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ORIGINAL ARTICLE

Bird traits in urban–rural gradients: how many functional groups are there?

Lucas M. Leveau

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Abstract Recent analyses of communities have examined the variation of species traits along environmental gradients. These papers highlight a combination of several traits, instead of variation of individual traits, to better explain the effect of urbanization on bird communities. Exploratory factor analysis (EFA) allows the identification of an underlying structure of a broad set of data. EFA can be a useful tool for generating functional groups from highly correlated biological traits in bird communities and determining its variation along gradients of urbanization. Birds were counted along an urban–rural gradient during spring 2009–summer 2010. Species were classified using 15 biological traits related to the use of space. The EFA was calculated from a matrix where rows were sampling units ($n = 75$), and columns represented counts of individuals with each trait ($n = 15$). Four functional groups were obtained. Functional group 1 comprised resident species feeding gregariously on the grond, nesting in buildings, having an omnivorous diet, and being most abundant in the more urbanized areas. Functional group 2 was most abundant at intermediate levels of urbanization and represented solitary species that nest in trees, feeding on vegetation and with carnivorous and nectarivorous diets. Migratory behavior, insectivorous and granivorous diets, aerial feeding and ground nesting were representative of two functional groups in rural areas. Responses to urbanization by these functional groups are consistent with the classifications of response guilds (urban exploiters, urban adapters, and urban avoiders). Thus, EFA allows a link between concepts generated from the analysis of species and the analysis based on biological traits.

Keywords Exploratory factor analysis · Urbanization · Guilds · Birds · Argentina · Land use

Zusammenfassung

Merkmale von Vögeln entlang von städtisch-ländlichen Gradienten: Wie viele funktionelle Gruppen gibt es?

In aktuellen Untersuchungen von Vogelgemeinschaften wurde die Variation von Merkmalen an Arten entlang von Umweltgradienten untersucht. Diese Untersuchungen betonen eine Kombination verschiedener Merkmale, anstatt einer Variation individueller Merkmale, um den Effekt der Urbanisierung auf Vogelgemeinschaften besser zu erklären. Eine Erklärende Faktoranalyse (EFA) erlaubt es, in einem großen Datensatz eine zugrundeliegende Struktur aufzudecken. EFA kann ein nützliches Werkzeug sein, um aus hoch miteinander korrelierten biologischen Merkmalen in Vogelgemeinschaften funktionelle Gruppen zu erzeugen und um deren Variation entlang von Urbanisierungsgradienten zu bestimmen. Vögel wurden entlang eines städtisch-ländlichen Gradienten während des Frühlings 2009 bis Sommer 2010 gezählt. Die Arten wurden anhand von 15 biologischen Merkmalen zur Raumnutzung klassifiziert. Die EFA wurde aus einer Matrix berechnet, deren Reihen den Zählstellen entsprachen ($n = 75$), und in deren Spalten die Anzahl der Individuen mit dem jeweiligen Merkmal ($n = 15$) stand. Wir erhielten vier funktionale Gruppen. Die

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L. M. Leveau (✉)
Universidad Nacional de Mar del Plata, Funes 3350,
7600 Mar del Plata, Argentina
e-mail: lucasleveau@yahoo.com.ar

funktionale Gruppe 1 bestand aus Arten, die Schwärme bilden, in Gebäuden nisten, eine omnivore Ernährung aufweisen und am häufigsten in den am meisten urbanisierten Gegenden vorkommen. Die funktionale Gruppe 2 war am häufigsten in Gebieten mittlerer Urbanisierung zu finden und bestand aus Arten, die in Bäumen nisten, die sich von Pflanzen ernährten und solchen mit carnivorer und nectarivorer Ernährung. Zugverhalten, insektivore und granivore Ernährung, Nahrungsaufnahme im Flug und Bodenbrüten waren kennzeichnend für zwei funktionelle Gruppen in ländlichen Gegenden. Die Reaktionen dieser funktionalen Gruppen auf Urbanisierung stimmen überein mit den sog. Reaktions-Gilden (Stadtnutzer, Stadtanpasser und Stadtvermeider). Daher erlaubt die EFA eine Verbindung zwischen Konzepten, die auf der Analyse der Art beruhen, mit Analysen, die auf biologischen Merkmalen fußen.

Introduction

Recent analyses on bird communities have examined the variation of species traits along environmental gradients (Diaz et al. 1999; Lavorel and Garnier 2002; McGill et al. 2006). The use of traits permits greater generality and predictability, whereas a focus on environmental gradients allows an explanation of why communities change in a systematic way in space (McGill et al. 2006).

In recent years, several studies in urban areas have dealt with these topics (McDonnell and Pickett 1990; Blair 1996; Reynaud and Thioulouse 2000; Blair and Johnson 2008; Burton et al. 2009; Møller 2009; Evans et al. 2011). These papers highlighted a combination of several traits, instead of variation of individual traits, to better explain the effect of urbanization on bird communities (Kark et al. 2007; Croci et al. 2008). However, there are no methodological approaches to explore the combinations of birds' traits along urban gradients, except for the relationships between nesting and feeding strategies (Conole and Kirkpatrick 2011).

Exploratory factor analysis (EFA) is a multivariate statistical tool to identify factors or latent variables of an extensive group of data (Ferrando and Anguiano-Carrasco 2010; Howit and Cramer 2011). EFA makes it possible to group variables that are highly correlated with each other into a smaller number of factors that can be interpreted as conceptual variables (Legendre and Legendre 1998; Pérez and Medrano 2010).

Exploratory factor analysis emerged in the early twentieth century in the study of intelligence, when it was thought that different skill tests reflected an underlying factor of intelligence (Spearman 1904; Pérez and Medrano 2010). Then, from 1930, these analyses were reformulated to determine a set of factors that characterize skills and personality (Thurstone 1947; Pérez and Medrano 2010). Subsequently, EFAs have been used for models in biology and economics (Ferrando and Anguiano-Carrasco 2010).

In ecology, statistical analyses to reduce the number of variables, such as principal component analysis (PCA) or EFA, have been used to summarize habitat variables or to explore environmental gradients in a few axes (Fernandez-Juricic 2000; Garaffa et al. 2009; du Toit and Cilliers 2011). Although PCA and EFA seem similar, they have important differences (James and McCulloch 1990). Whereas PCAs consider the total variance among variables, EFAs take into account that variables have sampling errors (Ferrando and Anguiano-Carrasco 2010). The aim of PCAs is to extract components to reduce dimensions and summarize variability among variables; in EFAs, the aim is to explore the resultant factors and relationships among the original variables (James and McCulloch 1990; du Toit and Cilliers 2011). Another statistical method of data reduction similar to EFA is nonmetric multidimensional scaling (NMS; James and McCulloch 1990), which does not require meeting assumptions of linearity among variables and normal distribution (James and McCulloch 1990). However, EFAs have rotational methods that allow a simple structure (Rabinowitz 1975). This simple structure is achieved when each variable has a correlation near to 1 with one factor and correlations near to 0 for the remaining factors (Pérez and Medrano 2010).

The development of response-guild concepts has been very useful in the advance of urban ecology (Blair 1996; McKinney 2002; Croci et al. 2008). These concepts are based on classifying species according to their response to different levels of urbanization (Blair 1996). However, these response-guilds tell us almost nothing about which function or traits characterize them (but see Croci et al. 2008; Conole and Kirkpatrick 2011).

Although EFA has been used a very few times by ecologists (Legendre and Legendre 1998), it can be a useful tool to generate functional groups from highly correlated traits and determine their variation along urbanization gradients. Moreover, depending upon the type of response that these functional groups have in relation to the level of urbanization, links to the response-guilds can be made.

The objective of this work is to generate functional groups from a series of traits of birds along an urban–rural gradient by using EFA. It is expected that scores of the functional groups will vary along the urbanization gradient according to different responses to human activities.

Methods

Study area

The study was made in Mar del Plata city (38°00′S, 57°34′W; >600,000 inhabitants) and surroundings. It is located in the southeastern part of Buenos Aires province (Argentina), within the subregional Austral Pampas in the Pampean Region (Soriano et al. 1991), surrounded by a landscape composed by crop fields, pastures, tree plantations and natural grasslands. The climate is temperate; mean annual temperature is 14 °C and annual precipitation is 920 mm (data from the National Meteorological Service).

Different components of an urban–rural gradient were recognized (Fig. 1): (1) the urban sector, represented by the commercial and administrative center of the city, is dominated by tall buildings; (2) the suburban sector is composed of detached houses located within the urban matrix, with lawned sidewalks, yards and paved roads; (3) the periurban sector is located on the boundary of the city and composed of detached houses with yards, high tree cover and unpaved roads; (4) the horticultural sector, which is placed 2 km from the urban fringe where cultivated crops include lettuce, onions and tomatoes; and (5) the agricultural sector is located 1 km from the urban fringe, where primarily soybeans and wheat are grown in fields larger than those present in the horticultural sector (L. Leveau, unpublished data).

Bird surveys

Morning surveys were conducted along transects 100 m long × 50 m wide, separated from each other by at least 100 m. Surveys were conducted three times on each transect during spring 2009 and summer 2010. These seasons correspond with the breeding period of most species in the study area (de la Peña 2010). I conducted 15 transects in each of the five sectors of the urban–rural gradient. The species identification was aided by use of 7 × 50 binoculars. All birds making use of sample unit were counted whether perched, singing, or feeding; high flying birds were not counted. Species were classified among 15 traits grouped in five categories (see Electronic supplementry material): (1) feeding sites (vegetation, ground, air), (2) diet (omnivore, granivore, insectivore, nectarivore, carnivore), (3) nest sites (trees, buildings, or herbaceous vegetation and ground), (4) resident status (resident, migratory), and (5) sociability (solitary or gregarious). These classifications were made based on data from the literature and personal observations (de la Peña 1988, 1989).

Measures of habitat

Measurements in two plots of 25-m radius in each transect along the gradient were made for the following habitat characteristics: (1) percentage cover of trees, shrubs, lawn (managed herbaceous vegetation), herbaceous vegetation, asphalt, buildings, and crops, (2) number of trees <5 m of height and number of trees >5 m of height, and (3) pedestrian and vehicle traffic for 3 min, measured simultaneously during the bird counts. The complexity of habitat within each transect was estimated by calculating the Shannon diversity index H (Zar 1999) using percentage of cover of trees, shrubs, lawn, buildings, herbaceous vegetation, and crops. For each transect, values of percentage cover and habitat diversity of the two circular plots were averaged.

Statistical analysis

A data matrix was generated with rows as sampling units ($n = 75$), and columns for the number of individuals for each trait ($n = 15$), considering the number of individuals with specific traits (Lim and Sodhi 2004; Leveau and Leveau 2004, 2005; Blair and Johnson 2008). This alternative would be most suitable to represent the functioning of a community (Blair and Johnson 2008).

Normality of data was assessed by analyzing values of skewness and kurtosis (Pérez and Medrano 2010). For those variables with skewness or kurtosis values above 1.5, the data were logarithmically transformed (Zar 1999). Although data transformations improved skewness and kurtosis for nectarivores and aerial feeders, data still remained above the threshold of 1.5 (nectarivores: skewness = 2.42, kurtosis = 6.21; aerial feeders: skewness = 2.20, kurtosis = 5.24). Barlett's test of sphericity was used to test the assumption of linearity among variables by evaluating the null hypothesis of no correlation among variables (Pérez and Medrano 2010). Barlett's test was 2,016.0 ($P < 0.001$), indicating that the variables were intercorrelated. In addition, I calculated an index of sampling adequacy using Kaiser–Meyer–Olkin (KMO) which produces a value between 0 and 1, with values near 1 indicating sampling adequacy (Kaiser 1970). This index was 0.54, and is above the cut-off value established by Kaiser (1970). Those factors with eigenvalues equal to or greater than 1 were selected (Kaiser 1960). An oblique factor extraction, using the minimum rank factor method with Promax rotation was performed because some factors had correlations above 0.32 between them (ten Berge and Kiers 1991; Tabachnick and Fidell 2001; Pérez and Medrano 2010). These methods were the most appropriate to generate a matrix of simple structure. Those loadings with correlation values greater than or equal to 0.40 were taken into account, and then the higher trait–factor correlations (Glutting 2002; Pérez and Medrano 2010). These tests were performed using the program FACTOR (Lorenzo-Seva and Ferrando 2006). FACTOR is easy to use software that contains several statistical analyses not available in other commercial software, and since its release in 2006 has been used in 29 papers of journals covered by ISI (Ferrando and Anguiano-Carrasco 2010).

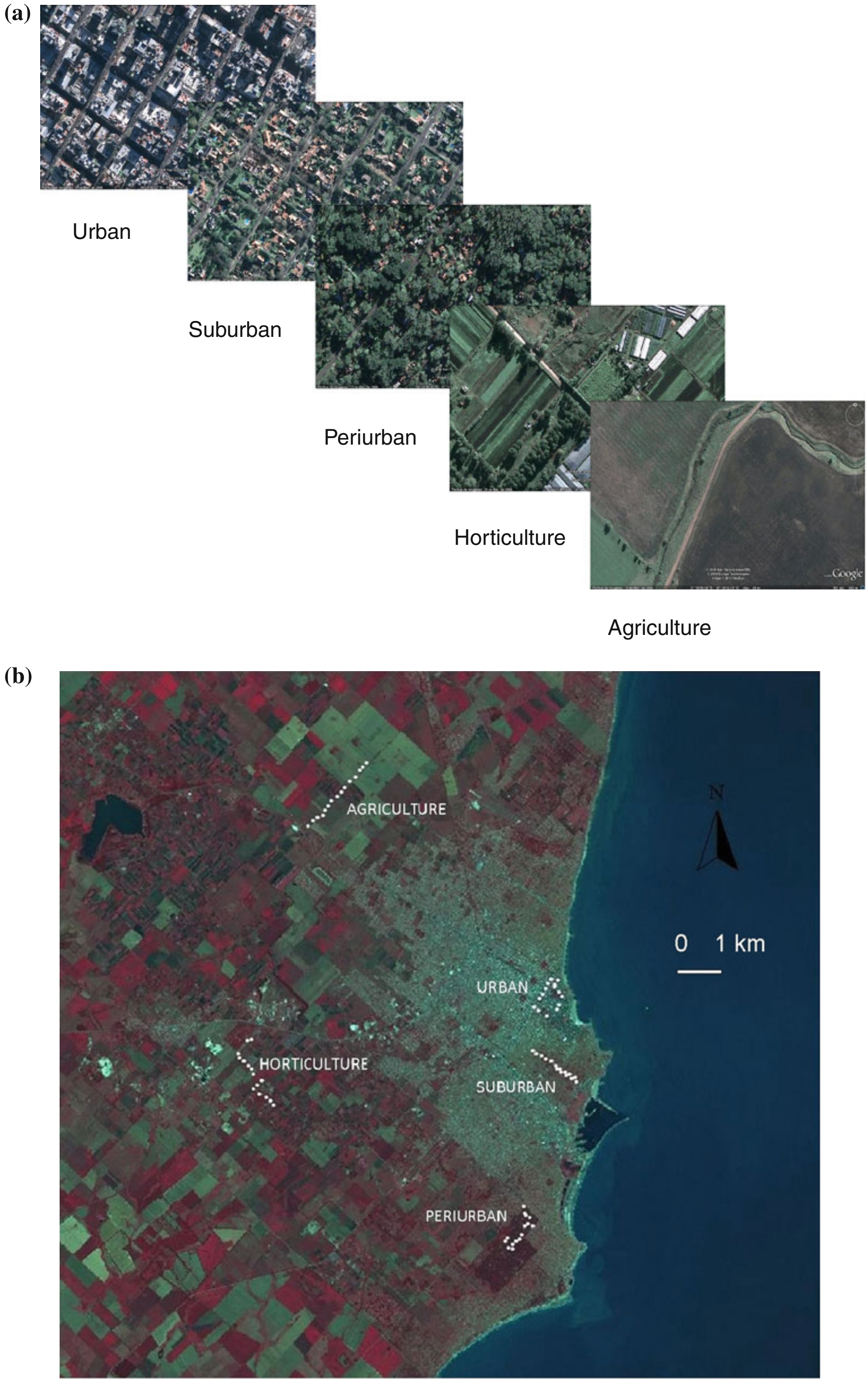

Fig. 1 The study area showing: **a** Google Earth images (580 m long × 380 m wide) of the five land use types surveyed in this study, and **b** false colour image of Mar del Plata (bands 2, 3, and 4 of Landsat TM) with the location of the transects along the urban–rural gradient

Scores along each axis were used to analyze the variation along the urban–rural gradient. Differences in the values of scores and measures of habitat were compared using the non-parametric Kruskal–Wallis and Nemeyi tests (Zar 1999).

Results

Coverage of buildings, asphalt, and variables related to human disturbance (traffic of cars, motorcycles, bicycles and pedestrians) were highest in the urban center and declined towards rural areas (Table 1). Coverage of lawn, shrubs, and trees were highest at intermediate levels of urbanization, leading to greater habitat diversity (Table 1). The number of tall trees was also highest at intermediate levels of urbanization, particularly in periurban areas (Table 1). Rural areas generally had high cover of herbaceous vegetation and crops (Table 1). However, horticulture sectors differed from agriculture sectors in having greater tree cover, fewer crops, and a greater diversity of habitat (Table 1).

Exploratory factor analysis produced four factors or functional groups (Table 2). These functional groups accounted for 84 % of the variance.

Functional group 1 was related to resident species that nest in buildings, have an omnivorous diet, and feed gregariously on the ground (Table 2). Functional group 2 was related to solitary individuals that nest in trees, and feed in vegetation with nectarivorous or carnivorous diets. Functional group 3 was defined by high loadings on migratory behavior, insectivorous diet and aerial feeding (Table 2). Finally, functional group 4 was related to species that nest on the ground and have a granivorous diet.

Functional group 1 showed significant differences along the environmental gradient ($H = 10.72$, $P = 0.03$). Values of scores were highest in urban and suburban areas compared to periurban, horticulture and agriculture areas, although there were no significant differences between habitats (Fig. 2) (Nemeyi test, $P > 0.05$). Functional group 2 showed significant differences along the gradient ($H = 42.78$, $P < 0.001$) with periurban areas having higher values than urban and agricultural sectors (Nemeyi test, $P < 0.05$). Suburban and horticulture sectors had higher values than urban sectors. Functional groups 3 and 4 also showed significant differences along the gradient (Fig. 2) ($H = 27.02$, $P < 0.001$; $H = 33.43$, $P < 0.001$, respectively). For both, urban sectors had lower values than other habitats (Nemeyi test, $P < 0.05$).

Discussion

The results indicate that urbanization leads to significant changes in the lifestyles of birds. Of the four functional groups defined from EFA, two were negatively affected by

Table 1 Environmental variables along the urban–rural gradient

	Urban	Suburban	Periurban	Horticulture	Agriculture	*H*
Trees[a]	10.97 (7.64) bc	20.98 (10.42) b	51.40 (12.02) a	15.10 (8.70) b	3.63 (5.22) c	51.54*
Shrubs[a]	0.77 (0.84) cd	5.23 (2.88) ab	10.90 (4.05) a	3.33 (3.42) bc	0 d	55.9*
Lawn[a]	1.00 (1.51) b	31.20 (12.67) a	34.13 (14.09) a	2.17 (3.52) b	0.33 (1.29) b	59.08*
Buildings[a]	60.97 (5.49) a	37.5 (10.99) ab	25.17 (10.01) b	6.33 (8.91) bc	0.10 (0.39) c	65.15*
Asphalt[a]	32.00 (0.00) a	27.67 (6.34) a	1.17 (3.11) b	0 b	0 b	69.57*
Herbaceous vegetation[a]	0 b	0 b	17.90 (16.06) ab	35.07 (15.22) a	36.17 (11.84) a	54.3*
Crops[a]	0 b	0 b	0 b	23.67 (17.34) a	42.83 (13.66) a	60.7*
Trees <5 m[b]	4.13 (2.48) b	9.93 (4.20) a	3.83 (1.45) b	14.70 (14.12) a	1.07 (1.12) c	41.65*
Trees >5 m[b]	3.73 (2.23) bc	3.83 (2.77) b	14.90 (3.85) a	5.03 (5.48) bc	0.77 (2.47) c	43.47*
H′ habitat[c]	0.25 (0.06) c	0.49 (0.05) ab	0.63 (0.07) a	0.49 (0.12) ab	0.35 (0.06) bc	56.95*
Pedestrians[b]	9.33 (6.98) a	0.96 (0.85) b	0.24 (0.30) bc	0.05 (0.12) c	0.02 (0.09) c	54.87*
Cars[b]	9.93 (5.69) a	2.67 (1.60) ab	0.96 (1.30) c	1.22 (0.76) bc	0.60 (0.42) c	47.3*
Motorcycle[b]	0.71 (0.47) a	0.11 (0.21) b	0.16 (0.31) b	0.02 (0.09) b	0.04 (0.12) b	36.45*
Bicycle[b]	0.56 (0.50) a	0.27 (0.14) ab	0.11 (0.16) ab	0.05 (0.179) c	0.07 (0.19) bc	26.95*

Data are means and standard deviations in parentheses. Column *H* represents the results of the nonparametric Kruskal–Wallis test. Different letters for each variable indicate significant differences according to Nemeyi nonparametric test ($P < 0.05$)

* $P < 0.001$

[a] Data of percentage cover obtained in 25-m radius in each transect

[b] Data is quantity/3 min in each transect

[c] Shannon diversity index

Table 2 Promax rotated EFA results of biological traits along an urban–rural gradient in Mar del Plata and surroundings

Traits	Factor 1	Factor 2	Factor 3	Factor 4
Resident	**0.81**	0.28	−0.05	0.26
Omnivorous	**0.96**	−0.08	0.07	−0.34
Build nest	**0.93**	−0.29	0.24	−0.34
Ground feeder	**0.88**	0.10	−0.10	0.32
Gregarious	**0.98**	−0.14	−0.06	0.09
Nectarivorous	−0.18	**0.76**	−0.04	−0.20
Carnivorous	−0.15	**0.83**	−0.06	−0.15
Vegetation feeder	−0.13	**0.70**	0.40	−0.17
Tree nester	0.25	**0.89**	−0.08	−0.02
Solitary	−0.04	**0.53**	0.41	0.30
Migrant	0.02	−0.02	**0.97**	0.00
Insectivorous	0.02	0.29	**0.66**	0.14
Air feeder	0.07	−0.15	**0.89**	0.01
Ground nester	−0.16	−0.61	0.20	**0.93**
Granivorous	0.07	0.11	−0.08	**0.92**
Eigenvalues	5.29	3.80	2.18	1.34
% Variance	35.26	25.34	14.56	8.92
% Cumulative	35.26	60.60	75.16	84.08

Higher trait-factor loadings are highlighted in bold

high levels of urbanization, one was dominant in intermediate levels of urbanization, and the remaining one dominant toward the more urbanized areas. Functional group 3 had highest values in areas of horticulture, including migratory species, insectivores and aerial foragers. Functional group 4 dominated in agricultural areas, and included granivores that nest on the ground. In general, these patterns are consistent with those of previous studies (Lim and Sodhi 2004; Leveau and Leveau 2005; Kark et al. 2007; Croci et al. 2008; Blair and Johnson 2008; Conole and Kirkpatrick 2011). Migratory species may be at a disadvantage to residents because they have less time to adapt to urban conditions (Croci et al. 2008). Most migratory species recorded in this study are insectivores and aerial foragers. In this sense, it is likely that these species do not persist at high levels of urbanization due to the scarcity of insect prey (Lim and Sodhi 2004; Blair and Johnson 2008). It is important to note that the number of migratory species in a given site is related to latitude (Newton and Dale 1996). So the geographical location of the city is a variable to consider when analyzing the impact of urbanization on the migratory behavior. On the other hand, most of the species recorded in this study that nest on the ground are also granivores. Ground nesters can be affected by high levels of predation and pedestrian disturbance in urban areas (Jokimäki and Huhta 2000; Jokimäki et al. 2005; Conole and Kirkpatrick 2011).

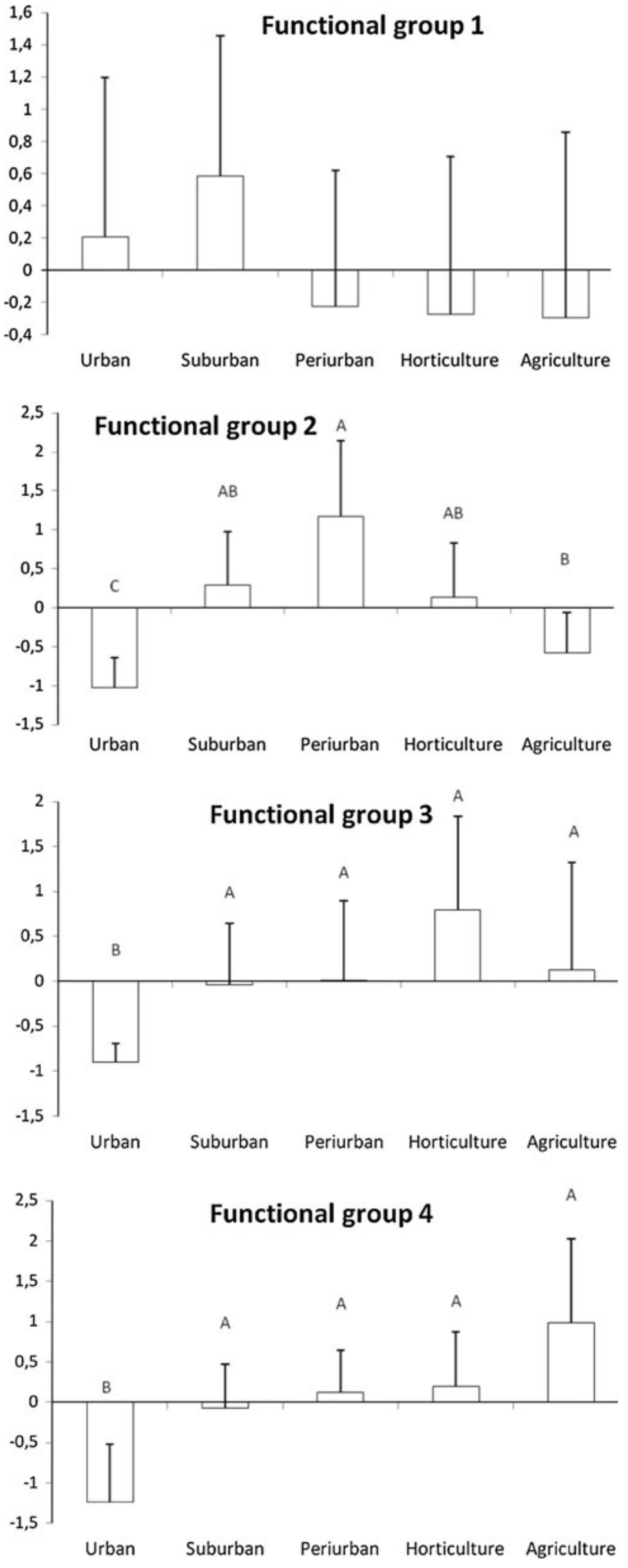

Fig. 2 Factor score values for the different factors or functional groups along the urban–rural gradient. *Bars* are means and *vertical lines* are standard deviations. Different *letters* indicate significant differences between land use types (Nemeyi test, $P < 0.05$)

Functional group 2, composed of tree nesters, carnivores and nectar feeders, and species foraging in vegetation, was dominant at intermediate levels of urbanization. These areas were characterized by a greater number of tall trees which would thus benefit those species that nest in trees. In addition, these residential areas have parks with an abundance of flowering plants that benefit nectarivorous birds (Montaldo 1984; Blair 1996). The high richness of birds in these areas may favor those carnivorous species that feed on eggs and nestlings such as *Milvago chimango* (Leveau and Leveau 2004).

Finally, functional group 1 comprises resident species that nest in buildings, are omnivorous, gregarious, and feed on the ground, and tended to be most abundant in more urbanized areas. Omnivorous species would benefit from the variety of foods offered directly or indirectly by humans in the more urbanized areas (Kark et al. 2007; Croci et al. 2008). The greater coverage and variety of buildings provides a greater availability of nesting sites for species that nest in buildings. Gregarious behavior aids in finding food and avoiding predators (Sol 2007; Kark et al. 2007). Overall, this functional group had characteristics that allow success in highly urbanized areas. Although the scores of this group tended to be highest in the more urbanized sites, the scores did not show significant differences among land use types, indicating that such a combination of traits related to a lifestyle in highly urbanized areas can also be successful in other less urbanized areas.

Results from this work show that factor analysis is a useful tool in determining different uses of space by bird communities. Factor analysis has shown which traits are affected along a gradient of urbanization. In this sense, analysis of functional groups can determine the potential impact of urbanization on ecosystem function and aid management measures to protect ecosystem services (Burton et al. 2009); for example, the case of insectivorous bird species and insect pest control (Hashimoto et al. 2005; Heyman and Gunnarsson 2011), or the case of raptors and their control of rodent populations (Chace and Walsh 2006; Bellocq et al. 2008).

Birds can be classified according to three types of responses to urbanization (Blair 1996; McKinney 2002; Marzluff 2005; Catterall 2009): (1) a positive response (urban exploiters, invaders or new urban arrivals), (2) a positive response to intermediate levels of urbanization (urban–suburban adapters), and (3) a negative response to the level of urbanization (urban avoiders). In short, birds have three types of responses to urbanization: (1) factor 1 tends to be most important in more urbanized areas, (2) factor 2 comprises birds that prefer intermediate levels of urbanization, and (3) factors 3 and 4 denote the "urban avoiders". EFA allows a link between concepts generated from analyses of species and analyses based on biological traits.

Exploratory factor analysis has several assumptions and requirements, and its use with data of bird abundance can be problematic because some variables may have non-normal distributions. A possible solution would be to use NMS as a complement, because this statistical method does not require meeting the same assumptions as EFA (López-Gonzalez et al. 2011).

When comparing bird communities in different continents, aspects related to the classification of traits and scale of study must be taken into account (Catterall 2009; du Toit and Cilliers 2011). The use of traits requires using the same classification of species in a global context. Different classifications for traits such as nesting site and diet for dominant cosmopolitan species (such as *Columba livia* and *Passer domesticus*) can lead to contrasting results. Comparisons of cities should be made considering same spatial scales. Differences in grain size or extent of the study may be associated with different responses of bird communities (Pautasso 2007).

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