UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Dissertação de Mestrado

ESTRUTURA FUNCIONAL E PROCESSOS ECOSSISTÊMICOS EM CAMPO NATIVO MEDIADOS PELA INTENSIDADE DE PASTEJO

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Porto Alegre, Fevereiro de 2013

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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, Fevereiro de 2013

AGRADECIMENTOS

A elaboração da presente dissertação envolve muito mais do que a titulação de mestre. Ela faz parte de uma fase concluída em uma escalada, um projeto de vida, e, se materializa como uma síntese de minha formação profissional, paixão pela ecologia e pela pesquisa.

Mesmo sendo um caminho solitário nunca teria obtido o presente êxito sem a companhia de diversas pessoas que estiveram ao meu lado e me apoiaram das mais distintas maneiras.

Primeiramente ao meu orientador, Prof. Dr. Valério De Patta Pillar não somente nesses dois anos de mestrado, mas também nos quatro anos de iniciação científica em que durante o longo trajeto acompanhou meu amadurecimento como pessoa e como profissional. Ele me incentivou e, principalmente, me instigou a desvendar padrões e processos onde só enxergamos grama, com sua "aura de lógica" que sempre tornava tão simples as questões com as quais eu matutava por horas sem esperanças de resolvê-las. Porém não posso prometer que assimilei, ou para ser franca aceitei todas as suas opiniões, mas espero não ter sido tão "cabeça dura" e ter seguido o caminho pelos quais ele me conduziu.

Aos colegas do laboratório de Ecologia Quantitativa, que também, durante esse tempo formaram uma família dinâmica, sempre disponível para ajudar no campo, nas análises, na escrita ou até mesmo em devaneios teóricos na hora do cafezinho. Mas, principalmente, agradeço por aguentarem meu autoritarismo e meu mau humor pela manhã. André Dresseno, Anaclara Guido, Gabriele Pilger, Luciana Mertins, Mariana de Ávila, Fernando Joner, Mark Leithead, Vanessa Panachuk, Rafael Machado, Bethânia Azambuja, Diógenes Machado.

Demais ajudantes de campo, pela força e determinação sob as horas de sol escaldante em meio aos espinhos de gravatá: Camila Bonilha, Robberson Setubal, Fábio Torchelsen, Mariana Vieira, Rosângela Rolim, Lidiane Boavista, Graziela Silva e Rodrigo Baggio.

Aos excelentes botânicos de plantão do Levcamp, pela ajuda na identificação do material e pelos ensinamentos: Profª. Ilsi Boldrini, Pedro Joel e Ângelo Schneider.

À equipe do Grupo de Pesquisa em Ecologia do Pastejo do Departamento de Plantas Forrageiras e Agrometeorologia por permitirem realizar o trabalho dentro do experimento de manejo de campo nativo e pela ajuda em campo: Prof. Paulo Carvalho, Júlio Azambuja Ian Cezimbra e Olivier Bonnet.

A Luciana Podgaiski pelas ideias e pela ajuda na metodologia de decomposição e na elaboração do segundo artigo.

Aos colegas mestrado pelo companheirismo nas disciplinas e momentos de descontração.

À minha família e ao Gabriel Pontalti pela compreensão e paciência com a minha ausência.

Aos meus amigos da graduação (*euamigos*), em especial Lindsey Cassini por me ajudar nessa *indiada*.

Ao CNPq pelo auxílio financeiro através do projeto PELD Campos Sulinos.

Ao Programa de Pós-Graduação em Ecologia da UFRGS pela oportunidade e pelos ótimos professores.

A CAPES pela bolsa.

RESUMO

O pastejo em campos nativos é um distúrbio que afeta a comunidade vegetal e processos por ela promovidos. O objetivo desse estudo foi determinar como a intensidade do pastejo afeta os padrões de distribuição de espécies e atributos funcionais e como essa mudança na vegetação afeta processos ecossistêmicos relativos à decomposição de serapilheira. Em uma área de campo nativo na região da Depressão Central do Rio Grande do Sul foi instalado um experimento com 14 potreiros submetidos a três diferentes intensidades de pastejo. Em cada um deles tomou-se a cobertura média de espécies e atributos funcionais das mesmas. Com o uso de *litter-bags e bait-lamina* avaliamos a decomposição da serapilheira e a atividade dos invertebrados detritívoros do solo. Comparamos a cobertura de espécies, e atributos e diversidade funcional entre os tratamentos. Exploramos a relação de variáveis estruturais do habitat, atributos e diversidade funcional aos processos avaliados. A intensidade de pastejo afetou significativamente a cobertura de espécies e atributos funcionais, aumentando a os valores médios de área foliar específica e diminuindo os de conteúdo de matéria seca, e a presença de espécies com rota fotossintética C4, cespitosas e hemicriptófitas, além de diversidade funcional. Nas áreas menos pastejadas a atividade de detritívoros também foi maior, relacionada à altura da vegetação, quantidade de biomassa morta e espécies com rota fotossintética C4, e negativamente relacionada à quantidade de solo descoberto e à diversidade funcional. A decomposição de serapilheira não foi afetada pela intensidade de pastejo, e sim pela presença de espécies com órgãos subterrâneos de reserva e pela maior diversidade funcional. Intensidade de pastejo seleciona espécies pelos seus atributos funcionais, atuando como um filtro ambiental. Sob alta pressão de pastejo, a intensa desfolhação permite apenas a persistência de espécies adaptadas a um rápido rebrote. Áreas menos pastejadas permitem o desenvolvimento de plantas com folhas resistentes e longas. A competição nessas comunidades promove uma diferenciação de nicho e alta diversidade funcional, resultando em um padrão de divergência nos atributos. Organismos detritívoros são beneficiados por essa vegetação densa, enquanto que a decomposição da serapilheira responde a outros fatores que não à atividade de organismos detritívoros.

Palavras-chave Pastagem nativa, atributos funcionais, convergência, divergência funcional, processos ecossistêmicos, decomposição de serapilheira, atividade de detritívoros.

ABSTRACT

Cattle livestock grazing is a disturbance that affects plant community and its processes. Our objective is to determine how grazing intensity affects plant species distribution patterns and their functional traits; and how these changes affect ecosystem processes related to litter decomposition. In a native grassland area in southern Brazil an experiment of 14 paddocks submitted to three different treatments of cattle grazing intensity was assessed. At each paddock we evaluated species cover and their functional traits. We also evaluated litter decomposition (litter-bag method) and detritivore activity (bait-lamina test). We compared species cover, functional traits and functional diversity between treatments. We explored the relations between habitat structure variables and the ecosystem processes. Increasing grazing intensity significantly affected species cover and functional traits, it increased community weighted means for SLA and decreased LDMC, proportion of species with C4 metabolic pathway, caespitose and hemicryptophytes; also increased functional diversity. Grazing intensity decreased detritivore activity, which was related to vegetation height, dead biomass cover and species with C4 photosynthetic pathway; and negatively related to bare soil and functional diversity. Litter decomposition was not affected by grazing intensity, but it was related to presence of species with belowground storage organs and higher functional diversity. Grazing intensity selects species by their functional traits, acting like an environmental filter. Under high grazing intensity, severe defoliation allows only persistence of similar species adapted to rapid resprout. Under low grazing intensity, the lack of frequent defoliation enables the development of species with high investment on strong and long-lived leaves. Competition in these plots promotes niche differentiation and high functional diversity, leading to a divergence pattern of communities' traits. Further, the dense vegetation benefit detritivore organisms, while litter decomposition is affected by other factors than detritivore activity.

Key-words Natural pasture, functional traits, convergent and divergent functional patterns, ecosystem processes, litter decomposition, detritivore activity.

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Introdução

Campos naturais provêm diversos serviços ambientais, como forragem para criações domésticas. O pastejo, no entanto, pode acarretar drásticas modificações no ambiente. Ao contrário do que ocorre em processos naturais de pastejo, onde populações de grandes herbívoros são determinadas pela disponibilidade de recursos e condições climáticas; em sistemas de pastejo manejados, a densidade da população é geralmente mantida acima da capacidade de suporte e artificialmente direcionada (Carvalho & Batello 2009).

Campos nativos do sul do Brasil compreendem um grande biodiversidade, com mais de 2.200 espécies vegetais (Boldrini 2009). Por se tratar de um ecossistema diferenciado do restante do Brasil, onde na sua maioria são de porte arbóreo ou arbustivo, o apelo para sua conservação fica em segundo plano. Mesmo a legislação brasileira, até 2004 não reconhecia o bioma Pampa como um dos tipos de vegetação (IBGE 2004). Histórica falta de reconhecimento de sua importância para a biodiversidade levou a uma negligencia na conservação desses ambientes.

Estudos comprovam que esse tipo de formação faz parte de uma vegetação relictual de um clima passado mais seco e frio (Behling & Pillar 2007). Ainda não está claro se estes campos são adaptados ao pastejo. Ou seja, se esse distúrbio pode ser considerado natural. Há evidencias de que esses campos originalmente sustentavam uma megafauna pastadora, e após a extinção de grande parte dessas espécies (grande extinção do Pleistoceno), os campos só voltaram a ser pastejados após a introdução de gado por colonizadores europeus na região (Pillar et al. 2010; Müller et al. 2012). Hoje, o pastejo por animais domésticos é um dos principais distúrbios que moldam os campos nativos, afetando sua manutenção, produtividade, proveito econômico, e manejo da biodiversidade.

O distúrbio promovido pelo pastejo se deve à remoção seletiva de espécies ou partes de plantas (Milchunas et al. 1988). Essa seletividade e a intensidade de desfolhação atua como um filtro ecológico na comunidade vegetal. Em ecologia de comunidades há muitas teorias sobre como e se as espécies se organizam no meio abiótico e quais os processos que definem esses padrões. Organismos são selecionados, ou seja, para se estabelecer em um local, devem ser capazes de ultrapassar diversos "filtros" (Keddy 1992). Para melhor compreendermos essas respostas devemos não apenas considerar a identidade do organismo como pertencente a uma espécie, e sim as características que conferem a ele a capacidade de ultrapassar esses filtros (Violle et al. 2007). Esses conjuntos de características ecologicamente ativas são denominados "atributos funcionais de resposta" (Keddy 1992; Lavorel et al. 2002; Canadell et al. 2007).

Espécies são capazes de afetar processos e serviços ecossistêmicos (Tilman 1997). Atributos que conferem a elas essa capacidade são os chamados "atributos funcionais de efeito" e eles podem ou não ser ao mesmo tempo atributo de resposta (Blanco et al. 2007; Harrington et al. 2010). Assim, somos capazes de inferir sobre os processos ecossistêmicos relacionados a atributos de espécies na comunidade (Bello et al., 2010; Lavorel, et al., 2011), bem como às combinações de atributos (diversidade funcional)(Díaz & Cabido 2001). A diversidade é funcionalmente importante porque aumenta a probabilidade de incluir espécies com fortes efeitos no ecossistema, assim, aumentando a eficiência da utilização dos recursos disponíveis (Chapin et al. 1997). Diversidade proporciona estabilidade à comunidade, resiliência e resistência frente a mudanças climáticas. Portanto, em comunidades naturais, a biodiversidade (em todos os níveis de organização) é ao mesmo tempo uma variável respondendo ao ambiente e um fator influenciando o funcionamento do ecossistema, e a depauperação de espécies ou tipos funcionais na comunidade pode por em risco esses processos (Chapin et al. 2000; Lavorel et al. 2011).

O uso de ecossistemas campestres como forragem para criações domésticas afeta a estrutura funcional da vegetação e, consequentemente, processos ecossistêmicos promovidos por ela. O pastejo influencia a distribuição de espécies de plantas de diferentes maneiras (Díaz et al. 2007). Assim, é um novo filtro atuante na comunidade, definindo a maneira como as espécies se relacionam, alterando sua composição. O impacto promovido pelo pastejo é evidente nos atributos de resposta das plantas da comunidade, porém esta variação pode também estar relacionada com a mudança nos atributos de efeito e, consequentemente, com os processos ecossistêmicos a eles relacionados.

Plantas, além de serem responsáveis pela produtividade primária da cadeia trófica, são também engenheiras do ecossistema, oferecendo abrigo e um microclima favorável para a fauna e a microbiota (Jones et al. 1997). Assim, indiretamente afetam os principais processos ecossistêmicos (Lavorel & Garnier 2002; Bello et al. 2010). Nesse sentido, a delimitação de atributos funcionais de efeito para as espécies vegetais é de suma importância para inferências de mudanças nos processos ecossistêmicos mediados por esses organismos.

Decomposição de serapilheira é um exemplo de processo ecossistêmico que é direta e indiretamente afetado pela estrutura da vegetação. Esse processo interfere profundamente nos ciclos globais de carbono e a ciclagem de nutrientes em ecossistemas terrestres, permitindo o retorno dos nutrientes no solo, mantendo a fertilidade e a produtividade do ecossistema (Hättenschwiler et al. 2005; Canadell et al. 2007).

Dentre os fatores que afetam a decomposição de serapilheira, a composição e a qualidade química do material foliar senescente definem a decomposabilidae. Além disso, o efeito de condições ambientais na decomposição inclui propriedades físico-químicas do solo (Vossbrinck et al. 1979), e condições climáticas que determinam umidade e a degradação física por intempéries e fotodegradação (Austin 2006). Outro fator crucial que define a decomposição da serapilheira é a abundância e a composição de organismos detritívoros. Muitos grupos de invertebrados de solo incluem espécies detritívoras, tais como nematoides, artrópodes (ácaros, colêmbolas, isópodes, diplópodes, cupins, e alguns besouros) e minhocas (Lavelle 1996). Artrópodes constituem um grupo megadiverso, e respondem rapidamente a distúrbios, principalmente quando estes afetam propriedades estruturais e microclimáticas do habitat. Portanto diferenciação na atividade alimentar de organismos detritívoros pode ser usada como uma aproximação da atividade de decomposição, contornando-se assim a necessidade de obtenção de dados de abundância e composição de espécies detritívoras (Reinecke et al. 2008). Atributos funcionais de plantas podem, então, afetar a decomposição da serapilheira diretamente através da decomposabilidade e indiretamente por determinar a estrutura do habitat e oferecer proteção contra fatores abióticos (radiação solar, vento e chuva) para os organismos detritívoros (de Bello et al. 2010a).

Nesta dissertação avalio a variação na estrutura de cobertura vegetal e atributos funcionais da comunidade, e se esta variação também se reflete nos processos ecossistêmicos mediados por esses atributos. O primeiro artigo, intitulado “Effects of grazing intensity on trait-based community patterns in South Brazilian native grasslands" avalia as principais efeitos causados pelo pastejo na comunidade vegetal, tendo como foco de estudo a cobertura de espécies, identificando as mais relacionadas aos níveis de intensidade de pastejo. Além disso, são também identificados, dentre vários atributos levantados, aqueles que melhor refletem respostas das comunidades ao pastejo e os que melhor representam a variação na diversidade funcional.

O segundo artigo, "Litter decomposition and soil detritivore activity respond to habitat structure changes related to grazing intensity in native grassland", tem como objetivo avaliar se a diferenciação na estrutura da vegetação (cobertura de espécies, atributos e diversidade funcional), resultante da intensidade de pastejo afetam a decomposição da serapilheira e a atividade alimentar de organismos detritívoros. Identifica também quais as variáveis mais relacionadas e possíveis relações causais para esses processos, envolvendo atributos funcionais e diversidade funcional.

Capítulo I

"Effects of grazing intensity on trait-based community patterns in South Brazilian native grasslands"

Abstract

Questions: How does grazing intensity affect species composition and species traits? What plant traits converge or diverge along ecological gradient?

Location: Natural grassland in southern Brazil, Estação Experimental Agronômica, UFRGS.

Methods: The study area (ca. 52 ha) is divided in 14 experimental units (paddocks) that have been subjected to more than 25 years of different treatments of grazing intensity. Treatments were defined by the availability of forage per live weight of bovine cattle. In each paddock we recorded average plant species cover and species functional traits in nine plots of 1 m^2. We tested the effect of grazing intensity on species and traits by using multivariate analysis of variance (MANOVA) with permutation testing. We also tested if treatments had an effect on functional diversity (Rao quadratic entropy).

Results: Species and traits cover were affected by grazing intensity. SLA increased with grazing intensity, while LDMC, presence of caespitose, hemicryptophytes and C4 species decreased. Rao quadratic entropy (for the traits leaf length, form, shrub habit,

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Artigo a ser submetido à revista Journal of Vegetation Science

caespitose growth form, erect, and hemicryptophyte life-form) decreased with grazing intensity.

Conclusions: Grazing intensity selects species, acting like an environmental filter, selecting them by their functional traits. Under high grazing intensity, frequent and severe defoliation allows only persistence of similar species adapted to resprout. Under low grazing intensity, the lack of frequent defoliation enables the development of species with high investment on strong and long-lived leaves, which leads to a double strata vegetation structure: the tussock one avoided by cattle, and a lower one that is overgrazed. Furthermore, competition in these plots promotes niche differentiation and a high functional diversity, leading to a divergence pattern of communities' traits.

Key words: Functional traits, convergence and divergence patterns, experimental disturbance levels.

Introduction

Natural grasslands are important ecosystems that provide services such as forage production for cattle livestock. The impact of grazing on community structure is a great concern for range management as well as for nature conservation. That is why grazing is one of the central issues affecting grasslands, linking their maintenance, productivity, economic use and biodiversity (Diaz 2007). While grazing by wild populations of large herbivores is mainly determined by resource availability and climate, in human-managed cattle production, the population density is usually maintained above ecosystem capacity and unnaturally directed, by means of fencing, supplementing, and input of fossil nutrients (Carvalho & Batello 2009).

Grazing can influence species distributions in plant communities by selective and differential removal of plant parts or species (Milchunas et al. 1988; Diaz 2007; Zheng et al. 2011), depending on their palatability and availability. Responses of plant community to grazing are very complex because it depends on many intrinsic and external factors. As any natural ecosystem, grassland communities are determined by environmental filters, and grazing can be considered as one. In general, abiotic filters only allow species with certain attributes to grow, selecting more similar species than is expected randomly (Keddy 1992), leading to convergence patterns of communities' traits (Pillar et al. 2009). Biotic interactions between species, mainly competition, determine restriction of coexistence between individuals with similar attributes (Cody & Diamond 1975). This competition leads to a divergence pattern in community functional traits (Keddy 1992). Thus, when considering species by their functional traits we are actually assessing how ecological processes define community patterns (Weiher et al. 1999; Violle et al. 2007). Once changes in species composition are linked to ecosystem processes (by means of functional *effec*t traits, Lavorel & Garnier 2002) understanding plant responses is a key issue to explore the impacts of variation in grazing intensity on ecosystems.

The historic origin of grasslands is tightly linked to the development of large herbivore mammals: species present in these communities have adaptations to prevent defoliation by grazing (Stebbins 1981; Milchunas et al. 1988). Different taxa can adopt distinct strategies of survival under this disturbance. Even Poaceae species present several different adaptations for evading or tolerating defoliation (Coughenour 1985). Most of the traits related to these adaptations are the ones linked to meristem location, shoot resprouting and turnover, belowground nutrient reserves and growth rate (Coughenour 1985; Díaz et al. 2007). But competition is a relevant restriction even in grazed areas. Tall growth forms, with relatively greater investment in aboveground rather that belowground production, are adaptations that enhance the grasses' competitiveness for light, but make them more vulnerable to grazing (Sims et al. 1978).

In a grazing intensity gradient it is possible to visualize the shifts in ecological filters by shifts in plant composition (de Bello et al. 2010) and their traits (Cruz et al. 2010). Here we analyze the effect of experimental manipulation of grazing intensity on grassland plant communities. We observed changes in species composition and in the experimental units then ascertained if these changes were explained by functional traits following the grazing intensity gradient. Furthermore, we also intended to identify several species traits, the ones that better reveal convergence and divergence assembly patterns, and how these patterns responded to controlled grazing intensity.

Methods

Our study was conducted in natural grassland in southern Brazil. The region is in a transition between tropical and temperate climatic zones, with a Cfa climate type in Koeppen's classification. The average annual precipitation is 1,445 mm and events of water deficits may occur from November to March (Bergamaschi et al. 2003). An experimental area of 52 ha at Agricultural Research Station of the Federal University of Rio Grande do Sul (30º06'00"S, 51º40'55"W) was subjected to treatments of different grazing intensities since 1986. The experiment is based on two blocks of seven treatments defined by forage dry matter offer (DMO). The blocks were defined by soil type. On the experimental units, the aboveground biomass present was considered as forage feed and the levels of DMO were established as dry matter per 100kg of cattle liveweight d^{-1} (%LW). If tussocks were present, their biomass was not included in the calculation. For the analysis we grouped the forage offer treatments based on three levels of grazing intensity: high (4% over the year), moderate (8 and 12 over the year, and 8 in spring with 12% over the rest of the year, 12 in the spring with 8% over the rest of the year) and low (16% over the year, and 16 in spring and 12% over the rest of the year).

In each experimental unit (paddock), during 2012 spring, we marked 9 plots of 1 x 1 m² that was evaluated by visual estimation of species of cover. It was categorized in levels of cover percentage (0.1, 0.5, 1, 2 … 10), than calculated the average cover on each experimental unit.

To analyze species cover we built two matrices: (1) experimental units described by species composition (matrix **W**) and (2) experimental units described by grazing intensity (matrix **G**). We evaluated the differences in plant composition, at each intensity level, using Multivariate Analysis of Variance (MANOVA) with Permutation Tests based on the Euclidean distance matrix with square root transformed values, restricting permutations within blocks (Pillar & Orlóci 1996). Principal Coordinate Analysis (PCoA) of matrix **W** (Legendre & Legendre 1998) ordination were plotted to show composition patterns, based on the Euclidean distance matrix between experimental units described by species cover (also square root transformed).

Data on species functional traits were used, rather than individual-based traits, as a practical approach and because the main effect of grazing intensity on plant functional groups were due to species turnover, not by intraspecific variation or phenotypic plasticity (at least for Poaceae species) (Cruz et al. 2010). The traits were assembled by field collections, literature and specialists consultation. Details on which traits were accessed and their functional importance are available in Table 1. As we could only get information about species functional traits for 153 of the 170 species, we performed the same previous analysis considering only these species. If there are no differences between results found with both sets of information then the 153 species set can represent the whole community and its responses to grazing intensity.

The analysis of functional traits structure was based on the scaling up of the data on species functional traits to the community level using the methodology described in

Pillar *et al.* (2009) (see also Pillar et al. (2013)). We ran the analysis using the software SYNCSA (available at http://ecoqua.ecologia.ufrgs.br). For the analysis, three input matrixes are needed: (1) species described by attributes (matrix **B**), (2) experimental units described by species composition standardized to unit total within units (matrix **W**) and (3) experimental units described by grazing intensity (matrix **G**). In general, the procedure is: (1) generate a matrix **X** of species by experimental units by weighing the species abundances in each plot by fuzzy sets defined by the species' pairwise trait similarities; (2) generate a matrix **T**= **B'W** with community weighted means for the traits in each experimental unit; (3) define the congruence r(**XG**) between matrices **X** and **G** based on Procrustes rotation (Peres-Neto & Jackson 2001; Legendre & Legendre 2012) and search for optimal trait subsets that maximize r(**XG**) using an algorithm based on Pillar & Sosinski (2003); (4) using the same method of Procrustes rotation and trait optimization algorithm, define the congruence r(**TG**) between matrices **T** and **G** and search for optimal trait subsets. Each element of matrix **X** is the probability of finding a given species in the experimental unit considering the similarities of this species to the species that occur in the same experimental unit (Pillar et al. 2009). We tested the significance of r(**XG**) against a null model based on the permutation of the species in the trait similarity matrix between species that defined **X** and the significance of r(**TG**) against a null model based on the permutation of the species in the trait matrix **B**. Analogously to Pillar et al. (2009), we interpreted the congruence r(**TG**) as a reflection of trait-convergence pattern (TCAP) related to the grazing intensity gradient, while the congruence r(**XG**) was an indication of both trait-divergence and trait-convergence.

For the traits that maximized TCAP we tested, by ANOVA with permutation testing, the relation between each one of the weighted traits on the communities and grazing intensity treatments. We also analyzed matrix **X** by Principal Coordinates Analysis (PCoA) to facilitate the interpretation of the patterns and their relation to grazing intensity.

For the traits that maximized r(**XG**), we used MANOVA to access how convergence and divergence respond to grazing intensity. We measured functional diversity using Rao's Quadratic Entropy (Rao 1982), which takes into account the species cover in the experimental units and the species' similarities in terms of traits. The variation of Rao's quadratic entropy among treatments was compared using ANOVA with permutation testing.

Results

We found a total of 170 species (see species list in Appendix 1) in the studied plots. Multivariate analysis of variance showed that grazing intensity affected significantly species composition over the three different grazing levels (p=0.002). However, the pairwise contrast between the high and low grazing intensity treatments was the only non-significant one (p=0.109). The ordination based on species composition (Fig.1) also showed a clear tendency of separation between experimental units of different grazing intensities (the first two axis contained 46.29% of total variation; p=0.17 for the first one and p=0.44 for the second one). Indeed, experimental units that were subjected to the highest grazing intensity were separated towards one extreme along the first ordination axis. The paddocks with low grazing intensities were separated on the second axis with lower scores for the plots in block B, and higher ones for the plots in block A. Species more positively related to the first axis are (axis 1 scores): *Ruelia morongi* (correlation=0.933), *Paspalum paucifolium* (0.873), *Stylosanthes leiocarpa* (0.867), *Eryngium ciliatum* (0.85) and *Cliococca selaginoides* (0.84); and species more negatively related are: *Eryngium horridum* (-0.826), *Aristida* *filifolia* (-0.69), *Aristida laevis* (-0.68) and *Senecio selloi* (-0.678). Species with greater correlation with the second axis are: *Briza rufa* (0.617), *Paspalum pumilum* (0.616), *Andropogon virgatus* (0.614) and species with greatter negative correlation are: *Aristida jubata* (0.858), *Aristida venustula* (0.845), *Krapovickasia flavecens* (0.76).

The analysis of species composition using only the 153 species subset for which trait data were available showed very similar results regarding differences between grazing intensity treatments and general patterns revealed by ordination (Appendix 2).

The functional traits analysis revealed a trait subset that maximized r(**TG**), for trait convergence, which were SLA, LDMC, presence of caespitose, hemicryptophyts and C4. For these traits subset r(**TG**)=0.841 and p=0.001, and ANOVA showed significant effect of grazing intensity for all traits in the subset except for LDMC (Tab. 2).

The ordination (PCoA) with the community weighted mean traits (matrix **T**) explained 96.54% of total variation in the first two axes among experimental units' (Fig 2). This ordination separated experimental units of different grazing intensities; high intensity ones were negatively related to both axes, while moderated ones were positively related to the second axis. High intensity experimental units were positively related to the first and negatively related to the second axis. At the ordination, we also plotted the community weighted mean traits that maximized r(**TG**) by their correlation with each axis.

The trait subset that maximized r(**XG**) was composed by leaf length, form, shrub habit, caespitose growth-form, erect, and hemicryptophyte life-form. For this trait subset r(**XG**)= 0.830 and p=0.015. Rao's quadratic entropy (for the selected traits subset) difference between treatments was significant (p=0.05) (Fig. 3).

Discussion

Our results revealed significant effects of grazing intensity on species composition and trait-based patterns. In both ordination analyses, using species composition or trait-based community data, experimental units subjected to the different grazing intensity treatments were clearly separated along the main axis of variation.

The analysis considering species cover on experimental units showed that there is a difference between treatments, and this difference can be clearly seen on the ordinations first axis. Also species related to this difference are identified by the correlation with this axis. Those species are not only the common ones and with great cover, but also more rare species exclusive of a specific treatment.

High grazing intensity experimental units are characterized by *Ruelia morongi*, *Paspalum paucifolium*, *Stylosanthes leiocarpa*, *Eryngium ciliatum* and *Cliococca selaginoides*, while plots with low grazing intensity characterized by *Eryngium horridum*, *Aristida filifolia*, *Aristida laevis* and *Senecio selloi*. The interesting fact about it is that all of these species (except *Paspalum paucifolium* and *Stylosanthes leiocarpa*) are not good for forage, and are considered as weed species. The ones related to high grazing intensity are small forbs while the ones from low grazing intensity are large, fibrous and unpalatable. The analysis with community weighted values of species functional traits give us more details in how these species are selected, and how it may affect grassland productivity and cattle growth. The functional traits issue will be discussed with more details hereafter.

But first it must be highlighted the variation among the ordinations second axis. This variation occurs primary between paddocks with low grazing intensities. What may occur due to the great filter imposed to communities on high grazing intensity plots. While plots with more relaxed grazing filter respond better to other environmental filters. In this case it may represent differences in soil type, the block criteria.

The analysis with community weighted values of species functional traits also showed some clear tendencies. Thus, indicating that changes in species cover can be also perceived on their traits. Actually, tendencies related to the grazing levels found with functional traits analysis were stronger than the ones found with species identity. While the ordination with species composition contained only 46% of total variation in the first two axes, the ordination with community-weighted means of functional traits (matrix **T**) contained 96% in the first two axes. These results corroborate the idea that plants are selected by the traits they carry, not by their species' identity *per se*, and ascertain that the selected traits are relevant for revealing community patterns related to grazing intensity.

Significant r(**TG**) and significant differences in community weighted mean traits between grazing intensity treatments indicate a trait convergence assembly pattern (Pillar et al. 2009). In this sense, grazing is acting as an ecological filter, selecting plant species carrying traits that allow them to persist under the conditions created by the different grazing intensities. This filter could be mainly through changes in soil properties by trampling. Also, the animal`s selectivity in plant defoliation.

We found that the most important traits related to grazing were: specific leaf area (SLA), leaf dry matter content (LDMC), and the presence of caespitose growth-form, hemicryptophyte life-form, and photosynthetic pathway (proportion C4/C3). Our selected traits are also seen in the literature as important ones related to grazing (Díaz et al. 2007; Saatkamp et al. 2010). SLA and LDMC are linked to a tradeoff between investing in leaf toughness with slow growth, or fragile laminas with rapid sprouting

(Cornelissen et al. 2003). The C4 photosynthetic pathway allows the plant for a more efficient use of water in photosynthesis under warmer temperatures; however it also confers leaf strength by a greater amount of fiber around the vessels (Sage 2004). Species with a caespitose growth form are tussock grasses, which confers more competitive capacity to the plant (Cornelissen et al. 2003).

Considering that the species in the study vegetation have likely coevolved with large grazers (MacFadden 1997; Müller et al. 2012), they have adaptations to this disturbance, but the strategy of survival will depend on the intensity of grazing. In one extreme of our gradient, the plants are submitted to intense and frequent defoliation. In this case, species must be able to rapidly resprout after defoliation, and doing so they would not be able to invest in durable, strong leaves (Diaz et al. 1992). This is explained, under high grazing intensity, by the reduced proportion of hemicryptophyte species and increasing community weighted mean for SLA. In the other extreme, plants are also defoliated, but less intensely and frequently. This low frequency allows the survival of plants that invest more energy and resources on producing strong leaves (small SLA, greater LDMC) and on building a caespitose habit (which includes dense tussocks). A similar tendency was found by Cruz et al. (2010) in the same experimental area, but considering only Poaceae species. This tendency is clear, for instance, for the species associated with low grazing intensity: *A. filifolia*, *A. laevis* and A. *jubata*, which present low values of SLA and high values of LDMC. Also, many other species that were not highlighted in the ordination of species composition form tussocks. One special case is *Andropogon lateralis,* which is a very common species in the experimental plots in all treatments, but under high grazing intensity adopts a prostrate short form.

The development of tussocks under low grazing intensity is also identified in other studies (Bakker et al. 1983; Cruz et al. 2010). This change on vegetation structure modifies the way cattle graze, avoiding tussocks because of their less palatable and fibrous leaves (NABINGER et al. 2000; Cruz et al. 2010; Trindade et al. 2012). Also, the lack of significance in the contrast of species cover, between extreme grazing levels, could be due to this formation of tussocks. Under low grazing intensity the vegetation develops a double strata, where the tussock stratum with less palatability is less consumed, forcing overgrazing on the lower stratum. Further, the greater tussock cover, the less space is left for palatable species. Despite the tussocks have been disregarded for estimating the amount of forage available for cattle consumption, which is used for the controlled grazing intensity treatment maintenance, overgrazing has been observed on the lower stratum. The overgrazing may be leading the lower stratum vegetation to become similar to the vegetation found in the experimental plots subject to high intensity grazing. This is an example of how a functional traits approach can be used for explaining patterns that could be evident by only examining species composition.

However, the development of double strata in the vegetation physiognomy is not usually welcome by cattle farmers. Tussock formation reduces the actual grazed area and leads to a poorer animal performance per hectare (Cruz et al. 2010; Trindade et al. 2012). A moderate grazing intensity is favorable because there is less formation of tussocks, and the problems related to overgrazing are avoided, *e.g.* increased bare soil and low productivity (Nabinger et al. 2000). Furthermore, a rotational grazing system, by reducing the frequency and increasing the intensity of defoliation, will allow a better control of grazing animals' selectivity and therefore has been considered a better management option (Briske et al. 2008; Quadros et al. 2011).

High grazing intensity plots in our study presented, for the selected traits, lower functional diversity than moderate and low intensity grazing plots. If we consider grazing as an environmental filter, then we would expect lower functional diversity under high grazing intensity, because species would tend to be more similar each other regarding their traits in response to the environmental restrictions. The opposite is expected under lower grazing intensities, where competition may lead to niche differentiation (Cody & Diamond 1975; Keddy 1992).

Conclusion

We gave an example of how grazing intensity affects plant species acting as an ecological filter, selecting them by their functional traits. At high grazing intensities, the severe restriction allows only similar specialized species to survive, selecting them by their traits. While, at low grazing intensity, there is a greater relation C4/C3 and the development of caespitose, and species with low SLA and high LDMC, which leads to a double strata vegetation structure, the tussock one avoided by cattle, and a lower one that can be overgrazed. Furthermore, competition in these plots may lead to niche differentiation and a divergence pattern on community traits.

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Table 1: List of traits used for the 153 species found at the experimental area of "Estação Experimental Agronômica da UFRGS". The protocols were modified after Cornelissen et al. (2003).

Trait	**code**	**Measure unit**	**Way of assesses**	**Function** (Cornelissen et al. 2003)
Leaf Traits			Average of 2 leafs of 5 to 10 individuals from each species measured with Area Meter*, weighted fresh and after oven drying	
Size	Lsiz	Cm	lamina area	Leaf energy and water balance
Length	Llen	cm	lamina comp	
Average width	Lwi	cm	average lamina width	
Form	Lfor	-	relation comp/max width	
Specific leaf area	Sla	cm/mg	relation leaf si/ dry weight	Trade-off between relative growth rate and investments on leaf defences (and long life span)
Dry matter content	ldmc	-	relation fresh/dry weight	Relative to growth rate and leaf life span
Tension	tens	N	total strength needed for fracturing leaf lamina	Protection against biotic and abiotic mechanical damage
Whole-plant traits			Literature and specialists consults	
Potential Height	hei	Cm	Max height described on literature	Competitive vigour
Growth form			Modified of cornelissen an expanded to binary	Plant strategy under climatic factors and land use
Graminoid	gr	0/1	Poaceae, Cyperaceae and Juncaceae	
Forb	forb	0/1	non graminoid, non lignification	
Shrub	shr	0/1	Presence of lignification tissues	
Caespitose	cesp	0/1	Tussock and non-reptant grasses	
Reptant	rep	0/1	reptant grasses	
Erect	eret	0/1	non prostrate forbs and shrubs	
Prostrate	pros	0/1	prostrate forbs and shrubs	
Rosette	ros	0/1	rosette forbs	
Life form			Modified from Cornelissen and expanded to binary	Plant strategy of resprouting after disturbances or annual climatic variation
Hemicryptophyte	hcr	0/1	periodic shoot reduction to a remnant shoot system.	
Geophyte	geof	0/1	Annual reduction of the complete shoot system to underground storage organs.	
Therophyte	tero	0/1	Non perene	
Chamaephyte	came	0/1	shoot system remains, but below 0.5 m	

Belowground storage (and clonality) organs			Modified from Cornelissen and expanded to binary	
Belowground storage (and clonally) organs	reser	0/1	Only presence of any of these organs	Competitive vigour, exploiting patches rich in resources. Persistence after disturbances.
Rhizome	rhiz	0/1	1= Presence	
Xylopodium	xylo	0/1	1= Presence	
Bulb	bulb	0/1	1= Presence	
Corm	corm	0/1	1= Presence	
Roots	raiz	0/1	1= Presence	
Stolon	stol	0/1	1= Presence	
Tuber	tube	0/1	1= Presence	
Photosynthetic pathway			Literature and specialists consults	
C4 photosynthetic pathway	C4	0/1	1= C4 Pathway, 0= C3 Pathway	Higher optimum temperature for photosynthesis and growth. Water and nutrient use efficiencies.

Table 2: Results from ANOVA comparing community weighted mean traits between treatments.

Trait	Low	Moderate	high	p
SLA	103.92	128.43	157.59	0.001
LDMC	0.299	0.303	0.271	0.109
C4	0.571	0.461	0.306	0.003
Cesp	0.524	0.383	0.134	0.001
Hcr	0.525	0.384	0.134	0.001

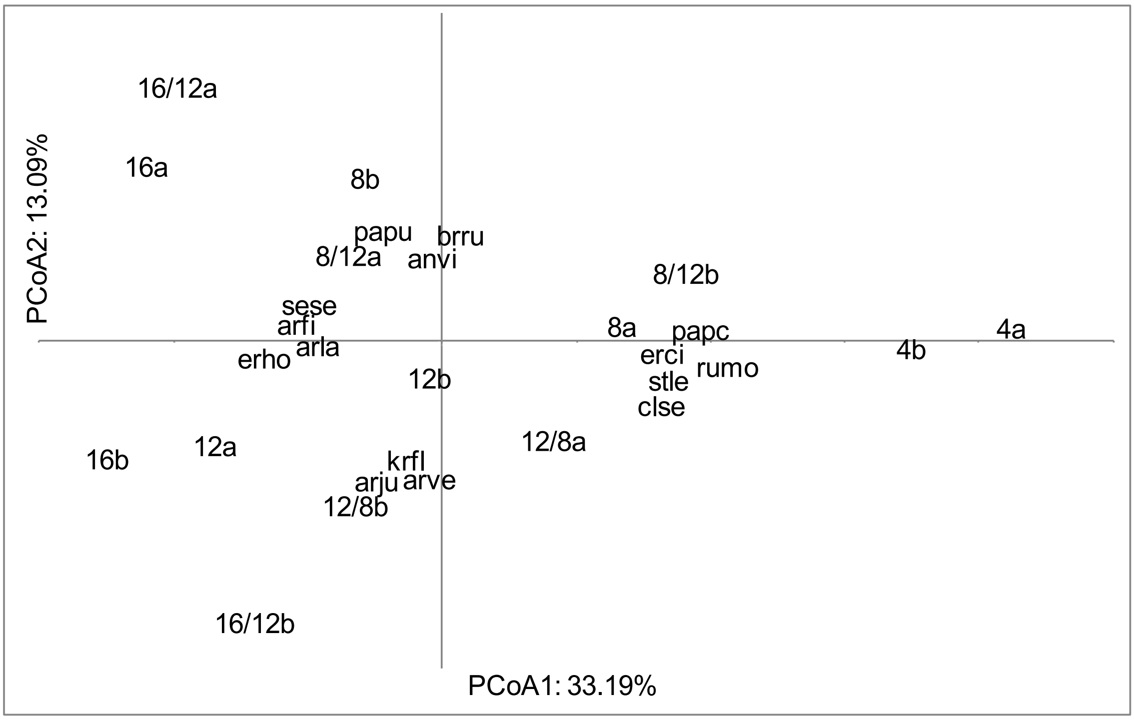

Figure 4: PCoA ordination of the 14 experimental units described by species composition. The numbers indicate percentage of forage offer in the experimental units (4=high; 8, 8/12, 12 and 12/8=moderated; 16/12 and 16=low grazing intensity). The letters “a” and “b” identify the experimental blocks. Species with greater positive and negative correlations with the axis are indicated by codes: anvi *Andropogon virgatus*, arfi *Aristida filifolia*, arju *Aristida jubata*, arla *Aristida laevis*, arve *Aristida venustula*, brru *Briza rufa*, clse *Cliococca selaginoides*, erci *Eryngium ciliattum*, erho *Eryngium horridum*, krfl *Krapovicasia flavescens*, papc *Paspalum paucifolium*, papu *Paspalum pumilum*, rumo *Ruelia morongi*, sese *Senecio selloi*, stle *Stylosanthes leiocarpa*.

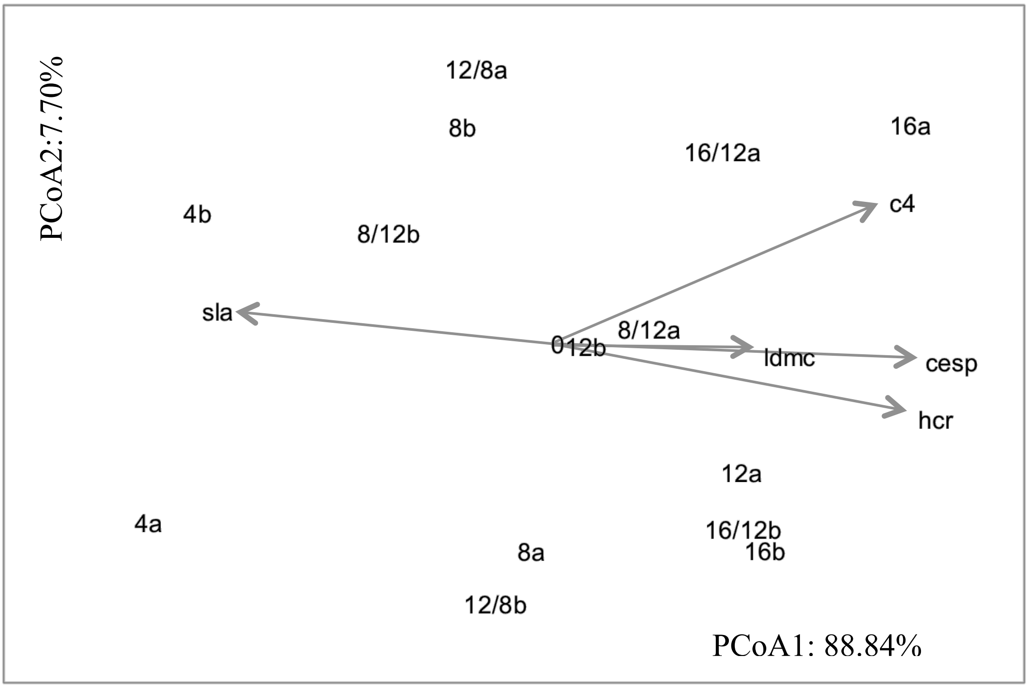

Figure 5: PCoA ordination of the matrix **T** 14 experimental units described by community weighted means of functional traits (selected to maximize correlation r(**TG**) with grazing intensity). The explanations of the first two axes are 88.84% and 7.70%. The numbers indicate percentage of forage offer of the experimental units (4=high; 8, 8/12, 12 and 12/8=moderated; 16/12 and 16=low intensity). The letters “a” and “b” indicates blocks. Traits are indicated by codes on Table 1.

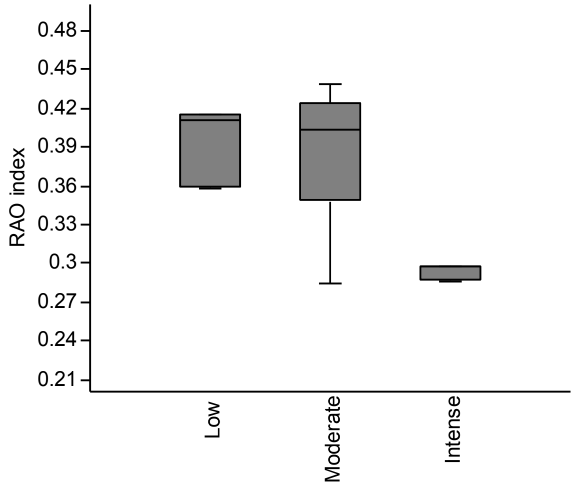

Figure 6: Box plot of functional diversity (Rao quadratic entropy), for the selected traits on different grazing intensity treatments. The selected traits were those that maximized Procrustes correlation r(**XG**) between functionally weighted community composition and grazing intensity.

Capítulo II

"Litter decomposition and soil detritivore activity respond to habitat structure changes related to grazing intensity in native grassland"

Abstract

Livestock production on natural grasslands may cause changes to ecosystem functions such as litter decomposition, a key ecosystem process. Our aim is to assess how grazing intensity affects litter decomposition (LD) and soil invertebrate detritivore activity (DA), and whether the effects are mediated by changes in habitat structure and functional patterns on plant communities. In an experiment with different grazing intensities in native grassland, southern Brazil, we evaluated LD (litter-bag method) and DA (bait lamina test). We analyzed how these variables relate to each other through analysis of variance (ANOVA). We also measured green biomass, dead biomass, vegetation height, cattle manure, bare soil, plant functional traits and diversity, selecting traits that better represent convergence and divergence patterns to LD (Rao_D) and

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Artigo a ser publicado na revista: Oecologia

DA(Rao$_A$); then, with these variables we plotted a PCA ordination. Grazing intensity was negatively related to DA, while LD was not related. Selected plant functional traits were: presence of species with C4 photosynthetic pathway (DA), and species with belowground storage organs (LD). For functional diversity, Rao$_A$ contained LDMC, SLA and presence of therophyte species; and Rao$_D$ contained: LDMC, leaf strength, presence of shrub and hemicryptophyte species. Grazing intensity separated experimental units by the first principal axis, Rao$_A$, bare soil and DA were positively related and C4 species, vegetation height and dead biomass were negatively related. By the second axis LD was positively related, together with Rao$_D$ and species with storage organs. Detritivore organisms are benefited by the dense vegetation habitat formed in low grazing intensity areas. Litter decomposition is favored by open canopy vegetation, which may increase photodegradation. It also affected functional diversity that could increase microbial decomposition.

Key-words: Plant community, functional effect traits, litter-bag, bait-lamina,

Introduction

Litter decomposition is a key ecosystem process of carbon and nutrient cycling in most terrestrial ecosystems (Hättenschwiler et al. 2005) by allowing nutrients to return to the soil, and maintaining ecosystem fertility and productivity (Davidson and Janssens 2006; Canadell et al. 2007). Among factors influencing litter composition, chemical composition and quality of leaves and other senescent plant organs determine decomposability (Fortunel et al. 2009). Further, the effect of the environmental conditions on litter decomposition rates is also well known, which includes soil physical chemistry properties (Vossbrinck et al. 1979) and the weather conditions controlling moisture and physical degradation by weathering and photodegradation (Austin 2006).

Another crucial factor that defines litter decomposition is abundance and composition of decomposer organisms. Many groups of soil invertebrates with detritivore roles include arthropods (mites, colembolas, isopods, diplopods, termites, some beetles) and earthworms (Lavelle 1996). Arthropods constitute a mega diverse group that rapidly responds to disturbances, mainly when they influence the structural and microclimatic habitat proprieties. Plant functional traits may directly affect decomposition through litter quality controlling biological activity, and indirectly through habitat structure affecting protection from abiotic factors such as sun radiation, wind and rain (de Bello et al., 2010).

The way plant communities contribute to ecosystem processes and services has received increasing attention lately. A conceptual framework linking species and ecosystem functioning based on plant functional traits was proposed by (Chapin et al. 2000; Vandewalle et al. 2010). While the functional *response* traits are the ones that confer to the organism capacity to survive under environmental adversities, the functional *effect* traits represent the effects of the organism on ecosystem functions (Lavorel and Garnier 2002). Functional diversity, as a whole, can also affect ecosystem processes, adding complexity and permitting several attributes to exist, thus increasing the probability of some species with important attributes to appear (Tilman 1997). Therefore, the delimitation of plant functional effect traits on litter decomposition is a key issue for inferring about changes over these ecosystem processes. Plants respond to disturbances in the habitat, thus a cascade of changes in the ecosystem could follow human controlled disturbances, such as the case when plant diversity and species composition are affected. Livestock production over natural grasslands is an example of that (Díaz et al. 2001).

Livestock grazing is one of the most important land uses worldwide, covering more than 25% of Earth's terrestrial surface (Asner et al. 2004), and represents a major drive of above- and below-ground communities and ecological processes. Large herbivores regulate grassland species composition and diversity by selective consumption (Milchunas et al. 1988), filtering out plants according to morphological and functional traits, e.g. favouring annual, short, prostate, stoloniferous and rosette plants over perennial, tall, erect and tussock species (Díaz et al. 2007). Shifts in plant communities, associated with grazing-induced habitat structural changes, such as heterogeneity (Reid and Hochuli 2007), canopy structure (Carrera et al. 2008) and soil compaction (Bouwman and Arts 2000) may influence directly faunal diversity and their mediated services.

The south Brazilian grassland biome is recognized by the rich plant biodiversity (Overbeck et al. 2007; Boldrini 2009). These grasslands provide forage for livestock production, which has been one of the main economic activities in the region (Carvalho and Batello 2009). But grazing may induce physiognomy changes and species turnover. Grazing influences plant species distribution by selective removal of species and plant parts. On the one hand, under high intensity grazing, the frequent removal of leaves forces species to rapidly resprout softer leaves instead of tough durable leaves (Chapter I). On the other hand, low grazing intensity allows vegetation to be taller, thus increasing competition for light and favoring tussock growth forms and shrubs (Chapter I). These life forms generate an upper stratum over the prostrate species. This double strata physiognomy is unwanted by cattle managers because animals avoid the unpalatable tall grasses and shrubs (Cruz et al. 2010; Trindade et al. 2012), thus diminishing their effective grazing. These are examples of how plant functional *response* traits are affected by grazing intensity (Lavorel and Garnier 2002). However, functional *effect* traits related to litter decomposition and soil biological activity in these ecosystems are still not well studied in a community framework.

Litter decomposition in this system of native grassland subjected to grazing may be controlled by several variables, but the effects may be masked by the high complexity of interactions. Grazing intensity may affect litter decomposition in different ways. Low intensity management allows taller caespitose grasses to survive (Chapter I) and results in greater accumulation of dry biomass. This would create a moist microenvironment, protected from weather, which facilitates the proliferation of detritivore organisms and, consequently, the total amount of decomposition. At the other extreme, under high grazing intensity, with the predominance of short, prostrate grasses and forbs, and a large proportion of uncovered soil, litter is left more exposed to sun radiation and weather conditions, and therefore decomposition may be faster.

Here we explore the long-term effects of experimentally controlled grazing intensity on leaf-litter decomposition and specifically on the soil invertebrate detritivore activity in native grassland. We also identify plant functional effect traits related to these processes. Then we investigate how changes in the grassland habitat structure (vegetation height, litter, manure and bare soil cover, plant functional traits and functional diversity) caused by grazing intensity are related to detritivore activity and litter decomposition.

Materials and Methods

Study site

The research was conducted in natural grassland ecosystems at the Agricultural Research Station of the Federal University of Rio Grande do Sul (30º06'00"S, 51º40'55"W, 46 m a.s.l.). The climate is Cfa, subtropical humid, with a warm summer. Average annual precipitation in the region is 1,440 mm. Mean monthly temperature varies between 9 and 25ºC. The vegetation is mainly composed of grasses with a clear differentiation of plant traits and composition derived from different grazing intensities (Chapter I).

Experimental paddocks were established in 1986 in an area of 52 ha. The experiment was a randomized block design, with two replicates (paddocks) for each of seven grazing treatment combinations, totaling 14 experimental units ranging from 3 to 5 ha each. The two blocks separate areas with different soil drainage capacity. Grazing treatments were defined by levels of forage dry matter on offer (DMO), established as aboveground dry matter per 100 kg of cattle live weight d^{-1} (%LW): (1) 4% over the year, (2) 8% over the year, (3) 12% over the year, (4) 8% in spring, and 12% in the rest of the year, (5) 12% in spring, and 8% in the rest of the year, (6) 16% over the year, and (7) 16% in spring, and 12% in the rest of the year. Further details on grazing treatments are given in (Trindade et al. 2012).

We marked eight quadrats of 1 x 1 m, spatially arranged on a 50 x 50 m grid, avoiding marshes, in each of our 14 experimental units, totaling 112 quadrats. Each quadrat was evaluated concerning decomposition rates of a standard leaf-litter, soil fauna feeding activity rates, habitat structural variables and composition and functional traits of dominant species in the plant community.

Litter decomposition

We collected standing dead biomass of *Andropogon lateralis* (Poaceae) from the study site. This is a native and very common grass species in natural grassland ecosystems from South Brazil. The collected material was cut into approx. 4cm length, and oven dried at 60°C. Approximately 1 g of the *A. lateralis* standard litter was inserted into litter-bags (10 × 10 cm; 1 mm^2 mesh size). We placed one litter-bag on the soil surface close to each 1 x 1 m quadrat in all experimental units on January 2012, and removed them in October 2012, totaling nine months of environmental exposure. The remaining material in litter-bags was cleaned, removing attached soil particles with distilled water and a brush, oven-dried to constant weight and weighed to determine the remaining mass. Litter decomposition was calculated as the percentage of weight loss in each litter-bag. The average of litter decomposition was calculated for each experimental unit.

Soil invertebrate detritivore activity

The role of invertebrates in litter decomposition was assessed using bait-lamina test. Bait-lamina consists of plastic strips of 120 mm length, 6 mm wide and 1.5 mm thick, with 16 perforations 5 mm from each other (Kratz 1998). Holes in the sticks were filled with a homogeneous mixture of cellulose (70%), wheat flour (27%), activated charcoal (3%) and distilled water to form a paste (e.g. (Gestel et al. 2003); (Römbke et al. 2006)). We inserted three bait-laminas sideways into the first centimeter of the soil in each quadrat. After 16 to 18 days of exposure, we pulled out all bait-lamina from the soil, and brought them to the lab. Under stereomicroscope, we counted in each stick partially consumed holes (category "1") and totally empty holes (category "2"), as indicative of soil fauna feeding activity. An average activity index was obtained per bait-lamina by attributing weights of 2 and 1 respectively to the holes with category 2 and 1. The average of activity index was calculated for each experimental unit.

Vegetation community and habitat structure

To assess habitat structure proprieties and characterize plant community functional traits in the different grazing treatments we visually estimated in each quadrat the cover percentage of: 1) green plant aerial biomass, 2) dead standing biomass and litter layer, 3) vegetation height (average of 5 points on the quadrat), 4) cattle manure, and 5) bare soil. We recorded plant species composition and visually estimated the cover of each species in the quadrats. Plant species (153 from 170 species [90%], Chapter I) were described by functional traits, as described in **Table 1**. Trait data assessment used protocols modified from Cornelissen et al. (2003) and based on plant specimens collected in the study region, and on the literature and consultation of specialists. Details on functional trait assessment and their functional importance for species fitness are given in **Table 1**.

Statistical analyses

For data analysis we grouped the forage offer treatments in three levels of grazing intensity: high intensity (1), moderate intensity (2, 3, 4, 5) and low intensity (6, 7). We used analysis of variance (ANOVA) in blocks, with permutation tests, to test for differences between the levels of grazing intensity concerning litter decomposition and soil fauna feeding activity. Additionally, we used simple linear regression to test the relationship between litter decomposition (percentage of weight loss in litter-bags) and the soil fauna feeding activity (activity index assessed with bait-lamina) considering all 14 experimental units.

We analyzed the functional traits structure by scaling up the data on species functional traits to the community level using the methodology described in Pillar *et al.* (2009) (see also and (Pillar et al. (2013)). We ran the analysis using the software

SYNCSA (available at http://ecoqua.ecologia.ufrgs.br). For the analysis, three input matrixes are needed: (1) species described by attributes (matrix **B**), (2) quadrats described by species composition standardized to unit total within quadrats (matrix **W**) and (3) quadrats described by one or more environmental variables (a vector or a matrix **E**). In general terms, the procedure is: (1) generate a matrix **X** of species by experimental units by weighting the species abundances in each plot by fuzzy sets defined by the species' pair wise trait similarities; (2) generate a matrix **T** = **B'W** with community weighted means for the traits in each experimental unit; (3) define the congruence r(**XE**) between matrices **X** and **E** based on Procrustes rotation (Peres-Neto and Jackson 2001; Legendre and Legendre 2012) and search for optimal trait subsets that maximize r(**XE**) using an algorithm based on (Pillar and Sosinski 2003)(Pillar and Sosinski 2003) ; (4) using the same method of Procrustes rotation and trait optimization algorithm, define the congruence r(**TE**) between matrices **T** and **E** and search for optimal trait subsets. Each element of matrix **X** is the probability of finding a given species in the experimental unit considering the similarities of this species to the species that occur in the same experimental unit (Pillar et al. 2009). As we were looking for effect traits linked to decomposition and detritivore activity, we ran the analysis two times, each one defining a vector $\mathbf{E_A}$ for detritivore activity and $\mathbf{E_D}$ for decomposition. Analogous to Pillar et al (2009), we interpreted the congruence r(**TE**) as a reflection of trait-convergence pattern (TCAP) related to the grazing intensity gradient, while the congruence r(**XE**) was an indication of both trait-divergence and trait-convergence.

For the traits that maximized r($\mathbf{TE_A}$) and r($\mathbf{TE_D}$) we calculated community weighted means in each experimental unit (paddock). For the traits that maximized r($\mathbf{XE_A}$) r($\mathbf{XE_D}$), we calculated, for each experimental unit, the functional diversity using Rao's Quadratic Entropy (Rao 1982), which takes into account the species cover in the experimental units and the species' similarities in terms of traits. Rao_A indicates Rao's Quadratic Entropy for the traits that maximized $r(\mathbf{XE_A})$ and Rao_D for the traits that maximized $r(\mathbf{XE_D})$.

We assessed the effects of grazing intensity treatments for all habitat structure variables (green biomass, dead biomass, vegetation height, bare soil, cattle manure, Rao_A, Rao_D, and community average weighs of the selected traits) using ANOVA in blocks, with permutation tests. We also calculated a correlation matrix between these variables and built a Principal Components Analysis ordination to visualize their relationships.

Results

The trait subset maximizing $r(\mathbf{TE_A})$, related to detritivore activity, contained only one trait: presence of plants with C4 photosynthetic pathway (r=0.32, p=0.03). For $r(\mathbf{TE_D})$, related to litter decomposition, the selected traits subset also contained only one trait: presence of species with underground storage organs (r= 0.31, p= 0.001).

Traits that maximized $r(\mathbf{XE_A})$ were LDMC, SLA and presence of therophyte life form. Rao_A was calculated with these traits. Traits that maximized $r(\mathbf{XE_D})$ were LDMC, leaf strength, presence of shrubs and hemicryptophyte life form. Rao_D was calculated for these traits.

The ordination based on the correlation between grazing intensity, detritivore activity, litter decomposition, and habitat structure variables (green biomass, dead biomass, vegetation height, cattle manure, bare soil, presence of species with C4 photosynthetic pathway and storage organs, Rao_A and Rao_D) (Fig. 1) showed a clear tendency of separation between grazing intensity treatments. The two ordination axes contain 63.1% of total variation between variables, but only the first axis is stable under bootstrap resampling (p=0.05). Indeed, experimental units that were subjected to the highest grazing intensity were separated towards one extreme (right) along the first ordination axis. Traits and habitat variables related to this axis, along with Rao_A, included bare soil, manure, and species with belowground storage organs. The paddocks on the negative side of the first axis were characterized by C4 species, taller vegetation height, increased dead biomass, and increased invertebrate detritivore activity. On the other hand, Rao_D, green biomass, species with belowground storage organs and decomposition appeared to increase along axis 2.

We found significant differences concerning soil fauna feeding activity (p=0.002; Fig. 2a), which decreased with higher grazing intensity On the other hand, leaf-litter decomposition rates after nine months were not significantly different between the grazing intensity treatments (p=0.345; Fig. 2b), despite presenting a tendency to be reduced at low grazing levels. Litter decomposition and detritivore activity in our experimental units (paddocks) did not present any significant correlation (Fig. 3).

Sites with high grazing intensity presented more bare soil (Fig. 4.e), presence of species with belowground storage organs (Fig. 4.g) and Rao_A (Fig. 4.h). Paddocks with low grazing intensity presented higher cover of dead biomass (Fig. 4.b), taller vegetation (Fig. 4.c) and significant more species with C4 photosynthetic pathway (Fig. 4.f). Green biomass and manure cover did not differ between treatments (Fig. 4.a) and 4.d). Rao_D was higher under medium grazing intensity paddocks (Fig. 4.i).

Discussion

Our results corroborate the general view that grazing management practices influence community assembly and ecological processes at a range of scales, but the magnitude of the impact is dependent upon their intensity (Díaz and Cabido 2001; Blanco et al. 2007; Cruz et al. 2010). Based on our assessment of the long-term experiment manipulating livestock grazing we found that the higher the grazing intensity, the lower the soil fauna feeding activity rates. However, litter decomposition was not affected by the experiment, which may indicate shifts in the process drivers along the management gradient. Habitat structural proprieties, as well as functional effect traits and functional diversity, were distinct among grazing treatments. Some of these variables may be causing the ecosystem processes here evaluated, while others only respond to the same factors.

As we postulated, our results show that detritivore activity is higher under lower grazing intensity. Grazing intensity determines changes in habitat structure, including plant traits (Chapter I; Díaz et al., 2001; Fortunel et al., 2009). Under low grazing intensity the infrequent defoliation permits plants to be taller (Fig. 4.c), thereby increasing the competition between them. Species with the C4 photosynthetic pathway presents a competitive advantage over C3 plants, by having a more efficient use of water in photosynthesis under warmer temperatures. The C4 pathway also confers leaf strength by a greater amount of fiber around the vessels (Sage 2004). The infrequent defoliation also causes more accumulation of dead biomass (attached to plants and litter). On the other extreme, under high grazing intensity, the frequent defoliation creates spots of bare soil, opening the community to other species to spread and develop. Therefore, it could increase functional diversity based on the traits LDMC, SLA and therophyte life form (Rao_A). The most favorable environmental conditions for the activity of soil detritivore invertebrates seem to be taller vegetation, with a larger amount of C4 species and dead biomass, which provide more protected sites from heating and the maintenance of soil moisture (Gongalsky et al. 2008). The conditions under high grazing intensity, with spots of bare soil and high functional diversity, however, are not optimal for soil faunal detritivore activity. So it is not possible to say that specific functional traits or functional diversity affects directly detritivore activity. It seems be a result of several microhabitat characteristics shift by cattle grazing under natural grassland ecosystem.

A similar conclusion can be taken from litter decomposition data. Our results indicated that litter decomposition is not directly affected by grazing intensity (Fig. 2b), but the ordination (Fig. 1) showed that it is clearly linked with habitat structure variables, Rao_D and species with belowground storage organs (Fig. 4g and 4i). Spatial heterogeneity inside each experimental unit may cause the lack of significance when comparing the averages between each one. This great heterogeneity fades the response pattern.

Rao_D is the only variable that responds non-linearly to treatment level, with greater values observed under moderate grazing intensity paddocks. Since litter decomposition was found functionally linked to both Rao_D and presence of species with belowground storage organs, the non-linear pattern in Rao_D response to grazing intensity may have disrupted the direct relation between litter decomposition and grazing intensity.

The presence of species with underground storage organs may alter litter decomposition by changing its physical environment. There is a tradeoff in plants that invest energy in building underground storage organs in detriment of shoots

(Cornelissen et al. 2003), creating a more open canopy, therefore, making litter susceptible to photodegradation (Austin 2006) and other abiotic physical brakes.

The non-linear pattern of Rao_D's (functional diversity for the traits: LDMC, leaf strength, presence of shrubs and hemicryptophyte life form) response to grazing intensity suggests an optimization for greater functional diversity under intermediate disturbance level (similar as observed by Connell (1978) with species diversity). Under moderate grazing, the defoliation by cattle grazing is not so severe, allowing several species to survive, but at the same time grazing is not light enough to permit competitive exclusion. This process can generate communities with coexistence of species with different values of LDMC, leaf strength, presence of shrubs and non-shrubs and hemicryptophyts and non-hemicryptophytes. Namely, it will become a plant community with several strategies of survival, some of them with a better resprouting (non-shrubs, hemicryptophyte, low LDMC and leaf strength (Chapter I; Cornelissen et al., 2003) best competitors (shrubs, high LDMC, and leaf strength (Chapter I), and non-hemicriptophyte (Cornelissen et al. 2003)). In the soil microbial community a turnover between fungal and bacterial decomposition pathways is observed in response to grazing management (Bardgett et al. 1996, 1998). This intermediate environment created by higher plant functional diversity could favor the development of both types of microorganisms, thus, increasing litter decomposition.

We found no linkage between invertebrate detritivore activity and litter decomposition, suggesting that invertebrate detritivore activity is not the only decomposition driver. Other variables, such as photodegradation and detritivore activity of other organisms (as bacteria and fungi), not sampled by bite lamina-test, could be blurring this effect. Despite the lack of information about these other litter decomposition drivers, they were likely affected by grazing intensity.

Grazing in natural grassland indeed affect plant functional traits, functional diversity and other structural variables in the habitat. A reduction in invertebrate detritivore activity is found in response to more intense grazing; however causality in this case is very difficult to disentangle. Litter decomposition is not responding to grazing intensity, but to some structural variables that are in turn affected by grazing, but apparently non-linearly. While some of the variables may be directly acting on the evaluated ecosystem processes, others are just responding to common factors. Future research work should explore causal models relating these variables by path analysis and structural equation modeling (Shipley 2000).

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Table 1: Traits used for the description of 153 species found at the experimental area of "Estação Experimental Agronômica da UFRGS". The protocols were modified after Cornelissen et al. (2003).

Trait	**code**	**Measure unit**	**Method**	**Function** (Cornelissen et al 2003)
Leaf Traits			Average of 2 leafs of 5 to 10 individuals from each species measured with Area Meter*, weighted fresh and after oven drying	
Size	Lsiz	cm	lamina area	Leaf energy and water balance
Length	Llen	cm	lamina comp	
Average width	Lwi	cm	average lamina width	
Form	Lfor	-	relation comp/max width	
Specific leaf area	Sla	cm/mg	relation leaf si/ dry weight	Trade-off between relative growth rate and investments or leaf defences (and long life span)
Dry matter content	ldmc	-	relation fresh/dry weight	Relative to growth rate and leaf life span
Tension	tens	N	total strength needed for fracturing leaf lamina	Protection against biotic and abiotic mechanical damage
Whole-plant traits			Literature and specialists consults	
Potential Height	hei	cm	Max height described on literature	Competitive vigour
Growth form			Modified of cornelissen an expanded to binary	Plant strategy under climatic factors and land use
Graminoid	gr	0/1	Poaceae, Cyperaceae and Juncaceae	
Forb	forb	0/1	non graminoid, non lignification	
Shrub	shr	0/1	Presence of lignification tissues	
Caespitose	cesp	0/1	Tussock and non-reptant grasses	
Reptant	rep	0/1	reptant grasses	
Erect	eret	0/1	non prostrate forbs and shrubs	
Prostrate	pros	0/1	prostrate forbs and shrubs	
Rosette	ros	0/1	rosette forbs	
Life form			Modified from Cornelissen and expanded to binary	Plant strategy of resprouting after disturbances or annual climatic variation
Hemicryptophyte	hcr	0/1	periodic shoot reduction to a remnant shoot system.	
Geophyte	geof	0/1	Annual reduction of the complete shoot system to storage underground organs.	
Therophyte	tero	0/1	Non perene	

Chamaephyte	came	0/1	shoot system remains, but below 0.5 m	
Belowground storage (and clonality) organs			Modified from Cornelissen and expanded to binary	
Belowground storage (and clonally) organs	reser	0/1	Only presence of any of these organs	Competitive vigour, exploiting patches rich in resources Persistence after disturbances.
Rhizome	rhiz	0/1	1= Presence	
Xylopodium	xylo	0/1	1= Presence	
Bulb	bulb	0/1	1= Presence	
Corm	corm	0/1	1= Presence	
Roots	raiz	0/1	1= Presence	
Stolon	stol	0/1	1= Presence	
Tuber	tube	0/1	1= Presence	
Photosynthetic pathway			Literature and specialists consults	
C4 photosynthetic pathway	C4	0/1	1= C4 Pathway, 0= C3 Pathway	Higher optimum temperature for photosynthesis and growth Water and nutrient use efficiencies.

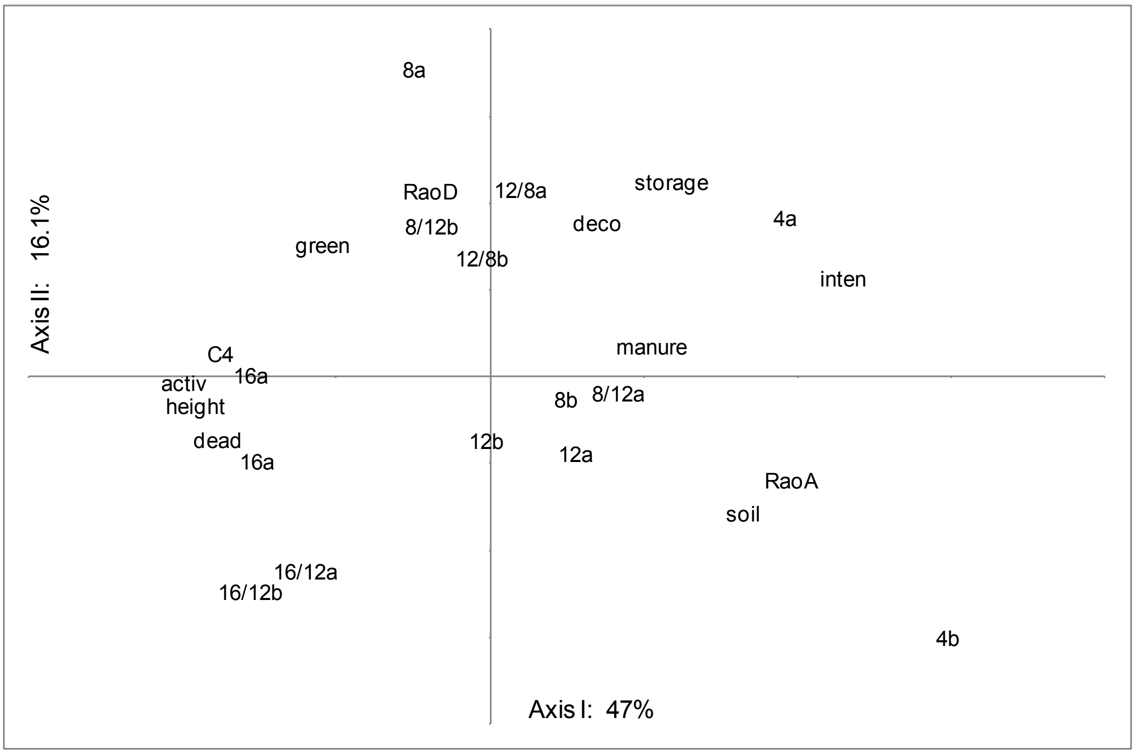

Figure 1: PCA ordination of 14 experimental units based on the correlation between variables. The first axis represents 47% of the total variation and the second axis represents 16.1%. The numbers indicate percentage of forage offer in the experimental units (4=high; 8, 8/12, 12 and 12/8= moderated; 16/12 and 16= low grazing intensity). The letters "a" and "b" identify the experimental blocks. The variables are *intens* (grazing intensity), *green* (green biomass cover), *dead* (dead stand biomass and litter layer), *height* (vegetation height), *manure* (cattle manure), *soil* (bare soil), *C4* (presence of species with C4 photosynthetic pathway), *storage* (presence of species with storage organs), *activ* (soil invertebrate detritivore activity), *deco* (litter decomposition), Rao_A and Rao_D.

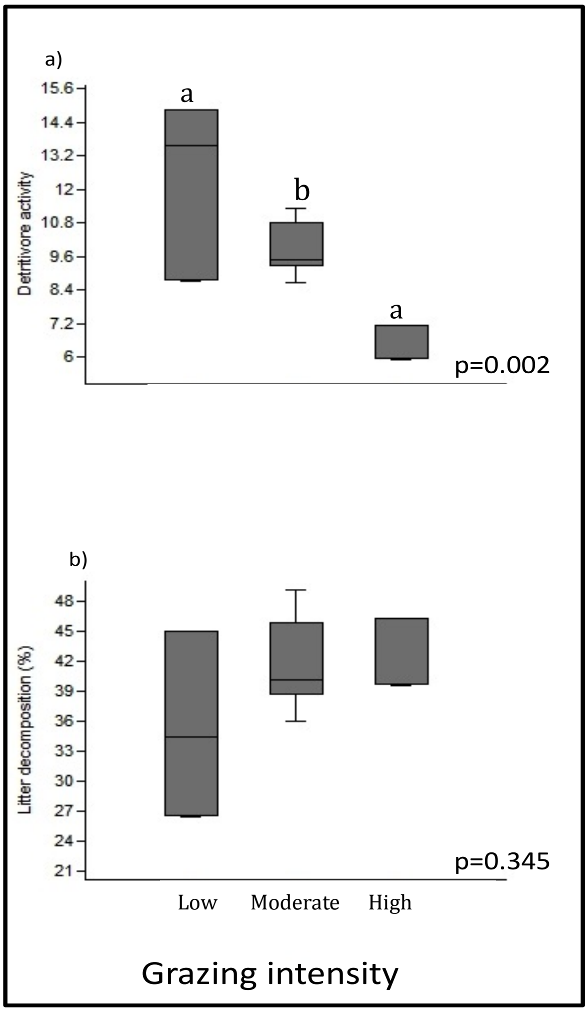

Figure 2: Differences on **a)** detritivore activity and average **b)** litter decomposition between grazing intensity treatments. Probability results from ANOVA in blocks with permutation testing. Letters indicate significant difference ($\alpha \leq 0.05$) in pairwise contrasts.

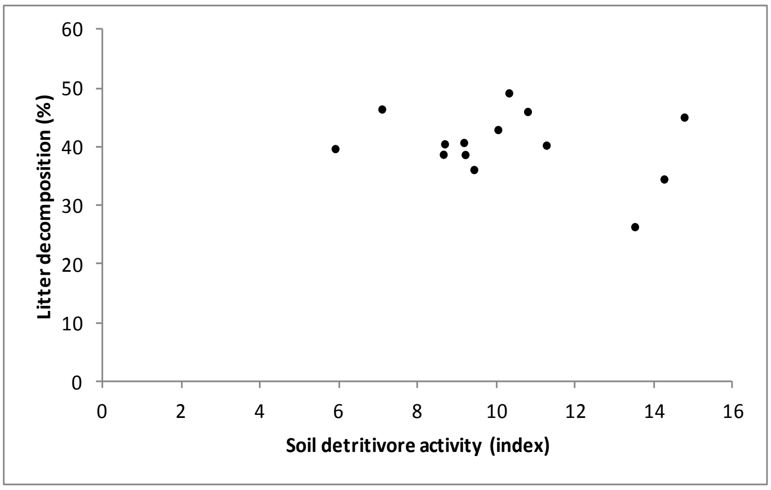

Figure 3: Relationship between detritivore activity and litter decomposition on the experimental units (p=0.3).

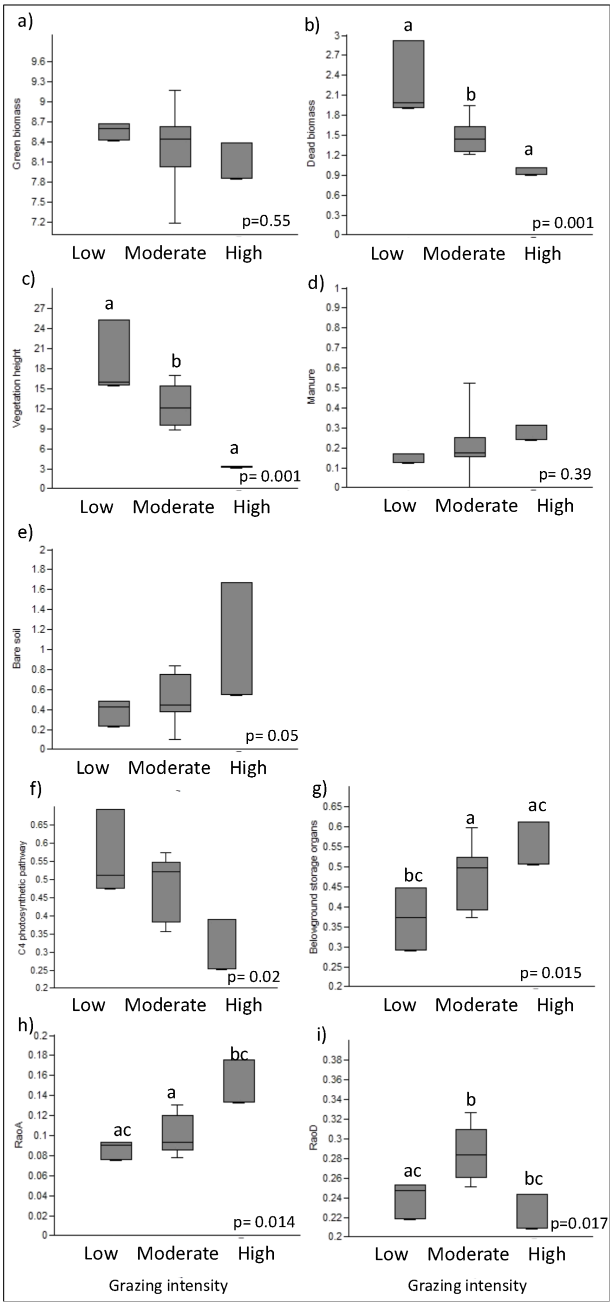

Figure 4: Differences on habitat structure variables between grazing intensity treatments. **a)** green biomass; **b)**dead biomass; **c)** vegetation height; **d)** bare soil; **e)** cattle manure; **f)** presence of species with C4 photosynthetic pathway **g)** Presence of species with belowground storage organs; **h)** Rao$_A$ and **i)** Rao$_D$. Probability results from ANOVA in blocks with permutation testing. Letters indicate significant difference in pairwise contrasts (higher p considered was 0.074)

Conclusão

O experimento de manipulação da intensidade de pastejo em campo nativo permitiu a avaliação dos efeitos desse distúrbio nas comunidades vegetais e processos ecossistêmicos por elas mediados. O fator intensidade de pastejo afeta a composição de espécies de plantas e seus atributos, atuando como um filtro ambiental e determinando padrões de convergência e divergência funcional na comunidade. Essas alterações nos padrões, somadas às mudanças na fisionomia da vegetação afetam processos ecossistêmicos ligados à decomposição da serapilheira, principalmente mediados pela atividade de invertebrados detritívoros.

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Apêndices

Appendix 1**:** List of species found in the sampling plots in the experimental unit

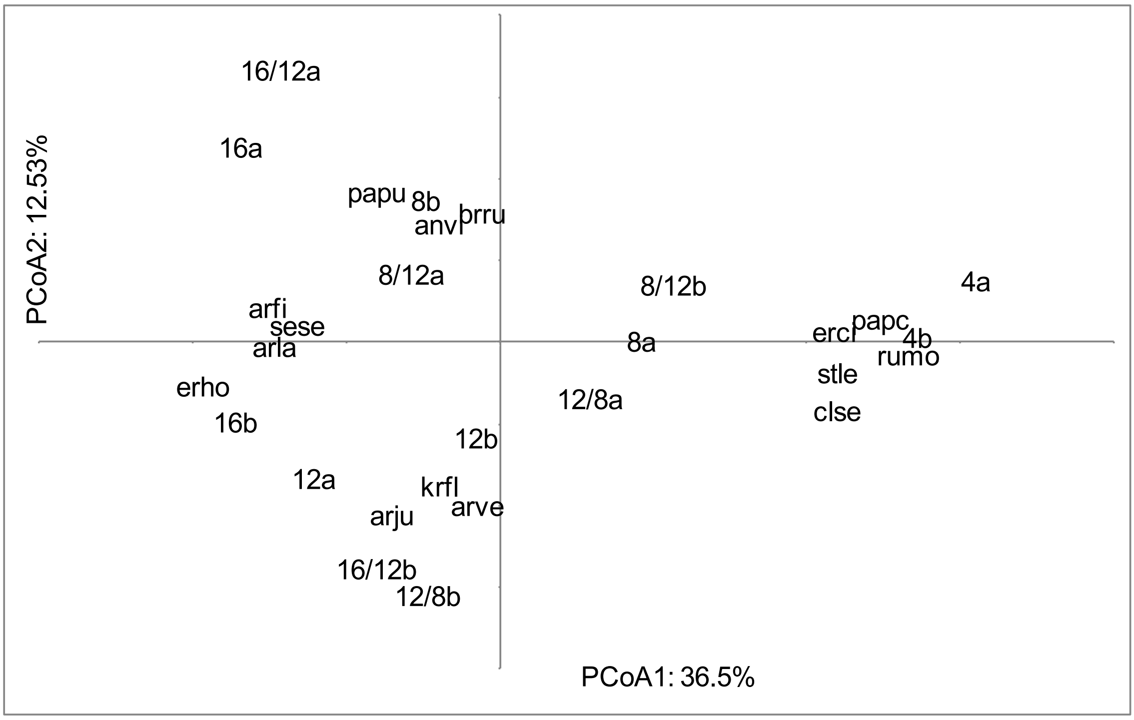
Family	**Species**	**Author**
Acanthaceae	Justicia reitzii	Leonard
Acanthaceae	Ruellia hypericoides	(Nees) Lindau
Acanthaceae	Ruellia morongii	Britton
Acanthaceae	Stenandrium diphyllum	Nees
Alliaceae	Nothoscordum minarum	Beauverd
Alliaceae	Nothoscordum montevidense	Beauverd
Amaranthaceae	Gomphrena graminea	Moq.
Amaranthaceae	Pfaffia tuberosa	(Spreng.) Hicken
Apiaceae	Centella asiatica	(L.) Urb.
Apiaceae	Cyclospermum leptophyllum	(Pers.) Sprague ex Britton & P. Wilson
Apiaceae	Eryngium ciliatum	Cham. & Schltdl.
Apiaceae	Eryngium elegans	Cham. Et Schlecht.
Apiaceae	Eryngium horridum	Malme
Apiaceae	Eryngium sanguisorba	Cham. Et Schlecht.
Araliaceae	Hydrocotyle exigua	Malme
Aristolochiaceae	Aristolochia sessilifolia	(Klotzsch) Duch.
Asteraceae	Acmella bellidioides	(Smith in Rees) R.K. Jansen
Asteraceae	Aspilia montevidensis	(Spreng.) Kuntze
Asteraceae	Baccharis coridifolia	DC.
Asteraceae	Baccharis dracunculifolia	DC.
Asteraceae	Baccharis trimera	(Less.) DC.
Asteraceae	Chaptalia exscapa	(Pers.) Baker
Asteraceae	Chaptalia piloselloides	(Vahl) Baker
Asteraceae	Chaptalia runcinata	Kunth
Asteraceae	Chaptalia runcinata	Kunth
Asteraceae	Chevreulia acuminata	Less.
Asteraceae	Chevreulia sarmentosa	(Pers.) Blake
Asteraceae	Conyza primulifolia	(Lam.) Cuatrec. & Lourteig
Asteraceae	Elephantopus mollis	Kunth
Asteraceae	Eupatorium ascendens	Sch. Bip. ex Baker
Asteraceae	Facelis retusa	(Lam.) Sch. Bip.
Asteraceae	Gamochaeta americana	(Mill.) Wedd.
Asteraceae	Hypochaeris albiflora	(O.K.) Azevêdo-Gonçalves & Matzenbacher
Asteraceae	Hypochaeris chillensis	(H.B.K.) Hieron
Asteraceae	Hypochaeris variegata	(Lam.) Baker
Asteraceae	Micropsis spathulata	(Pers.) Cabrera
Asteraceae	Orthopappus angustifolius	Gleason
Asteraceae	Pterocaulon angustifolium	DC.
Asteraceae	Senecio brasiliensis	(Spreng.) Less.
Asteraceae	Senecio brasiliensis	(Spreng.) Less.

Asteraceae	Senecio heterotrichius	DC.
Asteraceae	Senecio leptolobus	DC.
Asteraceae	Senecio selloi	(Spreng.) DC.
Asteraceae	Soliva sessilis	Ruiz et Pavón
Asteraceae	Stenachaenium campestre	Baker
Asteraceae	Vernonia flexuosa	Sims
Asteraceae	Vernonia nudiflora	Less.
Caryophyllaceae	Cerastium humifusum	Cambess. ex A. St.-Hil.
Cistaceae	Helianthemum brasiliense	(Lam.) Pers.
Commelinaceae	Commelina erecta	L.
Convolvulaceae	Dichondra macrocalyx	Meisn.
Convolvulaceae	Dichondra sericea	Sw.
Convolvulaceae	Evolvulus sericeus	Sw.
Cyperaceae	Abildgaardia ovata	(L.) Vahl
Cyperaceae	Bulbostylis capillaris	(L.) C.B. Clarke
Cyperaceae	Bulbostylis sphaerocephala	(Boeck.) C.B. Clarke
Cyperaceae	Carex phalaroides	Kunth
Cyperaceae	Eleocharis viridans	Kük. ex Osten
Cyperaceae	Fimbristylis dichotoma	(Retz.) Vahl
Cyperaceae	Kyllinga odorata	Vahl
Cyperaceae	Rhynchospora barrosiana	Guagl.
Cyperaceae	Rhynchospora rugosa	(Vahl) Gale
Cyperaceae	Rhynchospora tenuis	Link
Cyperaceae	Scleria distans	Poir.
Droseraceae	Drosera brevifolia	Pursh.
Euphorbiaceae	Euphorbia selloi	(Klotzsch & Garcke) Boiss.
Euphorbiaceae	Tragia bahiensis	Müll. Arg.
Fabaceae	Chamaecrista repens	(Vogel) H.S. Irwin & Barneby
Fabaceae	Clitoria nana	Benth.
Fabaceae	Desmanthus virgatus	(L.) Willd.
Fabaceae	Desmodium barbatum	(L.) Benth.
Fabaceae	Desmodium incanum	DC.
Fabaceae	Galactia marginalis	Benth. ex Benth. & Hook. f.
Fabaceae	Galactia pretiosa	Burkart
Fabaceae	Macroptilium prostratum	(Benth.) Urb.
Fabaceae	Rhynchosia diversifolia	Micheli
Fabaceae	Stylosanthes leiocarpa	Vogel
Fabaceae	Stylosanthes montevidensis	Vogel
Fabaceae	Trifolium polymorphum	Poir.
Fabaceae	Zornia cryptantha	Arechav.
Hypoxidaceae	Hypoxis decumbens	L.
Iridaceae	Herbertia pulchella	Sweet
Iridaceae	Sisyrinchium annuum	Ravenna
Iridaceae	Sisyrinchium micranthum	Cav.
Iridaceae	Sisyrinchium ostenianum	Beauverd
Iridaceae	Sisyrinchium sellowianum	Klatt

Juncaceae	Juncus capillaceus	Lam.
Juncaceae	Juncus tenuis	Willd.
Lamiaceae	Peltodon longipes	Kunth. ex Benth.
Lamiaceae	Scutellaria racemosa	Pers.
Linaceae	Cliococca selaginoides	(Lam.) C. M. Rogers & Mild
Lythraceae	Cuphea glutinosa	Cham. & Schltdl.
Malvaceae	Krapovickasia flavescens	(Cav.) Fryxell
Melastomataceae	Tibouchina gracilis	(Bonpl.) Cogn.
Moraceae	Dorstenia brasiliensis	Lam.
Myrtaceae	Campomanesia aurea	O.Berg
Myrtaceae	Psidium salutare var. mucronatum	(Cambess.) Landrum
Orchidaceae	Brachystele camporum	(Lindl.) Schltr.
Orchidaceae	Habenaria parviflora	Lindl.
Oxalidaceae	Oxalis brasiliensis	Lodd.
Oxalidaceae	Oxalis conorrhiza	Jacq.
Oxalidaceae	Oxalis eriocarpa	DC.
Oxalidaceae	Oxalis lasiopetala	Zuccarini
Oxalidaceae	Oxalis perdicaria	(Molina) Bertero
Oxalidaceae	Oxalis tenerrima	Knuth
Passifloraceae	Piriqueta selloi	Urb.
Passifloraceae	Turnera sidoides	L.
Plantaginaceae	Mecardonia tenella	(Cham. & Schltdl.) Pennell
Plantaginaceae	Plantago myosuros	Lam.
Plantaginaceae	Plantago tomentosa	Lam.
Poaceae	Andropogon lateralis	Nees
Poaceae	Andropogon selloanus	Hack.
Poaceae	Andropogon ternatus	(Spreng.) Nees
Poaceae	Andropogon virgatus	Desv. ex Ham.
Poaceae	Aristida filifolia	(Arechav.) Herter
Poaceae	Aristida flaccida	Trin. & Rupr.
Poaceae	Aristida jubata	(Arechav.) Herter
Poaceae	Aristida laevis	(Nees) Kunth
Poaceae	Aristida venustula	Arechav.
Poaceae	Axonopus affinis	Chase
Poaceae	Briza poaemorpha	(J.Presl) Henrard
Poaceae	Briza rufa	(J. Presl) Steud.
Poaceae	Briza subaristata	Lam.
Poaceae	Briza uniolae	(Nees) Steud.
Poaceae	Coelorachis selloana	(Hack.) Henr.
Poaceae	Danthonia cirrata	Hack. & Arechav.
Poaceae	Dichanthelium sabulorum	(Lam.) Gould & C.A. Clark
Poaceae	Digitaria violascens	(L.) Link
Poaceae	Eleusine tristachya	(Lam.) Lam.
Poaceae	Eragrostis neesii	Trin.
Poaceae	Melica brasiliana	Ard.

Poaceae	Paspalum dilatatum	Poir.
Poaceae	Paspalum lepton	Schult.
Poaceae	Paspalum maculosum	Trin.
Poaceae	Paspalum notatum	Fluegge
Poaceae	Paspalum pauciciliatum	(Parodi) Herter
Poaceae	Paspalum paucifolium	Swallen
Poaceae	Paspalum plicatulum	Michx.
Poaceae	Paspalum pumilum	Nees
Poaceae	Piptochaetium bicolor	(Vahl) Desv.
Poaceae	Piptochaetium montevidense	(Spreng.) Parodi
Poaceae	Piptochaetium stipoides	(Trin. & Rupr.) Hack.
Poaceae	Saccharum angustifolium	(Nees) Trin.
Poaceae	Schizachyrium tenerum	Nees
Poaceae	Setaria parviflora	(Poir.) Kerguélen
Poaceae	Setaria parviflora	(Poir.) Kerguélen
Poaceae	Setaria vaginata	Spreng.
Poaceae	Sporobolus indicus	(L.) R.Br.
Poaceae	Steinchisma hians	(Elliott) Nash.
Poaceae	Stipa nutans	Hack.
Polygalaceae	Polygala australis	A. W. Benn.
Rubiaceae	Borreria capitata	(Ruiz & Pav.) DC.
Rubiaceae	Borreria eryngioides	Cham. & Schltdl.
Rubiaceae	Diodia dasycephala	Cham. & Schltdl.
Rubiaceae	Galianthe fastigiata	Griseb.
Rubiaceae	Galium hirtum	Lam.
Rubiaceae	Galium richardianum	(Gillies ex Hook. & Arn.) Endl. ex Walp.
Rubiaceae	Richardia brasiliensis	Gomes
Rubiaceae	Richardia grandiflora	(Cham. & Schltdl.) Steud.
Rubiaceae	Richardia humistrata	(Cham. et Schlecht.) Steud.
Rubiaceae	Richardia stellaris	(Cham. & Schltdl.) Steud.
Rubiaceae	Spermacoce verticillata	L.
Verbenaceae	Glandularia marrubioides	(Cham.) Tronc.
Verbenaceae	Verbena montevidensis	Spreng.

Appendix 2: Analysis with species covers for the 153 species which data on functional traits were assessed.



PCoA ordination of the 14 experimental units. The numbers indicates percentage of forage offer on the experimental units (4=high; 8, 8/12, 12 and 12/8= moderated; 16/12 and 16= low grazing intensity). The letters “a” and “b” indicates blocks. Species with greater positive and negative correlations with the axis are indicated by codes: anvi *Andropogon virgatus*, arfi *Aristida filifolia*, arju *Aristida jubata*, arla *Aristida laevis*, arve *Aristida venustula*, brru *Briza rufa*, clse *Cliococca selaginoides*, erci *Eryngium ciliattum*, erho *Eryngium horridum*, krfl *Krapovicasia flavescens*, papc *Paspalum paucifolium*, papu *Paspalum pumilum*, rumo *Ruelia morongi*, sese *Senecio selloi*, stle *Stylosanthes leiocarpa*.

Results of MANOVA comparing species cover between treatments.

Comparation	p
Between groups	0.001
Contrasts :	
High X Moderate	0.05
High X Low	0.091
Moderate X Low	0.018