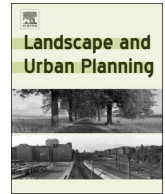




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Research Paper

Predicting the seasonal dynamics of bird communities along an urban-rural gradient using NDVI

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ABSTRACT

The normalized difference vegetation index (NDVI) is a strong and widely used proxy for bird species richness in urban environments. However, its potential to predict composition and seasonal dynamics of bird communities in urban areas remains unexplored. Our main objective was to analyze the power of NDVI to predict the seasonal dynamics of bird communities along urbanization gradients. Birds were surveyed in the breeding and non-breeding seasons. Bird species richness was estimated using COMDYN, and bird community composition was summarized in two axes using Non-metric Multidimensional Scaling (NMDS). For each of the breeding and non-breeding seasons, bird richness and the NMDS axis scores were related to both the mean NDVI of the season and the annual seasonal variation of NDVI (mean NDVI of the breeding season – mean NDVI of the non-breeding seasons). Results showed that NDVI decreased towards the most urbanized areas, with the highest seasonal variation occurring in agricultural areas. Single-family houses surrounded by yards held a high NDVI in both seasons and the lowest seasonal variation. Bird richness increased at intermediate levels of NDVI and was negatively related to the seasonal variations of the NDVI. Seasonal variation in bird community composition increased with annual mean and seasonal variation of the NDVI predicting higher seasonal stability of assemblage composition in urban than in non-urban areas. The results suggest that urbanization alters ecosystem functioning by reducing seasonal dynamics and the amount of primary productivity, which in turn promotes seasonal homogenization of urban avifauna relative to non-urban areas.

1. Introduction

Urbanization is a global and expanding process that results in profound changes in bird diversity and composition (Blair & Johnson, 2008; Jokimäki, Clergeau, & Kaisanlahti-Jokimäki, 2002; Lepczyk et al., 2008; Leveau, Leveau, Villegas, Cursach, & Suazo 2017; Leveau, Jokimäki, & Kaisanlahti-Jokimäki, 2017). Consequently, urban expansion requires planning and management to promote conservation of biodiversity. The use of remote sensing is a useful and convenient tool to predict species distributions in large areas at low costs and short time intervals (Leyequien et al., 2007; Travaini et al., 2007; Turner et al., 2003). Remote sensors collect information of environmental variables, which can be handled to build predictive maps of species presence in a given area (Guisan & Zimmermann, 2000; Travaini et al., 2007). Spatial prediction of biodiversity patterns from field data has been recognized as an important component of conservation planning, contributing to

the identification of areas with potential threats for biological diversity (Coops, Wulder, & Iwanicka, 2009; Coops, Waring, Wulder, Pidgeon, & Radeloff, 2009; Guisan & Zimmermann, 2000; Luoto, Virkkala, Heikkinen, & Rainio, 2004; Venier, Pearce, McKee, McKenney, & Niemi, 2004).

Satellite-collected data on phenology and the amount and distribution of vegetation are essential in studies on terrestrial ecology, because they are strongly related to animal distribution and population and community dynamics (Nieto et al., 2015; Pettorelli et al., 2005). The Normalized Difference Vegetation Index (NDVI) is a widely used indicator of net primary productivity (Rouse, Haas, Schell, Deering, & Harlan, 1974; Pettorelli et al., 2005). In turn, net primary productivity is an indicator of resource availability.

According to the species-energy hypothesis (Evans, Warren, & Gaston, 2005), sites with high primary productivity hold more species because resource availability allows for larger population sizes, thus

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reducing the risk of local extinctions (Rowhani et al., 2008). On the other hand, the ecosystem stress hypothesis states that vegetation loss due to urbanization has a negative influence on the number of species through a reduction in habitat and resource availability (Rapport, Regier, & Hutchinson, 1985). At the local scale, most studies conducted along urbanization gradients supported the ecosystem stress hypothesis (Lepczyk et al., 2008). Indeed, several studies showed that a loss of vegetation in urban environments, as indicated by changes of NDVI, affected negatively bird richness (Bino et al., 2008; Haedo, Blendinger, & Gasparri, 2010; Lee, Ding, Hsu, & Geng, 2004). At large spatial scales, more productive systems tend to support more species and more people, showing a positive correlation between species richness and human population (Lepczyk et al., 2008; Luck, Ricketts, Daily, & Imhoff, 2004; Pautasso, 2007).

The intermediate disturbance hypothesis (Connell, 1978) states that more species occur at intermediate frequencies and intensities of disturbance. Indeed, several studies along urbanization gradients have found that bird species richness peaks at intermediate levels of urbanization (Blair, 1996; Lepczyk et al., 2008; Leveau & Leveau, 2005; Marzluff, 2005). Those peaks, however, are generally related to the presence of widely distributed species associated with forest edges and early successional bird species (Marzluff, 2005; McKinney, 2006). Therefore, the analysis of community composition is important to assess the effects of urbanization on bird communities because it distinguishes species adapted to urban environments from those that avoid them. The use of remote sensors to map bird composition along urban-rural gradients is a powerful tool to predict the effect of urban expansion on native species intolerant to urbanization processes.

Although many studies use NDVI to predict bird species richness along environmental gradients, only a few used this index to predict the composition of bird assemblages (Bar-Massada, Wood, Pidgeon, & Radeloff, 2012; Debinski, VanNimwegen, & Jakubauskas, 2006; Foody, 2005; Müller, Stadler, & Brandl, 2010). To our knowledge, few studies have attempted to predict bird community composition in urban environments using data derived from remote sensors (but see Lin, Lin, & Fang, 2008; Lin, Yeh, Deng, & Wang, 2008).

Urban areas may be characterized by lower seasonal variation in habitat structure and resource availability than the surrounding non-urban areas, because humans manage vegetation with pruning, fertilizers and irrigation, providing food and nesting places for birds (Buyantuyev & Wu, 2012; Duckworth, 2014; Leveau, 2018; Shochat, Warren, Faeth, McIntyre, & Hope, 2006). The reduced environmental variability in urban areas may lower the seasonal variability of bird communities (Caula, Marty, & Martin, 2008; La Sorte, Tingley, & Hurlbert, 2014; Leveau, 2018; Leveau, Isla, & Bellocq, 2015; Leveau & Leveau, 2016). Furthermore, highly urbanized areas may negatively affect the presence of migratory species due to the scarce vegetation cover and food abundance (Leveau, 2013; MacGregor-Fors, Morales-Pérez, & Schondube, 2010), thus lowering the seasonal variation of bird communities. Since temporal variation of NDVI is related to temporal dynamics of vegetation cover and primary productivity in urban environments (Bino et al., 2008; Buyantuyev & Wu, 2012), it could be a good predictor of the seasonal dynamics of bird communities along urban-rural gradients.

The objectives of this study were to evaluate the use of NDVI and its seasonal variation along an urbanization gradient of Mar del Plata city to predict: 1) the spatial variation of bird richness and composition during the breeding and non-breeding seasons; and 2) the seasonal dynamics of bird richness and composition in the study area. In our study system, a previously published study (Leveau et al., 2015) indicated that temporal changes of bird richness and composition were negatively correlated with impervious cover. Therefore, we expected that reduced primary productivity promoted reductions of the seasonal variation of bird community attributes. Moreover, urban areas can reduce the seasonal variation of primary productivity, which in turn may decrease the seasonal variation of bird communities. Few studies have

attempted to predict the seasonal dynamics of bird richness and composition using data derived from remote sensors (Hurlbert & Haskell, 2003). Finally, we constructed a Distributional Uncertainty Map (DUM, sensu Rocchini et al., 2010) to account for the uncertainty when mapping the predictive patterns of bird richness and composition (Rocchini et al., 2010) and discussing the validity of our predictive maps.

2. Materials and methods

2.1. Study area

Bird surveys were conducted in Mar del Plata city (618 989 inhabitants, 2010 National Census) (38° 00' S; 57° 33' W, [Supplementary material 1, Fig. S1a](#)). Mar del Plata is a coastal city surrounded by crop fields, pastures, and a few small fragments of native grasslands and woodlots. Phytogeographically, Mar del Plata is located in the ecotone between the Espinal and the Pampean provinces (Cabrera, 1976). The average minimum temperature occurs in July (6.7 °C) and the maximum in January (21.1 °C); most rainfalls occur in January (124.2 mm), whereas June is the driest (21.5 mm) month (Servicio Meteorológico Nacional). Mean annual rainfall is 924 mm/year.

2.2. Study design

To study the relationship between productivity and bird communities, five sectors along the urban-rural gradient were considered, which spanned an impervious surface cover range from 0 to 100%. Sectors represented different land use types: 1) urban center, represented by the commercial and administrative center of the city, is dominated by tall buildings (mean percentage coverage of 61%); 2) suburban area composed by single-family houses surrounded by yards (mean building coverage of 27%); 3) periurban area composed by single-family houses surrounded by yards and unpaved streets on the boundary of the city (mean building coverage of 25%); 4) horticultural area, with crops of lettuce, onions and tomatoes (mean building coverage of 6%); and 5) agricultural area, where primarily soybeans and wheat are grown in fields larger than those of the horticultural sector (mean building coverage of 0.10%; see Leveau, 2013 and Leveau et al., 2015 for details). In each sector, 15 strip transects (100 × 50 m) were established at a minimum of 100-m intervals ([Supplementary material 1, Fig. S1b](#)). Of the total of 75 transects, 40 (located at least 300 m apart) were selected systematically (alternately) in each sector to model the relationship between NDVI, bird species richness and bird composition (represented by the axis scores of an ordination analysis). The remaining 35 transects were used to assess the performance of the predictive models. Coordinates of transects were obtained using a GPS Trimble Navigation Ensign XL. In those transects with poor signal the coordinate data were positioned by Google Earth.

2.3. Bird surveys

Surveys were conducted along transects during four hours after sunrise from May 2010 to February 2013; transects were visited three times in the same order during each of the breeding (spring-summer) and non-breeding seasons (autumn-winter). Birds were surveyed by an observer who walked along each transect (100 m) and recorded individuals on both sides of the transect (25 m each) during three to five minutes. Duration of the survey at each line transect was affected primarily by the recording time depending on the number of birds detected (Dobkin & Rich, 1998; Verner & Ritter, 1985). On each visit, birds were identified by sight or sound on days with favorable meteorological conditions, without strong wind or rain. Surveys were performed by the same observer (LML). Both resident and migrant birds were counted.

2.4. Habitat structure and NDVI

To measure habitat structure, we visually surveyed the percent cover of buildings, shrubs, trees, lawn, cultivated land and pavement, and the number of trees lower than 5 m and higher than 5 m along each transect on the ground in two circles of 25-m radius separated by 50 m. One circle was located in the center of the first 50 m along each transect and the other in the center of the remaining 50 m. We used visual estimation of vegetation coverage in the field because satellite sensors fail to provide information on overlapped vegetation strata, such as lawn, shrubs and trees and therefore underestimate the tree cover (Jiang et al., 2017). Habitat variables were related to the mean NDVI of each season and the seasonal change of NDVI. Therefore, we expected: 1) a positive relationship between mean NDVI and percentage coverage of trees, shrubs, lawn, herbaceous vegetation and cultivated land during the breeding season; 2) a positive relationship between mean NDVI and percentage coverage of trees, shrubs and lawn during the non-breeding season; and 3) a higher seasonal change of NDVI in transects with higher proportion of herbaceous vegetation and cultivated land.

2.5. NDVI estimation

The product MOD13Q1 from the MODerate resolution Imaging Spectroradiometer (MODIS sensor; Terra satellite) was used (Justice et al., 2002), available in https://lpdaac.usgs.gov/products/modis_products_table, which provides NDVI values at 16-day intervals with a spatial resolution of 250 m (Huete et al., 2002). For each period, an algorithm applies a filter based on quality, cloud cover and viewing geometry. Then, the best observation of each pixel was selected as the NDVI value of that period. The MODIS products are distributed according to tiles, which have 1200×1200 km in a sinusoidal projection. In this study, the h13v12 tile images were downloaded. For each year, six and seven images corresponding to the breeding (reference composite date from 17 November to 18 February) and the non-breeding seasons (from 25 May to 29 August) were handled, respectively. Therefore, images overlapped with the time of bird surveys. Images were referenced using the MODIS reprojection Tool software, using the UTM projection. Then, the images were reprojected again to the Argentina Gauss-Krüger projection. NDVI values during each season were averaged for each transect. Although MODIS products also include the enhanced vegetation index (EVI), which includes coefficients that minimize noise from the atmosphere (Phillips, Hansen, Flather, & Robison-Cox, 2010), several studies showed that NDVI is a better predictor of bird species richness than the EVI (Phillips, Hansen, & Flather, 2008; Phillips et al., 2010).

The seasonal variation of NDVI (hereafter seasonal NDVI) was calculated by subtracting the mean NDVI of the non-breeding season from the mean NDVI of the breeding season. There was not a significant relationship between mean NDVI of the breeding season and the seasonal NDVI (Pearson correlation, $r = 0.11$, $n = 75$, $P = 0.369$), although there was a significant negative relationship between the mean NDVI during the non-breeding season and seasonal variation ($r = -0.37$, $n = 75$, $P < 0.001$).

2.6. Statistical analysis

Habitat structure of the 75 transects and their relationship with the mean NDVI of each season and the seasonal NDVI was analyzed by Non-metric Multidimensional Scaling (NMDS), an ordination technique that determines the relationship among sampling sites regarding their habitat structure based on measurements of similarity in a few axes (Zuur, Ieno, & Smith, 2007). Since the variables had different units, the dissimilarity in habitat structure between transects was estimated using the Gower dissimilarity index (Oksanen, 2008). The NMDS was performed using the function metaMDS in the package vegan (Oksanen et al., 2008) of the R statistical environment (R Development Core

Team 2011). The ordisurf function explored the habitat-NDVI relationships by fitting smooth surfaces for NDVI variables into the ordination space, using thin plate splines with cross-validated selection of smoothness (Oksanen, 2008).

Bird community composition along the 75 transects of the urban-rural gradient was also analyzed using NMDS. For each season, the dissimilarity in bird community composition between transects was estimated by the Bray-Curtis dissimilarity index (Oksanen, 2008), ignoring those species recorded only once. Abundance values of species were $\log(x + 1)$ transformed to limit the effects of extreme values. Feilhauer and Schmidtlein (2009) proposed a method to relate variables derived from remote sensors to community composition based on ordination and regression analysis. Ordination methods can transform composition data into a manageable set of response variables ready for regression (Schmidtlein, Zimmermann, Schüpferling, & Weiss 2007). Community composition may be summarized in a few axes using Detrended Correspondence Analysis (DCA) or Non-metric Multidimensional Scaling (NMDS) from a species-by-site matrix. NMDS is considered a good and convenient ordination technique because of its flexibility with respect to the kind of data that it handles and its lack of assumptions of linearity or normal distribution among variables (Zuur et al., 2007). NMDS summarizes similarity in species composition among sites along two or three axes. Thus, a range of scores is produced, representing community composition in each sampling unit; those scores can then be related to reflectance values and/or vegetation indices derived from remote sensors.

Bird species richness for each season and year were estimated using the COMDYN software, available at <http://www.mbr-pwrc.usgs.gov/comdyn.html>. This software estimates species richness of a site and the associated variance by taking into account differences in detectability among species and sites (Hines, Boulinier, Nichols, Sauer, & Pollock, 1999). COMDYN requires information of detected and undetected species in a series of visits to a given site. The average estimated species richness among the three breeding and the three non-breeding seasons were considered in the analysis. There was no significant variation of bird richness among years ($P > 0.05$).

We selected 40 transects separated by at least 300 m to determine the relationship between the response variables and NDVI values. In each of the five sectors containing 15 transects separated by 100 m, we systematically selected the first transect, left out the next one and selected the following one, located at 300 m from the first one. Therefore, eight transects from each sector (a total of 40 transects) were selected to construct the models, and seven transects from each sector (a total of 35) were used for model adequacy. Relationships between dependent variables and NDVI of each season and the seasonal NDVI were analyzed with Generalized Additive Models (GAMs), applying the mgcv package in R (R Development Core Team, 2011). Given that bird richness data were averaged for the three years, all dependent variables were continuous, and a Gaussian distribution of errors was assumed. In some cases, normality and homoscedasticity were improved by transforming the dependent variables to $\log(x + 1)$ (Zar, 1999). Models were obtained by backward elimination of non-significant variables ($P > 0.05$) from the full model using the anova function (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Moreover, we used an information theoretic approach by estimating the Akaike Information Criterion modified for small sample size (AICc) of all the possible models (Burnham, Anderson, & Huyvaert, 2011), using the MuMIn package (Bartoń, 2016). The best model had the minimum AICc value and a $\Delta AICc$ value > 2 to the next best model. Plots of the regression models were constructed with the visreg package (Breheny and Burchett, 2013).

To assess the adequacy of models to predict the bird community variables in the 35 transects, the observed values of dependent variables in these transects were compared with predicted values using the mean NDVI and its seasonal dynamics. Model performance was assessed by analyzing the precision and accuracy of predicted values. Precision

measures the proximity between the predicted values and the model's ability to predict similar values consistently, whereas accuracy measures the proximity between observed and predicted values (Tedeschi, 2006). Precision was measured by calculating the Pearson coefficient between the model-predicted and the observed values (Zar, 1999). Hinkle, Wiersma, and Jurs (2003) established different degrees of correlation: from 0.0 to 0.3, very low correlation; 0.3 to 0.5, low; 0.5 to 0.7, moderate; 0.7 to 0.9, high; and 0.9 to 1.0, very high. Accuracy was measured using a paired *t*-test of the difference between observed and model-predicted values that removes the covariance between values (Tedeschi, 2006). The acceptance of the null hypothesis ($P > 0.05$) indicates that the difference between predicted and observed values is not significant. Predictive maps were produced for models of bird richness and composition with adequate precision and accuracy using the raster package in R (Hijmans & van Etten, 2014). A map of the coefficient of variation for bird richness between seasons was performed based on the predictive maps of bird species richness in both seasons. Furthermore, the seasonal variation of species composition was assessed by calculating the Bray-Curtis similarity index between seasons in each transect during the three years of surveys. Similarity indices were averaged among years and related to the mean NDVI between seasons (hereafter annual NDVI) and to the seasonal NDVI.

A Distributional Uncertainty Map was constructed using the software Idrisi 32 (Eastman, 1999), considering the spatial configuration of the sampling units. Five linear vectors were created by joining transects from each of the five sampling sectors (Supplementary material 1, Fig. S1b). The vectors were transformed to raster files, and a map of the distance from each sector was performed. As the distance to the sectors increases, so does the uncertainty of the predictive maps because of the lack of sampling units. Therefore, indices of uncertainty were calculated by dividing all distances by the maximum distance in the map, and an index from 0 (null uncertainty) to 1 (maximum uncertainty) was obtained.

3. Results

We identified 72 identified bird species, of which 52 were recorded during the non-breeding and 63 during the breeding seasons. For the ordination analysis, we included the 51 species observed on more than one occasion (Supplementary material 2, Table S1). On the other hand, mean NDVI was lowest in the urban center during both seasons, whereas it was higher in the periurban sector during the non-breeding season and higher in periurban, horticulture and agriculture during the breeding season (Fig. 1). The difference of mean NDVI between seasons was highest in the agriculture sector.

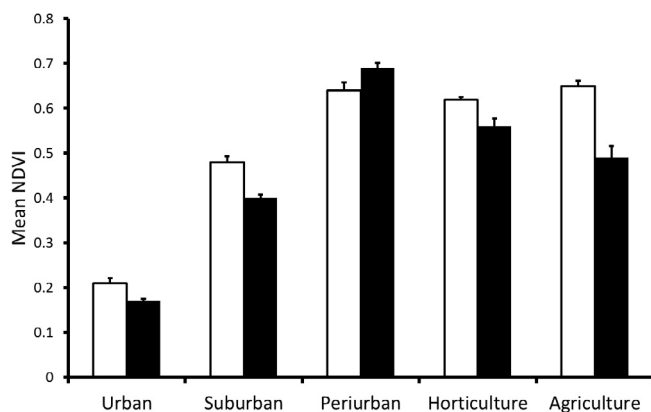


Fig. 1. Mean values of NDVI along the urban-rural gradient of Mar del Plata city during the breeding (white) and non-breeding season (black). Vertical bars indicate standard errors.

3.1. Habitat structure and NDVI

During the breeding season, the highest NDVI values were related to residential areas that are associated with the percent cover of trees, shrubs, lawn and high trees, and also the highest NDVI values were related to the percent cover of herbaceous vegetation and crops (Supplementary material 3, Fig. S2a). During the non-breeding season, the highest values of NDVI were associated with vegetation typical of residential areas (Supplementary material 3, Fig. S2b). During both seasons, the lowest NDVI values were associated with areas dominated by impervious surfaces. Finally, the highest seasonal variation of NDVI corresponded to crop and herbaceous vegetation areas (Supplementary material 3, Fig. S2c).

3.2. Predictive power of NDVI on bird species richness

Models containing the mean NDVI and the seasonal NDVI were the best explaining the variation of bird richness along the urbanization gradient during both seasons (Supplementary material 4, Table S3). During the breeding season bird richness peaked at mean NDVI values of 0.3–0.4 and remained relatively constant (Fig. 2a), whereas during the non-breeding seasons bird richness peaked at mean NDVI values of 0.2–0.3 and remained constant (Fig. 2b). During both seasons, bird richness was negatively related to the seasonal variation of NDVI. NDVI explained a greater percentage of variation and deviance in bird richness in the breeding than in the non-breeding season (Table 1). Nevertheless, the predictive models were similarly appropriate to estimate bird richness in the additional transects during both seasons (Supplementary material 4, Table S4 and Fig. S3). Within Mar del Plata city, areas of predicted low bird richness matched highly urbanized areas (Fig. 3a, b). Along the urban-rural gradient, maps showed that bird richness had the lowest predicted values in rural areas during the non-breeding season (Fig. 3a), whereas during the breeding season the lowest predicted values were found only within the city (Fig. 3b). Accordingly, the lowest predicted change in bird richness between seasons occurred within the city, whereas some parts of the non-urban areas had the highest seasonal variation of bird richness (Fig. 3c).

3.3. Predictive power of NDVI on bird community composition

The bird community during the breeding season showed three groups of species (Fig. 4a): 1) species typical of densely urbanized areas or urban exploiters (see Blair, 1996), such as the Rock Dove (*Columba livia*), the Eared Dove (*Zenaidura macroura*) and the House Sparrow (*Passer domesticus*), were related to the negative values of NMDS1 and NMDS2 (see Blair, 1996); 2) species associated with residential areas or urban adapters associated with the negative values of NMDS1 and positive values of NMDS2, such as the Picazuro Pigeon (*Patagioenas picazuro*), the White-throated Hummingbird (*Leucochloris albicollis*), the Tropical Parula (*Setophaga pititayumi*) and the Small-billed Elaenia (*Elaenia parvirostris*); and 3) species typical of rural areas or urban avoiders, related to positive values of NMDS1 and negative values of NMDS2, such as the Red-winged Tinamou (*Rhynchotus rufescens*), the Correndera Pipit (*Anthus correndera*), the Grassland Yellow Finch (*Sicalis luteola*), the Fork-tailed Flycatcher (*Tyrannus savana*) and the Double-collared Seedeater (*Sporophila caerulea*).

During the breeding season, models containing the mean NDVI and the seasonal NDVI were the best explaining the spatial variation of NMDS scores (Supplementary material 5, Table S5). NDVI variables explained 80% and 84% of the variability in the scores of axes 1 and 2, respectively (Table 2; Supplementary material 5, Fig. S4). The NMDS1 scores were the highest between mean NDVI values of 0.6 and 0.7, and showed a positive relationship with seasonal NDVI. The NMDS2 scores were negatively related to the seasonal NDVI and were highest at mean NDVI values of 0.5 and 0.7. Therefore, species typical of densely urbanized areas were related to low mean NDVI and seasonal NDVI. On

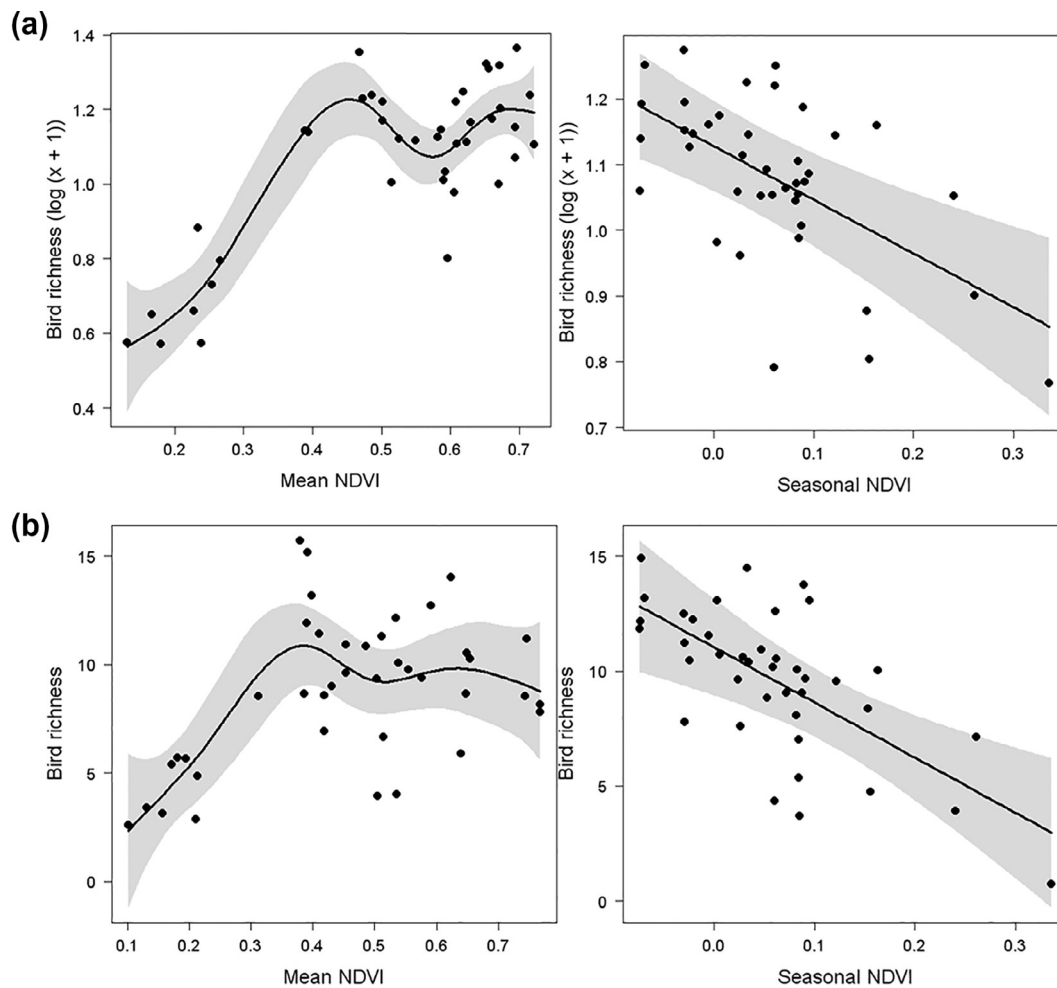


Fig. 2. Responses of bird species richness (number of species per transect, y axis) to the mean NDVI and the seasonal NDVI along the urban-rural gradient of Mar del Plata during the a) breeding seasons and b) non-breeding seasons. Graphs show the smoothed curves estimated by the Generalized Additive Models. The black line represents the fitted curve and the grey areas are the confidence intervals at 95%.

Table 1

Generalized additive models between the NDVI variables and the bird species richness during the breeding and the non-breeding seasons. ANOVA tests (F), estimated degrees of freedom (edf), P values, and percent of variation explained by the models (r^2).

	Mean NDVI			Seasonal NDVI			r^2
	F	edf	P	F	edf	P	
Breeding season	19.35	5.57	< 0.001	16.31	1.00	< 0.001	0.77
Non-breeding season	5.95	4.47	< 0.001	13.05	1.00	< 0.001	0.54

the other hand, species associated with residential areas were related to high mean NDVI and low seasonal NDVI. Finally, species typical of rural areas were related to both high mean NDVI and seasonal NDVI.

The bird community during the non-breeding season also showed three groups of species (Fig. 4b): 1) urban exploiters such as the Rock Dove, the Eared dove and the House Sparrow, associated with negative values of NMDS1; 2) urban adapters occupying the negative values of NMDS2, such as the Picazuro Pigeon, the White-throated Hummingbird, and the Tropical Parula; and 3) urban avoiders such as the Southern Lapwing (*Vanellus chilensis*) and the Grassland Yellow Finch, related to positive values of NMDS2.

During the non-breeding season, the mean and seasonal NDVI were in the best models (Supplementary material 5, Table S5), and these variables explained the variability in the scores of axes 1 (88%) and 2

(59%) (Table 2; Supplementary material 5, Fig. S5). In general, the NMDS1 scores were positively related to NDVI, and had the highest values with the increase of the seasonal NDVI. The NMDS2 score values were highest at low mean NDVI and at values between 0.5 and 0.6, and had a positive relationship with seasonal NDVI. Therefore, species typical of highly urbanized areas were related to low NDVI and seasonal NDVI, whereas species associated with residential areas were related to high NDVIs and low seasonal NDVI. Finally, species typical of rural areas were associated with moderate values of mean NDVI and high seasonal NDVI.

During both seasons, the predictive models were appropriate to estimate the axis scores in additional transects, indicating that NDVI was successful to predict the bird composition (Supplementary material 5, Table S6 and Fig. S6). Therefore, predictive maps of bird composition during both seasons were proposed (Fig. 5). Mapping of the NMDS1 scores showed that positive values comprised bird communities during the breeding season characterized by the presence of the Red-winged Tinamou, the Correndera Pipit, the Grassland Yellow Finch and the Rufous-collared Sparrow (*Zonotrichia capensis*) (Fig. 5a). Regarding the NMDS2 scores during the breeding season, positive values represented communities characterized by the presence of the Picazuro Pigeon, the White-throated Hummingbird, Tropical Parula and the Rufous-bellied Thrush (*Turdus rufiventris*) (Fig. 5b). Given that during the breeding season axis scores dominated by the Rock Dove matched those corresponding to residential species (negative values of the NMDS1) and rural species (negative values of the NMDS2), both NMDS axes were

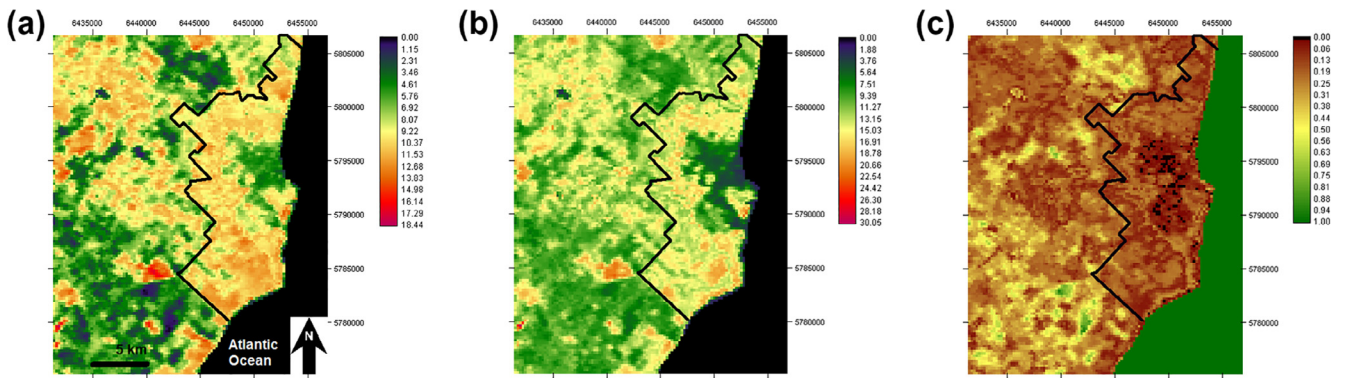


Fig. 3. Maps depicting the expected bird species richness (number of species per transect) during a) the non-breeding season b), during the breeding season and c) the expected seasonal variability (CV) of the bird species richness along the urban rural gradient of Mar del Plata c). The thick line represents the city limits.

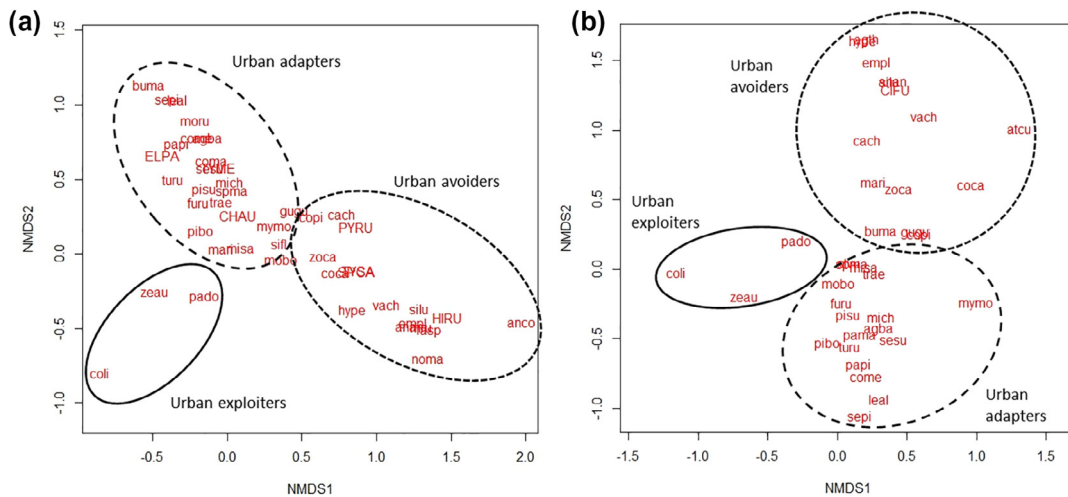


Fig. 4. NMDS ordination biplots of bird community composition during the a) breeding season (Stress = 0.11) and b) the non-breeding season (Stress = 0.13). Bird species are grouped according to different responses to urbanization (see Blair, 1996). Urban exploiters are species associated to highly urbanized areas; urban adapters are species associated to moderately urbanized areas, and urban exploiters are species related to non-urban areas. Their scientific names are depicted by the first two letters of the genus and the first two letters of the specific name (see Supplementary material, Table S1).

Table 2

Generalized additive models between the NDVI variables and axis scores of the NMDS during the breeding and the non-breeding seasons. ANOVA tests (F), estimated degrees of freedom (edf), P values, and percent of variation explained by the models (r^2).

		Mean NDVI			Seasonal NDVI			r^2
		F	edf	P	F	edf	P	
Breeding season	NMDS1	8.26	5.58	< 0.001	6.54	8.25	< 0.001	0.80
	NMDS2	20.63	5.24	< 0.001	47.74	1.62	< 0.001	0.84
Non-breeding season	NMDS1	29.10	2.55	< 0.001	12.24	6.62	< 0.001	0.88
	NMDS2	4.07	3.95	0.006	19.68	1.00	< 0.001	0.59

added for a better mapping of the assemblage. Therefore, score values lower than -1 would represent communities dominated by the Rock Dove (Fig. 5c). Negative values of NMDS1 scores represented communities during the non-breeding season dominated by the Rock Dove, the Eared Dove and the House Sparrow (Fig. 5d). Regarding the NMDS2, negative values represented bird communities during the non-breeding season composed of the Picazuro Pigeon, the White-throated Hummingbird and the Rufous-bellied Thrush, whereas positive values represented bird communities dominated by the Southern Lapwing, the Grassland Yellow Finch and the Rufous-collared Sparrow (Fig. 5e).

In general, mapping results showed that the predicted distribution of species typical of heavily urbanized areas was within the city (Fig. 5c and d). Predicted distribution of species associated with residential

areas matched peripheral areas of the city and some non-urban areas (Fig. 5b and e). Finally, the predicted distribution of species typical of rural areas was exclusively in non-urban areas (Fig. 5a and e).

Bird community similarity between seasons was negatively related to the mean NDVI and its seasonal variability (Model $r^2 = 0.64$; mean NDVI: $F = 42.57$, $P < 0.001$, $edf = 1.00$; seasonal NDVI: $F = 37.49$, $P < 0.001$, $edf = 1.00$; Fig. 6). In other words, areas with high mean primary productivity and high seasonal variation showed the highest seasonal change of bird composition. The predictive model was suitable to estimate the similarity values in additional transects ($r = 0.76$, $t_{MB} = -0.70$) (Supplementary material 6, Fig. S7). Thus, a predictive map was proposed, in which the least seasonal variation in bird community composition was expected within the city (Fig. 7).

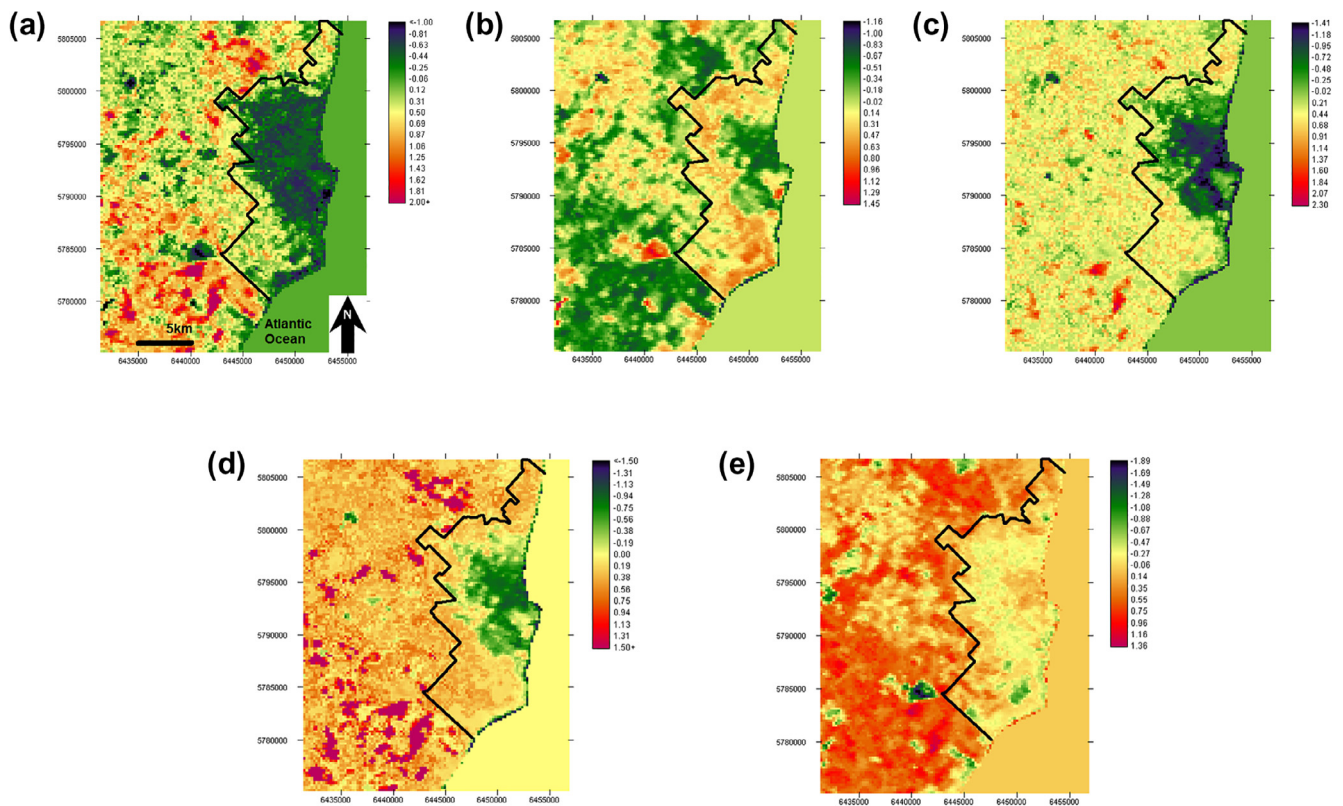


Fig. 5. Maps depicting a) the expected NMDS1 scores during the breeding season b), the expected NMDS2 scores during the breeding season c), the added expected scores of NMDS1 and NMDS2 during the breeding season d), the expected NMDS1 scores during the non-breeding season, and e) the expected NMDS2 scores during the non-breeding season along the urban-rural gradient of Mar del Plata. The black line represents the city limits.

3.4. Distributional uncertainty map

The DUM showed areas with low coverage of sampling units and, therefore, high predictive uncertainty. Those areas were located in the southwest and northwest parts of the study area, where the distance to the sampling units was the maximum (Supplementary material 7, Fig. S8). Within the city, sectors near the city boundaries also showed a relative uncertainty (index values between 0.3 and 0.5).

4. Discussion

Our results show that different levels of impervious surface cover were related to changes in spatial and temporal dynamics of primary productivity, which in turn were good predictors of bird community dynamics along the urban-rural gradient of Mar del Plata. Low values of primary productivity were associated with a decrease of bird richness in both breeding and non-breeding seasons. Over the year, urbanization had the lowest seasonality of primary productivity, which in turn buffered the seasonal variation of bird communities.

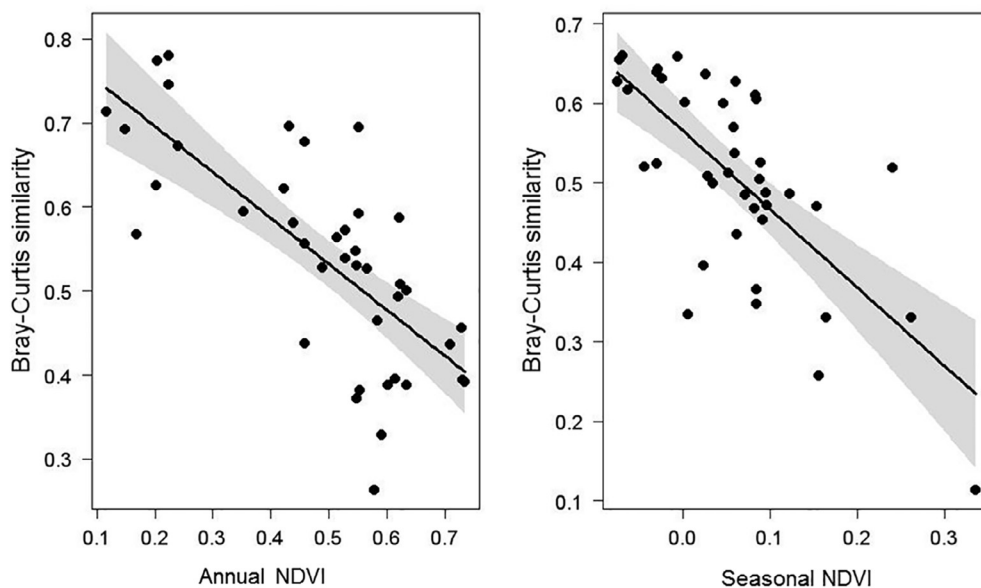


Fig. 6. Response of bird community composition similarity (Bray-Curtis similarity index/transect, y axis) between seasons to the annual NDVI (left panel) and the seasonal change of NDVI (right panel) along the urban-rural gradient of Mar del Plata. The graph shows the smoothed curve estimated by the Generalized Additive Models. The black line represents the fitted curve and the grey areas are the confidence intervals at 95%.

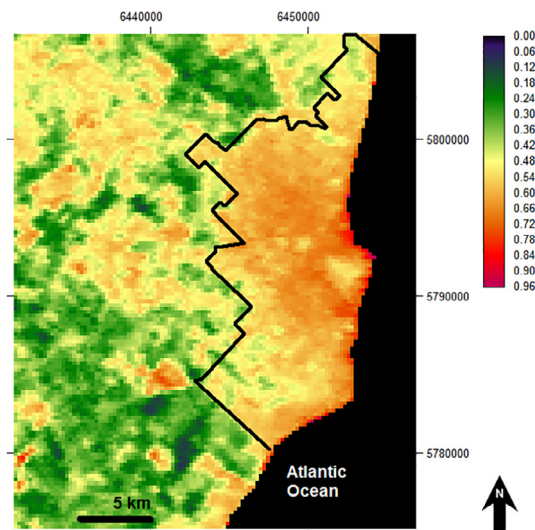


Fig. 7. Map depicting the expected seasonal variability in bird community composition (Bray-Curtis similarity) along the urban rural gradient of Mar del Plata. The black line represents the city limits.

4.1. Urbanization effects on primary productivity

Our analysis indicates that sites with the highest impervious cover were related to the lowest levels of primary productivity and its seasonal variation. These results agree with other studies conducted along urban-rural gradients, which showed negative relationships between urbanization and NDVI (Bino et al., 2008; Di Bella, Paruelo, & Straschnoy, 2004; Haedo et al., 2010; Lee et al., 2004) and a lower seasonal variation of NDVI in urbanized areas than in rural areas (Buyantuyev & Wu, 2012; Leong & Roderick, 2015). The low seasonal variation of primary productivity may be related to the frequent use of fertilizers, irrigation, pesticides and tillage (Buyantuyev & Wu, 2012; Faggi & Dadon, 2011; Leong and Roderick, 2015) and the presence of perennial tree species such as *Pinus* sp. and *Eucaliptus* sp. (Faggi & Dadon, 2011). Furthermore, the low seasonal variation of NDVI in the urban center may be related to the joined effect of low vegetation cover and high impervious surface. Conversely, rural areas dominated by crops are characterized by frequent seasonal fluctuations of NDVI, which have a peak of primary productivity in summer and a decrease during the fall-winter due to harvest and the presence of plowed fields (Lunetta, Knight, Ediriwickrema, Lyon, & Worthy, 2006; Sakamoto et al., 2005). Furthermore, seasonality in horticultural and agricultural areas may be related to the presence of unmanaged vegetation influenced by the annual changes in temperature and precipitation, and these changes were related to spatio-temporal responses of bird richness and species composition.

4.2. Predictive power of NDVI on the spatial variation of bird communities

During both seasons, bird richness increased at intermediate values of NDVI and then remained relatively constant. This result agrees with findings reported by Koh, Lee, and Lin (2006), who studied the relationship between NDVI and bird richness in northern Taiwan using a similar statistical approach by fitting LOWESS smoothing regression between variables. On the other hand, studies across urbanized landscapes indicate a positive linear relationship between bird richness and NDVI (Bino et al., 2008; Haedo et al., 2010), although non-linear relations were not explored. Overall, the results found in our study and others show that NDVI values below 0.5 are a limit beyond which bird richness decreases significantly along urban-rural gradients.

During both seasons, bird richness was negatively related to the seasonal variation of NDVI. Sites with high mean values of primary

productivity and low seasonal variation should be related to a constant supply of food throughout the year, favoring the coexistence of a large number of species, unlike non-urban areas with similar mean values of primary productivity but a higher seasonality (Shochat et al., 2006). On the other hand, in Mar del Plata, sites with high NDVI but low seasonal variation were related to high habitat heterogeneity, composed of several vegetation strata (Supplementary material 3, Fig. S2c). Indeed, sites with moderate and high NDVI values and low seasonal variation of NDVI were inhabited by the Picazuro Pigeon, the White-throated Hummingbird, the Tropical Parula, the Small-billed Elaenia and the Green-barred Woodpecker (*Colaptes melanochlorus*); these are species typical of residential areas (Leveau & Leveau, 2004; Leveau & Leveau, 2005), nesting in trees and feeding in lawns, shrubs and trees (De la Peña, 2010).

Sites with high seasonal NDVI were characterized by the presence of bird species that feed and nest on herbaceous vegetation and crops, and are negatively affected by urbanization, such as the Red-winged Tinamou, the Southern Lapwing and the Grassland-yellow Finch (Leveau & Leveau, 2005). Conservation strategies that address bird species excluded from cities (the so-called urban avoiders) should be planned by mapping the predicted values of the NMDS axis scores. Geographic information systems can identify areas inhabited by bird species typical of rural areas and, therefore, more vulnerable to urban expansion. Our maps showed two areas located near the northern and southern limits of Mar del Plata that are predicted to hold urban-avoider species and therefore vulnerable to urban expansion.

Sites with low NDVI values and their seasonality were associated with highly urbanized areas, dominated by the Rock Dove, the House Sparrow and the Eared Dove. The Rock Dove and the House Sparrow are invasive species that nest on buildings and feed on the ground, taking advantage of food left by humans (Devictor, Julliard, Couvet, Lee, & Jiguet, 2007; Suhonen & Jokimäki, 1988). The Eared dove is very common in central Argentina (Narosky & Di Giacomo, 1993), nesting in trees and buildings and taking advantage of human-provided food.

Our results agree with those of Lin et al. (2008), who found three types of bird assemblages associated with different land uses, elevations and NDVIs: 1) species typical of densely populated city areas related to low NDVI values; 2) species associated with suburban areas, related to moderate NDVI values and 3) forest species, associated with high NDVI values. Our study included estimations of the seasonal dynamics of primary productivity that allowed us to discriminate between bird communities of vegetated residential areas and crop areas; these two habitat types are hard to distinguish, since they have similar NDVI values.

The mapping results showed a progressive increase of bird richness from the downtown area towards the city limits due to lower building cover and higher NDVI. The patterns agreed with those reported by other authors who, using geostatistical approaches, found that the low values of bird diversity matched metropolitan areas (Lin et al., 2008). However, our maps showed a mixture of sites with high and low species richness along the non-urban areas, corresponding generally to horticultural and crop areas, respectively (Leveau, 2014). Horticultural areas have greater habitat diversity than croplands (Leveau, 2013) because they have a more similar proportion of crops, herbaceous vegetation, trees and shrubs, promoting the coexistence of a larger number of species.

Contrary to our expectations, the relationship between bird richness and NDVI was similar between seasons, a result that has also been reported in other studies (Apellaniz, Bellocq, & Filloy, 2012; H-Acevedo & Currie, 2003; Hurlbert & Haskell, 2003). Our results suggest that possible changes in habitat use and behavior in birds would not have affected the relationship between primary productivity and bird richness. Moreover, our results in Mar del Plata showed that NDVI is a good predictor of bird richness during both seasons. However, NDVI variables explained more variation in bird richness and bird composition

during the breeding than during the non-breeding season. These results suggest a more restricted habitat use during the breeding season, possibly due to space limitations related to the nesting territory (Delgado & Moreira 2000; Hutto, 1985; Wiens, 1989). Moreover, the weaker fit of the model during the non-breeding season should be related to the use of food resources not directly related to primary productivity, such as seeds, dead arthropods or food provided by humans (Hurlbert & Haskell, 2003).

4.3. Predictive power of NDVI on the seasonal dynamics of bird communities

Our predictive maps representing the expected seasonal variation of bird richness showed the lowest values within the city. In non-urban areas, there were sites with seasonal variation of bird richness higher than 50%, corresponding to crop fields (see Leveau, 2014). Similarly, the highest seasonal variation of bird composition was in non-urban areas. In fact, both predictive maps were very similar regarding the spatial variation of temporal change in bird communities (Figs. 3c and Fig. 7). Within the city, the spatial configuration of the seasonal dynamics was more homogeneous than in the non-urban areas; in the latter, areas that have undergone abrupt temporal changes in bird communities were contiguous to areas exhibiting low changes.

The seasonal variation of bird composition was directly related to the annual NDVI and its seasonal dynamics. As suggested previously, the degree of change in primary productivity between seasons determines the amount of migrant species in the community (Hurlbert & Haskell, 2003). Our results showed that, the increase in the number of migratory species during the breeding season was related to sites with highest seasonal variation of NDVI. These species included the Fork-tailed Flycatcher, the Vermilion Flycatcher (*Pyrocephalus rubinus*), the Barn Swallow (*Hirundo rustica*) and the Double-collared Seedeater. The first three species are aerial hawkers that hunt for insects over the herbaceous vegetation (Marone, 1991). The herbaceous vegetation of rural areas occurs generally along field edges, which have a greater abundance of arthropods than crops (Weyland & Zaccagnini, 2008). Arthropods may show seasonal fluctuations in abundance in response to temperature, with abundances being higher during summer (Davis & Gray, 1966; Danks, 2007). On the other hand, the Double-collared Seedeater depends on unmanaged field edges for nesting and feeding (De la Peña, 2010), where vegetation typically increases in volume during spring-summer. Resident species may also respond to the seasonal variation of resources by showing a nomadic behavior, such as the Rufous-collared Sparrow and the Grassland Yellow-finch (Fjeldså & Krabbe, 1990; Narosky & Yzurieta, 2003). These species concentrate in flocks during the non-breeding season in search of food, whereas during the breeding season they use unmanaged field edges for nesting and feeding (Leveau & Leveau, 2011).

The resulting maps confirmed previously proposed patterns (Catterall, Kingston, Park, & Sewell, 1998; Caula et al., 2008; Clergeau, Savard, Mennechez, & Falardeau, 1998; Leveau et al., 2015), in which bird communities had the lowest seasonal variation within the city. Accordingly, urbanization induces a seasonal stabilization in the dynamics of primary productivity that, in turn, is thought to affect the temporal changes in bird composition. Moreover, our mapping results revealed a spatial pattern of homogenization in the temporal variation of bird communities promoted by urbanization.

4.4. Caveats

This study did not include some land uses such as industrial areas, golf courses or woodlots; consequently, the predictive capacity of the models depicting the spatial and temporal variation of bird richness and composition on these land uses may be reduced. Moreover, the DUM showed areas where the predictive power of the models may be low due to a null coverage of sampling units. Including a greater number of

sampling units that cover more land use types in the southwest and northwest parts of the study area may improve the quality of the predictive models; thus, better predictive maps of bird richness and composition in the urban-rural gradient may be constructed.

MODIS data have an excellent temporal scale for an appropriate estimation of NDVI patterns during bird surveys; however, data spatial resolution are larger than the transect size used in this study. Therefore, the predictive maps of bird richness and composition have a spatial resolution that may be too coarse to get information for planning or management. For example, future urbanization changes produced in areas smaller than four hectares (MODIS pixel size) cannot be detected in our predictive maps.

5. Conclusions

Mapping the distribution of bird richness and composition results very useful to make conservation and management decisions along urbanization gradients. We found that mean NDVI and its seasonal variation (based on MODIS images) were appropriate to predict the spatial variation of bird richness and composition along an urban-rural gradient of central Argentina. Maps of bird composition allow the survey of areas inhabited by urban-avoider species, which are vulnerable to urban expansion. On the other hand, NDVI indices provided an appropriate prediction of the seasonal variation of bird composition, showing a more homogeneous spatial pattern within the city than in rural areas. Urbanization stabilized the seasonal dynamics of primary productivity which, in turn, was related to a reduced temporal dissimilarity of bird communities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.landurbplan.2018.04.007>.

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