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Campos do bioma Pampa no contexto de silvicultura: uso da terra, manejo e fatores ambientais como determinantes da vegetação campestre

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Introdução geral

Mudanças no uso da terra são um dos principais fatores que afetam a dinâmica de ecossistemas no mundo (Sala 2000), com impactos sobre a biodiversidade e funções ecossistêmicas, muitos dos quais estão relacionados com a biodiversidade (Millennium Ecosystem Assessment 2005, Perrings et al. 2010). Os campos no sul do Brasil (tanto no bioma Pampa, como em mosaicos com floresta no bioma Mata Atlântica) abrigam uma alta biodiversidade e prestam importantes serviços ecossistêmicos. Para a vegetação campestre do estado do Rio Grande do Sul (RS), atualmente são conhecidos 2.600 táxons de plantas (Boldrini et al., em prep.; ver também Boldrini 2009a), e há 125 aves e 25 mamíferos exclusivamente campestres (Bencke 2009).

No entanto, a conservação de áreas campestres tem sido negligenciada no Brasil (Overbeck et al. 2007). Segundo dados do IBGE (2012), o Pampa é o segundo bioma mais degradado do Brasil, apresentando, em 2009, 54% da sua área original convertida em outros usos. Somente uma pequena porção (2,6%; Brandão et al. 2009) dos campos no RS encontra-se em unidades de conservação (UCs), porém, o manejo realizado nestas muitas vezes não é adequado para a conservação de ecossistemas campestres (Pillar & Velez 2010): Em UCs de proteção integral todo tipo de interferência antrópica é proibido, e estudos evidenciam que tal exclusão de manejo gera a perda de diversidade e substituição dos campos por vegetação arbustiva ou florestal (Oliveira & Pillar 2004; Müller et al. 2012). Os campos sulinos, assim como muitas áreas de campos ou de savanas no mundo, devido a sua própria história evolutiva (Anderson 2006; Gibson 2009; Bond 2010), dependem da remoção de biomassa por pastejo e/ou fogo para a sua manutenção, e as suas espécies são adaptadas a estes distúrbios (Overbeck et al. 2005, 2007, Fidelis et al. 2010). No entanto, a legislação ambiental atual, os conceitos e as práticas de conservação não consideram esta necessidade de manejo da vegetação campestre (Overbeck et al. 2007; Pillar & Vélez 2010), mesmo que teoricamente haja grandes possibilidades de conciliar a conservação da biodiversidade com a produção agropecuária, visto que no bioma Pampa esta atividade é realizada em campos nativos, não cultivados (Sparovek et al. 2007). Por outro lado, em áreas campestres sob pastejo, o manejo inadequado, principalmente o sobrepastoreio, contribui para a perda de espécies, a invasão por espécies exóticas e a erosão, resultando em campos degradados, com baixa diversidade e produtividade (Nabinger et al. 2009). Há exemplos de outras regiões do mundo, em que áreas originalmente campestres, após um histórico de outros usos, não continuam a ter os mesmos níveis de diversidade mesmo após sua restauração (Zaloumis & Bond 2011). Para o sul do Brasil, este tipo de informação ainda é inexistente, e a necessidade de criação e aplicação de técnicas conservativas é urgente, visto a intensa conversão de campos está em níveis alarmantes, ainda mais com a falta de subsidios legais para a aplicação de técnicas de restauração ecológica em campos do bioma Pampa.

Diante desta situação, Áreas de Preservação Permanente (APP) podem apresentar um importante potencial para a conservação de campos no sul do RS, sobretudo em regiões com fortes mudanças no uso da terra (por exemplo, onde houve plantios de eucalipto). No entanto, é necessário que as mesmas permaneçam sob um tipo de manejo que efetivamente proteja a diversidade campestre – o que atualmente nem sempre é o caso. Tem sido mostrado, para áreas experimentais, que níveis intermediários de pastejo possuem efeitos positivos tanto para a biodiversidade, quanto para a produção animal (Nabinger et al. 2009). O manejo também influencia as taxas de incorporação de material orgânico no solo, sendo assim uma ferramenta que contribui para a mitigação do efeito estufa (Conceição et al. 2007). Porém, de forma geral, os dados disponíveis ainda são escassos e restritos a poucas localidades. Nesse sentido, estudos que avaliem os efeitos do manejo em paisagens fragmentadas pelo uso da terra são de grande relevância para se discutir a polêmica questão sobre como manejar a vegetação campestre para a sua conservação, e para divulgar a alta, porém pouco considerada, diversidade deste ecossistema ameaçado. Adicionalmente, interpretar o efeito dos filtros ambientais (Clima, solos e uso e ocupação da paisagem) em comunidades campestres extremamente ricas em espécies raras, endêmicas, e ameaçadas de extinção é fundamental para o planejamento em escala regional.

Assim potencializar a real função ambiental de uma APP ou RL, buscando preservar os recursos hídricos, a paisagem, a estabilidade geológica e a biodiversidade, facilitar o fluxo gênico de fauna e flora, proteger o solo e assegurar o bem-estar das populações humanas (Lei nº 12.651/12).

O presente trabalho aborda a questão dos impactos da silvicultura sobre a composição de comunidades de plantas campestres na região sul do bioma Pampa, mais especificamente, na Serra do Sudeste, a qual tem sofrido, principalmente na última década, um grande aumento da silvicultura, especificamente de plantios de Eucalipto. Os efeitos destas mudanças de uso nas diferentes escalas não têm sido abordados até agora, nem existem muitos estudos sobre as comundiades campestres da região. Desta maneira, o presente trabalho aborda:

- no Capitulo 1: O potencial de regeneração da vegetação campestre após longos períodos de uso de silvicultura, num estudo de caso realizado em três locais na região Sul do Rio Grande do Sul
- no Capitulo 2: A composição da vegetação campestre na parte sul da Serra do Sudeste, em um estudo comparativo em áreas de manejo tradicional e áreas de conservação no contexto de plantios de Eucalipto, contemplando um total de 58 sítios;
- no Capitulo 3: A análise dos diferentes drivers – climáticos, edáficos, e relacionados ao uso da terra – que influenciam a diversidade alfa e beta em comunidades de plantas campestres na região sul da Serra do Sudeste, nos mesmo 58 sítios como no Cap. 2.

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Chapter 1:

Do subtropical grasslands recover spontaneously after afforestation?

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Short title: Grassland recovery after afforestation

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Abstract

South American Pampa grasslands have been intensely converted into afforestation. While necessity for restoration grows, no information on restoration potential of grasslands after afforestation exists. We evaluated the spontaneous recovery of grasslands with a long history (50 years) of eucalyptus plantation. We sampled grassland vegetation at post-eucalyptus sites (with and without resprouting) ten years after clearclutting and in natural grasslands. Species richness and vegetation cover were higher in reference grassland than in resprout-areas, but did not differ from post-eucalyptus areas. Exotic species cover was significantly higher in areas with afforestation history. In terms of total composition, natural grasslands differed significantly from areas with past plantation use, with some vicinty of grassland types in the ordination diagram. Indicator species analyses revealed considerable differences in typical species as well as functional group composition when comparing the reference grassland to the grassland with history of afforestation. In conclusion, vegetation development led to grassland communities that are still quite distinct from reference sites. Likely, it is the specificity of grassland management, which was not controlled in our study, that determines vegetation trajectories in time. The influence of management for grassland recovery and restoration needs to be addressed in more studies.

Keywords: conservation, Pampa, restoration, southern Brazil, vegetation management

Introduction

Changes in land use act on ecosystem processes and biogeochemical cycles, promoting habitat loss and local extinction of species, biological invasions, erosion processes and changes in primary productivity and hydrological cycles (Ellis et al. 2010). Grasslands in southeastern South America, the Rio de la Plata grasslands (Soriano 1992), of natural original and considered to be old growth grasslands (Veldman et al. 2015) recently are being intensively converted to other land uses, including into tree plantations (Brockerhoff et al. 2008; Cordeiro & Hasenack 2009; Vega et al. 2009). Recent studies show the clear effects of afforestation on soil features and plant communities in and close to afforested areas (Céspedes-Payret et al. 2012; Saraiva and Souza 2012).

In Brazil, approximately 5.4 million hectares are currently covered by forest plantations, 55% of it by eucalyptus (Brockerhoff et al. 2008). The rapid expansion of commercial forestry (mainly *Pinus*, *Acacia* and *Eucalyptus*) is being encouraged by the government as a means of rural development. Thus, a further increase in the area of commercial forest plantations in the next decade is likely (Brockerhoff et al. 2008), increasing pressure on natural ecosystems. Non-forest ecosystems, primarily affected by establishment of tree plantations, however, are poorly protected, despite their high biodiversity and important ecosystem services(Overbeck et al. 2015). For example at present, only 1.48% of the original grassland area in Rio Grande do Sul state is protected in conservation units(Brandão et al. 2007), and more than 50% has already lost to conversion to other uses (Overbeck et al. 2015).

To reach conservation aims, for example the Aichi criteria (The Strategic Plan for Biodiversity 2011-2020), restoration of degraded areas thus becomes necessary. Restoration does not only contribute to biodiversity conservation, but also to the maintenance of important ecological services to humanity. This, as well as the legal requirements for restoration, turn knowledge about the potential of vegetation recovery into an important basis for an assessment of the need for active restoration and for the development of the necessary techniques. Before deciding on the necessity of active restoration measures, we need to understand the potential of spontaneous recovery of natural vegetation after degradation: in the best case, no or very few restoration activities are necessary. In Brazil, restoration studies still are scarce (Le Stradic et al. 2014), and in the South Brazilian grassland region, restoration of degraded grasslands has not been considered priority in conservation (Overbeck et al. 2013). Studies in other southern hemisphere grasslands have shown contrasting results: while some studies had promising results (Fensham et al. 2015), in other cases full recovery of the vegetation was not possible (Tognetti et al. 2010; Zaloumis & Bond 2011).

In this study, we aim at analyzing composition and structure of grassland vegetation with a history of eucalyptus plantations in order to assess recovery potential and restoration need of these areas. Our references are natural grasslands that have not seen any land-use change. We hypothesized that areas with history of eucalyptus would differ from reference grasslands in terms of floristic and functional composition and would present lower species richness.

Materials and Methods

Study Region

Our study region comprised four sites in the southeastern part of the Pampa Biome, in the coastal plain in the extreme south of Brazil, comprising the municipalities of Pedro Osório, Capão do Leão and Pelotas. Climate is temperate, with cold winters and hot summer without rainy season (Cfa according to the Koppen-Geigen classification; (Alvares et al. 2013). Topography is slightly rolling (average height ±30m a. s.) and soils are deep and nutrient-poor clay soils (Streck et al. 2008). Grasslands are the dominating vegetation physiognomy in the region.

Sampling design and data collection

The study was conducted at four sites (blocks), each consisting of two areas with history of eucalyptus plantations (with or without regrowth of eucalyptus) and of a natural grassland as reference area. Per site, these areas were situated at a maximum distance of 3 km to each other and were considered as a block. Post-eucalyptus grassland (PEG) developed after use of eucalyptus for approximately 50 years (1950-2000). After cutting of trees, sites were left for spontaneous recovery without any active restoration measures, and were subjected to low intensity grazing. Fire was used as an additional management tool to reduce excess biomass not consumed by grazers (personal communication by property owners). In areas with eucalyptus regrowth (ERG), with tree in regrowth state reaching 3 m high and 2 m spacing between trees, the canopy structure is discontinuous with the presence of clearings, management is not standardized (different intensities of grazing) and cutting twigs is not fully realized. Reference grasslands (RG) have no afforestation history and have been submitted to livestock management with an intermediate stocking rate for decades.

Vegetation data

Species composition data was obtained in 20 plots of 1 m^2 per area, distributed randomly. In each plot, we identified all vascular plant species and estimated their cover according to the Londo (1976) scale. Additionally, we recorded vegetation height (measured at 5 points), percentage of plant litter (excluding eucalyptus leaves), litter of eucalyptus, manure and exposed soil. Vegetation parameters were calculated according to Muller-Dombois & Ellenberg (1974): relative cover (RC), relative frequency (RF), and importance value index (IVI).

Species were classified regarding their origin (native/exotic; Rolim et al. 2014) and degree of threat of species was checked in the current Red List for the state (Rio Grande do Sul 2014). Plants were classified into life forms using a modified classification by Ferreira et al. (submitted), resulting in 12 growth form classes: Solitary evergreen tussocks (SET), Stolonoiferous evergreens (SE), Rhizomatous evergreens (RE), Evergreen subshrubs (ESS), Decumbent evergreens (DE), Evergreen forbs (EF), Connected evergreen tussocks (CET), Prostate rosette evergreens (PRE), Erect rosette evergreens (ERE), Therophytes (TH), Bulbous geophytes (BG), Evergreen shrubs (ES).

Data Analysis

For all analyses, we pooled the plot data to the paddock level (i.e., treatment per site). General patterns of species composition of the sites were explored by Principal Coordinate Analysis (PCoA), using the matrix of species mean cover per site. Only species with IVI above 1% were included in the ordination analysis. To compare treatments regarding the contribution of the principal species, cover values of the species with correlations > |0.7| to the first axis of the ordination were compared by randomization testing. For the analysis of functional composition, we used all species, both in a PcoA and in Randomization testing, after classification of species into twelve life forms. Additionally, we compared mean cover values of the three most important botanical families, Asteraceae, Fabaceae and Poaceae, the latter divided into prostrate and tussock species. Treatments were also compared by randomization tests regarding, separately, vegetation height, total vegetation cover, bare soil, litter and manure. We used Euclidian distance for univariate analyses and Chord distance for multivariate analyses, 999 permutations, and $\alpha = 0.05$ as probability limit for rejection of null-hypothesis. Site was used as block factor in all analyses. These analyses ware performed using the software MULTIV (available at: http://ecoqua.ecologia.ufrgs.br/). To test the preference of species and functional composition to reference grasslands, to sites with history of eucalyptus plantations, and to combination of sites, we applied indicator species analysis (Dufrene and Legendre 1997), using function ‘indicspecies’ of the R package ‘multipatt’, based on the ‘correlation index (r)’ (De Cáceres et al. 2010).

Results

Vegetation description

Overall, 281 plant species were identified in the study. The most important families in terms of species numbers were Poaceae (64 species), Asteraceae (59), Cyperaceae (20) and Fabaceae (12), together constituting 55% of all species. In areas with eucalyptus regrowth phase (ERG) and post-eucalyptus grassland (PEG), we recorded 188 species (111 forbs, 30 shrubs, 45 grasses and 2 ferns) and 225 species (147 forbs, 22 shrubs, 55 grasses, 1 fern), respectively. In contrast, in grassland areas without afforestation history (RG), we identified 183 species (115 forbs, 8 shrubs, 55 grasses).

Vegetation of RG was dominated by prostrate grasses such as *Paspalum notatum* and *Axonopus fissifolius*, with a summed value 39% of relative cover (RC) in this physiognomy. In PEG, *Eryngium horridum* and *Paspalum notatum* were the most important species, summing 19% of RC. In ERG areas, tussock grasses such as *Saccharum angustifolium* and *Piptochaetium montevidense* showed the highest RC (16%). Both species richness and vegetation cover had higher mean values in RG than in ERG, but did not differ from PEG (Figure 1).

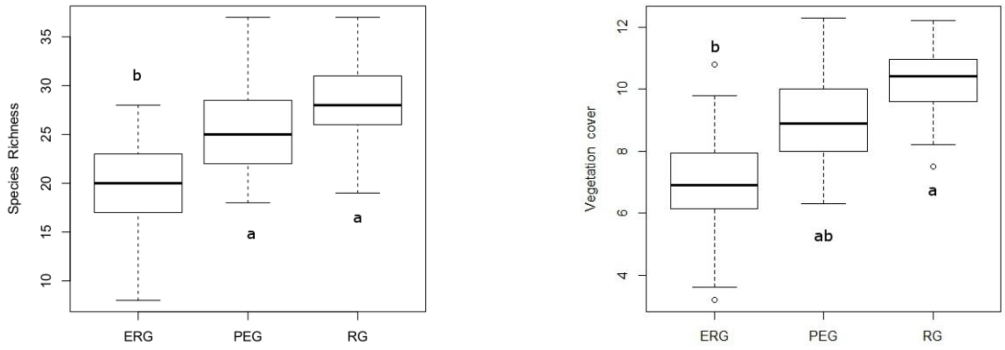

Figure 1 – Variation in vegetation cover and species richness among the three sampled sites (mean values and 25 quartiles). Different letters represent significant differences between treatments (p<0.05). PEG = post-eucalyptus grassland, ERG = eucalyptus regrowth, RG = reference grasslands.

In the 240 sampled plots, only one species included in the list of endangered species was recorded: *Gomphrena sellowiana* (Amaranthaceae), found in PEG at one site. Of the species sampled, 15 were exotic, and total cover of exotic species was significantly higher in PEG and ERG when compared to RG (p = 0.05). The invasive grass *Eragrostis plana* showed marginally significance differences between treatments, with lowest values in RG (p < 0.1).

The PcoA ordination reflected compositional differences in herbaceous communities between RG and former plantation areas (PEG and ERG), with RG to the right, and eucalyptus areas to the left, but with considerable overlap. The first and second axes of the PCoA with species composition data together explained 78% of the variation in the vegetation composition (Figure 2 - A). The first axis separated sites with high cover of *Paspalum notatum* (0.86% correlation to the axis) and *Axonopus fissifolius* (0.72%), on the right side of the figure, from areas with high cover of *Saccharum angustifolium* (-0.90%), *Aspilia montevidensis* (-0.89%) *Eryngium horridum* (-0.87%), *Baccharis dracunculifolia* (-0.83%), *Aristida laevis* (-0.82%), *Desmodium incanum* (-0.78%) and *Schizachyrium microstachyum* (-0.73%), on the left side. Along the second axis the species with the highest correlation was *Centella asiatica* (-0.74%) and *Elephantopus mollis* (-0.88%), a native species with a ruderal character, associated to ERG plots.

The first and second axes of the PCoA based on life form composition (Figure 2 - B) together accounted for 88% of the variation in the data. The first axis separated sites with high cover of Rhizomatous evergreens (correlation to axis: 0.94%) and Stoloniferous evergreens (0.83%), situated at the right side, from sites with high cover of Erect rosette evergreens (-0.94%), Solitary evergreen tussocks (-0.93%), Evergreen shrubs (-0.89%), Evergreen sub-shrubs (-0.87%), to the left. The second axis explained only 16% of the variation of the data.

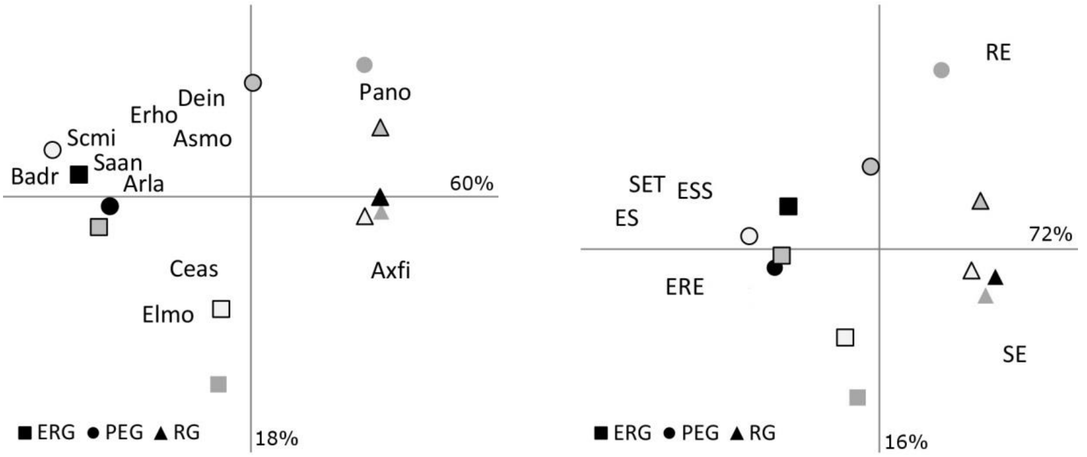

Figure 2 – Principal coordinate ordination diagram, based on chord distance, showing the first two axes. Only species with high correlations to the axes are shown (corr.>0.5). Symbols represent the sites, with color of symbols indicating the blocks (black, white with black edge, grey with black edge, grey without black edge). (A) PCoA using species data. The letters represent the initials of the genus and the epithet. (B) PCoA using life form data. In both figures, only species or life forms with high correlations to the axes are shown (corr.>0.7). PCoA (A) – Axfi: *Axonopus fissifolius*, Arla: *Aristida laevis*, Asmo: *Aspilia montevidensis*, Brdr: *Baccharis dracunculifolia*, Ceas: *Centella asiatica*, Dein: *Desmodium incanum*, Elmo: *Elephantopus mollis*, Erho: *Eryngium horridum*, Pano: *Paspalum notatum*, Saan: *Saccharum*

angustifolium, Scmi: *Schizachyrium microstachyum*. PCoA (B) - SET: Solitary evergreen tussocks, SE: Stolonoiferous evergreens, RE: Rhizomatous evergreens, ESS: Evergreen subshrubs, ERE: Erect rosette evergreens, ES: Evergreen shrubs. PEG = post-eucalyptus grassland, ERG = eucalyptus regrowth, RG = reference grasslands.

Both using floristic and functional composition (all species with IVI > 1), RG differed significantly from the other two vegetation types in multivariate randomization tests. Of the eleven species with higher vegetation cover and highest correlation (>70%) to axis 1 and 2, only four species showed significant differences between groups four (Table 1). Cover of the most abundant species showed significant differences between treatments, especially when comparing RG with the afforestation sites. Cover of tussock grasses was significantly higher for RG, while cover or prostrate grasses and Asteraceae was significantly lower than in ERG and PEG. Vegetation cover, vegetation height, eucalyptus litter and bare soil differed significantly between treatments (p<0.05; Table 1).

Table 1 – Differences in cover of species and species groups (families and growth forms of grasses) as well as parameters indicating vegetation structure between treatments. Different letters represent significant differences between treatments (p<0.05). PEG = post-eucalyptus grassland, ERG = eucalyptus regrowth, RG = reference grasslands. * indicates exotic species.

	RG	ERG	PEG
Aspilia montevidensis (%)	0.2^{b}	0.7^{ab}	1.1^{a}
Axonopus fissifolius (%)	20^{a}	3^{b}	3.4^{b}
*Eragrostis plana** (%)	0.1^{b}	0.7^{b}	2.9^{a}
Eryngium horridum (%)	0.7^{b}	3.6^{ab}	9.6^{a}
Paspalum notatum (%)	22^{a}	3.3^{b}	5.3^{b}
Asteraceae (%)	7^{b}	14^{a}	15^{a}
Fabaceae (%)	6^{a}	2^{b}	3^{ab}
Poaceae - tussocks (%)	11^{b}	19^{ab}	28^{a}
Poaceae - prostrate grasses (%)	56^{a}	12^{b}	17^{b}
Exotics species (%)	1.6^{b}	4.1^{ab}	5.6^{a}
Stolonoiferous evergreens (%)	33^{a}	8^{b}	10^{b}
Rhizomatous evergreens (%)	25^{a}	4^{ab}	7^{b}
Evergreen shrubs (%)	0.1^{b}	3.5^{a}	4^{a}
Evergreen subshrubs (%)	2.6^{b}	5.7^{a}	6.7^{a}
Erect rosette evergreens (%)	3^{b}	7^{ab}	12^{a}
Vegetation Height (cm)	8 (±2)^{b}	16 (±9)^{ab}	20 (±9)^{a}
Vegetation cover (%)	98 (±1)^{a}	67 (±2)^{ab}	88 (±3)^{b}
Litter cover (%)	3.6 (±2)^{b}	4.6 (±6)^{ab}	11.5 (±6)^{a}

Eucalyptus Litter cover (%)	0 (±0)^{b}	18 (±12)^{a}	0 (±0)^{b}
Bare soil cover (%)	4 (±4)^{b}	15 (±8)^{a}	10 (±8)^{ab}
Manure cover (%)	2 (±3)^{a}	1 (±1)^{a}	1 (±2)^{a}

From 49 species (IVI>1%) tested in indicator species analysis, 37 species were selected ($p<0.05$), 25 species associated to one group and 12 species associated to two groups. Nine species were selected as indicative of both grasslands with history of tree plantation (ERG and PEG), and four of them had correlation intensity values above 40%: *Saccharum angustifolium* (r=0.43; p=0.00), *Baccharis dracunculifolia* (r=0.42; p=0.00), *Eupatorium ascendens* (r=0.41; p=0.00), *Eryngium horridum* (r=0.40; p=0.00). Two species were indicative for ERG, with *Elephantopus mollis* having the highest correlation vale (r=0.30; p=0.00). For PEG, four indicator species were found, one of them the exotic grass *Eragrostis plana* (r=0.24; p=0.00). For RG, a total of 19 species were selected, nine species showed values above 40%, such as *Paspalum notatum* (r=0.54; p=0.00) and *Axonopus fissifolius* (r=0.45; p=0.00). Additionally, three species were selected as indicative for RG and PEG, and the species with the highest intensity correlation was *Andropogon lateralis* (r=0.38; p=0.00). The complete list of species selected by the indicator species analysis is presented in the appendix. In the indicator species analyses based on life forms, we noted the preference of erect rosette evergreens (r=067; p=0.03) to PEG and of stoloniferous evergreens (r=0.93; p=0.00) and rhizomatous evergreens (r=0.82; p=0.01) for RG. Three life forms were selected as indicative for ERG and PEG, with high indicator values: evergren shrubs (r=0.72; p=0.02), evergreen subshrubs (r=0.70; p=0.04) and solitary evergreen tussocks (r=0.65; 0.05). Evergreen forbs were indicative for the combination of PEG and RG (r=0.73; p=0.03).

Discussion

With more than half of the areas of the Pampa grasslands biome in Brazil now converted into plantations (Cordeiro & Hasenack 2009), including afforestation (Brockerhoff et al. 2008), studies on vegetation recovery and restoration potential of grasslands are urgent if losses in biodiversity and ecosystem services are to be avoided and if legal requirements for restoration are to be met (MMA 2015). Until now, information on the effects of eucalyptus plantations on grassland (Saraiva and Souza 2012) and, especially, information on vegetation development after use for tree plantations is scarce, despite growing concern with restoration of degraded grasslands (Overbeck et al. 2013). Our study represents a first step to fill this gap. Our results indicate that, for our study region, original grassland areas that had been used for tree plantations do develop to grassland, even after long times of afforestation, but that structure and composition of these plant communities differ considerably from reference sites.

Zaloumis & Bond (2011), in their comparison of restored and original grasslands in South Africa, observed strong differences in species richness between both types of community and especially evidenced losses of long-lived, resprouting forbs in vegetation with a history of other land uses. In our study, areas with history of eucalyptus differed in terms of physical vegetation structure, with increased height of the vegetation and more open soil and in terms of abundance patterns, but not in terms of species richness, even though richness was lower in sites with resprouting eucalyptus. We found increasing dominance of shrubs and tussock grasses in areas with afforestation history, in contrast to reference grassland characterized by rhizomateous and stoloniferous species. Markedly higher cover of the invasive grass *Eragrostis plana* and of ruderal and exotic species in general, as well of the disturbance specialist *Eryngium horridum* (Fidelis et al. 2008) in PEG and ERG indicated the degradation caused by tree plantations, just as has been observed for old-field sucession in the Argentinian Pampa (Tognetti et al. 2010). This variation between the floristic composition of natural and formally planted grassland may partially be attributed to afforestation induced changes, especially changes of soil characteristics (Wallace and Good 1995; Céspedes-Payret et al. 2012). Quite obviously, areas where eucalyptus was allowed to resprout show highest degrees of degradation, including by high cover of eucalyptus litter and open soil.

While the indicator species analyses pointed out considerable contrasts in terms of composition, nontheless we did not identify losses in richness or of species from a particular functional group, such as found by (Zaloumis & Bond 2011). This may be result of the specific situation of our study region: grasslands in the region show rather low rates of endemism and are mostly composed of generalist species. According Boldrini (2009), six endemic species are found in coastal grasslands, while for subtropical highland grasslands in the north of RS, numbers are much higher (296; Iganci et al. 2011). Thus, in our system the number of species with restricted distribution and with poor dispersal ability should be lower, and differences between treatment were more pronounced regarding mean cover of species and particular functional groups. More studies in other regions of the Campos Sulinos are needed to assess whether species with more restricted distribution patterns are able to recolonize original grassland areas after land use change. Most likely, grasslands with high endemism rates or higher presence of specialist species will be less likely to recovery their composition (see also Veldman 2015).

The ordination analysis showed the high dispersion of the sampling sites with a history of eucalyptus plantings, particularly PEG areas, in the ordination space, indicating considerable heterogeneity of plots and areas of this group: some sites had considerable similarity, in terms of floristic and functional composition, to the reference areas, while others differed greatly. This heterogeneity among sites most likely is related to differences in management regimes after cutting of Eucalyptus trees, which lead to different trajectories of vegetation development. The importance of grazing and fire as management tools in grassland restoration has been shown for the North American prairie (Fuhlendorf et al. 2006). Both factors are of high importance for maintenance of grasslands and their diversity under productive climatic conditions (Milchunas et al. 1998; Overbeck et al. 2005), and contribute to patch heterogeneity and environmental functionality (Fuhlendorf and Engle 2001). Nontheless, use of these ‘disturbances’ for conservation is still considered as a taboo in Brazil (Pillar and Vélez 2010). For our study, no control-sites without grazing or fire were available, and we also were not able to quantify management intensities. However, the fact that some of the PEG sites, under management, developed into a grassland with considerable similarities to RG conditions, including high cover of rhizomateous and stoloniferous species, indicates that grazing and fire can have positive effects on vegetation recovery, likely due to the reduction of dominance of few species(Overbeck et al. 2005), as well as by the transport of seeds by animals (Traba et al. 2003).

Despite the differences evidenced between reference grassland and areas with a history of Eucalyptus plantations after a period of more than ten years, our results are good news for grassland conservation as they indicate that recovery seems possible in principle. While we did not specifically address the role of grazing or fire for grassland restoration in our region, further studies should explicitly analyze the effects of different management types and intensities for the restoration of degraded grasslands. Experimental approaches seem especially important, as well as more detailed studies on specific effects of grazing, e.g. on dispersal and establishment processes. At any rate, given the differences pointed out by the Indicator Species analyses, the introduction of seeds and the control of exotic species seem to be important steps for grassland restoration, just as pointed out elsewhere (Tognetti et al. 2010).

Given the scarcity of studies on vegetation recovery in the Campos Sulinos region, we certainly need to be cautious to extrapolate our results to sites under different condition or after different types of degradation. It seems likely, for instance, that afforestation by pine trees will not allow for recovery in the magnitude as shown here, due to the accumulation of pine litter. And recovery of grassland after Eucalypt planting may be different in regions with higher endemism rate – or even after affestoration with other management techniques. More studies on vegetation recovery after degradation are needed in different grassland types, after different types of degradation and in different regions of the Pampa biome in order to establish a sound scientific basis for grassland restoration.

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Table 1: Species cover in three grassland types (PEG = post-eucalyptus grassland, ERG = eucalyptus regrowth, RG = reference grasslands) at the twelve study sites in southern Rio Grande do Sul, South Brazil. For species considered in the analysis of indicator species the significance level is indicated with the respective cover value (in one or two groups): *** < 0.001, ** < 0.01, * < 0.05. Exotic species are identified with *after the species name, according to Rolim (2015).

Families / Species	PEG	ERG	RG
Acanthaceae			
Justicia axilaris (Nees) Lindau	0.01	0.00	0.00
Ruellia morongii Britton	0.01	0.00	0.03
Stenandrium diphyllum Nees	0.00	0.00	0.01
Amaranthaceae			
Gomphrena sellowiana Mart.	0.00	0.03	0.00
Pfaffia tuberosa (Spreng.) Hicken	0.36	0.18	0.23
Amaryllidaceae			
Habranthus tubispathus (L´Hér.) Traub	0.01	0.00	0.13
Nothoscordum gracile (Aiton) Stearn	0.05	0.00	0.04
Nothoscordum montevidense Beauverd	0.11	0.04	0.20
Zephyranthes minima Herb.	0.13	0.00	0.00
Anacardiaceae			
Lithraea brasiliensis Marchand	0.00	0.05	0.00
Schinus polygamus (Cav.) Cabrera	0.05	0.18	0.00
Schinus weinmanniflius Engl.	0.01	0.00	0.00
Anemiaceae			
Anemia tomentosa (Sav.) Sw.	0.04	0.00	0.00
Apiaceae			
Centella asiatica (L.) Urb.	1.68	2.09	1.9***
Ciclospermum leptophyllum (Pers.) Sprague var. leptophyllum	0.00	0.16	0.14
Eryngium ciliatum Cham. & Schltdl.	0.38	0.00	0.00
Eryngium elegans Cham. Et Schlecht.	0.33	0.00	0.00
Eryngium horridum Malme	9.6***	3.56***	0.74
Eryngium nudicaule Lam.	0.18	0.13	1.68***
Eryngium sanguisorba Cham. Et Schlecht.	0.51	0.03	0.11
Apocynaceae			
Oxypetalum tomentosum Wight ex Hook. & Arn.	0.01	0.00	0.00
Aquifoliaceae			
Ilex dumosa Reissek	0.03	0.00	0.00
Araliaceae			
Hydrocotyle bonariensis Lam.	0.09	0.15	0.00
Hydrocotyle exigua Malme	0.16	0.49	0.76**
Asparagaceae			
Asparagopsis setacea Kunth*	0.00	0.05	0.00
Asteraceae			
Achyrocline satureioides (Lam.) DC.	0.18	0.13	0.08
Acanthostyles buniifolius (Hook. ex Arn.) R.M. King & H. Rob.	0.96	0.38	0.15
Aspilia montevidensis (Spreng.) Kuntze	1.14***	0.74	0.23

Aster squamatus (Spreng.) Hieron.	0.03	0.01	0.04
Baccharis articulata (Lam.) Pers.	0.08	0.15	0.00
Baccharis crispa Spreng.	1.35	1.26	0.88
Baccharis dracunculifolia DC.	2.85^{***}	1.53^{***}	0.00
Baccharis ochracea Spreng.	0.03	0.00	0.00
Baccharis patens Baker	0.00	0.01	0.00
Baccharis psiadioides (Less.) Joch.Müll.	0.00	0.16	0.00
Baccharis riograndensis I.L.Teodoro & J.Vidal	0.00	0.00	0.25
Baccharis spicata (Lam.) Baill.	0.03	0.10	0.00
Baccharis tridentata Vahl	0.63	0.00	0.00
Badilloa steetzii (B.L.Rob.) R.M.King & H.Rob.	0.08	0.13	0.00
Calea pinnatifida (R. Br.) Less.	0.00	0.23	0.00
Calea uniflora Less.	0.03	0.00	0.04
Chaptalia exscapa (Pers.) Baker	0.08	0.10	0.23
Chaptalia integerrima (Vell.) Burk.	0.05	0.13	0.00
chaptalia nutans (l.) polak	0.00	0.08	0.00
Chaptalia runcinata Kunth	0.16	0.05	0.40
Chaptalia sinuata (Less.) Baker	0.31	0.14	0.04
Chevreulia acuminata Less.	0.06	0.00	0.03
Chevreulia sarmentosa (Pers.) Blake	0.25	0.38	0.93^{***}
Chromolaena ascendens (Sch. Bip. ex Baker) R.M. King & H. Rob.	0.75^{***}	0.58^{***}	0.03
Chrysolaena flexuosa (Sims) H.Rob	0.43	0.25	0.15
Cirsium vulgare (Savi) Ten.*	0.89	0.25	0.00
Conyza bonariensis (L.) Cronquist	0.19	0.31	0.01
Conyza primulifolia (Lam.) Cuatrec. & Lourteig	0.35	0.50	0.19
Crepis capillaris (L.) Wallr.*	0.03	0.15	0.00
Elephantopus mollis Kunth	0.16	1.96^{***}	0.43
Facelis retusa (Lam.) Sch. Bip.	0.08	0.11	0.6^{***}
Gamochaeta americana (Mill.) Wedd.	0.53	0.63	0.66
Gochnatia polymorpha (Less.) Cabrera	0.00	0.25	0.00
Grazielia intermedia (DC.) R.M. King & H. Rob.	0.00	0.23	0.00
Hypochaeris albiflora (O.K.) Azevêdo-Gonçalves & Matzenbacher	0.00	0.00	0.03
Hypochaeris chillensis (H.B.K.) Hieron	0.01	0.01	0.33
Hypochaeris radicata L.*	0.03	0.20	0.06
Lessingianthus sellowii (Less.) H. Rob.	0.08	0.04	0.01
Lucilia acutifolia (Poir.) Cass.	0.01	0.08	0.00
Lucilia nitens Less.	0.44	0.33	0.56^{*}
Micropsis spathulata (Pers.) Cabrera	0.06	0.00	0.05
Noticastrum diffusum (Pers.) Cabrera	0.00	0.03	0.00
Orthopappus angustifolius (Sw.) Gleason	0.13	0.34	0.00
Picrosia longifolia D. Don	0.03	0.00	0.03
Pluchea sagittalis (Lam.) Cabrera	0.00	0.03	0.00
Porophyllum ruderale (Jacq.) Cass.	0.04	0.13	0.00
Pterocaulon alopecuroides (Lam.) DC.	0.00	0.03	0.00

Pterocaulon angustifolium DC.	0.53	0.45	0.08
Pterocaulon rugosum (Vahl) Malme	0.09	0.05	0.03
Pterocaulon balansae Chod.	0.00	0.05	0.00
Senecio brasiliensis (Spreng.) Less.	0.08	0.06	0.00
Senecio heterotrichius DC.	0.19	0.14	0.15
Senecio leptolobus DC.	0.01	0.00	0.03
Senecio madagascariensis Poir.*	0.11	0.18	0.13
Senecio selloi (Spreng.) DC.	0.15	0.30	0.14
Solidago chilensis Meyen	0.21	0.08	0.00
Soliva pterosperma (Juss.) Less.	0.04	0.11	1.01^{***}
Stenachaenium megapotamicum (Spreng.) Baker	0.50	0.89	0.00
Brassicaceae			
Lepidium ruderale Benth.*	0.08	0.01	0.00
Campanulaceae			
Wahlenbergia linarioides (Lam.) A.DC.	0.11	0.03	0.05
Caryophyllaceae			
Anagallis arvensis L.*	0.11	0.06	0.00
Cerastium glomeratum Thuill.*	0.00	0.05	0.00
Paronychia communis Cambess.	0.03	0.00	0.05
Cistaceae			
Helianthemum brasiliense (Lam.) Pers.	0.06	0.00	0.04
Commelinaceae			
Commelina erecta L.	0.06	0.04	0.00
Tradescantia crassula Link & Otto	0.08	0.02	0.00
Convolvulaceae			
Dichondra macrocalyx Meisn.	0.04	0.00	0.13
Dichondra sericea Sw.	0.71	1.48	1.49^{***}
Evolvulus sericeus Sw.	0.64^{***}	0.28	0.11
Cyperaceae			
Abildgaardia ovata (Burm. f.) Kral	0.00	0.00	0.14
Bulbostylis consanguinea (Kunth) C.B. Clarke	0.00	0.00	0.03
Bulbostylis scabra (J. Presl & C. Presl) C.B. Clarke	0.04	0.11	0.01
Carex phalaroides Kunth	0.20	0.35	0.67^{***}
Carex sororia Kunth	0.01	0.03	0.08
Cyperus aggregatus (Willd.) Endl.	0.08	0.08	0.20
Cyperus reflexus Vahl	0.14	0.19	0.20
Eleocharis cf. montana (Kunth) Roem. & Schult.	0.00	0.00	0.01
Eleocharis viridans Kük. ex Osten	0.33	0.00	0.38
Fimbristylis autumnalis (L.) Roem. & Schult.	0.00	0.00	0.01
Fimbristylis complanata (Retz.) Link	0.01	0.03	0.11
Fimbristylis dichotoma (Retz.) Vahl	0.06	0.00	0.01
Kylinga vaginata Lam.	0.00	0.00	0.21
Kyllinga brevifolia Rottb.	0.01	0.05	0.41
Kyllinga odorata Vahl	0.30	0.29	0.13

Rhynchospora barrosiana Guagl.	0.50	0.34	0.39
Rhynchospora megapotamica (A. Spreng.) H. Pfeiff.	0.01	0.01	0.08
Rhynchospora setigera (Kunth) Boeck.	0.11	0.09	0.09
Rhynchospora tenuis Link	1.48	0.81	0.55
Scleria distans Poir.	0.13	0.03	0.00
Dennstaedtiaceae			
Pteridium arachnoideum (Kaulf.) Maxon	0.05	0.06	0.00
Droseraceae			
Drosera brevifolia Pursh.	0.00	0.00	0.06
Erythroxylaceae			
Erythroxylum argentinum O.E.Schulz	0.00	0.05	0.00
Euphorbiaceae			
Bernardia multicaulis Müll. Arg.	0.03	0.03	0.00
Croton montevidensis Spreng.	0.00	0.00	0.03
Euphorbia papillosa A.St.-Hil.	0.14	0.00	0.00
Euphorbia stenophylla Boiss.	0.00	0.01	0.03
Tragia bahiensis Müll. Arg.	0.24	0.08	0.00
Fabaceae			
Clitoria nana Benth.	0.06***	0.01	0.00
Desmanthus tatuhyensis Hoehne	0.54	0.15	0.04
Desmodium adscendens (Sw.) DC.	0.09	0.15	0.78
Desmodium barbatum (L.) Benth.	0.03	0.03	0.00
Desmodium incanum DC.	2.40	1.95	4.06***
Galactia marginalis Benth.	0.04	0.00	0.00
Macroptilium prostratum (Benth.) Urb.	0.23	0.00	0.13
Rhynchosia diversifolia Micheli	0.03	0.00	0.00
Stylosanthes leiocarpa Vogel	0.29	0.03	0.73
Stylosanthes montevidensis Vogel	0.01	0.04	0.01
Zornia orbiculata Mohlenbr.	0.10	0.00	0.08
Zornia sericea Moric.	0.08	0.00	0.01
Gesneriaceae			
Sinningia lutea Buzatto & R. Singer	0.04	0.00	0.00
Hypericaceae			
Hypericum connatum Lam.	0.00	0.01	0.00
Hypoxidaceae			
Hypoxis decumbens L.	0.60	1.06	0.63
Iridaceae			
Cypella fucata Ravenna	0.03	0.01	0.04
Herbertia lahue (Molina) Goldblatt	0.04	0.00	0.06
Herbertia pulchella Sweet	0.26	0.01	0.21
Sisyrinchium megapotamicum Malme	0.08	0.00	0.05
Sisyrinchium micranthum Cav.	0.26*	0.13	0.43*
Sisyrinchium palmifolium L.	0.05	0.00	0.00
Sisyrinchium sellowianum Klatt	0.06	0.00	0.08

Juncaceae			
Juncus capillaceus Lam.	0.00	0.00	0.13
Juncus microcephalus Kunth	0.05	0.05	0.05
Juncus tenuis Willd.	0.46	0.31	1.03^{***}
Lamiaceae			
Hyptis mutabilis (Rich.) Briq.	0.36	0.15	0.00
Scutellaria racemosa Pers.	0.08	0.05	0.11
Linaceae			
Cliococca selaginoides (Lam.) C. M. Rogers & Mild	0.01	0.00	0.01
Lythraceae			
Cuphea calophylla Cham. & Schltdl.	0.03	0.00	0.01
Cuphea glutinosa Cham. & Schltdl.	0.18	0.28	0.20
Malpighiaceae			
Aspicarpa pulchella (Griseb.) O´Donell & Lourteig	0.15	0.04	0.01
Galphimia australis Chodat	0.08	0.00	0.00
Janusia guaranitica (A. St.-Hil.) A. Juss.	0.00	0.03	0.05
Malvaceae			
Krapovickasia flavescens (Cav.) Fryxell	0.24	0.09	0.03
Melochia chamaedrys A. St.-Hil.	0.01	0.00	0.00
Pavonia glechomoides A. St.-Hill.	0.06	0.00	0.00
Pavonia hastata Cav.	0.09	0.00	0.00
Sida regnellii R.E. Fr.	0.01	0.03	0.00
Sida rhombifolia L.	0.08	0.25	0.35
Wissadula glechomifolium (A. St.-Hil.) R.E. Fr.	0.01	0.00	0.01
Melastomataceae			
Tibouchina gracilis (Bonpl.) Cogn.	0.16	0.10	0.09
Moraceae			
Dorstenia brasiliensis Lam.	0.00	0.08	0.00
Myrtaceae			
Blepharocalyx salicifolius (Kunth) O.Berg	0.00	0.06	0.00
Campomanesia aurea O.Berg	0.36	0.20	0.00
Eugenia uniflora L.	0.00	0.05	0.00
Psidium salutare var. *mucronatum* (Cambess.) Landrum	0.04	0.03	0.00
Psidium salutare var. *sericeum* (Cambess.) Landrum	0.00	0.00	0.13
Orchidaceae			
Brachystele camporum (Lindl.) Schltr.	0.05	0.00	0.01
Habenaria parviflora Lindl.	0.03	0.03	0.09
Orobanchaceae			
Agalinis communis (Cham. & Schltdl.) D'Arcy	0.03	0.01	0.00
Oxalidaceae			
Oxalis bifrons Progel	0.10	0.03	0.00
Oxalis bipartita A. St.-Hil.	0.23	0.15	0.30
Oxalis eriocarpa DC.	0.04	0.00	0.23
Oxalis floribunda Lehm.	0.01	0.00	0.00

Oxalis lasiopetala Zuccarini	0.13	0.04	0.34
Oxalis perdicaria (Molina) Bertero	0.08	0.04	0.28
Oxalis sellowiana Zucc.	0.06	0.00	0.09
Passifloraceae			
Passiflora caerulea L.	0.00	0.08	0.00
Passiflora suberosa L.	0.00	0.05	0.00
Piriqueta suborbicularis (A. St.-Hil. & Naudin) Arbo	0.06	0.05	0.01
Turnera sidoides L.	0.00	0.06	0.03
Plantaginaceae			
Gratiola peruviana L.	0.00	0.00	0.24
Mecardonia procumbens (Mill.) Small	0.00	0.00	0.10
Mecardonia tenella (Cham. & Schltdl.) Pennell	0.20	0.00	0.31
Plantago tomentosa Lam.	0.13	0.34	0.4^{**}
Scoparia montevidensis (Spreng.) R.E. Fr.	0.05	0.01	0.04
Poaceae			
Agrostis montevidensis Spreng. ex Nees	0.04	0.25	0.20
Andropogon lateralis Nees	2.6^{**}	1.00	4.27^{**}
Andropogon selloanus (Hack.) Hack.	0.78	0.46	0.43
Andropogon ternatus (Spreng.) Nees	0.21	0.06	0.14
Anthoxanthum odoratum L.*	0.00	0.03	0.00
Aristida laevis (Nees) Kunth	2.63^{***}	2.78^{***}	0.03
Aristida venustula Arechav.	0.16	0.06	0.14
Axonopus argentinus Parodi	0.26	0.00	0.00
Axonopus compressus (Sw.) P. Beauv.	0.04	0.23	0.43
Axonopus fissifolius (Raddi) Kuhlm.	3.43	2.96	19.55^{***}
Axonopus purpusii (Mez) Chase var. *glabrescens* Valls	0.43	0.03	0.00
Briza minor L.*	0.05	0.00	0.16
Calamagrostis viridiflavescens (Poir.) Steud.	0.09	0.00	0.08
Chascolytrum calotheca (Trin.) Essi, Longhi-Wagner & Souza-Chies	0.11	0.06	0.03
Chascolytrum lamarckianum (Nees) Matthei	0.06	0.03	0.10
Chascolytrum poomorphum (J. Presl) Essi, Longhi-Wagner & Souza-Chies	0.15	0.03	0.29
Chascolytrum rufum J. Presl	0.08	0.03	0.09
Chascolytrum subaristatum (Lam.) Desv.	0.66	0.65	1.20
Chascolytrum uniolae (Nees) L. Essi, Longhi-Wagner & Souza-Chies	0.21	0.03	0.21
Cynodon dactylon (L.) Pers.	0.98	0.75	0.08
Danthonia cirrata Hack. & Arechav.	0.08	0.04	0.01
Danthonia secundiflora J. Presl	0.01	0.00	0.00
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	2.30	3.01^{*}	1.54
Digitaria ciliaris (Retz.) Koeler	0.06	0.00	0.01
Eleusine tristachya (Lam.) Lam.	0.04	0.08	0.14
Eragrostis airoides Nees.	0.00	0.14	0.00
Eragrostis bahiensis Schrad. ex Schult.	0.09	0.18	0.08
Eragrostis cataclasta Nicora	0.00	0.00	0.78
Eragrostis lugens Nees	0.18	0.08	0.10

Eragrostis neesii Trin.	0.14	0.30	0.68^{**}
Eragrostis plana Nees	2.94^{**}	0.68	0.09
Eragrostis polytricha Nees	0.10	0.11	0.03
Eustachys retusa (Lag.) Kunth	0.11	0.00	0.00
Eustachys uliginosa (Hack.) Herter	0.08	0.00	0.00
Ischaemum minus J. Presl	0.25	0.00	3.74^{***}
Leersia hexandra Sw.	0.00	0.00	0.03
Leptocoryphium lanatum (Kunth) Nees	0.05	0.00	0.03
Lolium multiflorum Lam.*	0.00	0.00	0.05
Melica hyalina Döll	0.13	0.00	0.00
Melica macra Nees	0.13	0.00	0.00
Mnesithea selloana (Hack.) de Koning & Sosef	0.39	0.28	2^{***}
Nassella nutans (Hack.) Barkworth	0.05	0.03	0.05
Panicum bergii var. *pilosissimum* Zuloaga	0.10	0.00	0.03
Paspalum corcovadense Raddi	0.04	0.00	0.00
Paspalum dilatatum Poir.	0.00	0.28	0.99
Paspalum lepton Schult.	0.10	0.00	0.50
Paspalum modestum Mez	0.03	0.00	0.00
Paspalum notatum Alain ex Flüggé	5.30	3.33	21.9^{***}
Paspalum paniculatum L.	0.00	0.03	0.00
Paspalum paucifolium Swallen	0.03	0.23	0.00
Paspalum plicatulum Michx.	1.46^{*}	1.43^{*}	0.70
Paspalum pumilum Nees	0.83^{*}	0.05	1.07^{*}
Paspalum umbrosum Trin.	0.00	0.19	0.05
Paspalum urvillei Steud.	0.04	0.13	0.03
Piptochaetium montevidense (Spreng.) Parodi	6.55	5.63	3.40
Saccharum angustifolium (Nees) Trin.	6.28^{***}	5.01^{***}	0.05
Schizachyrium microstachyum (Desv. ex Ham.) Roseng.	1.72^{***}	0.96^{***}	0.06
Schizachyrium tenerum Nees	0.00	0.00	0.03
Setaria parviflora (Poir.) Kerguélen	0.8^{**}	1.43^{**}	0.30
Setaria vaginata Spreng.	0.50	0.50	0.08
Sporobolus indicus (L.) R.Br.	1.29	0.43	0.45
Steinchisma decipiens (Nees ex Trin.) W.V. Br.	0.01	0.00	0.00
Stenchismia hians (Elliott) Nash	0.36	0.21	0.93^{***}
Vulpia bromoides (L.) Gray*	0.06	0.03	0.56
Polygalaceae			
Monnina resedoides A. St.-Hil. & Moq.	0.08	0.03	0.00
Polygala adenophylla A. St.-Hil. & Moq.	0.03	0.00	0.03
Polygala australis A. W. Benn.	0.03	0.00	0.19
Polygala brasiliensis L.	0.06	0.00	0.03
Polygonaceae			
Rumex acetosella L.*	0.05	0.00	0.00
Primulaceae			

Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	0.00	0.10	0.00
Rubiaceae			
Borreria capitata (Ruiz & Pav.) DC.	0.03	0.00	0.00
Borreria dasycephala (Cham. & Schltdl.) Bacigalupo & E.L. Cabral	0.03	0.03	0.05
Borreria eryngioides Cham. & Schltdl.	0.09	0.00	0.09
Borreria verticillata (L.) G. Mey.	0.24	0.23	0.09
Galianthe centranthoides (Cham. & Schltdl.) E.L.Cabral	0.06	0.00	0.00
Galianthe fastigiata Griseb.	0.23	0.08	0.03
Galium hirtum Lam.	0.03	0.11	0.13
Galium hypocarpium (L.) Endl. ex Griseb.	0.00	0.08	0.04
Galium richardianum (Gillies ex Hook. & Arn.) Endl. ex Walp.	0.16	0.03	0.18
Guetarda uruguaiensis Cham. & Schltdl.	0.03	0.00	0.00
Oldenlandia salzmannii (DC.) Benth. & Hook. f. ex B.D. Jacks.	0.04	0.00	0.18
Richardia humistrata (Cham. et Schlecht.) Steud.	0.84	0.68	1.11
Sapindaceae			
Cupania vernalis Cambess.	0.00	0.13	0.00
Smilacaceae			
Smilax campestris Griseb.	0.35	0.44	0.00
Solanaceae			
Cestrum euanthes Schltdl.	0.19	0.21	0.00
Petunia axillaris (Lam.) Britton, Sterns & Poggenb.	0.03	0.00	0.05
Solanum laxum Spreng.	0.00	0.03	0.00
Solanum reflexum Schrank	0.00	0.03	0.00
Solanum sisymbrifolium L.	0.01	0.05	0.04
Thymelaeaceae			
Daphnopsis racemosa Griseb.	0.00	0.55	0.25
Verbenaceae			
Glandularia marrubioides (Cham.) Tronc.	0.05	0.00	0.03
Glandularia selloi (Spreng.) Tronc.	0.21	0.20	0.20
Verbena bonariensis L.	0.00	0.03	0.05

Chapter 2:

Conservation of species-rich subtropical grasslands: traditional management vs. legal conservation requirements in the context of Eucalypt plantations

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Short title: Grasslands conservation in preserved areas

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Abstract

Land use change is the main cause of global losses in biodiversity, and in the case of grasslands, this includes not only change to other uses, but also changes in management intensity. In the last 10 years, afforestation area of grasslands in the understudied Serra do Sudeste region, situated in the southern part of the South Brazilian Pampa, has increased considerably, turning the region into a mosaic of tree plantations, remnant grasslands under traditional grazing regimes, set-aside areas within the tree plantations that have not been planted due to conservation requirements and are not under traditional management, and other land use types. Here, we evaluated the patterns of plant structure and composition in conservation areas considering two distinct types of land use history (former use prior to plantation: agricultural use or traditional grazing, i.e. secondary grassland in conservation area and primary grassland in conservation area) in comparison to grasslands under traditional management (primary grasslands, traditionally grazed). The study was carried out at 58 sites, using two sizes of sampling plots:1m^2 and 25m^2. We used ordination techniques to observe the distribution of the data and analysis of indicator species for the typical ones of each type of grassland. Additionally, we evaluated the influence of shrubs and structural parameters of vegetation on species richness. Our results – total of 518 species accounted for in the sampling – confirm the high biodiversity of the region. We demonstrated differences in vegetation structure and composition in secondary grasslands in conservation areas (SGCA), in contrast to primary grasslands in conservation areas (PGCA). Differences between PGCA and PGTM are associated to management intensity, with sites under lower grazing intensity suffering from changes in grassland physiognomy due to increased cover of shrubs and higher cover of tussock grasses. Our study emphasized the need to increase conservation efforts in the region, and points out that current conservation approaches should be evaluated critically regarding their effects for biodiversity conservation.

Keywords: PAMPA, Serra do Sudeste, conservation areas, biodiversity, management

Introduction

The leading driver of the loss of biodiversity in the world is human land use (Sala et al. 2000; Millennium Ecosystem Assessment 2005). The modification of natural landscapes for agricultural production has led to widespread destruction of habitats and to the fragmentation of previously continuous habitat into smaller and more isolated fragments. Habitat fragmentation exposes small fragments to negative edge effects and constrains dispersal between them, often with negative consequences for population dynamics (Fahrig 2003; Hanski et al. 2013; Damschen et al. 2014; Haddad et al. 2015). Contrasts in land-use intensity and the specific management history of remaining fragments induce variable habitat qualities and select different species combinations and cover (Freschet et al. 2013; Allan et al. 2015; Newbold et al. 2015). In the specific case of grasslands, land use change consists both of complete replacement of the original vegetation and in changes of management intensity of grasslands (Koch et al. 2016).

In the South Brazilian grasslands, plantations of Eucalypt have expanded greatly in area in the past ten years (AGEFLOR 2016). Usually, entire farms are transformed into eucalyptus plantations, but some areas are not planted, as Brazilian legislation (law 12.651/2012) requires establishment of Permanent Preservation Areas (APP) and Legal Reserve (RL). APPs have to be established until a certain distance around creeks (30 to either side in the case of small creeks), rivers and wetlands as well as on steep hillslopes and tops of hills and mountains). RL are a part of the rural property (20% in the Pampa biome, with possibility to include APP areas in the calculation) where natural vegetation cannot be removed and only sustainable use is possible. In APPs, in contrast, no economic use is possible. These areas of APP and RL in the context of Eucalypt plantations are spared from planting trees. In some cases, this may include areas that had been used for agriculture previous to tree planting, i.e. where then secondary grasslands will develop.

APPs usually are not under grazing management, in contrast to RL areas. However, in the latter, traditional management is abandoned in most cases. Often cattle, usually from neighboring properties, still is present in the areas, but usually at low and not controlled stocking rates. It is well established that grassland in regions that allow forest development depends on grazing for maintenance of their structure and biodiversity (Briggs et al 2002; Enyedi et al. 2008; Lezama et al 2014; Blanco et al. 2014; Veldman et al. 2015). When placed into conservation schemes and grazing intensity declines considerably, management thus may not anymore be suitable for the conservation of grasslands.

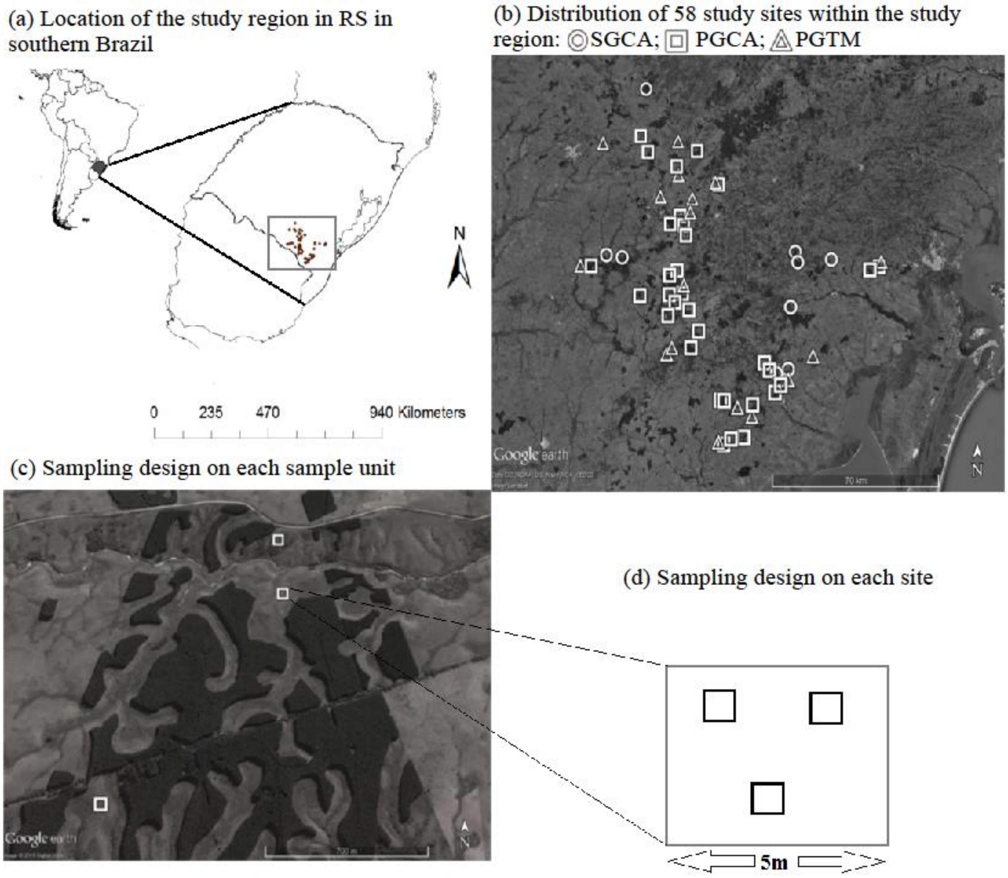
While the overall level of land use change in the grassland region, i.e. substitution of native grasslands by other land use, has been quantified (Andrade et al. 2015), quantification of effects of changed management within grazed grasslands is more difficult (Koch et al. 2016) and has not been undertaken for grasslands in the Pampa region. Mitigating the negative effects of changes on biodiversity requires immediate and effective conservation measures (Pimm et al. 2014; Ceballos et al. 2015). The challenge is to determine the level of degradation in secondary and abandoned grasslands, where the natural potential is strongly dependent on the evolutionary history of the grassland with grazers or fire (Milchunas et al 1988.) and on grassland productivity (Proulx & Mazumder 1998, Lezama et al 2014; Fraser et al 2015).

According to AGEFLOR (2016), in the state of Rio Grande do Sul (RS) the area planted with afforestation is 593.15 thousand ha, of which 309 thousand ha are planted with Eucalypt. The companies of the sector maintain 525 thousand hectares of protected areas in the RL, APP and Private Reserves of Natural Heritage (RPPN) in the RS. This area represents an area almost equivalent to the existing conservation areas in the state of RS, with 575 thousand hectares in conservation areas. The Serra do Sudeste region, situated on granitic rocks in the southeastern part of the state, is especially affected by Eucalypt plantations (Gautreau P & Vélez E 2011). At the same time, the region poorly studied regarding plant species composition and conservation value, even though considered a high-priority region for conservation (MMA 2000). In this study, we aim at analyzing composition and structure of grassland vegetation in primary and secondary grasslands in conservation areas established in the context of Eucalypt plantations (afforestation) in order to assess conservation status of these areas. Our references are primary grassland subjected to traditional grazing management. We hypothesized that areas without formal management and within the context of afforestation areas differ from reference grasslands in terms of floristic composition and structure. Specifically, we expected to find 1) higher abundance of woody species (both grassland shrubs and pioneer forest species) in these areas without formal management; 2) lower species richness in areas where traditional management had been abandoned, in consequence of lower grazing pressure, and 3) higher importance of exotic species in areas where conservation areas included secondary grasslands that established spontaneously on former agricultural land.

Materials and Methods

Study Region

Our study region, situated in the Brazilian Pampa Biome, comprises the southern part of the Serra do Sudeste mountain range in the extreme south of Brazil, comprising the area between the municipalities of Bagé, Jaguarão and Pelotas (Fig. 1). The region is a conservation priority area in the Pampa Biome by the Brazilian government due to high levels of endemism among herbaceous plant species (MMA 2000). Geologically the oldest region of southern Brazil, it consists of a mosaic of geological formations with dominance of granitic and magmatic formations. Climate is temperate, with cold winters and hot summer without rainy season, average temperature of the coldest month above 11.3° C, and no dry season (Cfa according to the Koppen-Geigen classification (Alvares et al 2013). The topography is slightly undulated to strongly accentuated (average altitude 30 to 430 m a. s.) and soils are poor in nutrients, ranging from deep to shallow soils, depending on relief features (Streck et al. 2008). The region is composed of forest-grassland mosaics. While forests occur mainly along river valleys, the predominant vegetation is dry grasslands, with the presence of many shrubs and subshrubs. In comparison to other regions of Rio Grande do Sul state, the region still contains a large proportion of primary grassland (Andrade et al. 2015), however, in the past decade, there has been a fast expansion of exotic tree plantations, mainly Eucalypt (Gautreau P & Vélez E. 2011).


(a) Location of the study region in RS in southern Brazil

(b) Distribution of 58 study sites within the study region: ◎SGCA; ▣ PGCA; △PGTM

(c) Sampling design on each sample unit

(d) Sampling design on each site

Fig. 1 (a) Location of the study region in the grasslands of Rio Grande do Sul (RS), southern Brazil; (b) distribution of 58 study sites throughout the study region (background map©Google Earth 2015): ▣ PGCA = primary grasslands in conservation areas; ◎ SGCA = secondary grassland in conservation areas; △ PGTM = primary grassland subjected to the traditionally management; (c) sampling design at each of the 1 sample unit containing three 25 m^2 study sites (plots); and (d) sampling design on each plot (25 m^2) containing three 1 m^2 subplots.

Sampling design and data collection

The study was conducted at a total of fifty eight sites, which included three distinct types of grasslands with contrasting land use histories and management intensities: 1) primary grasslands in conservation areas (PGCA) without formal management (i.e. varying cattle stocking rates) and long history of livestock grazing, located around the eucalyptus plantations; 2) secondary grassland in conservation areas (SGCA), recovering from conversion to arable land with grazing at variable stocking rates, located around the eucalyptus plantations; 3) primary grassland subjected to the traditionally management (PGTM) of the region (extensive livestock: cattle average 0.5-1 animals per hectare). We consider as "conservation areas" those areas in the context of the Eucalypt plantation where no trees were planted, i.e. mostly the APP and RL areas. The study was conducted in spring and summer of the years 2013 and 2014. The Eucalypt plantations has been established 7 - 8 years (2006) before our sampling, and tree height varied from 8 to 12 m.

Vegetation data

At each site, we randomly allocated three plots of 25m^2, with a distance of at least 1km from each other. For site selection, we used a buffer of 30 m to native forest, Eucalypt plantations, roads and any other type of land use besides grasslands. All sites were located in predominantly dry grasslands (humid grasslands or wetlands not included into the sampling design). In these plots, we identified the average height and abundance of shrub and sub-shrub species, additionally we recorded the occurrence of species listed on the Red List of endangered species in RS state (SEMA) and of species endemic to the Pampa biome (according to Boldrini et al. in prep.). In each 25m^2 plot, we randomly selected three plots of 1m^2 where we identified all vascular plant species and estimated their cover according to the Londo (1976) scale. Additionally, we recorded vegetation height (measured at 5 points), percentage of plant litter, manure and exposed soil. Vegetation parameters were calculated according to Muller-Dombois & Ellenberg (1974): relative cover (RC), relative frequency (RF), and importance value index (IVI). In the 25m^2 plots, we recorded identity and height of all shrubs, sub-shrubs and trees. Species were classified regarding their origin (native/exotic; Rolim, 2014) and degree of threat of species was checked in the current Red List for the state (Rio Grande do Sul 2014).

Data Analysis

For all analyses, we pooled the plot data to the site level. General patterns of species composition were explored by Principal Coordinate Analysis (PCoA), using the matrix of species mean cover per site, for both the herbaceous layer and the shrub/tree layer. Only species with IVI above 1% were included in the ordination analysis of the herbaceous layer. To compare treatments regarding the contribution of the principal species, cover values of the species with correlations > |0.7| to the first axis of the ordination were compared by randomization testing. For the analysis of composition, we used all species, both in a PcoA and in Randomization testing. Additionally, we compared mean cover values of the three most important botanical families, Asteraceae, Fabaceae and Poaceae, the latter divided into prostrate and tussock species. Treatments were also compared by randomization tests regarding, separately, vegetation height, total vegetation cover, bare soil, litter and manure. We used Euclidian distance for univariate analyses and Chord distance for multivariate analyses, 999 permutations, and $\alpha = 0.05$ as probability limit for rejection of null-hypothesis. Site was used as block factor in all analyses. These analyses ware performed using the software MULTIV (available at: http://ecoqua.ecologia.ufrgs.br/). To test the preference of species and shrub and sub-shrubs to reference grasslands, to sites with eucalyptus plantations, and to combination of sites, we applied indicator species analysis (Dufrene & Legendre 1997), using function 'indicspecies' of the R package 'multipatt', based on the 'correlation index (r)' (De Cáceres Legendre, & Moretti 2010). In addition, linear regression was used to test the effect of the average height of the vegetation and the abundance of shrubs in the richness of species. For this, data were transformed in logarithm to obtain normality.

Results

Vegetation description

Overall, 518 plant species were identified at the 58 grassland sites. The most important families in terms of species numbers were Poaceae (110 species), Asteraceae (104 species), Fabaceae (37 species), Cyperaceae (33 species), together constituting 55% of all species. In the 174 sampled plots ($25m^2$), twenty five species included in the list of endangered species (Rio Grande do Sul, 2014) was recorded: 21 were found in PGCA and 14 in PGTM; in SGCA, no endangered species were recorded. Species richness (Figure 1- a) on the site and plot level was significantly ($p = 0.02$) higher in reference grasslands than in conservation grasslands with a history of agriculture. In primary grasslands in conservation areas (PGCA), mean species number per site in subplots was 31 and in plots of $25m^2$, 109. Grasslands with a history of agriculture before afforestation (SGCA) showed an average 21 species in subplots of 1m^2 and 75 species in plots of 25m^2 per site. In grassland areas under traditional management (PGTM), we identified a total of 345 species, found 34 species in subplots of 1m^2, and 102 species in plots with 25m^2.

The shrub and sub-shrubs species with highest cover values recorded in 25 m^2 plots were: *Baccharis trimera, Eupatorium bunifolium, Baccharis riograndensis, Baccharis dracunculifolia.* The number of shrub individuals differed significantly between SGCA and PGTM, but not between PGTM and PGCA ($p = 0.05$; Figure 1-B). The abundance of shrubs in 25m^2 plots showed negative effect on the richness of herbaceous community in 1m^2 plots ($R^2 = 0.30$; $p = 0.00$). This result is mainly associated with the presence of *Baccharis dracunculifolia*, which had the largest number of individuals in SGCA and PGCA and differed significantly from PGTM in terms of abundance ($p = 0.00$). Additionally, we tested the effect of the average height of vegetation in species richness, the result shows that the sites with the highest height of vegetation have lower species richness ($R^2 = 0.24$; $p = 0.00$).

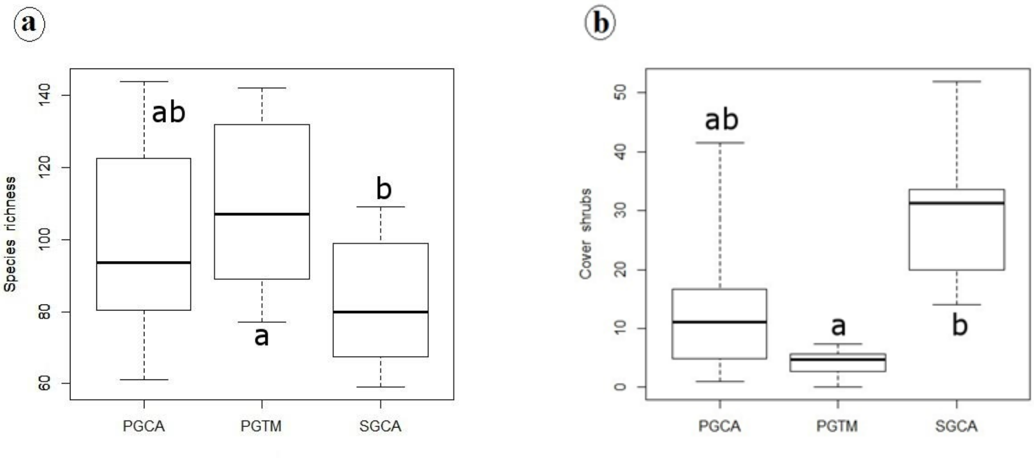


Figure 1 – Variation in species richness (a) and average number of shrubs (b) among the fifty eight sampled sites (mean values and 25 quartiles). Different letters represent significant differences between treatments ($p<0.05$). PGCA = primary grasslands in conservation areas, SGCA = secondary grassland in conservation areas, PGTM = primary grassland subjected to the traditionally management.

Of the species sampled, 29 were exotic, and total cover of exotic species was significantly higher in PGCA and SGCA when compared to PGTM ($p = 0.00$). The invasive plants *Cynodon* *dactylon*, *Eragrostis plana*, *Cirsium vulgare* showed significance differences between treatments, with higher values in SGCA (p < 0.01). *Senecio madagascariensis* and *Ulex europaeus,* two other invasive species that are abundant in the region, did not show significant differences between treatments.

The PCoA ordination reflected compositional differences in herbaceous communities between PGTM and SGCA, with traditionally management to the left, and secondary grassland to the right, but with considerable overlap between PGCA and the other two types of grassland. The first and second axes of the PCoA with species composition data together explained 52% of the variation in the vegetation composition (Figure 2 - a). The first axis separated sites with high cover of *Paspalum notatum* (-0.96% correlation to the axis) and *Axonopus affinis* (-0.50%), on the left side of the figure, from areas with high cover of the exotic grass *Cynodon dactylon* (0.61%) and the native shrubs *Baccharis dracunculifolia* (0.54%) and *Eupatorium buniifolium* (0.52%), on the right side. Along the second axis the species with the highest correlation was *Axonopus suffultus* (0.93%), *Danthonia cirrata* (0.69%), *Piptochaetium stipoides* (0.61%), *Schizachyrium tenerum* (0.59%) and *Aristida venustula* (0.52%), all associated to PGCA plots.

The first and second axes of the PCoA based on shrub and sub-shrubs composition (Figure 2 - b) together accounted for 46% of the variation in the data. The first axis separated sites with high cover of *Eupatorium buniifolium* (0.85%), *Baccharis dracunculifolia* (0.59%) and *Sida rhombifolia* (0.54%), situated at the right side, from sites with high cover of *Baccharis riograndensis* (0.-68%) to the left. The second axis explained 19% of the variation of the data, species with the highest correlation was *Baccharis crispa* (0.83%) and *Baccharis ochracea* (0.62%),

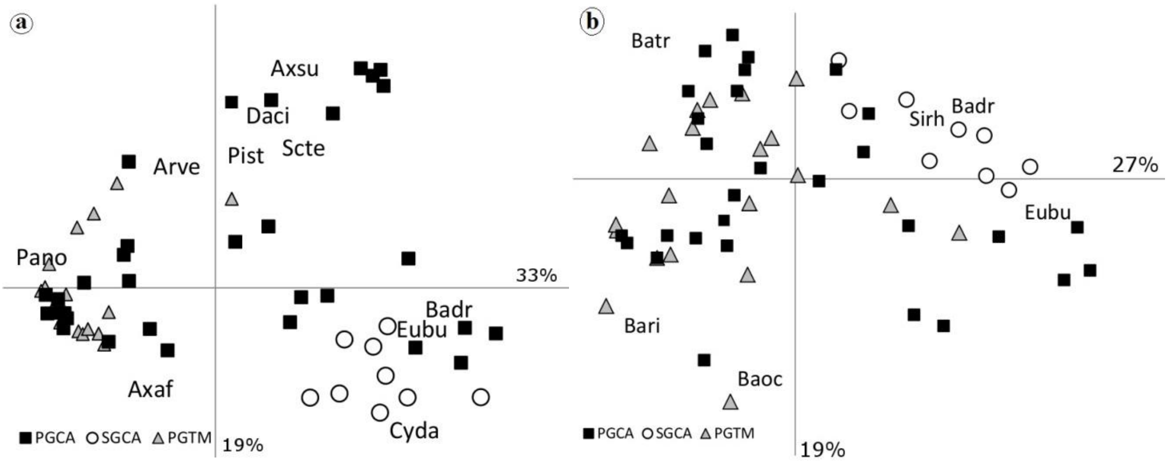


Figure 2 – Principal coordinate ordination diagram, based on chord distance, showing the first two axes. Symbols represent the sites. Letters represent the initials of the genus and the epithet of species with high correlations to the axes (corr.>0.5). (a) PCoA using grassland species data. (b) PCoA using shrub and sub-shrubs species data. In both figures, only species with high correlations to the axes are shown (corr.>0.5). PCoA (a) – Arla: *Aristida venustula*, Axaf: *Axonopus affinis*,Axsu: *Axonopus suffultus*, Brdr: *Baccharis dracunculifolia*, Cyda: *Cynodon dactylon*, Daci: *Danthonia cirrata*, Eubu: *Eupatorium buniifolium*, Pano: *Paspalum notatum*, Pist: *Piptochaetium stipoides*; Scte: *Schizachyrium tenerum*. PCoA (b) - Brtr: *Baccharis trimera;* Bari: *Baccharis riograndensis*; Baoc: *Baccharis ochracea;* Eubu: *Eupatorium buniifolium;* Sirh: *Sida rhombifolia*.

Both using floristic and shrub and sub-shrubs (all species with IVI > 1), PGTM differed significantly from the other two grassland types in multivariate randomization tests. However, of the four species with higher vegetation cover and highest correlation (>60%) to axis 1 and 2, only four species showed significant differences between grasslands (Table 1). Average number of individuals of shrub and sub-shrubs species was significantly higher for SGCA and PGCA and lower than in PGTM. Vegetation cover, vegetation height, litter and bare soil differed significantly between treatments ($p<0.05$; Table 1).

Table 1 – Differences in number of individuals and cover of species and species groups (exotics species) as well as parameters indicating vegetation structure between treatments. Different letters represent significant differences between treatments. PGCA = primary grasslands in conservation areas, SGCA = secondary grassland in conservation areas, PGTM = primary grassland subjected to the traditionally management. * indicates exotic species.

		PGTM	SGCA	PGCA	P value
Plot 1m^2	*Cynodon dactylon** (%)	0.3^{b}	9.9^{a}	1.3^{b}	0.001
	*Eragrostis plana** (%)	0.2^{b}	3.2^{a}	1^{b}	0.007
	Axonopus suffultus (%)	1.2^{b}	0^{ab}	4^{a}	0.004
	Danthonia cirrata (%)	0.5^{a}	0^{b}	1.3^{a}	0.001
	Paspalum notatum (%)	24^{a}	3^{b}	11^{a}	0.055
	Piptochaetium stipoides (%)	0.4^{a}	0^{b}	0.7^{a}	0.001
Plot 25m^2	*Baccharis riograndensis* (ind)	3.3^{a}	0.6^{b}	3^{a}	0.009
	Baccharis dracunculifolia (ind)	0.2^{a}	4.2^{b}	2^{b}	0.001
	Eupatorium buniifolium (ind)	1.6^{a}	4.6^{b}	3.8^{b}	0.044
Shrub abundance (ind)		4^{a}	30^{b}	12^{ab}	0.023
Shrub richness (species)		2.6^{a}	9.6^{b}	6.3^{c}	0.001
Exotics species (%)		0.1^{b}	0.6^{a}	0.1^{b}	0.001
Vegetation Height (cm)		12 (±6)^{a}	52 (±29)^{b}	30 (±18)^{c}	0.016
Litter cover (%)		3.6 (±2)^{a}	10 (±5)^{b}	8 (±3)^{b}	0.027
Litter cover in the plant (%)		3 (±1.6)^{a}	6 (±3)^{b}	7.3 (±5)^{b}	0.049
Bare soil cover (%)		4 (±5)^{b}	14 (±7)^{a}	8 (±10)^{ab}	0.083
Manure cover (%)		2 (±3)^{a}	0.5 (±1)^{b}	0.3 (±2)^{b}	0.002

From 39 species (IVI>1%) tested in indicator species analysis, 21 species were selected ($p<0.05$), 14 species associated to one group and 7 species associated to two groups. Seven species were selected as indicative for the combination of reference grasslands and grasslands with afforestation (PGTM and PGCA), and six of them had correlation intensity values above 40%: *Oxalis eriocarpa* (r=0.53; p=0.00), *Piptochaetium stipoides* (r=0.46; p=0.00), *Evolvulus sericeus* (r=0.44; p=0.00), *Mnesithea selloana* (r=0.43; p=0.00), *Aristida venustula* (r=0.41; p=0.00), *Aspilia montevidensis* (r=0.40; p=0.01). Five species were indicative for SGCA, one of them is the invasive exotic grass *Cynodon dactylon* (r=0.61; p=0.00), also the species with the highest correlation value. The other species were: *Baccharis dracunculifolia* (r=0.50; p=0.00), *Sisyrinchium micranthum* (r=0.49; p=0.00), *Hypoxis decumbens* (r=0.46; p=0.00), *Eryngium horridum* (r=0.40; p=0.00). For PGCA, three indicator species were found: *Danthonia cirrata* (r=0.46; p=0.00), *Paspalum plicatulum* (r=0.43; p=0.00), *Axonopus suffultus* (r=0.40; p=0.00). For PGTM, a total of five species were selected and showed correlation values above 40%, such as *Richardia humistrata* (r=0.53; p=0.00), *Paspalum notatum* (r=0.53; p=0.00), *Eragrostis neesii* (r=0.46; p=0.00), *Dichondra sericea* (r=0.44; p=0.00), and *Steinchisma hians* (r=0.40; p=0.00). The complete list of species selected by the indicator species analysis is presented in the appendix.

Discussion

High plant species richness in an undersurveyed region

Our study is the first to comprehensively conduct vegetation sampling in the species rich Serra do Sudeste on a larger scale. The region is one of the best preserved areas of the Brazilian Pampa biome if we consider the total percentage of remaining natural vegetation (Andrade et al. 2015). Due to a high proportion of shallow and poor soils, suitability for cultivation of annual crops is low. However, in recent years, the region has been intensely occupied by Eucalypt plantations which are not demanding in terms of site conditions under the productive climatic conditions, and because the land value is lower than in other parts of the state. As relief is wavy to strongly wavy and the presence of vegetation native forest is common in valley areas and some slopes, plantations end up directly affecting the natural grassland areas, often leaving only grasslands in flaps surrounding hill tops, rock outcrops, small creeks and springs where protection of native vegetation in APPs is mandatory.

With our sample we recorded 1/4 of the total number of grasslands plants present in the Pampa biome in Brazil (Boldrini et al. in prep.). Despite this high species richness in the region, these grasslands are scarcely studied, as evidenced by the occurrence of one Asteraceae species, *Aspilia foliacea*, that had previously been considered probably extinct in the region and of one *Baccharis* sp. new to science (Torchelsen et al. in preparation). The occurrence of the high number of 20 endemic species, likely is a consequence of the situation of grasslands in the geologically oldest region of the Pampa (Bossi J. & Gaucher C. 2014). However, up to now, the region has been neglected by scientific research on its vegetation resources and by conservation actions: no conservation units have actually been implemented, and the region suffers from increasing conversion to other land uses causes fragmentation, with known negative effects on biodiversity and ecosystem services (Overbeck et al 2007; Andrade et al 2015; Koch et al, 2016; Modernel et al 2016). Legal obligations for establishment of APP and RL – if managed in a way to conserve grassland biodiversity, see below – are important, only one approach for conservation and should be complemented by other approaches that are more effective in conservation of priority areas and prevention of fragmentation, especially if we keep in mind the meet Aichi Biodiversity Target (CBD 2010).

Historical use and diversity in secondary grassland

In our study, we observed that the historical use directly influences the structure and species composition, as has been found in other studies (Alrababah et al. 2007; Koch et al, 2016; Modernel et al 2016). For the study region, re-establishment of grasslands after other land uses seems possible, but these secondary grasslands differ from primary grasslands in terms of composition and structure (Koch et al. 2016; Torchelsen et al., submitted). In general, secondary grasslands on sites with former agricultural use are characterized by distinct concentrations of nutrients, promoting changes in successional trajectories (Céspedes-Payret et al 2014; Andrade et al 2015; Vink et al 2016). In our case, secondary grasslands showed lower total species richness and species composition differed from that of traditionally managed grasslands. No endangered species were found in SGCA, which shows the impact of change in land use and the low potential recovery of these populations in secondary grasslands. Cover and number of exotic species in SGCA, on the other hand, was higher than that found in PGCA and PGTM, with the presence of three problematic invasive species, *Ulex europaeus*, *Cynodon dactylon* and *Eragrostis plana*. Our results underline that without proper management, or possibly active restoration efforts, secondary grasslands do not resemble natural grasslands. The presence of exotic plants is especially important, as these species may here establish large populations that then constitute source populations for dispersal into native grasslands in the region (Leon et al 2016 a,b).

Grasslands in preservation areas without effective management differ in plant diversity and species composition from traditionally grazed areas

A conspicuous result of our study it the heterogeneity of the grasslands in conservation areas, in terms both of composition of the herbaceous layer and of the woody species component. This can be explained by three factors: first of all, the sites under conservation schemes span sites with different site condition. For instant, the species related to PGCA areas along the second axis of the ordination analysis are mostly indicative of shallow soils and rather low and open grasslands. Even though our traditionally managed sites also include some heterogeneity, it is likely that the bias to more extreme sites is higher within the PGCA category, as decition of where Eucalypt are not planted is influenced by both legal obligation (especially in the case of the APPs) and of selection of sites where plantings likely are less productive (or more difficult to work with) due to topographic and soil conditions for RL. Secondly, PGCA sites differ in grazing management and grazing history. Some sites are still grazed at low intensity, and without additional management practices (such as periodic mowing to reduce the shrub component in grasslands). Other are in the process of spontaneous succession after long periods with livestock grazing. Here, grasslands are dominated by tall-growing tussock grasses and present higher importance of woody species, mostly grassland shrubs, both processes that reduce species richness (Overbeck et al. 2005; Lezama et al. 2014), evidenced here by the negative correlation between vegetation height and species richness, and between the abundance of woody species and vegetation richness. These results were influenced mainly by the abundance of *Baccharis dracunculifolia* and *Eupatorium buniifolium*, both grassland shrubs that are controlled in abundance by traditional management. These results are also in line with model predictions by Milchunas et al. (1988), a recent study on effects of land management for highland grasslands in southern Brazil (Koch et al. 2016), and studies from other grassland systems that showed a decline in species number (Hinman & Brewer 2007; Klimes et al. 2013), or marked changes in species composition (Uys et al. 2004; Loydi et al. 2012) when fire or grazing were excluded. The accumulation of litter observed in PGCA and SGCA of our study and in other regions (Enyedi et al. 2008) can additional reduce species number (Morgan & Lunt 1999). The afforestation around the grasslands, as well as the establishment of shrubs that will occur in the absence of management, have been shown to have marked consequences for microclimatic conditions, i.e. reduced radiation, air temperature, connectivity between fragments and wind speed that may reduce biodiversity (Saraiva 2012; Sousa et al. 2013). These effects act in synergy and lead to decreased species richness with plantation age after grassland around afforestation (Bremer & Farley 2010). Thirdly, it needs to be recognized that these processes need time, and that speed of succession will depend on the initial conditions of the vegetation, site features that govern productivity, and adjacent vegetation patches that present seed sources for species from different species groups. Clearly, after only 7 to 8 years, we still cannot expect any dramatic changes as they have been evidenced in grasslands abandoned after longer periods (e.g. Overbeck et al. 2005). Overall, we thus find differences between grassland types under different management. On a regional scale, this certainly contributes to diversity and thus may be considered efficient for conservation, likely not only for plant species (evaluated in this study), but also for other species groups that depend on grassland structure (see Overbeck et al. 2016)

The need to discuss effectiveness of APP and RL for grassland conservation

Permanent Preservation Areas (APP and RL) are areas with the environmental function of preserving water resources, landscape, geological stability, biodiversity, the genetic flow of animals and plants, protecting the soil and ensuring the well-being of human populations (law 12.651/2012). Even though APPs are placed at sites with specific conditions regarding topography and presence of water bodies, they thus are to be multifunctional in their conservation objectives. RS, on the other hand, aims at preserving natural vegetation under the perspective of human use. The important question to which point both conservation approaches are effective for conservation of grassland vegetation is not the main issue of this paper, but – based on the discussion above – our results do allow some comments on the matter. As grasslands have evolved with the presence of disturbances such as fire and grazing (Oesterheld et al. 1999; Lezama et al 2014; Veldman et al. 2015), their conservation requires different strategies that include the presence of disturbance management. This also offers opportunities for sustainable use and economic benefits, i.e. allow for conservation that increases needs of local population, a point much focused on in the current conservation debate (e.g. Kareiva & Marnier 2012). In Brazil, this is accepted for RL areas, but not much applied in case of APPs, where usually no management is considered. If we consider a landscape where natural vegetation is mostly formed by grasslands and conversion to other land uses is high, it seems reasonable that conservation should give priority to the maintenance of the original vegetation types and not per se exclude disturbances or management that will cause successional processes. Furthermore, shrub encroachment due to absence of management in former grassland sites now in APP, may lead to changes in ecosystem processes, such as carbon sequestration in the soil (Jackson et al. 2002), water infiltration into the soil (Farley 2005) and habitat suitability for other species group that should also be considered when making decisions on conservation approaches (Overbeck et al. 2016), such as inclusion or not of management. This is even more important in a region with fast land use change and inexistence of protected areas, such as in the Pampa biome, the biome with the highest Conservation Risk Index of all Brazilian biomes (Overbeck et al. 2015). Under such circumstances, the effectiveness of the existing – and working – legal instruments such as APP and RL are of high importance, together with the development of strategies for restoration of degraded grasslands, such as the secondary grasslands analyzed in our study.

Conclusion

The increasing demand for the production of wood in a grassland region promotes changes in the structure and composition of permanent grasslands. Fragmented grassland landscapes in regions with high biological diversity demonstrate different structure and composition. When the history of use of these grasslands is marked by intensive practices of land management (agriculture), divergence from reference systems is considerably greater, and the presence of invasive exotic species contributes to losses of typical grassland diversity. Grasslands with long history of grazing where this use has then been abandoned or declined prove to be better preserved, however their future is uncertain and successional trajectories should be studied over longer periods. Our results show that some grassland species are able to persist under reduced or abandoned management, but species richness is generally reduced. Consequently, this abandonment option has long-term negative consequences for conservation and would not be suitable for conservation units, as evidenced also in the highland grasslands of Rio Grande do Sul (Pillar & Velez 2010). Neglecting the use of management is condoning the environment to a secondary succession, promoting changes in species composition and consequently the loss of grasslands environments. PGCAs were the grasslands with the greatest species richness; however the competitive strategies of tussocks, shrubs and invasive exotic species are a threat to most of the rare, endangered and endemic species found in the region. To implement strategies dedicated to the conservation of grasslands is necessary for the efficiency of conservation areas, considering the persistence of a neglected biome with high biological diversity in fragmented grasslands.

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Table 1: Species cover in three grassland types (PGCA = primary grasslands in conservation areas, SGCA = secondary grassland in conservation areas, PGTM = primary grassland subjected to the traditionally management) at the fifty-eight study sites in southern Rio Grande do Sul, South Brazil. For species considered in the analysis of indicator species the significance level is indicated with the respective cover value (in one or two groups): *** < 0.001, ** < 0.01, * < 0.05. Exotic species are identified with *after the species name, according to Rolim (2015).

Families / Species	PGCA	SGCA	PGTM
Acanthaceae			
Stenandrium diphyllum Nees	0.06	0.00	0.11
Justicia axilaris (Nees) Lindau	0.02	0.02	0.03
Ruellia morongii Britton	0.04	0.00	0.01
Ruellia hypericoides (Nees) Lindau	0.01	0.00	0.01
Stenandrium dulce (Cav.) Nees	0.01	0.00	0.01
Justicia laevilinguis (Ness) Lindau	0.00	0.00	0.00
Amaranthaceae			
Pfaffia tuberosa (Spreng.) Hicken	0.27	0.12	0.17
Gomphrena graminea Moq.	0.08	0.00	0.03
Pfaffia gnaphaloides (L. f.) Mart.	0.10	0.00	0.04
Gomprena perenis L.	0.01	0.00	0.00
Alternanthera sp.	0.01	0.00	0.00
Gomphrena sellowiana Mart.	0.01	0.00	0.00
Amaryllidaceae			
Nothoscordum montevidense Beauverd	0.06	0.00	0.08
Habranthus tubispathus (L´Hér.) Traub	0.06	0.00	0.07
Nothoscordum gracile (Aiton) Stearn	0.00	0.04	0.01
Nothoscordum gaudichaudianum Kunth	0.02	0.00	0.00
Zephyranthe sp.	0.01	0.00	0.00
Zephyranthes cf. *candida* (Lindl.) Herb.	0.01	0.00	0.00
Nothoscordum inodorum (Aiton) G. Nicholson	0.01	0.00	0.00
Ipheion uniflorum Raf.	0.01	0.00	0.00
Anacardiaceae			
Lithraea brasiliensis Marchand	0.07	0.10	0.01
Schinus polygamus (Cav.) Cabrera	0.06	0.05	0.00
Anemia tomentosa (Sav.) Sw.	0.02	0.00	0.00
Apiaceae			
Eryngium horridum Malme	2.45	4.88**	1.55
Centella asiatica (L.) Urb.	0.55	0.90	0.54
Eryngium nudicaule Lam.	0.16	0.01	0.69
Eryngium sanguisorba Cham. Et Schlecht.	0.36	0.07	0.22
Apium leptophyllum F. Muell. ex Benth.	0.12	0.15	0.31
Eryngium echinatum Urb.	0.00	0.00	0.29
Eryngium megapotamicum Malme	0.05	0.00	0.00
Eryngium pristis Cham. & Schltdl.	0.05	0.00	0.00
Eryngium elegans Cham. Et Schlecht.	0.00	0.09	0.03
Eryngium ciliatum Cham. & Schltdl.	0.03	0.00	0.00
Eryngium ebracteatum Lam.	0.00	0.00	0.03

Daucus pusillus Michx.*	0.01	0.00	0.00
Eryngium eriophorum Cham. Schltdl.	0.00	0.00	0.00
Apocynaceae			
Macrosiphonia pinifolia (A.St.-Hil.) Pichon	0.01	0.00	0.00
Oxypetalum solanoides Hook. & Arn.	0.01	0.00	0.00
Asclepias curassavica L.	0.01	0.01	0.00
Asclepia sp.	0.03	0.00	0.00
Mandevilla coccinea (Hook. & Arn.) Woodson	0.01	0.00	0.00
Asclepias campestres Vell.	0.00	0.00	0.00
Aquifoliaceae			
Ilex dumosa Reissek	0.01	0.05	0.00
Araliaceae			
Hydrocotyle exigua Malme	0.08	0.11	0.24
Asparagaceae			
Clara ophiopogonoides Kunth	0.02	0.00	0.01
Asteraceae			
Baccharis trimera (Less.) DC.	4.66	3.88	2.81
Eupatorium buniifolium Hook. ex Arn.	2.04	4.02*	1.20
Aspilia montevidensis (Spreng.) Kuntze	0.79*	0.27	0.63*
Baccharis dracunculifolia DC.	0.68	4.62**	0.14
Baccharis riograndensis I.L.Teodoro & J.Vidal	0.56*	0.00	0.73*
Gamochaeta americana (Mill.) Wedd.	0.27	0.31	0.23
Elephantopus mollis Kunth	0.26	1.42	0.10
Vernonia flexuosa Sims	0.39	0.01	0.25
Senecio selloi (Spreng.) DC.	0.21	0.64	0.25
Lucilia nitens Less.	0.29	0.09	0.28
Baccharis ochracea Spreng.	0.32	0.01	0.36
Senecio brasiliensis (Spreng.) Less.	0.31	0.57	0.02
Chevreulia sarmentosa (Pers.) Blake	0.12	0.16	0.57
Chaptalia runcinata Kunth	0.13	0.02	0.16
Facelis retusa (Lam.) Sch. Bip.	0.07	0.16	0.20
Vernonia sellowii Less.	0.17	0.00	0.17
Bidens pilosa L.	0.09	0.23	0.00
Conyza primulifolia (Lam.) Cuatrec. & Lourteig	0.14	0.33	0.08
Chaptalia exscapa (Pers.) Baker	0.10	0.01	0.15
Eupatorium ascendens Sch. Bip. ex Baker	0.20	0.06	0.12
Hypochaeris chillensis (H.B.K.) Hieron	0.07	0.25	0.19
Solidago chilensis Meyen	0.14	0.75	0.01
Sommerfeltia spinulosa (Spreng.) Less	0.24	0.00	0.05
Soliva pterosperma (Juss.) Less.	0.03	0.22	0.25
Baccharis spicata (Lam.) Baill.	0.19	0.38	0.01
Vernonia brevifolia Less.	0.20	0.00	0.01
Lucilia acutifolia (Poir.) Cass.	0.16	0.00	0.04
Hypochaeris albiflora (O.K.) Azevêdo-Gonçalves & Matzenbacher	0.09	0.00	0.07
Pterocaulon angustifolium DC.	0.10	0.09	0.05

Pterocaulon rugosum (Vahl) Malme	0.07	0.11	0.05
Criscia stricta (Spreng.) Katinas	0.13	0.00	0.04
Vernonia megapotamica (Spreng.) Sch.Bip.	0.20	0.00	0.00
Senecio madagascariensis Poir.*	0.04	0.16	0.10
Calea uniflora Less.	0.12	0.00	0.09
Senecio leptolobus DC.	0.06	0.01	0.10
Conyza bonariensis (L.) Cronquist	0.07	0.05	0.05
Senecio heterotrichius DC.	0.03	0.12	0.08
Eupatorium subhastatum Hook. & Arn.	0.09	0.07	0.02
Panphalea commersonii Cass.	0.05	0.00	0.08
Baccharis coridifolia DC.	0.02	0.00	0.37
Chevreulia acuminata Less.	0.04	0.00	0.10
Heterotalamus alienus (Spreng.) Joch.Müll.	0.15	0.20	0.00
Achyrocline satureioides (Lam.) DC.	0.09	0.02	0.00
Porophyllum linifolium (L.) DC.	0.08	0.01	0.03
Stenachaenium campestre Baker	0.05	0.00	0.10
Chaptalia mandoni Burkart	0.05	0.00	0.07
Eclipta prostrata (L.) L.	0.01	0.02	0.23
Calea pinnatifida (R. Br.) Less.	0.04	0.15	0.00
Noticastrum diffusum (Pers.) Cabrera	0.05	0.02	0.00
Hypochaeris radicata L.*	0.01	0.12	0.06
Aster squamatus (Spreng.) Hieron.	0.01	0.02	0.05
Noticastrum gnaphalioides (Baker) Cuatrec.	0.07	0.00	0.01
Vernonia hipochaeris (DC.) H.Rob.	0.05	0.00	0.00
Calea cymosa Less.	0.06	0.00	0.01
Hysterionica filiformis (Spreng.) Cabrera	0.05	0.00	0.02
Gamochaeta filaginea (DC.) Cabrera	0.01	0.00	0.12
Stenachaenium megapotamicum (Spreng.) Baker	0.01	0.20	0.00
Eupatorium squarrulosum Hook. & Arn.	0.04	0.00	0.00
Pterocaulon alopecuroides (Lam.) DC.	0.02	0.00	0.03
Baccharis cultrata Baker	0.11	0.00	0.00
Micropsis spathulata (Pers.) Cabrera	0.01	0.02	0.07
Stevia sp.	0.04	0.00	0.01
Trichocline cisplatina E.Pasini & M.R.Ritter	0.10	0.00	0.04
Gamochaeta coarctata Willd.	0.01	0.04	0.03
Pterocaulon polystachyum DC.	0.00	0.02	0.07
Acmella bellidioides (Smith in Rees) R.K. Jansen	0.03	0.00	0.02
Chaptalia nutans (l.) polak	0.01	0.07	0.01
Baccharis patens Baker	0.05	0.00	0.01
Cirsium vulgare (Savi) Ten.*	0.03	0.05	0.01
Pluchea sagittalis (Lam.) Cabrera	0.00	0.09	0.00
Schlechtendalia luzulifolia Less.	0.08	0.00	0.00
Crepis capillaris (L.) Wallr.*	0.01	0.04	0.00
Vernonia nudiflora (Less.) H.Rob.	0.01	0.00	0.07
Baccharis articulata (Lam.) Pers.	0.02	0.00	0.03

Gamochaeta simplicicaulis (Willd. ex Spreng.) Cabrera	0.00	0.00	0.05
Baccharis tridentata Vahl	0.00	0.07	0.01
Picrosia longifolia D. Don	0.00	0.00	0.05
Orthopappus angustifolius (Sw.) Gleason	0.00	0.02	0.01
Mutisia coccinea A.St.-Hil.	0.01	0.07	0.00
Bidens pilosa L	0.01	0.09	0.00
Eupatorium tanacetifolium (Gillies ex Hook. & Arn.) D.J.N.Hind & Flann	0.02	0.00	0.00
Baccharis cognata DC.	0.02	0.00	0.00
Chaptalia sinuata (Less.) Baker	0.01	0.00	0.00
Gamochaeta falcata (Lam.) Cabrera	0.01	0.00	0.00
Heterothalamus alienus (Spreng.) O.Kuntze	0.01	0.00	0.01
Stevia lundiana DC.	0.01	0.00	0.01
Noticastrum decumbens (Baker) Cuatrec.	0.02	0.00	0.00
Eupatorium intermedium (DC.) R.M.King & H.Rob.	0.00	0.15	0.00
Mikania glomerata Spreng.	0.01	0.02	0.00
Micropsis dasycarpa (Griseb.) Beauverd	0.00	0.00	0.03
Viguiera nudicaulis Baker	0.01	0.00	0.00
Panphalea sp.	0.01	0.00	0.00
Hypochaeris megapotamica Cabrera	0.00	0.01	0.01
Gochnatia polymorpha (Less.) Cabrera	0.00	0.05	0.00
Baccharis cf. *linearifolia* (Lam.) Pers.	0.01	0.00	0.00
Holocheilus brasileiensis (L.) Cabrera	0.01	0.00	0.00
Hypochaeris brasiliensis (Less.) Benth. & Hook. f. ex Griseb.	0.00	0.00	0.01
Hypochaeris petiolaris (Hook. & Arn.) Griseb	0.01	0.00	0.00
Porophyllum ruderale (Jacq.) Cass.	0.00	0.00	0.00
Senecio bonariensis Hook. & Arn.	0.00	0.00	0.01
Soliva macrocephala Cabrera	0.00	0.00	0.01
Trichocline incana (Lam.) Cass.	0.00	0.00	0.00
Berberidaceae			
Berberis laurina Thunb.	0.01	0.05	0.00
Brassicaceae			
Lepidium bonariense L.	0.01	0.02	0.16
Raphanus raphanistrum L.*	0.00	0.10	0.00
Lepidium aletes Regel & Körn.	0.00	0.00	0.01
Bromeliaceae			
Dyckia leptostachya Baker	0.01	0.00	0.00
Cactaceae			
Gymnocalycium denudatum (Link & Otto) Pfeiff. ex Mittler	0.02	0.00	0.00
Frailea pygmaea (Speg.) Britton & Rose	0.00	0.00	0.00
Calyceraceae			
Acicarpha tribuloides Juss.	0.00	0.02	0.11
Campanulaceae			
Wahlenbergia linarioides (Lam.) A.DC.	0.08	0.00	0.10
Lobelia hederacea Cham.	0.00	0.00	0.06

Triodanis perfoliata (L.) Nieuwl.*	0.00	0.01	0.00
Caryophyllaceae			
Cerastium glomeratum Thuill.*	0.01	0.14	0.00
Paronychia communis Cambess.	0.01	0.05	0.00
Silene gallica L.*	0.00	0.00	0.01
Cerastium commersonianum Ser.	0.00	0.00	0.01
Cistaceae			
Helianthemum brasiliense (Lam.) Pers.	0.29	0.01	0.25
Commelinaceae			
Commelina erecta L.	0.01	0.01	0.01
Commelina diffusa Burm. f.	0.00	0.05	0.00
Tradescantia crassula Link & Otto	0.01	0.00	0.00
Convolvulaceae			
Dichondra sericea Sw.	0.80	0.86	1.31**
Evolvulus sericeus Sw.	0.97*	0.20	0.69*
Dichondra macrocalyx Meisn.	0.00	0.02	0.05
Cyperaceae			
Rhynchospora setigera (Kunth) Boeck.	0.33	0.05	0.22
Carex phalaroides Kunth	0.14	0.06	0.25
Abildgaardia ovata (L.) Vahl	0.13	0.00	0.23
Kyllinga odorata Vahl	0.05	0.67	0.21
Bulbostylis sphaerocephala (Boeck.) C.B. Clarke	0.16	0.00	0.08
Cyperus aggregatus (Willd.) Endl.	0.06	0.11	0.08
Rhynchospora barrosiana Guagl.	0.29	0.12	0.09
Bulbostylis capillaris (L.) Kunth ex C.B. Clarke	0.03	0.15	0.14
Cyperus reflexus Vahl	0.04	0.19	0.04
Rhynchospora tenuis Link	0.11	0.21	0.15
Kyllinga brevifolia Rottb.	0.05	0.06	0.03
Rhynchospora megapotamica (A. Spreng.) H. Pfeiff.	0.13	0.00	0.10
Eleocharis viridans Kük. ex Osten	0.00	0.06	0.39
Carex sororia Kunth	0.03	0.06	0.07
Fimbristylis complanata (Retz.) Link	0.02	0.02	0.10
Fimbristylis dichotoma (Retz.) Vahl	0.02	0.01	0.14
Kyllinga vaginata Lam.	0.00	0.01	0.22
Fimbristylis autumnalis (L.) Roem. & Schult.	0.03	0.02	0.03
Pycreus polystachyos (Rottb.) P.Beauv.	0.00	0.11	0.05
Scleria distans Poir.	0.03	0.06	0.01
Bulbostylis communis var. *scabrida* M.G. López & D.A. Simpson	0.01	0.00	0.10
Fimbristylis sp.	0.00	0.00	0.09
Cyperus rotundus L.*	0.00	0.15	0.00
Rhynchospora rugosa (Vahl) Gale	0.03	0.00	0.02
Bulbostylis juncoides (Vahl) Kük. ex Herter	0.01	0.00	0.00
Eleocharis maculosa (Vahl) Roem. & Schult.	0.00	0.00	0.05
Eleocharis flavescens (Poir.) Urb.	0.00	0.00	0.04
Carex longii Mack.	0.00	0.00	0.03

Eleocharis bonariensis Nees	0.00	0.02	0.00
Eleocharis minima Kunth	0.00	0.00	0.01
Bulbostylis consaguinea (Kunth) C.B.Clarke	0.00	0.00	0.00
Eleocharis sellowiana Kunth	0.00	0.00	0.01
Scleria balansae Maury ex Micheli	0.00	0.00	0.01
Droseraceae			
Drosera brevifolia Pursh.	0.00	0.00	0.01
Euphorbiaceae			
Tragia bahiensis Müll. Arg.	0.14	0.00	0.06
Euphorbia stenophylla Boiss.	0.05	0.01	0.00
Euphorbia selloi (Klotzsch & Garcke) Boiss.	0.02	0.01	0.02
Bernardia multicaulis Müll. Arg.	0.03	0.00	0.02
Croton gnaphalii Baill.	0.02	0.00	0.03
Euphorbia sp.	0.01	0.00	0.01
Croton parvifolius Müll.Arg.	0.02	0.00	0.00
Fabaceae			
Desmodium incanum DC.	1.03	1.12	1.58
Rhynchosia diversifolia Micheli	0.39	0.05	0.17
Stylosanthes montevidensis Vogel	0.24	0.00	0.22
Desmanthus tatuhyensis Hoehne	0.23	0.06	0.09
Galactia marginalis Benth.	0.22	0.00	0.21
Trifolium polymorphum Poir.	0.17	0.04	0.35
Macroptilium prostratum (Benth.) Urb.	0.23	0.04	0.12
Stylosanthes leiocarpa Vogel	0.25	0.00	0.24
Galactia gracillima Benth.	0.10	0.00	0.04
Rhynchosia senna Gillies ex Hook.	0.07	0.01	0.03
Zornia sericea Moric.	0.05	0.00	0.05
Ulex europaeus L.*	0.31	0.00	0.00
Arachis burkartii Handro	0.03	0.00	0.10
Lathyrus subulatus Lam.	0.02	0.05	0.00
Clitoria nana Benth.	0.02	0.00	0.01
Adesmia incana Vogel	0.02	0.00	0.04
Desmodium uncinatum (Jacq.) DC.	0.00	0.11	0.00
Zornia orbiculata Mohlenbr.	0.02	0.00	0.03
Lupinus bracteolaris Desr.	0.01	0.00	0.01
Desmodium adscendens (Sw.) DC.	0.01	0.02	0.03
Vachellia caven (Molina) Seigler & Ebinger	0.03	0.17	0.00
Chamaecrista repens (Vogel) H.S. Irwin & Barneby	0.01	0.00	0.01
Mimosa cruenta Benth.	0.04	0.00	0.00
Collaea stenophylla (Hook. & Arn.) Benth.	0.04	0.00	0.00
Lotus corniculatus L.*	0.00	0.17	0.00
Trifolium repens L.*	0.00	0.06	0.00
Mimosa pudica L.	0.04	0.00	0.00
Indigofera asperifólia Bong. ex Benth.	0.01	0.00	0.00
Mimosa schleidenii Herter	0.01	0.00	0.00

Poiretia tetraphylla (Poir.) Burkart	0.01	0.00	0.00
Adesmia securigerifolia Hert.	0.00	0.00	0.01
Desmodium barbatum (L.) Benth.	0.00	0.02	0.00
Mimosa rocae Lorentz & Niederl.	0.01	0.00	0.00
Rhynchosia corylifolia Mart. ex Benth.	0.01	0.00	0.00
Lathyrus cuniculifolia L.	0.00	0.00	0.00
Lathyrus linearifolius Vogel	0.00	0.00	0.00
Gentianaceae			
Zygostigma australe (Cham. & Schltdl.) Griseb.	0.02	0.00	0.00
Centaurium pulchellum (Sw.) Druce*	0.00	0.06	0.00
Hypericaceae			
Hypericum connatum Lam.	0.03	0.01	0.01
Hypericum polyanthemum Klotzsch ex Reichardt	0.01	0.00	0.00
Hypericum pirai Arechav.	0.00	0.00	0.01
Hypoxidaceae			
Hypoxis decumbens L.	0.30	0.75**	0.35
Iridaceae			
Sisyrinchium micranthum Cav.	0.16	0.90***	0.42
Herbertia lahue (Molina) Goldblatt	0.09	0.00	0.26
Sisyrinchium vaginatum Spreng.	0.19	0.02	0.08
Herbertia pulchella Sweet	0.15	0.04	0.10
Sisyrinchium sellowianum Klatt	0.15	0.04	0.10
Sisyrinchium scariosum I.M.Johnst.	0.05	0.00	0.19
Cypella herbertii Hook.	0.03	0.00	0.08
Sisyrinchium palmifolium L.	0.06	0.00	0.00
Sisyrinchium megapotamicum Malme	0.03	0.00	0.01
Onira unguiculata (Baker) Ravenna	0.02	0.01	0.00
Cypella falcata Ravenna	0.03	0.00	0.00
Cypella pussila (Link & Otto) Benth. & Hook.f. ex B.D.Jacks.	0.02	0.00	0.03
Kilissa brasiliensis (Baker) Ravenna	0.01	0.00	0.00
Juncaceae			
Juncus tenuis Willd.	0.12	0.43	0.31
Juncus capillaceus Lam.	0.10	0.05	0.44
Juncus microcephalus Kunth	0.31	0.05	0.01
Lamiaceae			
Scutellaria racemosa Pers.	0.02	0.04	0.10
Glechon spatulata Benth.	0.04	0.00	0.05
Hyptis sp.	0.07	0.00	0.00
Salvia procurrens Benth.	0.03	0.01	0.01
Hyptis mutabilis (Rich.) Briq.	0.01	0.28	0.00
Peltodon longipes Kunth ex Benth.	0.01	0.00	0.00
Linaceae			
Cliococca selaginoides (Lam.) C. M. Rogers & Mild	0.22	0.00	0.20
Linum erigeroides A.St.-Hil.	0.01	0.00	0.00
Loganiaceae			

Spigelia stenophylla Progel	0.00	0.00	0.01
Lythraceae			
Cuphea glutinosa Cham. & Schltdl.	0.21	0.16	0.28
Heimia myrtifolia Cham. & Schltd.	0.07	0.00	0.02
Cuphea calophylla Cham. & Schltdl.	0.01	0.00	0.01
Malpighiaceae			
Aspicarpa pulchella (Griseb.) O´Donell & Lourteig	0.24	0.00	0.12
Janusia guaranitica (A. St.-Hil.) A. Juss.	0.03	0.02	0.00
Galphimia australis Chodat	0.01	0.00	0.01
Malvaceae			
Krapovickasia flavescens (Cav.) Fryxell	0.26	0.00	0.23
Sida rhombifolia L.	0.15	0.53	0.05
Ayenia mansfeldiana (Herter) Herter & Cristóbal	0.25	0.00	0.22
Pavonia glechomoides A. St.-Hill.	0.03	0.00	0.01
Melochia chamaedrys var. *chamaedrys* A. St.-Hil.	0.03	0.00	0.01
Pavonia orientalis Krapov.	0.02	0.00	0.00
Abutilon terminale (Cav.) A.St.-Hil.	0.02	0.00	0.00
Wissadula glechomifolium (A. St.-Hil.) R.E. Fr.	0.02	0.00	0.00
Pavonia friesi Krapov.	0.00	0.04	0.00
Sida regnellii R.E. Fr.	0.00	0.01	0.01
Melastomataceae			
Tibouchina gracilis (Bonpl.) Cogn.	0.02	0.04	0.03
Miconia hyemalis A. St.-Hil. & Naudin	0.00	0.00	0.02
Moraceae			
Dorstenia brasiliensis Lam.	0.09	0.00	0.06
Myrtaceae			
Campomanesia aurea O.Berg	0.20	0.01	0.32
Psidium salutare var. *mucronatum* (Cambess.) Landrum	0.20	0.00	0.18
Psidium salutare var. *sericeum* (Cambess.) Landrum	0.11	0.00	0.05
Eugenia uniflora L.	0.00	0.04	0.00
Blepharocalyx salicifolius (Kunth) O.Berg	0.01	0.00	0.00
Eugenia uniflora L.	0.01	0.00	0.00
Onagraceae			
Oenothera indecora Cambess.	0.00	0.00	0.01
Ludwigia peploides (Kunth) P.H.Raven	0.02	0.02	0.00
Orchidaceae			
Brachystele camporum (Lindl.) Schltr.	0.03	0.00	0.02
Habenaria parviflora Lindl.	0.01	0.00	0.03
Orobanchaceae			
Agalinis communis (Cham. & Schltdl.) D'Arcy	0.02	0.09	0.28
Buchnera integrifolia Larrañaga	0.05	0.00	0.03
Buchnera longifolia Kunth	0.01	0.00	0.00
Oxalidaceae			
Oxalis eriocarpa DC.	0.33**	0.06	0.36**
Oxalis conorrhiza Jacq.	0.09	0.00	0.08

Oxalis lasiopetala Zuccarini	0.10	0.07	0.05
Oxalis sellowiana Zucc.	0.09	0.02	0.03
Oxalis bifrons Progel	0.05	0.06	0.01
Oxalis brasiliensis G. Lodd.	0.02	0.16	0.01
Oxalis bipartida A. St.-Hil.	0.01	0.14	0.01
Oxalis corymbosa DC.	0.02	0.00	0.00
Oxalis floribunda Lehm.	0.01	0.05	0.01
Oxalis articulata Savigny	0.02	0.05	0.01
Oxalis perdicaria (Molina) Bertero	0.02	0.00	0.01
Oxalis teneri (Molina) Bertero	0.00	0.00	0.01
Oxalis myriophylla A. St.-Hil.	0.01	0.00	0.00
Passifloraceae			
Turnera sidoides L.	0.09	0.00	0.03
Piriqueta suborbicularis (A. St.-Hil. & Naudin) Arbo	0.03	0.01	0.01
Passiflora caerulea L.	0.02	0.00	0.00
Passiflora misera Kunth	0.01	0.00	0.00
Plantaginaceae			
Plantago tomentosa Lam.	0.14	0.43	0.34
Mecardonia tenella (Cham. & Schltdl.) Pennell	0.01	0.05	0.16
Scoparia montevidensis (Spreng.) R.E. Fr.	0.02	0.00	0.10
Plantago brasiliensis Sims	0.08	0.01	0.02
Scoparia ericacea Cham. & Schltdl.	0.03	0.00	0.05
Gratiola peruviana L.	0.00	0.00	0.08
Veronica arvensis L.*	0.00	0.05	0.00
Linaria canadensis (L.) Dum. Cours.*	0.00	0.00	0.02
Mecardonia procumbens (Mill.) Small	0.01	0.00	0.02
Angelonia integerrima Spreng.	0.01	0.00	0.00
Stemodia verticillata (Mill.) Hassl.	0.00	0.00	0.01
Stemodia palustris A. St.-Hil.	0.00	0.00	0.01
Poaceae			
Paspalum notatum Alain ex Flüggé	11.35	2.94	24.75***
Axonopus affinis (Raddi) Kuhlm.	6.29	5.90	11.04
Piptochaetium montevidense (Spreng.) Parodi	3.19	3.46	3.84
Axonopus suffultus (J.C.Mikan ex Trin.) Parodi	4.03*	0.00	1.25
Cynodon dactylon (L.) Pers.*	1.35	9.95***	0.31
Paspalum plicatulum Michx.	1.95**	0.51	1.15
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	1.40	0.90	1.02
Saccharum angustifolium (Nees) Trin.	1.69	2.47	0.85
Coelorachis selloana (Hack.) Henr.	1.15*	0.23	1.50*
Briza subaristata Lam.	0.85	0.47	0.74
Danthonia cirrata Hack. & Arechav.	1.30**	0.00	0.56
Setaria parviflora (Poir.) Kerguélen	0.62	0.81	0.79
Aristida venustula Arechav.	1.05*	0.00	1.18*
Lolium multiflorum Lam.*	1.05	1.94	1.31
Piptochaetium stipoides (Trin. & Rupr.) Hack.	0.71**	0.07	0.44**

Aristida laevis (Nees) Kunth	1.15	0.47	0.62
Andropogon lateralis Nees	0.85	0.40	1.20
Stenchismia hians (Elliott) Nash	0.45	0.22	0.78**
Schizachyrium tenerum Nees	1.41	0.19	0.22
Eragrostis neesii Trin.	0.25	0.27	1.18**
Andropogon ternatus (Spreng.) Nees	0.56	0.32	0.41
Eragrostis plana Nees*	0.96	3.22	0.23
Stipa setigera J. Presl.	0.43	0.20	0.21
Piptochaetium lasianthum Griseb.	0.48	0.05	0.20
Eragrostis lugens Nees	0.33	0.00	0.34
Andropogon selloanus (Hack.) Hack.	0.21	0.02	0.40
Paspalum dilatatum Poir.	0.34	0.26	0.29
Aristida murina Cav.	0.31	0.00	0.27
Sporobolus indicus (L.) R.Br.	0.11	0.67	0.38
Schizachyrium microstachyum (Desv. ex Ham.) Roseng.	0.39	0.11	0.05
Bothriochloa laguroides (DC.) Herter	0.15	0.00	0.42
Eragrostis bahiensis Schrad. ex Schult.	0.17	0.12	0.08
Eragrostis airoides Nees.	0.29	0.07	0.05
Melica hialina Döll	0.21	0.00	0.12
Agrostis montevidensis Spreng. ex Nees	0.14	0.23	0.12
Leptocoryphium lanatum (Kunth) Nees	0.28	0.02	0.05
Vulpia bromoides (L.) Gray*	0.04	0.44	0.37
Piptochaetium ruprechtianum Desv.	0.14	0.07	0.15
Briza poaemorpha (J.Presl) Henrard	0.14	0.02	0.09
Erianthecium bulbosum Parodi	0.31	0.00	0.08
Trachypogon montufari (L. f.) Kuntze	0.29	0.00	0.16
Briza minor L.*	0.05	0.11	0.07
Paspalum polyphyllum Nees ex Trin.	0.23	0.00	0.03
Stipa paposa Nees	0.20	0.00	0.18
Aristida filifolia (Arechav.) Herter	0.19	0.74	0.16
Aristida circinalis Lindm.	0.17	0.00	0.16
Poa lanigera Nees	0.15	0.00	0.07
Setaria vaginata Spreng.	0.09	0.26	0.04
Agenium villosum (Nees) Pilg.	0.21	0.00	0.08
Briza lamarckiana Nees	0.10	0.00	0.03
Schizachyrium imberbe (Hack.) A. Camus	0.24	0.00	0.09
Paspalum pumilum Nees	0.03	0.20	0.60
Melica brasiliana Ard.	0.06	0.04	0.16
Calamagrostis viridiflavescens (Poir.) Steud.	0.07	0.06	0.03
Panicum bergii var. *pilosissimum* Zuloaga	0.11	0.00	0.02
Paspalum urvillei Steud.	0.13	0.20	0.05
Eragrostis sp.	0.42	0.00	0.00
Danthonia secundiflora J.Presl	0.04	0.00	0.01
Melica rigida Cav.	0.08	0.02	0.05
Paspalum lepton Schult.	0.06	0.00	0.30

Eleusine tristachya (Lam.) Lam.	0.02	0.25	0.05
Paspalum corcovadense Raddi	0.00	0.00	0.72
Stipa megapotamia Spreng. ex Trin.	0.09	0.02	0.02
Bromus auleticos Trin. ex Nees	0.06	0.00	0.00
Eragrostis cataclasta Nicora	0.08	0.00	0.10
Stipa nutans Hack.	0.05	0.01	0.03
Eragrostis polytricha Nees	0.03	0.02	0.02
Paspalum umbrosum Trin.	0.02	0.20	0.00
Bromus catharticus Vahl	0.10	0.28	0.00
Andropogon macrothrix (Spreng.) Nees	0.03	0.00	0.03
Stipa charruana Arechav.	0.06	0.00	0.05
Eustachys uliginosa (Hack.) Herter	0.03	0.07	0.00
Stipa juergensii Hack.	0.05	0.00	0.02
Calamagrostis alba (J. Presl) Steud.	0.03	0.00	0.07
Steinchisma decipiens (Nees ex Trin.) W.V. Br.	0.00	0.00	0.12
Melica macra Nees	0.06	0.00	0.01
Axonopus compressus (Sw.) P. Beauv.	0.14	0.00	0.00
Sorghastrum pellitum (Hack.) Parodi	0.11	0.00	0.00
Schizachyrium spicatum (Spreng.) Herter	0.03	0.00	0.01
Vulpia australis (Nees ex Steud.) C.H. Blom	0.06	0.00	0.00
Briza uniolae (Nees) Steud.	0.02	0.02	0.00
Paspalum sp.	0.03	0.00	0.00
Bouteloua megapotamica (Spreng) Kuntze	0.02	0.00	0.00
Eustachys retusa (Lag.) Kunth	0.01	0.05	0.00
Danthonia montana Döll	0.03	0.00	0.00
Briza rufa (J. Presl) Steud.	0.01	0.02	0.01
Tripogon spicatus (Nees) Ekman	0.02	0.00	0.00
Aristida spegazini Arechav.	0.01	0.00	0.06
Poaceae 1	0.00	0.00	0.01
Bromus brachyanthera Döll	0.03	0.00	0.00
Ischaemum minus J. Presl	0.03	0.00	0.00
Melica eremophila Torres	0.01	0.00	0.01
Trachypogon spicatus (L.f.) Kuntze	0.00	0.00	0.03
Briza calotheca (Trin.) Hack.	0.01	0.00	0.00
Stipa melanosperma (J.Presl) Barkworth	0.01	0.00	0.00
Digitaria ciliaris (Retz.) Koeler	0.00	0.00	0.01
Axonopus siccus (Nees) Kuhlm.	0.03	0.00	0.00
Holcus lanatus L.*	0.00	0.03	0.00
Avena strigosa Schreb.*	0.00	0.05	0.00
Poaceae 2	0.00	0.00	0.01
Paspalum paniculatum L.	0.00	0.00	0.01
Anthoxanthum odoratum L.*	0.01	0.00	0.00
Aira caryophyllea L.*	0.00	0.00	0.01
Agrostis sp.	0.00	0.00	0.00
Aira caryophyllea L.	0.00	0.01	0.00

Briza scabra (Nees ex Steud.) Ekman	0.00	0.00	0.00
Eustachys brevipila (Roseng. & Izag.) Caro & E.A.Sánchez	0.00	0.00	0.01
Panicum gouinii E. Fourn.	0.01	0.00	0.00
Paspalum paucifolium Swallen	0.00	0.01	0.00
Kikuyuochloa clandestina (Hochst. ex Chiov.) H. Scholz*	0.01	0.00	0.00
Polygalaceae			
Polygala australis A. W. Benn.	0.06	0.00	0.04
Polygala brasiliensis L.	0.00	0.02	0.09
Polygala bonariensis Grond.	0.01	0.02	0.07
Polygala adenophylla A. St.-Hil. & Moq.	0.03	0.00	0.01
Polygala molluginifolia A. St.-Hil.	0.03	0.01	0.01
Monnina oblongifolia Arechav.	0.02	0.00	0.01
Polygala riograndensis Lüdtke & Miotto	0.01	0.00	0.02
Polygala pulchella A. St.-Hil. & Moq.	0.00	0.00	0.02
Polygonaceae			
Rumex acetosella L.*	0.01	0.16	0.00
Primulaceae			
Anagallis arvensis L.*	0.02	0.11	0.02
Anagallis minima (L.) E.H.L.Krause*	0.00	0.00	0.03
Pteridophita			
Pteridophita	0.04	0.00	0.00
Rhamnaceae			
Discaria americana Gillies & Hook.	0.08	0.00	0.00
Scutia buxifolia Reissek	0.01	0.05	0.00
Rubiaceae			
Richardia humistrata (Cham. et Schlecht.) Steud.	0.43	0.58	1.18***
Galium richardianum (Gillies ex Hook. & Arn.) Endl. ex Walp.	0.26	0.16	0.29
Galianthe fastigiata Griseb.	0.43	0.01	0.08
Borreria capitata (Ruiz & Pav.) DC.	0.15	0.01	0.14
Borreria verticillata (L.) G.Mey.	0.09	0.11	0.05
Galium hirtum Lam.	0.06	0.11	0.05
Borreria eryngioides Cham. & Schltdl.	0.09	0.00	0.13
Richardia brasiliensis Gomes	0.08	0.15	0.04
Richardia stellaris (Cham. & Schltdl.) Steud.	0.04	0.00	0.02
Galianthe centranthoides (Cham. & Schltdl.) E.L. Cabral	0.06	0.00	0.02
Borreria dasycephala (Cham. & Schltdl.) Bacigalupo & E.L.Cabral	0.04	0.04	0.03
Galium hypocarpium (L.) Endl. ex Griseb.	0.01	0.05	0.00
Galium uruguayense Bacigalupo	0.01	0.00	0.01
Diodella radula (Willd. ex Roem. & Schult.) Delprete	0.00	0.01	0.01
Oldenlandia salzmannii (DC.) Benth. & Hook. f. ex B.D. Jacks.	0.00	0.02	0.03
Coococypselum lanceolatum (Ruiz & Pav.) Pers.	0.00	0.02	0.00
Salicaceae			
Xylosma tweediana (Clos) Eichler	0.08	0.00	0.00
Sapindaceae			
Dodonaea viscosa (L.) Jacq.	0.16	0.01	0.00

Allophylus edulis (A.St.-Hil., A.Juss. & Cambess.) Radlk.	0.00	0.01	0.00
Selaginellaceae			
Selaginella sp.	0.00	0.00	0.00
Smilacaceae			
Smilax campestris Griseb.	0.04	0.02	0.00
Solanaceae			
Neirembergia riograndense Hunz. & A.A. Cocucci	0.02	0.00	0.08
Solanum reflexum Schrank	0.03	0.14	0.00
Calibrachoa humilis (R.E.Fr.) Stehmann & Semir	0.04	0.00	0.04
Bouchetia anomala (Miers) Britton & Rusby	0.01	0.00	0.04
Solanum sisymbrifolium Lam.	0.03	0.09	0.01
Solanaceae 1	0.01	0.07	0.00
Nierembergia sp.	0.00	0.00	0.01
Solanum americanum Mill.	0.00	0.42	0.20
Petunia linearis Hook	0.00	0.04	0.00
Petunia axillaris (Lam.) Britton et al.	0.00	0.02	0.00
Petunia integrifolia (Hook.) Schinz & Thell.	0.00	0.00	0.00
Thymelaeaceae			
Daphnopsis racemosa Griseb.	0.08	0.42	0.20
Gerardia arvensis (L.) Coss. & Germ.	0.03	0.09	0.00
Verbenaceae			
Glandularia selloi (Spreng.) Tronc.	0.18	0.53	0.26
Verbena montevidensis Spreng.	0.01	0.33	0.06
Glandularia marrubioides (Cham.) Tronc.	0.11	0.00	0.04
Glandularia thymoides (Cham.) N. O' Leary	0.01	0.00	0.01
Lippia hieraciifolia Cham.	0.06	0.00	0.04
Verbena bonariensis L.	0.02	0.05	0.01
Lantana montevidensis (Spreng.) Briq.	0.12	0.00	0.00
Aloysia chamaedryfolia Cham.	0.06	0.01	0.00
Glandularia peruviana (L.) Small	0.02	0.00	0.00
Verbena rigida Spreng.	0.01	0.02	0.00
Lippia romboi Moldenke	0.01	0.00	0.00
Phyla canescens (Kunth) Greene*	0.00	0.05	0.00
Verbena intermedia Gillies & Hook. ex Hook.	0.00	0.00	0.00
Violaceae			
Hybanthus bicolor (Saint-Hilaire) Baill.	0.01	0.05	0.00
Vitaceae			
Cissus striata Ruiz & Pav.	0.00	0.05	0.00
Cissus palmata Poir.	0.02	0.00	0.00
Unidentified species			
Plant 1	0.01	0.00	0.00
Plant 2	0.01	0.00	0.00
Plant 3	0.01	0.00	0.00
Plant 4	0.00	0.00	0.00
Plant 5	0.00	0.01	0.00

Chapter 3

The effect of environmental features in determining patterns in the presence of exotic plants, shrubs and drivers for alpha and beta diversity in metacommunitys of the subtropical grasslands.

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Short title: The effect of environmental features in subtropical grasslands metacommunity.

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Introduction

The metacommunity concept aims at identifying the factors behind changes in composition and richness of communities in space, by explicitly considering how diversity of plants among localities might interact with local environmental conditions to determine variation in community structure among localities (Leibold 2011). The metacommunity perspective explicitly integrates ecological processes that work at different spatial scales, and thus goes beyond classical approaches in Ecology that focus either on local factors, factors working on ecological gradient, or on population- and community-level processes such as dispersal. Empirical tests of the concept in grasslands are still few (Gibson 2009).

The definition of a metacommunity as a "*set of local communities that are linked by dispersal of multiple potentially interacting species*" (Leibold et al. 2004) reflects the view that community structure can be understood in the light of regional dispersal processes. There are, however, different scenarios of how dispersal, local site conditions, and the species' ecological characteristics might actually regulate community patterns. Leibold et al. (2004) and Leibold (2011) formalize four classes of metacommunity models, which differ in the importance they ascribe to dispersal processes, variation in local site factors over a larger region, and species' characteristics as drivers of community assembly Importantly, previous investigations of alpha and beta diversity in fragmented landscapes have shown that diversity patterns reflect past rather than present habitat connectivity (Lindborg & Eriksson 2004; Helm et al. 2006; Purschke et al. 2012). This scenario can thus be considered as a special case of dispersal assembly in which variation in local community structure is explained by past dispersal processes (Fukami 2015) and beta diversity thus related to variation in historical landscape configuration. Mechanisms leading to nestedness and turnover are similar to the dispersal-driven assembly scenario, with the exception that the dispersal processes happened in the past and are no longer occurring in the contemporary landscape.

Even under scenarios that emphasize the role of dispersal, differences in local community structure are determined by interspecific differences in resource requirements and physiological tolerance limits that confine species to certain sections of environmental features and gradients, leading to an important role of environmental variation for explication of beta diversity (Chase & Myers 2011). In fragmented landscapes, environmental sorting might be an important driver of community structure because habitat patches often differ in soil properties due to contrasting land-use histories (Verheyen et al. 1999; Freschet et al. 2013). In the environmental sorting scenario, environmental variation can produce nestedness when soil gradients reach into marginal habitats where only a subset of species can survive. Alternatively, high resource availability may lead to competitive displacement of many species by a subset of few competitive species (Harpole & Tilman 2007). It can also produce spatial turnover when different species replace each other along environmental gradients. When environmental sorting is important, nestedness might also result from variation in soil spatial heterogeneity because of the contrasting numbers of niches provided (Tilman 1982; Adler et al. 2013).

Here, we aim at identifying the direct and indirect effects of environmental features on grassland plant community composition. Specifically, we tested the variation in alpha and better diversity of grassland plant community as well as differences in presence of shrub and exotic species, using 58 grassland sites in the South Brazilian grassland region. As land use change, specifically afforestation by exotic trees, has been strong in the region, we expected that environmental features explained most of the total variation in community composition. Specifically, we tested the following hypotheses: 1) Grasslands situated in less fragmented landscapes show high alpha and beta diversity, and differ in species composition from those of fragmented landscapes with show more shrubs and exotic species; 2) Physical features of the environment, such as soil characteristics (fertility, depth, texture) and topography are drivers that influence changes in structure and composition of grassland plant ; 3) Climatic differences in the region also influence the presence of shrubs, with more humid (more subtropical regions) showing a higher proportion of shrubs in grasslands, which in turn influences alpha and beta diversity negatively.

Materials and methods

Study region

Our study region comprised 58 sites in the Brazilian Pampa Biome, in the Serra do Sudeste mountain range in the extreme south of Brazil, comprising the area between the municipalities of Bagé, Jaguarão and Pelotas (Fig. 1). The region is a conservation priority area in the Pampa Biome by the Brazilian government due to high levels of endemism among herbaceous plant species (MMA, 2000). Geologically the oldest region of southern Brazil, it consists of a mosaic of geological formations with dominance of granitic and magmatic formations. Climate is temperate, with cold winters and hot summer without rainy season, average temperature of the coldest month above 11.3° C, and no dry season (Cfa according to the Koppen-Geigen classification; Alvares et al. 2013). The topography is slightly undulated to strongly accentuated (average altitude 30 to 430 m a. s.) and soils are poor in nutrients, ranging from deep to shallow soils, depending on relief features (Streck et al., 2008). The region is composed of forest-grassland mosaics while forests occur mainly along river valleys, the predominant vegetation is dry grasslands composed of grasses and herbs, with the presence of many shrubs and subshrubs.

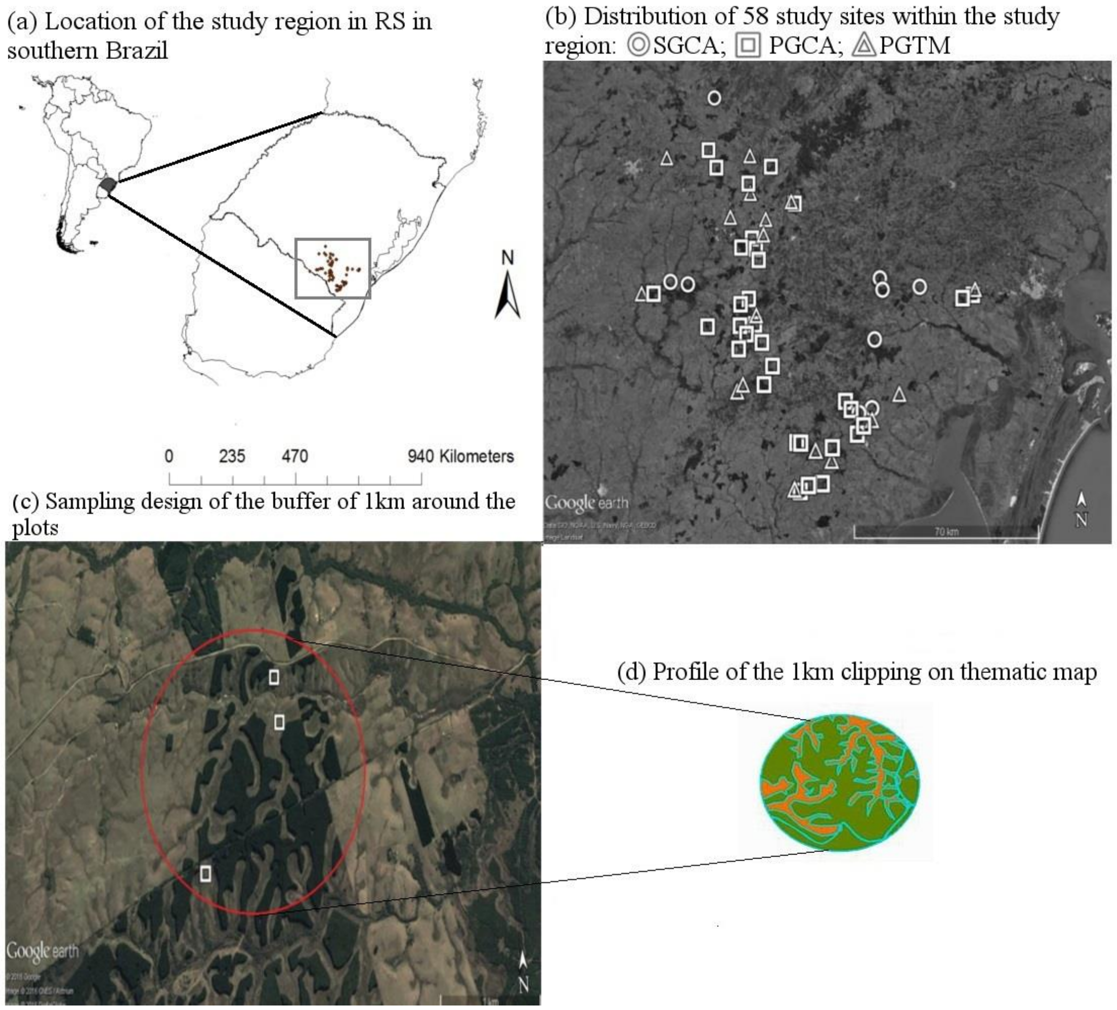


Fig. 1 (a) Location of the study region in the grasslands of Rio Grande do Sul (RS), southern Brazil; (b) distribution of 58 study sites throughout the study region (background map©Google Earth 2015): ▣ PGCA = primary grasslands in conservation areas; ◎ SGCA = secondary grassland in conservation areas; △ PGTM = primary grassland subjected to the traditionally management; (c) sampling design of the buffer of 1km around the 25 m^2 study sites (plots); and (d) Profile of 1km clipping on thematic map, showing the variations on landscape elements.

Sampling design and vegetation data

The study was conducted at a total of fifty eight sites, each consisting of three distinct types of grasslands with contrasting land use histories and management intensities: 1) primary grasslands in conservation areas (PGCA) without formal management and long history of livestock, located around the eucalyptus plantations; 2) secondary grassland in conservation areas (SGCA), recovering from conversion to arable land with grazing at variable stocking rates, located around the eucalyptus plantations; 3) primary grassland subjected to the traditionally management (PGTM) of the region (extensive livestock: cattle average 0.5-1 animals per hectare). The study was conducted in the spring and summer of the years 2013 and 2014, the eucalypt plantations has been established 7 - 8 years (2006) before our sampling, and tree height varied from 8 to 12 m.

Within the three land-use types 58 sites were selected based on a stratified design (Fig. 1). This design ensured that sampling sites of all land-use types were distributed as randomly on the treatments over the entire study region using as base images of google earth. Criteria for the inclusion of a site in the study are the distance of the 30 m to native forest, eucalyptus plantations, roads and other site. The all sites were located in predominantly dry grasslands

At each site, we established three plots of 25 m^2 per area, allocated randomly In each plot, we randomly selected three plots of 1m^2 and identified all vascular plant species and estimated their cover according to the Londo (1976) scale. Additionally, we recorded vegetation height (measured at 5 points), percentage of plant litter, manure and exposed soil. Vegetation parameters were calculated according to Muller-Dombois & Ellenberg (1974): relative cover (RC), relative frequency (RF), and importance value index (IVI). In the 25 m^2 plots, we recorded identity and height of all shrubs, sub-shrubs and trees. Species were classified regarding their origin (native/exotic; Rolim et al. 2014) and degree of threat of species was checked in the current Red List for the state (Rio Grande do Sul, 2014).

Species and functional diversity

We measure grassland species diversity within and between sample units through Whittaker's components of diversity (Whittaker, 1972). We defined alpha diversity as the local diversity within sample and beta diversity as the variation in community composition among sample units in the study region, i.e., the variation in composition among the pastures constitute our metacommunity. The variable alfa diversity was composed by the effective number of species (Jost et al., 2011). The variable beta diversity was represented by the first axes (r^2= 31.3) of a principal coordinates analysis (PCoA) of vegetation data based on the Chord distance (standardized Euclidean) matrix. The chord distance is a measure of dissimilarity evaluating the values from the Euclidean distance between two sample units (MacCune and Grace, 2002).

Variable exotic plants and shrubs were determined from the average vegetation cover of exotic species (Rolim, 2014) and shrub species. In our sample were recorded 29 exotic species, of which 5 are invasive species. We define as shrub, woody or herbaceous plants with potential to reach more than 1m in height. In our sampling data, 61 species with these characteristics were registered.

Environmental descriptors

Environmental features were grouped by nine blocks of variables: climate, landscape, relief, soil type, fertility, drainage, depth, stoniness and texture. Each block of environmental predictors represents a latent variable (LV) in our path modeling framework. We consider the LV as the variable group observed, containing information which reflect aspects of their latent variable (Grace, 2006; Grace et al., 2010). In our case, the LV consist of representative values of the nature of the direct and indirect effects on the studied metacommunity. For climate, we selected the folloing variables of Worldclim (global climate layers): Annual Mean Temperature, Mean Diurnal Range, Isothermality, Temperature Seasonality, Max Temperature of Warmest Month, Min Temperature of Coldest Month, Annual Precipitation, Precipitation Seasonality (Coefficient of Variation). Latent landscape was built from the Project PROBIO (Plant Cover of the Pampa Biome) shape (UFRGS-IB-Centro de Ecologia 2016), consindering: dry grassland, afforestation, grassland with forest and rocky outcrops, native forests, agriculture, degraded grassland, mixed vegetation, water and roads. Soil data were collected from thematic map with adaptations of Brazilian soil map (Cunha, 2006; Flores, 2009), using the following variables: texture, classified by the percentage of clay, sand and organic matter; effective depth, classified as very deep (> 200 cm), deep (100-200 cm), half shallow (50 - 100 cm), shallow (<50 cm), very shallow (<25 cm); relief was classified according to the steepness of the terrain, such as flat (0-3%), soft wavy (3-8%), wavy (8-20%), strong corrugated (20-45%), mountainous (45-75%), cliff (> 75%); drainage refers to the amount and speed with which the water received by the soil infiltrates and flows thus created were the following classes: heavily and excessively drained, sharply drained, well-drained, moderately drain, imperfectly drained, poorly drained; fertility was classified as the base saturation (V%), determining the following variables: high fertility, medium and low; the stony refers to the portion (%) of rocky outcrops ("boulders"), classified as: absent (0 to 0.1), low (0.1 to 0.3), moderate (3 to 15), abundant (greater than 15). We use the environmental characteristics to evaluate the effect of the variables in the local grassland metacommunity.

Description of the analysis

Principal Components Analysis (PCA)

In order to reduce dimensionality, the environmental variables were submitted to Principal Component Analysis (PCA), with different PCAs for each set of variables. Before running the analysis the data were transformed into "normal scores" to give equal weights and reduce the outliers. The first two principal components (PC) presented greater potential for explanation of the environmental variation (Table 1), therefore the scores of axis 1 and axis 2 were used as explanatory variables of the environmental set.

Table 1 - Pearson correlation of environmental variables with principal component (PC) scores of grasslands in fifty eight landscapes with contrasting in conservation state in southern Brazil. Percentage values below PCs are their explained variance:

Clime	PC1 (38%)	PC2 (28%)
Annual Mean Temperature	0.51	0.02
Mean Diurnal Range	0.01	0.42
Isothermality	-0.17	0.57
Temperature Seasonality	0.21	-0.42
Max Temperature of Warmest Month	0.57	0.1
Min Temperature of Coldest Month	0.38	0.26
Annual Precipitation	-0.45	-0.1
Precipitation Seasonality	0.05	-0.49

Landscape	PC1 (27%)	PC2 (20%)
Grassland	0.32	-0.6
Afforestation	-0.09	0.58
Forest-grassland mosaic	0.46	-0.15
Forest	-0.47	0.37
Crop land	-0.33	0.19
Grassland degraded	-0.01	0.48
Mixed vegetation	-0.04	-0.31
Water	0.05	0.11
Roads	-0.3	0.14

Soil class	PC1 (45%)	PC2 (28%)
Argissolo	0.55	-0.41
Chernossolo	0.49	0.05
Luvissolo	-0.07	-0.53
Neossolo	-0.29	0.38
Planossolo	0.05	0.37
Gleissolo	0.5	0.22
Vertissolo	0.5	0.29

Soil drainage	PC1 (47%)	PC2 (21%)
Markedly drained	-0.59	-0.13
Well drained	0.62	-0.43
Excessively drained	-0.33	-0.02
Heavily drained	-0.34	-0.05
Imperfectly drained	0.11	0.71
Poorly drained	0.16	0.53
Moderately drained	0.07	-0.02

Soil fertility	PC1 (59%)	PC2 (40%)
High fertility	-0.19	0.73
Low fertility	0.89	-0.16
Average fertility	-0.66	-0.42

Depth of soil	PC1 (54%)	PC2 (45%)
Little profound	0.76	-0.16
Deep	0.82	-0.26
Shallow	-0.59	0.56

Boulders	PC1 (43%)	PC2 (34%)
Abundant	-0.54	0.57
Absent	0.69	-0.28
Moderate	0.07	0.46
Few	0.61	-0.23

Relief	PC1 (60%)	PC2 (27%)
Strong wavy	-0.52	0.63
Wavy	0.75	0.0021
Plan	-0.31	-0.55
Soft wavy	-0.27	-0.55

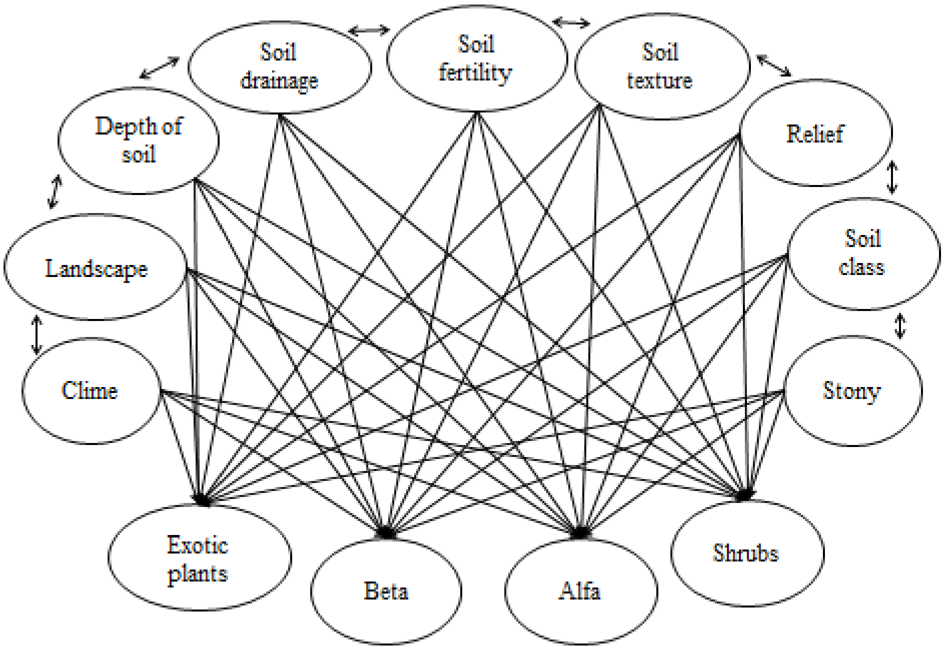
Soil texture	PC1 (94%)	PC2 (6%)
Sandy	-0.34	0.91
Clayey	-0.64	-0.4
Medium texture	0.69	0.08

Path analysis

We used Wright's path analysis (Wright 1921) in order to identify the direct and indirect effects of environmental features on exotic species, abundance of shrubs, alfa and beta diversity of grasslands in the Serra do Sudeste. In this approach, the correlation between predictor (x) and response (y) is partitioned as the sum of two types of effects: the direct effect of x on y (single path) and the indirect effect of x on y through one or more predictor variables (compound path) (McCune and Grace 2002). Thus, the total effect is the sum of all direct and indirect effects of one variable on another. For instance, the partitioning of the correlations between two predictor variables (x_1, x_2) and one response variable (y_1) involves the direct effects estimates of x_1 and x_2 on y_1 and indirect effects of x_1 on y_1 through x_2 and x_2 on y_1 through x_1 (Wright 1934). When x_1 and y_1 are only connected through a single path, the path coefficient for this relationship is equivalent to the bivariate regression coefficient (Grace 2006). On the other hand, when x_1 and y_1 are connected through x_2, the path coefficient corresponds to the partial regression coefficient (Grace 2006). According to Shipley (2000), the partial regression coefficient is a function of the partial correlation coefficient which measures the degree of linear association between two variables after to remove ('partialling out') the effect of one or more variables.

We used the environmental variables as LV (Figure 1), in order to determine the direct and indirect effects in the grasslands. In addition, we tested the environmental variables individually, forming a single set of variables (model 1), this matrix was decomposed into 5 other models determined from the values of correlation between variables, excluding variables with more than three correlations above 70%.

Figure 1 - Conceptual structural model illustrating predictive relationships among predictor and response latent variables (straight arrows) and associative (correlational) relationships among latent predictor variables (small arrows).



Results

Spatial and biogeographical components of species distribution

We sampled a total of 518 species in the 58 grasslands located in the Serra do Sudeste region. The sites were initially separated into three types of grasslands: PGCA with 445 species; SGCA with 238 species; PGTM with 345 species. Differences in structure and composition among these three types are discussed in Torchelsen et al. (in preparation/Chapter 2, this thesis).

Drivers of alpha, beta diversity, exotic species and abundance of shrubs

Overall variation in community composition among natural and semi-natural grasslands resulted mainly from climate, soil and landscape turnover, with 27 significant models (p>0.05; Table 2). After exclusion of variables with more than three variables with high correlation (<70%), there remained 14 LV, as soil texture (texture 1 and 2), relief (relief 2) and climate (climate 2) were removed.

The contrast with more significant variables was driven by environmental factors in the landscape, with turnover between the presence of primary grasslands and transformed landscapes, with direct and indirect effects in the composition of species. A higher proportion of natural ecosystems in LV landscape 1 promotes higher values of alpha and beta diversity, in contrast the effect is negative for the cover of exotic and abundance shrubs. In LV landscape 2, the transformed ecosystems produced positive effects on the abundance of shrubs and the cover of exotic species, in contrast the effect was negative for alpha and beta diversity.

Factors related to environmental filtering also determined structure and composition. The positive values for alpha and beta diversity were determined by direct and indirect effects of the latent variables of climate 1, soil fertility 1, stony 2 and soil class 1 and 2. In contrast, positive values for exotic species and abundance of shrubs were determined by soil drainage 2, depth of soil 2, soil fertility 2.

Table 2 - Direct and total effects of the environmental latent variables for the path modeling. Direct effects are given by the standardized path coefficients and the total effects as the sum of both the direct and indirect effects. Only values of significant variables (P> 0.05) are shown.

LV	Way	Alpha	Beta	Exotic cover	Abundance shrubs
Landscape					
Landscape 1	Direct	0.09	0.42	-0.18	-0.46
r total		0.27	0.45	-0.23	-0.47
Landscape 2	Direct	-0.15	-0.24	0.1	
r total		-0.32	-0.28	0.22	

Climate					
Climate 1	Direct	0.15			
r total		0.29			
Soil drainage					
Soil drainage 2	Direct	-0.01		0.34	
r total		-0.33		0.27	
Soil fertility					
Soil fertility 1	Direct	0.13	0.08		
r total		0.26	0.24		
Soil fertility 2	Direct			0.05	
r total				0.24	
Depth of soil					
Depth of soil 1	Direct	-0.34			
r total		-0.38			
Depth of soil 2	Direct	0.02	0.02	0.19	-0.02
r total		-0.32	-0.31	0.34	0.28
Stony					
Stony 2	Direct	0.37	0.1	0.1	
r total		0.43	0.24	-0.24	
Relief					
Relief 1	Direct				-0.28
r total					-0.23
Soil class					
Stony 1	Direct	0.25			-0.21
r total		0.27			-0.25
Stony 2	Direct	0.11		-0.52	-0.38
r total		0.26		-0.4	-0.22

To determine how the entire set of specific variables influenced species composition in our metacommunity, we assemble the matrix with 48 environmental variables, we excluded the variables with more than three variables with high correlation (<70%), reaching a total of 19 specific variables. We consider all the variables as part of the functioning of the ecosystem under study and influence directly and indirectly the composition of species in the grasslands (Table 3).

Table 3 - Direct and total effects of the specific environmental variables for the path modeling. Direct effects are given by the standardized path coefficients and the total effects as the sum of both the direct and indirect effects. They were only included the values of the significant variables (P> 0.05).

Specific variables	Way	Alpha	Beta	Exotic cover	Abundance shrubs
Landscape					
Grassland	Direct	0.21	0.15	-0.2	-0.05
r total		0.37	0.51	-0.29	-0.4
Afforestation	Direct		-0.24		0.42
r total			-0.43		0.48
Agriculture	Direct	-0.13	-0.26		
r total		-0.35	-0.28		
Degraded grassland	Direct	0.19	-0.15		
r total		-0.27	-0.22		
Roads	Direct			0.17	
r total				0.24	
Climate					
Annual Mean Temperature	Direct	-0.21	-0.19	0.46	0.33
r total		-0.38	-0.34	0.35	0.27
Annual Precipitation	Direct	0.15			
r total		0.27			
Soil drainage					
Sharply drained	Direct		-0.03		
r total			0.25		
Imperfectly drained	Direct	-0.01		0.33	
r total		-0.29		0.32	
Fertility					
High fertility	Direct			-0.15	
r total				0.26	
Depth of soil					
Deep	Direct		-0.15	0.31	0.18
r total			-0.32	0.33	0.33
Shallow	Direct	0.28		0.18	
r total		0.49		-0.31	
Stony					
Abundant	Direct	0.15			
r total		0.38			
Absent	Direct	-0.36	0.07	-0.12	
r total		-0.36	-0.26	0.28	
Relief					
Strong corrugated	Direct		-0.16		0.02

r total			-0.23		0.25
Soil class					
Chernossolo	Direct	0.09	-0.34	0.05	
r total		-0.24	-0.38	0.23	
Neossolo	Direct	0.43	0.18	-0.3	-0.27
r total		0.36	0.23	-0.32	-0.29
Planossolo	Direct	0.01			-0.13
r total		-0.22			-0.12

Supplementary Table (S1) present the indirect scores of the path coefficient, responsible for the total r of the climate, soil and landscape variables.

The effect of interaction between alpha and beta diversity vs. coverage of exotic species and abundance of shrubs.

The prediction performance of the path modeling was high for the predictive variables, with low correlation between variables, the model showed significance in all interactions (Figure 3). The results show positive relationships in the interaction between alpha and beta diversity, the direct effect of beta diversity (r^2=0.28) in alpha diversity, and alpha diversity in beta diversity (r^2=023) reveals relatively close relationships, however they represent independent components. The best scores obtained in the framework were from indirect results, considering the variables contributed to strengthen the effects of the model. Especially the relations between exotic and shrubs (r^2=0.58), alpha and beta (r^2=0.38) and beta and shrubs (r^2=-0.56).

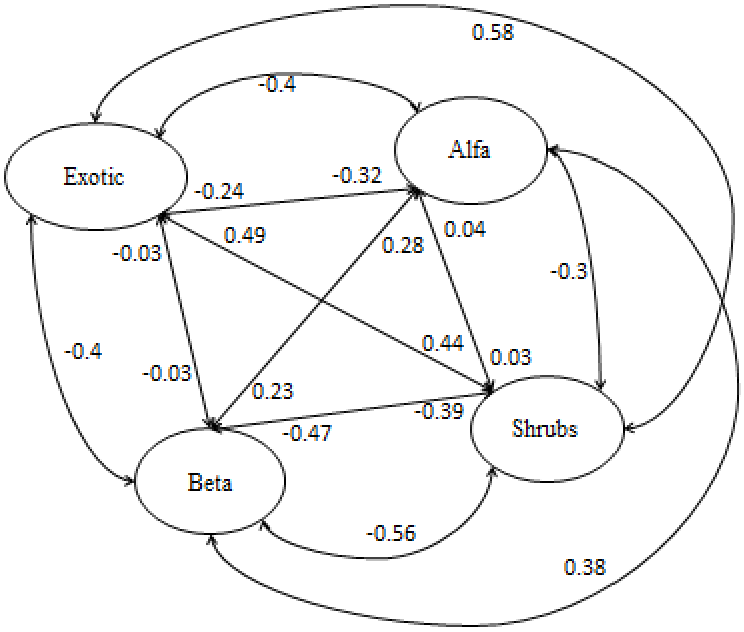


Figure 3 - Path modeling showing the strength and direction of the interaction effect among variables. Direct (straight arrows) and indirect (curved arrows) effects are shown through path coefficients.

Discussion

Environmental drivers for community assembly in a region with recently fragmented grasslands

This study contributes to a better understanding of how different environmental variables, including those related to recent anthropogenic land use, shape alpha and beta diversity in species rich subtropical grasslands. Our method allows us to discriminate between direct and indirect drivers and to identify. Overall, our results indicate that the species-sorting model is useful in understand environmental filtering in grassland communities in our study region.

Natural variation of environmental features – related to climate and soil – but especially factors related to anthropogenic land use change were identified as main drivers for diversity patterns at both the site (alpha diversity) and regional (beta diversity) scales. Specifically, in the case of our study region, we see clear effects of silviculture on grasslands. However, it is important to recognize that the effect of fragmentation per se cannot easily be separated from that of management changes in the context of Eucalypt plantions (see also Chapter 2). Studies with metacommunity in fragmented grasslands are rare, however it has been shown in other studies that the historical presence of grassland influences the current community assembly processes in extant grasslands (Helm et al. 2006; Purschke et al. 2012). In our study a considerable proportion of grasslands directly situated in the context of Eucalypt plantations still present typical communities of the region, as the occupation of the region by afforestation is relatively recent (10 years). Nonetheless, this process leads to changes in management – abandonment of traditional practices – which in turn leads to changes in the plant community, e.g. higher presence of shrubs or invasion of exotic species. Altogether, we can thus see that the intensity of management acts as driver for of the structure and the grasslands, leading to changes from the reference state that can be considered as degradation (Andrade et al. 2015; Koch et al. 2016).

Grassland communities are also directly associated with natural drivers. In our study, community composition and thus alpha and beta diversity varied in relation to environmental filters, specifically climate and soil features. For instance, higher annual temperature and lower rainfall favored alpha diversity. Low soil fertility was positive for alpha and beta diversity. These findings show clear diversity patterns on a regional scale, even though we may not forget the apparent clear filtering at high fertility sites may result from the fact that under these conditions, a relatively small number of widely-distributed plants that are highly competitive may dominate (Zobel 2015).

Drivers of exotic plant invasions and shrub encroachment

At regional scales, climate has been considered the major driver of invasive species occurrence (Ibáñez et al. 2009), as temperature and precipitation are key factors of resource availability, which limits survival, growth and reproduction of plants (Woodward 1987). Our study reveals a positive relationship between the presence of exotic species and annual temperature, but not precipitation. Importantly, the most expressive alien invasive species in the region (Chapter 2) are *Eragrostis plana*, with origin in South Africa, and *Cynodon dactylon*, likely of Mediterranean origin. These species are clearly benefitted from higher temperature, just as the shrub *Ulex europaeus*, especially invading abandoned sites in the context of *Eucalypt* plantations is.

Habitat fragmentation is an important driver of exotic species invasions Elton (1958) and increasing levels of human transformation of ecosystems, such as roads and roadsides (Vilà and Ibañéz 2011) contribute to spread of exotics. This has also been shown for our study region, as shown, for instance, by Guido et al. (2016). In our analysis, better conserved landscapes (landscape 1) negatively influenced the presence of exotic, contrasting fragmented landscape that showed a greater propensity for the establishment of exotic species. We also found a positive relation between the presence of roads and the occurrence of exotic species. In contrast, grasslands situated in less fragmented landscapes showed higher levels of alpha and beta diversity, confirming our hypothesis.

Encroachment of woody species in grasslands and savannas is a process occurring around the world, reflecting ecosystem changes and resulting in negative changes of important ecosystem processes such as carbon storage, water discharge, and biodiversity (Stevens et al. 2016), For South Brazilian grasslands, a number of studies has shown that the absence of disturbances, such as fire and grazing results not only in changes of the dominant grasses (e.g. Boldrini & Eggers 1996, Lezama et al. 2014), but, on a medium or long-term scale, also on succession from grassland to forest (e.g. Oliveira & Pillar, Müller et al. 2012, Blanco et al. 2014). In our study, shrub encroachment is related to a number of natural (climatic and soil related factors), but also the landscapes changes observed. This reflects, principally, the changes in grassland management when traditional grazing management is abandoned (Torchelsen et al. in prep.; Chapter 2), and also seems related to the fact that a changed landscape configuration, with degradation patterns, will also increase the presence of wind-dispersed shrubs, such as species of the *Baccharis* genus, i.e. of a ruderal character.

Alpha and beta diversity in relation to presence of exotic species and shrubs

Martin & Wilsey (2015) present a hierarchical concept of factors influencing alpha and beta diversity of plant communities. According to this concept, community composition changes, first of all, due to species sorting according to abiotic conditions, such as soil types or climates, as shown in our model as well. Assembly may, secondly, depend on dispersal processes that vary in the environment, as also evidenced in our study). Their third level, animal activities, that can alter plant species composition among patches and increase beta diversity (Steinauer and Collins 1995) was only studied indirectly by us, as it relates to land management by grazing. Last, beta diversity needs to be considered in the context of metacommunity theory through current dispersal rates and connectivity of habitat patches.

The introduction of alien plant species, and especially invasive plants, is a factor with considerable potential to change patterns of alpha and beta diversity (Hobbs et al. 2006). However, no general effect of exotic species on beta diversity has been found in a study comparing a large set of grassland vegetation data, over different climate zones and spatial scales (Martin & Wisley 2015). Here, we found that direct negative influence in alpha diversity is clear (r2=-32), but for beta diversity the effect was only slightly negative (r2=-0.04). Based on our data, we thus cannot affirm that exotic plant invasions lead to an overall homogenization and general losses of plant communities when considering a regional scale (beta diversity), even though there are clear effects on a the local (alpha) scale. Possibly, the lack of effects on beta diversity is related to the rather recent landscape changes in the region which still is considered one of the best preserved of the South Brazilian grasslands (Andrade et al. 2015). Shrub encroachment, on the other hand, had a strong negative effect on beta diversity (-0,56), indicating losses of typical grassland species, as discussed above.

Conclusion

The present study provides empirical evidence for the relative contributions of local environmental conditions, contemporary landscape spatial configuration, and historical landscape context for alfa and beta diversity in fragmented grasslands. We show that alpha and beta diversity patterns reflect complex interactions between different sets of variables, and that especially human induced land-use changes, in our case, tree plantations, are important drivers of assembly processes. Importantly, we here only talk of indirect effects, as we do not consider losses of grasslands per se due to expansion of forest plantations, but only changes in remaining grassland fragments. Nonetheless, clear negative effects on alpha and beta diversity were shown. From a theoretical perspective, our results confirm the species sorting model for grassland plant community assembly. From an applied perspective, our results indicate that conservation actions should be coordinated at a regional level, taking into account climatic and soil-related variation, as well as landscape-related processes.

Acknowledgements

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Conclusão Geral

De forma geral, os estudos presentes na tese abordam diferentes aspectos das mudanças indiretas em comunidades campestres, principalmente em relação aos plantios de eucalipto no bioma Pampa. Os dados levantados demosntram o potencial da vegetação campestre se recuperar mesmo após longos períodos de uso, mas também que as comunidades secundarias diferem das comunidades primarias. No entanto, há evidencias que o manejo tem um papel importante nos processos de manutenção e restauração dos campos, no emtanto, mais estudos são necessários para poder indicar como a restauração da vegetação campestre torna-se mais eficiente. O manejo também foi apontando, na presente tese, como fator principal que define a composição e o estado de conservação de áreas de campo em diferentes contextos ambientais (com ou sem silvicultura no entorno, com ou sem histórico de agricultura), e mudanças no uso, de forma geral, demontram influenciar diretamente a variação na diversidade alfa e beta de comunidades campestres, em conjunto com outras variáveis ambientais. Desta forma, a presente tese evidencia o marcante efeito antrópico para comunidades de plantas campestres, em diversas escalas. Fica evidente que estratégias de conservação tem de considerar estes efeitos, e deverão considerar o manejo como elemento principal na conservação da biodiversidade da região.

Futuros estudos devem buscar interpreter qual a intensidade de manejo adequada para a efetiva conservação de cada fisionomia campestre, considerando indicadores de qualidade ambiental, como por exemplo: a riqueza de espécies, a altura da vegetação, a abundância de arbustos, a presença de espécies invasoras, etc.. Testar práticas como o diferimento (exclusão do gado por determinados períodos) é uma alternativa, visando à heterogeneidade de plantas e habitas em areas de preservação. Implementar a coleta e a introdução de sementes nativas em areas degradadas, manejar os campos secundários, são alguns dos desafios necessários para a manutenção campos, e assim conservar de forma efetiva a biodiversidade e os serviços ambientais prestados pelos campos do bioma Pampa.