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journal homepage: www.elsevier.com/locate/landurbplan

# Changes in bird species richness through different levels of urbanization: Implications for biodiversity conservation and garden design in Central Brazil

# Elivânia Reis<sup>a,b</sup>, Germán Manuel López-Iborra<sup>b,\*</sup>, Renato Torres Pinheiro<sup>a</sup>

<sup>a</sup> Grupo de Pesquisa em Ecologia e Conservação de Aves, Universidade Federal do Tocantins, Av. NS 15, 109 Norte, Estação Experimental 77020-120, Palmas, Tocantins, Brazil <sup>b</sup> Departamento de Ecología/IMEM Ramon Margalef, Universidad de Alicante, Campus de San Vicente del Raspeig, Apdo. correos 99, 03080 Alicante, España, Spain

#### ARTICLE INFO

Article history: Received 6 July 2011 Received in revised form 25 January 2012 Accepted 11 April 2012 Available online 7 May 2012

Keywords: Species loss Effects of urbanization Neotropical birds Urban planning Urban ecology Cerrado

# ABSTRACT

Urban processes lead to species loss. Palmas is a young city under construction; thus, it provides a rare opportunity to analyze changes in bird richness in a developing city. Eighty city blocks, which were classified into five different categories according to different levels of urbanization, were sampled. Bird counting took place during a dry season and a rainy season in four parallel transects in each block. In these blocks, we estimated 20 variables related to woody vegetation, land cover and type of urban use. The estimated bird species richness for the study area was very high (151 species); nevertheless, species reduction occurred as a function of the urbanization processes. Although representing only 11% of the city surface, the not-urbanized blocks showed the highest species richness, which corresponded to 96.3% of the richness estimated in the city. The average species richness for most trophic groups, families, openfield or forest species and resident or migratory species decreased significantly in urbanized blocks. According to a Hierarchical Partitioning analysis the environmental variables that made the greatest positive contribution to the variation in bird species richness in urbanized blocks were the percentage of block area planned for residential use, the density of native trees and the percentage area covered by unpaved roads, whereas the commercial block density, the density of exotic trees and the percentage of block area built had the greatest negative contribution. Based on our results, policies aimed to maintain Cerrado native species in urbanized blocks would contribute to reduce bird species loss.

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# 1. Introduction

Urbanization changes natural environments by transforming the landscape and drastically reducing local biodiversity (Beardsley, Throne, Roth, Gao, & McCoy, 2009; MacGregor-Fors, Ortega-Álvarez, & Schondube, 2009, 2011). The urban occupation process is usually fast and focused on the satisfaction of the human population's primary needs (Fontana, Burger, & Magnusson, 2011). As a consequence, urban landscapes often form a scattered environmental mosaic, characterized by green native areas mixed with constructed areas varying in terms of size, form and the level of human occupation (MacGregor-Fors, 2011; McKinney, 2006). The understanding of the effects of urbanization on biodiversity has an essential role in successful management and conservation (Marzluff, Bowman, & Donnelly, 2001).

Birds are considered good models for the understanding of the effects of urbanization on habitat structure and composition (Chace & Walsh, 2006; MacGregor-Fors et al., 2009). Detailed studies evaluating bird species richness in urban areas are important to understand the environmental impacts and to propose effective urban planning strategies that contribute to the conservation of bird diversity in cities (Freeman & Buck, 2003; Fuller, Tratalos, & Gaston, 2009). Previous research in urban environments has shown a significant loss of bird richness and/or biodiversity due to urban growth (Ortega-Álvarez & MacGregor-Fors, 2011; Rottenborn, 1999). According to Marzluff et al. (2001), bird communities are directly affected by urbanization, and the extent of the effects varies among species. Although urbanization can favor some species that can exploit urban habitats (DeGraaf & Wentworth, 1986), other species cannot maintain stable populations in the modified areas.

In the urban areas of temperate regions, bird species richness is usually low and dominated by a few native and/or introduced species (Beissinger & Osborne, 1982; Emlen, 1974). However, studies of urban birds are still scarce in tropical regions, despite the higher biodiversity and the spreading of urban environments in the tropics, (Marzluff et al., 2001; Ortega-Álvarez & MacGregor-Fors, 2011). For example, Ortega-Álvarez and MacGregor-Fors (2009) found in Mexico City that a few generalist species dominate in commercial areas and that species richness decreased according to the

<sup>\*</sup> Corresponding author. Tel.: +34 965903400x2255.

*E-mail addresses:* elivania.reis@yahoo.com (E. Reis), german.lopez@ua.es, german.lopeziborra2@gmail.com (G.M. López-Iborra), renatopin@uft.edu.br (R.T. Pinheiro).

<sup>0169-2046/\$ -</sup> see front matter © 2012 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.landurbplan.2012.04.009

level of urbanization. In Brazil, Fontana et al. (2011) investigated the community composition of birds in a longitudinal gradient in Porto Alegre; they demonstrated that bird composition varied according to the level of urban occupation and that factors such as noise and human density considerably affected the number of species.

The city of Palmas, the capital of the Brazilian state of Tocantins, was founded in 1989 (Instituto de Planejamento Urbano de Palmas, 2002). Since its conception, the Basic Urban Plan has aimed to maintain environmental quality; the minimization of anthropogenic impacts is included in its objectives. In this way, the city occupation strategy was planned to be controlled and uniform, using built-in modules that would be progressively added according to the development stage. However, the actual process of urbanization has been characterized by the clearing of native vegetation and its substitution by exotic species (Adorno & Fighera, 2005). Palmas city is still under construction, and the present urban landscape is characterized by a mosaic of urbanized and semi-urbanized areas mixed with preserved ones. In general, studies of birds in urbanized environments have been conducted in well-consolidated cities. Thus, Palmas, which was only 20 years old at the time of this study, offers an extraordinary opportunity to analyze the effect of urbanization processes on bird diversity; the results of this study will serve in the development of management measures for bird conservation before irreversible changes occur.

This study is focused on bird species richness as an indicator of biodiversity loss triggered by urbanization and has the following objectives: (1) to estimate bird richness in the Palmas urban area; (2) to compare blocks with different levels of urbanization in order to evaluate how the progression of urbanization affects bird species richness; and (3) to estimate the importance of environmental variables that may affect bird richness in the urbanized areas of Palmas.

#### 2. Materials and methods

#### 2.1. Study area

This study was performed in the Palmas urban area, Tocantins state, Brazil. This city covers an area of 15 km (North/South) × 7 km (East/West) and has approximately 210,000 inhabitants (Instituto Brasileiro de Geografia e Estatística, 2010). The climate is hot and humid, with two well-defined periods: a dry season (May–October) and a rainy season (November–April). The mean annual precipitation is 1700 mm, and the average annual temperature is about 28 °C. The natural vegetation in the area is comprised of cerrado *sensu stricto, cerradão* (dry forested cerrado), gallery forests and grasslands (Secretaria do Planejamento, 2008). The Palmas central area is bordered on the north by the Água Fria brook, on the south by the Taquaruçú Grande brook, on the west by the Luis Eduardo Magalhães electric power station lake and on the east by the motorway TO 050 (Fig. 1).

Palmas was designed in a checkerboard format, in which roads and blocks present a defined pattern of form and size (Adorno & Fighera, 2005). The urban plan proposed a functional separation of land uses in which 38% of the city area was designated for residential use, 8% for commercial use, 24% for green areas, 18% for administrative buildings and 12% for roads (Instituto de Planejamento Urbano de Palmas, 2002). The dimension of most blocks are approximately 400 m × 600 m for commercial blocks and 400 m × 700 m for the residential blocks, although some blocks of half this size exist close to brooks.

### 2.2. Urban habitats

There are approximately 150 blocks in the study area, and we selected 80 blocks representative of the stages of urbanization that can be found in the city (Fig. 1). Blocks were selected systematically along the entire city in the areas where they are more uniform in size and shape. These blocks were classified into five categories based on land use and occupation, and the blocks were evaluated by field observations and satellite image analyses from Google earth obtained in July, 2008. The five categories are described as follows (with number of sampled blocks between parentheses). (i) Not urbanized (11); almost all blocks of this category were covered by cerrado sensu stricto vegetation, which was characterized by small and medium-sized trees and scrubs adapted to periodic fires (Eiten, 1993). In a few of these blocks, cerrado vegetation was more dense and classified as *cerradão*, a forest type with several species not found in cerrado sensu stricto (Ribeiro & Walter, 1998). (ii) Not urbanized with unpaved roads (5); these were blocks in which paths had already been opened but were still unpaved and in which the original cerrado or cerradão vegetation was maintained. (iii) Not urbanized with open vegetation (5); these were blocks in which the original vegetation was cleared but construction had not begun. In these blocks, the vegetation consisted of grasslands with scattered trees and shrubs. (iv) Semi-urbanized (12); these were blocks where the proportion of constructed area was less than 20%; (v) Urbanized (47); these were blocks where the proportion of constructed area was greater than 20%, and the proportion of vegetation cover was less than 20%.

These criteria differ from those of Marzluff et al. (2001), who considered preserved areas to be those including a percentage of edification between 0 and 2%, sub-urban areas to be those with 30–50% of area constructed and urban areas to be those with over 50% of the area constructed. However, these criteria were proposed for structured and consolidated cities and are not applicable to Palmas, a city which is still under development.

# 2.3. Bird sampling

For each block, four linear transects (Bibby, Burguess, Hill, & Mustoe, 2000) that were parallel to and the same length as the longest axis were selected: two on opposite edges and two in the interior. The distance between adjacent transects in the same block was approximately 130 m. Birds were counted up to 30 m on both sides of the transect lines in the interior transects and just on the inside band of edge transects. The counts started at sunrise and lasted until 8 h:30 min; this period of time was sufficient for sampling two non-adjoining blocks per day. Birds were counted every day that the meteorological conditions were favorable, but alternating in consecutive days the type of block visited. To account for seasonal variations in bird richness, the transects were sampled twice: once during the dry season (September/October 2008) and once during the rainy season (January/February 2009).

The bird species were classified in several groups according to the following criteria: (a) trophic guild; granivores (GRA), insectivores (INS), omnivores (OMN), frugivores (FRU), carnivores (CAR), nectarivores (NEC) and necrophagous (NCR) (Sick, 1997); (b) habitat preference; open area species (C1), species that prefer open areas but also use forested areas (C2), species exclusive to the forest (F1) and forest species that also use open areas (F2) (Sick, 1997; Silva, 1995); (c) migratory status; resident or migratory (Silva, 1995); and (d) family; since species belonging to the same family may share characteristics related to behavior or nesting ecology that may influence the way they are affected by the urbanization process. For statistical reasons only families with more than four species detected in the area were included in these analyses.



Fig. 1. Map of the study area showing the different categories of urban blocks described in the text as well as industrial blocks (not studied), cerrado vegetation remnants and green areas. Sampled blocks are marked with black dots. The frame shows UTM coordinates. The small Brazil map depicts the location of Tocantins state (shaded) and the city of Palmas (point).

# 2.4. Environmental variables sampling

In each block, we estimated 20 environmental variables belonging to four categories: (a) woody plants richness and density; (b) the vertical structure of woody plants; (c) land use and cover; and (d) urban use type (residential or commercial) (Table 1). In this paper we utilize land use and cover variables estimated in all blocks but the rest of variables were used only in urbanized blocks analyses.

The vegetation variables were measured using circular plots with a radius of  $10 \text{ m} (314 \text{ m}^2)$  distributed regularly at 25 m intervals along the bird counting transects (Felfili and Resende, 2003). On the borders, plots were placed only on the interior side of the transects, whereas in the interior transects, the plots were

distributed alternately on both sides of the transect. In both cases, the plots were located 3 m from the transect line. Overall, 7119 plots were sampled in the 80 selected blocks, in which only woody plants with trunk circumferences equal to or greater than 10 cm were recorded. Plants were identified and their height was measured using a graduated aluminum pole. Plant species that could not be identified in the field were collected and identified later using field guides (Lorenzi, 1998a, 1998b; Lorenzi & Souza, 2001; Lorenzi, Medeiros-Costa, & Cerqueira, 2003; Lorenzi, Souza, Torres, & Bacher, 2003; Lorenzi, Bacher, & Lacerda, 2006) and/or by comparison with species deposited at the Tocantins Federal University Herbarium at Porto Nacional campus. The classification of tree species followed the recommendations of Mendonça et al. (2008).

#### Table 1

Habitat variables estimated in blocks in which birds were surveyed in Palmas, Central Brazil.

Tree richness and density	
SNat	Species Richness of native trees
	calculated by Jackknife1 estimator
DNat	Density of native trees (trees/hectare)
SExot	Richness of exotic trees calculated by
	Jackknife1 estimator
DExot	Density of exotic trees (trees/hectare)
Vertical structure of tree stratum	
DNatH1	Density of native trees with height
Diatin	<3.5 m
DNatH2	Density of natives trees $>3.6$ and
Ditutil2	<64m
DNatH3	Solution Density of native trees with beight
Divatilis	>65m
DEvotU1	$\geq$ 0.5 m Density of evotic trees with height
DEXOLITI	2.5 m
DEvent 12	≤5,5111 Density of eventia traces ≥ 2 Cm and
DEXOLH2	Density of exotic trees $\geq$ 3.6 m and
DEvent12	≤0.4 III
DEX0[H3	Density of exotic trees with height
	≥6.5 m
Land use and cover	
DistBlockProtA	Distance (m) between the block and
	the closest protected areas
% Grass	Percentage block area covered by grass
% Coverage of trees and shrubs	Percentage block area covered by
	woody vegetation exotic and native
% Paved roads	Percentage block area covered by
	paved roads
% Upaved roads	Percentage block area covered by
	unpaved roads
% Exposed soil	Percentage block area covered by
	exposed soil
% Built area	Percentage block area covered by
	buildings
Urban use type	
DResBuildings	Density of residential buildings
DComBuildings	Density of commercial buildings
% Residential	Percentage of block area planned for
	residential uses

Woody plants were classified into three height categories defined from the lower and upper quartiles of the vertical height distribution of all sampled individuals: (i) low ( $\leq$ 3.5 m); (ii) medium ( $\geq$ 3.6 m and  $\leq$ 6.4 m); (iii) high ( $\geq$ 6.5 m). We estimated woody plant species richness in each block using the Jackknife1 estimator (Hortal et al., 2006) from the EstimateS 8.2 program (Colwell, 2008).

The estimates of land use variables were obtained from satellite images of Google Earth 4.2 in July 2008, georeferenced and converted into layers on a 1:5000 scale. Constructed areas and areas covered with shrubs and trees, grass, unpaved or paved roads or exposed soil were identified on the images; these features were digitalized as polygons, and their surfaces were measured in meters using the Arc-Gis 9.2 program. The area of each block was also measured in meters, and the percentage of cover of the above variables was calculated. The number of residential and commercial buildings constructed and planned for each block was obtained from the Palmas financial bureau (December 2009). This information was used to calculate the actual density of residential and commercial buildings as well as the percentage of block area planned for residential use.

# 2.5. Statistical analysis

To analyze block type variability and its potential overlap, a Non-metric Multidimensional Scaling (NMDS) ordination of blocks (Quinn and Keough, 2002) was performed, using the land use and cover variables. To estimate bird species richness in the study area and in each block type, the Jackknife1 non-parametric estimator



**Fig. 2.** Non-metric Multidimensional Scaling (NMDS) ordination of blocks sampled in Palmas, Tocantins. Ordination is based on land use and cover variables estimated in each block (see Table 1). Blocks were classified into five categories (identified by different symbols) that represent an increasing urbanization gradient from not urbanized to urbanized blocks.

was calculated using EstimateS 8.2 (Colwell, 2008). Even though discussion about which richness estimator is the best persists, Jack-knife1 is usually one of the estimators recommended, especially when data have the same grain resolution (Hortal et al., 2006).

We used ANOVA to test whether the mean species richness per block differed among block types. The data were square root transformed to homogenize variances. If the variance did not homogenize (according to Levene test), a Kruskal-Wallis nonparametric test was performed instead. We tested for the existence of spatial autocorrelation among residuals by calculating the Moran's I index (Dale et al., 2002). If this statistics was significant then a Nearest Neighbor (NN) method for adjusting residuals was applied (Dixon, 2002). In this procedure the residuals of the blocks whose centers were located within a 1000 m radius from each block were averaged (weighted by the inverse of their distance) and the resulting value was considered a measure of the effect of spatial autocorrelation. The 1000 m radius included all adjacent blocks and was chosen after inspection of variograms, which were essentially flat after that distance. Then the square root transformed data were corrected by subtracting the averaged residuals and the Moran's I was calculated again with the new resulting residuals, to test if spatial autocorrelation had been removed. If Moran's I was still significant the procedure was repeated until this statistic was not significant. This second step was only needed to adjust two variables (richness in the dry season and richness of F1 species). The post hoc Tukey test was used to identify different block types after significant ANOVAs. After a significant Kruskal-Wallis test, all block types were compared pair-wise using the Mann-Whitney test with a Bonferroni correction (Holm, 1979).

To investigate which environmental characteristics influenced bird richness in the urbanized blocks, a hierarchical partitioning (HP) analysis was performed (Chevan and Sutherland, 1991). This analysis is used to quantify the explaining capacity of the independent variables individually by partitioning each variable's pooled contribution from other correlated variables (Quinn and Keough, 2002). Hierarchical partitioning computes all of the possible hierarchical models that can be developed with a set of independent predictive variables and their explanatory power is segregated in the independent effect 'I' and the effects caused jointly with other variables 'J' (MacNally, 2000). Hierarchical Partitioning analyses were conducted only for the urbanized blocks using the "hier.part" package (Walsh and MacNally, 2003) in the R software. For these analyses, bird richness was the dependent variable of the linear regression models with Poisson error, and  $R^2$  was used as the adjustment measure of the models. The significance of

the independent contribution of the environmental variables was evaluated using randomization tests based on 999 randomizations (MacNally, 2002). Such analyses were performed in two steps. First, an HP analysis was conducted for each of the four groups of environmental variables separately. The effect of spatial autocorrelation was controlled by including five linear and quadratic geographical variables in each analysis (longitude, longitude<sup>2</sup>, latitude, latitude<sup>2</sup> and longitude × latitude) calculated from the UTM coordinates of the center of each block (Legendre, 1993). During the second step, an HP analysis was performed using a set of predictors that included the environmental variables that were determined to be significant in the previous analyses together with the five coordinate variables (see López-Iborra et al., 2011 for a similar approach).

Domestic pigeon *Columba livia* and House sparrow *Passer domesticus*, were excluded from the species richness estimates because we were interested on the effect of urbanization on native species.

# 3. Results

## 3.1. Urban habitats

The Non-metric Multidimensional Scaling (NMDS) ordination of blocks according to soil use and cover variables distributed block categories along the first axis. Non-urbanized blocks were placed at the negative extreme of this axis, and urbanized blocks were localized to the opposite end; thus, this axis represents a gradient of urbanization (Fig. 2). Semi-urbanized blocks were spread along a wide portion of this gradient, which suggests a high degree of heterogeneity within this block category, whereas urbanized blocks appeared to be much more homogeneous and were concentrated in a smaller range of the urbanization gradient.

### 3.2. Variation in bird species richness among block types

During this study, 135 bird species belonging to 36 families were detected (Appendix A), 89.8% of which were residents and 10.2% were migrant species. Most species were insectivores (43.0%), followed by omnivores (29.6%), frugivores (8.6%) granivores (7.0%), carnivores (4.4%), nectarivores (5.9%) and necrophagous (1.5%) species. The bird species richness estimated with Jackknife1 (Fig. 3) tended to stabilize after 10 blocks were sampled for each block type. The final slopes of the Jackknife1 curves for the urbanized, semiurbanized and non-urbanized block types were 0.07, 0.61 and 0.38, respectively. However, for the block types for which fewer blocks were sampled, richness tended to grow. The final slopes for the non-urbanized blocks with unpaved roads and the non-urbanized blocks with open vegetation were 2.05 and 4.43, respectively. The total bird species richness was estimated as 151 using Jackknife1 (Table 2). This suggests that we have detected about 90% of the species present in the study area. There was a gradual decrease of estimated species richness along the gradient of increasing urbanization. The estimated number of species in the non-urbanized blocks represented 91.6% of the richness estimated for the entire city and was significantly higher than those of the urbanized block types. Semi-urbanized blocks and non-urbanized blocks with some degree of alteration had similar species richnesses, while urbanized blocks showed the lowest species richness; these blocks included only 45% of the species estimated for the whole city (Table 2).

The mean species richness decreased from non-urbanized to urbanized blocks both in the dry and rainy seasons for most species groups (Table 3). In general, *post hoc* tests showed that urbanized blocks had fewer species of most groups than the other block types, while semi-urbanized blocks had intermediate richness. Only the species richness of nectarivores and species belonging to



**Fig. 3.** Bird species richness estimated by Jackknife1 as a function of the number of blocks sampled in Palmas. (a) Species richness estimated using Jackknife1 and observed species richness (Sobs Mao Tau) for all the blocks analyzed altogether, (b) species richness estimated using Jackknife1 separately for each block type. Note the different scales of the horizontal axes.

the Trochilidae, Falconidae and Icteridae families were not significantly different among the block types (Table 3).

#### 3.3. Factors affecting richness in urbanized blocks

The results of the hierarchical partitioning (HP) analyses performed with the urbanized blocks are shown in Table 4. When analyzed separately, all groups of variables included at least one variable with a significant independent contribution to explain the variation in bird species richness. In the first group of variables, the most important variables were the density and richness of native trees, with a positive correlation with bird species richness; the density of exotic trees, however, had a negative effect. The native tree species that were most often planted in urbanized blocks were Anaccardium occidentale L., Caryocar brasiliense L. and Sapindus saponaria L., which were present in 93.6%, 61.7% and 53.4% of blocks, respectively. These species produce fruits that are attractive to birds. Among the variables related to the vertical structure of vegetation, the density in the medium height category of both native and exotic trees had the greatest independent contribution, which, once again, was positive for native trees and negative for exotic tree species. Within the land use and cover variable category, only three variables had a significant contribution; the "% unpaved roads" and "% coverage of trees and shrubs" had a positive correlation with species richness, while the effect of "% built area" was negative (Table 4). Among the variables related to the type of urban use in the block, the density of commercial use buildings was significant and had a negative relationship to bird richness, whereas the percentage of area planned for residential use in the block had a positive significant contribution (Table 4).

Table 4 also shows the results of the overall HP analysis performed using the variables that had been deemed significant by the previous analyses. The densities of native and exotic trees were

# 36 **Table 2**

Bird species richness (S) and standard deviation (SD) estimated by Jackknife1 for the whole sampled area and for each block type in Palmas, Central Brazil. Cl 95%: confidence interval; %S: percentage of global richness estimated to exist in each block type.

Urban blocks	S	SD	CI 95%		%S
Whole sampled area	150.78	7.69	132.63	168.92	100.0
Not urbanized	138.18	7.72	120.96	155.39	91.6
Not urbanized but with unpaved roads	102.60	4.31	90.61	114.58	68.0
Not urbanized with open vegetation	99.80	5.85	83.53	116.06	66.2
Semi-urbanized	95.58	5.32	83.87	107.28	63.6
Urbanized	67.81	3.01	61.75	73.86	45.0

not considered in this analysis despite being significant (Table 4) because these variables included the density of medium and high trees and, thus, were highly correlated with these measurements. The overall model had an  $R^2$  higher than any of the partial models (Table 4) and identified six variables as having a significant independent contribution to the variation in bird species richness in urbanized blocks (Fig. 4). Variables related to the type of urban use were determined to be the most important by this analysis, showing that bird species richness was greater in residential blocks and was negatively affected by the increasing density of commercial buildings. The density of medium native trees had the third most significant contribution to the variability in bird species richness, followed by the percentage of constructed area. The percentage of area covered by unpaved roads was positively correlated to bird species richness, whereas the density of medium height exotic trees had a negative effect (Table 4, Fig. 4).

### 4. Discussion and conclusions

#### 4.1. Variation in bird species richness among block types

Our results have shown that the urbanization process produced a decrease in the bird species richness in the urbanized areas of Palmas and that this process affected total richness, as well as most trophic guilds and some families. The loss of species due to urbanization is a general pattern also found in other studies (Fontana et al., 2011; Fuller et al., 2009; MacGregor-Fors, Moralez-Pérez, & Shondube, 2010). However, in the city of Palmas, we are witnessing the ongoing process of urbanization because blocks in different stages of urbanization coexist. Compared to other cities the Palmas urban area maintains a high number of species, which we have estimated, using a non-parametric estimator, to be 151 species. This represents only 54.7% of the 276 species recorded in Palmas urban

#### Table 3

Mean bird species richness ( $\pm$ SD) calculated for each block type. Bird species have been analyzed together and separately by groups defined by season, trophic guild, family, migratory behavior (resident or migrant) and habitat preferences (C1, C2, F1, F2, see Section 2). Means were compared using ANOVA ( $F_{4,75}$ ) performed on square root transformed data in order to homogenize variances. The *post hoc* Tukey test was used to identify significant different groups of blocks after significant ANOVA findings, which are identified by different letters as superscripts. When square root transformation did not homogenize the variances, Kruskal–Wallis tests were conducted (marked with \* in  $F_{4,75}$  column), and *post hoc* comparisons were performed using the Mann–Whitney test with a Bonferroni correction. NN identifies variables that were adjusted by the Nearest Neighbor method after detecting significant spatial autocorrelation of residuals.

Species richness	Block type					F <sub>4.75</sub>	р
	Not urbanized	Not urbanized with unpaved roads	Not urbanized with open vegetation	Semi-urbanized	Urbanized		
Total	$49.36\pm9.99^{d}$	$45.60 \pm 4.82^{c,d}$	$37.00 \pm 3.39^{b,c}$	$28.33\pm7.85^{b}$	$16.11\pm4.72^a$	76.21	0.000
Dry season <sup>NN</sup>	$39.18 \pm 10.40^{b}$	$32.20 \pm 7.05^{b}$	$32.00 \pm 2.91^{b}$	$20.75 \pm 7.02^{a,b}$	$12.11 \pm 4.81^{a}$	10.49	0.000
Rainy season <sup>NN</sup>	$24.36 \pm 7.32^{b,c}$	$27.20 \pm 9.68^{\circ}$	$11.80 \pm 5.54^{a}$	$16.42 \pm 4.64^{a,b}$	$10.0\pm3.73^a$	20.20	0.000
Granivores	$6.09 \pm 1.04^{c}$	$6.20\pm1.64^{b,c}$	$6.40 \pm 1.14^{b,c}$	$4.50\pm1.16^{b}$	$2.06\pm0.81^a$	58.46	0.000
Insectivores <sup>NN</sup>	$17.00 \pm 3.97^{\circ}$	$17.20 \pm 2.38^{\circ}$	$12.60 \pm 2.60^{b,c}$	$9.17 \pm 2.72^{b}$	$4.38\pm2.81^a$	50.16*	0.000
Omnivores <sup>NN</sup>	$16.36 \pm 3.69^{\circ}$	$14.60 \pm 2.96^{b,c}$	$10.80\pm4.49^{\rm b}$	$10.33 \pm 3.42^{b}$	$6.32\pm2.36^a$	27.00	0.000
Frugivores <sup>NN</sup>	$5.45 \pm 2.01^{b}$	$4.20\pm1.09^{b}$	$3.20\pm0.83^{\rm b}$	$3.00 \pm 1.53^{a,b}$	$1.45\pm1.03^a$	17.80	0.000
Carnivores	$1.45\pm0.82^{b}$	$1.00 \pm 0.70^{\underline{a},b}$	$1.00 \pm 0.00^{a,b}$	$1.00\pm0.95^{b}$	$0.49\pm0.62^a$	16.61*	0.002
Nectarivores <sup>NN</sup>	$2.64 \pm 1.91$	$2.00\pm0.70$	$2.20\pm0.83$	$1.17\pm0.93$	$1.19\pm0.99$	2.02	0.100
Tyrannidae	$8.18\pm2.60^{\rm b}$	$7.60 \pm 1.51^{b}$	$5.40\pm1.14^{\rm b}$	$2.83\pm1.69^a$	$1.79\pm1.04^a$	36.96	0.000
Bucconidae <sup>NN</sup>	$2.64\pm2.11^{\text{b}}$	$3.40\pm2.88^b$	$1.40\pm0.89^{a,b}$	$1.25 \pm 1.35^{a,b}$	$0.53 \pm 0.77^{a}$	22.54*	0.000
Emberizidae	$4.00\pm0.89^{\circ}$	$3.60 \pm 1.51^{b,c}$	$4.00 \pm 1.00^{\circ}$	$2.25\pm0.86^{b}$	$0.38\pm0.64^a$	60.12*	0.000
Psittacidae	$3.64 \pm 1.43^{b}$	$3.20\pm0.83^{b}$	$2.80 \pm 1.09^{a,b}$	$2.50 \pm 1.24^{a,b}$	$1.53\pm0.88^a$	8.98	0.000
Picidae	$2.45\pm0.93^{c}$	$2.20\pm1.30^{b,c}$	$1.20\pm0.83^{\rm b}$	$1.08\pm0.51^{b}$	$0.14\pm0.31^{a}$	56.36	0.000
Thraupidae <sup>NN</sup>	$9.64 \pm 2.97^{b}$	$7.40 \pm 2.79^{b}$	$5.40 \pm 3.28^{\underline{a},b}$	$5.67 \pm 2.96^{a,b}$	$2.36 \pm 1.48^{a}$	14.20	0.000
Trochilidae <sup>NN</sup>	$2.00\pm1.78$	$1.00\pm0.70$	$1.60\pm0.54$	$0.92\pm0.99$	$1.04\pm0.72$	1.08	0.373
Falconidae	$0.36\pm0.50$	$0.40\pm0.54$	$0.80\pm0.83$	$0.67\pm0.49$	$0.62\pm0.64$	0.65	0.630
Thamnophilidae	$1.91 \pm 1.13^{\circ}$	$1.60 \pm 1.14^{b,c}$	$0.80 \pm 0.83^{a,b,c}$	$0.58 \pm 0.66^{b}$	$0.00\pm0.00^a$	52.24*	0.000
Columbidae	$2.36\pm0.50^{\text{a,b}}$	$2.80\pm0.44^{b}$	$2.60\pm0.54^{\rm b}$	$2.42\pm0.66^{a,b}$	$1.74\pm0.48^{\rm a}$	9.15	0.000
Icteridae	$0.36\pm0.50$	$0.60\pm0.89$	$0.20\pm0.44$	$0.42\pm0.51$	$0.47 \pm 0.54$	1.36*	0.851
Resident species <sup>NN</sup>	$44.45 \pm 8.81^{\circ}$	$40.80 \pm 4.97^{\circ}$	$32.80 \pm 3.42^{b,c}$	$26.00 \pm 6.79^{b}$	$14.96\pm4.37^a$	55.26	0.000
Migrant species	$4.91 \pm 2.11^{\circ}$	$4.80 \pm 0.83^{\circ}$	$4.20 \pm 0.83^{b,c}$	$2.33 \pm 1.49^{a,b}$	$1.13 \pm 1.03^{a}$	45.55*	0.000
C1	$9.27 \pm 2.10^{b,c}$	$9.00 \pm 3.53^{b,c}$	$10.40 \pm 0.54^{c}$	$7.00 \pm 2.33^{b}$	$2.81 \pm 1.39^{a}$	42.89	0.000
C2	$19.91 \pm 3.20^{\circ}$	$19.20 \pm 2.95^{b,c}$	$17.00 \pm 2.12^{b,c}$	$14.08 \pm 4.01^{b}$	$8.23\pm2.85^a$	39.18	0.000
F1 <sup>NN</sup>	$1.55\pm2.46$	$1.00 \pm 1.00$	$0.20\pm0.44$	$0.25\pm0.45$	$0.0\pm0.00$	11.39*	0.022
F2 <sup>NN</sup>	$18.64\pm6.50^{\circ}$	$16.40\pm3.78^{c}$	$9.4\pm4.72^{b,c}$	$7.00\pm3.43^{a,b}$	$5.06\pm2.07^{a}$	31.68	0.000

#### Table 4

Results of the hierarchical partitioning analyses performed with each group of habitat variables and a global analysis conducted with a selection of the variables that were determined to be significant by the former analyses (see Section 2). Only urbanized blocks are included in these analyses. *I* and *J* are, respectively, the independent and joint contribution of a variable. *XI* is the percentage of the total *I* accounted for by each habitat variable. Coordinates headings correspond to the sum of *I* and *XI* values of the five variables relative to the UTM coordinates of each block. *Z* score is the randomization test for the independent contributions of each predictor variable calculated from 999 randomizations.

Variables	Variables g	roup analyses			Global analysis			
	I	J	%I	z score	Ι	J	%I	z score
Tree richness and density								
SNat	0.071	0.098	16.03	$1.67^{*}$	0.035	0.213	6.88	1.11
DNat	0.097	0.092	21.94	2.73**				
SExot	0.014	-0.011	3.06	-0.29				
DExot	0.073	0.045	16.61	1.81*				
Coordinates	0.187		42.33					
R <sup>2</sup>	0.425							
Vertical structure of tree stratum								
DNatH1	0.028	0.006	6.29	0.82				
DNatH2	0.119	0.218	26.91	6.69***	0.069	0.258	13.74	3.56***
DNatH3	0.052	0.064	11.70	2.31**	0.025	0.087	5.04	0.58
DExotH1	0.026	-0.026	5.79	0.53				
DExotH2	0.080	0.123	17.91	3.79***	0.041	0.155	8.17	1.94*
DExotH3	0.046	0.058	10.3	$1.73^{*}$	0.024	0.077	4.73	0.48
Coordinates	0.094		21.07					
R <sup>2</sup>	0.444							
Land use and cover								
DistBlockProtA	0.012	-0.008	3.42	-0.39				
% Grass	0.036	0.093	10.21	1.06				
% Paved roads	0.032	0.088	9.17	0.89				
% Unpaved roads	0.057	0.172	16.22	$2.48^{**}$	0.045	0.171	8.95	1.82*
% Coverage of trees and shrubs	0.055	0.168	15.53	$2.40^{**}$	0.038	0.172	7.56	1.30
% Exposed soil	0.015	-0.005	4.21	-0.25				
% Built area	0.077	0.237	21.95	4.16**	0.053	0.242	10.64	2.64**
Coordinates	0.068		19.27					
$R^2$	0.352							
Urban use type								
DResBuildings	0.040	0.020	9.64	0.9				
DComBuildings	0.088	0.121	21.48	2.09**	0.073	0.234	14.59	4.19***
% Residential	0.129	0.095	31.37	3.44***	0.076	0.253	15.15	3.79**
Coordinates	0.154		37.50					
R <sup>2</sup>	0.415							
Global coordinates					0.023		4.52	
R <sup>2</sup> global					0.502			

\* *p* < 0.05.

\*\* p < 0.01.

<sup>\*\*\*</sup> *p* < 0.001.

area by Pinheiro et al. (2008). However, our study has focused on realized and projected blocks, while this check-list encompasses other environments within the urban perimeter, such as wetlands and protected forest areas.

Within Brazil, few studies have evaluated the effect of urbanization on bird richness, and none of these studies was performed in a city in the cerrado. Studies performed in other Brazilian cities located in cerrado areas, such as Brasilia or Goiânia, focused on particular habitats within the city, such as parks, lakes and university campuses (Faria, 2007; Monteiro and Brandão, 1995); thus, their results are not comparable with the results of this study.

The non-parametric estimates of species richness per block type tended to stabilize when the sample size was greater than 10 blocks; thus, meaningful comparisons can be made at least among the three block types with most data. Non-urbanized blocks had a species richness level that was 91.6% of the estimated species richness, while accounting for only 11% of the city area. In contrast, the species richness in semi-urbanized blocks and urbanized blocks was 63.6% and 45.0% of the total estimated richness, respectively, despite the fact that these blocks covered a larger area. Thus, nonurbanized blocks are the cause of the high bird species richness in the study area. These results show that the urbanization process produces a quick decrease in bird species richness and that this process starts with the first alterations of the block because the opening of unpaved roads in non-urbanized blocks seemed to reduce richness by about 24%. If this process continues, our results predict that bird species richness will have decreased to half the present value once all projected blocks are urbanized. Thus, it is of paramount importance to understand how the urbanization process could be modified to maintain a higher percentage of the present richness. Conserving the present protected forest areas will be also necessary to achieve this aim.

In general, mean species richness per block, calculated for all bird species or for bird species groups defined by several criteria (season, trophic guild, family, migratory behavior and habitat preference) also experienced a progressive reduction with increased urbanization. Exceptions to this pattern were the richness of nectarivores and hummingbirds (Trochilidae), the main family in this trophic guild, which were fairly constant in block types. Other studies have also found similar species richness for nectarivores in areas with different degrees of urbanization and have suggested that this trophic guild benefits from urban gardening (Parsons, French, & Major, 2003; Reichard, Chalker-Scott, & Buchanan, 2001; White, Antos, Fitzsimons, & Palmer, 2005). Nectarivorous birds seem to be able to use the nectar of exotic species (Hodgson, Fresch, & Major, 2007), and in this study, we have observed some hummingbird species foraging on exotic plants such as Lophantera lactescens Ducke and Plumeria rubra L., in urbanized and semi-urbanized blocks. The average richness of Falconidae and Icteridae was low and also did not vary among block types. The presence of some



**Fig. 4.** Relationship between bird species richness observed in urbanized blocks sampled in Palmas and the habitat variables that were significant in the global hierarchical partitioning analysis (Table 4). The residential character of the block, the existence of unpaved roads and the density of native trees contribute to increase species richness, while percentage of block area built, the density of commercial buildings and the density of exotic trees have the opposite effect.

generalist species in these families, such as *Falco sparverius* and *Milvago chimachima*, in the former, and *Gnorimopsar chopi* and *Cacicus cela*, in the latter, would explain this lack of differences.

# 4.2. Factors affecting richness in urbanized blocks

The Hierarchical Partitioning analysis demonstrated that within urbanized blocks, which NMDS characterized as the most homogeneous block category, several environmental variables are important in determining the observed bird species richness. The most important determinant of species richness was the residential or commercial nature of the block. The percentage of block area planned for residential use had the highest independent contribution to species richness, both in the global model and when comparing the models by groups of variables; it exerted a positive influence on species richness. The distribution of this variable shows that blocks may be assigned unambiguously as residential or commercial because the percentage of buildings planned for each of these uses is always greater than 80%, and residential blocks

had, on average, more bird species than commercial ones. The density of commercial buildings actually constructed was the second most important variable in both HP analyses and was negatively correlated with species richness. Another related variable, the percentage of block area built, was also significant and had a negative effect on species richness. Thus, it can be inferred that within urbanized blocks, the percentage of area that is covered by buildings has an inverse relationship with bird diversity but that this relationship depends on the commercial or residential use of the block. Other studies have also found that commercial blocks harbor fewer bird species than do residential ones; this difference has been attributed to the reduction in area covered by vegetation and the increase in built area in commercial blocks (Blair, 2001; Heezik, Smyth, & Mathieu, 2008; Mathieu, Freeman, & Aryal, 2007; Ortega-Álvarez and MacGregor-Fors, 2009). While this may be true, our global HP analysis includes variables related to vegetation cover (native and exotic tree densities) together with variables descriptive of the block type, and both have a significant independent contribution to the variation in bird species richness. This means that there is an effect of the commercial-residential dichotomy that should be independent of the extent of vegetation reduction in commercial blocks. Thus, it seems that other characteristics of commercial blocks that were not analyzed here, such as the greater density of people, vehicles, noise or some specific features of commercial buildings, may negatively affect bird species richness (Fontana et al., 2011; Ortega-Álvarez and MacGregor-Fors, 2009). However, given that the distribution and structure of commercial and residential block types is already planned and approved, managers should focus on other variables affected by the urbanization process. Unpaved roads also had a significant effect on species richness; the few urbanized blocks that contained this type of road reached high richness values, probably due to the presence of bushes and herbaceous vegetation on the perimeter of the roads. However, this was the weakest of the significant effects, and it is likely that unpaved roads will eventually be paved; thus, the ability to incorporate these into a management policy is limited.

The third most important independent contribution to species richness was the density of mid-height native trees. The density of exotic trees was also significant, but this variable was negatively correlated with bird species richness. The number of native or exotic tree species was only significant in the partial analysis and lost significance when analyzed together with tree density. Thus, it appears that the densities of native and exotic trees are important block features in determining bird species richness that may be managed during the urbanization process (MacGregor-Fors, 2008). Cerrado native trees may offer food and areas for refuge and nesting that birds have adapted to use. In contrast, exotic tree species, while they may offer fruits or nectar, seem to be suitable for fewer species. The negative effect of the density of exotic trees cannot be attributed to a few dominant species, since we have detected 88 exotic species in urbanized blocks and the average number of exotic tree species per block doubles the number of native species (own data). The results showed a significant influence only for medium height trees in the global analysis. While taller trees were important only in the partial analysis, the conservation of tall trees should not be regarded as unimportant because they may be used by certain species.

#### 4.3. Concluding remarks

This study has shown that the progress of the urbanization process will produce a considerable decrease in bird species richness in Palmas, a recently established city that is still under construction. Given that a high number of blocks are currently not urbanized or are partially urbanized, our findings should be used by managers and decision makers to promote strategies to mitigate the expected loss of bird diversity. We have identified that, among the features that are amenable to management, the density of native trees is the variable that most influences bird species richness. Thus, strategies directed to keep these species in private or public gardens, as well as on streets, will contribute substantially to the maintenance of bird diversity. The process of developing the city's blocks has entailed the elimination of native vegetation and trees; thus, the exotic and native trees now found in the urbanized blocks were planted after urbanization. Based on our findings, we recommend that whenever possible native trees should be kept during the transformation of blocks to promote the conservation of these native trees in owners' gardens. The town council formerly mandated that 15% of the area of each block should be comprised of vegetation (Adorno and Fighera, 2005), but these policies did not indicate that native species should be given priority. Although these regulations were eliminated, our results suggest that if these regulations could be recovered and improved to promote the conservation of a certain percentage of native trees during development and to give incentives to plant native tree species, the expected loss of bird species richness would be largely mitigated.

# Acknowledgements

We thank José Emílio Martínez-Pérez (University of Alicante), Bruno M. Carneiro (Tocantins Catholic Faculty) and Dianes G. Marcelino (Tocantins Federal University), who helped us with GIS, and Cristiano Borges, Suélen Amâncio, Yanna Leite, Vanílcia Clementino and Natália Freire (Tocantins Federal University) for his assistance in identifying plant species. We are grateful to Dárius Pukenis Tubelis, Luís Fábio Silveira and Daniel Blamires that reviewed an initial version of the manuscript and made valuable suggestions. We also would like to thank CAPES for the Master's scholarship granted to E.S.R. and the Neotropical Grassland Conservancy for the field equipment donated. The city of Palmas and Tocantins State Government provided data on city planning and state of lots development and some bibliography.

## Appendix A.

Bird species recorded in Palmas, Tocantins, Central Brazil. Taxonomy follows the Brazilian Committee of Ornithological Records (CBRO, 2011). Blocks types: (B1) not urbanized; (B2) not urbanized with unpaved roads; (B3) not urbanized with open vegetation; (B4) semi-urbanized; (B5) urbanized. Status: (R) Resident species. (M) Migrant species; Habitat: (C1) open area species; (C2) species that prefer open areas but use also forested areas; (F1) species exclusive to forests; (F2) forest species that use also open areas; Trophic guilds: (GRA) granivores, (INS) insectivores, (OMN) omnivores, (FRU) frugivores, (CAR) carnivores, (NEC) nectarivores and (NCR) necrophagous. References: 1 – Moojen et al. (1941); 2 – Schubart et al. (1965); 3 – Sick (1997); 4 – Remsen et al. (1993); 5 – Willis (1979); Endemic's: EnA – Amazon Endemic (Stotz et al., 1996). EnC – Cerrado Endemic (Cavalcanti, 1999; Silva, 1997; Silva & Santos, 2005).

Species	$B_1$	$B_2$	B <sub>3</sub>	$B_4$	$B_5$	Status	Habitat	Trophic
Tinamidae								
Crypturellus	×	×	×	×		R	C2	OMN <sup>1,2</sup>
parvirostris								
Rhynchotus	×		×			R	C2	OMN <sup>2</sup>
rufescens								
Cracidae								
Penelope	×	×		×		R	F1	FRU <sup>2</sup>
superciliaris								
Threskiornithidae								
Theristicus	×	×	×	×		R	C2	OMN <sup>2</sup>
caudatus								
Cathartidae								
Cathartes aura	×	×	×			R	C2	NCR <sup>2,3</sup>
Coragyps atratus	×	×	×	×	×	R	C2	NCR <sup>2,3</sup>
Accipitridae								
Elanoides		×	×	×	×	М	F2	INS <sup>2,3</sup>
forficatus								
Ictinia plumbea		×			×	R	F2	INS <sup>2</sup>
Gampsony		×	×	×	×	R	F2	CAR <sup>2,3</sup>
swainsonii								
Rupornis	×	×	×	×	×	R	C2	CAR <sup>1,2</sup>
magnirostris								
Falconidae								
Caracara plancus			×		×	R	C2	OMN <sup>2,3</sup>
Milvago	×		×	×	×	R	C2	CAR <sup>1,2,3</sup>
chimachima								
Falco femoralis			×	×	×	R	C1	CAR <sup>3</sup>
Falco sparverius	×	×	×	×	×	R	C1	INS <sup>1,2</sup>
Herpetoteres	×	×		×		R	C2	CAR <sup>2</sup>
cachinnans								
Charadriidae						_		
Vanellus chilensis	×	×	×	×	×	R	C1	INS <sup>2</sup>

Species	$B_1$	$B_2$	B3	B4	<b>B</b> <sub>5</sub>	Status	Habitat	Trophic	SI
Columbidae						_		122	
Columbina	×	×	×	×	×	R	C2	GRA <sup>1,2,3</sup>	
Columbina	×	×	×	×	×	R	C2	GRA <sup>1,2,3</sup>	
squammata						_		122	Tl
Patagioenas	×	×	×	×	×	R	C2	GRA <sup>1,2,3</sup>	
Leptotila rufaxilla	×	×		×		R	F2	GRA <sup>1,2,3</sup>	
Columba livia				×	×	R	C1	GRA <sup>1,2,3</sup>	
Psittacidae						р	<b>C</b> 2	<b>FDI 1</b> 2 3	
Ara araraana Aratinga	×	×	×	×	×	к R	C2	FRU <sup>1,2,3</sup>	
leucophthalma							02	THO .	D
Aratinga aurea	×	×	×	×	×	R	C2	FRU <sup>2,3</sup>	
Forpus	×					R	F2	FRU <sup>2,3</sup>	
Brotogeris chiriri	×	×	×	×	×	R	F2	FRU <sup>2,3</sup>	
Amazona	×	×	×	×	×	R	F2	FRU <sup>2,3</sup>	
amazonica						P	50	<b>FDU</b> <sup>2</sup> 3	Fı
Orthopsittaca manilata	×	×				к	F2	FKU <sup>2,5</sup>	
Cuculidae									
Piaya cayana	×	×		×		R	F2	INS <sup>1,2</sup>	
Crotophaga ani	×	×	×	×	×	R	C2	INS <sup>1,2</sup>	Ty
Strigidae	×	×	×	×	×	к	12	IINS <sup>1,2</sup>	
Megascops	×	×		×		R	F2	INS <sup>1,2</sup>	
choliba						_			
Glaucidium	×	×		×	×	R	F2	CAR <sup>1,2</sup>	
Athene			×	×	×	R	C2	INS <sup>1,2</sup>	
cunicularia									
Caprimulgidae						P	61	NIC <sup>2</sup>	
Poaager nacunaa Nyctidromus	×	×	×	×	×	к R	F2	INS <sup>2</sup> INS <sup>2,3</sup>	
albicollis		~	~	~		ĸ	12	1110	
Trochilidae						_			
Phaethornis	×	×		×		R	F2	NEC <sup>3</sup>	
Phaethornis ruber	×	×				R	F1	NEC <sup>3</sup>	
Anthracothorax	×	×		×	×	R	C2	NEC <sup>2,3</sup>	
nigricollis						P	50	NEC <sup>23</sup>	
furcata	×	×		×		к	F2	NEC <sup>2,5</sup>	
Amazilia	×			×	×	R	F2	NEC <sup>3</sup>	
versicolor						-		ND 23	
Amazilia fimbriata	×	×		×	×	R	C2	NEC <sup>3</sup>	
Eupetomena	×	×	×	×	×	R	F2	NEC <sup>1,2,3</sup>	
macroura									
Trogonidae						р	<b>F1</b>	OMN <sup>24</sup>	
Galbulidae	×	×		×		к	FI	UMIN <sup>2,4</sup>	
Galbula ruficauda	×	×		×	×	R	F2	INS <sup>2</sup>	
Bucconidae						-		m (c1 2 2	
Bucco tamatia <sup>EnA</sup>	×	×	~	~	~	R	F1 C1	INS <sup>1,2,3</sup> INS <sup>1,2,3</sup>	
Nystalus	×	×	×	×	×	R	C2	INS <sup>1,2,3</sup>	
maculatus									
Notharchus tectus	×					R	F1	INS <sup>1,2,3</sup>	
Chenaoptera tenebrosa	×	×		×		к	F2	INS <sup>1,2,5</sup>	
Ramphastidae									
Ramphastos toco	×	×	×	×	×	R	C2	OMN <sup>1,2,3,4</sup>	
Pteroglossus	×	×		×		R	F2	FRU <sup>1,2,3,4</sup>	
Picidae									
Picumnus	×	×		×		R	F2	INS <sup>3</sup>	Pi
albosquamatus						_			
Melanerpes	×	×	×	×	×	R	C2	INS <sup>2</sup>	Ti
Colaptes	×	×		×		R	C2	INS <sup>3</sup>	V
melanochloros				-			-	-	• ·
Colaptes	×	×	×	×	×	R	C2	INS <sup>1,2</sup>	
campestris Celeus flavescens	×	×		×		R	F2	INS <sup>1,2</sup>	C
Celeus jiuvescells	~	~		~		N	12	1140	C

Species	<b>B</b> <sub>1</sub>	<b>B</b> <sub>2</sub>	<b>B</b> <sub>3</sub>	B4	B <sub>5</sub>	Status	Habitat	Trophic
Dryocopus lineatus	×	×		×		R	C2	INS <sup>2</sup>
Campephilus rubricollis <sup>EnA</sup>	×					R	F1	INS <sup>3</sup>
Thamnophilidae	~	~		v		P	C	INIS <sup>2</sup>
torquatus Thampophilus	<u>`</u>	<sup>^</sup>		^		D	C2	INS <sup>2</sup>
pelzelni	x	×				л р	C2	INS <sup>-</sup>
formicivora grisea Formicivora mifa	×	×		×		ĸ	FZ	INS <sup>-,-</sup>
Dendrocolaptidae	×	×	x	×		ĸ	C2	INS <sup>2,5</sup>
Sittasomus griseicapillus	×					R	F1	INS <sup>2,3</sup>
Dendroplex picus Lepidocolaptes	× ×	×	×	×	×	R R	F2 C2	INS <sup>2,3</sup> INS <sup>1,2</sup>
angustirostris Furpariidae								
Furnarius rufus		×	×	×		R	C2	INS <sup>1,2</sup>
Synallaxis albescens	×	×				R	C2	INS <sup>3</sup>
Xenops rutilans	×	×		×		R	F1	INS <sup>3</sup>
Tyrannidae Hemitriccus	~	~				R	F1	INS <sup>3</sup>
striaticollis	~	~				D	50	INC <sup>3</sup>
garitaceiventer	×	×				ĸ	FZ	INS <sup>3</sup>
cinereum	×	×		×		ĸ	F2	INS <sup>3</sup>
Myiopagis caniceps	×	×				R	F2	INS <sup>3</sup>
Elaenia cristata Elaenia	× ×	× ×	×	× ×		M R	C2 C2	INS <sup>3</sup> OMN <sup>3</sup>
flavogaster Elaenia	×	×	×	×		М	C1	OMN <sup>2</sup>
chiriquensis Elaenia	×					R	C1	OMN <sup>3</sup>
parvirostris Camptostoma	×	×	×	×		R	F2	OMN <sup>2,3</sup>
obsoletum Fuscarthmus	×					R	F2	INS <sup>3</sup>
meloryphus Tolmomyias	~		~	~		R	F1	INS <sup>2</sup>
sulphurescens	^		^	^		ĸ	11	
Myiophobus fasciatus	×					R	C2	INS <sup>2</sup>
Legatus Iaucophaius	×	×	×			R	F2	INS <sup>2</sup>
Pitangus	×	×	×	×	×	R	C2	OMN <sup>1,2,3</sup>
sulphuratus Myiodynastes	×	×	×	×	×	R	F2	OMN <sup>1,2,3</sup>
maculatus Megarynchus	×	×	x	×	×	R	F2	OMN <sup>1,2,3</sup>
pitangua Griseotyrannus	×	×	×			М	C2	INS <sup>2</sup>
aurantioatro- cristatus								
Tyrannus albogularis	×	×	×	×	×	М	C1	INS <sup>3</sup>
Tyrannus melancholicus	×	×	×	×	×	М	C2	INS <sup>2,3</sup>
Tyrannus savana Myiarchus	×	×	× ×	× ×	×	M R	C1 F2	INS <sup>3</sup> INS <sup>2</sup>
swainsoni Tolmomyas	×	×		×		R	F2	INS <sup>2</sup>
sulphurescens Pipridae								
Pipra fasciicauda	×	×				R	F1	FRU <sup>3</sup>
Tityra cayana	×					R	F1	OMN <sup>2</sup>
Cyclarhis	×	×	×	×	×	R	F2	INS <sup>2</sup>
gujanensis Vireo olivaceus	×	×		×		R	F2	INS <sup>2</sup>
Corvidae Cyanocorax	×	×	×	×	×	R	C1	OMN <sup>3</sup>
cristatellus <sup>EnC</sup>								

Species	$B_1$	$B_2$	$B_3$	$B_4$	$B_5$	Status	Habitat	Trophic
Cyanocorax	×	×		×		R	F2	OMN <sup>3</sup>
cyanopogon								
Progne tanera	~	×	~	×	×	R	C2	INS <sup>1,2</sup>
Progne chalybea	~	~	~	x	×	M	C2	INS <sup>1,2</sup>
Troglodytidae								4.5
Troglodytes	×	×	×	×	×	R	C2	INS <sup>1,2</sup>
Polioptilidae								
Polioptila	×	×	×	×	×	R	F2	INS <sup>2</sup>
dumicola								
Turdus	~	~	~	~	~	R	F2	OMN <sup>1,2</sup>
leucomelas	~	~	~	~	~	R	12	omit
Mimidae								
Mimus saturninus	×	×	×	×	×	R	C1	OMN <sup>1,2</sup>
Coereba flaveola	×	×	×	×	×	R	F2	NEC <sup>3</sup>
Thraupidae								
Saltator maximus	×			×		R	F2	INS <sup>2</sup>
Saltatricula atricollis <sup>EnC</sup>	×	×	×	×		R	C1	INS <sup>2</sup>
Schistochlamys			×			R	C2	OMN <sup>2</sup>
melanopis								
Schistochlamys	×	×		×		R	C2	OMN <sup>2</sup>
Neothraunis	×	×	×	×		R	C1	OMN <sup>2</sup>
fasciata <sup>EnC</sup>								
Nemosia pileata	×	×	×	×		R	F2	OMN <sup>2</sup>
Thlypopsis	×	×	×			R	F2	OMN <sup>1,2</sup>
Cypsnagra	×	×	×	×		R	C1	OMN <sup>3</sup>
hirundinacea								
Tachyphonus	×		×			R	F2	OMN <sup>2</sup>
rujus Ramphocelus	×	×	×	×	×	R	F2	OMN <sup>2</sup>
carbo								
Tangara sayaca	×	×	×	×	×	R	C2	OMN <sup>1,2</sup>
Tangara palmarum	×	×	×	×	×	ĸ	F2	OMN <sup>2</sup>
Tangara cayana	×	×	×	×	×	R	C2	OMN <sup>1,2</sup>
Tersina viridis	×	×		×		R	F2	OMN <sup>2</sup>
Dacnis cayana	×	×	×	×	×	R	F2	$OMN^{1,2}$
cyaneus	×	×		x		ĸ	I'I	Olvin
Hemithraupis	×	×	×	×		R	C2	OMN <sup>2</sup>
guira Coniroctrum						D	F2	OMN <sup>2</sup>
speciosum	×	×				ĸ	FZ	Olvin-
Emberizidae								
Ammodramus		×	×			R	C1	GRA <sup>2</sup>
numerans Emberizoides		×	×			R	C1	INS <sup>2</sup>
herbicola								
Volatinia jacarina	×	×	×	×	×	R	C1	GRA <sup>2</sup>
Sporophila	×	×	×	×	×	R	C1	GRA <sup>2</sup>
Sporophila		×	×			М	C2	GRA <sup>2</sup>
nigricollis								_
Charitospiza	×	×	×	×		R	C1	INS <sup>2</sup>
Corvphospingus	×	×		×		R	C2	GRA <sup>2</sup>
pileatus								
Cardialidae						р	<b>C</b> 2	OMD112
Piranga flava Parulidae	×	×	×	×		к	(2	UIVIN <sup>1,2</sup>
Basileuterus	×	×				R	C2	INS <sup>3</sup>
culicivorus						_		
Basileuterus flaveolus	×	×		×		R	C2	INS <sup>3</sup>
Icteridae								
Psarocolius		×			×	R	F2	OMN <sup>2</sup>
decumanus						р	53	OMD <sup>2</sup>
Cucicus ceia Icterus cavanensis	×			×	×	ĸ	г2 F2	OMN <sup>2</sup>
Gnorimopsar	×	×	×	×	×	R	C2	OMN <sup>1,2</sup>
chopi								

Species	$B_1$	<b>B</b> <sub>2</sub>	<b>B</b> <sub>3</sub>	B4	<b>B</b> <sub>5</sub>	Status	Habitat	Trophic			
Fringillidae											
Euphonia	×	×	×	×	×	R	C2	FRU <sup>3</sup>			
chlorotica											
Euphonia violacea	×					R	F2	FRU <sup>3</sup>			
Passeridae											
Passer domesticus				×	×	R	C1	OMN <sup>2</sup>			
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