

ESCOLA DE CIÊNCIAS DA SAÚDE E DA VIDA  
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**VARIAÇÃO TEMPORAL NA COMUNIDADE E NA REPRODUÇÃO DE AVES CAMPESTRES  
EM ÁREAS QUEIMADAS NOS CAMPOS DE ALTITUDE NO SUL DO BRASIL**

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PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL  
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NO SUL DO BRASIL**

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**TESE DE DOUTORADO  
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*"In the end,  
we will conserve only what we love,  
we will love only what we understand,  
and we will understand only what we are taught."*

**Baba Dioum**

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## RESUMO

Os campos da América do Sul vêm sofrendo uma intensa transformação nas últimas décadas, principalmente devido à conversão do campo nativo em áreas de silvicultura ou lavouras. O uso correto do fogo, geralmente associado à pecuária, tem sido apontado como uma forma de manejo para conservação de áreas campestres em várias partes do mundo. O objetivo desse estudo foi avaliar as mudanças ocorridas nas comunidades, na reprodução e nos territórios de aves campestres ao longo do tempo, em áreas submetidas a diferentes históricos de distúrbio por fogo nos campos de altitude no sul do Brasil. As comunidades de aves foram amostradas através de pontos de contagem durante quatro temporadas (2015 – 2018), enquanto as buscas por ninhos e territórios de *Emberizoides ypiranganus* e *Sporophila melanogaster* ocorreram em três (2013, 2016 e 2017) e duas (2016 e 2017) temporadas reprodutivas, respectivamente. Fizemos comparações da riqueza, abundância e composição de espécies nos diferentes anos. As taxas de sobrevivência diária dos ninhos foram calculadas com o programa MARK e os territórios foram medidos com o estimador kernel 95%. A riqueza, abundância e composição de espécie variou significativamente na temporada em que ocorreu a queimada, retornando aos valores iniciais (ano anterior ao fogo) dois anos após o distúrbio. Em áreas queimadas anualmente ou em áreas sem fogo também houve diferenças entre as temporadas, mas sem um padrão claro. Ainda nas análises da comunidade, das seis espécies avaliadas individualmente quanto à densidade, três responderam significativamente ao tempo decorrido desde o fogo. Quanto à reprodução, nós monitoramos 237 ninhos (178 de *E. ypiranganus* e 59 de *S. melanogaster*). A probabilidade de sobrevivência e a produtividade dos ninhos de ambas espécies não mostraram diferenças significativas entre as temporadas reprodutivas, tanto na área queimada ocasionalmente como na área frequentemente queimada. No entanto, o tamanho e o número de territórios de *E. ypiranganus* variaram ao longo do tempo na área queimada ocasionalmente, havendo menos territórios e estes sendo menores na temporada do fogo. O número de territórios de *S. melanogaster* foi menor um ano após o fogo em comparação com a temporada em que ocorreu a queimada. Na área com fogo frequente não houve mudanças no número e no tamanho dos territórios medidos. Nosso estudo é o primeiro a abordar a dinâmica temporal dos efeitos do fogo sobre as comunidades e aspectos importantes da história de vida de aves campestres no sul do Brasil. Os resultados obtidos permitem saber o tempo que a comunidade de aves ou os parâmetros territoriais de aves campestres levam para se recuperar após um evento de fogo. Embora os resultados mereçam a devida cautela na sua extrapolação devido ao número de áreas que foi possível amostrar, informações sobre a frequência com que o fogo pode ser utilizado são importantes para o planejamento e a implementação de práticas que usam o fogo como uma ferramenta de manejo em áreas campestres. Estudos adicionais deveriam avaliar os efeitos de longo prazo causados pela mudança no regime de fogo, quando uma área onde não havia queimadas regulares passa a ser manejada com fogo ou quando esse distúrbio é excluído de uma área que era frequentemente queimada.

Palavras-chave: aves campestres, conservação, *Emberizoides ypiranganus*, manejo, sobrevivência de ninhos, *Sporophila melanogaster*, território

## ABSTRACT

Temporal variation in bird community and breeding of grassland birds in burned areas in highland grasslands of southern Brazil

Grasslands of South America have been suffering an intense transformation in the last decades, mainly due to the conversion of native grasslands to agriculture or afforestation areas. The correct use of fire, often associated to cattle raising, has been pointed as a form of management to conserve grassland areas over the world. We aimed to assess changes in communities, breeding, and territories of grassland birds over the time, in areas under different histories of fire disturbance in highland grasslands of southern Brazil. Bird communities were sampled through point counts during four seasons (2015 – 2018), while search for nests and territories of *Emberizoides ypiranganus* and *Sporophila melanogaster* occurred in three (2013, 2016 e 2017) and two (2016 e 2017) breeding seasons, respectively. We made comparisons of richness, abundance and species composition in different years. Daily survival rates of nests were calculated with MARK program, and territories were measured using the 95% kernel estimator. Richness, abundance and species composition varied significantly in the season of the fire, returning to the initial values (year before the fire) two years after the disturbance. In areas occasionally burned or areas without fire there were differences among the seasons either, but not with an equally clear pattern. Still in the analysis on the communities, of the six species assessed individually for density, three responded significantly to time since the fire. Considering breeding, we monitored a total of 237 nests (178 of *E. ypiranganus* and 59 of *S. melanogaster*). Cumulative survival probability and productivity of the nests of both species did not show statistically significant differences among breeding seasons, both in the area burned occasionally and in the area frequently burned. However, the size and number of territories of *E. ypiranganus* varied over time in the area burned occasionally, with small and less territories in the season of the fire. The number of territories of *S. melanogaster* was lower one year after the fire in comparison with the season of the fire. In the area with frequent fire there were no changes either in the number or in the size of the measured territories. Our study is the first one to address the temporal dynamics of the effects of fire on communities and important aspects of natural history of grassland birds in southern Brazil. The results allow to know the time taken for the bird community or the territorial parameters of grassland birds to recover after a fire disturbance. Although the results deserve caution in their extrapolation due to the number of areas that it was possible to sample, information about how often fire can be used is important for planning and implementing practices that use fire as a management tool in grassland areas. Further studies should assess long-term effects caused by changes in fire regime, when an area where there was no regular fire becomes managed with fire or when this disturbance is excluded from an area that was often burned.

Keywords: conservation, *Emberizoides ypiranganus*, grassland birds, management, nest survival, *Sporophila melanogaster*, territory



## APRESENTAÇÃO

No sul do Brasil, aproximadamente 25% dos campos foram perdidos em decorrência de mudanças no uso da terra nas últimas três décadas, causadas, principalmente, por atividades antrópicas como agricultura e silvicultura (Overbeck et al. 2007). Esta perda e degradação dos habitats têm consequências diretas sobre a avifauna associada a áreas abertas, levando a declínios populacionais, como já observado em estudos realizados em diferentes partes do mundo (e.g., Di Giacomo e Di Giacomo 2004, Donald et al. 2006, Askins *et al.* 2007). Apesar disso, pouca importância é dada aos campos, e nem sempre as leis atuais são cumpridas para reverter a perda dos ecossistemas não-florestais no Brasil, pois as políticas de conservação no país estão fortemente voltadas para os biomas florestais (Overbeck et al. 2015). Exemplo disso é o grau de proteção dos campos no sul do Brasil, onde menos de 0,5% de sua área está protegida em unidades de proteção integral (Overbeck et al. 2007, Pillar e Véllez 2010). Os campos de altitude do sul do Brasil, localizados no nordeste do Rio Grande do Sul e nos estados de Santa Catarina e Paraná muitas vezes são negligenciados por estarem localizados em encaves de vegetação campestre no bioma Mata Atlântica e, por esse motivo, também merecem atenção. Esses campos possuem uma relação histórica com distúrbios como o fogo e o pastejo (Behling e Pillar 2007), sendo tradicionalmente manejados com fogo no final do inverno, no intuito de queimar a biomassa acumulada e estimular o rebrote da vegetação para alimentação do gado (Overbeck e Pfadenhauer 2007, Andrade et al. 2019). Sabe-se que na ausência desses distúrbios as formações florestais tendem a avançar sobre as áreas de campo, levando à descaracterização e perda das formações campestres (Overbeck et al. 2005, Behling e Pillar 2007, Buisson et al. 2018).

Por outro lado, distúrbios podem impactar negativamente algumas espécies da fauna. O sobrepastejo, pisoteio pelo gado e queimadas anuais dos campos são apontados como ameaças a espécies campestres no Rio Grande do Sul (Fontana et al. 2003). O fogo também pode ter efeitos negativos diretos (destruindo ninhos) ou indiretos (aumentando as taxas de predação e parasitismo) na reprodução de aves campestres (Rohrbaugh et al. 1999, Reinking 2005).

Diante disso, entender os efeitos do fogo sobre a biodiversidade é fundamental para subsidiar ações de conservação que utilizem o fogo como uma ferramenta de manejo de áreas campestres. Abordagens que avaliem a dinâmica temporal dos efeitos do fogo sobre as aves são de grande necessidade, dada a carência desses estudos na América do Sul. Portanto, desenvolvemos o primeiro estudo abordando a questão temporal do fogo em relação à reprodução de aves nos campos no sul do Brasil. O trabalho também configura o primeiro

estudo que avaliou comunidades de aves ao longo de quatro anos na região, com dados desde o período anterior ao fogo até dois anos após o distúrbio. Assim, nossos resultados contribuem para o conhecimento dos efeitos do fogo na reprodução e na comunidade de aves, auxiliando na tomada de decisões para o planejamento de ações de manejo em áreas campestres.

A tese está dividida em dois capítulos, os quais estão estruturados na forma de artigos científicos. No primeiro capítulo (artigo 1), avaliamos os parâmetros da comunidade de aves (riqueza, abundância e composição) em áreas com diferentes históricos de distúrbio provocado por fogo, buscando verificar quais mudanças ocorrem ao longo do tempo e qual o período necessário para recuperação desses parâmetros após uma queimada. Esse artigo foi submetido para publicação no periódico *PloS ONE*, Qualis Capes A1. Além disso, os resultados parciais deste artigo foram apresentados no XXVI Congresso Brasileiro de Ornitologia, em 2019. O segundo capítulo (artigo 2) avalia os efeitos temporais do fogo na reprodução e nos territórios de duas espécies de aves associadas a campos altos (*Emberizoides ypiranganus* e *Sporophila melanogaster*). Este artigo será submetido para publicação no periódico *Ibis*, Qualis Capes A1. Os resultados parciais foram apresentados no XXV Congresso Brasileiro de Ornitologia, em 2018, onde o trabalho recebeu o prêmio Helmut Sick (2º lugar) na categoria apresentação oral pós-graduação.

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## **CAPÍTULO 1**

### **Temporal changes in bird communities in areas with different histories of fire disturbance in highland grasslands of Brazil**

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Temporal changes in bird communities in areas with different histories of fire disturbance in  
highland grasslands of Brazil

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## 22 **Abstract**

23           Despite the importance and ubiquity of grasslands, the degradation and loss of these  
24 habitats has negatively affected bird populations throughout the world. The use of fire to  
25 manage grassland areas in some regions of southern Brazil can help to maintain these areas but  
26 can also influence the bird community in different ways. We assessed temporal changes in  
27 richness, abundance, and composition of bird communities in areas with different histories of  
28 fire disturbance in highland grasslands of southern Brazil, the most extensive remnant of  
29 grassland of the Atlantic Forest biome. We censused birds during four breeding seasons (2015–  
30 2018), through point counts in areas burned only once in the last ten years (OF, n = 3), areas  
31 burned annually (AF, n = 2), and areas without fire in the last ten years (WF, n = 2). In OF the  
32 richness, abundance, and species composition changed in the year of the fire, compared to the  
33 previous year, and returned to the initial values two years later. In AF and WF we found some  
34 differences among the years, but not with an equally clear pattern. Three of the six grassland  
35 species assessed individually for density responded significantly to temporal habitat  
36 modification caused by fire. Our results show that two years without fire were enough time for  
37 the bird community to recover after a fire, but some responses are species-specific. Therefore,  
38 fire can be used as a management tool for grasslands and may help in the conservation of birds  
39 of southern Brazil, as long as with a minimum interval between fires in an area is guaranteed.

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42 *Keywords:* abundance, bird community, composition, disturbance, fire, southern Brazilian  
43 grasslands

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## 45 **Introduction**

46 Grasslands occupy about 13.7 million ha of South Brazil and have been undergoing  
47 extensive transformation in recent decades, mainly from conversion of native grassland areas  
48 to agriculture or afforestation [1,2]. The degradation and loss of grassland areas have negatively  
49 affected bird populations throughout the world [1]. The biodiversity in southern Brazilian  
50 highland grasslands, located in northeastern Rio Grande do Sul and the states of Santa Catarina  
51 and Paraná, has also been impacted by anthropic actions [3–5]. This region houses about 70%  
52 of the bird species associated with grassland landscapes in southeastern South America,  
53 including endemic, migratory and/or threatened species [1,6–8].

54 The two main ways of managing grasslands are fire and grazing, and these disturbances  
55 are usually associated with cattle raising, an activity that allows to combine production and  
56 conservation in southern Brazil [3,9,10]. In southern Brazilian highland grasslands, fire is  
57 traditionally used to manage them at the end of winter, in order to burn the accumulated biomass  
58 and stimulate the regrowth of vegetation for cattle feed [11,12]. In the last years laws have been  
59 introduced in order to allow the use of controlled fire in grasslands in some municipalities of  
60 northeastern Rio Grande do Sul state, but this decision is usually based more on political and  
61 cultural issues than on scientific studies that assess the impacts of fire on animal and plant  
62 communities. Although the use of fire is already recommended as a management tool for  
63 protected areas in Brazil, its application is not yet a reality in these areas, and this issue is still  
64 a taboo [13,14].

65 It is known that in the absence of any disturbance (e.g., grazing or fire), grasslands show  
66 a high dominance of a few species of caespitose grasses (that form tussocks) and a low diversity  
67 of forbs, resulting in a homogenization of the vegetation structure [2,15] and a consequent  
68 reduction of the bird diversity [16,17]. In the long term, in abandoned grasslands (i.e. long

69 periods without grazing or fire), the floristic richness can be reduced and the grassland  
70 vegetation itself can be lost due to encroachment of shrubs [12,18,19]. A recent study in  
71 highlands of southern Brazil estimated in 30 years the time needed for shrubs to encroach into  
72 99% of grasslands without management [20]. Fire exclusion also leads to the accumulation of  
73 flammable biomass and, consequently, can increase fire intensity and risk of catastrophic fire  
74 [13,19,21]. However, when in excess (e.g., overgrazing, cattle trampling and high frequencies  
75 of fire) these disturbances can cause the decline of threatened bird species, mainly those  
76 dependent of tall grasslands, as observed for Rio Grande do Sul state in Brazil [5,22]. Thus, the  
77 threshold between sustainable use and degradation seems to be subtle when we consider fire is  
78 a factor in maintaining the integrity of grasslands [9].

79         In North America, the probability of occurrence of several grassland bird species has  
80 decreased significantly in areas where the coverage of tall shrubs and trees has increased [23].  
81 Some species increase in density in recently burned areas, and may be excluded from unburned  
82 areas [24–26]. For other species, the reductions in the abundance of individuals and the number  
83 of nests suggest that fire has a strong negative effect [26,27]. Since fire can directly (nest  
84 destruction) or indirectly (changes in vegetation structure) affect the bird community in  
85 different ways [28], studies that assess the effects of burning are necessary for the proper  
86 management of grassland areas.

87         In South America most of the studies about fire effects on birds in non-forest habitats  
88 have been conducted in Argentina (e.g., [29–32]) or in Central Brazil (e.g., [33–36]). Few  
89 studies have specifically assessed this issue in southern Brazilian highland grasslands, and most  
90 have only compared burned and unburned areas (e.g., [37–39]). Despite temporal scale strongly  
91 influences both the ecosystem responses to fire and the effects of fire [40], long-term studies  
92 are uncommon, and temporal aspect of the effects of certain variables (e.g., intensity, period  
93 and frequency of fire) on bird response to fire is seldom discussed [41], particularly in



94 Neotropical region. Therefore, approaches that evaluate temporal dynamics of fire effects,  
95 including pre- and post-fire periods, are needed to assess possible changes associated with fire  
96 in local populations and bird community. Our study is the first that considers the temporal  
97 dynamics of fire on bird community in highland grasslands of South Brazil.

98         Here, we assessed the parameters of the grassland bird community (richness, abundance  
99 and composition) over four breeding seasons, in areas with different histories of fire  
100 disturbance, aiming to determine the effects of fire on grassland birds over time. We  
101 hypothesized that: (1) Bird community structure in areas with a constant history of management  
102 over time (i.e. annual fire or without fire) does not change temporally, or may present a different  
103 variation pattern when compared with areas burned occasionally; (2) Richness, abundance and  
104 bird composition changes after an occasional fire and return to pre-disturbance levels as time  
105 goes by; and (3) Since we know that birds respond differently to variations in habitat structure  
106 caused by fire [28,30], and differences in vegetation height is an important driver of species  
107 sorting [42], the predict abundance of tall-grass species will reduce and the abundance of short-  
108 grass species will increase in grasslands in the year of the fire.

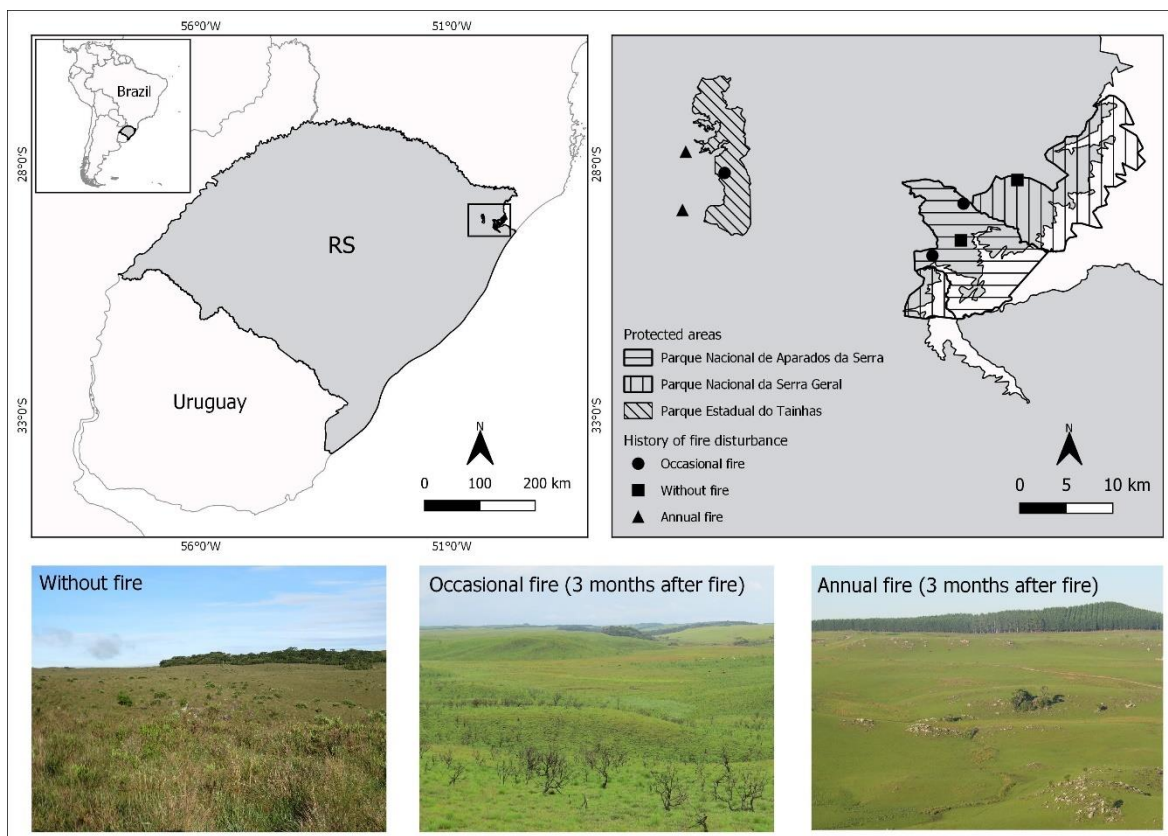
109

## 110 **Materials and methods**

### 111 **Study area**

112         The study areas are situated in the southern Brazilian highland grasslands (*sensu* [14]),  
113 in the Atlantic Forest biome. We selected seven areas of native grassland, in three protected  
114 areas (Parque Nacional de Aparados da Serra, Parque Nacional da Serra Geral and Parque  
115 Estadual do Tainhas) and on nearby farms, in northeastern Rio Grande do Sul state (Fig 1). We  
116 categorized areas according their histories of fire disturbance: (1) occasional fire (OF) – areas

117 burned (accidentally) only once in the last ten years (n = 3); (2) annual fire (AF) – areas burned  
 118 annually (n = 2); and (3) without fire (WF) – areas without fire in the last ten years (n = 2). The  
 119 fires occurred between August and October in the study areas, even those burned accidentally.  
 120 All areas (including the protected areas) are used for cattle raising and have similar low grazing  
 121 pressure (0.3 to 0.5 animal unit per hectare). Our study areas are composed mainly by large  
 122 extensions of native grasslands interspersed with marshes, rocky outcrops, and patches of  
 123 *Araucaria* forests (*Araucaria angustifolia*). Surrounding areas also have these features and, in  
 124 addition, usually have exotic pine (*Pinus* spp.) plantations and crops (mainly maize, potatoes,  
 125 and soybean).



126  
 127 **Fig 1. Locations of the study areas in highland grasslands in northeastern Rio Grande**  
 128 **do Sul (RS) state, Brazil.** Pictures are examples of landscapes of the three histories of fire  
 129 disturbance in our study areas.

130

131           The landscape of the study areas resembles typically the grasslands in the Atlantic Forest  
132 biome of South Brazil. Southern Brazilian highland grasslands cover about 60,000 km<sup>2</sup> and  
133 consist of a mosaic of grasslands and *Araucaria* forest, together with other vegetation types in  
134 a minor contribution, such as wetlands and peat bogs, with an undulating relief and mean  
135 altitude of 900–1,000 m a.s.l. [1,5,12,14]. These grasslands are characterized by dominance of  
136 perennial grass species in terms of cover and by high levels of endemism and high overall  
137 species richness, where Poaceae (mostly represented by tussock species such as *Andropogon*  
138 *lateralis*, *Axonopus siccus*, and *Schizachyrium tenerum*), Asteraceae, Fabaceae and Cyperaceae  
139 are the main families in species number [14,43]. The mean annual temperature in the region  
140 ranges from 16 °C to 22 °C and the precipitation is evenly distributed throughout the year  
141 (1,500–2,000 mm), reaching up to 2,500 mm in certain subregions [44,45].

142

## 143 **Data collection**

144           Bird surveys were conducted during four consecutive breeding seasons (2015–2016 to  
145 2018–2019), between November and February, the breeding period of most species in the  
146 region [46]. Birds were recorded in point counts of 10 min with an 80 m radius [47]. All  
147 individuals sighted and/or heard inside the circle were counted and their distances from the  
148 observer were estimated. Samplings were carried out from dawn to 10:00 a.m., in suitable  
149 weather conditions (without rain and with wind less than 10 km/h). The number of point counts  
150 was distributed according to the size and availability of the area in each breeding season (S1  
151 Table), with a proportional number of points located in dry grasslands and near wetlands in  
152 each area. The minimum distance between two point-count centers was 300 m, and they were  
153 sited in open areas at a minimum distance of 150 m from the edges of other vegetation types  
154 (e.g., forests) or from fences. Each point was sampled twice per breeding season (see statistical

155 analysis) in order to record the bird richness more accurately. The procedures adopted to avoid  
156 double counts and ensure independence among counts were: (1) sampling was conducted only  
157 in the breeding season, when individuals tend to keep their breeding territories; (2) minimum  
158 distance of 300 m between point counts; (3) counting only birds using the area within the point  
159 radius, excluding those merely flying over the area; (4) not counting groups of birds that move  
160 over large distances or are difficult to count (e.g., swallows, swifts, and birds of prey).

161 We sampled vegetation (height) and ground-cover variables (percentage of vegetation  
162 cover, bare ground, rocks, and water) of each point in four quadrats ( $1 \times 1$  m). These quadrats  
163 were placed at different distances from the point count: 10 m to the north, 25 m to the west, 50  
164 m to the south, and 75 m to the east. Vegetation height was measured at five points in each  
165 quadrat (at the center and at the four vertices). These data were grouped as mean values at the  
166 point-count level. The vegetation was sampled at the end of each breeding season, immediately  
167 after the end of bird counts.

168

## 169 **Statistical analysis**

170 Differences in bird species richness between breeding seasons were assessed through  
171 the rarefaction and extrapolation method, based on sample coverage [48]. This method allows  
172 comparisons of richness based on samples with the same coverage (completeness) rather than  
173 the same size, which would be an advantage when comparing areas or years with very different  
174 degrees of diversity [48]. The species richness was calculated for each breeding season, based  
175 on the lowest sample coverage among the four values obtained in each history of disturbance.  
176 The 95% confidence intervals were obtained with 999 iterations by bootstrap resampling.  
177 Significant differences at the 5% level are guaranteed when the confidence intervals do not

178 overlap [48]. This analysis was performed with the *iNEXT* package, using the *estimateD*  
179 function [49,50].

180 We used generalized linear mixed models (GLMM) with the Poisson error distribution  
181 to test for differences in bird abundance and vegetation height between breeding seasons. For  
182 the bird abundance analysis, we used only the maximum number of individuals recorded in the  
183 two samples taken in each point count per breeding season, to avoid overestimates caused by  
184 re-counting the same individual. We created models for each history of fire disturbance  
185 (occasional fire, annual fire, and without fire) separately, in order to assess only the temporal  
186 changes within each history, not among them. In all models the year was considered as fixed  
187 effect, while areas and point counts were treated as random effects, to control spatial and  
188 temporal variations, considering the dependence in our data. The model analyses were carried  
189 out in the *lme4* package using the *glmer* function [51]. The significance of the fixed effect (year)  
190 was assessed via likelihood-ratio tests, with an ANOVA between the model with the  
191 explanatory variable (fixed effect) and the model without this variable (null model) [51,52].  
192 Differences among the four breeding seasons were evaluated via post-hoc Tukey pairwise  
193 comparisons, using the *multcomp* package [53].

194 In order to determine the responses of species to the time since fire (i.e. years since the  
195 last burn), we initially estimated the density (individuals/ha) of some species in occasional-fire  
196 areas, because only these areas had changes in their history of disturbance during our study. We  
197 used the Distance 7.3 program to adjust detectability issues [54]. Only species with more than  
198 30 records were included in this analysis [55]. The estimates of density generated were tested  
199 for normality via a Shapiro-Wilk test, with the *RVAideMemoire* package [56], showing normal  
200 distribution. Therefore, we used linear mixed models (LMM) to assess the effect of the time  
201 since fire on the density of each species. In all models the year was considered as fixed effect  
202 and the areas as random effect, accounting for temporal dependence in the data (same areas

203 sampled in four consecutive breeding seasons/years). The model analyses were carried out in  
204 the *lme4* package, using the *lmer* function [51]. Again, the significance of the fixed effect was  
205 evaluated using an ANOVA between the model with the explanatory variable and the null  
206 model (without this variable), and differences among breeding seasons were evaluated via post-  
207 hoc Tukey pairwise comparisons.

208 In order to test for differences in the composition of the bird community between  
209 breeding seasons, for each history of fire disturbance, we used permutational multivariate  
210 analysis of variance (PERMANOVA) with 999 iterations, using the *Adonis* function in the  
211 *vegan* package [57]. We used post-hoc Tukey pairwise comparisons to assess differences  
212 between seasons, using the *pairwiseAdonis* package [58]. We plotted only the results for  
213 occasional-fire areas in order to show associations between bird species and time since fire,  
214 through a non-metric multidimensional scaling (NMDS), using the Bray-Curtis index as a  
215 dissimilarity measure, with the *metaMDS* function in the *vegan* package. Environmental  
216 variables were then fitted in the NMDS plot and their statistical significance tested with 999  
217 permutations, using the *envfit* function in *vegan*. For this analysis we used only grassland-  
218 dependent bird species (*sensu* [1]). All analyses were performed using R 3.4.0 [59].

219

## 220 **Results**

### 221 **Bird richness and abundance**

222 We recorded 73 bird species and 2,828 individuals during the study (S2 Table). Of this  
223 total, 59 species and 1,325 individuals were recorded in areas with occasional fire (OF), 58  
224 species and 1,093 individuals in areas burned annually (AF), and 34 species and 410 individuals  
225 in areas without fire (WF). Eight species were exclusive to OF, nine to AF, and four to WF.  
226 Seven other species occurred in areas with all histories of fire disturbance and in all breeding

227 seasons. The Ochre-breasted Pipit (*A. nattereri*) and the Saffron-cowled Blackbird (*X. flavus*),  
 228 two species of conservation concern, did not occur in areas without fire or in the breeding  
 229 season before the burn (in the case of OF), while in areas burned annually, these species were  
 230 recorded in all four breeding seasons sampled.

231 The high values of estimated sample coverage (ranges from 0.94 in WF to 0.98 in OF  
 232 and AF) indicate that the sampling was sufficient to detect most species. Considering the lowest  
 233 sample coverage of each history of fire disturbance no overlap in confidence intervals showed  
 234 a significant difference in richness over the breeding seasons in OF and AF (Table 1, Fig 2). In  
 235 the OF areas, richness was higher in the year of the fire (47 species) and one year post-fire (46  
 236 species), compared to the year before the burn (31 species) and two years after the burn (34  
 237 species). In the AF areas, richness was higher in the third year (2017: 47 species) than in the  
 238 others (2015: 33 species; 2016: 36 species; 2018: 37 species). In the WF areas, bird richness  
 239 did not vary significantly during the four years.

240

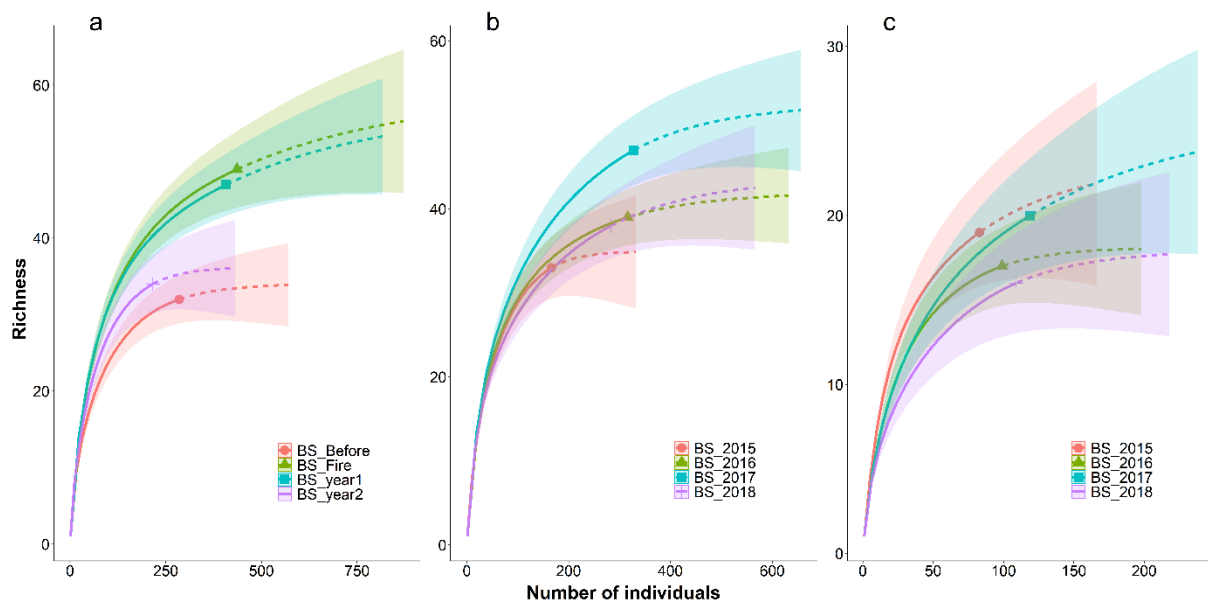
241 **Table 1. Bird richness in areas with different histories of fire disturbance during four**  
 242 **breeding seasons (2015–2018) in highland grasslands in northeastern Rio Grande do Sul**  
 243 **state, Brazil.**

<b>History / Breeding season</b>	<b>S.obs</b>	<b>SC</b>	<b>S</b>	<b>CI</b>
Occasional fire / before	32	0.98	31	27.9 – 33.8 <sup>A</sup>
Occasional fire / fire	49	0.98	47	43.0 – 51.9 <sup>a</sup>
Occasional fire / 1 year post-fire	47	0.98	46	41.4 – 50.4 <sup>a</sup>
Occasional fire / 2 years post-fire	34	0.97	34	30.6 – 37.4 <sup>A</sup>
Annual fire / 2015	33	0.96	33	29.6 – 36.4 <sup>B</sup>
Annual fire / 2016	39	0.98	36	33.6 – 39.3 <sup>B</sup>

History / Breeding season	S.obs	SC	S	CI
Annual fire / 2017	47	0.97	47	42.3 – 51.0 <sup>b</sup>
Annual fire / 2018	38	0.97	37	33.4 – 41.2 <sup>B</sup>
Without fire / 2015	19	0.94	19	15.8 – 22.2 <sup>C</sup>
Without fire / 2016	17	0.97	16	13.5 – 18.0 <sup>C</sup>
Without fire / 2017	20	0.95	19	15.9 – 22.2 <sup>C</sup>
Without fire / 2018	16	0.96	15	12.3 – 16.9 <sup>C</sup>

244 S.obs = observed richness; SC = sample coverage; S = richness based on the lowest sample  
 245 coverage for that history of disturbance; CI = 95% confidence interval. Differences between  
 246 letters (upper and lower case) next to CI of a same history (A/a for occasional fire, B/b for  
 247 annual fire, C/c for without fire) indicate significant differences between breeding seasons.

248



249

250 **Fig 2. Species richness of birds recorded during four breeding seasons (BS) in grasslands**  
 251 **with three histories of fire disturbance in northeastern Rio Grande do Sul state, Brazil.**

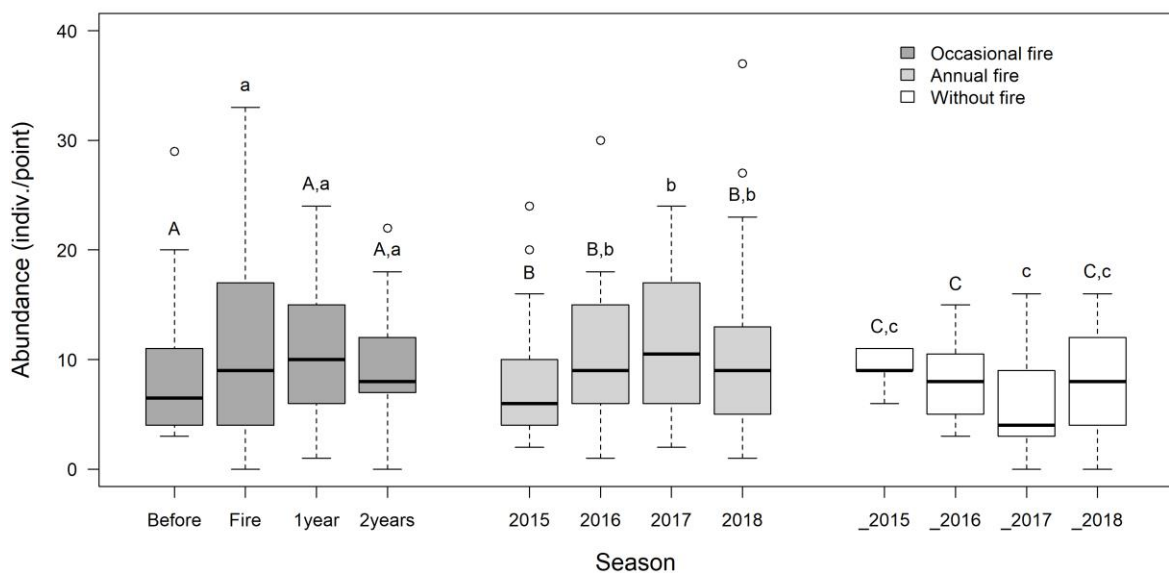
252 Histories of fire disturbance are occasional fire (a), annual fire (b), and without fire (c). In  
 253 occasional fire breeding seasons refer to the year before the burn (before), in the year of the



254 burn (fire), and one and two years post-fire (year1 and year2, respectively). Solid and dashed  
 255 lines are interpolated and extrapolated data, respectively, based on rarefaction and extrapolation  
 256 method, with their associated 95% confidence intervals.

257

258 There was significant temporal variation in bird abundance in OF ( $\chi^2 = 16.05$ ;  $p =$   
 259  $0.001$ ). Post-hoc tests showed that the number of individuals recorded increased in the year of  
 260 the fire ( $Z = -3.76$ ;  $p = 0.001$ ), and did not differ in the following years (1 year post-fire:  $Z = -$   
 261  $2.39$ ;  $p = 0.07$ ; 2 years post-fire:  $Z = -1.01$ ;  $p = 0.74$ ) in relation to the year before the  
 262 disturbance (Fig 3). Bird abundance also changed significantly in AF ( $\chi^2 = 8.89$ ;  $p = 0.03$ ) and  
 263 WF ( $\chi^2 = 10.31$ ;  $p = 0.02$ ). In AF, the number of records differed significantly only between the  
 264 first and third years ( $Z = 2.79$ ;  $p = 0.02$ ), while in WF the number of records differed  
 265 significantly between the second and third years ( $Z = -2.7$ ;  $p = 0.03$ ).



266

267 **Fig 3. Abundance of birds recorded during four breeding seasons (2015 – 2018) in**  
 268 **grasslands with three histories of fire disturbance in northeastern Rio Grande do Sul**  
 269 **state, Brazil.** In occasional fire breeding seasons refer to the year before the burn (before), in

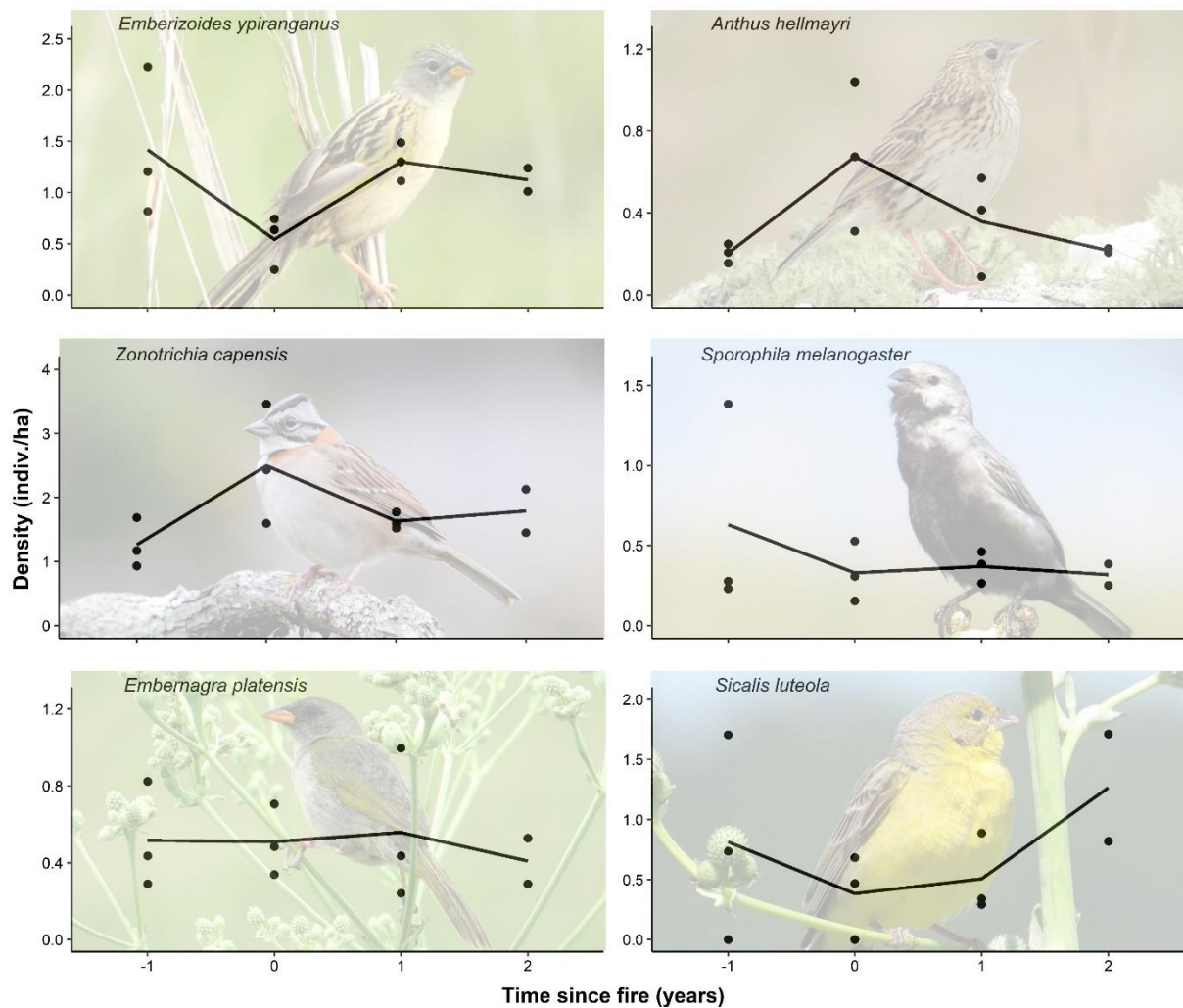
270 the year of the burn (fire), and one and two years post-fire (1 year and 2 years, respectively).  
271 Differences between letters (upper and lower case: A/a for occasional fire, B/b for annual fire,  
272 C/c for without fire) indicate significant differences between breeding seasons, based on  
273 generalized linear mixed models. The line inside each box represents the median; top and  
274 bottom of each box represent upper and lower quartiles, respectively; whiskers represent  
275 maximum and minimum values; circles are outliers.

276

277         Considering the six species analyzed for density (for which the minimum number of  
278 records was obtained), three of them responded significantly in relation to time since fire (Fig  
279 4). The time since fire positively affected the density of the Lesser Grass-Finch (*Emberizoides*  
280 *ypiranganus*;  $\chi^2 = 8.03$ ;  $p = 0.04$ ). Post-hoc tests showed that the density of the species was  
281 significantly higher one year post-fire ( $Z = 2.89$ ;  $p = 0.02$ ) and before the burn ( $Z = 3.35$ ;  $p =$   
282  $0.004$ ) compared to the year of the disturbance. The density of the Lesser Grass-Finch did not  
283 vary between the year before the fire and one year ( $Z = 0.45$ ;  $p = 0.97$ ) or two years post-fire  
284 ( $Z = 0.81$ ;  $p = 0.85$ ). For Hellmayr's Pipit (*Anthus hellmayri*), the time since fire negatively  
285 affected its density ( $\chi^2 = 8.04$ ;  $p = 0.04$ ). The density of the species was significantly higher  
286 in the year of the fire than in the year before the disturbance ( $Z = -3.24$ ;  $p = 0.007$ ) and two  
287 years post-fire ( $Z = -2.74$ ;  $p = 0.03$ ). The density of the Hellmayr's Pipit did not differ between  
288 the year before the fire and one year ( $Z = -1.02$ ;  $p = 0.71$ ) or two years post-fire ( $Z = -0.14$ ;  $p$   
289  $= 0.99$ ). Similarly, the time since fire negatively affected the density of the Rufous-collared  
290 Sparrow (*Zonotrichia capensis*;  $\chi^2 = 7.88$ ;  $p = 0.04$ ). The density of the Rufous-collared  
291 Sparrow was significantly higher in the year of the fire than in the year before the disturbance  
292 ( $Z = -3.3$ ;  $p = 0.005$ ), while there was no difference between the year before the fire and one  
293 year ( $Z = -0.98$ ;  $p = 0.76$ ) or two years post-fire ( $Z = -1.26$ ;  $p = 0.58$ ). For the other three species,

294 their densities not changed with the time since fire (*S. melanogaster*:  $\chi^2 = 1.98$ ;  $p = 0.58$ ; *E.*  
 295 *platensis*:  $\chi^2 = 0.53$ ;  $p = 0.91$ ; *S. luteola*:  $\chi^2 = 4.23$ ;  $p = 0.24$ ).

296



297

298 **Fig 4. Density of six grassland birds one year before (“-1”), just following (“0”), and for**  
 299 **two years after fire in highland grasslands in northeastern Rio Grande do Sul state, Brazil.**

300 Line represents the mean density of the species in each year. Only densities of *E. ypiranganus*,  
 301 *A. hellmayri*, and *Z. capensis* varied significantly over time ( $p < 0.05$ ), based on linear mixed  
 302 models.

303

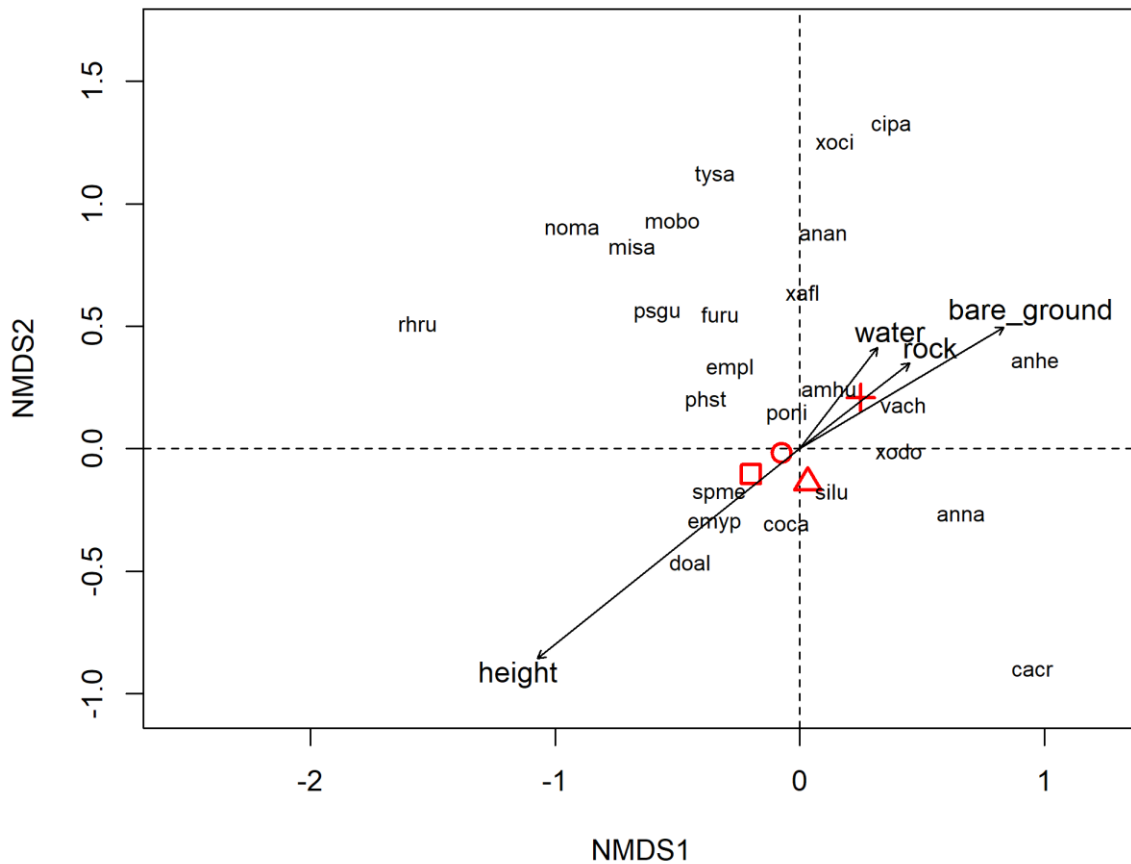
304

305

## 306 **Species composition and environmental variables**

307           The species composition of grassland birds changed over time in OF ( $F = 3.99$ ,  $df = 3$   
308 and 121;  $r^2 = 0.09$ ;  $p = 0.001$ ). Post-hoc tests revealed significant differences between the year  
309 of the burn and the other three breeding seasons (before:  $r^2 = 0.11$ ;  $p_{adj} = 0.006$ ; one year post-  
310 fire:  $r^2 = 0.05$ ;  $p_{adj} = 0.03$ ; two years post-fire:  $r^2 = 0.10$ ;  $p_{adj} = 0.006$ ). Temporal changes also  
311 occurred in the species composition in AF ( $F = 1.73$ ,  $df = 3$  and 93;  $r^2 = 0.05$ ;  $p = 0.02$ ) and in  
312 WF ( $F = 2.93$ ,  $df = 3$  and 46;  $r^2 = 0.16$ ;  $p = 0.002$ ). In AF areas, the species composition in the  
313 first year was significantly different from the third ( $r^2 = 0.06$ ;  $p_{adj} = 0.02$ ) and fourth year ( $r^2 =$   
314  $0.07$ ;  $p_{adj} = 0.01$ ). In the WF areas, there were significant differences between the first and third  
315 years ( $r^2 = 0.13$ ;  $p_{adj} = 0.04$ ) and between the third and fourth years ( $r^2 = 0.12$ ;  $p_{adj} = 0.02$ ).

316           As shown by the average of the breeding season scores (centroids), and reflecting the  
317 results of the tests in OF, the post-fire years (1 and 2 years) were more closely related to the  
318 year before the burn than to the year of the fire (Fig 5). Vegetation height ( $r^2 = 0.24$ ;  $p = 0.001$ )  
319 and percentage of bare ground ( $r^2 = 0.11$ ;  $p = 0.005$ ) were the environmental variables  
320 significantly associated with the structure of the bird community in this history of fire  
321 disturbance. The other variables did not show significant values (rock:  $r^2 = 0.04$ ;  $p = 0.09$ ;  
322 water:  $r^2 = 0.03$ ;  $p = 0.12$ ). In AF areas, vegetation height ( $r^2 = 0.24$ ;  $p = 0.001$ ) and percentage  
323 of bare ground ( $r^2 = 0.13$ ;  $p = 0.002$ ) also were the environmental variables associated with the  
324 species composition, while in WF areas only vegetation height ( $r^2 = 0.13$ ;  $p = 0.03$ ) was  
325 significant. The percentage of plant cover was strongly correlated with vegetation height and  
326 was not evaluated in this analysis.



327

328 **Fig 5. Non-metric multidimensional scaling (NMDS) plot illustrating the association**  
 329 **among the grassland birds, four environmental variables (vegetation height, bare ground,**  
 330 **rocks, and water) and a time gradient in relation to the fire disturbance.** Results based on  
 331 the species abundance (Bray-Curtis dissimilarity index) in areas with occasional fire (i.e.  
 332 burned only once during the study). Stress = 0.22. Symbols represent the mean scores  
 333 (centroids) of each breeding season (square = before the fire; cross = year of fire; circle = one  
 334 year post-fire; triangle = two years post-fire). Acronyms are formed by the first two letters of  
 335 the genus and species epithet of each species in S2 Table.

336

337 The vegetation height varied significantly over time in OF ( $\chi^2 = 535.72$ ;  $p < 0.001$ ),  
 338 decreasing after the burn and increasing in subsequent years (Table 2). Post-hoc comparisons

339 indicated significant differences among all breeding seasons (in all combinations,  $Z > 8.5$ ;  $p <$   
340  $0.001$ ), except between one year and two years post-fire ( $Z = 2.45$ ;  $p = 0.07$ ). There were also  
341 changes in vegetation height between the breeding seasons in AF ( $\chi^2 = 56.17$ ;  $p < 0.001$ ) and  
342 WF ( $\chi^2 = 15.98$ ;  $p = 0.001$ ). In AF areas, the vegetation height in the third year was significantly  
343 lower than in the others (2015:  $Z = -6.73$ ;  $p < 0.001$ ; 2016:  $Z = -3.85$ ;  $p < 0.001$ ; 2018:  $Z = 5.98$ ;  
344  $p < 0.001$ ) and there were also differences between the first and second years ( $Z = -3.36$ ;  $p =$   
345  $0.004$ ). In WF areas, the vegetation height in the first year was higher than in the second ( $Z = -$   
346  $3.06$ ;  $p = 0.01$ ) and third years ( $Z = -3.71$ ;  $p = 0.001$ ).  
347

348 **Table 2. Measurements of four environmental variables in areas with different histories of fire disturbance during four breeding seasons**  
 349 **(2015–2018) in highland grasslands in northeastern Rio Grande do Sul state, Brazil.**

History	Season	Vegetation height (cm)	Bare ground <sup>a</sup>	Rock <sup>a</sup>	Water <sup>a</sup>
Occasional fire	Before	63.2 ± 22.4 (31.2–109.6)	0.08 ± 0.45 (0–2.5)	2.04 ± 5.22 (0–25)	2 ± 6.34 (0–25)
	Fire	22.7 ± 12.2 (9.7–66.4)	15.6 ± 12.6 (1.5–47.5)	0.92 ± 2.93 (0–16.2)	1.57 ± 4.24 (0–21.2)
	1 year	34.4 ± 10.8 (15.3–54.2)	1.61 ± 3.43 (0–20.5)	0.67 ± 2.88 (0–17.5)	0.81 ± 3.50 (0–21.2)
	2 years	40.5 ± 11.2 (25.2–70.7)	0.2 ± 0.48 (0–2)	0.53 ± 1.98 (0–9.25)	0.29 ± 0.99 (0–4.5)
Annual fire	2015	25.5 ± 11.4 (7.1–46.2)	0 ± 0 (0–0)	7.51 ± 12.0 (0–40.6)	3.79 ± 8.36 (0–31.2)
	2016	20.9 ± 14.9 (9.5–75.1)	3.5 ± 3.51 (0.25–14.7)	2.74 ± 4.39 (0–20.5)	0.98 ± 3.09 (0–13.7)
	2017	16.2 ± 10.3 (5.6–38.7)	2.57 ± 3.04 (0–12.5)	3.68 ± 4.29 (0–16)	0.47 ± 0.90 (0–3.75)
	2018	24.4 ± 9.17 (9.1–40.8)	0.64 ± 1.06 (0–3.75)	2.72 ± 4.04 (0–16)	0.30 ± 0.89 (0–3.75)
Without fire	2015	59.6 ± 12.4 (41–78.8)	0 ± 0 (0–0)	1.38 ± 2.40 (0–6.25)	4.51 ± 8.43 (0–25)
	2016	46.6 ± 11.2 (26.1–61.9)	0 ± 0 (0–0)	1.14 ± 2.79 (0–8.75)	0 ± 0 (0–0)
	2017	44.7 ± 10.8 (30.8–67.8)	0.2 ± 0.41 (0–1.75)	0.14 ± 0.37 (0–1.25)	0.73 ± 1.55 (0–6.25)
	2018	50.3 ± 8.6 (31–67.5)	0 ± 0 (0–0)	0.07 ± 0.26 (0–1)	1.25 ± 4.01 (0–15)

350 Values correspond to mean ± SD (minimum–maximum).

351 <sup>a</sup> Mean percentage of cover in quadrats of 1 m<sup>2</sup> within bird point counts.

## 352 **Discussion**

353 We found that the richness, abundance, and species composition in the study areas  
354 changed over time in different ways. A more regular pattern of variation was found in areas  
355 that burned occasionally, where all parameters changed in the year of the fire and returned to  
356 the same levels as in the year before the fire one or two years after the disturbance. In areas  
357 burned annually or in areas without fire, changes did not occur (e.g., richness in areas without  
358 fire) or occurred in different years, without a definite temporal pattern. Lindenmayer et al. [60]  
359 also reported a different pattern of temporal changes between burned and unburned sites, where  
360 the rate of increase of bird richness was higher in burned sites.

361 The increase in bird richness observed shortly after the fire in areas that have gone  
362 through a long period without a burn may be related to a greater habitat heterogeneity. After a  
363 fire, the dry grassland has the shortest vegetation, while wetlands, depending on the fire  
364 intensity, are less impacted and have a different vegetation structure. The lower intensity of fire  
365 in wetlands than in dry grasslands observed in Brazilian *Cerrado* grasslands can be attributed  
366 to the higher soil water availability [61]. The heterogeneity of the vegetation structure increases  
367 the habitat variability and the diversity of the grassland bird community [16,62]. Thus, in our  
368 study areas, species associated with tall grasses (e.g., *Emberizoides ypiranganus*, *Sporophila*  
369 *melanogaster*, and *Phacellodomus striaticolis*, *sensu* [1]) did not disappear after the fire, but  
370 tended to occupy areas with tall vegetation such as *Eryngium* marshes, and were often restricted  
371 to these habitats. The dry grassland, in turn, provided habitat for species associated with low  
372 grasses (e.g., *Vanellus chilensis*, *Cinclodes pabsti*, *Anthus* spp.) that did not previously occur  
373 there or were less abundant before the fire. In fact, our results showed that some species are  
374 more associated with sites with taller vegetation, while other species occupy sites with shorter  
375 vegetation and more bare ground (Fig 5).



376           On the other hand, in the breeding season that the areas were unburned for long periods,  
377 we observed lower bird richness compared to years when these areas had been burned (Table  
378 1). Probably in these cases, the greater homogenization of the habitat structure, due mainly to  
379 the presence of tall grasses, disadvantages species that occupy short grasslands. Sites without  
380 disturbances for long periods usually present an increase in vegetation height and plant biomass,  
381 which leads to a homogenization of vegetation structure [15,18]. The diversity of vegetation  
382 and structural differences, such as vegetation height, are important variables that determine the  
383 response of grassland birds [16,32,42,63]. We did not record some species in areas unburned  
384 for a long period, such as the Saffron-cowled Blackbird (*X. flavus*) and the Ochre-breasted Pipit  
385 (*A. nattereri*), two globally threatened species [64]. In the Brazilian Cerrado, *A. nattereri* has  
386 been recorded in native grasslands affected by fire [65,66]. Grasslands with more than two years  
387 of post-fire succession and no grazing, even in sites with favorable relief, do not seem to favor  
388 the occurrence of the Ochre-breasted Pipit [67]. In southern Brazil, the Saffron-cowled  
389 Blackbird used burned areas more frequently and avoided habitats with tall grasses and  
390 developed vegetation [37]. The species was absent from a protected area that has not  
391 experienced fires in nearly three decades [37], since the Saffron-cowled Blackbird depends on  
392 marshes to breed but also uses dry, short-grass areas to forage [37,68,69]. In Argentina, Isacch  
393 and Martinez [30] observed that areas with more tall-grass coverage had higher richness and  
394 abundance of birds. However, the authors noted that they did not sample sites with 100% tall-  
395 grass coverage (probably equivalent to WF areas in our study), and that in this situation, the  
396 richness is likely lower due to the loss of ground-feeding species.

397           In grasslands of the Serra da Canastra National Park, southeastern Brazil, burnings  
398 triggered profound and immediate changes in bird assemblages, increasing the number of  
399 species and individuals right after the fire [35]. Bahía and Zalba [32] found that the abundance  
400 and richness of birds were lower one year after a burn and increased significantly two years

401 afterward. Besides the increase in richness, our data also showed an increase in abundance of  
402 individuals after fire. Probably the occurrence of some common species in our areas, such as  
403 the Rufous-collared Sparrow (*Z. capensis*), Hellmayr's Pipit (*A. hellmayri*), and Southern  
404 Lapwing (*V. chilensis*) contributes to this higher abundance. In North America, some species  
405 occurred in higher abundances in areas with fire disturbance [16,24,25].

406 Three species assessed individually showed responses to fire, in different ways. The  
407 densities of Rufous-collared Sparrow and the Hellmayr's Pipit (a non-grassland and a short-  
408 grass species, respectively, according to [1]) increased with a burn and later decreased over  
409 time after the fire. In contrast, the density of the Lesser Grass-Finch (a tall-grass species)  
410 decreased in the year of the fire, increasing again as the time since the fire lengthened (Fig 4).  
411 This is expected and occurs because some species are favored and others disadvantaged by fire  
412 disturbance, responding to variations in habitat structure [28,30]. Lesser Grass-Finch tends to  
413 be disadvantaged by fire disturbance due to the loss of suitable habitat, since it depends on a  
414 specific vegetation structure to nest, forage and seek refuge [70]. Some species of conservation  
415 concern that occur in the region of our study might be more frequent and abundant in areas  
416 burned frequently (e.g., *Cinclodes pabsti*, *Anthus nattereri* and *Xanthopsar flavus*), where short  
417 grasses are predominant, while others might be more frequent and abundant in areas with  
418 reduced fire management or without it (e.g., *Scytalopus iraiensis*, *Limnortites rectirostris* and  
419 *Sporophila melanogaster*), where vegetation is higher [39]. Although we assumed that grazing  
420 pressure was constant at our study sites, it is important to note that grazing influences directly  
421 the vegetation structure and plant taxonomic diversity, promoting effects on plant and arthropod  
422 communities [15], and, consequently, may have additional effects on grassland birds. Several  
423 tallgrass-dependent birds are threatened in South America and are affected by the lack of  
424 tallgrass vegetation caused by the intensive disturbance of grassland due to cattle raising [1,42].

425           The present results also showed changes in grassland-bird species composition over the  
426 years, but the spatial dependence of the data used in the analysis requires caution in interpreting  
427 the effects of fire on community structure. Vegetation height was the main variable associated  
428 with species composition, corroborating other studies (e.g., [42,71]). Our data point to an effect  
429 of fire in areas that burned occasionally, but differences in species composition were also found  
430 among the years in areas burned annually and in areas without fire. Annual variation in areas  
431 without changes in the fire regime over the years may be the result of climatic variation.  
432 Temporal fluctuations of bird communities can be indirectly caused by both changes in  
433 temperature and precipitation, which determine the amount of resources available to birds  
434 [72,73]. Areas burned annually, for example, may have variable amounts of primary  
435 productivity, depending on rainfall and temperatures, affecting the stability of the grassland  
436 bird community [17].

437           Our results converge to the ideas that grasslands should be managed in a way that forms  
438 mosaics with a spatial and temporal arrangement of both short and tall grass, creating vegetation  
439 heterogeneity and promoting bird diversity [16,17,42]. Patch-burn management has been  
440 recommended for grassland bird conservation, because it creates the entire gradient of  
441 vegetation structure required to maintain grassland bird species that differ in habitat preferences  
442 [16,74]. Increasing heterogeneity at landscape scales also results in higher stability of bird  
443 communities over time [17]. Thus, management of grasslands that creates a shifting mosaic,  
444 using prescribed fires in areas with different times since burnings and areas with different  
445 histories of fire disturbance, can be useful in conservation of grassland birds and habitats. Fire  
446 in highland grasslands of southern Brazil has already been recommended as an important  
447 management tool to ally cattle raising with bird conservation [39].

448           This study is the first to use data covering the period before and after a burn in southern  
449 Brazilian grasslands, since we are not allowed to burn large areas for experiments, especially

450 in Brazilian protected areas. We took advantage of three events of occasional (accidental) fire  
451 in the protected areas where we usually develop bird monitoring to answer relevant questions  
452 to grassland conservation in southern Brazil. Our results showed that two years without fire was  
453 a period long enough for the evaluated parameters of the bird community and the density of  
454 some species to return to levels estimated before the disturbance. The recovery of the vegetation  
455 after a fire and the response time of the birds, in one or two breeding seasons, depending on the  
456 species, were also observed in Argentina [32]. In southeastern Australia, an endangered bird  
457 species either remained continuously on burned sites or returned to previously occupied sites  
458 within two years after an unplanned fire [75]. Another study in Argentina, with a threatened  
459 grassland bird, found that the species did not show avoidance of the burned patch in the third  
460 breeding season after the prescribed fire, suggesting burning intervals longer than two years  
461 [31]. This kind of information is useful for planning the periodicity with which fire can be used  
462 to manage grassland areas.

463 We showed that the use of fire in highland grasslands of southern Brazil should consider  
464 a period of at least two years (or two breeding seasons) without burnings in the same grassland  
465 patch, to ensure the recovery of the bird community of the area. Another point of concern is  
466 that fire must occur before the breeding season of most grassland birds (which is the austral  
467 spring and summer in southern Brazil [76]) to avoid burning active nests, and do not affect  
468 wetlands to avoid losing important sites of refuge and/or nest sites for tall-grass birds, including  
469 migratory and philopatric species such as *Sporophila melanogaster*. However, it is needed to  
470 consider that management decisions and a better understanding of the effects of fire require an  
471 analysis that integrates different taxonomic groups of animals and plants.

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705 **Supporting information**

706 **S1 Table. Areas used to sample birds in highland grasslands in northeastern Rio Grande**  
 707 **do Sul state, Brazil, and history of fire disturbance.** Numbers in each breeding season  
 708 represent the years since fire (“0” indicates the year when the area was burned) and the quantity  
 709 of count points sampled (between parentheses). APA = area in Parque Nacional de Aparados  
 710 da Serra or Parque Nacional da Serra Geral; TAI = area in the region of Parque Estadual do  
 711 Tainhas.

Area	Area size (ha)	History of disturbance	Breeding Season			
			2015–16	2016–17	2017–18	2018–19
APA 1	250	Occasional fire	≥ 8 (8)	0 (12)	1 (12)	2 (12)
TAI 1	210	Occasional fire	≥ 8 (10)	0 (14)	1 (14)	2 (11)
APA 3	220	Occasional fire	-	>8 (12)	0 (12)	1 (12)
TAI 2	210	Annual fire	0 (11)	0 (14)	0 (14)	0 (14)
TAI 3	170	Annual fire	0 (10)	0 (12)	0 (12)	0 (12)
APA 2	180	Without fire	-	>10 (12)	>10 (12)	>10 (4)
APA 4	150	Without fire	>10 (9)	-	>10 (9)	>10 (10)

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718 **S2 Table. Relative abundance (number of individuals/point) of bird species recorded during four breeding seasons (2015–2018) in**  
719 **grasslands with three histories of fire disturbance (occasional fire, annual fire, and without fire) in northeastern Rio Grande do Sul state,**  
720 **Brazil.** In occasional fire breeding seasons refer to the year before the burn (before), in the year of the burn (fire), and one and two years after a  
721 fire (1year and 2years, respectively). Species are in alphabetical order.

Species	Occasional fire				Annual fire				Without fire			
	before	fire	1year	2years	2015	2016	2017	2018	2015	2016	2017	2018
<i>Agelaioides badius</i>	-	-	-	-	0.10	-	-	-	-	-	-	-
<i>Amazonetta brasiliensis</i>	0.10	0.08	0.05	-	-	0.08	-	-	-	0.33	-	-
<i>Ammodramus humeralis</i>	-	0.29	0.18	0.09	0.24	0.23	0.19	0.08	-	-	-	-
<i>Anas flavirostris</i>	-	0.05	-	-	-	0.12	0.08	-	-	0.17	-	-
<i>Anas georgica</i>	-	-	0.05	-	-	0.19	-	-	-	-	0.05	-
<i>Anthus hellmayri</i>	0.33	1.11	0.55	0.35	0.57	1.12	0.92	0.85	1.11	0.42	0.33	0.14
<i>Anthus nattereri</i>	-	0.08	0.08	0.26	0.62	0.42	0.27	0.04	-	-	-	-
<i>Anumbius annumbi</i>	-	0.26	0.16	0.04	0.05	0.23	0.54	0.08	0.33	-	-	-
<i>Ardea alba</i>	-	-	-	-	-	-	-	-	-	-	0.05	-
<i>Butorides striata</i>	-	-	-	-	-	-	-	-	0.11	-	-	-
<i>Cariama cristata</i>	-	0.05	0.05	0.04	-	-	0.04	0.04	-	-	-	-
<i>Chlorostilbon lucidus</i>	0.10	0.18	0.18	0.09	-	0.08	0.04	-	0.22	0.17	0.05	0.21
<i>Ciconia maguari</i>	-	-	-	-	-	-	-	0.04	-	-	-	-
<i>Cinclodes pabsti</i>	-	-	0.03	-	0.10	0.27	0.19	-	-	-	-	-



Species	Occasional fire				Annual fire				Without fire			
	before	fire	1year	2years	2015	2016	2017	2018	2015	2016	2017	2018
<i>Colaptes campestris</i>	0.17	0.42	0.26	-	0.38	0.50	0.92	0.73	-	0.33	-	-
<i>Colibri serrirostris</i>	0.07	-	-	-	-	-	-	-	-	-	-	-
<i>Donacospiza albifrons</i>	0.37	0.11	0.21	0.17	0.10	-	0.08	-	0.22	0.25	0.19	0.36
<i>Elaenia parvirostris</i>	-	0.05	-	-	-	-	-	-	-	-	-	-
<i>Emberizoides ypiranganus</i>	1.77	0.74	1.76	1.52	0.52	0.88	0.73	0.69	1.11	2.92	1.76	2.14
<i>Embernagra platensis</i>	0.83	0.89	1.00	0.78	0.10	0.58	0.81	0.88	0.67	0.58	0.57	0.50
<i>Furnarius rufus</i>	-	-	0.03	0.04	-	-	0.19	-	-	-	-	-
<i>Gallinago paraguaiiae</i>	-	0.03	-	0.09	-	0.04	0.15	0.19	0.11	0.08	0.05	0.07
<i>Geothlypis aequinoctialis</i>	0.27	0.13	0.18	-	0.05	0.04	0.15	0.15	-	-	-	0.14
<i>Gnorimopsar chopi</i>	-	-	-	-	1.48	0.42	0.62	0.46	-	-	-	-
<i>Guira guira</i>	-	-	-	-	-	-	0.04	-	-	-	-	-
<i>Hylocharis chrysura</i>	-	0.03	-	-	-	-	-	-	-	-	-	-
<i>Jacana jacana</i>	-	-	-	-	-	-	-	-	0.11	-	-	-
<i>Knipolegus lophotes</i>	-	-	-	-	-	-	0.08	-	-	-	-	0.07
<i>Knipolegus nigerrimus</i>	-	-	-	-	-	-	-	-	-	-	0.10	-
<i>Laterallus leucopyrrhus</i>	0.07	-	0.11	-	-	0.12	0.08	0.12	-	0.08	0.05	-
<i>Leucochloris albicollis</i>	-	0.08	0.08	-	-	-	-	-	-	0.17	-	-
<i>Limnortyx rectirostris</i>	0.20	0.16	0.21	-	0.05	0.15	0.19	0.08	0.22	-	0.10	-
<i>Mimus saturninus</i>	-	0.03	0.05	-	0.19	-	0.15	0.08	-	-	-	-

Species	Occasional fire				Annual fire				Without fire			
	before	fire	1year	2years	2015	2016	2017	2018	2015	2016	2017	2018
<i>Molothrus bonariensis</i>	-	0.05	0.03	0.13	-	-	-	-	-	-	-	-
<i>Myiarchus swainsonii</i>	0.03	0.03	-	-	-	-	-	-	-	-	-	-
<i>Myiophobus fasciatus</i>	0.03	0.08	0.08	0.04	-	-	-	0.04	-	-	-	-
<i>Nothura maculosa</i>	0.03	0.03	0.08	0.09	0.19	0.04	0.04	0.04	-	-	-	-
<i>Pardirallus sanguinolentus</i>	0.07	0.11	0.08	-	0.10	0.08	0.08	0.23	-	-	-	0.14
<i>Patagioenas cayennensis</i>	-	0.03	-	-	0.10	-	-	-	-	-	-	-
<i>Patagioenas picazuro</i>	-	-	0.03	-	0.05	-	-	0.04	-	-	-	-
<i>Phacellodomus striaticollis</i>	0.07	0.18	0.13	0.09	0.05	0.12	-	-	-	-	-	-
<i>Pipraeidea bonariensis</i>	-	0.03	0.03	-	-	-	-	-	-	-	-	-
<i>Pitangus sulphuratus</i>	0.10	0.16	0.11	0.13	0.10	0.23	0.04	0.27	0.33	0.08	-	-
<i>Plegadis chihi</i>	-	-	-	-	-	-	0.46	-	-	-	-	-
<i>Poospiza nigrorufa</i>	-	-	0.03	-	-	0.08	0.04	0.04	-	-	-	-
<i>Pseudoleistes guirahuro</i>	0.33	0.45	0.24	0.26	0.52	0.31	0.62	0.69	-	-	-	-
<i>Rhynchotus rufescens</i>	0.10	0.08	0.05	-	0.05	-	-	-	0.11	0.17	0.10	-
<i>Satrapa icterophrys</i>	-	0.03	0.03	-	-	0.04	0.08	0.08	-	-	-	-
<i>Scytalopus iraiensis</i>	0.13	0.13	0.08	0.13	-	-	-	-	0.33	-	0.14	0.07
<i>Serpophaga subcristata</i>	0.17	0.08	0.03	0.04	-	-	-	-	-	-	0.14	-
<i>Sicalis flaveola</i>	0.13	0.13	0.29	0.26	-	-	0.08	0.12	-	-	0.14	0.07
<i>Sicalis luteola</i>	1.03	0.58	0.61	1.52	0.19	0.50	0.19	0.69	1.22	0.33	0.19	1.93

Species	Occasional fire				Annual fire				Without fire			
	before	fire	1year	2years	2015	2016	2017	2018	2015	2016	2017	2018
<i>Spinus magellanicus</i>	-	0.08	-	0.17	-	0.19	0.04	0.12	-	-	-	-
<i>Sporophila caerulescens</i>	0.03	0.16	0.16	0.13	-	-	-	0.04	-	-	-	-
<i>Sporophila melanogaster</i>	0.67	0.37	0.39	0.35	0.24	0.31	0.23	0.35	0.67	0.92	0.76	1.00
<i>Stephanophorus diadematus</i>	-	-	-	-	-	-	0.08	-	-	-	-	-
<i>Sturnella superciliaris</i>	-	-	-	-	-	-	0.04	-	-	-	-	-
<i>Synallaxis spixi</i>	0.10	0.08	0.16	0.09	-	-	0.04	0.08	-	-	-	-
<i>Syrigma sibilatrix</i>	-	-	-	-	-	0.08	0.08	-	-	-	-	-
<i>Tangara sayaca</i>	-	-	-	0.17	-	-	-	-	-	-	-	-
<i>Thamnophilus ruficapillus</i>	0.07	0.08	-	-	-	0.04	-	-	-	-	-	0.14
<i>Theristicus caudatus</i>	-	-	-	-	0.10	0.12	0.15	0.15	-	-	-	-
<i>Troglodytes musculus</i>	0.03	0.32	0.39	0.13	0.10	0.08	0.31	0.08	-	-	0.05	-
<i>Turdus amaurochalinus</i>	-	0.03	0.03	-	-	-	0.04	0.04	-	-	-	-
<i>Turdus rufiventris</i>	0.03	0.03	-	-	-	-	-	-	-	-	-	-
<i>Tyrannus melancholicus</i>	-	-	0.11	0.22	0.14	0.04	0.04	-	0.11	-	-	-
<i>Tyrannus savana</i>	0.17	0.21	0.21	0.22	0.19	0.42	0.15	0.12	-	-	-	-
<i>Vanellus chilensis</i>	-	0.21	0.26	0.09	0.33	0.54	1.04	0.81	0.67	-	-	-
<i>Xanthopsar flavus</i>	-	0.21	0.13	-	0.14	2.00	0.88	0.88	-	-	-	-
<i>Xolmis cinereus</i>	-	0.05	-	0.09	0.14	0.23	0.08	0.27	-	-	-	-
<i>Xolmis dominicanus</i>	0.10	0.29	0.37	0.35	0.14	0.31	0.35	0.38	0.67	0.67	0.24	0.21

Species	Occasional fire				Annual fire				Without fire			
	before	fire	1year	2years	2015	2016	2017	2018	2015	2016	2017	2018
<i>Zenaida auriculata</i>	-	-	0.03	0.04	-	0.12	0.08	-	-	-	-	-
<i>Zonotrichia capensis</i>	1.13	2.45	1.37	1.17	0.52	0.85	0.92	0.85	0.89	0.58	0.62	0.57
Total	8.83	11.47	10.74	9.39	7.90	12.15	12.62	10.88	9.22	8.25	5.67	7.79

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## **CAPÍTULO 2**

### **Implications of fire on breeding of grassland-dependent birds in highland grasslands of southern Brazil**

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Implications of fire on breeding of grassland-dependent birds in highland grasslands of  
southern Brazil

Short title: Response of grassland birds to fire

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## ABSTRACT

Grasslands have been closely related to fire disturbances, which play an important role in their dynamics. Despite this, little is known about temporal dynamics of fire effects on breeding of birds, mainly in South America. We assessed the temporal changes on nesting success, productivity, and territories of grassland-dependent bird species in natural grassland ecosystems under different fire regimes. We based our study on two tall-grass species, Lesser Grass-Finch (*Emberizoides ypiranganus*) and Black-bellied Seedeater (*Sporophila melanogaster*). We searched for nests and territories during three breeding seasons (2013–2014, 2016–2017 and 2017–2018) in sites with occasional fire (OF) and frequent fire (FF), both located in a Conservation Unit at northeastern Rio Grande do Sul state, Brazil. We monitored a total of 237 nests (178 of Lesser Grass-Finch and 59 of Black-bellied Seedeater). Cumulative survival probability and productivity of the nests of the two species did not show statistically significant differences among breeding seasons both in OF and FF. Size and number of territories of Lesser Grass-Finch varied over breeding seasons only in OF, with fewer and smaller territories in the year of the fire. The number of territories of Black-bellied Seedeater in OF was lower one year after fire in comparison with the season of the fire, but did not differ in FF. Our study is the first to assess temporal effects of fire on breeding and territories of grassland birds in southern Brazilian grasslands and provides information to support that controlled prescribed fire can be used as a tool to manage and conserve highland grasslands in South America.

Keywords: conservation, fledglings, *Emberizoides ypiranganus*, grassland birds, management, nest survival, *Sporophila melanogaster*

## INTRODUCTION

Grassland ecosystems are largely spread around the world, covering about 40% of the Earth's surface (White *et al.* 2000), and their distribution has been related to regions where tree cover is limited by edaphic or climate conditions, or by disturbances regimes such as fire, herbivory, or flooding (Leys *et al.* 2018). Although the factors that control the distribution of grasslands around the world throughout history are varied and debated, it is recognized that fire is a consistently strong predictor (Staver *et al.* 2011, Leys *et al.* 2018). Fire plays an important role in the dynamics of open ecosystems like grasslands, with evolutionary effects on their biodiversity (Bond *et al.* 2005, Pausas & Keeley 2009).

Grassland bird populations have been declining in several parts of the world, and the main causes are loss and fragmentation of native grasslands, intensification of agricultural practices, and use of pesticides (Donald *et al.* 2001, Butchart, S.H.M., Stattersfield *et al.* 2004, Askins *et al.* 2007, Azpiroz *et al.* 2012b). Management of grasslands that promotes habitat uniformity instead of heterogeneity (e.g., annual burning and overgrazing) has also contributed to the decline in grassland bird diversity and abundance (Fuhlendorf *et al.* 2006). Despite widespread recognition of the importance of grasslands for global biodiversity, and varied attempts to protect these ecosystems, managing and conserving their essential processes remain a significant challenge (Leys *et al.* 2018).

In Southeastern South America Grasslands (SESA Grasslands sensu Azpiroz *et al.* 2012b) there is a natural portion of grasslands often neglected in open ecosystems bird studies, probably because they are located in the portion of Atlantic Forest Biome in Brazil (Fontana *et al.* 2008). Such portion is known as southern Brazilian highland grasslands (SBHG), located in northeastern Rio Grande do Sul state and part of Santa Catarina and Paraná states (Andrade *et al.* 2016). Grasslands of SBHG are usually burned at the end of winter, in order to renew and stimulate the regrowth of vegetation for cattle feed (Overbeck & Pfadenhauer 2007, Andrade



*et al.* 2019). The traditional practice of fire can be one of the sustaining elements of these grasslands over the centuries (Behling & Pillar 2007). This statement is proved by studies showing that in the absence of fire or grazing for long periods in regions of grassland/forest mosaics like the ones found at SBHG, grassland vegetation can be replaced by shrubs (Overbeck *et al.* 2005, Pillar & Vélez 2010, Andrade *et al.* 2019, Sühs *et al.* 2020). Fire and grazing exclusion can also increase the risk of catastrophic fire due to the accumulation of flammable biomass (Pillar & Vélez 2010, Buisson *et al.* 2018). However, disturbances such as overgrazing, cattle trampling and annual grassland burning have been pointed as a cause of decline of populations of threatened grasslands bird species in Rio Grande do Sul (Fontana *et al.* 2003), what makes studies on the effects of fire on bird populations necessary for future conservation policies.

In contrast with North America, where there are several studies aiming specifically to assess the fire effects on breeding of grassland birds (e.g., Winter 1999, Churchwell *et al.* 2008, Hovick *et al.* 2012, Verheijen *et al.* 2019), little is known about this issue in South America (e.g., Di Giacomo *et al.* 2011, Bahía & Zalba 2019). In southern Brazilian grasslands none of the studies done on fire and birds (Petry & Krüger 2010, Petry *et al.* 2011, Bettio 2017) have analyzed in detail how fire affects the reproductive success and territories of grassland bird populations. These issues were only briefly discussed in few studies that accessed breeding biology of some grassland species in the region (Rovedder 2011, Franz 2013, Chiarani & Fontana 2015, Repenning & Fontana 2016). The lack of studies on breeding biology of several Neotropical bird species has been reported (Heming *et al.* 2013, Xiao *et al.* 2017), and a probable reason for this is the difficulty of collecting breeding data, because searching for nests takes a long time in the field, increasing the costs of the studies. The current deficiency in financial resources in Brazil, due to the political crisis on science funding (Magnusson *et al.* 2018), makes this type of research more difficult.

Another important issue little investigated worldwide is the temporal dynamics of fire effects. Fuhlendorf *et al.* (2011) in a review found that only 12.5% of the studies in North America assessed fire frequency, a temporal response to fire. Temporal scale strongly influences both the ecosystem responses to fire and the effects of fire (Fuhlendorf *et al.* 2011). Therefore, conservation purposes need to incorporate temporal dynamics to understand the effects of fire on territory size, local population density, and reproductive aspects of grassland birds, mainly if management based on fire is recommended as a strategy for grassland conservation (Churchwell *et al.* 2008, Fuhlendorf *et al.* 2011, Verheijen *et al.* 2019). In southern Brazil, the use of fire has already been recommended to manage grasslands even in protected areas, although this is still a taboo issue (Pillar & Vézlez 2010, Andrade *et al.* 2016).

Fire may have negative impact on reproductive success of grassland birds, destroying their nests if burn occurs during the breeding period (Reinking 2005, Repenning & Fontana 2016), or increasing rates of nest predation and brood parasitism due to higher nest exposition caused by reduced vegetation cover in burned areas (Rohrbaugh *et al.* 1999, Churchwell *et al.* 2008, Davis *et al.* 2016). Fire may also affect size, habitat type, density, and choice of breeding territories of tall-grass species (Rovedder 2011, Chiarani & Fontana 2015). In SBHG, for a grassland-dependent bird species, burned sites showed fewer and smaller territories in comparison with unburned sites, due to the low availability of tall vegetation (which provides appropriate sites for shelter, foraging, and nest building) in burned dry grasslands (Chiarani & Fontana 2015). Fire effects on territory size and local population density should be better investigated, since these parameters are key drivers of population dynamics (Brown 1969, Winter 1999, Verheijen *et al.* 2019).

Here, we assessed temporal changes in nesting success, productivity, territory size, and number of breeding territories of two grassland-dependent species: the Lesser Grass-Finch (*Emberizoides ypiranganus*) and the Black-bellied Seedeater (*Sporophila melanogaster*), a

least concern and a near-threatened species (regionally vulnerable), respectively. Our aim was to compare these reproductive and territory parameters over breeding seasons for each species in areas under different fire regimes (an area burned only once in the last years and an area frequently burned). We expected that in the area burned only once, the breeding parameters (e.g., nesting success and productivity) would decrease in the breeding season in which fire occurred in comparison with the breeding seasons before or after fire, while in the area frequently burned there would be no changes over the years. In relation to breeding territories, we expected that in the area burned only once, size and number of territories would decrease in the breeding season following the fire, while no changes among breeding seasons would be observed in the area frequently burned.

## **METHODS**

### **Study area**

Our study was conducted in Parque Estadual do Tainhas (PET), a protected area with 6,654 ha located in northeastern Rio Grande do Sul state, Brazil (29° 05' 58" S, 50° 21' 50" W). PET is a conservation unit that includes significant extensions of natural grasslands (Bencke & Duarte 2008), and recognized due to its role in the conservation of birds, including threatened, migratory and/or endemic species (Bencke *et al.* 2006, Chiarani & Fontana 2019). To date, 208 species of birds are reported for PET, of which ten are under some level of threat (Chiarani & Fontana 2019). The landscape of PET includes grasslands, marshes, peat bogs, rocky outcrops, araucaria forests, crops and exotic tree plantations (Bencke & Duarte 2008). The area is situated in the southern Brazilian highland grasslands, in the Atlantic Forest biome, with an undulating relief and mean altitude of 900–1,000 m (Fontana *et al.* 2016). The mean annual temperature ranges from 16 °C to 22 °C and the precipitation is evenly distributed

throughout the year (1,500–2,000 mm), reaching up to 2,500 mm in certain subregions (Almeida 2009, Fontana *et al.* 2016).

We assessed temporal changes over three breeding seasons, 2013–2014, 2016–2017 and 2017–2018 (hereafter BS1, BS2, and BS3, respectively) in areas of native grassland with two different histories of fire disturbance: (1) occasional fire (OF) – a 250 ha area burned accidentally only once in the last ten years, in late August 2016; and (2) frequent fire (FF) – a 100 ha area where the use of fire is frequent, burned annually or biennially for cattle raising in the last decade (in all breeding seasons sampled during our study there was fire in this area). In both areas there is low grazing pressure (about 0.5 animal unit per hectare).

### **Study species**

Lesser Grass-Finch is a grassland species that inhabits marshes and grasslands with dense vegetation in southeastern and southern Brazil, southeastern and northern Uruguay, northeastern Argentina, and eastern Paraguay (Ridgely & Tudor 1989, Sick 1997, Tobias *et al.* 1997, Claramunt & Cuello 2004). In our study area, Lesser Grass-Finch is a regular and common species (Chiarani & Fontana 2019) that uses the area to nest from early October to early March, building open-cup nests in grass clumps, mainly *Andropogon lateralis*, *Schizachyrium tenerum*, and *Sorghastrum setosum* (Chiarani & Fontana 2015). Little is known about its feeding habits, but invertebrates probably make up most of its diet (EC, pers. obs.). Lesser Grass-Finch is considered a species of Least Concern (BirdLife International 2019). In Brazil the species is non-threatened but in Argentina and Uruguay it is Vulnerable (Azpiroz *et al.* 2012a, MAyDS & AA 2017).

Black-bellied Seedeater is a tall-grass species often associated to marshy areas (Ridgely & Tudor 1989, Sick 1997). The species is endemic to Brazil and breeds only in a small portion of northeast of Rio Grande do Sul and southeast of Santa Catarina states from November to

March, and later migrates north as far as Minas Gerais and southern Goiás, in central Brazil (Rovedder 2011, Fontana & Repenning 2014, Malacco 2018). In our study area, Black-bellied Seedeater is a regular species during the breeding season, building its nests in small shrubs and grass clumps, both in marshes and dry grasslands (Chiarani & Fontana 2019). Its diet is mainly composed of grass seeds, but invertebrates may eventually be used to feed nestlings (Rovedder 2011). Although Black-bellied Seedeater is Vulnerable in Brazil (MMA 2014), where the entire world population occurs, it is considered a Near-Threatened species at global level (BirdLife 2019). Habitat loss and captures for cage bird trade are the main threats (Fontana & Repenning 2014).

We selected Lesser Grass-Finch and Black-bellied Seedeater because they are grassland-dependent species associated with tallgrass (Azpiroz *et al.* 2012a), with different feeding habits. The two species are abundant in our study area, but Black-bellied Seedeater is a migrant that only occurs there from November to March, and its local breeding population seems to be smaller than Lesser Grass-Finch, a resident species (Chiarani & Fontana 2019). Thus, understanding fire effects on these species may facilitate management initiatives that can also benefit other tall-grass species. The main group of threatened grassland birds in South America is formed by birds fully or partially associated with tall-grass habitats (Azpiroz *et al.* 2012a). Moreover, fire has important effects on breeding territories and nest site of Lesser Grass-Finch and Black-bellied Seedeater (Rovedder 2011, Chiarani & Fontana 2015).

### **Nest searching and monitoring**

We systematically searched for nests of Lesser Grass-Finch in the two areas (OF and FF) during three breeding seasons (BS1, BS2, and BS3) from October to March, totaling 322 days of field work. In the area occasionally burned, the breeding seasons correspond to the period before the fire, the year of the fire, and one year after the fire, respectively. Nests of

Black-bellied Seedeater were searched in the same areas during two breeding seasons (BS2 and BS3) from November to March (because the species arrives at SBHG only in November for breeding), totaling 189 days of field work.

Nest search was conducted by direct observation of the adults' behavior in their breeding territories. Nests found were georeferenced with a handheld GPS device, and then marked with a colored tape placed about 5 m from the nest to facilitate its subsequent location and monitoring. We visited the nests at intervals of 1–5 days, varying according to the nest stage (i.e. shorter interval when events such as laying, hatching or fledging young were approaching). Nests were monitored from the time they were found until they became inactive in order to verify their contents (eggs or nestlings) and fate (successful or unsuccessful).

### **Nesting survival and productivity**

Nests were considered successful when at least one nestling fledged. We considered a nest had been depredated when the contents (eggs or nestlings) disappeared between two consecutive visits, taking into account if nestlings would be old enough to fledge (Pretelli *et al.* 2015). A nest was considered abandoned if the female had not been seen on the nest and a small green leaf placed by us inside the nest had not been removed in more than two consecutive visits (Chiarani & Fontana 2015). As soon as a nest was successful, we followed the parents on feeding fledglings to confirm the nest fate and the number of young individuals, in order to calculate productivity.

### **Territories**

We systematically searched for mated pairs and recorded the total number of territories found in each area during three breeding seasons for Lesser Grass-Finch and two breeding seasons for Black-bellied Seedeater. We captured adult individuals using mist nets and marked

them with unique combinations of colored bands and one aluminum band (standard CEMAVE/ICMBio, Federal Brazilian Banding Agency). To delimit the breeding territories, we used a handheld GPS device to record all points where individuals manifested some territory-defense behavior or where processes associated with breeding occurred. Territory-defense behavior includes singing perches or boundaries defended by males in relation to other individuals of the same species, while mating, nest building, and feeding/rearing of young are breeding process, following the reproductive-territory definition type A proposed by Nice (1941) or type I according to Welty & Baptista (1988).

### **Data analysis**

We estimated nesting success by the daily survival rate (DSR) generated by program MARK (White & Burnham 1999). We excluded from the survival analysis nests that did not provide all the basic information that the program requires to build an encounter history, such as abandoned nests. DSR and duration of the nesting cycle (i.e. from the laying of the first egg until birds fledged) were used to estimate cumulative probabilities for nest survival, that is the probability of a nest to survive for a complete nesting cycle. We defined nesting cycle as 26 days for Lesser Grass-Finch (Chiarani & Fontana 2015) and 23 days for the Black-bellied Seedeater (Rovedder 2011). We obtained the variance for cumulative survival probabilities using the delta method, that allows to approximate the variance when the daily nest survival rate is extrapolated to another temporal scale of survival estimate (Powell 2007, Pretelli *et al.* 2015). We used program CONTRAST (Hines & Sauer 1989) to compare cumulative survival probabilities among breeding seasons for each species in each area.

We calculated the annual production of fledglings by dividing the number of fledglings in each season by the total number of nests in the respective season (Ricklefs & Bloom 1977). Productivity of successful nests was obtained similarly, but in this case we divided the number

of fledglings by the number of successful nests only. We tested if productivity differed among breeding seasons using the nonparametric Kruskal-Wallis tests.

We used the 95% fixed kernel estimator to calculate territory size of the Lesser Grass-Finch, using the least-squares cross-validation smoothing parameter (Worton 1989, Seaman & Powell 1996). Only territories for pairs with  $\geq 30$  locations were measured, to avoid bias in the size estimates (Seaman *et al.* 1999). This analysis was performed with the *adehabitatHR* package (Calenge 2006), using R 3.4.0 (R Development Core Team 2019). Then, we used Kruskal-Wallis tests to compare territory size among the three breeding seasons in each area (Of and FF). We measured only territories of Lesser Grass-Finch, for which we were able to define with precision the territory boundaries. In order to assess if the number of breeding territories was distributed with equal proportions among breeding seasons, we used a binomial test, considering only territories occupied by mated pairs (for both species). All comparisons were made among breeding seasons instead of between areas due to differences in sample size and because we were interested in assessing temporal changes. The level of significance considered in all tests was  $P < 0.05$ .

## RESULTS

We found and monitored a total of 237 nests of the two species (Table 1). One hundred seventy-eight Lesser Grass-Finch nests were monitored during three breeding seasons: 130 in the area occasionally burned (51 in BS1, 30 in BS2, and 49 in BS3) and 48 in the area with frequent use of fire (12 in BS1, 13 in BS2, and 23 in BS3). Fifty-nine Black-bellied Seedeater nests were monitored in two breeding seasons: 36 in the area occasionally burned (30 in BS2, and six in BS3) and 23 in the area frequently burned (13 in BS2, and 10 in BS3). We banded 57 individuals of Lesser Grass-Finch, and 27 individuals of Black-bellied Seedeater.



## Nest survival

Daily survival rates varied over the breeding seasons (Table 2), but the cumulative survival probability of the nests did not show significant differences among years for both species in the two monitored areas. Nest survival probability for Lesser Grass-Finch in OF was 0.390 in BS1 (before the fire), 0.365 in BS2 (year of the fire), and 0.278 in BS3 (one year after the fire), not differing significantly among breeding seasons with or without fire ( $\chi^2_2 = 1.55$ ,  $P = 0.46$ ; Fig. 1). In FF, where fire regimes did not vary through the years, nest survival probability for the species was 0.485 in BS1, 0.312 in BS2, and 0.200 in BS3, not differing significantly among seasons ( $\chi^2_2 = 2.65$ ,  $P = 0.26$ ; Fig. 1). For Black-bellied Seedeater, cumulative probability of nest survival in OF was 0.208 in BS2 (year of the fire), and 0.060 in BS3 (one year after the fire), not differing significantly between breeding seasons ( $\chi^2_1 = 1.74$ ,  $P = 0.19$ ; Fig. 1). In FF, nest survival probability for Black-bellied Seedeater was 0.293 in BS2 and 0.441 in BS3, not differing significantly between breeding seasons either ( $\chi^2_1 = 0.35$ ,  $P = 0.55$ ; Fig. 1).

## Productivity

Production of fledglings per nest did not differ among breeding seasons in the area burned only in 2016 (occasional fire), for both Lesser Grass-Finch ( $H = 0.66$ ,  $P = 0.72$  all nests;  $H = 0.31$ ,  $P = 0.85$  only successful nests) and Black-bellied Seedeater ( $H = 0.16$ ,  $P = 0.69$  all nests;  $H = 0.93$ ,  $P = 0.34$  only successful nests; see Table 1 for values). In the area with frequent fire there was no significant difference among breeding seasons either, for both Lesser Grass-Finch ( $H = 1.02$ ,  $P = 0.60$  all nests;  $H = 0.85$ ,  $P = 0.65$  only successful nests) and Black-bellied Seedeater ( $H = 0.41$ ,  $P = 0.52$  all nests;  $H = 1.00$ ,  $P = 0.32$  only successful nests).

**Table 1.** Number and productivity of nests of two grassland birds in areas with occasional fire (OF) and areas with frequent fire (FF) in Parque Estadual do Tainhas, northeastern of Rio Grande do Sul, Brazil. Nests were monitored during three breeding seasons (BS1 – BS3) for Lesser Grass-Finch, and two breeding seasons (BS2 and BS3) for Black-bellied Seedeater. Nests are defined as number of successful (S) or unsuccessful (U) nests (percentages between parenthesis), and productivity is the mean of fledglings per nest  $\pm$  sd. The area with occasional fire was burned in 2016–2017 (BS2).

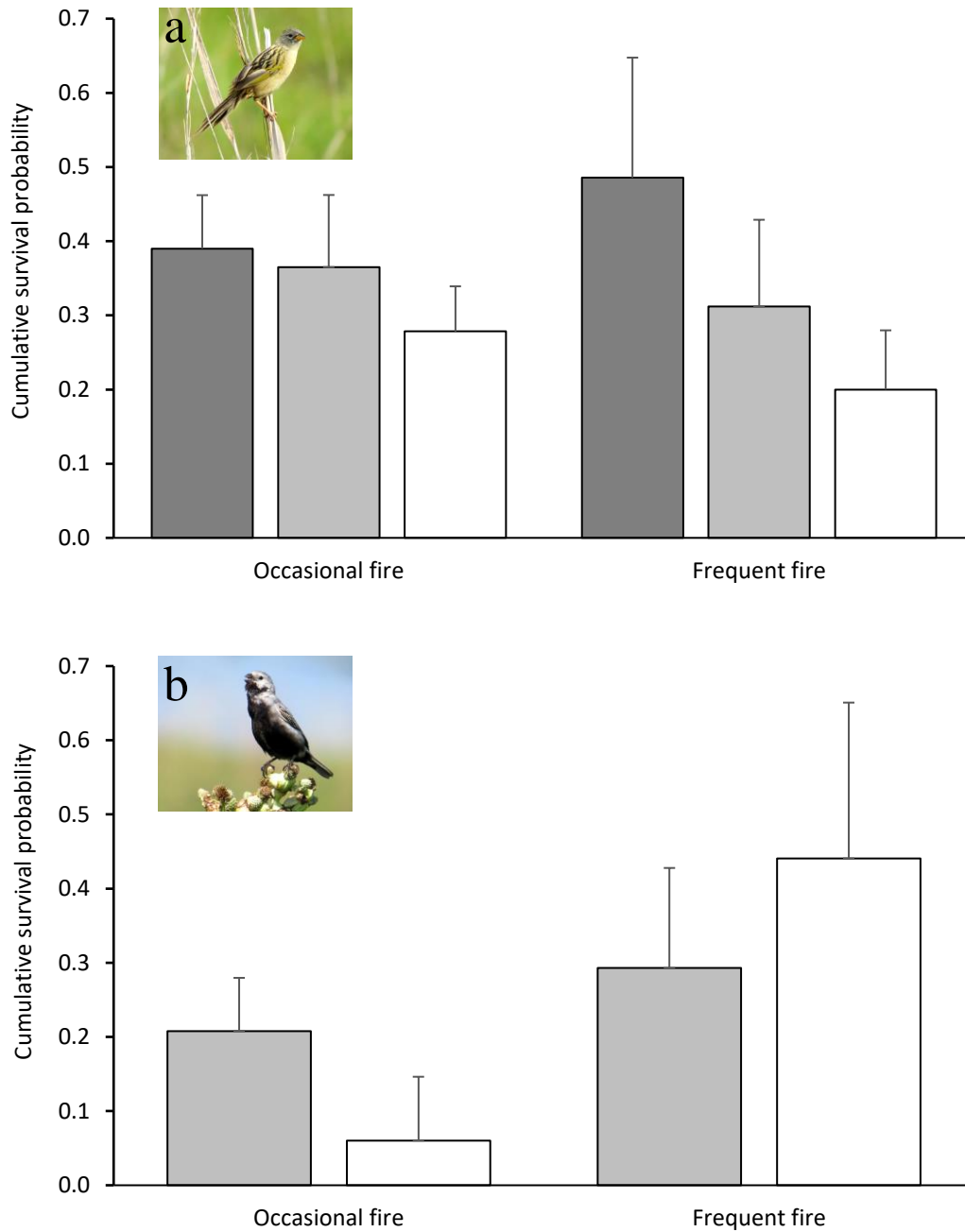
Species	Area	2013-14 (BS1)			2016-17 (BS2)			2017-18 (BS3)		
		S	U	Productivity <sup>a</sup>	S	U	Productivity <sup>a</sup>	S	U	Productivity <sup>a</sup>
Lesser Grass-Finch	OF	22 (43.1)	29 (56.9)	0.84 $\pm$ 1.1	11 (36.7)	19 (63.3)	0.77 $\pm$ 1.14	16 (32.7)	33 (67.3)	0.67 $\pm$ 1.05
				1.95 $\pm$ 0.79			2.09 $\pm$ 0.83			2.06 $\pm$ 0.68
	FF	6 (50)	6 (50)	1.33 $\pm$ 1.44	4 (30.8)	9 (69.2)	0.77 $\pm$ 1.3	8 (34.8)	15 (65.2)	0.78 $\pm$ 1.2
				2.67 $\pm$ 0.52			2.5 $\pm$ 1			2 $\pm$ 0.89
Black-bellied Seedeater	OF				6 (20)	24 (80)	0.4 $\pm$ 0.86	2 (33.3)	4 (66.7)	0.5 $\pm$ 0.84
							2 $\pm$ 0.63			1.5 $\pm$ 0.71
	FF				5 (38.5)	8 (61.5)	0.69 $\pm$ 0.95	5 (50)	5 (50)	1 $\pm$ 1.05
							1.8 $\pm$ 0.45			2 $\pm$ 0
Total nests		28	35		26	60		31	57	

<sup>a</sup> considering all nests (first value) and only successful nests (second value).

**Table 2.** Daily survival rates ( $\pm$  se) for Lesser Grass-Finch and Black-bellied Seedeater nests monitored in areas with two fire histories during three breeding seasons (only two for Black-bellied Seedeater), estimated using program MARK.

Species	Occasional fire			Frequent fire		
	2013-14	2016-17 <sup>a</sup>	2017-18	2013-14 <sup>a</sup>	2016-17 <sup>a</sup>	2017-18 <sup>a</sup>
Lesser Grass-Finch	0.964 (0.007)	0.962 (0.010)	0.952 (0.008)	0.972 (0.012)	0.956 (0.014)	0.940 (0.016)
Black-bellied Seedeater		0.934 (0.014)	0.885 (0.055)		0.948 (0.019)	0.965 (0.020)

<sup>a</sup> corresponds to breeding seasons in which fire occurred.



**Figure 1.** Cumulative survival probability for Lesser Grass-Finch (a) and Black-bellied Seedeater (b) nests monitored in different breeding seasons and areas with two fire histories in Parque Estadual do Tainhas, northeastern of Rio Grande do Sul, Brazil. Dark gray bar corresponds to 2013-2014 breeding season (BS1), light gray bar corresponds to 2016-2017 breeding season (BS2), and white bar corresponds to 2017-2018 breeding season (BS3).

Whiskers are standard errors, calculated using the delta method. All comparisons are non-significant at  $P < 0.05$ .

## **Territories**

Territory size of Lesser Grass-Finch was significantly different over the breeding seasons in OF ( $H = 27.76$ ,  $df = 2$ ,  $P < 0.001$ ; Table 3). Post-hoc tests showed that in the season before the fire (BS1) territories were larger than in the season of the fire (BS2;  $z = 2.58$ ,  $P = 0.008$ ) and one year after the fire (BS3;  $z = 5.27$ ,  $P < 0.001$ ) but territories did not differ between BS2 and BS3 ( $z = 2.06$ ,  $P = 0.055$ ). There were not differences in the territory size of Lesser Grass-Finch over the breeding seasons in FF ( $H = 0.44$ ,  $df = 2$ ,  $P = 0.801$ ; Table 3).

The number of territories of Lesser Grass-Finch in OF was lower in the season of the fire in comparison with the season before the fire (BS2: 14 vs. BS1: 29,  $P = 0.03$ ), and in relation to one year after the fire (BS2: 14 vs. BS3: 31,  $P = 0.01$ ; Supporting Information Figure S1). The number of territories did not differ between the season before the fire and one year after fire (BS1: 29 vs. BS3: 31,  $P = 0.90$ ). In FF the number of territories of Lesser Grass-Finch did not differ among breeding seasons (BS1: 11; BS2: 9; BS3: 11; all comparisons  $P \geq 0.82$ ). The number of territories of Black-bellied Seedeater in OF was lower one year after the fire in comparison with the breeding season of the fire (BS3: 5 vs. BS2: 18,  $P = 0.01$ ). In FF the number of territories of Black-bellied Seedeater did not differ among breeding seasons (BS2: 11 vs. BS3: 9,  $P = 0.82$ ).

**Table 3.** Territory size (in ha) of Lesser Grass-Finch in areas with two fire histories during three breeding seasons (BS1 – BS3) in Parque Estadual do Tainhas, northeastern of Rio Grande do Sul, Brazil. Values are presented as mean  $\pm$  sd (with sample size) and the results of Kruskal-

Wallis test among breeding seasons. The breeding season 2016–2017 corresponds to that in which the area with occasional fire was burned.

Area	2013-14 (BS1)	2016-17 (BS2)	2017-18 (BS3)	<i>H</i>	<i>P-value</i>
Occasional fire	3.77 ± 1.04 (19)	2.58 ± 0.88 (14)	1.9 ± 0.73 (26)	27.76	< <b>0.001</b>
Frequent fire	1.74 ± 0.5 (11)	2.03 ± 0.91 (9)	1.94 ± 1.09 (11)	0.44	0.8

## DISCUSSION

We found no temporal changes on nest survival and production of fledglings of Lesser Grass-Finch and Black-bellied Seedeater, both in the area burned occasionally and in the area with frequent fire. Although the daily survival rates of Lesser Grass-Finch showed a decrease across the years in both areas it was not statistically different (Fig. 1). This refutes our hypothesis that nest success and productivity would be smaller in the breeding season following the fire in the area burned only once. In Argentina a prescribed fire did not affect the nest survival, clutch size, hatching success, and chick survival of Strange-tailed Tyrant *Alectrurus risora*, in comparison with the years before and after the fire (Di Giacomo *et al.* 2011). Interannual differences on nest survival were not detected between burned areas either, nor between unburned areas for grassland birds in the Argentine Pampas during two breeding seasons following a fire (Bahía & Zalba 2019). In North America, comparisons between two typical methods of grazing (patch-burn grazed pastures and traditionally managed pastures with annual fire) showed little difference in nest survival rates for grasshopper sparrows *Ammodramus savannarum* (Hovick *et al.* 2012). However, our results on nest survival of Black-bellied Seedeater must be interpreted with caution due to the small sample size (number of nests) in the breeding season one year after the fire.

The low number of Black-bellied Seedeater nests found one year after the fire is a result of the decrease of the number of territories in this breeding season. This may be related to a

response of birds to the fire occurred one year before and possible changes in their territories, since this species has a philopatric behavior (Rovedder 2011). The potential benefits of returning to previously successful breeding sites could be denied if nesting habitat is variable and suffers disturbances, becoming unsuitable in a given time (Jones *et al.* 2007). Some grassland birds have adapted to this variability, often resulting in fluctuations in local population densities (Winter *et al.* 2005).

Territories of Lesser Grass-Finch were fewer and smaller in the breeding season following the fire in the area burned only once, corroborating our hypothesis. This probably occurred due to the loss of tall-grass vegetation in dry grasslands and, consequently, lower availability of suitable habitat for the species in this year. Fire affects both the composition and the structure of vegetation (Reinking 2005), and after fire, dry grasslands have low vegetation that does not provide appropriate sites for shelter, foraging, and nest building, restricting the territories of Lesser Grass-Finch to wetlands (Chiarani & Fontana 2015). Territories fully located on dry grassland were lost in the breeding season of the fire. One year after the fire some territories in this area occupied portions of dry habitats (some nests were even built in dry grasslands in this breeding season) but remained smaller than in the breeding season before fire, probably because the number of territories increased. In contrast, in the area frequently burned, fire seems not to affect territory stability of the Lesser Grass-Finch over years, because in this area there are few suitable habitats for the species outside the wetlands, being the territories in marshes less affected by fire. Lesser Grass-Finch occupies less dry grasslands in burned areas than in unburned areas (Chiarani & Fontana 2015). Thus, the smaller territory size in areas recently burned is probably related to habitat availability. An important issue in further studies would be to know if an area with frequent fire will present more territories and with larger size if fire disturbance is excluded for some years. Density and territory size are also often related to local habitat quality, which is usually determined by food availability (Marshall & Cooper

2004, Verheijen *et al.* 2019). The smaller territory size of Lesser Grass-Finch in areas recently burned may be also a consequence of the increased abundance of invertebrates. Although we do not have data on this assumption, studies show that the diversity and abundance of arthropods increase in the months following a fire (Swengel 2001, Podgaiski *et al.* 2013).

Our results show that temporal variations occurred in territories in the area burned occasionally, and no changes over years were observed on breeding in both occasional and frequent fire areas. For both species, the reduced number of territories in the year of the fire or one year after the fire shows that we should avoid burning the whole area (i.e. using patch-burn method) when it remains a long time without fire in order to prevent loss of breeding territories. Patch-burn management has been recommended as a useful tool for grassland bird conservation, because it creates the entire gradient of vegetation structure required to maintain grassland bird species that differ in habitat preferences (Fuhlendorf *et al.* 2006, Churchwell *et al.* 2008). In Argentina in the years when accidental fires did not affect the whole area the birds breed in the remaining unburned patches (Di Giacomo *et al.* 2011). Even with no effects on nest survival, a drastic loss of territories should be a major concern because it reduces the number of breeding birds in the population and consequently reduces the number of fledglings per year. For Strange-tailed Tyrant, Di Giacomo *et al.* (2011) consider that if the appropriate size and intensity of the fire are chosen, taking into consideration season and frequency of fire, the impact of prescribed fires on its reproduction can be minimized.

The number of territories of Lesser Grass-Finch returned to previous values (i.e. values recorded before the fire) one year after the fire, suggesting that for this species to recover its density of territories in an area with occasional fire the interval between burns should be at least two years. Interestingly for Black-bellied Seedeater the number of territories was reduced one year after the fire, and a longer study period is required to understand this relation of territory with time since fire. However, this result indicates that Black-bellied Seedeater probably needs



a longer interval between fire disturbances than Lesser Grass-Finch. This information is of great concern since the species is threatened in Brazil, which encompasses its entire distribution. Results for Saffron-cowled Blackbird *Xanthopsar flavus*, another grassland threatened species that occurs in the same region of our study, showed that the species returned to a burned marshland to breed three breeding seasons after the fire (Petry & Krüger 2010). The same was observed in Argentina, where Strange-tailed Tyrant showed not to avoid a burned patch in the third breeding season after the prescribed fire (Di Giacomo *et al.* 2011).

Fire is an important structuring factor of natural communities in grasslands (Leys *et al.* 2018). However, management policies in protected natural areas of southern South America are frequently limited to preventing and extinguishing fire, which can lead to loss of biodiversity (Pillar & Vélez 2010, Bahía & Zalba 2019). Our study is the first about temporal effects of fire on breeding and territories of grassland birds in South Brazil and provides information to support management actions in grasslands. Although caution is needed for extrapolations of results due to the number of areas that it was possible to sample, our findings support that controlled prescribed fire can be used in some areas for managing grasslands without effects on breeding of Lesser Grass-Finch and Black-bellied Seedeater. However, the effects on territories of these species suggest that this management must consider the maintenance of portions of grasslands without fire and the interval between burns. Because responses of bird density and nesting success may vary among regions, years, and species, land managers need to provide grasslands with different types of vegetation structure (Winter *et al.* 2005). Another point of major concern is that the fire must occur before the breeding season of birds to avoid burning nests. Further studies could include areas without fire in analyzes, despite the difficulties in finding grassland areas that remain a long time without burn. Additionally, studies should consider long-term effects caused by changes in fire regime of an area, to know,

for example, what happens when an area that was occasionally burned starts to be burned more often.

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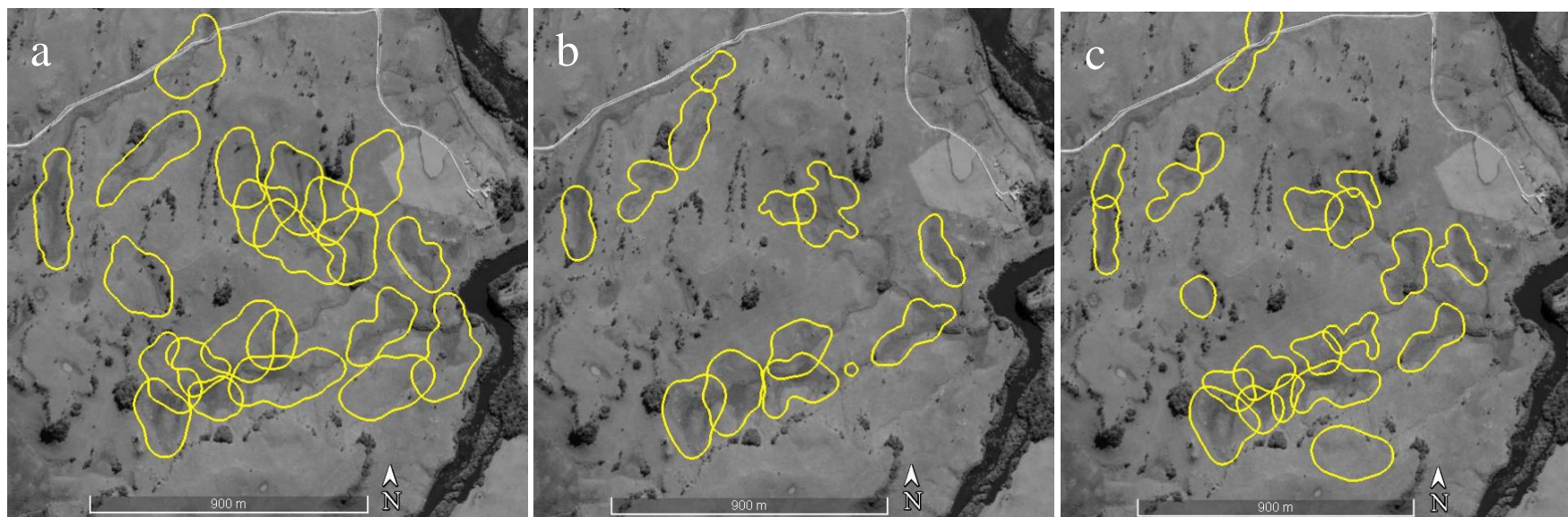
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## SUPPORTING INFORMATION



**Supporting Information Figure S1.** Territories of Lesser Grass-Finch during three breeding seasons (a, season before the fire; b, season following the fire; c, season one year after the fire) in an area occasionally burned in Parque Estadual do Tainhas, northeastern of Rio Grande do Sul, Brazil. Polygons represent some territories monitored in each breeding season and delimited using the 95% kernel estimator.

## CONCLUSÕES GERAIS

Esse trabalho permitiu o entendimento de como o fogo influencia a comunidade e a reprodução de aves campestres em uma escala temporal. A resiliência da avifauna mostrou que o fogo pode ser uma opção de manejo dos campos, desde que feito de forma correta, ou seja, respeitando o período e a periodicidade das queimadas. O período é importante para a queima não coincidir com a época de reprodução das aves (i.e., deve ocorrer anteriormente), e a periodicidade implica dar o tempo necessário para uma área se recuperar após uma queimada. Durante o estudo, algumas espécies de aves (inclusive ameaçadas) só foram registradas em áreas recentemente queimadas, enquanto outras espécies tiveram sua abundância reduzida após o fogo. Isso mostra que o fogo deveria ser usado de forma a criar mosaicos de áreas com diferentes tempos desde a última queimada, gerando, assim, uma paisagem heterogênea de locais com alturas de vegetação variadas para favorecer um maior número de espécies de aves.

A utilização do fogo como ferramenta de manejo de áreas campestres é muito debatida em todo o mundo, embora essa questão seja mais abordada em relação aos efeitos das queimadas sobre a vegetação, como ocorre no Brasil. Uma melhor compreensão dos efeitos do fogo passa por uma análise que integre diferentes grupos taxonômicos da fauna e da flora. Apesar de muitos estudos demonstrem que distúrbios como o fogo são importantes para a manutenção de áreas campestres em algumas regiões do Brasil, essa temática ainda é vista como um tabu para a conservação, especialmente dentro de áreas protegidas. Após uma regulamentação, queimadas prescritas para fins científicos e/ou econômicos do campo deveriam ser mais utilizadas e estudadas no Brasil, pois uma das principais dificuldades de trabalhos com fogo é o encontro de áreas para desenvolver estudos de longo prazo. É frequente a ocorrência de queimadas acidentais (ou criminosas) que geram incêndios de grandes proporções, comprometendo projetos de pesquisa.

Nos campos de altitude do sul do Brasil, a pecuária possui uma estreita ligação com o uso do fogo. Além de questões econômicas, a proibição do uso do fogo contribuiu para mudanças significativas no uso da terra nas últimas décadas na região, transformando campos nativos que eram usados para criação de gado em áreas de lavouras ou silvicultura. Por isso, estudos que elucidem os efeitos do fogo sobre o campo são fundamentais para permitir que uma atividade econômica capaz de conciliar o uso do campo com sua conservação não continue sendo substituída por outras que resultam na perda desse importante ecossistema.



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