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Passive restoration contributes to bird conservation in Brazilian Pampa grasslands

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ABSTRACT. The global decline of biodiversity makes it important to find affordable ways to conserve and restore habitats. Restoration is useful for conserving native grasslands, with passive restoration defined as either natural colonization or unassisted recovery. Grasslands in southeastern South America have been transformed into croplands and impacted by other human activities. We describe the first assessment of passive restoration as a management tool to conserve birds in the Pampa grasslands of Brazil. We compared bird species richness using coverage-based rarefaction and extrapolation, applying PERMANOVA for composition, and the abundance of bird communities between sites undergoing passive restoration (PR) and sites with native grasslands (NG). We employed fitted generalized linear mixed models (GLMM) to quantify relationships between bird occurrence and vegetation structure and cover. We recorded 61 species of birds during our study (45 in PR and 46 in NG) and 762 individuals (333 in PR and 429 in NG). Of these species, 15 were restricted to PR and 16 to NG. Grassland specialists and threatened species were found in both PR and NG, and only vegetation height differed between PR and NG. We detected eight species of conservation concern, including three recorded only in PR, three only in NG, and two in both PR and NG. The absence of marked differences in species richness and composition of bird communities between passive-restoration and native grasslands in our study suggests that grasslands in the process of passive restoration can provide habitat for many species of grassland birds and that passive restoration is an appropriate management tool for biodiversity conservation in Brazilian grasslands.

RESUMEN. **La restauración pasiva contribuye a la conservación de las aves en los pastizales de las pampas Brasileñas**
La disminución global de la biodiversidad hace que sea importante encontrar formas asequibles para conservar y restaurar los hábitats. La restauración es útil para conservar los pastizales nativos, con la restauración pasiva definida como colonización natural o recuperación no asistida. Los pastizales en el sureste de Sudamérica se han transformado en tierras agrícolas e impactados por otras actividades humanas. Describimos la primera evaluación de la restauración pasiva como una herramienta de manejo para conservar las aves en las praderas de las pampas en Brasil. Comparamos la riqueza de especies de aves utilizando rarefacción y extrapolación basadas en la cobertura, aplicando PERMANOVA para la composición y la abundancia de comunidades de aves entre sitios sometidos a restauración pasiva (RP) y sitios con pastizales nativos (PN). Empleamos modelos mixtos lineales generalizados ajustados (GLMM) para cuantificar las relaciones entre la presencia de aves y la estructura y cobertura vegetal. Registramos 61 especies de aves durante nuestro estudio (45 en RP y 46 en PN) y 762 individuos (333 en RP y 429 en PN). De estas especies, 15 estaban restringidas a RP y 16 a PN. Se encontraron especialistas en pastizales y especies amenazadas tanto en PR como en PN, y solo la altura de la vegetación difirió entre RP y PN. Detectamos ocho especies de interés para la conservación, incluidas tres registradas solo en RP, tres registradas solo en PN y dos registradas en RP y PN. La ausencia de marcadas diferencias en la riqueza de especies y la composición de las comunidades de aves entre la restauración pasiva y los pastizales nativos en nuestro estudio sugiere que los pastizales en el proceso de restauración pasiva pueden proporcionar hábitat para muchas especies de aves de pastizales, y que la restauración pasiva es un herramienta de manejo apropiado para la conservación de la biodiversidad en pastizales Brasileños.

Key words: abandonment, agriculture, conservation, degradation, grassland birds

Natural habitats have been converted for human land uses, impacting biodiversity globally (Newbold et al. 2015). Vegetation restoration has been used to recover altered ecosystems that have been degraded, damaged, or destroyed (Zaloumis and Bond 2011, McAlpine et al. 2016). Where the aim is restoration for faunal recovery, restoration programs must provide suitable habitat and

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associated key resources, such as for nesting, foraging, and shelter (Fletcher and Koford 2002, 2003, Sudduth et al. 2011, McAlpine et al. 2016).

Broadly, there are two types of restoration, active and passive. Whereas active restoration involves human intervention and a range of management techniques applied to influence the successional trajectory of recovery, passive restoration relies on natural colonization or unassisted recovery (i.e., secondary succession) without additional remedial actions (Rey Benayas et al. 2008, Holl and Aide 2011, Suding 2011). Passive restoration typically occurs after abandonment of land uses such as agriculture, and the spontaneous recovery may allow colonization of disturbed areas by native and/or non-typical or alien species of plants (Rey Benayas et al. 2008, Andrade et al. 2015). The effectiveness of passive restoration for conservation depends on factors such as the length of time land has been used for other purposes, whether seeds of native plants remain in the soil, the intensity and duration of past land management, landscape context, and soil conditions (Prober and Thiele 2005, Andrade et al. 2015, Crouzeilles et al. 2016, McAlpine et al. 2016).

Ecological restoration has advanced worldwide as an academic discipline in the last two decades (Selwood et al. 2009, Brudvig 2011), with restoration initiatives undertaken in many ecosystems and countries (Bullock et al. 2011, Crouzeilles et al. 2016). Grasslands require extensive restoration because they have been widely degraded (Hoekstra et al. 2005) and their biodiversity is affected by land-use pressures (Newbold et al. 2016), mainly by conversion to agriculture, establishment of pastures of exotic grasses for livestock, and afforestation (Overbeck et al. 2015). Grassland restoration may range from improvement of a degraded site to major interventions to recover grasslands on sites that have been entirely cleared (Gibson 2009). Globally, abandonment of farmland has increased, influenced by rural-urban migration (Aide and Grau 2005, Cramer et al. 2008, Rey Benayas and Bullock 2012), and is therefore the major form of passive restoration of grasslands.

Although investigators have evaluated the responses of plants to grassland restoration, less is known about the responses of other groups such as birds (Brudvig 2011, Kollmann et al. 2016). Birds can serve as indicators of habitat change because they perform important ecological functions and may serve as a proxy for the overall recovery of biodiversity during ecosystem restoration (Rey-Benayas et al. 2010, Latja et al. 2016, Batisteli et al. 2018). Vegetation structure directly influences bird communities because birds require particular structures for nesting, foraging, and perching (Azpiroz and Blake 2016).

In the Brazilian Pampa region (177,000 km^2), only 36% of the native grasslands remains (MMA 2011) and only 1.38% of this area is protected (MMA 2007). Approximately 90 species of grassland birds depend on this habitat during all or part of their life cycle, and 21% of these species are globally and/or regionally threatened (Fontana and Bencke 2015). Despite this, there are no published studies of birds in grasslands undergoing restoration in South America, including the Brazilian Pampa grasslands or even in Argentina, where grasslands occupy ~ 33% of the entire country (Bilenca and Miñarro 2004). Thus, our objective was to compare the structure of bird communities (species richness, abundance, and composition) in grasslands undergoing passive restoration to those of native grasslands (reference areas) in the Brazilian Pampa. We also assessed the ways that vegetation attributes (structure and cover) influenced the occurrence of bird species. Further, we compared the vegetation structure and cover of passively restored and native grasslands, given that some key attributes of grasslands important for birds are lost with human disturbance (Öster et al. 2009, Fisher and Davis 2010). We hypothesized that native grasslands would have greater species richness than passive-restoration sites because their habitat features may support more niches and other resources for birds (MacArthur and MacArthur 1961).

METHODS

Our study was conducted in the Brazilian Pampa grasslands, part of the grasslands of southeastern South America (SESA grasslands) and one of the most extensive grassland ecosystems in the Neotropics (Azpiroz et al. 2012). The study region—Central Depression and Southwestern—was characterized by intensive agricultural activity and cattle

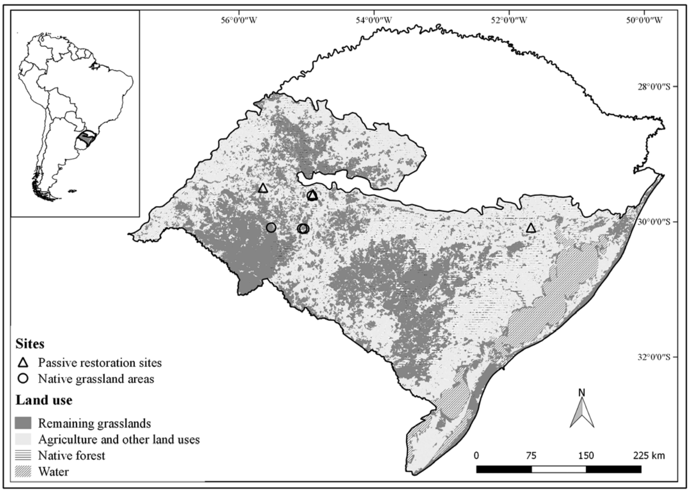

Fig. 1. Eight sites sampled in grasslands of the Brazilian Pampa biome, including four passive-restoration sites and four native grasslands (i.e., reference areas).

grazing and was broadly representative of the ~ 32% of the degraded grasslands of southern Brazil (Andrade et al. 2015). Native grassland with low levels of cattle stocking is almost non-existent in our study region. Plant species that dominated the study region included *Paspalum notatum*, *Andropogon lateralis*, *Axonopus affinis*, *Eryngium horridum*, and *Aristida jubata* (Andrade et al. 2019).

We conducted fieldwork at four sites undergoing passive restoration (PR) and four native grassland areas (NG; Fig. 1). Passive-restoration areas were either abandoned soybean (*Glycine max*) or rice (*Oryza sativa*) fields, with time since abandonment ranging from 10 to 35 years. These areas have not been subject to any type of subsequent human intervention and were the only areas where grassland vegetation had been recovered after more intensive land use. However, we acknowledge that we did not analyze the composition of the vegetation so cannot confirm that the plant community was totally restored. We assumed that these areas could serve as replicates of passive restoration, even though they differed in time since abandonment. We based this assumption on our field experience of more than 20 years (C. S. Fontana) as well as on the results of studies indicating that plant species richness (Torchelsen et al. 2019) and floristic composition of grassland remnants (Fensham et al. 2016) can recover within ~ 10 years of abandonment, even if some differences to reference grasslands may remain both in terms of structure and floristic composition (Tognetti et al. 2010). In addition, Fedrigo et al. (2018) evaluated the vegetation of Pampa grasslands and found high restoration capacity within ~ 3 months after a long period of intense grazing.

Three of the four passive-restoration sites in our study were on private land, ranged in size from 65 to 600 ha, and had similar altitudes, relief, soil types (hydromorphic and depth), and climates (Hasenack et al. 2010). They were located in three municipalities, including Eldorado do Sul (PR1, public land; 30.0854°S, 51.6769°W), Manoel Viana (PR2; 29.4950°S, 55.6441°W), and São Francisco de Assis (PR3 and PR4; 29.5978°S, 54.9090°W; 29.6046°S, 54.9105°W).

Native grasslands in our study were typical Brazilian Pampa grasslands that have been used as benchmark grasslands by botanists and correspond to the same physiognomy of grasslands as PR. These sites were located on either public or private land in three municipalities, ranged in size from 260 to 1200 ha, and were designated as NG1 and NG2 (Rosário do Sul, public lands; 30.1021°S, 55.0640°W; 30.1039°S, 55.0339°W), NG3 (São Francisco de Assis, private land; 29.6157°S, 54.9119°W), and NG4 (Alegrete, private land; 30.0860°S, 55.5231°W).

The PR and NG sites were lightly grazed, with a low cattle stocking rate (≤ 1 animal unit per ha). Extensive grazing has been part of the culture and management of these grasslands for at least two centuries so grasslands not used for grazing are almost non-existent in our study region. Cattle grazing is intrinsic to the landscape of the Brazilian Pampa and is important for its maintenance and diversity (Overbeck et al. 2007, Andrade et al. 2015). For each site, the sampled area was ~ 180 ha, except for PR4 where the entire 65 ha was sampled.

Bird sampling. We sampled birds during the breeding season (austral spring–summer, November–February), once in 2015–2016 and once in 2016–2017, using 80 point counts in PR ($N = 40$; PR1: 12, PR2: 12, PR3: 10; PR4: 6 point counts) and NG ($N = 40$; 10 point counts at each site) distributed randomly. We used 5-min, 100-m radius point counts (Bibby et al. 2000, Matsuoka et al. 2014, Fontana et al. 2018) all completed by one observer (T.W. da Silva). Point-count centers were at least 300 m apart and located at least 150 m from the nearest habitat edge. To standardize detection, point counts were conducted for a maximum of 3 h beginning immediately after sunrise on days of favorable weather (i.e., no rain or strong wind). We recorded all birds observed or heard; birds in flight were not considered. We used information from Azpiroz et al. (2012) to classify grassland bird species in southeastern South America and global (IUCN 2017) and regional (DOE 2014) lists to determine their conservation status. We used unadjusted counts for all species because many grassland birds are easily detected, and many assumptions used to estimate detection probabilities are difficult to apply to grassland systems (Lockhart and Koper 2018).

Vegetation structure sampling. We surveyed vegetation structure and cover at all locations where we conducted point counts and at the same time of year (November–February, once in 2015–2016 and once in 2016–2017). We surveyed five quadrats at each point-count location ($N = 400$), one at the central point and the others in each cardinal direction (north, south, east, and west) and 50 m from the central point.

During surveys, we recorded vegetation height, percent of visual obstruction, and percent soil cover. In each quadrat, we used a plastic frame measuring 1 × 1 m and divided internally into 16 quadrants (each 0.25 × 0.25 cm) (Daubenmire 1959). We placed graduated plastic rods vertically in the center and at the four corners of the frame to measure vegetation height (cm). To determine visual obstruction (density), we placed the frame vertically on one side of the quadrat, with the observer 4 m away from the frame recording the number of quadrants filled by vegetation (Robel et al. 1970). To measure soil cover, we positioned the quadrat horizontally and measured the number of quadrants filled with different functional groups of plants: short grasses (≤20 cm), tall grasses (>21 cm), herbs, shrubs, *Eryngium* spp., *Baccharis* spp., exposed soil, water, and cattle dung (Fuhlendorf et al. 2006, Bencke and Dias, unpubl. data). *Eryngium* and *Baccharis* are native plants, woody vegetation (*Baccharis)* provides important resources for birds (Dias et al. 2014), and some birds use *Eryngium* as a perch site (Dias et al. 2017). To obtain a mean value for vegetation variables at the point-count level, we calculated the mean for each of the five quadrats per point count. All vegetation sampling was conducted by the same observer (T. W. da Silva).

Statistical analysis. To assess differences in species richness between PR and NG, we used coverage-based rarefaction and extrapolation (Chao and Jost 2012) using the estimateD function of the iNEXT package (Hsieh et al. 2019). Non-overlapping 95% confidence intervals are considered to indicate a difference in species richness in two types of grassland. We used generalized linear mixed models (GLMM) to compare total bird abundance between PR and NG, using the glmer function in the lme4 package (Bates et al. 2015) and Poisson family of models. Our models included type of grassland and a null model, together with two random effects (point-count and site) to account for spatial variation. Of the two models, we selected the one with the lower AIC_c value (see below for more details).

We modeled the effects of vegetation variables on the occurrence of individual species of grassland birds separately. Only species observed in at least 10% of the point counts were analyzed individually to model abundance, using a Poisson distribution. We used the pairs function in the FactoMiner package to quantify the level of correlation among vegetation-cover variables (Le et al. 2008). We found that visual obstruction and tall grass were positively correlated with vegetation height ($r = 0.81$ for both), whereas short grass was negatively correlated with vegetation height ($r = -0.77$). Therefore, these three variables were dropped from the analysis. We therefore used only vegetation height and herbs as independent variables, in addition to the type of grassland (PR and NG). For all models, we used two random effects, point count and site. Our full model for the response variable (occurrence of individual species) was as follows: "x = glmer (response variable ~ type of grassland + vegetation height + herbs + (1|Point-count) + (1|Site), family = Poisson)." We ran all possible models and compared them using the second-order AIC corrected for small sample sizes (AIC_c) with the dredge function of the MuMIn package (Barton 2016). The model with the lowest AIC_c value was selected as the best model. All analyses were performed using R 3.4.3 (R Core Team 2018) at a significance level of $\alpha = 0.05$.

To compare the composition of grassland bird species in PR and NG, we performed a non-metric multidimensional scaling (NMDS) with the Jaccard dissimilarity index, using the metaMDS function in the vegan package in R (Oksanen et al. 2017). We tested the NMDS significance with the manyglm function of the mvabund package in R, using the binomial family (Wang et al. 2017). To examine differences in the structure and composition of vegetation (response variables) for eight variables between PR and NG (fixed effects), we used the GLMM with a Poisson distribution and two random effects (point-count and site). The best model was the one with the lowest AIC_c value.

RESULTS

We recorded 61 species of birds (45 in PR, and 46 in NG) and 762 individuals (333 in PR, and 429 in NG) (Table 1). Of these species, 15 were restricted to PR and 16 to NG. Grassland Sparrows (*Ammodramus humeralis*) were recorded in most point counts ($N = 101$) and were the most abundant species for both PR ($N = 68$ individuals) and NG ($N = 82$ individuals). Of the 61 species recorded, 34 are associated with grasslands in southeastern South America (PR = 28 species; NG = 25 species) (Table 1). Twenty-five species are considered grassland specialists, i.e., restricted solely to, or make extensive use of grassland habitats (Azpiroz et al. 2012). We found six grassland specialists only in PR, including Burrowing Owls (*Athene cunicularia*), Chimango Caracaras (*Milvago chimango*), Spectacled Tyrants (*Hymenops perspicillatus*), Streamer-tailed Tyrants (*Gubernetes yetapa*), Blue-black Grassquits (*Volatinia jacarina*), and Chestnut Seedeaters (*Sporophila cinnamomea*), and six only in NG, including Greater Rheas (*Rhea americana*), Southern Caracaras (*Caracara plancus*), Gray Monjitas (*Xolmis cinereus*), Ochre-breasted Pipits (*Anthus nattereri*), Marsh Seedeaters (*Sporophila palustris*), and Long-tailed Reed Finches (*Donacospiza albifrons*). Thirteen species occurred in both PR and NG. We detected eight species of conservation concern, including Streamer-tailed Tyrants, Chestnut Seedeaters, and Rusty-collared Seedeaters (*Sporophila collaris*) recorded only in PR, Greater Rheas, Ochre-breasted Pipits, and Marsh Seedeaters recorded only in NG, and Sedge Wrens (*Cistothorus platensis*) and Pearly-bellied Seedeaters (*Sporophila pileata*) recorded in both PR and NG (Table 1).

We found no significant difference in estimated rarified species richness between PR and NG, after considering the overlap in confidence intervals (45 [39.15–50.85] and 41.88 [38.81–44.95], respectively; Fig. 2). However, total bird abundance was greater in NG than PR (GLMM, $Z = 2.5$, $P = 0.013$) (Table 2). Of the 11 species of grassland birds analyzed, four responded significantly to habitat associations (Table 2), including Wedge-tailed Grass-Finches (*Emberizoides herbicola*) present in taller vegetation, Hellmayr's Pipits (*Anthus hellmayri*) and Grassland Yellow-Finches (*Sicalis luteola*) in shorter vegetation. Hellmayr's Pipits responded significantly to NG, and Spotted Nothuras (*Nothura maculosa*) responded to coverage of herbs.

Composition of grassland bird species did not differ between PR and NG (manyglm binomial, $P = 0.24$; Fig. 3). Of the eight vegetation variables, only one differed between PR and NG, with shorter vegetation in NG (GLMM, $Z = -3.5$, $P < 0.001$; Fig. 4). The

Table 1. Number of individuals of each bird species sampled from 2015 to 2017 in passive-restoration (PR) and native grasslands (NG) of the Brazilian Pampa biome, and the frequency of occurrence at the eight sites.

Family and species	Habitat PR	Habitat NG	Frequency of occurrence (%)
Rheidae			
Greater Rhea (*Rhea americana*)*,†	0	1	12.5
Tinamidae			
Red-winged Tinamou (*Rhynchotus rufescens*)*	6	1	25
Spotted Nothura (*Nothura maculosa*)*	5	9	50
Anatidae			
Brazilian Teal (*Amazonetta brasiliensis*)	2	1	25
Columbidae			
Eared Dove (*Zenaida auriculata*)	0	2	25
Ruddy Ground Dove (*Columbina talpacoti*)	1	0	12.5
Cuculidae			
Guira Cuckoo (*Guira guira*)	5	4	25
Smooth-billed Ani (*Crotophaga ani*)	1	0	12.5
Charadriidae			
Southern Lapwing (*Vanellus chilensis*)*	1	3	25
Scolopacidae			
South American Snipe (*Gallinago paraguaiae*)	1	4	50
Jacanidae			
Wattled Jacana (*Jacana jacana*)	2	2	25
Threskiornithidae			
Plumbeous Ibis (*Theristicus caerulecens*)	0	1	12.5
Strigidae			
Burrowing Owl (*Athene cunicularia*)*	4	0	12.5
Picidae			
Campo Flicker (*Colaptes campestris*)*	4	1	37.5
Falconidae			
Southern Caracara (*Caracara plancus*)*	0	2	25
Chimango Caracara (*Milvago chimango*)*	1	0	12.5
Furnariidae			
Rufous Hornero (*Furnarius rufus*)*	1	4	50
Firewood-gatherer (*Anumbius annumbi*)*	5	8	62.5
Stripe-crowned Spinetail (*Cranioleuca pyrrhophia*)	0	1	12.5
Chotoy Spinetail (*Schoeniophylax phryganophilus*)	2	3	37.5
Tyrannidae			
White-crested Tyrannulet (*Serpophaga subcristata*)	0	1	12.5
Bran-colored Flycatcher (*Myiophobus fasciatus*)	0	1	12.5
Spectacled Tyrant (*Hymenops perspicillatus*)*	1	0	12.5
Yellow-browed Tyrant (*Satrapa icterophrys*)	1	0	12.5
Gray Monjita (*Xolmis cinereus*)*	0	1	12.5
Streamer-tailed Tyrant (*Gubernetes yetapa*)*,‡	2	0	12.5
Cattle Tyrant (*Machetornis rixosa*)*	1	0	12.5
Great Kiskadee (*Pitangus sulphuratus*)	3	2	37.5
Tropical Kingbird (*Tyrannus melancholicus*)	1	6	37.5
Fork-tailed Flycatcher (*Tyrannus savana*)*	13	7	75
Hirundinidae			
Brown-chested Martin (*Progne tapera*)*	1	3	37.5
Troglodytidae			
House Wren (*Troglodytes aedon*)	0	2	12.5
Sedge Wren (*Cistothorus platensis*)*,‡	6	5	50

Table 1. Continued

Family and species	Habitat		Frequency of occurrence (%)
	PR	NG	
Turdidae			
Creamy-bellied Thrush (*Turdus amaurochalinus*)	1	0	12.5
Mimidae			
Chalk-browed Mockingbird (*Mimus saturninus*)*	3	6	50
Motacillidae			
Ochre-breasted Pipit (*Anthus nattereri*)*,§,¶	0	1	12.5
Hellmayr's Pipit (*Anthus hellmayri*)*	1	55	62.5
Thraupidae			
Grassland Yellow-Finch (*Sicalis luteola*)*	24	62	87.5
Blue-black Grassquit (*Volatinia jacarina*)*	12	0	37.5
Red-crested Finch (*Coryphospingus cucullatus*)	0	2	12.5
Pearly-bellied Seedeater (*Sporophila pileata*)*,¶	9	1	50
Marsh Seedeater (*Sporophila palustris*)*,¶,**	0	1	12.5
Chestnut Seedeater (*Sporophila cinnamomea*)*,†,‡	8	0	12.5
Double-collared Seedeater (*Sporophila caerulescens*)	2	2	25
Rusty-collared Seedeater (*Sporophila collaris*)*,†	5	0	12.5
Green-winged Saltator (*Saltator similis*)	0	1	12.5
Golden-billed Saltator (*Saltator aurantiirostris*)	0	1	12.5
Great Pampa-Finch (*Embernagra platensis*)*	7	4	62.5
Wedge-tailed Grass-Finch (*Emberizoides herbicola*)*	18	4	87.5
Long-tailed Reed Finch (*Donacospiza albifrons*)*	0	2	12.5
Red-crested Cardinal (*Paroaria coronata*)	1	2	25
Sayaca Tanager (*Thraupis sayaca*)	1	0	12.5
Emberizidae			
Grassland Sparrow (*Ammodramus humeralis*)*	67	81	100
Rufous-collared Sparrow (*Zonotrichia capensis*)	27	25	100
Parulidae			
Masked Yellowthroat (*Geothlypis aequinoctialis*)	6	7	62.5
Icteridae			
Chestnut-capped Blackbird (*Chrysomus ruficapillus*)	2	0	12.5
Yellow-rumped Marshbird (*Pseudoleistes guirahuro*)*	4	1	37.5
Grayish Baywing (*Agelaioides badius*)	0	2	12.5
Screaming Cowbird (*Molothrus rufoaxilaris*)*	1	0	12.5
Shiny Cowbird (*Molothrus bonariensis*)*	1	2	25
White-browed Meadowlark (*Sturnella superciliaris*)*	5	14	62.5

*Species representative of southeastern South America grasslands (Azpiroz et al. 2012).
†Near threatened globally.
‡Near threatened in Rio Grande do Sul.
§Vulnerable globally.
¶Vulnerable in Rio Grande do Sul.
**Endangered globally.

other seven variables (herbs, shrubs, *Eryngium* spp., *Baccharis* spp., exposed soil, water, and cattle dung) either did not differ ($P > 0.05$) or the best model was null (Table 2).

DISCUSSION

We found similar bird species richness and community composition between the PR and NG areas, although levels of total abundance were different. Grassland specialists and threatened species were found in both PR and NG, and only vegetation height differed between PR and NG. Depending on management, grasslands become more structurally complex and richer in plant species as more time elapses since land use change and previous clearing (Pulsford et al. 2016, Torchelsen

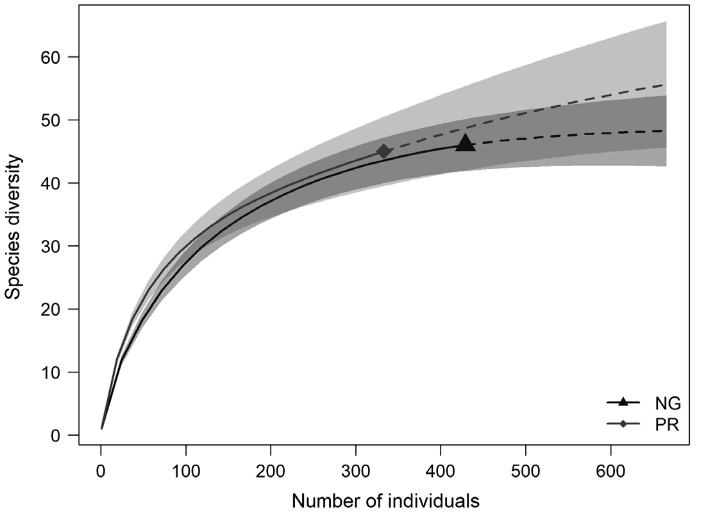

Fig. 2. Estimated-rarified species richness based on sample coverage for passive-restoration sites (PR) and native grasslands (NG).

et al. 2019), potentially explaining the few differences in vegetation structure and cover between PR and NG. Although surveying more sites was not possible either because they did not exist (Overbeck et al. 2015) or landowners would not provide access, our results represent a first attempt to understand how grassland bird communities might respond to passive grassland restoration in southern Brazil.

We found no significant differences in the bird species richness and composition between PR and NG, but some species were restricted to each type of grassland and the frequency of occurrence of these species was generally low (<40% of the sites). The results of previous studies have revealed that regeneration of native grasslands on abandoned agricultural land may be important for conserving biodiversity (Fletcher and Koford 2002, Thogmartin et al. 2014, Valkó et al. 2016). For example, species richness and total abundance of grassland birds in abandoned grasslands in Japan were similar to those in areas of reference habitat (Katayama et al. 2015, Kitazawa et al. 2019). Although grasslands under restoration may differ from native grasslands in terms of vegetation structure, they may nevertheless provide suitable habitat for grassland birds (Fletcher and Koford 2002, Kennedy et al. 2009).

We recorded several species of endangered birds in both PR and NG, suggesting that the resources these species require were available in both types of grasslands. However, restored habitats sometimes do not support specialist species or those that are sensitive to disturbance (Aerts et al. 2008), so additional studies are needed to better understand relationships between birds and changes in habitats and landscapes (Katayama et al. 2015).

We observed grassland-specialist birds in both passive-restoration and native grasslands, but some were exclusive to either PR or NG. One factor likely contributing to this difference was the difference between the two grassland types in vegetation height, a variable that influenced the occurrence of three species. The results of some studies suggest that vegetation height is an important predictor of the occurrence of grassland birds, in addition to the amount of bare ground and litter depth (Fisher and Davis 2010, Dias et al. 2014). In our study, Blue-black Grassquits and Chestnut Seedeaters were only observed in PR and Wedge-tailed Grass-Finches were more abundant in PR, the grassland type with taller vegetation and greater coverage of tall grass. Other investigators have also noted that these three species are most commonly found in grasslands with taller vegetation (Azpiroz

Table 2. GLMM results for the total abundance, occurrence of individual species of grassland birds, and structure and composition of vegetation compared between passive-restoration sites and native grasslands of the Brazilian Pampa biome. Models with the lowest AIC_c value are presented, with the significance level of their variables.

Models	Estimate (SE)	Z value	P*
Total abundance			
Intercept	1.30 (0.09)	14.1	< 0.001
Type of grassland	0.31 (0.12)	2.5	**0.013**
Spotted Nothura			
Intercept	–3.25 (0.52)	–6.3	< 0.001
Type of grassland	0.96 (0.57)	1.7	0.093
Herbs	0.69 (0.20)	3.4	**< 0.001**
Firewood-gatherer			
Intercept	–3.46 (0.81)	–4.3	< 0.001
Fork-tailed Flycatcher			
Intercept	–3.03 (0.80)	–3.8	< 0.001
Herbs	0.44 (0.27)	1.6	0.11
Sedge Wren			
Intercept	–7.58 (1.84)	–4.1	< 0.001
Chalk-browed Mockingbird			
Intercept	–5.51 (2.72)	–2.0	0.043
Hellmayr's Pipit			
Intercept	–5.32 (1.38)	–3.9	< 0.001
Type of grassland	3.11 (1.44)	2.2	0.031
Vegetation height	–1.75 (0.54)	–3.2	**0.001**
Grassland Yellow-Finch			
Intercept	–0.70 (0.33)	–2.1	0.034
Vegetation height	–0.38 (0.18)	–2.2	**0.030**
Great Pampa-Finch			
Intercept	–2.95 (0.49)	–6.0	< 0.001
Herbs	–0.74 (0.48)	–1.5	0.13
Wedge-tailed Grass-Finch			
Intercept	–2.43 (0.39)	–6.3	< 0.001
Vegetation height	0.85 (0.19)	4.5	**< 0.001**
Grassland Sparrow			
Intercept	–0.16 (0.25)	–0.7	0.51
White-browed Meadowlark			
Intercept	–3.10 (0.66)	–4.7	< 0.001
Vegetation height			
Intercept	3.73 (0.11)	34.2	< 0.001
Type of grassland	–0.55 (0.15)	–3.5	**< 0.001**
Herbs			
Intercept	2.19 (0.22)	9.8	< 0.001
Shrubs			
Intercept	–2.40 (0.68)	–3.5	< 0.001
Eryngium spp.			
Intercept	–2.56 (0.94)	–2.7	0.006
Baccharis spp.			
Intercept	–1.14 (0.51)	–2.2	0.025
Exposed soil			
Intercept	–1.32 (0.37)	–3.6	< 0.001
Water			
Intercept	–4.87 (1.57)	–3.1	0.002
Type of grassland	–2.02 (1.31)	–1.5	0.12
Cattle dung			
Intercept	–1.22 (0.44)	–2.8	0.006
Type of grassland	1.11 (0.57)	2.0	0.050

*Significant *P* values are indicated by bold font.

et al. 2012, Dias et al. 2017). In contrast, Hellmayr's Pipits and Grassland Yellow-Finches were more abundant in NG, i.e., sites with shorter vegetation (and more extensive coverage of short grass). Other investigators, however, have reported that these species also occupy areas with intermediate-height and tall grass (Azpiroz et al. 2012, Dias et al. 2014, Steffen 2017). Grassland Sparrows, for example, were more abundant in NG, but were also abundant in PR. Clearly, bird populations respond to habitat modification, and understanding their responses to restored habitats is essential for managing and conserving grassland bird species (Fletcher and Koford 2003).

Passive regeneration depends on the degree of degradation and the duration and intensity of agricultural practices (Scowcroft and Yeh 2013). Development of a level of vegetation structure similar to native grasslands depends on adjacent seed sources and the distance to an adequate matrix of remnant grasslands (Ruprecht 2006, Fensham et al. 2016). The results of some studies suggest that recovery may occur relatively rapidly, i.e., within 10 to 40 years (Suding 2011). In other studies, longer periods have been required to restore grasslands to a condition similar to reference areas, e.g., up to 50 years in Europe (Öster et al. 2009) and 60 years in North America (Samuel and Hart 1994). Our results suggest that passive restoration following 10 to

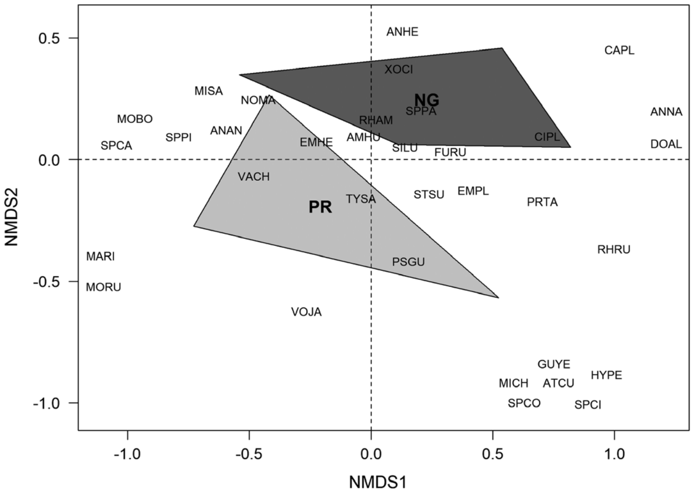

Fig. 3. NMDS of bird species in passive-restoration sites (PR) and native grasslands (NG) in the Brazilian Pampa biome based on the presence/absence of bird species and using the Jaccard dissimilarity index, stress = 0.08. Species acronyms are formed by the first two letters of the genus and species, as in Table 1.

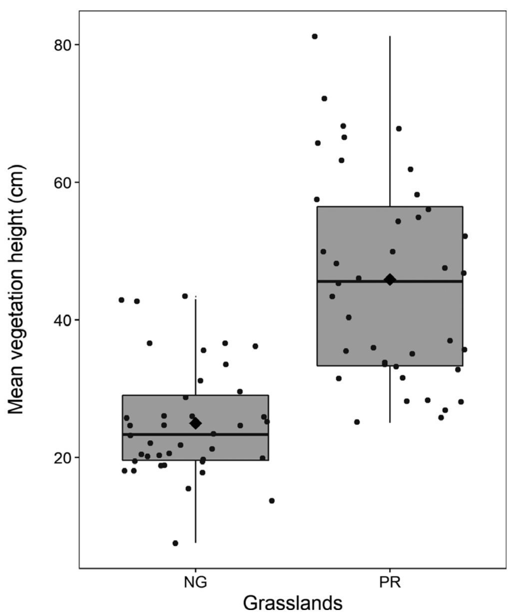

Fig. 4. Mean vegetation height in passive-restoration sites (PR) and native grasslands (NG), the only significant vegetation variable ($P < 0.05$) between these types of grassland. Box-plot values are represented by medians (horizontal black lines) and means (diamonds).

35 years of abandonment can make an important contribution to the conservation for grassland birds. Different results reported in different studies may be a consequence of measuring different variables of recovery success or a consequence of specific conditions at the site and surrounding landscape that influence vegetation recovery. Clearly, more studies on the recovery of vegetation and its drivers are needed.

Implications for management and conservation. The absence of marked differences in species richness and composition of bird communities between passive-restoration and native grasslands in our study suggests that grasslands in the process of passive restoration can provide habitat for many species of grassland birds, even though we did not determine whether restoration sites are also similar to native grasslands in plant species composition. However, the absence of some species of grassland birds from recovering grasslands in our study suggests a need to ensure that existing undisturbed grasslands are not subject to further clearing and land conversion.

Passive restoration is a potentially cost-effective option for ecosystem recovery (Jones et al. 2018), mainly because the use of advanced technology and direct establishment of seedlings (i.e. planting) is not necessary. To promote grassland conservation, we recommend designating passive-restoration areas as new conservation units along with the few areas that are currently preserved.

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