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## Urbanization impacts on the trophic guild composition of bird communities

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### ABSTRACT

Urbanization transforms the landscape and generates loss of pristine habitats. We investigated the urbanization effect on bird communities in a growing South American city (Santa Fe, Argentina) and hypothesized that if habitat structure and human disturbance change along an urban gradient, the richness and abundance of trophic guilds should also vary accordingly. We placed 50 transects 100 m long × 50 m wide in five districts with different levels of urbanization, determined by habitat structure variables. We recorded the number and abundance of species and the amount of pedestrians and vehicles passing through each transect. We recorded 23% of all bird species known for the Santa Fe province and categorized them within 19 trophic guilds. The percentage of area covered by herbaceous vegetation, water bodies and trees and shrubs had a positive relationship with the richness and abundance of most of trophic guilds (hawking aerial, terrestrial, bark and foliage insectivores; terrestrial and generalized granivores; generalized, aquatic diving and foliage omnivores; hawking aerial, aquatic diving and striding carnivores; nectarivores; and aquatic filters). Pavement surface and human disturbance variables had a negative relationship with the richness, and high buildings and pavement surface had a positive relationship with the abundance of terrestrial omnivores and coursing aerial insectivores. Variation partitioning revealed that habitat structure and human disturbance were better predictors of the richness than the abundance of each trophic guild. Results showed that trophic guilds associated to vegetation strata were seen to increase their richness and abundance towards green areas, even if they presented generalist or specialist habits. Urban planners should conserve or manage the surrounded natural spaces when the growth of the city is directed to these areas and increase the availability of environmental features within the urban matrix.

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structure; trophic guilds

## Introduction

Urbanization replaces pristine environments and agricultural areas mainly by pavement, buildings and green spaces dominated by exotic vegetation (Pauchard et al. 2006). As a result, urban systems are more similar among themselves worldwide than to previous pristine habitats (McKinney 2006). This process alters biogeochemical cycles, weather, hydrological systems and biodiversity at different temporal and spatial scales (Grimm et al. 2008; Long et al. 2016; Cao et al. 2017) and generates the loss of natural habitats and native species (Giraudou 2009). Most of the world human population inhabits urban areas and the United Nations (2008) hopes that it will reach 70% by 2050. Urban environments will continue to expand and per capita resource consumption will increase accordingly (Kennedy et al. 2007). Knowledge about the effects of urban areas on biota is needed in order to protect biodiversity (Threlfall et al. 2016). The urban–rural gradient approach has been widely used by urban ecologists to quantify variation in the ability of species to adapt to changes along the gradient (McDonnell and Pickett 1990; McKinney 2006). These studies have found that both natural and anthropogenic habitat features induce changes in bird communities (MacGregor-Fors and Schondube 2011). Urbanization acts as a filter of species on the basis of their biological traits (Crocì et al. 2008; Silva et al. 2016). For example, omnivorous and granivorous guilds are better represented in the cities by both native and exotic species with wide geographical distributions (Chace and Walsh 2006). Generalist habits allow consumption of the various resources that belong to human systems. Therefore, insectivorous and frugivorous species prefer larger green spaces with higher vegetation cover and diversity, whilst generalist and opportunistic species are favoured by urban infrastructure features such as cables, lightning rods and building height and cover (Kark et al. 2007; Carbó-Ramírez and Zuria 2011; MacGregor-Fors and Schondube 2011). Knowledge of the proportional representation of guild members of a community in different levels of urbanization can therefore be useful to determine causes of avifaunal changes related to urbanization (Kark et al. 2007; Meffert and Dziöck 2013).

Habitat structure is a relevant factor that explains the diversity of bird assemblages in urban systems. The presence, distribution and extent of parks and natural patches within the urban matrix can increase both habitat dimensions and available niches, and consequently the diversity of native species (van Rensburg et al. 2009; Fontana et al. 2011; Vignoli et al. 2013; Matsuba et al. 2016). Raptor and falcon species may be favoured by urbanization because they are free from persecution and could have an adequate food supply in green spaces such as parks (Chace and Walsh 2006). However, there are patterns that need to be clarified. Significant positive associations between high levels of urbanization and richness of nectarivores in tropical cities such as Singapore were reported (Lim and Sodhi 2004), while in cities with diverse climatic conditions the opposite was observed (Reynaud and Thioulouse 2000; Pauw and Louw 2012). Most species that achieve colonization of the urban matrix usually have broader environmental tolerances (Bonier et al. 2007). Nevertheless, the management of urban green spaces in a way to compensate the loss of pristine areas and resources may increase the opportunities of colonization of many native species (Fontana et al. 2011).

Human disturbance seems to be another important factor affecting urban bird communities. MacGregor-Fors and Schondube (2011) found that passing cars and

pedestrian rate, as well as the number of dogs, do not limit generalist species associated with highly urbanized areas, but do limit native species. González-Oreja et al. (2012) reported a negative relationship between human disturbance, as measured by background noise levels, and species richness of the songbird assemblages in parks of a Mexican city, which implied that the louder the background noise level, the poorer the site. In addition, Lin et al. (2012) indicated that bird species with a high propensity to disperse and with large population sizes tend to tolerate more human disturbance, in terms of flight-initiation distance. Herrera-Montes and Aide (2011) found that anthropogenic noise reduces the bird community diversity by interfering with or masking important social signals in species with low frequency songs.

Both human disturbance and urban system structure produce a taxonomic and functional simplification of the urban bird community (McKinney 2006). Cities homogenize the physical environment because they are built to meet the relatively narrow human needs, regardless of the bioregion where they are located. Synanthropic species adapted to intensely modified built habitats at the urban core consist mainly of generalist species and are found in cities worldwide. Therefore, urbanization may favour similar groups of birds and traits across the different biogeographical regions (Silva et al. 2016; Leveau et al. 2017). Research on the effects of urbanization on bird communities would help planners and environmental managers to develop strategies for structuring cities in order to maintain or enhance native biodiversity and counteract the homogenizing effect of urbanization (e.g. Meffert and Dziocck 2013; Vignoli et al. 2013).

Most of the studies have been carried out in the Northern Hemisphere. Studies from South American urban areas are still scarce (e.g. Leveau 2013; Silva et al. 2016). The avifauna of the Santa Fe province (Argentina) is almost completely recorded and includes 431 species, which places Santa Fe among the most diverse regions of the subtropical-temperate South America (Fandiño and Giraudo 2010). Nevertheless, the response of birds to anthropogenic disturbances in this area is poorly known, with only two studies that analysed the effect of agricultural development in a unique threatened species (Filloy and Bellocq 2006) and the effect of rural housing in gallery forest bird communities (Rossetti and Giraudo 2003). However, the urbanization effect on bird assemblages remains poorly understood. In addition, in order to face the growth of the population in the Santa Fe city during the last years (5.8% for the period 1991–2001), an increase of the extension of the Santa Fe city towards the north has been proposed, as well as the creation of a ‘metropolitan space’ that connects Santa Fe and the surrounding cities (Soijet et al. 2012). The region where these cities are settled is part of the floodplain of the Parana River, the second largest river system in South America and it is also included in the southernmost of the ‘Atlantic Forest Biodiversity Hotspot’, one of the most biodiverse and threatened ecosystems in the world (Giraudo et al. 2003; Ribeiro et al. 2009). The region that include Santa Fe city was proposed as both regional and worldwide priority area for conservation efforts (Dinerstein et al. 1995; Myers et al. 2000; Arzamendia and Giraudo 2012). As the increase in the extension of Santa Fe city towards the surrounding cities may impact on biodiversity, we investigated the relationship between the urban matrix structure and bird communities in order to establish some base guidelines to contribute to its growth. We hope this will contribute to urban planning in other growing cities like Santa Fe in the biodiversity hotspot of the Paraná river system. We used a ‘guild approach’ and an ‘urban gradient approach’ to represent

the bird community and the urban areas, respectively (McDonnell and Pickett 1990). We hypothesized that if habitat structure and human disturbance, as measured by passing pedestrian and vehicle rates, are substantially different along an urban gradient, the diversity of trophic guilds should also vary accordingly (Blair 1996).

## Material and methods

### Study area

The study was conducted in Santa Fe city (31°38'0" S, 60°42'0" W), Argentina (Figure 1). Santa Fe covers an approximate area of 1156 km<sup>2</sup> and houses 525,093 people (INDEC 2010). It has a temperate climate; the mean daily temperature is about 19.55°C and the approximate annual rainfall is 990.4 mm (National Meteorological Services, <http://www.smn.gov.ar/>). The topography is flat. The major primeval vegetation types in Santa Fe have been included in the Paranaense (Interior Atlantic Forest) and Espinal phytogeographic province confluence, and the area is strongly influenced by the flood valley of the Paraná River, which is composed of subtropical wet forest and gallery forest where the most abundant species are *Salix humboldtiana*, *Tessaria integrifolia*, *Nectandra falciifolia*, *Albizia inundata*, *Erythrina crista-galli* and different types of flooded savannahs and wetlands (rivers, streams, ponds and estuaries) (Cabrera 1994; Arzamendia and Giraudó 2004). Santa Fe is bordered by the confluence between the Salado River and streams of the Paraná floodplain to the south, by the Salado River to the west and by Colastiné River and Setúbal Lake to the east.

### Urban gradient

According to Leveau and Leveau (2004), Perepelizin and Faggi (2009) and Sequeira et al. (2003), we determined different levels of development inside Santa Fe city to place our transects (Figure 1): (1) the urban sector, represented by the commercial and administrative centre of the city, is dominated by tall buildings and there are not green spaces available; (2) the suburban sector, composed of detached houses located within the urban matrix, with lawned sidewalks, yards and paved roads; (3) the periurban area, located on the boundary of the city and composed of detached houses with yards and unpaved roads, is near rural zones and natural patches and there is green space available; (4) the forested sector, represented by urban parks which are green spaces surrounded by urbanized areas and composed of both exotic and native vegetation planted by man; (5) the natural or semi-natural area which includes the biological reserve located inside the National University of the Littoral and adjacent areas, and consists of a remnant of native vegetation.

### Bird surveys

We placed 10 transects 100 m long × 50 m wide in each level of development, separated from each other by at least 200 m. In the forested and natural strata, transects were separated at least by 150 m due to the smaller area of the strata. We consider that these distances were enough to avoid pseudo-replication (getting records of birds that could

come from nearby transects). Several works on urban birds use similar distances (e.g. Leveau 2013). Morning walking surveys were conducted along transects approximately from 7:00 to 11:00 am on days without wind or rain. In each transect, the observer walked along 100 m in a 10 min period four times, one for each season during 2012. All birds making use of sample units were counted whether perched, singing, or feeding. High flying birds were not counted. The species identification was aided by use of binoculars. Species were categorized by feeding habits and preferred foraging strata of vegetation, according to Giraudo et al. (2008) and Casenave and Filipello (1995), as follows: aquatic diving carnivore; aquatic striding carnivore; hawkling aerial carnivore; aquatic filter; foliage granivore; generalized granivore; terrestrial granivore; coursing aerial insectivore; foliage insectivore; hawkling aerial insectivore; bark insectivore; generalized insectivore; terrestrial insectivore; nectarivore; foliage omnivore; generalized omnivore; terrestrial omnivore; aquatic diving omnivore; and aquatic striding omnivore. We differentiated the carnivore species from insectivores due to the ecological differences between 'strict insectivores', and the recorded carnivore species which basically feed on vertebrates (Ortega-Álvarez and MacGregor-Fors 2009).

### **Measures of habitat**

In each transect, we estimated the percentage of area covered by trees/shrubs, herbaceous vegetation, pavement, high and low buildings (two-story building as threshold), water bodies and bare soil through direct field observations. We corrected our field measures with those obtained from the detailed Google Earth 2012 images (Table 1). In each transect there were two researchers, so the counts of the numbers of pedestrians and vehicles were done simultaneously with the bird survey. Percentage values of coverage of habitat structure variables and human disturbance rates were averaged between all seasons.

### **Statistical analyses**

We defined the trophic guild richness and abundance for each transect as the total number of trophic guilds recorded and total number of individuals recorded per trophic guild, respectively. We first calculated a detrended correspondence analysis (DCA) to estimate the gradient length covered by the data. A length of first DCA axis <3 indicates a linear response, a length of >4 a unimodal response (Lepš and Šmilauer 2003). In our

**Table 1.** Habitat structure and human disturbance variables along the urban gradient in Santa Fe city.

Variable	Code	Mean	Standard deviation
High buildings	BHIGH	4.28	9.40
Low buildings	BLOW	33.70	30.39
Pavement	PAVEM	12.57	10.98
Herbaceous vegetation	GRASS	34.31	32.16
Trees and shrubs	TREESHUB	23.00	27.64
Bare soil	UNPSOIL	1.26	2.88
Water bodies	WATERB	4.97	11.35
Pedestrian rate	PEDESR	2.69	6.62
Vehicle rate	VEHICLR	2.46	3.67

case, the first DCA axis had lengths of 1.7409 and 1.9211 for trophic guild richness and abundance, respectively. Therefore, we chose a redundancy analysis (RDA), instead of a canonical correspondence analysis (CCA), as a constrained ordination technique (Ter Braak and Smilauer 2002). RDA uses a linear model of relationships among the variables in the response matrix and between the variables in the explanatory and response matrices. RDA consists of a series of multiple linear regressions followed by an eigenvalue decomposition of the table of fitted values. The canonical ordination vectors obtained are linear combinations of the response variables. This means that each ordination vector is a one-dimensional projection of the distribution of the objects in a space that preserves the Euclidean distances among them. These ordination vectors are also constrained to be linear combinations of explanatory variables. Therefore, RDA provides the proportion of variance of the response data that is accounted for by the explanatory variables (Legendre and Legendre 1988; Markarenkov and Legendre 2002).

As spatial autocorrelation can inflate Type I errors in statistical analyses (Diniz-Filho et al. 2003), we incorporated the spatial structure of the data within the modelling process. Spatial autocorrelation can be defined as the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations (Legendre 1993). Similarly, environmental variables used to describe the study area are structured by physical processes causing gradients and/or patchy structures. One consequence of this general property of ecological variables is that the assumption of independence of the observations is not respected (Legendre 1993). In addition, geographically contagious biotic processes (such as population growth, geographic dispersal, differential fertility or mortality, social organization, or intra and interspecific interactions) also can promote spatial autocorrelation in species distribution (Griffith and Peres-Neto 2006). We computed a matrix of shortest distances (portion of a great circle) among the centroids of transects, using the 'earth.dist' function from the 'fossil' package (Vavrek 2011). Principal coordinates of neighbour matrices (PCNM) were used to generate spatial variables (Borcard and Legendre 2002; Dray et al. 2006), using the 'pcnm' function from the vegan package (Oksanen et al. 2016). PCNM variables represent a spectral decomposition of the spatial relationships among the study sites that can be computed for regular or irregular sets of points in space (Borcard et al. 2004). The latter was the case for our sampling design. In order to truncate the distance matrix, the threshold value used in the PCNM analysis was the minimum distance that kept all sampling sites connected using a minimum-spanning-tree procedure. We included only coordinates corresponding to positive eigenvalues in the data analyses as spatial predictor variables.

We carried out two redundancy analyses (Ter Braak and Smilauer 2002) to test whether environmental and spatial variables were associated with a fraction of the urban trophic guild richness and abundance variation. For environmental variables, the variance inflation factor (VIF) was used for detecting the presence of multicollinearity among the environmental variables in the RDA.  $VIF > 10$  indicates multicollinearity (Zuur et al. 2010). We retained all the environmental variables into the subsequent analysis, except the percentage of area covered by low buildings ( $VIF = 12.36$ ). We performed a forward selection of parameters, including only significant variables in the final model. In all cases the alpha level of significance was set to 0.05. Only the significant terms were



incorporated in the subsequent ordination constrained analyses to avoid the artificial increase of explained variation by chance.

By making two canonical ordinations, each of them constrained by one set of explanatory variables, we obtained a measure of the effects of the environmental conditions and the spatial structure that are not independent because of the spatially structured environmental descriptors (Smith and Lundholm 2010). We applied variation partitioning to assess the unique and joint fractions of variation explained by the environmental and spatial datasets. This partition is possible by using the sum of all canonical eigenvalues of two canonical ordinations, each of them constrained by one set of explanatory variables, and of two partial canonical ordinations, each of them constrained by one set of explanatory variables while controlling for the effect of the others (covariables) (Borcard et al. 1992). Variation partitioning was implemented as function 'varpart' in the 'vegan' package (Oksanen et al. 2016). We reported the variation explained in each RDA model as the adjusted R<sup>2</sup> (R<sup>2</sup><sub>adj</sub>), which takes the number of predictor variables and sample size into account to prevent the inflation of R<sup>2</sup> values (Peres-Neto et al. 2006). When a negative R<sup>2</sup><sub>adj</sub> was obtained, we interpreted it as a zero value (Peres-Neto et al. 2006), meaning that not all fractions of one variation partitioning always add up to a perfect 100%. To test the significance of the influence of both explanatory matrices, we used the function 'permutest' that is a permutation test with 99,999 permutations. This test shows whether a fraction of variables significantly explains variation in the response matrix.

In our study, the trophic guild richness and abundance matrices consisted of the average amount of species and individuals per trophic guilds between all seasons (columns) and transects (rows), respectively. The environmental explanatory matrix consisted of the percentage of area covered by trees/shrubs, herbaceous vegetation, pavement, high buildings, low buildings, water bodies, bare soil, passing pedestrian and vehicle rate (columns) per transect (rows). And the spatial explanatory matrix consisted of the coordinates corresponding to positive eigenvalues obtained from the PCNM.

The RDA allows a visual interpretation of multiple habitat dimensions by plotting trophic guilds and environmental variables in the ordination diagram formed by two canonical axes obtained by the 'environmental' RDA. Type-2 scaling was used to make the biplots. On such a biplot, environmental variables are depicted by lines. The length of each line represents the relative importance of the environmental variable to the community distribution (in the two-dimensional plane under consideration) (Ter Braak 1986). The further the trophic guild points are from the origin, the more informative the ordination: a cluster of species near the origin is difficult to interpret and indicates a weak trophic guild-environment relationship (Ter Braak 1986).

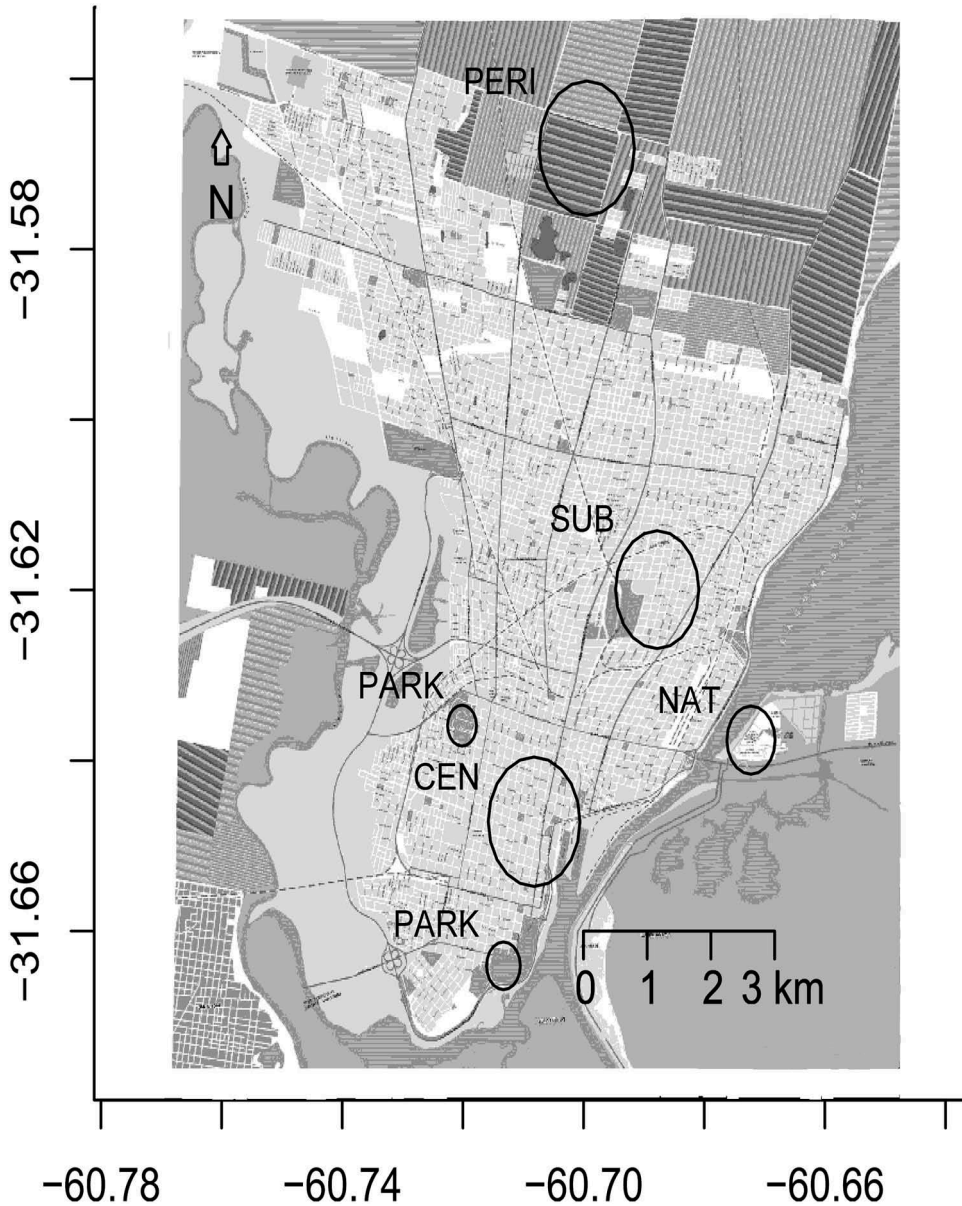
## Results

### *Avian assemblage composition*

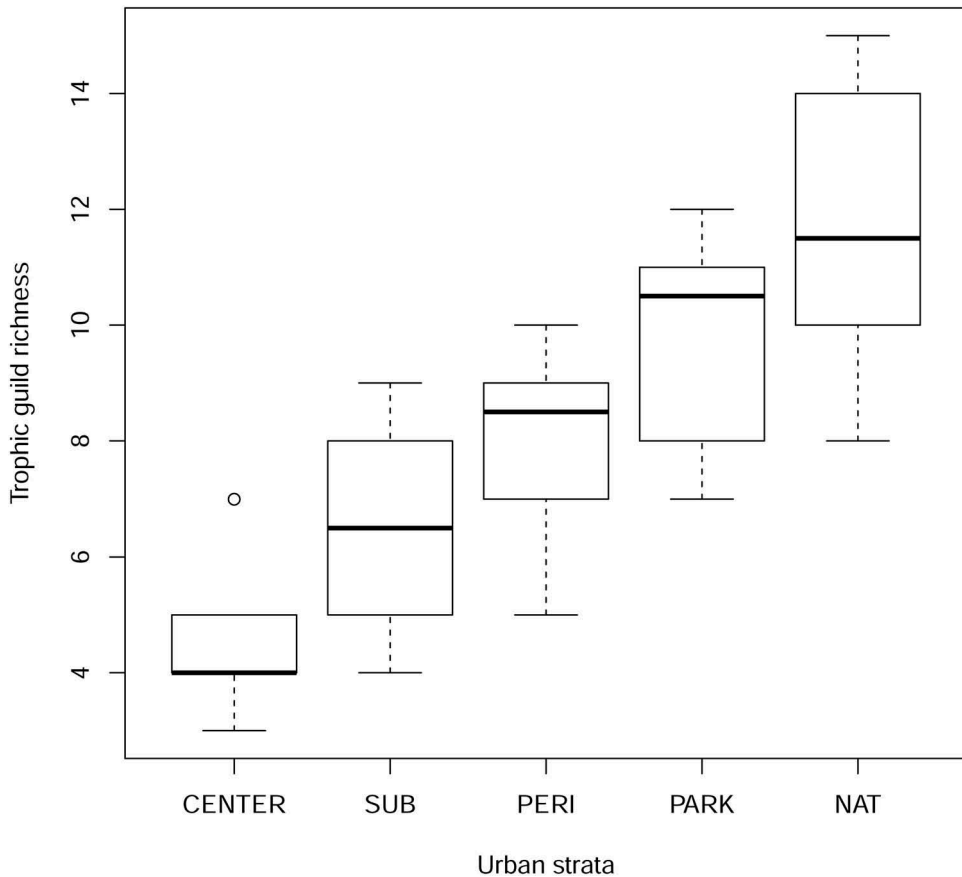
We obtained 6452 records from 99 bird species (Appendix A). A total of 1251 records came from 12 species in the urban sector, 936 records from 19 species in the suburban area, 1011 records from 26 species in the periurban sector, 2079 records from 43 species



in the forested sector, and 1175 records from 79 species in the natural area. The number of species recorded in Santa Fe city corresponds to the 23% of all known bird species for Santa Fe province (Fandiño and Giraudo 2010). The amount of trophic guilds increased as the level of urbanization decreased (Figure 2).



**Figure 1.** Santa Fe city and strata of the urban gradient indicated by circles. The urban matrix is represented by white and water bodies and forested areas with shades of grey. References: urban (CEN), suburban (SUB), periurban (PERI), forested (PARK) and natural (NAT) sectors.

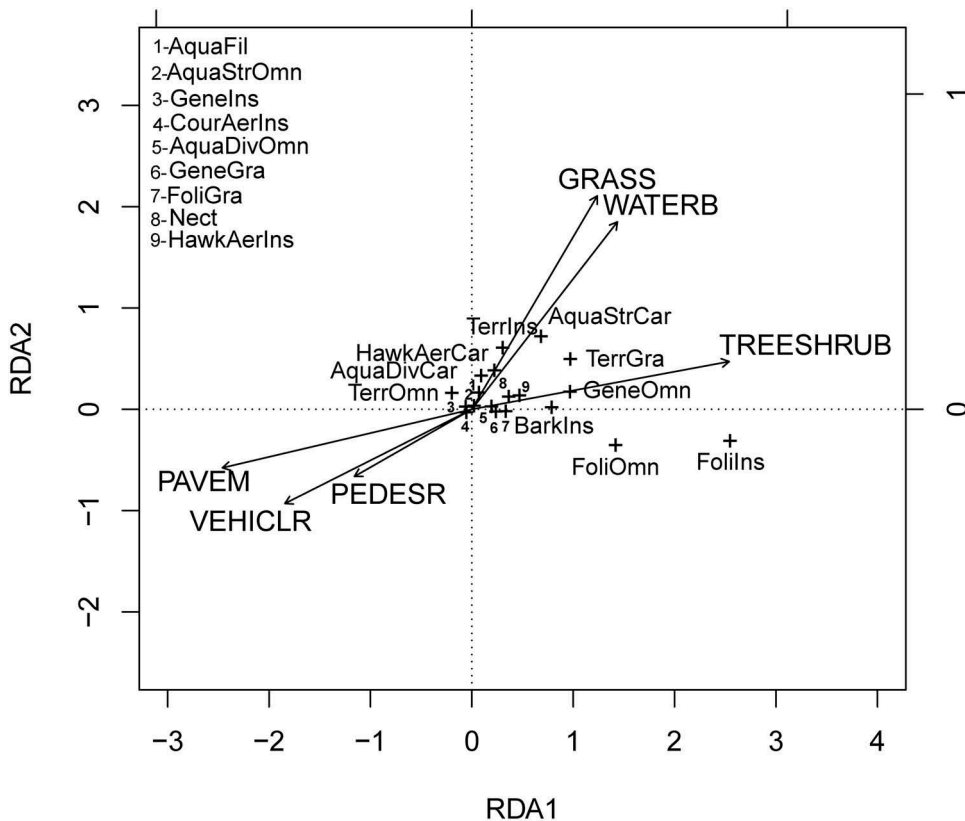


**Figure 2.** Exploratory boxplot showing the richness of trophic guilds (number of trophic guilds per transect) at each urban stratum of the urban gradient. References: urban (CENTER), suburban (SUB), periurban (PERI), forested (PARK) and natural (NAT) sectors.

### ***Factors affecting trophic guild composition of the bird community in the urban environment***

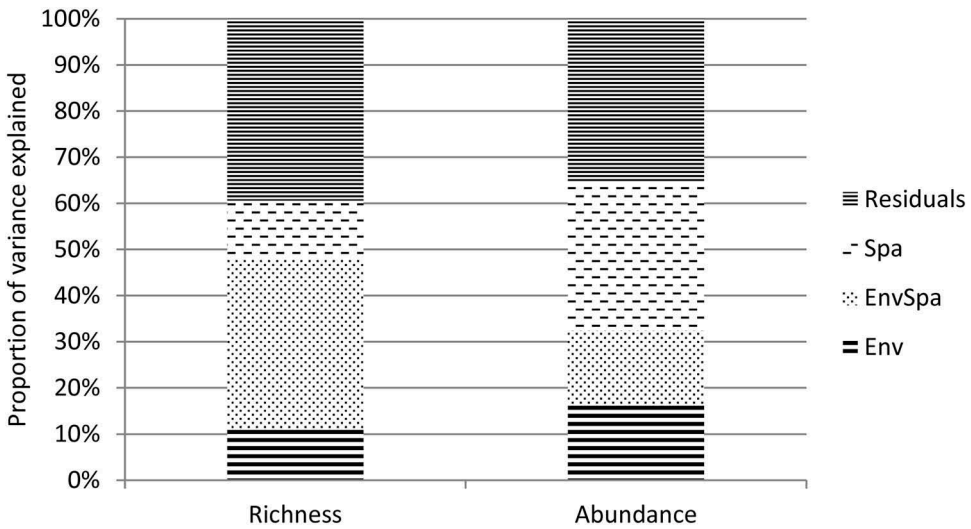
#### ***Guild richness***

We obtained a significant relationship between the richness trophic guilds and the habitat structure variables of percentage of area covered by trees/shrubs, herbaceous vegetation, pavement, water bodies and human disturbance variables (RDA: adjusted- $R^2 = 0.47951$ ,  $F = 8.523538$ ,  $P = 1e-05$ ). Most of the trophic guilds had a positive relationship with the percentage of area covered by trees and shrubs, water bodies and herbaceous vegetation and had negative relationships with pavement and human disturbance variables (pedestrian and vehicles rate) (Figure 3). Trophic guilds associated to some of the vegetation strata in terms of their food resources (such as foliage insectivores, foliage omnivores, bark insectivores and nectarivores) or foraging behaviour (such as hawking aerial insectivores and hawking aerial carnivores) increased their richness towards urban green spaces and natural areas. Availability of water bodies determined a higher richness of the aquatic diving carnivores in the



**Figure 3.** Biplot of redundancy analysis (RDA) showing the association between the richness of each trophic guild and significant habitat structure and human disturbance variables along the urban gradient. Arrow length indicates the importance of the variable in the model and arrow orientation, the direction of the variable increase. References: percentage of area covered by trees/shrubs (TREESHURB); herbaceous vegetation (GRASS); water bodies (WATERB); pavement (PAVEM); pedestrian rate (PEDES); and vehicle rate (VEHICLR). Guilds: aquatic diving carnivore (AquaDivCar); aquatic diving omnivore (AquaDivOmn); aquatic filter (AquaFil); aquatic striding carnivore (AquaStrCar); aquatic striding omnivore (AquaStrOmn); bark insectivore (Barklns); coursing aerial insectivore (CourAerlns); foliage granivore (FoliGra); foliage insectivore (FoliIns); foliage omnivore (FoliOmn); generalized granivore (GeneGra); generalized insectivore (Genelns); generalized omnivore (GeneOmn); hawking aerial carnivore (HawkAerCar); hawking aerial insectivore (HawkAerlns); nectarivore (Nect); terrestrial granivore (TerrGra); terrestrial insectivore (Terrlns); and terrestrial omnivore (TerrOmn).

forested and natural sectors, whereas generalized omnivores, terrestrial granivores and terrestrial insectivores seemed to increase their richness towards natural habitats (Figure 3). Environmental matrix (i.e. environmental alone and spatial structure of environmental variables) accounted for 60.59% of the variation in the trophic guild richness. Spatial component of the variation partitioning explained 12.64% of variation in the response matrix. Thirty-nine per cent of the variance in the trophic guild richness remained unexplained (Figure 4). We did not find a clear relationship between environmental variables and aquatic striding omnivores, generalized insectivores and coursing aerial insectivores. This may be because of the small sample size of some of their component species.



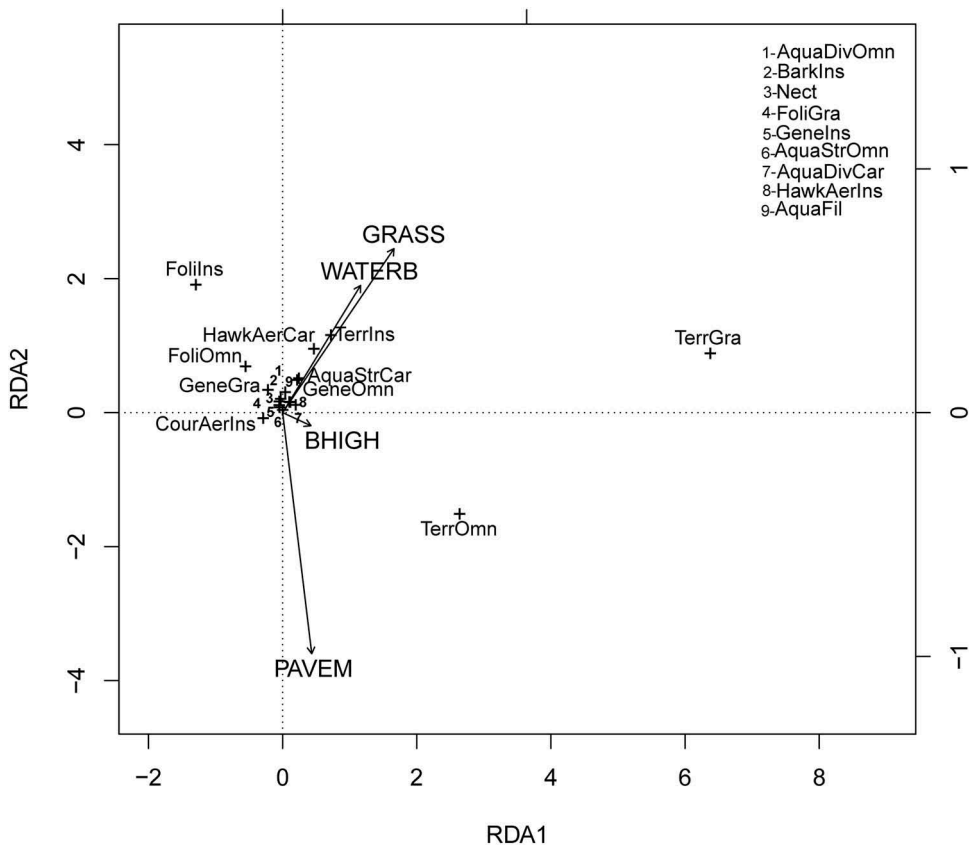
**Figure 4.** Proportion of variance of the purely environmental (Env), spatially structured environmental (EnvSpa) and purely spatial components (Spa) which explain the richness (left) and abundance (right) of trophic guilds across the Santa Fe city.

### **Guild abundance**

We found a significant relationship between the abundance of trophic guilds and the habitat structure variables of the percentage of area covered by herbaceous vegetation, pavement, tall buildings and water bodies (RDA: adjusted-R<sup>2</sup> = 0.32448, F = 6.884082, P = 8e-05). Conversely, we did not detect significant relationship between trophic guild abundances and percentage of area covered by bare soil and tree/shrub. However, since the latter had a *p*-value of 0.064 – slightly higher than 0.05 – it was not included in the model. No significant relationships between guild abundance and human disturbance variables were detected. Most of the trophic guild abundance had a positive relationship with the percentage of area covered by herbaceous vegetation and water bodies and had a negative relationship with pavement and high buildings (Figure 5). The trophic guilds associated to urban habitats were terrestrial omnivores and coursing aerial insectivores, whose abundances were higher as levels of urbanization increased. Variation partitioning revealed that both environmental and spatial matrices accounted for 64.6% of the variation in the trophic guild abundance. Spatial component of the variation partitioning explained 32.16% of variation in the response matrix, the environmental component explained 16.42% of the variation and the spatially structured environmental component accounted for 16.02% of the explained variation. Thirty-five percent of the variance in the trophic guild abundance remained unexplained (Figure 4).

### **Discussion**

We showed that urbanization was strongly associated to the functional composition of the urban bird community in terms of diet and foraging habits. Among trophic guilds, terrestrial omnivores and terrestrial granivores were composed of species that were related to high levels of urbanization and shared with other urban assemblages around



**Figure 5.** Biplot of redundancy analysis (RDA) showing the association between trophic guild abundance and significant habitat structure variables along the urban gradient. Arrow length indicates the importance of the variable in the model and arrow orientation, the direction of the variable increase. References: percentage of area covered by herbaceous vegetation (GRASS); pavement (PAVEM); high buildings (BHIGH) and water bodies (WATERB). Guilds: aquatic diving carnivore (AquaDivCar); aquatic diving omnivore (AquaDivOmn); aquatic filter (AquaFil); aquatic striding carnivore (AquaStrCar); aquatic striding omnivore (AquaStrOmn); bark insectivore (BarkIns); coursing aerial insectivore (CourAerIns); foliage granivore (FoliGra); foliage insectivore (FoliIns); foliage omnivore (FoliOmn); generalized granivore (GeneGra); generalized insectivore (GeneIns); generalized omnivore (GeneOmn); hawkling aerial carnivore (HawkAerCar); hawkling aerial insectivore (HawkAerIns); nectarivore (Nect); terrestrial granivore (TerrGra); terrestrial insectivore (TerrIns); and terrestrial omnivore (TerrOmn).

the world (Chace and Walsh 2006). Although the abundance of terrestrial omnivores was high in higher levels of urbanization, most trophic guilds identified in this study had peaks in richness and abundance at the forested and the natural sectors where natural features predominated. Moreover, most of the migrant species feeding on aerial insects and some trophic guilds related to aquatic habitats were recorded only where the natural features became prominent. No significant relationships were obtained between the abundance of trophic guilds and human disturbance. Hence, a growing city surrounded by natural patches and green spaces like Santa Fe should conserve the natural features and regulate the human activity across the urban system in order to enhance

the diversity of the bird community. Our results agree with studies which postulate that the higher the level of urban development, the lower the diversity of functional groups (Concepción et al. 2017; Suri et al. 2017). In addition, our urban gradient was determined with variables similar to those used in other studies around the world (Clergeau et al. 2006; MacGregor-Fors and Schondube 2011). Similar tendencies in the proportion of the cover of both anthropogenic and natural features in the urban matrix are due to the ecological structures produced by human activity in different biogeographical areas (Clergeau et al. 2001). Hence, human activity favoured the spread of natural and anthropogenic features which increase the homeostatic conditions of cities worldwide (McKinney 2006). The great abundance of terrestrial omnivores in the most urbanized side of the gradient and the wide variety of trophic guilds in the forested and natural sectors agreed with previous studies in different parts of the world (Conole and Kirkpatrick 2011; Ikin et al. 2012).

Most of the species identified along the urban gradient were generalist species in terms of their food resources and geographic distribution (Menon and Mohanraj 2016). *Passer domesticus* and *Columba livia* are common with other urban assemblages around the world and typical of the most intensely urbanized central business districts or downtown areas (Conole and Kirkpatrick 2011; Paker et al. 2014). *Zenaida auriculata*, *Molothrus bonariensis* and *Zonotrichia capensis* were also frequent along the urban gradient and are common with other urban assemblages at a more regional scale (Leveau and Leveau 2004, 2006; Juri and Chani 2005). These species are mainly omnivorous and granivorous, the most abundant trophic guilds identified in urban systems (Chace and Walsh 2006). In this study, the abundance of terrestrial omnivores and terrestrial granivores peaked at the forested sector, although only terrestrial omnivore abundance was also high in the most urbanized areas. The forested sector presented the highest values of coverage of herbaceous vegetation and a great amount of large trees. This favoured the foraging success of species included in these trophic guilds, e.g. *Passer domesticus*, *Columba livia* and *Zenaida auriculata*, which may subsist on supplementary foods such as bread and grains that are put out by people (Kark et al. 2007; Perepelizin and Faggi 2009; Tiwary and Urfi 2016). The high abundance of the coursing aerial insectivores in the urban sector can be explained only by the presence of *Progne chalybea*, the Grey-breasted Martin, a species that nests and feeds mainly in urban areas. By contrast, in the natural area, we found trophic guilds with both generalist and specialist habits. Since urban environments change constantly at temporal and spatial scales, generalist species may be more favoured than species that heavily depend on specific resources, environmental conditions and certain spatial and ecological processes for their survival (Sattler et al. 2010; Meffert and Dziocck 2013; Banville et al. 2017). Like in Leveau and Leveau (2004), trophic guilds associated to the vegetation strata were seen to increase their richness and abundance towards green areas (forested and sub-natural sectors), even if they presented generalist (such as foliage omnivores, generalized omnivores, generalized granivores) or specialist (such as foliage insectivores, bark insectivores, nectarivores, foliage granivores, hawking aerial insectivores and hawking aerial carnivores) habits. We agreed with Clergeau et al. (2006) who established that habitat quality and availability are important limiting factors in the urban colonization of many species. Although the nectarivore guild was composed of three species and results should be interpreted with care, we recorded a negative impact of urbanization. Leveau



(2013) established that the nectarivores were benefited by areas characterized by a great amount of flowering plants, while Pauw and Louw (2012) stated that the different response to urbanization within this trophic guild was mainly because of differences in feeding ecology. As was expected, bark insectivore species were highly related to natural habitats. On the other hand, both richness and abundance of woodpeckers and woodcreepers increased with increasing availability of trees and shrubs, as was also observed by Myczko et al. (2014). In addition, the strong relationship between these trophic guilds and forested and natural sectors was probably caused by a greater availability and diversity of native food resources (McKinney 2008; Fattorini 2011; Threlfall et al. 2016; Tiwary and Urfi 2016).

Habitat structure was greatly associated to the trophic guild composition of the urban bird community. Our results agree with previous findings, showing that trophic guild richness of the urban bird community was positively related to natural features (such as coverage of tree/shrub, herbaceous vegetation and water bodies) and negatively related to anthropogenic features (such as coverage of high buildings and pavement) (Leveau 2013; Silva et al. 2016). The availability of water bodies in parks and natural areas was strongly related to the appearance of aquatic diving carnivores and aquatic striding carnivore, whose food resource is obtained from water. The former predominated in the park though the latter, in natural areas. Adding more natural features, which are uncommon in the urban matrix, to the habitat structure, would help to enhance the avian diversity by increasing the spectrum of resources that cities offer to birds (Melles et al. 2003; Suri et al. 2017). Although most of the abundance patterns recorded in Santa Fe city cannot be explained in this study (the analysis explains 35% of data variability), results show that urbanization significantly affects the abundance of the different trophic guilds (Blair 2004; van Heezik et al. 2008), a fact that may be explained by predictors acting in different spatial or temporal scales (Melles et al. 2003; Blair 2004; Lee and Rotenberry 2015). Also, the increase of the trophic guild richness towards lower levels of urbanization and the presence of the richest trophic guilds such as bark insectivores and foliage insectivores in the greenest sectors indicate urban intensity affects negatively the urban bird communities, thus differing from previous studies reporting peaks in avian diversity at intermediate levels of urbanization (Blair 2004).

Previous studies showed that the richness and abundance of Neotropical migrants increase with increasing coverage of natural habitats. Migrant species were highly associated to vegetation structure (Chace and Walsh 2006; MacGregor-Fors et al. 2010). In this study we identified 11 migrant species, *Progne tapera* and *Progne chalybea* being the only migrant species that appeared also in areas with higher levels of urbanization. The rest of the migrant species were identified only in the natural sector. *Progne chalybea* may nest on buildings, feed on aerial insects and take advantage of resources that are not used by other insectivore species in the urban sector (Leveau and Leveau 2004; Kark et al. 2007). *Progne tapera* feeds on aerial insects, may take advantage of the resources found in the surrounding areas and heavily depends on abandoned nests of *Furnarius rufus* (Carpintero and Aramburú 2007).

Many studies have reported the influence of human disturbance variables in the diversity and functional composition of urban bird communities. Ortega-Álvarez and MacGregor-Fors (2009) found that the abundance and richness of species were



negatively related to passing cars and positively related to passing pedestrian rate. Carbó-Ramírez and Zuria (2011) and González-Oreja et al. (2012) observed that richness tended to increase in urban greenspaces where human disturbance variables, as measured by passing pedestrian and vehicle rate and background noise levels, were lower. Not all the general patterns described in previous studies can be applied in all cities worldwide since Meffert and Dziocck (2012) did not find human intrusion or occurrence of dogs to have a measurable effect on any of the bird species under study, while Paker et al. (2014) concluded the opposite. In this study, many trophic guilds increased their richness towards lower level of urbanization and only the abundance of terrestrial omnivores was positively associated to human disturbances.

Finally, we found that the richness and abundance of trophic guilds had a spatial structure. On the one hand, we could determine the proportion of the variation in the trophic guild composition explained by the habitat structure and human disturbances and the proportion explained by spatial predictors, with the least bias as possible (Lennon 2000; Diniz-Filho et al. 2003; Peres-Neto et al. 2006); and on the other hand, spatial structure may imply the occurrence of neutral mechanisms (Sattler et al. 2010). Therefore, future studies should consider multiple scales analyses to discover the neutral mechanisms that are operating in the bird assemblage in Santa Fe city and explain the variation in the trophic guild composition that could not be explained in this study.

## Conclusion

We demonstrated that the greater the availability of natural features belonging to previous pristine habitats in the urban matrix and the less human activity, the greater the spectrum of trophic guilds that are present. The forested and natural sectors were composed of natural features that are also found in the flood valley of the Paraná River where Santa Fe city is sited. The availability of different vegetation strata and water bodies are common features in the subtropical wet forest, gallery forest and wetlands. In these sectors, we recorded a wider variety of trophic guilds than in the more urbanized sectors. The growth of cities must be carried out in such a way as to protect natural patches and manage urban green spaces and the intensity of human activity across the city in order to counteract the filter imposed by urban systems on bird species (Kark et al. 2007; Croci et al. 2008; Yang et al. 2015; Silva et al. 2016). This may allow many species to colonize the urban matrix (Shimazaki et al. 2016). Finally, we hope that our study can contribute to the conservation of bird species in other growing cities like Santa Fe within the Paraná river system, because it provides a knowledge base to the management of the growing urban system structure.

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## References

- Arzamendia V, Giraudo A. 2004. Usando patrones de biodiversidad para la evaluación y diseño de áreas protegidas : las serpientes de la provincia de Santa Fe (Argentina) como ejemplo. *Revista Chilena de Historia Natural*. 77:335–348.
- Arzamendia V, Giraudo AR. 2012. A panbiogeographical model to prioritize areas for conservation along large rivers. *Divers Distrib*. 18:168–179.
- Banville MJ, Bateman HL, Earl SR, Warren PS. 2017. Decadal declines in bird abundance and diversity in urban riparian zones. *Landsc Urban Plan*. 159:48–61.
- Blair R. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecol and Society*. 9(5):2. <http://www.ecologyandsociety.org/vol9/iss5/art2>
- Blair RB. 1996. Land use and avian species diversity along an urban gradient. *Ecological Appl*. 6 (2):506–519.
- Bonier F, Martin PR, Wingfield JC. 2007. Urban birds have broader environmental tolerance. *Biol Lett*. 3(August):670–673.
- Borcard D, Legendre P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Modell*. 153:51–68.
- Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H. 2004. Dissecting the spatial structure of ecological data at multiple scales statistical reports. *Ecology*. 85(7):1826–1832.
- Borcard D, Legendre P, Drapeau P. 1992. Partialling out the spatial component of ecological variation. *Ecology*. 73(3):1045–1055.
- Cabrera AL. 1994. Regiones fitogeográficas argentinas. In: En Kugler WF, editor. *Enciclopedia argentina de agricultura y jardinería*. Tomo 2. 2da. edición. 1ra. reimpresión, Fascículo 1. Acme: Buenos Aires, Argentina; p. 1–85.
- Cao W, Li R, Chi X, Chen N, Chen J, Zhang H, Zhang F. 2017. Island urbanization and its ecological consequences: A case study in the Zhoushan Island, East China. *Ecol Indic*. 76:1–14.
- Carbó-Ramírez P, Zuria I. 2011. The value of small urban greenspaces for birds in a Mexican city. *Landsc Urban Plan*. 100(3):213–222.
- Carpintero DL, Aramburú RM. 2007. Presencia de *Caminicimex furnarii* (Hemiptera: Cimicidae) en nidos de golondrina (Passeriformes: Hirundinidae) en Argentina. *Rev la Soc Entomol Argentina*. 66:153–156.
- Casenave LD, Filipello AM. 1995. Las aves acuáticas de la Reserva Costanera Sur: cambios estacionales en la composición específica y en la abundancia de poblaciones y gremios. *El Hornero*. 14:9–14.
- Chace JF, Walsh JJ. 2006. Urban effects on native avifauna: a review. *Landsc Urban Plan*. 74(1):46–69.
- Clergeau P, Croci S, Jokimäki J, Kaisanlahti-Jokimäki M-L, Dinetti M. 2006. Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biol Conserv*. 127(3):336–344.
- Clergeau P, Jokimäki J, Savard J-PL. 2001. Are urban bird communities influenced by the bird diversity of adjacent landscapes? *J Appl Ecol*. 38(5):1122–1134.

- Concepción ED, Götzenberger L, Nobis MP, de Bello F, Obrist MK, Moretti M. 2017. Contrasting trait assembly patterns in plant and bird communities along environmental and human-induced land-use gradients. *Ecography (Cop)*. 40:753–763.
- Conole LE, Kirkpatrick JB. 2011. Functional and spatial differentiation of urban bird assemblages at the landscape scale. *Landsc Urban Plan*. 100(1–2):11–23.
- Croci S, Butet A, Clergeau P. 2008. Does urbanization filter birds on the basis of their biological traits? *Condor*. 110(2):223–240.
- Dinerstein E, Olson DM, Graham DJ, Webster AL, Primm SA, Bookbinder MP, Ledec G, World Wildlife Fund. 1995. A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. Washington (DC): The World Bank.
- Diniz-Filho JAF, Bini LM, Hawkins BA. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol Biogeogr*. 12:53–64.
- Dray S, Legendre P, Peres-Neto PR. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol Modell*. 196(3):483–493.
- Fandiño B, Giraudó AR. 2010. Revisión del inventario de aves de la provincia de Santa Fe, Argentina. *Revista FABICIB*. 14:116–137.
- Fattorini S. 2011. Insect extinction by urbanization: A long term study in Rome. *Biol Conserv*. 144(1):370–375.
- Filloy J, Bellocq MI. 2006. Spatial variations in the abundance of *Sporophila* seedeaters in the southern Neotropics: contrasting the effects of agricultural development and geographical position. *Biodivers Conserv*. 15:3329–3340.
- Fontana S, Sattler T, Bontadina F, Moretti M. 2011. How to manage the urban green to improve bird diversity and community structure. *Landsc Urban Plan*. 101(3):278–285.
- Giraudó A. 2009. Deforestación, defaunación como consecuencia de las actividades humanas en la llanura del Chaco Argentino. In: Morello JH, Rodríguez AF, editors. *El Chaco sin bosques: La Pampa o el desierto del futuro*. Buenos Aires: Orientació; p. 315–345. doi:10.1017/CBO9781107415324.004
- Giraudó AR, Krauczuk E, Arzamendia V, Povedano H. 2003. Critical analysis of protected areas in the Atlantic forest of Argentina. En: Galindo-Leal C, Câmara IG, editors. *State of the hotspots: atlantic forest*. Center for Applied Biodiversity Science. Washington (DC): Island Press.
- Giraudó AR, Matteucci SD, Alonso J, Herrera J, Abramson RR. 2008. Comparing bird assemblages in large and small fragments of the Atlantic Forest hotspots. *Biodivers Conserv*. 17(5):1251–1265.
- González-Oreja JA, De La Fuente-Díaz-Ordaz AA, Hernández-Santín L, Bonache-Regidor C, Buzo-Franco D. 2012. Can human disturbance promote nestedness? Songbirds and noise in urban parks as a case study. *Landsc Urban Plan*. 104(1):9–18.
- Griffith DA, Peres-Neto PR. 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology*. 87(10):2603–2613.
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. 2008. Global change and the ecology of cities. *Science (New York, N.Y.)*. 319(5864):756–760.
- Herrera-Montes MI, Aide TM. 2011. Impacts of traffic noise on anuran and bird communities. *Urban Ecosyst*. 14(3):415–427.
- Ikin K, Knight E, Lindenmayer DB, Fischer J, Manning AD. 2012. Linking bird species traits to vegetation characteristics in a future urban development zone: implications for urban planning. *Urban Ecosyst*. 15:961–977.
- INDEC Dirección Nacional de Estadísticas Sociales y de Población. 2010. Dirección de Estadísticas Sectoriales en base al Censo Nacional de Población, Hogares y Viviendas 2010. World Wide Web. [accessed 2016 May 25]. [www.indec.mecon.gov.ar](http://www.indec.mecon.gov.ar).
- Juri MD, Chani JM. 2005. Variación en la composición de comunidades de aves a lo largo de un gradiente urbano (Tucumán, Argentina). *Acta Zoológica Lilloana*. 49:49–57.
- Kark S, Iwaniuk A, Schalimtzek A, Banker E. 2007. Living in the city: can anyone become an 'urban exploiter'? *J Biogeogr*. 34(4):638–651.
- Kennedy C, Cuddihy J, Engel-Yan J. 2007. The changing metabolism of cities. *J Ind Ecol*. 11(2):43–59.

- Lee MB, Rotenberry JT. 2015. Effects of land use on riparian birds in a semiarid region. *J Arid Environ.* 119:61–69.
- Legendre P. 1993. Spatial autocorrelation: trouble or New Paradigm. *Ecology.* 74(6):1659–1673.
- Legendre P, Legendre L. 1988. *Numerical ecology, volume 24 (Developments in Environmental Modelling) (Vol. 24)*. doi:10.1017/CBO9781107415324.004
- Lennon JJ. 2000. Red-shifts and red herrings in geographical ecology. *Ecography.* 23:101–113.
- Lepš J, Šmilauer P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge: Cambridge University Press.
- Leveau C, Leveau L. 2006. Ensembles de aves en calles arboladas de tres ciudades costeras del sudeste de la provincia de Buenos Aires, Argentina. *Hornero.* 21(1):25–30.
- Leveau L, Leveau C. 2004. Comunidades de aves en un gradiente urbano de la ciudad de Mar del Plata, Argentina. *Hornero.* 19(1):13–21.
- Leveau LM. 2013. Bird traits in urban–rural gradients: how many functional groups are there? *J Ornithol.* 154(3):655–662.
- Leveau LM, Leveau CM, Villegas M, Cursach JA, Suazo CG. 2017. Bird communities along urbanization gradients: a comparative analysis among three neotropical cities. *Ornitol Neotrop.* 28:77–87.
- Lim HC, Sodhi NS. 2004. Responses of avian guilds to urbanisation in a tropical city. *Landsc Urban Plan.* 66:199–215.
- Lin T, Coppack T, Lin Q, Kulemeyer C, Schmidt A, Behm H, Luo T. 2012. Does avian flight initiation distance indicate tolerance towards urban disturbance? *Ecol Indic.* 15(1):30–35.
- Long X, Ji X, Ulgiati S. 2016. Is urbanization eco-friendly? An energy and land use cross-country analysis. *Energy Policy.* 2006:387–396.
- MacGregor-Fors I, Morales-Pérez L, Schondube JE. 2010. Migrating to the city: responses of neotropical migrant bird communities to urbanization. *Condor.* 112(4):711–717.
- MacGregor-Fors I, Schondube JE. 2011. Gray vs. green urbanization: relative importance of urban features for urban bird communities. *Basic Appl Ecol.* 12(4):372–381.
- Markarenkov V, Legendre P. 2002. Nonlinear redundancy analysis and canonical correspondence analysis based on polynomial regression. *Ecol.* 83(4):1146–1161.
- Matsuba M, Nishijima S, Katoh K. 2016. Effectiveness of corridor vegetation depends on urbanization tolerance of forest birds in central Tokyo, Japan. *Urban Forest Urban Green.* 18:173–181.
- Mcdonnell AMJ, Pickett STA. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology published by: Ecological Society of America Stable. 71(4):1232–1237. <http://www.jstor.org/stable/1938259>.
- McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. *Biol Conserv.* 127(3):247–260.
- McKinney ML. 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst.* 11:161–176.
- Meffert PJ, Dziocck F. 2012. What determines occurrence of threatened bird species on urban wastelands? *Biol Conserv.* 153:87–96.
- Meffert PJ, Dziocck F. 2013. The influence of urbanisation on diversity and trait composition of birds. *Landsc Ecol.* 28(5):943–957.
- Melles S, Glenn S, Martin K. 2003. Urban bird diversity and landscape complexity: species – environment associations along a multiscale habitat gradient. *Conserv Ecol.* 7(1):5.
- Menon M, Mohanraj R. 2016. Temporal and spatial assemblages of invasive birds occupying the urban landscape and its gradient in a southern city of India. *J Asia-Pacific Biodivers.* 9(1):74–84.
- Myczko L, Rosin ZM, Skórka P, Tryjanowski P. 2014. Urbanization level and woodland size are major drivers of woodpecker species richness and abundance. *PLoS One.* 9(4):e94218.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J. 2000. Biodiversity hotspot for conservation priorities. *Nature.* 403:853–858.
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, et al. 2016. *Vegan: Community Ecology Package*. R package version 2.4-1. [accessed 2016 July 25]. <https://CRAN.R-project.org/package=vegan>.

- Ortega-Álvarez R, MacGregor-Fors I. 2009. Living in the big city: effects of urban land-use on bird community structure, diversity, and composition. *Landsc Urban Plan.* 90(3–4):189–195.
- Paker Y, Yom-Tov Y, Alon-Mozes T, Barnea A. 2014. The effect of plant richness and urban garden structure on bird species richness, diversity and community structure. *Landsc Urban Plan.* 122:186–195.
- Pauchard A, Aguayo M, Peña E, Urrutia R. 2006. Multiple effects of urbanization on the biodiversity of developing countries: the case of a fast-growing metropolitan area (Concepción, Chile). *Biol Conserv.* 127(3):272–281.
- Pauw A, Louw K. 2012. Urbanization drives a reduction in functional diversity in a guild of nectar-feeding birds. 17(2):27. doi:10.5751/ES-04758-170227
- Perepelizin PV, Faggi AM. 2009. Diversidad de aves en tres barrios de la ciudad de Buenos Aires, Argentina. *Multequina.* 18:71–85.
- Peres-Neto PR, Legendre P, Dray S, Borcard D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology.* 87(10):2614–2625.
- Reynaud P, Thioulouse J. 2000. Identification of birds as biological markers along a neotropical urban–rural gradient (Cayenne, French Guiana), using co-inertia analysis. *J Environ Manage.* 59:121–140.
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. Brazilian Atlantic Forest: how much is left and how is the remaining forest distributed? Implications for conservation. *Biol Conserv.* 142:1141–1153.
- Rossetti MA, Giraudo AR. 2003. Comunidades de aves de bosques fluviales habitados y no habitados por el hombre en el río Paraná Medio, Argentina. *Hornero.* 18(2):89–96.
- Sattler T, Borcard D, Arlettaz R, Bontadina F, Legendre P, Obrist MK, Moretti M. 2010. Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology.* 91(11):3343–3353.
- Sequeira G, Vanasco G, Enria D, Calderon G, Canal A. 2003. Distribución de Pequeños Mamíferos en la Ciudad de Santa Fe, Argentina. *Revista FAVE-Ciencias Veterinarias.* 2(1):7–17.
- Shimazaki A, Yamaura Y, Senzaki M, Yabuhara Y, Akasaka T, Nakamura F. 2016. Urban permeability for birds: an approach combining mobbing-call experiments and circuit theory. *Urban Forest Urban Green.* 19:167–175.
- Silva CP, Sepúlveda RD, Barbosa O. 2016. Nonrandom filtering effect on birds: species and guilds response to urbanization. *Ecol Evol.* 6(11):3711–3720.
- Smith TW, Lundholm JT. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography.* 33(November 2009):648–655.
- Soijet M, Rodríguez M, Tonini R, Mantovani G, Gramaglia V, Celeste M, ... Uriarte Y. 2012. Observatorio Del Área Metropolitana Santa Fe-Paraná (Amsf-P). *Cuaderno Urbano Espacio Cultura Sociedad.* 13(13):149–174.
- Suri J, Anderson PM, Charles-Dominique T, Hellard E, Cumming GS. 2017. More than just a corridor: a suburban river catchment enhances bird functional diversity. *Landsc Urban Plan.* 157:331–342.
- Ter Braak CJ, Smilauer P 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Ithaca, New York: Microcomputer Power. [www.canoco.com](http://www.canoco.com)
- Ter Braak CJF. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology.* 67(5):1167–1179.
- Threlfall CG, Williams NSG, Hahs AK, Livesley SJ. 2016. Approaches to urban vegetation management and the impacts on urban bird and bat assemblages. *Landsc Urban Plan.* 153:28–39.
- Tiwary NK, Urfi AJ. 2016. Spatial variations of bird occupancy in Delhi: the significance of woodland habitat patches in urban centres. *Urban Forest Urban Green.* 20:338–347.
- United Nations. 2008. World urbanization prospects: the 2007 revision. In United Nations, Department of Economic and Social Affairs, Population Division [CD-ROM]. CD-ROM: Data in digital form (POP/DB/WUP/Rev.2007).
- van Heezik Y, Smyth A, Mathieu R. 2008. Diversity of native and exotic birds across an urban gradient in a New Zealand city. *Landsc Urban Plan.* 87(3):223–232.

- van Rensburg BJ, Peacock DS, Robertson MP. 2009. Biotic homogenization and alien bird species along an urban gradient in South Africa. *Landscape Urban Plan.* 92(3–4):233–241.
- Vavrek MJ 2011. Fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica*. [accessed 2016 July 25]:[14:1T]. [http://palaeo-electronica.org/2011\\_1/238/index.html](http://palaeo-electronica.org/2011_1/238/index.html).
- Vignoli L, Scirè S, Bologna MA. 2013. Rural–urban gradient and land use in a millenary metropolis: how urbanization affects avian functional groups and the role of old villas in bird assemblage patterning. *Web Ecol.* 13(1):49–67.
- Yang G, Xu J, Wang Y, Wang X, Pei E, Yuan X, Wang Z. 2015. Evaluation of microhabitats for wild birds in a Shanghai urban area park. *Urban Forest Urban Green.* 14(2):246–254.
- Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol.* 1:3–14.