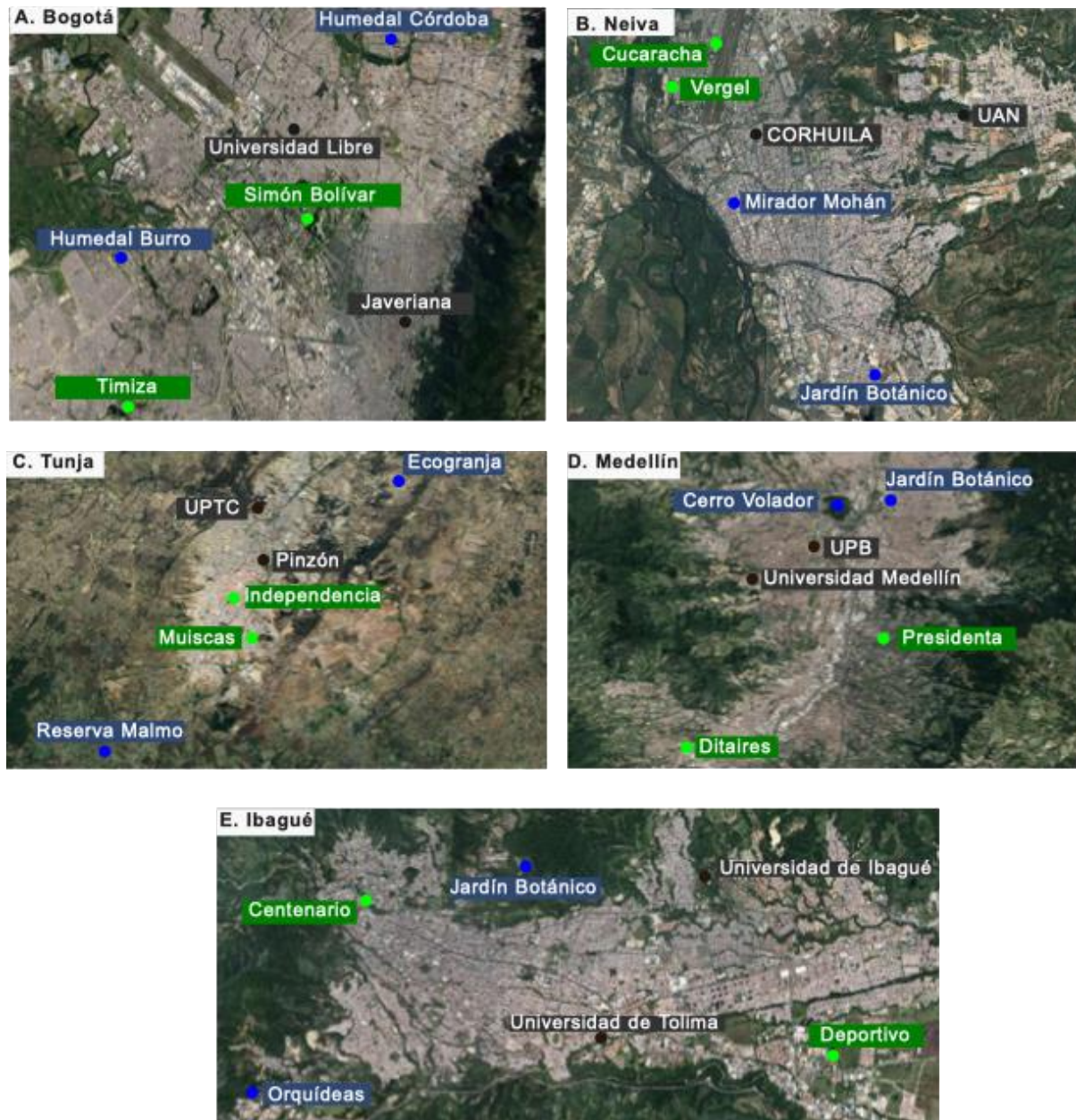


Figure 2. Map highlighting the selected study sites in Bogotá, Medellín, Ibagué, Tunja and Neiva. Sites represented an urbanization gradient ranging from natural sites highlighted by blue bubbles, parks highlighted by green bubbles and residential areas highlighted by gray bubbles. This image was recovered from Google Earth.

Table 1. Percentage of impervious surface of each of the selected cities and study sites. Impervious surface for each selected city and study site was calculated using the Zonal Statistics tool in QGIS (QGIS Development Team 2018) on the 2024 Global Artificial Impervious Area (GAIA) raster covering the study region (Gong et al. 2020).

City (Impervious surface %)	Site	Site category	Impervious surface %
Bogotá (67.5)	Humedal Burro	Natural site	9.49
	Humedal Córdoba		1.86
	Simon Bolívar	Park	26.94
	Timiza		25.79
	Javeriana	Residential area	60.54
	Libre		32.6
Medellín (65.55)	Cerro Volador	Natural Site	1.88
	Jardín Botánico		12.5
	Humedal Ditaires	Park	43.75
	Presidenta		34.61
	Universidad de Medellín	Residential area	75
	UPB		68.44
Tunja (61.79)	Ecogranja	Natural site	1.82
	Reserva Malmo		0.81
	Independencia	Park	42.8
	Muisacas		47.23
	Pinzon	Residential area	57.89
	UPTC		95.55
Neiva (57.81)	Jardín Botánico	Natural site	0.25
	Mirador Mohan		0.57
	Vergel	Park	25.56
	Cucaracha		42.5
	UAN	Residential	73.4
	Corhuila		68.98

Data collection

First, we selected three locations within each study site varying in their proximity to urban infrastructure and vegetation (Figure 2). The first patch (Grey Edge) was located within five meters of urban infrastructure (i.e., near) but more than five meters from vegetation (i.e., far). The second patch (Core) was near vegetation but far from urban infrastructure. The third patch (Green Edge) was situated near both vegetation and urban infrastructure. We considered urban infrastructure elements from the ecosystem that were part of its streetscape and would lead to landscape fragmentation such as concrete sidewalks, streets, recreational and residential areas and buildings (following Ehrenfeucht and Loukaitou-Sideris 2010). Locations were at least 100 meters apart from each other to avoid pseudo-replication. We recorded the distance of each location to its closest vegetation cover and urban infrastructure using a laser rangefinder (BOSCH GLM 20).

Once locations were selected, an observer (Melissa Ardila-Villamizar) conducted the visual surveys (i.e., point counts) along a 20x50 meter transect from them (i.e., local patches illustrated in Figure 3). Point counts were conducted by recording all the species seen or heard in the local patches during a 10-minute period within birds' peak activity hours (07:00–10:00 AM) (following Mitchell et al., 2020). Each local patch was surveyed twice on different days. Lastly, the observer also recorded the number of pedestrians and domestic animals (e.g., cats and dogs) passing through the patches during each point count (hereby, pedestrian density and pet density) to assess the disturbance level of each patch.

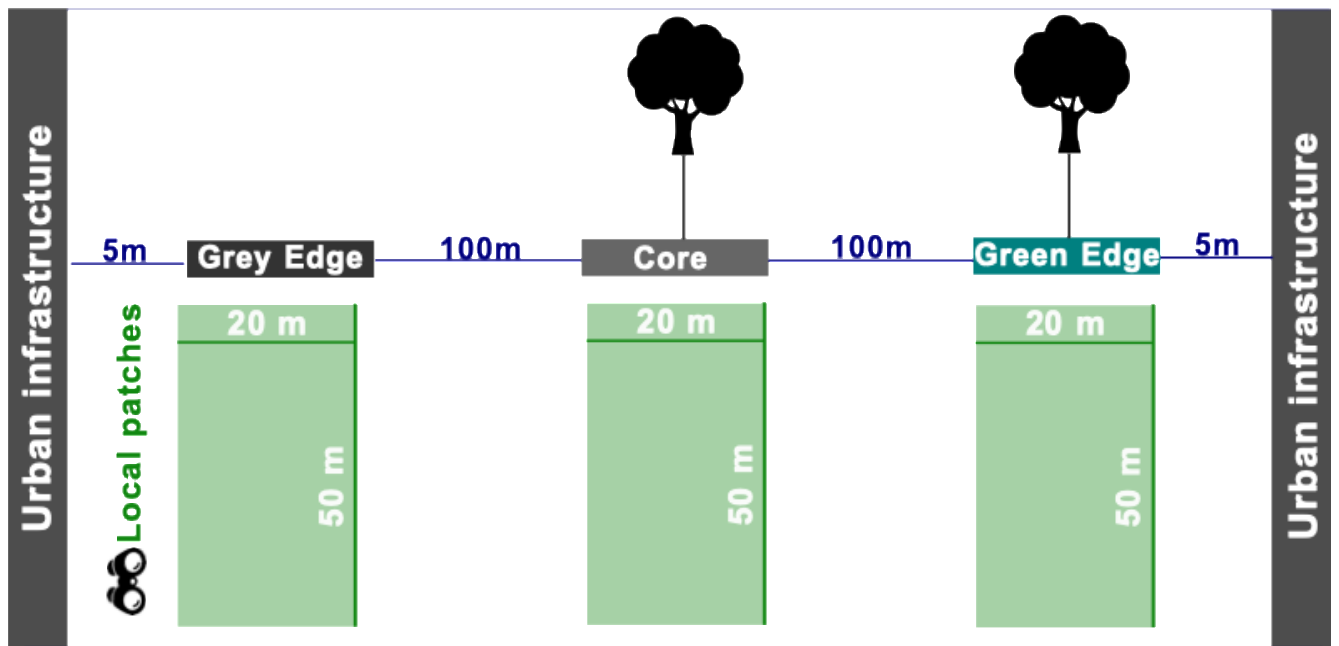


Figure 3. Schematic representation of local patches within each study site. Each site contained three patches labelled as Edge A, Core, and Edge B varying in their proximity to vegetation cover and urban infrastructure.

Data analysis

Quantification of the diversity metrics of the local patches

We calculated the species richness, relative abundance, evolutionary distinctiveness, and functional diversity of each local patch. Species richness was calculated as a sum of the unique species observed at each patch (following Tucker et al. 2017). Relative abundance was assessed as the proportion of individuals observed at each patch relative to the total number recorded across its study site (following Tucker et al. 2017).

Relative evolutionary distinctiveness (ED) quantified how phylogenetically unique the species within each patch were compared to the overall assemblage at their study site. It was estimated using the sum of phylogenetic branch lengths from a tree (Tucker et al. 2017) including all recorded species, generated with the Ericson backbone via birdtree.org. Each branch was assigned a value equal to its

length divided by the number of species subtending it using the `evol.distinct` function from the “picante” package v1.8.2 (Kembel et al. 2010). First, we calculated the community-level ED of each patch by summing the ED scores of its species and then calculated each patch’s relative contribution to the total ED of the site community (following Ibáñez-Álamo et al. 2017). Lastly, functional diversity measured how diverse assemblages were in terms of two traits: primary lifestyle (generalist or specialist) and trophic guild (insectivore, scavenger, carnivore, nectivore, or omnivore). We assessed functional diversity using Rao’s Q entropy index, a mathematically measure of the functional diversity in a community based on multiple traits (Tucker et al. 2017). Rao’s Q was calculated using the avian niche traits provided by the AVONET dataset (Tobias et al. 2022), and using the `rao.diversity` function from the “SYNCSA” package (Debastiani and Pillar 2012). Diversity measures were calculate using R v 4.4.3 (R Core Team 2021).

Assessing the effect of spatial arrangement of urban features in the diversity of local patches

We performed four Generalized Linear Mixed Models (GLMM) using Template Model Builder (TMB) each fitting the diversity metric (species richness, relative abundance, relative evolutionary distinctiveness and functional diversity) as a response variable and distance to closest vegetation, distance to closest urban infrastructure, pedestrian density and pet density as scaled predictors using the `glmmTMB` function of the “glmmTMB” package v 1.1.11 (Bolker 2019). Additionally, we included a nested random effect with location nested within site, and site nested within city in each model. The models fitting relative abundance, relative evolutionary distinctiveness and functional diversity were performed under a beta distribution and the model fitting species richness under a Poisson distribution given the nature of their variables (proportions and count data, respectively). Moreover, the general performance of the models specifically the multicollinearity of their predictors, outliers, heteroscedasticity and convergence was checked using the `check_collinearity`, `check_outliers`, `check_heteroscedasticity` and `check_convergence` function of the package “performance” v 0.13.0 (Lüdtke et al. 2021). Lastly, statistical significance was assessed at the $\alpha = 0.05$ level.

RESULTS

We conducted 180-point count surveys in which we identified 1,459 individuals from 84 species from 15 orders and 30 families. In average, local patches were (mean \pm SD) 12.11 ± 5.68 meters from urban infrastructure, 3.35 ± 2.21 meters from vegetation and had 1.48 ± 2.95 walkers per minute and 0.24 ± 2.05 dogs per minute. As a general trend, 8.58 ± 3.78 species were recorded at each patch that exhibited a relative abundance of 0.33 ± 0.11 , relative evolutionary distinctiveness of 0.4 ± 0.11 and functional diversity of 0.67 ± 0.08 .

Local patches with closer vegetation, lower pedestrian density and higher pet density had a higher species richness.

The GLMM models indicated that there was a significant negative relationship between distance to vegetation cover, pedestrian density and species richness and a significant positive relationship between pet density and species richness (Table 2). Local patches that had closer vegetation, lower pedestrian density and higher pet density exhibited greater species richness (Figure 4). Lastly, although there was a positive relationship between distance to urban cover and species richness, it was not statistically significant (Table 2).

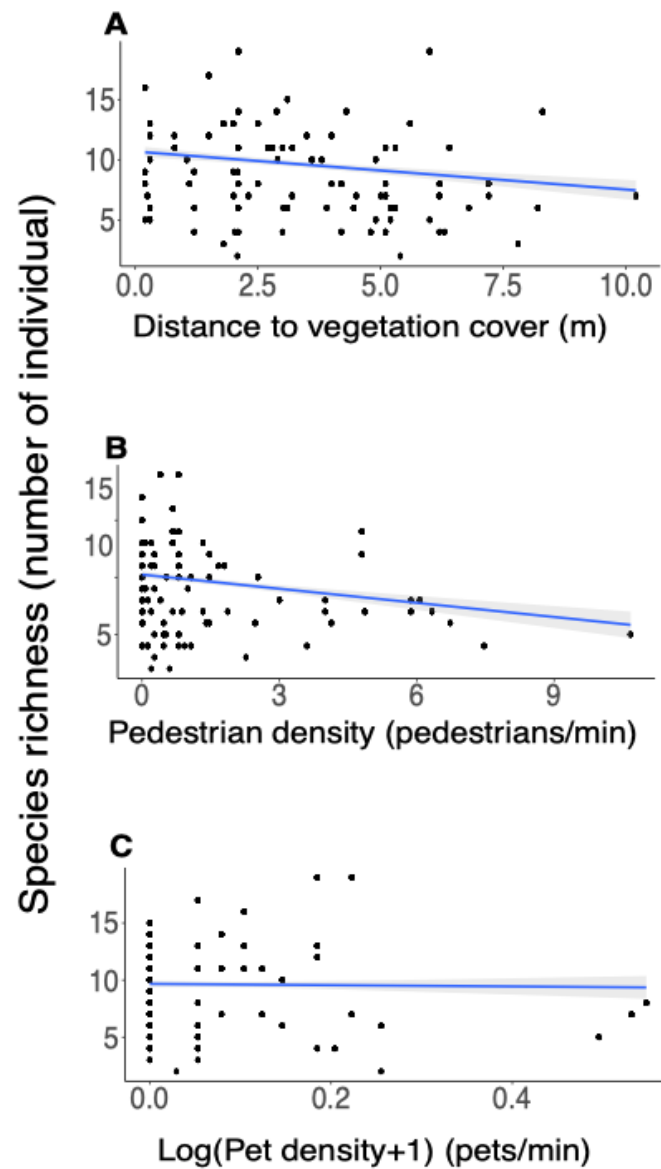


Figure 4. Relationship between distance to vegetation cover (A), pedestrian density (B) and pet density (C) and species richness (N=1459). The plot shows the regression line for the main effect fitted using the GLMM results included in Table 2 (blue line) and its corresponding 95% confidence interval (shaded zone). Dots represent the raw data. Data of Figure 3C was log-transformed for visualization purposes.

Table 2. Coefficients, standard errors and p-values from four generalized mixed models built using Template Model Builder (glmmTMB) evaluating the influence of distance to urban infrastructure, distance to vegetation, pedestrian density and pet density (fixed terms) on diversity metrics. Each diversity metric: species richness, abundance, evolutionary distinctiveness (ED) and functional diversity (FD) was fitted as a response variable of the fixed terms. Bold values indicate statistical significance at $\alpha = 0.05$. N = 1459 corresponds to the total number of individuals included in the regression models. The AIC fitting species richness as a response variable was 6496.9, the model fitting relative abundance -2554.9, the model fitting evolutionary distinctiveness -2316.7 and the model fitting functional diversity -5019.3.

Fixed terms	Estimate				SE				P-value			
	Richness	Abundance	ED	FD	Richness	Abundance	ED	FD	Richness	Abundance	ED	FD
Intercept	2.13	-0.56	-0.70	0.71	0.08	0.06	0.02	0.06	<0.001	< 0.001	<0.01	<0.01
Distance to urban infrastructure	0.01	0.05	-0.002	-0.03	0.01	0.01	0.01	0.01	0.60	< 0.001	0.85	<0.01
Distance to vegetation	-0.06	-0.12	-0.005	0.0003	-0.06	0.01	0.01	0.01	<0.01	<0.01	0.74	0.962
Pedestrian density	-0.07	-0.07	0.06	-0.07	-0.07	0.03	0.03	0.01	0.01	0.01	0.06	<0.01
Pet density	0.23	0.45	-0.04	0.04	0.23	0.08	0.03	0.03	<0.01	<0.01	0.08	0.130
Random effects	Variance				SE							
	Richness	Abundance	ED	FD	Richness	Abundance	ED	FD				
city:site:site_category	0.19	0.12	0.01	0.1	0.43	0.35	0.08	0.32				

Patches with closer vegetation, lower pedestrian density, higher pet density and further urban infrastructure exhibited higher relative abundance.

There was a significant negative relationship between distance to vegetation cover, pedestrian density and relative abundance and a significant positive relationship between pet density and distance to urban infrastructure and relative abundance (Table 2). Local patches that had closer vegetation, lower pedestrian density, higher pet density and further urban infrastructure exhibited higher relative species abundance (Figure 5).

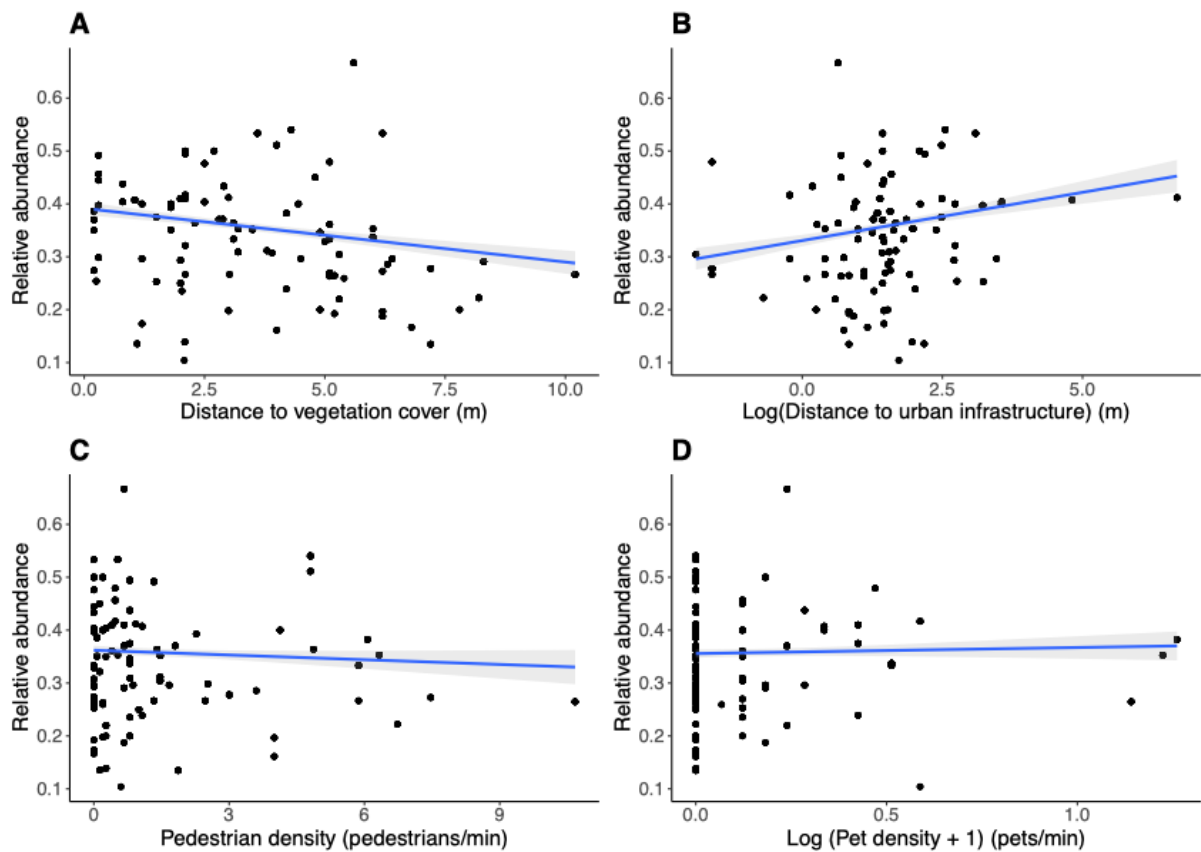


Figure 5. Relationship between distance to vegetation cover (A), distance to urban infrastructure (B) pedestrian density (C) and pet density (D) and relative abundance (N=1459). The plot shows the regression line for the main effect fitted using the GLMM results included in Table 2 (blue line) and its corresponding 95% confidence interval (shaded zone). Dots represent the raw data. The y axis of the distance to urban infrastructure and pet density graphs (C and D) were transformed for visualization purposes.

276 *Evolutionary distinctiveness was not influenced by any ecological factors.*

277 Although the evolutionary distinctiveness of local patches tended to increase with closer urban
278 infrastructure and vegetation, as well as higher pedestrian density, and lower pet density, these trends
279 were not statistically significant (Table 2). Thus, none of the evaluated ecological factors influenced
280 the evolutionary distinctiveness of local patches.

281

282 *Local patches with closer urban infrastructure and higher pedestrian density exhibited higher*
283 *functional diversity (FD).*

284 There was a significant negative relationship between distance to urban infrastructure and FD and a
285 positive relationship between pedestrian density and FD (Table 2). Local patches that had closer urban
286 infrastructure and higher pedestrian density had a higher functional diversity (reflected as a higher
287 Rao's Q entropy index) (Figure 6). Note that although the figure illustrating the relationship between
288 functional diversity and pedestrian density displays a negative relationship between the variables
289 (Figure 6B), possibly driven by outliers; their overall estimate remains positive.

290

291 Lastly, although there was a positive relationship between distance to vegetation and pet density and
292 functional diversity, it was not statistically significant (Table 2).

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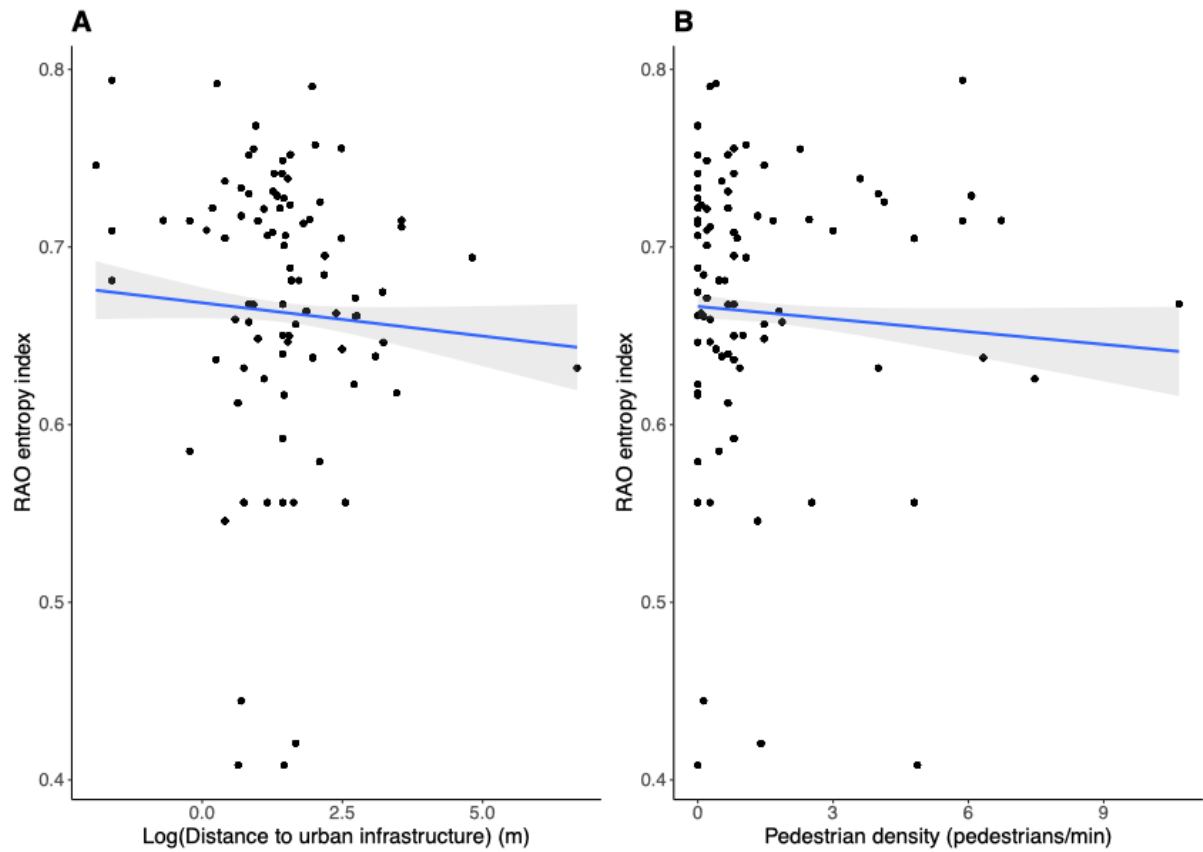


Figure 6. Relationship between distance to urban infrastructure (A) and pedestrian density (B) and functional diversity (assessed with Rao entropy index) (N=1459). The plot shows the regression line for the main effect fitted using the GLMM results included in Table 2 (blue line) and its corresponding 95% confidence interval (shaded zone). Dots represent the raw data. The y axis of the distance to urban infrastructure graphs (A) was log-transformed for visualization purposes. Note that Figure 5B displays a negative relationship between the variables, driven by outliers; however, the overall estimate remains positive.

DISCUSSION

As urbanization expansion exacerbates pressures on biodiversity, there is an urgent need to design urban landscapes responsive to the needs of animal communities and capable of supporting local biodiversity (McKinney 2002). Here, we found that local patches with closer vegetation, lower pedestrian density, and higher pet density supported greater species richness and abundance. Interestingly, evolutionary distinctiveness remained unaffected by the evaluated ecological variables whilst functional diversity was highest in patches near urban infrastructure with higher pedestrian density. Overall, these findings highlight the importance of (1) preserving larger green areas with lower human disturbance to maintain biodiversity within urban ecosystems, (2) habitat edges to promote functional diversity in urban ecosystems and (3) incorporating taxonomic, phylogenetic, and functional dimensions when assessing ecological dynamics. Thus, our study contributes to the understanding of the drivers of biodiversity loss in urban ecosystems in the Neotropics and highlights key urban design features that support diverse bird communities. These findings offer guidance for urban planning supportive of biodiversity in rapidly growing tropical cities.

Local patches with proximate vegetation and lower pedestrian density tending to support greater species richness and abundance supports the idea of continuous and less disturbed green areas offering better habitat quality for birds and consequently, hosting diverse bird communities (Callaghan et al. 2018). Human-induced disturbances, such as pedestrian activity, can disrupt bird foraging behaviour; hence, areas with lower disturbance intensity may allow individuals to forage for longer due to fewer environmental disruptions, contributing greater species richness and abundance (Ditchkoff et al. 2006; Bateman and Fleming 2014). Moreover, less fragmented green spaces can facilitate animal movement and offer a greater variety of foraging resources, promoting population connectivity and enhancing habitat quality and thus, supporting avian diversity (Cramer et al. 2023). The diversity of patches being enhanced by closer vegetation and less intensity of disturbances aligns with our initial hypothesis and previous studies in tropical ecosystems finding that patches proximate

to native vegetation (Muñoz-Pacheco and Villaseñor 2023), high levels of woody cover (Muñoz-Pedreros et al. 2018) and with a reduced pedestrian density (Oropeza-Sánchez et al. 2024) were associated with higher avian diversity. Similar patterns have also been observed in temperate ecosystems (Barbe et al. 2018). Overall, this finding suggests that vegetation availability within urban matrices and lower intensity of disturbance play a crucial role in maintaining local avian diversity and thus, should be a key factor to consider in urban planning and management aiming to support and conserve wildlife in the neotropics.

Two sources of human-induced disturbances were considered in this study, pedestrian and pet density. Only pedestrian density followed our initial hypothesis and was negatively related to bird diversity, while pet density was positively related to diversity. This contrasting finding suggests that not all sources of human-induced disturbance exert the same ecological pressure on local avian diversity (as seen in Fernández-Juricic 2002). This pattern could have been caused by pedestrian activity being unpredictable and generating frequent disruptions such as movement off paths, that birds might have perceived as high-risk, reducing habitat suitability (Miller et al. 2001). In contrast, pets in public spaces that are typically accompanied and often leashed, may represent a more predictable and less threatening form of disturbance (Miller et al. 2001). Moreover, the presence of domestic animals, especially dogs, tends to be higher in well-maintained and vegetated areas that offer higher habitat quality which are typically those with a higher diversity (Aronson et al. 2017). Furthermore, higher domestic animal density can be related to lower density of natural predators of birds such as raptors (Loss et al. 2013). Thus, the positive relationship between diversity and pet density might be a result of pets being more present in well-maintain areas that support more diversity due to their characteristics and dogs not representing a greater disturbance. However, note that most pets included in the pet density measure were leashed dogs, not free-ranging animals or cats. Therefore, the results could have differed if the metric was composed primarily by cats or unleashed free-ranging dogs (as seen in Banks and Bryant 2007; Sims et al. 2008). Further research is needed to

determine the specific influence of these different types of domestic animals on avian diversity. Overall, these findings highlight the need to distinguish between types of human presence when assessing the impact of urbanization on biodiversity. Future studies should determine whether these patterns reflect actual tolerance to pets or are linked to habitat conditions, and explore variation across urban contexts, disturbance types, and bird species responses to inform urban management.

The decline in species abundance but not richness as distance to urban infrastructure increases could be driven by edge effects limiting the population size but not the presence of species (Schneider et al. 2015). Edge zones tend to exhibit higher levels of disturbances and increase species exposure to predators and brood parasites, which can reduce the population size of species over time and explain the observed reduction in species abundance as distance to urban infrastructure increased (Chalfoun et al. 2002). This finding aligns with our initial hypothesis and other studies showing that bird abundance decreased as distance to urban edges increased, but richness seemed unaffected (Schneider et al. 2015) and songbird abundance decreased as housing density increased likely due to increases in brood parasitism (Burhans and Thompson III 2006). Nonetheless, further studies are needed to understand the underlying mechanism driving the decrease in abundance but no richness of urban dwellers by directly assessing the influence of distance to urban infrastructure on predation exposure, brood parasitism and disturbance.

Contrary to our hypothesis, evolutionary distinctiveness was not influenced by any of the ecological factors considered. The lack of phylogenetic variation among patches with differing urban features and disturbance levels suggests that variation in spatial arrangement alone may be insufficient to filter phylogenetic traits. However, this finding contrasts with previous studies reporting that sites with denser urban infrastructure supported less evolutionary unique communities (La Sorte et al. 2018; Morelli et al. 2024). Such discrepancies may be driven by differences in spatial scale, as this study focused on small urban patches, whereas previous studies have often examined broader urban

environments. Additionally, these studies were conducted in temperate ecosystems that might exhibit different patterns of urban filtering compared to tropical regions. Nonetheless, further studies are needed to assess if this effect persists in larger urban tropical ecosystems and to compare phylogenetic urbanization filtering processes among temperate and tropical ecosystems.

Although spatial arrangement regarding distance to urban infrastructure and disturbance levels such as pedestrian activity did not affect evolutionary distinctiveness, it did affect functional diversity. This suggests that filtering processes might be occurring on a trait and not phylogenetic level (Aronson et al. 2017). Functional homogenization as distance to urban infrastructure decreases might be due to urbanization favoring species with a broader range of functional traits (Evans et al. 2009), as species more tolerant to the high level of disturbances present around edge areas are expected to possess a variety of traits to exploit more heterogeneous ecosystems (Aronson et al. 2017). Moreover, edge areas are transition zones within the ecosystems and thus, might favor the diversity of functional traits in the community (Barbaro et al. 2014). Nonetheless, this finding is contrasting with previous studies reporting functional homogenization in edge areas and our initial hypothesis (Morelli et al. 2024). This difference between previous findings and our results might be related to variation in the size of the study areas and ecosystems, and in their relative difference in urbanization pressure. However, further studies are needed to establish this.

Overall, this study assessed the influence of the spatial arrangement of urban features and human disturbance on avian biodiversity in local patches in the neotropics. While species richness and abundance were higher in patches with proximate vegetation and lower pedestrian activity, functional diversity was higher in more disturbed patches closer to urban infrastructure, indicating that edge environments may favor a broader range of functional traits. Interestingly, pet density was positively associated with diversity, suggesting that not all forms of human presence may exert the same ecological pressure on avian diversity. Evolutionary distinctiveness was not influenced by any

ecological factors, indicating that ecological filtering might be occurring at functional and not phylogenetic scale. Thus, these findings highlight the importance of larger green areas with reduced human activity for maintaining biodiversity within urban ecosystems and the importance of considering both functional and evolutionary dimensions in biodiversity assessments. Further studies should assess if these patterns persist at different spatial scales and compare temperate and tropical contexts to better our understanding of the processes underlying ecological filtering in urban ecosystems.

ACKNOWLEDGEMENTS

We want to thank the universities, regional and local institutions, reserves, and communities that generously allowed us to conduct visual surveys on their territories. We also thank the editor and reviewers for their thoughtful feedback, which strengthened the quality of this work.

REFERENCES

- Ardila-Villamizar M, Alarcón-Nieto G, Maldonado-Chaparro AA (2022) Fear in urban landscapes: conspecific flock size drives escape decisions in tropical birds. *R Soc Open Sci* 9:221344. <https://doi.org/10.1098/rsos.221344>
- Aronson M, Lepczyk C, Evans K, et al (2017) Biodiversity in the city: key challenges for urban green space management. *Front Ecol Environ* 15:. <https://doi.org/10.1002/fee.1480>
- Aronson MFJ, La Sorte FA, Nilon CH, et al (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences* 281:20133330. <https://doi.org/10.1098/rspb.2013.3330>
- Banks PB, Bryant J V (2007) Four-legged friend or foe? Dog walking displaces native birds from natural areas. *Biol Lett* 3:611–613. <https://doi.org/10.1098/rsbl.2007.0374>
- Barbaro L, Giffard B, Charbonnier Y, et al (2014) Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. *Divers Distrib* 20:149–159. <https://doi.org/https://doi.org/10.1111/ddi.12132>
- Barbe L, Morel R, Rantier Y, et al (2018) Bird communities of a temperate forest: spatio-temporal partitioning between resident and migratory species. *J Ornithol* 159:457–469. <https://doi.org/10.1007/s10336-017-1523-y>
- Bateman PW, Fleming PA (2014) Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *J Zool* 294:93–98. <https://doi.org/https://doi.org/10.1111/jzo.12156>
- Bolker B (2019) Getting started with the glmmTMB package. *Cran R-project vignette* 9:
- Burhans DE, Thompson III FR (2006) Songbird Abundance And Parasitism Differ Between Urban And Rural Shrublands. *Ecological Applications* 16:394–405. <https://doi.org/https://doi.org/10.1890/04-0927>
- Callaghan C, Major R, Lyons M, et al (2018) The effects of local and landscape habitat attributes on bird diversity in urban greenspaces. *Ecosphere* 9:. <https://doi.org/10.1002/ecs2.2347>
- Chalfoun A, Thompson F, Ratnaswamy M (2002) Nest Predators and Fragmentation: a Review and Meta-Analysis. *Conservation Biology USA* Paper submitted July 16:. <https://doi.org/10.1046/j.1523-1739.2002.00308.x>
- Cramer AN, Hoey JA, Dolan TE, et al (2023) A unifying framework for understanding ecological and evolutionary population connectivity. *Front Ecol Evol* 11:
- Debastiani VJ, Pillar VD (2012) SYNCSEA—R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. *Bioinformatics* 28:2067–2068. <https://doi.org/10.1093/bioinformatics/bts325>
- Ditchkoff SS, Saalfeld ST, Gibson CJ (2006) Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst* 9:5–12
- Dominoni D, Smit JAH, Visser ME, Halfwerk W (2020) Multisensory pollution: Artificial light at night and anthropogenic noise have interactive effects on activity patterns of great tits (*Parus major*). *Environmental Pollution* 256:113314. <https://doi.org/https://doi.org/10.1016/j.envpol.2019.113314>

- Ehrenfeucht R, and Loukaitou-Sideris A (2010) Planning Urban Sidewalks: Infrastructure, Daily Life and Destinations. *J Urban Des* (Abingdon) 15:459–471. <https://doi.org/10.1080/13574809.2010.502333>
- Evans KL, Newson SE, Gaston KJ (2009) Habitat influences on urban avian assemblages. *Ibis* 151:19–39. <https://doi.org/https://doi.org/10.1111/j.1474-919X.2008.00898.x>
- Fernández-Juricic E (2002) Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia* 131:269–278. <https://doi.org/10.1007/s00442-002-0883-y>
- Fontana CS, Burger MI, Magnusson WE (2011) Bird diversity in a subtropical South-American City: effects of noise levels, arborisation and human population density. *Urban Ecosyst* 14:341–360
- Forrest A, St. Clair CC (2006) Effects of dog leash laws and habitat type on avian and small mammal communities in urban parks. *Urban Ecosyst* 9:51–66. <https://doi.org/10.1007/s11252-006-7903-3>
- Fraixedas S, Lindén A, Piha M, et al (2020) A state-of-the-art review on birds as indicators of biodiversity: Advances, challenges, and future directions. *Ecol Indic* 118:106728. <https://doi.org/https://doi.org/10.1016/j.ecolind.2020.106728>
- Gong P, Li X, Wang J, et al (2020) Annual maps of global artificial impervious area (GAIA) between 1985 and 2018. *Remote Sens Environ* 236:111510
- Hanh Nguyen H, Venohr M, Gericke A, et al (2023) Dynamics in impervious urban and non-urban areas and their effects on run-off, nutrient emissions, and macroinvertebrate communities. *Landsc Urban Plan* 231:104639. <https://doi.org/https://doi.org/10.1016/j.landurbplan.2022.104639>
- Hughes AC, Orr MC, Lei F, et al (2022) Understanding drivers of global urban bird diversity. *Global Environmental Change* 76:102588. <https://doi.org/https://doi.org/10.1016/j.gloenvcha.2022.102588>
- Ibáñez-Álamo JD, Rubio E, Benedetti Y, Morelli F (2017) Global loss of avian evolutionary uniqueness in urban areas. *Glob Chang Biol* 23:2990–2998. <https://doi.org/https://doi.org/10.1111/gcb.13567>
- Kembel SW, Cowan PD, Helmus MR, et al (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kondratyeva A, Knapp S, Durka W, et al (2020) Urbanization Effects on Biodiversity Revealed by a Two-Scale Analysis of Species Functional Uniqueness vs. Redundancy. *Front Ecol Evol* 8:
- La Sorte FA, Lepczyk CA, Aronson MFJ, et al (2018) The phylogenetic and functional diversity of regional breeding bird assemblages is reduced and constricted through urbanization. *Divers Distrib* 24:928–938. <https://doi.org/https://doi.org/10.1111/ddi.12738>
- Leveau C, Leveau L (2005) Avian community response to urbanization in the Pampean region, Argentina. *Ornitol Neotrop* 16:501–503
- Leveau LM (2019) Primary productivity and habitat diversity predict bird species richness and composition along urban-rural gradients of central Argentina. *Urban For Urban Green* 43:126349. <https://doi.org/10.1016/j.ufug.2019.05.011>
- Loss SR, Will T, Marra PP (2013) The impact of free-ranging domestic cats on wildlife of the United States. *Nat Commun* 4:1396. <https://doi.org/10.1038/ncomms2380>

Lüdecke D, Ben-Shachar MS, Patil I, et al (2021) performance: An R package for assessment, comparison and testing of statistical models. *J Open Source Softw* 6: 6.

McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst* 11:161–176. <https://doi.org/10.1007/s11252-007-0045-4>

McKinney ML (2002) Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience* 52:883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)

Miller SG, Knight RL, Miller CK (2001) Wildlife Responses to Pedestrians and Dogs. *Wildlife Society Bulletin* (1973-2006) 29:124–132

Mitchell SL, Bicknell JE, Edwards DP, et al (2020) Spatial replication and habitat context matters for assessments of tropical biodiversity using acoustic indices. *Ecol Indic* 119:106717. <https://doi.org/10.1016/j.ecolind.2020.106717>

Morelli F, Reif J, Díaz M, et al (2024) Dense city centers support less evolutionary unique bird communities than sparser urban areas. *iScience* 27:108945. <https://doi.org/10.1016/j.isci.2024.108945>

Morelli F, Tryjanowski P, Ibáñez-Álamo JD, et al (2023) Effects of light and noise pollution on avian communities of European cities are correlated with the species' diet. *Sci Rep* 13:4361. <https://doi.org/10.1038/s41598-023-31337-w>

Müller N, Ignatieva M, Nilon CH, et al (2013) Patterns and Trends in Urban Biodiversity and Landscape Design. In: Elmqvist T, Fragkias M, Goodness J, et al. (eds) Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities: A Global Assessment. *Springer Netherlands*, Dordrecht, pp 123–174

Muñoz-Pacheco CB, Villaseñor NR (2023) Is there a relationship between socioeconomic level, vegetation cover, free-roaming cats and dogs, and the diversity of native birds? A study in a Latin American capital city. *Science of The Total Environment* 891:164378. <https://doi.org/10.1016/j.scitotenv.2023.164378>

Muñoz-Pedrerros A, González-Urrutia M, Encina-Montoya F, Norambuena H V (2018) Effects of vegetation strata and human disturbance on bird diversity in green areas in a city in southern Chile. *Avian Res* 9:38. <https://doi.org/10.1186/s40657-018-0130-9>

Narango DL, Tallamy DW, Marra PP (2017) Native plants improve breeding and foraging habitat for an insectivorous bird. *Biol Conserv* 213:42–50. <https://doi.org/10.1016/j.biocon.2017.06.029>

Neate-Clegg MHC, Tonelli BA, Youngflesh C, et al (2023) Traits shaping urban tolerance in birds differ around the world. *Current Biology* 33:1677–1688.e6. <https://doi.org/10.1016/j.cub.2023.03.024>

Oropeza-Sánchez MT, Solano-Zavaleta I, Cuandón-Hernández WL, et al (2024) Urban green spaces with high connectivity and complex vegetation promote occupancy and richness of birds in a tropical megacity. *Urban Ecosyst* 28:50. <https://doi.org/10.1007/s11252-024-01612-3>

Perillo A, Mazzoni LG, Passos LF, et al (2017) Anthropogenic noise reduces bird species richness and diversity in urban parks. *Ibis* 159:638–646. <https://doi.org/10.1111/ibi.12481>

QGIS Development Team (2018) QGIS Geographic Information System

- Qi K, Fan Z, Xie Y (2021) The influences of habitat proportion and patch-level structural factors in the spatial habitat importance ranking for connectivity and implications for habitat conservation. *Urban For Urban Green* 64:127239. <https://doi.org/https://doi.org/10.1016/j.ufug.2021.127239>
- R Core Team (2021) R: A Language and Environment for Statistical Computing
- Schneider SC, Fischer JD, Miller JR (2015) Two-sided edge responses of avian communities in an urban landscape. *Urban Ecosyst* 18:539–551. <https://doi.org/10.1007/s11252-014-0418-4>
- Sims V, Evans KL, Newson SE, et al (2008) Avian assemblage structure and domestic cat densities in urban environments. *Divers Distrib* 14:387–399. <https://doi.org/https://doi.org/10.1111/j.1472-4642.2007.00444.x>
- Smit W (2021) Urbanization in the Global South. *Oxford Research Encyclopedia of Global Public Health*. Retrieved 20 Jun. 2025, from <https://oxfordre.com/publichealth/view/10.1093/acrefore/9780190632366.001.0001/acrefore-9780190632366-e-251>.
- Sun B, Lu Y, Yang Y, et al (2025) Urbanization affects spatial variation and species similarity of bird diversity distribution. *Sci Adv* 8:eade3061. <https://doi.org/10.1126/sciadv.ade3061>
- Tobias JA, Sheard C, Pigot AL, et al (2022) AVONET: morphological, ecological and geographical data for all birds. *Ecol Lett* 25:581–597. <https://doi.org/https://doi.org/10.1111/ele.13898>
- Tucker CM, Cadotte MW, Carvalho SB, et al (2017) A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* 92:698–715. <https://doi.org/https://doi.org/10.1111/brv.12252>
- Xie S, Marzluff JM, Su Y, et al (2022) The role of urban waterbodies in maintaining bird species diversity within built area of Beijing. *Science of The Total Environment* 806:150430. <https://doi.org/https://doi.org/10.1016/j.scitotenv.2021.150430>