

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

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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

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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

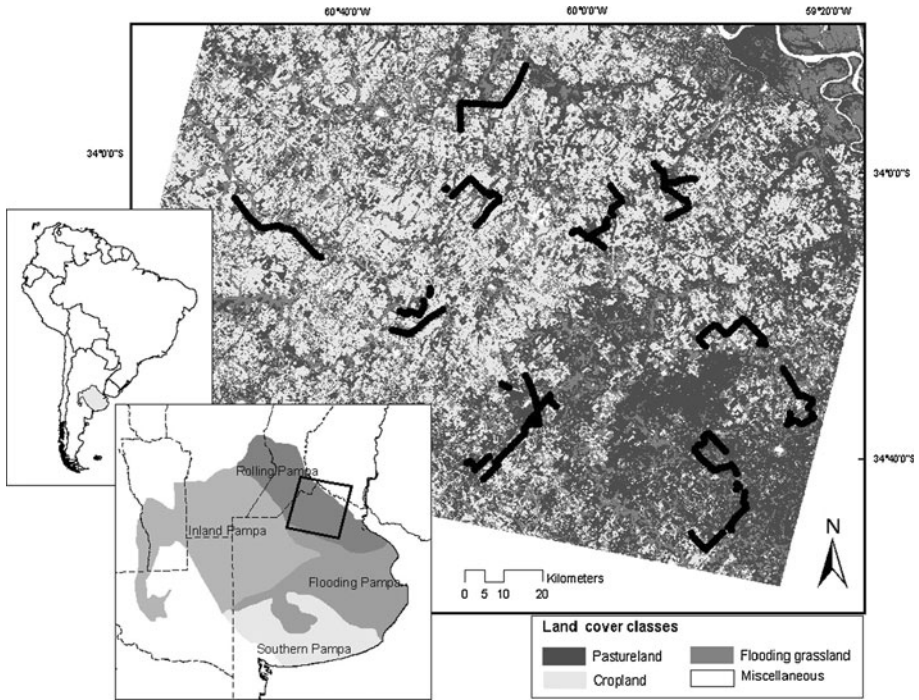


Fig. 1 Study region in the Rolling Pampa of Argentina; locations of bird sampling routes (as black lines) are shown (see “Bird surveys” in “Methods” for more details)

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).

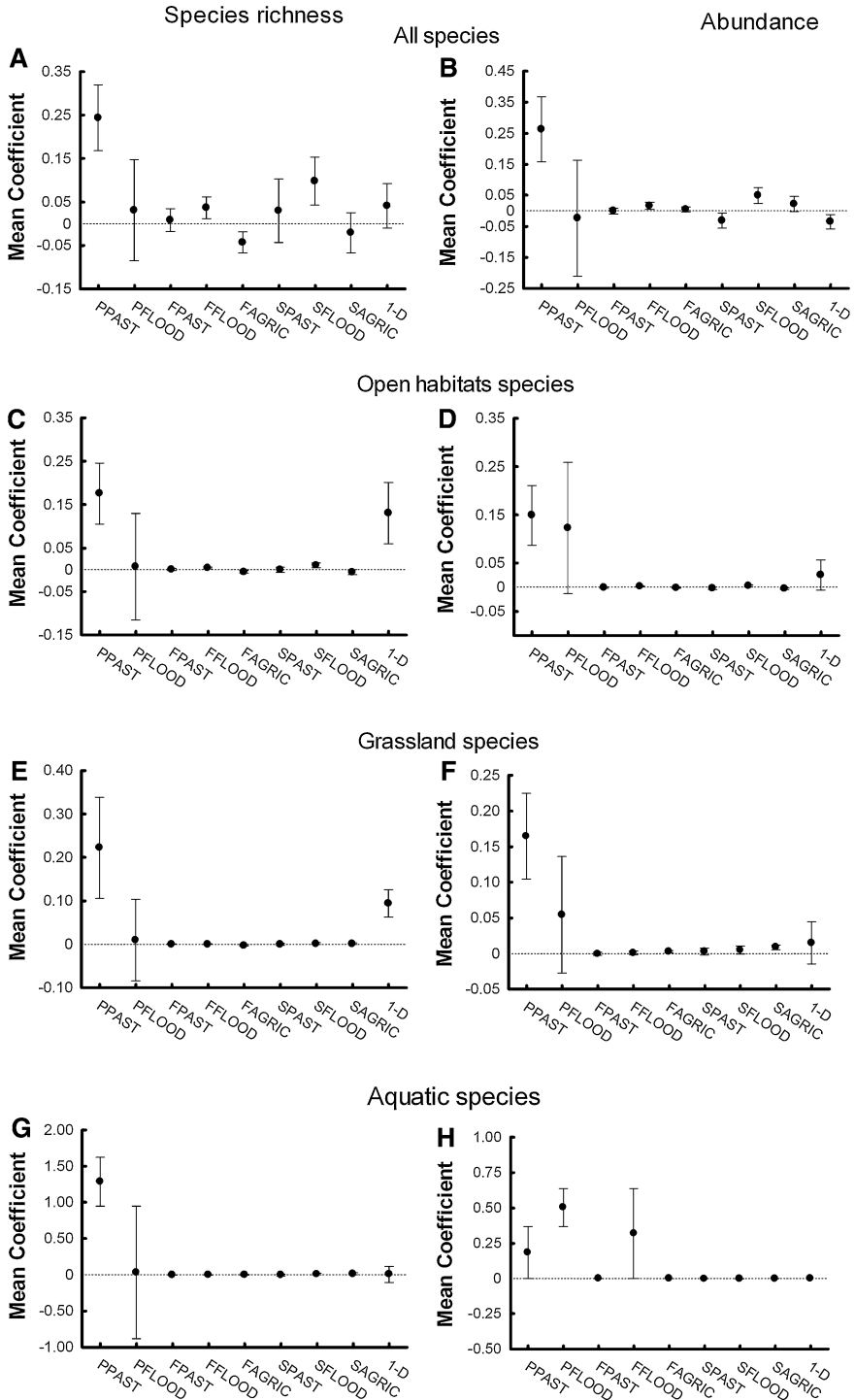


Table 2 Model AICc and Akaike weight (w_i) values for all fitted models and species groups

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

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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 platatea</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 cucularia</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 chrysur</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 cucularia</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 | 0.01 | <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)

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