

Pasture area and landscape heterogeneity are key determinants of bird diversity in intensively managed farmland

Alexis Cerezo · María Cecilia Conde · Santiago L. Poggio

Received: 2 December 2010 / Accepted: 15 June 2011 / Published online: 23 June 2011
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Abstract Agriculture intensification has drastically altered farmland mosaics, while semi-natural grasslands have been considerably reduced and fragmented. Bird declines in northern temperate latitudes are attributed to habitat loss and degradation in farmed landscapes. Conversely, landscape-modification effects on grassland/farmland bird communities are less studied in the South American temperate grasslands. We investigated how bird communities were influenced by landscape characteristics in the Rolling Pampa (Argentina). We sampled bird communities in 356 landscapes of 1-km radius that varied in cover and configuration of pastureland, flooding grassland and cropland. Using generalized linear models, we explored the relationship between both bird species richness and abundance, and landscape structure. Analyses were carried out for all species, and open-habitat, grassland and aquatic species. Pasture area was far the most important factor, followed by landscape composition, in predicting species richness and abundance, irrespective of specific habitat preferences, followed by partially-flooded grassland cover and its mean shape index. Grassland fragmentation did not affect species richness or abundance. When comparing the effects of landscape variables on bird richness and abundance (using mean model coefficients), pasture and grassland area effects were on average more than four times greater than those of compositional heterogeneity, and about ten times greater than shape effects. To conserve species-rich bird communities persisting in Rolling Pampa farmland, we recommend the

A. Cerezo · M. C. Conde
Departamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía,
Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina
e-mail: acerezo@agro.uba.ar

A. Cerezo ·
e-mail: acerezo@agro.uba.ar

M. C. Conde
e-mail: mconde@agro.uba.ar

S. L. Poggio (✉)
CONICET/Cátedra de Producción Vegetal, Departamento de Producción Vegetal, Facultad de
Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina
e-mail: spoggio@agro.uba.ar

preservation of pasture and grassland habitats, irrespective of their fragmentation level, in intensively managed farmland mosaics.

Keywords Agricultural intensification · Agro-ecosystems · Biodiversity · Landscape modification · Land-use patterns · Pampas

Abbreviations

A	Area
AICc	Second-order Akaike Information Criterion
C	Configuration
Crop	Cropland
Flood	Flooding grassland
F	Fragmentation
GLM	Generalized linear models
Grass	Pastureland
H	Heterogeneity
IBA	Important Bird Areas
1-D	Compositional heterogeneity
OLS	Ordinary least-squares
P	Proportional area
S	Mean patch shape
w_i	Akaike weights

Introduction

Farmland complexity has changed rapidly in most cropping systems worldwide during the twentieth century due to agricultural intensification and land use change (Krebs et al. 1999; Benton et al. 2003). Intensification of modern agriculture, and the concomitant abandonment of traditional farming, has drastically altered farmland mosaics, while non-crop habitats such as semi-natural grasslands have been considerably reduced and fragmented (Söderström et al. 2001; Petit 2009). Simultaneously, a sharp decline in the abundance and distribution of grassland birds has been observed in agricultural landscapes of Europe (Donald et al. 2001, 2006) and North America (Peterjohn and Sauer 1999). The decline of bird populations in grasslands has been attributed to the loss and degradation of these habitats in farmed landscapes (Chamberlain et al. 2000; Vickery et al. 2001; Donald et al. 2001, 2006). A similar process of agricultural intensification has occurred in the Pampas of Argentina, formerly an extensive grassland region that has become one of the largest agricultural regions of the world (Hall et al. 1992). Furthermore, there is an increasing concern for the conservation of grassland birds in the Pampas, since 24 species of grassland specialists are considered of conservation concern (Di Giacomo and Krapovickas 2005).

Habitat modifications (i.e., changes in the proportional cover or configuration of patches) at patch and landscape levels have affected bird assemblages of temperate grasslands in the northern hemisphere. At the patch scale, several studies found that the area of grassland fragments has positive effects on the occurrence and abundance of grassland specialists (Herkert 1994; Vickery et al. 1994; Winter and Faaborg 1999; Johnson and Igl 2001). Concerning patch configuration, Helzer and Jelinski (1999) found a strong negative effect of the edge-to-area ratio on the occurrence and species richness of birds. At the landscape

scale, grassland cover was a more important correlate of community composition than mean patch size and grassland core size (Coppedge et al. 2001). Cover-type diversity, measured around prairie grassland fragments in south-central Wisconsin (U.S.A.), was negatively correlated with grassland species richness (Ribic and Sample 2001). More interestingly, patch and landscape level factors interacted in their effect on bird occurrence in mixed-grass and tallgrass prairie patches in South Dakota (U.S.A.) (Bakker et al. 2002). Effects on species richness of low-intensity land use also interacted with forest land cover at the landscape scale in a farmland region of Sweden (Wretenberg et al. 2010). Finally, Fletcher and Koford (2002), in addition to patch-scale variables, found that landscape edge density negatively affected the abundance of tallgrass prairie birds in northern Iowa (U.S.A.), and grassland bird abundance was negatively related to the total length of boundaries in managed grassland patches in the Hungarian Great Plain (Batáry et al. 2007).

Effects of habitat modifications at the landscape level on the grassland and farmland bird communities are much less studied in the temperate grasslands of South America. Codesido et al. (2008) found that bird richness was lowest in the Rolling Pampa, a region dominated by cropland, compared to the other two neighboring regions, one where a mixture of pasture and cropland prevail, the Inland Pampa, while the other, the Flooding Pampa, is characterized by extensive grasslands (Soriano 1991). Filloy and Bellocq (2007) observed that the density of most bird species studied (13 of 20) decreased as the proportion of croplands in the landscape increased, and Schrag et al. (2009) found that bird species richness increased with decreasing cover of annual crops. Although these studies have surveyed birds with respect to varying levels of cover types, other variables regarding landscape composition, compositional heterogeneity and configuration of patches have not been evaluated yet with respect to their effects on grassland and agricultural bird communities.

Here, we investigated how species richness and abundance of bird assemblages were influenced by landscape structure and composition in the Rolling Pampa of Argentina. We tested the hypothesis predicting that species richness and abundance of birds would increase as landscape becomes increasingly heterogeneous. Alternatively, we also hypothesized that the species richness and abundance of birds specialized in grassland and open habitats would be mainly determined by the extent and configuration of grassland patches. Thus, our main objective was to elucidate whether pasture and grassland habitat areas, sub-division (as a measure of fragmentation), landscape compositional or land-cover heterogeneity, or some particular combination of these landscape attributes, are chiefly affecting the bird communities occurring in the study area. We discuss our findings by pondering the importance of preserving the extant patches of semi-natural grassland for conserving birds in the highly intensified farmland mosaics of the Pampas. Finally, we also compare our results to similar studies from Europe, where grasslands have been extensively and intensively used for centuries.

Methods

Study area

The study was carried out in the central area of the Rolling Pampa, one of the sub-regions of the Pampas (Soriano 1991). The Rolling Pampa is located between 32–34°S and 59–61°W in the north of the Buenos Aires province of Argentina (Fig. 1). Climate is temperate and sub-humid, with no marked dry seasons and warm summers (Hall et al. 1992). Climate limits are set by the 17°C isotherm to the north and the 14–15°C isotherms

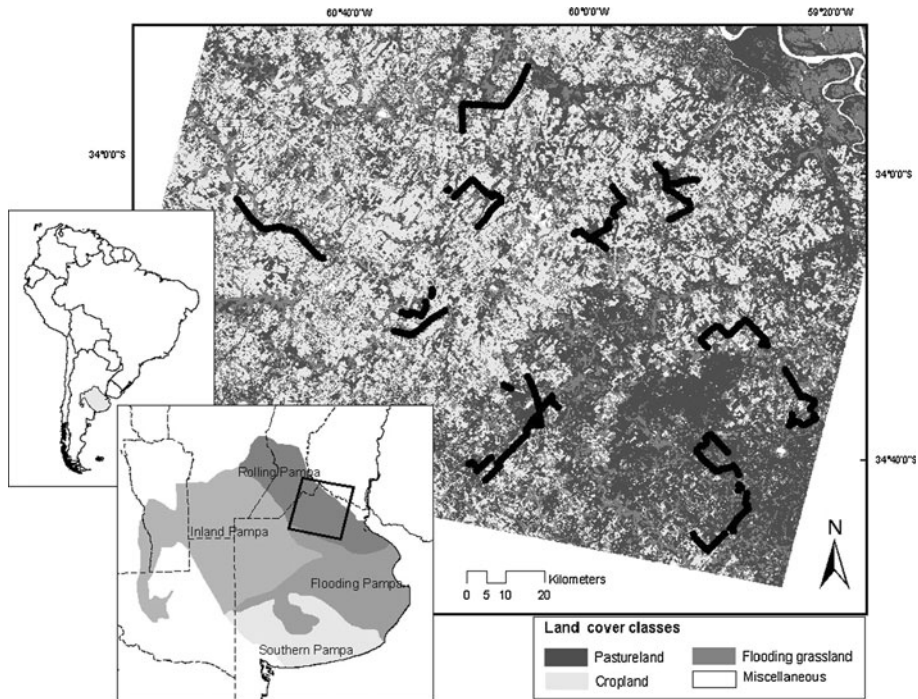


Fig. 1 Study region in the Rolling Pampa of Argentina; locations of bird sampling routes (as black lines) are shown (see “Bird surveys” in “Methods” for more details)

to the south, respectively. Average annual rainfall ranges from ca. 1,000 mm in the northeast to ca. 800 mm in the southwest (Hall et al. 1992). A gently undulated topography characterizes the landscapes of the Rolling Pampa, where flat, extensive cropland areas are intermingled with riparian zones surrounding both shallow lagoons and narrow streams.

Extensive and treeless grasslands characterized the pristine landscapes the Rolling Pampas before the expansion of agriculture since late nineteenth century, which entirely transformed the original grassland habitats into extensive croplands. Most mesic grasslands in the Rolling Pampa, associated to well-drained soils, have been entirely plowed to sown pastures and row crops (Burkart et al. 2011). Habitat loss and fragmentation have been the prevailing factors driving landscape transformation. Rolling Pampa farmland has been thus intensively fragmented by the extension of complex networks of main and secondary roads, railroads and wire-fencerows. Landscapes in this area comprise extensive, almost continuous croplands (ca. 70% of the study region, Viglizzo et al. 2011), with large fields averaging ca. 60 ha in size and small perimeter/area ratios (Poggio et al. 2010). Soybean is the prevalent warm-season crop (ca. 75% of cropland, DPEBA 2011). Maize was the dominant summer crop for decades, but has been rapidly displaced by soybean after the inception of both no-tillage and herbicide-tolerant GM cultivars in 1996 (ca. 10% of cropland, DPEBA 2011). Soybean is also sown as a relay crop immediately after the harvest of winter crops, mostly wheat, which is the dominant cool-season crop in this region (ca. 15% of cropland, DPEBA 2011). Practically all field crops are nowadays sown using no-tillage; plowing has become very infrequent and almost exclusively used to grow maize (Satorre 2001; Manuel-Navarrete et al. 2009). Soybean and maize crops differ

markedly in their agronomic management. While herbicide control in soybean fields relies exclusively on glyphosate application, residual herbicides (e.g., atrazine) are commonly used in growing maize.

Pastureland is characterized by pasture paddocks in well-drained soils sown with mixtures of grasses (e.g., *Bromus catharticus*, *Dactylis glomerata*, *Festuca arundinacea*, *Lolium multiflorum*) and legumes (e.g., *Medicago sativa*, *Trifolium repens*, *T. pratense*). Agrochemical applications in pastures are not unusual in the study region, mostly to ensure implantation during the first years after sowing. Cattle density is usually higher in pastures than in temporally flooded grasslands. Recent agriculture intensification, mostly after the inception of GM-soybean, has promoted the conversion of pastureland into cropland, the elimination of fencerow to enlarge fields, and the opportunistic cultivation of road verges. Conversely, remnant grassland habitats remain scattered in the cropland matrix, mainly associated to riparian zones, fields comprising poorly drained, and temporally-flooded soils unsuitable for cropping, and to the margins of fences, road and rail networks. Thus, intensive agriculture is the main driver of habitat loss for grassland-dependent birds (and Pampean biota) in the Rolling Pampa.

Bird surveys

Bird surveys were carried out along transects established using a stratified design. An 8 km × 8 km grid was placed over a land-cover classification for the study region. The four strata were defined based on five landscape indices (class area, number of patches, mean patch size, coefficient of variation in patch size, total edge, and mean patch shape index), calculated for five land-cover classes (maize, soybean, wheat–soybean relay crop, pastureland, and riparian zones consisting mainly of temporally-flooded grassland, henceforth, “flooding grassland”), using the FRAGSTATS software (McGarigal and Marks 1995). The four strata were identified using cluster analysis, with the Pearson correlation (r) as a distance measure between cells ($1 - r$), and the nearest neighbor group linkage method.

Within each of the four strata, we located three transects, each comprising 30 sampling points (90 points per stratum or landscape type). Points along each transect were 1 km apart. First points of each route were located by randomly selecting starting locations within each landscape type, and then locating the nearest secondary road to this point. Bird sampling was carried out between November 2005 and January 2006 using the unlimited-radius point count methodology (Ralph et al. 1993). During 5 min, all bird species and individuals observed or heard were registered at each sampling point.

To achieve regional inference capability, we chose to sample a greater number of different landscapes, instead of carrying out repeated (i.e., temporal re-sampling of a single site) or sub-sampling (sampling of several sites per landscape) of studied landscapes. Consequently, our study considers the influence of landscape context on local-scale bird diversity at each point, and in this sense is closer to a focal-patch (Brennan et al. 2002) or patch-landscape approach (McGarigal and Cushman 2002). Consequently, our results do not address the “effects of landscape mosaics on the conservation value of mosaics” (Bennett et al. 2006), but rather the effect the landscape mosaic on local bird communities.

Landscape characteristics of sampling points

Landscape structure and composition around each sampling point was characterized within circles of 1-km radius surrounding them. Hence, the experimental units were circular

landscape areas of 1 km radius. We calculated the proportion of each land-cover class, fragmentation via the landscape division index (Jaeger 2000), mean shape index, and compositional heterogeneity via the Simpson diversity index (using the five original classes). Thus, we only consider heterogeneity associated with the relative proportional cover of each land-cover class. We merged the three crop classes in one (“cropland”), so cover and configuration indices were calculated for pastureland, flooding grassland and cropland. Four sampling points were excluded from the analyses, since cloud cover over them impeded adequate land-cover classification. Hence, all statistical analyses were carried out on 356 sampling points (circular landscape sectors of 1-km radius), considering each one as a replication (i.e., experimental unit).

Statistical analysis

We evaluated seven statistical models as competing predictions of our hypotheses to elucidate which landscape attributes, whether individually or in some combination, best explained the variation of species richness and abundances of bird assemblages. Response variables in the models corresponded to all species, and three sets of species grouped according to habitat preference (open-habitat, grassland, and aquatic). Information for grouping species was obtained from Stotz et al. (1996). Open-habitat species were those for which any type of grassland, shrub land or agricultural land was identified as their primary habitat (i.e., the habitat the species uses most commonly over most of its range, according to Stotz et al. 1996). Grassland and aquatic species were those for which any type of grassland or aquatic habitat was identified as their primary habitat, respectively. Thus, “open-habitat” species include grassland species. Explanatory variables included in the models were (1) the proportional cover of pastureland and flooding grasslands (proportion of agricultural cover was not included in models because it was highly correlated with proportional pastureland cover, $r = -0.91$); (2) landscape division index for the three classes; (3) mean shape index for the three classes; and (4) compositional (land-cover) heterogeneity. Models are described in Table 1.

We used generalized linear models (GLM) to evaluate the relationships of both species richness and abundance of birds as a function of the candidate predictive variables in the above described models (Table 1). Poisson multiple regression was used to relate species richness to landscape structure and composition, a special type of GLM for discrete,

Table 1 Description of evaluated models

Model	Effects	Predictive variables
1	A + C + H	F _{crop} , S _{crop} , P _{grass} , F _{grass} , S _{grass} , P _{flood} , F _{flood} , S _{flood} , 1-D
2	A + C	F _{crop} , S _{crop} , P _{grass} , F _{grass} , S _{grass} , P _{flood} , F _{flood} , S _{flood}
3	A + H	P _{grass} , P _{flood} , 1-D
4	C + H	F _{crop} , S _{crop} , F _{grass} , S _{grass} , F _{flood} , S _{flood} , 1-D
5	A	P _{grass} , P _{flood}
6	H	1-D
7	C	F _{crop} , F _{grass} , F _{flood}

See the text for further information. Effects are area (A), configuration (C), and compositional heterogeneity (H). Predictive variables included in the different models are combinations of the proportional area (P), fragmentation (F) and mean patch shape (S) for cropland (sub index “crop”), pastureland (sub index “past”) and flooding grassland (sub index “flood”) habitats, and landscape heterogeneity (1-D)

highly-skewed distribution of the dependent variable, such as species richness (Vincent and Haworth 1983). Models were tested and adjusted for over-dispersion, according to the highest estimated single variance inflation factor ($\hat{c}$) of the most parameterized models, estimated as the ratio of the deviance statistic and its degrees of freedom ($\hat{c} = \text{deviance}/\text{df.}$). Ordinary least-squares (OLS) multiple regression was used to analyze the association between bird abundance and landscape heterogeneity, considering the sum of individuals of all species as the independent variable. We applied a $\log_{10}(X + 0.1)$ transformation to abundance data to conform to model assumptions, specifically, a log-normal distribution of the transformed dependent variable (Vincent and Haworth 1983).

In order to detect and minimize problems associated with multicollinearity, the Spearman correlation coefficient was used to evaluate the correlations between landscape metrics. When correlations were ≥ 0.6 , we performed partial linear regression analysis (Legendre and Legendre 1998). When configuration or heterogeneity variables were highly correlated with area, the latter was used as the predictive variable in the partial regression whereas the other two were the response variables. We then used the residuals of these partial regressions as independent indices of either landscape configuration or heterogeneity. Using this procedure, we thus obtained measures of landscape patch configuration and heterogeneity that were independent of cover.

The second-order Akaike Information Criterion (AICc) and Akaike weights (w_i) were used to choose the best-fitting models (Burnham and Anderson 1998). Using AICc is advocated when $n/K < 40$, where n is sample size and K the number of estimated parameters. The AIC belongs to a family of model selection criteria that not only consider the goodness-of-fit of the model but also its complexity, which allows the simultaneous comparison of several models (Johnson and Omland 2004). AIC values reflect the amount of “information” lost when a model is used to approximate conceptual reality. Thus, the model with the lowest AIC value is selected as the best model (Burnham and Anderson 1998). When differences between AIC values are small (less than two AIC units), Akaike weights (w_i) can be used as indicators of the strength of evidence supporting each model. The w_i is interpreted as the approximate probability that model i is the best one among the set of models being evaluated (Burnham and Anderson 1998). We only show results for those models whose sum of w_i values was approximately equal to or greater than 0.95, also known as the “confidence set” of models (Burnham and Anderson 1998). To compare the relative effects of area, configuration and heterogeneity, we used multi-model inference, or model averaging (Burnham and Anderson 1998). For each species groups, we obtained mean model coefficients for each effect, weighted by w_i .

In spatially structured data, the assumption of independence between observations is often violated due to spatial dependence between points closer in space (Dormann et al. 2007). The presence of spatial autocorrelation in a dataset can have serious negative consequences on hypothesis testing and prediction because it violates the assumption of independently and identically distributed errors and hence inflates type I errors (Dormann et al. 2007), causing a form of pseudoreplication by overestimating effective degrees of freedom (Carl and Kühn 2007). Spatial autocorrelation in residual variance, i.e., variance not explained by the predictor variables, is problematic, particularly in hypothesis testing, since estimated error or variance terms are used in calculating test statistics. We used general estimating equations (GEE) to account for spatial autocorrelation in data analyses (Carl and Kühn 2007; Dormann et al. 2007). When responses are measured repeatedly through time or space, the GEE method takes correlations within “clusters” of sampling units into account by means of a parameterized correlation matrix, while correlations between clusters are assumed to be zero (Dormann et al. 2007). In our study, clusters were

Fig. 2 Mean coefficient values (with standard errors) for each landscape variable in models for species richness and abundance, and all species groups. Mean values shown were calculated by averaging model coefficients for the models in the confidence set, weighted by corresponding Akaike weights (w_i)

routes of sample points. All GEE analyses were carried out using the GENMOD procedure in SAS statistical package (SAS Institute 1999).

Results

A total of 103 species were detected, which belong to 39 families and 14 orders (“Appendix”). The families having the greatest number of species were *Tyrannidae* (new world flycatchers) and *Anatidae* (ducks, geese and swans), both with nine species. Other well-represented families were *Furnariidae* (ovenbirds), with seven species, *Columbidae* (doves and pigeons), *Emberizidae* (sparrows and seedeaters), and *Icteridae* (blackbirds), each one comprising six species. Among all species surveyed, 54 are partially dependent on grassland habitats, that is, grassland is its second or third most important habitat type according to Stotz et al. (1996), whereas 24 are considered grassland-dependent, that is, their main habitat type is grassland. Of the remaining 49 species, 22 species are distinctive of aquatic habitats and 27 are woodland-dependent (their main habitat type is an aquatic or forested habitat, respectively, according to Stotz et al. 1996). We did not find any species under any category of risk (“critically endangered”, “endangered”, “vulnerable”, or “near-threatened”) according to Birdlife International (2000) standards.

Models included in the confidence set ranged from 2 to 4, but the average number of models in the set for the different species groups and dependent variables (species richness or abundance) was 2.75 ± 0.89 (all values shown henceforth are mean and standard deviations). Considering the seven models we evaluated, on average the area model had the highest w_i (model 5, 0.52 ± 0.15 , see Table 1), followed by the area and compositional heterogeneity model (model 3, 0.34 ± 0.13). These two models were, in general, much more supported by data. Mean model support for the area and configuration model (model 2) and the full model respectively were 0.08 ± 0.10 and 0.05 ± 0.07 , whereas models 4 and 7 had null support. These results were consistent for both bird richness and abundance, and for the three species groups. Nonetheless, more complex models, the full and the area and configuration models, had substantial support for all species and for aquatic species (Tables 2, 3).

Overall, area effects were much greater than either configuration or compositional heterogeneity effects (Fig. 2). The mean coefficient, obtained by averaging all land-use types and species groups, was higher for habitat area (0.23 ± 0.33) than for either subdivision (0.00 ± 0.01), patch shape (0.01 ± 0.02), or compositional heterogeneity (0.04 ± 0.05). When comparing effects of landscape variables on bird richness and abundance (using mean model coefficients), pasture and flooding grassland area effects were on average 6.7 times greater than compositional heterogeneity effects, and 29.9 times greater than shape effects. Compositional heterogeneity effects were 4.5 times greater than patch shape effects. Species richness and abundance of all groups were positively associated to compositional heterogeneity, but there was no association with habitat subdivision and pastureland and cropland mean patch shape (i.e., mean coefficient values are close to 0). Nonetheless, total species richness was positively associated to flooding grassland mean shape index (Fig. 2, top left).

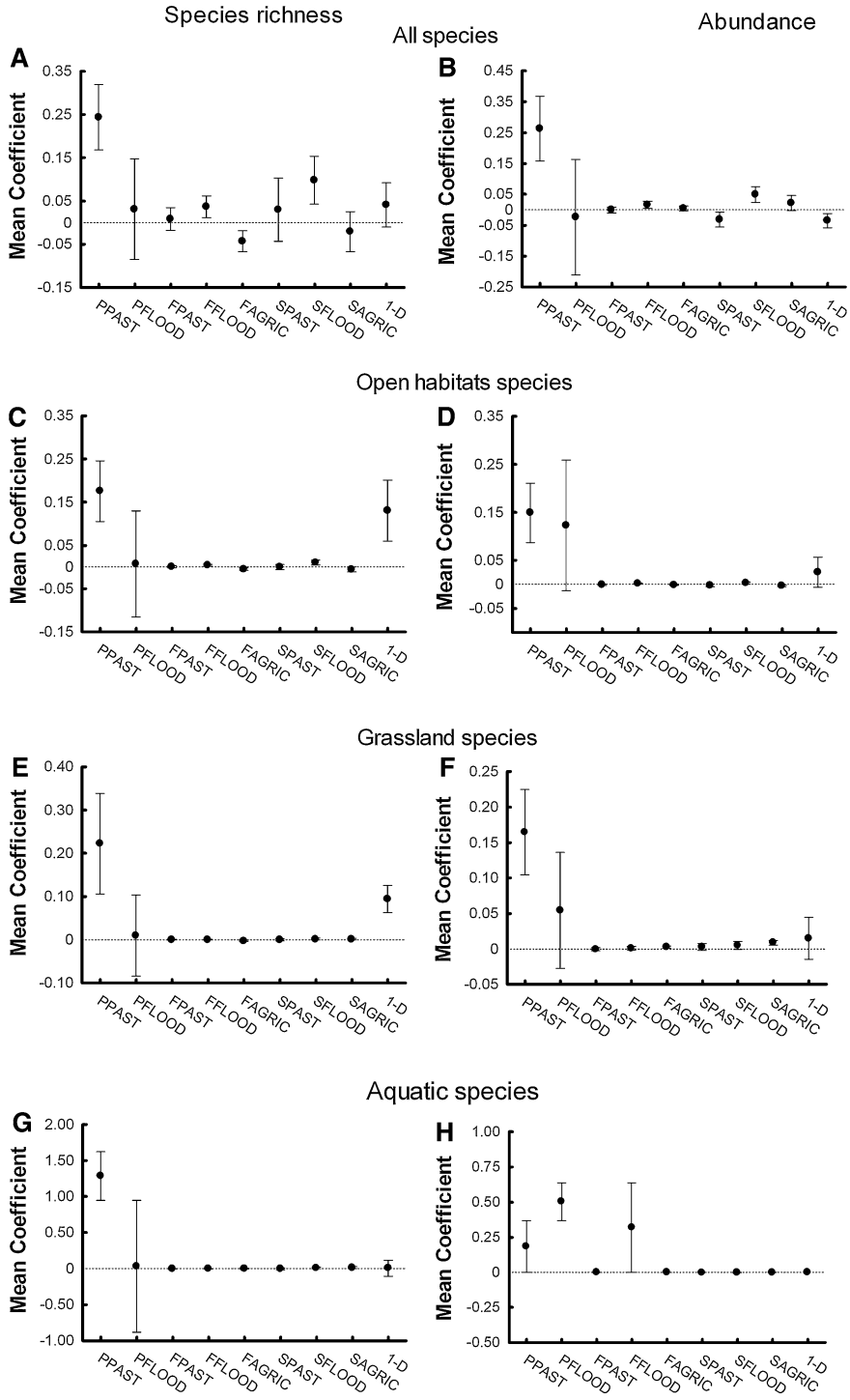


Table 2 Model AICc and Akaike weight (w_i) values for all fitted models and species groups

Model	AICc	w_i
All species		
$P_{\text{past}} + P_{\text{flood}}$	313.70	0.34
$P_{\text{past}} + P_{\text{flood}} + 1\text{-D}$	314.13	0.29
$-F_{\text{agric}} - S_{\text{agric}} + P_{\text{past}} + F_{\text{past}} + S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	316.83	0.19
$-F_{\text{agric}} - S_{\text{agric}} + P_{\text{past}} + F_{\text{past}} + S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}}$	316.46	0.18
$-F_{\text{agric}} - S_{\text{agric}} - F_{\text{past}} + S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}}$	334.24	0.00
$-F_{\text{agric}} - S_{\text{agric}} - F_{\text{past}} + S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	335.69	0.00
1-D	338.56	0.00
Open-habitat species		
$P_{\text{past}} + P_{\text{flood}} + 1\text{-D}$	250.49	0.61
$P_{\text{past}} - P_{\text{flood}}$	251.53	0.33
$-F_{\text{agric}} - S_{\text{agric}} + P_{\text{past}} + F_{\text{past}} + S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	258.54	0.03
1-D	257.64	0.01
$-F_{\text{agric}} - S_{\text{agric}} + P_{\text{past}} + F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}}$	259.44	0.01
$F_{\text{agric}} S_{\text{agric}} F_{\text{past}} S_{\text{past}} F_{\text{flood}} S_{\text{flood}} 1\text{-D}$	262.74	0.00
$-F_{\text{agric}} - S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}}$	262.69	0.00
Grassland species		
$P_{\text{past}} - P_{\text{flood}}$	211.18	0.50
$P_{\text{past}} + P_{\text{flood}} + 1\text{-D}$	211.48	0.46
1-D	217.34	0.02
$-F_{\text{agric}} + S_{\text{agric}} + P_{\text{past}} + F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}}$	220.85	0.01
$-F_{\text{agric}} + S_{\text{agric}} + P_{\text{past}} + F_{\text{past}} + S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	221.42	0.01
$-F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}}$	223.87	0.00
$-F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	224.98	0.00
Aquatic species		
$P_{\text{past}} + P_{\text{flood}}$	365.83	0.68
$P_{\text{past}} + P_{\text{flood}} + 1\text{-D}$	367.59	0.30
$-F_{\text{agric}} + S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} - F_{\text{flood}} + S_{\text{flood}}$	375.30	0.01
$-F_{\text{agric}} + S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} - F_{\text{flood}} + S_{\text{flood}} - 1\text{-D}$	377.57	0.01
$F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}}$	385.05	0.00
$F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}} - 1\text{-D}$	387.37	0.00
1-D	387.73	0.00

Signs indicate the relationship between species richness and landscape variables

When only considering the estimated area effects, coefficients of pastureland were much larger than those of flooding grassland. The mean area coefficients for species richness, averaged over all species groups, were 0.48 ± 0.54 and 0.02 ± 0.04 for pastureland and flooding grassland, respectively. The mean coefficient for abundance was 0.24 ± 0.10 for pastureland, while that for flooding grassland was 0.20 ± 0.30 , but the former average was high compared to the average for pastureland because of its large effect on aquatic species abundance (Fig. 2, lower right). With this exception, flooding grassland area effects were nearly null and highly variable for all other species groups, whether we considered richness or abundance.

When area and compositional heterogeneity effects were compared, the effect of pastureland area was much more important, and these effects were consistent between species

Table 3 Model AICc and Akaike weight (w_i) values for all fitted models and species groups

Model	AIC	w_i
All species		
$P_{\text{past}} - P_{\text{flood}}$	158.31	0.61
$P_{\text{past}} - P_{\text{flood}} - 1\text{-D}$	160.09	0.25
$F_{\text{agric}} + S_{\text{agric}} + P_{\text{past}} + F_{\text{past}} + S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} - S_{\text{flood}}$	161.87	0.10
$F_{\text{agric}} + S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}} - 1\text{-D}$	163.87	0.04
$F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}}$	176.57	0.00
$F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}} - 1\text{-D}$	178.51	0.00
-1-D	181.48	0.00
Open-habitat species		
$P_{\text{past}} + P_{\text{flood}}$	-127.9	0.66
$P_{\text{past}} + P_{\text{flood}} + 1\text{-D}$	-126.5	0.32
$-F_{\text{agric}} - S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}}$	-120	0.01
$-F_{\text{agric}} - S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	-118.6	0.01
$-F_{\text{agric}} - S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}}$	-107.9	0.00
$-F_{\text{agric}} - S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	-105.9	0.00
1-D	-98.8	0.00
Grassland species		
$P_{\text{past}} + P_{\text{flood}}$	-36.09	0.68
$P_{\text{past}} + P_{\text{flood}} + 1\text{-D}$	-34.35	0.28
$F_{\text{agric}} + S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} + S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}}$	-29.78	0.03
$F_{\text{agric}} + S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} + S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	-27.82	0.01
$F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} + S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}}$	-13.79	0.00
1-D	-12.3	0.00
$F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} + S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}} + 1\text{-D}$	-12.16	0.00
Aquatic species		
$P_{\text{past}} + P_{\text{flood}}$	710.76	0.72
$P_{\text{past}} + P_{\text{flood}} + 1\text{-D}$	712.76	0.27
$F_{\text{agric}} - S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}}$	720.81	0.00
$F_{\text{agric}} - S_{\text{agric}} + P_{\text{past}} - F_{\text{past}} - S_{\text{past}} + P_{\text{flood}} + F_{\text{flood}} + S_{\text{flood}} - 1\text{-D}$	722.78	0.00
-1-D	723.06	0.00
$F_{\text{agric}} - S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}}$	727.71	0.00
$F_{\text{agric}} + S_{\text{agric}} - F_{\text{past}} - S_{\text{past}} + F_{\text{flood}} + S_{\text{flood}} - 1\text{-D}$	729.06	0.00

Signs indicate the relationship between abundance and landscape variables

richness and abundance. However, species richness on average was more affected by compositional heterogeneity than the area of flooding grassland, and abundance was more affected by the latter landscape variable than the former (Fig. 2).

Discussion

Our results suggest that landscape structure strongly affects the bird communities occurring in the Rolling Pampa. Overall, species richness and abundance was higher in landscapes having a greater proportion of land covered by pasturelands and higher compositional

heterogeneity (Tables 2, 3; Fig. 2). We also demonstrated that habitat area is much more important than patch configuration, here characterized as habitat sub-division and mean patch perimeter–area ratio, in determining species richness and abundance. Much greater support (i.e., higher Akaike weights) for area models (see model 5, Table 1), compared to the other models (Tables 2, 3), and mean model coefficients (Fig. 2) provide strong evidence for this conclusion. Moreover, our findings are in agreement with previous studies in other temperate regions of the world: bird species occurrence and community structure is mainly affected by the amount of habitat area (Coppedge et al. 2001; Bennett et al. 2006).

Following pastureland area, compositional heterogeneity was the second most important variable associated to higher numbers of species, a result also concurring with other studies (Pino et al. 2000; Atauri and de Lucio 2001; DeVicor and Jiguet 2007; Báldi 2008). We also found that compositional heterogeneity was relatively important for open-habitat and grassland species, but to a lesser extent than pastureland area (Fig. 2). According to Stotz et al. (1996), grassland-dependent species are not entirely restricted to grassland habitats; thus, it seems reasonable to conclude that some species, because of their relatively ample habitat breadth, are able to use other habitats for breeding, feeding or as transit habitats, to supplement resources at the landscape level (*sensu* Dunning et al. 1992). Only one species detected in the study (*Anthus chacoensis*, Chaco Pipit) is reported as being a specialist of (i.e., only found in) southern temperate grasslands (Stotz et al. 1996). Fuller et al. (2004) found that 16 out of 28 farmland bird species in Great Britain occurred in landscapes not dominated by farmland: less than half of their breeding range was associated with high cover of lowland farmland. They also appeal to (and provide evidence of) landscape complementation and supplementation mechanisms (Dunning et al. 1992) to explain their results.

The ability of some bird species to use other habitats might also make them less vulnerable or invulnerable to fragmentation effects (Fig. 2). Habitat sub-division may disrupt population dynamics and increase the risk of local extinctions (Hanski 1998), because of decreased levels of structural connectivity (Moilanen and Hanski 2001). The ability of a species to use different habitats may affect its vulnerability to landscape fragmentation (Ricketts 2001), because species having wider habitat breadth may find less resistance to move through the landscape matrix and therefore will be less susceptible to fragmentation effects. Consequently, species that depend, in greater or lesser degrees, on grassland habitat observed in our study are probably able to disperse throughout the agricultural matrix to reach optimal habitat. Habitat area at the landscape level thus seems to be the main factor affecting the persistence of some bird populations in the farmland mosaics of the Rolling Pampa. Species with a wider habitat breadth (i.e., “generalist” species) are those that were more tolerant to the process of agricultural intensification in Britain and north-west Europe (Robinson and Sutherland 2002).

In addition to pastureland cover and compositional heterogeneity, the increase of the perimeter–area ratio for flooding grassland patches was relatively important for explaining the species richness increase of the whole taxonomic group (Fig. 2a). This result differs from other empirical studies, because an edge increase (relative to the area of the patch) has been found to negatively affect the abundance of grassland specialists in North America (Helzer and Jelinski 1999; Fletcher and Koford 2002) and Eastern Europe (Batáry et al. 2007). Flooding grassland habitats primarily occur along streams and rivers, which results in a large perimeter–area ratio (i.e., patches are elongated and narrow in natural circumstances). Many species detected in our study have been reported to use the vegetation bordering riparian zones for breeding and foraging (Canevari et al. 1991), hence it

seems reasonable to expect species richness to increase at higher perimeter–area ratios of flooding grassland patches.

Differences in the effects of landscape modification on species richness and abundance do not have a straightforward explanation. In general, species abundance shows practically no response to either landscape configuration or compositional heterogeneity (Fig. 2), as opposed to species richness, but has a strong response to pastureland cover. We attribute this result to density compensation effects (Gonzalez and Loreau 2009). Along the landscape modification gradient, individuals of species having decreasing population sizes are replaced by individuals from other species favored by changes in the gradient and therefore having increases in population. Hence, there would have been no noticeable changes in the total abundance for the group in the explored gradient. Such compensation may not necessarily involve local extinctions, but does imply a reorganization of the patterns of community dominance in response to environmental change (Gonzalez and Loreau 2009). In practical terms, species richness seems to be a more sensitive indicator than species abundance to the effects of habitat configuration and compositional heterogeneity at the landscape scale on bird community structure.

Conclusions

Overall, our results suggest that maintaining the cover of pastureland is critical for preserving the bird community structure in the Rolling Pampa of Argentina. This is especially relevant given the extensive conversion of pastureland by cropland during the past 25 years (Viglizzo et al. 2011). Furthermore, it is noteworthy that pastureland cover is much more important than fragmentation. This result leads to the simple conservation recommendation of conserving extant grassland patches, whatsoever their spatial distribution. In addition to pastureland area, landscape compositional heterogeneity should be promoted by increasing habitat diversity, which will positively impact bird diversity.

Our research results also calls for a major change in bird conservation strategies in the Rolling Pampas. The near-complete absence of southern temperate grassland specialist species, and the complete absence of species considered at risk by conventional standards (Birdlife International 2000) are indicators of the devastating effects that the expansion and intensification of agriculture have produced on these species in this Pampean subregion (Di Giacomo and Krapovickas 2005; Di Giacomo et al. 2007; Codesido et al. 2008). In less modified subregions of the Pampas, where native grasslands are still present in relatively high cover proportions, species of conservation concern are found, but they make little or no use of pasturelands and croplands (Codesido et al. 2008; Di Giacomo et al. 2007). It is thus reasonable to conclude that these grassland obligates have become locally extinct because of extensive habitat elimination and conversion.

We thus recommend the adoption of conservation initiatives adapted to agricultural landscapes for the Rolling Pampas. This perspective assumes that part of the biota, usually restricted to the original habitat, has been largely extirpated, and thus focuses on the part that still survives in agroecosystems, a biota that nevertheless possesses important conservation value (Altieri 1999; Fahrig et al. 2011). Ongoing agricultural intensification in the Pampas, which is increasingly promoting the opportunistic cultivation of marginal habitats of lower crop yield potential, will imply further habitat reduction at the local and landscape scales in areas outside proposed Important Bird Areas (IBA). Hence we also consider that determining the importance of non-agricultural habitats for biodiversity conservation in Pampean agro-ecosystems deserves greater research efforts. Broadening

the spectrum of conservation strategies from endangered bird species to a community approach at the landscape scale should reduce further loss of biodiversity in the Pampas region.

Acknowledgments We would like to thank The Rufford Maurice Laing Foundation for financial support (Rufford Small Grants for Nature Conservation), and the Regional Analysis and Teledetection Laboratory (LART, Laboratorio de Análisis Regional y Teledetección) of the School of Agronomy, University of Buenos Aires, for providing the land cover classification. We also extend our most sincere gratitude to Gabriel Rocha for his assistance with field surveys, and to Teresa Boca, at the Institute of Climate and Water, National Institute of Agricultural Technology (Instituto de Clima y Agua, INTA-Castelar) of Argentina, for allowing us to perform statistical analyses with the SAS package at their facilities.

Appendix

See Table 4.

Table 4 List of species detected in the study, and proportion of study sites where the species was detected in three grassland cover (%) categories

Scientific name	English name	Main habitat	Grassland cover		
			<35%	35–65%	>65%
<i>Rhynchotus rufescens</i>	Red-winged Tinamou	Grassland	0.26	<u>0.29</u>	0.14
<i>Nothura maculosa</i>	Spotted Nothura	Grassland	0.53	<u>0.60</u>	0.59
<i>Phalacrocorax brasilianus</i>	Neotropic Cormorant	Aquatic	0.01	0.01	<u>0.02</u>
<i>Syrigma sibilatrix</i>	Whistling Heron	Grassland	0.14	0.13	<u>0.17</u>
<i>Ardea cocoi</i>	Cocoi Heron	Aquatic	<0.01	–	<u>0.02</u>
<i>Ardea alba</i>	Great Egret	Aquatic	0.01	–	<u>0.02</u>
<i>Egretta thula</i>	Snowy Egret	Aquatic	0.01	0.01	<u>0.02</u>
<i>Bubulcus ibis</i>	Cattle Egret	Pasture/Agric.	0.25	0.20	<u>0.35</u>
<i>Ciconia maguari</i>	Maguari Stork	Grassland	0.03	0.02	<u>0.06</u>
<i>Plegadis chihi</i>	White-faced Ibis	Aquatic	0.48	<u>0.54</u>	0.48
<i>Ajaia ajaja</i>	Roseate Spoonbill	Aquatic	<0.01	–	<u>0.02</u>
<i>Chauna torquata</i>	Southern Screamer	Aquatic	0.07	0.04	<u>0.19</u>
<i>Dendrocygna viduata</i>	White-faced Whistling-Duck	Aquatic	0.06	<u>0.08</u>	0.05
<i>Cygnus melanocorypha</i>	Black-necked Swan	Aquatic	<u>≤0.01</u>	–	–
<i>Amazonetta brasiliensis</i>	Brazilian Teal	Aquatic	0.03	0.04	<u>0.05</u>
<i>Anas flavirostris</i>	Mallard	Aquatic	0.01	0.01	<u>0.02</u>
<i>Anas georgica</i>	Yellow-billed Pintail	Aquatic	0.01	0.01	<u>0.02</u>
<i>Anas bahamensis</i>	Speckled Teal	Aquatic	0.01	<u>0.02</u>	–
<i>Anas versicolor</i>	Silver Teal	Aquatic	<0.01	–	<u>0.02</u>
<i>Anas platalea</i>	Red Shoveler	Aquatic	<0.01	<u>0.01</u>	–
<i>Netta peposaca</i>	Rosy-billed Pochard	Aquatic	0.01	<u>0.02</u>	0.02
<i>Elanus leucurus</i>	White-tailed Kite	Pasture/Agric.	0.03	<u>0.04</u>	0.03
<i>Rostrhamus sociabilis</i>	Snail Kite	Aquatic	0.01	0.02	<u>0.03</u>
<i>Circus cinereus</i>	Cinereous Harrier	Grassland	<u>≤0.01</u>	–	–
<i>Buteo albicaudatus</i>	White-tailed Hawk	Grassland	<u>0.01</u>	–	–
<i>Buteo magnirostris</i>	Roadside Hawk	Forest	<u>0.08</u>	0.07	0.05
<i>Caracara plancus</i>	Southern Caracara	Scrub	0.18	0.17	<u>0.30</u>
<i>Milvago chimango</i>	Chimango Caracara	Grassland	<u>0.81</u>	0.78	0.78

Table 4 continued

Scientific name	English name	Main habitat	Grassland cover		
			<35%	35–65%	>65%
<i>Falco sparverius</i>	American Kestrel	Grassland	0.04	0.03	<u>0.05</u>
<i>Falco femoralis</i>	Aplomado Falcon	Grassland	0.01	–	<u>0.02</u>
<i>Aramus guarauna</i>	Limpkin	Aquatic	0.01	0.01	<u>0.05</u>
<i>Aramides ypecaha</i>	Giant Wood-Rail	Forest	<0.01	–	<u>0.02</u>
<i>Himantopus melanurus</i>	White-backed Stilt	Aquatic	<0.01	–	<u>0.02</u>
<i>Vanellus chilensis</i>	Southern Lapwing	Grassland	0.74	0.85	<u>0.89</u>
<i>Tringa flavipes</i>	Lesser Yellowlegs	Aquatic	0.01	0.01	<u>0.02</u>
<i>Larus maculipennis</i>	Brown-hooded Gull	Aquatic	0.04	<u>0.09</u>	0.05
<i>Columba livia</i>	Rock Pigeon	Scrub	0.04	<u>0.04</u>	0.03
<i>Patagioenias picazuro</i>	Picazuro Pigeon	Forest	<u>0.81</u>	0.80	0.75
<i>Patagioenias maculosa</i>	Spot-winged Pigeon	Forest	0.06	<u>0.07</u>	0.06
<i>Zenaida auriculata</i>	Eared Dove	Scrub	0.67	<u>0.74</u>	0.56
<i>Columbina picui</i>	Picui Ground Dove	Scrub	0.17	<u>0.25</u>	0.17
<i>Leptotila rufaxilla</i>	Gray-fronted Dove	Forest	0.02	<u>0.04</u>	–
<i>Myiopsitta monachus</i>	Monk Parakeet	Forest	0.51	0.60	<u>0.67</u>
<i>Guira guira</i>	Guira Cuckoo	Scrub	<u>0.53</u>	0.51	0.51
<i>Athene cunicularia</i>	Burrowing Owl	Grassland	0.10	<u>0.11</u>	0.10
<i>Chlorostilbon aureoventris</i>	Glittering-bellied Emerald	Scrub	0.03	<u>0.05</u>	0.03
<i>Hylocharis chrysura</i>	Gilded Sapphire	Forest	<0.01	<u>0.01</u>	–
<i>Leucochloris albicollis</i>	White-throated Hummingbird	Forest	<0.01	<u>0.01</u>	–
<i>Colaptes melanochloros</i>	Green-barred Woodpecker	Forest	0.07	0.09	<u>0.11</u>
<i>Colaptes campestris</i>	Colaptes campestris	Grassland	0.42	0.43	<u>0.48</u>
<i>Geositta cunicularia</i>	Common Miner	Grassland	<u>≤0.01</u>	–	–
<i>Furnarius rufus</i>	Rufous Hornero	Scrub	0.79	<u>0.88</u>	0.81
<i>Leptasthenura platensis</i>	Tufted Tit-Spinetail	Forest	<u>≤0.01</u>	–	–
<i>Schoeniophylax phryganophila</i>	Chotoy Spinetail	Riparian Veg.	<u>0.02</u>	0.02	0.02
<i>Synallaxis spixi</i>	Chicli Spinetail	Scrub	<0.01	<u>0.01</u>	–
<i>Phacellodomus striaticollis</i>	Freckle-breasted Thornbird	Riparian Veg.	0.04	0.03	<u>0.08</u>
<i>Anumbius amumbi</i>	Firewood-gatherer	Grassland	0.10	0.12	<u>0.22</u>
<i>Lepidocolaptes angustirostris</i>	Narrow-billed Woodcreeper	Forest	0.03	<u>0.05</u>	0.03
<i>Thamnophilus ruficapillus</i>	Rufous-capped Antshrike	Riparian Veg.	<u>0.01</u>	–	–
<i>Elaenia parvirostris</i>	Small-billed Elaenia	Forest	0.01	–	<u>0.02</u>
<i>Serpophaga subcristata</i>	White-crested Tyrannulet	Forest	<u>0.01</u>	–	–
<i>Sublegatus modestus</i>	Southern Scrub-flycatcher	Forest	<0.01	<u>0.01</u>	–
<i>Myiophobus fasciatus</i>	Bran-colored Flycatcher	Scrub	<0.01	<u>0.01</u>	–
<i>Pyrocephalus rubinus</i>	Vermilion Flycatcher	Pasture/Agric.	0.01	<u>0.01</u>	<u>0.02</u>
<i>Hymenops perspicillata</i>	Spectacled Tyrant	Aquatic	0.02	0.01	<u>0.03</u>
<i>Machetornis rixosus</i>	Cattle Tyrant	Pasture/Agric.	0.04	<u>0.08</u>	0.06
<i>Myiarchus swainsoni</i>	Swainson's Flycatcher	Forest	<0.01	<u>0.01</u>	–
<i>Pitangus sulphuratus</i>	Great Kiskadee	Forest	0.51	0.58	<u>0.63</u>

Table 4 continued

Scientific name	English name	Main habitat	Grassland cover		
			<35%	35–65%	>65%
<i>Myiodynastes maculatus</i>	Streaked Flycatcher	Forest	≤0.01	–	–
<i>Tyrannus melancholicus</i>	Tropical Kingbird	Forest	0.12	<u>0.14</u>	0.08
<i>Tyrannus savana</i>	Fork-tailed Flycatcher	Grassland	0.38	<u>0.45</u>	0.41
<i>Progne tapera</i>	Brown-chested Martin	Grassland	0.08	0.09	<u>0.19</u>
<i>Progne chalybea</i>	Gray-breasted Martin	Scrub	0.09	0.13	<u>0.17</u>
<i>Tachycineta leucorrhoa</i>	White-rumped Swallow	Grassland	0.18	<u>0.25</u>	0.14
<i>Notiochelidon cyanoleuca</i>	Blue-and-white Swallow	Scrub	0.06	0.06	<u>0.14</u>
<i>Anthus correndera</i>	Correndera Pipit	Grassland	≤0.01	–	–
<i>Anthus furcatus</i>	Short-billed Pipit	Grassland	<u>0.01</u>	–	–
<i>Anthus lutescens</i>	Yellowish Pipit	Pasture/Agric.	0.01	0.01	<u>0.02</u>
<i>Anthus chacoensis</i>	Chaco Pipit	Grassland	<u>0.01</u>	<u>0.01</u>	–
<i>Troglodytes aedon</i>	House Wren	Scrub	0.49	<u>0.52</u>	0.46
<i>Cistothorus platensis</i>	Sedge Wren	Grassland	<u>0.01</u>	<u>0.01</u>	–
<i>Turdus rufiventris</i>	Rufous-bellied Thrush	Forest	0.16	<u>0.21</u>	0.19
<i>Turdus amaurochalinus</i>	Creamy-bellied Thrush	Forest	0.01	0.02	<u>0.03</u>
<i>Mimus saturninus</i>	Chalk-browed Mockingbird	Scrub	0.31	<u>0.37</u>	0.25
<i>Poliophtila dumicola</i>	Masked Gnatcatcher	Forest	≤0.01	–	–
<i>Vireo olivaceus</i>	Red-eyed Vireo	Forest	≤0.01	–	–
<i>Basileuterus culicivorus</i>	Golden-crowned Warbler	Forest	<0.01	<u>0.01</u>	–
<i>Thraupis bonariensis</i>	Blue-and-yellow Tanager	Forest	0.01	0.01	<u>0.02</u>
<i>Sporophila caerulea</i>	Double-collared Seedeater	Scrub	<u>0.51</u>	0.41	0.32
<i>Sicalis flaveola</i>	Saffron Finch	Scrub	0.21	<u>0.24</u>	0.17
<i>Sicalis luteola</i>	Grassland Yellow-Finch	Grassland	0.74	0.71	<u>0.76</u>
<i>Embernagra platensis</i>	Great Pampa-Finch	Grassland	0.03	<u>0.04</u>	0.03
<i>Ammodramus humeralis</i>	Grassland Sparrow	Grassland	<u>0.50</u>	0.49	0.35
<i>Zonotrichia capensis</i>	Rufous-collared Sparrow	Scrub	<u>0.94</u>	0.93	0.90
<i>Saltator aurantirostris</i>	Golden-billed Saltator	Forest	≤0.01	–	–
<i>Sturnella superciliaris</i>	White-browed Blackbird	Pasture/Agric.	0.32	0.34	<u>0.44</u>
<i>Molothrus badius</i>	Bay-winged Cowbird	Scrub	0.17	0.19	<u>0.21</u>
<i>Molothrus bonariensis</i>	Shiny Cowbird	Forest	0.44	0.47	<u>0.49</u>
<i>Molothrus rufoaxillaris</i>	Screaming Cowbird	Scrub	0.01	<u>0.02</u>	0.02
<i>Icterus cayanensis</i>	Epaulet Oriole	Forest	<0.01	–	<u>0.02</u>
<i>Pseudoleistes virescens</i>	Brown-and-yellow Marshbird	Pasture/Agric.	<0.01	<u>0.01</u>	–
<i>Carduelis magellanica</i>	Hooded Siskin	Scrub	0.03	0.02	<u>0.03</u>
<i>Passer domesticus</i>	House Sparrow	Scrub	0.13	<u>0.19</u>	0.06

Underlined data is the highest constancy value in three cover categories. “Grassland cover” is the sum of pastureland and flooding grassland cover. Data for each species’ main habitat was taken from Stotz et al. (1996). Taxonomic order is according to Clements (2000)

References

- Altieri MA (1999) The ecological role of biodiversity in agroecosystems. *Agric Ecosyst Environ* 74:19–31
- Atauri JA, de Lucio JV (2001) The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landsc Ecol* 16:147–159
- Bakker KK, Naugle DE, Higgins KP (2002) Incorporating landscape attributes into models for migratory grassland bird conservation. *Conserv Biol* 16:1638–1646
- Báldi A (2008) Habitat heterogeneity overrides the species–area relationship. *J Biogeogr* 35:675–681
- Batáry P, Báldi A, Erdős S (2007) Grassland versus non-grassland bird abundance and diversity in managed grasslands: local, landscape and regional scale effects. *Biodivers Conserv* 16:871–881
- Bennett AF, Radford JQ, Haslem A (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biol Conserv* 133:250–264
- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol Evol* 18:182–188
- BirdLife International (2000) Threatened birds of the world. Lynx Ediciones and BirdLife International, Barcelona and Cambridge
- Brennan JM, Bender DJ, Contreras TA, Fahrig L (2002) Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. In: Liu J, Taylor WW (eds) Integrating landscape ecology into natural resource management. Cambridge University Press, Cambridge
- Burkart SE, León RJC, Conde MC, Perelman SB (2011) Plant species diversity in remnant grasslands on arable soils in the cropping Pampa. *Plant Ecol* 212:1009–1024
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York
- Canevari M, Canevari P, Carrizo GR et al (1991) Nueva Guía de las Aves Argentinas, vol 2. Fundación Alindar, Buenos Aires
- Carl G, Kühn I (2007) Analyzing spatial autocorrelation in species distributions using gaussian and logit models. *Ecol Model* 207:159–170
- Chamberlain DE, Fuller RJ, Bunce RGH et al (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J Appl Ecol* 37:771–788
- Clements JF (2000) Birds of the world: a checklist, 5th edn. Cornell University Press, Ithaca
- Codesido M, Fischer CG, Bilenca D (2008) Asociaciones entre diferentes patrones de uso de la tierra y ensambles de aves en agroecosistemas de la región pampeana, Argentina. *Ornitol Neotrop* 19(suppl):575–585
- Coppedge BR, Engle DM, Masters RE, Gregory MS (2001) Avian response to landscape change in fragmented southern Great Plains grasslands. *Ecol Appl* 11:47–59
- Devictor V, Jiguet F (2007) Community richness and stability in agricultural landscapes: the importance of surrounding habitats. *Agric Ecosyst Environ* 120:179–184
- Di Giácomo A, Krapovickas S (2005) Conserving the Grassland Important Bird Areas (IBAs) of Southern South America: Argentina, Uruguay, Paraguay, and Brazil. In: Ralph CJ, Rich TD (eds) Bird conservation implementation and integration in the Americas: 3rd international partners in flight conference. Gen Tech Rep PSW-GTR-191, Albany
- Di Giácomo AS, De Francesco MV, Coconier EG (2007) Áreas importantes para la conservación de las aves en Argentina. Sitios prioritarios para la conservación de la biodiversidad. Aves Argentinas/Asociación Ornitológica del Plata, Buenos Aires
- Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc R Soc Lond B Biol Sci* 268:25–29
- Donald PF, Sanderson FJ, Burfield IJ, van Bommel FJP (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agric Ecosyst Environ* 116:189–196
- Dormann CF, McPherson JM, Araújo MB et al (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628
- DPEBA (2011) Dirección Provincial de Estadística, Ministerio de Economía, Provincia de Buenos Aires, Argentina. <http://www.ec.gba.gov.ar/Estadistica/index.htm>. Accessed 12 April 2011
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175
- Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin J (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol Lett* 14:101–112

- Filloy J, Bellocq MI (2007) Patterns of bird abundance along the agricultural gradient of the Pampean region. *Agric Ecosyst Environ* 120:291–298
- Fletcher JR Jr, Koford RR (2002) Habitat and landscape associations of breeding birds in native and restored grasslands. *J Wildl Manag* 66:1011–1022
- Fuller RJ, Hinsley SA, Swetnam RD (2004) The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. *Ibis* 146:22–31
- Gonzalez A, Loreau M (2009) The causes and consequences of compensatory dynamics in ecological communities. *Annu Rev Ecol Evol Syst* 40:393–414
- Hall AJ, Rebella CM, Ghersa CM, Culot P (1992) Field crop systems of the Pampas. In: Pearson CJ (ed) *Ecosystems of the world 19: field crops ecosystems*. Elsevier, New York
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Helzer CJ, Jelinski DE (1999) The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecol Appl* 9:1448–1458
- Herkert JR (1994) The effects of habitat fragmentation on midwestern grassland bird communities. *Ecol Appl* 4:461–471
- Jaeger JAG (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landsc Ecol* 15:115–130
- Johnson D, Igl L (2001) Area requirements of grassland birds: a regional perspective. *Auk* 18:24–34
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Krebs JR, Wilson JD, Bradbury RB, Siriwardena GM (1999) The second silent spring? *Nature* 400:611–612
- Legendre P, Legendre L (1998) *Numerical ecology*. Elsevier, Amsterdam
- Manuel-Navarrete D, Gallopín GC, Blanco M et al (2009) Multi-causal and integrated assessment of sustainability: the case of agriculturalization in the Argentine Pampas. *Environ Dev Sustain* 11:621–638
- McGarigal K, Cushman S (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation. *Ecol Appl* 12:335–345
- McGarigal K, Marks BJ (1995) FRAGSTATS—spatial pattern analysis program for quantifying landscape structure. USDA Forest Service Gen Tech Rep PNW 351, Corvallis
- Moilanen A, Hanski I (2001) On the use of connectivity measures in spatial ecology. *Oikos* 95:147–151
- Peterjohn BG, Sauer JR (1999) Population status of North American grassland birds. *Stud Avian Biol* 19:27–44
- Petit S (2004) The dimensions of land use change in rural landscapes: lessons learnt from the GB Countryside Surveys. *J Environ Manag* 90:2851–2856
- Pino J, Rodà F, Ribas J, Pons X (2000) Landscape structure and bird species richness: implications for conservation in rural areas between natural parks. *Landsc Urban Plan* 49:35–48
- Poggio SL, Chaneton EJ, Ghersa CM (2010) Landscape complexity differentially affects alpha, beta, and gamma diversities of plants occurring in fencerows and crop fields. *Biol Conserv* 143:2477–2486
- Ralph CJ, Geupel GR, Pyle P et al (1993) *Handbook of field methods for monitoring landbirds*. Gen Tech Rep PSW-GTR-144, Albany
- Ribic C, Sample DW (2001) Associations of grassland birds with landscape factors in southern Wisconsin. *Am Midl Nat* 146:105–121
- Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *Am Nat* 158:87–99
- Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *J Appl Ecol* 39:157–176
- SAS Institute (1999) SAS/STAT user's guide version 8 (online doc). SAS Institute, Cary
- Satorre EH (2001) Production systems in the Argentine Pampas and their ecological impact. In: Solbrig OT, Paarlberg R, di Castri F (eds) *Globalization and the rural environment*. Harvard University Press, Cambridge
- Schrag AM, Zaccagnini ME, Calamari N, Canavelli S (2009) Climate and land-use influences on avifauna in central Argentina: broad-scale patterns and implications of agricultural conversion for biodiversity. *Agric Ecosyst Environ* 132:135–142
- Söderström B, Svensson B, Vesspy K, Glimskär A (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodivers Conserv* 10:1839–1863
- Soriano A (1991) Río de la Plata grasslands. In: Coupland RT (ed) *Ecosystems of the world 8. Natural grasslands*. Elsevier, Amsterdam
- Stotz DF, Fitzpatrick JW, Parker TA III, Moskovitz DK (1996) *Neotropical birds: ecology and conservation*. University of Chicago Press, Chicago
- Vickery PD, Hunter ML Jr, Melvin SM (1994) Effects of habitat area on the distribution of grassland birds in Maine. *Conserv Biol* 8:1087–1097
- Vickery JA, Tallowin JR, Feber RE et al (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *J Appl Ecol* 38:647–664

- Viglizzo EF, Frank FC, Carreño LV et al (2011) Ecological and environmental footprint of 50 years of agricultural expansion in Argentina. *Glob Change Biol* 17:959–973
- Vincent PJ, Haworth JM (1983) Poisson regression models of species abundance. *J Biogeogr* 10:153–160
- Winter M, Faaborg J (1999) Patterns of area sensitivity in grassland-nesting birds. *Conserv Biol* 13:1424–1436
- Wretenberg J, Pärt T, Berg A (2010) Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. *Biol Conserv* 143:375–381