

# Bird diversity patterns in Neotropical temperate farmlands: The role of environmental factors and trophic groups in the spring and autumn

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**Abstract** Productivity, habitat heterogeneity and environmental similarity are of the most widely accepted hypotheses to explain spatial patterns of species richness and species composition similarity. Environmental factors may exhibit seasonal changes affecting species distributions. We explored possible changes in spatial patterns of bird species richness and species composition similarity. Feeding habits are likely to have a major influence in bird–environment associations and, given that food availability shows seasonal changes in temperate climates, we expect those associations to differ by trophic group (insectivores or granivores). We surveyed birds and estimated environmental variables along line-transects covering an E–W gradient of annual precipitation in the Pampas of Argentina during the autumn and the spring. We examined responses of bird species richness to spatial changes in habitat productivity and heterogeneity using regression analyses, and explored potential differences between seasons of those responses. Furthermore, we used Mantel tests to examine the relationship between species composition similarity and both the environmental similarity between sites and the geographic distance between sites, also assessing differences between seasons in those relationships. Richness of insectivorous birds was directly related to primary productivity in both seasons, whereas richness of seed-eaters showed a positive association with habitat heterogeneity during the spring. Species composition similarity between assemblages was correlated with both productivity similarity and geographic proximity during the autumn and the spring, except for insectivore assemblages. Diversity within main trophic groups seemed to reflect differences in their spatial patterns as a response to changes between seasons in the spatial patterns of food resources. Our findings suggest that considering different seasons and functional groups in the analyses of diversity spatial pattern could contribute to better understand the determinants of biological diversity in temperate climates.

**Key words:** environmental similarity, habitat heterogeneity, primary productivity, species richness, species turnover.

## INTRODUCTION

Understanding the mechanisms that create and drive spatial diversity patterns has been a challenge for ecologists for about 200 years (Hutchinson 1959; Evans *et al.* 2005). While many studies have examined spatial changes in species richness and species composition similarity, few have accounted for the temporal dynamics of the spatial patterns of diversity in seasonal climates (H-Acevedo & Currie 2003; Hurlbert & Haskell 2003; Laiolo 2005). Species distributions may change over time because of resource availability and their own physiological or ecological requirements (Hurlbert & Haskell 2003).

The most widely accepted hypotheses to explain diversity patterns over large geographic scales rely on species–environment relationships. The productivity

and the habitat heterogeneity hypotheses have gained extensive empirical evidence to explain spatial patterns of species richness (Benton *et al.* 2003; Hawkins *et al.* 2003). The former states that energy limits species richness through the available energy flowing in food webs (Hawkins *et al.* 2003). The habitat heterogeneity hypothesis predicts increasing species richness with increasing habitat types (i.e. landscapes with high variety of land uses), because more species are able to coexist at increasing niche availability (Cramer & Willig 2005). Moreover, it has been documented that the spatial turnover in species composition increases with increasing geographic distance (or distance-decay in species composition similarity *sensu* Nekola & White 1999) or with decreasing environmental similarity between sites (Steinitz *et al.* 2006), because both dispersal abilities and species capability of adapting to different environmental conditions ultimately drive species composition similarity between assemblages (Qian & Ricklefs 2007).

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In temperate climates, spatial patterns of productivity, habitat heterogeneity and environmental similarity may exhibit seasonal changes caused by climate or anthropogenic land uses (H-Acevedo & Currie 2003; Laiolo 2005). Given that increases in primary production are expected to lead to increases in secondary production (Loreau *et al.* 2001), seasonal changes in primary productivity likely lead to changes in food resources for birds. Besides, the seasonal dynamics of human land use may also alter bird resources independently of primary productivity (Atkinson *et al.* 2002). Studying the seasonal variations in diversity patterns and environmental factors may help clarify the true relationship between species distributions and their potential explanatory variables (Hurlbert & Haskell 2003).

Focusing on functional groups may provide a comprehensive framework to understand the seasonal dynamics of diversity–environment relationships and the spatial patterns. Specifically, we expect that the abundance of different food types, such as seeds and invertebrates, reflects seasonal variations in both climatic conditions and land use (Vickery *et al.* 2001). If bird–environment associations are influenced by the species feeding habits (Atkinson *et al.* 2002), the diversity within main trophic groups may show seasonal differences in their spatial patterns as a response to the seasonal dynamics in the spatial patterns of food resources.

Our aim was to explore possible variations between the autumn and the spring in spatial patterns of species richness and species composition similarity between bird assemblages, and to examine the environmental determinants of those patterns in Neotropical temperate farmlands. We took two approaches to analyse bird responses. First, we consider the whole bird assemblages; then, we assigned each species into a feeding group based on its primary food (granivores or insectivores). Specifically, we examined the spatial distribution of bird species richness during the autumn and the spring in relation to spatial changes in environmental variables describing primary productivity (rainfall, actual evapotranspiration (AET), normalized difference vegetation index (NDVI)) and habitat heterogeneity (diversity of land uses), and investigated differences between seasons. If any of the species richness hypotheses were correct, we would expect that increases in the explanatory variable (productivity/habitat heterogeneity) should determine increases in species richness during both seasons, irrespectively of possible changes between seasons in the spatial pattern of the explanatory variable. However, we would expect changes between autumn and spring in the explanatory factor of species richness if species (or species groups) have different environmental requirements according to the season. Furthermore, species composition similarity between assemblages was analysed in

response to both environmental similarity (including productivity and anthropogenic factors) and geographic distance between sites in the autumn and the spring. If species composition similarity was responding to any environmental similarity factor, we would expect the relation to be maintained between the autumn and the spring, independently of the geographic distance between sites or changes between seasons in environmental similarity between them.

## METHODS

### Study area

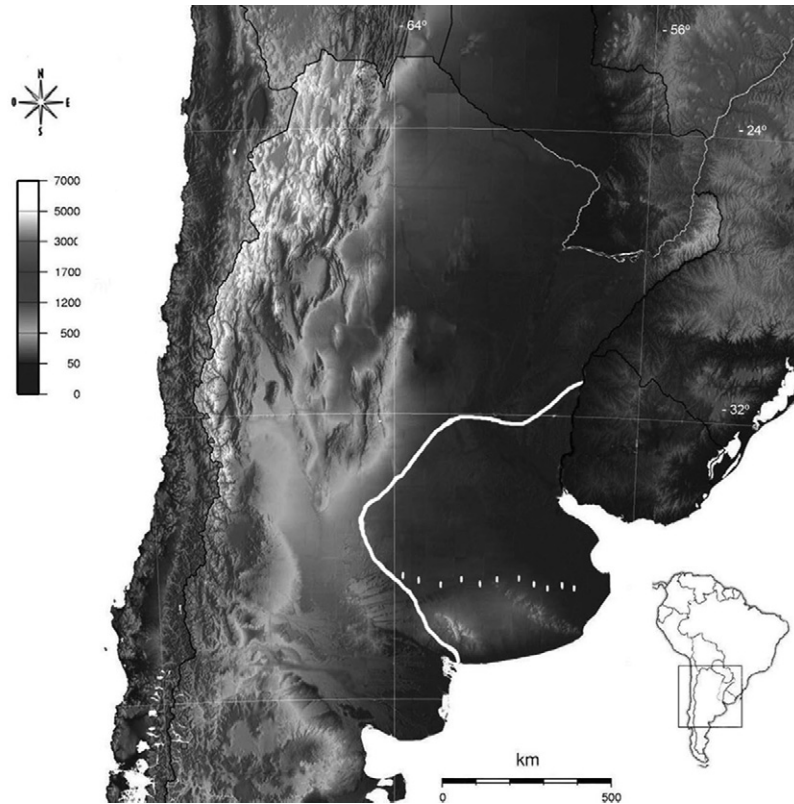
The study was conducted in the Pampean Region in central-eastern Argentina, approximately between 31–39°S and 58–63°W (Fig. 1). The region has a temperate climate with temperatures ranging 7.5–9.5°C in July and 21.5–23°C in January; rainfall is evenly distributed throughout the year, decreasing from east (1100 mm year<sup>-1</sup>) to west (600 mm year<sup>-1</sup>). Although steppes were dominated by grasses such as *Stipa*, *Piptochaetium*, *Aristida*, *Melica*, *Briza*, *Bromus*, *Eragrostis* and *Poa* (Cabrera 1971), composition of the native grass community has been modified by agriculture and livestock for over two centuries (Viglizzo *et al.* 2001). Trees are virtually absent in the region but small and isolated woodlots are often found in association to cattle-shelter, windbreaks, farms or towns. Cattle production involves steer fattening and cow–calf operations on perennial and annual pastures, and the main crops are wheat, maize, soybean and sorghum (Krapovickas & Di Giacomo 1998).

Until the early 1970s, the model dominant production in this region was the alternation between agriculture and livestock, allowing for a partial recovery of soil structure and nutrients. The massive conversion of natural grasslands into croplands, and the intensification of agriculture, pesticide use and forestry in the last decades have caused a markedly decline of most grassland bird populations (Krapovickas & Di Giacomo 1998, Zaccagnini 2005), and the extinction of four grassland birds (*Numenius borealis*, *Xanthopsar flavus*, *Alectruru risora*, *Rallus antarcticus*) in the Pampean region (Narosky & Di Giacomo 1993).

### Study design

The study was conducted during the autumn (May–June) and the spring (October–November) of 2008. Birds were surveyed and environmental variables were measured along the E–W gradient of decreasing mean annual rainfall, a positive covariate of net primary productivity (NPP) in temperate regions (Paruelo *et al.* 1999) (the productivity gradient hereafter).

Using satellite images we placed 11 line-transects along the gradient covering 500 km. Transects were 10 km long, located on secondary roads with N–S direction and 30–40 km apart (Fig. 1). All transects were located at similar latitudes (36.5–37.5°S) and altitude (90–150 m.a.s.l.), minimizing other potential environmental effects.



**Fig. 1.** Location of bird survey transects (white dots) along the rainfall/primary productivity gradient in the Pampean region (white line) of Argentina. The coloured scale provides the elevation (m.a.s.l.).

### Bird surveys

Birds were surveyed using the point-count method with a fixed 200 m radius (Ralph *et al.* 1995). Along each transect, 11 point count sites were established systematically 1 km apart along secondary roads with a random starting point. Sampling over secondary roads allowed us to thoroughly cover the study area; besides, it increases the efficiency of data collection given that birds are counted in the same proportion as off roads but with reduced time travel between sampling sites, enabling researchers to survey a larger number point counts in one morning (Ralph *et al.* 1995). Surveys were conducted on clear and calm days, from dawn to the following 4 h. At each point-count site, all terrestrial birds seen or heard over 5 min (the standard counting period when travel time between point-count sites is less than 15 min; Ralph *et al.* 1995) were recorded except birds flying overhead. The same two observers conducted all surveys.

We surveyed transects twice during each season (the spring and the autumn), and considered the total number of different species recorded (including both visits) as the transect species richness. Species composition similarity was estimated between all pairs of transects. Species were classified as insectivorous (species that feed on arthropod in any life stage) or granivorous (species with a diet mainly composed by seeds) according to their primary food (Montaldo 2005; de la Peña 2006; Bó *et al.* 2007); birds that were not classified within those groups were excluded from analyses by feeding groups. Trophic group analysis was conducted on

the basis of insectivores and granivores because they were the most abundant groups, and because land use management mainly affects invertebrate and seed diversities, and thus food availability for insectivorous and granivorous birds (Benton *et al.* 2003).

### Environmental variables

The NPP is commonly used in studies of species-energy relationships as an estimate of the potential productivity available to high trophic levels (Mittelbach *et al.* 2001). We worked with three of the NPP estimators most commonly used in the literature: NDVI, AET and rainfall (Evans *et al.* 2005). We located transects in 5TM LANDSAT satellite images from the last 5 years, and established an area of  $10 \times 20$  km around each transect where we calculated NDVI. We obtained a daily average NDVI per transect and season. From a database of daily AET maps available for central and eastern Argentina (Di Bella *et al.* 2000), we obtained AET values for each transect and season for the last 5 years, and estimated a daily AET average value. Values of mean annual rainfall were obtained from a climatic database for all localities of Argentina with averages of 50 years. We calculated habitat heterogeneity based on the diversity of land uses recorded along transects (considering pasture and different crop types as different categories of land use) using the Shannon–Wiener diversity index.

## Data analysis

### *Quantification of the productivity gradient*

Given the controversy on which is the best estimator of NPP at the meso and macro scales, we performed principal component analysis (PCA) using a matrix based on the three NPP estimators to quantify the productivity gradient for each season. Following the Kaiser Criterion, only axes with associated eigenvalues greater than one were considered (Kaiser 1958). This method allow to take into account the different NPP estimates and combine them into a new productivity variable (from now on productivity component) obtaining a more complete description of the east-west productivity gradient along the Pampas region for each season.

To investigate the spatial variation of productivity during the autumn and the spring, we analysed the relationship between the axes scores of the productivity component (dependent variable) and the longitudinal geographic coordinates (independent variable). We ran regression models. When finding two or more significant models we followed a model selection employing the Akaike information criterion (AIC) (Johnson & Omland 2004). We ran all possible linear and non-linear regression models containing the longitudinal geographic coordinates and its square component as explanatory variables, respectively. Following the AIC, we select the better model to describe the productivity gradient for each season.

### *Species richness*

We examined the influence of NPP and habitat heterogeneity on bird species richness with multiple regression models for each season. We included the number of species as the dependent variable (the total number, and the number of granivores and insectivores), and the productivity component extracted from the PCA and the land use diversity index as the independent variables. There was no multicollinearity among independent variables. We examined the relationships between species richness and the predictor variable for each season. To study the spatial structure of species richness and its relationship with the associated explanatory variables, we performed partial regression analyses for total species richness and for bird feeding groups. The model included the geographic coordinates (spatial variable) and the significant environmental predictors as independent variables. We identified the proportion of variation in species richness explained by: (i) environmental factors, independently of any spatial structure; (ii) the spatially structured environmental variation; (iii) the space alone, or spatial structured variation unexplained by our environmental variables; and (iv) unexplained variation and stochastic fluctuations. All the analyses were performed using the software Spatial Analysis in Macroecology v.4 (SAM, Rangel *et al.* 2010).

### *Species composition*

We explored changes in species composition and the environmental determinants for each season. Species composi-

tion similarity between all pairs of transects was estimated using the complementary distance measurement of the Sørensen similarity index for the whole assemblage, and for granivores and insectivores. Environmental similarity based on productivity factors (average rainfall and AET) was estimated using the complementary distance measurement based on Gower index (Legendre & Legendre 1998), and similarity based on anthropogenic factors (land use) was estimated using the complementary quantitative Bray–Curtis distance index. The distance index interpretation in terms of similarity was: the larger the distance between two sites was, the less the similarity between the assemblages.

Associations between species composition and environmental similarities (productivity/land use) were evaluated by simple Mantel tests run for each season (Steinitz *et al.* 2006). Simple Mantel tests were also used to evaluate the correlation between species composition similarity based on its distance complement (total and by trophic groups) and geographic distance. Geographic distance between all pairs of transects was estimated from geographic coordinates using Euclidean distance. Then, we conducted partial Mantel tests to assess the correlation between species composition and the significant environmental dissimilarity while controlling for the effect of geographic distance and vice versa. Mantel analyses were performed using ZT version 1.1 (Bonnet & Van de Peer 2001).

## RESULTS

### **Productivity gradient**

We recorded five and 10 different types of land uses (including pasture and crops) during the autumn and the spring, respectively. Habitat heterogeneity showed changes between seasons along the productivity gradient due to land use dynamics. Land use was relatively homogeneous during the autumn because cattle pastures dominated the landscape. In contrast, a mix of agricultural and pastoral farming resulted in a more heterogeneous landscape in the spring (Appendix S1).

Primary productivity was summarized into a single productivity component obtained from the PCA, and the three NPP estimators had high positive correlations with the productivity component in both seasons (Table 1). As expected, the productivity component increased from west to east during the autumn and the spring; however, differences were observed between seasons (Fig. 2). The spatial variation in productivity scores was best explained by a linear model in the autumn ( $t_9 = 10.756$ ,  $P < 0.0001$ ;  $R^2 = 0.93$ ) (Fig. 2a; Table 2), and by a quadratic model in the spring ( $F_{2,8} = 49.94$ ;  $P < 0.0001$ ;  $R^2 = 0.91$ ) (Fig. 2b; Table 2).

### **Species richness**

We recorded a total of 68 bird species, of which 41 were classified as insectivores, 12 as granivores and the



remaining 15 species were excluded from the analysis by feeding groups because they did not classify as either granivore or insectivore (Appendix S2). Of the total bird species recorded, we identified 52 during the autumn (2879 individuals): 11 granivores (1152 individuals), 27 insectivores (616 individuals) and 14 species were excluded from the analysis by trophic groups. In the spring, we recorded 57 bird species (3624 individuals) including 11 granivores (1506 individuals), 35 insectivores (1758 individuals) and 11 species had other diets.

Multiple regression analysis indicated that productivity explained spatial variation in the total number of species in both seasons (autumn:  $t_8 = 2.883$ ,  $P = 0.020$ ; spring:  $t_8 = 3.367$ ,  $P = 0.009$ ), unlike habitat heterogeneity (autumn:  $t_8 = 1.087$ ,  $P = 0.309$ ; spring:  $t_8 = 0.548$ ,  $P = 0.599$ ). Similarly, richness of insectivores was positively related to productivity (autumn:  $t_8 = 2.617$ ,  $P = 0.031$ ; spring:  $t_8 = 3.537$ ,  $P = 0.008$ ) but not to habitat heterogeneity (autumn:  $t_8 = 1.892$ ,  $P = 0.095$ ; spring:  $t_8 = 0.273$ ,  $P = 0.791$ ). Richness of granivores, however, showed variations between seasons in the association with environmental factors. During the autumn, there was no significant association with either productivity ( $t_8 = 0.62$ ,

$P = 0.552$ ) or habitat heterogeneity ( $t_8 = -1.02$ ,  $P = 0.335$ ); in the spring, richness was positively associated with habitat heterogeneity ( $t_8 = 2.708$ ,  $P = 0.027$ ) but not with productivity ( $t_8 = 1.043$ ,  $P = 0.327$ ).

Simple regressions revealed a positive relationship between species richness and the productivity component that was consistent between seasons (autumn:  $t_9 = 2.75$ ,  $P = 0.011$ ; spring:  $t_9 = 3.53$ ,  $P = 0.003$ ; Fig. 3a,b). Increases in insectivore richness were associated with increasing productivity in both the autumn ( $t_9 = 2.14$ ,  $P = 0.031$ ) and the spring ( $t_9 = 3.88$ ;  $P = 0.002$ ) (Fig. 3c,d). In contrast, spatial patterns of granivore richness differed between seasons, showing no response to changes in habitat heterogeneity in the autumn ( $t_9 = 1.14$ ;  $P = 0.142$ ) (Fig. 3e) and a positive association in the spring ( $t_9 = 2.49$ ;  $P = 0.017$ ) (Fig. 3f).

Partial regressions indicated that the highest proportion of variation in total species richness and in insectivore richness was explained by productivity during both seasons (Fig. 4). The highest proportion of spring variation in granivore richness was explained by habitat heterogeneity regardless of any spatial structure (Fig. 4).

**Table 1.** Correlations of environmental variables and factor loadings for the first component of the productivity principal component analysis during the autumn and the spring

	Autumn	Spring
Seasonal average precipitation	0.904	0.982
AET daily average	0.895	0.906
NDVI daily average	0.845	0.849
$R^2$	0.778	0.836

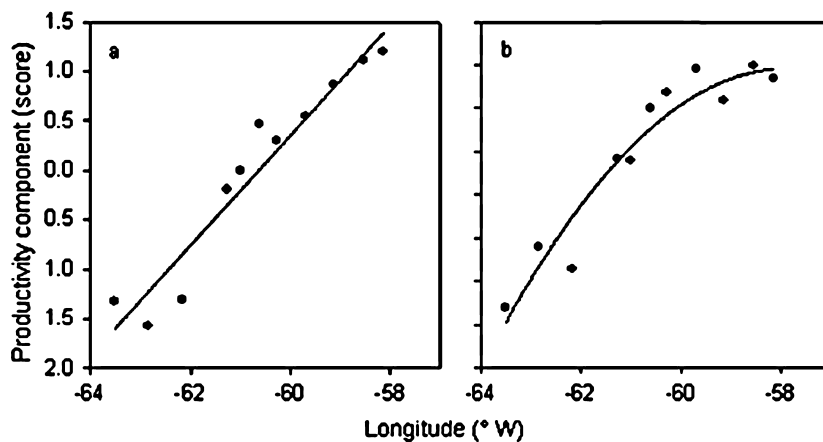
AET, actual evapotranspiration; NDVI, normalized difference vegetation index.

**Species composition**

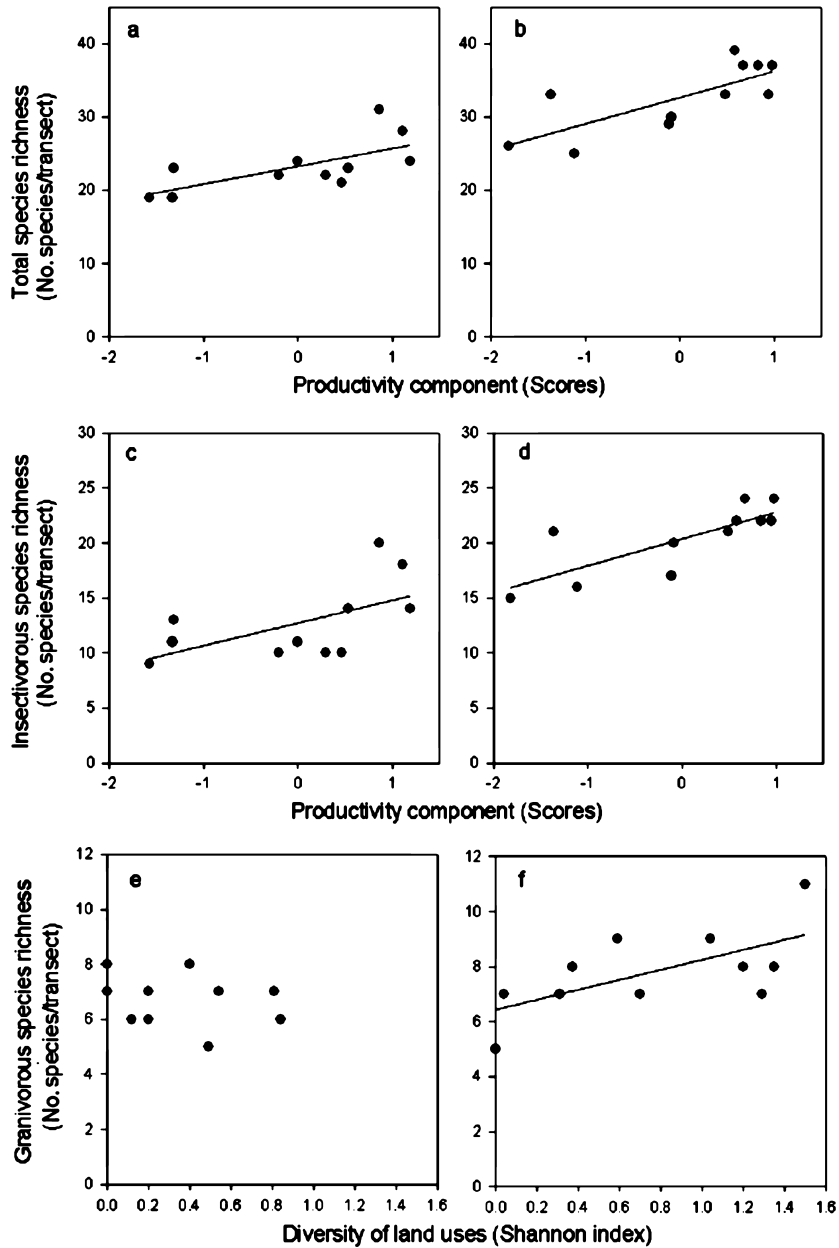
Simple Mantel tests for all groups (total, granivores and insectivores) showed that species composition dis-

**Table 2.** Akaike information criterion (AIC) values of the model selection procedure during the autumn and the spring

	Autumn AIC	Spring AIC
Linear regression model	10.675	17.507
Quadratic regression model	14.917	16.217



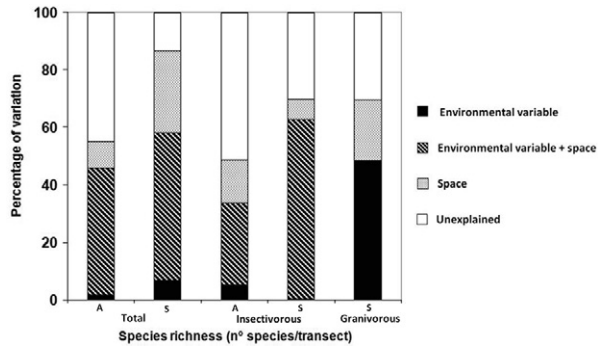
**Fig. 2.** Longitudinal pattern of environmental productivity during the autumn (a) and the spring (b).



**Fig. 3.** Relationship between the productivity component derived from principal component analysis for total species richness (a,b), insectivore richness (c,d), and relationship between land use diversity and granivore richness (e,f), during the autumn (a,c,e) and the spring (b,d,f).

similarity between transects was never correlated with environmental dissimilarity due to anthropogenic factors, while it was generally positively correlated to productivity factors (Table 3). The more environmentally similar the sites were due to productivity, the greater the species composition similarity between assemblages was. The correlation between species composition and productivity similarity was consistent between seasons except for insectivorous birds. During the autumn, insectivore assemblages were relatively similar along the productivity gradient.

Simple Mantel tests for species composition dissimilarity and geographic distance showed positive correlations for bird assemblages and seasons (Table 3). The closer the sites were the greater the species composition similarity between assemblages was during both seasons. Partial Mantel tests revealed that the correlation between species composition and environmental dissimilarity due to productivity factors was no longer significant when controlling for the effect of space over species composition dissimilarity (Table 3). In contrast, the correlation between species composition



**Fig. 4.** Percentage of variation of the total bird richness and insectivore richness explained by the productivity component, the space and the unexplained variation; and granivore richness explained by land use diversity, space and the unexplained variation.

tion dissimilarity and geographic distance remained significant when productivity dissimilarity was controlled, except for seed-eaters in the spring (Table 3).

## DISCUSSION

### Patterns of species richness

Primary production seemed to be a key factor in determining spatial patterns of bird species richness in temperate farmlands of the Pampas during both the spring and the autumn. Previous large-scale studies also reported seasonal consistency in bird richness–productivity relationships (H-Acevedo & Currie 2003; Hurlbert & Haskell 2003). Considering the whole bird assemblage, species richness showed no evidence of positive responses to habitat diversity. However, our results showed that the role of NPP and environmental heterogeneity in determining spatial patterns of bird richness in different seasons differed between trophic groups. The relationship between the number of insectivorous species and primary productivity was consistent between seasons regardless of the changes in the spatial pattern of productivity between the autumn and the spring. Thus, the distribution of insectivorous birds appears to respond to food production (i.e. insect abundance) all year round regardless of human land use. Insect responses to unfavourable weather conditions include decreasing activity such as diapause (Curry 1994). Consequently, richness of insectivores could be the highest where climatic conditions are more benign (i.e. in the east of the region during the autumn and central-east during the spring) and a higher primary production could lead to higher abundance of invertebrates. In contrast, granivore richness seems to depend on habitat heterogeneity, rather than on productivity, only during the spring. It has been

documented that a reduction in habitat heterogeneity, such as we observed in the autumn, could result in decreasing food resources (i.e. seeds) affecting bird species distributions (Benton *et al.* 2003; Heikkinen *et al.* 2004). Previous studies showed that seed-eating birds are more abundant in areas with mixed land uses than in homogeneous areas (Vickery *et al.* 2001; Atkinson *et al.* 2002).

Although our data showed spatial autocorrelation, variations in the total species richness and insectivore richness are likely a consequence of the spatial-structure primary productivity along the Pampean region. Partial regressions showed that the proportion of variation in species richness explained by the space was lower than that explained by the spatially structured environmental variables, indicating that regressions were little affected by the residual autocorrelation (Borcard *et al.* 1992).

### Patterns of species composition similarity

Both environmental similarity due to productivity factors and geographic distance between sites influence the species composition similarity among bird communities during the autumn and the spring. Thus, the more productively similar and proximate the sites are, the more similar the assemblage composition will be. At global scale, He and Zhang (2009) found a positive correlation between species composition similarity and productivity similarity primarily in temperate regions, suggesting that species' natural spatial boundaries (such as the biogeographical affinity, *sensu* Harrison & Grace 2007) could play a critical role in shaping the relation between species composition and productivity similarity. Our findings suggest that, at the mesoscale, species composition patterns may be explained in terms of both ecological and historical effects: species may be distributed according to their niche requirements related to productivity conditions (that covary with geographic distance) and their own dispersal abilities related to the geographic distance itself (Qian *et al.* 2009).

An inconsistency between seasons in the associations between species composition similarity and productivity similarity/geographic distance arose only when assigning species into trophic groups. The composition of insectivores was influenced by productivity in the spring but not in the autumn. These results suggest that when arthropods scapes during the autumn (Denlinger 1980), several species of insectivorous birds enlarge their occupancy area, tolerating broader productivity conditions in order to fulfil their food requirements. Thus, a low association between insectivore composition similarity and geographic distance was found during the autumn. Species composition of seed-eating birds was influenced by

**Table 3.** Simple and partial Mantel correlations between species composition dissimilarity and environmental dissimilarities and geographic distance

Correlation between taxonomic dissimilarity and:	All species		Insectivores		Granivores	
	Autumn	Spring	Autumn	Spring	Autumn	Spring
Productivity dissimilarity	0.528**	0.656**	0.237	0.682**	0.427**	0.316*
Anthropogenic dissimilarity	0.055	0.119	0.101	0.033	0.101	0.184
Geographic distance	0.636***	0.734***	0.288*	0.762***	0.544**	0.291*
Productivity dissimilarity, controlling geographic distance	0.052	0.173	–	0.193	–0.007	0.165
Geographic distance, controlling productivity dissimilarity	0.421*	0.463**	–	0.493**	0.373*	0.06

Analysis based on all species, insectivores and granivores, for the autumn and the spring. \* $P = 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

productivity, which accounted for the spatial structure only in the spring. Possibly, some unaccounted spatially structure factor influenced the spatial pattern of granivore composition during the autumn. When seeds are abundant and readily available during the autumn (Thompson & Grime 1979), seed-eaters may reduce their occupancy area to more favourable sites. Further studies are required to better understand the seasonal and spatial dynamics in the composition of trophic groups.

Our results showed that land use similarity is unlikely a key factor determining bird community composition. The Pampean original grasslands have been transformed by agricultural development for over two centuries (Viglizzo *et al.* 2001). According to our results, sites under different land uses (e.g. different crops or pastures) are similarly composed because many species that currently occur in the study area are adapted to agriculture. Previous research conducted in the Pampas suggested that the lack of response to the agricultural dynamics revealed that many bird species are tolerant to changes in land use over time and space (Fillooy & Bellocq 2007).

The correlation between geographic distance and species composition similarity was lower when controlling for the effect of productivity similarity. The fact that all common effects between productivity similarity and geographic distance over species composition similarity are associated to the variable that is being controlled (i.e. space; Steinitz *et al.* 2006), together with the difference between simple and partial Mantel correlations, suggests that the spatial pattern of productivity similarity contributed partially to the spatial pattern of species composition similarity among assemblages. However, the decrease in species composition similarity with geographic distance could also be the result of other spatially autocorrelated factors not measured here.

The overall result of this work suggests differences in the spatial patterns of bird species richness by trophic groups, as well as a continuous species turnover along

the environmental gradient. Pattern consistency between seasons was largely dependent on the species primary food, revealing that the factors influencing bird diversity across space may change between seasons. Analyses incorporating different seasons and functional groups could contribute to better understand the determinants of biological diversity in temperate climates, which is crucial in the development of land use policies for biodiversity conservation.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Longitudinal distribution of land use categories.

**Appendix S2.** List of bird species recorded.