UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Tese de Doutorado

Estratégias de manejo adaptativo para os campos Sulinos

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Porto Alegre, março de 2017

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Tese de Doutorado 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 Doutor em Ciências com ênfase em Ecologia.

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Porto Alegre, abril de 2017

Vou num carro são
Sigo essa frente fria
Pampa a dentro e através
Desde o que é Libre sigo livre
E me espalho sob o céu
Que estende tanta luz
No campo verde a meus pés
(...)
Oigalê, que tal!
Sou o futuro imperfeito
De um passado sem lugar
Com a missão de olhar pra tudo
E em tudo viajar
Pra não ser só um cego
Num espaço sem ar

Eu acho que é bem
Eu indo ao Pampa
O Pampa indo em mim

Diz um capitão:
"Seja bem-vindo, hombre
Nosso tempo é todo teu
Tempo de morte, dor e fome
Mas tempo de pelear
Onde as ideias
Não são cegas sem ar"
(...)
Eu indo ao Pampa
O Pampa indo em mim

Indo ao Pampa, Vitor Ramil (1997).

AGRADECIMENTOS

Primeiramente, gostaria de agradecer à universidade pública brasileira que, apesar de ser desacreditada por muitos, realiza pesquisa de excelência e ajuda a superar o atraso científico, tecnológico e cultural ainda muito marcante no Brasil. Essa instituição, que só existe em razão da luta de inúmeras pessoas, é responsável por grande parte do que conhecemos da biodiversidade brasileira.

Agradeço ao orientador Valério De Patta Pillar pela confiança depositada, pelo intenso aprendizado, assim como pela amizade construída ao longo do doutorado.

Ao professor da UFSM Fernando Quadros por toda a sua ajuda na concepção do experimento e pela paciência nos momentos decisivos que tivemos.

Ao pesquisador da EMBRAPA/ Pecuária Sul José Pedro Trindade por todo o seu suporte ao projeto esta pesquisa e pela amizade firmada.

À toda minha família que tem me acompanhado durante este tempo que passei dentro da UFRGS. Em especial agradeço à minha mãe Elisabeth Meinke Baggio e ao meu pai José Guilherme Baggio, pois participaram intensivamente da construção da minha educação.

À minha companheira Suzana Hoppe Oderich, pelo constante incentivo ao estudo assim com por todo o suporte emocional. Sem ela possivelmente não teria realizado este doutorado. Também agradeço à sua família, em especial a sua mãe Myriam Hoppe Oderich e o seu pai Ernesto Oderich pela amizade e todo o suporte proporcionado.

Ao produtor e biólogo Claudio Nery Martins proprietário da Estância Cinco Salsos, primeiro por propor esta parceria e em segundo pela amizade que se formou ao longo destes anos. A relação de confiança formada entre o Claudio e os pesquisadores do projeto PELD-Campos Sulinos tem sido fundamental para avançar no desenho de estratégias de manejo sustentáveis.

Todos os funcionários da estância Cinco Salsos, em especial ao veterinário Paulo Krause para além a parceria, pelo apoio constante a realização deste projeto. Ao capataz Mano pela amizade. Ao alambrador Santo Soares que tem sido responsável pela manutenção da água e das cercas, sem ele possivelmente este experimento teria sido muito mais difícil de conduzir. Também agradeço aos peões Anastácio (Xiru) e João Carlos.

Um agradecimento especial ao colega André Alfredo Coelho pela sua dedicação na condução deste experimento e na resolução das dificuldades encontradas.

Todo o apoio das pessoas que ajudaram na instalação do experimento, nos três levantamentos florísticos, na pesagem dos animais e no levantamento de artrópodes: Murilo Zanini David, Luiza Baggio, Gustavo Viegas, Gustavo Rolim, Rafael Martel, entre tantas outras pessoas que auxiliaram em algum momento os trabalhos de campo.

Todos colegas do ECOQUA pela parceria nestes 4 anos. Em especial agradeço ao Vasso Balogianni tanto pela ajuda no campo muitas vezes em condições difíceis, quanto pela revisão dos artigos presentes nesta tese. Também agradeço ao Vanderelei Debastiani e ao Vinícius Bastazini pelo suporte estatístico.

Aos colegas do LEVCAMP pela paciência em me receber e em especial agradeço à professora Ilsi Boldrini, a qual identificou muitas coletas que fiz nos três levantamentos florísticos.

Agradeço todo o suporte do Programa de Pós-graduação em Ecologia da UFRGS. À CAPES pela bolsa de estudos que recebi e ao CNPq pelo financiamento do projeto PELD/Campos Sulinos.

E por fim, agradeço a Alexandra Elbakyan e toda a equipe do site *scihub* por facilitar o acesso gratuito ao conhecimento produzido em todo o mundo.

RESUMO

Os ecossistemas campestres que caracterizam os Campos Sulinos contêm alta biodiversidade e a sua manutenção está associada aos regimes de distúrbio como o fogo e o pastejo. Apesar de sua ampla contribuição social, nas últimas décadas esses ecossistemas têm sido substituídos por lavouras anuais e silvicultura, em razão de uma suposta vantagem econômica em relação à pecuária. Portanto, urge a consolidação de estratégias de manejo que conciliem a manutenção da diversidade biológica, dos processos ecossistêmicos e dos serviços ecológicos, com a viabilidade econômica aos produtores. Neste sentido, esta tese pretende colaborar com a concepção de estratégias de manejo para distintas formações dos Campos Sulinos. No Capítulo 1 discutimos a perspectiva de manejo adaptativo para a conservação de mosaicos de campos e florestas, propondo alternativas para serem testadas. Os Capítulos 2 e 3 abordam respostas das comunidades de plantas às três estratégias de manejo implementadas em um experimento conduzido em Aceguá/RS. No Capítulo 2 tratamos das mudanças na diversidade funcional e na estratégia de utilização dos recursos pelas plantas em resposta às estratégias de manejo. Em três escalas espaciais estudadas houve efeitos significativos dos diferentes manejos avaliados, incluindo o tratamento controle definido pelo manejo adotado na propriedade. No Capítulo 3 tratamos do efeito da roseta espinhenta *Eryngium horridum* sobre as comunidades de plantas, em resposta a um gradiente de altura da vegetação e aos dois sistemas de manejo conservativos implementados. Mesmo em uma pequena escala de tempo, neste estudo tivemos uma amostra da produção secundária dos campos de *solos profundos* e das respostas das comunidades de plantas às diferentes estratégias manejo aplicadas.

Palavras-chave: Campos Sulinos, manejo adaptativo, diversidade funcional, interações positivas, manejo rotativo, oferta de forragem, *Eryngium horridum*.

ABSTRACT

The Southern Brazil grassland ecosystems (Campos) contain high biodiversity and their maintenance is related to disturbance regimes as fire and grazing. Despite their contribution to society, in the last decades these ecosystems have been converted to crops and tree plantations due to the alleged economic advantage compared to livestock farming on the native grasslands. Therefore, it is urgent to consolidate management strategies that could combine the maintenance of biological diversity, ecosystem processes and ecological services, with economically viable livestock farming. In this sense, this thesis intends to collaborate with the design of management strategies for distinct grassland formations of the South Brazilian Campos. In Chapter 1 we discuss the concept of adaptive management as applied to grassland/forest mosaics that characterize southern Brazil formations, and propose management options to be tested. In Chapters 2 and 3 we refer to the responses of plant communities to three grazing management treatments implemented in an experiment conducted in Aceguá/RS. In Chapter 2 we investigated changes in plant functional diversity and resource use strategies in response to three grazing managements. At the three studied spatial scales we found differences between rotational grazing and the management used in farm. Finally, in the chapter 3 we study the effect of thorny rosette *Eryngium horridum* in plant communities, in response to the vegetation height gradient and the two conservative grazing managements. Even in a short time, in this work we verify the first results of the secondary production and the responses of plant communities to the applied management strategies.

Key-words: South Brazilian Campos, adaptive management, functional diversity, facilitation, rotational grazing, forage allowance.

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Considerações finais

Introdução geral

Os ecossistemas campestres estão entre aqueles com a maior diversidade de plantas em todo o planeta (Wilson et al. 2012) e suportam cerca de 800 milhões de seres humanos (Reynolds et al. 2005). Os processos oriundos desses ecossistemas contribuem amplamente para a sociedade, através da produção de forragem para a pecuária (Nabinger et al. 2009), da redução da poluição da água (Schilling et al. 2015), o acúmulo de carbono no solo (Fornara & Tilman 2008; Soussana & Lemaire 2014), a diminuição de pragas para culturas anuais, a polinização (Werling et al. 2014), assim como contribui através da formação de valores culturais. A existência e a manutenção destes elevados níveis de diversidade e dos processos ecossistêmicos e serviços ecológicos fundamentais para a sociedade, estão diretamente associados à manutenção de regimes de distúrbio como o pastejo, fogo e a fenação (Wilson et al. 2012; Veldman et al. 2015). Apesar desta vasta importância, os ecossistemas campestres são regiões fortemente ameaçados pela ação humana, notadamente em decorrência da conversão para a agricultura e silvicultura (Veldman et al. 2015).

Os ecossistemas que caracterizam a região dos Campos Sulinos estão presentes em três estados brasileiros e são considerados, por setores do Agronegócio, como uma das últimas fronteiras agrícolas do sul do país destinadas ao avanço de cultivos anuais. Em 2002 no RS se estimou que mais de 60% da cobertura campestre original já havia sido suprimida principalmente devido à expansão da agricultura e silvicultura (Cordeiro & Hasenack 2009). Mesmo assim, o avanço das culturas anuais sobre essas áreas campestres permanece constante tanto no Rio Grande do Sul quanto na Argentina.

Figura 1. Foto tirada no município de Bagé/RS em 2014 vinculada à notícia "Soja avança sobre áreas de pecuária". Crédito: Fernando Gomes/Agencia RBS (http://zh.clicrbs.com.br/rs/fotos/veja-imagens-do-avanco-da-soja-na-metade-sul-41259.html endereço acessado no dia 27/02/2015)

E esse processo tem acontecido principalmente na nova fase de financeirização das grandes corporações que o coordenam o agronegócio na América Latina desde os anos 2000 (Golfarb 2015). Portanto, em função desta nova fase, no Rio Grande do Sul a partir de 2000 o aumento da área plantada de soja na região nos ecossistemas campestres remanescentes apresentou picos de incremento entre os anos 2005 e 2015 (Figura 2) (FEE/RS 2017).

No último ano avaliado (Figura 2), todas as regiões alcançaram um coeficiente de área plantada superior aos demais períodos analisados. Considerando todas estas regiões, entre os anos de 2010 e 2015 o incremento anual da área de soja foi superior a 340 mil hectares. Há, contudo, uma relação entre o avanço da soja e a perda dos ecossistemas campestres cujas transformações da paisagem são facilmente visualizadas em visitas ao campo nestas regiões, notícias na imprensa regional (Figura 1) e relatos de produtores ao longo do período analisado. No entanto, existem poucos estudos recentes sobre a área dos ecossistemas campestres remanescentes nestas regiões(Oliveira et al. 2017).

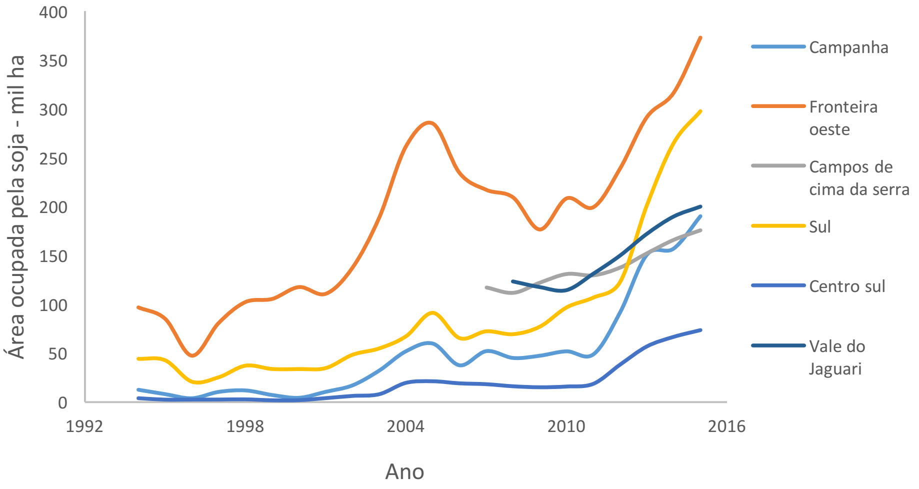

Figura 2. Evolução da plantação de soja no RS em diferentes regiões do estado (COREDES) em áreas caracterizadas pelo predomínio de formações campestres (FEE/RS 2017).

Manejo de ecossistemas

A estrutura e os processos dos ecossistemas suportam funções que potencialmente provêm serviços ecossistêmicos à sociedade. Entretanto, o sistema socioeconômico em que vivemos é, de um só modo, dependente e transformador dos sistemas ecológicos, pois usufrui diversos bens e serviços – comida, água, fibras, polinização, nutrientes, ar limpo, regulação do clima, bem-estar, etc. (Leff 1993; MA 2005; Häyhä & Franzese 2014). Portanto, a gestão e o manejo dos ecossistemas precisa ser combinada com a responsabilidade pela manutenção dos níveis desejáveis das funções ecossistêmicas. Ao sintetizar os objetivos oriundos de distintas perspectivas de manejo, Grumbine (1994) propôs: manter as populações viáveis de todas as espécies nativas *in situ*; representar dentre as áreas protegidas todos os tipos de ecossistemas com a sua amplitude de variação natural;

preservar processos evolutivos e ecológicos (e.g., regimes de distúrbios, processos hidrológicos, ciclo de nutrientes, entre outros); manejar por um período suficiente para manter o potencial evolutivo das espécies e ecossistemas; e, por fim, acomodar o uso e a ocupação humana dentre esses limites. Esses objetivos, no entanto, contrapõem diversas iniciativas governamentais de uso dos ecossistemas em vastas partes do globo.

As contradições existentes no modo de organização social, tornam complexa e intrinsicamente conflitante a gestão de recursos naturais (Leff 1993). Assim, parte significativa das decisões de manejo dos ecossistemas causam divergências entre os atores envolvidos. Dentre esses atores destacam-se os legisladores, pesquisadores das universidades e centros de pesquisa (e.g., EMBRAPA, INPA), agentes de fiscalização do Estado (e.g., SEMA e FEPAM/RS, IBAMA), os administradores das reservas ambientais (ICMbio, SEMA/RS), os produtores rurais e suas associações (e.g., Farsul, Fetraf, CNA), representantes de ONGs e de corporações nacionais e multinacionais ligadas ao Agronegócio (e.g., JBS, BRF, Monsanto, Bayer).

Recentemente, no Rio Grande do Sul, evidenciou-se o conflito de interesses na tomada de decisões acerca do manejo dos ecossistemas campestres. Com a emissão do Decreto Estadual 52.431/2015 pelo governo do Estado do Rio Grande do Sul, as áreas de campo nativo presentes nos biomas Pampa e Mata Atlântica poderiam ser declaradas no Cadastro Ambiental Rural como áreas rurais consolidadas. Entretanto, há evidências (Andrade et al. 2016; Fedrigo et al. 2017) de que o uso pastoril mantém a vegetação campestre nativa e, portanto, não causa sua supressão como estaria indicando o referido Decreto. Além disso, o uso pastoril é essencial para a conservação desses ecossistemas, pois estudos paleoecológicos indicam coevolução destes campos com regimes de distúrbios como o pastejo e o fogo (MacFadden 1997; Strömberg 2011). A declaração de campos nativos como áreas de uso consolidado em que teria ocorrido a supressão da vegetação nativa fragilizaria ainda mais a sua conservação, ao comprometer a exigência de Reserva Legal em ecossistemas campestres. Salienta-se, contudo, que os efeitos de Decreto foram suspensos por iniciativa do Ministério Público estadual. Portanto, o governo do Rio Grande do Sul, estimulado pela expansão da agricultura para as áreas ocupadas pela pecuária, explicitamente procurou beneficiar setores específicos da economia em detrimento da conservação dos ecossistemas campestres.

Alternativas de manejo e conservação dos campos Sulinos

Em contrapartida à vertiginosa degradação dos ecossistemas campestres, parte dos objetivos dos artigos que compõe esta tese é auxiliar na proposição de alternativas sustentáveis de manejo para os campos Sulinos. Abordando, assim, os efeitos das opções de manejo sobre processos ecossistêmicos e serviços ecológicos. Dessa forma, o experimento base para os Capítulos 2 e 3 iniciou em 2014, através da iniciativa de um grupo de pesquisadores vinculados ao projeto de Pesquisa Ecológica de Longa Duração - Campos Sulinos. Sua finalidade, portanto, é testar em um sistema real de produção, alternativas de manejo sustentável para os campos nativos dessa região criadas e aplicadas nas áreas experimentais da UFRGS, UFSM e da EMBRAPA Pecuária Sul (Carvalho & Batello 2009; Barbieri et al. 2014). Assim, através de uma parceria com o proprietário da Estância Cinco Salsos, Sr. Claudio Neri Martins, foi possível o estabelecimento do experimento de Manejo Adaptativo no âmbito do projeto PELD Campos Sulinos.

A Estância Cinco Salsos desenvolve atualmente, dentre outras atividades, a produção de gado de corte da raça Hereford com ciclo completo, ou seja, todas as fases de criação dos animais (cria, recria e engorda) até a venda para os frigoríficos são realizadas dentro da propriedade. Nesse sentido, o experimento foi inserido no sistema produtivo da Estância com a finalidade de recriar fêmeas. Sendo assim, as novilhas entram no experimento com cerca de um ano e aproximadamente 190 kg de peso vivo e, no ano posterior, devem sair em condições para serem inseminadas e iniciarem a gestação (em função da condição corporal e aproximadamente 270kg de peso vivo). Ao contrário de um estudo dentro da área experimental de uma universidade ou centro de pesquisa, na qual se controla uma série de variáveis, a viabilidade deste experimento também dependeu do sistema produtivo da propriedade. Assim, outras atividades desenvolvidas não relacionadas ao experimento também repercutiram direta e indiretamente na sua condução.

A área destinada ao experimento (31°39'07"S, 54°09'59"W) possui 160 ha e está localizada no município de Aceguá/RS com a predominância de Vertissolos. A vegetação é caracterizada como *campos de solos profundos* com a predominância de gramíneas prostradas como o *Paspalum notatum*, *Axonopus fissifolius* (Boldrini 2009), dos subarbustos *Baccharis crispa* (carqueja) e *Baccharis coridifolia* (mio-mio) e da roseta espinhosa *Eryngium horridum* (gravatá ou caraguatá). Os campos desta propriedade são classificados como úmidos (*mesic grasslands*) com média pluviométrica anual da região de 1130 mm (Worldclim Hijmans et al. 2005). Acerca do histórico de uso da área, o produtor relatou que desde 1932 – ano em que sua família adquiriu a propriedade – a área cedida ao experimento jamais foi convertida em lavoura ou pastagem plantada. Maiores detalhes sobre a área onde foi instalado o experimento podem ser encontrados na seção Methods do Capítulo 2.

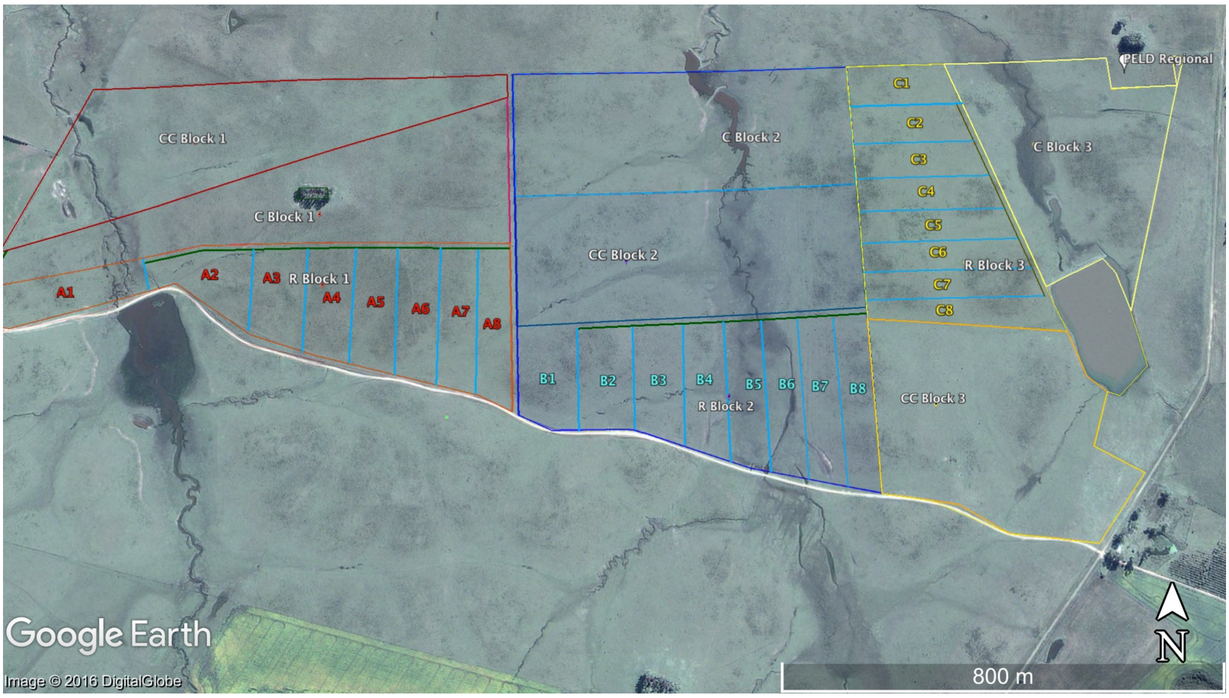

Figura 3. Imagem de satélite do experimento Manejo Adaptativo do projeto PELD-Campos Sulinos no município de Aceguá-RS. São três blocos (bloco 1 em vermelho, bloco 2 em azul e o bloco 3 em amarelo) com três tratamentos cada: Convencional (C), Contínuo conservativo (CC), e o Rotativo (R). Google 2016, DigitalGlobe 2016. http://www.earth.google.com [26 de Abril de 2016].

Neste experimento três formas de manejo do campo estão sendo testadas, duas propostas de manejo sustentável e a outra conforme o praticado pelo produtor:

(1) Manejo contínuo conservativo (CC): o gado tem acesso à toda unidade experimental sem limitações. A carga animal é ajustada de acordo à oferta de forragem almejada, que é a razão da disponibilidade de biomassa seca por hectare para cada kg de peso vivo de gado (Sollenberger et al. 2005). De setembro de 2014 a abril de 2015 a carga ajustada efetiva foi em média 4.7 Kg de biomassa seca / kg de peso vivo e nos demais

períodos as ofertas foram superiores (Tabela 1 e Apêndice S4 do Capítulo 3) em função da indisponibilidade de um número suficiente de animais para o experimento.

(2) Manejo rotativo (R) ou *Multi-paddock*: o acesso do gado à pastagem é controlado através da divisão de cada unidade experimental em oito potreiros. Cada potreiro passa por um período de descanso visando o crescimento da vegetação após o período sob pastejo. Períodos de descanso mais curtos beneficiarão grupos funcionais de plantas de rápido desenvolvimento, e períodos mais longos beneficiarão grupos funcionais de plantas com estratégias de conservação de recursos (Cruz et al. 2010). Tem sido proposto (Teague et al 2013) que o controle do acesso do gado à forragem através de múltiplos potreiros pode permitir o adequado reestabelecimento da vegetação em áreas sobre pastejadas, a ampliação da área utilizada pelos animais, o aumento da capacidade de suporte das áreas, a regulação da intensidade de pastejo. No experimento, utilizamos a soma térmica de 550 graus-dia como base para o período de descanso, que corresponde a um valor intermediário entre a soma térmica de 375 graus-dia, necessária para que espécies de plantas de rápido desenvolvimento expandam 2,5 folhas por perfilho, e 750 graus–dia, soma térmica necessária para espécies de desenvolvimento lento e vinculadas à estratégia conservação de recursos expandam 1,5 folhas por perfilho (Barbieri et al. 2014). A disponibilidade de forragem foi ajustada periodicamente em proporções similares ao manejo contínuo conservativo. Maiores informações sobre as ofertas utilizadas e o método de ajuste de carga em conformidade a disponibilidade de forragem estão descritas no Capítulo 2 em *Methods* e no Apêndice S4, de forma mais completa;

(3) Manejo convencional: o manejo destas unidades experimentais foi coordenado pelo capataz da estância. Portanto, o modo de condução resultou tanto do próprio conhecimento, quanto do seu aprendizado através do convívio com os pesquisadores e das

demandas da propriedade. No primeiro ano estas áreas ficaram submetidas a baixas cargas, e o fluxo de animais deveu-se aos ajustes da oferta de forragem das unidades experimentais sob manejo conservativo. A partir de agosto de 2015, essas áreas foram submetidas a períodos de altos níveis de oferta de forragem bem como outros períodos com altas cargas e baixas ofertas (Capítulo 3, Tabela 1 – Apêndice S4).

Objetivos gerais

Diante da intensa perda de campos naturais para a agricultura, precisamos consolidar alternativas de produção pecuária que, a um só tempo, mantenham processos evolutivos e ecológicos. E, por fim, que proporcionem sustentabilidade econômica de longo prazo aos produtores rurais como uma alternativa econômica à esta expansão. Através das experiências desenvolvidas pela pesquisa, sabemos que a pecuária produzida em campo nativo é economicamente viável e pode proporcionar resultados superiores aos da produção de soja (Nabinger et al. 2009). Porém, os efeitos destas alternativas de manejo em uma escala real de manejo de uma propriedade, ainda demandam estudos. Neste sentido, o Capítulo 1 da presente tese discute a importância dos regimes de distúrbio como o pastejo para a conservação de mosaicos de campo/floresta dos campos. Já, os Capítulos 2 e 3 tem por objetivo contribuir para o estudo das repostas dos ecossistemas campestres às alternativas de manejo através de uma abordagem experimental. O Capítulo 2 analisa as primeiras mudanças na diversidade funcional das comunidades submetidas aos três regimes de manejo e o Capítulo 3 avalia o efeito dos manejos conservativos e da intensidade de pastejo sobre o processo de facilitação nas comunidades de plantas pelo Caraguatá (*Eryngium horridum*).

Capítulo I: Conservation of South Brazilian Campos: why not adopting adaptive management?[*]

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[*] Este artigo será submetido à revista Brazilian Journal for Nature Conservation.

Conservation of forest-grasslands mosaics in South Brazilian Campos: why not adopt adaptive management?

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The recent debate in scientific community about conservation strategies for the South Brazil Campos has offered contrasting perspectives for the management of forest-grassland mosaics that characterize natural ecosystems in this region (Luza et al. 2014; Carlucci et al. 2016; Overbeck et al. 2016). The debate started with Luza et al. (2014) stating that intensively grazed and/or subjected to fire grasslands present reduced diversity of small mammals, which led the authors to recommend anthropogenic fire and livestock grazing in protected areas at the highest level (IUCN categories I and II, according to Dudley, 2008) for conserving the grassland–forest mosaic in southern Brazil. As for private protected areas (IUCN categories III, IV, V e VI), the authors recommended forms of sustainable grazing management. Overbeck et al. (2016), in response argued that there is no direct relationship between these disturbances and diversity decrease and proposed that, if the goal is to maintain grasslands ecosystems in the context of mosaics and all associated biodiversity, protected areas of any level should be subjected to management plans that include livestock grazing or controlled fire. Finally, Carlucci et al. (2016) argued that forests and shrub vegetation need to be protected from grazing in mosaics. In this article we aim to clarify some misunderstandings related to the apparent contradiction between conservation of native ecosystems and grazing by large herbivores, as well as to offer adaptive management options to be tested both in public and private protected areas with forest-grassland mosaics.

In ecosystem management, is common to simplify complex systems to make the ecosystem response more predictable to human needs (Holling & Meffe 1996). But these simplifications are not always able to match the real responses to management decisions, because we do not have the knowledge of all important processes that influence the path of the complex ecosystems. Therefore, it is necessary that the same decision-making process in the management of complex ecosystems also helps us to increase the knowledge about their functioning. In those situations, the adoption of adaptive management is important for even if we have knowledge about some processes of an ecosystem (Holling 1978; Walters 1986; Walters & Holling 1990; Allen & Gunderson 2011). The application of adaptive management is better when both uncertainty and controllability are high and where it is possible to conduct experimentation (Allen & Gunderson 2011). Thus, by testing the most plausible alternatives for forest-grassland mosaics management, we can begin reducing the uncertainties and answer which is the most appropriate conservation action.

The southern Brazil grasslands are ecosystems with high diversity that coevolved with grazing by large herbivores and fire (Macfadden 1997; Behling et al. 2007; Müller et al. 2012). In the last 50-300 years shrub encroachment and/or the presence of woody species has been observed largely in response to climatic changes, especially with increasing humidity (Archer et al. 1995; Müller et al. 2012). However, this process can be accelerated under low intensity or suppression of grazing and fire disturbances (Overbeck et al. 2007; Loiola et al. 2010). Yet, increase of humidity and the exclusion of grazing or fire are not only the sole factors that are degrading the grasslands ecosystems in Brazil. As well reports Veldman et al. (2015) for the *old-growth* ecosystems (including grasslands, savannas and woodlands) and Overbeck et al. (2007) for South Brazilian Campos, the land use change with conversion of grasslands to crop or silviculture areas, overgrazing or poorly management using domestic livestock, woody encroachment and invasive species are also important for the loss of biodiversity in this ecosystems. Therefore, if we aim at keeping these forest-grassland mosaics with high complexity in their dynamics and structure, we need to learn how to use and test the set of tools that we have at hand. And generalizations about grazing and fire may lead us to ignore low cost tools with an important potential to attract "allies" rather than "opponents" in the conservation of the South Brazilian Campos.

Grazing as a tool

Grazing, which is in the centre of the argumentation in this debate, has been used in a general way by Luza et al. 2014, Carlucci et al. 2016 and Overbeck et al. 2016. Grazing is a complex process and can both induce changes and is dependent of the ecosystems structure (McNaughton 1984; Anderson & Briske 1994; Augustine & McNaughton 1998a; Cingolani, Noy-Meir, et al. 2005; Díaz et al. 2007). The effects of grazing in spatial and temporal scales depend on the body size and digestive system of grazing animals (i.e. mouth and rumen format) (Schwartz & Ellis 1981; McNaughton 1984; Senft et al. 1987; Hodgson et al. 1991; Milne 1991; Osoro et al. 2013; Tóth et al. 2016), grazing intensity (amount of animals/time and area) (McNaughton 1984; Hobbs & Swift 1988; Belsky 1992; Teague et al. 2013), life stages (young, adult, lactating females) and management methods (continuous, herds, different types of rotational and grassland deferrals) (Walker et al. 1989; Bailey & Provenza

2006; Teague et al. 2011). Therefore, for using grazing as a management tool we have to predict the impact of grazing in grasslands spatial heterogeneity (Adler et al. 2001).

Large grazers interact with the ecosystems resources at different scales, and their behaviour is strongly influenced by grazing choices on both temporal and spatial scales (Senft et al. 1987; Olff & Ritchie 1998). Thus, large grazers was influenced by evaluation of the resources following since a plant individual scale (or animal feeding station), the plant community, landscapes and regional systems scale (Bailey et al. 1996). For example, at medium scales, abiotic factors such as topography, water distance, and temperature are often constraints within which the animals select grazing sites at finer scales considering forage quality and quantity (Hobbs & Swift 1988; Coughenour 1991; Jefferies et al. 1994). At fine scales, large herbivore behaviour is strongly influenced by the biotic factors. Therefore, when selecting plants and feeding stations, herbivores choices depends on abundance of biomass, the highest concentration of nutrients and lowest levels of toxins (McNaughton 1984; Senft et al. 1987; Jefferies et al. 1994; Bailey et al 1996). However, studies have shown that gregarious animal behaviour can decrease selective grazing within grazed areas (Augustine & McNaughton 1998a). WallisDeVries et al. (1999), using artificial mosaics of vegetation also verified that large grazers displayed more intense selective behaviour among large areas when compared to small patches (feeding stations scale). Therefore, relatively random grazing behaviour should occur at small scale among higher generalist grazers in plant communities where differences in species or patches palatability is small (homogeneous grasslands without shrubs or trees), and with herd rather than solitary large herbivores (Adler et al. 2001).

Distribution of grazing by large herbivore is the main theme for *old growth* ecosystems managers (Bailey et al. 1996), and it is more intensely discussed among scientists and managers of rangeland ecosystems such as the western of United States, arid areas of Argentina, African continent as in Australia (Fuhlendorf & Engle 2001; Witten et al. 2005; Jacobo et al. 2006; Müller et al. 2007; Bertiller & Ares 2008; Fynn 2012; Briske et al. 2013; Teague et al. 2013). Numerous studies have demonstrated the relationship between uneven grazing distribution and increases in soil erosion process, as well changes in habitat conditions of endangered species, at both lower and higher grazing intensities (Bailey et al. 1996; Hobbs 1996; Fuhlendorf & Engle 2001; Briske et al. 2011). Many of the existing strategies for controlling grazing heterogeneity have been in used for more than 45 years in rangeland management conservation in USA, but by the low adhesion of the rangeland managers many problems of ecosystem conservation still persist. The reasons for not adopting these management techniques are the lack of managers knowledge and the costs required for implementation (Bailey 2004; Briske et al. 2008). Below we will discuss some of existing knowledge with potential to be used in adaptive management experiments to maintain forest-grassland mosaics.

Some of the management strategies currently used aim to satisfy the grazers demands with artificial structures. For example, areas with woody or shrub component are mainly used for protection from heat and cold winds as well as for their proximity of water sources. Providing water points away from riparian vegetation decreases the use of these areas and often improves animal performance due to the better quality of the water (Porath et al. 2002). Artificial shading structures may also decrease the use of these areas mainly during the hottest times of the day(Bailey 2004). A direct way of conserving highly sensitive to grazing areas is the exclusion of large grazers through fencing. Fences can also be used to homogenize grazing behaviour by temporally concentrating the animals in certain areas, while allowing the recovery of others. The use of resource attractors such as molasse bars, mineral salt (or other dietary supplements) and herds management also can help to maintain large herbivores away from water sources or other resources. The combination of grazing supplementation and herding has been shown to be effective in reducing the use of riparian vegetation by large grazers (Bailey & Provenza 2006).

Type of grazing animal also plays a key role in heterogeneity of grazing. For example, even among cattle breeds there are very different grazing behaviors. Comparing species of herbivores, Schwartz and Ellis (1981) verified different patterns of feeding in response to different months and plant functional groups (warm season grass, cool season grass, warm season forbs, cool season forbs and shrubs). The authors found that larger bison and cattle prefer more abundant grasses while the smaller pronghorn's often prefer low-fiber, high digestibility forbs. Sheep, the smallest domestic grazer often studied, select more grasses (both C3 and C4) than expected and consequently their diets were with higher proportions of fiber. The consumption by bison and cattle was uniformly high throughout the period and despite the loss of forage quality (Schwartz & Ellis 1981).

Locally, in southern Brazil, goats and sheep are used by numerous small producers in the forest-grassland mosaic present along Camaquã river valley. Comparing with sheep, goats select more woody species and less herbaceous plants, thus have the potential to control shrub encroachment in grasslands (Milne 1991; Osoro et al. 2013; Fleming et al. 2016). It has been proposed that mixed grazing by sheep and goats can be used as a management option in these communities to improve forage utilization due to their complementary grazing behavior (Osoro et al 2013).

Fire and grazing

Similar to grazing, fire is an important disturbance regime that affects ecosystems structure and processes (Westoby et al. 1989; Belsky 1992; Hobbs 1996; Overbeck et al. 2005; Kraaij & Ward 2006; Podgaiski et al. 2013; Vasconcelos et al. 2016) and is constantly used in management of both public and private areas of open ecosystems (Hobbs 1996; Macdonald et al. 2007; Kyser et al. 2008; Kirkpatrick et al. 2016). Grassland plant diversity appears to be resilient in response to variable frequencies and seasons of burning (O'Connor et al. 2010; Fidelis et al. 2012). However, one important issue in fire management is the season of its applications, since, depending on the applied season, it can be harmful for important plant species and almost extinguish them from an given ecosystem (O'Connor et al. 2010; Fidelis & Blanco 2014). In southern Brazil grasslands, mostly on highland grasslands, fire is commonly applied in the end of the winter when there is a high quantity of dead biomass remaining from the summer in order to promote the regrowth of palatable species (Heringer & Jacques 2002). However, Fidelis & Blanco (2014) argue that due to the frequent use of fire in the end of the winter there is a tendency towards a decrease in the presence in C3 grasses.

Fire and grazing by large grazers are key factors that interact in determining the dynamics of grassland formations throughout the world (Hobbs 1996; Koerner & Collins 2014). Although there is a great deal of knowledge about the effect of each disturbance individually in plant communities, little is known on how communities respond to the interaction of fire and grazing (Veen et al. 2008; Kirkpatrick et al. 2016). In general, grazing reduces the biomass of plants available for burning and thus can reduce the frequency, and intensity of fires (Hobbs 1996; Overbeck et al. 2005). Vegetation recovering from fire is very attractive to large herbivores due to its high palatability and nutrients concentration and this can result in changes in communities structure and eventually differentiate these communities from communities that are only burned or only grazed (Collins & Smith 2006; Kirkpatrick et al. 2016). Grazing after burning are predominantly associated with an impeded recovery of woody plants (Leigh et al. 1987; Hill and French 2004), but also it is associated with an increased in cover of unpalatable woody plants (Radloff et al. 2014). Testing the effect of the interaction between fire and grazing on different temporal and spatial scales, Collins & Smith (2006) found that the individual effects of grazing and fire on spatial and temporal heterogeneity are scale independent, but their interaction is dependent on the measured scale. They also verified that annually burned sites were characterised by lowest spatial and temporal heterogeneity than infrequently burned sites (20 years), present highest at all scales. At small scales (10 m^2) grazing after annually burned sites increased spatial and temporal heterogeneity but in patches scales (50m^2) grazing decreased the spatial heterogeneity on sites burned every 4 years and had no effect witjh other fire frequencies management (Collins & Smith 2006).

Therefore, both grazing and fire are used around the world as an instrument for the management of non-forest ecosystems. Like any instrument, they have limitations. However, taking into account the possibilities created by the application of this environmental legislation approved in 2012 which allows the combination of sustainable use with the income of the cattle producers, the use of these disturbance regimes in a controlled way gains allies for the conservation of these ecosystems. In order to consolidate and validate strategies for the management of grasslands and forest mosaics, it would be important to combine experimentation as a way to reduce the uncertainties of decision making strategies.

And the viability of these initiatives will be conditioned the interaction between livestock producers, researchers, decision makers of the state inspection bodies.

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Capítulo II: Grazing strategies promote changes in opposite directions of functional diversity in a native grassland[*]

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[*] Este artigo será submetido ao periódico Applied Vegetation Science

Grazing strategies promote changes in opposite directions of functional diversity in a native grassland

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ABSTRACT:

Question: The dynamics of plant diversity in grasslands are strongly influenced by grazing behaviour. Management systems often seek to control the impact of intensive grazing on different scales. Could different grazing managements with similar forage allowance change the functional strategy of plant communities?

Location: Subtropical native grassland of southern Brazil (Campos); 31°39'07"S, 54°09'59"W; 170 m a.s.l.

Material & Methods: We analysed functional changes in plant communities under three cattle grazing management systems: (1) continuous conservative grazing with systematic adjustment of stocking rate to carrying capacity, (2) multi-paddock, rotational grazing with equivalent stocking rate adjustment of (1), and (3) control treatment under continuous grazing management used in the farm without systematic adjustment of stocking rate to the carrying capacity. The experiment adopted a randomized complete block design with three replicates of 16 ha (paddocks) for each treatment. Within each experimental unit we systematically marked 256 plots of 1.6 x 0.2 m, and each plot was divided into eight 0.2 x 0.2 m sub-plots, where the presence/absence of all plant species were recorded in the 2014 and 2016 surveys. We summarized by PCA ordination the variation of 13 traits describing 98 species and used one significant PCA axis to calculate community weighted mean (CWM) and Rao quadratic entropy for each experimental unit. Rao entropy was also partitioned into the α, β and γ spatial components across different scales (whole experimental unit, relief gradient positions, and plot scale).

Results: PCA axis I reflected a resource acquisition trade-off ranging from a conservative acquisition strategies of C4 grass species, with solitary tussocks and high leaf dry-matter content (LDMC), to rapid acquisition strategies of C3 forb species with protected meristems and high specific leaf area (SLA). Rotational grazing decreased α functional diversity at the experimental unit scale, and increased the proportion of conservative strategies in humid patches and in plots with less preferred species. Continuous conservative grazing effect was similar to rotational grazing regarding α functional diversity at experimental unit scales but maintain higher α functional than rotational in humid patches. The control treatment increased α functional diversity at different scales and enhanced species with fast resource acquisition strategies and protected meristems at all scales.

Conclusion: Even in the short-term, different grazing management strategies affected functional composition plant community by both grazing intensity and selectivity in different scales.

Keywords: humid grasslands, rotational management, functional diversity, adaptive management, CWM, Rao quadratic entropy.

Nomenclature: The Taxonomic Name Resolution Service. iPlant Collaborative. Version 3.2 accessed on 08 Jun 2014. URL: http://tnrs.iplantcollaborative.org.

Introduction

Grazing by large herbivores is one of the most important drivers of biodiversity in grassland ecosystems (Huntly 1991). Since vegetation structure is affected by grazing and at the same time strongly influences grazing behaviour (McNaughton 1984; Olff & Ritchie 1998; Adler et al. 2001; Bailey & Provenza 2006), the interactions between resource availability in the ecosystem and the behaviour of grazing animals can alter ecosystems processes such as primary productivity, nutrient cycling, disturbance regimes, pathways of energy flow (McNaughton 1984; Hobbs 1996; Adler et al. 2001; Altesor et al. 2006; Díaz et al. 2007). The primary disturbance caused by large herbivores on plant communities is defoliation, which affects individual plant performance and competitive ability through the changes on plant resource acquisition capacity (Olff & Ritchie 1998; Augustine & McNaughton 1998b; Hendon & Briske 2002). However, defoliation by grazers is selective and may vary across ecosystem types and feeding stations (defined as the area a large herbivore can graze without moving) (Senft et al. 1987; Adler et al. 2001). This unequal effect of herbivory also depends on the animal species, body size, previous experience and age, the spatial arrangement of other resources (e.g. water, shading), and the grazing management system (Bailey, Gross, Laca, Rittenhouse, Coughenour, Swift, Sims, et al. 1996; Bailey & Provenza 2006; Teague et al.

2011). Thus, herbivory can affect plant diversity by creating environmental heterogeneity at different spatial scales (McNaughton 1984; Olff & Ritchie 1998; Adler et al. 2001).

At the fine scale, large herbivores often select plant species and thereby place them at a competitive disadvantage relative to undefoliated or more leniently defoliated neighbours (Hendon & Briske 2002). Such a behaviour is highly influenced by biotic factors as biomass quantity, nutrient concentration and leaf toxins (Senft et al. 1987). But there is empirical evidence that unselective grazing (random) can occur at fine scales with generalist grazers, in more uniform communities or patches (less differences in plant quality among species and grasslands rather than grass-shrub steppes), and with herding (Augustine & McNaughton 1998b; Adler et al. 2001). Grazing behaviour also depends on both the quality (e.g. protein content) and the quantity of available forage (Hobbs & Swift 1988) which are also important sources of grazing spatial heterogeneity (Jefferies et al. 1994). There is a body of evidence for humid productive grasslands that, insofar as an area is intensively grazed, the response of the plant community is the increase in forage quality (Hobbs 1996; Augustine & McNaughton 1998; Cingolani et al. 2005) which is a key factor to form frequently grazed patches (Adler et al. 2001). The increase in plant quality is likely explained by a decrease in the amount of senescent leaves, which are maintained in an early phenological state (Hobbs 1996) and also the increase of available nitrogen in the soil (Holland & Detling 1990). However, overgrazing is a problem in pastoral systems when the density of grazing animals (stocking rate) is maintained beyond the grassland's carrying capacity (O'Connor et al. 2010). To avoid overgrazing, systematic adjustment of stocking rate to carrying capacity has been advocated (Carvalho & Batello 2009). Further, trying to lessen the grazing selectivity effect at the landscape scale, grassland managers often adopt changing the distribution of water points, and fencing multi-paddock systems and herding for allowing deferred grazing or rotational grazing (Bailey & Provenza 2006; Teague et al. 2011).

Given the fact that grazing is often spatially and temporally heterogeneous, a crucial question in grassland management is the prediction of plant community responses to the grazing pattern (Milchunas et al. 1988; Hobbs 1996; Augustine & McNaughton 1998b). Numerous models have been proposed seeking the understanding of this relationship using simple functional traits (Díaz et al. 2007). Basing on analyses with global data and considering the generalized model (Milchunas et al. 1988), competitor-stress tolerator-ruderal (Grime 1977) model and the range succession model (Dyksterhuis 1949; Arnold 1955), Díaz et al (2007) concluded that the effect of grazing on plant community traits is mostly modulated by climate and herbivory history. The generalized model (Milchunas et al. 1988) was the one which better explained the observed patterns. The traits most associated with grazing intensity on humid grasslands and long history of coevolution, such as the Southern Brazilian Campos studied here (McFadden et al. 2011; Müller et al. 2012), were annual *life history*, short *canopy height*, prostate *habit*, stoloniferous and rosette *architecture*. No relationship was found between grazing and plant palatability (Díaz et al. 2007).

Other attributes are also being often used to study the response of communities to grazing, such as photosynthetic pathway, SLA and LDMC (Westoby 1998; Grime 2006; Al Haj Khaled et al. 2006; de Bello et al. 2009; Cruz et al. 2010; Öster & Eriksson 2012). Compared to C3, C4 plants tend to perform better in warm, sunny and relatively dry grasslands (Pérez-Harguindeguy et al. 2013). Plants with higher values of LDMC correlate negatively with potential relative growth rate (RGR), palatability, and positively with leaf lifespan (Pérez-Harguindeguy et al. 2013). Forage digestibility, at least for grass species, negatively correlates with LDMC (Pontes et al. 2007) and positively with SLA. Plant species with high values of LDMC are often opposite to plants with high values of SLA, the latter correlated negatively with leaf longevity, investment in important secondary compounds (tannins or lignin), and correlated positively with shoot regrowth ability (Westoby 1998; Díaz et al. 2001; Cingolani et al. 2005; Pérez-Harguindeguy et al. 2013). However, herbivore's selectivity for these leaf traits (considered good indicators of resource exploitative vs. conservative strategies) remains poorly tested (Mládek et al. 2013).

Here we analyse the early changes in functional diversity of plant communities at different spatial scales in response to three grazing management systems in an experiment established in humid native grassland. We tested the following treatments (1) continuous conservative grazing with systematic adjustment of stocking rate to carrying capacity, (2) multi-paddock, rotational grazing with equivalent stocking rate adjustment of (1), and (3) control treatment under continuous grazing management used in the farm without systematic adjustment of stocking rate to the carrying capacity. For that analyses, we considered community weighted mean traits (Ricotta & Moretti 2011) and functional diversity partitioned into the α, β and γ spatial components based on Rao quadratic entropy as proposed by De Bello et al. (2010), both based on the main PCA ordination axis of species described by traits (Fischer et al. 2016). After three years of the experiment, we tested the hypotheses that (1) the adjustment of stocking rate to carrying capacity would increase functional diversity and forage quality at paddock scale by reducing overgrazing of species that are preferred by grazers, and (2) that multi-paddock, rotational grazing would further reduce spatial heterogeneity on large scales by avoiding the creation of preferred, often overgrazed patches, and less preferred patches with less functional diversity and where we expect species with slow growth and higher lifespan. Also, as a response to more pronounced grazing selectivity, we also expected (3) higher β functional diversity under continuous than rotational grazing.

Methods

Site area

The experiment was established in 2013 in 160 ha of humid subtropical native grassland (31°39'07"S, 54°09'59"W, 175 m a.s.l., Appendix S1) located at *Estância Cinco Salsos* farm, municipality of Aceguá, Rio Grande do Sul state, Brazil. The soils are Vertisols (IUSS Working Group 2015) and the climate is Cfa (Köppen classification, Alvares et al. 2013), with 1130 mm annual mean precipitation and frequent summer dry spells. The annual mean temperature is 20.2 ºC, with 21.7 ºC in the warmest quarter and 11.8 °C in the coldest quarter (Worldclim Hijmans et al. 2005). The grassland vegetation is characterized by the dominance of prostrated (e.g. *Paspalum notatum*, *Axonopus affinis*) and some caespitose grasses (e.g. *Mnesithea selloana*, *Paspalum dilatatum*, *Nassela sp.*, and *Piptochaetium sp.*), with subshrubs (e.g. *Baccharis coridifolia*, *B. crispa*) and the tall rosette *Eryngium horridum.*

Experimental design and grazing management

The experiment was a randomized block design with three replicates (Appendix S1), each one with three experimental units (paddocks) which were randomly allocated to one of the three grazing management treatments (see below). The experimental units ranged from 16 to 21 ha and were separated by permanent electric fences. This experiment was part of the Brazilian Long-Term Ecological Research (LTER) network and aimed at testing the effects of grazing management treatments with cattle (Hereford heifers and young cows) in ecosystem processes and services.

The experimental units were delimited in such a way to maximize within-block similarity among experimental units regarding the distribution of vegetation physiognomies and relief positions. For this task, within each experimental unit we identified homogeneous patches according to relief position and soil humidity: (1) inundated, (2) humid, (3) talweg, and (4) mesic. Inundated patches are frequently inundated; humid patches have fewer periods of flooding, talweg patches are in the line of lowest elevation (drainage) of the mesic patches, and mesic patches are drier without any period of flooding. Before installing the experiment, the humid patches apparently were preferred by livestock grazing. We also identified patches historically less preferred by livestock, which are predominantly in mesic soils and are composed mostly of two species: *Eryngium horridum* and *Baccharis crispa*. *E. horridum* is a thorn plant that when adult may reach 30 cm in diameter, and the inflorescence emitted during spring (also with thorns) may reach about 1.5 m (Fidelis et al. 2007). *B. crispa* is a subshrub with up to 0.5 m and has phenolic compounds (Cabrera 1953; De Oliveira et al. 2012)

Starting in September 2014, the following grazing management treatments were applied to the experimental units:

(1) *Continuous conservative* grazing (CC): In this treatment, cattle had unlimited access to the entire experimental unit, and the stocking rate was adjusted periodically to maintain a forage allowance ratio of approximately 4.5:1 (i.e., 4.5 kg of aboveground dry biomass per kg of live cattle weight). For this, the amount of above-ground biomass was estimated using the method described in Appendix S4.

(2) *Multi-paddock, rotational grazing* (MP): Rotational grazing was applied maintaining approximately the same forage allowance of 4.5:1 applied to the CC treatment, but each experimental unit was subdivided into eight sub-paddocks with similar area. Each sub-paddock was grazed at intervals defined by a thermal sum of 550 degree days (Barbieri et al. 2014), which is enough for allowing leaf elongation of two most predominant functional groups of grasses in Southern grasslands (Cruz et al. 2010). While functional groups A and B (*Axonopus affinis* and *Paspalum notatum*) require 375 degree days for elongation of 2.5 leaves per tiller, the groups C and D (*Aristida laevi*s, *Saccharum trinii*) need 750 degree days treatment for elongation of 1.5 leaves per tiller. The periodical adjustment of the stocking rate considered the pre-grazing aboveground dry biomass in a given sub-paddock, which was extrapolated for the whole experimental unit. We also assumed a post-grazing dry biomass of 50% of the pre-grazing mass (see more in Appendix S4).

(3) Control treatment under *conventional* grazing management (C)**: This** was the grazing management system used in the farm with continuous grazing (cattle had unlimited access to the entire experimental unit) and forage allowance fluctuating according to seasonal grassland productivity and total stocking numbers of the farm. Between September 2014 and April 2015, it was frequent for experimental units to have higher or similar biomass values than the conservative grazing systems (see more in Table 1 of Appendix S4), but from August 2015 until November 2016 due to the high stocking rates of this period, the experimental units usually showed low and uniform aboveground biomass.

Data collection

We marked 256 plots of 1.6 x 0.2 m distributed systematically 75 m away from each other according to a virtual grid covering the whole experiment (Appendix S1). Each plot was divided into eight 0.2 x 0.2 m sub-plots (Appendix S2), where we recorded the presence/absence of all plant species, and the mean vegetation height (totalling eight measures per plot). Based on their location and observations in the field, we classified each plot in one of the abovementioned patch types.

Species composition surveys used here were conducted during the spring of 2014 and 2016, from November to December, namely 3 and 27 months after the start of the experiment. More than 140 species were identified in the study area. The ten most common species found in the 1.6 x 0.2 m plots at both surveys were *Paspalum notatum* (C4 Grass), *Axonopus fissifolius* (C4 Grass), *Steinchisma hians* (C3 Grass), *Mnesithea selloana* (C4 Grass), *Rhynchospora megapotamica* (C3 Cyperaceae), *Danthonia montevidensis* (C3 Grass), *Paspalum dilatatum* (C4 Grass), *Piptochaetium montevidense* (C3 Grass), *Chevreulia sarmentosa* (Forb) and *Eleocharis viridans* (C3 Cyperaceae).

Traits

For analysis of functional traits, we used 98 of the total of 145 species, based on their frequency in the sampling and the availability of trait data. We considered the following traits: Specific leaf area (SLA), leaf dry-matter content (LDMC), photosynthetic pathway (C4 or C3), and Raunkiaer's life-form classification (Raunkiaer et al. 1935) modified by Ferreira (2014, see the description and list of species with each corresponding life-forms in Appendix S3).We use leaf traits of the species present in our database which were measured following Pérez-Harguindeguy et al.(2013) and photosynthetic pathway was compiled from the literature.

Data analysis

We applied Principal Components Analysis (PCA) to the correlation matrix between traits computed from the species by traits matrix, and used for further analyses the most relevant axes summarizing independent dimensions of the spectrum of plant functional strategies (Figure 1, see species scores in Appendix S5). This approach avoids potential bias caused by correlated and redundant traits (Díaz et al. 2015; Fischer et al. 2016) and can also reduce the limitations caused by missing values in trait data (Josse & Husson 2016). For this analysis, the nominal traits (photosynthetic pathway and life-form) were expanded into binary traits. Missing data comprised 6% of the cells in the species by expanded traits matrix. The significance of the ordination axes was tested by bootstrap resampling (Pillar 1999), which indicated that only PCA axis I was significant (P = 0.03), i.e., with stable species scores across the resampling process.

For the scaling-up of the trait information to the community level we considered the following nested community units: (1) species presence/absence in each 0.2 x 0.2 m subplot, (2) species frequency, i.e., proportion of 0.2 x 0.2 m subplots with the species present, in each 1.6 x 0.2 m plot, (3) average species frequency considering the plots in the homogeneous patches previously identified within each experimental unit based on soil moisture and grazing preference, and (4) average species frequency considering all the plots in each experimental unit. Based on the species scores on axis I of the PCA, we computed community-weighted mean values (CWM, or Matrix T in Pillar et al. 2009) for each community unit from levels 2 to 4, and Rao's quadratic entropy index (Ricotta & Moretti 2011) for each community unit from levels 1 to 4. We computed the CWM values for each species composition survey (2016 and 2014) and then we subtracted CWM values between the two surveys to analyse the changes in mean trait values during this period.

Rao entropy was partitioned into spatial components according to de Bello et al. (2010). For this we computed α_{Eqv} (the Jost-equivalent average of α Rao entropy computed for the units within the nesting community unit), and γ_{Eqv} (Rao entropy calculated with the average species composition in the nesting community unit). By using α_{Eqv}, γ_{Eqv} and the number of units in each nesting community unit we calculated $\beta_{Norm\text{-}prop}$ functional diversity (equation 14 in de Bello et al. 2010). Here as well we considered for further analyses the differences in α_{Eqv}, $\beta_{Norm\text{-}prop}$ and γ_{Eqv} values between the last (2016) and the first (2014) species composition survey.

The effects of grazing treatments on the changes in CWM and Rao entropy values described above, computed at the experimental unit level, considering the experimental unit as a whole or restricted to types of homogeneous patches, were tested by univariate analysis of variance using permutation testing (Pillar & Orlóci 1996; Pillar 2013). Since it was a randomized block design, permutations were restricted within blocks. Note that in these analyses we considered the average value per experimental unit (or homogeneous patch type per experimental unit), thus there was no pseudo-replication. The same test was also applied to assess the effects of the presence of *E. horridum* and *B. crispa* on the abovementioned variables computed at the level of homogeneous patches (only mesic patches), and the interaction between this factor and the grazing treatments, but in these tests the permutations between the two types of patches (considering the averages per patch type) were restricted within each nesting experimental unit. The PCA and the analysis of variance were performed using Multiv software, available at http://ecoqua.ecologia.ufrgs.br. The Rao quadratic entropy and CWM were calculated by R program package SYNCSA (Debastiani & Pillar 2012).

Results

The PCA ordination of the species described by functional traits (Figure 1) revealed one significant axis that comprised 21.2% of the total variation. Axis I mostly reflected variation ranging from C4 photosynthetic pathway, solitary tussocks (Te) life-form, and high LDMC, to C3 photosynthetic pathway, therophytes (Th), geophytes (Geo), herbaceous forbs (Hf), subshrubs (Ss), rosettes (Ro) and decumbent (De) life-forms, and high SLA. Therefore, axis I separated two opposing strategies of the fundamental trade-off involving plant development: from conservation of resources at the negative end of the axis, to rapid acquisition of resources at the positive end of the axis (Shipley et al. 2006; Hodgson et al. 2011).

Changes in functional diversity between 2014 and 2016 surveys at the experimental unit scale were significantly affected by grazing management (Table 1). Average α diversity increased more in the conventional grazing treatment (C) compared to the conservative grazing management treatments (CC and MP). We did not find any effect of grazing treatments on the changes in β and γ functional diversity values. Further, conventional grazing significantly increased CWM values on the main axis of trait variation (PCA axis I), indicating an increase in the proportion of species with fast resource acquisition strategies. The opposite, though only marginally significant ($P<0.08$), was observed under multi-paddock rotational grazing (MP), which decreased the proportion of species with fast resource acquisition strategies.

Similar effects of grazing treatments were observed considering only mesic patches (Table 1), where conventional grazing significantly increased the proportion of species with fast resource acquisition strategies. Again, we did not find any effect of grazing treatments on the changes of α, β and γ functional diversity values. Comparing the functional changes in humid patches (Table 1), average α and γ diversity increased more in both continuous grazing treatments (C and CC) compared to the multi-paddock rotational grazing (MP). We did not find any effect of grazing treatments on the changes in β functional diversity values in humid patches. Further, in humid patches, conventional grazing treatment (C) increased CWM values on the main axis of trait variation (PCA axis I), indicating an increase in the proportion of species with fast resource acquisition strategies, though the difference was only marginally significant. The opposite, was observed under multi-paddock rotational grazing (MP), which significantly decreased the proportion of species with fast resource acquisition strategies.

The analysis of functional diversity at micro scale (Table 2) calculated by the Rao quadratic entropy values of each plot and nested subplots (1.6 x 0.2 m and 0.2 x 0.2 m respectively) indicated that α^{micro} and γ^{micro} functional diversity and CWM values $_{micro}$ were affected by grazing managements only in mesic patches. Average of CWM values $_{micro}$, α_{micro} (considering all the 0.2 x 0.2 m subplots in mesic patches in each experimental unit) and γ_{micro} functional diversity (considering all the 1.6 x 0.2 m plots in mesic patches in each experimental unit) was higher in both continuous grazing treatments (C and CC) than in MP grazing rotational treatment. Also at micro scale in mesic patches (Table 3), plots with the presence of *Eryngium horridum* (thorny rosette) and *Baccharis crispa* (subshrub) present significantly higher ($P=0.04$) proportion of species with slow growth and greater investment in structural compounds than in their absence (indicating an increase in species with fast resource acquisition strategies). In the absence of *E. horridum* and *B. crispa* we did not found any significant difference between treatments. However, the γ^{micro} functional diversity and

CWM values were higher (P=0.04 and P=0.04 respectively) in both continuous grazing treatments (C and CC) than in MP grazing rotational treatment in presence of *E. horridum* and *B. crispa*. Further, we did not find any effect of grazing treatments on the change in β functional diversity at micro scale in mesic patches.

At plot scale, we found a linear negative significant relationship between CWM values and average of vegetation height (P=0.0001) considering all plots (Figure 2). Accordingly, shorter average vegetation height was more frequently observed with higher CWM values on PCA axis I, which indicated an increase in the proportion of species with fast resource acquisition strategies, and this relationship was found independently of grazing management regime and soil moisture patches. The correlation between functional diversity (α^{micro}, β^{norm}_{micro} and γ^{micro}) measured at plot scale and soil moisture levels (1-inundated, 2- humid, 3 – talweg, 4- mesic soils) was linear and positive for α^{micro} and γ^{micro} functional diversity (Figure 3) under conventional and continuous conservative treatments (P=0.02 and P=0.002 respectively), and marginally significant under multi-paddock grazing management (γ^{micro} P= 0.06). Therefore, under both continuous grazing systems, drier patches presented greater α^{micro} and γ^{micro}, which tended to decrease with increasing soil moisture patches.

Discussion

After 27 months of the experiment, our results demonstrated significant changes in plant functional diversity mediated by grazing management systems at the three spatial scales: whole experimental units, homogeneous vegetation patches, and plots. At the scale of the experimental unit, the grazing management treatments affected community weighted mean trait values along the resource conservation (grazing avoidance) vs. fast regrowth (grazing tolerance) trade-off. Contrary to our expectations, the control treatment with continuous grazing without systematic adjustment of stocking rate increased the proportion of forbs and grasses with structures adapted to intense grazing (i.e. protected meristems) and greater investment on rapid acquisition of resources with shoot regrowth ability, while decreasing the proportion of lower forage quality species, mostly grasses, with slow growth, higher lifespan and greater investment in structural compounds (Fraser & Grime 1999; Cingolani et al. 2005; Shipley et al. 2006; Pérez-Harguindeguy et al. 2013). The opposite was observed under rotational, multi-paddock grazing with systematic adjustment of stocking rate to the grassland's carrying capacity. This pattern of change along the resource exploitation trade-off in conventional and multi-paddock grazing also was found when we analysed the effect of treatments considering separately mesic or humid homogeneous vegetation patches, and also mesic patches with or without the thorny rosette *Eryngium horridum* and the subshrub *Baccharis crispa*.

The α and γ diversity patterns presented differences according to the scale analysed. Contrary to what we expected, the changes in functional diversity for the whole experimental units in management systems were similar, and the mean of plot values of conventional grazing increase functional diversity more than both conservative grazing (CC and MP). The reduction of the functional diversity of multi-paddock grazing system become clearly at homogeneous vegetation patches and at plot scale. There was a decrease of functional diversity for multi-paddock grazing in humid patches, which were preferred by cattle for grazing prior to application of treatments, and in mesic patches plots with thorny rosette *Eryngium horridum* and the subshrub *Baccharis crispa.*

The continuous conservative grazing system, as well as conventional management, promotes the continuous access of cattle throughout the experimental unit. The main difference with conventional management is the systematic adjustment of stocking rate to the grassland's carrying capacity. Even though the effective forage allowance fluctuated temporally during the evaluation period due to a certain mismatch between the temporal variation in grassland productivity and in availability of livestock in the farm, they were adjusted to be consistently equivalent in the two conservative management systems (CC and MP, see Appendix S4 – Table 1). In the first year the forage allowance was closer to the expected 4.5 kg of dry biomass to kg of live weight, but in the second year, due to unavailability of animals, the forage allowance was higher during some periods (Appendix S4 – Table 1). In any case, considering all the events of stocking rate adjustment, the median forage allowance was 4.9:1 in the continuous conservative management, and 4.3:1 in the multi-paddock, rotational grazing treatment.

Thus, in response to recent higher forage allowance, continuous conservative grazing keeps in humid patches a similar functional diversity than conventional grazing. But in mesic patches the continuous conservative grazing also increased the proportion of the lower forage quality species, mostly grasses, with slow growth, higher lifespan and greater investment in structural compounds. Nevertheless, in the mesic patches the continuous conservative grazing maintained similar levels of functional diversity than conventional grazing. This response is probably due to maintenance of humid as the preferred areas for grazing, with higher quality (low LDMC and high SLA) than the mesic patches, which also pre-exist highest frequency of the thorny rosette *E. horridum* and subshrubs *B. crispa*. In mesic patches, constantly selective grazing probably also are contributing to maintaining higher levels of functional diversity than multi-paddock grazing. While rotational grazing promoted rest time and thus, allows the regrowth of species with slower development (Teague et al. 2013), in continuous grazing with high forage allowance the selective grazing maintain both frequently grazed feeding stations with more palatable species with shoot regrowth ability and structures adapted to intense grazing and feeding stations less grazed which promote species with slow growth, higher lifespan and greater investment in structural compounds (Anderson & Briske 1994; Milchunas & Noy-Meir 2002).

During this first stage (27 months) of this experiment, the multipaddock grazing management system had similar forage allowance than continuous conservative. But was driven into a rotational system in which each sub-paddock had the rest time of 550 degree-days. As it was hypothesized, this management system proposes the greater development of a set of grasses that contemplate both strategies: the resource conservation (grazing avoidance) and fast regrowth (grazing tolerance) (Cruz et al. 2010). On this first stage, the communities submitted to the multi-paddock grazing maintained their functional diversity in the experimental unit scale, while decreased in the humid patches as well as presented lower values within the mesic patches in plot scale. The decrease of functional diversity probably was intensified due to the greater forage allowance promoted in the last year of management (Appendix S4-Table1). Therefore, the combination of rest time with high forage allowance promoted the increased the presence of C4 grasses linked to the resource conservation strategy. This process should be strongly linked to the competitive exclusion promoted by the greater development of C4 solitary tussock grasses with higher LDMC, to the detriment of species with rapid growth and adapted to intense grazing (protected meristems and higher SLA). The relationship with competitive exclusion is reinforced by the correlation between CWM values and the average height of the communities in each plot, whereas the average height increase as the CWM values of the community decrease. The effect of the competitive exclusion process in response to resting time also help to explain the decrease of the heterogeneity between the patches, inducing the species replacement in historically intense grazed patches.

In the last year, in response to lack of forage in other paddocks of the farm, the farmer used high stocking rate in the experimental units in which he manages and this promoted high grazing pressure to the plant community. This grazing intensity probably induced the increase verified of the functional diversity of species correlated with strategies of rapid acquisition of resources, shoot regrowth ability and adapted to intense grazing (protected meristems) regardless of scale. This increase is probably a response to grazing in larger herds, which exerts greater grazing pressure and less selectivity on the different cattle consumption scales (McNaughton 1984; Augustine & McNaughton 1998b; Adler et al. 2001).

In grasslands under continuous grazing management systems, the formation of intensely grazed patches in response to higher forage quality, proximity to water sources, size of paddock or even mineral salt are commonly reported (Senft et al. 1987; Bailey, Gross, Laca, Rittenhouse, Coughenour, Swift, Sims, et al. 1996; Bailey 2004; Briske et al. 2008; Moreno García et al. 2014). But the functional response of plant communities to grazing intensity, whether in a feeding stations, patches or for whole areas, remains controversial (Hendon & Briske 2002; Rodríguez et al. 2003; Vesk et al. 2004; Cingolani et al. 2005; Díaz et al. 2007; Jones et al. 2011; Vandewalle et al. 2014; Komac et al. 2015; Török et al. 2015). Our results indicate that the variations of the functional diversity in the less preferred patches under continuous grazing can be a response to selective grazing intensity promoted by different levels of forage allowance. Therefore, the amount of feeding stations frequently grazed probably will be greater with less forage allowance (Bailey et al.1996). In patches that are preferably grazed, both continuous management of this experiment presented increases in functional diversity linked to frequency of species with morphological and physiological adaptations to intense grazing. And this response is consistent with the generalized model proposed Milchunas et al (1988) and extensively tested by the Díaz et al. (2007) meta-analysis, in which productive and historically intense grazed grasslands the common response is the predominance of species with fast resource acquisition strategies, annuals, short, prostate, stoloniferous and rosette plants.

One of the major reasons to justify the use of rotational grazing systems (like the MP) is the control of grazing selectivity on both the feeding stations and landscape scales (Briske et al. 2008). Therefore, through controlling the intensity and both the time it is submitted to grazing and the rest, rotational grazing systems seeks to avoid degradation of grassland ecosystems by overgrazing and to increase primary and secondary productivity of the system (Teague et al. 2011; Teague et al. 2013). Before the beginning of the experiment, when we think about the strategy to be applied in the multi-paddock grazing management, we sought a balance of the trade-off between grasses with fast resource acquisition strategies and conservative strategies (Cruz et al. 2010). However, the combination of the rest time applied, selective grazing promoted by mild stoking rates (resulted of the high forage allowance maintained) and three growing seasons with above-average rainfall with the highest accumulation of biomass, probably induced this fast change in plant communities with higher predominance of traits linked to conservative strategy. Rotational grazing systems with low intensity of stoking rate also allows selective grazing mainly on the feeding station scale (Teague et al. 2011). Each grazing behaviour probably reflects on maintenance of functional heterogeneity through the similar values of β functional diversity to the other treatments, even with decrease in α functional diversity values in whole experimental units (Table 1 and Table 2).

Some questions still need to be answered to complement the understanding of the factors that are transforming the grassland functional structure, ecological processes and ecosystem services that are being modified. For example, does increasing functional diversity or the proportion of fast resource acquisition strategies also induce increased primary and secondary productivity? What are the changes in the balance of nutrients in the ecosystem? What are the effects of the transformations imposed by management on other organisms? These and other questions are important and remain open to understand which management system is best suited for this ecosystem and therefore to guide the discussions around this experiment.

Our results demonstrated that functional responses of the communities was coherent with the strategy of grazing management adopted. The analysis of functional diversity through the use of Rao quadratic entropy and CWM values (both based on the main axis of trait variation) at different spatial scales seems to be an effective tool for guiding the management of grassland ecosystems due to its sensitivity, even with short-term results. It not yet possible to evaluate if a grazing management strategy would be better or worse in the long run for their increase or decrease of the functional diversity or for maintaining a certain community structure. But they help us to better understand the processes affected by each management aiming at the biodiversity conservation.

Acknowledgments

This experiment was part of the Long-Term Ecological Research (LTER) network coordinated and funded by CNPq (Brazil). We thank especially Murilo Zanini, Luiza Baggio, Suzana H. Oderich that assisted in data collection, Ilsi Boldrini and colleagues at the

Laboratory of Grassland Vegetation for help identifying species, Émerson Soares, André Coelho and others members of the Natural Grassland Ecology Research Group (Lepan-UFSM) who helped in keeping this experiment alive, and the owner Claudio Martins and the farm employees of *Estância Cinco Salsos* for the partnership we have built during the last three years.

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Appendix list

Appendix S1 – Scheme of experimental area.

Appendix S2 - Permanent vegetation plots with 1.6 x 0.2 m composed of eight 0.2 x 0.2 m subplots.

Appendix S3 - Description of Raunkiaer’s adapted life-form classification.

Appendix S4. Biomass sampling and forage allowance adjustment.

Appendix S5 Values of the only significant axis obtained through the PCA of the species described by the attributes.

Table 1. Effects of grazing treatments on changes in functional diversity, CWM values on the main axis of trait variation (PCA axis I, see Fig. 1) between 2016 and 2014 surveys considering two spatial scales: whole experimental unit and homogenous patches related to soil moisture (mesic or humid). Positive changes in CWM indicate increase in the proportion of species with fast resource acquisition strategies.

Scale	Treatment	α_{Eqv}	$\beta_{Norm\text{-}prop}$	γ_{Eqv}	CWM values
	P-value	*0.062*	*0.30*	*0.16*	*0.029*
Experimental unit	C	0.024^{a}	- 0.0038	0.081	0.021^{a}
	CC	0.017^{b}	- 0.0020	0.061	0.0029^{b}
	MP	0.0054^{b}	0.0073	0.035	-0.011^{b*}
	P-value	*0.11*	*0.24*	*0.19*	*0.002*
Mesic	C	0.087^{a}	-0.0022	0.086	0.020^{a}
	CC	0.066^{a}	-0.0010	0.065	-0.0011^{b}
	MP	0.027^{a*}	0.0077	0.042	-0.013^{b}
	P-value	*0.049*	*0.24*	*0.10*	*0.028*
Humid	C	0.067^{a}	- 0.016	0.054^{a}	0.025^{a*}
	CC	0.045^{a}	- 0.0016	0.045^{a}	0.008^{a}
	MP	-0.045^{b}	0.0070	-0.042^{b}	-0.024^{b}

Values followed with the same letter had no significant differences (P<0.05). An asterisk (*) indicates marginally significant difference in a multiple contrast to the other grazing management treatments taken together (P<0.08).

Table 2. Functional diversity values under grazing management systems in plots (γ^{micro} - 1.6 x 0.2m) and subplots (α^{micro} – average of α from 8 subplots of 0.2m x 0.2m) on **2016** survey and in **mesic** patches:

Treatment	$\alpha_{eq\ micro}$	$\beta_{norm\ micro}$	$\gamma_{eq\ micro}$	CWM values $_{micro}$
P test	*0.049*	*0.99*	*0.007*	*0.08*
C	1.90^{a}	0.039	1.98^{a}	-0.039^{a}
CC	1.90^{a}	0.040	1.98^{a}	-0.039^{a}
MP	1.86^{b}	0.040	1.93^{b}	-0.057^{b}

Values followed with the same letter had no significant differences ($p<0.05$).

Table 3. Functional diversity values under grazing management systems in plots (γ^{micro} - 1.6 x 0.2m) and subplots (α^{micro} – average of α from 8 subplots of 0.2m x 0.2m) on **2016** survey and in **mesic** patches with and without the presence of the *Baccharis crispa* (subshrub) and the *Eryngium horridum* (thorny rosette).

	Treatment	$\alpha_{eq\ micro}$	$\beta_{norm\ micro}$	$\gamma_{eq\ micro}$	CWM values $_{micro}$
	P test	*0.42*	*0.44*	*0.28*	*0.34*
Without	C	1.91	0.046	2.00	-0.032
	CC	1.89	0.036	1.97	-0.041
	MP	1.88	0.037	1.95	-0.057
	P test	*0.18*	*0.48*	*0.10*	*0.06*
With	C	1.90	0.037	1.97^{a}	-0.041^{a}
	CC	1.89	0.042	1.98^{a}	-0.045^{a}
	MP	1.83	0.045	1.92^{b}	-0.068^{b}
	P test	*0.09*	*0.17*	*0.20*	*0.05*
Without		1.88^{*}	0.042	1.97	-0.049^{b}
With		1.90^{*}	0.038	1.96	-0.037^{a}

Values followed with the same letter had no significant differences ($p<0.05$). An asterisk (*) indicates marginally significant difference ($P=0.09$).

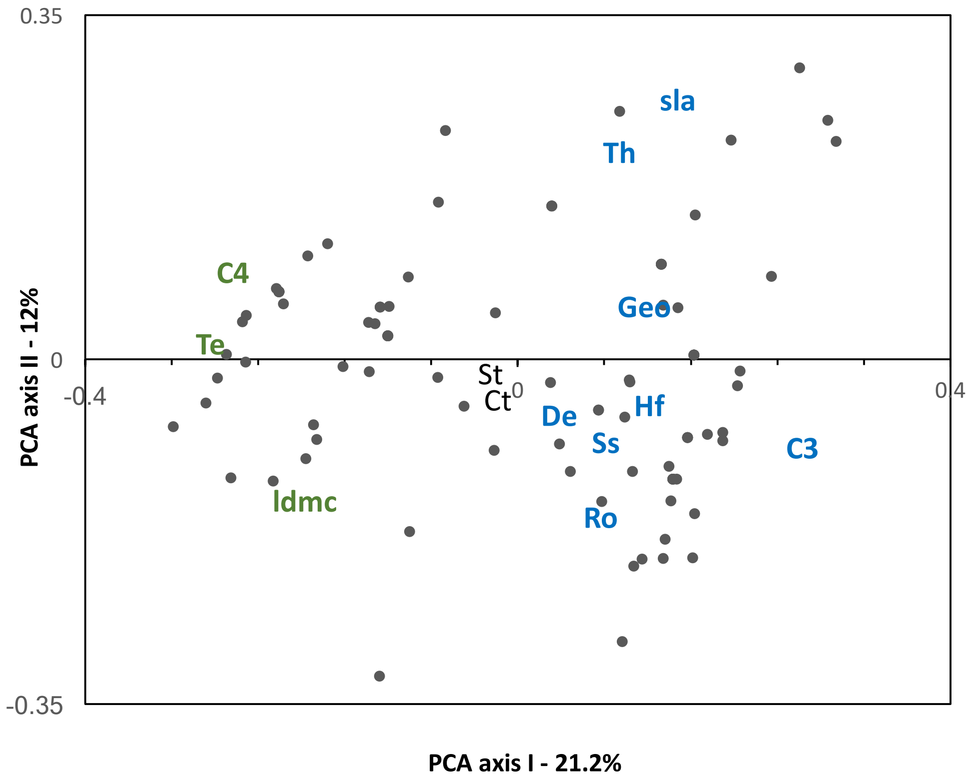


Figura 1. Scatter diagram of two axes resulted from PCA of the matrix describing 98 species by 12 traits. On the left, are species with high values of leaf dry matter content (LDMC), C4 photosynthetic pathway, and solitary tussocks (Te). On the right, are species with high values of leaf dry matter content (LDMC), C4 photosynthetic pathway, and solitary tussocks (Te). On the right, are species with high values of SLA, therophytes (Th), geophytes (Geo), herbaceous forbs (Hf), subshrubs (Ss), rosettes (Ro), or decumbent (De). In the intermediate positions are stoloniferous or rhizomatous (St) species, or with connected tussocks (Ct).

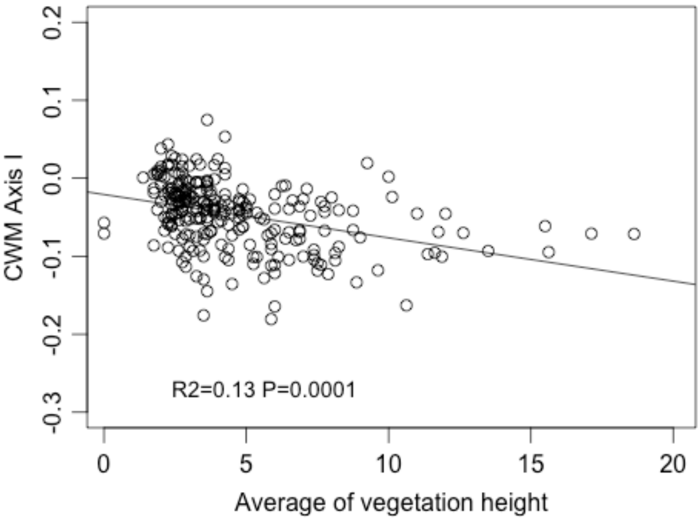


Figura 1. Relationship between average of vegetation height in the 2016 survey and CWM values on the main axis of trait variation (PCA axis I, see Fig. 1) computed at plot scale.

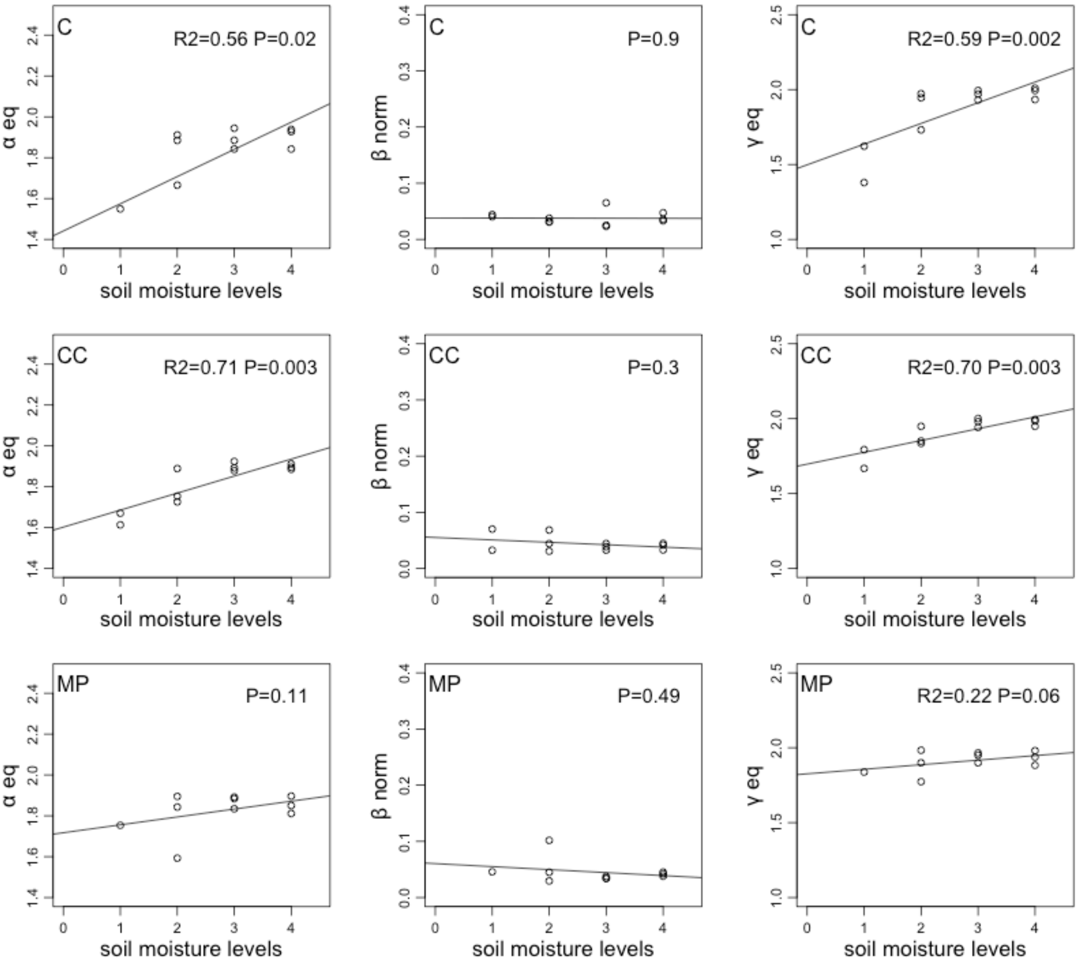
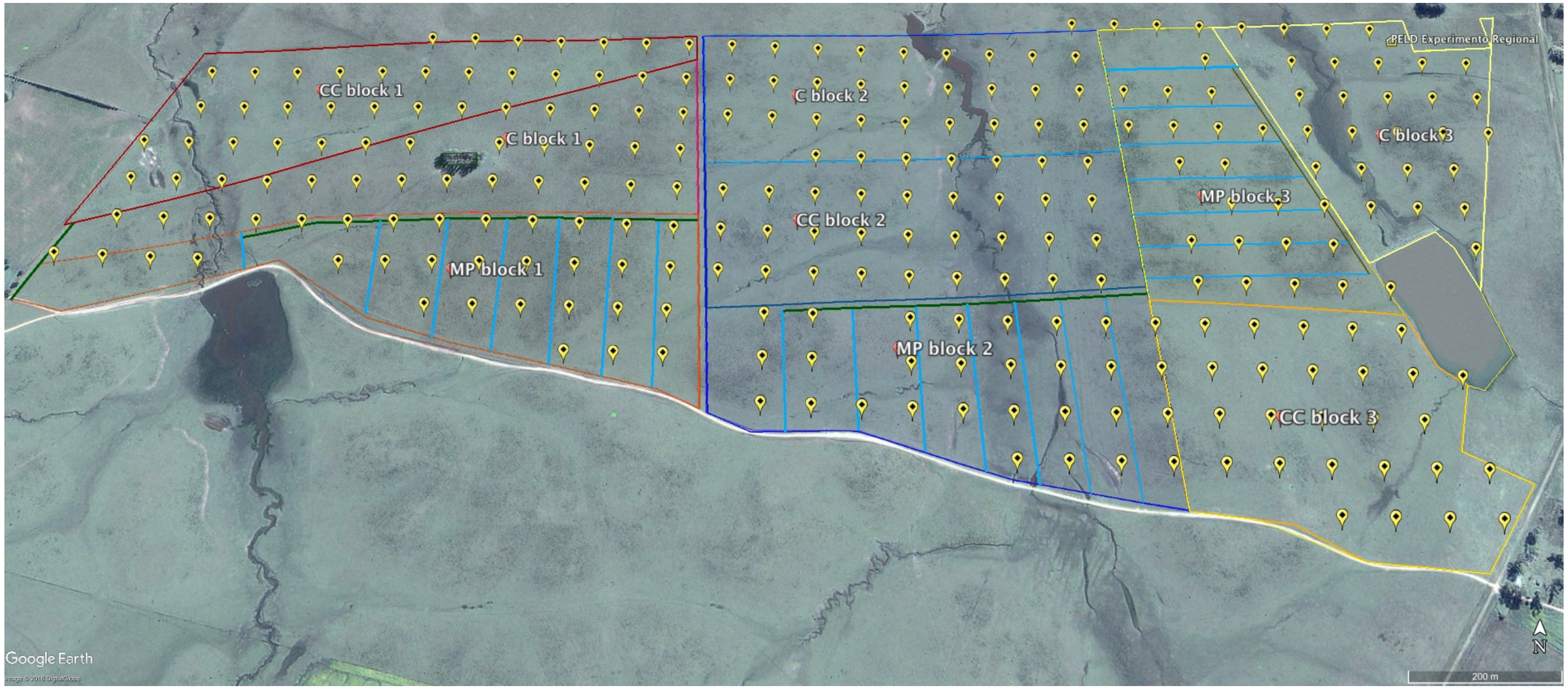
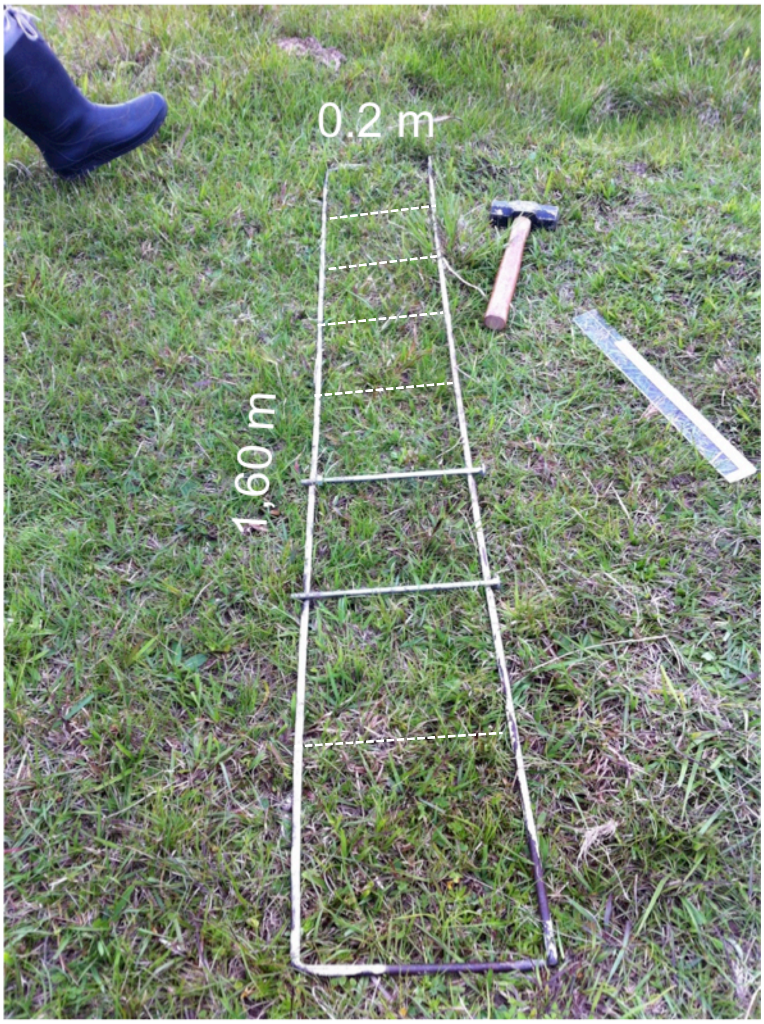


Figure 2. Relationship between functional diversity (α^{micro}, β^{norm} micro and γ^{micro}) measured at plot scale and levels of soil moisture (1-inundated, 2- humid, 3 –talweg, 4- mesic soils) for each grazing management system (C – conventional, CC – continuous conservative and MP – multi-paddock)



Appendix S1. The total area of experiment is 160 ha. C correspond the Conventional treatment, CC the Continuous Conservative and MP correspond the Multi-paddock grazing treatment. The latter are divided into 8 sub-paddocks with similar area. Blocks are marked in different colours: red (1), blue (2) and yellow (3). Points in yellow are the plots where we did the floristic surveys. Google Earth Pro 7.1.5.1557. (June 20, 2006). Aceguá/BR, 31° 39’ 18”S, 54° 09’ 16”W, Eye alt 2.2 km. Google 2016, DigitalGlobe 2016. http://www.earth.google.com [April 26, 2016].

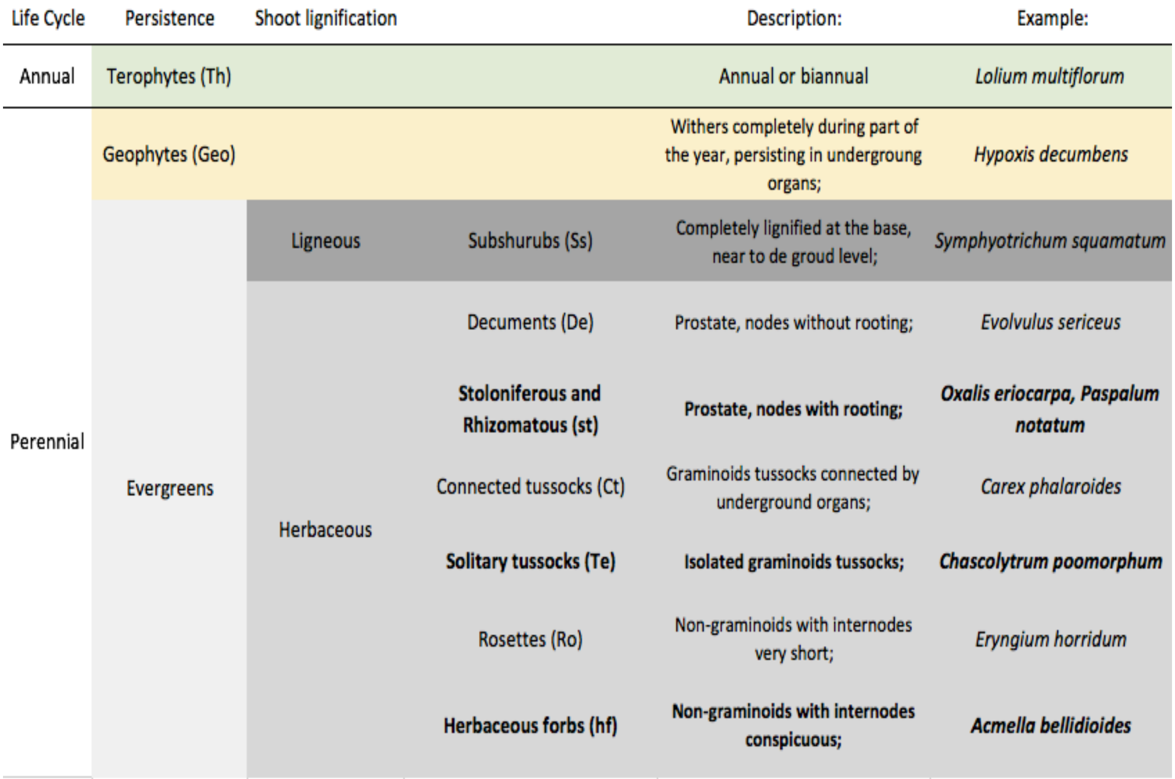
Appendix S2. Permanent vegetation plots with 1.6 x 0.2 m composed of eight 0.2 x 0.2 m subplots.



Appendix S3. Description of Raunkiaer’s adapted life-form classification (after Ferreira 2014).

The modified classification of *life-forms* was based on plant characteristics related to adaptation to herbivory and fire, comprising four hierarchical levels of refined categories. From Raunkiaer’s original classification, Chamaephytes and Geophytes were maintained (Figure 1 S3). Annual or biennial were classified as Terophytes, and Chamaephytes were treated as “Evergreens”. Based on shoot classification, within Evergreens category, were divided on Herbaceous and Ligneous. Plants lignified or slightly lignified at the base at the ground level we classified as *Ligneous* (Ss) (Ferreira 2014).

Other category used within *Evergreen/Herbaceous* was *Erect* with four sub-categories: *Rosettes* (Ro) as forbs with short internodes and *Herbaceous forbs* (Hf) with internodes conspicuous, *Solitary tussocks* (Te) as graminoids tussocks not connected and *Connected tussocks*(Ct) as graminoids connected by underground organs. Lastly, also within *Evergreen/Herbaceous* but to *Prostrate* plants as horizontal occupation strategy we also used (St) for both *Stoloniferous* and *Rhizomatous* and (De) for *Decumbent* plants (Ferreira 2014).



Life Cycle	Persistence	Shoot lignification		Description:	Example:
Annual	Terophytes (Th)			Annual or biannual	*Lolium multiflorum*
Perennial	Geophytes (Geo)			Withers completely during part of the year, persisting in undergroung organs;	*Hypoxis decumbens*
	Evergreens	Ligneous	Subshurubs (Ss)	Completely lignified at the base, near to de groud level;	*Symphyotrichum squamatum*
		Herbaceous	Decuments (De)	Prostate, nodes without rooting;	*Evolvulus sericeus*
			Stoloniferous and Rhizomatous (st)	**Prostate, nodes with rooting;**	***Oxalis eriocarpa, Paspalum notatum***
			Connected tussocks (Ct)	Graminoids tussocks connected by underground organs;	*Carex phalaroides*
			Solitary tussocks (Te)	**Isolated graminoids tussocks;**	***Chascolytrum poomorphum***
			Rosettes (Ro)	Non-graminoids with internodes very short;	*Eryngium horridum*
			Herbaceous forbs (hf)	**Non-graminoids with internodes conspicuous;**	***Acmella bellidioides***

Appendix S3a. Diagram with four hierarchical levels of refined categories of life-forms adapted from Raunkiaer’s life-form classification (Ferreira 2014).

Appendix S3b. Raunkiaer adapted life form classification for the species used in the analysis.

Species	Adapted life-form
Acmella_bellidioides	hf
Agalinis_communis	hf
Agrostis_hygrometrica	th
Agrostis_montevidensis	th
Anagallis_minima	st
Andropogon_ternatus	te
Aristida_murina	te
Aristida_uruguayensis	te
Aristida_venustula	te
Axonopus_fissifolius	st
Axonopus_argentinus	te
Baccharis_coridifolia	ss
Baccharis_crispa	ss
Bothriochloa_laguroides	te
Briza_minor	th
Carex_phalaroides	ct
Carex_sororia	te
Chascolytrum_poomorphum	te
Chascolytrum_rufun	te
Chaptalia_runcinata	pr
Conyza_bonariensis	th
Conyza_primunifolia	th
Chascolytrum_subaristatum	te
Chevreulia_sarmentosa	st
Desmanthus_tatuhyensis	ss
Eragrostis_bahiensis	te
Cuphea_glutinosa	hf
Cyclospermum_leptophyllum	th
Cynodon_dactylon	st
Danthonia_montevidensis	te
Eragrostis_plana	te
Dichanthelium_sabulorum	de
Facelis_retusa	st
Dichondra_sericea	st
Eleocharis_viridans	ct
Fimbristylis_autumnalis	st
Eragrostis_lugens	te
Eragrostis_neesii	th
Galactia_marginalis	ss
Glandularia_selloi	st
Eryngium_horridum	ro
Eryngium_nudicaule	pr
Evolvulus_sericeus	de
Juncus_capillaceus	te
Melica_brasiliana	te
Nierembergia_riograndensis	ss
Galium_richardianum	de
Gamochaeta_americana	hf
Paspalum_cf_recortado	rh
Hydrocotyle_exigua	st
Plantago_myosuros	th
Juncus_microcephalus	te
Juncus_tenuis	te
Leersia_hexandra	te
… continuing	…
Chaptalia_exscapa	pr
Chaptalia_piloselloides	pr
Dichondra_macrocalyx	st
Eryngium_echinatum	ro
Herbertia_lahue	geo
Hypochaeris_chillensis	geo
Hypoxis_decumbens	geo
Lolium_multiflorum	th
Luziola_peruviana	te
Mnesithea_selloana	te
Nothoscordum_montevidense	geo
Nothoscordum_sp.	geo
Oxalis_brasiliensis	geo
Oxalis_eriocarpa	st
Oxalis_perdicaria	geo
Paspalum_cf_lepton	rh
Paspalum_dilatatum	te
Paspalum_notatum	rh
Paspalum_plicatulum	te
Pfaffia_tuberosa	hf
Piptochaetium_montevidense	te
Piptochaetium_stipoides	te
Polygala_linoides	th
Pterocaulon_alopecuroides	hf
Rhynchospora_megapotamica	st
Richardia_humistrata	de
Richardia_stellaris	st
Schizachyrium_microstachyum	te
Scutelaria_racemosa	hf
Setaria_parviflora	te
Sisyrinchium_micranthum	th
Sisyrinchium_platense	hf
Soliva_sessilis	th
Sporobolus_indicus	te
Steinchisma_hians	te
Stenandrium_dulce	pr
Stipa_charruana	te
Stipa_filiculmis	te
Stipa_setigera	te
Symphyotrichum_squamatum	ss
Trachypogon_molle	te
Trifolium_polymorphum	st
Verbena_montevidensis	hf
Vulpia_bromoides	th

Appendix S4. Biomass sampling and forage allowance adjustment:

The periodic adjustment of the forage allowance was carried out through a systematic method of triple sampling of dry biomass. In each sampling unit, biomass was sampling in the form of W at 40 points for C and CC and at 25 points for MP grazing management (Figure 1 S4). In the sample units submitted to the MP, samplings were performed in the sub-paddocks in which the animals will enter as shown in Figure 1 S4.

For each sampling point, the following information were collected in a 0.5 x 0.5 m square:

- Five points of height of the vegetation, one in each vertex and the last one in the center of the square;
- Comparative visual estimation of biomass on a scale of zero to three;
- Of the total points made in the whole experiment, more than 35 dry biomass samples were cut, dried and weighed.

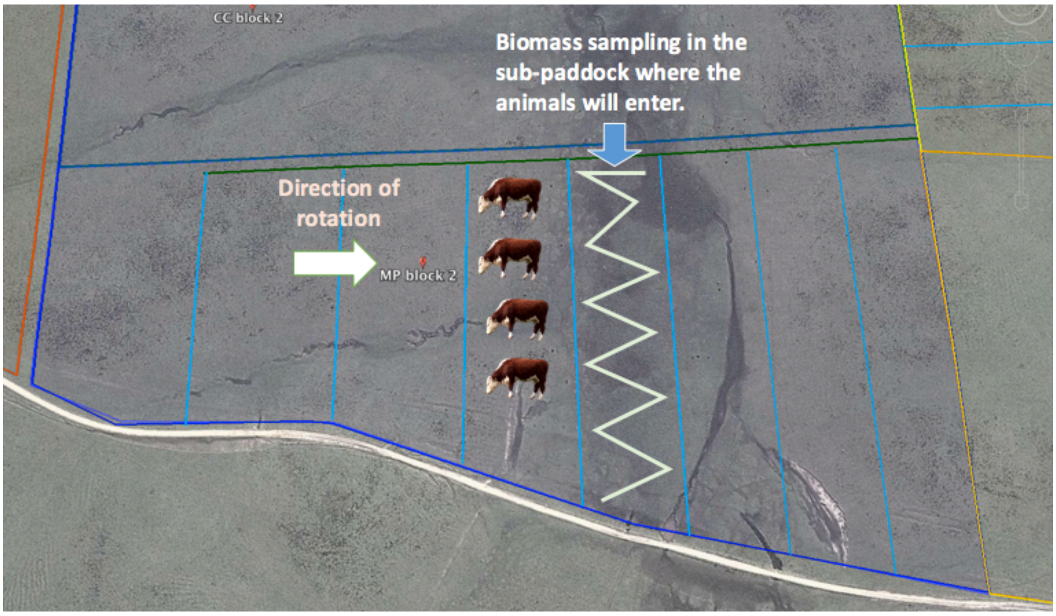


Figure 1 S4. Method of the biomass sampling used for the periodically adjustment of forage allowance in the sample units submitted to Multi-paddock grazing management.

The biomass collected remains 72 hours in the greenhouse at 60 degrees. With the values of the dry biomass we make two simple linear regressions between the dry biomass and both the visual estimate and the average of the five heights of the vegetation. Among the two equations generated, the one that presents the best adjustment (R^2) is taken into account (Figure 2 S4). To estimate the dry biomass of whole experimental unit we applied the equation to the other values obtained, or average height of the vegetation or the visual estimation of the dry biomass.

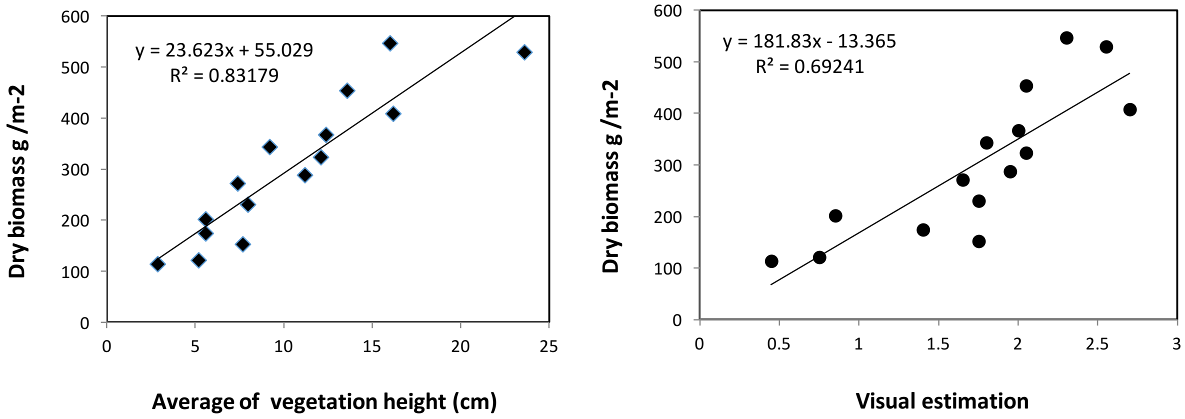


Figure 2 S4. Comparative forms of generating the linear equation for September of 2016. The higher R^2 value determines whish equation will be used, in that case we choose the equation provided by dry biomass and average of vegetation height.

Finally, to obtain the corresponding stoking rate for each paddock of the CC grazing management, we divided the biomass obtained by the desired ratio of dry biomass per live weight in following proportions: 4:1 in the growing season and approximately 5:1 in the autumn and winter. For the MP grazing management, we consider that the available biomass less the post-grazing dry biomass is, on average, the available biomass that the animals will find in each moment that they switch from sub-paddock. We also assumed a post-grazing dry biomass of 50% of the pre-grazing mass and use the same forage allowance than CC grazing management. For more details of these equations see in (Sollenberger et al. 2005).

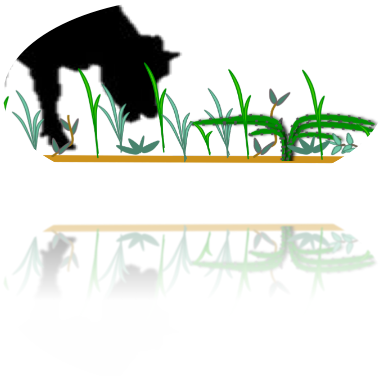
Appendix S4 Table 1. Average of dry aboveground biomass (kg/ha) and effective forage allowance (kg of dry aboveground biomass/ kg live weight) in each forage allowance adjustment for each grazing management system since the experiment beginning. Treatment C represent the common treatment applied in farm, CC is continuous conservative grazing system and MP is a multi-paddock grazing system. In multi-paddock grazing system the forage allowance represents de above-ground biomass measured before the entrance of cattle less the biomass consumed (aprox. 40%). In Nov 2015 and Dec 2016 we estimate the MP allowance allowance taking into account the aboveground biomass of the entire experimental unit.

	Treatment	Sep-14	Nov-14	Dec-14	Jan-15	Feb-15	Mar-15	Apr-15	Aug-15	Nov-15	Feb-16	Jul-16	Dez-16
Dry Biomass	C	2137	NA	1487	2930	1736	2614	1182	1574	1574	921	1698	1264
	CC	1994	542	985	2643	2197	2006	844	1657	1296	1538	1695	1216
	MP	1454	478	816	2651	1879	1487	1135	1527	1487	1606	1801	1192
Forage allowance	C	NA	NA	NA	NA	NA	NA	5.2	11.7	NA	2.7	5.5	2.1
	CC	4.8	4.4	4.6	4.9	4.7	4.9	5.0	10	6	6.1	5.7	3.6
	MP	4.4	4.1	4.2	4.4	4.2	4.3	4.5	9.5	6.4	5.9	6.1	3.5

Appendix S5 Values of the only significant axis obtained through the PCA of the species described by the attributes:

Species	Axis I	Species	Axis I
Aristida_venustula	-0.319463	*Vulpia_bromoides*	0.030619
Schizachyrium_microstachyum	-0.289081	*Dichondra_macrocalyx*	0.0378071
Sporobolus_indicus	-0.278253	*Eleocharis_viridans*	0.0482809
Andropogon_ternatus	-0.269784	*Facelis_retusa*	0.0739549
Richardia_stellaris	-0.266011	*Glandularia_selloi*	0.0739549
Eragrostis_lugens	-0.255061	*Evolvulus_sericeus*	0.0770881
Axonopus_argentinus	-0.252529	*Lolium_multiflorum*	0.0934667
Bothriochloa_laguroides	-0.251766	*Eryngium_horridum*	0.0962777
Danthonia_montevidensis	-0.227057	*Anagallis_minima*	0.0984221
Mnesithea_selloana	-0.224029	*Dichondra_sericea*	0.102461
Aristida_murina	-0.221254	*Oxalis_eriocarpa*	0.103019
Aristida_uruguayensis	-0.221254	*Galium_richardianum*	0.105365
Carex_sororia	-0.221254	*Eryngium_echinatum*	0.106771
Eragrostis_bahiensis	-0.221254	*Chaptalia_piloselloides*	0.114228
Eragrostis_plana	-0.221254	*Conyza_bonariensis*	0.132077
Juncus_capillaceus	-0.221254	*Conyza_primunifolia*	0.132077
Trachypogon_molle	-0.221254	*Plantago_myosuros*	0.132077
Paspalum_plicatulum	-0.217592	*Polygala_linoides*	0.132077
Stipa_setigera	-0.196462	*Chaptalia_runcinata*	0.133969
Setaria_parviflora	-0.194536	*Chevreulia_sarmentosa*	0.134208
Piptochaetium_stipoides	-0.189585	*Stenandrium_dulce*	0.135462
Piptochaetium_montevidense	-0.186661	*Richardia_humistrata*	0.139289
Paspalum_dilatatum	-0.17637	*Baccharis_crispa*	0.141276
Steinchisma_hians	-0.162283	*Baccharis_coridifolia*	0.142653
Paspalum_cf_lepton	-0.138553	*Desmanthus_tatuhyensis*	0.142653
Chascolytrum_subaristatum	-0.138177	*Galactia_marginalis*	0.142653
Carex_phalaroides	-0.132673	*Nierembergia_riograndensis*	0.142653
Trifolium_polymorphum	-0.128476	*Sisyrinchium_platense*	0.146505
Fimbristylis_autumnalis	-0.127948	*Hydrocotyle_exigua*	0.147331
Paspalum_cf_recortado	-0.127948	*Acmella_bellidioides*	0.156512
Chascolytrum_poomorphum	-0.120808	*Agalinis_communis*	0.156512
Chascolytrum_rufun	-0.120808	*Verbena_montevidensis*	0.156512
Melica_brasiliana	-0.120808	*Eryngium_nudicaule*	0.161099
Stipa_charruana	-0.120808	*Herbertia_lahue*	0.162195
Stipa_filiculmis	-0.120808	*Hypochaeris_chillensis*	0.162195
Axonopus_fissifolius	-0.119845	*Nothoscordum_montevidense*	0.162195
Paspalum_notatum	-0.101805	*Nothoscordum_sp.*	0.162195
Juncus_tenuis	-0.100712	*Oxalis_perdicaria*	0.162195
Luziola_peruviana	-0.074596	*Chaptalia_exscapa*	0.162698
Cynodon_dactylon	-0.0741019	*Cyclospermum_leptophyllum*	0.163679
Eragrostis_neesii	-0.0673157	*Gamochaeta_americana*	0.174722
Rhynchospora_megapotamica	-0.0503699	*Pfaffia_tuberosa*	0.188759
Juncus_microcephalus	-0.0222602	*Symphyotrichum_squamatum*	0.189138
Leersia_hexandra	-0.0211314	*Sisyrinchium_micranthum*	0.19699
Dichanthelium_sabulorum	0.0295795	*Pterocaulon_alopecuroides*	0.202403
Agrostis_hygrometrica	0.030619	*Scutelaria_racemosa*	0.204796
Agrostis_montevidensis	0.030619	*Briza_minor*	0.206534
		Cuphea_glutinosa	0.23399
		Soliva_sessilis	0.26038
		Oxalis_brasiliensis	0.286388
		Hypoxis_decumbens	0.293671

Capítulo III: Grazing management affects the sign of inter-specific interactions induced by *Eryngium horridum* in subtropical grassland[‡]



[‡] Este artigo será submetido à revista Journal of Applied Ecology.

Grazing management affects the sign of inter-specific interactions induced by *Eryngium horridum* in subtropical grassland

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ABSTRACT

Question: Can different grazing intensities in grassland reverse the sign of inter-specific interactions? Here, we investigate how the presence of the spiny Apiaceae *Eryngium horridum* affects richness of functional types in plant communities under varying vegetation height and grazing management treatments.

Location: Subtropical native grassland of south Brazil (Campos); 31°39'07"S, 54°09'59"W; 170 m a.s.l.

Methods: Each experimental unit, in a randomized block design with three replicates, was a paddock of ca. 16 ha subjected to a grazing treatment: Continuous grazing (CC) with stocking rates adjusted to the carrying capacity; and multi-paddock (MP) under rotational grazing and the same forage allowance as treatment CC. We systematically marked 1.6 x 0.2 m plots, and each plot was divided into eight 0.2 x 0.2 m sub-plots, where the presence/absence of all plant species and mean vegetation height were recorded. For the analysis, we selected a subsample of plots where the presence of *E. horridum* had been recorded in at least one subplot. We computed the Relative Neighbour Effect index (RNE) to quantify the effect of *E. horridum* on species richness considering different plant functional types.

Results: We found significant effect of vegetation height on the sign and the strength of RNE. The effect changed clearly according to the grazing management treatment. Under multiple-paddock grazing management, RNE responded linearly (from negative to positive, i.e., from competition to facilitation) with increasing vegetation height in the subplot without *E. horridum*, while under continuous grazing RNE decreased with vegetation height. Under CC, RNE considering C_3 and C_4 graminoids decreased sharply from positive to negative with increasing vegetation height. Further, under MP vegetation height affected negatively the richness of forbs in both subplots with and without *E. horridum*.

Conclusions: Under CC management, facilitation by the refuge effect induced by *E. horridum* becomes more important with decreasing vegetation height (more intense grazing pressure) of grazed patches. Under MP, facilitation by neighbouring habitat amelioration in gaps created around *E. horridum* spine leaves becomes stronger with increasing vegetation height of grazed patches. Our study reinforces the importance of spiny *E. horridum* on promoting biodiversity in native grassland vegetation under changing grazing pressures and managements systems.

Keywords: Facilitation, competition, positive interactions, grazing management, stress-gradient hypothesis, selective herbivory.

Nomenclature: The Taxonomic Name Resolution Service. iPlant Collaborative. Version 3.2 accessed on 08 Jun 2016. URL: http://tnrs.iplantcollaborative.org.

Introduction

The stress-gradient hypothesis (Bertness & Callaway 1994) suggested that facilitation (positive interactions) should have a significant role in communities developing under high physical stress and with high consumer pressure, while positive interactions should be rare in communities with relatively benign physical environment and less severe consumer pressure, where competitive interactions should be the dominant structuring forces (Brooker et al. 2008; Maestre et al. 2009). Although positive interactions are well documented in the literature, studies have shown that they can vary depending on the way multiple factors such as the performance measure used (Goldberg et al. 1999; Maestre et al. 2005), the nature of the stress factor involved (resource or non-resource; Maestre et al. 2009), the ontogenetic stage of the interacting species (Soliveres et al. 2010), the ecological requirements of the interacting plants (Liancourt et al. 2005; Chu et al. 2008) and the evolutionary relationships of the species involved (Suzuki & Suzuki 2012; Estapé et al. 2013; Soliveres et al. 2014).

Positive interactions between plants have been studied in grassland ecosystems and they often involve generalist large herbivores (Milchunas & Noy-Meir 2002; Baraza et al. 2006). Likewise, associational avoidance strategies where palatable plants are protected from herbivores by living in close association with less preferred plants (Pfister & Hay 1988; Graff et al. 2007; Fidelis et al. 2009) have been suggested to be of a great importance in habitats with heavy grazing pressure (Bertness and Callaway 1994, Baraza et al. 2006). However, selective grazing behaviour is affected by the amount of available forage per individual grazer, so that the actual grazing pressure on a given patch may vary according to the grazing management strategy (Senft et al. 1987). Large herbivores interact with the forage resources at several spatial resolutions, making decisions in a hierarchal fashion by choosing plant communities at a landscape scale, feeding stations within a plant community, and individual plants or plant parts at the bite scale (Senft et al. 1987; Milchunas & Noy-Meir 2002). As a result, a gradient with different intensities of grazing pressure can be found within the same system. The most common form of grazing management on rangelands is continuous stocking of livestock (Sollenberger et al. 2005). Since under this form of grazing management the grazing animals can freely access the whole paddock, choosing where and when to graze, the vegetation is characterised by patches with preferred plants repeatedly and heavily grazed, and lightly used or completely avoided patches elsewhere (Witten et al. 2005). The use of multiple paddocks restricts spatially and temporally the area available to the grazers, thus it tends to decrease selective grazing behaviour and, as a consequence, the heterogeneity of the vegetation (Bailey, Gross, Laca, Rittenhouse, Coughenour, Swift, & Sims 1996; Teague et al. 2011). Therefore, the relative importance of positive interactions on grasslands ecosystems is expected to vary between continuous or multi-paddock management as well as with different grazing pressure promoted by herbivore behaviour.

The subtropical grasslands of South America have large species diversity and productivity and grazing is considered a key tool for maintaining the biodiversity and ecological properties of these ecosystems (Lezama et al. 2014). However, on the one hand overgrazing causes decreased vegetation cover and replacement of productive forage species by species that are less productive and of lower forage quality (Overbeck et al. 2005). On the other hand, extremely low grazing pressure can result in dominance of tall grasses of low nutritional value and other species of low forage quality, mainly from the genera *Baccharis* (Asteraceae) and *Eryngium* (Apiaceae) (Nabinger et al 2000). One of these species is *Eryngium horridum*, which is a rosette growth-form considered a weed by livestock farmers because of its spiny leaves (Lombardo 1980; see photos in Appendix S5), presenting predominantly vegetative reproduction and spreading under disturbance, such as frequent fire (Fidelis et al. 2007) or when it is cut in inappropriate periods (Lallana et al. 2004). However, studies (Fidelis et al. 2009; Estapé et al. 2013) found evidence that, in grazed areas, *E. horridum* can interact positively with other plant species, protecting them as a biotic refuge for more palatable species and thus influencing plant community structure. In contrast, under grazing exclusions, *E. horridum'* s architecture can provide gaps with more light for plant establishment and survival, thus decreasing competition by the dominant tall grasses (Fidelis et al. 2009).

Here we evaluated the role of *E. horridum* on grassland community structure under different grazing management. As hypothesized in previous work (Bertness & Callaway, 1994), we propose here that facilitation by a refuge effect would be more prominent under intense grazing where competition would be less intense, which should be found on intense grazed patches of continuous grazing management. Although negative interactions would be expected in less grazed patches under both continuous or multi-paddock grazing management, we also hypothesize that neighbouring habitat amelioration by gaps created around *E. horridum* can induce positive interactions (Fidelis et al. 2009; Estapé et al. 2013).

Methods

Site area

The experiment was established in 160 ha of subtropical native grassland (31°39'07"S, 54°09'59"W, 175 m a.s.l., Appendix S1) located at *Estância Cinco Salsos* farm, municipality of Aceguá, Rio Grande do Sul, Brazil. The soils are Vertisols (IUSS Working Group 2015). The climate is Cfa (according to Köppen classification, Alvares et al. 2013), with 1130 mm annual mean precipitation and frequent summer dry spells, and mean temperature of 20.2º C across the year, 21.7 ºC in the warmest quarter and 11.8 °C in the coldest quarter (Worldclim Hijmans et al. 2005). The vegetation is characterized by the dominance of prostrated (e.g. *Paspalum notatum*, *Axonopus affinis*) and caespitose grasses (e.g. *Mnesithea selloana*, *Paspalum dilatatum*, *Nassela setigera*, and *Piptochaetium stipoides*), with scattered shrubs (e.g. *Baccharis coridifolia*, *B. crispa*) and patches with *Eryngium horridum*. Cattle and horses have likely grazed the area since their introduction in the region in the 17th Century. However, there is evidence the grassland vegetation coevolved with large grazers until their extinction by the end of the Pleistocene (MacFadden 1997; Müller et al. 2012).

Experimental design

The experiment used a randomized block design with three replicates (Appendix S1). The blocks had three experimental units (paddocks) each, with areas ranging from 16 to 21 ha depending on the block. The delimitation of the experimental units within each block was done using permanent electric fences in such a way to maximize the within-block similarity among experimental units in terms of distribution of vegetation physiognomies and relief position. The experiment tested the effects of three grazing management treatments with cattle (Hereford heifers and young cows). Here we restrict our analysis using the results of two treatments:

(1) *Continuous conservative* (CC): In this treatment, cattle had unlimited access to the entire experimental unit; stocking rate was adjusted monthly in order to maintain a forage allowance ratio of approximately 4.5:1 (i.e., 4.5 kg of aboveground dry biomass per kg of live

cattle weight) between September 2014 and August 2015, and approximately 9.5:1 between August 2015 and November 2015.

(2) *Multi-paddock* (MP): For this treatment, we applied rotational grazing with the same level of forage allowance of the CC treatment, as recommended by Sollenberger et al. (2005). For this, each experimental unit was fenced into eight sub-paddocks of equal size, which were grazed at intervals defined by a thermal sum of 550 degree days. This thermal sum is adequate for enough leaf elongation of two most predominant functional groups of grasses in these grasslands (Cruz et al. 2010). For the monthly adjustment of the stocking rate we considered the pre-grazing aboveground biomass available in a given sub-paddock, which was extrapolated for the whole experimental unit (Sollenberger et al. 2005). Further, we assumed a post-grazing forage mass of 50% of the pre-grazing mass.

Data collection

We systematically marked 256 1.6 x 0.2 m plots at nodes 75 m away from each other according to a grid over the whole experiment (Appendix S1). Each plot was divided into eight 0.2 x 0.2 m sub-plots, where we recorded the presence/absence of all plant species, and the mean vegetation height (Appendix S4). For this study, we selected the plots in which *E. horridum* was present in at least one sub-plot and absent in at least another subplot (Appendix S1). To avoid possible confounding effects, plots with adult shrubs were not selected. In this way, a sample of 32 1.6 x 0.2 m plots was used for the analyses.

Floristic survey was conducted in Spring 2015, from November to December, namely 15 months after the start of treatment. More than 150 species were identified in the study area, with 88 of these found in plots with *E. horridum.* The ten most common species found in the 1.6 x 0.2 m plots with *E. horridum* (in ascending order) were *Dichondra sericea* (forb), *Chevreulia sarmentosa* (forb), *Evolvulus sericeus* (forb), *Piptochaetium montevidense* (C_3 graminoid), *Rhynchospora megapotamica* (C_4 graminoid), *Oxalis brasiliensis* (forb), *Paspalum dilatatum* (C_4 graminoid), *Axonopus affinis* (C_4 graminoid), *Mnesithea selloana* (C_4 graminoid) and *Paspalum notatum* (C_4 graminoid).

Vegetation height

We used the mean vegetation height of the three highest plants in the 0.2 x 0.2 m subplot as a proxy of grazing pressure on each subplot. In evaluations done in the same experimental units we found a significant correlation between aboveground biomass and vegetation height of 0.5 x 0.5 m plots ($R^2 = 0.8$, $P = 0.001$). Lower vegetation height was taken as an indication of preferred (higher frequency of consumption), while taller vegetation was an indication of rejected patches (low preference) (Carvalho 2013). We believe it is reasonable to assume that soil conditions are relatively homogenous among the plots where *E. horridum* was found(Appendix S1).

Data analysis

To measure the impact of *E. horridum* in the community composition, we used an automated procedure to randomly select in each plot a pair of non-adjacent subplots: one subplot with and another without *E. horridum*. We used the Relative Neighbour Effect index (RNE) to quantify the effect of *E. horridum* on species richness of the plant communities. The RNE was estimated for each plot pair, where RNE = -1 * (Xt - Xc)/max(Xt, Xc), where X_t is species richness in the absence, and X_c in the presence of individuals of *E. horridum*, and max(Xt, Xc) is the highest value among Xt and Xc. The values of RNE range from -1 (negative interactions) to 1 (positive interactions) (Callaway et al. 2002). We then assessed by linear regression the effect of vegetation height on the RNE within each grazing management treatment. Also, we calculated RNE considering species richness within each functional group (forbs, and C_3 and C_4 graminoid species), in which case subplot pairs with less than two species of the corresponding functional group were ignored in the computations. This procedure, starting with the random selection of a pair of non-adjacent subplots with and without *E. horridum* in each plot, followed by the computation of corresponding RNE and the adjustment of a linear regression model for the effect of vegetation height on RNE within each grazing management treatment, was repeated many (1000) times. With these we computed confidence limits for the regression coefficients. The procedure was programmed using R.

For assessing the effects of the presence of *E. horridum* on total species richness, as well as on the richness of forbs, C_3 and C_4 graminoids species, we used univariate analysis of variance with permutation testing (Pillar & Orlóci 1996; Torres et al. 2010), by restricting the permutations within each subplot pair. These analyses were performed using Multiv software, available at http://ecoqua.ecologia.ufrgs.br/ecoqua/MULTIV.html. We also used the Akaike information criterion for small samples (Hurvich & Tsai 1989) for selecting the regression model with the best fit to the data. For this we compared the AICc and weights of the null (y=mean), linear, exponential, asymmetric curve and quadratic models using the R package *bbmle* available at https://cran.r-project.org/web/packages/bbmle/.

Results

We found significant relationships between vegetation height and the sign and the strength of the effect of *E. horridum* on community species richness, expressed by the RNE. Further, the effect changed clearly according to the grazing management treatment (Fig. 1a-b). That is, under multiple paddocks (MP) grazing management, RNE responded linearly (from negative to positive) with increasing vegetation height in the subplot without *E. horridum* (R^2 = 0,23, P = 0.03, AIC weight = 0.32), while under continuous grazing (CC) RNE decreased with vegetation height (Fig 1 a-b, R^2 = 0.22, P = 0.047, AIC weight = 0.25,). Under CC, RNE considering C_3 and C_4 graminoids decreased sharply from positive to negative values of RNE with increasing vegetation height (Fig. 1c, asymmetric curve for C_3, P =0.069, AIC weight=0.3, and linear for C_4, P=0.06, AIC weight =0.23). In contrast, under MP, RNE considering C3 graminoids tended to increase with vegetation height, but the fit was not significant (Fig. 1d AIC weight = 0.19, R^2=0.13, P=0.12). See Appendix S2 for detailed results. The vegetation height of subplots, as expected, was lower in the subplots without than with *E. horridum* (Tab. 1). Further, the subplots under CC were in average shorter and more variable than under MP.

We also examined the relations between vegetation height and species richness within each functional group in the subplots with and without *E. horridum*. Under MP management (Fig. 2 c-d), there was a negative effect of vegetation height on the richness of forbs in both subplots with and without *E. horridum* (respectively, a linear effect with P= 0.075, and asymmetric curve effect with P=0.001). However, under MP the effect of vegetation height on C3 graminoids was only significant in the subplots without *E. horridum*

(Fig. 2c, linear effect, P = 0.005). Under CC (Fig. 2a-b) the effect of vegetation height was not significant for any functional group and with or without *E. horridum*. See Appendix S3 for detailed results.

By comparing the subplots solely by species richness irrespective of vegetation height (i.e., in average across varying heights), under CC richness of C_3 and C_4 graminoids was not any different between subplots with and without *E. horridum*, but it was different for forbs (P = 0.01, Fig. 3a). Under MP, greater richness of C_4 graminoids was found in the subplots without *E. horridum* (P = 0.01, Fig. 3b).

Discussion

Our results have demonstrated that at fine plot scale the effect of grazing management systems on species richness of different plant functional groups is mediated by the presence of the spiny plant *E. horridum*, even with such short-term evaluation after application of the grazing treatments. Under continuous grazing, the results indicated *decreased* positive interactions (RNE > 0) induced by *E. horridum* as vegetation height increased in the nearby microsites without *E. horridum* and the same response was also found for RNE of C3 and C4 graminoids. The opposite trend was observed for total species richness under multiple-paddock grazing management, where positive interactions induced by the presence of *E. horridum* increased as the vegetation height increased in the nearby microsites without *E. horridum*. Further, under MP the effect of vegetation height on the *richness* of C_3 graminoids in the absence of *E. horridum* was negative, but was neutral in its presence. As for forbs richness, the effect of vegetation height was negative in microsites both with and without *E. horridum.*

If we accept that soil conditions of the community microsites where *E. horridum* was found are relatively homogeneous (see Methods and Appendix S1), variation in vegetation height reflected mainly differential grazing pressure, i.e., preference by the grazers, and not pre-existing soil differences affecting productivity. Also, RNE was computed considering each subplot pair within a 1.6 x 0.2 m plot, which by definition controlled richness variation among plots. Thus, considering that continuous and multiple-paddock grazing management depicted opposite trends on the effect of vegetation height, it is unlikely that the effects on RNE of the presence of *E. horridum* and vegetation height could be confounded with pre-existing differences in available soil resources (Steinbauer et al. 2016).

The results indicated that under continuous grazing management microsites without *E. horridum* were predominantly subjected to higher levels of grazing pressure than they were under multiple-paddock grazing management. This suggests that highly palatable species may suffer more intense and constant grazing in the absence of *E. horridum*, while these species may be protected by the presence of the spiny leaves of *E. horridum*, corroborating earlier findings by Fidelis et al. (2009) and Estapé et al. (2013). Indeed, many C_3 grasses, such as *Chascholitrum subaristatum, Chascholitrum poomorphum, Briza minor, Nassella setigera, Nassella charruana,* and *Piptochaethium stipoides* are known as palatable plants, which present the peak of their development in the spring (Estapé et al. 2013), when forage availability for cattle grazing is often limited (Scottá & da Fonseca 2015). Thus, facilitation by *E. horridum* under high local grazing pressure, by the provision of *grazing protection refugia*, was more frequently observed under continuous than multiple-paddock grazing management.

On the other hand, high local grazing intensity may lower the competitive exclusion potential (Milchunas et al. 1988; Bakker et al. 2006) by dominant species in intensively grazed patches. The control of the dominants by grazing allows the coexistence of short prostrate and rosette forb species which are unable to grow taller or support shaded environments (such as *Chevreulia sarmentosa* and *Eryngium nudicaule*) with some short or stoloniferous grass (i.e. *Paspalum notatum*), which can withstand higher grazing intensities in grasslands (Díaz et al. 2007). Frequent grazing causes intense removal of aboveground biomass (Bakker et al. 2006; Segre et al. 2016), compromising the competitive ability and population persistence of some species by reducing tiller recruitment, tiller longevity, plant longevity, seed production and seedling establishment (Briske et al. 2008). Thus, continuous grazing management may generate patches subject to intense biomass removal, which may filter out species that cannot support such high levels of herbivory (Díaz et al. 2007).

Selective grazing behaviour is also observed in multi-paddock grazing management, where preferred patches are more intensively grazed. However, since cattle are eventually removed to another paddock, preferred grazed patches can recover, which may not the case under continuous grazing. Thus, under multi-paddock grazing, lower grazing pressure in nearby microsites without *E. horridum*, favoured richness of C_4 graminoids, which have higher competitive potential to use light resources compared to forbs and C_3 graminoids (Segre et al. 2016). Thus, the provision of *competition avoidance refugia* may explain the increase of positive interaction for C3 graminoids by the presence of *E. horridum* when the nearby microsites were less intensively grazed. Taking into account the low correlation between the functional groups and increasing vegetation height, we also verify which species have benefited from positive interactions by the presence of *E. horridum* under vegetation height increase. We found species with traits related to survive in conditions encountered among (i.e, decumbent forb *Galactia marginalis* and decumbent C3 graminoid *Dichanthelium sabulorum*) and below (i.e. tall and erect C4 graminoid *Axonopus argentinus*) its spiny leaves, which reinforces the hypothesis that under vegetation height increase, plants of *E. horridum* provide changes in competition conditions.

Therefore, we confirmed both of our initial hypotheses. For one, we conclude that positive interactions between *E. horridum* and C_3 and C4 graminoids species in continuous grazing through the refuge effect becomes more important as the vegetation height decrease, a conclusion also supported by literature (Bertness & Callaway 1994; Fidelis et al. 2009; Estapé et al. 2013). Further, we also hypothesize that positive interactions influence the community structure through neighbouring habitat amelioration by gaps created around *E. horridum* (Bertness & Callaway 1994; Fidelis et al. 2009) and that effect benefits C_3 graminoids but also species adapted to *E. horridum* shape. Therefore, in agreement with previous work (Fidelis et al. 2009; Estapé et al. 2013), our study reinforces the importance of *E. horridum* on promote biodiversity refugia to the grassland flora under changing grazing pressures and managements systems. Our results also support the need to maintain some patches with *E. horridum* aimed at guaranteeing the viability of grazing susceptible species under changes in management systems.

Acknowledgments

This experiment was part of the Long-Term Ecological Research (LTER) network coordinated and funded by CNPq (Brazil). We thank especially Murilo Zanini, Luiza Baggio, Suzana H. Oderich that assisted in data collection, Ilsi Boldrini and colleagues at the Laboratory of Grassland Vegetation for help identifying species, José Pedro Trindade and others professionals of Embrapa - Pecuária Sul for all the collaborations regarding the experiment design and maintenance, Fernando Quadros, André Coelho and others members of the Natural Grassland Ecology Research Group (Lepan-UFSM) who helped in keeping this experiment alive, and the owner Claudio Martins and the farm employees of *Estância Cinco Salsos* for the partnership we have built during the last three years.

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Appendix list

Appendix S1 – Photo with the scheme of experimental area.

Appendix S2 - Akaike information criterion (AIC) for RNE and vegetation height models in each management system and functional group.

Appendix S3 - Akaike information criterion (AIC) for richness ande vegetation height models for each management system and functional group

Appendix S4 - Permanent vegetation plots with 1.6 x 0.2 m and with eight 0.2 x 0.2 m subplots.

Appendix S5 – Photos of the effect of *Eryngium horridum* under different management systems.

Table 1. Mean values of vegetation height and the standard deviation for each subplot with and without *E. horridum* in three grazing management treatments (CC: Continuous conservative, MP: Multi-paddock). In lines, values followed by the same letter do not differ significantly ($P < 0.05$).

Eryngium horridum

	Without		With	
Treatment	Height (cm)	StdDev	Height (cm)	StdDev
CC	4.11_b	2.45	8.11_a	4.14
MP	6.05_b	1.91	9.19_a	4.74

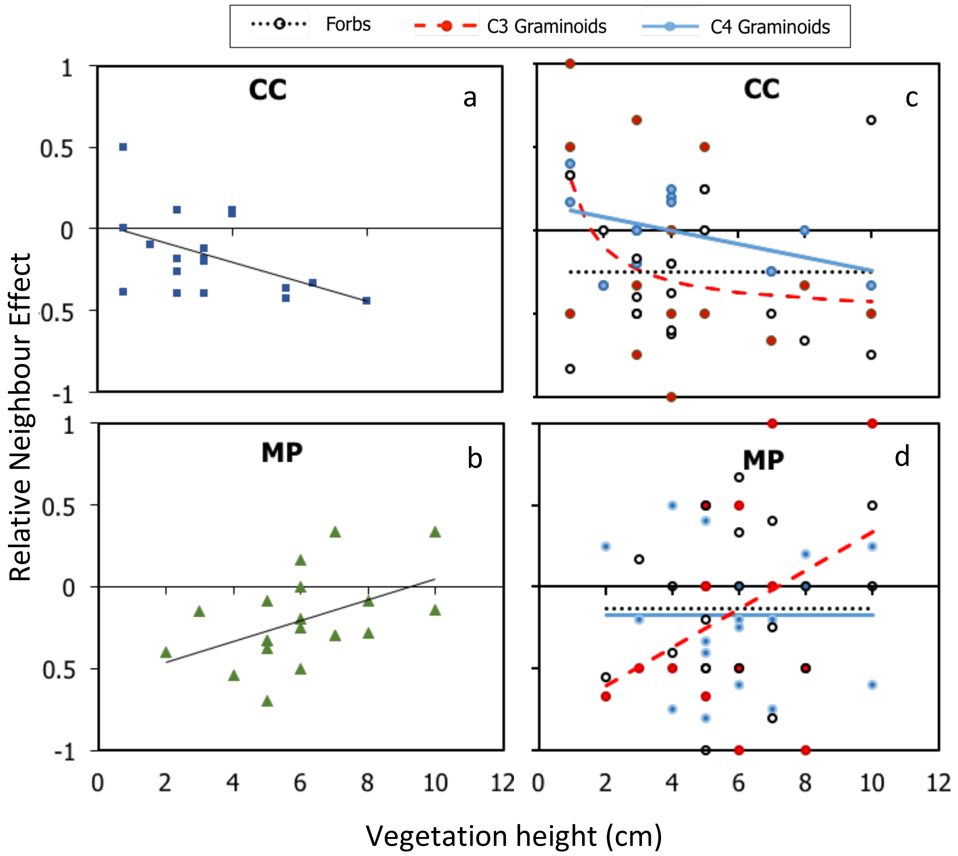


Figura 1. Relative Neighbour Effect (RNE) related to vegetation height (cm) of the subplot where Eryngium horridum was absent, under two grazing management treatments (CC: Continuous conservative - AIC weight=0.25, R^2=0.22, P=0.047, y = -0.043x + 0.103, MP: Multi-paddock - AIC weight=0.32, R^2=0.23, P=0.03, y=0.062x - 0.45) in *a* and *b* with all species. In *c* and *d* the fit models found for the functional groups are shown: Under MP the response was linear and positive for C3 graminoids (AIC weight=0.19, R^2=0.13, P=0.12, y=12x+0.84) and in CC it was an asymmetric curve for C3 graminoids (AIC weight= 0.3, y=-0.51+0.81/x, P=0.069) and linear for C4 graminoids (AIC weight= 0.23, R^2=0.20, y=-0.04x+0.16, P=0.06). Points above zero on the RNE axis indicate facilitation, whereas points below zero indicate competition.

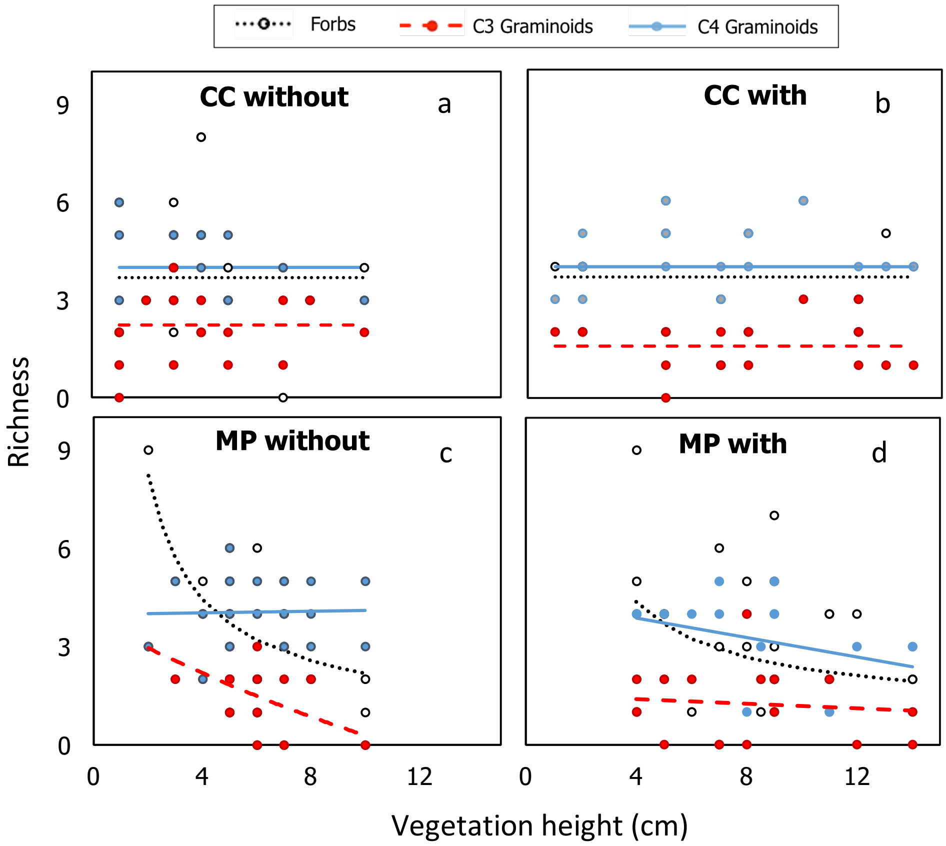


Figura 2. Relations between functional group richness and vegetation height (cm) of the subplot where *Eryngium horridum* was present (a and c) and absent (b and d) in two grazing management treatments (CC: Continuous conservative, MP: Multi-paddock). Under MP with *E. horridum* the response was linear negative for C4 graminoids (AIC weight= 0.21, R^2=0.14, P=0.11, y=-0.15x+4.48) and asymmetric curve for forbs (AIC weight=0.25, P=0.075, y=0.97+13.61/x). And in MP without *E. horridum* the response was negative linear for C3 graminoids (AIC weight = 0.49, R^2=0.32, P=0.005, y=-0.98x + 7.42) and asymmetric curve for forbs (AIC weight = 0.68, P=0.001, y=0.67+15.09/x).

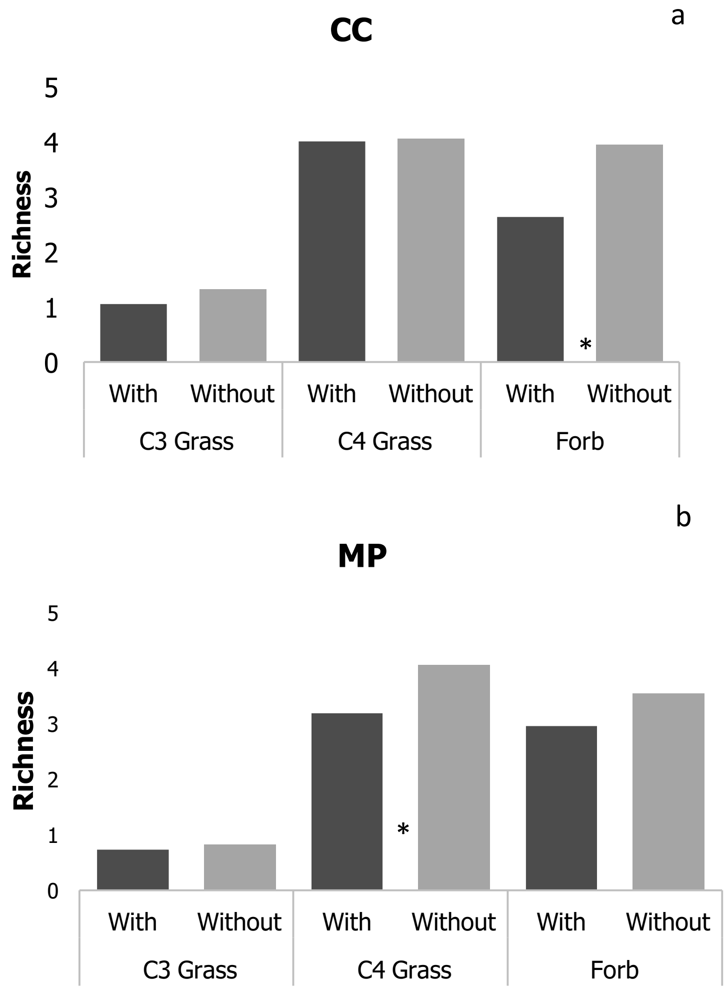
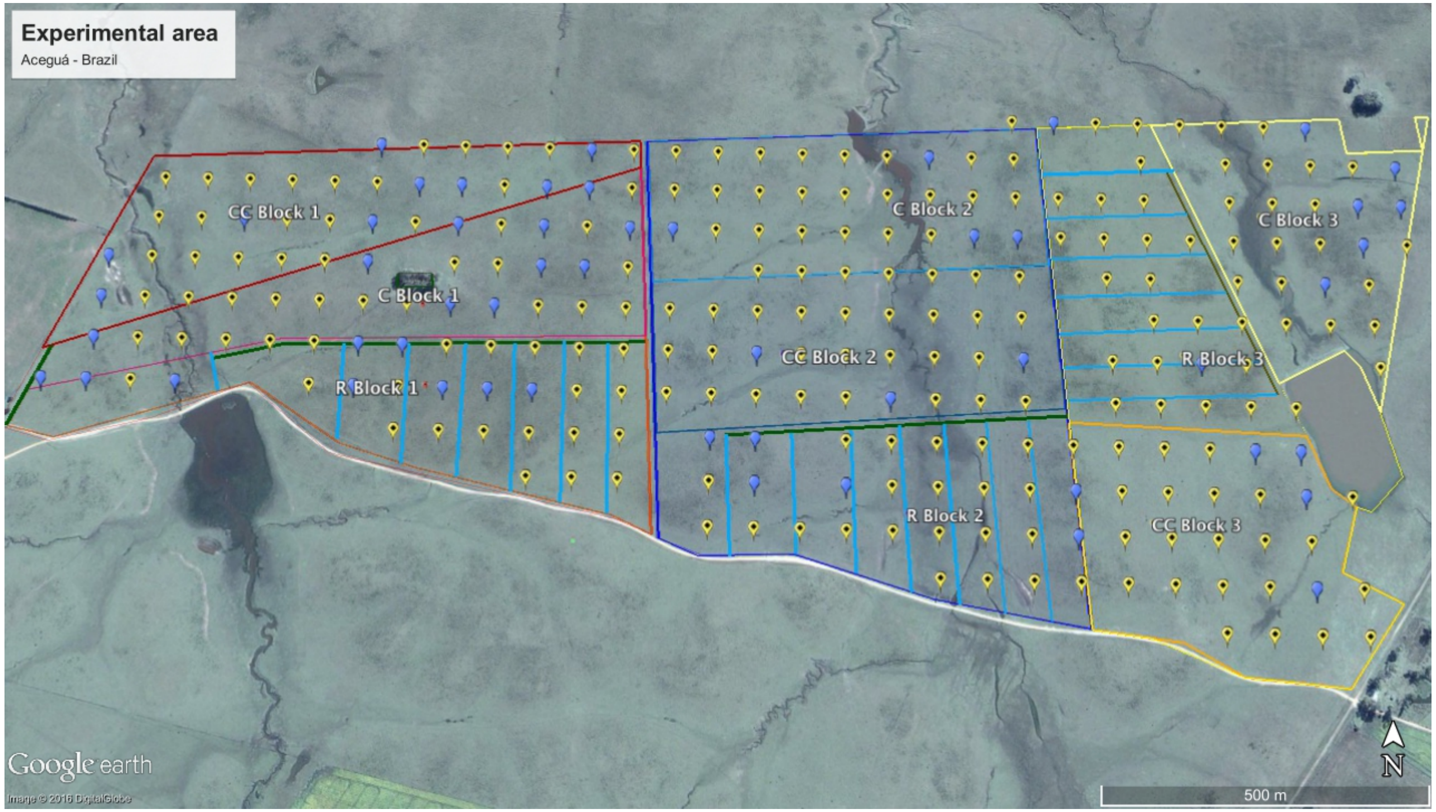


Figura 3. Richness of C3 and C4 graminoids, and forbs in two grazing management treatments (CC: Continuous conservative and MP: Multi-paddock) with and without *E. horridum.* Bars with an asterisk between showed significant differences ($P < 0.05$) among the plots with and without *E. horridum.*



Appendix S1. The total area of experiment is 160 ha. C correspond the Conventional treatment, CC the Continuous Conservative and MP correspond the Multi-paddock treatment. The latter are divided into 8 paddocks with similar area. Blocks are marked in different colours: red (1), blue (2) and yellow (3). Points in blue are the plots selected to this study (with *Eryngium horridum* and without *Baccharis crispa*). Google Earth Pro 7.1.5.1557. (June 20, 2006). Aceguá/BR, 31° 39’ 18”S, 54° 09’ 16”W, Eye alt 2.2 km. Google 2016, DigitalGlobe 2016. http://www.earth.google.com [April 26, 2016].

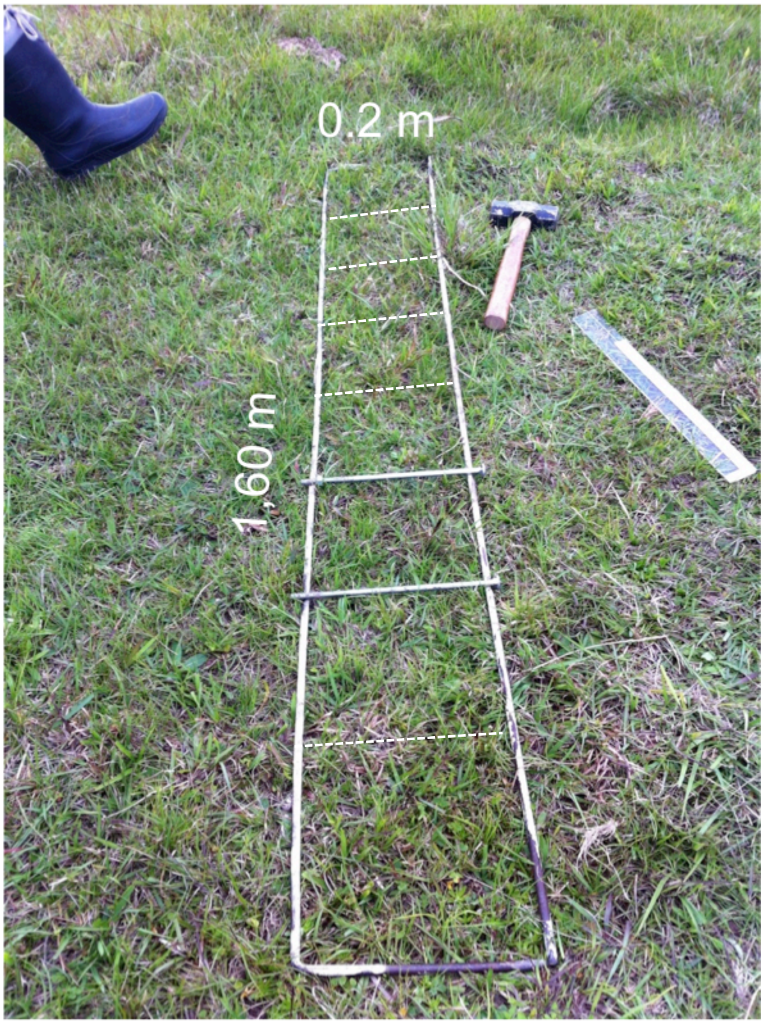
Appendix S2. Akaike information criterion (AIC) for RNE and vegetation height models in each management system and functional group. The model weight values with an asterisk presented better fit to the data.

Treatment	Functional group	AICc	dAICc	df	Weight	Model
Continuous conservative	Forbs	24.6	0	2	0.48*	Null
		26.8	2.2	3	0.16	Asymmetric curve
		27.1	2.6	3	0.13	Exponential
		27.4	2.9	3	0.11	Linear
		27.4	2.9	3	0.11	Quadratic
	C4 Graminoids	-1.1	0	3	0.23*	Linear
		-1.1	0	3	0.23	Quadratic
		-1	0.2	3	0.21	Exponential
		-1	0.2	3	0.21	Asymmetric curve
		0	1.1	2	0.13	Null
	C3 Graminoids	31.1	0	3	0.3*	Asymmetric curve
		31.6	0.5	3	0.24	Exponential
		32	0.9	2	0.19	Null
		32.7	1.6	3	0.13	Linear
		32.7	1.6	3	0.13	Quadratic
	Total RNE	3.6	0	3	0.25*	Linear
		3.6	0	3	0.25	Quadratic
		3.7	0.2	3	0.23	Exponential
		4.5	0.9	3	0.16	Asymmetric curve
		5.2	1.7	2	0.11	Null
Multi-paddock	Forbs	27.5	0	2	0.47*	Null
		29.9	2.4	3	0.14	Asymmetric curve
		30	2.5	3	0.13	Exponential
		30.1	2.6	3	0.13	Linear
		30.1	2.6	3	0.13	Quadratic
	C4 Graminoids	22.9	0	2	0.47*	Null
		25.0	2.1	3	0.16	Asymmetric curve
		25.4	2.5	3	0.13	Exponential
		25.6	2.7	3	0.12	Linear
		25.6	2.7	3	0.12	Quadratic
	C3 Graminoids	33.9	0	2	0.31*	Null
		34.9	1.0	3	0.19*	Linear
		34.9	1.0	3	0.19	Quadratic
		35.1	1.2	3	0.17	Asymmetric curve
		34.4	1.5	3	0.15	Exponential
	Total RNE	5.3	0	3	0.321*	Linear
		5.3	0	3	0.321	Quadratic
		6.4	1.2	3	0.18	Exponential
		7.7	2.5	2	0.094	Null
		7.9	2.7	3	0.084	Asymmetric curve

Appendix S3. Akaike information criterion (AIC) for richness and vegetation height models for each management system and functional group. The model weight values with an asterisk presented better fit to the data.

Treatment	Functional group	AICc	dAICc	df	weight	Model
Continuous Conservative Without	Forbs	87.8	0	2	0.46*	Null
		89.9	2.2	3	0.16	Linear
		89.9	2.2	3	0.16	Quadratic
		90.5	2.7	3	0.12	Asymmetric curve
		90.6	2.8	3	0.11	Exponential
	C4 Graminoids	55.4	0	2	0.3*	Null
		56.4	1	3	0.18	Exponential
		56.5	1.1	3	0.17	Asymmetric curve
		56.5	1.1	3	0.17	Linear
		56.5	1.1	3	0.17	Quadratic
	C3 Graminoids	60.1	0	2	0.36*	Null
		60.4	0.2	3	0.32	Asymmetric curve
		62	1.9	3	0.14	Exponential
		62.8	2.7	3	0.09	Linear
		62.8	2.7	3	0.09	Quadratic
Multi-paddock With	Forbs	86.7	0	3	0.25*	Asymmetric curve
		87.1	0.3	3	0.21	Exponential
		87.4	0.6	3	0.18	Linear
		87.4	0.6	3	0.18	Quadratic
		87.6	0.8	2	0.17	Null
	C4 Graminoids	69.3	0	3	0.21*	Linear
		69.3	0	3	0.21	Quadratic
		69.3	0.1	3	0.21	Exponential
		69.4	0.1	2	0.2	Null
		69.7	0.4	3	0.17	Asymmetric curve
	C3 Graminoids	105.5	0	2	0.64*	Null
		108.1	2.6	3	0.18	Linear
		108.1	2.6	3	0.18	Quadratic
Multi-paddock Without	Forbs	79.5	0	3	0.682*	Asymmetric curve
		81.9	2.4	3	0.2071	Exponential
		84.7	5.1	3	0.0522	Linear
		84.7	5.1	3	0.0522	Quadratic
		88.9	9.3	2	0.0064	Null
	C4 Graminoids	55.4	0	2	0.3*	Null
		56.4	1	3	0.18	Exponential
		56.5	1.1	3	0.17	Asymmetric curve
		56.5	1.1	3	0.17	Linear
		56.5	1.1	3	0.17	Quadratic
	C3 Graminoids	90.1	0	3	0.487*	Linear
		90.1	0	3	0.487	Quadratic
		96	5.9	2	0.026	Null

Appendix S4. Permanent vegetation plots with 1.6 x 0.2 m and with eight 0.2 x 0.2 m subplots.



Appendix S5. Photos of the effect of *Eryngium horridum* under different management system:

- Under CC management:

Under MP management:

Considerações finais

O recente avanço da agricultura sobre regiões historicamente ocupadas pela pecuária de corte causa inquietação principalmente àqueles que defendem a conservação dos Campos Sulinos – sua importância biológica, econômica e para a formação cultural da região. A alternativa mais plausível para sua conservação é a manutenção de regimes de distúrbio como o fogo e o pastejo. Entretanto, é certo que estes distúrbios não podem ser aplicados irrestritamente, pois há uma grande variação nas respostas dos ecossistemas campestres às diferentes intensidades, frequências e épocas aplicadas.

Neste sentido, no Capítulo I foram abordadas várias possibilidades de manejo através do uso controlado do pastejo e do fogo, atentando à complexidade dos mosaicos de campo e floresta existentes nos Campos Sulinos. Essas alternativas devem testadas numa perspectiva de manejo adaptativo ativo. Ou seja, abordando experimentalmente, tanto em áreas públicas quanto privadas, e monitorando as variáveis chaves dos ecossistemas para dirimir a incerteza das ações de manejo.

No Capítulo II percebemos que, mesmo num prazo curto a partir da aplicação de diferentes sistemas de manejo do campo, houve detecção de efeitos na diversidade funcional. Em especial, na diversidade e na proporção das estratégias de utilização dos recursos nas comunidades de plantas em três escalas da paisagem. É possível que tais mudanças decorram de respostas da comunidade de plantas a uma maior ou menor seletividade do pastejo e do descanso proporcionado pelo manejo rotativo.

Por fim, no Capítulo III demonstramos que em escala fina (20 x 20 cm) o efeito do manejo pastoril na riqueza de espécies é mediado pela presença de *Eryngium horridum.* Sob o manejo contínuo com ajuste sistemático da carga animal à capacidade suporte da vegetação campestre, as interações de facilitação mediadas pela presença de *E. horridum* decresceram na medida em que aumentou a altura da vegetação em subparcelas próximas sem *E. horridum.* Um padrão oposto foi encontrado no manejo rotativo com o mesmo ajuste sistemático da carga animal à capacidade suporte da vegetação campestre, em que foram intensificadas as interações de facilitação mediadas pela presença de *E. horridum* com o aumento da altura média da vegetação nas subparcelas próximas sem *E. horridum.* Nos dois últimos capítulos mostramos que a dinâmica dos processos que estruturam as comunidades de plantas nos campos é amplamente influenciada pela estratégia de manejo utilizada. Para possibilitar uma avaliação mais profunda das melhores estratégias a serem utilizadas na conservação das formações campestres dos Campos Sulinos faz-se necessário o monitoramento de longo prazo das respostas das comunidades em diferentes níveis tróficos assim como de outros processos ecossistêmicos e serviços ecológicos (e. g. ciclo dos nutrientes, dinâmica do C, ciclo da água, produção de forragem).

Um dos objetivos deste experimento foi avaliar a produção secundária através do desenvolvimento dos animais. Para tanto, monitoramos o desenvolvimento das fêmeas jovens indicado pelo ganho de peso e pela condição corporal. Durante esta primeira etapa (setembro de 2014- dezembro de 2016), tivemos algumas limitações concernentes à disponibilização de água para os animais em todas as unidades experimentais; à imprecisão das balanças usadas para pesar os animais; às questões sanitárias; assim como a insuficiência de animais que possibilitassem alcançar a oferta de forragem almejada (entre 3,5 e 4 kg de biomassa seca / kg de peso vivo Sollenberger et al. 2005). Tais limitações foram superadas ao longo desta primeira etapa, permitindo que os próximos ciclos possam gerar resultados mais confiáveis.

Apesar das limitações, obtivemos valores de ganho médio diário de peso das novilhas para o período de novembro de 2015 a fevereiro de 2016 (Tabela 1) consideravelmente positivos, se comparados a outros experimentos semelhantes em campo nativo no estado do Rio Grande do Sul (Fagundes et al. 2003; Barbieri et al. 2014; Carvalho et al. 2015). Estes valores possivelmente resultam de um período com maior pluviosidade que média dos anos no verão e da alta oferta de forragem de qualidade. O ganho de peso por hectare obtido nos diferentes tratamentos resultou das baixas cargas que aplicamos durante todo o período analisado. A não existência de diferenças significativas entre os tratamentos provavelmente deve-se a semelhança da oferta de forragem mantida. Esperamos que estes níveis de produtividade possam ser superados nas próximas avaliações, mesmo com a diminuição da oferta de forragem e a elevação da carga de animais. Pois o ajuste das condições experimentais limitantes e a alta qualidade das espécies predominantes nestes campos têm nos mostrado incrementos satisfatórios no desenvolvimento das fêmeas em avaliações recentes. Informações sobre a oferta de forragem de setembro de 2014 a dezembro de 2016 podem ser encontrados na Tabela 1 do Apêndice S4, Capítulo 2. Na próxima etapa deste experimento é essencial avaliar, para além do desenvolvimento das fêmeas, o conjunto de condições que determinam as respostas de desenvolvimento animal encontradas. Isso inclui, entre outros, o estudo do comportamento animal durante o pastejo e a sua relação com a estrutura da vegetação.

Por fim, para frear a perda dos ecossistemas campestres é insuficiente a simples consolidação de estratégias de manejo que assegurem aos pecuaristas rendas superiores à agricultura. É notória a pujança das corporações que estão coordenando o agronegócio brasileiro. Essas, juntamente a um conjunto de instituições (mídia, órgãos de pesquisa e extensão, cooperativas e sindicatos rurais), têm difundido uma única forma de produção, que se restringe à utilização massiva de insumos. Assim, nos últimos vinte anos de expansão da agricultura, o Estado brasileiro também aportou um expressivo volume de recursos em benefício desse tipo de agricultura, e manteve frágeis os órgãos de fiscalização, como o Ibama. Em contraposição a esta tendência, a fim de avançarmos na conservação dos Campos Sulinos, precisamos tanto de um Estado que efetivamente regule a conversão dos ecossistemas quanto difunda as alternativas para seu uso sustentável. Os sistemas de manejo testados nesta e em outras experiências citadas, oferecem importantes direções para o uso sustentável dos ecossistemas campestres nativos, mas que ainda precisam ser reconhecidas pelo Estado e pelos produtores como alternativas economicamente viáveis de conservação da biodiversidade.

Tabela 1. Resultados provisórios do desenvolvimento de novilhas da raça Hereford no experimento PELD - Manejo Adaptativo entre novembro de 2015 e novembro de 2016. São demonstrados as variáveis ganho de peso (GP – Kg de PV), ganho médio diário (GMD – Kg de PV/dia), ganho de peso por hectare (GP/ha – Kg de peso vivo/ha) e a oferta de forragem aplicada (Kg de biomassa aérea/Kg de peso vivo) em cada período para os sistemas de manejo convenvional, contínuo conservativo e rotativo. A oferta média de 09/16 à 11/16 (*) foi obtida a partir da média da biomassa aérea coletada nas duas datas. Não houveram diferenças significativas entre os tratamentos.

	De 11/15 à 10/02			De 10/02 à 09/16			De 09/16 à 11/16			Todo o período analisado			
Tratamento	GP	GMD	Oferta	GP	GMD	Oferta	GP	GMD	Oferta média*	GP	GMD	GP/ha	Oferta média
Convencional	48.5	0.59	6.5	-4	-0.02	4.2	33	0.61	5.9	80	0.225	102.9	5.5
Contínuo Conservativo	48.3	0.59	6	9	0.04	6.1	30	0.55	5.7	81	0.227	106.3	5.9
Rotativo	52.4	0.64	6.4	2	0.01	5.9	31	0.57	6.1	83	0.232	109.9	6.1

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