Universidade Federal do Rio Grande do Sul
Instituto de Biociências
Programa de Pós-Graduação em Ecologia

Dissertação de Mestrado

Respostas funcionais da vegetação campestre ao manejo pastoril

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Porto Alegre, maio de 2016

Respostas funcionais da vegetação campestre ao manejo pastoril

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Porto Alegre, maio de 2016

“Pampa e flor, olhos de terra

querência que quero bem

todo mundo busca um sonho

mas poucos sabem que tem...

Sou planura, sombra e vento

horizonte de sol pôr...

Por muito mais sou querência

pois sou assim, pampa e flor....”

Pampa e flor... – Gujo Teixeira

AGRADECIMENTOS

Agradeço primeiramente à CAPES pela minha bolsa de mestrado, ao CNPq pelo financiamento da maior parte das saídas de campo para coleta de dados (PELD Campos Sulinos, 558282/2009-1) e ao PPG-Ecologia UFRGS pelo financiamento de parte das saídas e pelo acolhimento. Agradeço também aos meus orientadores, Prof. Gerhard Overbeck e Prof. Pedro Maria Ferreira, que com suas sugestões e críticas tiveram papel determinante na qualidade do presente trabalho e na minha formação.

Agradeço também aos colegas do LEVCamp, principalmente àqueles que participaram das expedições de campo: Camila Bonilha, Luciana Menezes, Cleusa Vogel-Ely. Quero deixar minha gratidão a todos os demais colegas do LEVCamp, pelo acolhimento e ensinamentos sobre a vegetação campestre, pelas rodas de chimarrão e também pelos momentos de descontração.

Por último, mas não menos importante, agradeço a todas aquelas pessoas que de alguma maneira foram importantes para que meu mestrado corresse bem e para que eu pudesse hoje cumprir mais esta etapa da minha carreira e, que porventura eu possa não ter mencionado aqui.

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Resumo

Os Campos Sulinos são ecossistemas típicos da região sul do Brasil, ocorrendo no bioma Pampa e no bioma Mata Atlântica, e possuem alta riqueza florística e estrutura únicas. A dinâmica dos campos está associada à ocorrência de distúrbios naturais, como o pastejo e as queimadas, que possibilitam a renovação dos processos sucessionais, impedindo que poucas espécies dominem a comunidade. O pastejo atua como filtro ambiental selecionando espécies com determinados atributos, resultando na organização das comunidades. Nesse estudo, utilizamos dados de atributos da vegetação campestre nos biomas Pampa e Mata Atlântica, no Sul do Brasil para compreender os efeitos de diferentes intensidades de pastejo sobre os padrões e variações funcionais das comunidades vegetais. Avaliamos a variação intra-específica de atributos foliares das espécies dominantes de cada sítio e classificamos as espécies de acordo com a classificação C-S-R. Avaliamos também a variação na diversidade funcional de atributos da vegetação campestre. Observamos um padrão de variação ao longo do gradiente de pastejo, em que a exclusão de pastejo tende a selecionar indivíduos com menor SLA, e maior LA e FT. Os resultados da classificação CSR mostraram uma predominância de espécies com estratégia de tolerância ao stress, enquanto espécies com características ruderais ou habilidades de competição não foram encontradas. Não houve diferença nas estratégias das plantas entre tratamentos ou entre os sítios do bioma Pampa e Mata Atlântica. As comunidades de plantas campestres diferiram entre os sítios dos biomas Pampa e Mata Atlântica quanto à sua composição de espécies. Também encontramos maior diversidade funcional nos sítios do bioma Pampa. Encontramos padrão de convergência de atributos em relação ao gradiente, em que as áreas de exclusão apresentam mais espécies perenes e entouceiradas, e menos espécies rizomatosas. Assim, confirmamos que diferentes intensidades de pastejo promovem uma resposta funcional que é muito variável, e dependente do atributo e da espécie em questão. Esse padrão de convergência encontrado pode ser causado por processos evolutivos, indicando que tanto filtros bióticos como abióticos estão atuando sobre a estrutura das comunidades.

Palavras-chave: Campos Sulinos; gradiente de pastejo; variação intra-específica; diversidade funcional.

Abstract

Campos Sulinos are ecosystems typical of southern Brazil, occurring in Pampa and Atlantic Forest biomes, and hold high species richness and unique structure. Grassland dynamics are associated with the occurrence of natural disturbances such as grazing and burning, which allow the renewal of successional processes, preventing a few species dominate the community. Grazing acts as an environmental filter by selecting species with certain traits, resulting in the community assembly. In this study, we used functional traits of grassland vegetation of biomes Pampa and Atlantic Forest in southern Brazil to understand the effects of different grazing intensities on the patterns and functional changes in plant communities. We evaluated the intra-specific variation of leaf traits of the dominant species for each site and classified the species according to the C-S-R scheme. We also evaluated the changes in functional diversity of plant traits. We observed a pattern of variation along the grazing gradient, in which the grazing exclusion tends to select individuals with lower SLA and greater LA and FT. CSR classification showed a predominance of species with stress-tolerance strategy, while species with ruderal characteristics or competition abilities were not found. There was no difference in the strategies of the plants between treatments or between sites in Pampa and Atlantic Forest biomes. The grassland communities differed in species composition between the sites of Pampa and Atlantic Forest biomes. We also found higher functional diversity in the Pampa biome sites. Found patterns of trait convergence along the gradient, where exclusion areas have more perennial and tussock species and less rhizomatous species. Thus, we confirm that different grazing intensities promote a functional response that is highly variable and dependent on the trait and the species concerned. Evolutionary processes, indicating that both biotic filters as abiotic are acting on the structure of communities, may cause the pattern of convergence found.

Keywords: *Campos Sulinos*; grazing gradient; intra-specific variation; functional diversity.

Introdução Geral

As formações campestres ocupam cerca de 40% da superfície da Terra, e ocorrem em climas tanto secos quanto úmidos, e são caracterizadas por seus solos rasos e vegetação herbácea em que espécies graminóides são dominantes (Suttie et al. 2005). Muitos dos biomas campestres do mundo ocorrem onde o clima pode suportar florestas de dossel fechado. Estudos recentes demonstram claramente que a extensão e distribuição desses biomas campestres não são determinados pelo clima por si só, mas também através de interações com fogo, herbívoros, e fatores edáficos que limitam o crescimento das árvores (Bond et al. 2005; Lehmann et al. 2011). Formações campestres enfrentam uma enorme pressão de alterações ambientais induzidas pelo homem, mas são classificadas como baixa prioridade de conservação em relação às florestas. Assim, os campos temperados e as savanas estão entre os biomas terrestres com a situação global mais crítica – 45,8% de conversão e apenas 4,6% de proteção (Hoekstra et al. 2004). No sul do Brasil, as formações campestres são caracterizados pela sua ocorrência em climas mésicos e por diferenças em suas fisionomias de acordo com o tipo de substrato na escala regional. Diferenças no substrato afetam as fisionomias de vegetação nestas pastagens, mas congruência também tem sido observado em espécies que ocorrem em locais com diferentes substratos (Moro & Carmo 2007).

Os Campos Sulinos são ecossistemas típicos da região sul do Brasil. Desenvolvem-se sob clima subtropical e úmido, com chuvas bem distribuídas ao longo do ano. Os campos do sul do Brasil representam uma vegetação remanescente de um clima mais seco e mais frio do que hoje (Behling & Pillar 2007). Situam-se no bioma Pampa e no bioma Mata Atlântica, neste último caso associados às florestas com Araucária, e possuem alta riqueza florística e estrutura únicas, resultantes da diversidade de fatores climáticos e edáficos e do manejo da vegetação (Boldrini et al. 2011). Apenas para o RS, são estimadas 2.577 espécies de plantas campestres, pertencentes a 90 famílias botânicas (Boldrini et al. 2011), formando diferentes fisionomias campestres em diferentes regiões do estado (Boldrini 2009). Os campos também possuem uma rica diversidade faunística, incluindo espécies endêmicas e ameaçadas de extinção (Bencke 2009). Apesar desta alta biodiversidade, os campos do bioma Pampa contam, atualmente, com 54% de sua área original convertida em outros usos, principalmente para uso agrícola para produção de soja e arroz, e cultivo de árvores exóticas para extração de celulose (Cordeiro & Hasenack 2009; Overbeck et al. 2013) e a sua conservação tem sido negligenciada (Overbeck et al. 2007). Essas alterações na cobertura e uso da terra provocam mudanças na estrutura e funcionamento do ecossistema campestre, e acarretam principalmente a perda de hábitat e biodiversidade associada (Overbeck et al. 2007; Herrera et al. 2014).

A dinâmica dos campos está associada à ocorrência de distúrbios naturais, como o pastejo pelo gado e queimadas. Distúrbios possibilitam a renovação dos processos sucessionais, impedindo que poucas espécies, competitivamente superiores, dominem a comunidade. Promovem a heterogeneidade espacial com a manutenção de várias fisionomias campestres e maximizam a diversidade de espécies. Estudos nos Campos Sulinos demonstraram a influência positiva de distúrbios na diversidade de espécies vegetais (Overbeck et al. 2007). A ação de pastejo modifica a estrutura da vegetação pela seleção entre plantas palatáveis e não palatáveis e influencia na microvariação topográfica, incrementando a heterogeneidade espacial dos hábitats (Morris 2000).

Organização das comunidades vegetais

Uma das principais questões abordadas em ecologia é como as comunidades vegetais estão organizadas (Götzenberger et al. 2012). Uma das teorias de organização de comunidades que vem se fortalecendo é a teoria das regras de montagem, ou *community assembly* (Diamond 1975), definida como o conjunto dos processos ecológicos selecionando a favor ou contra espécies do *pool* regional, determinando, assim, a composição da comunidade local (Keddy 1992). Esses processos de seleção são relacionados a filtros ambientais que atuam em diferentes escalas, por exemplo, fatores climáticos na escala regional e diferentes tipos de manejo, como o pastejo no caso da vegetação campestre, numa escala local (Blanco et al. 2007; Cruz et al. 2010). Uma abordagem funcional de organização de comunidades pode revelar padrões relacionados a esses filtros, pois os organismos possuem características que respondem a condições ambientais ou processos do ecossistema, e podem determinar a aptidão do organismo através de efeitos no crescimento, reprodução e sobrevivência (Keddy 1992; Violle et al. 2007).

A partir da medição de atributos das espécies de uma comunidade, podemos obter uma medida de diversidade funcional, um componente da biodiversidade que busca entender as comunidades ou ecossistemas baseando-se na função que os organismos desempenham nesse ambiente (Petchey & Gaston 2006). Ela se refere à medida de variação dos atributos funcionais dos organismos dentro de determinado ambiente (Petchey & Gaston 2006), e quanto menor a amplitude dessa variação em uma determinada comunidade, menor será a sua diversidade funcional. Explorando o padrão de distribuição de atributos funcionais de comunidades, entende-se a divergência de atributos como resultado de limitação de similaridade, enquanto que a convergência de atributos é uma consequência da ação local de filtros ambientais (Grime 2006; Wilson 2007).

Variação intraespecífica e estratégia das plantas

Estudos recentes sobre a estrutura funcional das comunidades de plantas sugerem a importância do papel da plasticidade fenotípica na explicação das regras de montagem das comunidades, uma vez que a competição e o uso dos recursos ocorrem a nível de indivíduo (Albert et al. 2010; Jung et al. 2010; Cianciaruso et al. 2012; Carlucci et al. 2012; Siefert et al. 2015). Considerar a variação intraespecífica dos atributos é importante para avaliar a resposta de uma espécie a gradientes ambientais, como a possibilidade de uma espécie ajustar suas características morfológicas e fisiológicas, expressas em valores de atributos, às condições e requisitos abióticos e limitação de similaridade ecológica com espécies concorrentes pode ser decisiva para a sua criação e reprodução numa comunidade (Jung et al. 2010). Além disso, na perspectiva de hierarquias competitivas, há uma gama de valores ótimos dos atributos que permite às espécies competir com sucesso por recursos limitados (Herben & Goldberg 2014; Fort et al. 2014), pois esse atributo ótimo pode mudar ao longo do gradiente ambiental. Se uma espécie é suficientemente plástica para ajustar a expressão de atributos relevantes para a aquisição de recursos e o volume de negócios para o ótimo necessário, será mais provável que persista em uma maior variedade de ambientes (Andrade et al. 2014).

As espécies individuais podem assim ajustar a expressão do seu atributo de acordo com os efeitos específicos de pastejo experimentados. Estudos mostram que uma alta pressão de pastejo resulta em uma dominância por espécies de hábito prostrado (Louault et al. 2005; Cruz et al. 2010; Lezama et al. 2014), enquanto uma menor pressão de pastejo resulta em uma vegetação composta tanto de espécies prostradas como entouceiradas, e, finalmente, a exclusão de pastejo leva ao domínio de espécies entouceiradas somente (Boldrini & Eggers 1996). Esse padrão está associado a diferentes estratégias de uso de recursos entre espécies de gramíneas, que podem ser demonstradas por suas características foliares (Cruz et al. 2010) e refletem as diferenças entre ambientes com níveis constantemente baixos ou altos de desfolhação por animais no pastejo. Espécies de gramíneas com uma estratégia de conservação de recursos apresentam folhas com maior teor de matéria seca foliar (LDMC, do inglês *Leaf Dry-Matter Content*) e área foliar específica menor (SLA, do inglês *Specific Leaf Area*) (Louault et al. 2005), sendo tipicamente associada com espécies de crescimento lento sob baixa pressão de pastejo. No entanto, as espécies caracterizadas pela estratégia de captação de recursos apresentam maior SLA e LDMC mais baixos, e tendem a ser dominantes em áreas com alta pressão de pastejo (Cruz et al. 2010).

Nesse estudo, utilizamos dados de atributos da vegetação campestre do Sul do Brasil para compreender os efeitos de diferentes intensidades de pastejo sobre os padrões e variações funcionais das comunidades vegetais. Desta forma, compreendemos que este estudo, além de investigar os processos ecológicos atuantes sobre as comunidades campestres, também é relevante para o conhecimento e conservação da vegetação dos Campos Sulinos.

O trabalho aqui apresentado tem os seguintes objetivos e hipóteses:

Objetivo geral

Analisar os padrões de organização da vegetação campestre, com foco na variação nos atributos funcionais em resposta a um gradiente de intensidade de manejo pastoril.

Objetivo específicos

(1) Avaliar os efeitos de diferentes intensidades de pastejo sobre a variação intra-específica nos atributos funcionais foliares da vegetação campestre no sul do Brasil.

Hipótese: Plantas com estratégia de captura de recursos devem apresentar maior plasticidade intra-específica em relação a plantas de estratégia de conservação de recursos devido ao seu crescimento rápido.

(2) Avaliar se há variação na diversidade funcional de atributos da vegetação campestre ao longo de um gradiente de intensidade de pastejo.

Hipótese: Áreas com exclusão de pastejo devem apresentar menor riqueza de espécies e menor diversidade funcional.

(3) Avaliar quais os atributos funcionais que estão associados às diferentes intensidades de pastejo.

Hipótese: Existem diferenças nos atributos de forma de vida ao longo do gradiente de pastejo, como a dominância de espécies entouceiradas e declínio de espécies prostradas em áreas de exclusão de pastejo.

Estrutura da Dissertação

Essa dissertação é apresentada na forma de dois artigos, com indicação de um possível periódico ao qual serão submetidos. O primeiro capítulo busca responder ao objetivo específico 1. Nele apresentamos os efeitos do pastejo sobre a variação intra-específica de atributos foliares, com enfoque nas estratégias expressas pelas plantas. No segundo capítulo, buscamos responder aos objetivos específicos 2 e 3, com enfoque voltado para as teorias ecológicas que buscam explicar a organização das comunidades.

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Capítulo 1. Intraspecific trait variation of grassland species under distinct grazing treatments depends on functional strategy *

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Printed journal page estimate: 5.509 words (6.8 pages), table 1.5 pages, figures 0.4 pages, total 8.7 pages.

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* Artigo formatado segundo as regras do periódico *Journal of Vegetation Science*.

Abstract

Question: Do different grazing intensities affect intraspecific variation in leaf functional traits of grassland vegetation in southern Brazil?

Location: Six sites of the LTER Campos Sulinos, situated in subtropical grasslands in Rio Grande do Sul State, Southern Brazil.

Methods: We measured functional traits of grassland plant species associated with competition for resources and environmental tolerance (specific leaf area – SLA, leaf-dry matter content – LDMC, leaf area – LA and leaf resistance to traction - FT) along three different grazing treatments in grassland vegetation of Pampa and Atlantic forest biomes in Southern Brazil. We quantified the proportion of intra- and interspecific variation through decomposition of trait variance, and explored patterns of intraspecific variation related to grazing treatments through randomization tests.

Results: In general, SLA showed lower values in the excluded treatment, unlike LA, which showed higher values in excluded treatment. LDMC did not show any effect and FT values in general were higher in the exclusion treatment. Altogether, species classified as resource conservation strategy showed more intraspecific variation among grazing treatments than the other groups.

Conclusion: Our study confirms that cessation of grazing leads to higher intraspecific variation in functional traits for most species and to a dominance of species with resource conservation strategy. However, differences in grazing regimes, such as cattle pressure, can also influence trait expression. The results from our study reforce that trait expression may be variable within a given species, and we show that this is the case, especially for species with a resource conservation strategy.

Keywords: *Campos Sulinos*; Environmental filtering; Functional ecology; Grassland; Grazing experiment; Intraspecific variability; Leaf traits; Management; Plasticity.

Nomenclature: Anon. (2016)

Abbreviations: CONV = conventional management; EXCL = exclusion management; FT = force to tear; ITV = intraspecific trait variation; LA = mean leaf area; LDMC = leaf dry-matter content; PFT = plant functional type; ROT = rotational management; SLA = specific leaf area.

Running head: Effects of grazing on plant intraspecific trait variation

Introduction

Plant functional traits can be defined as traits that respond to variation in the environment and impact fitness indirectly via their effects on plant growth, reproduction and survival (Díaz et al. 2001; Violle et al. 2007). Recent studies on the functional structure of plant communities suggest the importance of the role of phenotypic plasticity in explaining community assembly, once competition and resource use occurs at individual level (Albert et al. 2010; Jung et al. 2010; Cianciaruso et al. 2012; Carlucci et al. 2012; Siefert et al. 2015). Additionally, functional traits can also have effects on ecosystem functioning (Weisser et al. 2017). Intraspecific trait variation should increase when individuals of a given species occupy specific parts of an environmental gradient. It reflects the capacity of a species to adjust its morphological and physiological features, expressed in trait values, to changes in the environmental conditions, which can be decisive for establishment and reproduction in a community (Jung et al. 2010). Furthermore, from the perspective of competitive hierarchies, there is an optimal range of trait values that allows species to successfully compete for limiting resources (Herben & Goldberg 2014; Fort et al. 2014), but this trait optimum may shift along environmental gradients. If a species is sufficiently plastic to adjust the expression of traits relevant for resource acquisition and turnover towards the required optimum, it will be more likely to persist in a broad range of environments (Andrade et al. 2014).

Grazing acts as an environmental filter on the plant community and plays an important role in defining structural and functional patterns of plants in grassland systems (Blanco et al. 2007; Cruz et al. 2010). The magnitude of its effects depends on intensity and frequency of the disturbance as well as on evolutionary history and productivity levels of the grassland (Cingolani et al. 2005; Lezama et al. 2014). One of the effects of grazing in productive systems is the reduction of dominance of competitively superior species, in contrast to situations without grazing where these species will exclude inferior competitors (Boldrini & Eggers 1996; Cingolani et al. 2005; Cruz et al. 2010). However, an excess of grazing can lead to a decline in biomass of grassland species (Mysterud 2006; Ruppert et al. 2012), while the cessation of grazing can be followed by increased dominance of a few species and associated decline of species adapted to grazing (Lezama et al. 2014). Several studies have shown that a high grazing pressure results in a dominance by prostrated species (Louault et al. 2005; Cruz et al. 2010; Lezama et al. 2014). Lower grazing pressure results in a vegetation composed both of prostrated and tussock species, and, finally, grazing exclusion, at least in productive systems, usually leads to dominance of tall tussock species only (Boldrini & Eggers 1996; Lezama et al. 2014). This pattern is associated to different strategies for resources use between grass species, which can be demonstrated by their leaf traits (Cruz et al. 2010) and reflects the differences between environments with constantly low or high levels of defoliation by grazing animals. Grass species with a resource conservation strategy present leaves with higher leaf dry-matter content (LDMC), and lower specific leaf area (SLA) (Louault et al. 2005; Garnier et al. 2007; Cruz et al. 2010). This strategy is typically associated with slow growth species under low pressure of grazing. However, species characterized by resource capture strategy present higher SLA and lower LDMC, and tend to be dominant in areas with high pressure of grazing (Cruz et al. 2010).

In addition to these differences in trait values among plants with contrasting plant strategies, individual plants may adjust their trait expression according to the specific grazing effects experienced. Whitworth-Hulse et al. (2016) found evidence for trait variation of grassland plants in grazed vs. ungrazed plots mainly for size-related traits; however, they did not include different grazing regimes. In our study, conducted in subtropical grasslands in southern Brazil, we aimed to evaluate the effects of different grazing intensities on the intraspecific variation in leaf functional traits of grassland species. Our work was conducted within the Long-term Ecological Research (LTER) Campos Sulinos project, an ongoing grazing experiment with three different treatments (grazing intensities), conducted at six study sites distributed in two separate regions (lowland grassland in the Pampa biome, and highland grasslands in the more humid and cooler Atlantic forest biome). We hypothesized that (1) plants with a resource capture strategy should show greater intraspecific plasticity than plants with resource conservation strategy, due to fast growth; (2) species in the grazing exclusion treatment, mainly the tussock grasses, should present traits characterizing competition strategy.

Materials and methods

STUDY AREA

The study was carried out at six sites in the South Brazilian grassland region (Fig. 1), three in the lowland *Pampa* biome grasslands (in Aceguá, Alegrete and Lavras do Sul municipalities) and three in municipalities in the highland grasslands in the Atlantic Forest biome (Cambará do Sul in Aparados da Serra National Park, Jaquirana in Tainhas State Park and São Francisco de Paula in Aratinga Ecological Station; Andrade et al. 2016). All sites are part of the LTER Campos Sulinos project whose objective is the analyses of the effect of different types of grazing management on vegetation and productivity patterns. Climate in the lowland *Pampa* region is Cfa, with mean annual rainfall of 1158mm, 1509mm and 1450mm, mean annual temperature of 17.9ºC, 18.9ºC and 17.8ºC, and mean altitude of

175m, 108m and 345m AMSL (Hijmans et al. 2005) for Aceguá, Alegrete and Lavras do Sul sites, respectively. Climate in the highland grasslands region is Cfb, with mean annual rainfall of 1917mm, 1981mm and 1636mm, mean annual temperature of 15 ºC, 15.2ºC and 16.9ºC, and mean altitude of 962m, 901m and 758m AMSL (Hijmans et al. 2005) respectively for Cambará do Sul, São Francisco de Paula and Jaquirana sites. The vegetation at all sites is natural grasslands, managed with cattle and, at the highland grasslands sites, traditionally also with fire (Overbeck et al. 2007).

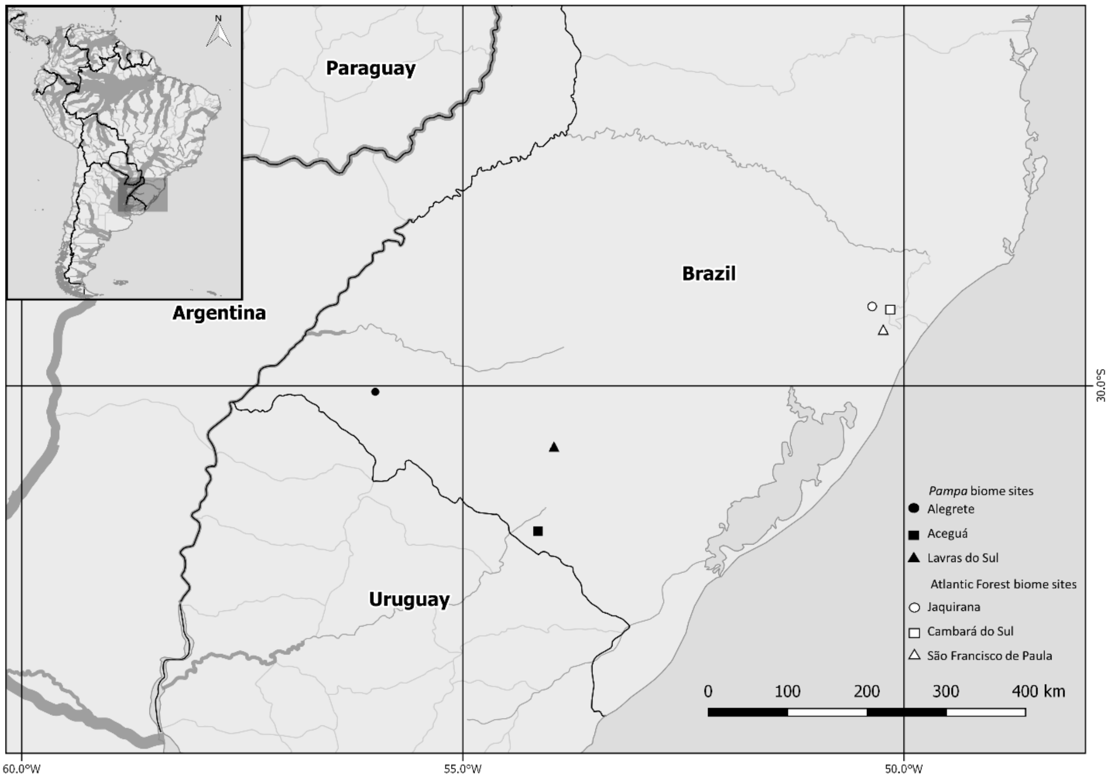

Figure 1: Location of LTER *Campos Sulinos* sampling sites of grassland vegetation in lowland *Pampa* biome grasslands and highland grasslands in Atlantic Forest biome.

GRAZING TREATMENTS

Leaf traits of plants under different types of grazing management were measured in the different treatments of the LTER Campos Sulinos project. At each site, three treatments are being applied in plots of 0.5 ha each: (1) grazing exclusion, (2) rotational management and (3) conventional management. Treatments are being applied since 2011, i.e., for four or five years prior to our sampling. The grazing exclusion plots and rotational management are fenced, while the plot subjected to conventional grazing is not fenced and is inserted in a larger area under the conventional management adopted by the local farmers. In the rotational management plot, the criteria used to determine the time interval between cattle access is the cumulative thermal sum of 700 degree-days, which aims to maintain the contribution of grasses with a strategy of resource conservation (Quadros et al. 2011). When this value is reached, cattle is placed in the paddock and remains there up to three days. In each treatment, the vegetation is analyzed in nine systematically allocated permanent quadrats with 1 x 1 m, with estimation of cover of all vascular plant species on a decimal scale (Londo 1976). For details on results of the treatments on plant community composition and structure, see Ferreira (2014).

SPECIES SELECTION AND TRAIT MEASUREMENT

Using the vegetation survey data of spring/summer 2014/2015, we computed the relative cover value (RC) of each of the 427 recorded species as the total cover value of the species in each experimental plot at each site of the experiment. Through the RC value of species, we selected the most abundant species in each treatment per site, in order to reach around 50% of relative cover of plant community. This selection resulted in 31 species, which accounted for the most important species in the communities. The minimum species collected per site was eight and the maximum was 16. Discrepancies in cover among treatments in some sites (in particular, at the abandoned plots) are due to the dominance of shrub species not selected for the study or to the high cover of accumulated dead biomass (Table 1). Also, to be selected, species had to occur in at least two treatments per site, which meant that many dominant species in the grazing exclusion treatment where not considered. Data collection included different life forms, as forb, grass and graminoid species.

Sampling of plant individuals for traits measurements was performed during southern hemisphere spring and summer, between November 2014 and March 2015, and between December 2015 and January 2016, depending on phenological development of the species. For each collected plant individual, we measured the following functional traits: specific leaf area (SLA), expected to be correlated with relative growth rate; leaf dry-matter content (LDMC), related to the average density of the leaf tissues; leaf area (LA), related to leaf energy and water balance; and leaf resistance to traction (FT – force to tear), related to the investment in structural protection of the photosynthetic tissues (Cornelissen et al. 2003). For each selected species, we collected five individuals with at least six expanded and healthy leaves per grazing intensity treatment. Sampling, storing and subsequent trait measurement followed the protocol described by Pérez-Harguindeguy et al. (2013).

Grass species were grouped based on SLA and LDMC values to define the resource use strategy (see Cruz et al. 2010). Species with low values of LDMC and high SLA were classified as resource capture strategy, while grasses with low SLA and high LDMC were classified as resource conservation strategy (Table 2). The grouping method used was cluster analysis with complete linkage in the software MULTIV v. 3.40β (V. Pillar, available at [http://ecoqua.ecologia.ufrgs.br]).

Table 1: Total relative cover of species collected in each treatment at each site. Treatments: CONV – conventional management; ROT – rotational management; EXCL – grazing exclusion.

Aceguá			*Cambará do Sul*		
CONV	ROT	EXCL	CONV	ROT	EXCL
41.90%	43.87%	14.15%	47.95%	73.87%	70.36%
Alegrete			*São Francisco de Paula*		
CONV	ROT	EXCL	CONV	ROT	EXCL
57.47%	62.37%	53.44%	76.31%	71.54%	75.39%
Lavras do Sul			*Jaquirana*		
CONV	ROT	EXCL	CONV	ROT	EXCL
72.85%	31.01%	13.15%	74.73%	63.60%	54.02%

Table 2: Groups of plant functional types (PFTs) based on leaf dry-matter content (LDMC; mg.g^{-1}) and specific leaf area (SLA; mm².mg^{-1}), following Cruz et al. 2010. Grouping by Cluster analysis using complete linkage as clustering method.

Trait / Group	LDMC (mg.g^{-1})	SLA (mm².mg^{-1})	Species
A	395	16	*Andropogon lateralis, Eragrostis airoides, Melica rigida, Piptochaetium lasianthum, Schizachirium tenerum, Sorghastrum setosum, Sporobolus indicus, Steinchisma hians, Nassella neesiana*

B	335	19	*Chascolytrum subaristatum, Cyperus reflexus, Mnesithea selloana, Paspalum maculosum, P.polyphyllum, Setaria vaginata*
C	270	24	*Axonopus affinis, Bothriochloa laguroides, Dichantelium sabulorum, Paspalum dilatatum, P. notatum, P. plicatulum, P. pumilum, Setaria parviflora*

DATA ANALYSES

The proportion of intra- and interspecific variation was quantified through decomposition of trait variance using nested factors at four levels: between sites, between treatments, inter- and intraspecific. This analysis was carried out in R 3.2.0 (R Development Core Team 2015) with the package *cati* (Taudiere & Violle 2015).

To test the effects of cattle grazing over intraspecific variation of the collected species, independent for each species, randomization tests were carried out. This analysis was carried out in MULTIV v. 3.40β (V. Pillar, available at [http://ecoqua.ecologia.ufrgs.br]) and the significance level considered was $\alpha \leq 0.05$. In all analysis, we considered as sample unit each experimental plot in each site. Analysis of variance was performed to detect general patterns of trait variance among grazing treatments, regarding the 834 plant individuals collected.

Results

In the overall evaluation, using the full data set of all collected species, trait variation was partitioned into within and among species, and among site and treatment components (Fig. 2): 22, 18, 25 and 37% of the total variance in LA, LDMC, SLA and FT, respectively, were explained by intraspecific trait variation. Interspecific variability in LA, LDMC, SLA and FT was

3, 5, 2.5 and 1.5-fold higher than intraspecific variation. SLA and FT varied significantly among sites, as opposed to the other traits. LA was the only trait that presented variation among treatments.

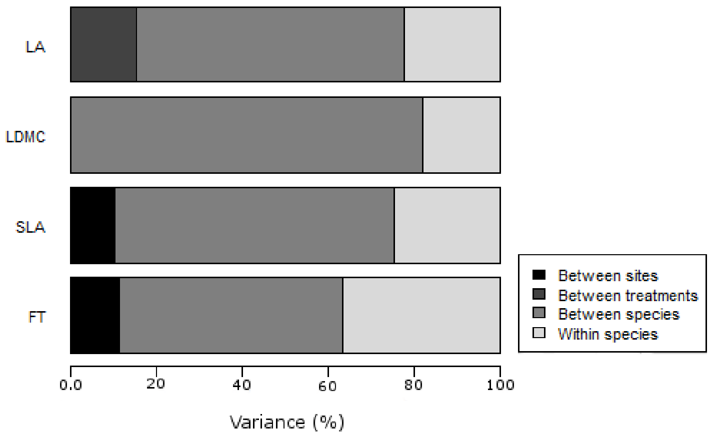

Figure 2: Sources of variation of leaf plant traits. Variance decomposition in inter- and intraspecific and among sites contributions for single-trait pattern. LA, leaf area; LDMC, leaf dry-matter content; SLA specific leaf area; FT, force to tear.

Overall, forb species showed no intraspecific variation between treatments for any of the tested traits, except for *Trifolium polymorphum*, which had a higher LDMC value under rotational management compared to conventional and excludes treatments (p = 0.02).

Only one (*Paspalum polyphyllum*) of the 23 graminoid species analyzed showed no intraspecific variation between treatments in any trait (Table 3; see also overview of results in Table 4). However, ten species showed variation only in LA, but maintained values for the other traits. Most of these species belong to the plant functional group C according to the classification proposed by Cruz et al. (2010), i.e., are characterized by a resource capture strategy. On the other hand, grass species classified as resource conservation strategist (PFT A) showed variation in at least one other trait besides LA. In general, the SLA showed lower values in excluded treatment, as well as LA. LDMC did not show a pattern of variance and FT values in general were higher in the exclusion treatment. Altogether, species of PFT group A showed more intraspecific variation among grazing treatments than the other groups (Table 4).

When considering all individuals in the comparison of treatments, analysis of variance (ANOVA) showed, in general, that LA varied among all treatments, while LDMC did not (Table 5). Also, conventional management showed significantly higher values for SLA (p = 0.03) and FT (p<0.001) when compared to rotational management.

Table 3: Randomization tests results for intraspecific variation for each trait between treatments, for graminoid species. CONV: conventional management; ROT: rotational management; EXCL: cattle exclusion. Different superscript letters indicate significant differences per trait/species.

Species	Group	Treat-ment	SLA ($mm^2.mg^{-1}$)	LDMC ($mg.g^{-1}$)	FT ($N.mm^{-2}$)	LA (mm^2)
Andropogon lateralis	A	CONV	13.41^a	375.30	1.24^a	710.51^a
		ROT	12.10^b	373.37	1.30^a	1063.70^b
		EXCL	11.88^b	379.23	1.94^b	1678.57^c
Eragrostis airoides	A	CONV	19.97	385.74	0.45	175.28^a
		ROT	19.01	395.70	0.64	149.42^a
		EXCL	19.82	384.17	0.31	277.85^b
Melica rigida	A	CONV	15.12	447.40^a	0.92	112.48^a
		ROT	12.97	389.70^b	0.76	132.80^a

		EXCL	14.58	380.63^{b}	1.22	231.66^{b}
Piptochaetium lasianthum	A	CONV	11.71	548.26^{a}	0.10	35.75^{a}
		ROT	14.94	386.50^{b}	0.38	129.41^{b}
		EXCL	16.89	419.54^{b}	0.32	365.10^{c}
Schizachyrium tenerum	A	CONV	18.82	435.08^{a}	0.54	132.96^{a}
		ROT	20.46	376.63^{b}	0.68	253.98^{a}
		EXCL	18.61	395.77^{ab}	0.79	445.97^{b}
Sorghastrum setosum	A	CONV	12.02^{a}	419.90	1.59^{a}	906.45^{a}
		ROT	10.28^{b}	407.06	1.19^{a}	770.86^{a}
		EXCL	10.10^{b}	405.25	2.65^{b}	1690.31^{b}
Sporobolus indicus	A	CONV	15.56^{a}	378.27^{a}	1.07	451.38^{a}
		ROT	13.79^{b}	401.86^{b}	1.14	762.30^{b}
		EXCL	13.50^{b}	402.23^{b}	1.48	1586.97^{c}
Steinchisma hians	A	CONV	21.62	363.05^{a}	0.62	218.01^{a}
		ROT	22.13	407.81^{b}	0.74	494.27^{b}
		EXCL	24.35	375.03^{a}	0.65	525.87^{bc}
Nassella neesiana	A	CONV	19.42^{a}	344.96^{a}	0.63	411.91^{a}
		ROT	17.72a^{b}	368.61^{a}	0.62	462.80^{a}
		EXCL	15.99^{b}	399.74^{b}	1.46	844.18^{b}
Chascolytrum subaristatum	B	CONV	21.41^{a}	342.19	0.52	300.69^{a}
		ROT	17.54^{b}	372.73	1.09	563.69^{b}
		EXCL	19.47^{ab}	342.98	0.79	620.55^{bc}
Cyperus reflexus	B	CONV	14.40	341.05	0.95	329.18^{a}
		ROT	12.43	330.98	2.14	948.88^{a}
		EXCL	12.85	304.70	1.67	2917.34^{b}
Mnesithea selloana	B	CONV	22.34	337.22	0.59	549.78^{a}
		ROT	19.05	346.37	0.69	584.07^{a}

		EXCL	20.65	332.09	0.56	864.62^{b}
Paspalum maculosum	B	CONV	13.89	293.91	0.65	373.03^{a}
		ROT	12.20	314.69	0.96	447.77^{a}
		EXCL	13.10	309.51	0.91	505.49^{b}
Paspalum polyphyllum	B	CONV	20.11	337.28	1.57	105.06
		ROT	19.20	342.73	2.16	120.49
		EXCL	19.84	350.08	1.75	95.68
Setaria vaginata	B	CONV	25.90	299.42	0.52	293.74^{a}
		ROT	22.69	322.93	0.46	263.29^{a}
		EXCL	25.59	332.43	0.37	736.38^{b}
Axonopus affinis	C	CONV	23.49	259.73^{ab}	0.87	526.41^{a}
		ROT	23.23	263.84^{a}	0.90	656.90^{a}
		EXCL	24.20	239.97^{b}	0.92	1244.20^{b}
Bothriochloa laguroides	C	CONV	33.81	253.14	0.37	301.98^{a}
		ROT	-	-	-	-
		EXCL	30.22	292.16	0.14	630.81^{b}
Dichantelium sabulorum	C	CONV	-	-	-	-
		ROT	22.43	271.75	1.00	69.31^{a}
		EXCL	21.24	301.11	1.52	265.26^{b}
Paspalum dilatatum	C	CONV	27.06	219.37	0.84	858.07^{a}
		ROT	22.89	227.55	1.19	1157.50^{b}
		EXCL	22.82	250.37	1.06	1095.93^{b}
Paspalum notatum	C	CONV	22.15	299.18	0.68	330.91^{a}
		ROT	22.17	296.56	0.78	530.28^{b}
		EXCL	22.54	285.07	0.63	811.02^{c}
Paspalum plicatulum	C	CONV	18.13^{a}	271.06^{a}	0.50^{a}	488.98^{a}
		ROT	16.07^{ab}	303.72^{b}	0.86^{b}	655.27^{a}

		EXCL	15.45^{b}	276.09^{a}	0.70^{ab}	875.68^{b}
Paspalum pumilum	C	CONV	20.68^{a}	249.01^{a}	1.19	497.60^{a}
		ROT	19.16^{a}	262.35^{a}	1.22	546.74^{a}
		EXCL	26.15^{b}	222.15^{b}	1.08	1380.85^{b}
Setaria parviflora	C	CONV	24.11	288.00	0.52	250.32^{a}
		ROT	25.17	298.02	0.40	286.75^{a}
		EXCL	28.04	267.58	0.51	484.23^{b}

Table 4: Synthesis table of results for intraspecific variation for each trait between treatments. We indicate the total number of species that showed variation for each trait in each plant functional group.

Group	Number of species	SLA ($mm^2.mg^{-1}$)	LDMC ($mg.g^{-1}$)	FT ($N.mm^{-2}$)	LA (mm^2)
A	9	4	6	2	9
B	6	1	0	0	5
C	8	2	3	1	8

Table 5: Analysis of variance (ANOVA) results for trait variation between treatments, for 834 collected plant individuals. CONV: conventional management; ROT: rotational management; EXCL: cattle exclusion. Superscript star indicate significant differences per treatments.

Trait Treatment	SLA	LDMC	LA	FT
CONV x ROT	0.004*	0.22	0.002*	0.24
CONV x EXCL	0.07	0.99	<0.001*	<0.001*
ROT x EXCL	0.24	0.2	<0.001*	0.008*

Discussion

The overall objective of this study was to quantify intraspecific trait variation under contrasting conditions as a way to assess how plants cope with varying levels of disturbance, in our case grazing, which has led to differences in plant community composition and thus competition. These environmental constraints were the result of a 5-year grazing management experiment. Grazing exclusion has led to clear changes in grassland composition and structure (Ferreira 2014), compared to sites with cattle grazing, mainly visible in the higher contribution of species classified as resource conservation strategy.

The range of intraspecific variation of functional traits (ITV) found in our study is similar to other studies evaluating grassland communities over environmental gradients (Jung et al. 2010; Andrade et al. 2014). SLA often shows considerable plasticity in response to environmental factors (Wilson et al. 1999), which may enhance plant performance under a range of conditions. SLA and LDMC reflect whole-plant strategies of resource acquisition and use, and the large variation of trait values within plots suggests species coexistence may be facilitated by differentiation of resource use strategies (Siefert 2012). This is consistent with previous studies finding extensive ITV in leaf economic traits arising from plastic responses to light, nutrients and other environmental factors. Nonetheless, variation in these traits was much lower than in leaf area (LA), which varied significantly for many species, clearly as a direct consequence of changed community composition. This agrees with the results by Cruz et al. (2010) for *Paspalum notatum*, classified as a resource capture strategist, where the final size of leaves increases with decreasing grazing pressures, but without consequences for leaf traits.

Plants with scleromorphic leaves, i.e. hard leaves, are expect to reduce both the palatability and digestibility of plant material, limiting herbivore fitness (Pérez-Barbería & Gordon 1998; Hanley et al. 2007). We expected plants in excluded treatment would show higher FT related to harder tissues and leaf longevity. However, FT was the most stable trait analyzed, which other authors support. For example, Diaz et al. (2001) showed that, in two-variable models for these grassland species, plant height, life history and life form were more important predictors of grazing resistance than force to tear. It seems that this is an important defense trait when considering small invertebrate herbivores (Hanley et al. 2007) and it is not relevant when it comes to large vertebrate herbivores like cattle. Additionally, we only measured traits for grass and forb species. Shrub species are more hard-leaved than grasses and forbs, and then this trait could play an important role in grazing avoidance (Hanley et al. 2007).

In contrast to our hypothesis, species classified as resource capture strategy (group C) showed less plasticity than species of the resource conservation strategy – except for the trait leaf area which indeed was highly plastic. The lower plasticity of structural traits had previously been indicated for *Paspalum notatum* (Cruz et al. 2010)*;* we here confirm this pattern for several other species of the same group. Most of the species that form group C have long rhizomes, i.e. a creeping habit, and are very rare in the exclusion treatment due to the vegetation height, where the increasing amount of dead biomass decreases light availability for prostrate species, which will eventually disappear (Boldrini & Eggers 1996; Overbeck et al. 2005; Lezama et al. 2014). As shown by Whitworth-Hulse et al. (2016), absence of grazing leads to changes in size-related traits, such as leaf area, which means that the plants can maintain their structural trait expression. Thereby, the capture strategy in the gradient would correspond rather to an adaptation to maximizing the interception of the light resource permitted in stoloniferous types of plant, which allows light interception to be optimized (Sinoquet et al. 1990). Also, high values of SLA are accompanied by a relatively short leaf life span, determining rapid biomass dynamics and release of nutrients as litter (Moreno García et al. 2014), which reflect in grazing tolerance (Louault et al. 2005).

Our study shows that differences in the management in grassland ecosystems, including differences in grazing regimes, can influence trait expression. Our main findings were that the response of individual traits to grazing intensities may be highly variable, species and trait-dependent, especially in the case of species of PFT A, i.e. species with a conservative resource use strategy. This means that some caution should be taken when using mean values of traits from databases without considering the environmental conditions under which traits were measured (Weisser et al. 2017). In addition, the large variation of trait values within plots suggests species coexistence may be facilitated by differentiation of resource use strategies. However, further information of ITV for the whole plant community are needed, to assess patterns of community assembly.

Acknowledgements

This study was conducted as part of the LTER/PELD Campos Sulinos project, coordinated by Valério Pillar and financed by CNPq (558282/2009-1). HS and LSM received a scholarship by CAPES and GEO was supported by a CNPq grant.

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Capítulo 2. Grazing intensity affects the functional structure of subtropical grasslands *

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Short title: Effects of grazing on functional structure of grasslands

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* Artigo submetido ao periódico *Flora*.

Abstract

Grazing is a disturbance affecting floristic composition, vegetation structure and functional patterns in grassland ecosystems. In this study, we aimed to assess the effect of grazing intensity on (1) functional trait diversity and (2) on traits of grassland vegetation. We experimentally assessed the effect of three grazing treatments (conventional, rotational and exclusion) on grassland vegetation in six sites situated in *Pampa* and Highland grasslands in Southern Brazil. We compiled functional traits associated to grazing from the literature. We explored the relations among different sites and grazing treatments through Principal Coordinate Analysis (PCoA). To analyze the effects of grazing treatments on community-weighted mean traits we used the method for discriminating trait-convergence assembly patterns (TCAP). Functional diversity was measured with Rao's quadratic entropy and related to the grazing treatments through two-way analysis of variance. Plant species richness was lower in the grazing exclusion treatment. Functional diversity differed significantly between grazing treatments, with lower values related to the exclusion treatment. We found TCAP affected by grazing intensity for the following traits: plant persistence, rhizomatous and tussock life form. PCoA revealed that in the excluded plots we have more perennial plants, less rhizomatous plants and more tussock plants. Species composition and the functional structure of communities in grasslands in southern Brazil are partially explained by grazing intensity. According to our hypothesis, grassland communities were affected by grazing intensity in terms of composition and functional traits.

Keywords: *Campos Sulinos*; community-weighted means; grassland; grazing experiment; trait convergence.

Abbreviations

FD, Functional diversity; PCoA, Principal Coordinates Analysis; TCAP, trait-convergence assembly patterns.

1. Introduction

Plant communities can be seen as the result of a hierarchy of abiotic (e.g. climatic, resource availability, disturbance) and biotic (e.g. competition, predation, mutualisms) conditions that successively constrain which species can persist at a site (Blanco et al., 2007; Díaz et al., 1998; Keddy, 1992; Levin et al., 2003). In grasslands, disturbances such as grazing affect floristic composition and vegetation structure, but the effect sizes depend on intensity and frequency of the disturbance, as well as on evolutionary history and productivity levels of the grassland (Cingolani et al., 2005; Lezama et al., 2014; Vandewalle et al., 2014). Grazing itself thus acts as an environmental filter on plant communities, and some studies have reported that grazing increases heterogeneity in species composition (Bakker et al., 2003).

One of the effects of grazing in productive systems is the suppression of high dominance by few competitively superior species, in contrast to systems without grazing where these species will exclude inferior competitors (Boldrini and Eggers, 1996; Cingolani et al., 2005; Cruz et al., 2010; Overbeck et al., 2005). In productive grasslands, the cessation of grazing is followed by increased dominance of a few species and associated decline of species adapted to grazing (Lezama et al., 2014). In contrast, an overgrazing can lead to a decline in biomass of grassland species and thus of productivity, and this phenomenon is a major cause of grassland degradation (Mysterud, 2006; Ruppert et al., 2012). Also, heavy grazing or intense competition in abandoned grasslands are expected to reduce the number of functional types of species that co-exist, and lead to a loss of functional diversity (McIntyre and Lavorel, 2001).

It has been shown before that grazing plays an important role in defining functional patterns of plants in grassland systems (Blanco et al., 2007; Díaz et al., 2001). A functional approach in studies of community assembly can reveal patterns associated to environmental filters, as the organisms have morphological features that respond to variations in the environment (Keddy, 1992; Violle et al., 2007), and can impact plant fitness indirectly via their effects on plant growth, reproduction and survival (Violle et al. 2007). Grazing-induced changes in species composition and diversity may result in predictable responses by plant life forms characterized by different functional traits (Díaz et al., 2007).

Gradients of abiotic conditions and biological interactions of species may induce non-random patterns of community assembly. From this perspective, the local action of environmental filters leads to a community whose species are more similar to each other regarding their functional traits than expected at random, which is result of trait convergence in community assembly (Keddy, 1992; Pillar et al., 2009). On the other hand, the role of biotic interactions in communities can generate limiting similarity, and species coexistence is only possible if its traits presented different patterns, resulting in a trait divergence assembly pattern (Grime, 2006; Pillar et al., 2009). Strong abiotic or biotic filtering effects, such as heavy grazing or intense competition in abandoned grasslands, are expected to reduce the number of functionally similar species that can co-exist, and lead to a loss of functional diversity (McIntyre and Lavorel, 2001; Pillar et al., 2009).

While some studies on the relationship between grazing and vegetation patterns and dynamics in grassland communities in Southeastern South America are available (e. g. Boldrini & Eggers 1996; Lezama et al. 2014), studies evaluating effects of different grazing levels and on functional composition are rare (Díaz et al., 2001). In this study, we analyzed the effects of grazing intensity levels defined by grazing treatments (conventional grazing, low-intensity grazing, and grazing exclusion) on functional patterns of grassland communities. We assessed the effect of grazing intensity on (1) functional trait diversity and (2) on plant traits itself. We hypothesized that (1) grazing exclusion reduce species richness and functional diversity; (2) life form traits are affected by grazing intensity, as cover of tussock species increases and that of prostrate species decreases from the heavy grazing to the grazing-exclusion treatment.

2. Material and methods

2.1. Study sites

The study was carried out at six sites characterized by species-rich native grasslands in southern Brazil (Table 1), in the framework of an ongoing long-term ecological research experiment, the PELD/LTER Campos Sulinos. Three sites were located in the Pampa grasslands (Aceguá, Alegrete and Lavras do Sul) and three in the Highland grasslands (Cambará do Sul in Aparados National Park, Jaquirana in Tainhas State Park and São Francisco de Paula in Aratinga State Park); the sites thus spanned over two contrasting grassland types (Overbeck et al., 2007). Climate in the Pampa region is Cfa and in the Highland region is Cfb. Details of bioclimatic data are shown in Table 1, extracted from WorldClim Database (Hijmans et al., 2005). The vegetation at all sites is natural grassland that had been under cattle grazing since its introduction during European colonization in the 17-18th Centuries. At sites in the Highland region, burning is common tool for pasture management.

2.2. The Experiment

The experiment was set up adopting a randomized block design, with one block at each site composed of three 70 x 70 m (0.5 ha) contiguous plots that were randomly allocated to three treatments: (1) grazing exclusion, (2) rotational management and (3) conventional management. Treatments were applied since spring of 2010, except for the rotational grazing treatment, which started a year later due to logistic limitations. The grazing exclusion plots and rotational management were fenced, while the plot subjected to conventional grazing was not fenced and was inserted in a larger area under the conventional management adopted by the local farmers. In the rotational management plot, the criteria used to determine the time interval between cattle access was the cumulative thermal sum of 700 degree-days, which aimed to maintain the contribution of conservative grass resources (Quadros et al., 2006). Duration of grazing in the rotational treatment was up to three days.

From September 2014 to January 2015 we described the vegetation in nine 1 m^2 permanent quadrats systematically located in each plot, using estimation of cover of all vascular plant species according to Londo's decimal scale (Londo, 1976).

2.3. Functional Traits

Traits expected to respond to grazing disturbance were compiled from literature. We selected the following traits: plant height – associated with competitive vigor and time to grow between disturbances (Cornelissen et al., 2003); life form – indicative of plant life strategy (Ferreira, 2014); belowground storage organs – related to the potential for vegetative reproduction and persistence after environmental disturbances (Cornelissen et al. 2003); persistence – related to perennial or annual plants; leaf morphometry – measured as maximum and minimum width and length, related to leaf energy and water balance (Cornelissen et al. 2003); diaspore type – related to dispersal strategies (Van der Pijl, 1969). Details on the measure unit and type of traits are described in Table 2.

We gave priority to compile functional traits to the species with the highest relative cover. At the end, we obtained traits for 104 species, which represented 64% of relative cover of communities.

2.4. *Data Analysis*

We compared species richness in the different grazing treatments through permutation analysis of variance, considering each 0.5 ha plot as sampling unit and the significance level as $\alpha \leq 0.05$. This analysis was carried out in R 3.2.0 (R Development Core Team 2015), using function *aovp* from package lmPerm. To explore the variation in species composition between grazing treatments, we submitted the vegetation data to Principal Coordinate Analysis (PCoA) using Chord distance as similarity measure between sampling units, considering as units each 0.5 ha plot. In order to highlight the differences, we calculated a mean value coverage for each species to each plot, and subtracted this value from the estimated coverage in field.

Functional diversity (FD) for each 0.5 ha plot was measured by Rao's quadratic entropy (Botta-Dukát, 2005) with the following traits: persistence, life form. FD was related to classes of grazing intensity and to each site through permutation analysis of variance. This analysis was carried out in R 3.2.0 (R Development Core Team 2015).

To study the response of functional traits of communities to grazing intensity, we used the method proposed by Pillar et al. (2009) for analyzing trait-convergence assembly patterns (TCAP), which consists of a Mantel correlation of distance matrices between each 0.5 ha plots based on community-weighted trait means (**T**) and on environmental matrix (**E**). For this, traits composed a matrix describing species by their traits (matrix **B**), the species composition data defined a species by plots matrix (**W**) containing species relative cover in each plot, and the grazing treatments defined dummy variables for the plots arranged in environmental matrix (**E**). Matrix **T** was generated by scaling-up species traits to the community level, by multiplying matrices **B** transposed and **W.** The Mantel correlation ρ(**TE**) of **T** and **E** indicates the strength of trait-convergence patterns related to grazing intensity. The significance of ρ(**TE**) was tested by permutation of the trait vectors among species, maintaining the other matrices fixed (Pillar et al. 2009). To assess the links between traits and grazing intensity, we submitted matrix **T** to a Principal Coordinates Analysis (PCoA) based on Euclidean distances between plots, after trait standardization. These analyses were performed in MULTIV v. 3.40β and SYNCSA v. 2.10.1 (V. Pillar, available at [http://ecoqua.ecologia.ufrgs.br]).

3. Results

We found 319 species distributed in 43 families among the six sampling sites. Plant species richness was lower in the excluded treatment (Fig. 1, P<0.001).

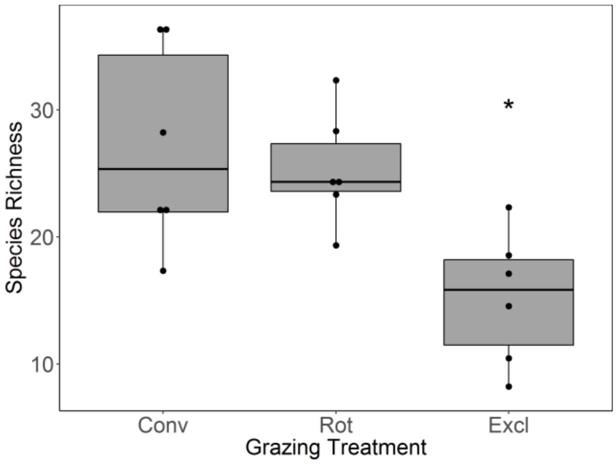

Figure 1: Species richness in the different treatments, considering all 0.5 ha plots. Grazing treatments labels are: Conv, conventional management; Rot, rotational management; Excl, cattle exclusion. Treatments indicated with asterisk differ significantly (P < 0.05).

The PCoA for sampling units revealed differences on taxonomic composition, separating the exclusion treatment from the other treatments (Fig. 2). The first two axis explained 20.5% and 17.6% of variation.

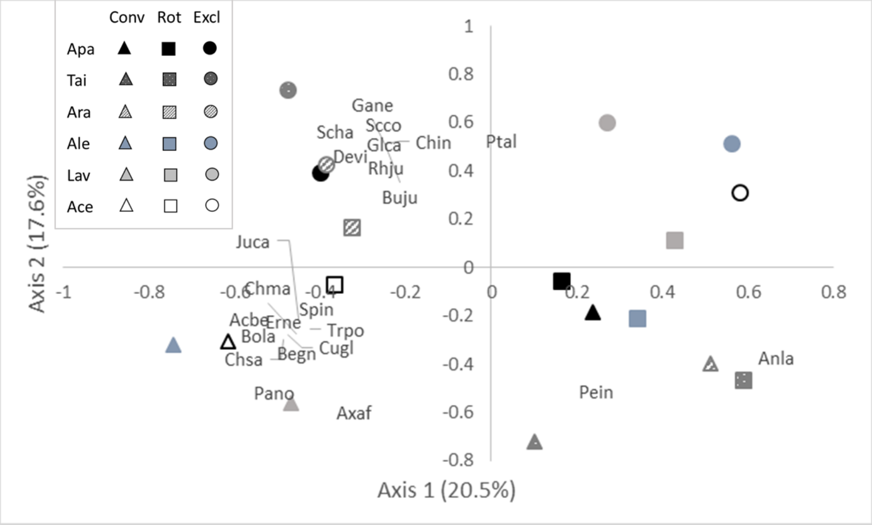

Figure 2: Ordination diagram of the PCoA of species density per plot, highlighting the compositional differences between Pampa biome sites and Atlantic forest sites. Site labels are: Pampa grasslands sites – Ale, Alegrete site; Lav, Lavras do Sul site; Ace, Aceguá site; Highland grasslands sites – Apa, Aparados site; Tai, Tainhas site; Ara, Aratinga site. Grazing treatments labels are: Conv, conventional

management; Rot, rotational management; Excl, cattle exclusion. Species with correlation ρ≥ 0.52 with the axis are shown in the ordination diagram; species labels are: Acbe, *Acmella bellidioides*; Anla, *Andropogon lateralis*; Axaf, *Axonopus affinis*; Begn, *Berroa gnaphalioides*; Bola, *Bothriochloa laguroides*; Buju, *Bulbostylis juncoides*; Chin, *Chaptalia integerrima*; Chma, *Chaptalia mandonii*; Chsa, *Chevreulia sarmentosa*; Cugl, *Cuphea glutinosa*; Devi, *Desmanthus virgatus*; Erne, *Eragrostis neesii*; Gane, *Galactia neesii*; Glca, *Glandularia catharinae*; Juca, *Juncus capillaceus*; Pano, *Paspalum notatum*; Pein, *Petunia integrifolia*; Ptal, *Pterocaulon alopecuroides*; Rhju, *Rhynchospora junciformis*, Scco, *Schizachyrium condensatum*; Scha, *Schizachyrium hatschbachii*; Spin, *Sporobolus indicus* and Trpo, *Trifolium polymorphum*.

Functional diversity differed significantly among grazing treatments (P < 0.001). Lower values of functional diversity were related to the exclusion treatment, while higher values were found for conventional and rotational treatments (Fig. 3).

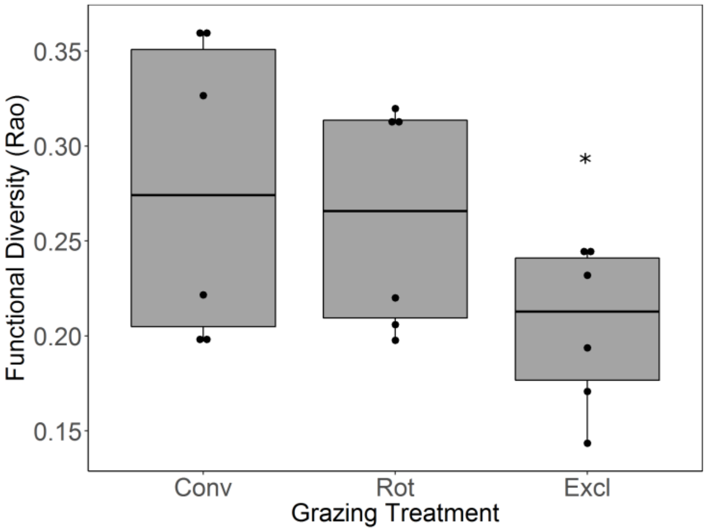

Figure 3: Boxplot of functional diversity values (Rao’s quadratic entropy) of plant traits at each grazing treatment. Grazing treatments labels are: Conv, conventional management; Rot, rotational management; Excl, cattle exclusion. Treatments indicated with asterisk differ significantly (P < 0.05).

We found trait-convergence assembly patterns (TCAP) related to the grazing gradient. The traits maximizing TCAP [ρ(**TE**)=0.13; P=0.003] were: plant persistence, rhizomatous and tussock life forms. The PCoA revealed that in the excluded plots we had more perennial plants, less rhizomatous plants and more tussock plants (Fig. 4). We can observe that excluded plots of Pampa grasslands are functionally similar to all Highland grasslands plots; also, for the latter, the three treatments of each site are much more uniform than those of the Pampa.

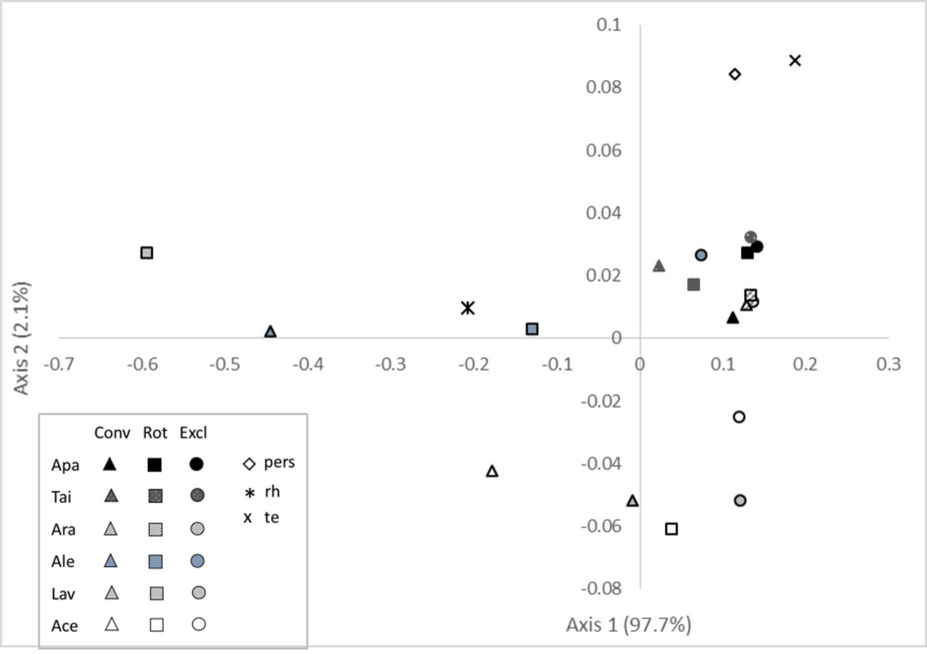

Figure 4: Diagram of Principal Coordinates Analysis (PCoA) of grassland communities described by the mean values of their plant traits. Site labels: Pampa biome – Ale, Alegrete site; Lav, Lavras do Sul site; Ace, Aceguá site; Atlantic forest biome – Apa, Aparados site; Tai, Tainhas site; Ara, Aratinga site. Grazing treatments labels: Conv, conventional management; Rot, rotational management; Excl, cattle exclusion. Functional traits labels: pers, plant persistence; rh, rhizomatous life form; te, tussock life form.

The analysis of variance of selected traits according to grazing treatment (Fig. 5) revealed that the rhizomatous life form had significantly higher cover in the conventional treatment. There was no difference in proportion of tussock life form or plant persistence between treatments (P-values = 0.05, 0.1, and 0.8, respectively).

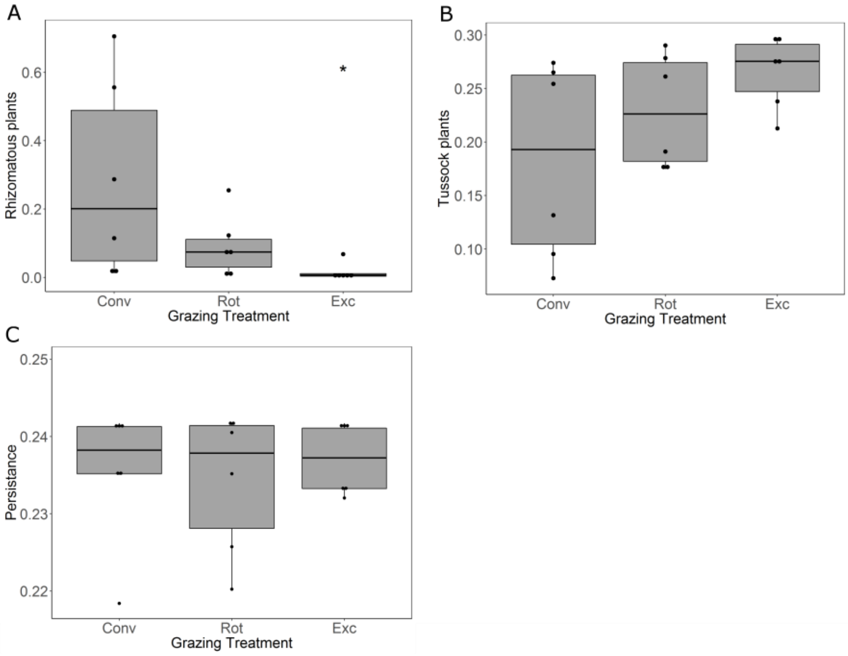

Figure 5: Boxplot of selected traits and grazing treatment. A. Community-weighted means for rhizomatous plants. B. Community-weighted means for tussock plants. C. Community-weighted means for persistence of plants. Grazing treatments labels: Conv, conventional management; Rot, rotational management; Excl, cattle exclusion. Treatments indicated with asterisk differ significantly (P < 0.05).

4. Discussion

After 4-5 years of applying three distinct grazing treatments in grassland, our study revealed significant effects in terms of taxonomic and functional diversity, as well as on community weighted mean traits. In a conceptual model for large-herbivore effects on grasslands, Milchunas et al. (1988) described that grazing effects on plant species composition depend on the position of a moisture gradient (with implications for productivity) and evolutionary history of grazing in the area. In our case, the sites in the Highland grasslands presents a lower grazing pressure than Pampa grasslands sites, even in the conventional management, which makes treatments within sites more similar. Additionally, the traditional use of fire in the region may also have acted as a filtering factor for certain plant types, e.g. tussock grasses at the expense of creeping grasses (e.g. Overbeck et al. (2005)). Despite these differences between grasslands from the two regions, general trends emerged in our study. Specifically, we found higher species richness in both grazed plots than in exclusion plots. Overall, these patterns correspond with predictions of conceptual models for large-herbivore effects on grasslands (Díaz et al., 2007; Milchunas et al., 1988) and other studies that found grazing producing differences in species composition, richness and dominant species cover (Bakker et al., 2003; Lezama et al., 2014; McIntyre and Lavorel, 2001). In productive grasslands, the cessation of grazing is followed by increased dominance of a few species and associated decline of species adapted to grazing (Lezama et al. 2014). Bakker et al. (2003) also found a strong correlation between light availability and species richness in response to grazing. Since ungrazed plots have low availability of light due to increasing amount of dead biomass (Boldrini & Eggers 1996; Overbeck et al. 2005; Lezama et al. 2014), lower species richness is expected in this situation.

In addition, we found higher plant functional diversity (FD) in the conventional and rotational management, while in the excluded treatment communities presents a loss of functional diversity. The higher FD represents communities with a broader range of values and also very different states of traits (Petchey and Gaston, 2002). FD is known to discriminate processes that rule community assembly related to biotic and environmental filters (De Bello et al., 2013; Grime, 2006). The absence of grazing promoted the homogenization of the communities by reducing the contribution of prostrate species and leading to a dominance of tussock species (Boldrini and Eggers, 1996), which can clearly be seen in the ordination diagram. One mechanism behind these changes should be the increasing amount of dead biomass in plots with grazing exclusion, where light become less available to prostrate species, that eventually disappear (Boldrini & Eggers 1996). This result is supported by other studies that found increased abundance of prostrate and annual plants in grazed areas, while tussocks and perennial plants are dominant in areas with low intensity of grazing (Díaz et al., 2007; McIntyre and Lavorel, 2001). Altogether, the importance of historical land-use patterns on functional composition of grasslands is well-known (Vandewalle et al., 2014); in our case, the use of fire as a management tool in the grasslands may have acted, together with the more similar climatic features at the Atlantic Forest sites, as homogenizing factors for grasslands in this region, making treatment effects weaker in this region.

We found a trait-convergence assembly pattern related to the treatments of grazing intensity. Moraes et al. (2016) found patterns of convergence for grasslands communities related to traits describing plant survival strategies on edaphic gradients and in relation to high light exposure. In our study, the traits reflecting convergence were those related to plant structure and life cycle. The contrasting life forms of grasses, tussock plants and rhizomatous species, have been linked to general strategies of resource acquisition of plants (Cruz et al., 2010). Additionally, they exert influence on vegetation structure and competitive interactions, thus driving the changes observed. The rotational management, i.e. the intermediate grazing intensity of our gradient, showed a higher heterogeneity in species considering the persistence of plant. Tussock life form is related to plant height, which is often related to the ability to efficient capture light (Grime, 2006). Thus, the selected traits showed a significant relationship with environmental variables and probably are the major traits for species selection during the assembly process. Community-weighted means differed between treatments indicating a pattern of trait-convergence concerning the grazing gradient.

5. Conclusions

In conclusion, our study shows that species composition and the functional structure of communities in grasslands in southern Brazil are partially explained by the position of grasslands among a grazing intensity gradient, and this pattern is consistent among distinct grassland regions. Patterns of trait convergence were found along this gradient and were partially determined by management history, which indicate that both abiotic and biotic filters are structuring the plant communities. In according to our hypothesis, grassland communities through grazing gradient differed in terms of composition and functional traits.

Funding

This study was conducted as part of the LTER/PELD Campos Sulinos project, coordinated by VDP and financed by CNPq (558282/2009-1). HS received a scholarship by CAPES. GEO, IIB and VDP was supported by a CNPq grant (310022/2015-0, 309934/2015-0 and 307689/2014-0, respectively).

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Tables

Table 1: Bioclimatic data of each study site, extracted from WorldClim Database (Hijmans et al., 2005), and mean species richness by site.

Site	Mean Annual Rainfall (mm)	Mean Annual Temperature (ºC)	Mean Altitude (m)	Mean species richness (per $1m^2$)
Aceguá	1158	17.9	175	24.3 ± 13.4
Alegrete	1509	18.9	108	28.6 ± 10.5
Lavras do Sul	1450	17.8	345	22.4 ± 7.7
Aparados	1917	15	962	22.7 ± 5.05
Aratinga	1981	15.2	901	17.2 ± 6.1
Tainhas	1636	16.9	758	20 ± 7.6

Table 2: Selected plant traits for this study. Life form states following Ferreira (2014): ct, connected evergreen tussocks; de, decumbent evergreens; ef, evergreen forbs; er, erect rosette evergreens; pr, prostate rosette evergreens; rh, rhizomatous evergreens; ss, evergreen subshrubs; st, stoloniferous evergreens; te, solitary evergreen tussocks; th, therophytes. Diaspore type: annx, diaspore with attached structure; fruit, entire fruit is dispersed; seed, seed is the dispersal structure.

Trait	Type of variable	Measuring unit or trait states
Plant height	Quantitative	cm
Life form	Categorical	ct de ef er pr rh ss st te th
Belowground storage organs	Binary	0/1
Persistence	Binary	0/1
Leaf morphometry	Quantitative	cm
Diaspore type	Categorical	annx fruit seed

Considerações Finais

A partir deste trabalho foi possível identificar os padrões funcionais das comunidades vegetais campestres ao longo de diferentes intensidades de pastejo. No primeiro capítulo focamos na variação intra-específica de atributos foliares das espécies dominantes de cada sítio. A partir dos principais resultados encontrados, pudemos observar um padrão de variação ao longo do gradiente de pastejo, em que a exclusão de pastejo tende a selecionar indivíduos com menor SLA, e maior LA e FT. Assim, confirmamos que diferentes intensidades de pastejo promovem uma resposta funcional que é muito variável, e dependente do atributo e da espécie em questão.

No segundo capítulo, abordamos os padrões funcionais no nível das comunidades vegetais. Os principais resultados mostraram que as comunidades de plantas campestres diferiram entre os sítios dos biomas Pampa e Mata Atlântica quanto à sua composição de espécies. Também encontramos maior diversidade funcional nos sítios do bioma Pampa. Os resultados analisando as diferenças entre os tratamentos de pastejo mostraram que a riqueza de espécies é menor quando há exclusão de pastejo. Quanto aos padrões funcionais, o tratamento excluído também apresentou menores índices de diversidade funcional. Esses resultados corroboram as hipóteses que a exclusão de pastejo leva à uma homogeneização da vegetação e perda de diversidade funcional. Sendo assim, a manutenção da biodiversidade dessa vegetação está adaptada à perturbações como o pastejo e o fogo.

Outro resultado importante foi a identificação das respostas funcionais das comunidades ao gradiente de pastejo. Encontramos padrão de convergência de atributos em relação ao gradiente, em que as áreas de exclusão apresentam mais espécies perenes e entouceiradas, e menos espécies rizomatosas. Esse padrão de convergência encontrado pode ser causado por processos evolutivos, indicando que tanto filtros bióticos como abióticos estão atuando sobre a estrutura das comunidades.

Visto que a pecuária é uma das principais atividades econômicas em áreas de campo, e a interação do pastejo com a vegetação é um dos principais fatores responsáveis pela manutenção dos campos do sul do Brasil, este estudo contribui para o entendimento das relações da vegetação com o pastejo, demonstrando que a manutenção da atividade é fundamental para a manutenção da diversidade biológica dos campos. Estudos futuros deveriam concentrar esforços nas relação da vegetação com características do solo e também em aumentar o banco de dados de atributos para toda a comunidade campestre, para elucidar questões ainda em aberto. Sobretudo, este estudo fornece dados taxonômicos e funcionais para diferentes formações campestres do Rio Grande do Sul.

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