

Urbanization as a driver of taxonomic, functional, and phylogenetic diversity losses in bird communities

Facundo X. Palacio, Lucía M. Ibañez, René E. Maragliano, and Diego Montalti

Abstract: Urbanization is one of the most important threats to biodiversity worldwide, as it drives declines in species diversity, functional diversity, and phylogenetic diversity and increases functional redundancy among species. We estimated taxonomic, functional, and phylogenetic diversities, as well as the abundance of several functional groups, in bird communities from a town in east-central Argentina in 1985–1986 and 30 years after (2015–2016). In 1985–1986, we found that taxonomic diversity (abundance, species richness, and alpha diversity), functional richness, and basal phylogenetic diversity were negatively related to building cover, whereas terminal phylogenetic diversity showed a positive relationship with building cover. Moreover, the abundance of specialized functional groups (ground, aerial, and foliage insectivores; nectarivores/insectivores; ground/canopy and ground granivores) decreased with increased building cover, whereas the reverse pattern for the abundance of generalists (medium-sized/large and small omnivores) was found. In 2015–2016, by contrast, taxonomic, functional, and phylogenetic diversities were not related to building cover. Our results not only support the hypothesis that urbanization affects the potential number of ecosystem functions, but also that this relationship may change through time. Given the accelerated rate of urbanization worldwide, an integrative approach between different facets of biodiversity is promoted to gain insight into the response of bird communities in urban environments.

Key words: bird community, functional evenness, functional divergence, functional redundancy, functional richness, functional traits.

Résumé : L'urbanisation est l'une des plus grandes menaces pesant sur la biodiversité à l'échelle planétaire puisqu'elle entraîne le déclin d'espèces, des baisses de la diversité fonctionnelle et phylogénétique et l'augmentation de la redondance fonctionnelle entre espèces. Nous estimons les diversités taxonomique, fonctionnelle et phylogénétique et l'abondance de plusieurs groupes fonctionnels dans des communautés d'oiseaux d'une ville du centre-est de l'Argentine, en 1985–1986, puis 30 ans plus tard (2015–2016). Nous constatons que, en 1985–1986, la diversité taxonomique (abondance, richesse spécifique et diversité alpha), la richesse fonctionnelle et la diversité phylogénétique basale étaient négativement reliées à la couverture d'immeubles, alors que la diversité phylogénétique terminale présentait une relation positive avec la couverture d'immeubles. En outre, l'abondance de groupes fonctionnels spécialisés (insectivores terrestres, aériens et du feuillage; nectarivores/insectivores; granivores terrestres/de la canopée et terrestres) diminuait quand augmentait la couverture d'immeubles, alors que la relation inverse était observée pour l'abondance des généralistes (moyens/grands et petits omnivores). En revanche, en 2015–2016, les diversités taxonomique, fonctionnelle et phylogénétique n'étaient pas reliées à la couverture d'immeubles. Nos résultats appuient non seulement l'hypothèse voulant que l'urbanisation ait une incidence sur le nombre potentiel de fonctions écosystémiques, mais également la notion voulant que cette relation puisse changer dans le temps. Étant donné l'accélération de l'urbanisation à l'échelle planétaire, une approche qui intègre diverses facettes de la biodiversité est recommandée dans l'étude des réactions des communautés d'oiseaux en milieu urbain. [Traduit par la Rédaction]

Mots-clés : communauté d'oiseaux, uniformité fonctionnelle, divergence fonctionnelle, redondance fonctionnelle, richesse fonctionnelle, caractères fonctionnels.

Introduction

Urbanization has become one of the most severe threats to biodiversity worldwide, as it negatively impacts on ecosystem functions and processes (Vitousek et al. 1997; Alberti 2005; Aronson et al. 2014). Numerous studies have shown the impairing effects of urban landscapes on bird diversity through a reduction of species richness and changes in species composition (e.g., increase of exotic species, replacement of specialists by more generalist species; for reviews see the following: Marzluff 2001; McKinney 2008). However, the vast majority of these studies have focused on the effects of urban environments on taxonomic di-

versity (McKinney 2008). Although these studies have provided valuable knowledge of the effects of urbanization on bird communities, functional diversity (FD), defined as the range and value of functional traits within communities (Tilman 2001), has been proposed as a more direct measure of ecosystem functioning than taxonomic diversity, given the link between FD and ecosystem processes (Tilman et al. 1997; Díaz and Cabido 2001). In particular, the development of human infrastructure is expected to reduce FD and increase functional redundancy among species in a community as a result of trait and, therefore, function loss, in a process termed “functional homogenization” (Olden and Rooney 2006; Clavel et al. 2011). For instance, Pauw and Louw (2012) found

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that increased levels of urbanization declined diversity of nectarivorous birds in South Africa. Luck et al. (2013), Sacco et al. (2015), and Schütz and Schulze (2015) found that higher urbanization concomitantly decreased bird FD across different land uses in Australia, in a small city from Brazil, and in urban parks of Vienna, respectively. More recently, de Castro Pena et al. (2017) found that exposure to noise was the most limiting factor for FD in bird communities from a largely urbanized city from Brazil. By contrast, the effects of urbanization on functional redundancy remain understudied. The replacement of specialists by generalists with increased disturbance suggests that urbanization should favor functional redundancy, because generalists may be considered redundant as a result of high niche overlap (Clavel et al. 2011). Nevertheless, it has also been shown little or no compensation for lost ecosystem functions in highly urbanized areas (Pauw and Louw 2012, Huijbers et al. 2015). For instance, Pauw and Louw (2012) and Huijbers et al. (2015) found that pollination by certain nectarivorous birds and carrion removal by raptors, respectively, were lost as ecosystem functions in highly urban areas, suggesting a limited functional redundancy in urban environments. Therefore, these studies highlight the need for further research to understand how urbanization affects both FD and functional redundancy to maintain ecological processes in urban landscapes, which is a matter little explored, particularly in Latin America (MacGregor-Fors and Escobar-Ibáñez 2017).

Similarly, phylogenetic diversity (PD), defined as the amount of evolutionary history represented in the species of a given community (Mouquet et al. 2012), may be altered by the impacts of urbanization (Sol et al. 2017). Like FD, PD may predict ecosystem functioning, assuming that phylogeny represents functional differences in species from a community (Webb 2000; Flynn et al. 2011). Under this scenario, a negative effect of urbanization on PD is also expected based on the premise that urbanization drives trait and ecosystem function loss (Flynn et al. 2011; Cadotte et al. 2012; Sol et al. 2017). This process would lead to phylogenetic clustering, in which closely related species tend to share similar niches as a result of environmental filtering, thus reducing PD (Webb et al. 2002; Cavender-Bares et al. 2004; Knapp et al. 2008). A minority of studies have assessed the impacts of urbanization on bird PD by comparing urban vs. nonurban areas, evidencing evolutionary homogenization of bird communities (Morelli et al. 2016; Ibáñez-Álamo et al. 2017; Sol et al. 2017). However, the role of urbanization in PD patterns within the urban landscape remains unclear (Sol et al. 2017). Altogether, the use of taxonomic diversity, FD, and PD, as well as functional redundancy, is expected to give a broader picture of the processes underlying the effects of urbanization on bird communities.

Here, we tested the hypothesis that urbanization drives reductions in different facets of biodiversity, namely taxonomic diversity, FD, and PD, and increases in functional redundancy. To this end, we assessed the relationship between building cover and bird communities from an Argentinian town in 1985–1986 and 2015–2016. Specifically, we addressed how urbanization was related to (i) diversity components of bird communities (taxonomic diversity, FD, and PD) and (ii) groups of species with specific traits linked to ecosystem functions (functional groups). The main predictions were that bird diversity (taxonomic diversity, FD, and PD) and the abundance of specialized functional groups decreased with increased urbanization and that functional redundancy increased with higher levels of urbanization.

Materials and methods

Study area

The study was carried out in Llavallol (34°48'S, 58°26'W), Lomas de Zamora city, northeast Buenos Aires province, Argentina. The city has about 41 463 inhabitants and is located near the Río de La Plata shore, with a surface area covering 17 500 ha (INDEC 2001).

From 1980 to 2010, its population has increased ca. 20% (510 130 to 613 192 inhabitants; Grassi 2011). The area encompasses (i) built-up areas including residential areas with numerous gardens and tree avenues, as well as an important industrial zone, and (ii) hardwood plantations composed of tree privet (*Ligustrum lucidum* W.T. Aiton), pine (species of the genus *Pinus* L.), araucaria (species of the genus *Araucaria* Juss.), acacia (species of the genus *Acacia* Mill.), sycamore (species of the genus *Platanus* L.), gum (species of the genus *Eucalyptus* L'Hér.), oak (species of the genus *Quercus* L.), and ceiba (species of the genus *Ceiba* Mill.) (Maragliano et al. 2009). The climate is humid temperate, with a mean annual precipitation of 1000 mm and a mean annual temperature of 16.5 °C (Grassi 2011).

Bird counts and transect characterization

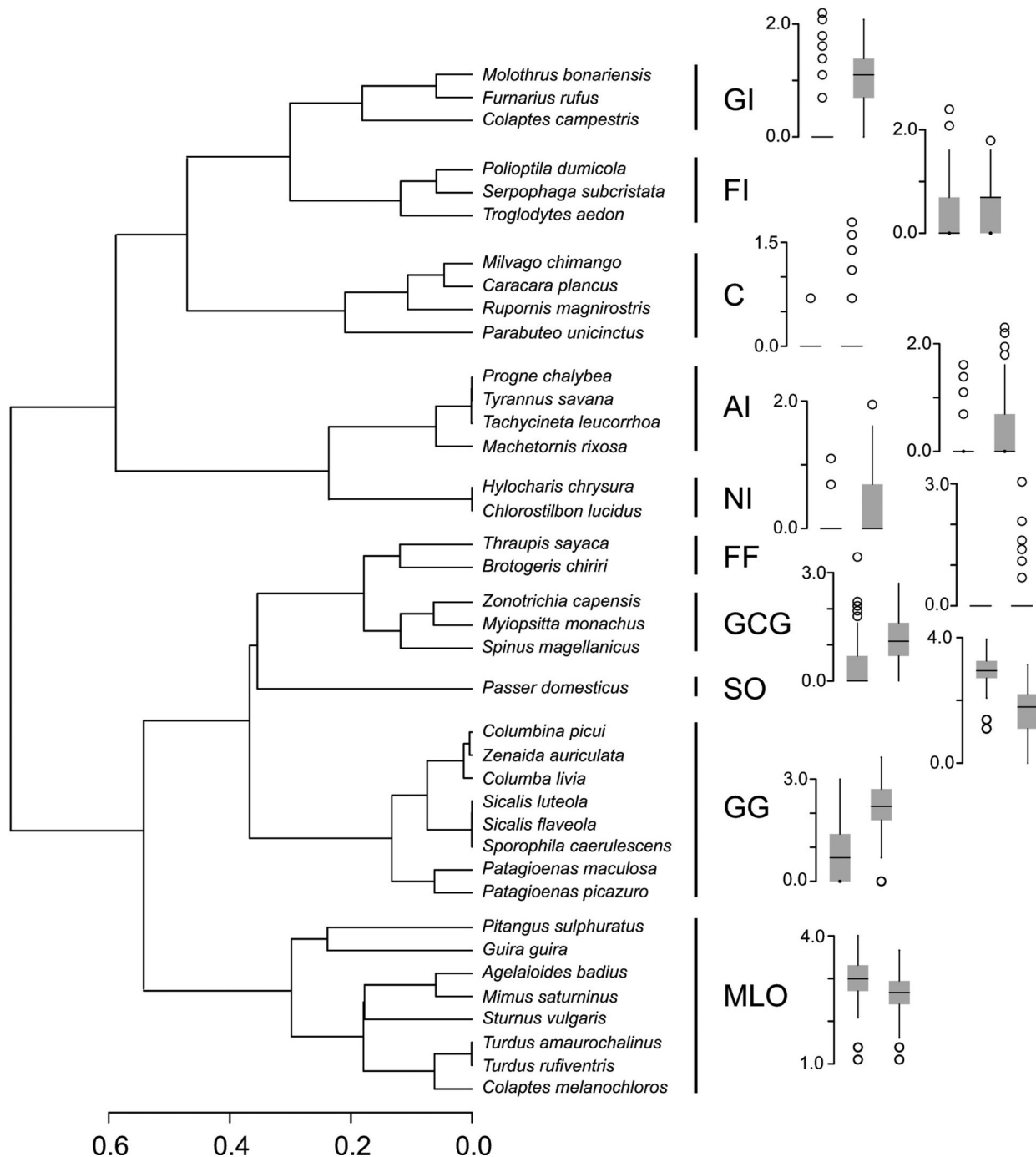
Bird counts were conducted following a line-transect method (Bibby et al. 2000) from April 1985 to March 1986 and from April 2015 to March 2016 (two complete years; hereafter referred to as years 1985 and 2015, respectively). Ten transects of 200 m × 50 m (1 ha) separated by at least 250 m were established on streets, in which the species and the number of all birds seen or heard were recorded. The sampled area represented 4.3% out of the entire study area (10 ha out of 232 ha). The same observer (R.E.M.) sampled the 10 transects every month in both years (except for June 1985 and February 1986 owing to inclement weather), within the 4 h after sunrise and in good weather conditions ($n = 100$ and 120 counts in 1985 and 2015, respectively). To characterize transects from each year, we measured the following environmental variables: tree cover (TC), lawn cover (LC), green cover (GC = TC + LC), building cover (BC), pavement cover (PC), concrete cover (CC = BC + PC), and bare soil (BS). Land-cover categories were measured on an aerial image provided by Instituto Geográfico Nacional (August 1984) and a GoogleEarth image (August 2015) from the study area using QGIS software (Quantum GIS Development Team 2011).

Diversity components

Abundance and species richness were estimated as the number of individuals and species, respectively, per transect and observation date. Alpha diversity was computed using the bias-corrected Shannon entropy estimator, a nearly unbiased estimator based on species accumulation curves outperforming other diversity measures (Chao et al. 2013). Species composition was characterized with nonmetric multidimensional scaling (NMDS; Kruskal and Wish 1978) based on a Bray–Curtis similarity matrix. NMDS is an ordination technique that functions iteratively by minimizing the difference between distance in the original matrix and distance in the reduced ordination space called “stress” (Legendre and Legendre 1998). The lower the stress, the better the approximation in reduced space. Empirical evidence and simulation studies have shown that a stress value of <0.2 gives an ordination sufficient to be interpreted in ecological terms (Clarke 1993). We then used the first two NMDS axes as variables accounting for species composition (Naidoo 2004; Cintra 2012). To assess which species accounted for differences in species composition between years, we used similarity percentages (SIMPER; Clarke 1993). This analysis first computes the mean Bray–Curtis similarity between all pairs of intergroup samples (i.e., samples from years 1985 vs. 2015). It then ranks the percentage species contributions to both within-group and between-group similarities (Clarke 1993). Species that contribute greatly to similarity within sites of a particular year are considered characteristic of that year. Most important species are considered to be those that contributed at least to 70% of the differences between years (Oksanen et al. 2015).

FD components were computed using the following functional traits (Palacio et al. 2016): mean body mass, food item (invertebrates, vertebrates, fruits, nectar, seeds), foraging substrate (water, ground, vegetation, air), and foraging method (pursuit, gleaning, reaching, pecking, scavenging, probing). Data (quantitative data for body mass and presence–absence data for the re-

Fig. 1. Functional relationships among 38 species recorded in Llavallol (northeast Buenos Aires province, Argentina) in 1985 and 2015. The dendrogram was produced by UPGMA (unweighted pair-group method with arithmetic averaging) algorithm of a Gower distance matrix computed from the functional traits of species. Horizontal distance represents separation in trait space. Boxplots depict mean log abundance per transect in 1985 (left) and 2015 (right). GI: ground insectivores; FI: foliage insectivores; C: carnivores; AI: aerial insectivores; NI: nectarivores/insectivores; FF: foliage frugivores; GCG: ground/canopy granivores; SO: small omnivores; GG: ground granivores; MLO: medium-sized/large omnivores.



main traits) were extracted from del Hoyo et al. (1994–2011), Wilman et al. (2014), and personal observations of the authors. The species by traits matrix was converted to a Gower distance matrix that was clustered through UPGMA (unweighted pair-group method with arithmetic averaging) algorithm to produce a dendrogram (Petchey and Gaston 2002; Fig. 1). We then computed four FD metrics that corresponded to four primary components of FD (Mouchet et al. 2010; Swenson 2014; McPherson et al. 2017): functional richness (FRic), functional evenness (FEve), functional

divergence (FDiv), and functional redundancy (FRed). FRic represents the amount of functional space occupied by a species assemblage, FEve corresponds to how regularly species abundances are distributed in the functional space, FDiv defines how far high species abundances are from the center of the functional space, and FRed represents the overlap between species in occupied functional space (Mouchet et al. 2010; McPherson et al. 2017). We used the measures detailed in Villéger et al. (2008) and Ricotta et al. (2016) to represent these four components. FD values were

Table 1. Descriptive measures of environmental variable changes (%) in the years 1985 and 2015 in Llavallol, northeast Buenos Aires province, Argentina.

Variable	Year 1985		Year 2015		Mean paired difference	t	P
	Mean	SD	Mean	SD			
Building cover	21.83	8.24	27.32	8.89	6.49	5.74	0.0003
Pavement cover	17.02	10.43	24.37	5.99	7.35	1.97	0.080
Concrete cover	38.87	16.95	51.70	12.75	12.83	3.08	0.014
Tree cover	13.64	6.19	12.10	8.55	-1.54	-0.75	0.472
Lawn cover	43.95	9.89	35.00	5.54	-8.95	-4.76	0.001
Green cover	57.56	12.23	47.09	11.29	-10.47	-4.10	0.003
Bare soil cover	3.57	6.53	1.21	2.47	3.57	1.33	0.217

Note: Results of paired t tests are shown. Values in boldface type are significant with $P < 0.05$.

standardized between 0.0 (lowest value) and 1.0 (highest value). Some transects had less than three species recorded, so FD values could not be computed. Complementarily, and to assess FD related to particular ecosystem functions (pollination, invertebrate and vertebrate pest control, seed dispersal, and waste removal; Luck et al. 2012), we classified species into 10 functional groups based on the functional dendrogram (Fig. 1): ground insectivores (three species), foliage insectivores (three species), carnivores (four species), aerial insectivores (four species), nectarivores/insectivores (two species), foliage frugivores (two species), ground/canopy granivores (three species), ground granivores (eight species), medium-sized/large omnivores (eight species), and small omnivores (one species). Foliage frugivores were only recorded in 2015.

As a complement to FD, we also computed PD. PD components were estimated from 100 phylogenies from <http://birdtree.org/> (Jetz et al. 2012) to account for phylogenetic uncertainty (Rubolini et al. 2015). These phylogenetic trees were generated by combining a backbone phylogeny (Hackett et al. 2008) using species placed on this phylogeny with either genetic or taxonomic information (i.e., 9993 bird species) and a pure-birth model of diversification (Jetz et al. 2012). We computed two PD measures according to Webb (2000): the mean pairwise distance (MPD) and the mean nearest taxon distance (MNTD). The MPD captures the overall phylogenetic distance of the taxa in a sample and is considered a “basal” metric of PD, whereas the MNTD measures the mean phylogenetic distance to its closest relative in the sample and thus is considered a “terminal” metric of PD (Swenson 2014). For each tree, we computed PD values and then averaged the 100 values for each metric (Rubolini et al. 2015). PD values were standardized between 0.0 (lowest value) and 1.0 (highest value).

Relationship between environmental attributes and diversity components

To analyze the effect of urbanization on diversity components in each year, we applied generalized additive mixed models (GAMMs), which are able to analyze nonlinear relationships between predictor and response variables (Zuur et al. 2009). Because of the high correlations among land covers (r values > 0.7), we used building cover as a surrogate for urbanization. We included this variable as a fixed effect and date as a smooth function (thin-plate regression spline). In each model, the transect identity was included as a random effect and a correlation structure was included to account for temporal autocorrelation of time series. An autoregressive model of order 1 was used, where errors at time t are modeled as a function of time $t - 1$ (Zuur et al. 2009). The following error distributions and link functions were used: Poisson and log link for abundance and species richness (corrected for overdispersion whenever required); normal and identity link for composition (values of NMDS axes), FD, and PD components. Finally, we analyzed diversity changes between 1985 and 2015, using

similar models (same autocorrelation function, error distributions, and link functions) but including only the factor “year” as a fixed effect.

All analyses and graphs were performed in R version 3.2.1 (R Core Team 2015) using the packages entropart (function bcShannon; Marcon and Herault 2015), vegan (functions metaMDS and simper; Oksanen et al. 2015), Hmisc (function rcorr; Harrell 2016), FD (function dbFD; Laliberté et al. 2014), picante (functions mpd and mntd; Kembel et al. 2010), and mgcv (function gamm; Wood 2006).

Results

A total of 38 species were recorded from the 2 years (Fig. 1): 2633 individuals from 27 species in 1985 and 3847 individuals from 36 species in 2015. On average, there were 26.33 ± 16.14 individuals (mean \pm SD) and 3.46 ± 2.95 species per transect in 1985 and 32.06 ± 11.04 individuals and 10.24 ± 2.38 species per transect in 2015. Four birds were exotic species (Rock Dove, *Columba livia* Gmelin, 1789; House Sparrow, *Passer domesticus* (Linnaeus, 1758); European Starling, *Sturnus vulgaris* Linnaeus, 1758; Yellow-chevrons Parakeet, *Brotogeris chiriri* (Vieillot, 1818)), two of which (European Starling and Yellow-chevrons Parakeet) were absent in 1985. In terms of urbanization changes, building and concrete covers significantly increased after 30 years, whereas green and lawn covers decreased (Table 1). The NMDS provided a good representation of species composition between years (stress = 0.159; Fig. 2). Species richness was highly positively correlated with alpha diversity, species composition (NMDS axis 1), and basal PD (Spearman's rank correlations > 0.80 , $P < 0.0001$), which indicates that an increase in species richness increased several metrics of diversity and also promoted differences in species composition. SIMPER analysis identified seven species that contributed strongly to differences in composition between years: the invader species House Sparrow (% contribution = 24.87) and European Starling (% contribution = 4.42); the native species Eared Dove (*Zenaida auriculata* (Des Murs, 1847)) (% contribution = 9.18), Rufous-bellied Thrush (*Turdus rufiventris* Vieillot, 1818) (% contribution = 3.95), Rufous Hornero (*Furnarius rufus* (Gmelin, 1788)) (% contribution = 3.68), Picazuro Pigeon (*Patagioenas picazuro* (Temminck, 1813)) (% contribution = 3.45), and Rufous-collared Sparrow (*Zonotrichia capensis* (P.L. Stadius Müller, 1776)) (% contribution = 3.04). The only species that decreased its abundance after 30 years was the House Sparrow, whereas the abundance of the remaining species increased.

In 1985, abundance, species richness, alpha diversity, FRic, and basal PD were negatively related to building cover, whereas terminal PD showed a positive relationship with this variable (Fig. 3, Supplementary Table S1¹). In contrast, Feve, FDiv, or FRed did not relate to building cover. Significant differences in species composition were also detected in 1985, revealed by changes in NMDS 1 with increased building cover (Fig. 3, Supplementary Table S1¹).

¹Supplementary tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0008>.

Fig. 2. Nonmetric multidimensional scaling (NMDS) of bird communities from northeast Buenos Aires province, Argentina. Circles represent transects (white: 1985; gray: 2015). Only extreme species (scores greater than 0.5 or lesser than -0.5) are shown for clarity. BCH: Yellow-chevroned Parakeet, *Brotogeris chiriri*; CCA: Campo Flicker, *Colaptes campestris* (Vieillot, 1818); CMC: Green-barred Woodpecker, *Colaptes melanochloros* (Gmelin, 1788); MCH: Chimango Caracara, *Milvago chimango* (Vieillot, 1816); PCY: Gray-breasted Martin, *Progne chalybea* (Gmelin, 1789); PDO: House Sparrow, *Passer domesticus*; PDU: Masked Gnatcatcher, *Poliophtila dumicola* (Vieillot, 1817); PUN: Harris's Hawk, *Parabuteo unicinctus* (Temminck, 1824); RMA: Roadside Hawk, *Rupornis magnirostris* (Gmelin, 1788); SCA: Double-collared Seedeater, *Sporophila caerulea* (Vieillot, 1823); SLU: Grassland Yellow-finch, *Sicalis luteola* (Sparman, 1789); TSY: Sayaca Tanager, *Thraupis sayaca* (Linnaeus, 1766).

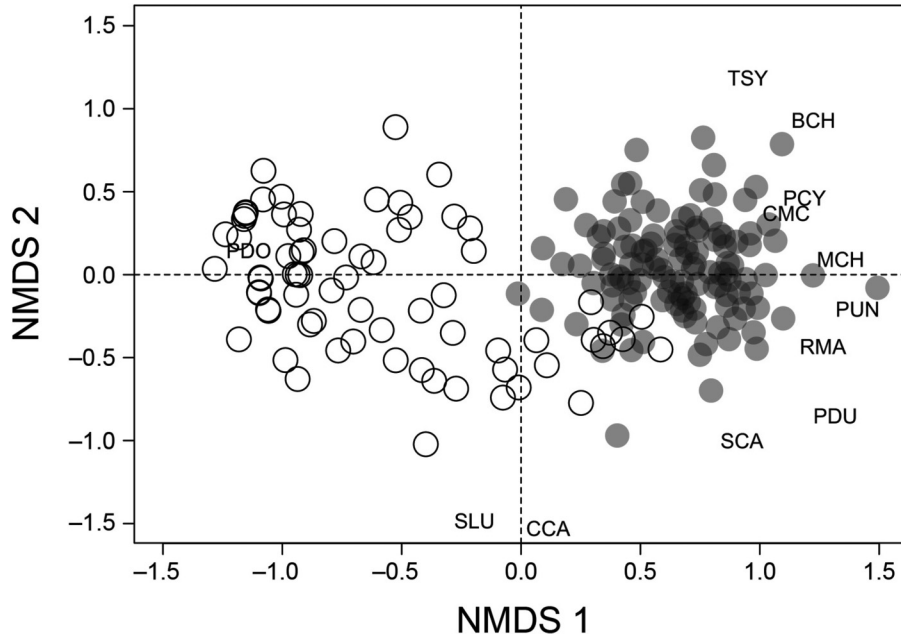
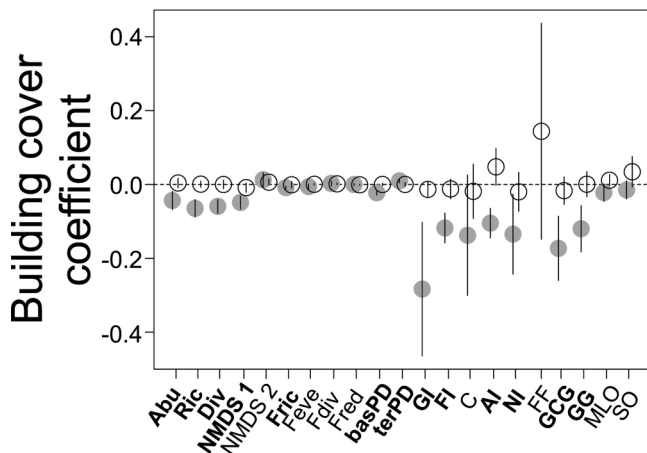


Fig. 3. Relationships between urbanization and diversity components in bird communities from northeast Buenos Aires province, Argentina. Shown are the magnitude of the effect of building cover on different diversity metrics resulting from generalized additive mixed models (circles) and 95% confidence intervals (black vertical lines). Gray and white circles depict years 1985 and 2015, respectively, and diversity components in boldface type represent significant effects ($P < 0.01$). Abu: abundance; Ric: species richness; Div: alpha diversity; NMDS: nonmetric multidimensional scaling; FRic: functional richness; FEve: functional evenness; FDiv, functional divergence; FRed: functional redundancy; basPD: basal phylogenetic diversity (mean pairwise distance); terPD: terminal phylogenetic diversity (mean nearest taxon distance); GI: ground insectivores; FI: foliage insectivores; C: carnivores; AI: aerial insectivores; NI: nectarivores/insectivores; FF: foliage frugivores; GCG: ground/canopy granivores; GG: ground granivores; MLO: medium-sized/large omnivores; SO: small omnivores.



Moreover, when functional groups were considered, a significant abundance decrease related to higher levels of urbanization was found for the most specialized groups (ground insectivores, foliage insectivores, aerial insectivores, nectarivores/insectivores, ground/canopy granivores, and ground granivores), whereas no pattern for generalist groups (small and medium-sized/large omnivores) was found (Fig. 3, Supplementary Table S1¹). In 2015, by contrast, building cover did not relate to taxonomic diversity, FD, PD, species composition, or abundance of species of functional groups (Fig. 3, Supplementary Table S1¹).

After 30 years, a significant increase in abundance, species richness, alpha diversity, FRic, FEve, and basal PD was detected (Supplementary Table S2).¹ Significant changes in species composition were also detected, revealed by changes in both NMDS 1 and NMDS 2 values. In contrast, no pattern on FDiv or functional redundancy was found. A significant abundance increase after 30 years was also found for most specialized functional groups (ground insectivores, carnivores, aerial insectivores, nectarivores/insectivores, ground/canopy granivores, and ground granivores), whereas a decrease for generalist groups (small and medium-sized/large omnivores) was found (Supplementary Table S2).¹

Discussion

Our study showed that urbanization was coupled with a significant loss of bird taxonomic diversity, FD, and PD in 1 year (1985) but not 30 years after. This was revealed by negative associations between building cover, species richness, alpha diversity, FRic, and basal PD and a positive association between building cover and terminal PD in 1985. This suggests that urbanization is related to a species loss which translates into (i) a decrease of species diversity, (ii) a reduction of the volume of the functional trait space, (iii) a loss of overall PD, and (iv) a loss of tips in the phylogenetic tree. For instance, in a global comparison of PD along urbanization gradients, Sol et al. (2017) found that highly urbanized environments supported, on average, 450 million fewer years

of evolutionary history than the surrounding natural areas, mainly resulting from species loss. Highly urbanized landscapes also supported fewer evolutionary distinctive species, and exotic species did not fully compensate for the loss of PD related to urbanization (Sol et al. 2017). The main mechanism proposed for this functional and phylogenetic trait loss is that urbanization decreases the availability of different resources, such as food, nests, and shelter, thus increasing competition, predation, and parasitism for most species (Marzluff 2001; Shochat et al. 2006). Therefore, this would lead to a decrease in species richness and the potential number of ecosystem functions (Alberti 2005; Chace and Walsh 2006; Shochat et al. 2006). Our results support previous studies showing a negative relationship between urbanization and bird FD (e.g., Devictor et al. 2007, 2010; Conole and Kirkpatrick 2011; Meynard et al. 2011; Pauw and Louw 2012; Meffert and Dzioczek 2013; Jokimäki et al. 2016). In a recent global comparison of bird FD between urban and nonurban areas, however, Oliveira Hagen et al. (2017) found that, after accounting for species richness, FD of urban bird assemblages was higher than that of nonurban assemblages. These authors suggest that greater habitat diversity within cities compared with seminatural areas dominated by a single habitat may promote FD in urban environments. Overall, these contrasting results indicate that further studies are needed to effectively assess the effects of urbanization on FD.

Moreover, we also found a relationship between urbanization and bird PD. In particular, urbanization was related to the loss of basal phylogenetic diversity, as well as the loss of terminal taxa in the phylogeny, in 1985. Besides, the relatively low to moderate correlations between FD and PD components ($r = -0.62$ to 0.10) suggest that PD may be representing other physiological or behavioral traits not covered by FD (Cadotte et al. 2012). In the only study that has addressed the role of urban land cover (among other land uses) in bird PD patterns, Meynard et al. (2011) found a negative relationship between the percentage of urban areas and the PD of breeding bird communities across France. In European and worldwide comparisons between urban and nonurban areas, Morelli et al. (2016) and Ibáñez-Álamo et al. (2017), respectively, found that urbanization reduced the evolutionary uniqueness (how unique are species in phylogenetic terms) of bird communities, supporting the idea that urban environments negatively affect PD. Although these studies differ from ours in the scale of study, this suggests that urbanization may drive the loss of PD at different spatial scales. These studies also support the idea that urbanization may act as an environmental filter clustering closely related species, thus reducing the ability of bird communities to cope with environmental change (Webb et al. 2002; Cavender-Bares et al. 2004; Helmus et al. 2010; Sol et al. 2017). Therefore, both FD and PD components may be crucial components to understand the effects of urbanization on bird communities.

When changes in particular functions were assessed through the delimitation of functional groups, most specialized groups were negatively related to urbanization in 1985, including ground insectivores, foliage insectivores, aerial insectivores, nectarivores/insectivores, ground/canopy granivores, and ground granivores, whereas generalist species (omnivores) were not related to changes in urbanization in either 1985 or 2015. This suggests that some ecosystem functions (particularly pollination, pest control, and seed dispersal) might be impaired by urbanization (Pauw and Louw 2012), a hypothesis that deserves further research. These results agree with previous studies, which have shown that urbanization alters ecosystem functioning by acting as an environmental filter of different functional traits (Crocini et al. 2008; Evans et al. 2011; Leveau 2013; Møller 2014). Omnivores, granivores, and cavity-nesting species are typically more abundant in urbanized areas, whereas insectivores and nectarivores tend to be more abundant at lower levels of urbanization (Crocini et al. 2008; Conole and Kirkpatrick 2011; Leveau 2013). In contrast, functional redundancy

did not change with higher levels of urbanization, suggesting that urban species compensated for the loss of ecosystem functions (Huijbers et al. 2015). The traditional view of the response of bird communities to urbanization is that a few generalist birds are benefited from cities (urban exploiters), whereas most species are negatively affected by this change (urban avoiders; Blair 1996; Crocini et al. 2008). This is explained by the hypothesis that a minority of species have adaptations for exploiting resources and avoiding risks of the urban environments (the “urban tolerance hypothesis”; Bonier et al. 2007; Clavel et al. 2011; Sol et al. 2014). Although the species loss linked to this phenomenon has been shown to be more pronounced in highly urbanized areas (i.e., city centers; Sol et al. 2014), our results support the idea that this mechanism could also act at a moderate degree of urbanization (i.e., detached houses with lawned sidewalks, gardens, yards, and parks).

After 30 years, we found an increase in taxonomic diversity, FD, and PD in the study area, along with changes in species composition. Even though urbanization has moderately increased during this period, this suggests an increase in the diversity of ecosystem functions. However, with only two points in time, it is difficult to attribute the observed changes to one specific factor, as different confounding factors might account for the differences between years. For instance, mean annual temperature also increased in the study area from 16.9°C in 1985 to 17.7°C in 2015 (Servicio Meteorológico Nacional, unpublished data). The increase of energy availability could be related to the availability of different resources promoting species diversity, as predicted by the energy-species theory (Wright 1983; Lennon et al. 2000; Evans et al. 2005; Honkanen et al. 2010). Although unmeasured, it is also plausible that changes in bird composition were related to changes in the habitat structure occurring at a broader scale, such as those related to the availability of habitat types in the surrounding urban landscape matrix (Clergeau et al. 2001; Evans et al. 2009; Meffert and Dzioczek 2013). These hypotheses remain to be tested in light of the different factors related to urbanization at a coarse resolution. Furthermore, significant associations detected in 1985 between FD, PD, and urbanization disappeared in 2015, indicating that these relationships may change through time. The increase in building cover at the expense of other land covers in all transects (i.e., reduced land-cover heterogeneity) resulted in a narrow urbanization gradient (building-cover range in 1985 = 4.0% – 32.5% vs. building-cover range in 2015 = 10.1% – 36.5%). Therefore, one likely explanation is that birds responded similarly to all levels of urbanization in 2015 due to low building-cover variation. As it has been pointed out by Petchey et al. (2007), both spatial and temporal dynamics of FD, functional redundancy, and by extension, PD are key to understanding the effects of urbanization on different assembly processes, which is a matter still poorly addressed.

Six species (European Starling, Eared Dove, Picauro Pigeon, Rufous-bellied Thrush, and Rufous-collared Sparrow) accounted for differences in species composition between 1985 and 2015. These species have typically benefited from urban areas across the Neotropics, and thus may be considered urban exploiters or synanthropic species (Bonier et al. 2007; MacGregor-Fors and Escobar-Ibáñez 2017). However, the only small omnivore and well-known urban exploiter House Sparrow has drastically declined its abundance in the study area. Although a decline in urban areas from Argentina was suspected (Montalti and Kopij 2001), we present the first quantitative evidence of an abundance decrease, which is consistent with the decline of the species worldwide attributed to increased predation, competition with other synanthropic species, and noise pollution (Summers-Smith 2003; Nakagawa and Pick 2016). Two other exotic species, the invasive European Starling (a medium-sized/large omnivore) and the Yellow-chevroned Parakeet (a foliage frugivore) were not present in the study area until 1987 (Peris et al. 2005) and the early 1990s (Scheffer et al. 2015), respectively. Both species are expanding

their distribution ranges and are increasing their population numbers (Scheffer et al. 2015; Zufiurre et al. 2016); thus, they are the focuses of major concern for their effects on native biota.

Overall, our study contributes to the understanding of the relationship between urbanization and different diversity components, some of which are more directly related to ecosystem functioning, such as FD and PD. Given the accelerated rate of urbanization worldwide, an integrative approach between different facets of biodiversity is promoted to better describe and gain insight into the response of bird communities in urban environments.

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