



Are abandoned grasslands within forest plantations effective for the conservation of grassland birds?

¿Son eficaces para la conservación de las aves de pastizal los pastizales abandonados dentro de plantaciones forestales?

Lucilene Inês Jacoboski¹, Allan de Oliveira de Oliveira² and Sandra Maria Hartz³

ABSTRACT. The decline and fragmentation of grasslands in recent years have stimulated efforts to preserve this ecosystem. However, even legally protected remnant grasslands are threatened by changes in the structure and composition of vegetation, which compromise their ecological functions. Shrub encroachment in grasslands is a global concern because it can reduce the occurrence of grassland birds. We evaluated the effectiveness of abandoned grassland areas under legal protection for the conservation of grassland avifauna, because the exclusion of disturbances, such as grazing and fire, favor the advancement of woody vegetation over grasslands. Birds were sampled during two periods in abandoned grasslands within farms of eucalyptus plantations. Significant differences in bird species composition were found between the two sampling periods as was a significant increase in species richness associated with shrubs and forests. There was no significant reduction in the number of grassland bird species between periods. Nineteen of the recorded species were recorded only in the second sampling period, of which only two are associated with grasslands. The results indicate that changes in vegetation mainly affect grassland specialist species and can lead to their local extinction in the long term. Furthermore, the studied grassland areas have, thus far, been effective for the conservation of birds. However, the results also demonstrate that the implementation of activities to manage woody vegetation can be a promising alternative for improving these areas for grassland birds over the medium and long term because shrub encroachment in these areas is evident.

RESUMEN. El declive y la fragmentación de los pastizales en los últimos años han estimulado los esfuerzos por conservar este ecosistema. Sin embargo, incluso los remanentes de pastizales legalmente protegidos se ven amenazados por cambios en la estructura y composición de la vegetación, que comprometen sus funciones ecológicas. La invasión de arbustos en los pastizales es una preocupación mundial porque puede reducir la presencia de aves de pastizal. Evaluamos la efectividad de las zonas de pastizales abandonados, que se encuentran bajo protección legal, para la conservación de la avifauna de pastizales, ya que la exclusión de perturbaciones, como el pastoreo y el fuego, favorecen el avance de la vegetación leñosa sobre los pastizales. Se tomaron muestras de aves durante dos periodos en pastizales abandonados dentro de fincas de plantaciones de eucaliptos. Se encontraron diferencias significativas en cuanto a la composición de las especies de aves entre los dos periodos de muestreo, así como un aumento significativo de la riqueza de especies asociadas a los arbustos y los bosques. No hubo una reducción significativa en el número de especies de aves de pastizal entre los dos periodos. Diecinueve de las especies registradas sólo se registraron en el segundo periodo de muestreo, de las cuales sólo dos están asociadas a los pastizales. Los resultados indican que los cambios en la vegetación afectan principalmente a las especies especialistas de pastizal y pueden provocar su extinción local a largo plazo. Es más, las zonas de pastizales estudiadas han sido, hasta ahora, eficaces para la conservación de las aves. Sin embargo, los resultados también demuestran que la implementación de actividades de manejo de la vegetación leñosa puede ser una alternativa prometedora para mejorar estas zonas para las aves de pastizal a mediano y largo plazo, ya que la invasión de arbustos en estas zonas es evidente.

Key Words: *avifauna; Brazilian Pampa grasslands; conservation; shrub encroachment; vegetation structure*

INTRODUCTION

Grasslands are among the most threatened ecosystems in the world as a result of strong anthropogenic pressure that has transformed and fragmented them (Hoekstra et al. 2005, Henwood 2010, Carbutt et al. 2017). The recent decline and fragmentation of grasslands has drawn attention to the preservation of this ecosystem, but conservation efforts remain relatively low (Pillar and Vélez-Martin 2010, Parr et al. 2014, Overbeck et al. 2015). Only 1% of the original extent of grasslands in southern South America is currently protected (Henwood 2010). In Brazil, existing legal measures to protect vegetation on private properties can prevent the conversion of native grasslands

to other uses, thereby preventing the loss of grassland biodiversity (Overbeck et al. 2007, 2015). However, even legally protected grasslands are threatened by changes in vegetation structure and composition, which compromise their ecological functions (Pillar and Vélez-Martin 2010, Archer et al. 2017, Sühs et al. 2020). The advance of woody vegetation over grasslands is a global concern and has been recorded throughout the world (Van Auken 2009, Eldridge et al. 2011, Archer et al. 2017, Sühs et al. 2020).

Historically, the dynamics of grasslands in southern South America have been associated with the occurrence of natural and anthropogenic disturbances, such as grazing and the use of fire to benefit the regrowth of grassland vegetation and the

¹Departamento de Ecologia, Universidade Federal do Rio Grande do Sul (UFRGS), Rio Grande do Sul, Brazil, ²Centro de Ecologia, Universidade Federal do Rio Grande do Sul (UFRGS), Rio Grande do Sul, Brazil, ³Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio Grande do Sul (UFRGS), Rio Grande do Sul, Brazil

maintenance of the grassland physiognomy (Overbeck et al. 2007, Pillar and Vélez-Martin 2010, Sühs et al. 2020). In this sense, management practices can be essential to ensure the conservation of grassland biodiversity, when conducted with adequate frequency and intensity (Andrade et al. 2015, Veldman et al. 2015). Native grassland vegetation predominates in the grasslands of the Pampa biome (IBGE 2004) in extreme southern Brazil, with forest formations in riparian areas and in regions of accentuated topography (Andrade et al. 2019). Livestock is an important economic activity in this region and cattle grazing shapes the grassland physiognomy by controlling the abundance of shrub species and, depending on grazing intensity, producing mosaics of vegetation of different heights (Overbeck et al. 2007, Andrade et al. 2019). When vegetation is legally protected, disturbances such as grazing are suppressed. Without disturbances, the composition of grassland communities becomes more homogeneous with a few dominant species, predominantly cespitose grasses forming clumps (Overbeck et al. 2007, Pillar and Vélez-Martin 2010), and there is gradual shrub encroachment (Oliveira and Pillar 2004, Blanco et al. 2014, Andrade et al. 2019). Sühs et al. (2020) studied altitude grasslands in southern Brazil and observed an accelerated proliferation of shrubs in protected areas, replacing grassland vegetation in a short period of time.

The dynamics of shrub encroachment after the exclusion of traditional management, e.g., grazing or fire, are little known for the grasslands of southern Brazil (Oliveira and Pillar 2004). Shrubs encroachment can alter grassland plant communities and ecosystem processes by negatively affecting grassland vegetation (Archer et al. 2017, Andersen and Steidl 2019, Sühs et al. 2020). Indeed, a decrease in plant species richness was detected in grasslands of southern Brazil (Overbeck et al. 2007). Other taxa are also affected, especially obligate grassland species (Blaum et al. 2009, Stanton et al. 2018) and those endemic to these ecosystems (Archer et al. 2017). For example, several studies have shown a reduced occurrence of grassland birds (Coppedge et al. 2004, Brennan and Kuvlesky 2005, Andersen and Steidl 2019), decreased diversity of mammals and amphibians (Stanton et al. 2018), and decreased abundances for some arthropod groups (Blaum et al. 2009). Changes in vegetation can alter the quality and quantity of habitat available to animal communities, especially grassland specialist species. Among birds the responses vary, but there is an overall reduction in grassland bird species and an increase in shrub-associated bird species (Coppedge et al. 2001, 2004, Sirami and Monadjem 2012, Andersen and Steidl 2019).

Studies in the grasslands of southern Brazil (Pampa biome, IBGE 2004) demonstrate the positive influence of disturbances on grassland bird diversity and indicate that low/moderate grazing intensities are beneficial for maintaining bird diversity (Develey et al. 2008, Fontana et al. 2016, Jacoboski et al. 2017). Furthermore, they show that the vertical heterogeneity of vegetation, shaped by grazing, forms mosaics of grasslands of different heights, which benefit bird species associated with short grasslands as well as those associated with the taller and denser vegetation of preserved grasslands, thereby maximizing the diversity of grassland birds (Dias et al. 2017, Jacoboski et al. 2017). Thus, bird diversity can vary among the different types of grasslands in the Pampa biome, either because of different grazing intensities or differences in climate, altitude, and soil type

(Fontana and Bencke 2015). Around 480 bird species, not counting wandering species, have been recorded in Brazilian Pampa grasslands (Develey et al. 2008), of which 95 are grassland birds (Fontana and Bencke 2015). Several of these species are threatened with extinction, especially those that do not tolerate disturbances such as grazing, because they need well-preserved vegetation to survive, that is, grasslands with tall and dense vegetation (Fontana and Bencke 2015). A total of 12 species of birds that live in Brazilian Pampa grasslands are threatened with extinction (Bencke 2016).

The present study is the first to assess the short-term effectiveness of abandoned grassland areas as habitat for grassland avifauna in southern South America. We consider short-term here to be a time span of up to 10 years, because Sühs et al. (2020) estimated a 30-year time period for the total replacement of vegetation after the exclusion of management. We aimed to assess whether abandoned grassland areas are effective as habitat for grassland avifauna in the short term. We used bird community and vegetation data collected by Jacoboski et al. (2017) collected in 2014–2015 and conducted sampling of the same areas four years later (2018–2019), thus representing two sampling periods. To meet our goal we tested four hypotheses: (1) the richness of bird species associated with shrub-forest vegetation will increase and the richness of grassland bird species will decrease; (2) bird species composition will change between sampling periods; (3) vegetation height, mean vegetation density, and percentage of native forest cover within the sampled areas will be higher in the second sampling period; and (4) vegetation structure will be crucial to explaining the richness and abundance of bird species in each sampling period. In general, vegetation structure is a key factor for bird distribution, as it is related to the availability of resources for food, nesting, and shelter (Fisher and Davis 2010).

METHODS

Study area

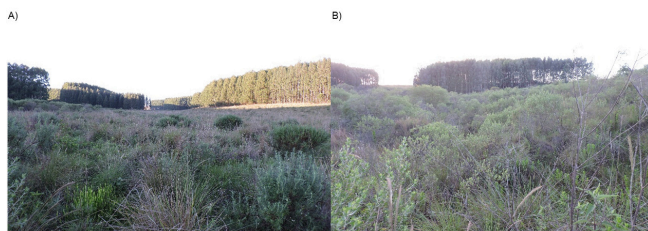
The study area is in the southernmost grasslands of Brazil, regionally known as the Pampa grasslands. These grasslands are part of the so-called grasslands of southeastern South America (SESA grasslands), the region with the largest extension of grassland ecosystems in the Neotropics (Azpiroz et al. 2012). Ten ecoregions, characterized on the basis of vegetation, altitude, and soil type, have been delimited within the portion that encompasses Brazilian grasslands (Hasenack et al. 2010). The study area is located in the mixed grassland of *Andropogoneae* and *Compositae* ecoregions, wherein prostrate species predominate in the lower stratum and grasses of the genus *Andropogon* spp. predominate in the upper stratum (Hasenack et al. 2010), and forests are more restricted to riparian zones (Andrade et al. 2019).

The sampled grasslands are legally protected by specific legislation and were abandoned about 10 years ago, when eucalyptus plantations were established. Each plantation is a mosaic of eucalyptus stands and native vegetation at different stages of development, ranging from grasslands to forest vegetation remnants. These areas of native vegetation within each plantation comprise Permanent Preservation Areas (PPAs). These PPAs within forest plantations comprise corridors of native vegetation around small watercourses surrounded by eucalyptus plantations. Brazilian legislation determines which margins of

watercourses must be preserved through the delimitation of a strip of vegetation for both banks, which varies according to watercourse width (CFB 2012). Therefore, since the establishment of eucalyptus plantations, all disturbances caused by cattle and fire have been excluded and there is no deliberate management, except for occasional records of invasion by cattle and accidental fire.

Sampling occurred in PPAs of eight eucalyptus plantation farms in the municipality São Gabriel (30°20'11"S, 54°19'12" W), located in the center-west portion of the state of Rio Grande do Sul. These areas were selected based on meeting two main requirements: predominance of grassland vegetation and a minimum width of 100 m for the application of the bird sampling method employed. The PPAs sampled in 2014–2015 (Jacoboski et al. 2017) had native grassland as the predominant vegetation, while in recent years there has been shrub encroachment in some of these areas (Fig. 1A, B).

Fig. 1. Permanent Preservation Areas (PPAs) in different stages of succession. (A) Grassland vegetation predominates with the beginning of shrub encroachment. (B) Shrub vegetation predominates in an advanced stage of succession.



In the Brazilian grasslands some shrub species, such as *Baccharis uncinella*, *B. dracunculifolia*, and *B. pentodonta*, may form a layer in the upper stratum of native grasslands (Boldrini et al. 2009, Andrade et al. 2019). These species are typical of grasslands in southern Brazil and characterize early stages of grassland succession in the absence of disturbances, such as grazing and fire (Oliveira and Pillar 2004).

Avifauna sampling

The data used were those of Jacoboski et al. (2017) from bird sampling during austral spring-summer (October to January) 2014 and 2015 and from re-sampling the same sites using the same methodology in 2018 and 2019, covering two reproductive seasons of the species. Two visits were made on two consecutive days at each of the eight sites in each period. The order of sampling the points of a given site on the second day was the opposite of that the first day. Abundance analyses used the highest abundance of the two sampling days for each species to avoid overestimates of abundance. Birds were sampled by the point-count method at points separated by a distance of at least 200 m (Bibby et al. 2000). Counting points were distributed according to site size such that there were from three to seven points per site with each site representing a sampling unit. All bird species seen or heard for a period of 10 minutes within a fixed radius of 50 m around each

point were recorded; birds in flight were not considered. Sampling started 10-minutes after sunrise and ended about three hours later. A total of 50 point-counts were performed, all sampled during favorable weather conditions, i.e., no strong wind or rain. Recorded bird species were classified according to habitat use following Azpiroz et al. (2012) for grassland birds and Stotz et al. (1996) for forest birds and those associated with shrub vegetation.

Vegetation sampling

Vegetation height and density were measured at each sampling point using a stick subdivided in centimeters (Dias and Scarano 2007). The stick was placed vertically on the ground and the following were recording: (1) density as the number of times vegetation touches the stick, and (2) height of each plant that touches the stick. Four such height and density measurements were performed at each sampling point ($n = 200$), at randomly determined cardinal directions (east, west, north, or south) and distances (5, 15, 30, and 50 m) from the center of the bird sampling point ($n = 200$), each of the four directed to each of the cardinal points direction (east, west, north, and south) and at four different distances (5, 15, 30, and 50 m), starting from the center of the counting sampling point. The distance and direction of the vegetation measurements were randomly determined. Statistical analyses used mean vegetation values per sampling site.

Categorization of land cover and use

Percentages of native woody and grassland vegetation within the sampled areas were quantified by land cover and land use change analysis using data from Phase 4 of the Brazil Annual Land Cover and Land Use Mapping Project (MapBiomias Project; Souza et al. 2020). This project annually maps land cover and land use throughout Brazil and monitors changes in territory using the Google Earth Engine platform (<https://earthengine.google.com/>). The annual maps of land cover and land use of MapBiomias were produced from pixel-by-pixel classification of images from Landsat satellites, with a spatial resolution of 30 x 30 m. These maps were then used to categorize land cover within each eucalyptus plantation farm for the bird sampling period (2014 to 2018). Coverage maps for the year 2019 were not yet available at the time of analysis. The maps were obtained, in geotiff format, through the Google Earth Engine platform, the same platform on which the maps (MapBiomias) were generated. Data visualization and analysis used the ArcMap program. Boundary data for the sampled farms were subsequently added and the areas of interest clipped, identifying which classes of land cover were present within each farm. The information about land cover classes, as well as the accuracy of the data (MapBiomias), were used to refine classes identified within farm boundaries (this process was made possible because MapBiomias performs mapping with a spatial cut aimed at Brazilian biomes, and in situ field verification allowed increased accuracy of the data). Percentages of each coverage were then calculated and compared annually. Land cover was classified into four different classes: native forest vegetation, planted forest, native grassland vegetation, and non-vegetated areas, i.e., roads or weirs. Percentages of planted forest and non-vegetated areas did not change over the years in each of the areas where the avifauna was sampled and so only the percentages of forest and grassland vegetation were included in the statistical analyses.

Data analysis

All hypotheses were tested using R software (R Development Core Team 2019). The vegan package (Oksanen et al. 2020) was used to test the first three hypotheses. For the first hypothesis, which predicted differences in bird species richness between the two sampling periods, rarefied richness was first calculated using the *rarefy* function. Differences in species richness and abundance between the two sampling periods, and also with respect to species classification, were then tested by ANOVA. The greatest number of individuals recorded in the two sampling periods was used for abundance to avoid recounting and overestimating individuals. The second hypothesis, which predicted differences in bird species composition between the two sampling periods, was tested by non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity. Permutational multivariate analysis of variance (PERMANOVA) was then employed to give statistical rigor to the clusters formed by NMDS and to test for differences in species composition (Anderson 2001). The contribution of each vegetation variable to explaining the clusters formed by NMDS was assessed using the *envfit* function with 9999 permutations, thus giving significance to the test. The third hypothesis, which predicted greater height and density of vegetation in the second sampling period, was also tested by ANOVA, as were differences in percentage of native forest and grassland vegetation within farms between the two periods.

The fourth hypothesis, which predicted effects of vegetation variables on species richness and abundance, was tested by generalized linear mixed models (GLMMs) using the Poisson family using the MuMIn package (Bartoń 2016). Models were created separately for rarefied richness and species abundance. The variables vegetation and year were considered fixed effects and site as a random effect for all models. A null model was also included in the models. None of the habitat variables (height, vegetation density, and percentage of vegetation cover) were significantly correlated. The created models were ranked by the Akaike information criterion corrected for small sample sizes (AICc), with the best being the one with the lowest AICc value. The *model.sel* function was used to select the models that best explained the richness and abundance of bird species in the communities using the fewest parameters (Burnham and Anderson 2002). Model weight (AICc weight) indicates the empirical support of a model in relation to other models. Models with Delta AICc > 2 units were considered to have low support (Burnham and Anderson 2002), and so only models with Delta AICc < 2 are included in the results

RESULTS

A total of 55 bird species were recorded during the two sampling periods (n = 35 in 2014–2015 and n = 47 in 2018–2019; Table 1), of which 20 were grasslands dependent. The most abundant species during the two sampling periods was *Zonotrichia capensis* (n = 44 and n = 90 individuals, in 2014–2015 and 2018–2019 respectively). Of the species recorded in the second period (2018–2019), 19 were not recorded in the first, two of which, *Phacellodomus striaticollis* and *Poospiza nigrorufa*, are grassland-dependent (Azpiroz et al. 2012). Three of the species not recorded in the second period are grassland-dependent: *Nothura maculosa*, *Vanellus chilensis*, and *Sporophila pileata* (Azpiroz et al. 2012). Two of the recorded species, *Culicivora caudacuta* (n = 25) and *Sporophila cinnamomea* (n = 4), are categorized as “Vulnerable”

Table 1. List of species recorded during the two sampling periods with the number of individuals per period and classification according to habitat dependence. Threat status follows DOE (2014) and IUCN (2022). Acronyms of Figure 3 are also shown.

Species	2014	2018	Habitat
<i>Agelaioides badius</i> (Agba)	3	0	Shrub
<i>Amazonetta brasiliensis</i> (Ambr)	10	8	Other
<i>Amodramus humeralis</i> (Amhu)	23	7	Grassland
<i>Chorostilbon lucidus</i> (Chlu)	1	1	Shrub
<i>Cistothorus platensis</i> [†] (Cipl)	1	4	Grassland
<i>Colaptes campestris</i> (Coca)	3	1	Grassland
<i>Columbina picui</i> (Copi)	0	1	Shrub
<i>Coryphospingus cucullatus</i> (Cocu)	0	5	Shrub
<i>Crotophaga ani</i> (Cran)	0	2	Shrub
<i>Culicivora caudacuta</i> [‡] (Cuca)	2	25	Grassland
<i>Cyclarhis gujanensis</i> (Cygu)	0	3	Forest
<i>Donacospiza albifrons</i> (Doal)	8	7	Grassland
<i>Emberizoides herbicola</i> (Emhe)	27	34	Grassland
<i>Emberizoides ypiranganus</i> (Emyp)	10	2	Grassland
<i>Embernagra platensis</i> (Empl)	27	28	Grassland
<i>Euscarthmus meloryphus</i> (Eume)	0	2	Shrub
<i>Furnarius rufus</i> (Furu)	1	6	Grassland
<i>Geothlypis aequinoctialis</i> (Geae)	4	19	Shrub
<i>Gnorimopsar chopi</i> (Gnch)	1	0	Other
<i>Heliobletus contaminatus</i> (Heco)	0	1	Forest
<i>Icterus pyrrhopterus</i> (Icpi)	1	1	Shrub
<i>Laterallus leucopyrrhus</i> (Lale)	1	0	Other
<i>Mustelirallus albicollis</i> (Mual)	2	15	Other
<i>Myiophobus fasciatus</i> (Myfa)	0	5	Shrub
<i>Myiopsitta monachus</i> (Mymo)	0	2	Forest
<i>Nothura maculosa</i> (Noma)	3	0	Grassland
<i>Paroaria coronata</i> (Paco)	4	7	Shrub
<i>Phacellodomus striaticollis</i> (Phst)	0	2	Grassland
<i>Pitangus sulphuratus</i> (Pisu)	1	8	Forest
<i>Poospiza nigrorufa</i> (Poni)	0	1	Grassland
<i>Progne chalybea</i> (Prch)	1	0	Shrub
<i>Progne tapera</i> (Prta)	1	2	Grassland
<i>Rhynchotus rufescens</i> (Rhru)	5	10	Grassland
<i>Saltator similis</i> (Sasi)	0	1	Forest
<i>Serpophaga subcristata</i> (Sesu)	1	15	Forest
<i>Setophaga pitayumi</i> (Sepi)	0	2	Forest
<i>Sicalis flaveola</i> (Sifl)	0	2	Shrub
<i>Sicalis luteola</i> (Silu)	7	20	Grassland
<i>Spinus magellanicus</i> (Spma)	1	11	Shrub
<i>Sporophila caerulea</i> (Spca)	5	10	Shrub
<i>Sporophila cinnamomea</i> [‡] (Spci)	3	4	Grassland
<i>Sporophila pileata</i> [§] (Sppi)	1	0	Grassland
<i>Synallaxis frontalis</i> (Syfr)	0	3	Forest
<i>Synallaxis spixi</i> (Sysp)	0	2	Shrub
<i>Tapera naevia</i> (Tana)	3	0	Shrub
<i>Thamnophilus ruficapillus</i> (Thru)	0	7	Shrub
<i>Troglodytes musculus</i> (Trmu)	2	46	Shrub
<i>Turdus amaurochalinus</i> (Tuam)	0	1	Forest
<i>Turdus leucomelas</i> (Tule)	0	2	Forest
<i>Tyrannus melancholicus</i> (Tyme)	0	1	Forest
<i>Tyrannus savana</i> (Tysa)	5	5	Grassland
<i>Vanellus chilensis</i> (Vach)	2	0	Grassland
<i>Volatinia jacarina</i> (Voja)	8	23	Grassland
<i>Zenaidura macroura</i> (Zeau)	1	1	Shrub
<i>Zonotrichia capensis</i> (Zoca)	44	90	Shrub

[†]Near threatened species in Rio Grande do Sul.

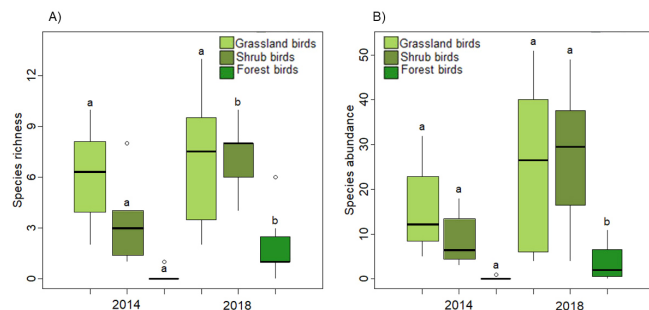
[‡]Vulnerable globally species.

[§]Vulnerable species in Rio Grande do Sul.

to extinction at the global level (IUCN 2022). Besides these, *Sporophila pileata* is categorized as “Vulnerable” at the regional level and *Cistothorus platensis* (n = 4), as “Near Threatened” at the regional level (DOE 2014).

Rarefied richness did not differ significantly between sampling periods (ANOVA, $F_{1,14} = 0.36$, $p = 0.31$), whereas abundance was significantly higher in the second sampling period ($F_{1,14} = 5.57$, $p = 0.03$). Classification of bird species according to vegetation dependence revealed a significant increase in the richness of species associated with shrub and forest vegetation in the second sampling period (ANOVA, $F_{1,14} = 15.19$, $p = 0.001$ and $F_{1,14} = 6.66$, $p = 0.02$, respectively; Fig. 2A). The richness of grassland birds did not differ between the two sampling periods (ANOVA, $F_{1,14} = 0.28$, $p = 0.60$; Fig. 2A). There was a significant increase in the abundance of species associated with forest vegetation in the second sampling period (ANOVA, $F_{1,14} = 8.61$, $p = 0.01$; Fig. 2B), while the abundance of grassland- and shrub-dependent birds did not differ significantly between sampling periods (ANOVA, $F_{1,14} = 0.30$, $p = 0.59$ and $F_{1,14} = 4.15$, $p = 0.06$).

Fig. 2. Boxplots showing (A) differences in bird species richness between the two sampling periods according to habitat dependence and (B) differences in the abundance of species between the two sampling periods according to habitat dependence. Different letters indicate significant differences between the two sampling periods.



Species composition differed significantly between the two sampling periods (PERMANOVA, $F_{1,16} = 2.42$, $p = 0.01$). Mean vegetation density was the variable most associated with bird species composition in the second sampling period (Fig. 3), while percentage of grassland vegetation within farms was most associated with species composition in the first sampling period. However, testing the importance of each of the vegetation variables to bird species composition found none to have a significant effect on composition (Table 2).

Mean vegetation height (ANOVA, $F_{1,14} = 4.31$, $p = 0.05$; Fig. 4A) and mean vegetation density increased in the second sampling period (ANOVA, $F_{1,14} = 10.49$, $p = 0.005$; Fig. 4B). Percentage of native forest cover did not differ significantly between sampling periods (ANOVA, $F_{1,14} = 0.13$, $p = 0.72$; Fig. 5A). Percentage grassland vegetation coverage was marginally significant (ANOVA, $F_{1,14} = 4.24$, $p = 0.058$), with a trend toward a reduction in coverage in the second period (Fig. 5B). The evaluation of the effect of vegetation variables on bird species richness and number of individuals in each community found the best model for species

richness to be the one that included only average vegetation height (Table 3), while for number of individuals the best model was the one that included the average vegetation height and average vegetation density (Table 3).

Fig. 3. Non-metric multidimensional scaling (NMDS) of bird species composition demonstrating the two sampling periods and their relationship to habitat variables. Acronyms for species names are provided in Table 1.

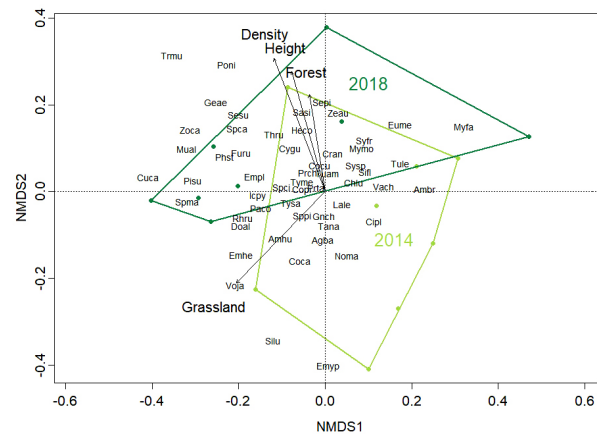


Table 2. Vector scores for habitat variables related to two axes of non-metric multidimensional scaling (NMDS).

Habitat variable	NMDS1	NMDS2	r ²	P
Mean vegetation density	-0.36022	0.93287	0.1421	0.3630
% Grassland vegetation	-0.69678	-0.71728	0.1126	0.4532
Mean vegetation height	-0.26969	0.96295	0.1078	0.4763
% Forest vegetation	-0.15912	0.98726	0.0670	0.6288

Fig. 4. Boxplots showing differences in (A) vegetation height and (B) vegetation density between sampling periods. Different letters indicate significant differences between the two sampling periods.

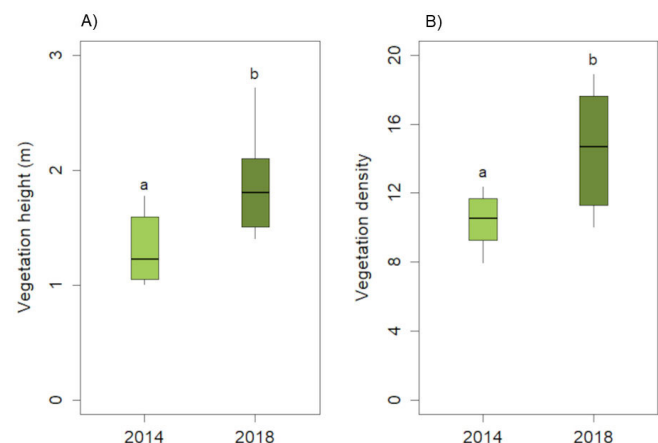


Fig. 5. Boxplots showing differences in (A) percentage of forest cover and (B) grassland coverage percentage between sampling periods. Equal letters indicate that there was no significant difference between the two sampling periods.

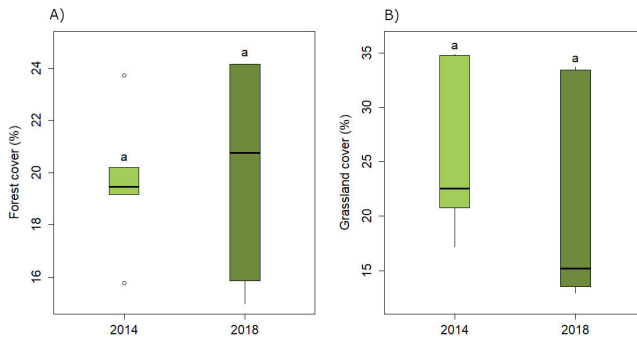


Table 3. Comparison of generalized linear mixed models (GLMMs), using Akaike's information criterion for small sample sizes (AICc), comparing the effects of vegetation variables on species richness and abundance. Only models with $\Delta AICc < 2$ are presented, in ascending order of AICc value (best to worst).

Model structure	df	logLik	AIC _c	ΔAIC	Model weight
Richness ~ height	3	-31.42	70.8	0.00	0.966
Abundance ~ height+density	4	-77.48	166.6	0.00	0.473
Abundance ~ height	5	-75.68	167.4	0.75	0.324
Abundance ~ height+density+% forest	5	-76.15	168.3	1.71	0.201

DISCUSSION

The results of the present study demonstrate that both the richness and abundance of grassland species remained stable between sampling periods, indicating that, thus far, the PPAs are effective for their maintenance. However, we found a significant increase in the richness of species associated with shrub and forest vegetation in the second sampling period. That is, differences in species richness were significantly related to species habitat. This result suggests that changes in vegetation structure may be shaping the distribution of bird species in the studied areas. The absence of disturbances such as grazing and fire may have influenced the results because these factors contribute to restraining shrub encroachment over grasslands (Andrade et al. 2019, Sühs et al. 2020). Other studies have shown that habitat for grassland specialists decreases with the transition from grassland to shrubland, so that the abundance and diversity of grassland birds also decreases (Coppedge et al. 2001, 2004, Grant et al. 2004, Sirami and Monadjem 2012, Andersen and Steidl 2019). These studies, however, involved long-term (i.e., 10+ years) evaluations (e.g., Coppedge et al. 2001, Sirami and Monadjem 2012). The present study involved a shorter period of time and only two sampling periods during which it was not possible to follow all stages of vegetation succession. In the long

term, shrub encroachment may reach more advanced stages and grassland species may be displaced to other areas as the needs of their niche may be suppressed by the woody component of the vegetation (e.g., Sirami et al. 2009, Archer et al. 2017, Andersen and Steidl 2019). In a study carried out in high-altitude grasslands in southern Brazil (Atlantic Forest biome; IBGE 2004), Sühs et al. (2020) estimated that 30 years is necessary for shrubs to dominate abandoned grasslands. These grasslands differ from the grasslands in the extreme south of Brazil (Pampa biome; IBGE 2004) because they have different climatic conditions, higher altitude, and frequent use of fire for vegetation management (Andrade et al. 2019). We do not know of any similar estimates for the Pampa grasslands, where our study was carried out. Considering that the woody element in this region is concentrated only in riparian regions, we suggest that this amount of time should be greater in this region.

Because of the lack of species-specific studies, we cannot say with certainty, but each bird species seems to have a different tolerance threshold in relation to the shrub encroachment. Thus, populations of bird species can expand, contract, or even be excluded locally according to the intensity of shrub encroachment (Andersen and Steidl 2019). In the present study, *Serpophaga suberistata* and *Geothlypis aequinoctialis*, species associated with shrub vegetation (Stotz et al. 1996), increased not only in abundance but also in frequency of occurrence in the second sampling period, whereas *Ammodramus humeralis*, a grassland vegetation-dependent species, experienced a decrease. These species-specific differences may be of interest in identifying species that are particularly vulnerable to shrub encroachment. For example, it is interesting to note that *C. caudacuta* experienced a significant population increase in the second sampling period (Table 1). In other words, this grassland-dependent species that selects habitat where shrub density is low (Sousa and Marini 2007, Kanegae et al. 2012) is, thus far, benefiting from PPAs. Initially registered at just one farm, the species came to occupy four of them. We recorded the presence of 11 nests of the species during our observations (*unpublished data*). The species occurs both in grassland areas and in areas with higher densities of shrubs and uses them for perching and building nests (*personal observation*). However, we do not know the threshold of shrub encroachment tolerated by this and other grassland specialist species in grassland, as shrub encroachment can decrease habitat quality for specialists and reduce their survival or reproductive success (Klug et al. 2010, Sirami and Monadjem 2012). For example, the risk of nest predation increases with increasing shrub cover, because snakes and predatory birds are known to use shrub habitat, resulting in decreased reproductive success of birds in areas invaded by woody plants (With 1994, Mason et al. 2005, Graves et al. 2010, Klug et al. 2010). Species-specific responses may explain why the effects of shrub encroachment on bird populations and communities vary with stage of encroachment; that is, whereas some specialist species can be displaced at an early stage of encroachment, others can tolerate more advanced stages (Archer et al. 2017, Andersen and Steidl 2019). Furthermore, different responses can be expected with regard to the predominant shrub species, the degree of density, and the geographic region involved (Ayers et al. 2001, Meik et al. 2002, Blaum et al. 2009, Archer et al. 2017).

One of the grassland species registered in the first sampling period and not in the second, *Vanellus chilensis*, is typical of grasslands with thinner and shorter vegetation (Azpiroz et al. 2012, Fontana and Bencke 2015), and thus ended up being displaced from the areas because of increased vegetation height and density. This species is very common in the studied region and may even benefit from anthropogenic landscapes. On the other hand, *Phacellodomus striaticollis* and *Poospiza nigrorufa*, recorded in the second period, use grasslands (Azpiroz et al. 2012) but depend on the occurrence of shrub and woody vegetation to nest and take refuge (*personal observation*). Specialist birds that are dependent on grasslands with tall vegetation (*Sporophila* spp.), many of which are threatened in southern South America (Fontana and Bencke 2015), are negatively affected by the loss of grassland habitat, be it in a natural (e.g., advance of woody species) or anthropogenic manner. Considering the accelerated conversion of the grassland ecosystem in the studied region, and the already known scarcity of tall and well-preserved grassland vegetation throughout the Pampa biome (e.g., Bencke 2009, Azpiroz et al. 2012), successful displacement may be unfeasible for many species.

The results here also demonstrate a restructuring of the bird community with significant changes in species composition. Although we did not detect a significant influence of vegetation structure on species composition, we saw that vegetation structure was a determinant of species richness and abundance. In this sense, differences in bird species composition between periods may be related to the biology of each bird species because each species has specific niche requirements associated with different vegetation structure (Fisher and Davis 2010, Azpiroz and Blake 2016). Although we did not observe a significant increase in forest vegetation cover between sampling periods, this variable was among the best models in our analyses of species abundance. Alterations to vegetation structure within the PPAs may indicate a more complex and sometimes more heterogeneous habitat, considering the density of shrubs, mainly of the genus *Baccharis* (*personal observation*), in some of the observed areas. These changes alter grassland communities as they reduce the quantity and quality of habitat available for species dependent on this vegetation type (Archer et al. 2017). In this way, the composition of bird communities change with increasing density of woody plants as new foraging opportunities, hiding places, and nesting sites become available (Coppedge et al. 2004, Archer et al. 2017, Stanton et al. 2018, Andersen and Steidl 2019). On the other hand, these new niche opportunities end up displacing bird species associated with grassland vegetation because of the loss of a specific niche. As areas dominated by grassland vegetation are invaded by shrubs and trees, a decline in grassland bird populations is imminent (Coppedge et al. 2001, 2004, Grant et al. 2004, Brennan and Kuvlesky 2005).

Our study is the first to present a temporal assessment of bird communities in abandoned grasslands in southern South America. Despite being a relatively short-term and only a 2-time point study, it showed changes in the structure of the bird community and in the structure of vegetation. Responding to our initial question, we found that, thus far, the abandoned grassland areas studied here are effective for the conservation of grassland bird species, especially those dependent on well-preserved, high vegetation grasslands. However, our results bring a warning about

the future of these species, especially grassland specialists. In line with other studies (e.g., Grant et al. 2004, Sirami et al. 2009, Graves et al. 2010, Andersen and Steidl 2019), our results confirm the general concern with grassland-dependent bird species, especially in southern South America. If there is an increase in the density of shrubs in grasslands in the medium and long term, the preservation of grassland avifauna in these areas may depend on some management activity directed at woody vegetation, such as mowing or selected cutting, to avoid shrub encroachment and the consequent local exclusion of grassland bird species by species associated with woody vegetation. Removing woody vegetation will increase grassland area, thereby improving habitat quality for grassland specialists, and may also reduce the occurrence of bird predators and nest brood parasites (Hauber and Russo 2000, Graves et al. 2010) as it eliminates the structures they use, such as woody vegetation as visual perches (e.g., With 1994). In addition, management actions for vegetation can have a cascade effect by benefiting grassland specialists of other taxa, i.e., plants, insects, and mammals (Archer et al. 2017, Andersen and Steidl 2019). We emphasize that our study was a short-term study, and it was not possible to follow the complete process of vegetation succession, so it is essential to continuously monitor these areas to investigate whether grassland bird populations will remain stable or, in the long term, become completely replaced by birds not associated with grassland vegetation. In this case, species-specific answers can help to elucidate issues related to the conservation of grassland specialists in these areas because their displacement to other areas may be impracticable.

Responses to this article can be read online at:

<https://journal.afonet.org/issues/responses.php/84>

Author Contributions:

Lucilene Inês Jacoboski and Sandra Maria Hartz conceived the ideas of the paper. Lucilene Inês Jacoboski collected the data in the field, conducted analysis, and lead the writing of the manuscript. Allan de Oliveira de Oliveira processed the satellite images and calculated the percentages of land cover. All authors contributed to writing the present paper and gave their final approval for submission.

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Data Availability:

The data/code supporting the findings of this study are available on request from the corresponding author, [L. I. J.]. None of the data/code are publicly available because of contractual restrictions by the financing company of the study.

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