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BIRD COMMUNITIES ALONG URBANIZATION GRADIENTS: A COMPARATIVE ANALYSIS AMONG THREE NEOTROPICAL CITIES

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Abstract · Urbanization is expanding continuously over rural and natural areas and it is imperative to analyze its effect on bird communities**.** Although the impact of urbanization on bird communities in the Neotropical region has been explored by several authors, there is a scarcity of comparative studies with standardized methodologies that allow establishing whether the effects of urbanization are similar in different ecoregions. We analyzed the urbanization impact on bird communities in three Neotropical cities. Cities were located in different biomes: La Paz (Bolivia) surrounded by a highland plateau and inter-Andean valleys; Mar del Plata (Argentina) surrounded by agroecosystems of the pampas; and Osorno (Chile), surrounded by agroecosystems, timber plantations, and remnants of temperate forests. In general, high levels of urbanization correlated negatively with bird richness in the three cities, but the response of bird richness to urbanization varied among cities, being linearly negative in La Paz and Osorno and declining only towards high levels of urbanization in Mar del Plata. The effect of urbanization was stronger in La Paz, where more bird species were absent toward higher urbanization levels. Bird abundance did not show significant responses to urbanization. Exotic bird abundance showed a positive relationship with urbanization in the three cities. Bird composition differed between cities and urbanization levels. The House Sparrow (*Passer domesticus*) was the most abundant species in more urbanized sites, the Eared Dove (*Zenaida auriculata*) in moderate levels of urbanization, whereas the Rufous-collared Sparrow (*Zonotrichia capensis*) was most abundant in the less urbanized sites. The results of our study showed that the impact of urbanization on bird communities in the Neotropical region varied among cities, probably as a result of latitude and the structure of rural areas.

Resumen · Comunidades de aves en gradientes de urbanización: un análisis comparativo entre tres ciudades Neotropicales

La urbanización se está expandiendo continuamente en áreas rurales y naturales, y siendo imprescindible analizar su efecto sobre las comunidades de aves. Aunque el impacto de la urbanización en el Neotrópico ha sido estudiado por varios autores, existe una escasez de estudios comparativos entre diferentes ecorregiones mediante el uso de metodologías estandarizadas. Por lo tanto, analizamos el impacto de la urbanización sobre comunidades de aves en tres ciudades Neotropicales. Las ciudades estuvieron localizadas en diferentes biomas: La Paz (Bolivia) rodeada por un altiplano y valles interandinos; Mar del Plata (Argentina) rodeada por agroecosistemas de las Pampas; y Osorno (Chile), rodeada por agroecosistemas, plantaciones de árboles y remanentes de bosques nativos. En general, altos niveles de urbanización se correlacionaron negativamente con la riqueza de aves en las tres ciudades. Sin embargo, la respuesta de la riqueza de aves a la urbanización varió entre ciudades, siendo negativamente lineal en La Paz y Osorno, para disminuir solo a partir de altos niveles de urbanización en Mar del Plata. El impacto sobre la riqueza fue mayor en La Paz, donde más especies de aves se perdieron hacia los niveles más altos de urbanización. Por otro lado, la abundancia de aves no se correlacionó con la urbanización. La abundancia de especies exóticas mostró una relación positiva con la urbanización en las tres ciudades. La composición de aves cambió entre niveles de urbanización;

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el Gorrión común (*Passer domesticus*) fue la especie más abundante en los niveles más altos de urbanización, la Torcaza (*Zenaida auriculata*) en sitios de urbanización moderada, mientras que el Chingolo (*Zonotrichia capensis*) fue la especie más abundante en los niveles más bajos de urbanización. Los resultados de nuestro estudio mostraron que el impacto de la urbanización sobre las comunidades de aves en la región Neotropical varió entre ciudades, probablemente como resultado de la latitud y la estructura de las áreas rurales.

Key words: Biotic homogenization · Bird abundance · Bird richness · Composition · Conservation · Exotic species · Urbanization

INTRODUCTION

Human population growth, more pronounced in developing countries, promotes the expansion of city limits by irreversibly using natural and pristine areas (Morello et al. 2000, McKinney 2002). Although urban areas represent nearly 3% of terrestrial surface, their ecological impact goes beyond city limits, generating environmental changes at local and even global scales (Grimm et al. 2008, Liu et al. 2014). As a consequence, several taxa are negatively affected by urbanization (Chmaitelly et al. 2009, Martinson & Raupp 2013, Villaseñor et al. 2014). In particular, birds are the most studied zootaxa (Marzluff et al. 2001, Garden et al. 2006), and several studies showed that urbanization altered bird communities by changing species richness, composition, and relative abundance (Blair 1996, Clergeau et al. 1998, Ortega-Álvarez & MacGregor-Fors 2009).

The relationship between urbanization and bird communities in the Neotropical region has been explored by several authors (Nocedal 1987; Leveau & Leveau 2004, 2005; Juri & Chani 2005, Faggi & Perepelizin 2006, Ortega-Álvarez & MacGregor-Fors 2009, Reis et al. 2012, Silva et al. 2016). However, there is a scarcity of comparative studies with standardized methodologies that allow establishing whether the effects of urbanization are similar in different ecoregions. This kind of information will allow a better knowledge of urban ecosystems and the establishment of proper management policies to preserve or enhance biodiversity (Niemelä 2000, Fernández-Juricic & Joki-mäki 2001).

Spatial variation in urbanization levels has been studied by ecologists using the gradient paradigm (Whittaker 1967, McDonnell & Picket 1990). Different studies have found a negative relationship between urbanization and bird species richness (Chace & Walsh 2006, Faeth et al. 2011). Intermediate levels of urbanization, however, can exhibit higher species richness than non-urban areas (Blair 1996, McKinney 2002, Leveau & Leveau 2005, Marzluff 2005, Chace & Walsh 2006, Villegas & Garitano-Zavala 2010). In general, the most urbanized areas have a higher total bird density than non-urban areas (Marzluff 2001, Garaffa et al. 2009, but see Saari et al. 2016), are inhabited by exotic or widespread species, and exclude migrants or species that nest in herbaceous vegetation (Clergeau et al. 2006, Croci et al. 2008, Leveau 2013). Behavioral plasticity can explain differences in bird species richness and invasive success in urban environments (Møller 2009).

Given that cities are built to satisfy human requirements, they have a very similar structure around the world (McKinney 2006). A few invasive species that are adapted to humans live in urban centers, whereas other widespread species adapt to residential and suburban areas (Blair 1996, McKinney 2002). This process, where highly urbanized areas in the world hold the same species, is known as biotic homogenization (McKinney & Lockwood 1999). In fact, urbanization is considered the major cause of biotic homogenization (McKinney 2006), and several studies carried out in urban gradients of the northern hemisphere support this idea (Blair 2001, Clergeau et al. 2001, 2006). However, the process of biotic homogenization has been little explored in the Neotropical region (Filloy et al. 2015). Therefore, it is important to analyze the effect of urbanization on bird community composition in the Neotropics to determine whether urban centers are dominated by the same exotic species.

The objective of this study was to evaluate the relationship between impervious cover (buildings and pavement) and bird richness, abundance and composition along urbanization gradients of three Neotropical cities which comprised different biomes from subtropical to temperate zones. Thus, we tested four predictions: 1) urbanization will have a negative relationship with bird species richness in the three cities; 2) the more urbanized sites will have the highest bird abundance; 3) urbanization will be related to a dominance of exotic bird species in the most urbanized sites of the three cities; and 4) bird composition will be more similar among the most urbanized sites than among the least urbanized sites.

METHODS

Study area. The study was conducted in three Neotropical cities (Figure 1): La Paz (Bolivia), Mar del Plata (Argentina), and Osorno (Chile). La Paz (16°29'S, 68°8'W) is located in the Central Andes in the valley of La Paz river, east of the Andean high plateau and north of adjacent mesothermic valleys (Liberman 1991). La Paz belongs to the Montane grasslands and shrublands biome (Olson et al. 2001). It has an irregular topography, with mountain ranges, canyons, terraces, and alluvial prairies, covering an elevational gradient from 2700 to 4100 m a.s.l. The city is surrounded by scattered crops, mountains, and the city of El Alto on the northwestern side. It has a subtropical highland climate with average annual temperature of 11°C (central area, downtown) and 13°C

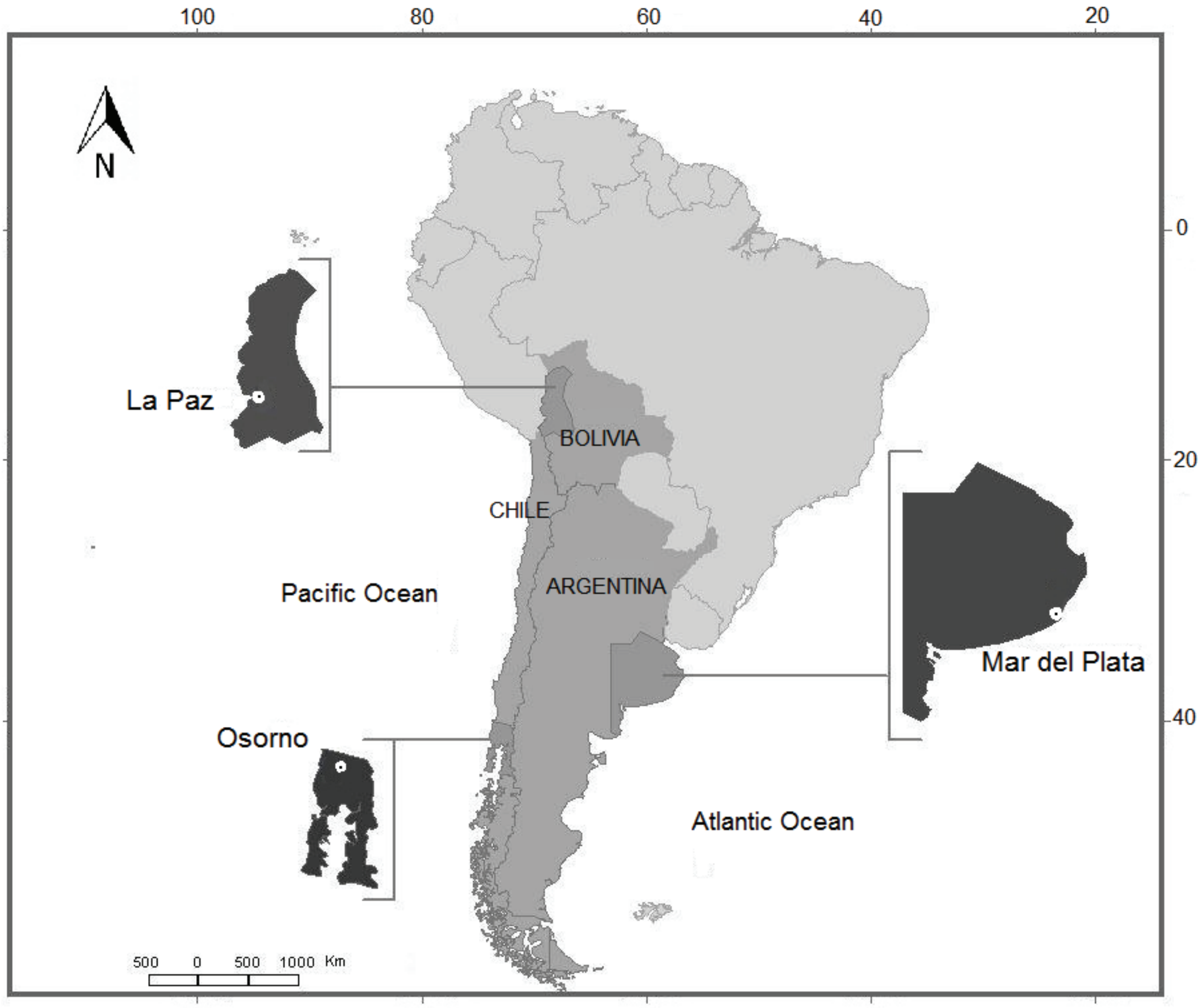

Figure 1. Map of South America showing the location of the three cities surveyed in this study.

(south area), respectively (García 1997, Kottek et al. 2006), and an average annual rainfall of 579 mm (Segaline Nieto & Cabré 1988). The city covers 180 km^2 and had (without considering the adjacent city of El Alto) approximately 839,594 inhabitants at the moment of our bird surveys (Instituto Nacional de Estadística 2016).

Mar del Plata (38°00’S, 57°33’W) is located on the southeastern coast of Buenos Aires province, in the so-called Pampean Region. It belongs to the Temperate grasslands, savannas, and shrubland biome (Olson et al. 2001). The surrounding landscape is dominated by crops, pastures, tree plantations, and the mountain range of Tandilia. It has an oceanic temperate climate with an average annual temperature of 14°C, and annual rainfall reaches 920 mm (Leveau & Leveau 2004, Kottek et al. 2006). The city covers 79.8 km^2 and had approximately 563,000 occupants in 2001 (2001 Census, INDEC).

Osorno (40°34’S, 73°9’W) is located in southern central Chile, in the convergence of the rivers Rahue and Damas. It belongs to the Temperate broadleaf and mixed forests biome (Olson et al. 2001) and presents an homogenous relief in the region called the ‘Intermediate depression’ with an elevation of *ca.* 35 m a.s.l., between the Andes and the coastal mountain range. The matrix, in which the city is established, is devoted to cattle farming, agriculture, and forestry (di Castri 1968). Osorno has a temperate oceanic climate with an annual rainfall of 1400 mm and an average temperature of 10°C (di Castri 1968, di Castri & Hayek 1976, Kottek et al. 2006). The city covers 36 km^2 and had 132,245 inhabitants at the moment of bird surveys (INE Chile 2005).

In each city, we analyzed three areas of the urbanization gradient (Figure 2): urban, suburban, and rural areas (hereafter, habitats). Urban areas are characterized by high density of buildings for commerce, service or industry, with more than 50% of building cover; suburban areas are characterized by moderate to high-density, single-family housing, with gardens and open fields (30–50% building cover); and rural areas have dispersed houses surrounded by natural and agricultural environments (5–20% building cover) (Marzluff et al. 2001).

Bird surveys. Bird surveys were performed by using 100 x 50 m transects, separated by 200 m, in which we counted the number of individuals of all bird species detected, from 06:30 h to 10:30 h. We placed 15

Figure 2. Example of study sites surveyed. Columns (from left to the right): La Paz (La Paz department, Bolivia), Mar del Plata (Buenos Aires province, Argentina), and Osorno (Osorno province, Chile). Rows (from top to bottom): rural, suburban, and urban habitats.

transects (i.e., sampling units) per habitat in each city, except for the rural area of Mar del Plata where 14 transects were placed. Each sampling unit was surveyed two times during September 2005–March 2006 by two observers, except for La Paz where one observer made the bird surveys. Therefore, comparisons of bird richness and density among cities should be taken with caution because La Paz values may be underestimated. The effect of different observers on bird richness values was taken into account by using an estimator (see below).

Urbanization measure. In the center of each transect, we placed a 25 m radius plot where we recorded the percentage cover of buildings and pavement. As showed by DeGraaf et al. (1991), environmental data obtained at the 25 m radius (0.2 ha) is representative of the environmental characteristics of the whole transect (0.5 ha). Therefore, we estimated the percent cover of impervious surface as a measure of urbanization level. We assumed that the habitat characteristics of the central plot represented the habitat of the entire sampling unit.

Statistical analyses. Since bird surveys were made necessarily by different observers, we needed to account for different detectability among observers to estimate bird richness. Hence, bird richness was calculated using a capture-recapture approach which assumes heterogeneity in detection probability among species, transects, and observers (Burnham & Overton 1979, Boulinier et al. 1998). This procedure uses a jackknife estimator associated with model M(h) (Burnham & Overton 1978, 1979; Otis et al. 1978), which estimates bird species richness and species detection probability. Therefore, we took into account possible differences in detectability among species, observers, and habitat types. To achieve this we used the program COMDYN (Hines et al. 1999) to estimate species richness. The program uses information on species detected and not detected in a series of sampling occasions (Hines et al. 1999). In this case, we estimated the species richness by using the information of the two visits in each transect. The abundance was the mean of individuals recorded on the two visits in each transect.

The correlation between bird richness and abundance and impervious surface cover was done using Generalized additive models (GAMs), which allow non-linear relationships (Zuur et al. 2009). These tests were performed with the *mgcv* package (Wood 2001) in the statistical software R (R Development Core

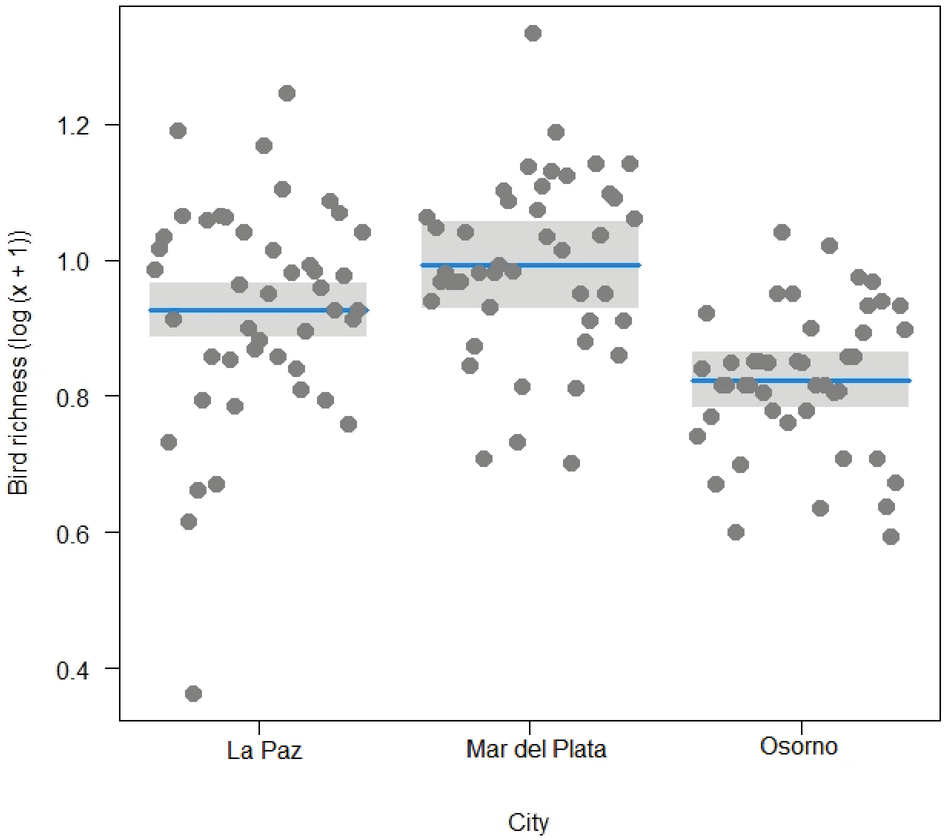

Figure 3. Bird richness per transect ($\log_{10}$ [x + 1] transformed) for the three Neotropical cities: La Paz (La Paz department, Bolivia), Mar del Plata (Buenos Aires province, Argentina), and Osorno (Osorno province, Chile). Individual data points are shown in dark grey, blue line represents the mean, and grey areas are 95% confidence intervals.

Team 2013). We obtained a geographic regression model for each city using the *by* argument and city as a categorical variable (Wood 2006). Bird richness and abundance were $\log_{10}$ (x + 1) transformed to improve normality and homoscedasticity. The package *visreg* (Breheny & Burchett 2015) was used to visualize the regression models.

Bird community composition among cities and different levels of urbanization was analyzed using the Multi-response permutation procedure (MRPP) with the function mrpp in the package *vegan* (Oksanen et al. 2015). MRPP is mathematically allied with analysis of variance in that it compares dissimilarities within and among groups (Oksanen et al. 2015), and it is robust to unbalanced designs through the use of permutation between groups (Carter & Feeney 2012). The mrpp statistic delta is the overall weighted mean of within-group means of the pairwise dissimilarities among sampling units. It then permutes the sampling units and their associated pairwise distances, and calculates an expected delta based on the permuted data. The significance test is simply the fraction of permuted deltas that are smaller than the observed delta, with a small sample correction (Oksanen et al. 2015). To convert the impervious surface variable in a categorical one, we classified transects among three levels: 1) low urbanization (0–33% impervious cover); 2) moderate urbanization (33–66% impervious cover); and 3) high urbanization (66–100% impervious cover). The Bray-Curtis dissimilarity index was used to analyze the composition among sampling units. We took into account the nested design in which urbanization levels were nested within cities with the term strata in function mrpp. If significant differences in species composition were detected among urbanization levels or cities, the simper function was used to identify species that contributed mostly to the dissimilarity among them. Average dissimilarity (Dissim) is the average contribution for each species to the overall dissimilarity. We focused on species with ratios greater than one of the average dissimilarity to standard deviation of the dissimilarity among cities or urbanization levels (Dissim/SD). This indicated species that contributed mostly to the dissimilarity, but also had low variation in inter-comparisons of all samples of cities or urbanization levels (Clarke & Warwick 2001). In order to visualize the distribution patterns of sampling units, a Non-metric multidimensional scaling (NMDS) was performed with the *vegan* package.

RESULTS

We recorded a total of 86 bird species and a total of 3301 individuals across the three cities (see Supple-

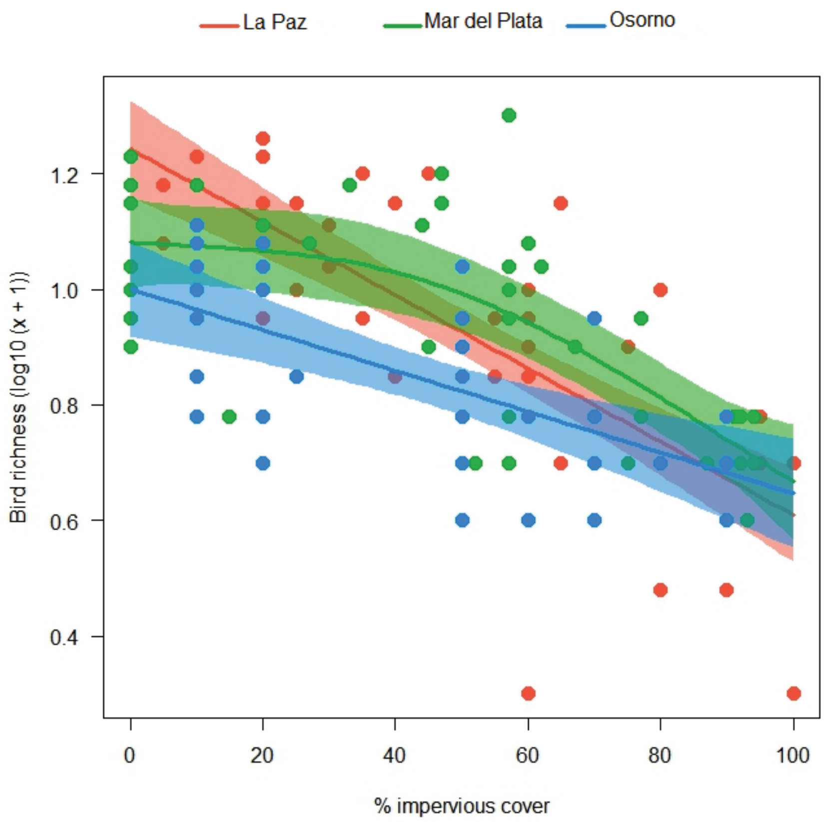

Figure 4. Relationship between impervious cover surface (%) and bird richness per transect (log_{10} [x + 1] transformed) along the three urbanization gradients in the Neotropical region: La Paz (La Paz department, Bolivia), Mar del Plata (Buenos Aires province, Argentina), and Osorno (Osorno province, Chile). Individual data points are dotted and shaded areas are 95% confidence intervals.

mentary online material). Mean bird species richness was higher in La Paz and Mar del Plata compared to Osorno (F = 139.1, df = 2, P < 0.001; Figure 3). The relationship between impervious cover and bird richness varied among cities (Figure 4): whereas in La Paz (F = 121.52, estimated degrees of freedom [edf] =1.67, P < 0.001) and Osorno (F = 61.71, edf = 1.42, P < 0.001) bird richness decreased monotonically with impervious surface, in Mar del Plata bird richness remained constantly high in low and moderate levels of impervious cover and only declined toward the highest levels of impervious cover (F = 15.90, edf = 2.43, P < 0.001). Moreover, at the non-urbanized sites bird richness was higher in La Paz than in Mar del Plata and Osorno, indicating that the impact of urbanization was higher in La Paz than in the other two cities. Bird abundance did not change among cities (F = 1.61, df = 2, P = 0.21) (Figure 5), but tended to increase with urbanization in La Paz (F = 1.81, edf = 7.69, P = 0.08), although did not show clear responses in Mar del Plata (F = 2.17, edf = 1.89, P = 0.11) and Osorno (F = 1.88, edf = 1.42, P = 0.16).

The abundance of exotic birds did not differ among cities (F = 0.45, df = 2, P = 0.64), but their abundance increased with impervious cover in the three cities (La Paz: F = 8.92, edf = 7.55, P < 0.001; Osorno: F = 27.23, edf = 2.43, P < 0.001; and Mar del Plata: F = 6.46, edf = 1.42, P = 0.04; Figure 6).

Bird composition varied among cities (MRPP: observed delta = 0.70, expected delta = 0.82, P < 0.001) and among impervious surface levels (MRPP: observed delta = 0.76, expected delta = 0.82, P < 0.001). The Rufous-collared Sparrow (*Zonotrichia capensis*) was more abundant in La Paz (mean = 2.60 individuals/transect), and contributed to the dissimilitude with Mar del Plata (ratio = 1.32, mean = 0.97 individuals/transect) and Osorno (ratio = 1.55, mean = 0.18 individuals/transect). The Eared Dove (*Zenaida auriculata*) was more abundant in Mar del Plata (mean = 1.53 individuals/transect) and contributed to the dissimilitude with La Paz (ratio = 1.11, mean = 1.40 individuals/transect) and Osorno (ratio = 1.02, mean = 0.00 individuals/transect). The House Sparrow (*Passer domesticus*) was more abundant in Mar del Plata (mean = 3.92 individuals/transect) and contributed to the dissimilitude with La Paz (ratio = 1.12, mean = 0.00 individuals/transect) and Osorno (ratio = 1.31, mean = 3.60 individuals/transect).

The House Sparrow was most abundant in the highly urbanized sites (mean = 3.71 individuals/transect) and contributed to the dissimilitude with the other urbanization levels (moderate urbanized sites, ratio = 1.18, mean = 2.87 individuals/transect; low-urbanized sites, ratio = 1.07, mean = 0.96 individuals/transect). The Eared Dove was the most abundant species in moderate urbanization levels (mean =

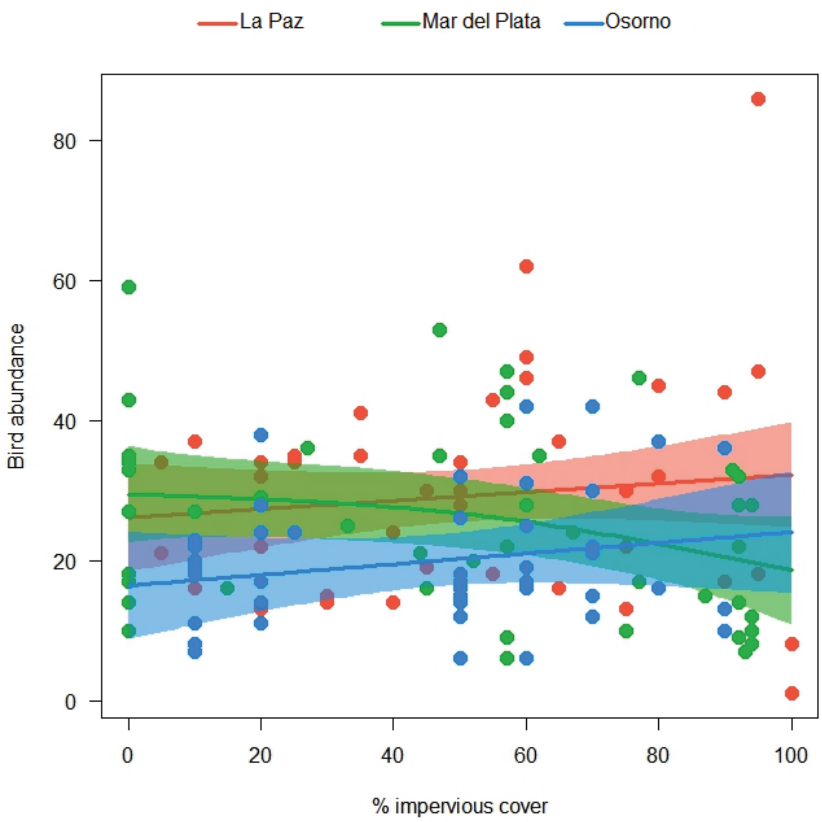

Figure 5. Relationship between impervious cover surface (%) and bird abundance per transect along the three urbanization gradients in the Neotropical region: La Paz (La Paz department, Bolivia), Mar del Plata (Buenos Aires province, Argentina), and Osorno (Osorno province, Chile). Individual data points are dotted and shaded areas are 95% confidence intervals.

1.54 individuals/transect) and contributed to the dissimilitude with highly urbanization levels (ratio = 1.05, mean = 0.85 individuals/transect). The Rufous-collared Sparrow was most abundant in low urbanization levels (mean = 1.56 individuals/transect) and contributed to the dissimilitude with moderate urbanization levels (ratio = 1.08, mean = 1.46 individuals/transect). The NMDS analysis revealed that the least urbanized transects of cities were more dissimilar (Figure 7), compared to the more urbanized transects which showed higher similarity, suggesting a process of biotic homogenization.

DISCUSSION

Our results showed that the relationship between bird richness and urbanization varied among cities. While in Osorno and La Paz bird richness declined monotonically with impervious surface cover, in Mar del Plata it declined only with high impervious cover. A possible explanation may be related to the type of native vegetation surrounding each city. Osorno and La Paz belong to forest and shrub type biomes respectively, whereas Mar del Plata belongs to a grassland type biome (Olson et al. 2001). Therefore, the loss of habitat heterogeneity in the former two cities is steeper than in Mar del Plata, where intermediate levels of urbanization may be composed by more vegetation layers (lawn, shrubs, and trees) than grassland and crops (Leveau & Leveau 2004). The habitat diversity in moderate levels of urbanization in Mar del Plata could allow comparable bird richness with non-urban habitats. Our data suggest that the relationship between urbanization and bird richness may be dependent of the biome in which the city is located; cities located in forested biomes probably will have a negative linear relationship, whereas cities located in grassland biomes will have only a decline in highly urbanized areas or a unimodal relationship (Leveau & Leveau 2005). However, contrary to our predictions other authors (Marzluff 2005, Blair & Johnson 2008) have found unimodal relationships between bird richness and urbanization in forested biomes. Other factors, such as the number of exotic species and the proportion of native vegetation in moderately urbanized sites, may play an important role in determining the relationship between bird richness and urbanization.

As expected, bird richness at null impervious cover followed a latitudinal gradient, being highest in La Paz. However, bird richness at the more urbanized sites was similar among cities. As a result, the impact of urbanization was more pronounced for La Paz, the northernmost city studied. Our results were similar to those of Filloy et al. (2015), who found that the impact of urbanization was higher in subtropical medium-sized cities than in temperate and semiarid ones. This suggests that the loss of species caused by

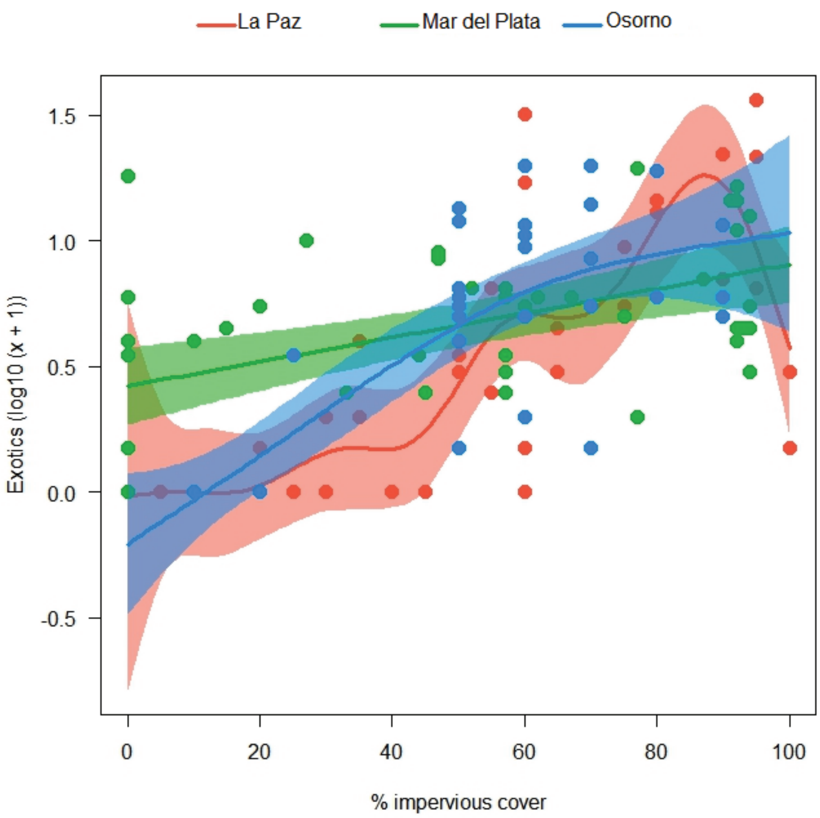

Figure 6. Relationship between impervious cover surface (%) and exotic bird abundance per transect ($\log_{10}$ [x + 1] transformed) along three urbanization gradients in the Neotropical region: La Paz (La Paz department, Bolivia), Mar del Plata (Buenos Aires province, Argentina), and Osorno (Osorno province, Chile). Individual data points are dotted and shaded areas are 95% confidence intervals.

urbanization will be higher in the tropics. Therefore, more management actions should be taken in these areas to promote more sustainable cities. On the other hand, the higher proportion of native vegetation in the rural areas of La Paz may also promote higher bird richness than in rural areas of Mar del Plata and Osorno. Finally, it is important to note that altitude in La Paz may have a negative effect on bird richness variation (Villegas & Garitano-Zavala 2010). Therefore, transects with the least urbanization but with highest altitude may have lower bird richness than those transects with similar urbanization level but at a lower altitude.

Contrary to a number of studies (Ortega-Álvarez & MacGregor-Fors 2009, van Rensburg et al. 2009, Barbosa de Toledo et al. 2012, Mikami & Mikami 2014), our results showed that bird abundance did not increase with urbanization. Møller et al. (2012) showed that the higher population densities of bird species in urban areas were related to their timing of urban colonization, reflecting their gradual adaptation to urban areas. Since the Neotropical cities used in this study are on average younger than European cities, our results may be related to a lower time of adaptation of bird species to urban conditions.

Exotic bird species showed similar responses to urbanization among cities. It is notable that the densities of exotic species converged in the most urbanized sites of the three cities. However, the contrast in exotic densities between low and highly urbanized sites was higher in La Paz and Osorno than in Mar del Plata. Rural areas of Mar del Plata covered by crops and scattered houses may provide food and nesting resources to House Sparrow and Rock Dove (*Columba livia*). On the other hand, in the absence of buildings House Sparrows may use abandoned nests of the Rufous Hornero (*Furnarius rufus*), allowing its presence in rural areas. Finally, the presence of House Sparrows in rural areas may affect negatively bird richness due to aggressive interactions with native species (MacGregor-Fors et al. 2010).

Bird composition varied among cities and urbanization levels. Differences among cities matched known biogeographical patterns in the region. For example, the House Sparrow can occur up to 4500 m a.s.l. (Summers-Smith 1988) and, therefore, the altitude of La Paz may constitute a distributional limit. As a result, the higher abundance of the Rufous-collared Sparrow in La Paz, even in highly urbanized areas otherwise occupied by the House Sparrow, may suggest competitive exclusion of the Rufous-collared Sparrow by the House Sparrow in lowland areas.

The most urbanized sites were dominated by House Sparrow and Rock Dove, exotic species introduced from Eurasia (Baptista et al. 2015, Summers-Smith et al. 2017). This result supports the idea that

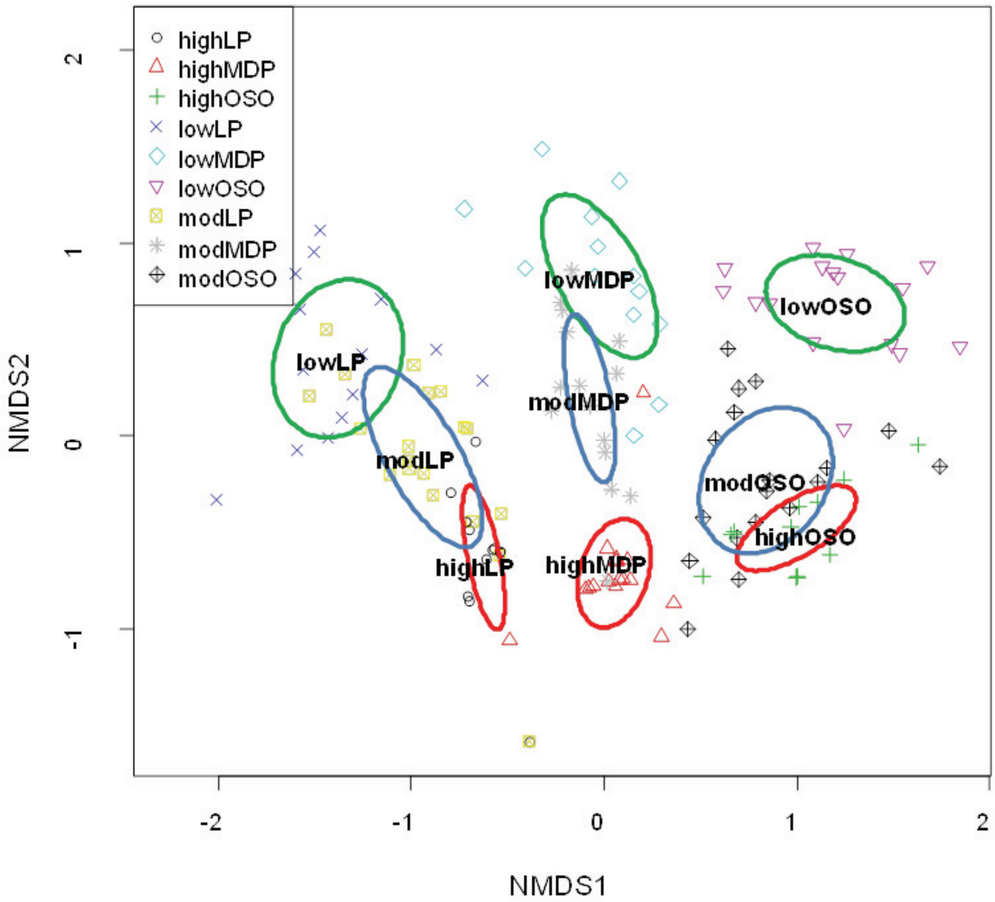

Figure 7. Plot of Non-metric Multidimensional Scaling (NMDS) showing the similarity in bird composition of transects with different urbanization levels (Stress = 0.17). Urbanization levels: high, moderate (mod), and low. Cities: LP, La Paz; MDP, Mar del Plata; OSO, Osorno. Centroids of urbanization levels for each city are depicted with ellipses of standard errors.

urbanization homogenizes the composition of bird communities by the replacement of native species by cosmopolitan species (McKinney 2006, Filloy et al. 2015). The native Eared Dove was more abundant in moderate levels of urbanization, and it appears to be the main suburban adapter in the three cities of this study and other Neotropical cities (Fontoura 2013, Fontoura & Orsi 2014).

Our study showed on the one hand that, although bird richness values converged at the most urbanized sites of the three cities, the loss was greatest in the most subtropical city, suggesting a higher impact of urbanization on taxonomical diversity toward the tropics. On the other hand, our results showed that bird abundance did not increase with urbanization, indicating that more comparative studies are necessary to understand when cities have higher bird density. Finally, the dominance of House Sparrow and Rock Dove in the most urbanized sites of the three cities suggests a process of biotic homogenization in Neotropical cities.

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