

Species-Area Relationships of Specialist Versus Opportunistic Pampas Grassland Birds Depend on the Surrounding Landscape Matrix

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Research Papers

SPECIES-AREA RELATIONSHIPS OF SPECIALIST VERSUS OPPORTUNISTIC PAMPAS GRASSLAND BIRDS DEPEND ON THE SURROUNDING LANDSCAPE MATRIX

LA RELACIÓN ESPECIES-ÁREA PARA AVES ESPECIALISTAS VERSUS OPORTUNISTAS DE LOS PASTIZALES DE LA PAMPA DEPENDE DE LA MATRIZ DE PAISAJE CIRCUNDANTE

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and Daniel Augusto CARDONI¹

SUMMARY.—Agriculture and urban development have been the main drivers of loss and fragmentation of grasslands worldwide. The Argentine Pampas has been highly transformed by human activities. However how birds respond to the size of grassland patches and landscape matrices is unknown. We studied the effects of these on the abundance and richness of both specialist and opportunist grassland birds. In addition, we evaluated the patch size effect in contrast with unfragmented grasslands. We surveyed birds in small and large patches of *Cortaderia selloana* grasslands embedded within agricultural, planted forest, dune and urban landscape matrices and, specifically in spring, in unfragmented grasslands. The abundance and richness of specialist grassland birds in small patches were lower than in large patches, but richness depended on the type of matrix and was lowest in patches surrounded by a forest matrix. Extensive grasslands are a key habitat for grassland specialists during the breeding season. In contrast, the abundance and richness of opportunist grassland birds were higher in patches than in unfragmented grasslands, and showed a negative effect of dune matrix in winter. Our results enable prediction of how bird species with different habitat requirements may vary in abundance and richness depending on the size of grassland patches and the type of land use following grassland replacement. —Pretelli, M.G., Isacch, J.P. & Cardoni, D.A. (2018). Species-area relationships of specialist versus opportunistic Pampas grassland birds depend on the surrounding landscape matrix. *Ardeola*, 65: 3-23.

Key words: agricultural landscape, Argentina, *Cortaderia selloana*, dunes, planted forest, urban landscape.

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RESUMEN.—El desarrollo agrícola y urbano han sido las principales causas de pérdida y fragmentación de los pastizales en todo el mundo. La región Pampeana de Argentina ha sido enormemente transformada por las actividades humanas; sin embargo se desconoce cómo las aves responden al tamaño de los parches de pastizal remanentes y a las matrices de paisaje. Estudiamos ambos efectos sobre la abundancia y riqueza de aves especialistas y oportunistas de pastizal. Además, evaluamos el efecto del tamaño del parche contrastándolo con pastizales sin fragmentar. Muestreamos aves en parches pequeños y grandes de *Cortaderia selloana* inmersos en matrices agrícolas, forestales, de dunas y urbanas, y específicamente en primavera, en pastizales sin fragmentar. La abundancia y riqueza de aves especialistas en parches pequeños fueron menores que en parches grandes, pero la riqueza dependió del tipo de matriz, y la menor ocurrió en parches rodeados de matriz forestal. Los extensos pastizales son un hábitat clave para las aves especialistas durante la estación reproductiva. Por el contrario, la abundancia y riqueza de aves oportunistas fueron mayores en parches que en pastizales sin fragmentar, y mostraron un efecto negativo de la matriz de dunas durante el invierno. Registramos un efecto del tamaño del parche sobre aves especialistas; sin embargo, este efecto estuvo modulado por el uso del suelo que domina el paisaje alrededor de los parches. Nuestros resultados permiten predecir cómo las aves, con diferentes requerimientos de hábitat, pueden variar en abundancia y riqueza dependiendo del tamaño del parche de pastizal y del uso de la tierra derivado de su reemplazo. —Pretelli, M.G., Isacch, J.P. y Cardoni, D.A. (2018). La relación especies-área para aves especialistas *versus* oportunistas de los pastizales de la Pampa depende de la matriz de paisaje circundante. *Ardeola*, 65: 3-23.

Palabras clave: Argentina, bosque plantado, *Cortaderia selloana*, dunas, paisaje agrícola, paisaje urbano.

INTRODUCTION

Agricultural expansion and urban development are the main causes of loss of native habitats throughout the world, resulting in increased fragmentation of natural landscapes (Wilcove *et al.*, 1986; Andrén, 1994). One of the main consequences of this fragmentation is that patches of different sizes are generated and, in general, both the abundance of organisms and species richness tend to decrease with the area of relict patches (Andrén, 1994; Fahrig, 2003). However, the response of species to fragmentation is not always uniform, because the suitability of remaining patches may change depending on the landscape matrices that surround them (Andrén, 1994; Prevedello & Vieira, 2010). As a consequence of native habitat replacement, patches are embedded in a new habitat, which often becomes the dominant element in the landscape (i.e., matrix; Forman, 1995). Thus, the type of matrix is a landscape element that needs to be considered for its po-

tential effect on organisms and ecological processes occurring within and between the habitat fragments (Kupfer *et al.*, 2006; Prevedello & Vieira, 2010). In addition, the ecological plasticity of species, associated with the ability to use a new landscape surrounding patches as alternative or secondary habitat, can modulate the effects of fragmentation (e.g., Sieving *et al.*, 1996; Sisk *et al.*, 1997; Hodgson *et al.*, 2007).

Birds have been good models for testing the effect of landscape matrices on biodiversity in fragmented habitats (see Prevedello & Vieira, 2010). Most such knowledge comes from forest habitats (e.g., Sieving *et al.*, 1996; Sisk *et al.*, 1997; Marzluff & Ewing, 2001; Brotons *et al.*, 2003; Watson *et al.*, 2005). The results of these studies show that the matrix type can control the nature and magnitude of edge effects, since certain bird species may use matrices with low structural contrast with the remnant habitats as an alternative habitat (Sisk *et al.*, 1997) or, conversely, high contrast can increase the isola-

tion effect of a patch (Marzluff & Ewing, 2001). Ultimately, the difference between a remnant patch and the matrix will be reflected in differential connectivity between the remaining patches (Sieving *et al.*, 1996), with negative effects on the density of habitat specialist species (Brotons *et al.*, 2003) or species richness when patches of similar size are surrounded by a matrix of high structural contrast (Watson *et al.*, 2005).

Grasslands, like other biomes, have been replaced and fragmented mainly due to agricultural expansion. Fragmentation has been identified as one of the main causes of decline in grassland bird populations (Askins *et al.*, 2007), as a consequence of the area sensitivity of most grassland species that do not find their ecological requirements in less suitable habitats, such as agricultural fields, forests or intensively grazed pastures (Herkert, 1994; Vickery *et al.*, 1994; Winter & Faaborg, 1999; Ribic *et al.*, 2009). However, area sensitivity is not always consistent (see Johnson & Igl, 2001; Horn & Koford, 2006), because the landscape matrix surrounding grasslands can influence the patch size effect and modify the density and relative abundance of grassland birds (Ribic & Sample, 2001; Horn & Koford, 2006; Renfrew & Ribic, 2008).

Grasslands in the southeastern South America (SESA) region are among the most extensive grassland ecosystems in the Neotropics (see Azpiroz *et al.*, 2012). This region includes the grasslands of the Pampas region, which occupies central-eastern Argentina (Soriano *et al.*, 1991). The vast grasslands that once dominated the SESA Pampas are now mostly reduced to a mosaic of patches with different land-uses, largely croplands and pastures (Baldi *et al.*, 2006). The proportion of land used for crops and pasture in a particular location depends on the soil conditions and areas dominated by natural grasslands are confined to soils unsuitable for agriculture because they flood

or are sandy or salty (Viglizzo *et al.*, 2001; Baldi *et al.*, 2006). These soils predominate along the coastal strip of the southeastern Pampas region in Argentina (Soriano *et al.*, 1991), where extensive patches of tall grasslands still remain, despite the expansion of agriculture in the last two decades (Herrera *et al.*, 2009). Tall grasslands of Pampas Grass *Cortaderia selloana* growing on sandy and flooded soils are the main native vegetation that extend along the coastal strip (Block, 2014). However, these grasslands are being increasingly threatened by forestry or urban developments which, alongside croplands, have contributed to the fragmentation of many remaining large grasslands (Demarías *et al.*, 2008; Faggi *et al.*, 2010).

The conversion of grasslands into croplands in the Pampas region has negatively affected bird populations at regional levels, particularly tall-grassland birds, leading to marked population declines, distributional changes and local extinctions (e.g., Filloy & Bellocq, 2007; Codesido *et al.*, 2011; Azpiroz *et al.*, 2012). Although the conservation of grassland bird populations depends strongly on the conservation of tall grass fragments (e.g., Azpiroz *et al.*, 2012), how the birds of temperate grasslands of the Pampas region respond to the size of remnant grassland patches and the landscape matrices surrounding them is unknown.

The habitat requirements of the grassland birds of the eastern Pampas are diverse (Isacch *et al.*, 2014). They include specialist species that are only adapted to live in tall grasslands (e.g., *Cistothorus platensis*, *Craniroleuca sulphurifera*) (Isacch *et al.*, 2004; Pretelli *et al.*, 2013; Agra *et al.*, 2015), generalist species that breed in tall grasslands but use many other habitats (e.g., *Zonotrichia capensis*, *Poospiza nigrorufa*), and species that use grasslands opportunistically as non-breeding habitat (e.g., *Pitangus sulphuratus*, *Tyrannus melancholicus*) (Filloy & Bellocq, 2007; Isacch & Cardoni, 2011;

Codesido *et al.*, 2012; Pretelli *et al.*, 2013). Therefore, it is expected that different species respond differently to grassland fragmentation, and to the landscape matrix surrounding grasslands. Given the lack of knowledge of the above effects, conservation needs and the current landscape scenario in the Pampas region, this study aimed to evaluate the effect of grassland patch sizes, matrix landscapes and seasonality on the abundance of individuals and richness of bird species with different dependence on tall grasslands.

Based on their different habitat requirements, we predicted that the abundance of individuals and richness of bird species adapted to live in tall grasslands (hereafter called specialists), would be lower in smaller patches and in matrices of high structural contrast with remnant patches, whereas no such effects would be expected on habitat generalists (hereafter called opportunists) is expected. The combination of these two factors enhances negative effects, that is, we expected the lowest values of individual abundance and richness of specialist species in smaller grassland patches embedded in matrices with high contrast with the grassland. In the south temperate grasslands of the Pampas region grassland birds show seasonal variations (Isacch & Martínez, 2001; Pretelli *et al.*, 2013; Isacch *et al.*, 2014), with many populations moving totally or partly northward after breeding (Pretelli *et al.*, 2013). Consequently, we expected the greatest effects of patch size to occur in spring, given the greater abundance of individuals and richness of bird species then rather than in fall-winter.

Finally, our results are interpreted with the objective of identifying grassland patch sizes and land use matrices supporting greater numbers of specialists, as a way of establishing management recommendations in a landscape that is changing rapidly and threatening the long-term survival of specialists (Azpiroz *et al.*, 2012).

METHODS

Study area

The study was performed along a 180 km-long coastal strip in the southeast Pampas region (see Pretelli *et al.*, 2013). The northernmost sampling site was close to Pinamar (37° 2' S; 56° 50' W) and the southern end was near Mar del Sud (38° 19' S; 57° 56' W), both cities located in Buenos Aires province, Argentina (Figure 1). Most of the coastland has brackish or sandy soils and floods frequently (Soriano *et al.*, 1991). Tall grasslands mostly dominated by Pampas Grass *Cortaderia selloana* (Block, 2014) grow on these soils. As a consequence of different land uses that have fragmented the tall grasslands, *C. selloana* grassland patches are embedded within different types of landscape matrices.

We identified four different landscape matrix types, three of them anthropogenic: i) agricultural, ii) forest, iii) urban, and iv) a natural dune system matrix (see Supplementary material appendix 1, Figure A1). The agricultural matrix consisted mainly of a combination of short grasses, pastures and crops. Short grasses consist of a variety of C3 (austral fall-winter-spring) and C4 species (austral spring-summer-fall) which include various species of the genera *Melica*, *Paspalum*, *Poa*, *Hordeum*, *Stipa*, and *Piptochaetium*. Pastures consisted of *Festuca arundinacea* and *Thyropiron ponticum*. Crops were wheat and maize. The sowing period for wheat was from June to mid-August and harvesting began in late December to early January. The sowing period for maize was from October to late November and harvesting began in late March and early April. After harvesting, stubbles of wheat and maize were maintained (M. Pretelli, pers. obs.). The forest matrix consisted of exotic tree species, mostly pines (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.). All tree

stands were over five years old with trees over six metres tall. The urban matrix was dominated by houses and parks with scattered trees. *C. selloana* grasslands are also naturally distributed in the form of patches along coastal sand dunes, growing in the humid soils of interdune areas. The native vegetation of coastal dunes is mainly com-

posed of *Poa lanuginosa*, *Panicum racemosum*, *Androtrichum trigynum* and *C. selloana* grasslands; shrublands; and mixed steppes of *Senecio crassiflorus*, *Achyrocline satureioides*, *Tessaria absinthioides*, *Baccharis notoserigila* and *Discaria americana* (Stellatelli *et al.*, 2013).

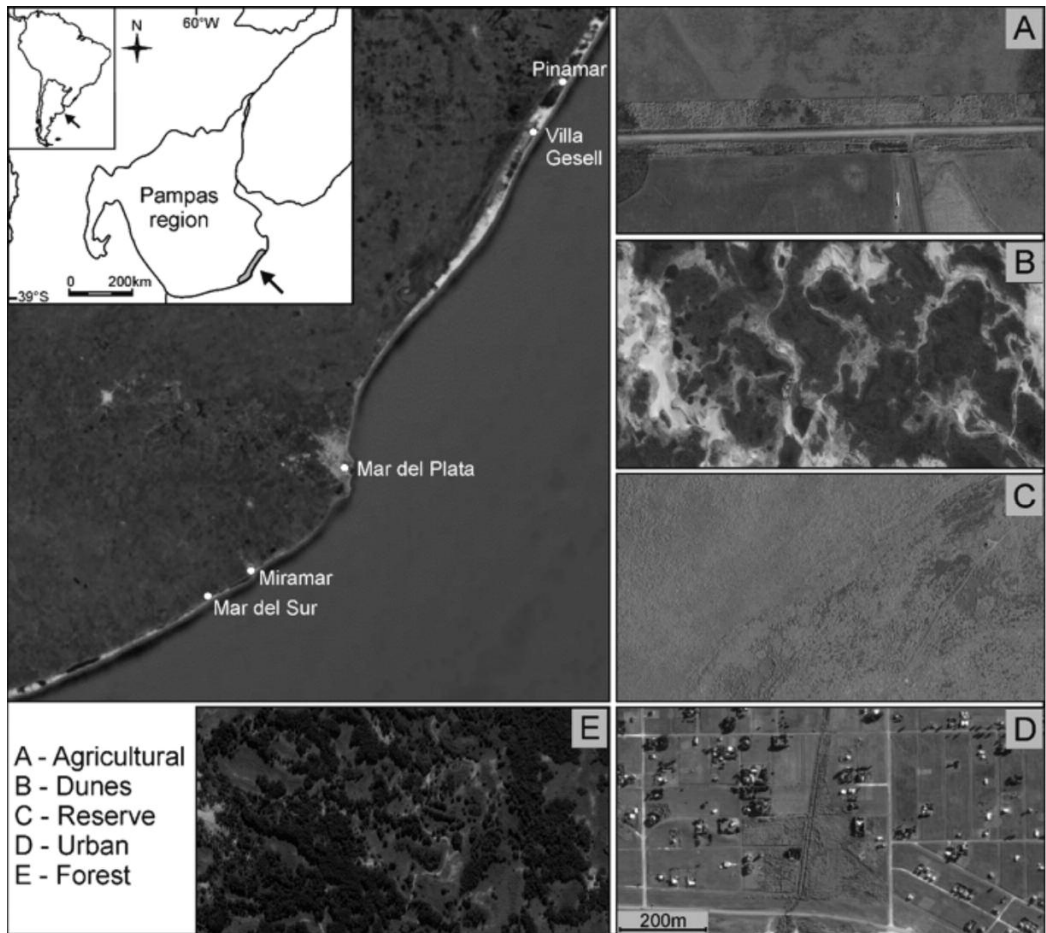


FIG. 1.—Location of the study area within the Pampas region of Argentina (top left of the figure), and satellite image of the study area showing in detail a *Cortaderia selloana* patch for each landscape matrix and continuous grasslands within the reserve.

[Localización del área de estudio dentro de la región Pampeana, Argentina (arriba a la izquierda de la figura), e imagen satelital del área de estudio mostrando en detalle un parche de *Cortaderia selloana* para cada matriz de paisaje y pastizales continuos dentro de la reserva.]

Sampling design

We selected 18 patches embedded within agricultural, forest and urban matrices, six patches for each matrix: three small patches (SP) and three large patches (LP), and ten more (five SP and five LP) in the dune matrix. Each patch was surrounded by its respective matrix to a distance of at least 1 km from the centre of the patch. As patch shape could modify effects of the landscape matrix itself, we selected patches with similar perimeter-to-area ratios (Davis, 2004). The area and perimeter of each patch was determined by using an on-line tool (<http://www.freemaptools.com/areacalculator.htm>). The study site was covered by a high-resolution image taken from Google Earth (date 1 July 2011) in which previously geopositioned patches were easily recognised. The average size of small patches was 2.8 ± 0.6 ha, with an average perimeter/area ratio of $7.6 \pm 1.4 \text{ m}^{-1}$ ($N = 14$ patches), while the average size of large patches was 8.1 ± 2.6 ha, with an average perimeter/area ratio of $2.7 \pm 0.9 \text{ m}^{-1}$ ($N = 14$ patches) (Supplementary material appendix 2, Table B1). While the patches of *C. selloana* grasslands are relatively evenly distributed in the region, we carefully selected patches for each matrix type in such a way that patches were distributed evenly within the study area, so as to cover the entire area and, thus minimise the isolation and connectivity effects among the selected patches. The patches within the dune matrix were an exception, since the distance between them was relatively shorter than in the rest of the matrices due to a peculiarity of the dune system. This aspect should be considered when interpreting the results. Likewise, in order to correct potential problems of isolation and distance effects among patches, we considered patch identity when analysing the data (see below). The average distances (\pm SD) between patches within each matrix were: agricultural 64 ± 40 km ($N = 6$), forest 51 ± 44 km

($N = 6$), urban 65 ± 41 km ($N = 6$) and dunes 5 ± 2 km ($N = 10$).

Birds of tall grasslands respond strongly to changes in grassland physiognomy resulting, for example, from fire and grazing (Isacch & Martínez, 2001; Isacch & Cardoni, 2011). We therefore sampled within patches where mature *C. selloana* was dominant and the physiognomy similar. In addition, we ensured that patches had not been burned or grazed for at least three years before being sampled. During spring, we also surveyed birds within two sites representing the near natural condition of *C. selloana* grassland. Both sites are nature reserves: the Mar Chiquita Coastal Lagoon Biosphere Reserve (26,488 ha) and the Faro Querandí Reserve (5,575 ha) (Bilenca & Miñarro, 2004), where *C. selloana* forms extensive tracts (see Supplementary material appendix 1, Figure A1). The incorporation of these two sites allows us to compare the abundance and species richness of specialists among all small and large patches, irrespective of the landscape matrix, and unfragmented grasslands (hereafter continuous grasslands).

We are aware that a natural experiment performed at a landscape scale including more than one factor may have restrictions associated with finding enough representative samples for all situations. In our case, we worked with two factors (patch size and landscape matrix), and the possibility of finding a representative number of samples for the whole combination of factors (i.e., small and large patches embedded within four matrix types) was limited. We thus offset our relative low sample size by choosing each patch meticulously, considering only those that most reliably represented the factors that we evaluated.

Bird sampling

Birds were surveyed seasonally between October 2010 and August 2011. Spring sur-

veys were conducted from 22 October to 7 December, summer surveys from 10 January to 11 February, autumn surveys from 5 May to 18 June, and winter surveys from 13 July to 17 August. Given that species detectability can vary with sampling date, especially during the breeding season, and modify patch size effects, both small and large patches were surveyed simultaneously throughout each season. At each patch, we surveyed birds along three strip transects that were walked and repeated on four occasions (once per season) by the same observer (M. Pretelli). Transects were placed along the longer axis of the patch, and these were 100 m long \times 60 m wide, spaced 100 m apart. All birds seen or heard within this area were recorded. Each transect was walked at a speed of five minutes per 100 m of transect length, and the time taken by the observer to follow each transect was the same in all patches. Transects were surveyed within four hours after sunrise. No surveys were conducted in bad weather conditions (Conner & Dickson, 1980). We always ran transects through grasslands. However, the transect width was a little larger than the patch width in two small patches of agricultural and urban matrices and in these cases we retained the 60 m width to survey birds, in order to have the same sampling unit area. In addition, in both cases, the spacing distance between adjacent transects was as short as possible so that the three transects could be fitted within the two smaller patches. Because these patches also included non-grassland habitat, we were cautious when interpreting these results. In the reserves, where grassland extended continuously, we sampled in seven sites (four in Mar Chiquita and three in Faro Querandí) that were randomly distributed although spaced at least 400 m apart. We also surveyed three transects per site here, as in the patches. The sites within both reserves were dominated by *C. selloana*. Within the fixed width of the transect we assumed that the detecta-

bility of all bird species was the same (see Isacch & Martínez, 2001; Isacch *et al.*, 2014).

To evaluate the effect of patch size, type of landscape matrix and seasonality on abundance and species richness, species were grouped specifically according to their affinity for *C. selloana* grassland (Pretelli *et al.*, 2013). Birds were assigned to two groups: i) specialists and ii) opportunists. The first group consisted of 11 species that are strongly dependent on *C. selloana* grassland for foraging and nesting in our region (Pretelli *et al.*, 2013; Isacch *et al.*, 2014), although this dependency can vary in some species within other regions (see Azpiroz *et al.*, 2012). These were: the Long-tailed Reed-finch *Donacospiza albifrons*, Sulphur-throated Spinetail *Cranioleuca sulphurifera*, Warbling Doradito *Pseudocolopteryx flavi-ventris*, Bay-capped Wren-spinetail *Sparto-noica maluroides*, Freckle-breasted Thornbird *Phacellodomus striaticollis*, Grassland Yellow-finch *Sicalis luteola*, Brown-and-yellow Marshbird *Pseudoleistes virescens*, Red-winged Tinamou *Rhynchotus rufescens*, Spectacled Tyrant *Hymenops perspicillatus*, Sedge Wren *Cistothorus platensis*, and Great Pampa-finch *Embernagra platensis*. The second group consisted of 12 species that use *C. selloana* grassland as an alternative habitat for foraging or even nesting (Pretelli *et al.*, 2013; Isacch *et al.*, 2014). These were: the Great Kiskadee *Pitangus sulphuratus*, Hooded Siskin *Spinus magellanicus*, Chalk-browed Mockingbird *Mimus saturninus*, Rufous-collared Sparrow *Zonotrichia capensis*, Double-collared Seedeater *Sporophila caerulea*, House Wren *Troglodytes aedon*, Black-and-rufous Warbling-Finch *Poospiza nigrorufa*, Tropical Kingbird *Tyrannus melancholicus*, Fork-tailed Flycatcher *Tyrannus savana*, Eared Dove *Zenaida auriculata*, Grayish Baywing *Agelaioides badius* and Shiny Cowbird *Molothrus bonariensis*. We followed Remsen *et al.* (2017) for taxonomy and nomenclature.

Data analyses

We calculated abundance and richness as the number of individuals and the number of bird species per transect, respectively. We used generalized linear mixed models, with a Poisson error distribution and log-link function (Crawley, 2007; Zuur *et al.*, 2009), to compare bird variables (i.e., bird abundance and species richness in spring) for each group of birds among the small patches, large patches and unfragmented grasslands (as a control site). Taking into account that bird abundances and richness in transects on the same patch are likely to be more similar to each other than those obtained from different patches, we considered the transect identity as a random factor nested within patch. Packages and functions used for the analysis of the bird variables data are given below.

To specifically assess the effect of patch size, landscape matrix and seasonality on abundance and richness of both groups of birds, we proceeded to the selection of models using an hypothesis testing approach (Burnham & Anderson, 2002). We started with a global model that includes all variables (i.e., patch size, landscape matrix and seasonality) and all their possible interactions. After that, we proceeded to remove, if not significant, first the more complex interactions (in this case the triple interaction), then the double interactions and finally the main effects. Thus, we obtained a suitable minimal model formed by those interactions or variables that were significant. For this we used generalized linear mixed models (Crawley, 2007; Zuur *et al.*, 2009). Analyses of the bird variables data were performed using the `glmmadmb` function in the `glmm-ADMB` package (Skaug *et al.*, 2013). A negative binomial error structure and a logit-link function were used for abundance, while a Poisson error structure and a log-link function were used for richness (Crawley, 2007). The Poisson distribution is typically used for

count data (Zuur *et al.*, 2009); however, in this case, for abundance models we used the negative binomial distribution as it had a better fit to the data in both cases. To compare goodness of fit between models (i.e., Poisson vs. negative binomial) likelihood ratio tests were calculated (Zuur *et al.*, 2009). We considered the patch size (small or large), the type of landscape matrix (agricultural, forest, dune or urban) and the season (spring, summer, autumn or winter) as fixed effects and the transect identity as a random factor nested within patch (Crawley, 2007; Zuur *et al.*, 2009).

Model fits were visually assessed by inspecting plots of standardized deviance residuals for each model. We assessed goodness of fit for all models and estimated the variance inflation factor (\hat{c}) as residual deviance divided by degrees of freedom (Burnham & Anderson, 2002; Crawley, 2007). The statistical significances of fixed and random effects were determined with the `lrtest` (likelihood ratio test, LRT) function in the `lrmtest` package. The likelihood ratio test statistic was calculated by subtracting the -2 log-likelihood between hierarchical models and referring the difference to a χ^2 distribution with the degrees of freedom associated (West *et al.*, 2006; Crawley, 2007). Additionally, an *a posteriori* Tukey's multiple comparison test of means was performed using `glht` function in the `multcomp` package when necessary. All statistical analysis were carried out using R software version 3.0.1 (R Development Core Team, 2013). Statistical tests were considered significant at $p < 0.05$.

RESULTS

Patches of grassland vs. Continuous grasslands

The abundance and richness of grassland birds during spring varied significantly

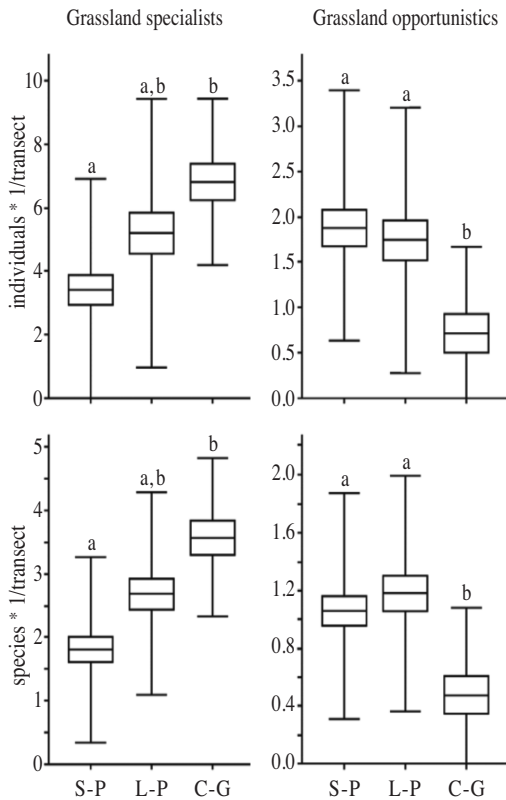


FIG. 2.—Abundance and species richness of specialist and opportunist grassland birds recorded in patches of different sizes (S-P: small patches, and L-P: large patches), and in an unfragmented grassland (C-G: continuous grassland) during the spring of 2010 in the southeast Pampas region, Argentina. Boxes represent the standard error, error bars the standard deviation and lines within boxes the mean values. The letters above the plot represent differences from an *a posteriori* Tukey test ($p < 0.05$).

[Abundancia y riqueza de especies de aves de pastizal y oportunistas del pastizal registradas en parches de diferentes tamaños (S-P: parches pequeños, y L-P: parches grandes), y en un pastizal sin fragmentar (C-G: pastizal continuo) durante la primavera de 2010 en el sudeste de la región Pampeana, Argentina. Las cajas representan el error estándar, las líneas la desviación estándar y la línea dentro de la caja el promedio. Las letras sobre las cajas representan diferencias de una prueba *a posteriori* de Tukey ($p < 0,05$).]

between patches and continuous grasslands (see Figure 2). The abundance and richness were significantly higher in continuous grasslands than in SP (GLMM: $Z = 2.35$, $p = 0.048$; $Z = 2.64$, $p = 0.022$, respectively) (Figure 2). However, the abundance and richness were similar between continuous grasslands and LP ($Z = 1.38$, $p = 0.346$; $Z = 1.57$, $p = 0.25$, respectively), and between LP and SP ($Z = 1.16$, $p = 0.473$; $Z = 1.26$, $p = 0.414$, respectively) (Figure 2). The abundance and richness of opportunistic grassland birds also varied significantly between continuous grasslands and patches during spring (Figure 2). However, the pattern was reversed, since both abundance and richness were significantly lower in the continuous grasslands than in SP ($Z = -2.56$, $p = 0.026$; $Z = -2.35$, $p = 0.049$, respectively) and LP ($Z = -2.55$, $p = 0.027$; $Z = -2.65$, $p = 0.020$, respectively), with no differences between LP and SP ($Z = -0.014$, $p = 0.999$; $Z = 0.53$, $p = 0.853$, respectively) (Figure 2).

Specialist grassland birds

During spring we recorded 11 specialist grassland bird species in continuous grasslands, ten in agricultural patches (nine in SP, eight in LP), ten in dune patches (nine in SP, seven in LP), eight in urban patches (seven in SP, eight in LP) and six in forest patches (three in SP, six in LP) (Table 1). The Spectacled Tyrant, Grassland Yellow-finch and Great Pampa-finch were notably frequent and abundant in the reserve. The Grassland Yellow-finch, Spectacled Tyrant and Brown-and-yellow Marshbird were more frequent and abundant in the agricultural and urban patches, regardless of patch size. The Spectacled Tyrant, Great Pampa-finch and Brown-and-yellow Marshbird were the most frequent and abundant in dune patches, while the Great Pampa-finch was the most frequent and abundant in forest patches (Table 1).

TABLE 1

Grassland specialists and opportunists recorded in small (SP) and large patches (LP) of *Cortaderia selloana* grasslands embedded in four different landscape matrices and in unfragmented grasslands within nature reserves during spring 2010 in the southeast Pampas region, Argentina (see Figure 1). Bird numbers represent the frequency of birds (F) (i.e., number of transects where the bird was present from the total of transects) and the total individuals per transect (T). Taxonomy and nomenclature follow Remsen *et al.*, (2017).

Species	Reserve		Dune			
	F	T	SP		LP	
			F	T	F	T
Grassland specialists						
Spectacled Tyrant	0.95	2.23	0.73	1.13	0.86	1.4
Grassland Yellow-finch	0.66	1.95	—	—	0.33	0.73
Brown-and-yellow Marshbird	0.19	0.29	0.33	0.6	0.53	1.2
Great Pampa-finch	0.57	1.05	0.46	0.66	0.8	1.26
Warbling Doradito	0.28	0.38	0.26	0.33	0.07	0.07
Sulphur-throated Spinetail	0.29	0.29	0.2	0.27	—	—
Sedge Wren	0.33	0.33	0.07	0.07	0.26	0.26
Red-winged Tinamou	0.2	0.2	0.13	0.13	0.13	0.13
Freckle-breasted Thornbird	0.05	0.05	0.07	0.07	—	—
Long-tailed Reed-finch	0.05	0.05	0.07	0.13	—	—
Bay-capped Wren-spinetail	0.05	0.05	—	—	—	—
Grassland opportunists						
Rufous-collared Sparrow	0.43	0.62	0.53	0.8	0.6	0.87
Shiny Cowbird	—	—	—	—	—	—
Eared Dove	—	—	—	—	—	—
House Wren	—	—	—	—	—	—
Black-and-rufous Warbling-finch	0.05	0.09	—	—	—	—
Grayish Baywing	—	—	—	—	—	—
Great Kiskadee	0.28	0.38	—	—	—	—
Chalk-browed Mockingbird	—	—	—	—	—	—
Hooded Siskin	—	—	—	—	0.06	0.26
Tropical Kingbird	—	—	—	—	—	—
Fork-tailed Flycatcher	—	—	—	—	0.07	0.07
Double-collared Seedeater	—	—	—	—	—	—

TABLE 1 (cont.)

[Aves especialistas y oportunistas del pastizal registradas en parches pequeños (SP) y grandes (LP) en pastizales de Cortaderia selloana inmersos en cuatro matrices de paisaje diferentes y en un pastizal sin fragmentar dentro de reservas naturales durante la primavera de 2010 en el sudeste de la región Pampeana, Argentina (véase Figura 1). Los números representan la frecuencia de aves (F) (i.e., número de transectas donde las aves estuvieron presentes en relación al número total de transectas) y el total de individuos por transecta (T). La taxonomía y nomenclatura se basaron en Remsen et al., (2017).]

Urban				Agricultural				Forest			
SP		LP		SP		LP		SP		LP	
F	T	F	T	F	T	F	T	F	T	F	T
0.55	1	0.77	2.11	0.88	1.77	0.77	1.55	0.11	0.11	0.22	0.22
0.66	1.66	0.44	1.66	0.55	1.88	0.77	3	—	—	0.22	0.22
0.22	1.11	0.77	2	0.55	1.66	0.55	1.88	—	—	—	—
0.33	0.44	0.55	0.55	0.44	0.66	0.66	1.11	0.22	0.22	0.33	0.33
0.11	0.11	0.22	0.33	—	—	0.11	0.22	0.11	0.11	0.11	0.22
0.11	0.11	0.22	0.22	0.11	0.11	—	—	—	—	0.11	0.11
—	—	—	—	0.11	0.11	0.11	0.22	—	—	—	—
—	—	—	—	0.11	0.11	0.33	0.33	—	—	—	—
0.22	0.22	0.11	0.11	0.11	0.22	0.11	0.11	—	—	0.11	0.11
—	—	0.11	0.11	0.11	0.11	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
0.77	1	0.66	1	0.43	0.33	0.66	1.44	0.33	0.44	0.77	1.22
—	—	0.22	0.33	0.22	0.33	0.33	0.44	—	—	—	—
0.11	0.22	0.11	0.33	0.11	0.11	0.22	0.44	—	—	—	—
—	—	0.33	0.33	—	—	—	—	0.11	0.11	0.33	0.33
0.11	0.22	0.11	0.11	—	—	—	—	—	—	—	—
0.11	0.22	—	—	0.11	0.11	—	—	—	—	—	—
0.11	0.22	—	—	—	—	—	—	0.11	0.11	0.22	0.22
—	—	0.22	0.33	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	0.22	0.22	—	—	—	—	—	—
—	—	0.11	0.11	—	—	—	—	—	—	—	—
—	—	0.11	0.11	—	—	0.22	0.22	—	—	—	—

Opportunist grassland birds

In spring, we recorded ten opportunist grassland bird species in urban patches (five in SP, eight in LP), seven in agricultural patches (six in SP, four in LP), three in forest patches (three in SP and LP), and three in dune patches (one in SP, three in LP), and two species in the reserve (Table 1). The

Rufous-collared Sparrow, Shiny Cowbird and Eared Dove were the most frequent and abundant species in agricultural and urban patches. The Rufous-collared Sparrow, House Wren and Great Kiskadee were the most frequent and abundant in forest patches, and the Rufous-collared Sparrow was also the most frequent and abundant in both continuous grasslands and dune patches.

TABLE 2

Generalized linear models result from assessing the effects of patch size (size), landscape matrix (matrix) and seasonality (season), as well as their interactions on the abundance of individuals and richness of species of specialist and opportunist grassland birds using patches of *Cortaderia selloana* grassland in the southeast Pampas region, Argentina.

[Resultados de los modelos lineales generalizados que resultan de evaluar los efectos del tamaño del parche (size), la matriz de paisaje (matrix) y la estacionalidad (season), y de sus interacciones sobre la abundancia de individuos y riqueza de especies de aves especialistas y oportunistas del pastizal, utilizando los parches de Cortaderia selloana del sudeste de la región Pampeana, Argentina.]

	df	Abundance		Richness	
		χ^2	p	χ^2	p
Grassland specialists					
Size:matrix:season	9	9.0	0.432	6.6	0.676
Matrix:season	9	15.6	0.075	2.7	0.974
Size:season	3	2.9	0.406	1.1	0.776
Size:matrix	3	7.6	0.054	9.8	0.020
Season	3	139.3	<0.001	115.0	<0.001
Matrix	3	29.1	<0.001	—	—
Size	1	7.2	0.007	—	—
Grassland opportunists					
Size:matrix:season	9	15.9	0.068	8.5	0.476
Matrix:season	9	24.8	0.003	21.9	0.009
Size:season	3	4.0	0.251	1.5	0.668
Size:matrix	3	6.7	0.081	5.2	0.153
Season	3	—	—	—	—
Matrix	3	—	—	—	—
Size	1	1.0	0.310	2.4	0.117

Effect of patch size, landscape matrix and seasonality

When the effects of patch size, landscape matrix and seasonality on the abundance of specialists were evaluated, we recorded an effect of patch size (Table 2), with greater abundance in large patches: $2.67 (\pm 3.2)$ than in small patches: $1.71 (\pm 2.2)$. The landscape matrix also affected the abundance of specialists (Table 2), with highest values recorded in the agricultural matrix: $3.81 (\pm 3.9)$, followed by the dune: $2.27 (\pm 2.3)$, urban: $1.98 (\pm 2.6)$, and forest matrices: $0.65 (\pm 1.2)$. Only in the forest matrix was abundance significantly lower than in the other matrices (Supplementary material appendix 2, Table B2).

We found a significant interaction effect between patch size and landscape matrix on specialists' richness (Table 2). Patch size negatively affected richness but only in the forest matrix (Figure 3A, and see Supplementary material appendix 2, Table B3). Among small patches, richness was only lower in the forest matrix, while there were no differences among the other matrices (Figure 3A). Among large patches the only significant difference was recorded between the agricultural and forest matrices (Figure 3A). For abundance, the pattern was similar but not significant (see Table 2, Figure 3B).

The abundance and richness of specialists also varied significantly with season. However, no statistically significant interaction between seasonality and patch size and/or the landscape matrix was recorded (Figure 4A, Table 2). The highest abundance was recorded in spring: 4.41 individuals per transect (± 3.9), then in summer: $2.42 (\pm 2.3)$, autumn: $1.05 (\pm 1.2)$, and the lowest in winter: $0.89 (\pm 1.2)$. Richness followed the same pattern with $2.35 (\pm 1.6)$ species per transect in spring, $1.60 (\pm 1.4)$ in summer, $0.74 (\pm 0.7)$ in autumn, and $0.67 (\pm 0.8)$ in winter. The

abundance and richness of specialists were significantly higher during spring than during the other seasons; in summer they were higher than in autumn and winter, while between autumn and winter there were no differences (Supplementary material appendix 2, Table B2).

The interaction between landscape matrix and season had a significant effect on both abundance and richness of opportunistic grassland birds (Table 2). The effect of landscape matrix on abundance and richness was recorded only in winter, with greater abundance and richness in the agricultural matrix than in the dune matrix (Figure 4B, Supplementary material appendix 2, Table B4). An effect of season only was observed in the dune matrix, with higher abundance and richness in spring than in winter. The abundance and richness of opportunistic grassland birds were unaffected by patch size (Table 2).

DISCUSSION

Bird species that inhabit the southeast Pampas region differ in their responses to the fragmentation of tall grasslands (i.e., patches vs. continuous grassland), patch size and type of landscape matrix, according to their affinity to grasslands. In the case of grassland specialists, abundance and richness were negatively affected by fragmentation, patch size and forest matrix. In contrast, patch size and the matrix type did not have an apparent effect on opportunistic grassland birds, whose abundance and richness were only affected during winter in the dune matrix. The observed patterns are clear and are a useful input to devising conservation guidelines. However, the extrapolation of these results to a regional level requires caution since the association between certain species and grasslands may vary depending

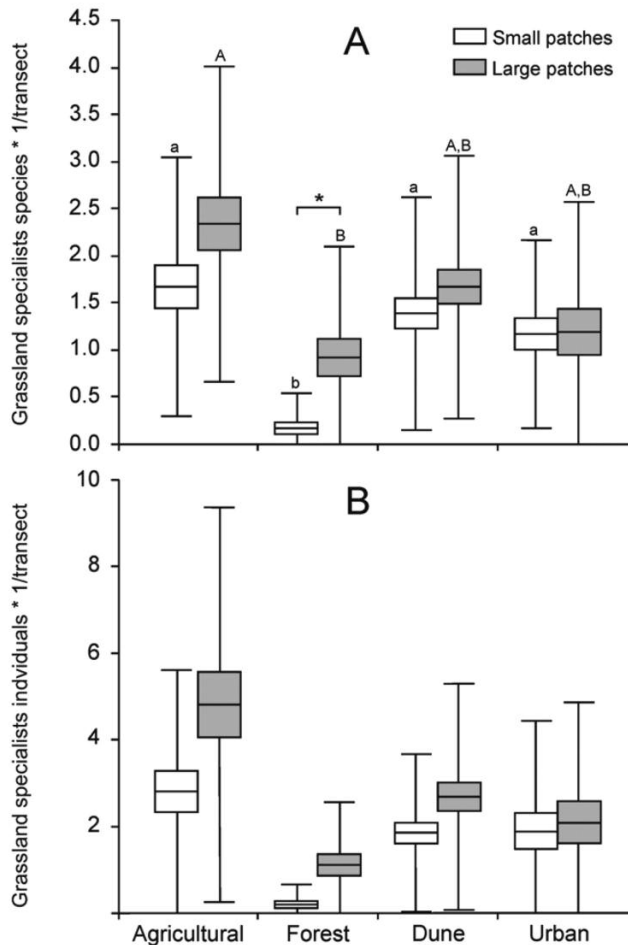


FIG. 3.—Grassland bird richness recorded in patches of *Cortaderia selloana* grassland embedded within four different landscape matrices in the southeast Pampas region, Argentina (see Figure 1). Boxes represent the standard error, error bars the standard deviation and lines within boxes the mean values. Letters above plots represent differences among matrices for each patch size (lower case letters for small patches and capitals for large patches). The asterisk above the horizontal line indicates significant differences between patches of different size within a matrix after performing GLMM (see Table 2) and an *a posteriori* Tukey test ($p < 0.05$) (Supplementary material appendix 2, Table B1). Absence of letters above plots means that there are no significant differences between values of a factor.

[Riqueza de aves de pastizal registradas en parches de *Cortaderia selloana* inmersos en cuatro diferentes tipos de matrices de paisaje en el sudeste de la región Pampeana, Argentina (véase Figura 1). Las cajas representan el error estándar, las líneas la desviación estándar y la línea dentro de la caja el promedio. Las letras sobre las cajas representan diferencias entre matrices para cada tamaño de parche (letras minúsculas para parches pequeños y letras mayúsculas para parches grandes). El asterisco sobre las líneas horizontales indica diferencias significativas entre parches de diferentes tamaños dentro de una matriz luego de realizar MLGM (véase Tabla 2) y una prueba *a posteriori* de Tukey ($p < 0,05$) (Apéndice B). La ausencia de letras sobre los gráficos indica la no diferencia entre niveles de un factor.]

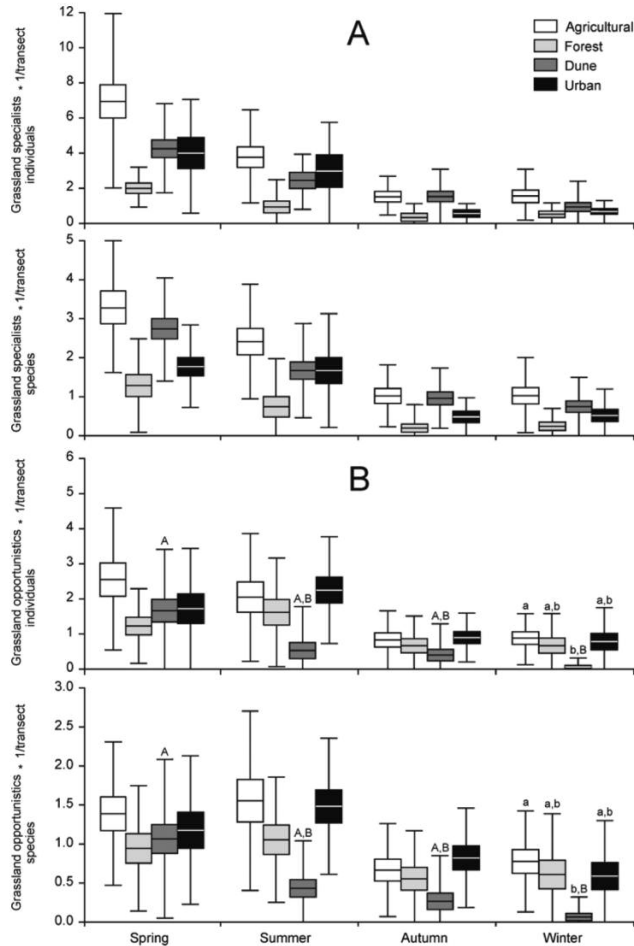


FIG. 4.—Abundance and species richness of grassland specialists (A) and grassland opportunists (B) recorded in patches of *Cortaderia selloana* grassland embedded within four different landscape matrices during each season of the year in the southeast Pampas region, Argentina (see Figure 1). Boxes represent the standard error, error bars the standard deviation and lines within boxes the mean values. The letters above the plot represent differences among treatments after performing GLMM (see Table 2) and an *a posteriori* Tukey test ($p < 0.05$) (Supplementary material appendix 2, Table B2). The lower case letters above the plot represent differences among landscape matrices, and capital letters represent differences between seasons. Absence of letters above plots means that there are no significant differences between values of a factor.

[Abundancia y riqueza de especies de aves de pastizal (A) y oportunistas del pastizal (B) registradas en parches de pastizal de *Cortaderia selloana* inmersos en cuatro diferentes matrices de paisaje durante cada estación del año en el sudeste de la región Pampeana, Argentina (véase Figura 1). Las cajas representan el error estándar, las líneas la desviación estándar y la línea dentro de la caja el promedio. Las letras sobre los gráficos representan diferencias significativas entre tratamientos después de realizar MLGM (véase Tabla 2) y una prueba *a posteriori* de Tukey ($p < 0,05$) (Apéndice C). Las letras minúsculas sobre los gráficos representan diferencias entre matrices de paisaje, y letras mayúsculas diferencias entre estaciones. La ausencia de letras sobre los gráficos indica la no diferencia entre niveles de un factor.]

on the study area within the region (see Azpiroz *et al.*, 2012).

In agreement with our prediction, the abundance of specialists was affected by patch size. It is important to note that, at least at group level, patch size sensitivity depends largely on the habitat requirements of species. Our results agree with previous studies that evaluated area sensitivity and the effects of habitat fragmentation on specialists. Such studies have found that many specialists require parcels of habitat much larger than their territory size on which to settle and reproduce (Herkert, 1994; Vickery *et al.*, 1994; Winter & Faaborg, 1999; Johnson & Igl, 2001; Davis, 2004). In our study, we found that specialists' abundance and richness were higher in continuous grasslands than in fragmented grasslands, and that abundance gradually decreased as the size of the patches became smaller. Codesido *et al.* (2013) reported a similar response at a larger scale in the Pampas region. In their study, they mention that most grassland specialists (e.g., the Great Pampa-finch, Brown-and-yellow Marshbird) were associated with pastoral landscapes that included large areas of continuous grasslands. This shows that the most important habitat for grassland specialists, at least during the breeding season (austral spring), are continuous *C. selloana* grasslands. In contrast, opportunistic grassland birds were unaffected by patch size and tolerated different patch sizes. This plasticity allows them to use grassland patches and the landscape matrix as alternative habitats (Sisk *et al.*, 1997; Brotons *et al.*, 2003). In addition, most opportunistic grassland species generally nest on planted shrubs, such as bushes (e.g., Eared Dove, Chalk-browed Mockingbird) or trees (e.g., Great Kiskadee, Grayish Baywing). The affinity of most opportunists towards anthropogenic or disturbed habitats (with bushes and trees) would explain their lower presence in the continuous grasslands within the reserves.

The abundance of specialists was also affected by the landscape matrix. We found a general trend partly explained by a decrease in abundance as the structural contrast between patch and matrix increased, regardless of the patch size. The abundance and richness values found in the agricultural and dune matrices were higher than those found in the urban and forest matrices. However, specialists' abundance was only significantly lower in patches embedded within the forest matrix. The high abundance and richness in the agricultural matrix could be due to the heterogeneity of this matrix in the study area (i.e., short grasses, pastures, and crops). Nevertheless, it should be noted that a homogeneous agricultural matrix (e.g., only soybean) can have a negative effect on the richness of specialists (da Silva *et al.*, 2015).

The urban and forest matrices have greater structural contrast when compared to the original grassland patch. However, the urban matrix is more similar to the grassland matrix than the forest matrix, because it has open green spaces and fewer trees. This underlines that afforestation negatively affected the presence of specialists. This pattern is consistent with previous studies that mention the negative effects of trees, either at patch edges (Winter *et al.*, 2000; Dias *et al.*, 2013) or at a landscape scale (Ribic & Sample, 2001; Cunningham & Johnson, 2006), since trees act as physical barriers hampering bird movements between patches (Fletcher & Koford, 2003). However, this structural contrast is not as marked in the other land uses, because movements between patches are less restricted in the urban, agricultural and dune matrices (Davis, 2004; Renfrew *et al.*, 2005). However, in the case of the urban landscape, it is important to consider that the contrast with natural grasslands will depend on the heterogeneity of the urban matrix (trees/houses/open green spaces ratio), since this may accentuate or mitigate the effects of the structural contrast (McLaughlin *et al.*, 2014).

It is striking that while the dune grasslands were mostly pristine areas formed by naturally scattered patches, there were no significant differences in abundance with patches embedded within agricultural and urban matrices. This shows that native grassland patches, although small, are highly sought after birds that require tall grasslands (Pretelli *et al.*, 2013; McLaughlin *et al.*, 2014; da Silva *et al.*, 2015).

We found an interaction between patch size and matrix type in specialists' richness. In the case of small patches, richness was significantly lower in the forest matrix when compared with the other matrices. In large patches, the matrix effect was attenuated and we only registered differences between patches embedded in the forest and agricultural matrices. These results agree with Hamer *et al.* (2006), who found that the richness of specialists species from North America (eastern Wyoming) was related to landscape matrix attributes that may restrict their movement. The landscape matrix also affected the abundance and richness of opportunistic grassland birds. This became evident in the dune matrix, particularly during winter, where we recorded the lowest abundance and richness values. The dune matrix consists of grassland patches that are naturally scattered and are more interconnected than in the other matrices. In this way, the dune matrix has some similarities with the continuous grasslands in the reserves.

The abundance and richness of specialists varied significantly between seasons but there was no interaction between seasonality and patch size or type of matrix. The highest values of abundance and richness occurred during spring, and then dropped in fall and winter. This seasonal variation coincides with the patterns observed for other specialists' assemblages of the region (Isacch & Martínez, 2001; Isacch *et al.*, 2004; Isacch & Cardoni, 2011). Seasonality was more marked in grassland specialists than in

opportunistic grassland birds, as the abundance and richness of the latter only varied significantly between seasons in the dune matrix. The observed seasonal variation in the abundance and richness of specialists could be partly explained by the arrival of migrants, such as Bay-capped Wren-spinetails, Spectacled Tyrants and Warbling Doraditos (Pretelli *et al.*, 2013). However, the abundance and richness of opportunistic species during winter was higher in the agricultural matrix than in the dune matrix. It is possible that the negative effect of the dune matrix may have increased in winter because some opportunists (Fork-tailed Flycatcher, Tropical Kingbird and Double-collared Seedeater) move northward during the non-breeding period. Also, during this period such species as the Shiny Cowbird and the Rufous-collared Sparrow occur more frequently in agricultural fields than in sand dunes (M. Pretelli pers. obs.).

One of the main consequences of grassland fragmentation is that the abundance and richness of birds that depend heavily on this environment are reduced as the level of fragmentation increases, manifested by a reduced patch size and increased perimeter/area ratio. An important contribution of this study is that patch size per se was not the only determinant factor of the abundance and richness of specialists but that there was also a modulating effect of the landscape matrix in which the patches were embedded. This was particularly evident in the forest matrix where specialists had the lowest abundance values. Conversely, grassland patches within the agricultural matrix were relatively more occupied.

Our findings have the potential to be used for practical purposes. For example, there is a strong demand to take advantage of misnamed *non-productive lands*. Therefore, decision makers require information (preferably local) to assess the impacts of different activities on natural grasslands and justify

their decisions. The coastal grasslands of the Pampas region are especially vulnerable to the increase of afforestation and urbanisation projects (Faggi *et al.*, 2010; Isla, 2013). Our results are particularly important in this context. Specifically, the possibility to develop more bird-friendly urbanisation should be considered instead of other landscape transformations, leaving grassland patches with low tree density. Grassland patches in agricultural matrices fulfill an important role since they are the habitat of a great abundance of both specialist and opportunist grassland birds. This shows that in a landscape under multiple land uses the lack of native tall grasslands forces birds to use small grassland patches, which are habitat islands in which birds can shelter, forage and nest (Pretelli *et al.*, 2013). Therefore, it is necessary to preserve small grassland patches, together with larger grassland areas, for a complete conservation of specialists.

To conclude, we recorded a patch-size effect on the abundance and richness of specialists inhabiting *C. selloana* grasslands in the Pampas region. However, the patch-size effect was modulated by the land-use that dominated the landscape matrix around the patches. In particular, matrices that are structurally different to tall grasslands (e.g., afforested areas) have a greater negative effect on specialists.

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- patches of grassland embedded within different landscape matrices, and among landscape matrices that contained patches of two sizes.
- Appendix 2. Table B4.** Interaction contrasts resulting from GLMM comparing the abundance and species richness of opportunistic grassland birds among different landscape matrices in different seasons, and between seasons but in different landscape matrices.

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SUPPLEMENTARY ELECTRONIC MATERIAL

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Appendix 1. Figure A1. Grasslands of *Cortaderia selloana* growing as patches embedded within four different landscape matrices, and unfragmented grassland within Mar Chiquita Coastal Lagoon Biosphere reserve.

Appendix 2. Table B1. Features of *Cortaderia selloana* grassland patches surveyed along a coastal strip in the southeast Pampas region, Argentina.

Appendix 2. Table B2. Fixed-factor contrasts resulting from GLMM comparing the abundance and species richness of specialists among different patch sizes, seasons of the year and landscape matrices.

Appendix 2. Table B3. Interaction contrasts resulting from GLMM comparing the species richness of specialists between small and large

