Bird diversity-environment relationships in urban parks and cemeteries of the Neotropics during breeding and non-breeding seasons

Lucas M. Leveau[1], Mariana Lucia Bocelli[1], Sergio Gabriel Quesada-Acuña[2], César González-Lagos[3,4], Pablo Gutiérrez Tapia[5], Gabriela Franzoi Dri[6], Carlos A. Delgado-V.[7], Álvaro Garitano-Zavala[8], Jackeline Campos[8], Yanina Benedetti[9], Rubén Ortega-Álvarez[10], Antonio Isain Contreras Rodríguez[11], Daniela Souza López[12], Carla Suertegaray Fontana[13], Thaiane Weinert da Silva[13], Sarah Sandri Zalewski Vargas[13], María Cecília Barbosa Toledo[14], Juan Andres Sarquis[15], Alejandro Giraudo[15], Ada Lilian Echevarria[16], María Elisa Fanjul[16], Maria Valeria Martínez[16], Josefina Haedo[17], Luis Gonzalo Cano Sanz[18], Yuri Peña[18], Viviana Fernandez[19], Verónica Marinero[19], Vinícius Abilhoa[20], Rafael Amorin[20], Juan Fernando Escobar Ibáñez[21], María Dolores Juri[22], Sergio Camín[23], Luis Marone[23], Augusto João Piratelli[24], Alexandre Gabriel Franchin[24], Larissa Crispim[24] and Federico Morelli[9]

[1] Universidad de Buenos Aires, Buenos Aires, Argentina
[2] Universidad Estatal a Distancia, San José de Costa Rica, Costa Rica
[3] Universidad Adolfo Ibáñez, Santiago de Chile, Chile
[4] Center of Applied Ecology and Sustainability (CAPES), Santiago de Chile, Chile
[5] Universidad de Santiago de Chile, Santiago de Chile, Chile
[6] University of Maine, Maine, United States
[7] Universidad CES, Medellín, Colombia
[8] Universidad Mayor de San Andrés, La Paz, Bolivia
[9] Czech University of Life Sciences Prague, Prague, Czechia
[10] Investigadoras e Investigadores por México del CONACYT, Dirección Regional Occidente, México
[11] Centro de Cultura Ambiental, Acuexcomatl, SEDEMA, Ciudad de México, México
[12] North American Birds Conservation Initiative, Ciudad de México, México
[13] Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil
[14] Universidade de Taubaté, Taubaté, Brazil
[15] Universidad Nacional del Litoral, Santa Fe, Argentina
[16] Fundación Miguel Lillo, San Miguel de Tucumán, Argentina
[17] Instituto de Ecología Regional, San Miguel de Tucumán, Argentina
[18] Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Arequipa, Perú
[19] Universidad Nacional de San Juan, San Juan, Argentina
[20] Museu de História Natural Capão da Imbuia, Curitiba, Brazil
[21] Instituto de Ecología, Xalapa, México
[22] Universidad Nacional de Chilecito, Chilecito, Argentina
[23] IADIZA-CONICET, Mendoza, Argentina
[24] Universidade Federal de São Carlos, Sorocaba, Brazil

Submitted 14 July 2022
Accepted 9 November 2022
Published 14 December 2022

Corresponding author
Lucas M. Leveau,
lucasleveau@yahoo.com.ar

Academic editor
José Maria Silva

Additional Information and Declarations can be found on page 12

DOI 10.7717/peerj.14496

ABSTRACT

Background: Urbanization will increase in the next decades, causing the loss of green areas and bird diversity within cities. There is a lack of studies at a continental scale analyzing the relationship between urban green areas, such as parks and cemeteries,

How to cite this article Leveau L. M., Bocelli ML, Quesada-Acuña SG, González-Lagos C, Gutiérrez Tapia P, Franzoi Dri G, Delgado-V. CA, Garitano-Zavala Á, Campos J, Benedetti Y, Ortega-Álvarez R, Contreras Rodríguez AI, Souza López D, Fontana, CS, da Silva TW, Zalewski Vargas SS, Barbosa Toledo MC, Sarquis JA, Giraudo A, Echevarria AL, Fanjul M. E., Martínez MV, Haedo J, Cano Sanz LG, Peña Y, Fernandez V, Marinero V, Abilhoa V, Amorin R, Escobar Ibáñez JF, Juri MD, Camín S, Marone L, Piratelli AJ, Franchin AG, Crispim L, Morelli F. 2022. Bird diversity-environment relationships in urban parks and cemeteries of the Neotropics during breeding and non-breeding seasons. **PeerJ 10:e14496 DOI 10.7717/peerj.14496**

and bird species richness in the Neotropical region. Bird diversity-environment relationships in urban parks and cemeteries may be influenced by latitudinal gradients or species-area relationships. However, the seasonal variation of species diversity- environment has not been analyzed at a continental scale in the Neotropics.
Methods: Bird surveys were conducted in 36 cemeteries and 37 parks within 18 Neotropical cities during non-breeding and breeding seasons. Bird diversity was assessed through Hill numbers, focusing on species richness, the effective number of species derived from Shannon index and the Simpson index. Environmental variables included latitude, altitude, and local scale variables such as area size, habitat diversity and pedestrian traffic.
Results: Species richness and Shannon diversity were higher during the breeding season, whereas Simpson diversity did not vary between seasons. During both seasons, species richness increased with area size, was negatively related to altitude, and was the highest at 20° latitude. Species richness was also positively related to habitat diversity, pedestrian traffic, and was highest in suburban areas during the non-breeding season. Shannon and Simpson diversity showed significant relationships with habitat diversity and area size during the breeding season. Bird diversity was similar between parks and cemeteries.
Discussion: Our results showed that urban parks and cemeteries have similar roles in conserving urban bird diversity in Neotropical cities. However, species diversity-environment relations at the continental scale varied between seasons, highlighting the importance of conducting annual studies.

Subjects Biodiversity, Biogeography, Conservation Biology, Zoology
Keywords Habitat heterogeneity, Latin America, Macroecology, Seasonality, Species-area relationships, Taxonomic diversity, Urbanization

INTRODUCTION

The global urban population is expected to be 60% by 2030 (*United Nations, 2018*), probably inducing the loss of green areas within cities (*Dallimer et al., 2011*). Green areas are urban habitats dominated by vegetation, generally constituting biodiversity hotspots within cities (*Kong et al., 2010*; *Dale, 2017*; *Morelli et al., 2017*; *Zuñiga-Palacios et al., 2020*). Therefore, analyzing bird-habitat relationships in urban green areas is important for guiding biodiversity conservation strategies in cities (*Nielsen et al., 2014*). Birds are the most studied taxa in urban green areas (*Nielsen et al., 2014*). They are easy to survey and identify and generally respond to environmental changes (*Lepczyk et al., 2017*).

Bird diversity has been regularly analyzed through several metrics, such as species richness, Shannon diversity, and Simpson diversity (*Magurran, 2005*; *Roswell, Dushoff & Winfree, 2021*). The most critical factors driving bird diversity in green areas are area size and habitat diversity (*Lussenhop, 1977*; *Latta et al., 2013*; *Nielsen et al., 2014*; *Garizábal-Carmona & Mancera-Rodríguez, 2021*). Green area size is generally positively related to species richness (*Tilghman, 1987*; *Jokimäki, 1999*; *Fernández-Juricic, 2000*; *Donnelly & Marzluff, 2004*; *Chamberlain et al., 2007*; *Leveau et al., 2019*). Large green areas may provide more habitats for species, enhancing species richness (*Connor & McCoy, 1979*; *Kisel et al., 2011*). In addition, large green areas may reduce the local extinction rates of species (*MacArthur & Wilson, 1963*; *Murgui, 2007*; *Dri, Fontana & de Sales Dambros, 2021*).

Anthropogenic factors such as pedestrian traffic in green areas and the surrounding urban landscape also can influence bird diversity. Increasing pedestrian rates have been negatively associated with bird diversity in urban areas (*Fernández-Juricic, 2001*; *Chang & Lee, 2016*; *Xie et al., 2016*). Moreover, the level of urbanization surrounding green spaces, such as the percentage of high buildings, has been negatively associated with bird diversity (*MacGregor-Fors & Ortega-Álvarez, 2011*; *Leveau & Leveau, 2016*; *Morelli et al., 2021*).

Urban parks are the most studied green area types regarding their effects on bird diversity (*Chiesura, 2004*; *Alvey, 2006*; *Nielsen et al., 2014*; *Estevo, Nagy-Reis & Silva, 2017*). On the other hand, cemeteries have also been identified as a potential reservoir of high biotic diversity (*Barrett & Barrett, 2001*; *Löki et al., 2019*). However, the role of cemeteries in conserving bird diversity in urban areas has been mainly in European contexts (*Tryjanowski et al., 2017*; *Morelli et al., 2018*). Meanwhile, the Neotropical region has been scarcely analyzed (*Villaseñor & Escobar, 2019*). In addition, most of the studies in parks and cemeteries have been performed during the breeding season (*Leveau et al., 2019*). Thus, an assessment of the environmental-bird diversity relationships along an annual cycle is essential (*Marra et al., 2015*). Due to birds during the non-breeding season having a broader habitat use, the relationships between habitat features and bird species richness might be weaker during the non-breeding season than in the breeding season (*Murgui, 2007*; *Leveau & Leveau, 2016*). Moreover, bird diversity in urban parks and cemeteries may increase during the breeding due to suitable resources for nesting in green areas compared to other urban habitats (*Leveau & Leveau, 2016*). Continental studies exploring the seasonal variations of bird diversity-environment relations are lacking in the Neotropics.

Global patterns of bird diversity have shown an increase in tropical regions (*Fischer, 1960*; *Tramer, 1974*; *Gaston, 2000*) and a general decrease in bird diversity with increasing altitude (*Able & Noon, 1976*; *Hunter & Yonzon, 1993*; *Rahbek, 1995*). Bird species richness in the Neotropics has been negatively related to latitude and altitude (*Rabinovich & Rapoport, 1975*; *Rahbek, 1997*; *Werenkraut & Ruggiero, 2011*) due to higher habitat heterogeneity and primary productivity at low altitudes and near the equator. Therefore, we expect that bird diversity in urban green areas will follow a similar trend increasing in the tropics and at low altitudes.

In this study, we conducted a continental comparative analysis of bird communities in urban parks and cemeteries of the Neotropics to analyze bird diversity–environment relations during an annual cycle. Most studies examining the continental variation of bird diversity in the Neotropics focused on species richness due to the available information on species presence/absence in distributional maps (*Rabinovich & Rapoport, 1975*; *Rahbek, 1997*; *Bellocq & Gómez-Insausti, 2005*). However, an analysis of different diversity components that consider the relative abundance of species, such as Shannon and Simpson diversities, may help to refine hypotheses and models of biodiversity responses to the environment (*Roswell, Dushoff & Winfree, 2021*). We assessed bird diversity through Hill numbers, transforming diversity indices values into the equivalent number of species (*Jost,*

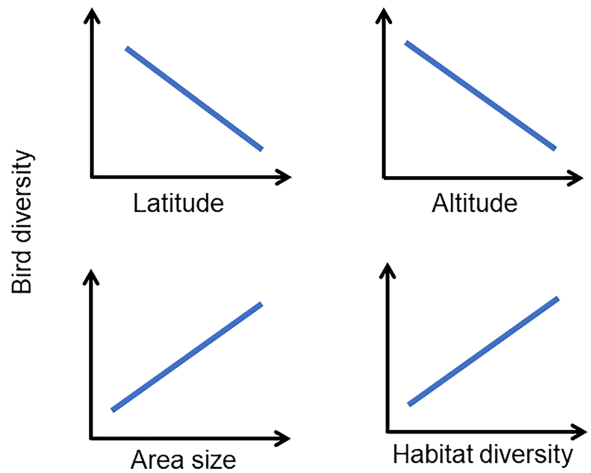

Figure 1 Conceptual schematic diagram showing the main hypotheses explaining bird diversity in urban green areas of the Neotropics. Bird diversity is expected to increase with decreasing latitude and altitude, and increase with more area size and habitat diversity.

Full-size DOI: 10.7717/peerj.14496/fig-1

2006). Therefore, we considered variations in species richness and the effective number of species derived from Shannon (Hill-Shannon) and the Simpson indices (Hill-Simpson) (*Jost, 2006*). Bird diversity is expected to increase during the breeding season, and the relationships between diversity and environmental variables should change between seasons. We expected an increase in bird diversity in the tropics and at low altitudes (Fig. 1). In addition, we expected that bird diversity would increase with area size and habitat diversity (Fig. 1).

MATERIALS AND METHODS

A total of 36 cemeteries and 37 parks belonging to 18 Neotropical cities were surveyed (Fig. 2; Tables S1 and S2). The cities were in eight countries with a broad range of biogeographical conditions, with latitudes between 6° N to 34° S and altitudes between 10 to 3,625 masl. However, a large portion of the tropics near the equator could not be sampled, which could affect the results obtained (see Discussion). In each city, cemeteries were selected according to availability. Then, parks with a similar size and location within the city were also chosen. Park size was estimated using Google Earth Pro (https://www.google.com/earth/versions/). Each park and cemetery was a sampling unit referred to as sites.

Bird surveys

The bird surveys were carried out in point counts with a radius of 100 m for 10 min, spaced at least by 200 m to ensure independence among points (*Bibby, Jones & Marsden, 1998*). All birds detected within the site were considered for green areas lower than 1 ha, excluding those seen outside the green space. The surveys were performed during the first 4 h after sunrise on weekdays with no rain or strong wind (*Bibby, Jones & Marsden, 1998*). Each point was visited twice by the same observer during the breeding season (spring) and twice during the non-breeding season (fall). In the Southern Hemisphere, the breeding season corresponded to surveys during the first 2 weeks of October and the last week of

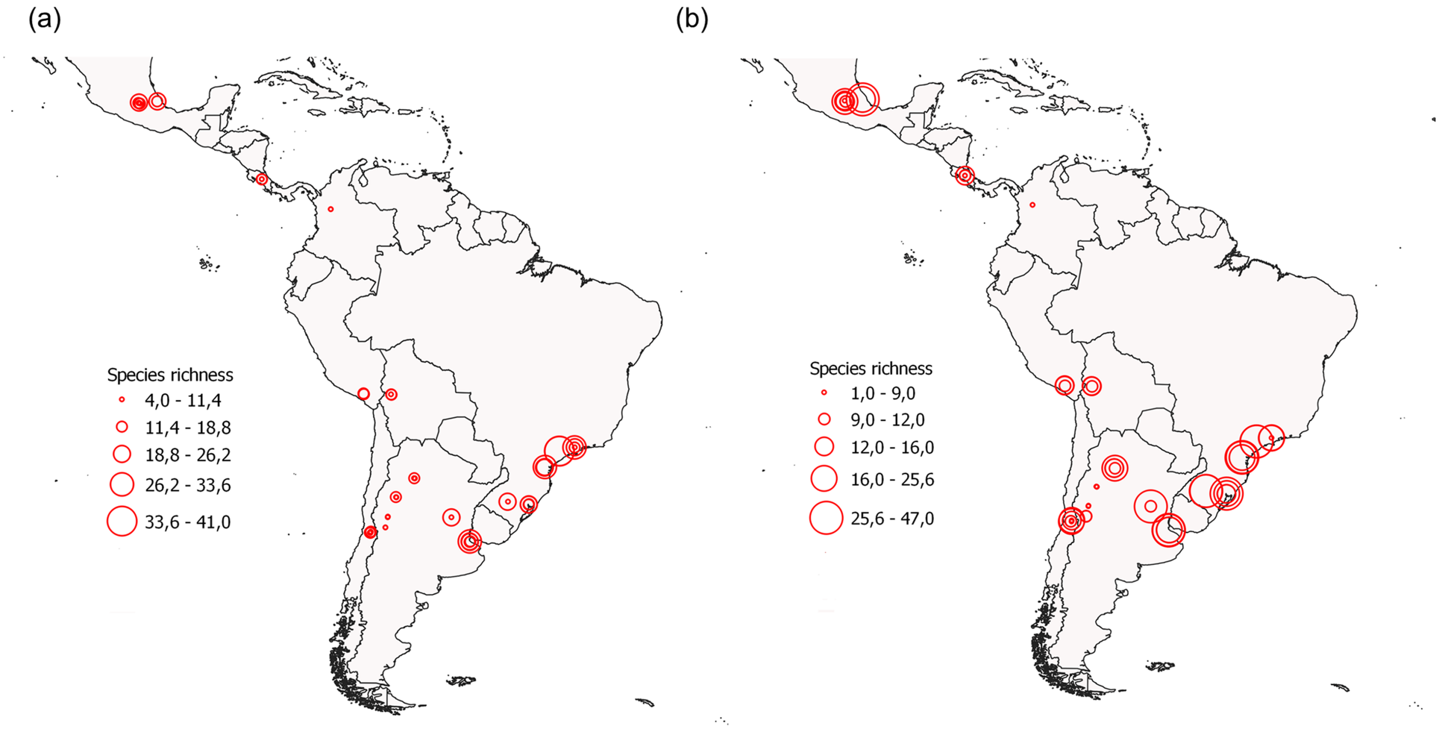

Figure 2 Location of the surveyed urban green areas, depicting their observed species richness values (red circles) during (A) the non-breeding season and (B) the breeding season. Each circle corresponds to each green area surveyed. Note that some circles may be overlapped due to similar species richness.
Full-size DOI: 10.7717/peerj.14496/fig-2

November or the first week of December. The non-breeding season corresponded to surveys during April, May or June. In the Northern Hemisphere, October–December corresponded to the non-breeding season, whereas April–June was the breeding season. The number of point counts per site ranged between one and 11, according to the space available to locate points spaced at least by 200 m. The location of points was determined by a stratified design, locating points in each microhabitat (wooded areas, lawned areas, *etc.*). Parks and cemeteries with less than 3 ha had one point, whereas larger sites had an increasing number of point counts proportional to their size.

Environmental variables

We analyzed eight environmental variables, at local, landscape and large spatial-scale (Table 1). Local-scale variables were within each green area, characterized by habitat diversity, habitat type, pedestrian traffic, park and cemetery area size. Habitat diversity was calculated using the Shannon index with the percent cover of built, tree, bush, grass, non-managed herbaceous vegetation, bare soil, and water. The built cover was included in habitat diversity because these areas may provide resources for birds, such as nesting places. When the percentage cover of habitat components exceeded 100% due to strata overlapping (*e.g.*, lawn overlapped by tree canopy), values were rescaled to 100%. These variables were estimated visually in the field at each point count. The variable values were averaged for each park and cemetery in the sites with more than one point count. Habitat

Table 1 Description of the predictor variables included in the statistical analysis.

Spatial scale	Variable	Mean	Range
Local	Habitat diversity (H′)	1.29	0.30–1.78
	Habitat type (park, cemetery)	–	–
	Pedestrian traffic (pedestrians/10 min)	15.18	0.5–175.5
	Area (ha)	11.48	0.33–97.60
Landscape	Urbanization level (urban, suburban, periurban)	–	–
	Population	3,493,619.61	41,179–22,597,699
Large-scale	Altitude (masl)	1,085.01	10–3,625
	Latitude	24.14	6.20–34.65

Note:
masl, meter above sea level.

types were cemeteries and parks, and a discriminant analysis revealed that cemeteries had more built cover and less pedestrian traffic than parks (Fig. S1). Pedestrian traffic was calculated as the number of pedestrians passing through each point count during bird surveys (pedestrians/10 min). A mean value of pedestrian traffic was obtained for each season.

Landscape variables were the surroundings of each green area within each city and characterized by the urbanization level and population size of each city. The urbanization level where each site was located was classified as urban, suburban, and periurban according to the impervious cover surrounding each area and its location in the city (see *Morelli et al., 2018*). The urbanization level was characterized with Google Earth Pro images by measuring impervious cover in four plots of 9 ha located in the cardinal points. Then, the four values of the impervious surface were averaged for each site. The urban level was characterized by >50% impervious (asphalted areas, buildings) cover. Suburban was characterized by <50% impervious cover within the city, whereas periurban areas were sites on the city fringe. The population size of each city was obtained from Wikipedia according to the last census information.

Large-scale variables were related to regional climate and vegetation variables and characterized by proxies such as latitude and altitude. Latitude was calculated as the mean latitude value of the point counts in each site using GPS. Altitude values for each city were obtained from Wikipedia.

Bird diversity

Bird diversity was assessed through Hill numbers, calculated with data on bird species abundance during each season. Hill numbers were estimated using the function hill_taxa of the hillR package (*Li, 2018*). Species richness was the total number of species in each site. Hill-Shannon diversity was the effective number of species derived from the Shannon diversity index, which gives more weight to species abundances and can be interpreted as the number of common species (*Chao, Chiu & Jost, 2014*). Hill-Simpson diversity was the effective number of species derived from the Simpson diversity index, which places more weight on species abundance than the Hill-Shannon index and can be interpreted as the number of dominant species (*Chao, Chiu & Jost, 2014*).

Statistical analysis

Differences in bird diversity between seasons in each site were analyzed through paired t-test with the function t.test of R (*R Development Core Team, 2017*). The relationship between the eight predictor variables (Table 1) and bird diversity was analyzed through a generalized additive mixed model (GAMM) with the function gamm4 of the gamm4 package (*Wood, Scheipl & Wood, 2017*). GAMMs are non-parametric regressions that model non-linear relationships between the response variable and predictors (*Zuur et al., 2009*). In the case of species richness, a Poisson error structure with the site as a random factor was used due to the presence of overdispersion. A Gaussian error structure was used to analyze the Hill-Shannon and Hill-Simpson diversities. Due to sites being nested within cities, the city was deemed a random factor. Heteroscedasticity and normality of residuals were checked.

Models were obtained by backward eliminating non-significant variables ($P > 0.05$) from the full model including the eight variables (Table 1) using the anova function. Final models were compared with null models using a Likelihood Ratio test (LRT test) ($P < 0.05$). Due to Pearson correlation coefficients between predictors being lower than 0.70, multicollinearity was considered low.

RESULTS

We registered a total of 17,978 individuals belonging to 281 species (Table S3). The most abundant bird species were the Rock Dove (*Columba livia*), the Eared Dove (*Zenaida auriculata*), and the Monk Parakeet (*Myiopsitta monachus*) (Table S3). Bird species richness per site varied between 4 and 41 species (mean = 14.52, standard deviation = 7.48) during the non-breeding season and between 1 and 47 (mean = 16.71, standard deviation = 9.75) during the breeding season (Fig. 2). Mean bird species richness and the Hill-Shannon diversity per site were higher during the breeding season compared to the non-breeding season (richness: paired t-test = 3.66, df = 72, $P < 0.001$; Shannon: paired t-test = 2.01, df = 72, $P = 0.048$, Figs. 2, 3A and 3B). The Hill-Simpson diversity was similar between seasons (paired t-test = 1.47, df = 72, $P = 0.147$; Fig. 3C).

During both seasons, species richness was significantly related to area size, latitude, and altitude (non-breeding: LRT = 31.69, df = 12, $P = 0.002$, $r^2 = 0.49$; breeding season: LRT = 30.91, df = 6, $P < 0.001$, $r^2 = 0.47$; Tables 2a and 2b). Species richness was the highest at 20° latitude (Figs. 2, 4A and 4B), whereas it had a negative relationship with altitude (Figs. 4A and 4B). The relationship between species richness and area size changed between seasons, being positive during the non-breeding season and showing an asymptote from 50 ha during the breeding season (Figs. 4A and 4B).

Urbanization level, pedestrian traffic, and habitat diversity only showed significant relationships during the non-breeding season. Bird species richness was higher in suburban landscapes and showed a positive relationship with pedestrian traffic (Fig. 4A). Moreover, bird richness positively correlated with habitat diversity (Fig. 4A).

The Hill-Shannon diversity during the non-breeding season was significantly related to latitude, area size and habitat diversity (LRT = 13.33, df = 6, $P = 0.038$, $r^2 = 0.48$; Table 2c). The Hill-Shannon diversity increased with increasing area size and habitat diversity and

Figure 3 Bow-plots showing the seasonal variation of bird diversity in urban green areas of the Neotropics. Box-plots show the species richness per site (A), the effective number of species derived from the Shannon index per site (B), and the effective number of species derived from the Simpson index per site (C), during non-breeding and breeding seasons in urban parks and cemeteries of the Neotropics. Full-size DOI: 10.7717/peerj.14496/fig-3

had the highest values between 20° and 30° latitude (Fig. 4C). During the breeding season, the Hill-Shannon showed a positive relationship with area size and habitat diversity (LRT = 24.85, df = 4, $P < 0.001$, $r^2 = 0.06$; Table 2d and Fig. 4D).

The Hill-Simpson diversity during the non-breeding season was not significantly related to any predictor (LRT = 6.50, df = 4, $P = 0.165$; Table 2e). During the breeding season, the Hill-Simpson diversity increased with increasing area size and habitat diversity (LRT = 21.27, df = 4, $P < 0.001$, $r^2 = 0.03$; Table 2f and Fig. 4F).

The remaining explanatory variables, such as habitat type and the population did not have a significant relationship with any bird diversity index.

DISCUSSION

Our results showed that species richness and the Hill-Shannon diversity were higher during the breeding season than in the non-breeding season in urban green areas of the Neotropics. In addition, species richness decreased with increasing altitude and increased at intermediate latitudinal values (between 20° and 30° latitude). Species richness was positively related to green area size during both seasons. However, the relationship between bird diversity and environmental variables was weaker during the non-breeding season and when considering Hill-Shannon diversity and Hill-Simpson diversity.

The increase in species richness during the breeding season could be related to three main factors. Firstly, species richness may increase due to the arrival of migrant species to temperate and subtropical cities in the Neotropics (*Joseph, 1997*; *Jahn et al., 2020*), such as the Fork-tailed Flycatcher (*Tyrannus savana*) and the Grey-breasted Martin (*Progne chalybea*) (Table S3). Secondly, bird species may be more present in green areas during breeding because these habitats provide suitable nesting places. Outside the breeding season, birds have a broader habitat use because they mainly focus on finding food (*Murgui, 2007*). Therefore, species may use other urban habitats, such as wooded streets or residential areas. Thirdly, bird species during the breeding season may be more conspicuous and, therefore, detectable because of their territorial behavior including vocalizations and displays.

Table 2 Final generalized additive mixed models between bird diversity and environmental variables.

Season	Predictor	Estimate	SE	edf	t/Chi.sq/F	*P*
(a) NB Species richness	Intercept	2.443	0.135		18.144	<0.001
	Habitat-Suburban	0.339	0.165		2.049	0.041
	Habitat-Urban	0.153	0.137		1.120	0.263
	Pedestrian			1.000	4.210	0.040
	Area (ha)			1.000	9.638	0.002
	Latitude			2.652	13.938	0.003
	Habitat diversity (H′)			1.000	5.448	0.019
	Altitude (m)			1.000	6.108	0.014
(b) B Species richness	Intercept	2.703	0.084		32.080	<0.001
	Area (ha)			2.115	38.360	<0.001
	Latitude			3.064	19.220	<0.001
	Altitude (m)			1.354	4.890	0.032
(c) NB Hill-Shannon	Intercept	9.717	0.935		10.390	<0.001
	Area (ha)			1.000	4.222	0.044
	Latitude			4.603	3.348	0.007
	Habitat diversity (H′)			1.000	7.020	0.010
d) B Hill-Shannon	Intercept	11.036	1.514		7.290	<0.001
	Area (ha)			1.945	9.948	<0.001
	Habitat diversity (H′)			1.234	7.312	0.009
(e) NB Hill-Simpson	Intercept	7.519	1.098		6.849	<0.001
(f) log(B Hill-Simpson)	Intercept	8.449	1.230		6.868	<0.001
	Area			1.642	7.885	0.001
	Habitat diversity (H′)			1.000	5.002	0.029

Note:
Final models showing the relationship between species richness (SR), Hill-Shannon (SH) diversity, Hill-Simpson (SI) diversity and environmental variables of urban parks and cemeteries in the Neotropics during the non-breeding (NB) and breeding (B) seasons SE: standard error; edf: estimated degrees of freedom.

The relationship between bird diversity and environmental variables was weaker during the non-breeding season. For example, the Hill-Simpson diversity showed no significant associations with the environmental variables. This pattern could be related to birds' broader habitat use during the non-breeding season (*Murgui, 2007*).

Although the species richness and the Hill-Shannon diversity increased during the breeding season, the Hill-Simpson diversity did not change significantly. Hill-Simpson diversity gives more weight to dominant species than the Hill-Shannon diversity, and species richness considers dominant, common, and rare species (*Roswell, Dushoff & Winfree, 2021*). Therefore, the patterns found suggest that the most significant seasonal change of species diversity in the green areas of the Neotropics is related to the change of rare species, which could respond to the availability of rare resources.

In general, the three components of bird diversity were positively associated with green area size during both seasons. This result agrees with a recent meta-analysis (*Leveau et al., 2019*), which found that green area size has a consistent global positive relationship with

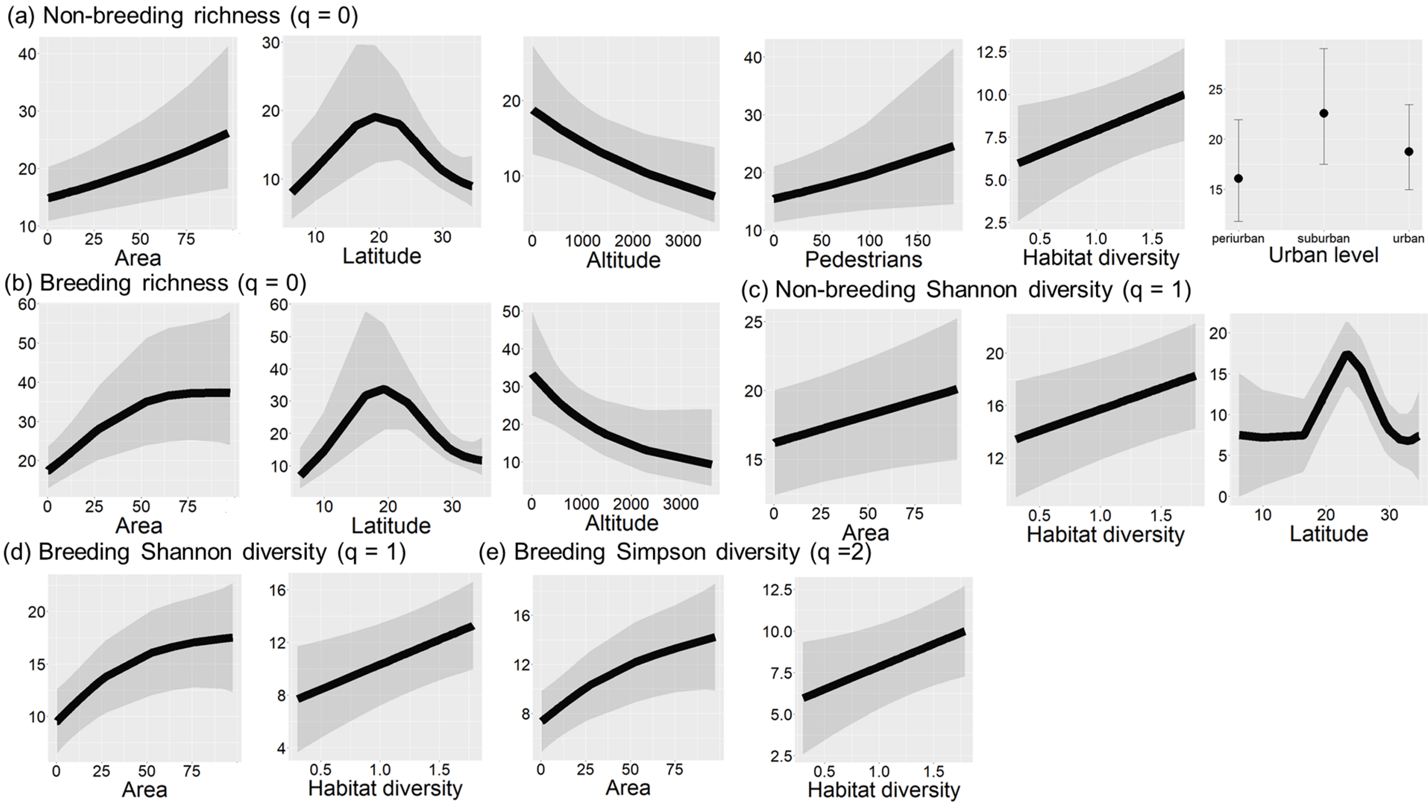

Figure 4 Final models of bird diversity-environment relationships in urban green areas of the Neotropics. Significant relationships ($P < 0.05$) between species richness and environmental variables during the non-breeding season (A) and breeding season (B), between Hill-Shannon diversity and environmental variables during non-breeding (C) and breeding season (D), and between Hill-Simpson diversity and environmental variables during the breeding season (E). Black lines are fitted models, and grey bands are 95% confidence intervals.

Full-size DOI: 10.7717/peerj.14496/fig-4

species richness in urban areas. Moreover, studies conducted at large scales in parks and cemeteries in Europe also found a positive relationship between species richness and area size (*Tryjanowski et al., 2017*; *Morelli et al., 2018*). The shape of the species-area relationship was asymptotic during the breeding season, suggesting that areas of 50 Ha are sufficient to conserve bird species. However, during the non-breeding season, the relationship was linear, indicating that the continuous increase in area size promoted the presence of more species. Therefore, our results highlight the importance of annual studies for a better understanding of the species-area relations in urban areas.

Habitat diversity was the second most important predictor of bird diversity in the green areas, related to different bird diversity components in both seasons. A similar proportion of habitat features, such as different vegetation strata, may provide food resources and shelter more bird species (*MacArthur & MacArthur, 1961*; *Tews et al., 2004*; *Leveau, 2013*).

Bird diversity was similar between habitat types. This result agrees with those found by Morelli and colleagues in Europe (*Tryjanowski et al., 2017*; *Morelli et al., 2018*). Therefore, our continental analyses support the idea that cemeteries work similarly to urban parks, maintaining a similar avian diversity.

The results showed that several bird diversity components increased between 20° and 30° latitude. This pattern disagrees with other authors in the Neotropics (*Rahbek, 1997*; *Herzog, Kessler & Bach, 2005*; *Bellocq & Gómez-Insausti, 2005*), who described an increasing bird species richness approaching the Equator. Our results may be related to a lack of sampling in the equatorial area. Alternatively, our tropical sites were dominated by Brazilian cities located between 20° and 30° latitude and surrounded by the Atlantic Forest, a biodiversity hotspot (*Chapa-Vargas et al., 2019*). Therefore, higher bird diversity in the regional pool surrounding cities could influence the species richness in urban green areas. However, the composition of plant species in green spaces, a variable that was not measured in our study, also could influence the bird diversity. Bird diversity has shown a positive relationship with native vegetation (*White et al., 2005*; *De Castro Pena et al., 2017*). Several studies have shown that native trees in urban areas are more common in tropical cities than in temperate cities of the Neotropics (*Leveau & Leveau, 2006*; *Barbosa de Toledo, Donatelli & Batista, 2012*; *De Castro Pena et al., 2016*). Therefore, more native vegetation species may favor bird diversity in urban green areas of the tropics.

As predicted, bird diversity declined with increasing altitude. In general, studies conducted in urban areas have also found a negative relationship between species richness and altitude (*Bhatt & Joshi, 2011*; *Morelli et al., 2018*), probably due to the decrease of temperature and habitat resources at high altitudes (*Kim et al., 2018*). However, other studies have found no or positive relationship between species richness and altitude in urban areas (*Sorace & Gustin, 2008*; *Daniels & Kirkpatrick, 2006*; *Villegas & Garitano-Zavala, 2010*). Differences among studies may be related to variations in the scale of analysis, site's altitude range and the biogeographic context of studies (*Rahbek, 2005*; *Werenkraut & Ruggiero, 2011*). On the other hand, the relationship between bird diversity and altitude disappeared when we considered common or dominant species. Therefore, our results suggest that diversity-altitude patterns were mainly driven by variations of rare species, which tracked the availability of rare resources or had physiologic limitations due to low temperatures. For example, the Violaceus Euphonia (*Euphonia violacea*) was only recorded in a park of Curitiba, located in the tropical lowlands of eastern Brazil.

Our results showed that pedestrian traffic was positively related to species richness during the non-breeding season. This pattern contrasts with other studies that have found a negative relationship between bird diversity and pedestrian traffic (*Chang & Lee, 2016*; *Leveau & Leveau, 2016*) or no relation between both variables (*Fernández-Juricic, 2004*; *Beninde, Veith & Hochkirch, 2015*; *Liordos et al., 2021*). The positive relationship between pedestrians and bird species richness could be related to food provided by humans to birds.

Bird species richness increased in sites surrounded by suburban landscapes. The heterogeneity of suburban landscapes, composed of buildings and green areas (*Leveau, 2019*), can favor the presence of a greater number of species in parks and cemeteries. This result partially agrees with other studies conducted at local scales (*MacGregor-Fors & Ortega-Álvarez, 2011*; *Leveau & Leveau, 2016*; *Villaseñor & Escobar, 2019*), where species richness increased in green areas surrounded by low urban cover. However, the large-scale analysis of urban parks and cemeteries conducted in Europe (*Clergeau, Jokimäki & Savard,* *2001*; *Morelli et al., 2018*) revealed no differences in the species richness of these urban green areas and the urbanization level surrounding them.

Although the researchers of this study had experience working with bird communities in urban areas, some bias can exist regarding bird detectability and habitat characterization. Therefore, the results obtained must be taken with caution.

CONCLUSIONS

Our analysis of environmental drivers of species diversity in urban green areas of the Neotropics revealed that the use of different components of bird diversity had other relations with the environmental predictors. However, area size and habitat diversity consistently showed a positive relationship with the different components of bird diversity. Cemeteries and parks had similar support for bird diversity to urban parks. Therefore, conserving large green areas and creating heterogeneous environments with different vegetation layers are fundamental for bird conservation in Neotropical cities. On the other hand, our results highlight the importance of considering the entire annual cycle for a better understanding of the species diversity-environment relations in urban areas.

ACKNOWLEDGEMENTS

CSF, TWS and SSZV are grateful to Eduardo Chiarani for his support during fieldwork. The comments of two anonymous reviewers and the Academic Editor, José Maria Silva, improved notably a previous version of the manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

Lucas Matias Leveau was supported by the Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación, PICT 2018-03871. César González-Lagos was supported by ANID PIA/BASAL FB0002 Sergio Gabriel Quesada-Acuña was supported by VI-UNED, PROY-2019-33. Carla Suertegaray Fontana was supported by CNPq grant (310608/2019-8). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación: PICT 2018-03871.
ANID PIA/BASAL: FB0002.
Sergio Gabriel Quesada-Acuña was supported by VI-UNED, PROY-2019-33.
CNPq grant (310608/2019-8).

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Lucas M. Leveau conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Mariana Lucia Bocelli performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Sergio Gabriel Quesada-Acuña performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- César González-Lagos performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Pablo Gutiérrez Tapia performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Gabriela Franzoi Dri performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Carlos A. Delgado-V. performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Álvaro Garitano-Zavala performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Jackeline Campos performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Yanina Benedetti conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Rubén Ortega-Álvarez performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Antonio Isain Contreras Rodríguez performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Daniela Souza López performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Carla Suertegaray Fontana performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Thaiane Weinert da Silva performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Sarah Sandri Zalewski Vargas performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- María Cecília Barbosa Toledo performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Juan Andres Sarquis performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Alejandro Giraudo performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Ada Lilian Echevarria performed the experiments, authored or reviewed drafts of the article, and approved the final draft.

- María Elisa Fanjul performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- María Valeria Martínez performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Josefina Haedo performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Luis Gonzalo Cano Sanz performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Yuri Peña performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Viviana Fernandez performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Verónica Marinero performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Vinícius Abilhoa performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Rafael Amorin performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Juan Fernando Escobar Ibáñez performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- María Dolores Juri performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Sergio Camín performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Luis Marone performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Augusto João Piratelli performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Alexandre Gabriel Franchin performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Larissa Crispim performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Federico Morelli conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw data are available in the Supplemental Files.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.14496#supplemental-information.

REFERENCES

Able KP, Noon BR. 1976. Avian community structure along elevational gradients in the northeastern United States. *Oecologia* **26(3)**:275–294 DOI 10.1007/BF00345296.

Alvey AA. 2006. Promoting and preserving biodiversity in the urban forest. *Urban Forestry & Urban Greening* **5(4)**:195–201 DOI 10.1016/j.ufug.2006.09.003.

Barbosa de Toledo MC, Donatelli RJ, Batista GT. 2012. Relation between green spaces and bird community structure in an urban area in Southeast Brazil. *Urban Ecosystems* **15(1)**:111–131 DOI 10.1007/s11252-011-0195-2.

Barrett GW, Barrett TL. 2001. Cemeteries as repositories of natural and cultural diversity. *Conservation Biology* **15(6)**:1820–1824 DOI 10.1046/j.1523-1739.2001.00410.x.

Bellocq MI, Gómez-Insausti R. 2005. Raptorial birds and environmental gradients in the southern Neotropics: a test of species-richness hypotheses. *Austral Ecology* **30(8)**:892–898 DOI 10.1111/j.1442-9993.2005.01533.x.

Beninde J, Veith M, Hochkirch A. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters* **18(6)**:581–592 DOI 10.1111/ele.12427.

Bhatt D, Joshi KK. 2011. Bird assemblages in natural and urbanized habitats along elevational gradient in Nainital district (western Himalaya) of Uttarakhand state, India. *Current Zoology* **57(3)**:318–329 DOI 10.1093/czoolo/57.3.318.

Bibby CJ, Jones M, Marsden S. 1998. *Bird surveys*. London: Expedition Advisory Centre.

Chamberlain DE, Gough S, Vaughan H, Vickery JA, Appleton GF. 2007. Determinants of bird species richness in public green spaces. *Bird Study* **54(1)**:87–97 DOI 10.1080/00063650709461460.

Chang HY, Lee YF. 2016. Effects of area size, heterogeneity, isolation, and disturbances on urban park avifauna in a highly populated tropical city. *Urban Ecosystems* **19(1)**:257–274 DOI 10.1007/s11252-015-0481-5.

Chao A, Chiu CH, Jost L. 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics* **45(1)**:297–324 DOI 10.1146/annurev-ecolsys-120213-091540.

Chapa-Vargas L, Ceballos G, Tinajero R, Torres-Romero EJ. 2019. Latitudinal effects of anthropogenic factors driving raptor species richness across the American continent. *Journal of Biogeography* **46(9)**:1948–1958 DOI 10.1111/jbi.13637.

Chiesura A. 2004. The role of urban parks for the sustainable city. *Landscape and Urban Planning* **68(1)**:129–138 DOI 10.1016/j.landurbplan.2003.08.003.

Clergeau P, Jokimäki J, Savard JPL. 2001. Are urban bird communities influenced by the bird diversity of adjacent landscapes? *Journal of Applied Ecology* **38(5)**:1122–1134 DOI 10.1046/j.1365-2664.2001.00666.x.

Connor EF, McCoy ED. 1979. The statistics and biology of the species-area relationship. *The American Naturalist* **113(6)**:791–833 DOI 10.1086/283438.

Dale S. 2017. Urban bird community composition influenced by size of urban green spaces, presence of native forest, and urbanization. *Urban Ecosystems* **21(1)**:1–14 DOI 10.1007/s11252-017-0706-x.

Dallimer M, Tang Z, Bibby PR, Brindley P, Gaston KJ, Davies ZG. 2011. Temporal changes in greenspace in a highly urbanized region. *Biology Letters* **7(5)**:763–766 DOI 10.1098/rsbl.2011.0025.

Daniels GD, Kirkpatrick JB. 2006. Does variation in garden characteristics influence the conservation of birds in suburbia? *Biological Conservation* **133(3)**:326–335 DOI 10.1016/j.biocon.2006.06.011.

De Castro Pena J, Magalhães DM, Mourao ACM, Young RJ, Rodrigues M. 2016. The green infrastructure of a highly-urbanized Neotropical city: the role of the urban vegetation in preserving native biodiversity. *Capa* **11(4)**:66–78 DOI 10.5380/revsbau.v11i4.63481.

De Castro Pena JDC, Martello F, Ribeiro MC, Armitage RA, Young RJ, Rodrigues M. 2017. Street trees reduce the negative effects of urbanization on birds. *PLOS ONE* **12(3)**:e0174484 DOI 10.1371/journal.pone.0174484.

Donnelly R, Marzluff JM. 2004. Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology* **18(3)**:733–745 DOI 10.1111/j.1523-1739.2004.00032.x.

Dri GF, Fontana CS, de Sales Dambros C. 2021. Estimating the impacts of habitat loss induced by urbanization on bird local extinctions. *Biological Conservation* **256**:109064 DOI 10.1016/j.biocon.2021.109064.

Estevo CA, Nagy-Reis MB, Silva WR. 2017. Urban parks can maintain minimal resilience for Neotropical bird communities. *Urban Forestry & Urban Greening* **27(3)**:84–89 DOI 10.1016/j.ufug.2017.06.013.

Fernández-Juricic E. 2000. Bird community composition patterns in urban parks of Madrid: the role of age, size and isolation. *Ecological Research* **15(4)**:373–383 DOI 10.1046/j.1440-1703.2000.00358.x.

Fernández-Juricic E. 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. *Biodiversity & Conservation* **10(8)**:1303–1316 DOI 10.1023/A:1016614625675.

Fernández-Juricic E. 2004. Spatial and temporal analysis of the distribution of forest specialists in an urban-fragmented landscape (Madrid, Spain): implications for local and regional bird conservation. *Landscape and Urban Planning* **69(1)**:17–32 DOI 10.1016/j.landurbplan.2003.09.001.

Fischer AG. 1960. Latitudinal variations in organic diversity. *Evolution* **14(1)**:64–81 DOI 10.1111/j.1558-5646.1960.tb03057.x.

Garizábal-Carmona JA, Mancera-Rodríguez NJ. 2021. Bird species richness across a Northern Andean city: effects of size, shape, land cover, and vegetation of urban green spaces. *Urban Forestry & Urban Greening* **64(4)**:127243 DOI 10.1016/j.ufug.2021.127243.

Gaston KJ. 2000. Global patterns in biodiversity. *Nature* **405(6783)**:220–227 DOI 10.1038/35012228.

Herzog SK, Kessler M, Bach K. 2005. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography* **28(2)**:209–222 DOI 10.1111/j.0906-7590.2005.03935.x.

Hunter ML, Yonzon P. 1993. Altitudinal distributions of birds, mammals, people, forests, and parks in Nepal. *Conservation Biology* **7(2)**:420–423 DOI 10.1046/j.1523-1739.1993.07020420.x.

Jahn AE, Cueto VR, Fontana CS, Guaraldo AC, Levey DJ, Marra PP, Ryder TB. 2020. Bird migration within the Neotropics. *The Auk* **137(4)**:ukaa033 DOI 10.1093/auk/ukaa033.

Jokimäki J. 1999. Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. *Urban Ecosystems* **3(1)**:21–34 DOI 10.1023/A:1009505418327.

Joseph L. 1997. Towards a broader view of Neotropical migrants: consequences of a re-examination of austral migration. *Ornitologia Neotropical* **8**:31–36.

Jost L. 2006. Entropy and diversity. *Oikos* **113(2)**:363–375 DOI 10.1111/j.2006.0030-1299.14714.x.

Kim JY, Lee S, Shin MS, Lee CH, Seo C, Eo SH. 2018. Altitudinal patterns in breeding bird species richness and density in relation to climate, habitat heterogeneity, and migration influence in a temperate montane forest (South Korea). *PeerJ* **6(12)**:e4857 DOI 10.7717/peerj.4857.

Kisel Y, McInnes L, Toomey NH, Orme CDL. 2011. How diversification rates and diversity limits combine to create large-scale species-area relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366(1577)**:2514–2525 DOI 10.1098/rstb.2011.0022.

Kong F, Yin H, Nakagoshi N, Zong Y. 2010. Urban green space network development for biodiversity conservation: identification based on graph theory and gravity modeling. *Landscape and Urban Planning* **95(1–2)**:16–27 DOI 10.1016/j.landurbplan.2009.11.001.

Latta SC, Musher LJ, Latta KN, Katzner TE. 2013. Influence of human population size and the built environment on avian assemblages in urban green spaces. *Urban Ecosystems* **16(3)**:463–479 DOI 10.1007/s11252-012-0282-z.

Lepczyk CA, La Sorte FA, Aronson MF, Goddard MA, MacGregor-Fors I, Nilon CH, Warren PS. 2017. Global patterns and drivers of urban bird diversity. In: Murgui E, Hedblom M, eds. *Ecology and Conservation of Birds in Urban Environments*. Cham: Springer, 13–33.

Leveau CM, Leveau LM. 2006. Ensambles de aves en calles arboladas de tres ciudades costeras del sudeste de la provincia de Buenos Aires, Argentina. *El Hornero* **21(1)**:25–30.

Leveau LM. 2013. Relaciones aves-habitat en el sector suburbano de Mar del Plata, Argentina. *Ornitologia Neotropical* **24**:201–212.

Leveau LM. 2019. Primary productivity and habitat diversity predict bird species richness and composition along urban-rural gradients of central Argentina. *Urban Forestry & Urban Greening* **43(3)**:126349 DOI 10.1016/j.ufug.2019.05.011.

Leveau LM, Leveau CM. 2016. Does urbanization affect the seasonal dynamics of bird communities in urban parks? *Urban Ecosystems* **19(2)**:631–647 DOI 10.1007/s11252-016-0525-5.

Leveau LM, Ruggiero A, Matthews TJ, Bellocq MI. 2019. A global consistent positive effect of urban green area size on bird richness. *Avian Research* **10(1)**:1–14 DOI 10.1186/s40657-019-0168-3.

Li D. 2018. hillR: taxonomic, functional, and phylogenetic diversity and similarity through Hill Numbers. *Journal of Open Source Software* **3(31)**:1041 DOI 10.21105/joss.01041.

Liordos V, Jokimäki J, Kaisanlahti-Jokimäki ML, Valsamidis E, Kontsiotis VJ. 2021. Patch, matrix and disturbance variables negatively influence bird community structure in small-sized managed green spaces located in urban core areas. *Science of the Total Environment* **801(5864)**:149617 DOI 10.1016/j.scitotenv.2021.149617.

Löki V, Deák B, Lukács AB, Molnár A. 2019. Biodiversity potential of burial places-a review on the flora and fauna of cemeteries and churchyards. *Global Ecology and Conservation* **18(1)**:e00614 DOI 10.1016/j.gecco.2019.e00614.

Lussenhop J. 1977. Urban cemeteries as bird refuges. *The Condor* **79(4)**:456–461 DOI 10.2307/1367725.

MacArthur RH, MacArthur JW. 1961. On bird species diversity. *Ecology* **42(3)**:594–598 DOI 10.2307/1932254.

MacArthur RH, Wilson EO. 1963. An equilibrium theory of insular zoogeography. *Evolution* **17(4)**:373–387 DOI 10.1111/j.1558-5646.1963.tb03295.x.

MacGregor-Fors I, Ortega-Álvarez R. 2011. Fading from the forest: bird community shifts related to urban park site-specific and landscape traits. *Urban Forestry & Urban Greening* **10(3)**:239–246 DOI 10.1016/j.ufug.2011.03.004.

Magurran AE. 2005. Biological diversity. *Current Biology* **15(4)**:R116–R118 DOI 10.1016/j.cub.2005.02.006.

Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM. 2015. A call for full annual cycle research in animal ecology. *Biology Letters* **11(8)**:20150552 DOI 10.1098/rsbl.2015.0552.

Morelli F, Benedetti Y, Ibáñez-Álamo JD, Tryjanowski P, Jokimäki J, Kaisanlahti-Jokimäki M-L, Suhonen J, Díaz M, Møller AP, Moravec D, Prosek J, Bussière R, Mägi M, Kominos T, Galanaki A, Bukas N, Marko G, Pruscini F, Tonelli M, Jerzak L, Ciebiera O, Reif J. 2021. Effects of urbanization on taxonomic, functional and phylogenetic avian diversity in Europe. *Science of the Total Environment* **795**:148874 DOI 10.1016/j.scitotenv.2021.148874.

Morelli F, Benedetti Y, Su T, Zhou B, Moravec D, Šímová P, Liang W. 2017. Taxonomic diversity, functional diversity and evolutionary uniqueness in bird communities of Beijing's urban parks: effects of land use and vegetation structure. *Urban Forestry & Urban Greening* **23**:84–92 DOI 10.1016/j.ufug.2017.03.009.

Morelli F, Mikula P, Benedetti Y, Bussière R, Tryjanowski P. 2018. Cemeteries support avian diversity likewise urban parks in European cities: assessing taxonomic, evolutionary and functional diversity. *Urban Forestry & Urban Greening* **36(3)**:90–99 DOI 10.1016/j.ufug.2018.10.011.

Murgui E. 2007. Effects of seasonality on the species-area relationship: a case study with birds in urban parks. *Global Ecology and Biogeography* **16(3)**:319–329 DOI 10.1111/j.1466-8238.2006.00304.x.

Nielsen AB, Van Den Bosch M, Maruthaveeran S, van den Bosch CK. 2014. Species richness in urban parks and its drivers: a review of empirical evidence. *Urban Ecosystems* **17(1)**:305–327 DOI 10.1007/s11252-013-0316-1.

R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation Project, GNU project, Boston, MA, USA. *Available at http://www.R-project.org/*.

Rabinovich JE, Rapoport EH. 1975. Geographical variation of diversity in Argentine passerine birds. *Journal of Biogeography* **2(3)**:141–157 DOI 10.2307/3037987.

Rahbek C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* **18(2)**:200–205 DOI 10.1111/j.1600-0587.1995.tb00341.x.

Rahbek C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. *The American Naturalist* **149(5)**:875–902 DOI 10.1086/286028.

Rahbek C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8(2)**:224–239 DOI 10.1111/j.1461-0248.2004.00701.x.

Roswell M, Dushoff J, Winfree R. 2021. A conceptual guide to measuring species diversity. *Oikos* **130(3)**:321–338 DOI 10.1111/oik.07202.

Sorace A, Gustin M. 2008. Homogenisation processes and local effects on avifaunal composition in Italian towns. *Acta Oecologica* **33(1)**:15–26 DOI 10.1016/j.actao.2007.07.003.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31(1)**:79–92 DOI 10.1046/j.0305-0270.2003.00994.x.

Tilghman NG. 1987. Characteristics of urban woodlands affecting breeding bird diversity and abundance. *Landscape and Urban Planning* **14**:481–495 DOI 10.1016/0169-2046(87)90061-2.

Tramer EJ. 1974. On latitudinal gradients in avian diversity. *The Condor* **76(2)**:123–130 DOI 10.2307/1366721.

Tryjanowski P, Morelli F, Mikula P, Krištín A, Indykiewicz P, Grzywaczewski G, Kronenberg J, Jerzak L. 2017. Bird diversity in urban green space: a large-scale analysis of differences between parks and cemeteries in Central Europe. *Urban Forestry & Urban Greening* **27**:264–271 DOI 10.1016/j.ufug.2017.08.014.

United Nations. 2018. World urbanization prospects 2018: highlights (ST/ESA/SER.A/421). United Nations, New York. *Available at https://population.un.org/wup/publications/Files/WUP2018-Highlights.pdf*.

Villaseñor NR, Escobar MA. 2019. Cemeteries and biodiversity conservation in cities: how do landscape and patch-level attributes influence bird diversity in urban park cemeteries? *Urban Ecosystems* **22(6)**:1037–1046 DOI 10.1007/s11252-019-00877-3.

Villegas M, Garitano-Zavala Á. 2010. Bird community responses to different urban conditions in La Paz, Bolivia. *Urban Ecosystems* **13(3)**:375–391 DOI 10.1007/s11252-010-0126-7.

Werenkraut V, Ruggiero A. 2011. Quality of basic data and method to identify shape affect richness-altitude relationships in meta-analysis. *Ecology* **92(1)**:253–260 DOI 10.1890/09-2405.1.

White JG, Antos MJ, Fitzsimons JA, Palmer GC. 2005. Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. *Landscape and Urban Planning* **71(2–4)**:123–135 DOI 10.1016/j.landurbplan.2004.02.006.

Wood S, Scheipl F, Wood MS. 2017. Package 'gamm4'. Am Stat, 45, 339. *Available at https://cran.r-project.org/web/packages/gamm4/gamm4.pdf*.

Xie S, Lu F, Cao L, Zhou W, Ouyang Z. 2016. Multi-scale factors influencing the characteristics of avian communities in urban parks across Beijing during the breeding season. *Scientific Reports* **6(1)**:1–9 DOI 10.1038/srep29350.

Zuñiga-Palacios J, Zuria I, Moreno CE, Almazán-Núñez RC, González-Ledesma M. 2020. Can small vacant lots become important reservoirs for birds in urban areas? A case study for a Latin American city. *Urban Forestry & Urban Greening* **47**:126551 DOI 10.1016/j.ufug.2019.126551.

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. *Mixed effects models and extensions in ecology with R*. Berlin: Springer Science & Business Media.