UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
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PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

ABORDAGEM QUALI-QUANTITATIVA E FUNCIONAL DE VEGETAÇÃO CAMPESTRE NOS BIOMAS PAMPA E MATA ATLÂNTICA

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Índice

“O começo de todas as ciências é o espanto de as coisas serem o que são”.

Aristóteles

“Eu acredito demais na sorte. E tenho constatado que, quanto mais duro eu trabalho, mais sorte eu tenho”.

Thomas Jefferson

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É injusto que uma tese de doutorado só tenha um nome na capa. Ela é o produto de incontáveis parcerias, discussões, almoços no RU e mesas de bar. Dito isto, vamos aos agradecimentos.

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Introdução Geral

As formações campestres em senso amplo (i.e., incluindo savanas, vegetação arbustiva e tundra), cobrem 52,5 milhões de quilômetros quadrados, o que corresponde a 40,5% da superfície da Terra, excluindo-se Groenlândia e Antártida (Suttie *et al.* 2005). Na América do Sul, as formações campestres, em senso amplo, cobrem cerca de 3,5 milhões de quilômetros quadrados, ou 350 milhões de hectares (Burkart 1975). No Brasil, os campos naturais cobrem 13.656.000 ha (IBGE 2006), se concentram na região sul do país e foram as formações dominantes na região durante o Pleistoceno recente, sendo sua distribuição atual interpretada como um indício de um clima anterior mais seco e frio (Behling 2002; Bredenkamp *et al.* 2002).

Os campos são as formações fitoecológicas predominantes no Rio Grande do Sul (RS), cobrem 62,2% da superfície do Estado (Cordeiro & Hasenack 2009) e se distribuem em dois biomas distintos: Pampa e Mata Atlântica (IBGE 2004; Boldrini 2009). No bioma Pampa são encontradas as maiores extensões contínuas de campo natural no Estado, distribuídas predominantemente em terras baixas de relevo suave-ondulado, enquanto que no bioma Mata Atlântica os campos apresentam distribuição em mosaico com as Florestas Ombrófilas Densa e Mista, predominantemente em regiões de altitudes e de relevo escarpado. Burkart (1975) classifica a vegetação campestre sul-brasileira em dois tipos: os “Campos do Brasil Central”, que abrangem as formações campestres do norte do RS, de Santa Catarina e do Paraná, e os “Campos do Uruguai e sul do Brasil”, que incluem os campos da metade sul do Estado e sua continuidade florística no Uruguai. A classificação proposta por Burkart (1975) coincide com a divisão atual dos biomas Mata Atlântica e Pampa no RS.

Considerando as áreas utilizadas para atividade pecuária sobre campo natural como fisionomias seminaturais, 68,62% da superfície do RS encontra-se convertida para uso humano, e estima-se que a taxa de conversão de fisionomias naturais para antrópicas seja de ca. 1000 km^2/ano (Cordeiro & Hasenack 2009). Dos 31,38% de fisionomias naturais ou seminaturais que ainda cobrem o Estado, 62,21% são compostas por formações campestres, fato que reflete o caráter ambientalmente sustentável da histórica prática da pecuária extensiva sobre campo nativo (Cordeiro & Hasenack 2009). Como apontado por Crawshaw *et al.* (2007), esta atividade, historicamente conduzida nos campos do RS, é um dos poucos exemplos de viabilidade econômica e sustentabilidade quando comparada à agricultura. Dentre os Estados que compõem a região Sul do Brasil, a maior área de campo natural preservada encontra-se no RS, tendo em vista que nos Estados do Paraná e Santa Catarina restam respectivamente 1.377 e 1.779 milhões de hectares de área campestre natural (IBGE 2006).

Os campos no RS são formações que apresentam elevada riqueza de espécies, além da presença de diversos táxons considerados endêmicos (Boldrini 2002). Boldrini (2009) aponta a ocorrência de cerca de 2200 espécies campestres no Estado, distribuídas nos biomas Pampa e Mata Atlântica. A alta diversidade biológica encontrada no Estado está, em grande parte, atrelada à grande variabilidade geológica, topográfica, de pluviosidade, de temperatura e de disponibilidade de água no solo (Boldrini 2009). Rambo (1954) chama a atenção para a riqueza e a importância ecológica da flora campestre sul-brasileira, apontando que somente as espécies herbáceas de Asteraceae presentes na região são mais numerosas do que toda a sua flora arbórea.

As formações campestres inseridas no bioma Mata Atlântica são caracterizadas por uma distribuição em mosaico com a Floresta com Araucária e turfeiras, sendo que *Andropogon lateralis* é a espécie de gramínea dominante na região, determinando sua fisionomia (Boldrini *et al.* 2009). A pecuária extensiva, sobre campos manejados com queimadas no fim do inverno visando ao rebrote da vegetação, é a atividade mais antiga da região, apesar de estar sendo gradativamente substituída por lavouras e pelo plantio de espécies arbóreas exóticas (Boldrini *et al.* 2009). Há evidências de que o uso do fogo como prática de manejo, devido à época e à frequência de aplicação, impeça o desenvolvimento de espécies hibernais na região, diminuindo, assim, diversidade e sustentabilidade da pastagem natural pelo predomínio de espécies entouceiradas de baixa qualidade forrageira (Jacques 2003). Caporal & Eggers (2005), em levantamento da flora agrostológica de uma área de campo natural preservado nos Campos de Cima da Serra do RS, apontam que 75% das espécies são estivais e apenas 25% hibernais. Nabinger *et al.* (2000) apontam a prática da queimada como agronomicamente improdutiva, tendo em vista o favorecimento de gramíneas “C4” e a conseqüente diminuição de forragem durante o inverno. Llorens & Frank (2004) relacionam o uso do fogo no inverno ou no início da primavera com diminuição da contribuição de espécies C3 e aumento das C4. Boldrini *et al.* (2009) listam a ocorrência de 1161 táxons para os campos da região, sendo que o maior número de espécies pertence à família Asteraceae (24%), seguida de Poaceae (20%), Fabaceae e Cyperaceae (ambas com 7%). Do total de espécies, 107 são consideradas endêmicas, 76 estão inseridas na lista de espécies ameaçadas do RS e quatro eram novas para a ciência. Segundo Boldrini (2009), o clima frio da região, aliado à alta pluviosidade, culminou na formação de diversos endemismos de plantas herbáceas.

No Brasil, o bioma Pampa está restrito ao RS, apresentando continuidade florística com o Uruguai e o Nordeste da Argentina (Burkart 1975; IBGE 2004; Boldrini 2009). Esta formação, que cobre ca. 63% da superfície do Estado, é apontada por Burkart (1975) como uma das regiões mais ricas em gramíneas do mundo. Os campos do bioma Pampa, apesar da aparente uniformidade fisionômica, apresentam uma enorme diversidade de táxons e formações vegetacionais decorrente da grande variabilidade edáfica da região (Boldrini 2009) e do seu caráter relictual (Behling 2002; Bredenkamp *et al.* 2002). Boldrini (2009) divide os campos da região em sete tipologias, baseadas em critérios florísticos, fisionômicos e edáficos: campos de barba-de-bode, de solos rasos, de solos profundos, de areais, do centro do Estado, litorâneos e vegetação savanóide (ou campos da Serra do Sudeste).

Apesar das conhecidas diferenças de solo, relevo, pluviosidade e composição florística entre os campos inseridos nos dois diferentes biomas presentes no Estado, não há trabalhos com abordagens quali-quantitativas estruturais comparando as duas formações.

Mesmo com o avanço do conhecimento em relação à flora campestre do Estado, estudos quali-quantitativos que tenham como objetivo a caracterização dos diversos subtipos de campos que existem no Estado (Boldrini 1997) são pontuais. Entre eles, Boldrini *et al.* (1998) realizaram um levantamento fitossociológico da vegetação campestre presente em um morro de embasamento granítico na região de Porto Alegre. Na mesma formação, Overbeck *et al.* (2006) avaliaram as diferenças florísticas e sua relação com fatores abióticos, como propriedades de solo e distância da borda da floresta. Levantamentos que empregaram metodologias semelhantes foram realizados por Caetano (2003), Garcia (2005), Boldrini *et al*. (2008), e Ferreira & Setubal (2009), todos na Planície Costeira do Estado. Caporal & Boldrini (2007) realizaram levantamento florístico e fitossociológico em uma área de campo pastejada na Serra do Sudeste do RS. Freitas *et al.* (2009) realizaram levantamento semelhante em um campo no sudoeste do Estado, sujeito à arenização. Estudos comparativos envolvendo a estrutura das comunidades campestres dos biomas Pampa e Mata Atlântica são imprescindíveis para futuras iniciativas de conservação e manejo dessas formações naturais características da região. Todavia, estudos de longo prazo que avaliem variáveis estruturais da comunidade atreladas à variável temporal são praticamente inexistentes. Overbeck *et al.* (2005) avaliaram as mudanças entre dois anos em comunidades campestres após eventos de queimada, utilizando uma área excluída de manejo para comparação. Os autores apontam que, na área queimada, o *turnover* de espécies foi maior no primeiro ano, decaindo nos anos subseqüentes devido ao aumento de cobertura de espécies cespitosas. Na área excluída de manejo, as espécies de gramíneas cespitosas apresentaram maior dominância, e a área apresentou valores menores de riqueza e diversidade quando comparada à área manejada com fogo.

Para entender os processos envolvidos na dinâmica desses ecossistemas campestres, tendo em vista sua já conhecida complexidade, espécies e populações podem ser resumidas em padrões funcionais gerais recorrentes (Walker 1992; Grime *et al.* 1996). Essa abordagem, embora tenha sido introduzida na ciência há tempo (e.g. Raunkiaer 1934; Box 1981; ver revisão em Westoby 1998), tem sido revisitada atualmente. Padrões consistentes de associação entre atributos de diferentes plantas foram encontrados para floras locais (ver revisão em Diaz & Cabido 1997), e a perspectiva de um método que permita classificar uma espécie, independentemente de sua distribuição, de acordo com sua estratégia ecológica permitiria desvendar padrões mais gerais através da análise de uma base de dados ampliada (Westoby 1998).

Partindo do princípio que certos atributos das plantas descrevam diferentes estratégias ecológicas, esses atributos poderiam ser usados para generalizar mudanças na composição de espécies ao longo do tempo (Weiher *et al.* 1999; Nygaard & Ejrnæs 2004). Mudanças significativas de atributos funcionais ao longo de um período de sucessão já foram observadas em formações campestres (Kahmen & Poschlod 2004; Lindborg & Eriksson 2005). Tendo em vista que a própria existência atual dos campos com sua configuração atual está atrelada a processos sucessionais após distúrbios como o fogo (Quadros & Pillar 2001, Behling 2002, Behling *et al.* 2004, Overbeck *et al.* 2005, Müller *et al.* 2007) e o pastejo (Senft *et al.* 1987; Coughenour 1991; Pillar & Quadros 1997), estudos que enfoquem as mudanças florísticas e estruturais ao longo do tempo são imperativos.

No bioma Pampa, mais especificamente na região da Campanha, onde o manejo utilizando fogo não é característico, o excesso de pressão de pastejo tem sido o problema (Boldrini 1997). Nos campos da região, praticamente não há áreas excluídas de pastejo e, portanto, não há estudos que enfoquem a dinâmica sucessional da vegetação campestre sem a presença do gado.

Como já abordado anteriormente, a fisionomia atual dos campos está relacionada a um regime de distúrbios. Assim sendo, a exclusão de qualquer prática de manejo permite visualizar o processo sucessional da comunidade, normalmente interrompido pelo manejo. Tendo em vista as já conhecidas diferenças de manejo e flora entre as formações campestres dos biomas Pampa e Mata Atlântica, espera-se que a resposta das comunidades de cada área seja diferente, de acordo com o tipo (ou a ausência) de manejo aplicado. Esperam-se grupos de plantas que compartilham atributos semelhantes entre si caracterizem a sucessão após cada distúrbio em cada área, e mesmo entre diferentes períodos sucessionais.

Para estudar a estrutura e a dinâmica da vegetação campestre, em ambos os biomas, levando em conta as práticas de manejo citadas e a variável temporal, é necessária a implantação de parcelas permanentes, para que seja possível obter informações de longo prazo padronizadas e futuramente comparáveis (Sanquetta 2008a).

Esta tese de doutorado foi realizada no âmbito do projeto de Pesquisa Ecológica de Longa Duração (PELD) Campos Sulinos (CNPq 558282/2009-1). Este projeto teve início simultâneo ao meu ingresso como aluno de doutorado no Programa de Pós-Graduação em Botânica da UFRGS. No âmbito deste projeto, foram estabelecidos seis sítios de pesquisa em diferentes pontos do Estado do Rio Grande do Sul (três no bioma Pampa e três no bioma Mata Atlântica), no ano de 2011. Na Figura 1 são apresentados todos os sítios que atualmente compõem a rede PELD Campos Sulinos. Esta tese foi realizada com base nos dados obtidos nos sitos 1, 2, 3, 4, 6 e 7 (Figura 1). Cada um destes sítios constitui um bloco de amostragem, composto de três potreiros sob diferentes tratamentos: manejo convencional, conservativo e exclusão de manejo (Figura 2). Detalhes sobre os tipos de manejo são fornecidos nos capítulos subsequentes da tese. Desde 2011, todos os sítios vêm sendo reamostrados anualmente.

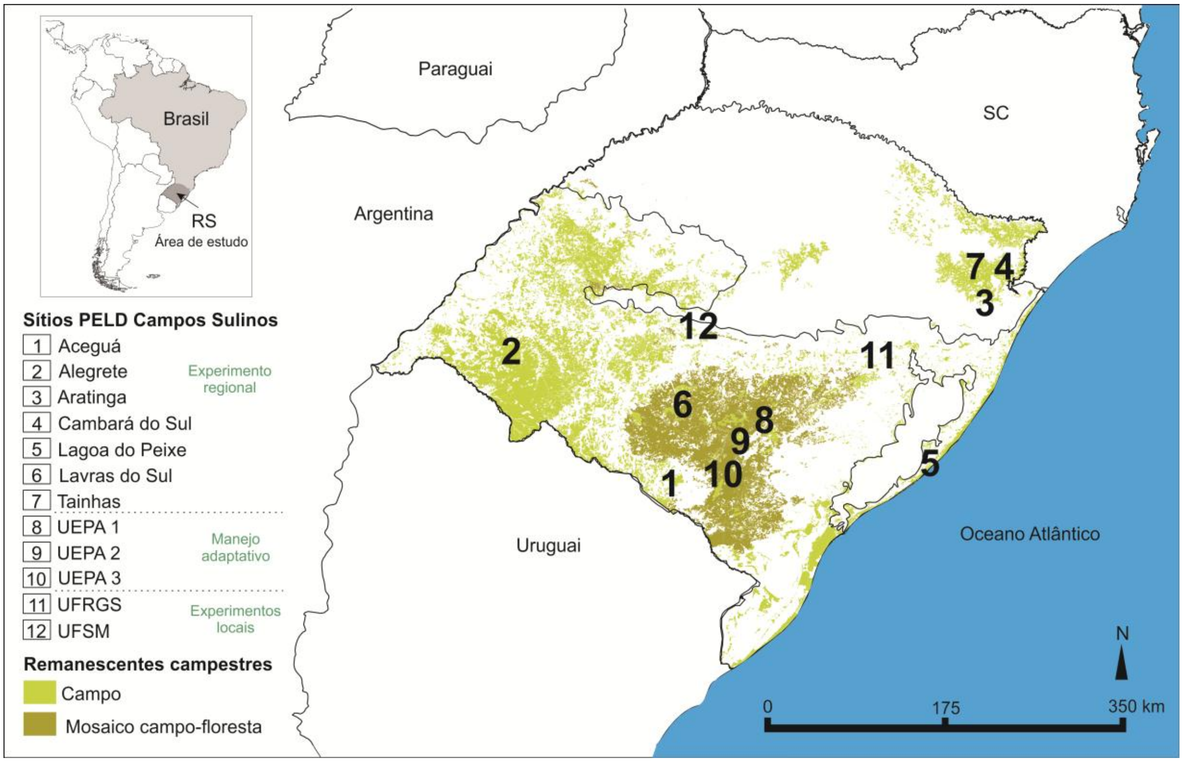

Figura 1. Sítios que atualmente fazem parte da Rede PELD Campos Sulinos. Os sítios englobados nesta tese são os do ‘experimento regional’, numerados de 1 a 7, com exceção do sítio número 5 que ainda não foi implementado.

Figura 2. Estrutura dos blocos de amostragem dos sítios da Rede PELD Campos Sulinos.

Os objetivos gerais desta tese, que são atingidos no conjunto dos artigos apresentados, foram os seguintes: (i) caracterizar e comparar comunidades campestres inseridas nos biomas Pampa e Mata Atlântica do Rio Grande do Sul em relação a sua composição florística e estrutural; (ii) avaliar a aplicabilidade do conceito clássico de forma de vida *sensu* Raunkiaer como descritor de padrões de vegetação campestre subtropical; (iii) identificar respostas das comunidades campestres inseridas nos dois biomas a diferentes práticas de manejo com animais pastadores e à exclusão de manejo e (iv) explorar as relações entre manejo, estrutura da vegetação, comunidades de artrópodes e processos ecossistêmicos (decomposição).

A tese está estruturada em capítulos que correspondem a manuscritos de artigos, já formatados para submissão em revistas científicas. O primeiro capítulo apresenta os dados obtidos no primeiro ano de levantamento do projeto (2011), consistindo na descrição da vegetação dos sítios, das diferenças entre sítios inseridos em diferentes biomas e em uma breve discussão sobre a influência de variáveis edáficas nos padrões encontrados. Este manuscrito está nas normas da revista Biodiveristy and Conservation. O segundo capítulo consiste em uma revisão do conceito de formas de vida aplicado em plantas, seguido de uma proposta de categorias de formas de vida para ser aplicada em ecossistemas campestres subtropicais. Este capítulo é finalizado com uma comparação entre a eficácia desta classificação proposta e classificações clássicas e amplamente utilizadas em descrever diferenças entre sítios com vegetação campestre sob níveis variáveis de pastejo. O manuscrito está nas normas da revista Austral Ecology. No terceiro capítulo são abordadas as relações entre manejo, estrutura da vegetação, comunidades de artrópodes e processos ecossistêmicos. Este manuscrito está nas normas da revista Ecography. Por fim, o quarto capítulo aborda aspectos da dinâmica da vegetação campestre sob diferentes manejos após quatro anos de monitoramento. Este manuscrito está nas normas da revista Journal of Vegetation Science.

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Capítulo 1

Differences in grassland vegetation from two South Brazilian biomes and implications for conservation

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Abstract

Conservation is a global concern, and can produce more effective results when encompassing simultaneous conservation and use of biodiversity. This paradigm highlights the importance of natural grasslands for conservation, since these ecosystems may be examples of sustainability by allying profitable use and maintenance of biodiversity. Grasslands in Southern Brazil are inserted in two biomes: Pampa and Atlantic Forest. Quantitative studies focusing on floristic and structural differences between grasslands in both biomes are so far lacking. This paper aims to evaluate differences in plant composition, richness, diversity and structural variables between natural grasslands from Pampa and Atlantic Forest biomes, and the implications of these differences for conservation. We also evaluated the correlation between soil features and vegetation patterns. Data were collected in 162 sampling units distributed in nine paddocks in six sites, three per biome. Data were submitted to cluster and ordination analyses. Relationships between soil features and vegetation were assessed with linear regression using ordination axes. Relationships between structural variables and plant community were estimated using correlation analysis. Sampling resulted in 382 plant taxa from 40 families (ca. 17% of the regional grassland flora). Sites between biomes shared 28 families and only 15% species. Average richness and diversity were higher in Pampa sites. Cluster and ordination analyses revealed two sharp groups among sampling units, consistent with biome separation. Dominance was higher in Atlantic Forest sites than in Pampa sites. We inferred that this vegetation structure is the result of past and present differences in management, soil and climate. The implication of our results is that conservation efforts must be equally focused on grasslands from both biomes in order to target: (1) a representative set of species, (2) different vegetation structures and (3) potentially different ecological processes and services. Also, we suggest that management planning that includes grazing and/or fire must be mandatory in Brazilian conservation units encompassing grasslands.

Keywords: management, soil-plant relationships, conservation units, sustainable use, grassland biodiversity, disturbance regime.

Introduction

Biodiversity conservation has been repeatedly pointed out as a priority task of societies worldwide (Sachs et al. 2009; Larigauderie and Mooney 2010). Although it was originally focused on preserving species, conservation is today a broad multidisciplinary science, and well-planned conservation efforts encompass species, landscapes and ecological processes alike (Heywood and Iriondo 2003). Human actions during the past few centuries have significantly reduced natural ecosystems in area and services offered (Millennium Ecosystem Assessment 2005), emphasizing the importance of conservation. Moreover, scientists and political actors are slowly converging towards the idea of allying conservation and use of natural resources (Aronson et al. 2006). Therefore, ecosystems dominated by natural grassland landscapes may be key assets for conservation, since they are natural forage sources for domestic herbivores (Hodgson 1990; Nabinger et al. 2000; Bilenca and Miñarro 2004) and their biodiversity is not impaired by this disturbance, at least when it does not occur in extreme intensities. In fact, grassland biodiversity and conservation status may be positively influenced by grazing (Olff and Ritchie 1998; Sebastià et al. 2008), thus configuring a 'natural' example of sustainable use.

Grassland ecosystems cover large areas in Southern South America. The Río de la Plata Grasslands extend over ca. 750,000 km2 in Argentina, Uruguay and Southern Brazil (Soriano et al. 1992; Bilenca and Miñarro 2004). Within Brazilian territory, these grasslands determine the landscape of the southern half of Rio Grande do Sul, the southernmost Brazilian state, in the region defined locally as the Pampa biome (IBGE 2004). However, grasslands are also present in the Atlantic Forest biome, in higher altitudes, milder climates and shaping mosaics with forests (Overbeck et al. 2007). The contact zone between these biomes is located near the 30oS parallel, a known threshold between tropical and subtropical/temperate vegetation (Cabrera and Willink 1980). This region is also a transition point considering geomorphology and soil types. Soils in the Atlantic Forest biome are mostly derived from basalt and show low pH values on average, whereas there is a higher diversity of soil types in the Pampa biome (Streck et al. 2008). Soils have been long hypothesized to influence vegetation patterns in South Brazilian grasslands, as it has been found for Uruguayan grasslands by Lezama et al. (2006), although no study has specifically focused on that relationship so far.

Temperate grasslands and savannas figure among the world's most critically endangered ecosystems, with 45.8% rate of conversion and only 4.6% of protection (Hoekstra et al. 2005). Conservation of South American ecosystems has long been identified as a problem (Mares 1986), and still remains overlooked (e.g., Ramirez-Villegas et al. 2012). Conservation of South Brazilian grasslands (locally known as campos) has been neglected. Less than 0.5% of the South Brazilian grasslands are protected in conservation units, and most of them are inserted in the Atlantic Forest biome (Overbeck et al. 2007). Moreover, there are no conservation units under IUCN's categories I to IV (Olson and Dinerstein 1998) in grasslands within the Pampa biome, increasing their vulnerability to land conversion and suppression of natural vegetation. There was a decrease of ca. 25% in total natural grasslands in Southern Brazil between 1970 and 2000 (Nabinger et al. 2000). Today, only 50% of original grassland cover in Rio Grande do Sul remains, and land conversion for human use is estimated to be of 1,000 km2 per year (Cordeiro and Hasenack 2009). Grasslands in the region have evolved under different levels of grazing (Milchunas et al. 1988) and fire disturbances (Behling et al. 2004; Behling et al. 2005), have been used since the seventeenth century as forage source for cattle breeding (Pillar and Quadros 1997) and are still used as such today (Nabinger et al. 2000). The use of natural grasslands as forage sources for extensive livestock breeding maintains grassland diversity, providing that adequate stocking rates are used (Hodgson 1990; Nabinger et al. 2009). In fact, conservation of grassland ecosystems around the world often involves herbivory and/or fire as management tools (e.g., Fuhlendorf et al. 2006; Hampicke and Plachter 2010; Houston 1982; Meagher 1973). However, land management within Brazilian conservation units is still a taboo subject, mostly due to misguided ecological concepts (Pillar and Vélez 2010) – even though, in fact, the very existence of these grassland ecosystems is linked to disturbances regimes such as grazing and fire (Behling et al. 2004; Quadros and Pillar 2001). Land management of grazed grasslands differs between biomes in Southern Brazil. In the Pampa, stocking rates are usually higher, fire is seldom used as a managing tool and mowing is used to control undesirable species. In the Atlantic Forest, stocking rates are usually lower, and undesirable species and accumulated dry biomass are controlled with yearly fire (Maraschin 2001; Nabinger et al. 2000). There is evidence that the use of fire with such periodicity reduces diversity and overall foraging value by removing intolerant species and favoring tussock C4 species (reviewed by Jacques 2003). It is likely that the difference in historical management between biomes has impacts on present vegetation structure, although this question is yet to be directly addressed.

Plant species diversity in South Brazilian grasslands is extremely high. Boldrini (1997) estimated 2,200 grassland plant species for Rio Grande do Sul state alone, and ongoing work by the same author and colleagues will soon provide an updated species list with roughly 2.600 taxa (Boldrini et al. unpubl.). Although the identity of plant species present in these ecosystems is relatively well known (Boldrini 2009), possible structural and floristic differences between grasslands inserted in the Pampa and in the Atlantic Forest biomes have not been elucidated. Evaluating such differences will provide valuable tools for future conservation efforts, since these must consider the representativeness of grassland ecosystems from different biomes (and possibly different regions within each biome), different management types and different disturbance history. Moreover, if floristics and/or community structure differs between grasslands from each biome, conservation efforts should encompass different strategies in each biome in order to maximize conservation of biodiversity, landscapes and ecological processes.

The objective of this paper is to evaluate differences between natural grassland areas from the Pampa and the Atlantic Forest biomes, and the implications of these differences for conservation. We hypothesize that these formations differ regarding plant composition, richness, diversity and structural variables. We also briefly consider the influence of soil features over vegetation patterns.

Material and Methods

Data collection took place in late 2010 and early 2011, in natural grasslands in Rio Grande do Sul, Southern Brazil. Vegetation surveys were carried out at six sites, three in the Pampa biome and three in the Atlantic Forest biome. Sites in the Pampa are inserted in farms predominantly focused on cattle breeding. Sites in the Atlantic Forest are inserted in Conservation Units. Acronyms for each sampling site were given according to municipalities or Conservation Units they were inserted. Pampa sites were Aceguá (ACE; 31º38’55”S, 54º09’26”W), Alegrete (ALE; 30º04’08”S, 55º59’27”W) and Lavras do Sul (LAV; 30º41’55”S, 53º58’11”W). Atlantic Forest sites were Aparados da Serra National Park (APA; 29º08’10”S, 50º09’21”W), Aratinga Ecological Station (ARA; 29º23’31”S, 50º14’30”W) and Tainhas State Park (TAI; 29º05’40”S, 50º22’03”W). Mean altitude in Pampa sites was 215 m AMSL and 930 m in Atlantic Forest sites. Grasslands in all sites are under cattle grazing, and have been under grazing for many years, with no known record of land conversion. In Atlantic Forest sites, yearly fires have also been used for many years, following a widespread regional management technique. Although grazing intensity (livestock units per area) varies from site to site, overall it is lighter in Atlantic Forest sites. We estimated grazing pressure in each site in animal units (AU = 450 kg of live weight) per hectare. Grazing pressure in each site was: ACE = 1.05 AU/ha, ALE = 0.9, LAV = 0.85, APA = 0.9, ARA = 0.6 and TAI = 0.45).

At each site we sampled three paddocks of 0.5 ha each using nine 1m2 permanent plots (systematically allocated in the paddock in a 3x3 grid with 17 m between plots), summing up to 162 sampling units across the six sites. This sampling layout was designed for an ongoing long-term ecological research (PELD Campos Sulinos; CNPq 558282/2009-1), and this paper reports results from the first season of sampling (Southern hemisphere summer 2010/2011). In each sampling unit, we surveyed all plant species that were present and estimated their cover using the decimal scale of Londo (1976). We also estimated cover of bare soil, litter, rock outcrops and overall vegetation cover per sampling unit. We calculated relative frequency and cover for each species (Ellenberg and Mueller-Dombois 1974).

We submitted vegetation data to cluster analysis with sum of squares as clustering criterion (Orloci 1967) and Principal Coordinate Analysis using chord distance as dissimilarity measure between sampling units. We used mean values of species cover in sampling units per paddock in all analyses. We performed additional multivariate analyses using presence/absence data to assess the importance of species composition alone over vegetation patterns. We evaluated the presence of sharp groups within cluster groups and stability and significance of ordination axes with bootstrap resampling methods (Pillar 1998; Pillar 1999a, b). For comparisons of diversity between sites we calculated the Shannon diversity index and evenness (Magurran 1988), and also used Hill's diversity profiles (Hill 1973; Tóthmérész 1995).

We collected soil samples in each sampling unit up to 10 cm depth. Air-dried soil samples were used for chemical and textural analysis (Silva 1999). The pH value was determined in water solution (1:1). Exchangeable cations, Mg^{+2}, Ca^{+2} and Al^{+3} were extracted with KCl $1molL^{-1}$. P and K were determined using the Mehlich I extraction method. Cation exchange capacity (CEC) was determined at pH 7. Organic carbon content of the soil was measured using the wet combustion method. Clay content was determined by densimeter method. In this paper, we do not wish to discuss soil characteristics in detail, since in-depth soil analysis will be discussed in a separate study (Andrade et al. unpublished). Rather, we used summarized soil data to estimate the influence of abiotic factors on grassland vegetation parameters. To do so, we used the ordination scores of sampling units from the first ordination axis obtained in a Principal Coordinate Analysis of sampling units described by an abiotic matrix containing the variables described above (162 sampling units described by 17 soil variables, see ESM 1). Then we explored the relationships between this axis and the axis obtained in the ordination of vegetation data (162 sampling units described by abundances of 382 plant species). Both vectors were normalized, submitted to correlation analysis (Pearson product-moment) and fitted with a linear regression model using the vegetation axis as dependent variable.

Differences between sites regarding richness, diversity, species composition and cover and structural variables were tested using randomization tests with 10,000 bootstrap resampling iterations (Pillar and Orlóci 1996). For comparisons between species composition and cover we used raw matrices (sampling units described by species mean percentage cover values). Correlation between variables was evaluated with Pearson product-moment correlation coefficient, using permutation tests to assess statistical significance. Only significant correlations were presented and discussed ($P<0.05$). Prior to correlation analysis, data subsets were submitted to Shapiro-Wilk's normality test, and vectors that failed the test were normalized. Analyses were conducted with the software Multiv (Pillar 1997) and on the R platform (R Development Core Team 2012).

Results

We found 382 plant taxa distributed in 40 families among the six sampling sites. Families with highest overall species richness and average cover were Poaceae, Asteraceae and Cyperaceae in both biomes, although the richness/cover ratio varied between biomes (Figure 1). The two groups of sites from each biome shared 28 families and had eight exclusive families each. Both sets of three sites within biomes had 27 species in common, whereas the two groups of sites from each biome shared 57 species overall (Figure 2).

Average species richness and diversity were overall higher in the Pampa biome, both at sampling unit and paddock levels. Richness values showed similar patterns in both biomes, with one site encompassing more species and two sites with less species and no significant difference between each other (Table 1). Considering only the Shannon index, diversity was similar among Atlantic Forest sites, whereas it was different among Pampa sites (Table 1). However, the diversity profiles revealed that diversities between biomes are different at low alpha values. Diversities were equivalent within the Pampa biome, whereas within the Atlantic Forest they differed with increasing alpha values (Figure 3). Randomization tests comparing species composition and cover resulted in significant differences between biomes at the paddock and site levels (P<0.05). All pairwise comparisons between sites of the same biome were not significant.

Differences between biomes were also consistent regarding structural variables. Vegetation cover and height showed higher values in site from the Atlantic forest biome, whereas open soil showed the opposite pattern (Table 2). Moreover, vegetation cover was more uniform in Atlantic Forest sites in comparison with Pampa sites. Cover of litter and rock outcrops did not differ between biomes, and showed significant differences only at the TAI site among Atlantic Forest sites (Table 2). Atlantic Forest sites showed high dominance of *Andropogon lateralis*, an erect tussock grass, whereas the prostrate grass *Paspalum notatum* was the most representative at Pampa sites (Table 3).

Across sites and biomes, mean bare soil was positively correlated to mean plant species richness (r=0.75, P=0.0013), Shannon diversity (r=0.93, P<0.001) and evenness (r=0.77, P<0.001). Evenness was negatively correlated to mean vegetation cover (r=-0.63, P<0.01) and positively correlated to rock outcrops (r=0.61, P<0.01). Grazing pressure was correlated to vegetation height (r=0.89, P<0.01), Shannon diversity (r=0.92, P<0.01) and species richness (r=0.68, P<0.01).

Cluster analysis revealed two sharp groups among paddocks. These groups are consistent with the biome separation. However, the distance between paddocks was different within each biome. Dissimilarity values between Pampa paddocks are on average twice as large as between Atlantic Forest paddocks, which resulted in a perfect clustering match for sites from the former and not for the latter (data not shown). Principal Coordinate Analysis revealed a pattern not entirely consistent with biome separation. Although Atlantic Forest paddocks clustered in the left side of the scatterplot, Pampa sites clustered in two groups: one comprising ACE and LAV paddocks, and the other comprising ALE paddocks (Figure 4). Ordination and cluster analyses performed with presence/absence data resulted in a similar pattern, although biome separation was clearer.

The first standardized ordination axis containing vegetation information was highly and significantly correlated to the first ordination axis containing soil information (r=0.86; see methods for details on soil data). The linear model using the vegetation axis as dependent variable showed that vegetation composition and structure can be predicted by soil features across our sampling units (Figure 5). Also, vegetation structural parameters were strongly correlated to individual soil variables, but these relationships will be discussed elsewhere (Andrade et al. unpubl.).

Discussion

We aimed at revealing principal differences in biotic composition of south Brazilian grassland sites included in two different biomes, Pampa and Atlantic Forest, for the first time based on analyses of quantitative data. Our results indicate that grasslands in the Pampa biome differ from those in the Atlantic Forest considering plant species composition and cover, richness (Table 1) and vegetation structural variables (Table 2). Cluster and ordination analyses (Figure 4) also showed a clear distinction between paddocks/sites from different biomes. The high dominance of *Andropogon lateralis* in Atlantic Forest sites (Table 3) corroborates earlier descriptive studies of the local flora (Boldrini 1997, 2009; Boldrini et al. 2009; Boldrini and Longhi-Wagner 2011), and partly explains the lower diversity values and structural differences between sites. This species forms dense tussocks, defining the landscape of this region. Dominance in Pampa sites, on the other hand, is more diluted among species (also shown in Figure 3, with similar diversity with increasing alpha values; see discussion on diversity profiles below), and the dominant grass is the prostrate *Paspalum notatum*, which also corroborates previous descriptive studies (Boldrini 1997; Díaz et al. 1992; Pinto et al. 2013; Rodríguez et al. 2003). It is important to mention that the Atlantic Forest Biome extends northwards along the entire Brazilian coast, whereas our sampling was restricted to grasslands in the southern portion of the biome. Grasslands in the northern Atlantic Forest, however, are usually related to high elevations, inserted in a more continuous forest matrix, have different structure and floristic composition and are known as altitude grasslands and campos rupestres (Vasconcelos 2011). The Pampa extends through Uruguay and Argentina and it is assumed to have a relative floristic and structural continuum throughout its distribution (Bilenca and Miñarro 2004; Ferreira and Boldrini 2011). However, this has not been evaluated quantitatively so far within Brazilian territory. Although our sampling does not allow extrapolation of floristic results for the two entire biomes, we did sample ca. 17% of the regional grassland flora, and also found structural patterns consistent with previous descriptive studies (e.g., Boldrini 2009; Boldrini et al. 2009).

Sites between biomes shared only 15% of their species, and the number of shared species in pairwise comparisons was slightly lower in Atlantic Forest sites (Figure 2). Also, the ordination analysis performed with presence/absence data resulted in a pattern of biome separation similar to the one found with cover data (data not shown). These results indicate that differences between biomes are also dependent on species composition. Distribution of species richness and relative cover values per family also differed between biomes (Figure 1). Poaceae species represented a slightly higher cover value in Atlantic Forest sites, although they were more numerous in Pampa sites. Asteraceae represented higher cover in Pampa sites, whereas Cyperaceae species richness and cover was more than two times higher in Atlantic Forest sites (this last could be related to more humid climate in the Atlantic Forest). Also, there was a high family turnover rate between biomes in less representative families. A regional literature-based floristic review found similar patterns, with the Pampa biome showing more exclusive species (Boldrini 2009). These differences in species composition (Table 3 and Figure 1) reflect differences in vegetation structure (Table 2) and community parameters (Table 1 and Figures 3 and 4). Differences in climatic variables such as mean annual rainfall (Nimer 1990), altitude and geological and soil features (Streck et al. 2008) are probably important variables that influence these differences. Also, areas from both biomes are under the influence of different floristic contingencies (Boldrini and Longhi-Wagner 2011; Cabrera and Willink 1980), which is also reflected in different species composition and vegetation structure.

Although pairwise comparisons of plant composition and cover between sites of the same biome showed no differences, variation of some parameters was different between biomes. Most structural parameters (Table 2) were more variable within the Pampa biome, as was Shannon diversity (Table 1). Diversity profiles showed that diversity in Atlantic Forest sites was overall slightly lower than in Pampa sites (Figure 3). Also, diversity among Pampa sites did not differ with increasing alpha values, whereas it did among Atlantic Forest sites. Changes in alpha values represent changes in sensitivity to abundant and rare species. Higher alpha values correspond to diversity indexes that give more weight to abundant species (Tóthmérész 1995). Therefore, differences in diversity between Atlantic Forest sites are related to the high dominance seen in these sites (Table 3), and are also reflected in the higher aggregation of paddocks in comparison with Pampa sites revealed in the ordination analysis (Figure 4).

The most striking structural differences in sites between biomes were mean vegetation height, cover and bare soil (Table 2). Some of these structural variables turned out to be good predictors of grassland plant community parameters. We found strong positive correlations between bare soil and species richness (r=0.75), Shannon diversity (r=0.93) and evenness (r=0.77) and between rock outcrops and evenness (r=0.61). Also, mean vegetation cover and evenness were negatively correlated (r=-0.63). Fire has been used to remove litter and standing dead biomass after winter for years in Atlantic Forest grasslands (Jacques 2003). This historical practice, combined with low stocking rates (Maraschin 2001; Nabinger et al. 2009) probably lead to the present structure: high dominance of C4 grasses that form dense tussocks, such as Andropogon lateralis, which accordingly grouped close to Atlantic Forest sites in the ordination analysis (Figure 4). Under light grazing pressures, such tussock species are allowed to grow both in height and tussock diameter, which may result in protection of growing buds, consequent resistance to future fire events and contributes to maintain dominance (Jacques 2003; Overbeck et al. 2005).

Evidence found in grasslands from other parts of the world (at least under relatively humid climate conditions) indicates that when disturbance (i.e. grazing and/or fire) is reduced or removed, plant species richness and/or diversity also reduce (Altesor et al. 2005; Fynn et al. 2004; McIntyre et al. 2003; Olff and Ritchie 1998; Overbeck et al. 2005; Rusch and Oesterheld 1997; Sebastià et al. 2008; Tremont 1994). Our results showed that sites with lower grazing pressures showed lower values of richness and diversity (Table 1), and overall less exclusive species (Figure 2). Coupled with the high correlation values we found between grazing pressure and richness, diversity and vegetation height, our results suggest a close relationship between management and grassland structure and composition. Management practices and the resulting high dominance are directly linked to increased mean vegetation cover and height in Atlantic Forest sites (Table 2), which in turn correlates to the lower values of richness and diversity.

High percentages of bare soil and rock outcrops are usually related to grasslands growing over shallow soils (e.g., Lezama et al. 2011; Pinto et al. 2013). Plant communities that thrive on such resource-limiting micro-environments are prone to show more evenly distributed abundances, less dominance and consequently higher values of evenness and diversity (e.g., Pinto et al. 2013; Setubal and Boldrini 2012). This explains the positive correlation between bare soil and rock outcrops and richness, diversity and evenness. Although mean values for bare soil were different between biomes and values for rock outcrop were not, they showed large variation between sites (Table 2), and even higher between sampling units. Nonetheless, both variables were strongly correlated to vegetation parameters, suggesting that soil features and vegetation structure are closely related. This could be a reflection of soil effects on vegetation patterns at two levels. The first depicts differences between biomes, mostly related to differences in soil acidity. The second shows natural vegetation heterogeneity related to local topography, which was found to be a strong driver structuring grassland communities at the landscape level (Sebastiá 2004). Relating abiotic and biotic factors is not a new topic in ecology (Austin et al. 1990; Gibson et al. 1993; Grime 1979; Tilman 1984). However, it is still used as a tool to explain grassland community organization (e.g., Cantero et al. 2003; Fynn and O'Connor 2005), although the relative contribution of biotic, abiotic and spatial factors in community assembly is still an open question in community ecology.

Diversity of soil types is higher in the Pampa biome when compared with the Atlantic Forest in southern Brazil (Streck et al. 2008). Although our sampling does not allow for broader extrapolations on soil-vegetation relationships, we did find an evident pattern linking abiotic and biotic variables within our data (Figure 5). Also, correlation between axes containing soil and vegetation information was significant and high (r=0.86), reinforcing the idea that vegetation patterns are related to soil features.

The Rio de La Plata Grasslands, in which the Brazilian Pampa biome is inserted, are characterized by a less seasonal environment in comparison with northern Hemisphere grasslands (Paruelo et al. 1995). Most studies from these subtropical and temperate grasslands indicate the predominance of prostrate growth forms (Rodríguez et al. 2003; Díaz et al. 1992 and our results for grasslands in the Pampa biome). In Atlantic Forest grasslands, however, the dominance of tussock species is similar to what is found in temperate grasslands such as North American prairies (Olff and Ritchie 1998). Grazed grasslands under moderate to high grazing pressures are dominated by prostrate growth forms, tend to accumulate less standing biomass, and are less prone to regular burning in comparison with grasslands dominated by erect tussock species (Altesor et al. 2005; Guerschman and Paruelo 2005). These differences in structure and management pose different challenges for conservation. In our personal observations during fieldwork over the past years, we have seen systematic substitution of natural grasslands, previously used as forage sources, by croplands and exotic tree plantations. Transformation of natural ecosystems to croplands represents one of the greatest threats to global biodiversity (Sala et al. 2000), and present conservation status of grasslands in the region is probably much worse than presently estimated, since the study by Cordeiro and Hasenack (2009) is based on remote sensing images from ten years ago.

According to current Brazilian environmental law, the use of fire or domestic herbivores is not allowed inside conservation units under the most restrictive categories, which supposedly are the ones that should provide the highest protection for biodiversity (MMA 2000; Olson and Dinerstein 1998). Herbivores are used as management tools in conservation of grasslands in North

America (Meagher 1973) and Europe (Hampicke and Plachter 2010), among other places. Furthermore, evidence of positive influence of grazing on ecosystems processes was found in experiments carried out inside conservation units (e.g., Frank et al. 2000; Frank and McNaughton 1993). To create or maintain conservation units encompassing large natural grassland landscapes that would remain unmanaged would be to repeat studies carried out worldwide that showed that management exclusion leads to species loss and decreasing diversity. In fact, the vast majority of preserved grassland ecosystems in southern Brazil are natural pasturelands used for extensive cattle breeding (Cordeiro and Hasenack 2009). Grasslands we sampled in the Atlantic Forest were inserted in conservation units, but as the areas were incorporated into these quite recently, grazing has not yet been excluded – but current management plans aim to do so. Our results indicated that grassland areas under lower grazing pressures harbor less species richness and diversity in comparison with more heavily grazed sites. It is likely that the complete exclusion of management would promote further biodiversity loss in these areas. If the prevailing Brazilian conservation policy is maintained, grazing and fire will indeed be suppressed from these grasslands (and many others throughout southern Brazil). This will ultimately lead, as discussed above, to declines in plant richness and diversity, besides negative effects on richness and diversity in other trophic levels as well as on ecosystem processes and services.

Our results indicated that grasslands in the Pampa and Atlantic Forest biomes differ from one another considering plant species composition and vegetation structure, in consequence both of environmental conditions (soil and climate) and current and past management. The implications of this conclusion for conservation are immediate: conservation efforts must be equally focused on grasslands from both biomes in order to target: (1) a set of species representative of the different grassland types; (2) different vegetation structures and (3) potentially different ecological processes and ecosystem services. Also, it is imperative that management is taken into account when planning future conservation efforts focusing on natural subtropical grasslands. Management is important not only due to its effects on biodiversity, but also because it is related to local culture and legal issues.

The next step to build a framework for conservation of grasslands in southern Brazil would be: (i) to bridge the gap between farmers and scientists, in order to provide the first the sustainable management alternatives that allow for simultaneous conservation and monetary gain and (ii) to propose standardized protocols for implementation and long-term maintenance of a disturbance regime in conservation units encompassing grasslands. Ongoing research projects in which our work was included aim to provide further contribution to build and thread these steps.

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Tables

Table 1 Mean species richness, diversity (Shannon's H') and respective standard deviations for grassland plant communities in six sites distributed in two biomes. Different letters represent significant differences (at paddock level) within columns and borders (P<0.05). P = Pampa sites, AF = Atlantic Forest sites

Biome	**Site**	**Species richness**		**Diversity (H')**	
		Mean	SD	Mean	SD
P		27.17^{a}	6.24	2.20^{a}	0.35
AF		22.86^{b}	4.81	1.73^{b}	0.34
P	ACE	33.04^{a}	5.18	2.43^{a}	0.28
	ALE	23.19^{b}	3.70	2.20^{b}	0.34
	LAV	25.30^{b}	4.85	1.98^{c}	0.29
AF	APA	25.63^{a}	5.58	1.83^{a}	0.21
	ARA	21.96^{b}	3.72	1.62^{a}	0.36
	TAI	21.00^{b}	3.71	1.74^{a}	0.40

Table 2 Mean values of structural variables for grassland plant communities in six sites distributed in two biomes from Southern Brazil. Different letters represent significant differences within biomes (P<0.05). P = Pampa sites, AF = Atlantic Forest sites

Biome	**Site**	**Vegetation cover (%)**	**Bare soil (%)**	**Rock outcrop (%)**	**Litter (%)**	**Vegetation height (cm)**
P		80.43^{a}	11.85^{a}	1.42^{a}	27.65^{a}	8.70^{a}
AF		91.91^{b}	2.38^{b}	1.05^{a}	14.10^{a}	27.64^{b}
P	ACE	89.07^{a}	13.15^{a}	-	25.56^{a}	9.53^{a}
	ALE	75.74^{b}	$13.98^{a,b}$	4.26	32.78^{a}	5.50^{b}
	LAV	76.48^{b}	8.43^{b}	-	24.63^{a}	11.06^{a}
AF	APA	92.41^{a}	2.50^{a}	0.09^{a}	19.89^{a}	$24.73^{a,b}$
	ARA	92.41^{a}	$3.15^{a,b}$	0.09^{a}	20.09^{a}	24.07^{a}
	TAI	90.93^{a}	1.48^{b}	2.96^{b}	2.31^{b}	34.13^{b}

Table 3 Relative cover (%) of the five most representative species per site of grassland communities in six sites distributed in two biomes from Southern Brazil

		Relative cover per site (%)					
		Pampa			**Atlantic Forest**		
Family	**Species**	ACE	ALE	LAV	APA	ARA	TAI
Poaceae	*Andropogon lateralis*	-	6.98	0.04	40.11	48.15	33.81
Poaceae	*Axonopus affinis*	3.59	0.54	6.39	1.52	4.87	0.94
Asteraceae	*Baccharis coridifolia*	-	4.85	4.56	-	-	-
Asteraceae	*Baccharis crispa*	1.04	-	9.54	0.43	1.61	2.48
Cyperaceae	*Bulbostylis* sp.	-	-	-	5.87	-	-
Poaceae	*Paspalum maculosum*	-	-	-	5.22	5.61	0.48
Poaceae	*Paspalum notatum*	18.02	7.80	32.04	-	-	3.96
Poaceae	*Paspalum plicatulum*	7.93	-	0.39	0.87	0.02	1.13
Poaceae	*Piptochaetium montevidense*	11.11	7.07	4.15	2.11	0.17	1.13
Cyperaceae	*Rhynchospora megapotamica*	8.91	0.02	-	-	-	-
Poaceae	*Saccharum angustifolium*	-	-	1.50	-	3.52	-
Poaceae	*Schizachyrium tenerum*	-	0.02	0.02	4.98	1.06	13.13
Total		**50.59**	**27.28**	**58.61**	**61.11**	**65.00**	**57.07**

Figures

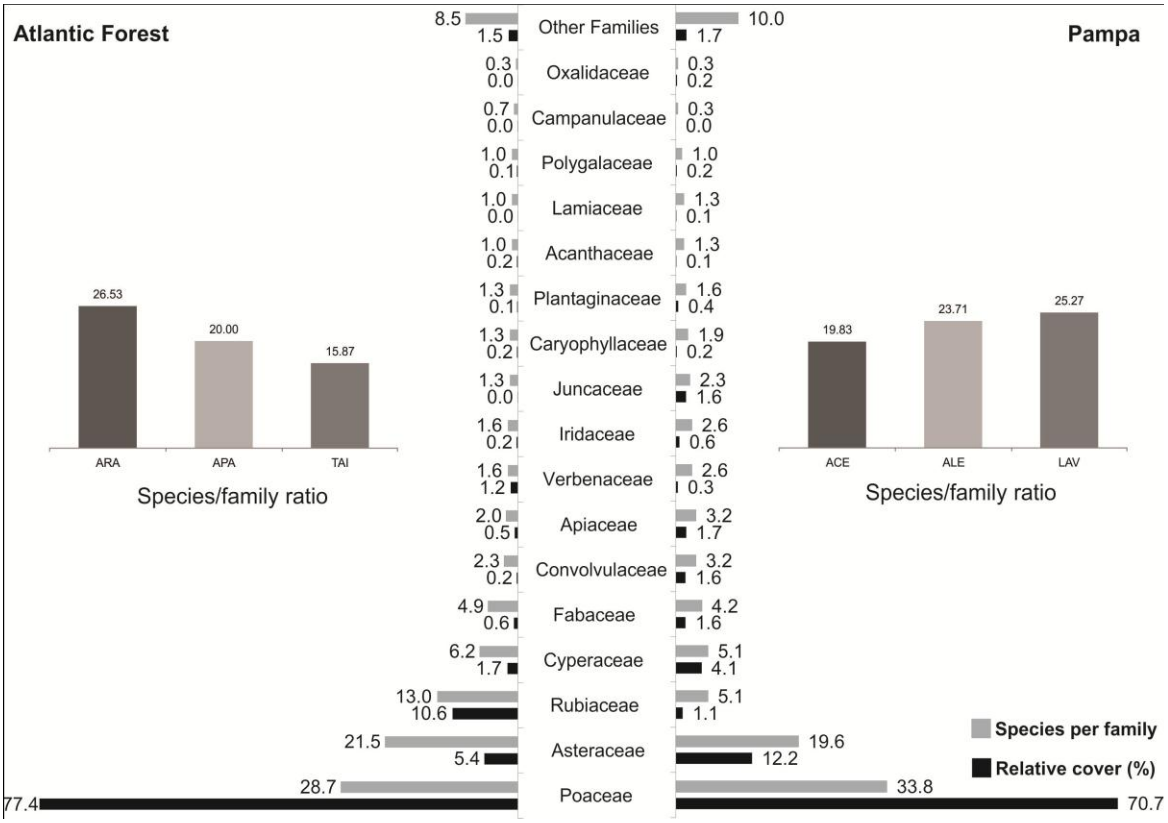


Fig. 1 Species richness, average cover per family and species per family ratio (number of species divided by number of families multiplied by 100) in six grassland communities distributed in the Pampa and Atlantic Forest biomes in Southern Brazil

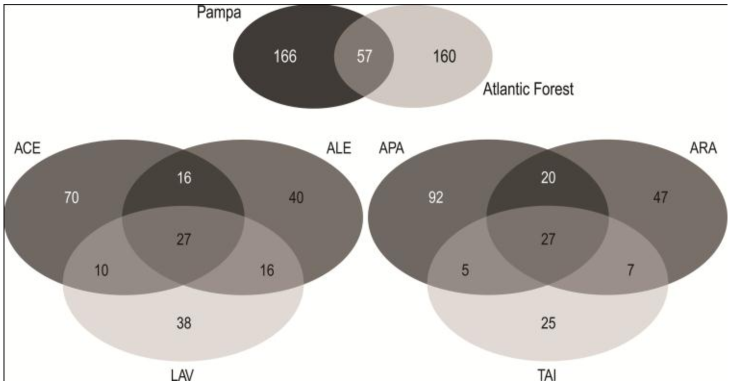


Fig. 2 Venn diagrams showing shared species between grasslands from two biomes and among the three sampling sites within each biome

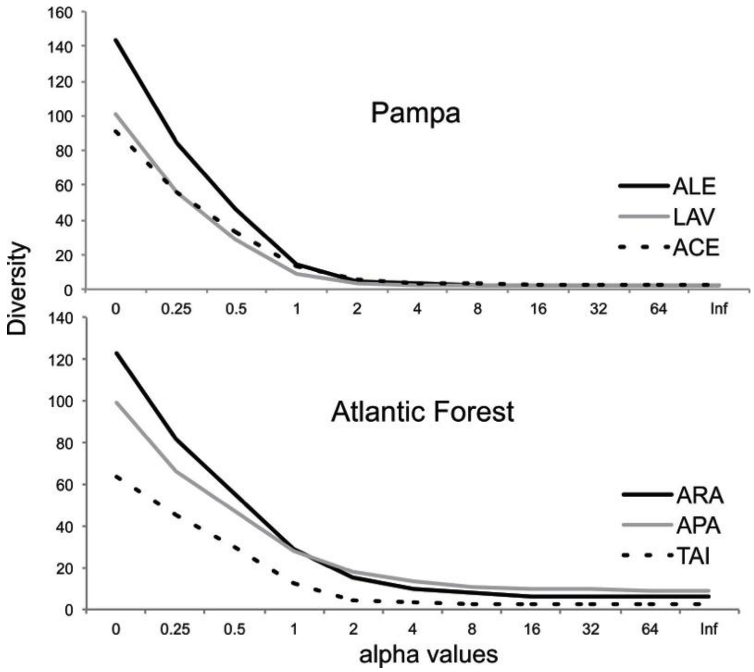


Fig. 3 Diversity profiles of grassland communities from six sampling sites distributed in two biomes in Southern Brazil. Alpha values represent Rényi entropy values

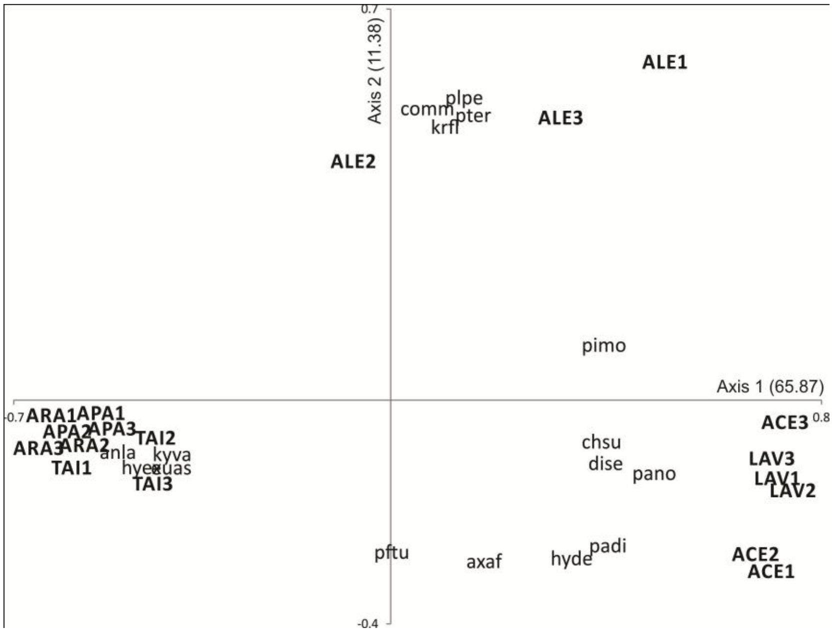


Fig. 4 Ordination diagram (Principal Coordinate Analysis) of six grassland communities (three paddocks each) described by 382 variables (plant species). Plotted variables were the most correlated with the first two ordination axes. Percentage of variation captured in both axes is shown in parenthesis. Legend for variables: anla = *Andropogon lateralis*; axaf = *Axonopus affinis*; chsu = *Chascolytrum subaristatum*; Comm = *Commelina* sp.; dise = *Dichondra sericea*; euas = *Eupatorium ascendens*, hyde = *Hypoxis decumbens*; hyex = *Hydrocotyle exigua*; krfl = *Krapovickasia flavescens*; kyva = *Kyllinga vaginata*; padi = *Paspalum dilatatum*; pano = *Paspalum notatum*; pftu = *Pfaffia tuberosa*; pimo = *Piptochaetium montevidense*; plpe = *Plantago penantha*; pter = Pteridophyta

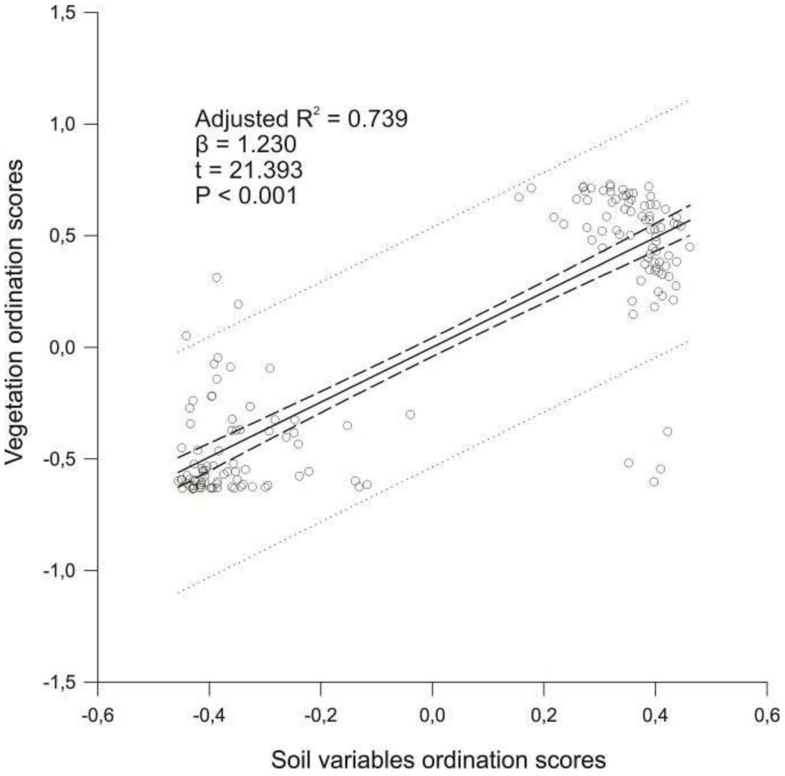
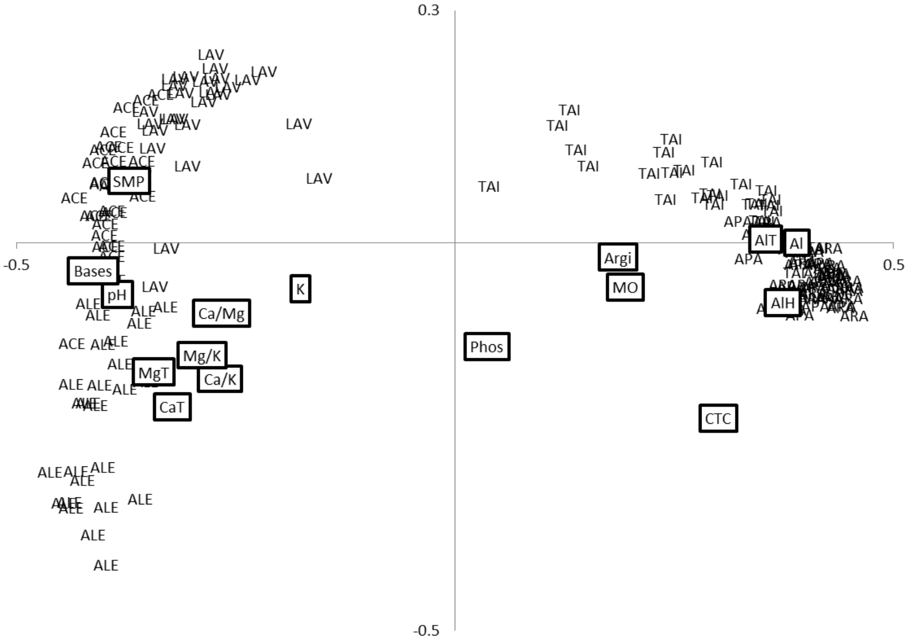


Fig. 5 Linear regression model showing the relationship between ordination axes containing information of vegetation (162 sampling units described by 382 plant species) and soil (162 sampling units described by 17 soil variables) from six grassland communities distributed in two biomes

Electronic supplementary material

ESM 1 Ordination diagram (Principal Coordinate Analysis) of six grassland communities (27 sampling units each) described by soil variables. Legend for variables: SMP = SMP pH method; Bases = percent base saturation; pH = pH (H_2O); Ca/Mg = Ca:Mg ratio; Mg/K = Mg:K ratio; K = potassium; MgT = exchangeable magnesium; CaT = exchangeable calcium; Phos = phosphorus; Argi = clay content; MO = organic matter; CTC = cation exchange capacity; AlT = exchangeable aluminum; Al = percent aluminum saturation; AlH = hydrogen-ion and aluminum concentrations



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Capítulo 2

Plant life forms revisited: are classic systems really applicable in all ecosystems?

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Plant life forms revisited: are classic systems really applicable in all ecosystems?

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Abstract

Plant life forms are coarse classifications of taxonomic entities used to describe biological patterns and processes. Such classifications are present in science since its early days, and are still used as descriptive tools in areas such as functional ecology and biogeography. Some classifications became widely accepted and applied worldwide. In this paper we present a review of plant life form classifications. We discuss the relevance and accuracy of using such all-encompassing classifications in any given ecosystem to answer varying ecological questions. We propose a multi-trait hierarchical classification of plant life forms for subtropical grasslands, using a case study from southern Brazil to compare its descriptive power with the widely used Raunkiaer and Ellenberg & Mueller-Dombois classifications. To perform such comparisons we used Mantel tests and Procrustes analyses in a multivariate matrix-based approach. Subtropical grassland species were mostly grouped into large heterogeneous categories in classic one-trait-based life form systems. These systems showed poor descriptive power of differences between areas with known differences in management, environmental factors and vegetation structure. Our classification was a better descriptor of species-based patterns in comparison with the existing ones. Our results indicated that the descriptive power of a life form classification lies in the criteria used to group species rather than in the number of categories alone. We pointed out that using a life form classification consistently within an ecological unit may reflect in future benefits, such as facilitating and improving the accuracy of meta-analyses and allowing the development of unified databases. This might be particularly important considering transnational biomes such as the subtropical and temperate South American grasslands. Although our classification was conceived in and for subtropical grasslands, we suggest that researchers using life forms as descriptive traits in other ecosystems consider the relatedness between the principles underlying the classification and the ecological question being addressed, as well as the ecosystem in question.

Keywords: Raunkiaer system, campos grasslands, growth forms, traits

Introduction

Scientists have relied on coarse classifications of taxonomic entities to describe biological patterns and processes since the dawn of ecology as a science. Earth’s biodiversity is simply too complex to be described using the specific level (Díaz and Cabido 1997; Walker 1992), and many ecological processes and patterns are better described by non-taxonomic units, although phylogenetic similarities between these units are also important (Westoby 2006). In plant ecology, classifications of life forms were extensively used from the descriptive works of the early nineteenth century until today in functional approaches. Many classification systems were proposed during all that time, although some became more accepted and widely used than others. Also, the applicability of life form classifications conceived for universal use was criticized in some ecosystems. In this paper we present a historical review of the use of plant life form classifications. We question the use of widely accepted classifications indiscriminately in any ecosystem, sometimes ignoring the relatedness between the principles underlying the classification and the ecological question being addressed. We also propose a classification of plant life forms for subtropical grasslands, and use a case study from southern Brazilian grasslands to compare it with two widely used classifications.

Brief history of plant life form classifications

During the past century, the name of the Danish botanist Christen Raunkiaer became nearly a metonym for plant life forms. However, grouping plant taxa into coarse and often taxonomy-independent classifications has been done for many years before his widely used classification (Raunkiaer 1934). The first known classification of life forms dates back to ca. 300 BC, to Theophrastus’ ‘Enquiry into plants’, in which the Greek philosopher defined four plant ‘classes’ that scientists have been using ever since: tree, shrub, under-shrub and herb (Hort 1916). Although science has moved from that exclusively descriptive approach, we still strive to find meaningful working units in plant ecology, and often go back to Theophrastus' four classes or minute variations of them.

The scientific literature of the nineteenth century teems with examples of plant classification systems, most of which comprising life forms based on physiognomic aspects. This focus on physiognomy arose from the need to define primary units for the description of plant communities (Du Rietz 1931). The system proposed by Humboldt (1806) was widely used by European botanists during the first half of that century. The alternative system of De Candolle (1818) was based on life span, and also included morphological features on its bases, thus being the only system not exclusively based on physiognomy at the time. Humboldt's system was subsequently extended by Grisebach (1872), resulting in 54 'physiognomic types'. By that time, the evolutionist paradigm (Darwin 1859) was already an influence, and plant classification systems slowed shifted their focus from physiognomy to characters reflecting biological importance (e.g., Kerner 1869). In fact, in his review of plant life forms, Du Reitz pointed out that 'it was probably only due to the personal influence of the strongly antievolutionist old Grisebach, that purely physiognomic systems of vegetation-forms remained predominating more than two decades after the publication of The Origin of Species' (Du Rietz 1931, p. 4).

The period of the late nineteenth and early twentieth century was marked by the transition between physiognomic and biological plant classification systems. Reiter (1885) was a pioneer by proposing a revision of the classic physiognomic systems under an evolutionary view. However, most of the systems conceived during this period were based on the Lamarckian concept of epharmony, in which the environment would directly induce transformations in individuals (Vesque 1882). Near the turn of the century, Warming (1895) published his first attempt of classification of plants into biological groups, mostly based on the work of De Candolle (1818), but including many additional morphological features and for the first time using the term 'life-form'. Warming progressively refined his system in the following years, and synthetized his views in his book

‘Oecology of Plants’ (Warming and Vahl 1909). In that book, Warming introduced the English term ‘growth-form’, although the corresponding terms in Danish and German from his previous works were ‘livsform’ and ‘Lebensform’ respectively. As Du Rietz (1931) argued later, he did so ‘without giving any reason for not using the term life-form in English’. Until today, life form and growth form are sometimes treated as synonyms. Oscar Drude, a severe critic of Humboldt’s and Grisebach’s systems, also proposed a ‘biological system’ (Drude 1896), upgraded in further publications and relatively influential at the time , being the foundation for some similar systems that followed. In the same year, Areschoug (1896) used for the first time the term ‘geophyte’ for plants with belowground renewal buds.

The first accounts of Raunkiaer’s life-form system are from publications in Danish and French between 1904 and 1907 (Raunkiaer 1904; 1905; 1907). In the following decades, the system underwent several changes (such as the increased number of species used in the calculation of the ‘normal spectra’) until the publication of ‘The life forms of plants and statistical plant geography’ (Raunkiaer 1934). Although Raunkiaer’s system became widely accepted and repeatedly used afterwards, not all his contemporary fellow scientists agreed with his views, and many kept on updating their systems or developing new ones (e.g., Sylvén 1906). Warming was probably one of his most prominent critics, but by far not the only one (see a review in Du Rietz 1931). One of the most common criticisms (or contributions) to Raunkiaer’s system was directed towards the establishment of consistent differences between Hemicryptophytes and Chamaephytes, as well as the wide diversity of life forms that both classes actually encompassed (e.g., Skottsberg 1929; Skottsberg 1913).

In 1920, the North American botanist Frederic Edward Clements published a new system, restoring the term ‘vegetation-form’ in place of life form (Clements 1920). For Clements, the dominant species played the central role in ecological processes, and thus their life forms were the ones that mattered. Following Clements’ work, in 1921 the Swedish biologist Gustaf Einar Du Rietz published his system, shifting back to an almost purely physiognomic-based classification (Du

Rietz 1921). Du Rietz was the first to establish a distinction between life and growth forms: the first was determined by physiognomy alone, whereas the latter encompassed subdivisions based on shoot architecture. Kerner's system was probably the first one purely based on morphology, and theoretically independent from taxonomy (Kerner 1929). In 1928 Josias Braun-Blanquet presented a classification based on Raunkiaer's, but including radically changed subdivisions of the original ten main categories (Braun-Blanquet 1928). Ellenberg and Mueller Dombois (1967) presented a refinement of Raunkiaer's system using finer categories (later re-edited in Ellenberg and Mueller Dombois 1974). It is important to note that, as Adamson (1939) pointed out, most of these classifications of life forms are solely based on the aerial parts of the plants, completely ignoring belowground differences.

After this period of copious production of plant classification systems, scientists moved towards progressively more complex questions, often involving relationships between multiple taxonomic levels and ecological processes. However, to answer many of these new questions, classifications of plant taxa into simple non-taxonomic entities, such as life forms, were (and still are) used. The most obvious example lies in functional ecology, which largely relies on recurrent relationships between species traits such as life form and ecosystem function (e.g., Díaz and Cabido 1997; McIntyre et al. 1995). Although it is known that some 'core traits' are better descriptors of ecological processes and environmental filters (Weiher et al. 1999; Westoby 1998), easy-to-measure traits such as life forms may also be useful, especially considering processes related to vegetation structure. Since Raunkiaer's system was simple, widely accepted and used for a good many years, it was the classification of choice for many researchers around the world until today. But would it be wise to keep using a classification system based solely on plant tolerance to a generalized unfavorable season in all ecosystems, to answer a vast array of ecological questions?

Life forms based on single or multiple traits?

We showed above that the first distinction between life and growth forms may have arisen from a language-related issue in Warming and Vahl (1909), as first noted by Du Rietz (1931). After that, Du Rietz (1921) used the term growth form to describe morphology-based subdivisions of his physiognomy-based life forms. Whittaker (1975) pointed out that life form (in Raunkiaer's system) considers only one characteristic (height of the perennating tissue in relation to ground level), whereas growth form reflects a mixture of characteristics. Accordingly, recent protocols that aim to standardize measurement of plant functional traits present growth and life forms as separate traits (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Be that as it may, we should keep in mind that this distinction between life and growth forms considers 'life form' as in Raunkiaer's one-character system. However, as we have discussed above, there are many other life form systems, most of which used multiple characters. Warming and Vahl (1909), for example, defined life/growth forms as the sum of adaptive characters in a species expressing the relationship between a plant and its environment. Although this definition may sound slightly outdated, it implies the multi-character approach used in many modern functional studies, in which sets of traits are used to group species into functional types to assess ecological processes in multiple organization levels. In this view, life forms may be based on a set of traits, which may include plant features usually related to 'growth forms', such as canopy structure. Therefore, from this point on we will use the term life form consistently, and will no longer use the term 'growth form', to avoid further confusion.

Plant life forms as predictors of ecological processes

'Structure without function is a corpse; function without structure is a ghost.'

(Vogel and Ewel 1972)

Under a functional perspective, plant life forms can be considered as functional groups based on a single character (in Raunkiaer's system; Solbrig 1993) or on multiple characters. Ewel and Bigelow (1996) postulated that, at least in tropical ecosystems, it is the diversity of life forms, and not species, that exerts major control over ecosystem functioning. For these statements to be true, life forms must to some degree reflect the ecological processes in question. Therefore, by using Raunkier's life forms, we assume that the relative position of growing buds is a functionally important character, and that his ten classes accurately represent the ecosystem being studied. Although this has been shown to hold true in many studies around the world (regions with a more or less clearly defined unfavorable season), not all researchers that used Raunkiaer's life forms did so without questioning. Already in the early 1900's, Skottsberg (1913) pointed out that plants from the Falklands classified as Hemicryptophytes actually behaved like Chamaephytes and, moreover, that they were in fact evergreen plants. More recently, Pillar and Orlóci (1993) were also skeptical regarding the use of assumedly universal classifications in any ecological context.

The applicability of Raunkiaer's system in tropical and subtropical ecosystems has been questioned mostly for two reasons: (i) it groups species in very few and apparently too broad, uninformative categories (e.g., Ewel and Bigelow 1996) and (ii) an unfavorable season is hardly a limiting factor in most tropical and subtropical realities, and Raunkiaer's whole system is based on plant resilience to this factor (Sarmiento and Monasterio 1983). In his studies on New Zealand vegetation, Allan (1937) found out that Raunkiaer's life form spectra did not actually reflect climatic conditions. He concluded that the delimitations of Hemicryptophytes and Chamaephytes were inadequate for austral floras, and that historical factors (i.e., the evolutionary history of the studied ecosystem) should be taken into account when classifying plants into life forms. Adamson (1939) pointed out that most classic plant life form classifications were based on floras from the North Temperate Zone, with limited or no confirmatory evidence from Southern Europe, let alone from the Tropics or Southern Hemisphere subtropical and temperate ecosystems. Considering grassland ecosystems, Willems (1985) argued that alternatives to Raunkiaer's system should be used, since most species from grasslands (in the Netherlands) would be classified as Hemicryptophytes, including obviously different life forms such as grasses and forbs in the same class, thus obscuring shifts in community dynamics unraveled by his simpler classification.

Considering grassland ecosystems, there are many examples of case-specific life form classifications that proved to be useful. Arnold (1955) presented a very simple classification based on life span and height to evaluate rangeland condition. He found that range productivity was dependent on the prevalent life forms according to his classification, which proved to be informative also in the evaluation of ecological dominance and susceptibility to grazing. Willems (1985) distinguished grassland plants in graminoids, forbs, rosettes and woody species, with some sub-categories and ten final life forms. Using this classification to compare different management regimes, he was able to establish relationships between biomass production and dominance, vegetation structure and diversity. In African Savannas, Cramer et al. (2012) discussed the role of underground competition in the coexistence of trees and grasses using the simplest life form classification possible in their case: trees and grasses.

Further examples of case-specific classifications and criticism on classic classifications of plant life forms are plentiful. However, our point here is that any classification of plants into a system of life forms should be based on two principal aspects: (i) the evolutionary history of the studied ecosystem and historical disturbance regimes it was submitted to, and (ii) the ecological question the classification is being used to answer. Classic and all-encompassing systems such as that of Raunkiaer may be useful to answer questions on a coarse scale, such as establishing broad differences between floras of different regions. However, when searching for more specific ecological processes that show little relatio to the theory underlying the classic life form system proposed by Raunkiaer, they should be adapted, or independent classifications should be used according to each case (as suggested by Allan 1937). In fact, examples of the use of case-specific life form classifications from various ecosystems and involving various questions are abundant in the recent literature (Aronson et al. 2007; Bhattarai and Vetaas 2003; Campanella and Bertiller 2008; Castanho et al. 2012; Collins and Calabrese 2012; Diaz et al. 2007; Gómez-Aparicio 2009; Hadar et al. 1999; Huang et al. 2009; Ivanova 2012; Lezama et al. 2013; López et al. 2013; Moustakas et al. 2013; Nelis 2012; Pekin et al. 2012; Skaer et al. 2012; Tsujino and Yumoto 2013).

Life forms in subtropical and temperate grasslands

In Southern South America, grasslands extend over ca. 750,000 km^2 in Argentina, Uruguay and Southern Brazil (Bilenca and Miñarro 2004; Soriano et al. 1992). These ecosystems evolved under different levels of grazing (Milchunas et al. 1988) and fire (Behling et al. 2005; Behling et al. 2004). They have been used as a natural forage source for cattle breeding since the seventeenth century (Pillar and Quadros 1997), and fire is still used as a management tool in some regions (Jacques 2003). Therefore, a classification of life forms that is ecologically meaningful for these ecosystems should take into account this historical disturbance regime. Life form categories should be based on characters potentially related to plant adaptations to fire and herbivory.

Previous studies carried out in South American grasslands have used different life form classifications. Some of them used adaptations based on Raunkiaer’s systems (e.g., Garcia et al. 2002; Overbeck and Pfadenhauer 2007). Other studies used case-specific classifications (e.g., Altesor et al. 2006; Lezama et al. 2006; Overbeck et al. 2006; Overbeck et al. 2005). In grasslands in the region, perennial species are predominant over annual species, and this ratio gradually changes towards higher latitudes and temperate climate (Burkart 1975). Raunkiaer's system is capable of detecting this change: the contribution of therophytes (frequency, cover and/or number of species) would increase with latitude.

However, the problem of using Raunkiaer’s system (or any posterior adaptation based on it) in these ecosystems is establishing the distinction between chamaephytes and hemicryptophytes. Hemicryptophytes are defined as plants with ‘periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface' (Ellenberg and Mueller-Dombois 1974; Ellenberg and Mueller Dombois 1967; Raunkiaer 1934). This definition is still used and reproduced in many works worldwide, including widely accepted protocols for measurement of plant traits (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Most plants from subtropical grasslands show no such behavior, and would actually be more accurately classified as chamaephytes. This problem was identified long ago for plants from the Falklands (Skottsberg 1913). In fact, by using Raunkiaer's original system, most of the non-therophytic grassland species from the subtropics would fall into chamaephytes, thus creating a large and heterogeneous group. Such an all-encompassing category is prone to show low descriptive power and to dim ecological patterns and processes.

In the following sections we propose a new classification of plant life forms for subtropical grasslands, based on plant characteristics related to herbivory and fire. We test the robustness and descriptive power of the new classification by comparing six grassland sites from Southern Brazil with different management history and vegetation structure. Also, we compare this new classification with the original system of Raunkiaer (1934) and the extended system proposed by Ellenberg and Mueller Dombois (1967).

Material and Methods

We used data from a grassland vegetation survey carried out in 18 paddocks at six sampling sites in Southern Brazil, three inserted in the Pampa Biome and three in the Atlantic Forest Biome. Details on surveyed sites, sampling methods and results are described in Ferreira et al. (unpublished [Capítulo 1]). Areas within each biome have been submitted to different management regimes in the past decades (grazing and sporadic mowing in the Pampa and grazing and yearly fire in the Atlantic Forest). Vegetation structure and community parameters differ between sites, mostly due to management, soil features and environmental variables Ferreira et al. (unpublished [Capítulo 1]). It is desirable that a classification of plant life forms also reflects these differences, since they are the product of the ecosystem’s evolutionary history. Plant species from the survey with relative cover value per site higher than five percent were classified in life forms according to Raunkiaer’s original system (Raunkiaer 1934, henceforth mentioned as 'Raunkiaer's system'), the extended system proposed by Ellenberg and Mueller Dombois (1967, henceforth mentioned as 'Ellenberg's classification') and the new classification we propose in this paper. We used specific taxonomic literature to classify each taxon. Species names were checked using The Taxonomic Name Resolution Service (Boyle et al. 2013).

Since most plant species from subtropical grasslands do not present the ‘periodic shoot reduction’ described for hemicryptophytes (i.e., they are evergreen plants), we considered that they were actually chamaephytes in Raunkiaer’s system. We are aware that many previous studies that used Raunkiaer’s system in similar ecosystems considered many species as hemicryptophytes. Tussock-forming grasses, for example, are commonly considered hemicryptophytes because their gems are slightly above the soil level, and often protected by the base of the tussock structure. However, similar species from subtropical grasslands do not present a key feature needed to be classified as hemicryptophytes: periodic shoot reduction, which implies they are evergreens. As shown in the previous section, this distinction has already been pointed out by Skottsberg (1913) for Argentinian temperate grasslands: most species actually behave like evergreen chamaephytes rather than hemicryptophytes sensu Raunkiaer. Although there may be arguments supporting subtropical and temperate species as hemicryptophytes, we will not delve further into this discussion in this paper, and will consider species that do not show periodic shoot reduction as chamaephytes. In fact, the distinction between categories does not affect our results and interpretations: we used Raunkiaer’s classification for the sake of comparison with other systems (see below), and all species that we classified as chamaephytes would remain under the same category regardless of the name we use to present it.

To assess the predictive power of our classification and compare it with the classic ones, we used a multivariate approach. First, we performed an ordination analysis (Principal Coordinate

Analysis) of a matrix containing the sampling areas described by species cover. We did the same analysis using averaged cover values of life form categories as descriptors of sampling areas, generating one ordination (sampling areas and life forms) per classification system. Based on the original species-based matrix and the different life form classification systems, we generated four matrices containing sampling units described by species and weighted by plant life forms. Since the number of categories may affect the predictive power and resolution of classifications, we tested two levels of our classification (five and 12 categories) to build two different life-form-weighted matrices. We did the same using randomly generated life forms with the same number of categories of all classifications. Methods to build trait-weighted matrices involve a series of matrix multiplications described by Pillar et al. (2009) and Pillar and Duarte (2010). We used Mantel tests and procrustes analyses (Peres-Neto and Jackson 2001) to evaluate the congruence between variations in the generated life-form-weighted matrices and the original matrix of sampling areas described by species cover. We performed all ordination analyses using chord distance as dissimilarity measure between sampling units. We assessed differences of life forms between areas from different biomes using randomization tests with 10,000 permutations (Pillar and Orlóci 1996). All analyses were carried out using softwares Multiv (Pillar 1997) and on the R platform (R Development Core Team 2012) with package ‘vegan’ (Oksanen et al. 2013).

Results

A classification of plant life forms for subtropical grasslands

We propose a hierarchical life form classification comprising four levels of progressively refined categories (Figure 1, Table 1). The classic categories ‘therophytes’ and ‘geophytes’ are maintained. However, Raunkiaer’s original chamaephytes are treated as ‘evergreens’, and then progressively sorted into finer categories based on level of lignification, plant architecture, habit and strategy of horizontal propagation (Table 1). In Electronic Supplementary Material 1 (ESM 1) we provide a data matrix containing the life form categories for the 193 grassland plant species we used in our analyses.

Comparison between classifications

Randomization tests showed significant differences ($P<0.05$) between areas from the different biomes using our classification and Ellenberg’s, but not when using Raunkiaer system. Therophytes, classified in the same way in all systems, showed significant higher cover values in areas from the Pampa biome ($P<0.01$). Considering the classes from Ellenberg’s classification, cover of herbaceous chamaephytes was significantly higher in Atlantic Forest areas ($P<0.05$). Among the categories from our classification, we found significant differences between areas from different biomes for solitary and connected tussocks, rhizomatous plants and stoloniferous plants ($P<0.01$). The most prominent overall differences between biomes were seen in tussocks and rhizomatous plants (Figure 2A).

Ordinations of matrices containing averaged cover values of life form categories resulted in different patterns according to each classification (Figure 3). Therophytes were highly associated with the second axis in all ordinations, segregating paddocks from site P1 from the others in varying levels of clarity. Patterns of biome separation and within-site aggregation were more clearly depicted by our classification (Figure 3A, B) in comparison with the other two systems. Using our classification, sites between biomes were separated along axis 1. Atlantic Forest sites were more associated with erect life forms, whereas Pampa sites P3 and P2 were more associated with prostrate and ligneous life forms. This pattern was mostly lost when using the other two classifications (Figure 3C, D).

Mantel tests and procrustes analyses revealed that matrices weighted by life form categories from our classification (levels C and D) are more correlated to the species-cover matrix in comparison with matrices weighted by Ellenberg's and Raunkiaer's classifications (Table 2 and Figure 4). Matrices weighted by randomly generated life forms showed low and nonsignificant correlation with species-described matrices.

Discussion

We have presented a new proposal of classification of plant life forms to be used in subtropical and temperate grasslands. We have structured the classification in progressively refined categories, so that it can be applicable at different levels of organization and scales (considering both grain and extent). Also, we tested the descriptive power of our classification and compared it with classic and broadly used classifications.

The second step in the system we proposed, in which we segregate 'Geophytes' from 'Evergreens' (Figure 1), deserves a brief discussion. The evergreens encompass the chamaephytes from Raunkiaer's classification (Table 1). Accordingly, in our view they are plants that do not have their aerial parts reduced during part of the year due to climatic limitations - such limitations are not common in subtropical grasslands. The geophytes, on the other hand, present this behavior, and are naturally reduced to underground organs during part of the year, from which they resprout in the next year. Although this adaptation may seem rather superfluous considering the present prevalent climatic conditions in the subtropics and temperate zones, they may derive from past conditions. During the late Pleistocene, grasslands were the dominant ecosystem in southern South America, under a colder and dryer climate and submitted to grazing and burning events (Behling et al. 2005; Behling et al. 2004; Bredenkamp et al. 2002; Milchunas et al. 1988). Therefore, this evolutionary history may be partly responsible for the presence of geophytes in these ecosystems, and may lead to a potential problem in segregating geophytes from evergreens: does the reduction in the aerial structure occurs without external interference or is dependent on disturbance (grazing and/or fire)? We considered that 'true geophytes' show the first behavior, i.e., reduction of above-ground shoots is an inherent characteristic of their life cycle, whereas the second corresponds to evergreen plants with underground storage organs that may allow post-disturbance resprouting (e.g., rhizomatous evergreens). These evergreen resprouters may contribute to the resilience of these ecosystems to historical disturbances (Fidelis et al. 2014; Fidelis et al. 2010). Although both life forms show obviously similar adaptations to fire/grazing, geophytes are reduced to their underground organs independently from disturbance events, possibly due to shared evolutionary history. Evergreens with storage organs are more likely to respond to disturbance gradients (e.g., Overbeck and Pfadenhauer 2007 and our results). Finally, we must consider that under extreme circumstances, such as a unusally dry season or after a severe frost, both geophytes and evergreens are likely to have their aboveground structures reduced.

Our classification (at levels C and D; Table 1 and Figure 1) was a better descriptor of the original species-based patterns in comparison with other classifications (Table 2, Figures 2, 3 and 4). At the level C, our classification comprises five categories, the same number of Ellenberg's classification. Even so, the first showed better descriptive power than the latter (and also than Raunkiaer's system with four categories). Also, randomly generated life forms with the same number of categories showed very limited descriptive power. This indicates that the descriptive power lies in the criteria used to group species into life forms rather than in the number of categories alone. Although this seems obvious, classic life form classifications have often been used without considering their underlying classification criteria, which consequently may have led to limitations regarding results and interpretations. For example, although differences in life forms between grassland sites with different grazing levels have been repeatedly found using case-specific classifications (e.g., Altesor et al. 2006; Diaz et al. 2007; Lezama et al. 2013), some authors have found no such differences using Raunkiaer's system (e.g., Vashistha et al. 2011). Our results indicate that such differences could be captured by the life form categories we have proposed, whereas coarse classifications such as that of Raunkiaer are not suited to answer specific ecological questions such as the effect of different land management. Therefore, when the goal of a given study is to sample general patterns, and not richness or diversity, these life form categories could even be used in the sampling process in place of species. Considering that only within Brazilian territory subtropical grasslands encompass more than 2,200 species (Boldrini 2009), this would speed up sampling and allow larger areas to be covered, ultimately improving the still poorly known general structural patterns of these ecosystems. However, sampling at such a coarse level and not considering species' identities would imply severe limitations, especially considering analytical possibilities, including the possibility to refine or adapt the life form classification at a later point in time.

In subtropical grasslands, Raunkiaer's chamaephytes actually encompass very different types of plants (Table 1), and using this system thus resulted in almost complete lack of differences between biomes (Figure 2B), less informative ordination patterns (Figure 3C) and the lowest congruence with species-based patterns (Figure 4). Previous works had already pointed out the 'chamaephyte problem', arguing that this category may actually encompass several life forms, depending on the ecological system in question (e.g., Adamson 1927; Allan 1937; Ewel and Bigelow 1996; Skottsberg 1929; Skottsberg 1913). The subdivisions of chamaephytes presented in Ellenberg's classification also encompass different life forms considering our classification (Table 1). Furthermore, they do not seem to enhance the system's refinement (at least considering the case-study we presented here), since they showed correlation values (Mantel and procrustes analyses) lower than those obtained with Raunkiaer's system (Table 2). However, we do not intend to suggest that these classic classifications should be abandoned. They have repeatedly proved to be applicable and informative, and the decision to use them should be dependent on the ecological system and specific questions. For example, Batalha and Martins (2002) suggested that Raunkiaer's system is not only applicable but also recommended considering the Brazilian Cerrado (tropical grasslands, or Savannas), on the basis that local factors (fire, waterlogging, oligotrophism, extreme dry season and aluminum toxicity) would be analogous to the unfavorable season his system was based upon.

Besides showing overall clearer vegetation patterns at a coarse level, our classification may be used to more accurately describe between-site differences in vegetation, and to link these differences to management history and local factors. Therophytes were strongly associated with the most austral site (P1; Figure 3A, B), corroborating the hypothesized increase in importance of the annual component in grassland vegetation towards higher latitudes. Differences between sites regarding tussocks (solitary and connected), subshrubs and rhizomatous plants were clearly shown by the averaged values of life form cover per biome (Figure 2A), and were largely responsible for site segregation in the ordination analysis (Figure 3A). These differences are to a large extent the reflection of land management. Atlantic Forest grasslands (sites A1, A2 and A3 in Figures 3 and 4) are historically submitted to low stocking rates and yearly burning (Maraschin 2001; Nabinger et al. 2009), which favors tussock C4 species (Jacques 2003) and may hamper the establishment of subshrubs and shrubs (Müller et al. 2007). Pampa sites, on the other hand, are managed with moderate to high grazing pressures, which favors prostrate growth forms (Altesor et al. 2005; Guerschman and Paruelo 2005).

The classification of life forms we presented and discussed here was conceived in and for subtropical grasslands and perhaps to some degree to temperate grasslands. Its usefulness towards higher temperate latitudes may be limited, since life forms we did not consider such as deciduous shrubs may increase in importance (e.g., Campanella and Bertiller 2008). Also, it is likely that 'true hemicryptophytes' (i.e., species that actually show partial or complete shoot reduction during part of the year) should be found towards the tropics (tropical grasslands, or Savannas), in altitude grasslands and in higher latitudes. Nevertheless, additional categories may be included in our classification in such situations, just as categories that are too refined to a given situation may be concatenated into a broader one (e.g., connected and isolated tussocks). Subtropical grasslands in South America present a unique floristic composition, with coexistence of winter and summer species, as well as some species also present in tropical and temperate areas (Boldrini 2009; Cabrera and Willink 1980). Such species may present a variation in life form along their distribution, behaving like evergreens in our case-study and like 'true hemicriptophytes' towards higher or lower latitudes. This plasticity deserves further attention in future works.

We did not intend to create an all-encompassing classification applicable to different ecosystems around the world, but our results have implications for researchers using plant life form classifications elsewhere. Any life-form system applied needs to be appropriate to the ecological system under study and must allow answering the questions asked. In our case, both Raunkiaer's and Ellenberg's system proved not to distinguish different plant strategies in a way that reflected the ecological properties and processes of the grassland system under study. Our suggestion of life form classification proved to be a more accurate descriptor of subtropical grasslands and allowed to perceive differences in functional plant composition between two subsets of our data that corresponded to grasslands under somewhat different climate and under different management. Generalizing these findings, we suggest that before using any existing classification, the relevance of the underlying criteria to the ecosystem under study should be critically reflected, in order to get meaningful answers. This seems to be important for other ecosystems worldwide, especially those with extremely different evolutionary histories in comparison with the ecosystems in which classic life form classifications were based on. Using easily obtained traits such as case-specific life form sytems such as the one we propose here may be a promising starting point in initiatives to compare communities in a regional scale, especially considering that a consistent trait database is still lacking for these ecological systems.

While case-specific classifications can be successfully used to answer various ecological questions in different ecosystems, they have one drawback: comparisons around the world may not be possible. Here, working on a coarser scale and reflecting basically climatic differences, the classical systems likely remain more useful. Nevertheless, we think that using a life form classification consistently within 'natural' ecological units may reflect in future benefits, such as facilitating and improving the accuracy of meta-analyses and allowing the development of unified databases. This might be particularly important considering transnational biomes such as the subtropical and temperate South American grasslands.

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Tables

Table 1. Hierarchical classification of plant life forms for subtropical and temperate grasslands, with four levels of progressively refined categories and the respective acronym (A-D). R and E: equivalent categories from Raunkiaer (1934) and Ellenberg and Mueller Dombois (1967) classifications. Th = therophytes, G = geophytes, Ch = chamaephytes, Ph = phanerophytes, Gb = bulbous geophytes, Gr = rhizomatous geophytes, HCh = herbaceous chamaephytes, RCh = reptant herbaceous chamaephytes, SCh = sufrutescent chamaephytes, FCh = frutescent chamaephytes.

A	**B**	**C**	**D**		**R**	**E**
Therophytes	Therophytes	Therophytes	Therophytes	Th	Th	Th
Geophytes	Geophytes	Geophytes	Bulbous geophytes	Bg	G	Gb
			Rhizomatous geophytes	Rg	G	Gr
Evergreens	Herbaceous	Prostrate	Prostate rosette evergreens	Pr	Ch	HCh
			Decumbent evergreens	De	Ch	RCh
			Rhizomatous evergreens	Rh	Ch	HCh
			Stoloniferous evergreens	St	Ch	HCh
		Erect	Solitary evergreen tussocks	Te	Ch	HCh
			Connected evergreen tussocks	Ct	Ch	HCh
			Evergreen forbs	Ef	Ch	HCh
			Erect rosette evergreens	Er	Ch	HCh
	Ligneous	Ligneous	Evergreen subshrubs	Ss	Ch	SCh
			Evergreen shrubs	Sh	Ph	FCh

Table 2. Results from Mantel tests and Procrustes analyses evaluating the congruence between life-form-weighted matrices and the original matrix of sampling areas described by species cover. SQ = Sum of squares.

	Mantel test		Procrustes analysis		
	r statistic	p-value	SQ	correlation	p-value
New classification (D)	0.7594	0.0001	0.3123	0.8293	0.0001
New classification (C)	0.4868	0.0002	0.4706	0.7276	0.0001
Ellenberg & Muller-Dombois	0.2349	0.0078	0.7223	0.5270	0.0125
Raunkiaer	0.2605	0.0086	0.6992	0.5485	0.0044

Figures

Figure 1. Hierarchical classification of plant life forms for subtropical and temperate grasslands, with four levels of progressively refined categories (A-D) and examples for each category (level D) based on species from south Brazilian grasslands.

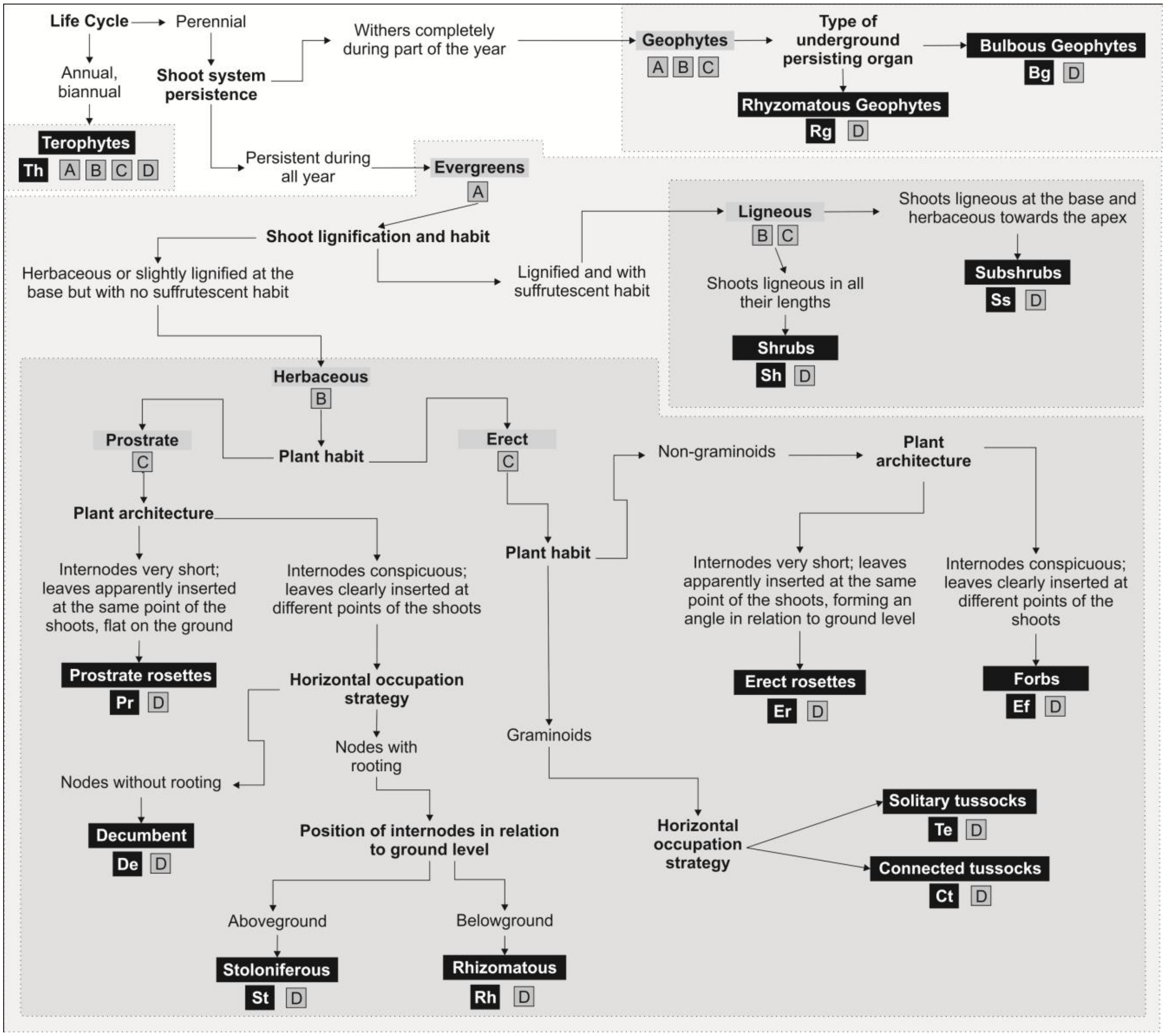


Figure 2. Cover values of life form categories from six grassland sites, averaged to biome level. Life form classes according to the new classification (A), Raunkiaer (B) and Ellenberg & Mueller Dombois (C). Th = therophytes, G = geophytes, Ch = chamaephytes, Ph = phanerophytes, Gb = bulbous geophytes, Gr = rhizomatous geophytes, HCh = herbaceous chamaephytes, RCh = reptant herbaceous chamaephytes, SCh = sufrutescent chamaephytes, FCh = frutescent chamaephytes. See legends for life form categories from the new classification in Table 1.

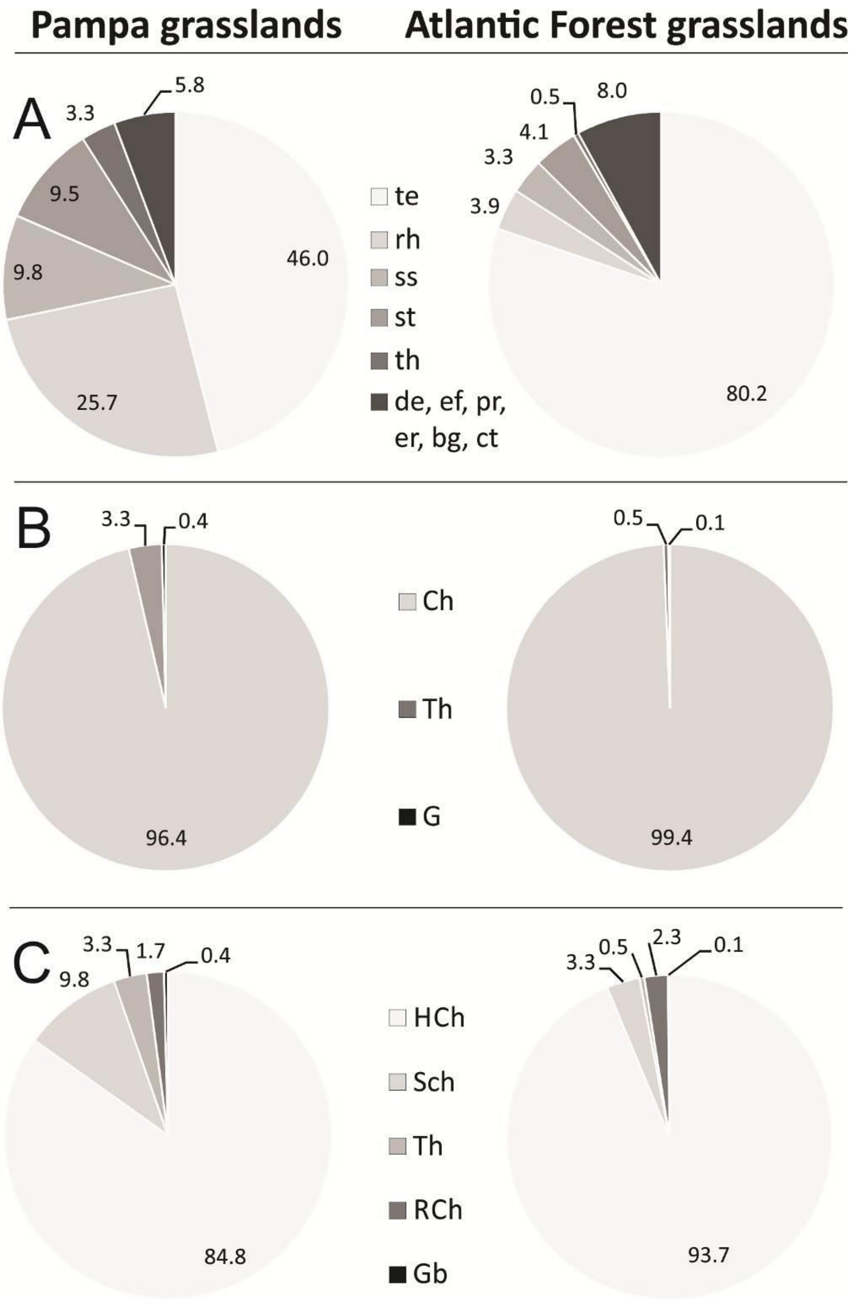


Figure 3. Ordination diagrams of averaged cover values of life form categories from different classification systems (A-D) as descriptors of sampling areas. Two levels of the proposed classification are shown ('D' and 'C'; see Table 1 for details). Legend: P = Pampa sites, A = Atlantic Forest sites, Th = therophytes, G = geophytes, Ch = chamaephytes, Ph = phanerophytes, Gb = bulbous geophytes, Gr = rhizomatous geophytes, HCh = herbaceous chamaephytes, RCh = reptant herbaceous chamaephytes, SCh = sufrutescent chamaephytes, FCh = frutescent chamaephytes. See legends for life form categories from the new classification in Table 1.

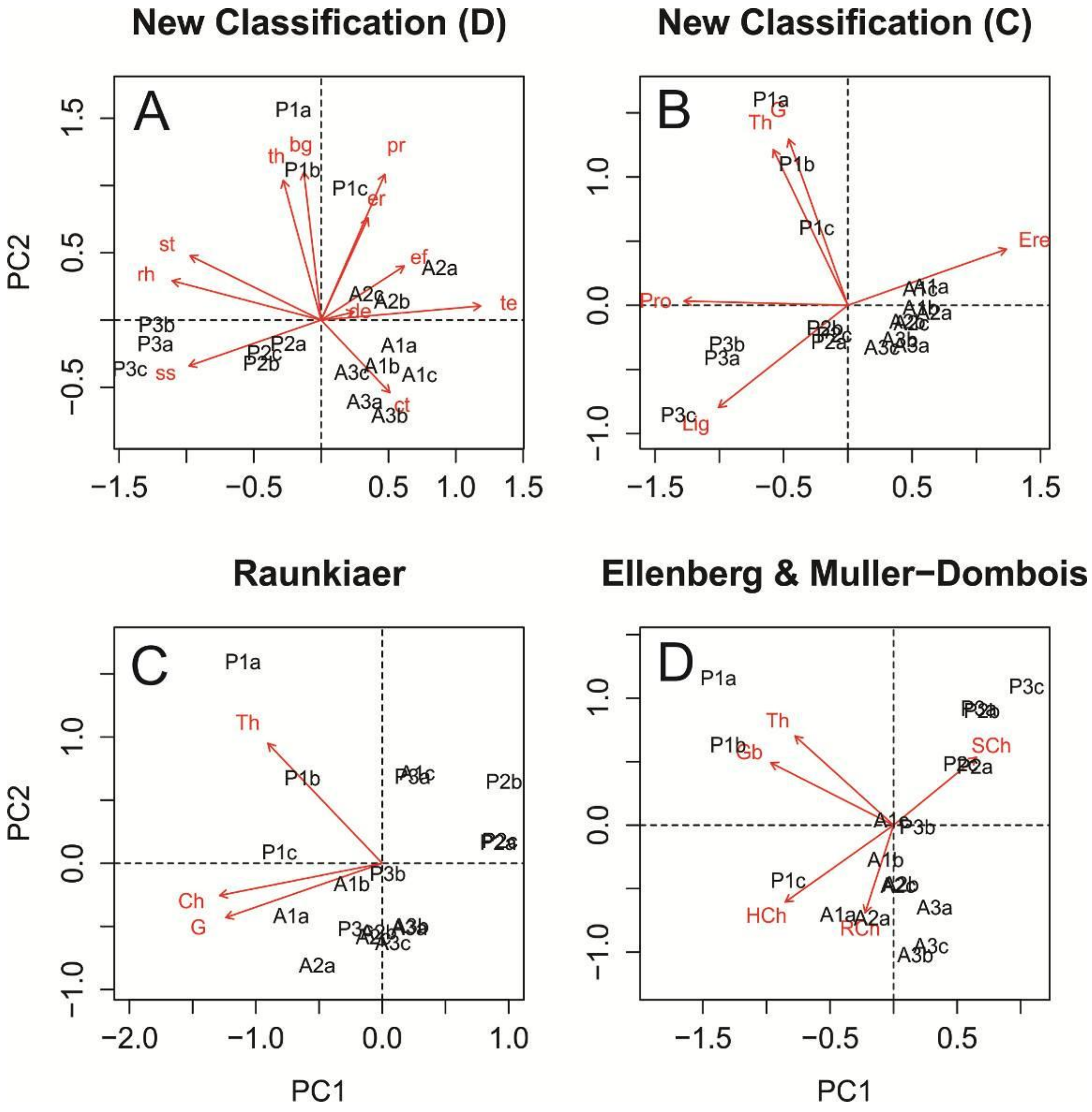
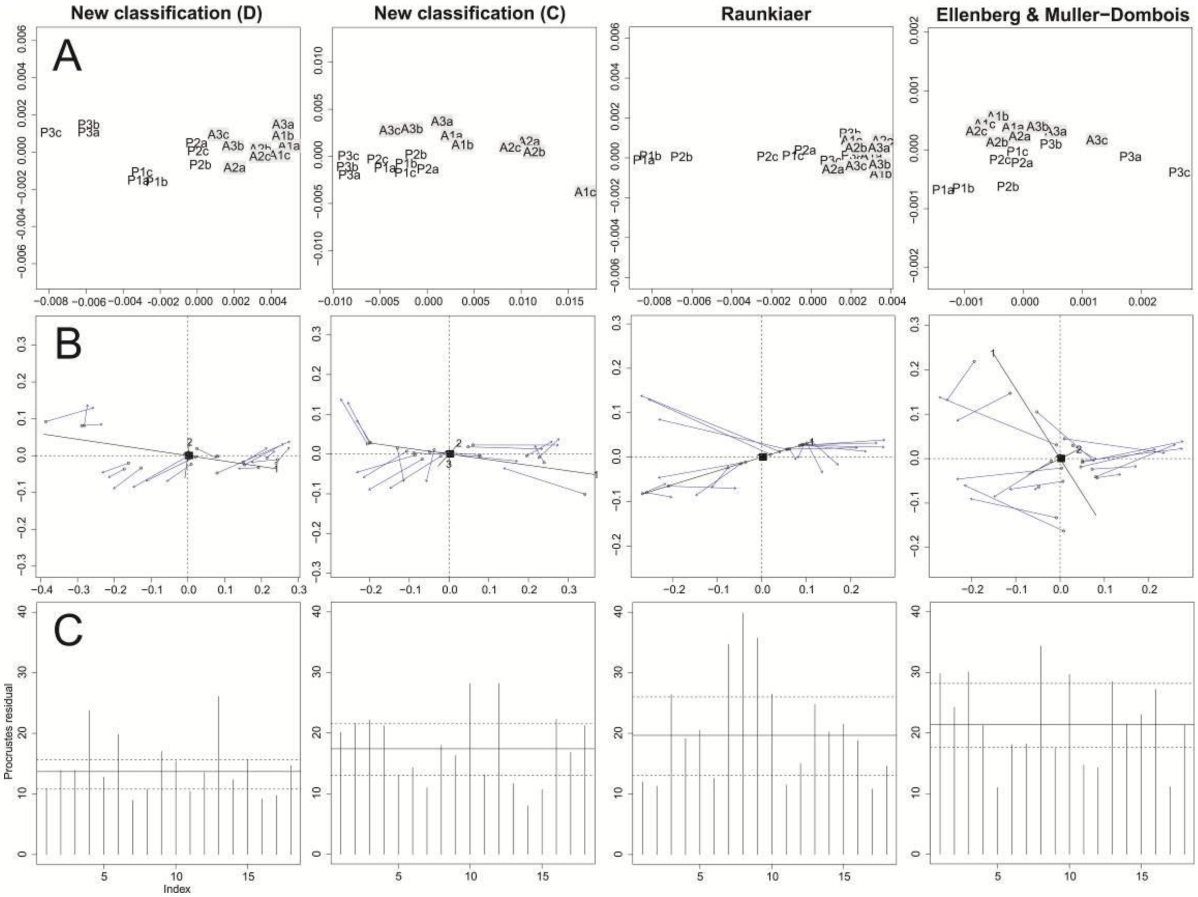


Figure 4. Procrustes analyses comparing ordinations of a species-described matrix of 18 grassland sampling paddocks with matrices weighted by life form categories from different classification systems. A. Ordinations of matrices weighted by life form categories. B. Procrustes rotation of ordination axes, with original and target locations of sampling units. C. Procrustes errors. P = sites from the Pampa biome; A = sites from the Atlantic Forest biome (also shaded in light gray).



electronic supplementary material

ESM 1 - Life form categories for the 193 grassland plant species used in the analyses. te = solitary evergreen tussocks; st = stolonoiferous evergreens; rh = rhizomatous evergreens; ss = evergreen subshrubs; de = decumbent evergreens; ef = evergreen forbs; ct = connected evergreen tussocks; pr = prostate rosette evergreens; er = erect rosette evergreens; th = therophytes; bg = bulbous geophytes; sh = evergreen shrubs

Family	Species	Author	Life form
Acanthaceae	*Stenandrium diphyllum*	Nees	pr
Amaranthaceae	*Pfaffia tuberosa*	Hicken	ef
Apiaceae	*Cyclospermum leptophyllum*	(Pers.) Sprague ex Britton & P. Wilson	th
Apiaceae	*Eryngium ebracteatum*	Lam.	pr
Apiaceae	*Eryngium echinatum*	Urb.	er
Apiaceae	*Eryngium horridum*	Malme	er
Apiaceae	*Eryngium nudicaule*	Lam.	pr
Araliaceae	*Hydrocotyle exigua*	Malme	st
Asteraceae	*Achyrocline satureioides*	(Lam.) DC.	ef
Asteraceae	*Acmella bellidioides*	(Smith in Rees) R.K. Jansen	ef
Asteraceae	*Aster squamatus*	(Spreng.) Hieron.	ss
Asteraceae	*Baccharis coridifolia*	DC.	ss
Asteraceae	*Baccharis dracunculifolia*	DC.	sh
Asteraceae	*Baccharis genistelloides*	(Lam.) Pers.	ss
Asteraceae	*Baccharis pentodonta*	Malme	ss
Asteraceae	*Baccharis riograndensis*	I.L. Teodoro & J.E. Vidal	ss
Asteraceae	*Baccharis subtropicalis*	G. Heiden	ss
Asteraceae	*Baccharis tridentata*	Vahl	ss
Asteraceae	*Calyptocarpus biaristatus*	(DC.) H. Rob.	th
Asteraceae	*Chaptalia exscapa*	(Pers.) Baker	pr
Asteraceae	*Chaptalia integerrima*	(Vell.) Burkart	pr
Asteraceae	*Chaptalia piloselloides*	(Vahl) Baker	pr
Asteraceae	*Chaptalia runcinata*	Kunth	pr
Asteraceae	*Chevreulia acuminata*	Less.	de
Asteraceae	*Chevreulia revoluta*	A.A. Schneid. & R. Trevis.	ef
Asteraceae	*Chevreulia sarmentosa*	(Pers.) S.F. Blake	st
Asteraceae	*Conyza bonariensis*	(L.) Cronquist	th
Asteraceae	*Elephantopus mollis*	Kunth	ef
Asteraceae	*Erigeron primulifolium*	(Lam.) Greuter	th
Asteraceae	*Eupatorium squarrulosum*	Hook. & Arn.	ef
Asteraceae	*Gamochaeta americana*	(Mill.) Wedd.	ef
Asteraceae	*Hypochaeris catharinensis*	Cabrera	pr
Asteraceae	*Lucilia linearifolia*	Baker	ef

Family	**Species**	**Author**	**Life form**
Asteraceae	*Noticastrum decumbens*	(Baker) Cuatrec.	de
Asteraceae	*Panphalea araucariophila*	Cabrera	th
Asteraceae	*Panphalea heterophylla*	Less.	th
Asteraceae	*Pterocaulon virgatum*	(L.) DC.	ef
Asteraceae	*Senecio heterotrichius*	DC.	ss
Asteraceae	*Senecio madagascariensis*	Poir.	th
Asteraceae	*Soliva sessilis*	Ruiz & Pav.	th
Asteraceae	*Trichocline catharinensis*	Cabrera	pr
Campanulaceae	*Wahlenbergia linarioides*	(Lam.) A. DC.	ef
Caryophyllaceae	*Cerastium glomeratum*	Thuill.	th
Caryophyllaceae	*Spergularia* sp.	-	th
Convolvulaceae	*Dichondra macrocalyx*	Meisn.	st
Convolvulaceae	*Dichondra sericea*	Sw.	st
Convolvulaceae	*Evolvulus sericeus*	Sw.	de
Cyperaceae	*Bulbostylis capillaris*	(L.) C.B. Clarke	te
Cyperaceae	*Bulbostylis juncoides*	(Vahl) Kük. ex Osten	te
Cyperaceae	*Bulbostylis* sp.	Kunth	te
Cyperaceae	*Bulbostylis sphaerocephala*	(Boeckeler) C.B. Clarke	te
Cyperaceae	*Carex bonariensis*	Desf. ex Poir.	te
Cyperaceae	*Carex phalaroides*	Kunth	ct
Cyperaceae	*Carex sororia*	Kunth	te
Cyperaceae	*Cyperaceae* sp.	-	te
Cyperaceae	*Cyperus aggregatus*	(Willd.) Endl.	te
Cyperaceae	*Cyperus hermaphroditus*	(Jacq.) Standl.	te
Cyperaceae	*Cyperus reflexus*	Vahl	te
Cyperaceae	*Eleocharis dunensis*	Kük.	ct
Cyperaceae	*Eleocharis nudipes*	(Kunth) H. Pfeiff.	te
Cyperaceae	*Eleocharis viridans*	Kük. ex Osten	ct
Cyperaceae	*Fimbristylis dichotoma*	(L.) Vahl	te
Cyperaceae	*Kyllinga odorata*	Vahl	te
Cyperaceae	*Kyllinga vaginata*	Lam.	ct
Cyperaceae	*Lipocarpha humboldtiana*	Nees	te
Cyperaceae	*Rhynchospora barrosiana*	Guagl.	te
Cyperaceae	*Rhynchospora emaciata*	(Nees) Boeckeler	ct
Cyperaceae	*Rhynchospora flexuosa*	C.B. Clarke	te
Cyperaceae	*Rhynchospora megapotamica*	(Spreng.) H. Pfeiff.	st
Cyperaceae	*Rhynchospora* sp.	-	te
Cyperaceae	*Rhynchospora tenuis*	Willd. ex Link	ct
Cyperaceae	*Scleria distans*	Poir.	ct
Euphorbiaceae	*Euphorbia selloi*	(Klotzsch & Garcke) Boiss.	de

Family	Species	Author	Life form
Fabaceae	*Aeschynomene falcata*	(Poir.) DC.	de
Fabaceae	*Crotalaria hilariana*	Benth.	ef
Fabaceae	*Desmanthus tatuhyensis*	Hoehne	ss
Fabaceae	*Desmanthus virgatus*	(L.) Willd.	ss
Fabaceae	*Desmodium incanum*	(Sw.) DC.	st
Fabaceae	*Galactia marginalis*	Benth.	ss
Fabaceae	*Galactia neesii*	DC.	ss
Fabaceae	*Macroptilium gibbosifolium*	(Ortega) A. Delgado	st
Fabaceae	*Macroptilium prostratum*	(Benth.) Urb.	de
Fabaceae	*Rhynchosia corylifolia*	Mart. ex Benth.	de
Fabaceae	*Stylosanthes montevidensis*	Vogel	ef
Fabaceae	*Trifolium polymorphum*	Poir.	st
Fabaceae	*Trifolium riograndense*	Burkart	st
Hypoxidaceae	*Hypoxis decumbens*	L.	bg
Iridaceae	*Herbertia lahue*	(Molina) Goldblatt	bg
Iridaceae	*Sisyrinchium micranthum*	Cav.	th
Iridaceae	*Sisyrinchium palmifolium*	L.	ef
Iridaceae	*Sisyrinchium platense*	I.M. Johnst.	ef
Juncaceae	*Juncus capillaceus*	Lam.	te
Juncaceae	*Juncus dichotomus*	Elliott	te
Juncaceae	*Juncus microcephalus*	Kunth	te
Juncaceae	*Juncus tenuis*	Willd.	te
Lamiaceae	*Cunila galioides*	Benth.	ss
Lamiaceae	*Scutellaria racemosa*	Pers.	ef
Malvaceae	*Ayenia mansfeldiana*	(Herter) Herter ex Cristóbal	ef
Melastomataceae	*Acisanthera alsinaefolia*	(DC.) Triana	ef
Melastomataceae	*Tibouchina gracilis*	(Bonpl.) Cogn.	ef
Myrtaceae	*Campomanesia aurea*	O. Berg	sh
Orobanchaceae	*Agalinis communis*	(Cham. & Schltdl.) D'Arcy	th
Oxalidaceae	*Oxalis brasiliensis*	G. Lodd.	bg
Oxalidaceae	*Oxalis eriocarpa*	DC.	st
Oxalidaceae	*Oxalis lasiopetala*	Zucc.	bg
Plantaginaceae	*Plantago australis*	Lam.	pr
Plantaginaceae	*Plantago myosuros*	Lam.	th
Plantaginaceae	*Plantago penantha*	Griseb.	th
Plantaginaceae	*Scoparia dulcis*	L.	ss
Poaceae	*Agrostis hygrometrica*	Nees	th
Poaceae	*Agrostis montevidensis*	Spreng. ex Nees	th
Poaceae	*Andropogon lateralis*	Nees	te
Poaceae	*Andropogon macrothrix*	Trin.	te

Family	Species	Author	Life form
Poaceae	*Andropogon ternatus*	(Spreng.) Nees	te
Poaceae	*Aristida flaccida*	Trin. & Rupr.	te
Poaceae	*Aristida murina*	Cav.	te
Poaceae	*Aristida uruguayensis*	Henrard	te
Poaceae	*Aristida venustula*	Arechav.	te
Poaceae	*Axonopus affinis*	Chase	st
Poaceae	*Axonopus argentinus*	Parodi	te
Poaceae	*Axonopus compressus*	(Sw.) P. Beauv.	st
Poaceae	*Axonopus fissifolius*	(Raddi) Kuhlm.	st
Poaceae	*Axonopus siccus*	(Nees) Kuhlm.	te
Poaceae	*Axonopus suffultus*	(Mikan ex Trin.) Parodi	te
Poaceae	*Bothriochloa laguroides*	(DC.) Herter	te
Poaceae	*Briza minor*	L.	th
Poaceae	*Briza uniolae*	(Nees) Nees ex Steud.	te
Poaceae	*Chascolytrum poomorphum*	(J. Presl) L. Essi, Longhi-Wagner & Souza-Chies	te
Poaceae	*Chascolytrum subaristatum*	(Lam.) Desv.	te
Poaceae	*Chloris grandiflora*	Roseng. & Izag.	te
Poaceae	*Cynodon dactylon*	(L.) Pers.	st
Poaceae	*Danthonia cirrata*	Hack. & Arechav.	te
Poaceae	*Danthonia secundiflora*	J. Presl	te
Poaceae	*Dichanthelium sabulorum*	(Lam.) Gould & C.A. Clark	de
Poaceae	*Eragrostis airoides*	Nees	te
Poaceae	*Eragrostis neesii*	Trin.	th
Poaceae	*Eragrostis polytricha*	Nees	te
Poaceae	*Eustachys brevipila*	(Roseng. & Izag.) Caro & E.A. Sánchez	te
Poaceae	*Melica eremophila*	Torres	te
Poaceae	*Melica rigida*	Cav.	te
Poaceae	*Microchloa indica*	(L. f.) P. Beauv.	te
Poaceae	*Mnesithea selloana*	(Hack.) de Koning & Sosef	te
Poaceae	*Paspalum almum*	Chase	te
Poaceae	*Paspalum compressifolium*	Swallen	te
Poaceae	*Paspalum dilatatum*	Poir.	te
Poaceae	*Paspalum lepton*	Schult.	rh
Poaceae	*Paspalum maculosum*	Trin.	te
Poaceae	*Paspalum notatum*	Alain ex Flüggé	rh
Poaceae	*Paspalum plicatulum*	Michx.	te
Poaceae	*Paspalum polyphyllum*	Nees ex Trin.	te
Poaceae	*Paspalum pumilum*	Nees	rh
Poaceae	*Piptochaetium lasianthum*	Griseb.	te
Poaceae	*Piptochaetium montevidense*	(Spreng.) Parodi	te

Family	Species	Author	Life form
Poaceae	*Piptochaetium stipoides*	(Trin. & Rupr.) Hack. ex Arechav.	te
Poaceae	*Saccharum angustifolium*	(Nees) Trin.	te
Poaceae	*Saccharum* sp.	-	te
Poaceae	*Sacciolepis vilvoides*	(Trin.) Chase	te
Poaceae	*Schizachyrium condensatum*	(Kunth) Nees	te
Poaceae	*Schizachyrium hatschbachii*	Peichoto	te
Poaceae	*Schizachyrium microstachyum*	(Desv. ex Ham.) Roseng., B.R. Arrill. & Izag.	te
Poaceae	*Schizachyrium spicatum*	(Spreng.) Herter	te
Poaceae	*Schizachyrium tenerum*	Nees	te
Poaceae	*Setaria fiebrigii*	R.A.W. Herrm.	te
Poaceae	*Setaria parviflora*	(Poir.) Kerguélen	te
Poaceae	*Sorghastrum* sp.	-	te
Poaceae	*Sporobolus indicus*	(L.) R. Br.	te
Poaceae	*Sporobolus monandrus*	Roseng., B.R. Arrill. & Izag.	te
Poaceae	*Steinchisma decipiens*	(Nees ex Trin.) W.V. Br.	te
Poaceae	*Steinchisma hians*	(Elliott) Nash	te
Poaceae	*Stipa filiculmis*	Delile	te
Poaceae	*Stipa juergensii*	Hack.	te
Poaceae	*Stipa setigera*	J. Presl	te
Poaceae	*Stipa* sp.	-	te
Poaceae	*Stipa tenuiculmis*	Hack.	te
Poaceae	*Trachypogon montufari*	(Kunth) Nees	te
Poaceae	*Trachypogon montufarii var. mollis*	(Nees) Andersson	te
Poaceae	*Vulpia bromoides*	(L.) Gray	th
Polygalaceae	*Polygala linoides*	Poir.	th
Polygalaceae	*Polygala molluginifolia*	A. St.-Hil. & Moq.	ef
Rosaceae	*Acaena eupatoria*	Cham. & Schltdl.	de
Rubiaceae	*Borreria eryngioides*	Cham. & Schltdl.	ef
Rubiaceae	*Galium humile*	Cham. & Schltdl.	de
Rubiaceae	*Galium richardianum*	(Gillies ex Hook. & Arn.) Endl. ex Walp.	de
Rubiaceae	*Richardia humistrata*	(Cham. & Schltdl.) Steud.	st
Rubiaceae	*Richardia stellaris*	(Cham. & Schltdl.) Steud.	de
Rubiaceae	*Spermacoce verticillata*	L.	ef
Selaginellaceae	*Selaginella* sp.	-	de
Solanaceae	*Nierembergia riograndensis*	Hunz. & A.A. Cocucci	ss
Solanaceae	*Solanum atropurpureum*	Schrank	ss
Verbenaceae	*Glandularia selloi*	(Spreng.) Tronc.	st
Verbenaceae	*Lippia angustifolia*	Cham.	ss
Verbenaceae	*Phyla nodiflora*	(L.) Greene	st
Verbenaceae	*Verbena montevidensis*	Spreng.	ss

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Capítulo 3

Exploring the relationships between habitat structure and arthropod diversity in South Brazilian grasslands: a functional perspective

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Exploring the relationships between habitat structure and arthropod diversity in South Brazilian grasslands: a functional perspective

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Abstract

Habitat structure is one of the major factors shaping biodiversity patterns, and plays a central role in ecological theory. Plant species define habitat structure in most ecosystems, and structurally complex habitats provide more niches and different ways of using resources, ultimately increasing diversity at multiple taxonomic levels. In grasslands, habitat structure is strongly influenced by disturbance regimes of fire and grazing. Diversity patterns of grassland arthropods are determined by plant diversity and structural architecture, although empirical data supporting this relationhip is limited for South American subtropical ecosystems. In this paper we explored the relationships between plant richness and diversity, habitat structure, and arthropod communities in six grassland sites under different grazing pressures from southern Brazil. We used four major groups of arthropod (Coleoptera, Araneae, Hemiptera and Formicidae) and vegetation height and plant functional diversity based on life form traits as descriptors of habitat structure. We searched for relationships between habitat structure and (1) plant species richness and diversity and (2) arthropod richness and diversity. Also, we explored the relationship between functional traits of arthropods and plants and estimate the magnitude of co-variation between community-weighted mean traits (CWM) using co-inertia analysis. Vegetation vertical structure and grazing pressure were, as expected, correlated. Sites under lower grazing pressure showed decreased habitat heterogeneity and plant richness and diversity. Plant diversity indexes and vegetation height were negatively correlated. Richness of arthropod orders was positively correlated to plant diversity and functional diversity. Co-inertia analyses showed a significant association between matrices with CWM traits of plants and all arthropod groups. The association was stronger in Coleoptera and Araneae and weaker in Hemiptera and Formicidae. Differences in patterns of association are related to different relationships between habitat structure and arthropod community in each group. Also, we found strong and group-specific pairwise correlations between arthropod and plant traits, providing further evidence that each group of arthropod responds differently to vegetation structure. Our results provided further evidence supporting the close relationship between grazing and grassland vegetation structure and diversity patterns. Grazing promotes habitat heterogeneity, which is turn influences diversity patterns of arthropods. Our results may guide future research focused on specific arthropod groups in subtropical grasslands.

Keywords: subtropical grasslands, plant life forms, co-inertia analysis, land management, disturbance, grazing

Introduction

Habitat structure is one of the factors that define biodiversity patterns in most ecosystems, and plays a central role in ecological theory (e.g., MacArthur, R. H. 1967, Simpson, E. H. 1949). According to the habitat heterogeneity hypothesis, habitats with complex structures provide more niches and different ways of using resources, ultimately increasing diversity (Bazzaz, F. 1975). Plant communities determine habitat structure in most terrestrial ecosystems, and as a result affect patterns of distribution and interaction of animal species (McCoy, E. and Bell, S. 1991, Tews, J. et al. 2004). Although a positive correlation between habitat heterogeneity and animal species diversity has been repeatedly found in many ecosystems and for different taxa, actual empirical support for this relationship is strongly biased towards vertebrate groups and non-natural habitats (review in Tews, J. et al. 2004). Moreover, the influence of habitat structure on animals is mostly evaluated on the basis of animal species richness and diversity, whereas functional aspects are often ignored (but see Podgaiski, L. R. et al. 2013). Understanding trait-environment links is a key step to determine community assembly in ecosystems, which has been shown to be important in studies on the animal response to habitat change after disturbances (Vandewalle, M. et al. 2010).

In grasslands, habitat structure is strongly influenced by disturbance regimes of fire and grazing, which in fact are the evolutionary drivers and maintainers of these ecosystems (Behling, H. et al. 2004, Bond, W. J. and Keeley, J. E. 2005, Knapp, A. K. et al. 1998, Milchunas, D. et al. 1988). Despite the apparent structural simplicity at first glance, grasslands can show high habitat heterogeneity, arising not only from disturbance (Fuhlendorf, S. D. and Engle, D. M. 2001, Kruess, A. and Tscharntke, T. 2002, Wardle, D. A. et al. 2005), but also because they can show a vast array of life forms and high species richness. Although grasses are responsible for ca. 80% of the aboveground biomass of grasslands, forbs and other life forms make up ca. 80% of the total plant species richness in these systems (Knapp, A. K. et al. 1998). Fire and grazing promote habitat heterogeneity by creating patches under different levels of disturbance and consequently selecting plant species that share similar traits (including structural traits that can are considered in life form classifications) compatible with each condition (Bond, W. et al. 2005, Diaz, S. et al. 2007, Grime, J. P. 2006). Although the heterogeneity promoted by filtering mechanisms is scale-dependent, any change in plant community structure will also have consequences for the diversity of coexisting animal species, which in turn may feedback to ecosystem function (Loreau, M. et al. 2002, Tews, J. et al. 2004).

Especially patterns of arthropod diversity in grassland ecosystem are, to a large extent, dependent on the plant diversity and structural architecture (review in Joern, A. and Laws, A. N. 2013). Arthropods comprise a large portion of grassland diversity (Fay, P. A. 2003, Tscharntke, T. and Greiler, H.-J. 1995) and also play key roles on ecosystem functioning (Belovsky, G. and Slade, J. 2000, Meyer, C. et al. 2002, Whiles, M. R. and Charlton, R. E. 2006). However, the bulk of evidence that links grassland habitat structure and arthropod biodiversity is mostly from data obtained in North American, Australian and European ecosystems, and is usually focused on a very specific taxonomic group or guild of organisms (Joern, A. and Laws, A. N. 2013 and references therein, Morris, M. 2000). Arthropods from natural grasslands of South America are considered highly diverse and abundant, but they remain extremely poorly documented and there is still a lack of knowledge regarding their role in ecosystem processes and functioning.

This study uses four major arthropod groups (Coleoptera, Araneae, Hemiptera and Formicidae) as model groups to explore the relationship between plant richness and diversity, habitat structure, and arthropod communities in grasslands from southern Brazil. We use vegetation height and plant functional diversity based on life form traits as descriptors of habitat structure. We search for relationships between habitat structure and (1) plant species richness and diversity and (2) arthropod richness and diversity. We also search for relationships between species and functional diversities in both trophic groups. Finally, we explore the relationship between functional traits of arthropods and plants and estimate the magnitude of co-variation between community-weighted mean traits using co-inertia analysis. We expect each group to respond differently to variation on habitat structure, due to contrasting overall habit and feeding behavior (Perner, J. et al. 2005).

Material and Methods

Study area

We carried out vegetation and arthropod sampling at five natural grassland sites in Rio Grande do Sul, Southern Brazil. Details on site locations and description of grassland vegetation can be found in Ferreira et al. (unpublished [Capítulo 1]). Grassland ecosystems in this region, known as *Campos*, are inserted in a transitional zone between tropical and temperate climates. Mean temperatures range from 9ºC in winter to 25ºC in summer and mean annual rainfall is ca. 1,440 mm mm (Moreno, J. A. 1961). Although it is assumed that climate in the region has no pronounced dry season (Cfa and Cfb in Köppen's system), there is a high probability of soil water deficit during the peak of summer in the Pampa biome, especially near the Brazilian border with Uruguay (Leivas, J. F. et al. 2006). Grasslands at all sites have been under grazing for many years, with no known record of land conversion. Prior to the surveys we estimated grazing pressure at each site in animal units (AU; corresponding to 450 kg of live weight) per hectare. Grazing pressure in each site was as follow: site 1 = 1.05, site 2 = 0.9, site 3 = 0.6, site 4 = 0.85 and site 5 = 0.45 AU/ha. *Campos* grasslands are relict ecosystems which covered larger areas in South America in past colder and dryer climates (Behling, H. and Pillar, V. 2008). Present climatic conditions favor forest expansion over grasslands, and this process is kept at bay by fire and grazing disturbances, which in fact maintain grassland physiognomy, structure and diversity (Overbeck, G. E. et al. 2005, Overbeck, G. E. and Pfadenhauer, J. 2007). The Brazilian Campos are the northernmost part of a larger formation known as the Rio de la Plata Grasslands, which cover ca. 750,000 km2 in Argentina, Uruguay and

Southern Brazil (Soriano, A. et al. 1992) and is known for its species richness, ecological relevance and high conservation potential (Bilenca, D. and Miñarro, F. 2004, Overbeck et al. 2007).

Plant and arthropod sampling

At each site, we delimited, in 2010, three permanent paddocks of 0.5 ha (70 x 70 m), which resulted in 15 paddocks across five sites. This sampling layout was designed for an ongoing long-term ecological research (PELD Campos Sulinos; CNPq 558282/2009-1). We sampled plants and arthropods within each paddock, and used average values per paddock for most analyses (see below).

Plant sampling took place in late 2010 and early 2011. Within each paddock, we sampled plant species in nine 1m2 plots, systematically allocated in a 3x3 grid with 17 m between plots (135 plots in total). We sampled all plant species present in each plot, and estimated their cover using a decimal scale (Londo, G. 1976). We categorized species in life form categories (Table 1) according to the classification for subtropical grasslands proposed by Ferreira et al. (unpublished [Capítulo 2]). In this classification, plant life forms are based on characteristics such as habit, architecture and strategy of horizontal occupation, and ultimately describe vegetation horizontal (and to some degree vertical) structural heterogeneity. We measured vegetation height in five points per plot as a descriptor of vegetation vertical structure and heterogeneity (675 measurements in total). We also estimated cover of bare soil, litter, rock outcrops and overall vegetation cover in each plot.

Arthropod community was sampled in each paddock using a sweep net (50 cm large; 0.1 m2). We swept the grassland vegetation along four transections equally distributed inside the paddocks. The organisms were preserved in alcohol 80% and sorted in major taxonomical groups. We described each of the focal study groups (Hemiptera, Araneae, Formicidae and Coleoptera) in morphological functional traits, which were measured under stereomicroscope with ocular micrometer. Also, we assigned each group/individual to generalized feeding habits. However, each group presented peculiarities concerning taxonomical identification and functional trait description. We provide the full description of functional traits in Table 1.

Formicidae were identified in genus and morphospecies. Morphological traits (body, relative leg and relative eye size) were measured in up to three individuals of each morphospecies in each paddock. We always selected the smaller individuals, and used the mean of these measurements as the value for each species in each paddock. We selected these morphological traits based on Bihn, J. H. et al. (2010). As a proxy for ant body size we measured head length, taking into account the strong correlation between both structures (Kaspari, M. and Weiser, M. 1999). Relative leg and eye size represented respectively the ratio of leg length (femur and tibia combined) and eye length to head length. Ant feeding behavior information (generalist, predator or leaf cutter) was obtained for all species based on genus level (Brandão, C. R. F. et al. 2012).

Coleoptera was identified in family and morphospecies. Morphological traits (body, relative leg and relative elytron size) were obtained from up to three randomly selected individuals from each morphospecies in each paddock, and then we used the average of these values per species per paddock. The pronotum length was used as a proxy for beetle body size, and for relative leg and elytron size we used respectively the ratio of tibia and elytron length to pronotum length. Beetle feeding habits (herbivore or predator) were assigned according to family affiliation (Marinoni, R. et al. 2001).

Spiders were identified solely in families, and all sampled individuals from each paddock had morphological traits (body and relative chelicerae size) measured. The body size was described in terms of the cephalothorax area (cephalothorax length x width), and the relative chelicerae size represented the ratio of chelicerae length to cephalothorax length. Spiders are exclusive predators, and we registered their behavior considering the construction of prey-capture web (web builders or hunters) based on family affiliation (Dias, S. C. et al. 2009).

Finally, Hemiptera was classified in family, and also all sampled individuals were measured in morphological traits (body and relative stylet size). Body size was estimated based on complete individual length (excluding wings), and relative stylet size represented the ratio between stylet length and body length. Based on family affiliation, all sampled hemipterans were considered plant-sucking herbivores.

We assumed the selected morphological traits to be related, in each arthropod group, to their adaptation to the environment, to the relationships with habitat structure and to resource use. Body size is considerate the most fundamental trait of an animal and is usually correlated with life history and physiological and ecological proprieties (e.g., Cushman, J. H. et al. 1993). Relative leg size in ants and beetles may be related to efficiency in locomotion, resource acquisition and may allow or prevent the use of specific microhabitats (Kaspari, M. and Weiser, M. 1999, Wiescher, P. T. et al. 2012). Relative eye size in ants is an important trait related to foraging (Bihn, J. H. et al. 2010). Relative elytra size in beetles has been related to dispersal ability (Barton, P. S. et al. 2011). Relative chelicerae size in spiders may be related to prey size and foraging (Podgaiski, L. R. et al. 2013) and finally, stylet size in hemipterans is related to sucking efficiency (Grimaldi, D. 2005). The feeding behavioral guilds, and hunting strategies in case of spiders, includes the organisms using the same class of resources, thus reflecting their direct connection with the habitat.

Data analysis

Our analyses aimed to (a) search for relationships between vegetation vertical structure, patterns of plant diversity and richness and the arthropod community; (b) estimate the magnitude and significance of the co-variation between plant and arthropod traits and (c) evaluate the role of habitat structure (based on vertical heterogeneity and plant life forms) over four abundant arthropod groups, as well as possible differences among groups regarding this role.

We organized the data in matrices containing community information (matrices **W** of species or individuals by paddocks) and functional information (matrices **B** of species or individuals by traits). Arthropod data was summarized in two matrices for each group: $\mathbf{W}_H$ and $\mathbf{B}_H$ for

Hemiptera, $\mathbf{W}_A$ and $\mathbf{B}_A$ for Araneae, $\mathbf{W}_F$ and $\mathbf{B}_F$ for Formicidae and $\mathbf{W}_C$ and $\mathbf{B}_C$ for Coleoptera. Coleoptera and Formicidae matrices contained information of morpho-species, whereas Araneae and Hemiptera matrices contained information of individuals. Matrices $\mathbf{W}_H$ and $\mathbf{W}_A$ are binary, whereas matrices $\mathbf{W}_C$ and $\mathbf{W}_A$ contain abundance information (see Table 1 for information on traits describing each matrix **B**). Plant data comprised two matrices: $\mathbf{W}_P$ (paddocks described by plant species average cover values) and $\mathbf{B}_P$ (plant species described by life form categories; see Table 1). All matrices **W** were standardized to unit total.

Using these matrices we calculated community weighted mean traits (CWM; see Podgaiski, L. R. et al. 2013 for details) for each paddock. We generated five matrices **T** with CWM trait values (one for each group of arthropod and one for plants) by matrix multiplication **T** = **WB** (Pillar, V. D. et al. 2009), where **W** and **B** were used according to each taxonomic group. The resulting matrices were $\mathbf{T}_P$ of plant CWM traits and matrices $\mathbf{T}_C$, $\mathbf{T}_F$, $\mathbf{T}_A$ and $\mathbf{T}_H$ of Coleoptera, Formicidae, Araneae and Hemiptera CWM traits, respectively. In cases when a given group of arthropods was absent from a paddock, the vector corresponding to that paddock was also removed from plant matrices $\mathbf{W}_P$ and $\mathbf{B}_P$ in order to obtain matrices **T** with compatible dimensions for both taxonomic groups (to enable co-inertia analysis; see below).

We calculated species diversity using Simpson’s 1-D (Magurran, A. E. and McGill, B. J. 2011) and functional diversity using Rao’s quadratic entropy (Botta-Dukát, Z. 2005) for plants and arthropods (for each order separately; species diversity only for Ants and Coleoptera). Rao’s index of functional diversity contains information on the extent of trait dissimilarity among taxa in a given community weighted by their relative abundance. Since plant traits consisted on life form categories, we interpreted plant functional diversity as a measure of habitat heterogeneity. We searched for associations between variables using pairwise correlation analysis with permutation and linear models. Pairwise correlation between vectors from matrices with CWM trait values was also tested to search for relationships between arthropod and plant traits. Possible associations between plant richness, diversity and functional diversity were tested at three different levels (area, paddock and plot), whereas all other associations were tested at the paddock level. We also searched for relationships between management intensity (grazing pressure) and vegetation structure and diversity. Finally, we calculated plant diversity using multiple diversity indexes (Simpson's D, Shannon, Evenness, Brillouin, Menhinick, Margalef, Equitability, Fischer-alpha and Berger-Parker; Magurran, A. E. and McGill, B. J. 2011) and estimated the correlation of each index with vegetation structure parameters and richness of arthropod orders. We only discussed significant correlations ($P < 0.05$), and only presented P values when they were lower than 0.01.

We used co-inertia analysis to further explore the relationship between functional traits of arthropods and plants (Dolédec, S. and Chessel, D. 1994). We tested the significance and estimated the magnitude of co-variation between matrix $\mathbf{T}_P$ of plant CWM traits and matrices $\mathbf{T}_C$, $\mathbf{T}_F$, $\mathbf{T}_A$ and $\mathbf{T}_H$ of arthropod CWM traits. In the next step we carried out Principal Coordinate Analyses (PCA) with all matrices **T** and reduced their dimensionality by selecting the principal axes. We maximized the concordance between each pair of matrices by rotation of the multivariate ordination space, which generated new axes (Dray, S. et al. 2003). We used permutation to test the significance of each association. All analyses were performed with the R platform (R Development Core Team 2012).

Results

Overall, across the five sampling sites, we sampled 376 plant species from 40 families and 2,579 arthropod individuals from 11 orders. Hemiptera (1,093 individuals), Araneae (500), Formicidae (188) and Coleoptera (141) represented 74% of the overall arthropod abundance sampled in the study. Differences in grazing pressures among sites resulted in differences of vegetation height and variance in vegation height among sites. These differences are, to a large extent, the reflection of different grazing pressures in each site, which influenced both vertical structure (Figure 3a,b) and plant diversity (Figure 3c,d). However, local factors such as soil composition and large-scale climatic factors may have also contributed to differences in vegetation structure among and within sites and paddocks.

Plant species diversity and functional diversity were lower in paddocks from sites 3 and 5 (Figure 2). Plant diversity (1-D) and functional diversity (Rao) were positively correlated at paddock level (r = 0.89, Figure 4b), but not correlated at site and plot levels. Similarly, plant species richness and functional diversity were positively correlated at paddock level (r = 0.81, p <0.01), but not correlated at site and plot levels. All plant diversity indexes were negatively correlated with average vegetation height and positively correlated with height variance and richness of arthropod orders (inverse relationships for Simpson's D and Berger-Parker's index).

Average vegetation height and plant species diversity were negatively correlated (r = -0.78, P < 0.01), as well as average vegetation height and plant functional diversity (r = -0.72, Figure 4a). Vegetation height variance and plant diversity were positively correlated (r = 0.78). Average percentage of bare soil and plant diversity were positively correlated (r = 0.88). Richness of arthropod orders was positively correlated to plant diversity (r = 0.63) and plant functional diversity (r = 0.73; Figure 5a). Plant functional diversity was also positively correlated to Coleoptera functional diversity (Figure 5b).

Co-inertia analyses showed a significant association between matrices **T** of plants and arthropods CWM trait values for all arthropod orders (Table 2). The association was stronger in Coleoptera and Araneae (RV = 0.683 and 0.438, respectively), and weaker in Hemiptera and Formicidae (RV = 0.332). The first two axes of the co-inertia biplot for each group of arthropods represented the differences in vegetation structure across the sampling sites (Figures 6a,d and 7a,d). Paddocks with overall higher and more homogeneous vertical vegetation structure (Figure 1) and lower values of plant diversity and functional diversity (Figure 2) were segregated from paddocks with lower and more heterogeneous vegetation, with higher plant diversity. This pattern was more evident for Coleoptera and Araneae (Figure 6) and less evident for Hemitera and Formicidae (Figure 7). It is likely that these differences are the reflection of different relationships between habitat structure and arthropod community in each group. Overall, paddocks from the same sites did not group together in the biplots, suggesting that vegetation structure is more important as a defining factor for arthropod community structure than spatial proximity alone.

Pairwise tests between vectors representing CWM traits for plants and arthropods (from matrices **T**) resulted in several significant associations. For spiders, 'stoloniferous plants' showed association with hunters (r = 0.71) and web-builders (r = -0.71); 'subshrubs', 'forbs' and 'decumbent plants' showed positive or negative association with relative size of chelicera (r = -0.54, 0.60 and 0.53, respectively; Figure 6b,c). For coleopterans, 'tussocks' was negatively associated with body size (r = -0.66), predators (r = 0.71) and herbivores (r = -0.71); 'forbs' was associated with body size (r = 0.69) and 'subshrubs' was associated with predators (r = 0.72), elytron size (r = 0.48) and leg size (r = 0.74; Figure 6e,f). Regarding ants, 'therophytes' was associated with leaf-cutters (r = 0.58), and 'shrubs' with body size (r = -0.64 , Figure 7b,c). For hemipterans, 'stoloniferous plants' showed negative association with body size (r = -0.78) and positive association with mouthparts (r = 0.65); 'subshrubs' showed negative association with mouthparts (r = -0.54) and positive association with body size (r = 0.73; Figure 7e,f). Finally, spider functional diversity and 'erect rosettes' were positively correlated (r = 0.66), as well as hemiptera and coleoptera functional diversities and 'shrubs' (r = 0.79 and 0.67, respectively).

Discussion

Our objective was to explore the relationships between vegetation structure and (1) plant diversity and (2) arthropod diversity in grasslands from Southern Brazil. Although our results represent a snapshot of these relationships, which may vary in time, we did find some clear patterns linking vegetation structure, plant diversity and arthropods. Moreover, our results provide further evidence that grassland vegetation structure is strongly associated with management, as differences in grazing pressures between our sampling sites are associated with variations in vertical vegetation structure and plant diversity (Figure 2). The role of disturbance (grazing and/or fire) on grassland vegetation heterogeneity is widely accepted (Bond, W. et al. 2005, Bond, W. J. and Keeley, J. E. 2005, Knapp, A. K. et al. 1998), but supporting evidence for this relationship, especially regarding the role of grazing, from subtropical and temperate grasslands is still scarce. Light grazing pressures promote the predominance of tussock grasses and the development of shrubs, which outcompete most prostrate life forms and ultimately reduce plant diversity. Our findings corroborate that relationship: vegetation height and height variance decrease linearly with decreasing grazing pressures (Figure 2a,b), and this pattern was recurrent for plant diversity (Figures 2, 3 and 4a). In a local scale, overgrazing may produce the same effect by creating uniform 'prostrate plant communities', although this was not the case in any of our sampling sites.

We used plant life forms as traits (Table 1) to calculate plant functional diversity (FD), as a proxy of habitat heterogeneity. The FD index we used estimates trait dissimilarity among taxa in the communities (each paddock) weighted by their relative abundances (Botta-Dukát, Z. 2005). Paddocks with low FD are largely dominated by few plant life forms, whereas in paddocks with high FD plant cover (our proxy for abundance) is more evenly distributed among different life forms, which promotes higher habitat heterogeneity.

Grassland arthropods are strongly influenced by habitat structure, which in turn is defined by plant species (Joern, A. and Laws, A. N. 2013). Evidence linking arthropod abundances to plant species richness is plentiful, but results encompass both positive and negative relationships (Koricheva, J. et al. 2000), and functional aspects of both taxa are mostly ignored. Moreover, studies that pursue plant/arthropod relationships often focus on small groups or single species. Our results indicate that areas with more heterogeneous habitats (i.e., with higher plant richness and FD) encompass increased richness of arthropod orders (Figure 5A). Structurally complex and diverse grassland areas provide an increased variety of niches and resources to be exploited in comparison with more homogeneous areas (Bazzaz, F. 1975), which should enable the existence of an arthropod community with more diverse habitat and resource requirements. Further, FD of spiders and beetles were also clearly positively related to plant FD. Podgaiski, L. R. et al. (2013) found similar results for spiders in grasslands from south Brazil in an experiment on effects of fire: more functionally diverse plant communities (induced by fire disturbance) sheltered more functionally diverse spider communities.

The functional traits of the different arthropod orders and trophic groups were affected by different components of grassland plant diversity and showed some interesting but yet unclear correlations with plant life form traits. For example, body size in each group was affected by different plant traits: body size of Hemiptera was influenced by subshrubs and stoloniferous plants; in Coleoptera it was affected by tussock grasses and forbs, while in ants it was more influenced by the proportion of shrubs in vegetation cover. Considering the size-grain hypothesis (Kaspari, M. and Weiser, M. 1999), morphological features of walking organisms (such as body size) indicate a trade-off in the manner they move over and through the environment and use the habitat. Smaller organisms experience a more rugose world with the possibility of enhanced penetration on microhabitats and interstices that larger organisms are not suited to enter (Sarty, M. et al. 2006). In our results, this could be noticed in the relationship between Coleoptera and habitat structure: coleopteran body size decreased following an increasing trend in the proportions of tussock grasses. The predominance of tussock grasses shapes habitats with high density of leaves, which would be best suited for smaller coleopterans.

Vegetation structure is particularly important for generalist predators such as spiders (Podgaiski, L. R. et al. 2013, Sunderland, K. and Samu, F. 2000). Non-web-building spiders (cursorials) have been shown to benefit in habitats with higher proportions of prostrate plant species, i.e. habitats that do not provide the necessary architecture to allow web building. Also, hunting spiders with larger chelicerae could benefit from such clear environments (Podgaiski, L. R. et al. 2013).

Our results showed that leaf-cutting ants were associated with higher proportion of annual plants. It has been shown that leafcutters may select pioneer leaves because of their low level of chemical defenses and high nutrient content (Farji-Brener, A. G. 2001), and our results confirm this ‘palatable forage hypothesis’, as annual plant species usually are poor in fiber and show high nutritious value.

Conclusions

Our results provide further evidence supporting the close relationship between disturbance (grazing) and grassland vegetation structure and diversity patterns. Although this relationship is well established, empirical evidence from subtropical grasslands is still scarce. Grazing promotes habitat heterogeneity, which in turn influences diversity patterns of arthropod. Although our results regarding the relationships between arthropods and vegetation structure are on the coarse level of four major orders, they may guide future directions for research on links between grassland vegetation and specific arthropod groups in subtropical grasslands, choosing for example animal traits that are more responsive to habitat structure in each group.

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Table 1. Description of arthropod and plant traits used in the study.

Group	Trait category	Trait	Acronym	Category	Description
Hemiptera	Morphological	Relative stylet size	Mouthp	Quantitative	Stylet (mm) / body lenght (mm)
	Morphological	Body size	Body	Quantitative	Body lenght (mm)
Araneae	Feeding behavior	Hunter	Hunt	Binary	
	Feeding behavior	Web builder	Web	Binary	
	Morphological	Body size	Body	Quantitative	Area of cephalothorax (mm^2)
	Morphological	Relative chelicera lenght	Chel	Quantitative	Chelicerae length (mm) / cephalothorax length (mm)
Formicidae	Feeding behavior	Generalist	Gen	Binary	
	Feeding behavior	Leaf cutter	Cutter	Binary	
	Feeding behavior	Predator	Pred	Binary	
	Morphological	Body size	Body	Quantitative	Head lenght (mm)
	Morphological	Relative leg size	Leg	Quantitative	Leg length (mm) / head length (mm)
	Morphological	Relative eye size	Eye	Quantitative	Eye length (mm) / head length (mm)
Coleoptera	Feeding behavior	Herbivore	Herb	Binary	
	Feeding behavior	Predator	Pred	Binary	
	Morphological	Body size	Body	Quantitative	Pronoto lenght (mm)
	Morphological	Relative leg size	Leg	Quantitative	Tibia lenght (mm) / pronoto lenght (mm)
	Morphological	Relative elytron size	Ely	Quantitative	Elytron length (mm) / pronoto length (mm)
Plants	Life form	Therophytes	Th	Binary	
	Life form	Bulbous geophytes	Bg	Binary	
	Life form	Rhizomatous geophytes	Rg	Binary	
	Life form	Prostate rosette evergreens	Pr	Binary	
	Life form	Decumbent evergreens	De	Binary	
	Life form	Rhizomatous evergreens	Rh	Binary	
	Life form	Stolonoiferous evergreens	St	Binary	
	Life form	Solitary evergreen tussocks	Te	Binary	
	Life form	Connected evergreen tussocks	Ct	Binary	
	Life form	Evergreen forbs	Ef	Binary	
	Life form	Erect rosette evergreens	Er	Binary	
	Life form	Evergreen subshrubs	Ss	Binary	
	Life form	Evergreen shrubs	Sh	Binary	

Table 2. Summarized results of co-inertia analysis using community-weighted mean traits of plants and each arthropod group.

	Hemiptera	**Araneae**	**Formicidae**	**Coleoptera**
RV	0.332	0.438	0.332	0.683
P-value	0.034	0.017	0.028	0.001
Axis 1 (%)	97.5	79.1	64.9	93.8
Axis 2 (%)	2.1	17.2	19.6	5.1
Cumulative (%)	99.6	96.3	84.5	98.9

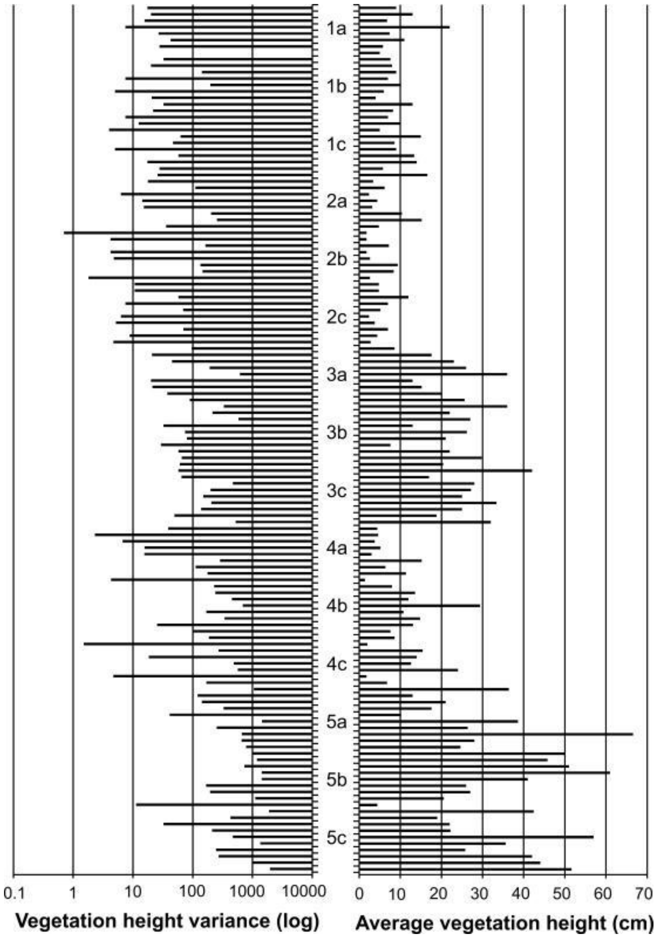

Figure 1. Vertical structure of grassland vegetation across five sampling sites (1 - 5) and 15 paddocks (a, b and c), nine sampling units per paddock.

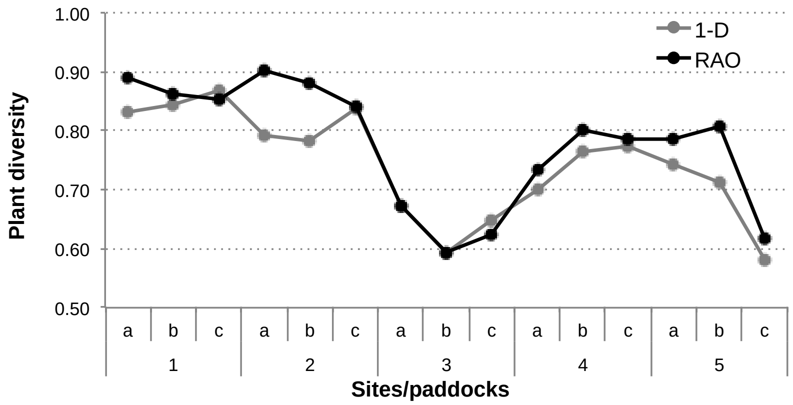

Figure 2. Plant species diversity (1-D) and functional diversity (Rao's quadratic entropy) across five sampling sites (1 - 5) and 15 paddocks (a, b and c).

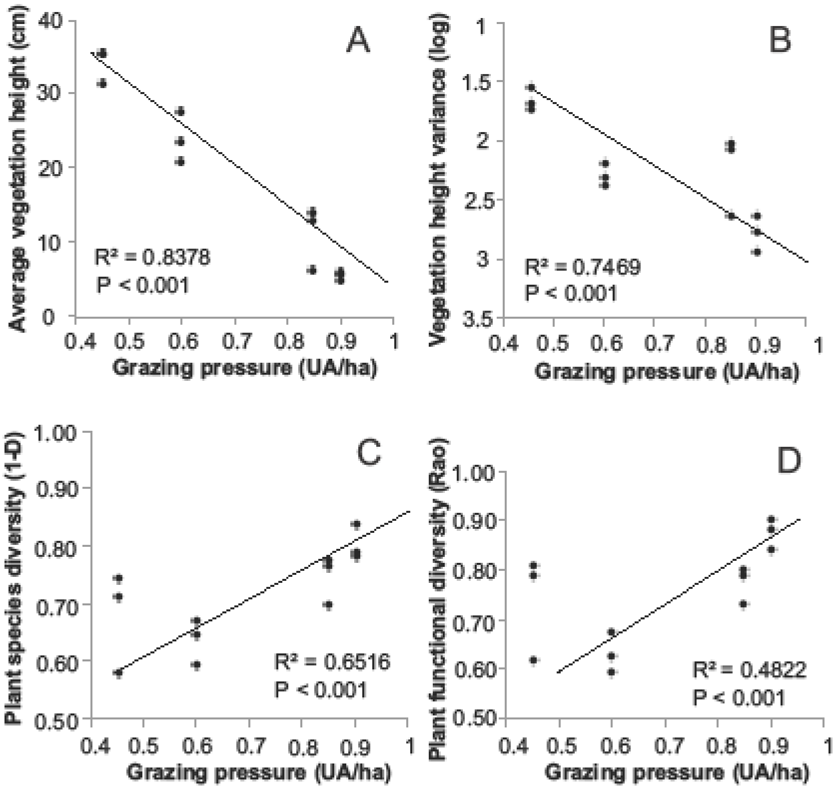

Figure 3. Relationships between grazing pressure and (A) vegetation height, (B) vegetation height variance, (C) plant species diversity and (D) plant functional diversity. UA = animal units (450 kg of live weight).

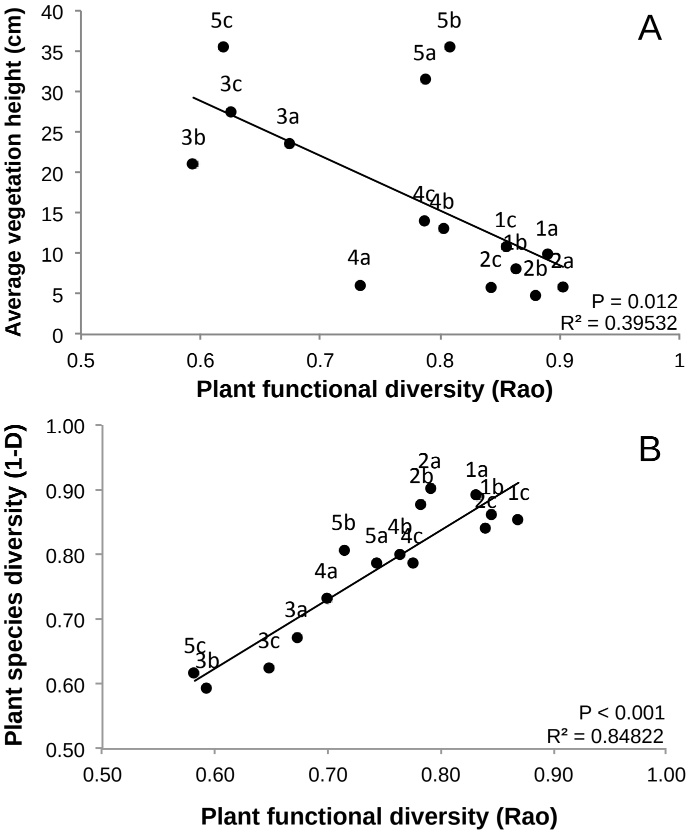

Figure 4. Relationships between vegetation vertical structure and plant functional diversity (A) and plant species and functional diversities (B). Labels: 15 paddocks (a, b and c) from five sampling sites (1 - 5).

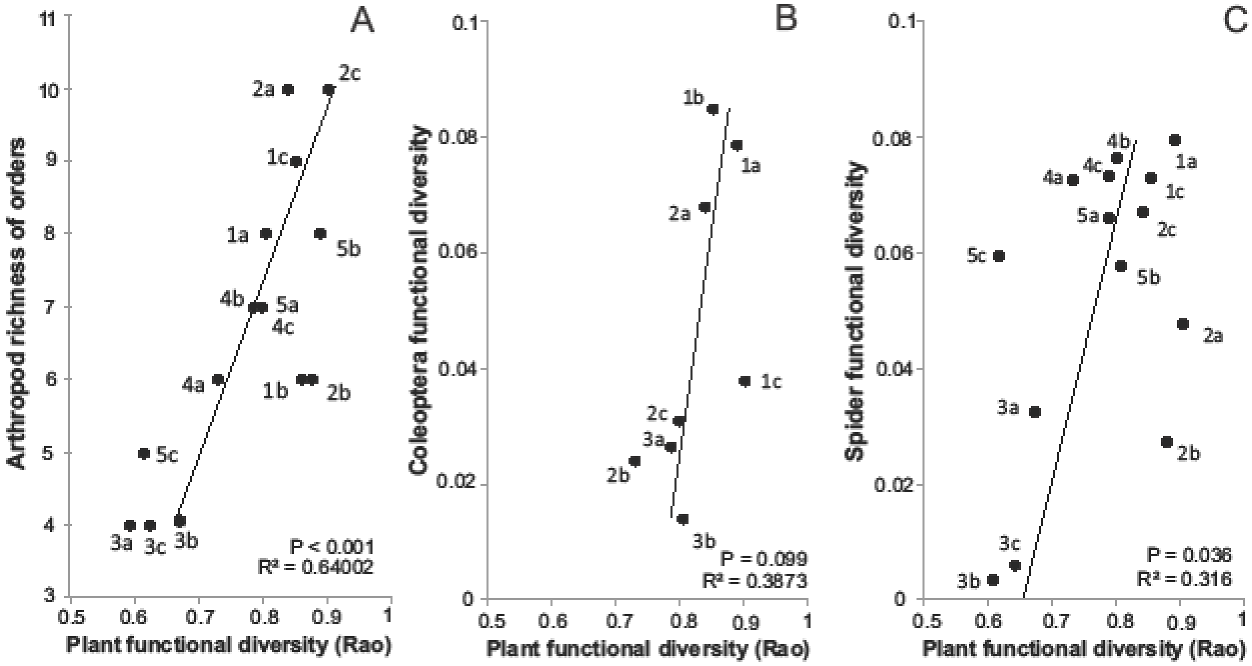

Figure 5. Relationships between plant functional diversity and: (A) richness of arthropod orders; (B) coleopteran functional diversity and (C) spider functional diversity. Labels: 15 paddocks (a, b and c) from five sampling sites (1 - 5).

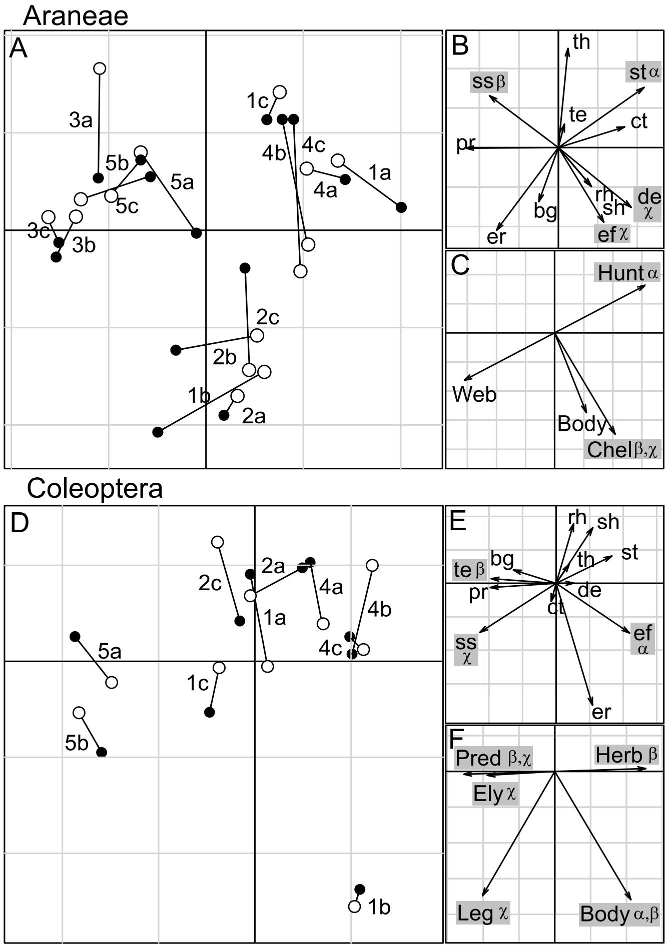

Figure 6. Results of co-inertia analysis using community-weighted mean traits of plants and spiders (A-C) and coleopterans (D-F). A and D: ordination of paddocks (a, b and c) from five sampling sites (1 - 5) based on plant (full circles) and arthropod (empty circles) traits. PCA of plant (B and E) and arthropod (C and F) traits. Highlighted traits indicate significant pairwise correlation (same symbol) between plant and arthropod traits within the same group. Legend for traits: see Table 1.

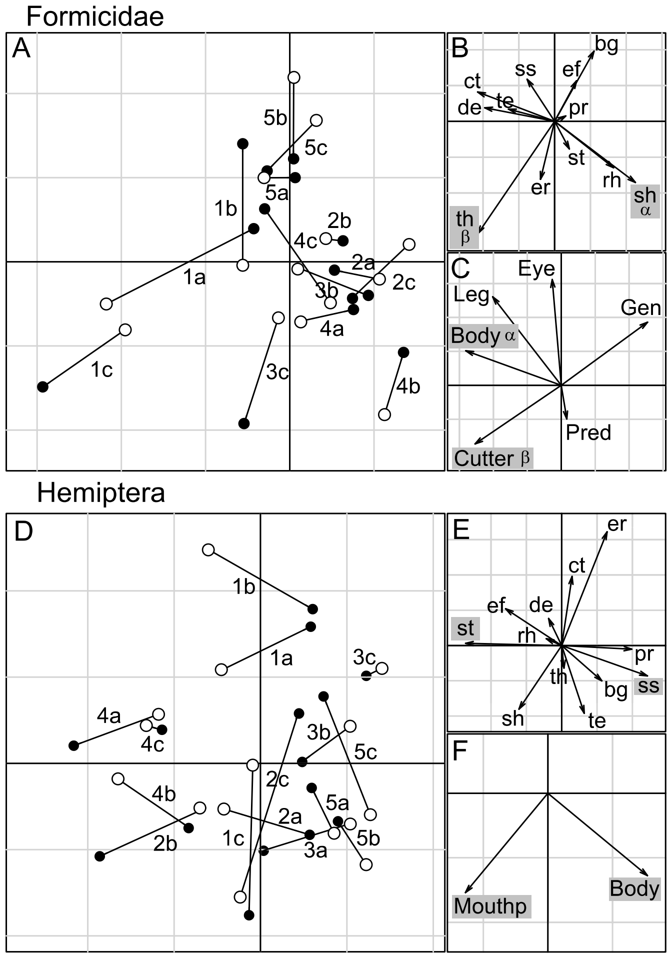

Figure 7. Results of co-inertia analysis using community-weighted mean traits of plants and ants (A-C) and trips (D-F). A and D: ordination of paddocks (a, b and c) from five sampling sites (1 - 5) based on plant (full circles) and arthropod (empty circles) traits. PCA of plant (B and E) and arthropod (C and F) traits. Highlighted traits indicate significant pairwise correlation (same symbol) between plant and arthropod traits within the same group. Legend for traits: see Table 1.

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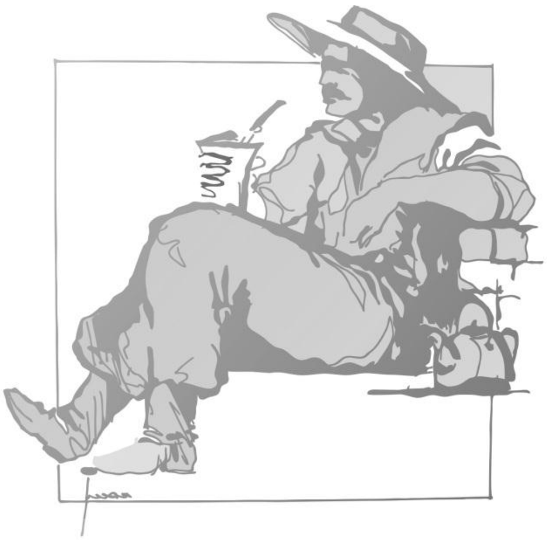

Capítulo 4

Long-term ecological research in subtropical grasslands: results from a four-year monitoring of different management practices in Southern Brazil

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Abstract

Questions: How do subtropical grassland communities respond to different intensities of grazing disturbance through time? Does this response affects litter decomposition?

Location: Subtropical grasslands, Southern Brazil (27º15'S - 31º54'S; 50º15'W - 56º15'W; 150 – 850 masl).

Method: We selected six sites with natural grassland vegetation under grazing. In each site we delimited three paddocks to which we randomly assigned one of three different managements with grazing animals: conventional, conservative or exclusion. The conventional treatment was our control, in which we maintained the grazing pressure used at each site. The conservative was a simulation of rotational grazing and the exclusion represented the cessation of disturbance. We repeatedly sampled plant communities using permanent plots in south hemisphere spring during four years. We searched for differences between treatments along time in species richness, diversity, functional diversity and functional redundancy. We used an alternative classification of plant life forms as functional traits, and also evaluated shifts in dominance of life forms between treatments. Finally, we estimated litter decomposition in two different experiments using litter-bags.

Results: Species richness decreased in exclusion paddocks after the second year of sampling. Management cessation promoted a short-term increase in species diversity. After the second year, species diversity dropped steadily in the exclusion, whereas it remained unchanged under the conservative management. Functional diversity also dropped after the second year of exclusion, but increased in the following years in the conservative treatment. Functional redundancy varied little in the control and conservative, whereas it increased linearly in the exclusion along the four years of sampling. Relations of dominance of life forms shifted in the exclusion and conservative treatments, with sharp decrease in cover of prostrate plants and increase in other life forms. Mean vegetation height and dead biomass increased more than two times in the exclusion. Many species were outcompeted due to shading. Decomposition experiments showed differences between treatments only after the third year of sampling, with higher decomposition rates in conventional paddocks and in Pampa sites. We concluded that these differences were mostly due to differential photodegradation promoted by differences in vegetation structure.

Conclusion: Interruption of grazing disturbance caused drastic changes in community parameters by shifting relationships of dominance, removing grazing-tolerant species and benefitting groups of species that were controlled by grazing. Structural differences arising from management exclusion also influenced litter decomposition. Our findings suggest that subtropical grasslands from South America may be in an intermediate position in a gradient of resistance/resilience to grazing in comparison with other systems such as shortgrass steppes and tallgrass prairies.

Keywords: diversity, grazing, Pastizales del Rio de la Plata, plant life forms, litter decomposition, ecosystem processes

Introduction

Grasslands, at least when under productive climatic conditions, are disturbance-prone ecosystems strongly shaped by fire and grazing regimes (Milchunas et al. 1988; Knapp et al. 1998; Bond & Keeley 2005). Disturbance can be defined as ‘any event in time that disrupts ecosystem, community, or population structure and changes resource pools, substrate availability, or the physical environment’ (Pickett 1985) or, more simply, as ‘any event partially or totally destroying plant biomass’ (Grime 1979). Either way, disturbance plays a key role on grassland species composition, diversity patterns on multiple scales and ecosystem functioning (e.g., Milchunas et al. 1988; Frank & McNaughton 1993; Frank & Evans 1997; Knapp et al. 1998; Frank et al. 2000; Bond et al. 2005; Grime 2006; Diaz et al. 2007).

Grazing animals can be very selective as to what they forage (Senft et al. 1987). In productive grasslands, where high-quality palatable plants can be found, herbivores preferably graze these plants, avoiding patches dominated by tall, less palatable taxa (Adler et al. 2001; McIntyre & Tongway 2005; McIvor et al. 2005). This selection promotes heterogeneity by creating a mosaic of patches under different grazing pressures in the landscape with the selection of plants that share traits compatible with each local disturbance situation (Grime 2006; Diaz et al. 2007). However, this selectiveness also depends on the amount of forage available per animal unit in a given paddock: the lower the forage availability, the less selective foraging will be , and the aforementioned patchiness may be converted in structural homogeneity (Senft et al. 1987; Coughenour 1991). The opposite also holds true: high forage availability may lead to higher selectiveness and to increasing dominance of plants characteristic of ungrazed or lightly grazed patches (Hobbs & Swift 1988).

To evaluate disturbance-driven grassland heterogeneity, or to compare shifts in grassland communities under different grazing intensities, plant species alone may not be the best working units. To answer such questions, the usefulness of a functional approach is well-established (Diaz et al. 2007). Based on recurrent findings of correlated plant traits, it has been suggested that reduced sets of traits such as life/growth forms may be good descriptors and predictors of ecosystem functioning under disturbance (McIntyre et al. 1995) or climate change (Chapin 1993). Although plant life forms sensu Raunkiaer (1934) may not be the ideal descriptors in all grassland ecosystems (Ferreira et al. unpublished [Capítulo 2]), alternative case-specific life/growth form classifications have been successfully used to answer different ecological questions in different places around the globe (e.g., Arnold 1955; Grime 1973; Sala 1988; Grime et al. 1997; Hadar et al. 1999).

Grazing by large herbivores also affects grassland ecosystem processes such as biomass decomposition. By modifying community habitat structure, plant species and functional composition, herbivores influence biological, physical and chemical properties of the soil environment, which ultimately enhances or reduces plant litter quality and decomposition rates (Bardgett & Wardle 2003; Güsewell et al. 2005; Semmartin et al. 2008). Habitat heterogeneity promoted by grazing can influence biological activity at the soil level by altering microclimatic features (Throop & Archer 2007; Araujo et al. 2012) or facilitating litter photodegradation (Verhoef et al. 2000; Pancotto et al. 2005). Large grazing animals also contribute with decomposable resources and nutrients by depositing urine and faeces, which may lead to increases in populations of decomposition microorganisms and also influence overall decomposition rates (Ruess & McNaughton 1987; Seagle et al. 1992; Bakker et al. 2004). Thus, it is expected that litter decomposition would be accelerated in grazed areas/patches in comparison with ungrazed or lightly grazed areas (e.g., Augustine & McNaughton 1998). However, this assumption did not hold true in South American temperate grasslands: Vaieretti et al. (2013) found no differences in decomposition rates comparing grazed and ungrazed patches in Argentina. Also working in Argentina, Carrera et al. (2008) found that leaf litter decomposed fast at the grazed sites due to changes in canopy structure induced by grazing disturbance. The relationship between grazing intensity and its implications on decomposition seems to remain unclear, especially considering South American subtropical grasslands, were few works addressing the question have been carried out, although there is evidence that fire affects litter decomposition in these ecosystems (Podgaiski et al. 2014).

Although the general importance of grazing for origin and maintenance of grasslands is well established, the impact of this disturbance on ecosystem structure and processes may vary with geographical location. The classic ‘generalized grazing model’ proposed by Milchunas et al. (1988) ascribe these differences in sensibility to grazing intensity (using plant diversity as indicator) to two principal variables: evolutionary history of grazing and moisture level of a given grassland ecosystem. Cingolani et al. (2005) provide further discussion of Milchuna’s model and suggests modifications that enhance its applicability. In another perspective, differences in ‘sensibility’ to disturbance may be related to two different ecological properties: resistance and resilience (Harrison 1979). Empirical evidence indicate that shortgrass steppes from Southern South America are highly resistant to grazing (Milchunas & Lauenroth 1993; Milchunas et al. 1998), whereas North American tallgrass prairies are less resistant but more resilient to grazing (Coffin et al. 1996; Baer et al. 2000).

The relationships between grazing, vegetation dynamics and ecosystem processes are still poorly studied in ecosystems from Southern Brazil, especially considering long-term monitoring. Grasslands in this region, locally known as ‘Campos’, are relict ecosystems from drier and cooler periods that are stabilized until today by the action of herbivores and fire (Behling & Pillar 2008). There is evidence of the presence of large grazing herbivores in South American grasslands since the early Miocene (MacFadden 1997, 2005). After their extinction, grazing by domestic herbivores has become widespread since the seventeenth century (Porto 1954), and today cattle breeding is one of the most important economic activities in the region (Pillar 2009). However, the degree of resistance/resilience of these systems to grazing remains unclear, as do the consequences of interrupting the disturbance regime. To answer such questions, long-term ecological research (LTER) is essential. Although LTER has greatly improved our understanding of ecosystem dynamics (reviews in Rees et al. 2001; Turner et al. 2003), very little of this evidence comes from the Southern Hemisphere, and almost none from grasslands in Southern South America (but see Boldrini & Eggers 1996).

In this paper we present the results of the first four years of an experiment in LTER sites established in 2010 in the South Brazilian grasslands. We examined shifts in grassland vegetation diversity patterns, relative dominance of plant life forms and biomass decomposition rates under different management intensities with grazing animals. We hypothesized that exclusion of management will lead to a decrease in species richness, diversity and functional diversity (as seen after fire disturbance in similar ecosystems; Overbeck et al. 2005). Accordingly, we expect that different grazing intensities will lead to shifts in dominance of plant life forms. Also, we expect that 'lighter' grazing pressures under rotational grazing will promote higher heterogeneity and increased species richness, diversity and functional diversity.

Material and Methods

Study sites and sampling design

Our study area comprised six sites in Southern Brazil. Since grassland ecosystems in the region are present in two different biomes, Pampa and Atlantic Forest, we selected three sites in each biome. Grasslands in the Pampa biome cover large continuous areas, and forests are mostly restricted to rivers. In the Atlantic Forest biome grasslands and forests shape mosaics in the landscape (Boldrini 1997; Boldrini et al. 2009). Pampa sites were Aceguá (31°38'55"S, 54°09'26"W), Alegrete (30°04'08"S, 55°59'27"W) and Lavras do Sul (30°41'55"S, 53°58'11"W). Atlantic Forest sites were Aparados da Serra National Park (29°08'10"S, 50°09'21"W), Aratinga Ecological Station (29°23'31"S, 50°14'30"W) and Tainhas State Park (29°05'40"S, 50°22'03"W). Grasslands at all sites are under cattle grazing probably since the introduction of domestic cattle in the 17th century in the Pampa and 18th century in the Atlantic Forest.

The experiment consisted in a randomized block design. At each site, we delimited three paddocks of 0.5 ha, and to each paddock we randomly assigned one of three treatments that represented different management of grazing animals: conventional, conservative or exclusion. The conventional treatment was the control, in which we maintained the grazing pressure (animal units per hectare) currently used at a given site. The exclusion treatment consisted on fenced paddocks that completely precluded the entry of grazing animals. The conservative treatment consisted on fenced paddocks with gates that allowed for controlled grazing during certain periods of time, simulating rotational grazing. In the interval between grazing events the conservative paddocks remained inaccessible to grazing animals. In the conservative management, the criterion used to determine the interval of cattle access to each paddock was the accumulated thermal sum of 700 degrees-day per site. The duration and number of animals used in each grazing event was calculated to obtain a post-grazing aboveground residual of ca. 1,200 kg of dry biomass per hectare. These procedures aim to maintain the contribution of resource-conserving grasses in the grassland community (Quadros et al. 2006), to promote habitat heterogeneity and less accumulation of dead biomass and ultimately to enhance ecosystem resilience (Soussana 2009).

We sampled the grassland vegetation in each site for the first time during south hemisphere spring/summer 2010, after which we carried out the construction of fences to start the different treatments. Cattle access into exclusion and conservative paddocks was blocked from late 2010 to spring/summer 2011. The conservative management started in late 2011. We resampled all sites during the same period in 2011, 2012 and 2013. In each paddock we sampled the vegetation using nine 1m^2 permanent plots (systematically allocated in a 3x3 grid with 17 m between plots). In each plot we surveyed all plant species that were present and estimated their cover using the decimal scale of Londo (1976). We also estimated vegetation height in five points per sampling unit, and estimated cover of bare soil, litter (aboveground dead biomass), rock outcrops and overall vegetation cover per sampling unit.

We performed two experiments to estimate litter decomposition under the different treatments using litter-bags (Wider & Lang 1982). In this procedure, we added a known mass of standardized dry material into 10 x 10 cm bags made of green nylon mesh (1 mm2), with five additional round perforations of 4 mm radius on each surface, which were fixed at ground level in each sampling paddock using four specks. We chose this configuration for the litter-bags to maximize camouflage in the environment, to minimize accidental loss of material and to allow the entry of invertebrates from the soil macro fauna, which also contribute to decomposition (Swift et al. 1979). After a determined period of time, we retrieved these bags, washed, dried and weighted their remaining contents and estimated the decomposition rate after subtracting the final mass from the initial mass. We used standardized materials in all sampling sites and paddocks, since we searched for differences between decomposition rates related to the micro-environments created by each treatment. Therefore, we did not take into account possible qualitative differences in litter (e.g. decomposability) produced in each site/treatment.

In the first experiment we installed 32 litter-bags per paddock in five sites (logistic problems made it impossible to install the experiment in one of the sites at the time), using dry leaves of two broadly distributed plant species: *Andropogon lateralis* (Poaceae, 1g) and *Eryngium horridum* (Apiaceae, 1.5g), with 16 bags each. The installation of this experiment took place in June 2011, and eight litter-bags of each species per paddock were removed six months later (December 2011), and the remaining litter-bags 18 months later (December 2012). The second experiment was installed in all six sites in December 2012, and lasted six months (June 2013). As *E. horridum* and *A. lateralis* materials presented extremely similar decomposition rates (based on the results from the first experiment), in the second experiment we opted to substitute the later for cellulose filter paper standard material which was expected to interact differently with the micro-environmental conditions (e.g., not being affected by photodegradation; Vaieretti et al. 2010). We installed 16 litter-bags per paddock, eight containing dry leaves of *E. horridum* (1g) and eight with cellulose filter paper (1g).

Data analysis

In our analyses we searched for differences between vegetation patterns among treatments during four consecutive years of sampling. We estimated these differences considering species composition and their relative abundances, species richness and diversity and functional aspects of the community based on plant life forms.

We organized plant community data in a matrix containing average cover values of species describing paddocks in each of the four years of sampling (matrix **W**). From matrix **W** we derived matrices containing information of treatments and/or years separately, according to each analysis. We classified plant species that were present in at least three paddocks in life form categories (Table 1) proposed by Ferreira et al. (unpublished [Capítulo 2]). In this classification, life forms are based on features such as habit, architecture, level of lignification and strategy of horizontal occupation, which are responsive to shifts in management and good descriptors of vegetation structure. Trait data were summarized in the binary matrix **B** of species described by life form categories. To evaluate changes in dominance of life forms across the years of sampling and under different treatments, we also generated a matrix **T** with community weighted mean traits by matrix multiplication **T** = **WB** (Pillar et al. 2009). We used chord distance as dissimilarity measure between sampling units in matrix **W** and Gower's index (Podani 1999) in matrix **B**.

We calculated species diversity using Simpson's index (Magurran & McGill 2011) and functional diversity using Rao's quadratic entropy (Botta-Dukát 2005). We also calculated functional redundancy using the method described in Pillar et al. (2013). Diversity indexes and functional redundancy were calculated at the paddock level, and for every year of sampling. We tested for correlations between diversity indexes and functional redundancy using correlation analysis with permutation. To test for differences in indexes between years we used Repeated Measures Analysis of Variance with permutation. We used ANOVA with permutation to evaluate differences between treatments in the same sampling year, and between decomposition rates between treatments. We restricted all permutations due to the blocked design of the experiment.

Results

Pairwise comparisons of species composition and abundance between years within each treatment resulted in significant differences only in the exclusion, and only between the first and the last two years (this difference vanishes when using only presence/absence data). Species richness dropped sharply after the second year of exclusion, and differences between treatments became significant after the third year, with higher values in the conventional treatment (Figure 1A). Plant species diversity increased after the first year of exclusion, after which conventional and conservative treatments maintained an increasing trend and exclusion decreased sharply. Differences in diversity between the control and the two treatments were evident after the first year of exclusion, became blurred in 2012 and were evident again in 2013 (Figure 1B). After four years, species diversity was higher in the conservative treatment, contrasting with results for species richness (Figure 1A). Considering the pooled data from the four years of monitoring, species richness was significantly different only between the exclusion and conventional treatments ($P<0.05$), and we found no significant differences considering species diversity.

Plant functional diversity showed little variation across four years in the control, whereas we found opposite trends in the conservative and exclusion treatments: steady increase in the first and sharp decrease in the latter (Figure 2A). Functional redundancy was overall lower in the conventional treatment, increased linearly in the exclusion and decreased in the conservative after the reintroduction of management in 2011 (Figure 2B).

The relative representativeness of life forms across years showed different trends in each treatment. Cover of prostate plants remained roughly constant in the conventional treatment, whereas it decreased in the conservative and exclusion (Figure 3A). Tussock cover was overall lower in the conventional treatment (Figure 3B), whereas the conservative treatment promoted an increase in cover of geophytes (Figure 3C). We found no clear pattern for annual plants (albeit a small number of species with little cover only), although there is an indication of decreasing cover in the exclusion after 2011 (Figure 3D). Forb cover increased after the first year of exclusion, but the pattern disappeared in the following years (Figure 3E). Cover of shrubs and subshrubs increased in the exclusion and remained unchanged in the conservative and conventional treatments (Figure 3F).

Relationships between functional diversity, species diversity and functional redundancy varied between treatments (pooled data of four years of sampling). Functional diversity and species diversity were significantly correlated in all treatments, although the magnitude of the correlation decreased in the conservative and even more in the exclusion. The relationship between functional redundancy and functional diversity followed the same pattern. Functional redundancy and species diversity were strongly correlated in the conventional treatment, but the correlation dropped considerably in the conservative and vanished in the exclusion (Figure 4).

Results of the first decomposition experiment showed no differences between treatments or materials after the first six and 18 months of grazing exclusion (Jun 2011 – Dec 2012; results not shown). However, results of the second experiment (Dec 2012 – Jun 2013) indicated differences in decomposition rates between treatments and materials. Average values per treatment showed higher decomposition rates of *E. horridum* in the conventional treatment ($P<0.05$; Figure 5A). After separating these results by location of sampling sites (southern Pampa sites vs. northern Atlantic Forest Sites), another pattern arose: decomposition rate of *E. horridum* was higher in conventional paddocks from Pampa sites ($P<0.01$), whereas it varied little between treatments in Atlantic Forest sites (Figure 5B). Decomposition rate of cellulose was less variable comparing treatments and sites, although it was on average higher in Pampa sites (Figure 5C). Vegetation height increased sharply in the conservative and exclusion treatments after one year, decreasing in the first and remaining constant in the latter afterwards (Figure 6A). The percentage of dead biomass increased in the exclusion and conservative managements across the years, and was significantly lower in the conventional management after 2012 (Figure 6B).

Discussion

We aimed to investigate, by means of a controlled, randomized experiment, differences in plant composition, diversity and ecosystem processes between grassland plant communities submitted to different grazing regimes during four years. The first year of grazing exclusion promoted a sharp increase in species diversity in the conservative (during the first year still without the conservative management) and exclusion paddocks (Figure 1B). The cessation of grazing produced a short-term decrease in the dominance of prostrate life forms, which was diluted among other groups such as forbs, therophytes and ligneous plants (Figure 3). The conservative management maintained the diversity levels achieved after one year of exclusion, although diversity in the conventional management also increased with time and differences between conservative management and exclusion were not significant after the third year of sampling. As expected, species richness and diversity dropped significantly in the exclusion treatment after 2011, i.e., one year of exclusion (Figure 1 A, B). In productive grasslands, the cessation of grazing is notably followed by increased dominance of a few species (usually the less palatable ones) and the associated decline of species adapted to grazing (e.g., Pucheta et al. 1998a; Pucheta et al. 1998b; Cingolani et al. 2003; Vaieretti et al. 2010). Accordingly, we recorded a steady decline in cover of prostrate plants (largely leaded by rhizomatous grass species) with concomitant increasing cover of other life forms such as tussocks (Figure 3). Under increasing amounts of dead biomass and overall taller vegetation (Figure 6), many species are outcompeted due to shading and tend to first decrease in cover and eventually disappear (Tilman & Wedin 1991; Collins et al. 1995). Declines in species richness in the exclusion treatment corroborate this hypothesis (Figure 1A). This competitive exclusion also affected other life forms such as annual species (Figure 3D). Geophytes were evenly represented among treatments prior to the experiment. Notwithstanding, after four years they were more representative in the conservative treatment in comparison with the conventional and exclusion, probably because they simply had their aerial parts removed by grazing in the first and were outcompeted in the latter (Figure 3C). Shrubs and subshrubs, on the other hand, have benefited from the exclusion of grazing (Figure 3F), and will probably play a key role on future shifts in vegetation structure and diversity patterns in exclusion paddocks during the following years. Although the conservative management also enabled different life forms to become more representative in the community, woody plants were not benefited by this treatment, indicating that no such shrub encroachment will take place under this management intensity.

Plant functional diversity (FD) was overall higher in the conventional treatment, although it rose steadily after 2011 in the conservative and dropped linearly in the exclusion (Figure 2A). Despite the overall higher FD in conventional paddocks prior to the experiment, the slight short-term increase and following maintenance of FD in this treatment may be attributed to the natural spatial heterogeneity (Adler et al. 2001; McIntyre et al. 2003; McIvor et al. 2005) and differential trait selection (Grime 2006; Diaz et al. 2007) promoted by grazing. We used plant life form categories as traits to calculate FD, and the index we used relates to limiting similarity and niche complementarity (Diamond 1975; Tilman et al. 1997; Wilson 1999) by measuring trait dissimilarities among taxa taking their relative abundances into account (Botta-Dukát 2005). Therefore, higher values of FD mean higher distribution of abundances among life forms, i.e., less dominance. The absence of grazing after 2011 promoted the homogenization of the community by greatly reducing the contribution of prostrate species (Figure 3). The disappearance of the natural patchiness was also reflected on average vegetation height, which doubled in the exclusion, reflecting the increasing dominance of tussock grasses (Figure 6A). After 2011, when the conservative management started, FD rose steadily and approached the control values, indicating that the lighter grazing pressures under the simulated rotational grazing promoted, besides higher species diversity (Figure 1B), more evenly distributed dominance of life forms (Figure 2A). Since grazing animals stayed in a very restricted area in each conservative paddock during grazing events (0.5 ha each), urine deposition may have also influenced heterogeneity by creating patches of high productivity (Steinauer & Collins 1995; Steinauer & Collins 2001). In the exclusion treatment, species became increasingly more redundant considering their life form through time (Figure 2B). Coupled with decreasing species richness (Figure 1A), this indicates that species loss due to management cessation may be taxonomically independent and very likely related to competitive ability of selected species (Tilman 1984; Collins et al. 1995; Collins et al. 1998). In fact, theories underlying plant-herbivore dynamics are largely based on tradeoffs between palatability and competitive ability (Pacala & Crawley 1992), and although short-range dispersal and rapid exploitation strategies may explain dynamics in annual plant communities (e.g., Bolker & Pacala 1999), the mechanisms underlying exploitation strategies in long-lived plant communities remain obscure (Rees et al. 2001).

Considering the pooled data from the four years of sampling, the relation between species diversity (D) and functional diversity (FD) was stronger in conventional paddocks, and progressively weakened in conservative and exclusion paddocks (Figure 4). This indicates that variation of FD through time tends to be independent of D with the cessation of management, whereas both variables share similar variation patterns under considerably heavier grazing pressure. The same relation held true between functional redundancy (FR) and FD: both variables are progressively less correlated in the conservative and exclusion treatments. Paddocks with low values of FD are dominated by few life forms, which would logically mean increased redundancy. However, this relationship tends to weaken under lower intensity of disturbance. Finally, correlation between FR and D is significant only in the conventional treatment, indicating that both variables are independent under lighter or no grazing. Pillar et al. (2013), working in grazed grasslands in the same region, showed that (at the plot scale) community stability was positively influenced by FR and negatively influenced by grazing intensity. Our results showed that FR increased under low (and under the absence of) grazing pressure (Figure 2B). Although our results represent mean values per paddock and do not account for between-plot variation, we can assume that species that are usually in ‘less palatable’ patches under grazing (Adler et al. 2001; McIntyre et al. 2003) are progressively excluding more palatable plants and dominating exclusion paddocks with increasing

FR (see also Figure 3). Therefore, exclusion of management may be leading these communities to increased resistance to grazing, considering resistance as the amount of external pressure needed to cause a given amount of disturbance in the system (Carpenter et al. 2001). However, the same communities are probably becoming less resistant to another common disturbance in grasslands: fire. Light grazing pressures lead to accumulation of biomass (Figure 6B), and may also increase fire intensity, extent and overall impact on grasslands and associated ecosystems (Bond & Keeley 2005; Fidelis et al. 2010). Moreover, cessation of management may be leading to decreased resilience (Harrison 1979; Carpenter et al. 2001). The progressive removal of grazing-tolerant species, the increase in woody species (Figure 3) and the shifting towards a closed and taller grass canopy (Figure 6) may in time prevent these communities of shifting back to the original stage (i.e., the conventional treatment), even if grazing is reintroduced. However, results obtained in the conservative treatment suggest high resilience after a short period (1 year) of exclusion, since most results were similar to the ones obtained in the control in the following years.

The absence of differences between treatments in the first decomposition experiment (Jun 2011 – Dec 2012) was probably time-related. Community structure was still in the process of changing due to grazing exclusion and conservative management, and differences between micro-habitats and related organisms were still incipient. Although the second experiment was shorter (6 months, Dec 2012 – Jun 2013), the higher rates of decomposition of *E. horridum* in conventional paddocks indicate that differences in vegetation structures promoted by different grazing pressures influenced decomposition. Lighter grazing pressures promote more accumulation of dead biomass and higher vegetation height (Figure 6), which probably decreased the rates of the litter decomposition promoted by solar radiation (photodegradation; Pancotto et al. 2005). Higher decomposition rates in grazed paddocks could also have been related to faeces and nitrogen deposition by herbivores (Ruess & McNaughton 1987; Seagle et al. 1992; Bakker et al. 2004), a factor that was absent in the exclusion. However, if such assumption was true, we would expect even higher decomposition rates in the conservative treatment, where density of grazers per hectare was much higher during grazing events, and so was deposition of faeces and urine. Also, decomposition of cellulose did not follow the same pattern, providing further evidence that differences between decomposition were most likely related to grassland canopy openness and the UV radiation incidence, which primarily generate the molecular fragmentation of lignin contributing to litter mass loss (Rutledge et al. 2010). When we separated decomposition results by site, we found out that southernmost sites inserted in the Pampa biome were responsible for most of the differences in decomposition of E. horridum between treatments (Figure 5B). When compared with the Atlantic Forest biome, grasslands inserted in the Pampa biome are characterized by lower canopies and less accumulation of biomass due to higher grazing pressures (Nabinger et al. 2000; Nabinger et al. 2009). Accordingly, vegetation structure showed differences between sites from different biomes prior to the implementation of the experiment we described here (Ferreira et al. unpublished [Capítulo 1]). Recent findings found higher litter decomposition rates in sites with more canopy openness in South Brazilian grasslands, which was probably due to increased photodegradation (Podgaiski et al. 2014).

We reported here differences in grassland vegetation structure and diversity patterns between paddocks that have been submitted to contrasting levels of grazing during four years. Interruption of the disturbance regime caused drastic changes in community parameters by shifting relationships of dominance, removing grazing-tolerant species and benefitting groups of species that were controlled by grazing. Structural differences arising from management exclusion also influenced litter decomposition. Our findings suggest that subtropical grasslands from South America may be in an intermediate position in a gradient of resistance/resilience to grazing in comparison with shortgrass steppes (Milchunas & Lauenroth 1993; Milchunas et al. 1998) and tallgrass prairies (Coffin et al. 1996; Baer et al. 2000). Although four years may be considered a short period of time to evaluate disturbance dynamics in comparison with studies carried out elsewhere (e.g., Knapp et al. 1998; Rees et al. 2001; Turner et al. 2003), this is the first attempt to do so in subtropical grasslands from South America. Also, all sites will be continuously monitored as part of an ongoing LTER (PELD Campos Sulinos; CNPq 558282/2009-1).

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Tables

Table 1. Life form categories used as binary traits to describe grassland plant communities. See details in Ferreira et al. (unpublished [Capítulo 2]).

Life form category	Acronym
Therophytes	Th
Bulbous geophytes	Bg
Rhizomatous geophytes	Rg
Prostate rosette evergreens	Pr
Decumbent evergreens	De
Rhizomatous evergreens	Rh
Stolonoiferous evergreens	St
Solitary evergreen tussocks	Te
Connected evergreen tussocks	Ct
Evergreen forbs	Ef
Erect rosette evergreens	Er
Evergreen subshrubs	Ss
Evergreen shrubs	Sh
Succulent evergreens	Su

Figures

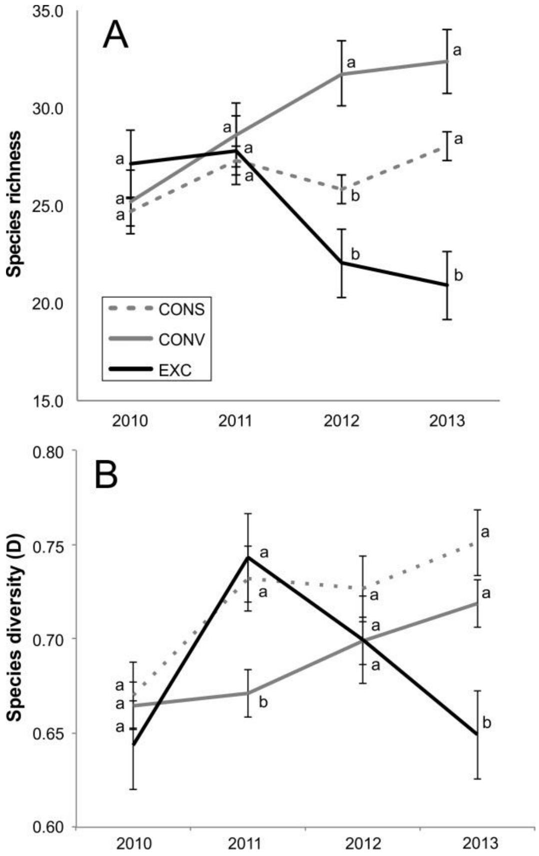

Figure 1. Species richness and diversity along four years under three different grazing treatments: conventional (conv), conservative (cons) and exclusion (exc). Mean values of six paddocks per treatment/year. Different letters correspond to significant differences (P<0.05) within each year.

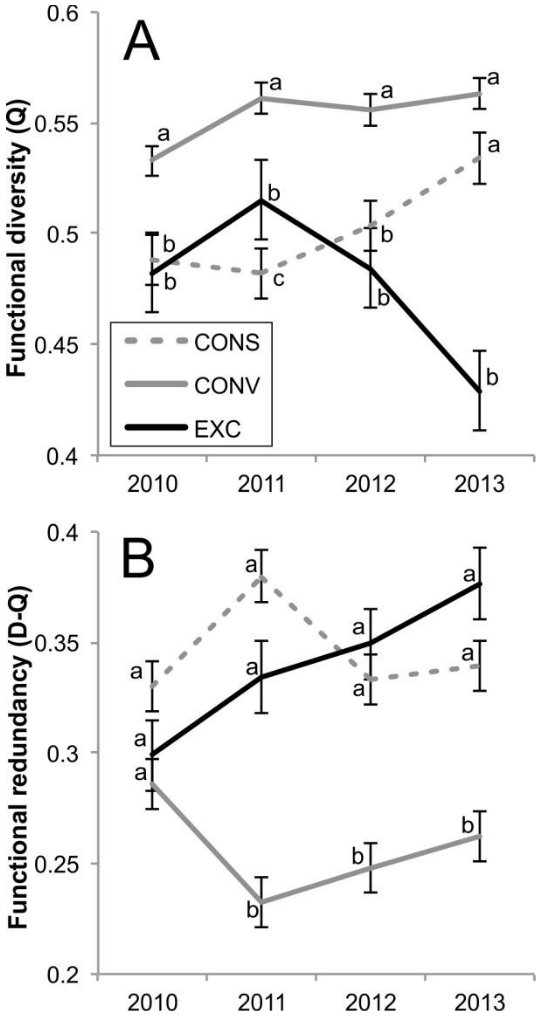

Figure 2. Functional diversity and redundancy along four years under three different grazing treatments: conventional (conv), conservative (cons) and exclusion (exc). Mean values of six paddocks per treatment/year. Different letters correspond to significant differences (P<0.05) within each year.

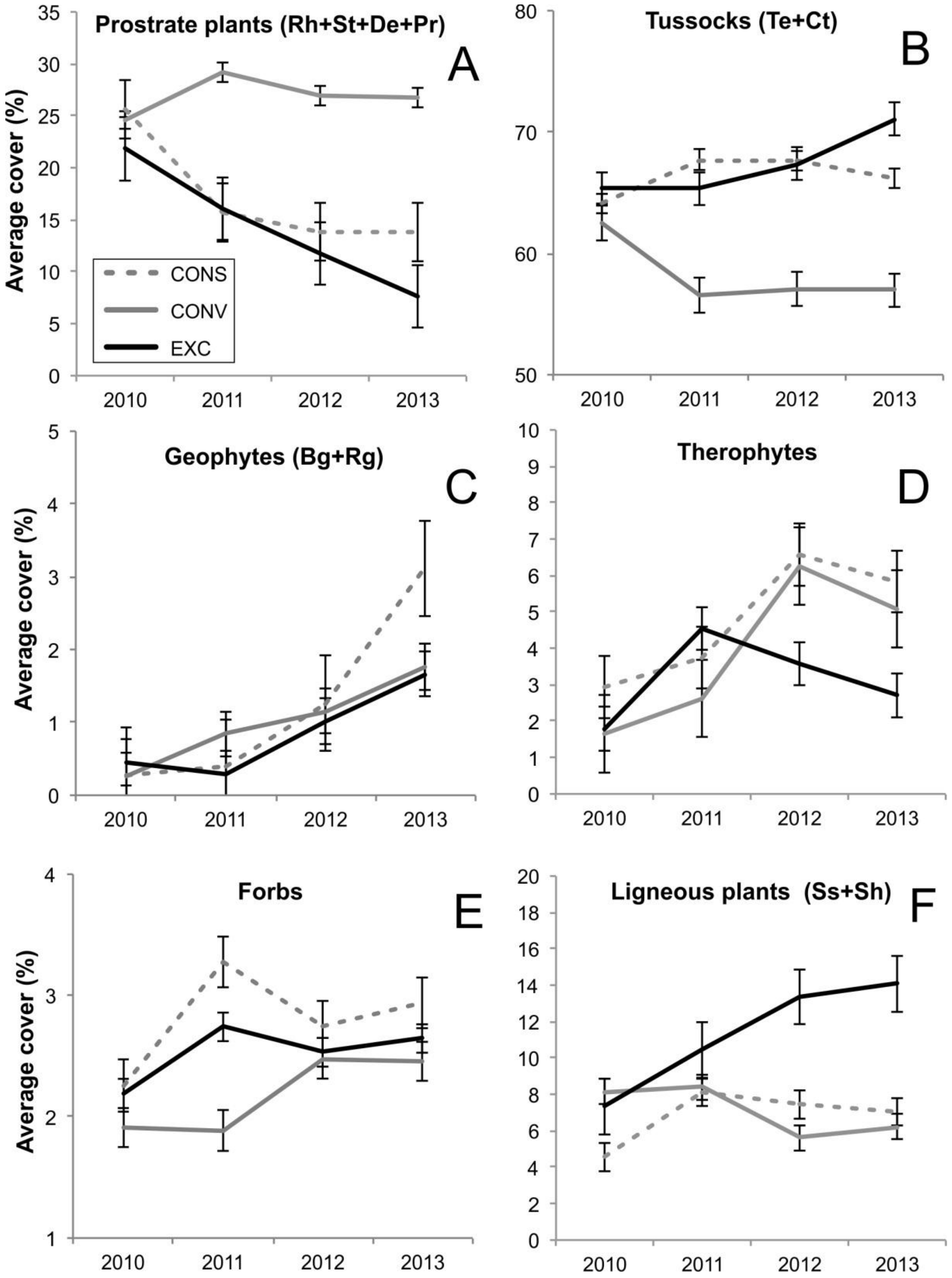

Figure 3. Mean cover values of different life forms along four years under three different grazing treatments: conventional (conv), conservative (cons) and exclusion (exc). Mean values of six paddocks per treatment/year. See Table 1 for life form acronyms.

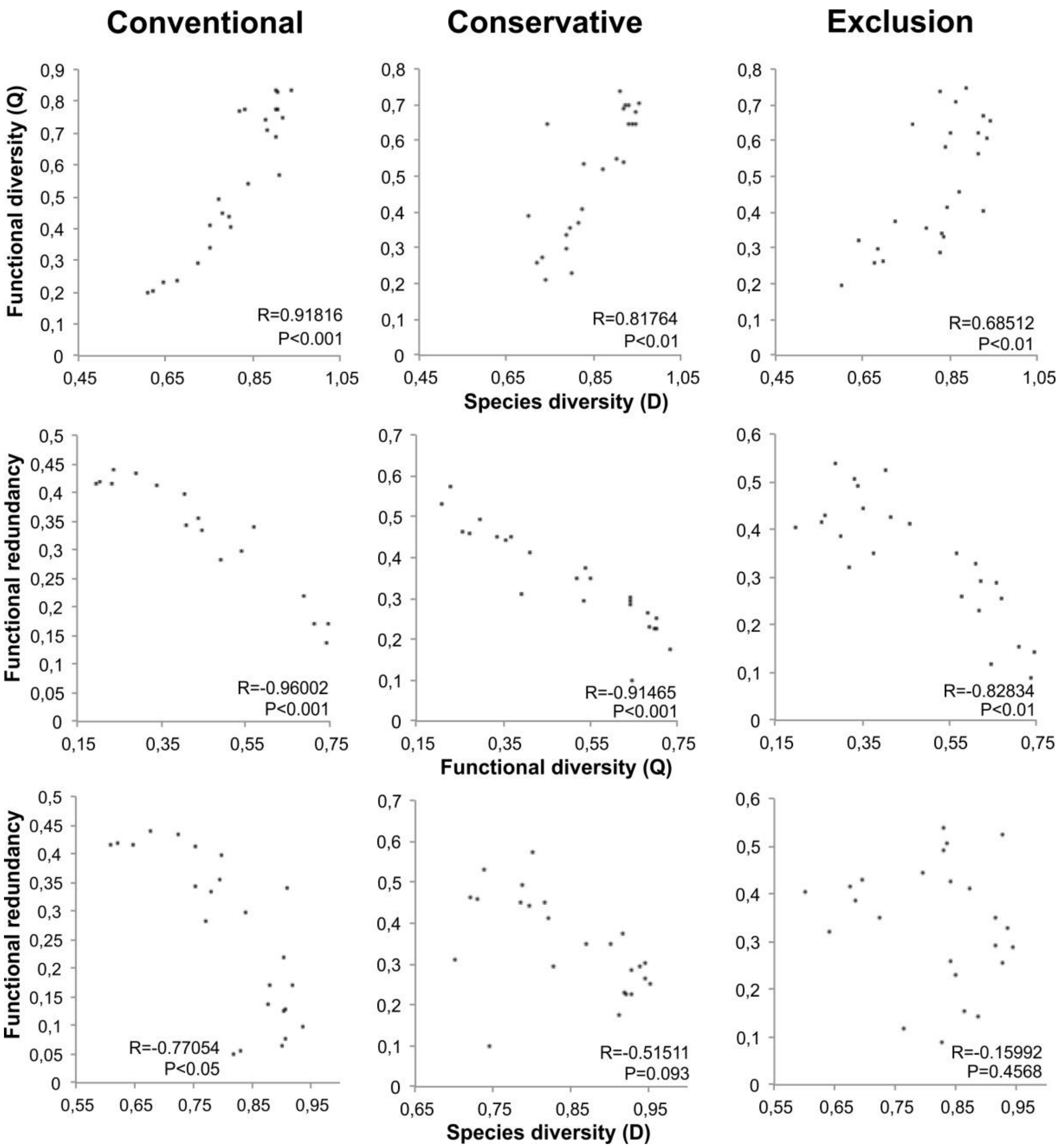

Figure 4. Correlation between functional diversity (Rao's Q), species diversity Simpson's D) and functional redundancy (FR) in grassland communities under three different grazing treatments. Mean values of six paddocks per treatment along four years of sampling (24 paddocks per analysis). Functional redundancy was calculated as FR = D – Q (Pillar et al. 2013). P-values obtained using restricted permutations.

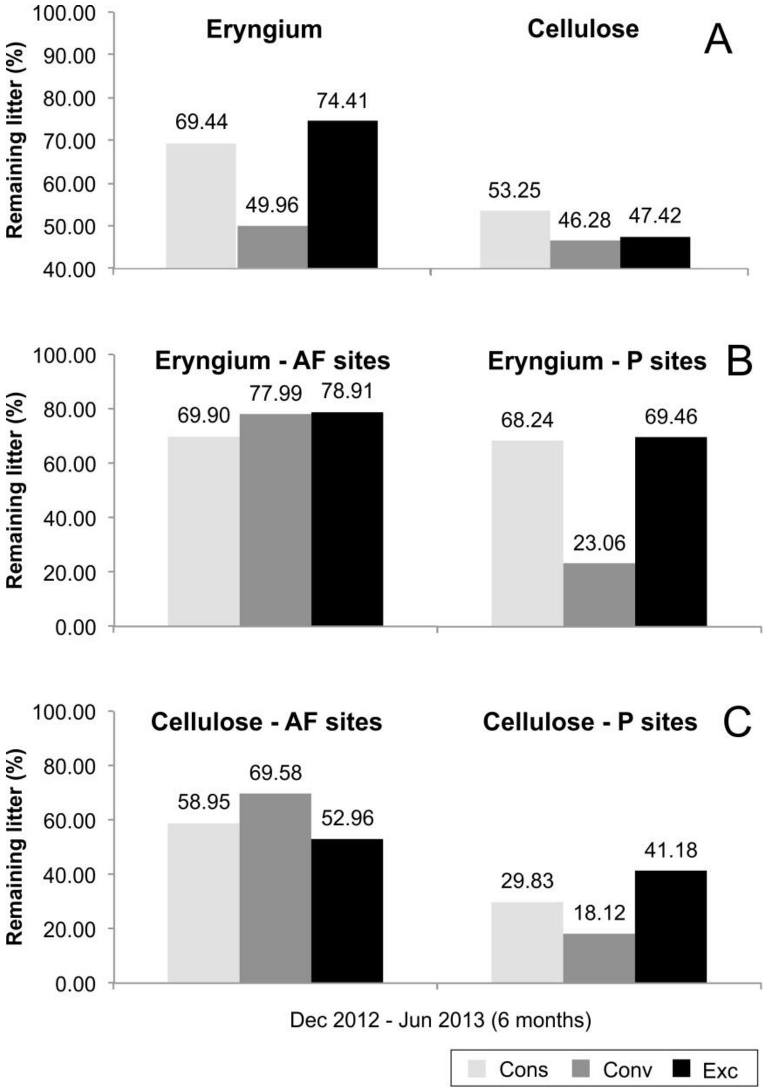

Figure 5. Percentage of litter mass remaining after six months in litter bags containing two different standardized materials (*Eryngium horridum* and cellulose paper), in grassland communities under three different grazing treatments: conventional (conv), conservative (cons) and exclusion (exc). A. Mean values of six sites (six paddocks per treatment). B,C. Mean values separated by biome (three paddocks each) in which sites were inserted (AF = Atlantic Forest; P = Pampa).

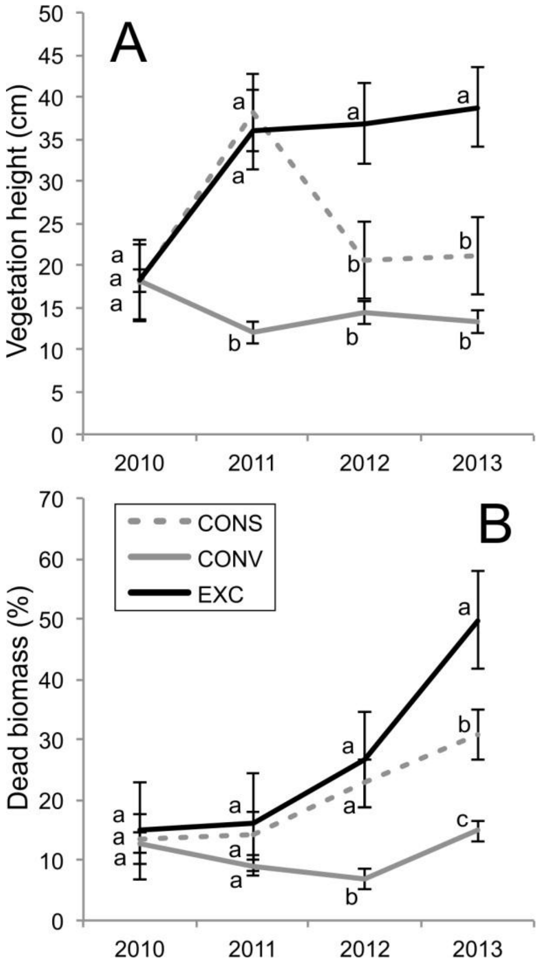

Figure 6. Vegetation height and percentage of dead biomass along four years under three different grazing treatments: conventional (conv), conservative (cons) and exclusion (exc). Mean values of six paddocks per treatment/year. Different letters correspond to significant differences ($P<0.05$) within each year.

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Considerações finais

Trabalhar com vegetação campestre é muito bom. Decidi iniciar esta breve seção final da tese com esta frase porque ela resume minha experiência ao longo do doutorado (e do mestrado também). Eu gosto do que faço, seja em campo de bombacha, bota e chapéu, seja de bermuda e chinelo no computador, brincando no R ou no Multiv. É claro que a companhia ajuda muito: tenho a sorte de trabalhar ao lado de pessoas (na maioria) ótimas. Trabalhar em um projeto grande como o PELD Campos Sulinos foi uma experiência extremamente desafiadora e recompensadora. Tenho orgulho de ter participado do início deste projeto, que tem a ambiciosa meta de estabelecer sítios de pesquisa permanentes (fato ainda raro no Brasil, sobretudo em ecossistemas campestres). Infelizmente não há espaço físico em uma tese de doutorado para inlcuir tudo o que foi feito ao longo de quatro anos (nem tempo para escrever, na verdade). Sei que muitos doutorandos são extremamente focados nas suas teses. Admiro estes colegas, mas eu não sou nada focado. Participei de diversos projetos paralelos nestes quatro anos, especialmente junto ao PPG Ecologia da UFRGS, no Laboratório de Ecologia Quantitativa (ECOQUA, para os íntimos). Provavelmente esta tese teria sido mais organizada, consistente e com mais capítulos se eu não tivesse feito isso, mas não me arrependo de absolutamente nenhum projeto paralelo ou conversa informal de quatro horas com algum colega sobre uma análise legal. Na verdade fui orientado a ser assim (obrigado, Ilsi).

Também é necessário ressaltar aqui o aspecto multidisciplinar de se trabalhar com vegetação campestre. Diferentemente de ecossistemas florestais, os campos bem conservados não estão em unidades de conservação, ou em áreas extremamente inacessíveis. Campos bem conservados estão nas propriedades rurais que bravamente mantêm a pecuária sobre campo nativo em seus mosaicos de produção. Trabalhar nestas propriedades é sair do computador na sala da Universidade e voltar no tempo para um mundo de estradas de chão, gado, cavalos e gaúchos (em extinção) que falam uma língua entre o português e o espanhol. É um processo de imersão cultural que pesquisadores das áreas sociais invejariam. O biólogo ‘típico’ não tem o costume de trabalhar neste meio, que geralmente é mais ligado ao agrônomo, veterinário ou zootecnista. O contato com estes profissionais leva à reflexão sobre conceitos tidos como óbvios nas ciências biológicas. Esta interação deveria ser mais estimulada em programas de pós-graduação, pois leva a um inegável crescimento mútuo advindo de diferentes experiências e visões da diversidade biológica. Trabalhos de várias partes do mundo (incluindo aqui as nossas singelas contribuições) apontam a importância do manejo da vegetação campestre na manutenção da sua diversidade em diversos níveis. Apesar disso, ainda há profissionais das áreas biológicas que consideram áreas de campo manejadas com fogo e/ou gado como ambientes degradados, e que a conservação passa obrigatoriamente pela exclusão total de intervenção humana. Esta visão dogmática desaparece em dez minutos de conversa com um ecólogo de pastagens, mas também com um pecuarista bem informado ou um peão de estância com 40 anos de lida, pois ambos veem na prática o que acontece com uma área campestre não manejada.

Acredito que o conjunto dos dados apresentados nesta tese forme uma contribuição consistente, porém pontual, ao estudo dos ecossistemas campestres do Rio Grande do Sul. O legado mais relevante destes quatro anos de trabalho talvez seja o conjunto bruto de dados obtidos em quatro anos consecutivos de levantamento da vegetação sob diferentes manejos em um experimento controlado. Estes dados serão a referência de comparação para os dados obtidos nos anos subsequentes deste projeto de longa duração.