



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



Tese de Doutorado

BIODIVERSIDADE DE PLANTAS DOS CAMPOS SULINOS:
PADRÕES DE DISTRIBUIÇÃO, DIVERSIDADE BETA E INTERAÇÕES

Luciana da Silva Menezes

Porto Alegre, junho de 2018

BIODIVERSIDADE DE PLANTAS DOS CAMPOS SULINOS:
PADRÕES DE DISTRIBUIÇÃO, DIVERSIDADE BETA E INTERAÇÕES

Luciana da Silva Menezes

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Botânica, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutora em Botânica.

Orientador: Dr. Gerhard Ernst Overbeck

Porto Alegre, junho de 2018

CIP - Catalogação na Publicação

Menezes, Luciana da Silva
Biodiversidade de plantas dos Campos Sulinos:
padrões de distribuição, diversidade beta e interações
/ Luciana da Silva Menezes. -- 2018.
158 f.
Orientador: Gerhard Ernst Overbeck.

Tese (Doutorado) -- Universidade Federal do Rio
Grande do Sul, Instituto de Biociências, Programa de
Pós-Graduação em Botânica, Porto Alegre, BR-RS, 2018.

1. Campos Sulinos. 2. Ecologia de comunidades. 3.
Riqueza. 4. Diversidade beta. 5. Ecologia funcional.
I. Overbeck, Gerhard Ernst, orient. II. Título.

Luciana da Silva Menezes

BIODIVERSIDADE DE PLANTAS DOS CAMPOS SULINOS:
PADRÕES DE DISTRIBUIÇÃO, DIVERSIDADE BETA E INTERAÇÕES

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Botânica, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutora em Botânica.

Aprovada em Porto Alegre, 29 de junho de 2018.

BANCA EXAMINADORA:

Prof. Dr. Pedro Maria de Abreu Ferreira
Pontífice Universidade Católica do Rio Grande do Sul (PUCRS)

Dr. Rodrigo Scarton Bergamin
Universidade Federal do Rio Grande do Sul (UFRGS)

Prof. Dr. Valério De Patta Pillar
Universidade Federal do Rio Grande do Sul (UFRGS)

AGRADECIMENTOS

Ao final desta jornada existem diversas pessoas às quais gostaria de agradecer. Porém, participando de um projeto tão grande como o PPBio Campos Sulinos muito provavelmente não lembrarei de todos envolvidos. Desta forma, se você esteve de alguma forma envolvido no desenvolvimento deste projeto, na concepção da ideia, seleção e delimitação das grades amostrais, contato inicial com os proprietários, ou qualquer outra função que eu não tenha citado, sintam-se contemplados pelo meu muito obrigado!

De forma mais específica agradeço profundamente ao meu orientador, prof. Gerhard Overbeck, por confiar em mim para o desenvolvimento do projeto integrado PPBio Vegetação Campestre. Mais do que isto, por ser um ótimo orientador, ler atentamente meus manuscritos, sempre com opiniões construtivas e contribuindo muito para a escrita desta tese.

Diversas pessoas participaram dos trabalhos de campo do PPBio, porém a mesma equipe foi responsável por 76,9% (sim, eu fiz a estatística) de todos os levantamentos. Cleusa, Dióber e Graziela, obrigada por toda ajuda nos trabalhos de campo! Sem vocês o trabalho teria sido muito mais difícil (impossível) e muito menos legal. Melhor do que todos os agradecimentos que posso oferecer para vocês são as memórias que formamos nas nossas viagens, os lugares que tivemos oportunidade de conhecer e todas as aventuras que vamos lembrar sempre nas conversas de bar.

Aos professores Ilsi Boldrini, Rafael Trevisan e Sérgio Bordignon, agradeço muito por compartilharem seu conhecimento, me auxiliando na identificação das plantas coletadas. Agradeço também aos colegas especialistas que me auxiliaram identificando as espécies de plantas dos gêneros com os quais trabalham: Camila Ignácio (Iridaceae/Sisyrinchium), Cleusa Vogel (Hypericaceae/Hypericum), Cristiano Buzatto (Orchidaceae), Dióber Lucas (Apiaceae/Eryngium), Fernanda Silveira (Fabaceae/Mimosa), Marlon Franco (Lythraceae/Cuphea), Michele Nervo (Pteridófitas), Pedro Joel (Cyperaceae/Rhynchospora), Rodrigo Ardizzone (Cyperaceae/Bulbostylis), Silviane Pesamosca (Onagraceae/Ludwigia). Provavelmente esqueci de vários, mas sintam-se todos agradecidos.

Em especial à professora Ilsi agradeço duplamente pelo agradável convívio diário no laboratório, as conversas na hora do café (ou a qualquer hora) e por sempre ceder a sua casa como uma segunda sede para o nosso laboratório. Falando em laboratório, não posso deixar de agradecer imensamente a toda turma do LEVCamp pela convivência alegre. Esse laboratório é um lugar onde sempre se encontra ajuda, tanto para o trabalho como para dividir as angústias da pós-graduação. Também se encontra facilmente no LEVCamp: um café, alguma coisa para comer (que provavelmente voltou de algum campo e nem sempre está na validade) e uma cerveja ou derivado na geladeira. É um local de convívio bastante saudável, recomendo.

Diversas pessoas participaram do projeto PPBio como estagiários, dedicando um pouco de seu tempo para colaborar no trabalho de campo ou nas identificações do material coletado. Silviane, Fernanda e Lukiel, vocês me ajudaram muito na organização do material coletado, sem essa ajuda estaria até agora embaixo de uma pilha de coletas que não passavam de um raminho com duas folhas (às vezes uma folha).

Agradeço ao PPG Botânica e à CAPES pela bolsa de doutorado concedida e ao Ministério da Ciência, Tecnologia, Inovações e Comunicações (MCTIC) pelo financiamento concedido ao projeto PPBio Vegetação Campestre (nº CNPq 457447/2012-5).

SUMÁRIO	
RESUMO GERAL	4
GENERAL ABSTRACT	5
INTRODUÇÃO GERAL	6
<i>Objetivo geral</i>	7
<i>Objetivos específicos</i>	7
Referências	7
CAPÍTULO 1: <i>Reference values and drivers of diversity for the South Brazilian grassland plant communities</i>	9
Abstract	11
Introduction	12
Material and methods	15
<i>Study region</i>	15
<i>Sampling design and procedures</i>	15
<i>Environmental variables</i>	16
<i>Data analysis</i>	17
Results	20
Discussion	22
<i>Environment-vegetation relations reflecting grasslands groups</i>	23
<i>Evenness, richness and diversity patterns</i>	25
<i>Establishing reference values for conservation and restoration</i>	26
Acknowledgements	28
References	28
Supplementary material	42
CAPÍTULO 2: <i>Plant species richness record in Brazilian Pampa grasslands and implications</i>	67
Abstract	69
Introduction	70
Materials and methods	72
Results	73
Discussion	76
<i>Need for conservation on private lands</i>	76
<i>Need for more field-based biodiversity assessments</i>	77

<i>Necessity to train field researchers</i>	78
Acknowledgements	79
References	80
Supplementary material	86
CAPÍTULO 3: <i>Spatial dependency of drivers and patterns of β-diversity, turnover and nestedness</i>	89
Highlights	90
Abstract	92
1. Introduction	93
2. Material and Methods	95
2.1. Study area	95
2.2. Spatial scale design	95
2.3. Data Analysis	96
2.4. Predictive variables	97
3. Results	99
4. Discussion	101
4.1. Do β-diversity, turnover and nestedness depend on the spatial scale?... 102	
4.2. Are there specific drivers for nestedness or turnover at the different spatial scales?	103
4.3. Implications for conservation decisions	104
References	105
Supplementary material:	109
Supplementary material	111
CAPÍTULO 4: <i>Functional beta diversity reveals hidden interactions: shrubs as keystone features for spiders</i>	115
Abstract	117
1. Introduction	117
2. Material and methods	119
2.1. Vegetation sampling and plant traits	120
2.2. Spider sampling and traits	120
2.3. Statistical analysis	122
3. Results	124
4. Discussion	125

<i>Functional diversity at alpha and gamma scales</i>	126
<i>Alpha diversity dependent, not only, of the specie pool</i>	126
<i>Functional beta diversity and shrubs influence</i>	127
References	129
Biosketch	131
Supplementary material	132
CONSIDERAÇÕES FINAIS	152

RESUMO GERAL

Os Campos Sulinos se estendem desde o extremo sul do estado do Rio Grande do Sul (RS) até o estado Paraná (PR). Na metade sul do RS os campos são predominantes e estão compreendidos pelo bioma Pampa, da metade norte do RS até o PR eles são representados por encraves campestres no bioma Mata Atlântica. Nesta tese, apresento resultados de uma pesquisa em ampla escala sobre a biodiversidade dos Campos Sulinos obtida em uma amostragem com desenho espacialmente aninhado e padronizado. No **primeiro capítulo** apresentamos uma descrição das comunidades de plantas, e valores de referência para conservação e restauração. Adicionalmente, observamos que as características de solo diferem entre os campos dos dois biomas e também evidenciamos a homogeneização das comunidades vegetais, provavelmente causada pelo pastejo excessivo. Um registro recorde de riqueza de plantas por metro quadrado é apresentado no **segundo capítulo**, aproveitamos para discutir questões relacionadas à conservação dos campos e a necessidade de maior reconhecimento dos estudos de base que envolvem levantamento da vegetação, também a importância de formar profissionais capacitados para reconhecer a biodiversidade dos campos. No **terceiro capítulo** a diversidade beta da vegetação campestre foi decomposta entre componentes de substituição de espécies (*turnover*) e aninhamento, buscamos quais fatores ambientais ou espaciais geram esses padrões em diferentes escalas. O padrão dominante nos Campos Sulinos é o *turnover* de espécies, na escala ampla esse padrão é gerado por filtros ambientais, que também geram aninhamento de espécies nesta escala. Na escala refinada a distância espacial foi a principal responsável pelo aninhamento e os resultados para *turnover* foram variáveis em cada local. No **quarto capítulo** testamos, com base na teoria da heterogeneidade de habitats, se a biodiversidade de plantas é determinante para comunidade associada de aranhas. A diversidade funcional de plantas afetou positivamente a diversidade funcional de aranhas nos níveis alfa e gama, porém para diversidade beta a relação foi inversa. Este padrão foi explicado pela cobertura de arbustos, que indica condições de pastejo amenas, favorecendo a manutenção de altos níveis de diversidade funcional alfa de aranhas ao longo de todas as unidades amostrais (baixa div. beta). As informações apresentadas nesta tese nos auxiliam a aprofundar de nosso conhecimento sobre as relações ecológicas da vegetação campestre com o ambiente, espaço e com outros grupos tróficos. Também contribuimos para geração de um amplo banco de dados sobre comunidades vegetais campestres que possui potencial para responder muitas outras questões sobre a dinâmica e ecologia dos Campos Sulinos.

Palavras-chave: campos; comunidades; ecologia funcional; riqueza; PPBio.

GENERAL ABSTRACT

The Campos Sulinos grasslands extend from the extreme south of Rio Grande do Sul state (RS) to Paraná state (PR). Grasslands dominate the landscapes in the southern half of RS, corresponding to the Brazilian Pampa Biome, while those in the northern half of RS and northwards are part of the Atlantic Forest Biome. In this thesis, I present results of a broad-scale study about Campos Sulinos biodiversity obtained in a nested and standardized sampling design. In the **first chapter**, we present a description of plant communities, considering alpha and beta diversity and its components, and reference values for conservation and restoration. Additionally, we found that soil characteristics differ among grasslands from the two regions and also evidenced homogenization of plant communities, probably related to overgrazing. A record register of plant species richness per square meter is presented in the **second chapter**; we took advantage of this register to discuss questions regarding grassland preservation, training of professionals and the need of higher valuation of field-based studies and vegetation description. In the **third chapter**, the beta diversity of grassland vegetation was decomposed into components of species substitution (turnover) and nestedness, and we looked for the environmental and spatial drivers of these patterns at different spatial scales. The dominant pattern in the *Campos Sulinos* is species turnover, at broad scale this pattern was driven by environmental filters that also are responsible for driving nestedness patterns at this scale. At the fine spatial, scale spatial distance was the most important driver of nestedness, while turnover drivers at this scale were very variable. In the **fourth chapter**, we tested, based on habitat heterogeneity theory, whether plant community biodiversity is determinant for the associated spider community. Plant functional diversity affected functional alpha and gamma diversities of spider communities positively. In contrast, for beta diversity the relationship was negative. This pattern was explained by shrub cover, associated to medium levels of grazing intensity, which favours the maintenance of higher levels of spider alpha functional diversity along all sampling units (low beta functional diversity). The results presented in this thesis help us to deepen our knowledge about ecological relationship of grassland plant communities and the environment, space and different trophic groups. We also contributed to create an extensive database on grassland plant community that harbors the potential to answer many other questions regarding ecological dynamics of the Campos Sulinos.

Key words: grasslands; community; functional ecology; richness; PPBio.

INTRODUÇÃO GERAL

Estima-se que no mundo ocorra aproximadamente 8,7 milhões de espécies (Mora et al., 2011), muitas dessas ainda desconhecidas pela ciência. Dentre as espécies cientificamente identificadas, um pequeno grupo recebe especial atenção, seja por apelo emocional ou por sua utilidade reconhecida para qualquer fim de interesse humano. Contudo isso não significa que as demais espécies são menos importantes, apesar de nem todas possuírem uma utilização econômica evidente, todas as espécies desempenham algum papel nos ambientes naturais.

Biodiversidade, conforme definido na Convenção Sobre Diversidade Biológica da Eco-92 (Decreto Legislativo nº 2, de 1994), diz respeito à variabilidade de organismos vivos de todas as origens. Compreende, dentre outros, os ecossistemas terrestres, marinhos e outros ecossistemas aquáticos e os complexos ecológicos de que fazem parte, incluindo a diversidade dentro de espécies, entre espécies e de ecossistemas. O conceito de biodiversidade valoriza as espécies por seu conjunto mais do que por sua individualidade. De fato, as iniciativas de conservação têm dado maior atenção para a biodiversidade de forma geral do que para as espécies separadamente (Heywood & Iriondo, 2003), por reconhecer que a interação entre as diferentes espécies e dessas com o meio é que promove os serviços ecossistêmicos, necessários para sobrevivência de todos os seres vivos.

Podemos pensar na biodiversidade e nos serviços ecossistêmicos como uma máquina funcionando com diversas engrenagens, retirando alguma dessas engrenagens a máquina pararia de funcionar, ou desempenharia sua função com muito mais dificuldade. Nessa analogia, as engrenagens são as espécies e remover uma engrenagem pode significar a extinção local ou definitiva de alguma espécie. Agora imagine que você sabe muito pouco sobre essa máquina, são tantas engrenagens que você não conhece todas, entende muito pouco sobre a função individual de cada uma e entende muito menos sobre o que aconteceria se uma ou outra fosse removida. É neste ponto que nos encontramos em relação à biodiversidade, principalmente em ambientes que foram historicamente negligenciados, como os Campos Sulinos (Overbeck et al., 2007; Pillar et al., 2009).

Na região do cone sul da América do Sul a vegetação campestre é predominante, se estendendo amplamente. No Brasil os campos se distribuem largamente no bioma Pampa e, entremeados com a floresta ombrófila mista, no bioma Mata Atlântica. Ao conjunto dessas formações campestres sul brasileiras denominamos Campos Sulinos (Pillar et al., 2009), que guarda uma riquíssima biodiversidade. O principal enfoque desta tese é a biodiversidade das plantas dessa região. Assim, esta tese foi elaborada com o objetivo de profundarmos os nossos conhecimentos sobre os Campos Sulinos de forma linear e crescente, acrescentando

complexidade ao longo dos capítulos. Dessa forma, cada um dos quatro capítulos aborda um tema específico, entrelaçados pelo tema geral.

Objetivo geral

Aprofundar o conhecimento existente sobre a vegetação campestre dos Campos Sulinos, abordando padrões de distribuição da biodiversidade, relacionando com filtros ambientais e espaciais e também explorar interações com outros grupos tróficos.

Objetivos específicos

- ❖ **Capítulo 1:** Descrever os padrões de distribuição espacial da biodiversidade de plantas dos Campos Sulinos, com base nos dados do projeto Programa de Pesquisa em Biodiversidade (PPBio) Vegetação Campestre. Relacionar os padrões de distribuição da vegetação com variáveis de solo.
- ❖ **Capítulo 2:** Reportar um registo de alta riqueza de espécies por metro quadrado nos Campos Sulinos, considerado um recorde. A partir deste registo, discutir pontos críticos para conservação: (i) se políticas conservacionistas estão incluindo áreas privadas que possuem alta riqueza de plantas; (ii) a valorização de estudos que realizam inventários da biodiversidade; (iii) a formação de profissionais capazes de identificar a biodiversidade dos Campos Sulinos.
- ❖ **Capítulo 3:** Utilizando diferentes escalas espaciais, analisar os padrões de substituição de espécies (*turnover*) e perda de espécies (aninhamento), na diversidade de plantas dos Campos Sulinos. Investigar se os padrões são mais relacionados com clima, solo ou espaço, nas diferentes escalas.
- ❖ **Capítulo 4:** Investigar de que forma a biodiversidade de plantas dos Campos Sulinos interage com a biodiversidade de aranhas, sob a ótica da diversidade funcional e também em diferentes escalas espaciais.

Referências

- Heywood, V.H. & Iriondo, J.M. (2003) Plant conservation: Old problems, new perspectives. *Biological Conservation*, **113**, 321–335.
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B., & Worm, B. (2011) How many species are there

on earth and in the ocean? *PLoS Biology*, **9**, 1–8.

Overbeck, G.E., Müller, S.C., Fidelis, A., Pfadenhauer, J., Pillar, V.D., Blanco, C., Boldrini, I.I., Both, R., & Forneck, E. (2007) Brazil's neglected biome: The South Brazilian Campos. *Perspectives in Plant Ecology Evolution and Systematics*, **9**, 101–116.

Pillar, V.D., Müller, S.C., Castilhos, Z., & Jacques, A.V.A. (2009) *Campos Sulinos - conservação e uso sustentável da biodiversidade*. Brasília.



CAPÍTULO 1

Reference values and drivers of diversity for the South Brazilian grassland plant communities

Luciana da Silva Menezes, Cleusa Vogel Ely, Dióber Borges Lucas, Graziela Har
Minervini-Silva, Eduardo Vélez-Martin, Heinrich Hasenack, Rafael Trevisan, Ilsi Iob
Boldrini, Valério D. Pillar e Gerhard Ernst Overbeck

Manuscrito submetido ao periódico *Brazilian Journal of Botany*.

Original article

Title

Reference values and drivers of diversity for the South Brazilian grassland plant communities

Authors

Luciana da Silva Menezes ^{1*} (orcid.org/0000-0002-2961-0190)

Cleusa Vogel Ely ¹ (orcid.org/0000-0001-9094-9524)

Dióber Borges Lucas ¹ (orcid.org/0000-0002-3293-492X)

Graziela Har Minervini-Silva ¹ (orcid.org/0000-0003-3835-7753)

Eduardo Vélez-Martin ² (orcid.org/0000-0001-8028-8953)

Heinrich Hasenack ³ (orcid.org/0000-0002-8521-1266)

Rafael Trevisan ⁴ (orcid.org/0000-0002-4817-3141)

Ilsi Iob Boldrini ^{1,5} (orcid.org/0000-0003-1028-8864)

Valério D. Pillar ² (orcid.org/0000-0001-6408-2891)

Gerhard Ernst Overbeck ^{1,5} (orcid.org/0000-0002-8716-5136)

Laboratório de Estudos em Vegetação Campestre, Programa de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul ¹

Laboratório de Ecologia Quantitativa Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul ²

Laboratório de Geoprocessamento, Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul ³

Departamento de Botânica, Universidade Federal de Santa Catarina ⁴

Departamento de Botânica, Universidade Federal do Rio Grande do Sul ⁵

* Correspondence author: 9500 Bento Gonçalves Av., CEP 91501-970, Porto Alegre, RS, Brasil. E-mail: luciana.menezes@ufrgs.br

Abstract

The South Brazilian grasslands (*Campos Sulinos*) form the dominant vegetation in southern Brazil. They are rich in plant species and occur under distinct geomorphological and climatic conditions but diversity spatial variation remains unknown. Here, we present a detailed description of plant communities across the region. Our data were obtained in 1080 plots, representing well-preserved grasslands in different ecological systems. Apart from describing alpha and beta diversity, we investigated the relations of plant communities with environmental features. We identified 759 plant species and found clear differences in community composition across the region. Highland grasslands, coastal grasslands and the inland Pampa grasslands were clearly distinct, related to climatic and edaphic features. While species abundance distribution was markedly uneven, local species richness was high, above 20 species/m² (except for coastal grasslands), especially in the Highlands and in Pampa sites on shallow soil. The predominant component of beta diversity was species turnover, which suggests that a network of well-conserved grasslands distributed across the region would be the best strategy to protect plant diversity. Our results establish regionalized reference values for richness and diversity that can be useful for initiatives of restoration and conservation of these grasslands.

Key words: beta diversity; conservation; diversity; environmental gradient; grassland; South Brazilian grasslands; species richness; turnover.

Introduction

Knowledge on biodiversity remains severely limited in many countries around the world, including Brazil, jeopardizing the conservation of natural resources (Bini *et al.* 2006, Oliveira *et al.* 2017). In the *Campos Sulinos* region (hereafter South Brazilian grasslands), located in the southernmost part of the country, we have seen an increase in the number of plant community studies over the last 25 years, but with a clear bias to few regions, primarily those situated close to research institutions (see Boldrini & Overbeck 2015). Only very recently the first comprehensive study on grasslands in the entire region was published (Andrade *et al.* 2019). This study used data obtained in standardized sampling at a total of 156 sites. It provided an important first step towards knowledge of grassland plant communities in the region as a whole. It also established, for the first time, a classification of South Brazilian grasslands based on quantitative data, confirmed floristic differences between Pampa and highland grasslands and defined indicator species for different grassland types. Quantitative vegetation sampling – as opposed to the recording of floristic lists – is of specific relevance for biodiversity science. Only quantitative data allows to understand the processes behind community assemblage, for instance by considering patterns of species co-occurrence, relationships between vegetation and environmental factors, and how plant species themselves may modify the local environment (Weiher & Keddy 2004; HilleRisLambers *et al.* 2012). Importantly, data from quantitative sampling may also be of relevance for environmental planning (Magnusson *et al.* 2005).

Understanding diversity changes across space (i.e. beta diversity) is essential to unveil the factors driving community structure, including deterministic processes (such as environmental filtering, species interactions) and neutral processes (such as random extinctions and ecological drift) (Chase & Myers 2011). Environmental filters are much

considered as drivers of plant community assembly (Laliberté *et al.* 2014). Understanding relationships between different drivers not only allows us to interpret current vegetation dynamics, but also to develop scenarios for the future, for example, in the face of climate changes, and to reveal particular habitat characteristics that need to be protected or restored. Moreover, the decomposition of beta diversity patterns into their turnover and nestedness components may be crucial to guide conservation (Socolar *et al.* 2016). When beta diversity is mainly due to species substitution from one site to the next (turnover), the best conservation option is to target multiple sites. However, when it is due to species loss from a richer set to a poorer one (nestedness), it may be more efficient to target the richest site. Importantly, both relations of environmental factors to biodiversity patterns and effective conservation strategies will vary with spatial scale (Bini *et al.* 2006).

Given that most parts of the globe are influenced by human activities, it is important – apart from the obvious and urgent need to reduce pressure on the environment and on biodiversity in general – to study biological communities and their ecological determinants in well-conserved regions in order to obtain reference data for conservation and restoration purposes. This is true for regions under rapid land-use change, such as the South Brazilian grasslands (Andrade *et al.* 2015), which include the Pampa grasslands, in the southern half of Rio Grande do Sul state, and the highland grasslands in the southernmost part of the Atlantic Forest (IBGE 2019; Overbeck *et al.* 2007; Andrade *et al.* 2019). A recent study conducted in the region has shown that even grassland areas in regions with an intermediate degrees of habitat loss (areas with more than 50% of natural grasslands), are affected by land-use change: suppression of grasslands leads to homogenization of remnant plant communities and to species losses within them (Stade *et al.* 2018). Furthermore, conservation through sustainable use (Boavista *et al.* 2019) and active restoration (Thomas *et al.* 2019) are increasingly relevant topics in the region but

are still in need of conceptual underpinning and field evidence, also to support restoration or conservation goals (e.g. Prach *et al.* 2019).

Here, we use the field data obtained in the PPBio *Campos Sulinos* project to investigate and discuss diversity patterns of the South Brazilian grasslands plant communities. The Brazilian Research Program on Biodiversity (acronym PPBio, from *Programa de Pesquisa em Biodiversidade*), established in the context of the Convention on Biological Diversity, includes a total of fifteen grids in the South Brazilian grassland region in which grassland plant communities, forest tree communities, amphibians, birds and fishes were sampled (e.g. Dala-Corte *et al.* 2016; Madalozzo *et al.* 2017; Fontana *et al.* 2018). Our first objective is to establish reference values for grassland plant community descriptors such as species richness and diversity at different spatial scales for use in grassland conservation and restoration. We present reference values for soft (easy to access) and popular indexes, such as species richness and Shannon diversity, but also more ecological meaningful indexes, as beta diversity and its components (turnover and nestedness). This kind of information so far has rarely been available in a comparative fashion beyond the point (i.e. sampling unit) scale, as studies often vary in terms of sampling design. Our second objective was to explore the relationship between species distribution patterns and environmental or spatial filters. Due to the large extent of the entire gradient (660 km) and differences in altitude (from the sea level to more than 900 m.a.s.l.), we expected to find strong effects of spatially structured climatic filters shaping species distribution patterns, especially related to temperature and precipitation.

Material and methods

Study region

The South Brazilian grasslands span the three southernmost states of Brazil, under subtropical climate, with the proportion of grasslands in the landscape increasing towards the south (Fig. 1). The climate in the region ranges from Cfa, at lower altitudes, to Cfb at altitudes above 600 m (Alvares *et al.* 2013). Precipitation is well distributed over the year, without a dry season, and ranges from 1000 mm to 2200 mm, with highest values in the north-eastern part of the region (Alvares *et al.* 2013). Historical data (2006 to 2016) indicates high rainfall variability: the average monthly rainfall in the driest year was 86 mm in Jaguarão municipality (coordinates 32°14' S; 53°46' W) and 341 mm in the rainiest year in Alegrete municipality (coordinates 29°46' S; 55°23' W). Different types of geological substrate occur in the study region: igneous volcanic rocks (basalt) in the northern part, igneous plutonic and metamorphic rocks (granite) in the south, and sedimentary material in the coastal region (for details on geology and soils see Andrade *et al.* 2019). Most grasslands in the region are under grazing regime by domestic livestock and fire is commonly used as a management tool only in the highland grasslands (Overbeck *et al.* 2007; Andrade *et al.* 2015). Both processes, fire and grazing, are known to influence vegetation structure and composition (e.g. Koch *et al.* 2016; Overbeck *et al.* 2018; Boavista *et al.* 2019). Under moderate intensity or frequency, they are considered key processes for maintenance of the characteristics of natural systems, as in other productive grassland systems around the world (Lezama *et al.* 2014).

Sampling design and procedures

PPBio sites were established in the different ecological systems defined for Rio Grande do Sul state by Hasenack *et al.* (submitted) and, additionally, in Santa Catarina

and Paraná states. Grassland vegetation sampling was conducted at eight sites in the Pampa grasslands and four sites in the highland grasslands (Fig. 1), i.e. with one site in each ecological system. Note that ecological systems are defined based on geomorphological/landscape features, not vegetation (see Hasenack *et al.* (submitted) for details). For site selection, an area of 5 km x 5 km with a low degree of conversion to other land uses was chosen in each ecological system. In the *Aristida* grassland system, located within the Pampa grasslands, where land-use change is especially strong (Andrade *et al.* 2015) it was not possible to find areas matching this requirement; this system thus was not considered in our study. At each site, a 5 km wide grid of five vertical lines and five horizontal lines was drawn with the orientation angle set to encompass grasslands remnants. From the 25 intersection points, nine were randomly chosen as sampling sites (totalling 108 sampling sites across the 12 grids). At each sampling site, we placed 10 plots (1 m x 1 m), equally distributed along a line of 250 m that followed the isocline to reduce heterogeneity. In each plot, the cover of all vascular plant species was estimated. All study sites were under grazing.

Field sampling was conducted during spring and summer in 2014, 2015, and 2016, and plant communities at each site were sampled only once. All vascular plants had their taxonomic identity verified with specific literature. Nomenclature follows the Brazilian Floristic List (BFG 2015).

Environmental variables

We obtained edaphic and climatic data for all 108 sampling sites. Soil samples were collected in three points per sampling site, until a depth of 30 cm whenever possible (but never less than 15 cm). The three samples were mixed into one combined sample. Chemical and physical soil features were analysed following protocols presented by

Tedesco *et al.* (1995). We considered the following edaphic variables (see Table. 1 for measurements units and analytical method for soil variables): percent of clay, percent of coarse sand, percent of fine sand, percent of silt, organic matter, pH, phosphorus, potassium, nitrogenous, aluminium, calcium, magnesium, cation exchange capability, base saturation and aluminium saturation. Complete data can be found in supplementary files (Suppl. 1 to 3).

Climatic data were obtained from 33 meteorological stations of the *Instituto Nacional de Meteorologia* (INMET), for a ten-year time series (2006 to 2016). Data from meteorological stations were interpolated through inverse distance weighting and extracted to the sampling sites coordinates with the help of Qgis software (version 3.4.10). We extracted the following variables: maximum daily temperature, minimum daily temperature, minimum daily air humidity, maximum monthly precipitation and minimum monthly precipitation.

As climatic variables are intrinsically spatially structured, we took into account the spatial distance among sampling sites by extracting ordination axes of a principal coordinate analysis based on central spatial coordinates of the sampling sites (MEM axes, Borcard *et al.* 2011). To produce the MEMs, the matrix of distance among pairs of coordinates must be truncated at the smallest distance that keeps all points connected, the truncation distance here was 221.2 km.

Data analysis

First, the sampling sites and sites were described by cover and species richness of plant families. To characterize the vegetation at each site, we calculated indexes of richness (S), Shannon diversity (H') and equivalent richness per site. Richness was additionally indicated on the sampling site and plot levels, always per grid. Equivalent

richness was calculated through the exponential of H' ; this estimate how many species with equitable abundances would be required to obtain the same value of H' (Magurran 1988). Once Shannon diversity may produce biased values dependent of species richness (alpha diversity) (see Jost (2006) for further discussion), we additionally calculated entropy of order 1 based on Hill numbers (Chao *et al.* 2014) to better describe grassland community diversity. To further describe plant species abundance relationships in the communities, we also calculated the evenness index (E), which expresses the ratio between observed diversity and maximum diversity (i.e., if all species were equally abundant in communities) (Magurran 1988).

We explored patterns of spatial heterogeneity in species composition by calculating beta diversity and its components, turnover and nestedness. We used the Jaccard-based multiple-site dissimilarity index (β -jac) to calculate beta diversity, turnover and nestedness (Baselga 2012), comparing species composition among the nine sampling sites at each site and thus obtaining one value representative of the heterogeneity per site.

In order to elucidate the relationship of plant species distribution patterns and the soil and climate characteristics, we performed a redundancy analysis (RDA) based on the Hellinger-transformed matrix of relative species cover per sampling site (Legendre & Gallagher 2001). We also performed a variance partitioning analysis (Borcard *et al.* 2011) to verify how much of compositional variance is related only to the environment (climate and soil), only to space (MEM) and to the shared effect of environment and space. To avoid inflation in both procedures, we first removed all environmental variables that had a collinearity factor greater than 10 (Oksanen *et al.* 2017). Collinearity was accessed using a variance inflation factor calculated for each environmental explanatory variable using the r^2 value of the regression of that variable against all other explanatory variables. As ordination axes, MEMs have the characteristic of being orthogonal to each other (Borcard

et al. 2011), and do not present collinearity. The remaining variables were submitted to forward selection of predictive variables. This procedure adds and drops variables in a model, aiming to maximize R^2 at every step, the procedure stops when the R^2 starts to decrease, or when the R^2 of the scope is exceeded (R^2 with all explanatory variables = 0.34), or when the p-value threshold ($p > 0.05$) is exceeded (Blanchet *et al.* 2008).

Based on plant species distribution, we tested if we could observe groups of plant communities within the South Brazilian grasslands. We performed a hierarchical clustering analysis, based on UPGMA method and using Jaccard-based pairwise species turnover, comparing pairs of sampling sites. Consistency of groups was tested with approximately unbiased p-values obtained via 999 multiscale bootstrap resampling (Shimodaira 2004). Groups with $p < 0.05$ were considered consistent. The dendrogram was cut at the height of 0.75, and the resultant five consistent and ecological meaningful groups were selected to discussion.

The analyses were performed in the R environment. Package ‘iNEXT’ and function ‘ChaoShannon’ were applied to calculate metrics of Shannon diversity and Hill numbers of order 1 (Chao *et al.* 2014). Package ‘betapart’ was used to calculate beta diversity, turnover and nestedness (Baselga & Orme 2012). From the package ‘vegan’ (Oksanen *et al.* 2017), we used functions ‘vif.cca’ to verify for collinearity in explanatory variables, ‘ordistep’ to perform forward selection of explanatory variables, ‘rda’ to run redundancy analysis and ‘varpart’ to run variance partitioning analysis. Hierarchical Clustering analysis was performed with the ‘pvclust’ package, function ‘pvclust’ (Suzuki & Shimodaira 2015).

Results

At the twelve sites (total of 108 sampling sites and 1080 plots), 759 plant species from 72 families were found (see Suppl. 2 for complete species list). Plants that could not be identified to the species level corresponded to 4% of total vegetation cover and were excluded from statistical analysis. The most species-rich families were Poaceae (154 species; Fig. 2b), Asteraceae (136), Cyperaceae (65), and Fabaceae (58). Considering species cover, clearly Poaceae stood out as the most important family (64.6%; Fig. 2a).

From the 759 plant species found, almost half (308) occurred in both Pampa and Highland grasslands. The Pampa grasslands presented the higher number of exclusive species (258) compared to the highland grasslands (193). Species richness varied from 119 species at the site in Tavares, located in the coastal region of the Pampa, to 262 species in the highland grasslands at the site in Soledade (Tab. 2). In all but two cases, the equivalent richness had a value of less than half of the mean species richness per plot, which indicates high dominance by few species at this scale in the South Brazilian grasslands (Tab. 2).

At all sites, the sum of the cover of the five most abundant species added up to more than 40% of total vegetation cover (Tab. 3). A large part of these abundant species occurred throughout most parts of the *Campos Sulinos*. A notable exception is the site in the coastal region (Tavares), characterized by the dominance of species that did not occur at other sites, such as *Axonopus* sp. and *Paspalum vaginatum*. Considering this list of 24 plant species with highest cover values per site, 17 were grasses. At three of the four highland grassland sites (Vacaria, Painei and Palmas), the grass *Schizachyrium tenerum* was very important and at all Pampa sites, the grasses *Paspalum notatum* or *Andropogon lateralis* were the most important plant species in terms of cover. Accordingly, the RDA shows the separation of highland grasslands dominated by *S. tenerum* (the positive

portion of RDA1 in Fig. 3) from the Pampa sites dominated by *A. lateralis* (the negative portion of RDA1). *P. notatum* is also descriptive of the Pampa sites, but positively correlated with the second RDA axis (RDA2, Fig. 3).

Although most abundant species were well distributed along the entire gradient, spatial heterogeneity per site was generally high, especially at the coastal grassland site ('tav' in Fig. 4). At all sites, the greater part of beta diversity was due to species substitution across sampling sites (the turnover component in Fig. 4).

Cluster analysis showed that species composition differed significantly across the sites (Fig. 5). The dendrogram shows the separation of sites from Pampa grassland and highland grassland (with two groups in the latter region) and additionally separating two groups of grasslands at the coastal grassland site in Tavares (part of the Pampa). A similar result could be observed in the RDA (Fig. 3) that evidenced the strong relation between vegetation and soil pH, with the highest concentration of aluminum, i.e. high acidity of soils, in highland grassland sites (see Tab. 1, aluminum has the highest R^2 and AIC values). Climatic variables were also important to explain species distribution patterns. In particular, minimum precipitation seems to be associated with Pampa sites and minimum temperature seems related to the northern highland grassland sites (Fig. 3). Indeed, the model with environmental variables explained 33% of species composition variance (Tab. 4). However, we highlight that the spatial variables had almost the same importance ($R^2=0.34$). Controlling the spatial influence in environmental variables, the explanation decreases ($R^2=0.13$), which shows the extent of spatial structuring of environmental variables along the climatic and edaphic gradients in the South Brazilian grassland region (Tab. 4).

Discussion

Around the world, grassland vegetation has been neglected in terms of science and conservation (Overbeck *et al.* 2015; Veldman *et al.* 2015). The results we present here contribute to a detailed characterization of still rather intact grassland landscapes in terms of species richness and of dominance patterns in the plant community and thus can serve to establish regional reference values for grassland conservation or restoration. The total number of species in our data set, 759, represents roughly one fourth of the 3000 plant species estimated for the South Brazilian grasslands as a whole (Overbeck *et al.* 2007). For the Pampa grasslands, 2.150 plant species have been confirmed (Andrade *et al.* 2018), and our sampling with 566 species thus also presents one fourth of the species from this region. However, it is important to recognize that our study was conducted mostly in the mesic grasslands that dominate the landscapes (with the exception for the coastal region, where humid grasslands cover considerable areas), and mostly in rather homogeneously grazed areas. We thus did not include extreme environments that are found inserted in the grassland matrix, such as rock outcrops or sand depositions. These environments often present a specific flora (Porembski & Barthlott 2000; Trindade *et al.* 2008) and are characterized by the presence of species-rich genera, such as *Parodia* (Cactaceae: 26 species in the region; Larocca & Zappi 2015) and *Dyckia* (Bromeliaceae: 29 species in the region; Forzza *et al.* 2015).

The high importance of Poaceae and Asteraceae in the South Brazilian grasslands in terms of species richness has been shown previously. Interestingly, however, Fabaceae, shown in many studies to be the third family in terms of species number (Ferreira *et al.* 2010; Andrade *et al.* 2016), was replaced by Cyperaceae in our study, a family previously shown to have high importance only in the shortgrass grasslands and coastal grasslands (Ferreira & Setubal 2009; Menezes *et al.* 2015; Bonilha *et al.* 2017). Until now, the high

richness of Cyperaceae in the South Brazilian grasslands might have been underestimated due to the lack of taxonomic treatment for species-rich genera. Improved knowledge of species from this group, resultant from descriptions of new species, now may reveal more accurately how important the family really is to the South Brazilian grasslands flora (e.g. Trevisan & Boldrini 2008; Hefler & Longhi-Wagner 2012; Silva-Filho *et al.* 2017).

Environment-vegetation relations reflecting grasslands groups

As to the climatic variables, minima of precipitation and temperature had influence over species distribution patterns in the South Brazilian grasslands (see Fig. 3). In the southern half of Rio Grande do Sul State (i.e., in the Pampa), some regions present historical registers of hydric deficits, especially in years of La Niña-Southern Oscillation events (Cordeiro *et al.* 2018). As to be expected due to their higher altitude, we observed a relation of highland grassland sites to minimum temperature. Lower temperature and more recurrent frost events were probably among the main factors generating, in the highland grassland region, a more or less treeless landscape over 3.000 years before present, in the region where now can today observe a mosaic of Araucaria forest and grasslands (Behling *et al.* 2004).

The two major grassland regions, Pampa and highland, do not only show separation due to climate but concomitantly by soil features. The concentrations of exchangeable aluminum (Al^{+3}) and potassium and differences in soil granulometry were the principal variables associated with the distinction of the Pampa and highland grasslands based on soil features (Tab. 1). The soils in the highland region are formed on volcanic rocks (basalt, rhyolite, rhyodacite), leading to high aluminum concentration. As aluminum has low mobility and is easily bounded by organic material (Li & Johnson 2016), both components are present in high proportion in the highland region.

When we discuss the role of environmental drivers shaping grassland community patterns, it is important to consider the shared effect of space and environment. Both environmental features and space (i.e. dispersal limitation) can be seen as filters of community assembly that act at different spatial scales (Menezes *et al.* 2016). Climatic variables, for instance, are intrinsically spatially structured at broader scales (Bell *et al.* 1993), which makes it difficult to discern between climate or dispersal limitation as responsible for changes in community composition. Soil properties, in contrast, are usually more influent at local spatial scales (Menezes *et al.* 2016).

Overall, the results presented here corroborate Andrade *et al.* (2019), separating the South Brazilian grasslands in similar groups of grasslands based on distinct species composition, edaphic and climatic characteristics. Classification of the South Brazilian grasslands historically had been based on physiognomic descriptors, such as ‘shrubby or dirty grassland’ (*campos arbustivos ou sujos*, sensu Lindman 1974) or considering very broadly defined environmental features, as in terms like ‘dry grasslands’ (*campos secos*, sensu Rambo 1942). Andrade *et al.* (2019) provided the first attempt to classify grasslands based on plant community composition, and our results are in agreement with their classification. We must recognize that data availability is still too limited for a fine-scale classification that would be important to define grassland habitats of specifically high conservation value or threat status.

A classification of landscapes based primarily on geomorphological variables (such as the classification by Hasenack *et al.* submitted; see Fig. 1) is useful for the description of different environments and regions. However, geomorphological features may not be directly related to species composition patterns. In fact, the classification of floristic regions, based on plant species composition, has yielded different result from previous classifications in other regions of Brazil as well (Silva & Souza 2018; Cantidio & Souza

2019; Silva-Souza & Souza 2020). Conservation and restoration planning at local or regional scales require larger data sets about plant community, and quantitative field sampling is necessary for this.

Evenness, richness and diversity patterns

Species abundance distribution at our sampling sites was remarkably uneven. The sum of cover of the five most abundant species per site represented over 40% of vegetation cover in all grids, despite the high species richness (average S in grids was 215) (Tab. 3). All sites studied are under traditional grazing management that also shapes grassland community composition and structure. Current legislation in the region obliges landowners to maintain rather high stocking rates, which can even lead to overgrazing (Carvalho & Batello 2009). This process possibly leads to dominance of few species that are adapted to rather strong disturbances (Sosinski Jr & Pillar 2004) and may also lead to a certain homogenization of plant communities, as found in general for biotic communities under land use intensification (Gossner *et al.* 2016). Lack of disturbance, i.e. exclusion from grazing or fire, on the other hand, has been shown to lead to biodiversity losses as few tall species become dominant; on the long term, it may lead to the substitution of natural grasslands by shrub- or tree-dominated ecosystems (Koch *et al.* 2016). Here, working on areas with cattle grazing throughout, we do not expect strong interference in the overall structure of grassland communities due to management as found in Andrade *et al.* (2019), where one ungrazed site clearly differed from the other sites. However, it would be interesting to investigate this further in future studies in order to better define optimum grazing levels (or fire frequencies, for that matter; see e.g. Overbeck *et al.* 2018) from both conservation and production perspectives.

While dominant species are widespread among regions (Tab. 3), rarer species differ more, even within sites. This was highlighted by the high beta diversity observed, with a greater contribution of species substitution (turnover) across sampling sites (Fig. 3). In fact, turnover seems to be the dominant pattern for most areas, while nestedness patterns are restricted to extreme climates in high latitudes (Dobrovolski *et al.* 2012). Concerning plant species conservation, high beta diversity due to turnover means that the best way to protect the greater part of biodiversity is having a network of well-conserved grasslands distributed over regions along the entire environmental gradient. Brazilian Native Vegetation Protection Law (Law 12.651/2012) obliges rural properties to maintain or restore native vegetation up to 20% of their total area as Legal Reserve for the conservation of biodiversity and ecosystem services (see Metzger *et al.* 2019). While our data indicate that the distribution of protected grassland remnants in space – as favored by the Legal Reserve – will be beneficial for conservation of plant diversity, other studies point negative effects of fragmentation (Staude *et al.* 2018). More studies on the relevance of scale and grain for conservation purposes are needed. Moreover, conservation requirements may differ among groups of organisms, since beta diversity, turnover and nestedness show specific behavior for organisms at different trophic levels and with dispersal capability, for instance (Soininen *et al.* 2018).

Establishing reference values for conservation and restoration

This study allows for a pragmatic definition of reference values for conservation and restoration purposes, with specific information for the major ecological systems in the South Brazilian grasslands. Species richness, for instance, is a valuable information regarding conservation (Wilson *et al.* 2012; Menezes *et al.* 2018). The richness values expressed here at three spatial scales (grids, sampling sites, plots) are informative in terms

of what to expect when conducting vegetation sampling in the different ecological systems of the South Brazilian grasslands. As shown by equivalent richness and evenness values, these grasslands can present highly uneven species abundance distribution, with high dominance of Poaceae species, especially *Andropogon lateralis*, *Paspalum notatum* and *Schizachyrium tenerum*. However, for evaluation of grassland conservation status or definition of restoration targets, it does not appear to be sufficient to consider only dominant species: the characteristic species richness needs to be taken into account. In fact, during the field sampling the ‘record’ value of 56 species per plot was registered at the Quaraí site, in the region of grasslands on shallow soil (Menezes *et al.* 2018). Thus, for conservation and restoration purposes, overall compositional patterns, dominant species and species richness should be used as reference simultaneously. Additionally, the presence of endangered or endemic species, should be taken into account for purposes of environmental licensing.

Scenarios point to continued pressure of agricultural expansion on natural ecosystems in southern Brazil (Dobrovolski *et al.* 2011), adding on to already fast land use change and resulting biodiversity losses (e.g. Staude *et al.* 2018). Only the implementation of effective conservation measures will be able to avoid more severe transformation of natural habitat that provides important ecosystem services (Metzger *et al.* 2019). We suggest that environmental agencies should establish clear criteria for environmental licensing and restoration/conservation monitoring based on information as presented here, and that these criteria should be periodically updated to include more recent data. We further urge to continue with standardized vegetation sampling in the region, in order to improve the information basis both for science and conservation.

Acknowledgements

We thank all landowners for allowing the research on their properties and anonymous reviewers and the editor for helpful comments that improved the manuscript. This research received financing from PPBio Rede Campos Sulinos - Vegetação Campestre MCTI/CNPq (457447/2012-5 to GEO and 457531/2012-6 to VDP) and was further supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES - Finance Code 001), National Institutes for Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation, MCTIC/CNPq (465610/2014-5) and FAPEG (201810267000023). EVM, CVE, DBL, GHMS and LSM were supported by MCTI/CNPq. RT (313306/2018-4), VDP (307689/2014-0) and GEO (310345/2018-9) received CNPq productivity grants.

References

- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711-728.
- Andrade BO, Bonilha CL, Ferreira PMA, Boldrini II, Overbeck GE. 2016. Highland grasslands at the southern tip of the Atlantic Forest biome: Management options and conservation challenges. *Oecologia Australis* 20: 37-61.
- Andrade BO, Bonilha CL, Overbeck GE, *et al.* 2019. Classification of South Brazilian grasslands: implications for conservation. *Applied Vegetation Science* 22: 1-17.
- Andrade BO, Koch C, Boldrini II, *et al.* 2015. Grassland degradation and restoration: A conceptual framework of stages and thresholds illustrated by southern Brazilian grasslands. *Natureza & Conservacao* 13: 95-104.
- Andrade BO, Marchesi E, Burkart S, *et al.* 2018. Vascular plant species richness and distribution in the Río de la Plata grasslands. *Botanical Journal of the Linnean Society* 188: 250-256.
- Baselga A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* 21: 1223-1232.
- Baselga A, Orme CDL. 2012. betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3: 808-812.
- Behling H, Pillar VDP, Orlóci L, Bauermann SG. 2004. Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203: 277-297.
- Bell G, Lechowicz MJ, Appenzeller A, *et al.* 1993. The spatial structure of the physical environment. *Oecologia* 96: 114-121.
- BFG - The Brazil Flora Group. 2015. Growing knowledge: an overview of Seed Plant diversity in Brazil. *Rodriguesia* 66: 1085-1113.

- Bini LM, Diniz-Filho JAF, Rangel TFLVB, Bastos RP, Pinto MP. 2006. Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. *Diversity and Distributions* 12: 475-482.
- Blanchet FG, Legendre P, Borcard D. 2008. Forward selection of explanatory variables. *Ecology* 89: 2623-2632.
- Boavista LR, Trindade JPP, Overbeck GE, Müller SC. 2019. Effects of grazing regimes on the temporal dynamics of grassland communities. *Applied Vegetation Science* 22: 326-335.
- Boldrini II, Overbeck GE. 2015. Estudos fitossociológicos em vegetação campestre. In: Eisenlohr PV, Felfili JM, Melo MMRF, Andrade LA, Meira-Neto JAA (eds.) *Fitossociologia no Brasil. Métodos e estudos de caso Volume II*. Viçosa, Editora UFV. p. 228-249.
- Bonilha CL, Andrade BO, Vieira MS, Silva-Filho PJS, Rolim RG, Overbeck GE, Boldrini II. 2017. Land management and biodiversity maintenance: a case study in grasslands in the Coastal Plain of Rio Grande do Sul. *Iheringia, Série Botânica* 72: 191-200.
- Borcard D, Gillet F, Legendre P. 2011. *Numerical ecology with R*. Springer, New York.
- Cantidio LS, Souza AF. 2019. Aridity, soil and biome stability influence plant ecoregions in the Atlantic Forest, a biodiversity hotspot in South America. *Ecography* 42: 1887-1898.
- Carvalho PCF, Batello C. 2009. Access to land, livestock production and ecosystem conservation in the Brazilian Campos biome: The natural grasslands dilemma. *Livestock Science* 120: 158-162.
- Chao A, Gotelli NJ, Hsieh TC, *et al.* 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84: 45-67.
- Chase JM, Myers JA. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2351-2363.
- Cordeiro APA, Berlato MA, Alves RDCM. 2018. Trend of the seasonal water index of Rio Grande do Sul State and its relationship with El Niño and La Niña. *Anuario do Instituto de Geociências* 41: 216-226.
- Dala-Corte RB, Giam X, Olden JD, Becker FG, Guimarães TF, Melo AS. 2016. Revealing the pathways by which agricultural land-use affects stream fish communities in South Brazilian grasslands. *Freshwater Biology* 61: 1921-1934.
- Dobrovolski R, Loyola RD, Júnior PDM, Diniz-Filho JAF, 2011. Agricultural expansion can menace Brazilian protected areas during the 21 st century. *Natureza & Conservação* 9: 208-213.
- Dobrovolski R, Melo AS, Cassemiro FAS, Diniz-Filho JAF. 2012. Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 21: 191-197.
- Ferreira PMA, Müller SC, Boldrini II, Eggers L. 2010. Floristic and vegetation structure of a granitic grassland in Southern Brazil. *Revista Brasileira de Botânica* 33: 21-36.
- Ferreira PMA, Setubal RB. 2009. Florística e fitossociologia de um campo natural no município de Santo Antonio da Patrulha , Rio Grande do Sul , Brasil. *Revista Brasileira de Biociências* 7: 195-204.
- Fontana CS, Chiarani E, Menezes LS, Andretti CB, Overbeck GE. 2018. Bird surveys in grasslands: do different count methods present distinct results? *Revista*

- Brasileira de Ornitologia 26: 116-122.
- Forzza RC, Costa A, Siqueira-Filho JA, *et al.* 2015. Bromeliaceae in Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro.
<http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB130195>. 27 Jul. 2019 (Date of last successful access).
- Gossner MM, Lewinsohn TM, Kahl T, *et al.* 2016. Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* 540: 266-269.
- Hasenack H, Weber EJ, Boldrini II, Trevisan R, Flores CA, Dewes H. (submitted). A functional landscape classification of subtropical grasslands in Southern Brazil as a support for conservation and land use planning. *Ecología Austral*.
- Hefler SM, Longhi-Wagner H. 2012. *Cyperus* L. subg. *Cyperus* (Cyperaceae) na Região Sul do Brasil. *Revista Brasileira de Biociências* 10: 327-372.
- HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics* 43: 227-248.
- IBGE. 2019. Biomas e sistema costeiro-marinho do Brasil: compatível com a escala 1:250 000. Rio de Janeiro: Relatórios metodológicos, v. 45.
<https://www.ibge.gov.br/apps/biomas/> 21 Jan. 2020 (Date of last successful access).
- Jost L. 2006 Entropy and diversity. *Oikos* 113: 363-375.
- Koch C, Conradi T, Gossner MM, *et al.* 2016. Management intensity and temporary conversion to other land-use types affect plant diversity and species composition of subtropical grasslands in southern Brazil. *Applied Vegetation Science* 19: 589-599.
- Laliberté E, Zemunik G, Turner BL. 2014. Environmental filtering explains variation in plant diversity along resource gradients. *Science* 345:1602-1605.
- Larocca J, Zappi D. 2015. Parodia in Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro.
<http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB114556>. 27 Jul. 2019 (Date of last successful access).
- Legendre P, Gallagher E. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271-280.
- Lezama F, Baeza S, Altesor A, Cesa A, Chaneton EJ, Paruelo JM. 2014. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation Science* 25: 8-21.
- Li W, Johnson CE. 2016. Relationships among pH, aluminum solubility and aluminum complexation with organic matter in acid forest soils of the Northeastern United States. *Geoderma* 271: 234-242.
- Lindman CAM. 1974. A vegetação no Rio Grande do Sul. São Paulo, Ed. da Universidade de São Paulo.
- Madalozzo B, Santos TG, Santos MB, Both C, Cechin S. 2017 Biodiversity assessment: selecting sampling techniques to access anuran diversity in grassland ecosystems. *Wildlife Research* 44: 78-91.
- Magnusson WE, Lima AP, Luizão R, *et al.* 2005. RAPELD: A modification of the Gentry Method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica* 5: 19-24.
- Magurran AE. 1988. Chapman & Hall Ecological diversity and its measurements. London, Chapman & Hall.
- Menezes LS, Müller SC, Overbeck GE. 2015. Floristic and structural patterns in South Brazilian coastal grasslands. *Anais da Academia Brasileira de Ciências* 87: 2081-2090.
- Menezes LS, Müller SC, Overbeck GE 2016. Scale-specific processes shape plant

- community patterns in subtropical coastal grasslands. *Austral Ecology* 41: 65-73.
- Menezes LS, Vogel-Ely C, Lucas DB, Minervini-Silva GH, Boldrini II, Overbeck GE. 2018. Plant species richness record in Brazilian Pampa grasslands and implications. *Revista Brasileira de Botânica* 41: 817-823.
- Metzger JP, Bustamante MMC, Ferreira J, *et al.* 2019. Why Brazil needs its Legal Reserves. *Perspectives in Ecology and Conservation* 17: 91-103.
- Oksanen J, Blanchet FG, Friendly M, *et al.* 2017. *vegan: Community Ecology Package*. R package version 2.4-3. <https://CRAN.R-project.org/package=vegan>. 15 Sep. 2018 (Date of last successful access).
- Oliveira U, Soares-Filho BS, Paglia AP, *et al.* 2017. Biodiversity conservation gaps in the Brazilian protected areas. *Scientific Reports* 7: 9141.
- Overbeck GE, Müller SC, Fidelis A, *et al.* 2007. Brazil's neglected biome: The South Brazilian Campos. *Perspectives in Plant Ecology Evolution and Systematics* 9: 101-116.
- Overbeck GE, Vélez-Martin E, Scarano FR, *et al.* 2015. Conservation in Brazil needs to include non-forest ecosystems. *Diversity and Distributions* 21: 1455-1460.
- Overbeck GE, Scasta JD, Furquim FF, *et al.* 2018. The South Brazilian grasslands - A South American tallgrass prairie? Parallels and implications of fire dependency. *Perspectives in Ecology and Conservation* 16: 24-30.
- Porembski S, Barthlott W. 2000. *Inselbergs Biotic Diversity of Isolated Rock Outcrops in Tropical and Temperate Regions*. Berlin, Springer.
- Prach K, Durigan G, Fennessy S, Overbeck GE, Torezan JM, Murphy SD. 2019. A primer on choosing goals and indicators to evaluate ecological restoration success. *Restoration Ecology* 27: 917-923.
- Rambo B. 1942. *A fisionomia do Rio Grande do Sul: ensaio de monografia natural*. Porto Alegre, Imprensa Oficial.
- Shimodaira H. 2004. Approximately unbiased tests of regions using multistep-multiscale bootstrap resampling. *Annals of Statistics* 32: 2616-2641.
- Silva AC, Souza AF. 2018. Aridity drives plant biogeographical sub regions in the Caatinga, the largest tropical dry forest and woodland block in South America. *PLoS ONE* 13: e0196130.
- Silva-Filho PJS, Boldrini II, Trevisan R. 2017. Revision of *Rhynchospora* (Cyperaceae) sect. *Luzuliformes*. *Systematic Botany* 42: 175-184.
- Silva-Souza KJP, Souza AF. 2020. Woody plant subregions of the Amazon forest. *Journal of Ecology* 00: 1-15.
- Socolar JB, Gilroy JJ, Kunin WE, Edwards DP. 2016. How Should Beta-Diversity Inform Biodiversity Conservation? *Trends in Ecology & Evolution* 31: 67-80.
- Soininen J, Heino J, Wang J. 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography* 27: 96-109.
- Sosinski Jr EE, Pillar VDP. 2004. Respostas de tipos funcionais de plantas à intensidade de pastejo em vegetação campestre. *Pesquisa Agropecuária Brasileira* 39: 1-9.
- Staude IR, Vélez-Martin E, Andrade BO, *et al.* 2018. Local biodiversity erosion in south Brazilian grasslands under moderate levels of landscape habitat loss. *Journal of Applied Ecology* 55: 1241-1251.
- Suzuki R, Shimodaira H. 2015. *pvclust: Hierarchical Clustering with P-Values via Multiscale Bootstrap Resampling*. R package version 2.0-0 <https://CRAN.R-project.org/package=pvclust>. 8 Aug. 2019 (Date of last successful access).
- Tedesco MJ, Gianello C, Bissani CA, Bohnen H. 1995. *Análises de solo, plantas e outros materiais*. 2nd ed. Porto Alegre, Departamento de Solos da UFRGS.

- Thomas PA, Schüler J, Boavista LR, Torchelsen FP, Overbeck GE, Müller SC. 2019. Controlling the invader *Urochloa decumbens*: Subsidies for ecological restoration in subtropical Campos grassland. *Applied Vegetation Science* 22: 96-104.
- Trevisan R, Boldrini II. 2008. O gênero *Eleocharis* R. Br. (Cyperaceae) no Rio Grande do Sul, Brasil. *Revista Brasileira de Biociências* 6: 7-67.
- Trindade JPP, Quadros FLF, Pillar VDP. 2008. Grassland vegetation of sandy patches of Rio Grande do Sul under grazing and exclosure. *Pesquisa Agropecuária Brasileira* 43: 771-779.
- Veldman JW, Buisson E, Durigan G, *et al.* 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* 13: 154-162.
- Weiher E, Keddy P. 2004. *Ecological Assembly Rules Perspectives, advances, retreats.* Cambridge, Cambridge University Press.
- Wilson JB, Peet RK, Dengler J, Pärtel M. 2012. Plant species richness: the world records. *Journal of Vegetation Science* 23: 796-802.

Figures and captions:

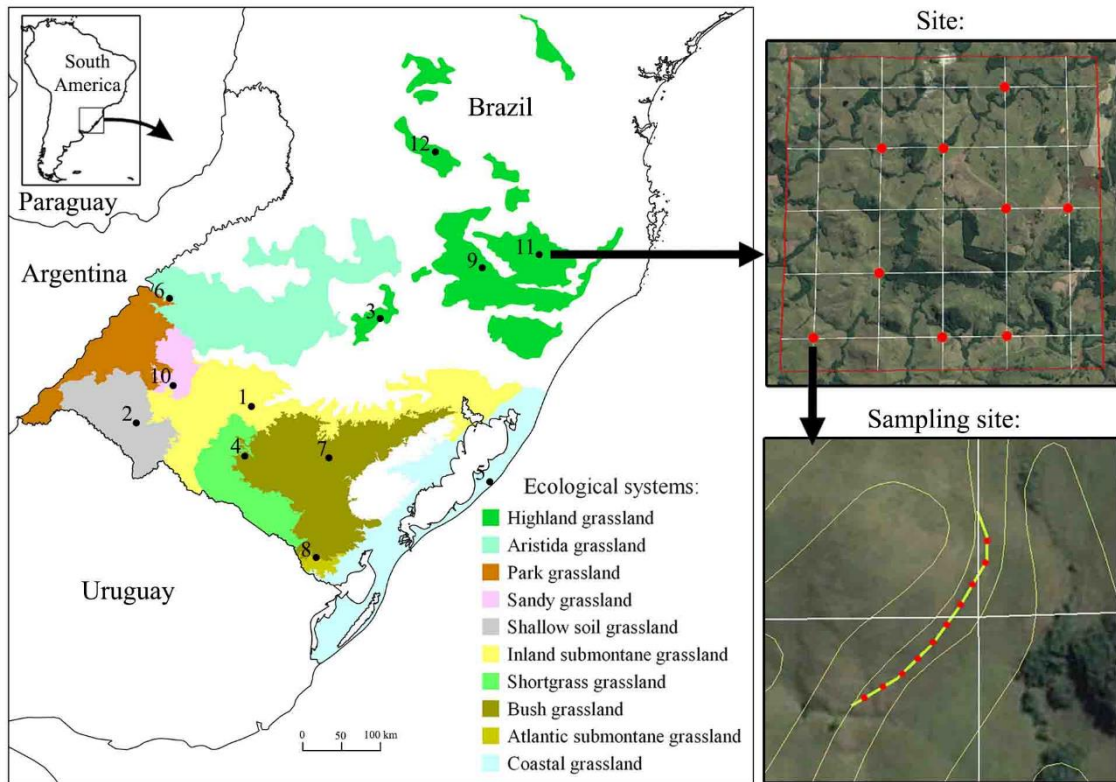


Figure 1: Spatial distribution of the 12 sites in the South Brazilian grasslands in the different ecological systems (based on Hasenack *et al.* submitted). Numbers correspond to the location of sites in the municipalities of: 1 São Gabriel (sgb), 2 Quaraí (qua), 3 Soledade (sol), 4 Lavras do Sul (lav), 5 Tavares (tav), 6 Santo Antônio das Missões (sam), 7 Santana da Boa Vista (sbv), 8 Jaguarão (jag), 9 Vacaria (vac), 10 Alegrete (ale), 11 Painel (pai) and 12 Palmas (pal). At right, representation of a site with nine randomly selected sampling sites and a detail of a sampling site, with the ten plots (1 m x 1 m) represented by the red dots.

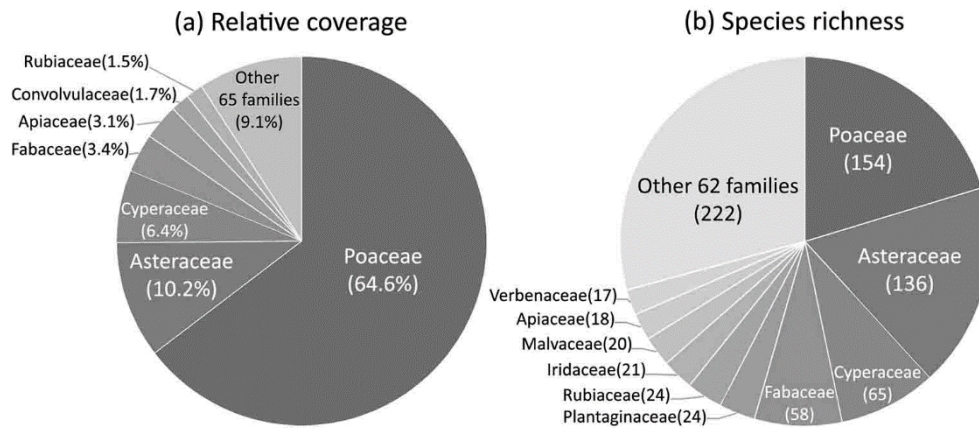


Figure 2: Principal plant families in the South Brazilian grasslands. (a) Percentage of total relative cover per family; (b) Species richness per family.

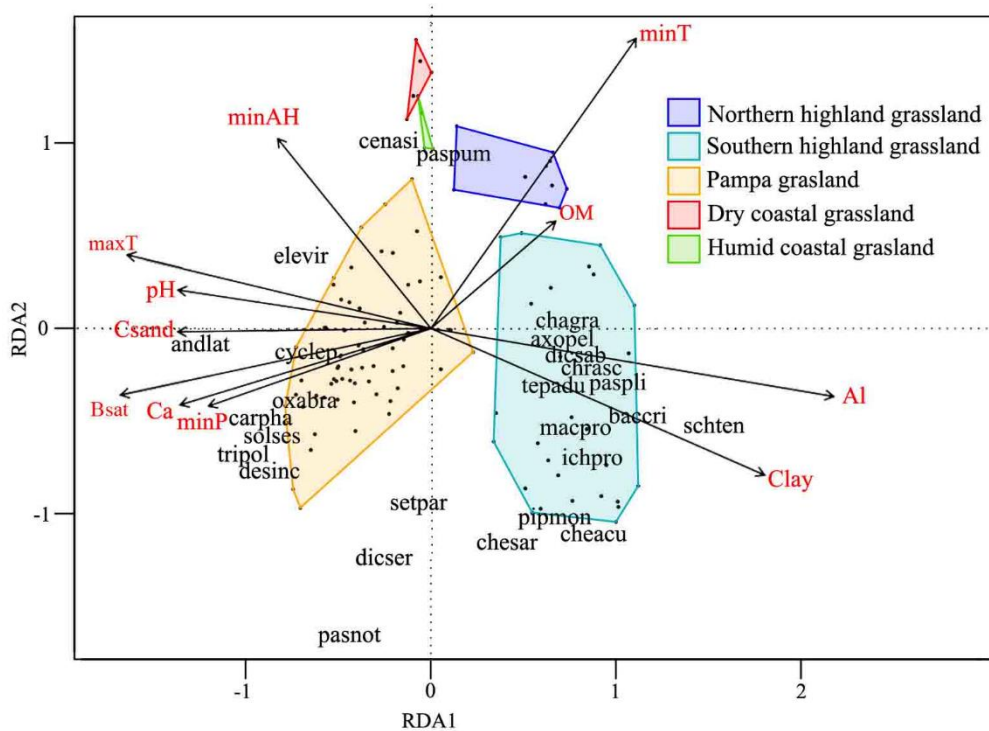


Figure 3: Redundancy analysis (RDA) based on relative frequency of plant species found in 108 sampling sites across the South Brazilian grasslands and predictive (edaphic and climatic) variables. Environmental variables explained 34% of species variance. Cluster analysis supported five groups of distinct plant species composition represented by the polygons (see Fig. 5). Predictive variables acronyms are given in Table 1. For better visualization only species highly correlated ($r^2 > 0.25$) with RDA axis were plotted.

Species acronyms are: andlat *Andropogon lateralis*, axopel *Axonopus pellitus*, baccri *Baccharis crispa*, cenasi *Centella asiatica*, cheacu *Chevreulia acuminata*, chesar *Chevreulia sarmentosa*, chrasc *Chrysolaena ascendens*, desinc *Desmodium incanum*, dicsab *Dichantheium sabulorum*, dicser *Dichondra sericea*, carpha *Carex phalaroides*, chagra *Chaetogastra gracilis*, cyclep *Cyclospermum leptophyllum*, elevir *Eleocharis viridans*, ichpro *Ichnanthus procurrens*, macpro *Macroptilium prostratum*, oxabra *Oxalis brasiliensis*, pasnot *Paspalum notatum*, paspum *Paspalum pumilum*, paspli *Paspalum plicatulum*, pipmon *Piptochaetium montevidense*, setpar *Setaria parvifolia*, schten *Schizachyrium tenerum*, solses *Soliva sessilis*, tepadu *Tephrosia adunca*, tripol *Trifolium polymorphum*.

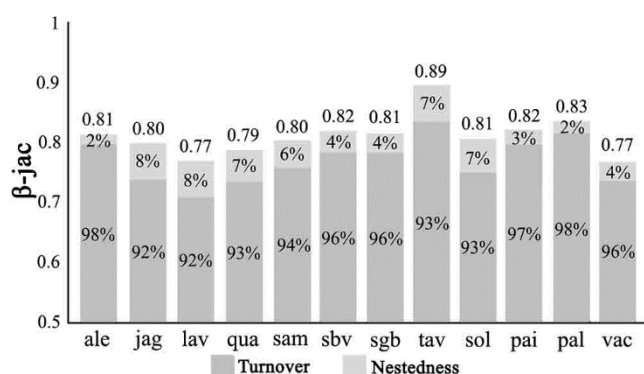


Figure 4: Beta diversity (numbers above bars), based on Jaccard-Index, decomposed into turnover and nestedness contribution at the twelve grassland sites in the South Brazilian grasslands.

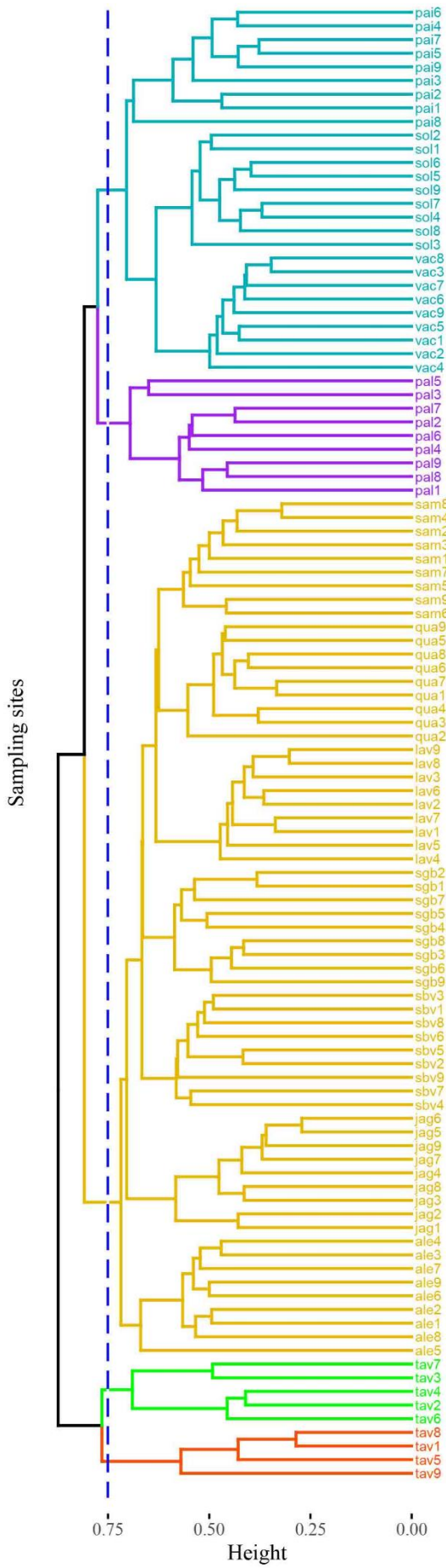


Figure 5: Hierarchical clustering analysis, based on UPGMA method and using Jaccard-based pairwise species turnover as dissimilarity metric, showing the separation of the 108 sampling sites from South Brazilian grasslands in five groups (top to bottom: Southern highland grassland (Vacaria, Soledade and Painei grids), Northern highland grassland (Palmas grid), Pampa grassland, Humid coastal grasslands (Tavares sampling sites 2, 3 4, 6 and 7) and Dry coastal grassland (Tavares sampling sites 1, 5, 8 and 9). Groups consistency were tested with approximately unbiased p-values obtained via 999 multiscale bootstrap resampling, groups with $p < 0.05$ were considered consistent (see Suppl. 5 for dendrogram with all p-values).

Tables and table heads:

Table 1: Environmental, spatial variables (and analytical method) and their correlation with grassland plant communities from South Brazilian grasslands. Only variables selected as significantly correlated ($p < 0.05$) with the species composition variance are shown. For complete set of explanatory variables see supplementary material.

Code	Variable	Unit	Method of analysis	R ²	AIC	p
<i>Environmental:</i>						
Al	Exchangeable aluminium	cmol _c /dm ³	Extracted with KCl 1mol L ⁻¹	0.12	208.38	0.002
minT	Minimum temperature	°C	Extracted from INMET database	0.05	203.00	0.002
Clay	Clay	%	Densimeter method	0.03	199.36	0.002
minAH	Minimum air humidity	%	Extracted from INMET database	0.03	196.22	0.002
minP	Minimum precipitation	mm	Extracted from INMET database	0.02	193.54	0.002
BSat	Base saturation	%	Bases extracted with ammonium acetate	0.02	187.99	0.002
Ca	Exchangeable calcium	cmol _c /dm ³	Same as Al	0.02	190.87	0.002
pH	pH	-	In water	0.02	189.37	0.002
maxT	Maximum temperature	°C	Extracted from INMET database	0.02	185.08	0.002
OM	Organic matter	%	Humid digestion	0.02	186.59	0.002
Csand	Coarse sand	%	Granulometry from 0.2 to 2 mm	0.01	184.30	0.004
<i>Spatial:</i>						
MEM1	1 st ordination axis	-	PCoA based on spatial coordinates	0.14	205.43	0.002
MEM2	2 nd ordination axis	-	PCoA based on spatial coordinates	0.03	186.78	0.002
MEM3	3 rd ordination axis	-	PCoA based on spatial coordinates	0.03	183.10	0.002
MEM4	4 th ordination axis	-	PCoA based on spatial coordinates	0.07	196.70	0.002
MEM5	5 th ordination axis	-	PCoA based on spatial coordinates	0.03	193.46	0.002
MEM6	6 th ordination axis	-	PCoA based on spatial coordinates	0.02	181.27	0.002
MEM12	12 th ordination axis	-	PCoA based on spatial coordinates	0.02	179.58	0.002
MEM13	13 th ordination axis	-	PCoA based on spatial coordinates	0.03	190.23	0.002

Table 2: Richness and diversity descriptive metrics from 12 sites of grassland vegetation in the South Brazilian grasslands. Ecological systems follow Hasenack *et al.* (submitted). Richness metrics (S) given for the three sampling scales. Shannon diversity (H') and equability (E) were calculated for each plot (1 m x 1 m), values presented are average and standard deviation for the 90 plots at each site. Equivalent richness (Equivalent S) is calculated based on H'. Hill numbers (q=1) were calculated for each site.

Municipality	Ecological system	Site (spp/25 km ²)	Samp. site (spp/250 m ²)	Plot (spp/1 m ²)	H' (nats/ind)	Equivalent S	E	Hill numbers (q=1)
Alegrete (ale)	Sandy grassland	175	70.33 (±4.72)	21.8 (± 4.61)	2.06 (± 0.31)	8.27 (± 2.76)	0.67 (± 0.07)	87.17 (± 2.49)
Jaguarão (jag)	Atlantic submontane grassland	196	83.33 (±18.28)	22.94 (± 5.15)	2.53 (± 0.3)	3.17 (± 4.18)	0.77 (± 0.05)	111.56 (± 2.21)
Lavras do Sul (lav)	Shortgrass grassland	197	87.77 (± 14.24)	24.45 (± 8.19)	2.36 (± 0.44)	11.62 (± 4.9)	0.72 (± 0.07)	97.45 (± 2.11)
Quaraí (qua)	Shallow soil grassland	252	111.55 (± 18)	30.5 (± 9.84)	2.51 (± 0.41)	3.32 (± 5.24)	0.74 (± 0.06)	140.304 (± 2.7)
Santo Antônio das Missões (sam)	Park grassland	196	84.22 (± 13.8)	25.48 (± 8.7)	2.23 (± 0.44)	0.24 (± 4.42)	0.7 (± 0.08)	105.83 (± 2.19)
Santana da Boa Vista (sbv)	Bush grassland	247	96.88 (± 14.53)	26.85 (± 6.33)	2.38 (± 0.32)	1.50 (± 3.97)	0.73 (± 0.08)	121.61 (± 2.77)
São Gabriel (sgb)	Inland submontane grassland	225	85.55 (± 11.41)	25.41 (± 6.15)	2.34 (± 0.32)	0.95 (± 3.62)	0.72 (± 0.06)	110.17 (± 2.99)
Tavares (tav)	Coastal grassland	119	30.77 (± 14.26)	10.41 (± 4.65)	1.56 (± 0.55)	5.40 (± 2.39)	0.69 (± 0.09)	63.14 (± 2.42)
Painel (pai)	Highland grassland	256	97.44 (± 10.52)	26.44 (± 6.15)	2.44 (± 0.33)	2.08 (± 3.61)	0.75 (± 0.07)	121.72 (± 2.71)
Palmas (pal)	Highland grassland	244	87 (± 8.8)	22.91 (± 5.85)	2.32 (± 0.35)	10.89 (± 4)	0.74 (± 0.06)	126.64 (± 3.36)
Soledade (sol)	Highland grassland	262	105.55 (± 20.01)	31.4 (± 6.9)	2.52 (± 0.38)	3.42 (± 5.37)	0.73 (± 0.07)	120.397 (± 3.04)
Vacaria (vac)	Highland grassland	218	98.77 (± 9.01)	30.85 (± 8.29)	2.52 (± 0.36)	3.28 (± 4.44)	0.74 (± 0.05)	103.526 (± 2.21)

Table 3: Relative cover of the five most abundant species occurring at each site. When one species is top five abundant for a given site its relative cover value is given for all sites where it was present. Acronyms for sites are given in Table 2.

Species	Sites											
	ale	jag	lav	qua	sam	sbv	sgb	tav	sol	vac	pai	pal
<i>Agenium villosum</i> (Nees) Pilg.	-	<0.1	-	-	-	-	-	-	1.1	1.2	4.3	-
<i>Andropogon lateralis</i> Nees	33.7	6.3	4.7	10.9	22.6	6.6	12.4	3.7	<0.1	-	0.5	4.3
<i>Andropogon macrothrix</i> Trin.	-	-	-	0.1	-	<0.1	-	-	0.1	<0.1	1.3	6.7
<i>Axonopus affinis</i> Chase	1.8	9	11.1	2.5	2.1	7.8	6.8	2.2	1.6	2.6	3.4	4.8
<i>Axonopus</i> sp.	-	-	-	-	-	-	-	12	-	-	-	-
<i>Baccharis crispa</i> Spreng.	0.3	1.8	1.6	0.4	-	2.1	1.6	-	4.3	3.1	3.1	1
<i>Centella asiatica</i> (L.) Urb.	0.1	3.5	-	-	<0.1	0.1	5.4	1.4	-	-	-	0.4
<i>Dichondra sericea</i> Sw.	2.8	1.2	2	1	1.4	2.2	1.1	0.3	1.7	1.2	0.5	0.2
<i>Eleocharis viridans</i> Kük. ex Osten	-	1.3	3.5	2.5	2.7	0.9	3	6.4	-	-	-	0.8
<i>Elionurus muticus</i> (Spreng.) Kuntze	-	-	-	-	-	-	-	-	0.1	-	-	4.9
<i>Eryngium horridum</i> Malme	-	0.3	1	0.4	0.1	4.2	0.5	-	6.7	-	-	0.1
<i>Ischaemum minus</i> J. Presl	-	0.2	-	-	-	-	<0.1	5.6	-	-	-	-
<i>Panicum aquaticum</i> Poir.	-	-	<0.1	<0.1	-	-	<0.1	5.5	-	-	-	<0.1
<i>Paspalum indecorum</i> Mez	-	-	-	5.2	4.9	-	-	-	-	-	-	-
<i>Paspalum notatum</i> Flügge	20.5	15.2	17.2	11.5	18.8	18.9	14.1	0.4	22.8	16.6	3.2	0.7
<i>Paspalum plicatulum</i> Michx.	0.5	2.9	0.3	1.1	0.7	0.5	<0.1	-	2.1	3.5	7.8	1.7
<i>Paspalum pumilum</i> Nees	0.3	6.6	0.9	-	-	0.1	1.2	4.4	0.3	-	4.8	2.1
<i>Paspalum vaginatum</i> Sw.	-	-	-	-	-	-	-	17.2	-	-	-	-
<i>Piptochaetium montevidense</i> (Spreng.) Parodi	2.7	3.2	1.9	1.7	0.7	5.5	1.7	-	7.6	7.8	5.7	7.1
<i>Saccharum angustifolium</i> (Nees) Trin.	-	0.1	6.2	-	0.1	-	-	-	1.7	-	2.3	2.3
<i>Schizachyrium tenerum</i> Nees	0.1	1.2	0.2	0.3	-	0.8	-	-	4.2	17.1	13.8	10.2
<i>Steinchisma hians</i> (Elliott) Nash	1.5	2.7	0.9	4.8	3.4	0.1	2.1	0.2	0.9	0.9	0.2	0.2
<i>Trifolium polymorphum</i> Poir.	-	0.2	5.9	0.6	1.1	0.6	0.5	-	-	-	-	-
<i>Vernonanthura nudiflora</i> (Less.) H. Rob.	0.4	-	-	0.3	-	0.2	3.5	0.2	-	0.1	1.2	<0.1
Total:	64.7	55.7	57.4	43.3	58.6	50.6	53.9	59.5	55.2	54.1	52.1	47.5

Table 4: Summary of the variation partitioning of species composition in the South Brazilian grasslands. Environmental and spatial features used as predictive variables are given in Table 1. Explanation factors are accepted as significant with $p < 0.05$, ‘n.t’ accounts for non-testable fractions.

Effect of the main variable	Explained variation (R ²)	Df	p
Total effect			
Environment + space	0.47	19	0.001
Partial effects			
Environment	0.33	11	0.001
Environment [space]	0.13	11	0.001
Space	0.34	8	0.001
Space [environment]	0.14	8	0.001
Shared effect			
Environment + space	0.20	-	n.t.
Residuals	0.53	-	n.t.

Supplementary material

Supplementary file 1: Plant species presence in the 12 sites of grassland vegetation across South Brazilian grasslands. Two letters code represents the municipality where each site is located: Alegrete (ale), Jaguarão (jag), Lavras do Sul (lav), Quaraí (qua), Santo Antônio das Missões (sam), Santana da Boa Vista (sbv), São Gabriel (sgb), Tavares(tav), Painei (pai), Palmas (pal), Soledade (sol), Vacaria (vac).

Family / Species	Sites											
	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac
Acanthaceae												
<i>Dyschoriste humilis</i> Lindau				1								
<i>Hygrophila costata</i> Nees								1				
<i>Justicia axillaris</i> (Nees) Lindau	1	1		1			1				1	
<i>Ruellia brevicaulis</i> (Nees) Lindau	1			1	1	1	1	1	1		1	1
<i>Ruellia bulbifera</i> Lindau	1			1							1	
<i>Ruellia geminiflora</i> Kunth												1
<i>Ruellia hypericoides</i> (Nees) Lindau	1			1	1	1		1			1	
<i>Ruellia morongii</i> Britton			1	1	1	1		1	1		1	
<i>Stenandrium dulce</i> (Cav.) Nees	1	1	1	1	1	1	1		1	1	1	1
Amaranthaceae												
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.								1				
<i>Gomphrena graminea</i> Moq.			1									
<i>Gomphrena perennis</i> L.				1			1					
<i>Pfaffia gnaphaloides</i> (L.f.) Mart.			1	1		1						
<i>Pfaffia tuberosa</i> (Spreng.) Hicken	1	1	1		1	1	1		1	1	1	1
<i>Salicornia fruticosa</i> L.									1			
Amaryllidaceae												
<i>Habranthus tubispathus</i> (L'Hér.) Traub			1									
<i>Nothoscordum bivalve</i> (L.) Britton				1				1			1	
<i>Nothoscordum bonariense</i> (Pers.) Beauverd						1						
<i>Nothoscordum gaudichaudianum</i> Kunth				1	1	1						1
<i>Nothoscordum gracile</i> (Aiton) Stearn				1		1						
<i>Nothoscordum montevidense</i> Beauverd			1	1	1	1	1			1	1	
Anacardiaceae												
<i>Lithraea brasiliensis</i> Marchand							1					
<i>Schinus lentiscifolius</i> Marchand									1			
<i>Schinus polygamus</i> (Cav.) Cabrera							1					
<i>Schinus weinmanniifolia</i> Mart. ex Engl.												1
Apiaceae												
<i>Ammoselinum rosengurtii</i> Mathias & Constance				1							1	
<i>Bowlesia incana</i> Ruiz & Pav.			1									
<i>Centella asiatica</i> (L.) Urb.	1	1			1	1	1	1		1		
<i>Cyclosporum leptophyllum</i> (Pers.) Sprague ex Britton & P. Wilson	1	1	1	1	1	1	1		1		1	
<i>Eryngium ciliatum</i> Cham. & Schldl.	1			1		1	1					

<i>Baccharis riograndensis</i> Malag. & J.Vidal	1	1			1		1					
<i>Baccharis subtropicalis</i> G.Heiden					1				1	1	1	
<i>Baccharis tridentata</i> Vahl					1			1	1	1		
<i>Baccharis uncinella</i> DC.									1			
<i>Barrosoa candolleana</i> (Hook. & Arn.) R.M.King & H.Rob.											1	1
<i>Calea cymosa</i> Less.									1	1		
<i>Calea uniflora</i> Less.	1										1	1
<i>Campuloclinium macrocephalum</i> (Less.) DC.									1		1	1
<i>Chaptalia exscapa</i> (Pers.) Baker			1	1	1	1			1	1	1	1
<i>Chaptalia integerrima</i> (Vell.) Burkart	1		1	1	1	1	1			1	1	1
<i>Chaptalia mandonii</i> Sch.Bip. ex Burkart									1	1	1	1
<i>Chaptalia piloselloides</i> (Vahl) Baker	1		1	1	1	1	1			1		
<i>Chaptalia runcinata</i> Kunth	1	1	1	1	1	1	1	1	1	1	1	1
<i>Chevreulia acuminata</i> Less.	1	1	1	1	1	1	1		1	1	1	1
<i>Chevreulia revoluta</i> A.A. Schneid. & R.Trevis.									1	1		
<i>Chevreulia sarmentosa</i> (Pers.) Blake	1	1	1	1	1	1	1		1	1	1	1
<i>Chromolaena ascendens</i> (Sch.Bip. ex Baker) R.M.King & H.Rob.	1						1		1	1	1	1
<i>Chromolaena congesta</i> (Hook. & Arn.) R.M. King & H. Rob.									1	1	1	
<i>Chromolaena ivifolia</i> (L.) R.M.King & H.Rob.										1		
<i>Chromolaena pedunculosa</i> (Hook. & Arn.) R.M.King & H.Rob.							1				1	
<i>Chromolaena squarrosula</i> (Hook. & Arn.) R.M. King & H. Rob.									1	1	1	1
<i>Chromolaena verbenacea</i> (DC.) R.M.King & H.Rob.											1	
<i>Chrysolepis flexuosa</i> (Sims) H.Rob.	1	1			1		1		1	1	1	1
<i>Conyza blakei</i> (Cabrera) Cabrera	1						1			1		1
<i>Conyza bonariensis</i> (L.) Cronquist	1	1	1	1	1	1	1	1	1	1	1	1
<i>Conyza canadensis</i> (L.) Cronquist		1										
<i>Conyza floribunda</i> Kunth	1											1
<i>Conyza primulifolia</i> (Lam.) Cuatrec. & Lourteig	1	1	1	1	1	1	1	1	1	1	1	1
<i>Dimerostemma arnotii</i> (Baker) M.D.Moraes									1	1		
<i>Disynaphia spathulata</i> (Hook. & Arn.) R.M.King & H.Rob.									1		1	1
<i>Eclipta prostrata</i> (L.) L.		1										
<i>Elephantopus mollis</i> Kunth	1		1	1	1	1	1			1	1	1
<i>Erechtites hieracifolius</i> (L.) Raf. ex DC.	1				1						1	
<i>Eupatorium inulifolium</i> Kunth										1		
<i>Facelis retusa</i> (Lam.) Sch.Bip.	1	1	1	1	1	1	1					
<i>Galinsoga parviflora</i> Cav.							1					
<i>Gamochaeta americana</i> (Mill.) Wedd.	1	1	1	1	1		1	1	1	1	1	1
<i>Gamochaeta argentina</i> Cabrera				1								
<i>Gamochaeta coarctata</i> (Willd.) Kerguélen	1	1	1	1	1	1	1				1	1
<i>Gamochaeta filaginea</i> (DC.) Cabrera	1	1					1					
<i>Gamochaeta stachydifolia</i> (Lam.) Cabrera						1	1					
<i>Gamochaeta simplicicaulis</i> (Willd. ex Spreng.) Cabrera	1			1			1	1		1	1	1
<i>Grazielia gaudichaudeana</i> (DC.) R.M.King & H.Rob.									1		1	1
<i>Grazielia intermedia</i> (DC.) R.M.King & H.Rob.											1	

<i>Senecio brasiliensis</i> (Spreng.) Less.	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Senecio conyzifolius</i> Baker									1	1			
<i>Senecio crassiflorus</i> (Poir.) DC.								1					
<i>Senecio heterotrichius</i> DC.		1	1		1	1	1		1	1	1	1	1
<i>Senecio juergensii</i> Mattf.										1			
<i>Senecio leptolobus</i> DC.		1				1						1	
<i>Senecio madagascariensis</i> Poir.		1											
<i>Senecio oxyphyllus</i> DC.							1					1	
<i>Senecio selloi</i> (Spreng.) DC.	1	1	1	1	1	1	1		1				
<i>Solidago chilensis</i> Meyen									1				1
<i>Soliva sessilis</i> Ruiz & Pav.	1	1	1	1	1	1	1	1		1			
<i>Sommerfeltia spinulosa</i> (Spreng.) Less.		1			1	1		1	1				1
<i>Stenachaenium campestre</i> Baker							1			1			1
<i>Stenachaenium megapotamicum</i> (Spreng.) Baker							1					1	
<i>Stenachaenium riedelli</i> Baker													1
<i>Stenocephalum megapotamicum</i> (Spreng.) Sch.Bip.									1	1	1	1	1
<i>Stevia alternifolia</i> Hieron.													1
<i>Stevia cinerascens</i> Sch.Bip. ex Baker									1				
<i>Stevia lundiana</i> DC.											1		
<i>Stevia selloi</i> (Spreng.) B.L.Rob.									1				
<i>Symphytotrichum squamatum</i> (Spreng.) G.L.Nesom		1					1						
<i>Trichocline catharinensis</i> Cabrera									1	1	1	1	1
<i>Vernonanthura beyrichii</i> (Less.) H. Rob.													1
<i>Vernonanthura catharinensis</i> (Cabrera) H.Rob.									1				
<i>Vernonanthura chamaedrys</i> (Less.) H. Rob.										1			1
<i>Vernonanthura discolor</i> (Spreng.) H.Rob.									1	1	1	1	1
<i>Vernonanthura nudiflora</i> (Less.) H. Rob.	1			1		1	1	1	1	1	1		1
<i>Vernonanthura phosphorica</i> (Vell.) H.Rob.												1	
<i>Vernonia echioides</i> Less.												1	
Begoniaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Begonia cucullata</i> Willd.							1						
Boraginaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Moritzia dusenii</i> I.M. Johnst.													1
Brassicaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Cardamine bonariensis</i> Pers.						1							
<i>Lepidium auriculatum</i> Regel & Körn.			1	1		1							
<i>Lepidium bonariense</i> L.					1								
<i>Lepidium ruderales</i> L.					1								
Cactaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Opuntia viridirubra</i> (F. Ritter) P.J. Braun & Esteves						1							
<i>Parodia ottonis</i> (Lehm.) N.P. Taylor							1						
Calyceraceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Acicarpa procumbens</i> Less.													1
Campanulaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Lobelia camporum</i> Pohl													1
<i>Lobelia hederacea</i> Cham.	1	1	1		1	1	1	1		1			

<i>Scleria balansae</i> Maury ex Micheli													1
<i>Scleria distans</i> Poir.								1	1	1			
<i>Scleria sellowiana</i> Kunth										1	1		
<i>Scleria spicata</i> (Spreng.) J.F.Macbr.						1							
Dennstaedtiaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Pteridium arachnoideum</i> (Kaulf.) Maxon										1	1	1	1
Droseraceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Drosera brevifolia</i> Pursh						1	1						
<i>Drosera communis</i> A.St.-Hil.											1		
Equisetaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Equisetum giganteum</i> L.							1						
Eriocaulaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Syngonanthus caulescens</i> (Poir.) Ruhland									1				
Escalloniaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Escallonia bifida</i> Link & Otto													1
Euphorbiaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Acalypha communis</i> Müll.Arg.												1	
<i>Croton didrichsenii</i> G.L.Webster				1									
<i>Croton glechomifolius</i> Müll.Arg.											1		
<i>Croton heterodoxus</i> Baill.	1					1							
<i>Croton lanatus</i> Lam.												1	
<i>Euphorbia papillosa</i> A.St.-Hil.	1							1	1				1
<i>Euphorbia peperomioides</i> Boiss.				1		1			1	1			
<i>Euphorbia selloi</i> (Klotzsch & Garcke) Boiss.	1	1			1				1				
<i>Euphorbia spathulata</i> Lam.													1
<i>Euphorbia stenophylla</i> (Klotzsch & Garcke) Boiss.		1		1								1	
<i>Tragia bahiensis</i> Müll.Arg.		1		1		1			1		1	1	
<i>Tragia geraniifolia</i> Klotzsch ex Müll.Arg.						1							
<i>Tragia uberabana</i> Müll.Arg.													1
Fabaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Adesmia bicolor</i> (Poir.) DC.				1	1								
<i>Adesmia ciliata</i> Vogel										1			
<i>Adesmia incana</i> Vogel				1									
<i>Adesmia latifolia</i> (Spreng.) Vogel										1			
<i>Adesmia sulina</i> Miotto											1		
<i>Adesmia tristis</i> Vogel										1			
<i>Aeschynomene falcata</i> (Poir.) DC.	1								1	1	1	1	1
<i>Ancistrotropis peduncularis</i> (Kunth) A. Delgado													1
<i>Arachis burkartii</i> Handro	1			1	1	1	1						
<i>Clitoria nana</i> Benth.							1						
<i>Crotalaria hilariana</i> Benth.										1	1	1	1
<i>Crotalaria incana</i> L.	1												
<i>Desmanthus tatuhyensis</i> Hoehne	1	1				1			1	1	1	1	
<i>Desmanthus virgatus</i> (L.) Willd.				1					1	1			
<i>Desmodium adscendens</i> (Sw.) DC.	1		1	1	1		1	1					1
<i>Desmodium affine</i> Schltdl.										1	1		

<i>Desmodium barbatum</i> (L.) Benth.							1					1
<i>Desmodium incanum</i> (Sw.) DC.	1	1	1	1	1	1	1	1	1	1	1	1
<i>Desmodium uncinatum</i> (Jacq.) DC.	1		1	1	1	1	1	1	1		1	
<i>Eriosema campestre</i> Benth.												1
<i>Eriosema longifolium</i> Benth.											1	
<i>Eriosema obovatum</i> Benth.											1	
<i>Eriosema tacuareamboense</i> Arechav.									1	1	1	1
<i>Galactia benthamiana</i> Micheli											1	
<i>Galactia gracillima</i> Benth.		1							1	1	1	1
<i>Galactia marginalis</i> Benth.	1	1	1	1					1		1	1
<i>Galactia neesii</i> DC.									1			1
<i>Indigofera asperifolia</i> Bong. ex Benth.					1							1
<i>Lathyrus crassipes</i> Gillies ex Hook. & Arn.		1		1		1						
<i>Lathyrus subulatus</i> Lam.						1						
<i>Leptospron adenanthum</i> (G. Mey.) A.Delgado									1		1	
<i>Lotus corniculatus</i> L.		1										
<i>Lupinus magnistipulatus</i> Burkart ex Planchuelo & D.B.Dunn									1			
<i>Macroptilium prostratum</i> (Benth.) Urb.	1	1							1		1	1
<i>Mimosa cruenta</i> Benth.												1
<i>Mimosa flagellaris</i> Benth.				1		1	1					
<i>Mimosa paupera</i> Benth.					1							
<i>Poiretia tetraphylla</i> (Poir.) Burkart									1	1		1
<i>Pomaria pilosa</i> (Vogel) B.B.Simpson & G.P.Lewis	1			1								
<i>Rhynchosia corylifolia</i> Mart. ex Benth.									1	1	1	1
<i>Rhynchosia diversifolia</i> Micheli		1	1	1		1					1	1
<i>Rhynchosia senna</i> Gillies ex Hook.				1							1	
<i>Stylosanthes leiocarpa</i> Vogel	1	1					1	1		1	1	
<i>Stylosanthes montevidensis</i> Vogel	1	1	1	1	1	1	1		1	1	1	1
<i>Tephrosia adunca</i> Benth.									1	1	1	1
<i>Trifolium argentinense</i> Speg.												1
<i>Trifolium polymorphum</i> Poir.		1	1	1	1	1	1					
<i>Trifolium repens</i> L.						1	1					
<i>Trifolium riograndense</i> Burkart									1		1	1
<i>Vachellia caven</i> (Molina) Seigler & Ebinger					1							
<i>Vicia graminea</i> Sm.			1			1					1	
<i>Vigna luteola</i> (Jacq.) Benth.								1				
<i>Zornia burkartii</i> Vanni											1	1
<i>Zornia contorta</i> Mohlenbr.						1						
<i>Zornia cryptantha</i> Arechav.				1			1			1	1	1
<i>Zornia multinervosa</i> Burkart ex N.M.Bacigal.	1	1										
<i>Zornia orbiculata</i> Mohlenbr.						1						
<i>Zornia pardina</i> Mohlenbr.										1		
Gentianaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac
<i>Cicendia quadrangularis</i> (Lam.) Griseb.	1					1	1					
<i>Zygostigma australe</i> (Cham. & Schldtl.) Griseb.				1		1						1
Geraniaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac

<i>Geranium albicans</i> A.St.-Hil.					1			1					1	
Hypericaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac		
<i>Hypericum brasiliense</i> Choisy										1	1			
<i>Hypericum connatum</i> Lam.										1		1	1	
<i>Hypericum gentianoides</i> (L.) Britton et al.								1						
<i>Hypericum mutilum</i> L.							1							
<i>Hypericum piriiai</i> Arechav.		1												
<i>Hypericum rigidum</i> A. St.-Hil.											1			
<i>Hypericum ternum</i> A.St.-Hil.											1			
Hypoxidaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac		
<i>Hypoxis decumbens</i> L.	1	1	1	1	1	1	1	1	1	1	1	1	1	
Iridaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac		
<i>Calydorea crocoides</i> Ravenna				1							1		1	
<i>Cypella discolor</i> Ravenna				1										
<i>Cypella hauthalii</i> (Kuntze) R.C.Foster				1	1									
<i>Cypella herbertii</i> (Lindl.) Herb.		1		1	1				1					
<i>Herbertia furcata</i> (Klatt) Ravenna				1										
<i>Herbertia lahue</i> (Molina) Goldblatt	1		1	1	1	1	1							
<i>Herbertia pulchella</i> Sweet		1		1	1	1								
<i>Herbertia quareimana</i> Ravenna				1										
<i>Kelissa brasiliensis</i> (Baker) Ravenna	1						1							
<i>Sisyrinchium angustifolium</i> Mill.		1												
<i>Sisyrinchium avenaceum</i> Klatt		1												
<i>Sisyrinchium hoehnei</i> I.M.Johnst.	1				1				1	1				
<i>Sisyrinchium megapotamicum</i> Malme		1										1	1	
<i>Sisyrinchium micranthum</i> Cav.	1	1	1	1	1	1	1		1	1	1	1	1	
<i>Sisyrinchium minutiflorum</i> Klatt		1		1	1	1								
<i>Sisyrinchium pachyrhizum</i> Baker				1	1									
<i>Sisyrinchium palmifolium</i> L.			1								1			
<i>Sisyrinchium scariosum</i> I.M.Johnst.							1			1				
<i>Sisyrinchium sellowianum</i> Klatt									1					
<i>Sisyrinchium setaceum</i> Klatt	1									1				
<i>Sisyrinchium vaginatum</i> Spreng.			1		1		1		1	1	1	1	1	
Juncaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac		
<i>Juncus bufonius</i> L.			1				1		1					
<i>Juncus capillaceus</i> Lam.	1	1	1	1		1	1				1	1		
<i>Juncus capitatus</i> Weigel				1		1								
<i>Juncus ilanquihuensis</i> Barros								1						
<i>Juncus imbricatus</i> Laharpe				1	1	1	1							
<i>Juncus microcephalus</i> Kunth	1	1	1	1	1	1	1		1	1				
<i>Juncus pallescens</i> Lam.								1						
<i>Juncus scirpoides</i> Lam.				1				1	1					
<i>Juncus tenuis</i> Willd.		1		1	1		1		1					
Lamiaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac		
<i>Cantinoa mutabilis</i> (Rich.) Harley & J.F.B.Pastore	1									1				
<i>Cunila galioides</i> Benth.									1	1				

<i>Oxalis brasiliensis</i> G.Lodd.	1	1	1	1	1	1	1	1		1				
<i>Oxalis conorrhiza</i> Jacq.	1	1	1	1	1	1	1	1	1			1	1	
<i>Oxalis eriocarpa</i> DC.	1	1	1	1	1	1	1							
<i>Oxalis floribunda</i> Lehm.				1										
<i>Oxalis hispidula</i> Zucc.							1	1						
<i>Oxalis lasiopetala</i> Zucc.	1	1	1				1	1			1	1		
<i>Oxalis paludosa</i> A.St.-Hil.				1						1				
<i>Oxalis subvillosa</i> Norlind							1							
<i>Oxalis tenerrima</i> Knuth														1
Plantaginaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac		
<i>Bacopa monnieri</i> (L.) Pennell		1				1		1						
<i>Gratiola peruviana</i> L.		1							1					
<i>Mecardonia procumbens</i> (Mill.) Small			1											
<i>Mecardonia procumbens</i> var. <i>flagellaris</i> (Cham. & Schltld.) V.C.Souza				1										
<i>Mecardonia procumbens</i> var. <i>herniarioides</i> (Cham.) V.C.Souza					1									
<i>Mecardonia procumbens</i> var. <i>tenella</i> (Cham. & Schltld.) V.C.Souza		1	1		1	1	1		1				1	
<i>Plantago australis</i> Lam.							1		1	1				
<i>Plantago coronopus</i> L.								1						
<i>Plantago guilleminiana</i> Decne.									1	1				
<i>Plantago myosuroides</i> Lam.	1	1	1	1	1	1	1		1					
<i>Plantago napiformis</i> (Rahn) Hassemer	1												1	
<i>Plantago penantha</i> Griseb.			1	1	1		1							
<i>Plantago tomentosa</i> Lam.	1	1	1	1	1	1	1		1	1	1	1	1	
<i>Plantago turficola</i> Rahn						1								
<i>Scoparia dulcis</i> L.			1	1			1							
<i>Scoparia ericacea</i> Cham. & Schltld.						1								
<i>Scoparia hassleriana</i> Chodat			1											
<i>Scoparia montevidensis</i> (Spreng.) R.E.Fr.		1		1	1	1	1							
<i>Stemodia lanceolata</i> Benth.									1					
<i>Stemodia stricta</i> Cham. & Schltld.						1								
<i>Stemodia verticillata</i> (Mill.) Hassl.			1	1	1	1	1			1				
<i>Veronica arvensis</i> L.			1											
<i>Veronica peregrina</i> L.						1								
<i>Veronica persica</i> Poir.			1	1										
Poaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac		
<i>Agenium villosum</i> (Nees) Pilg.		1							1		1	1		
<i>Agrostis montevidensis</i> Spreng. ex Nees		1	1					1	1		1	1		
<i>Agrostis tandilensis</i> (Kuntze) Parodi					1								1	
<i>Andropogon bicornis</i> L.		1												
<i>Andropogon lateralis</i> Nees	1	1	1	1	1	1	1	1	1	1	1	1		
<i>Andropogon leucostachyus</i> Kunth								1					1	
<i>Andropogon macrothrix</i> Trin.				1		1			1	1	1	1	1	
<i>Andropogon selleanus</i> (Hack.) Hack.		1	1	1		1		1	1		1	1	1	
<i>Andropogon ternatus</i> (Spreng.) Nees		1	1	1			1				1	1	1	
<i>Anthaenaria lanata</i> (Kunth) Benth.		1										1		

<i>Paspalum leptum</i> Schult.	1	1	1	1	1	1	1	1	1	1	1
<i>Paspalum maculosum</i> Trin.								1	1	1	1
<i>Paspalum modestum</i> Mez		1									
<i>Paspalum notatum</i> Flügge	1	1	1	1	1	1	1	1	1	1	1
<i>Paspalum pauciciliatum</i> (Parodi) Herter			1	1	1		1			1	1
<i>Paspalum paucifolium</i> Swallen			1			1					
<i>Paspalum plicatulum</i> Michx.	1	1	1	1	1	1	1		1	1	1
<i>Paspalum polyphyllum</i> Nees ex Trin.	1		1						1	1	1
<i>Paspalum pumilum</i> Nees	1	1	1			1	1	1	1	1	1
<i>Paspalum umbrosum</i> Trin.											1
<i>Paspalum urvillei</i> Steud.		1	1		1		1		1	1	1
<i>Paspalum vaginatum</i> Sw.								1			
<i>Phalaris angusta</i> Nees ex Trin.							1				
<i>Phalaris platensis</i> Henrard ex Wacht.				1							
<i>Piptochaetium bicolor</i> (Vahl) Desv.											1
<i>Piptochaetium lasianthum</i> Griseb.		1	1	1							
<i>Piptochaetium montevidense</i> (Spreng.) Parodi	1	1	1	1	1	1	1		1	1	1
<i>Piptochaetium ruprechtianum</i> Desv.		1	1	1		1	1				
<i>Piptochaetium stipoides</i> (Trin. & Rupr.) Hack. ex Arechav.		1	1	1	1	1	1			1	1
<i>Piptochaetium uruguense</i> Griseb.	1			1	1		1				
<i>Poa annua</i> L.			1	1	1	1	1				
<i>Saccharum angustifolium</i> (Nees) Trin.		1	1		1				1	1	1
<i>Saccharum villosum</i> Steud.					1				1		
<i>Sacciolepis vilvoides</i> (Trin.) Chase									1	1	
<i>Schizachyrium bimucronatum</i> Roseng., B.R.Arrill. & Izag.	1										
<i>Schizachyrium condensatum</i> (Kunth) Nees									1		
<i>Schizachyrium gracilipes</i> (Hack.) A.Camus										1	1
<i>Schizachyrium hatschbachii</i> Peichoto				1					1	1	1
<i>Schizachyrium imberbe</i> (Hack.) A. Camus		1		1							
<i>Schizachyrium microstachyum</i> (Desv. ex Ham.) Roseng., B.R.Arrill. & Izag.	1	1	1	1	1		1		1	1	1
<i>Schizachyrium plumigerum</i> (Ekman) Parodi								1		1	
<i>Schizachyrium spicatum</i> (Spreng.) Herter		1		1				1			
<i>Schizachyrium tenerum</i> Nees	1	1	1	1		1			1	1	1
<i>Setaria parviflora</i> (Poir.) M.Kerguelen	1	1	1	1	1	1	1	1	1	1	1
<i>Setaria vaginata</i> Spreng.		1		1	1	1	1		1	1	
<i>Sorghastrum pellitum</i> (Hack.) Parodi							1		1	1	1
<i>Sorghastrum setosum</i> (Griseb.) Hitchc.											1
<i>Spartina ciliata</i> Brongn.								1			
<i>Sporobolus aeneus</i> var. <i>angustifolius</i> (Doll) S.Denham & Aliscioni										1	1
<i>Sporobolus indicus</i> (L.) R.Br.	1	1	1	1	1	1	1	1	1	1	1
<i>Sporobolus monandrus</i> Roseng., B.R.Arrill. & Izag.										1	
<i>Sporobolus pseudairoides</i> Parodi											1
<i>Steinchisma decipiens</i> (Nees ex Trin.) W.V.Br.	1	1		1			1		1	1	1
<i>Steinchisma hians</i> (Elliott) Nash	1	1	1	1	1	1	1	1	1	1	1
<i>Stenotaphrum secundatum</i> (Walter) Kuntze									1		

<i>Trachypogon montufarii</i> (Kunth) Nees	1			1						1			1
<i>Trachypogon spicatus</i> (L.f.) Kuntze						1		1				1	1
<i>Trichantheium parvifolium</i> (Lam.) Zuloaga & Morrone										1			
<i>Trichantheium schwackeanum</i> (Mez) Zuloaga & Morrone										1		1	
<i>Urochloa decumbens</i> (Stapf) R.D.Webster	1												
<i>Vulpia australis</i> (Nees ex Steud.) C.H. Blom			1										
<i>Vulpia bromoides</i> (L.) Gray	1	1	1	1	1	1	1	1				1	
<i>Vulpia myuros</i> (L.) C.C.Gmel.				1									
Polygalaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Polygala adenophylla</i> A.St.-Hil. & Moq.					1	1					1		
<i>Polygala altomontana</i> Lüdtke et al.											1		
<i>Polygala aphylla</i> A.W.Benn.				1									
<i>Polygala australis</i> A.W.Benn.		1	1	1	1	1	1	1			1		1
<i>Polygala bonariensis</i> Grondona				1	1								
<i>Polygala brasiliensis</i> L.			1		1	1					1	1	1
<i>Polygala campestris</i> Gardner										1			
<i>Polygala duarteana</i> A.St.-Hil. & Moq.					1								
<i>Polygala extraaxillaris</i> Chodat										1			
<i>Polygala linoides</i> Poir.				1									
<i>Polygala molluginifolia</i> A.St.-Hil. & Moq.				1	1						1		
<i>Polygala paniculata</i> L.													1
<i>Polygala pulchella</i> A.St.-Hil. & Moq.		1	1	1	1	1	1		1	1			
Polygonaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Persicaria punctata</i> (Elliott) Small								1					
Portulacaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Portulaca grandiflora</i> Hook.									1				
<i>Portulaca oleracea</i> L.									1				
Primulaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Lysimachia arvensis</i> (L.) U.Manns & Anderb.		1	1			1	1	1					
<i>Lysimachia filiformis</i> (Cham. & Schltld.) U.Manns & Anderb.			1	1	1	1		1	1				
<i>Lysimachia minima</i> (L.) U.Manns & Anderb.	1		1	1	1	1	1	1		1			
Pteridaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Adiantopsis chlorophylla</i> (Sw.) Fée			1			1				1	1		
<i>Adiantopsis per fasciculata</i> Sehnem	1												
Ranunculaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Ranunculus flagelliformis</i> Sm.										1			
<i>Ranunculus platensis</i> Spreng.			1										
Rhamnaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Discaria americana</i> Gillies & Hook.			1										
<i>Scutia buxifolia</i> Reissek						1							
Rosaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Acaena eupatoria</i> Cham. & Schltld.										1	1	1	
<i>Agrimonia hirsuta</i> Bong. ex C.A.Mey.									1				
<i>Aphanes arvensis</i> L.	1		1			1	1						
<i>Aphanes parodii</i> (I.M.Johnst.) Rothm.						1	1						

Urticaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Urtica circularis</i> (Hicken) Sorarú			1			1	1						
Verbenaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Aloysia chamaedryfolia</i> Cham.						1							
<i>Aloysia gratissima</i> (Gillies & Hook.) Tronc.				1									
<i>Glandularia balansae</i> (Briq.) N.O'Leary									1				
<i>Glandularia catharinae</i> (Moldenke) N.O'Leary & P.Peralta									1				
<i>Glandularia marrubioides</i> (Cham.) Tronc.			1	1		1			1	1	1	1	
<i>Glandularia peruviana</i> (L.) Small			1	1		1	1	1		1			
<i>Glandularia selloi</i> (Spreng.) Tronc.		1	1		1		1			1			
<i>Lantana fucata</i> Lindl.						1							
<i>Lantana montevidensis</i> (Spreng.) Briq.												1	
<i>Lippia asperrima</i> Cham.					1								
<i>Lippia coarctata</i> Tronc.				1	1								
<i>Lippia turnerifolia</i> Cham.	1												
<i>Verbena gracilescens</i> (Cham.) Herter				1									
<i>Verbena intermedia</i> Gillies & Hook. ex Hook.			1										
<i>Verbena litoralis</i> Kunth									1				
<i>Verbena montevidensis</i> Spreng.		1	1	1	1				1	1		1	
<i>Verbena rigida</i> Spreng.		1							1				
Violaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Pombalia bicolor</i> (A.St-Hil.) Paula-Souza				1								1	
<i>Pombalia parviflora</i> (Mutis ex L.f.) Paula-Souza						1			1			1	
Vivianiaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Viviania albiflora</i> (Cambess.) Reiche						1					1	1	1
Xyridaceae	ale	jag	lav	qua	sam	sbv	sgb	tav	pai	pal	sol	vac	
<i>Xyris jupicai</i> Rich.									1				

Supplementary file 2: Soil variables analysed in each sampling site in the South Brazilian grasslands. Letters code represents the municipality where each site is located: Alegrete (ale), Jaguarão (jag), Lavras do Sul (lav), Quaraí (qua), Santo Antônio das Missões (sam), Santana da Boa Vista (sbv), São Gabriel (sgb), Tavares(tav), Painei (pai), Palmas (pal), Soledade (sol), Vacaria (vac). For more information regarding measurement unit and method of analysis see Table 1 in the main text.

	Clay	Csand	Fsand	Silt	OM	pH	P	K	N	Al	Ca	Mg	CEC	Bsat	AlSat
ale1	13	42	42	2	1.6	5	1.9	47	0.06	0.3	0.9	0.8	4.9	37	14.1
ale2	15	31	53	1	1	5	2.9	41	0.06	0.4	0.7	0.5	4.1	32	23.5
ale3	13	41	41	5	1.3	5	3.1	29	0.06	0.4	1.1	0.8	5.4	36	16.8
ale4	18	30	45	7	1.7	4.8	3.1	68	0.11	0.8	1.6	1.1	9	32	21.8
ale5	9	46	40	4	0.9	5	2.8	28	0.04	0.3	0.6	0.4	3.3	33	21.9
ale6	15	38	40	6	1.8	4.9	1.8	42	0.1	0.6	1.2	1.1	5.5	44	20
ale7	13	29	49	8	1.9	5.1	13	64	0.1	0.3	2	1	7.5	42	8.7
ale8	13	43	41	3	1.4	4.9	1.4	44	0.05	0.4	0.7	0.5	3.8	35	23.4
ale9	13	42	37	8	1.5	5.2	2.2	47	0.06	0.2	0.7	0.5	3.5	38	13.2
jag1	19	54	14	19	4	4.6	3	64	0.14	0.3	3.8	1.8	12	48	4.8
jag2	25	6	6	63	3	5.1	4.6	77	0.26	0.1	4.6	2.5	13.8	53	1.3
jag3	18	44	24	14	3.4	4.8	3.5	143	0.1	0.5	1.9	1.3	8	45	12.2
jag4	21	34	17	28	3.8	4.7	3.6	55	0.14	0.8	2.6	1.3	11.9	34	16.3
jag5	21	37	19	23	4.1	4.9	3.6	182	0.2	0.5	2.7	1.6	11	43	9.4
jag6	20	54	17	9	3.1	4.7	3.6	96	0.1	0.6	1.7	0.8	8.9	31	17.7
jag7	22	33	18	27	4.9	4.9	23	108	0.22	0.9	6.5	3.3	19.9	51	8.1
jag8	19	37	18	26	5.8	5.2	12	116	0.26	0.1	5.1	2.7	14.3	56	1.2
jag9	24	39	18	19	4.2	4.8	5.4	125	0.18	0.3	2.1	1.3	9.9	37	7.3
lav1	22	29	20	25	3.5	5.2	3.7	52	0.22	0.2	8.5	3.3	18.1	66	1.6
lav2	28	28	16	25	4.3	5	8.3	118	0.22	0.3	10.8	7.2	25.2	73	1.6
lav3	21	35	17	23	3.4	5	3.2	83	0.2	0.4	6	3.7	16.8	59	3.9
lav4	28	18	17	37	3.1	5.1	3.8	106	0.2	0.2	7.9	2.4	18.3	58	1.9
lav5	18	39	23	19	2.7	5.1	7	59	0.14	0.2	5.9	2.2	13.1	63	2.4
lav6	25	36	22	17	3.4	5.1	3.8	137	0.22	0.2	5.8	2.9	11.8	77	2.2
lav7	14	43	22	18	3.1	4.6	2.9	77	0.17	0.3	3.7	1.9	8.6	68	4.9
lav8	14	50	18	17	3.1	4.8	3.6	67	0.15	0.4	3.4	1.4	8.4	59	7.4
lav9	16	33	24	26	3.3	4.7	2.4	55	0.2	0.3	4.1	1.6	10.2	57	4.9
pai1	54	10	2	34	8.4	5	3.7	116	0.42	1.8	3	1.9	20.7	25	25.5
pai2	43	13	1	43	8.5	5.1	3.7	126	0.43	1.8	3.3	1.6	22.5	23	25.5
pai3	54	9	2	35	7.2	4.7	2.2	102	0.31	2.9	2	0.9	18.7	17	46.9
pai4	59	10	1	30	6.3	4.6	2.9	158	0.32	2.5	1.3	0.9	18.1	14	48.2
pai5	54	10	3	33	6	4.6	1.7	107	0.31	2.2	2.1	1.3	19.3	19	36.2
pai6	57	13	2	28	6.1	4.4	2.6	98	0.27	1.5	1.4	1	15.2	17	34
pai7	60	8	2	25	6	4.5	1.2	158	0.26	2	1	0.7	14.5	15	47
pai8	51	12	5	32	5.5	4.8	2.5	78	0.36	1.3	3.2	1.5	22.5	22	20.1
pai9	60	10	3	26	4.7	4.7	1.5	101	0.29	2.8	1.5	1	15.1	18	49.2
pal1	47	13	2	36	6.9	4.2	3.4	130	0.4	5.4	1	0.6	32.7	6	73.4
pal2	38	15	1	41	7	4.4	2.5	101	0.46	6.5	0.9	0.4	32.3	5	80.2

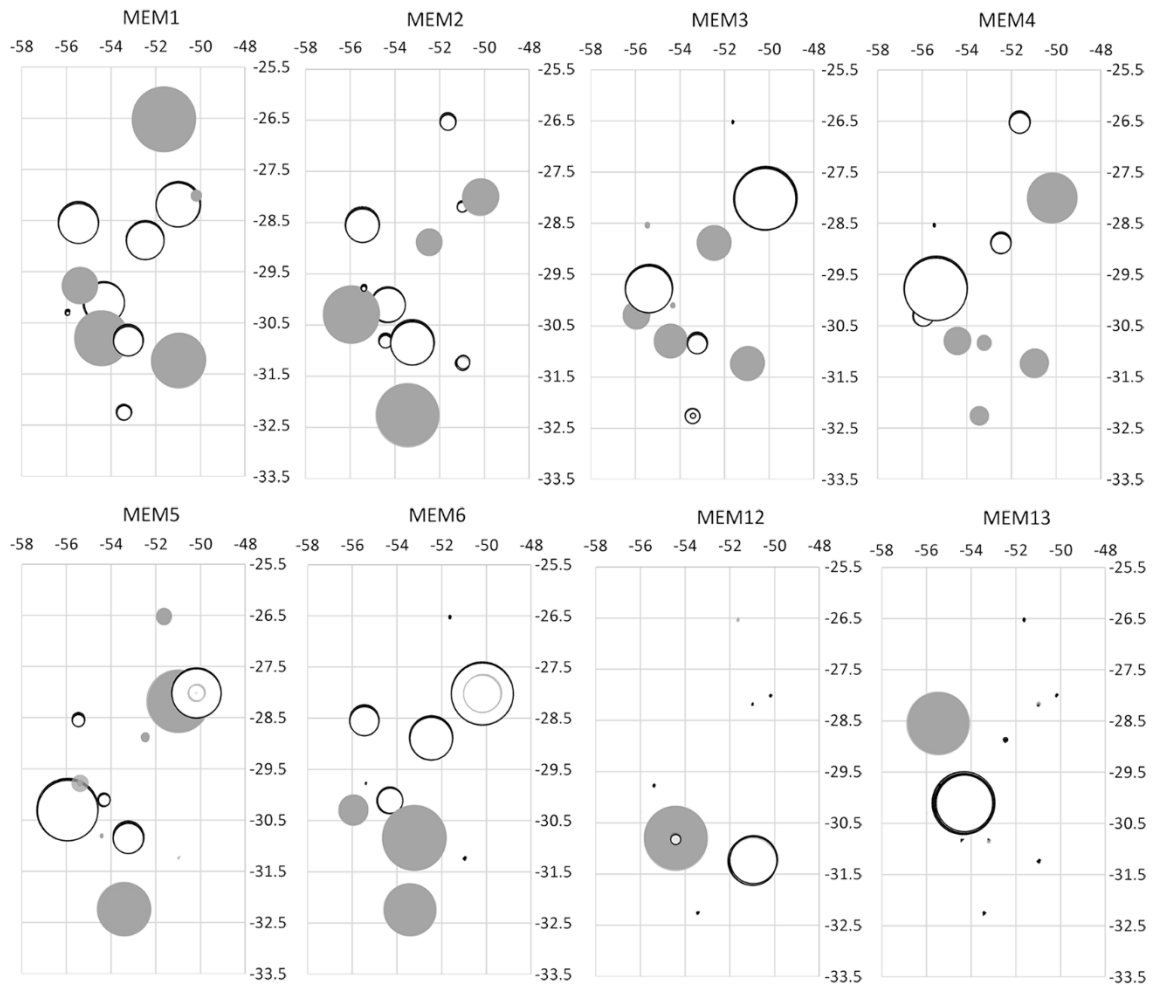
pal3	28	15	1	51	7.8	4.6	3.6	148	0.46	3.2	1	0.4	19.2	9	63.1
pal4	35	15	2	46	7.8	4.4	1.4	74	0.38	3.6	0.5	0.2	28.3	3	80
pal5	15	13	1	57	8.3	4.7	3.7	110	0.6	2.9	1	0.5	19.1	9	61.6
pal6	39	14	2	43	6.5	4.4	1.8	100	0.48	3.6	0.7	0.6	23.3	7	69.5
pal7	28	12	1	53	7.4	4.4	1.9	124	0.38	3.8	0.8	0.6	29.1	6	68.7
pal8	34	16	4	38	6.4	4.4	1.6	81	0.37	4	0.6	0.3	22.9	5	78
pal9	36	12	3	40	6.2	4.5	2.5	167	0.31	3.1	1.2	1	22.1	12	53.7
qua1	22	8	2	68	5.7	4.9	5.2	129	0.3	0.2	4.6	1.9	21	47	1.9
qua2	50	9	3	38	5.6	6.5	2.8	116	0.24	0	35.7	12.4	50.9	95	0
qua3	28	16	2	54	7.9	5.3	7.3	185	0.52	0.2	10.3	2.8	23.5	58	1.4
qua4	24	31	6	39	6.8	5.2	15	395	0.42	0.2	7.9	3.3	19.3	63	1.6
qua5	26	16	3	55	6.7	5.1	5	117	0.33	0.1	10.4	3	23.6	58	0.7
qua6	22	13	3	62	6.4	5	7.7	279	0.43	0.2	9.2	2.7	22.5	56	1.5
qua7	24	17	7	52	7.4	5.1	8.3	183	0.44	0.2	11.4	5.1	25.8	66	1.2
qua8	30	9	5	56	8.2	5.6	5.9	157	0.56	0	17.5	7.5	31.6	80	0
qua9	28	24	1	47	7.4	5.6	4.6	115	0.32	0	30.7	14.1	50	90	0
sam1	32	24	13	31	4.2	4.6	0.9	140	0.19	0.3	11.7	5.4	29.7	59	1.7
sam2	40	19	10	31	5.5	5.2	1.1	79	0.25	0	18.3	9.1	37.3	74	0
sam3	36	17	11	36	4.3	5.1	1.4	53	0.17	0.2	13.2	5.5	32.6	58	1.1
sam4	34	29	14	23	5.7	4.9	0.2	78	0.25	0.2	20.9	9.5	46	66	0.6
sam5	40	17	17	26	6	5.2	2.1	86	0.26	0.1	20.9	8.7	42.1	71	0.3
sam6	36	23	12	29	4.4	5.1	1.9	117	0.23	0.2	12.1	7.2	30.5	64	1
sam7	34	30	14	22	5	4.9	2.2	85	0.24	0.2	6.4	4.9	21.3	54	1.7
sam8	34	22	13	31	4.4	5.2	1.4	73	0.21	0.1	16.9	9.7	35.5	76	0.4
sam9	36	8	10	29	5.7	5	2.4	96	0.26	0.1	21	7.9	44.6	65	0.3
sbv1	18	41	29	12	2.7	4.7	1.4	49	0.15	0.8	1.9	0.3	9.2	25	25.6
sbv2	14	47	28	11	2.8	4.4	4.7	157	0.11	0.3	2	0.9	7.7	43	8.3
sbv3	14	51	27	8	2.5	4.5	5.5	100	0.14	1	1.1	0.3	8.6	19	37.7
sbv4	18	51	18	13	3.2	4.3	5.5	118	0.16	1	2.4	1.5	12.9	33	19.2
sbv5	20	29	36	15	3.2	4.2	7.8	181	0.14	0.9	3	1.4	14.6	33	15.6
sbv6	24	38	23	15	3.8	4.9	100	105	0.18	0.1	7.5	3.4	18.1	62	0.9
sbv7	20	44	21	15	2.3	4.7	3.3	58	0.15	0.9	1.8	0.4	9.3	25	27.7
sbv8	24	33	26	17	3	4.7	3.6	114	0.12	0.2	2.6	2.1	11.1	45	3.9
sbv9	18	20	48	14	2.3	4.5	3.4	101	0.14	0.4	3.1	0.9	10.4	41	8.6
sgb1	18	34	39	9	2	4.4	2.8	43	0.09	2	1.7	0.7	13.4	19	44.3
sgb2	12	34	52	2	1.9	4.2	1.2	19	0.06	1.6	0.3	0.2	6	9	74.5
sgb3	18	22	47	13	2.5	4.7	2.9	172	0.08	2.5	3.4	2	23.1	25	30
sgb4	22	18	41	19	2.6	5	3.2	65	0.13	0.8	2.7	1.1	11.7	34	16.8
sgb5	13	25	54	8	1.7	4.8	2	50	0.06	0.9	3	0.6	8.1	46	19.4
sgb6	24	16	38	22	3.1	5	3.7	202	0.15	0.7	6.9	2.3	17.5	56	6.7
sgb7	10	42	45	3	1.4	4.6	2.9	86	0.04	0.8	0.8	0.4	5.3	27	36
sgb8	12	37	50	1	2.1	4.7	8.2	144	0.1	0.4	1.8	0.9	6.2	50	11.5
sgb9	12	32	52	4	1.9	4.9	5.5	83	0.09	0.4	1.8	0.8	6.3	45	12.5
sol1	36	13	10	36	4.2	4.1	2	103	0.2	3.4	1.5	1	11.4	24	55.2
sol2	36	10	8	45	5	4.3	2.5	245	0.36	2.6	2.2	1.5	14.1	31	37.5
sol3	32	26	13	23	4	4.3	3.2	76	0.19	2.9	1.2	0.3	10.4	16	63.1

sol4	36	13	10	41	4.5	4.6	4.1	400	0.26	2.1	3.7	2.5	17.1	43	22.2
sol5	38	22	7	31	4.9	4	2.7	231	0.32	3.4	3	2.2	15.5	37	37
sol6	36	11	7	43	5.3	3.8	3.2	101	0.28	4.6	1.8	1	16.8	18	60.1
sol7	42	11	7	36	4.6	4.1	1.4	183	0.22	3	2	1.1	10.5	34	45.7
sol8	33	11	9	43	4.8	4	2.4	194	0.23	3.4	1.7	1.1	14.2	23	50.8
sol9	35	10	10	43	3.9	4.3	2.9	192	0.21	4.1	1.6	1.1	16.9	19	56.2
tav1	36	35	50	3	4	5.3	8.9	145	0.17	0	4.5	2.5	9.8	75	0
tav2	13	6	4	76	10	5	14	72	0	0.1	3.4	3.1	18.9	35	1.5
tav3	10	29	52	6	1.3	4.8	2.6	20	0.04	0.3	0.5	0.2	4.6	16	28.5
tav4	10	4	1	76	10	4.2	8.2	50	1.4	0.3	2.4	2.9	36.1	15	5.2
tav5	11	27	53	7	1.3	5.5	5.6	217	0.08	0	1.3	2.5	8.2	53	0
tav6	8	22	11	51	10	4	26	157	1.1	1.2	3.2	1.6	48.5	11	18.7
tav7	9	33	47	9	1	4.7	25	14	0.03	0.3	0.5	0.1	4.1	15	31.9
tav8	29	22	29	13	4.3	4.9	15	400	0.3	0	2.9	8.4	18.9	67	0
tav9	25	24	28	18	3.7	5.3	6.5	400	0.26	0	2.9	6.8	15.3	71	0
vac1	60	8	4	27	4.2	4.6	2.5	88	0.23	4.2	0.9	0.6	23.5	7	70.9
vac2	60	10	6	21	4.3	4.6	3	78	0.21	3.5	1.2	0.6	23.8	8	63.6
vac3	60	9	4	26	4	4.6	2.6	149	0.21	3	1.2	1.1	16.4	16	52.8
vac4	59	10	4	27	4	4.6	2.1	106	0.21	3.9	0.9	0.6	21.2	8	68.8
vac5	60	10	6	21	4.1	4.6	2.1	67	0.2	4.2	0.7	0.4	23	6	76.8
vac6	60	7	3	29	4.6	4.7	1.6	131	0.21	3.3	1	0.9	21.6	10	59.6
vac7	60	7	5	25	4.1	4.6	1.4	87	0.19	3.8	0.8	0.8	21.2	9	67.6
vac8	60	9	6	20	4.4	4.5	1.7	96	0.19	4.2	0.9	0.6	23.5	7	70.6
vac9	60	8	5	22	4.8	4.6	3.1	111	0.22	4.2	1	0.8	23.8	9	66.8

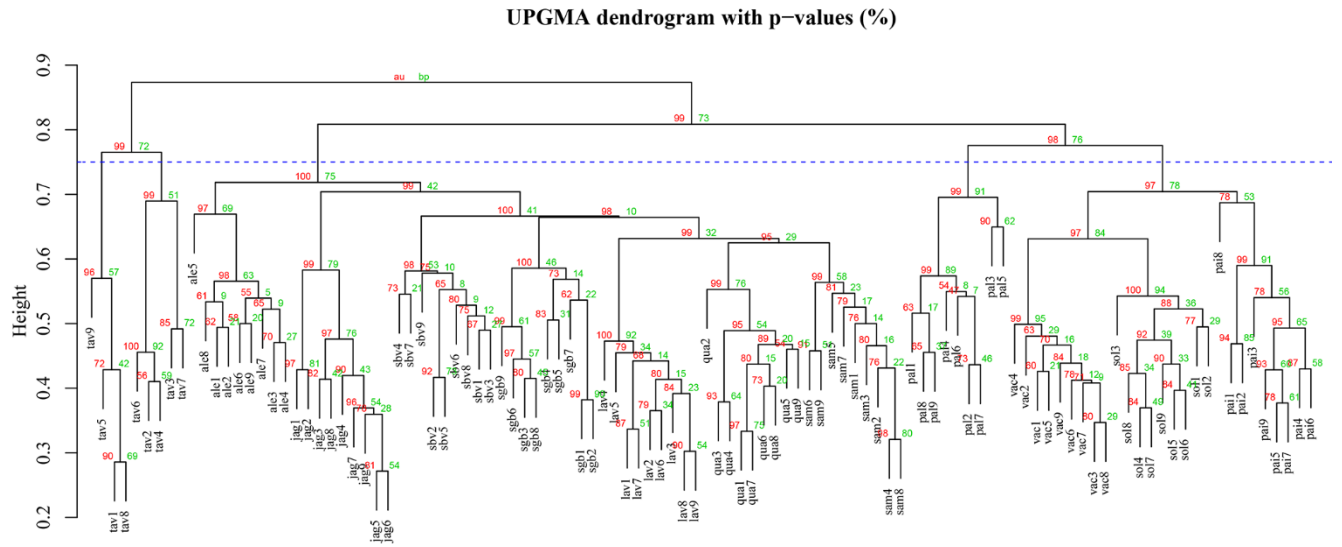
Supplementary file 3: Climatic variables extracted from INMET database for a ten-year time series (2006 to 2016). Variables are: 'maxT' maximum temperature (°C), 'minT' minimum temperature (°C), 'minAH' minimum air humidity (%), 'maxP' maximum precipitation (mm) and 'minP' minimum precipitation (mm). Letters code represents the municipality where each grid is located: Alegrete (ale), Jaguarão (jag), Lavras do Sul (lav), Quaraí (qua), Santo Antônio das Missões (sam), Santana da Boa Vista (sbv), São Gabriel (sgb), Tavares(tav), Paniel (pai), Palmas (pal), Soledade (sol), Vacaria (vac). Also showing the year of sampling of each grid.

Municipality	Year of sampling	maxT	minT	minAH	maxP	minP
ale	2015	38.25	-1.54	0.20	341.45	157.13
jag	2015	38.22	0.40	0.24	124.13	86.35
lav	2015	37.78	-1.24	0.25	168.42	110.11
pai	2015	37.70	1.63	0.22	191.79	92.62
pal	2015	35.87	0.10	0.20	200.75	106.52
qua	2014	38.65	-1.58	0.19	229.70	116.03
sam	2014	37.77	-0.40	0.21	218.94	115.98
sbv	2014	37.74	-0.13	0.22	160.87	104.12
sgb	2014	37.78	-0.64	0.22	207.90	115.94
sol	2014	36.83	-0.06	0.20	185.68	88.85
tav	2016	38.35	1.00	0.23	150.17	90.39
vac	2014	35.73	-1.08	0.19	188.74	97.87

Supplementary file 4: Representation of the eigenvalues from spatial ordination axes (MEMs). Showing only axes selected as significantly correlated ($p < 0.05$) with species composition variance through the forward selection of predictive variables. First MEMs (MEM1 to MEM6) capture spatial variation in broad scale, representing spatial variance of the entire gradient. Last MEMs (MEM12 and MEM13) capture spatial variation at finer scales, representing spatial variance inside the grids represented by the larger circles.



Supplementary file 5: Hierarchical clustering analysis, based on UPGMA method and using Jaccard-based pairwise species turnover as dissimilarity metric, showing the separation of the 108 sampling sites from South Brazilian grasslands in five groups. Groups consistency were tested with approximately unbiased p-values obtained via 999 multiscale bootstrap resampling. Red values above the nodes ('au', approximately unbiased) are computed by multiscale bootstrap resampling, is a better approximation to an unbiased p-value (see Shimodaira 2004). While green values above the nodes ('bp') are the values computed by normal bootstrap resampling. Groups with bootstrap values ('au' and/or 'bp') above 95% (p-value<0.05) were considered consistent. The dendrogram was cut at the height of 0.75 where five consistent and ecological meaningful groups were selected to the discussion.



CAPÍTULO 2

Plant species richness record in Brazilian Pampa grasslands and implications

Luciana da Silva Menezes, Cleusa Vogel Ely, Dióber Borges Lucas,
Graziela Har Minervini Silva, Ilsi Iob Boldrini & Gerhard Ernst Overbeck

Publicado no periódico *Brazilian Journal of Botany*, em dezembro de 2018,
volume 41 (4), pp 817–823 (doi.org/10.1007/s40415-018-0492-6).



(Parcela recorde em Quaraí - RS, Foto: Dióber Borges Lucas)

1 **Plant species richness record in Brazilian Pampa grasslands and implications¹**

2

3 Luciana da Silva Menezes^{1*}, Cleusa Vogel Ely¹, Dióber Borges Lucas¹, Graziela Har

4 Minervini Silva¹, Ilsi Iob Boldrini^{1,2} and Gerhard Ernst Overbeck^{1,2}

5

6 ¹Universidade Federal do Rio Grande do Sul, Programa de Pós-graduação em Botânica,

7 Av. Bento Gonçalves, 9500, CEP 91501-970, Porto Alegre, RS, Brasil. ²Departamento

8 de Botânica. *luciana.menezes@ufrgs.br

9

¹ Published in Brazilian Journal of Botany n 41, vol 4, pages 817–823.

10 **Abstract**

11 (Plant species richness record in Brazilian Pampa grasslands and implications)

12 Species richness remains one of the most valuable type of information for biodiversity
13 conservation. Here, we report a plant richness record in the Brazilian Pampa. We found
14 56 vascular plant species in a single plot of 1×1 m in a privately owned grazed
15 grassland in a region with shallow soils. This number is considerably higher than
16 common species numbers in similar surveys and highlights the high plant diversity in
17 South Brazilian grasslands. We take our register as an opportunity to reflect on some
18 issues of high importance if we wish to reach conservation goals: much of the
19 biodiversity is inside private lands, and these should be more in the focus of
20 conservation efforts; field-research, especially quantitative sampling, continues to be
21 essential to improve knowledge on biodiversity and its distribution patterns; training
22 biologists to be able to carry out biodiversity assessments and to interpret the results
23 should be a key issue for universities. We hope that the communication of this record
24 will encourage new scientific discoveries and raise social interest about the grasslands
25 conservation in South Brazil.

26

27 **Keywords:** biodiversity, Campos Sulinos, conservation, field-based research.

28

29 **Introduction**

30 How many plant species can coexist in one square meter? This is an intriguing
31 and fascinating question. Science, of course, is not primarily about the documentation of
32 records, although scientists keep collecting records since long ago, also in vegetation
33 science (see Wilson et al. 2012). Information on species richness patterns, including
34 maximum values, is an important tool to advance in ecological knowledge and theory.
35 Communication of records made in science may also contribute to increase public
36 interest for scientific issues. For biodiversity conservation this last aspect is crucial.
37 Conservation science aims to solve conservation problems or, at least, provide scientific
38 basis for it. However, implementation of conservation actions depends on political and
39 public interests, which depends critically on information and awareness.

40 The neglecting of non-forest ecosystems in conservation and restoration around
41 the world, and also in Brazil, has been widely documented and discussed (Overbeck et
42 al. 2015, Veldman et al. 2015). In southern Brazil, wide areas of grasslands extend
43 across the Pampa biome, and grassland patches are also found within the mixed
44 ombrophilous forest region in the Atlantic Forest biome; collectively, these grasslands
45 are called Campos Sulinos (Pillar et al. 2009). The Pampa has been especially neglected
46 in terms of conservation (Overbeck et al. 2015). Decisions made without scientific basis
47 or adequate technical analysis has been repeatedly compromising grassland
48 conservation in southern Brazil. A recent example is a Decree of the Governor of Rio
49 Grande do Sul state (State Decree 52,431 of 23 Jun 2015) that, if it had not been
50 overruled, would have immensely jeopardized biodiversity in the Pampa region. The
51 decree addressed the implementation of the Rural Environmental Cadaster (CAR) in the
52 Pampa, considering cattle grazing as an activity that suppressed natural vegetation, i.e.
53 turned grazed areas into consolidated rural areas. Thus, land owners would have be

54 exempt from the requirement of presenting Legal Reserve (specific percentage of area
55 inside private lands that should be destined to conservation, according to the federal
56 law), as all grazed areas would be considered converted to rural use and not native
57 vegetation. This decree was later overruled by a federal court, as it violated federal
58 legislation, but there even was an attempt to reverse this overruling decision (see:
59 <https://www.mprs.mp.br/noticias/ambiente/41865/>). Considering that environmental
60 conservation should be a priority in governmental agendas, the fact that this decree was
61 issued and signed by a government leader points to the lack of understanding or interest
62 of our governments on ecological or environmental issues. One problem may be that we
63 are failing in communicating with policy makers about ecology, conservation and value
64 of grassland ecosystems (see also Overbeck et al. 2007; Parr et al. 2014). The
65 publication of basic information, e.g. on species richness, should be helpful here. This
66 may be especially the case for ecosystems that critically depend on management for
67 maintenance of their biodiversity, and whose value is often less recognized than that of
68 systems whose biodiversity does not depend on such factors; the South Brazilian
69 grasslands constitute a good example of this (Pillar and Vález 2010). Grazing and/or
70 fire at adequate frequencies and intensities – disturbances, in ecological terms – are
71 intrinsic processes of the grassland ecosystem (Overbeck et al. 2016; Overbeck et al.
72 2018b). In the Pampa region, almost all large native herbivores are long extinct (Prado
73 et al. 2015), and domestic animals have taken their ecological role and have contributed
74 to biodiversity conservation.

75 Historically, conservation efforts in Brazil have focused mostly on forest
76 environments. Only in 2012, our most important federal environmental law had its name
77 changed from “Forestal Code” to “Native Vegetation Protection Law” (Federal law
78 12,651 of 25 May 2012). The Campos Sulinos, as much as other grasslands ecosystems

79 in Brazil, still lack a more specific legislation, because our knowledge about biological
80 characteristics of those environments had been incipient in the past, which has changed
81 more recently. Here, we report a species richness record from the Brazilian Pampa and
82 use this datum to reflect on some issues of high relevance to biodiversity conservation,
83 especially in open ecosystems. Our expectation is that the communication of records,
84 such as ours, will stimulate research and the conservation debate in all Brazilian
85 ecosystems, and will call attention to the biodiversity and conservation of these systems.

86

87 **Materials and methods**

88 Within the Brazilian National Research Program on Biodiversity (acronym in
89 Portuguese: PPBio; Magnusson et al. 2016) and the affiliated project on South Brazilian
90 grassland vegetation, we conducted extensive sampling in grasslands of the Campos
91 Sulinos region. Sampling followed a standardized protocol (RAPELD; Magnusson et al.
92 2005), with adaptations to the ecosystem under focus in our study. Overall, we sampled
93 grasslands in 13 regions, with ten linear plots of 250×1 m per region. Each plot was
94 characterized by ten 1×1 m sampling units. Sampling totalized 1,170 sampling units.

95 The survey from which the results reported here comes from was performed in the
96 municipality of Quaraí, in the Campanha region in the southwestern Rio Grande do Sul
97 (geographical coordinates $30^{\circ}18'39.4''\text{S}$ and $55^{\circ}58'00.4''\text{W}$), in the Brazilian Pampa.
98 Soils of the region are shallow and interspersed with rock outcrops; they belong to the
99 class leptosol, according to FAO (2009) or “neossolo litólico”, according to IBGE
100 (2007). Climate is temperate, with hot summers and without dry season, corresponding
101 to a Cfa climate according to Köppen’s classification (Alvares et al. 2013).

102 Our record plot was situated in a privately-owned grassland, grazed for livestock
103 production (Fig. 1). Stocking rates in the region generally are rather high, often

104 resulting in overgrazing (Carvalho and Batello 2009). In this region fire is not a
105 common management practice, some land owners recur to mowing as a management
106 technique, especially to remove undesirable species for cattle grazing.

107 Sampling was performed in November 2014, i.e. the flowering season of most
108 taxa. Species were identified in the field; when this was not possible, samples were
109 collected for posterior taxonomic identification and compared to vouchers already
110 deposited at ICN/UFRGS herbarium. Species classification into families followed APG
111 IV (2016).

112

113 **Results**

114 We recorded 56 vascular plant species in a plot of 1×1 m (Tab. 1). This number is
115 still considerably below the current world record for grassland plots of this size, 89
116 species in mountain grasslands in Argentina (Wilson et al. 2012). Nonetheless, our
117 number lies well above the maximum values indicated in the literature for other regions
118 in the South Brazilian grasslands, for example 22 species/m² in coastal grasslands
119 (Menezes et al. 2015) and 35 species/m² in the granitic hills of Porto Alegre (Ferreira et
120 al. 2010). The Campanha region, where our record plot is situated, is particularly rich in
121 species: within the course of our PPBio project, we found maximum species numbers of
122 31 species/m² in Alegrete municipality, 40 species/m² in São Gabriel and 43 species/m²
123 in Lavras do Sul (PPBio project, unpublished data). Another two plots from the survey
124 in the region accounted for 51 and 54 species each (data in Suppl. 1). From the 56
125 species recorded in the plot, only two were naturalized non-natives (*Cerastium*
126 *commersonianum* DC. and *Vulpia bromoides* (L.) Gray).

127

128 **Table 1.** List of the 56 plant species recorded in 1 m² in the Brazilian Pampa biome,
 129 Quaraí municipality, Rio Grande do Sul state, and respective vouchers deposited in the
 130 ICN herbarium. Naturalized non-native species are indicated with *.

Families and species	ICN vouchers
Acanthaceae	
<i>Ruellia morongii</i> Britton	ICN63373
<i>Stenandrium dulce</i> (Cav.) Nees	ICN189883
Apiaceae	
<i>Cyclospermum leptophyllum</i> (Pers.) Sprague ex Britton & P. Wilson	ICN115378
<i>Eryngium echinatum</i> Urb.	ICN156576
Araliaceae	
<i>Hydrocotyle exigua</i> Malme	ICN145069
Asteraceae	
<i>Chaptalia piloselloides</i> (Vahl) Baker	ICN167329
<i>Chevreulia sarmentosa</i> (Pers.) S.F. Blake	ICN157289
<i>Conyza bonariensis</i> (L.) Cronquist	ICN173455
<i>Hypochaeris megapotamica</i> Cabrera	ICN142569
<i>Micropsis spathulata</i> (Pers.) Cabrera	ICN93567
<i>Panphalea heterophylla</i> Less.	ICN185947
<i>Soliva sessilis</i> Ruiz & Pav.	ICN158239
Brassicaceae	
<i>Lepidium aletes</i> J.F. Macbr.	ICN8515
Campanulaceae	
<i>Wahlenbergia linarioides</i> (Lam.) A. DC.	ICN155429
Caryophyllaceae	
<i>Cerastium commersonianum</i> DC.*	ICN188188
Cistaceae	
<i>Crocanthemum brasiliensis</i> Spach	ICN195441
Convolvulaceae	
<i>Dichondra sericea</i> Sw.	ICN142579
<i>Evolvulus sericeus</i> Sw.	ICN44622
Cyperaceae	
<i>Bulbostylis communis</i> M.G. López & D.A. Simpson	ICN181036
<i>Fimbristylis dichotoma</i> (L.) Vahl	ICN143269
Fabaceae	
<i>Adesmia incana</i> Vogel	ICN185932
<i>Desmodium incanum</i> (Sw.) DC.	ICN35797
<i>Galactia marginalis</i> Benth.	ICN137519
<i>Rhynchosia diversifolia</i> Micheli	ICN144905

<i>Stylosanthes montevidensis</i> Vogel	ICN43731
<i>Trifolium polymorphum</i> Poir.	ICN44680
Iridaceae	
<i>Cypella discolor</i> Ravenna	ICN180156
<i>Sisyrinchium vaginatum</i> Spreng.	ICN158800
<i>S. micranthum</i> Cav.	ICN189984
Linaceae	
<i>Cliococca selaginoides</i> (Lam.) C.M. Rogers & Mildner	ICN45387
Malvaceae	
<i>Ayenia mansfeldiana</i> (Herter) Herter ex Cristóbal	ICN148601
<i>Krapovickasia flavescens</i> (Cav.) Fryxel	ICN153660
Onagraceae	
<i>Oenothera affinis</i> Cambess.	ICN179470
Plantaginaceae	
<i>Plantago myosuroides</i> Lam.	ICN121884
<i>P. tomentosa</i> Lam.	ICN121352
Poaceae	
<i>Andropogon lateralis</i> Nees	ICN190842
<i>A. macrothrix</i> Trin.	ICN155444
<i>Aristida venustula</i> Arechav.	ICN82424
<i>Chascolytrum subaristatum</i> (Lam.) Desv.	ICN129863
<i>Danthonia cirrata</i> Hack. & Arechav.	ICN134473
<i>Eragrostis neesii</i> Trin.	ICN175993
<i>Mnesithea selleana</i> (Hack.) de Koning & Sosef	ICN62178
<i>Nassella neesiana</i> (Trin. & Rupr.) Barkworth	ICN679040
<i>Paspalum notatum</i> Alain ex Flügge	ICN174125
<i>Piptochaetium montevidense</i> (Spreng.) Parodi	ICN35223
<i>Setaria parviflora</i> (Poir.) Kerguelen	ICN134741
<i>Steinchisma hians</i> (Elliott) Nash	ICN130129
<i>Vulpia bromoides</i> (L.) Gray*	ICN157870
Polygalaceae	
<i>Polygala aphylla</i> A.W. Benn.	ICN123444
<i>P. pulchella</i> A. St.-Hil. & Moq.	ICN193314
Primulaceae	
<i>Lysimachia minima</i> (L.) U. Manns & Anderb.	ICN176105
Rubiaceae	
<i>Galium hirtum</i> Lam.	ICN151577
<i>G. uruguayense</i> Bacigalupo	ICN117409
<i>Richardia stellaris</i> (Cham. & Schltl.) Steud.	ICN24961
Solanaceae	
<i>Calibrachoa ovalifolia</i> (Miers) Stehmann & Semir	ICN112720

131

132 **Discussion**

133 We hope that this record will challenge colleagues working in other grasslands in
134 Brazil or in other ecosystems to strive to establish new records by conducting field-
135 based biodiversity surveys. Diversity records can be important in science divulgation,
136 calling attention to the high biodiversity of Brazilian ecosystems, such as the Campos
137 Sulinos, and the need for their conservation. For scientists, the record itself may not
138 matter too much; nonetheless, we wish to use our record to call attention to some issues
139 of higher importance for conservation that are not in the center of the conservation
140 debate, and that often may even be overlooked by conservation specialists in
141 government agencies or science.

142

143 *Need for conservation on private lands*

144 From the original 178,243 km² of natural grasslands in the Brazilian Pampa
145 (IBGE 2004), only 41,055 km² (23%) remains and about 59% of the original area was
146 transformed to anthropic uses (Hasenack and Cordeiro 2006). Public areas under legal
147 protection (state or federal) add up 2,450 km² of grasslands, around 1.4% of the original
148 Pampa grasslands (Brandão et al. 2008). While the protection of pristine areas, e.g. in
149 protected areas, often is considered to be the prime approach for conservation, private
150 lands should also gain attention in conservation politics. Shortcomings of protected
151 areas for biodiversity conservation are well known (Mora and Sale 2011), just as the
152 need to integrate conservation issues into land use policy (Arsanjani et al. 2016).
153 Conservation on private lands can contribute to better habitat conditions throughout the
154 landscapes, including in agricultural landscapes, or by forming ecological corridors with

155 larger public protected areas, and a number of approaches for this exist (e.g. Kamal et
156 al. 2014). The Legal Reserve (Federal law 12,651 of 25 May 2012), if properly
157 implemented, is a promising conservation tool in this regard, including in grassland
158 regions. Private rangelands, if under proper management, have a high potential for
159 conservation and sustainable use, allowing, at the same time, for economic returns
160 (Nabinger et al. 2009). Furthermore, grasslands, if adequately managed, have potential
161 to provide important environmental and economic services, such as biodiversity
162 maintenance and carbon storage (e.g. McSherry and Ritchie 2013, Fuhlendorf and Engle
163 2001). In our study region, initiatives such as the Alianza del Pastizal provide excellent
164 examples for the successful combination of livestock production and grassland
165 conservation (Parera et al. 2014).

166

167 *Need for more field-based biodiversity assessments*

168 In an era of readily available sophisticated analytical methods and increasing
169 availability of global data sets, we advance in ecological knowledge, but basic
170 biodiversity research is lacking (Helm et al. 2014). Large databases, such as sPlot
171 (Dengler et al. 2014) for plant communities or TRY (Kattge et al. 2011) for functional
172 traits, depend on data that had been collected in the field. Gaps in data availability,
173 especially pronounced for tropical and subtropical regions, is a problem even for the
174 most complete databases. We need more field-based research, and data collection in the
175 field needs to be better valued, as it is the basic step for most ecological research.
176 Scientific research programs that aim to foster biodiversity assessments, like the PPBio
177 in Brazil (Peixoto et al. 2016), in the course of which our record was taken, are of high
178 relevance to improve knowledge on biodiversity patterns. At first, the focus of these
179 studies may be rather descriptive (biodiversity inventories), but they can create the basis

180 for hypothesis-driven work later on, at least when following a systematic sampling
181 approach that allows to connect plant community composition with the drivers from the
182 different environments. Additionally, data collected in these studies contribute to the
183 information necessary for modeling species niche and provide valuable data to assess
184 the extinction risk of plant species according to the IUCN's red lists criteria (IUCN
185 2017).

186

187 *Necessity to train field researchers*

188 Ecosystems with high species-richness, such as the South Brazilian grasslands and
189 many other Brazilian ecosystems, are a challenge for biodiversity research, independent
190 of the species group. The lack of field-guides of easy use in many tropical and
191 subtropical regions complicates field-based research and teaching of biodiversity.
192 Lewinsohn et al. (2015) recently addressed the need to change approaches in Ecology
193 teaching towards a 'problem-based perspective' that should enable students to tackle
194 real-world environmental problems. We can extend this to Botany: knowledge acquired
195 in universities should be applicable in the ecosystems outside the university's doorstep.
196 Traditional course curricula in Biology, and related courses, often include many credits
197 for rather theoretical courses, e.g. plant systematics, and little emphasis on becoming
198 acquainted with the species in the region and the vegetation types in their surroundings.
199 Solid theoretical foundations are important, but should not be laid at the cost of
200 applicable knowledge. Professors should critically evaluate if they are teaching students
201 what they need to know in their future career, e.g. when working with vegetation
202 sampling as a consultant or when evaluating vegetation data as analyst of an
203 environmental protection agency, to just cite two examples.

204 Scientific research and applied conservation highly depend on fieldwork, so data
205 collection is fundamental and the first step for ecological studies and for conservation.
206 The Brazilian Native Vegetation Protection Law from 2012 (Federal Law 12,651)
207 defines that areas with native vegetation require prior authorization for conversion to
208 other land uses. For southern Brazil, and likely other regions as well, no criteria for
209 suppression of grasslands exist so far for Pampa biome (but see CONAMA resolution
210 423/2010, for grasslands inserted in the Atlantic Forest biome). Composition (including
211 information on native species, rare or endemic species, threatened species), as well as
212 species richness itself, certainly constitute basic information for the evaluation if a
213 license for conversion to other uses should be granted or not. To secure our biodiversity
214 and the services provided by natural ecosystems and to advance in conservation, we
215 need more field sampling of our ecosystems, and we need qualified people to do so.
216 Unfortunately, the current public funding situation in sciences is not favorable for better
217 knowledge of Brazil's biodiversity, or for training of young scientists, which likely will
218 jeopardize conservation goals (Fernandes et al. 2017; Overbeck et al. 2018a). We hope
219 that records such as the one presented here will also contribute to public awareness of
220 biodiversity, including in policy. Investment into biodiversity knowledge thus is
221 strategic for a better management of natural resources and returns go beyond
222 biodiversity itself, but include the many benefits nature provides for people.

223

224 **Acknowledgements**

225 Our work was supported by MCTIC and CNPq within the Research Program on
226 Biodiversity (PPBio), network Campos Sulinos (grant 457447/2012-5). We thank
227 Eduardo Vélez for support and landowners for allowing the research. Two last authors

228 received productivity grants from the National Counsel of Technological and Scientific
229 Development. We thank Valério DePatta Pillar for comments on the manuscript.

230

231 **Authors' contributions** LSM, CVE, DBL, GHMS conducted fieldwork, GEO
232 lead the research project, IOB identified plant species, and all authors wrote and
233 reviewed the manuscript.

234

235 **References**

- 236 Alvares CA, Stape JL, Sentelhas PC, Moraes Gonçalves JL, Sparovek G (2013)
237 Köppen's climate classification map for Brazil. *Meteorol Z* 22: 711-728.
- 238 APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the
239 orders and families of flowering plants: APG IV. *Bot J Linn Soc* 181: 1-20.
- 240 Arsanjani JJ, Tayyebi A, Vaz E (2016) GlobeLand30 as an alternative fine-scale global
241 land cover map: Challenges, possibilities, and implications for developing
242 countries. *Habitat Int* 55: 25-31.
- 243 Brandão T, Trevisan R, Both R (2008). Unidades de Conservação e os Campos do Rio
244 Grande do Sul. *Rev Bras Biocienc* 5: 843-845.
- 245 Carvalho PCF, Batello C (2009) Access to land, livestock production and ecosystem
246 conservation in the Brazilian Campos biome: The natural grasslands dilemma.
247 *Livest Sci* 120: 158-162.
- 248 Dengler J, Bruehlheide H, Purschke O, et al. (2014) sPlot – the new global vegetation-
249 plot database for addressing trait-environment relationships across the world's
250 biomes. In: Mucina L, Price JN, Kalwij JM. (eds.) *Biodiversity and vegetation:
251 patterns, processes, conservation*. Perth, Kwongan Foundation. p. 90.

252 FAO (2009) Harmonized world soil database. Food and Agriculture Organization, 43p.
253 <http://www.fao.org/nr/Water/docs/Harm-World-Soil-DBv7cv.pdf> (accessed 2018
254 Apr. 18)

255 Fernandes GW, Vale MM, Overbeck GO, et al. (2017) Dismantling Brazil's science
256 threatens global biodiversity heritage. *PECON* 15: 239-243.

257 Ferreira PMA, Müller SC, Boldrini II, Eggers L (2010) Floristic and vegetation
258 structure of a granitic grassland in Southern Brazil. *Braz J Bot* 33: 21-36.

259 Fuhlendorf SD, Engle DM (2001) Restoring Heterogeneity on Rangelands: Ecosystem
260 Management Based on Evolutionary Grazing Patterns. *BioScience* 51: 625-632.

261 Hasenack H, Cordeiro JLP (2006) Mapeamento da cobertura vegetal do Bioma Pampa.
262 <http://www.mma.gov.br/biomas/pampa/mapa-de-cobertura-vegetal> (accessed 2016
263 Sept. 30)

264 Helm A, Kalamees R, Zobel M (2014) Vegetation patterns and their underlying
265 processes: where are we now? *J Veg Sci* 25: 1113-1116.

266 IBGE (2004) Mapa da vegetação do Brasil e Mapa de Biomas do Brasil.
267 <http://www.ibge.gov.br> (accessed 2018 Apr. 24).

268 IBGE (2007) Manuais Técnicos em Geociências número 4 Manual Técnico de
269 Pedologia. Ministério do Planejamento, Orçamento e Gestão, Rio de Janeiro. 316 p.

270 IUCN Standards and Petitions Subcommittee (2017) Guidelines for Using the IUCN
271 Red List Categories and Criteria. Version 13. Prepared by the Standards and
272 Petitions Subcommittee.
273 <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>. (accessed 2017 Oct.
274 6)

275 Kamal S, Grodzińska-Jurczak M, Brown G (2014) Conservation on private land: a
276 review of global strategies with a proposed classification system. *J Environ Plann*
277 *Man* 58: 576-597.

278 Kattge J, Díaz S, Lavorel S, et al. (2011) TRY – a global database of plant traits. *Glob*
279 *Change Biol* 17: 2905-2935.

280 Lewinsohn TM, Attayde JL, Fonseca CR, et al. (2015) Ecological literacy and beyond:
281 Problem-based learning for future professionals. *Ambio* 44: 154-62.

282 Magnusson WE, Bergallo HG, Cerqueira R, et al. (2016) O programa de pesquisa em
283 biodiversidade. In: Peixoto AL, Pujol-Luz JR, Brito MA. (eds.) *Conhecendo a*
284 *Biodiversidade*. Brasília, Ministério da Ciência, Tecnologia, Inovações e
285 *Comunicações, Conselho Nacional de Desenvolvimento Científico e Tecnológico,*
286 *Programa de Pesquisas em Biodiversidade*. p. 15-33.

287 Magnusson WE, Lima AP, Luizão R, et al. (2005) RAPELD: A modification of the
288 Gentry Method for biodiversity surveys in long-term ecological research sites.
289 *Biota Neotrop* 5: 19-24.

290 McSherry ME, Ritchie ME (2013) Effects of grazing on grassland soil carbon: a global
291 review. *Glob Change Biol* 19: 1347-1357.

292 Menezes LS, Müller SC, Overbeck GE (2015) Floristic and structural patterns in South
293 Brazilian coastal grasslands. *An Acad Bras Cienc* 87: 2081-2090.

294 Mora C, Sale P (2011) Ongoing global biodiversity loss and the need to move beyond
295 protected areas: a review of the technical and practical shortcomings of protected
296 areas on land and sea. *Mar Ecol Prog Ser* 434: 251-266.

297 Nabinger C, Ferreira ET, Freitas AK, Carvalho PCF, Sant'anna DM (2009) Produção
298 animal com base no campo nativo: aplicações de resultados de pesquisa. In: Pillar
299 VD, Müller SC, Castilhos ZMS, Jacques AVA. (orgs.) *Campos Sulinos:*

300 Conservação e Uso Sustentável da Biodiversidade. Brasília, Ministério do Meio
301 Ambiente. p. 175-198.

302 Overbeck GE, Bergallo HG, Grelle CEV, Akama A, Bravo F, Colli GR, Magnusson
303 WE, Tomas WM, Fernandes GW (2018a) Global Biodiversity Threatened by
304 Science Budget Cuts in Brazil, *BioScience* 68: 11–12.

305 Overbeck GE, Ferreira PMA, Pillar VD (2016) Conservation of mosaics calls for a
306 perspective that considers all types of mosaic-patches. Reply to: Luza, A.L. et al.
307 *Nat. Conserv.*, 14: 152-154.

308 Overbeck GE, Müller SC, Fidelis A, et al. (2007) Brazil's neglected biome: The South
309 Brazilian Campos. *Perspect Plant Ecol* 9: 101-116.

310 Overbeck GE, Vélez EM, Scarano FR, et al. (2015) Conservation in Brazil needs to
311 include non-forest ecosystems. *Divers Distrib* 21: 1455-1460.

312 Overbeck GE, Scasta JD, Furquim FF, et al. (2018b) The South Brazilian grasslands - A
313 South American tallgrass prairie? Parallels and implications of fire dependency.
314 *Persp Ecol Conserv* 16: 24-30.

315 Parera A, Paullier I, Weyland F. (2014) Índice de Contribución a la Conservación de
316 Pastizales Naturales del Cono Sur: Una herramienta para incentivar a los
317 productores rurales. *Aves Uruguay, Argentina*. 181 p.

318 Parr CL, Lehmann CER, Bond WJ, Hoffmann Wa, Andersen AN (2014) Tropical
319 grassy biomes: misunderstood, neglected, and under threat. *Trends Ecol Evol* 29:
320 205-213.

321 Peixoto AL, Pujol-Luz JR, Brito MA (2016) Conhecendo a biodiversidade. Ministério
322 da Ciência, Tecnologia, Inovações e Comunicações, Conselho Nacional de
323 Desenvolvimento Científico e Tecnológico, Programa de Pesquisas em
324 Biodiversidade, Brasília. 196 p.

- 325 Pillar VD, Müller SC, Castilhos Z, Jacques AVA (2009) Campos Sulinos - conservação
326 e uso sustentável da biodiversidade, MMA, Brasília. 408 p.
- 327 Pillar VD, Vélez EM (2010) Extinção dos Campos Sulinos em Unidades de
328 Conservação: um Fenômeno Natural ou um Problema Ético? PECON 8: 84-86.
- 329 Prado JL, Martinez-Maza C, Alberdi MT (2015) Megafauna extinction in South
330 America: A new chronology for the Argentine Pampas. *Palaeogeogr Palaeoclimatol*
331 *Palaeoecol* 425: 41-49.
- 332 Vélez EM, Chomenko L, Schaffer W, Madeira MM (2009) Um panorama sobre as
333 iniciativas de conservação dos Campos Sulinos. In: Pillar VD, Müller SC, Castilhos
334 ZMS, Jacques AVA. (orgs.) Campos Sulinos: Conservação e Uso Sustentável da
335 Biodiversidade. Brasília, Ministério do Meio Ambiente. p. 356-379.
- 336 Veldman JW, Overbeck GE, Negreiros D, et al. (2015) Tyranny of trees in grassy
337 biomes. *Science* 347: 484-485.
- 338 Wilson JB, Peet RK, Dengler J, Pärtel M (2012) Plant species richness: the world
339 records. *J Veg Sci* 23: 796-802.

340 **Fig. 1** A. Typical landscape with grazed grassland inside private properties. B. Field
341 work in the PPBio ‘Campos Sulinos – Vegetação campestre’ project. The dominant
342 bunchgrass is *Andropogon lateralis*.



343

344 **Supplementary material**

345

346 **Supplement 1:** In addition to the record plot, two other plots in the same region
 347 (Quaraí/RS) also presented high species richness, with more than 50 species each.

Family/Species	Presence	
Acanthaceae		
<i>Ruellia morongii</i> Britton	1	1
<i>Stenandrium dulce</i> (Cav.) Nees		1
Amaranthaceae		
<i>Gomphrena perennis</i> L.	1	
<i>Pfaffia gnaphaloides</i> (L.f.) Mart.	1	
Apiaceae		
<i>Cyclospermum leptophyllum</i> (Pers.) Sprague ex Britton & P.Wilson	1	1
<i>Eryngium echinatum</i> Urb.	1	1
<i>E. nudicaule</i> Lam.		1
Asteraceae		
<i>Acmella leptophylla</i> (DC.) R.K.Jansen		1
<i>Baccharis coridifolia</i> DC.	1	1
<i>Chaptalia piloselloides</i> (Vahl) Baker		1
<i>Chevreulia sarmentosa</i> (Pers.) Blake	1	1
<i>Facelis retusa</i> (Lam.) Sch.Bip.	1	1
<i>Gamochoaeta argentina</i> Cabrera		1
<i>Hypochaeris megapotamica</i> Cabrera	1	
<i>Soliva sessilis</i> Ruiz & Pav.	1	1
Campanulaceae		
<i>Wahlenbergia linarioides</i> (Lam.) A.DC.	1	1
Caryophyllaceae		
<i>Cerastium commersonianum</i> Ser.	1	
<i>Paronychia chilensis</i> DC.		1
<i>Polycarpon tetraphyllum</i> (L.) L.	1	
Cistaceae		
<i>Crocantemum brasiliensis</i> Spach	1	1
Convolvulaceae		
<i>Dichondra sericea</i> Sw.	1	1
<i>Evolvulus sericeus</i> Sw.	1	1
Cyperaceae		
<i>Bulbostylis glaziovii</i> (Boeckeler) C.B.Clarke	1	
<i>Carex phalaroides</i> Kunth	1	1
<i>Cyperus aggregatus</i> (Willd.) Endl.	1	
Fabaceae		
<i>Adesmia incana</i> Vogel		1
<i>Galactia marginalis</i> Benth.	1	1
<i>Lathyrus crassipes</i> Gillies ex Hook. & Arn.		1
<i>Mimosa flagellaris</i> Benth.	1	

<i>Rhynchosia senna</i> Gillies ex Hook.	1	1
<i>Stylosanthes montevidensis</i> Vogel	1	
<i>Trifolium polymorphum</i> Poir.	1	1
<i>Zornia cryptantha</i> Arechav.	1	
Iridaceae		
<i>Cypella hauthalii</i> (Kuntze) R.C.Foster	1	
<i>Sisyrinchium micranthum</i> Cav.		1
Linaceae		
<i>Cliococca selaginoides</i> (Lam.) C.M. Rogers & Mildner		1
Lycopodiaceae		
<i>Lycopodiella alopecuroides</i> (L.) Cranfill		1
Lythraceae		
<i>Cuphea glutinosa</i> Cham. & Schldl.	1	1
Malvaceae		
<i>Ayenia mansfeldiana</i> (Herter) Herter ex Cristóbal	1	1
<i>Krapovickasia flavescens</i> (Cav.) Fryxell	1	1
<i>Sida spinosa</i> L.	1	
Onagraceae		
<i>Oenothera affinis</i> Cambess.		1
Orchidaceae		
<i>Habenaria parviflora</i> Lindl.	1	
Oxalidaceae		
<i>Oxalis conorrhiza</i> Jacq.		1
Plantaginaceae		
<i>Plantago myosuroides</i> Lam.	1	1
Poaceae		
<i>Andropogon ternatus</i> (Spreng.) Nees		1
<i>Aristida murina</i> Cav.	1	
<i>A. venustula</i> Arechav.	1	1
<i>Bothriochloa laguroides</i> (DC.) Herter	1	
<i>Chascolytrum subaristatum</i> (Lam.) Desv.	1	1
<i>Danthonia cirrata</i> Hack. & Arechav.	1	
<i>Eleusine tristachya</i> (Lam.) Lam.	1	
<i>Eragrostis lugens</i> Nees	1	1
<i>E. neesii</i> Trin.		1
<i>Melica rigida</i> Cav.	1	
<i>Mnesithea selloana</i> (Hack.) de Koning & Sosef	1	1
<i>Nassella nutans</i> (Hack.) Barkworth	1	
<i>Paspalum leptum</i> Schult.	1	1
<i>P. notatum</i> Flüggé	1	1
<i>P. plicatum</i> Michx.		1
<i>Piptochaetium montevidense</i> (Spreng.) Parodi	1	1
<i>P. stipoides</i> (Trin. & Rupr.) Hack. ex Arechav.	1	
<i>Schizachyrium imberbe</i> (Hack.) A.Camus	1	
<i>S. spicatum</i> (Spreng.) Herter		1
<i>S. tenerum</i> Nees		1

<i>Setaria parviflora</i> (Poir.) M.Kerguelen	1	1
<i>Steinchisma hians</i> (Elliott) Nash	1	
Polygalaceae		
<i>Polygala bonariensis</i> Grondona	1	
<i>P. pulchella</i> A.St.-Hil. & Moq.	1	1
Rubiaceae		
<i>Galium richardianum</i> (Gillies ex Hook. & Arn.) Endl. ex Walp.	1	1
<i>Richardia humistrata</i> (Cham. & Schltdl.) Steud.	1	1
<i>R. stellaris</i> (Cham. & Schltdl.) Steud.		1
Solanaceae		
<i>Nicotiana bonariensis</i> Lehm.		1
Verbenaceae		
<i>Lippia coarctata</i> Tronc.	1	1
<hr/>		
Total species richness	54	51
<hr/>		

348



CAPÍTULO 3

Spatial dependency of drivers and patterns of β -diversity, turnover and nestedness

Luciana da Silva Menezes, Eduardo Vélez-Martin & Gerhard Ernst Overbeck

Manuscrito submetido ao periódico *Perspectives in Plant Ecology, Evolution and Systematics*, formatado nas normas do periódico a exceção das figuras e legendas que foram embebidadas no texto para fluência da leitura.

1 **Highlights**

2

3 β -diversity and turnover in the *Campos Sulinos* are dependent of grain size.

4

5 Distinct processes shape turnover and nestedness, also spatially dependent.

6

7 Spatially-structured environment drives turnover at wider scales, finer scales results
8 diverge.

9

10 Nestedness is related to environment at wider scales and space at finer scales.

11

12 Understanding β -diversity, its components and drivers is important for conservation
13 decisions.

14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35

Title

Spatial dependence of patterns and drivers of β -diversity, turnover and nestedness

Short running title

Turnover and nestedness in different scales

Authors

Luciana da Silva Menezes^{a,*}, Eduardo Vélez-Martin^b and Gerhard Ernst Overbeck^a

^a Laboratório de Estudos em Vegetação Campestre, Programa de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul.

^b Laboratório de Ecologia Quantitativa, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul.

* Corresponding author: 9500 Bento Gonçalves Av., CEP 91501-970, Porto Alegre, Brazil. E-mail: lu.silva.menezes@gmail.com

Acknowledgements

The authors thank the more than 50 landowners that allowed to work on their lands. Special thanks to the field work team of the UFRGS Laboratory of Grassland Vegetation Studies for data collection. LSM was supported by CAPES, EMV and GEO were supported by CNPq. This study was developed within the PPBio Campos Sulinos network, financed by MCTIC through grant CNPq 457447/2012-5 to GEO.

36 **Abstract**

37 Species substitution and loss are opposite processes that may generate the same β -
38 diversity values. Those processes can be separately analyzed by the partition of β -
39 diversity into turnover and nestedness. Here we investigate patterns of turnover and
40 nestedness across spatial grains in the species rich *Campos Sulinos* grasslands, a
41 206km² grassland region in subtropical Brazil that commonly is divided into two maior
42 regions, Pampa and highland grasslands. Additionally, we sought for the specific
43 drivers that may generate turnover and/or nestedness at different spatial extents. We
44 applied a nested sampling design, comprising three grains (fine, medium and coarse)
45 and three extents (full, regional and local). Turnover and nestedness were calculated
46 for each spatial grain with the multiple site Jaccard-based index. Partial regressions
47 were applied to verify the influence of environment, space and shared effect on
48 turnover and nestedness at each spatial extent. *Campos Sulinos* grasslands presented
49 much higher turnover than nestedness. Total β -diversity and turnover were higher at
50 finer grains, decreasing with coarser grain. This can be explained by species are
51 relationship, since with coarser grains the initial species pool is higher and few species
52 are added with new sampling units, resulting in lower β -diversity and turnover.
53 Nestedness was explained by environment at full extent and by space at regional
54 extent. Turnover was related to spatially structured environment in the full extent and
55 in highland grasslands but was explained by dispersal limitation in Pampa. At the local
56 scale relationships varied, the only general pattern found was environment with
57 turnover in highland grasslands areas. Processes that shaped turnover and nestedness
58 patterns were distinct and spatially dependent. This can be decisive to conservation
59 planning, especially considering sets communities from different trophic levels that
60 interact with the environment at different spatial resolutions. No consistent overall
61 picture of turnover and nestedness drivers appears at the local scale, likely because
62 other non-measured factors, including historical processes, are decisive for community
63 composition.

64

65 **Keywords:** beta-diversity, biodiversity, Campo Sulinos, drivers, grasslands,
66 nestedness, turnover.

67

68 1. Introduction

69

70 Changes in community richness and composition across gradients (β -diversity)
71 are among the most perceptible patterns in nature and have been of interest already
72 to early ecologists. Disentangling the processes that generate β -diversity along
73 gradients and at different spatial scales has been a major objective in ecology over the
74 past century (Chave, 2013; Levin, 1992; Velázquez et al., 2016). The current general
75 hypothesis about the spatial dependence of niche and neutral processes relates
76 habitat association (niche) to wider spatial scales and stochastic processes (neutral)
77 with finer spatial scales (Garzon-Lopez et al., 2014).

78 In parallel, the study of the complex relationship among β -diversity patterns and
79 their underlying processes has gained new momentum with the decomposition of β -
80 diversity into species replacement (turnover pattern) and richness differences
81 (nestedness pattern) (Baselga, 2012; Legendre, 2014). When β -diversity is quantified,
82 the same values may arise from communities where the main pattern is species
83 turnover, i.e. species substitution across sampling units, or where it is nestedness, i.e.
84 where the dissimilarity is due to the loss of species from a richer sample to a poorer
85 one (Baselga, 2010). This should not be understood as an imprecision in the calculation
86 of β -diversity, as changes in local communities along gradients can occur by two ways:
87 loss and substitution of species. If one is interested in isolating the amount of β -
88 diversity that is due to turnover or nestedness, specific indexes to separate
89 components of replacement and nestedness-resultant or richness-difference should be
90 applied (Baselga and Leprieur, 2015; Podani and Schmera, 2016), which provide
91 complementary information to β -diversity.

92 The degree at which the two components contribute to β -diversity is of high
93 relevance in conservation decisions (Banda-R et al., 2016; Bergamin et al., 2017;
94 Socolar et al., 2016). When nestedness prevails within or across communities, species
95 composition from poorer samples are subsets of a sample with higher species number.
96 This means that, for conservation of the species that make up the communities, it
97 should be sufficient to select the area that contains the overall highest species richness
98 and, for instance, place a large protected area there. Turnover-dominated
99 communities, on the other hand, are characterized by higher importance of species
100 substitution, where new samples will have few species in common with previous
101 samples. In this case, several protected areas will be required along the gradient to
102 protect the highest portion of biodiversity.

103 A better understanding of turnover and nestedness patterns and the processes
104 driving it, will contribute to our understanding of community assembly and,
105 consequently, improve conservation decisions. However, size of sampling unit (grain)
106 and total area sampled (extent) has been demonstrated to influence values of β -
107 diversity, turnover and nestedness (Antão et al., 2019; Keil et al., 2012; Steinbauer et
108 al., 2012). Total β -diversity and turnover were found to decrease as spatial grain
109 increase (Keil et al., 2012). Moreover, as overall patterns of β -diversity, turnover and
110 nestedness are dependent on the organism (Soininen et al., 2018), the same holds for
111 spatial scaling of those patterns (Antão et al., 2019), i.e. different spatial scaling behavior
112 is expected for organisms with different environmental requirements and dispersal
113 capabilities.

114 Also, contrasting relationships of turnover and nestedness with deterministic and
115 stochastic processes has been observed. In polychaeta communities, the lack of
116 nutrients generated nestedness patterns (Stuart et al., 2017). The opposite happened
117 in zooplankton communities: nutrient enrichment generated nestedness patterns
118 under dispersal limitation conditions, and increased dispersal increased the role of
119 species replacement in total β -diversity (Gianuca et al., 2017). In semi-natural
120 grasslands, dispersal limitation was related to nestedness, while relevance of turnover
121 was shown to depend on soil properties: in areas of high fertility, the nutrients
122 phosphorus and nitrate were important in generating turnover, while in areas of low
123 soil fertility dispersal processes drove the same pattern (Conradi et al., 2017).
124 Moreover, we can expect that drivers of turnover and nestedness patterns are also
125 organism dependent, since each organism interact with the environment in a specific
126 way.

127 Here we are looking for patterns and drivers of turnover and nestedness in
128 grassland vegetation in the Brazilian *Campos Sulinos* region, using different spatial
129 grains (i.e. sampling unit size). We aim to answer two questions:

130

131 ***(i) Do β -diversity, turnover and nestedness depend on the grain size?***

132

133 Sampling grain is expected to affect β -diversity because with finer grain the initial
134 species pool is rather low and adding new sampling units will add many new species to
135 the pool, generating high β -diversity. While with coarser sampling grain, values of β -
136 diversity should be lower, as the initial species pool is higher and fewer species will be
137 added to the pool as adding new sampling units (Barton et al., 2013).

138 To test for the grain size dependence of β -diversity, turnover and nestedness we
139 used three spatial grains: 1 m², 250 m² and 25 km². To compare the different grain
140 sizes we obtained coarser grains by pooling small sampling units, i.e. finer grains. This
141 leads to a decreasing number of sampling units as grain increase. To deal with the
142 uneven number of sampling units we applied a procedure of resampling across equal
143 number of sampling units (n = 8) to control for the influence of n (Barton et al., 2013;
144 Baselga, 2012).

145

146 ***(ii) Are there specific drivers for turnover and nestedness at the different spatial***
147 ***scales (extents)?***

148

149 Processes that generate β -diversity patterns are spatially structured. For total β -
150 diversity, we can expect that environmental drivers will be more effective at the broad
151 scale, while stochastic processes will be more important at finer scales (Garzon-Lopez
152 et al., 2014; Menezes et al., 2016). Here we test these assumptions for turnover and
153 nestedness, using a fixed medium grain (250 m²) and three spatial extents: local (25
154 km²), regional (175,000 km² of Pampa grasslands and 31,500 km² of highland
155 grasslands) and full extent (206,500 km² of grasslands in the *Campos Sulinos* region).

156 We expect to find specific relationship of environment and dispersal with
157 nestedness and turnover, respectively. Our first hypothesis is that when a strong
158 environmental filter is acting, species will be excluded along the gradient, with lower
159 replacement by new species and gradual reduction of species richness, showing a
160 clearly nested pattern. As environmental filters are more effective in broader scales,

161 we expect to observe this relationship over our full extent. Our second hypothesis is
162 that turnover patterns will be related to dispersal limitation (i.e. spatial distance), at all
163 spatial scales.

164

165 **2. Material and Methods**

166

167 **2.1. Study area**

168

169 The *Campos Sulinos*, literally translated as “Southern Grasslands”, is the
170 Portuguese designation given to the Brazilian portion of the temperate grassland
171 biome in Southeastern South America (Dixon et al., 2014) and adjacent areas. The
172 *Campos Sulinos* include the northern part of the Río de la Plata grasslands (Andrade et
173 al., 2018) and the highland grasslands in southern Brazil that are found in mosaic with
174 Araucaria forest (Overbeck et al., 2007). Vegetation of the region harbours high
175 biodiversity, with estimates of total number of grassland plants above 3000 taxa
176 (Boldrini et al., 2015), and maximum species number per square metre above 50
177 (Menezes et al., 2018). In the Brazilian vegetation classification, grasslands in the
178 southern half of Rio Grande do Sul state are considered as part of the Brazilian Pampa
179 (from now on: Pampa grasslands), and those in highland region in northern Rio Grande
180 do Sul, Santa Catarina and Paraná states make part of the Atlantic Forest (in the
181 following: highland grasslands) (Fig. 1). A recent analysis has revealed clear floristic
182 differences between grasslands from Pampa and highlands (Andrade et al., 2019).

183 Looking for the best spatial representation of the entire *Campos Sulinos* area we
184 selected twelve sites for sampling, avoiding, as much as possible, fragmented
185 landscapes due to its known negative effect on plant communities (Staudé et al.,
186 2018). In each site, a 5 x 5 kilometres grid was delimited and, starting 500 m from
187 the border, five horizontal and five vertical lines were drawn. From the 25
188 intersections points of the grid, nine were randomly selected to delimitate a 250 x 1 m
189 transect, keeping the same ground level curve (i.e. more homogenous vegetation)
190 (Magnusson et al., 2005). Along each transect, plant species presence was recorded in
191 ten plots of 1 x 1 m equally distributed. Floristic surveys were conducted during spring
192 and summer, in 2014 and 2015. Each area was sampled only once. Sampling sites were
193 located, mostly, inside private properties. Landowners applied traditional management
194 with cattle and sheep grazing at different intensities. Fire management is commonly
195 used in highland grasslands, but none of our sampled areas presented signals of recent
196 fire.

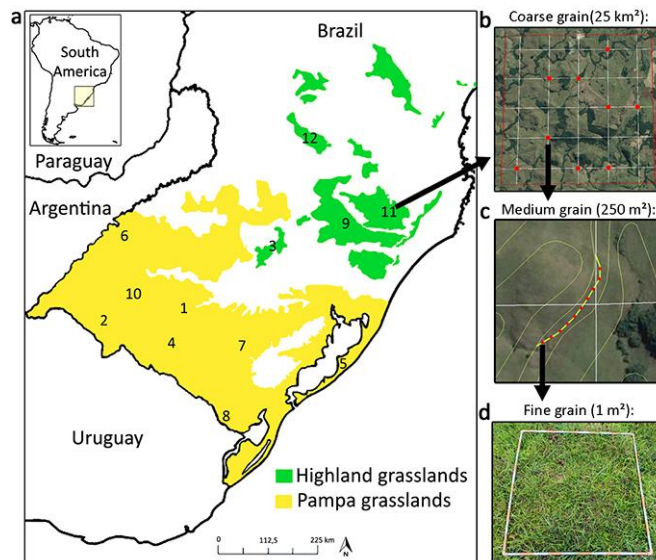
197

198 **2.2. Spatial scale design**

199

200 Spatial scale is defined by two properties: grain and extent. Grain is the size of
201 the fundamental sampling unit. Extent is the size of the area sampled. Our sampling
202 design was nested, i.e. wider scales were obtained by pooling smaller scales. The
203 fundamental sampling units were plots of 1 x 1 m (Fine grain, Fig. 1d). By pooling the
204 group of ten plots we represented the area of the transect (Medium grain, 250 m², Fig.
205 1c) and pooling the nine transects we obtained the total grid area (Coarse grain, 25
206 km², Fig. 1b).

207 As to the extents, the entire gradient of the *Campos Sulinos* comprises an area
 208 around 206,500 km² (green plus yellow area in Fig. 1a), and this we call here “full
 209 extent”. Our “regional extent” is formed by the separation of the two grassland regions
 210 of the *Campos Sulinos*: Pampa grasslands (175,000 km², yellow area in Fig. 1a) and
 211 highland grasslands (31,500 km², green area in Fig. 1a). The “local extent” was the area
 212 of each landscape unit (25 km²).
 213



214 **Figure 1:** Location of the study area. Numbers from 1 to 12 represent location of
 215 landscape units. Also showing area of grassland in the Atlantic Forest (highland
 216 grasslands, in green) and in the Pampa (Pampa grasslands, in yellow). At right side the
 217 three spatial grains are illustrated.
 218
 219

220 **2.3. Data Analysis**

221
 222 We used Jaccard based multiple-site dissimilarity index to calculate total β -
 223 diversity (β_{jac} , Baselga, 2010). Based on β_{jac} we decomposed the turnover and
 224 nestedness values. Other methods to calculate turnover and nestedness have been
 225 developed recently (Baselga and Leprieur, 2015; Podani and Schmera, 2016), but we
 226 opted to use β_{jac} because the alternative possibility (Sorensen based indexes) give
 227 uneven values to species in the communities, valuing more the unique species
 228 (Baselga, 2012). β_{jac} , turnover and nestedness were calculated with help of betapart
 229 package in R (Baselga and Orme, 2012).

230 To answer our first question, we calculate β -diversity, turnover and nestedness
 231 using three spatial grains: fine (1 m²), medium (250 m²) and coarse (25 km²). The
 232 number of sampling units (n) greatly influences values of multiple-site β -diversity and
 233 we have a wide variation in n in our sampling design: fine grain n = 1080; medium grain
 234 n = 108; coarse grain n = 12. To solve the problem of different n number, Baselga’s
 235 framework (β_{jac}) applies resampling across equal number of randomly chosen sampling
 236 units, and we used n = 8. The resampling was repeated 1000 times for each procedure.

237 To answer the second question, we run variation partitioning procedures to
 238 verify the relative contribution of environment, space and the shared effect, to
 239 turnover and nestedness variation at each spatial extent. As our response matrix was
 240 always composed by only one variable (turnover or nestedness at a given spatial scale)

241 the variation partitioning procedures were made by partial regressions, instead of
242 partial redundancy analysis (as is the default of the varpart function in R, see Oksanen
243 et al., 2012). The significance of the pure fractions produced (purely environmental
244 and purely spatial) was tested through permutation test under a $p < 0.05$ interval. All
245 variation partitioning procedures were conducted using function varpart, from vegan
246 package in R (Oksanen et al., 2012).

247 Turnover and nestedness were calculated at the transect level, comparing
248 species composition from the ten plots within each transect.

249 - Full extent: turnover and nestedness were calculated at the grid level, by
250 comparing species composition of the nine transects within each grid. This resulted in
251 twelve turnover values and twelve nestedness values that were used as response
252 variables in two variation partitioning procedures (one to explain turnover variation
253 and one to explain nestedness variation).

254 - Regional extent: at this extent, areas from Pampa were separated from
255 highland grasslands. Turnover and nestedness were calculated at the transect level,
256 comparing species composition from the ten plots within each transect. This resulted
257 in a total of 72 turnover values and 72 nestedness values for Pampa grasslands and of
258 48 turnover values/48 nestedness values for highland grasslands. Those were applied
259 as response variables in four variation partitioning procedures: two to explain turnover
260 variation (one for Pampa turnover and one for highlands turnover) and two to explain
261 nestedness variation (one for Pampa nestedness and one for highlands nestedness).

262 - Local extent: at this spatial extent turnover and nestedness were calculated
263 through the comparison of the ten plots within each transect. As this extent comprises
264 the landscape unit we had a total of 9 turnover and 9 nestedness values per landscape
265 unit. We repeated variation partitioning procedure 24 times: 12 to explain turnover
266 variation inside each landscape unit, and 12 to explain nestedness variation.

267

268 **2.4. Predictive variables**

269

270 We investigate the relative influence of space and environment shaping turnover
271 and nestedness patterns at the three spatial extents. Variables used to predict
272 nestedness and turnover at the regional and local extents were:

273 - *Environment*: percentage of bare soil and rocks were estimated in the 10 plots
274 per transect. Percentage of native grasslands was quantified, based on remote sensing
275 data, in a 2 kilometres buffer, around the central coordinate of the transect. This
276 variable aims to inform connectivity with other grasslands around. Data was extracted
277 from land use classification based on high resolution Landsat images (1:250,000).
278 Three soil samples (depth: approx. 15 cm) per transect were collected and mixed
279 together to one composite soil sample that was analysed regarding chemical and
280 physical features. For soil chemistry, we evaluated pH, aluminium, potassium, nitrogen
281 and phosphorus content, following protocol from Tedesco et al. (1995). The following
282 granulometric classes were used for soil physical description: clay (< 0.002 mm), silt
283 (0.002 to 0.05 mm) and sand (0.05 to 2 mm).

284

285 - *Space*: spatial distance was used as a proxy for dispersal limitation: we assume
286 that the greater the distance between pairs of sampling units, the greater the chance
287 of presenting different community composition. To model spatial distance, we used

288 Moran's eigenvector maps (MEM, Dray et al., 2012). MEM analysis uses geographical
289 coordinates of the sampling units to perform a multivariate ordination. Each
290 ordination axis, or each MEM, represents an independent spatial filter. First MEMs,
291 with lower eigenvalues, represent the finer spatial gradients (closer distances). While
292 the last MEMs, with higher eigenvalues, represent the coarser spatial gradients (longer
293 distances). MEMs were calculated with help of the *adespatial* package in R (Dray et al.,
294 2017). To the medium spatial grain, we used spatial coordinates from the centroid of
295 each transect to generate the MEMs.

296 Variables used to predict nestedness and turnover at the full extent were:
297 - *Environment*: we took the mean value of percentage of bare soil and rocks from
298 the nine transects, composing one value per landscape unit. The percentage of native
299 grasslands within a 10 kilometres buffer from the central point of each landscape unit
300 was calculated using a land cover map based on LANDSAT 2009 data (Weber et al.,
301 2016). Chemical soil features were the same used for medium grain, but using the
302 mean value of the nine transects for each landscape unit. At the coarse grain, we
303 obtained soil granulometric variables with a pixel resolution of 1 km from SoilGrids
304 database (Hengl et al., 2017). We considered the mean value for the pixels inside the
305 landscape unit.

306 At the coarse spatial grain, we added climatic variables to the set of
307 environmental predictors. Temperature (maximum and minimum to the period,
308 average temperature of the rainy month and average temperature of the driest
309 month) and precipitation (maximum and minimum to the period) were obtained from
310 the Brazilian Institute of Meteorology database (INMET, available online:
311 <http://inmet.gov.br/>), for 33 climatic stations in the region. We extracted a ten-year
312 time series, before vegetation sampling (2006-2016). Values were obtained by
313 polynomial interpolation of climatic station data and extracted using a central spatial
314 coordinate for each landscape unit. Interpolation and extraction were made in QGIS
315 software, version 2.18.7.

316 - *Space*: at coarse spatial grain we used central coordinates of each landscape
317 unit to generate the MEMs.

318 Before all variation partitioning procedures, all matrices of explanatory variables
319 (environmental and spatial) were submitted to variables selection. First, to avoid
320 variance inflation, we verified collinearity among environmental variables.
321 Environmental variables with high variance inflation factor (above 10) were excluded
322 (Oksanen et al., 2012). Spatial variables (MEMs) are orthogonal to each other,
323 therefore not collinear. The remaining environmental variables and all spatial variables
324 were submitted to forward selection procedures (Blanchet et al., 2008). This
325 proceeding consists in sorting variables from the explanatory matrix, correlating with
326 the response matrix and testing. The proceeding stops when one of the two previously
327 determined stopping criteria is reached: alpha (given significance level) and R^2
328 (maximum correlation). We adopted the significance level of $\alpha = 0.2$, to all sets of
329 variables. The adopted R^2 threshold varied according to the R^2 of the global model (i.e.
330 model with all explanatory variables), this way one of the subsets of selected variables
331 can't explain more than the full model, avoiding the inflation effect. Values of R^2
332 threshold for each selection procedure are given in supplementary material
333 (Supplementary Tab. 1 to 3).

334

335 **3. Results**

336

337

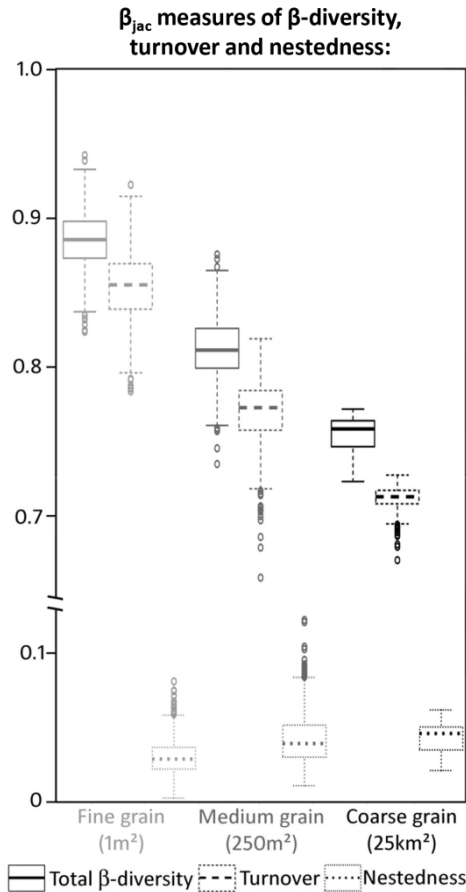
338

339

340

341

The decomposition of β_{jac} showed that regardless of spatial grain, turnover represented a considerably higher proportion of β -diversity (Fig. 2). β -diversity and turnover decreased with coarser grain sizes. Nestedness did not differ between coarse and medium grains and increased from fine to medium grain.



342

343

344

345

346

347

Figure 2: Box-and-whiskers plots present dispersal and median values of total β -diversity, turnover and nestedness. To calculate multiple site β -diversity, turnover and nestedness we kept the number of sampling units fixed in 8, to all spatial grains. Resampling was repeated 1000 times.

348

349

350

351

352

353

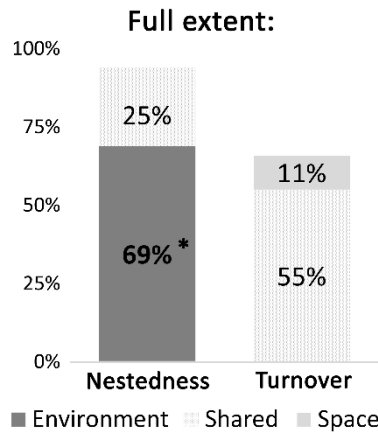
354

355

356

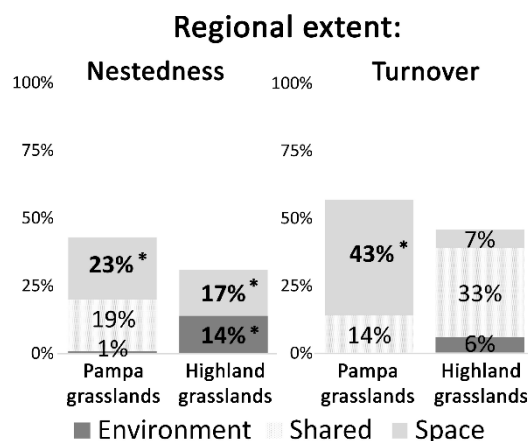
357

As to the drivers of turnover and nestedness, environment was the main, and only significant, driver of nestedness patterns at the full extent (Fig. 3). The most important environmental variables related to nestedness were maximum temperature (r^2 0.45, $p < 0.01$), soil potassium and aluminium content (r^2 0.24 and 0.12, p 0.06 and 0.04, respectively). Turnover did not present exclusive environmental relationships at this scale, but the shared effect of spatially structured environmental variables was strong (55%). This was due to the high correlation of spatial variable MEM4 with the environmental variables: percentage of bare soil (r^2 0.57) and minimum temperature (r^2 0.38).



358
 359 **Figure 3:** Relative influence of environment, space and the shared effect, on
 360 nestedness and turnover for the entire gradient (full extent). Nestedness and turnover
 361 were calculated to the twelve landscape units by comparing species composition of
 362 the nine transects within each landscape unit. Negative fractions are not shown.
 363 Fractions that presented significant explanation ($p < 0.05$) are in bold and marked with
 364 “*”.

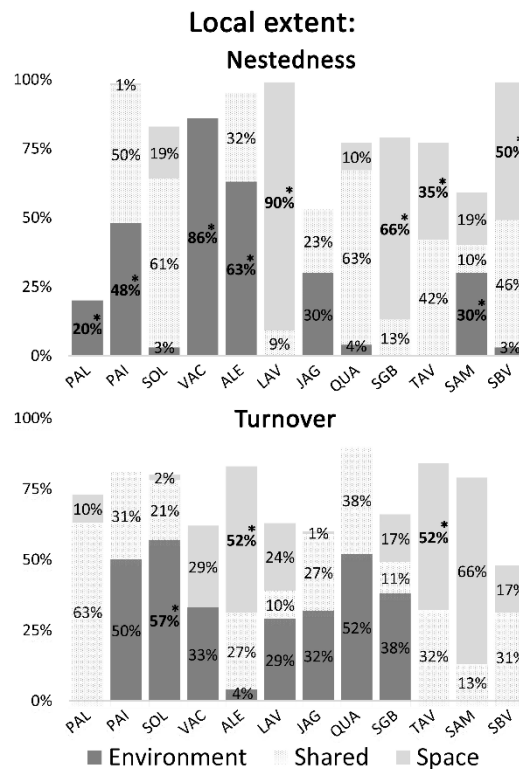
365
 366 Decreasing extent, i.e. dividing the entire region into the Pampa and highland
 367 regions, we observed contrasting drivers in comparison to the full extent. In Pampa
 368 grasslands, nestedness and turnover were related to spatial distance (Fig. 4, 23%* and
 369 43%*, respectively), both greatly influenced by the spatial variables MEM2 (local scale
 370 spatial filter) and MEM13 (medium scale spatial filter). In highland grasslands,
 371 nestedness was likewise related to spatial filters (17%), but with a similar contribution
 372 of environment (14%), mainly represented by soil phosphorus content (r^2 0.18 and p
 373 0.03). Turnover in the highland grasslands, otherwise, presented the same pattern of
 374 the full extent analysis, with higher explanation of spatially structured environment.
 375 The most important variables related were soil nitrogen (r^2 0.31 and $p < 0.01$) and the
 376 broad scale spatial filter MEM1 (r^2 0.2 and $p < 0.01$).
 377



378
 379 **Figure 4:** Relative influence of environment, space and the shared effect, on
 380 nestedness and turnover for each grassland region (regional extent). Nestedness and
 381 turnover were calculated to the 72 transects of Pampa grasslands and 48 transects of
 382 highland grasslands by comparing species composition of the ten plots within each of
 383 them. Negative fractions are not shown. Fractions that presented significant
 384 explanation ($p < 0.05$) are in bold indicated with “*”.

385
 386
 387
 388
 389
 390
 391
 392
 393
 394
 395
 396

At the local extent, each landscape unit seems to present specific relationships of turnover and nestedness with environment and space (Fig. 5). Generally, we observed that in landscape units of the highland regions (PAL, PAI, SOL and VAC), nestedness and turnover were more related to environmental and spatially structured environmental variables. In some of the Pampa landscape units we could observe that spatial features generated nestedness patterns (LAV, SGB, TAV and SBV); however, in other landscape units in the Pampa (ALE, SAM), nestedness was more related to environmental filters. Turnover patterns also presented varied explanations in the Pampa landscape units, but the only two significant correlations ($p < 0.05$) were with the purely spatial fraction, from ALE and TAV.



397
 398
 399
 400
 401
 402
 403
 404

Figure 5: Relative influence of environment, space and the shared effect, on nestedness and turnover for each landscape unit (local extent). Nestedness and turnover were calculated to the nine transects of each landscape unit by comparing species composition of the ten plots from each transect. Negative fractions are not shown. Fractions that presented significant explanation ($p < 0.05$) are in bold indicated with “*”. Acronyms for the municipalities of the landscape units are given in Figure 2.

405 **4. Discussion**

406
 407
 408
 409
 410
 411
 412

Turnover and nestedness are antithetic natural phenomenon (Staude et al., 2018) that may lead to the same β -diversity values. Therefore, diversity partitioning is important to reveal underlying patterns of β -diversity. The distinction between turnover and nestedness patterns brings new contributions to our understanding about community assembly, especially when associated to models with multiple spatial scales. In the South American *Campos Sulinos* region, studies about community

413 assembly still are rather scarce and mostly have focused on the role of disturbances
414 including fire (e.g. Overbeck et al., 2005), fire and mowing (e.g. Fidelis et al., 2012), and
415 grazing (e.g. Blanco et al., 2007), working usually at the local scale. So far, few
416 contributions have addressed community patterns and processes at different spatial
417 scales and over environmental gradients (but see: Menezes et al., 2016). To our
418 knowledge, this is the first contribution to the region that explores patterns and
419 drivers of turnover and nestedness in the *Campos Sulinos* grasslands as a whole and at
420 different spatial scales. Overall, considering the full extent, our results indicate the
421 importance of turnover, i.e. species substitution in space and along gradient, and a
422 much smaller contribution of nestedness, in shaping β -diversity patterns in the
423 *Campos Sulinos* region.

424

425 **4.1. Do β -diversity, turnover and nestedness depend on the spatial scale?**

426

427 The dependence of β -diversity on spatial grain is evident in our result, as total β -
428 diversity varied across the grain sizes (Fig. 2). Here we found that turnover was
429 influenced by the spatial grain in the same way as total β -diversity, but no clear
430 pattern was observed to nestedness. Similar spatial scaling of β -diversity and turnover
431 was found in other studies (Antão et al., 2019; Keil et al., 2012; Steinbauer et al.,
432 2012). Antão et al. (2019) attribute the observed spatial scaling to two possible
433 mechanisms: species aggregation patterns (SAP) and species area relationship (SAR).
434 SAP mechanism relates species spatial distribution patterns with spatial distance,
435 which was not tested here. In relation to our results the SAR mechanism is of special
436 relevance. It predicts that species richness will increase as area sampled increases. So,
437 with coarser spatial grains the initial species pool is higher and fewer species will be
438 added to the pool as adding new sampling units (Barton et al., 2013), resulting in lower
439 β -diversity and turnover. β -diversity would approach zero as grain increases until the
440 point that the grain species richness matches the richness from the entire sampled
441 region (Antão et al., 2019).

442 In our study, turnover had a much higher contribution to total β -diversity than
443 nestedness over all spatial grains. Species replacement has already been registered as
444 the dominant pattern for β -diversity for other taxa in high diversity systems from
445 Brazil, as for example frogs (Melchior et al., 2017) and trees (Bergamin et al., 2017) in
446 Atlantic Forest. Certainly, more studies, with different species groups are needed, but
447 it seems plausible that the reason for the high importance of turnover lies within the
448 past and present favorable environmental conditions that promote high biodiversity
449 (Dobrovolski et al., 2012). Since recent studies tend to use β -diversity measures
450 independent of species pool (γ -diversity), those patterns should not be understood as
451 an effect of the sampling (Kraft et al., 2011).

452 However, when looking at different species groups, it is important to keep in
453 mind: generalizations about β -diversity patterns should be made with caution as
454 patterns may vary for different species groups (Antão et al., 2019), especially when
455 comparing values from groups sampled at the same sites, but at different spatial scales
456 (e.g. varying plot size for different groups of organisms). Nonetheless an interesting
457 future approach for ecologists might be to compare different trophic groups in terms
458 of β -diversity, or seeking for areas with high turnover of different species groups
459 (“turnover hotspots”), especially in species rich regions, such as the *Campos Sulinos*

460 grasslands. When comparing groups from different trophic levels, in terms of β -
461 diversity and turnover, we should have extra attention for spatial scale influence.

462 Regarding nestedness, this portion of β -diversity represented a lower part of the
463 total β -diversity in the *Campos Sulinos* (most values below 0.1, Fig. 2), which seems to
464 be the prevalent pattern for most tropical and subtropical ecosystems, nestedness
465 prevails only in high altitude and temperate regions (Dobrovolski et al., 2012). As
466 nestedness did not present a clear pattern of spatial scaling across sampling grains,
467 few conclusions about spatial scaling can be made.

468

469 **4.2. Are there specific drivers for nestedness or turnover at the different spatial** 470 **scales?**

471

472 Despite the lower values of nestedness, we observed significant explanations for
473 its patterns. As hypothesized, we observed that environmental variables generated
474 nestedness patterns at the full extent. Nestedness represented a lower part of the
475 total β -diversity in the *Campos Sulinos* grasslands, even at the coarse scale. Nestedness
476 seems to prevail within communities where there is a strong biotic filtering, limiting
477 species composition (Stuart et al., 2017). When strong environmental filter act along
478 the gradient, species will be excluded from local communities without replacement for
479 new species due to the highly limiting conditions, leaving a nested pattern. In the
480 *Campos Sulinos* grasslands, the environmental filters generating nestedness were
481 maximum temperature and soil characteristics (potassium and aluminium content).

482 Processes that generated nestedness differed at the other spatial extents, being
483 more related to dispersal limitation in the regional extent for both grasslands regions.
484 Conradi et al. (2017) found that in semi-natural grasslands at medium extents (average
485 21 ha per fragment), nestedness was generated by historical connectivity among
486 fragments, i.e. dispersal limitation. Although the nestedness pattern observed by
487 Conradi et al. were attributed to the historical connectivity of the areas, influenced by
488 past uses, dispersal limitation seems to be an important process that generates
489 nestedness at this scale even in areas with no prior conversion history, such as those
490 analyzed by us.

491 As to our second hypothesis, that turnover patterns would be generated by
492 dispersal limitation at all spatial scales, turnover was explained by dispersal limitation
493 in the Pampa grasslands (i.e. at our medium extent), but at the local extent, only in
494 two of the eight areas in the Pampa (Alegrete - ALE and Tavares – TAV, situated in
495 distinct regions of the *Campos Sulinos*. At the full extent, spatial variables were
496 structured with environment and both together explained turnover. Especially
497 minimum temperature and percentage of bare soil were of great importance to
498 turnover patterns (Tmin: r^2 0.23 and p 0.04; %BareSoil: r^2 0.25 p 0.05), both were
499 correlated with the most influent spatial variable at this scale, MEM4 (correlations
500 with Tmin 0.38 and %Sand 0.55). Climate has intrinsic spatially structured variation
501 (Bell et al., 1993), making it difficult to separate the influence of environment and
502 space at wider scales.

503 In the highland grasslands, turnover patterns were highly correlated with soil
504 nitrogen content, which was spatially structured at the broader spatial scale
505 (correlation between MEM1 and N -0.77). Nitrogen is also a factor that generates
506 turnover in fertile pastures in Europe (Conradi et al., 2017). In areas where nitrogen

507 content is a limiting factor to plant growth, other important soil nutrients might be
508 lacking, as phosphorus (Vitousek et al., 2010). This means that areas with higher
509 nitrogen content tend to higher content of other important nutrients too, which seems
510 to favor species turnover.

511 We did not observe many common patterns at the local extent, especially for
512 Pampa grasslands. Our sampling design aimed at representing the different grasslands
513 physiognomies recognized by Hasenack et al. (2010). The diverse relationships among
514 environment and space with nestedness and turnover observed at this scale likely not
515 only reflect the environmental differences themselves, but also the different and
516 specific historical processes that acted to generate those different grasslands
517 physiognomies (see Conradi et al., 2017). Few general patterns emerge: in highland
518 grasslands, both turnover and nestedness were more strongly related to
519 environmental and spatially structured environmental processes, reaffirming the
520 importance of the edaphic heterogeneity in this region.

521 Despite our high total explanation of turnover and nestedness patterns at local
522 scale (Fig. 5, models explain over 50% of total variance), we must consider that a
523 diversity of other processes that we did not capture with the variables selected by us
524 might be acting to shape turnover and nestedness. Previous experimental research
525 conducted by Segre et al. (2014) has shown that competitive exclusion resulted in
526 lower richness values at local scales, and consequently higher values of β -diversity.
527 Although Segre et al. (2014) did not decompose β -diversity into turnover and
528 nestedness, their results shown that other processes, not spatial or environmental,
529 might also be important at the local scale.

530

531 **4.3. Implications for conservation decisions**

532

533 Total β -diversity is often precipitously used as a synonym for species turnover
534 (Jewitt et al., 2016). However, β -diversity might also increase with species loss, by
535 increasing the nestedness component. Popular indices of β -diversity, as Jaccard and
536 Sørensen, are useful, but it should be kept in mind that their values are the result of
537 distinct - and possibility antithetic - processes. When one is interested in β -diversity
538 patterns to discuss conservation options for a specific area, it is recommended to
539 access not only total β -diversity, but also turnover and nestedness components
540 (Banda-R et al., 2016; Bergamin et al., 2017; Socolar et al., 2016).

541 Our results indicate that for better conservation of *Campos Sulinos* biodiversity,
542 networks of protected areas should contemplate different portions of the climatic and
543 edaphic gradient of the region as a whole. As turnover is the dominant pattern,
544 biodiversity would benefit from conservation efforts, e.g. by help of protected areas,
545 over the full environmental gradient, rather than concentrated in space, e.g. within
546 one or few large and isolated areas. To achieve this, it could be useful to define a
547 minimum percentage of grassland area that is to be maintained; to this end, it is
548 necessary to evaluate effects of land conversion and fragmentations on biological
549 communities. Similar patterns were registered for forests in the Southern Brazil region
550 (Bergamin et al., 2017). In the Pampa grasslands, spatial processes seem to be of great
551 importance to species replacement, this highlights the needing for connectivity among
552 grasslands to facilitate dispersal. For the highland grasslands, environment and
553 spatially structure environment were of greater importance for turnover, especially

554 nitrogen, which is intrinsically related to other soil nutrients, stressing the importance
555 of conservation of the diversity of habitats - distinguished e.g. by soil features - to
556 grasslands preservation in this region. However, the local extent analysis indicates that
557 each grassland area presents specific relationships of turnover and nestedness with
558 environment and space. Therefore, initiatives for conservation at the local extent
559 should include efforts to better understand plant community patterns and processes
560 at the specific scale.

561

562 **References**

563

- 564 Andrade, B.O., Bonilha, C.L., Overbeck, G.E., Vélez-Martin, E., Rolim, R.G., Bordignon,
565 S.A.L., Schneider, A.A., Vogel-Ely, C., Lucas, D.B., Garcia, É.N., Santos, E.D.,
566 Torchelsen, F.P., Vieira, M.S., Silva-Filho, P.J., Ferreira, P.M. de A., Trevisan, R.,
567 Hollas, R., Campestrini, S., Pillar, V.D., Boldrini, I.I., 2019. Classification of South
568 Brazilian grasslands: implications for conservation. *Appl. Veg. Sci.* 22, 168–184.
569 <https://doi.org/10.1111/avsc.12413>
- 570 Andrade, B.O., Marchesi, E., Burkart, S., Setubal, R.B., Lezama, F., Perelman, S.,
571 Schneider, A.A., Trevisan, R., Overbeck, G.E., Boldrini, I.I., 2018. Vascular plant
572 species richness and distribution in the Río de la Plata grasslands. *Bot. J. Linn. Soc.*
573 188, 250–256. <https://doi.org/10.1093/botlinnean/boy063>
- 574 Antão, L.H., McGill, B., Magurran, A.E., Soares, A.M.V.M., Dornelas, M., 2019. B-
575 Diversity Scaling Patterns Are Consistent Across Metrics and Taxa. *Ecography*
576 (Cop.). 42, 1012–1023. <https://doi.org/10.1111/ecog.04117>
- 577 Banda-R, K., Delgado-Salinas, A., Dexter, K.G., Linares-Palomino, R., Oliveira-Filho, A.,
578 Prado, D., Pullan, M., Quintana, C., Riina, R., Rodriguez M., G.M., Weintritt, J.,
579 Acevedo-Rodriguez, P., Adarve, J., Alvarez, E., Aranguren B., A., Arteaga, J.C.,
580 Aymard, G., Castano, A., Ceballos-Mago, N., Cogollo, A., Cuadros, H., Delgado, F.,
581 Devia, W., Duenas, H., Fajardo, L., Fernandez, A., Fernandez, M.A., Franklin, J.,
582 Freid, E.H., Galetti, L.A., Gonto, R., Gonzalez-M., R., Graveson, R., Helmer, E.H.,
583 Idarraga, A., Lopez, R., Marcano-Vega, H., Martinez, O.G., Maturo, H.M.,
584 McDonald, M., McLaren, K., Melo, O., Mijares, F., Moggi, V., Molina, D., Moreno,
585 N. d. P., Nassar, J.M., Neves, D.M., Oakley, L.J., Oatham, M., Olvera-Luna, A.R.,
586 Pezzini, F.F., Dominguez, O.J.R., Rios, M.E., Rivera, O., Rodriguez, N., Rojas, A.,
587 Sarkinen, T., Sanchez, R., Smith, M., Vargas, C., Villanueva, B., Pennington, R.T.,
588 2016. Plant diversity patterns in neotropical dry forests and their conservation
589 implications. *Science* (80-.). 353, 1383–1387.
590 <https://doi.org/10.1126/science.aaf5080>
- 591 Barton, P.S., Cunningham, S. a, Manning, A.D., Gibb, H., Lindenmayer, D.B., Didham,
592 R.K., 2013. The spatial scaling of beta diversity. *Glob. Ecol. Biogeogr.* 22, 639–647.
593 <https://doi.org/10.1111/geb.12031>
- 594 Baselga, A., 2012. The relationship between species replacement, dissimilarity derived
595 from nestedness, and nestedness. *Glob. Ecol. Biogeogr.* 21, 1223–1232.
596 <https://doi.org/10.1111/j.1466-8238.2011.00756.x>
- 597 Baselga, A., 2010. Partitioning the turnover and nestedness components of beta
598 diversity. *Glob. Ecol. Biogeogr.* 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- 599
- 600 Baselga, A., Leprieur, F., 2015. Comparing methods to separate components of beta

601 diversity. *Methods Ecol. Evol.* 6, 1069–1079. <https://doi.org/10.1111/2041->
602 210X.12388

603 Baselga, A., Orme, C.D.L., 2012. betapart : an R package for the study of beta diversity.
604 *Methods Ecol. Evol.* 3, 808–812. <https://doi.org/10.1111/j.2041->
605 210X.2012.00224.x

606 Bell, G., Lechowicz, M.J., Appenzeller, a., Chandler, M., DeBlois, E., Jackson, L.,
607 Mackenzie, B., Preziosi, R., Schallenberg, M., Tinker, N., 1993. The spatial
608 structure of the physical environment. *Oecologia* 96, 114–121.
609 <https://doi.org/10.1007/BF00318038>

610 Bergamin, R.S., Bastazini, V.A.G., Vélez-Martin, E., Debastiani, V., Zanini, K.J., Loyola, R.,
611 Müller, S.C., 2017. Linking beta diversity patterns to protected areas: lessons from
612 the Brazilian Atlantic Rainforest. *Biodivers. Conserv.* 26, 1557–1568.
613 <https://doi.org/https://doi.org/10.1007/s10531-017-1315-y>

614 Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory
615 variables. *Ecology* 89, 2623–2632. <https://doi.org/10.1890/07-0986.1>

616 Blanco, C.C., Sosinski, E.E., Santos, B.R.C., Silva, M.A., Pillar, V.D. V.D., 2007. On the
617 overlap between effect and response plant functional types linked to grazing.
618 *Community Ecol.* 8, 57–65. <https://doi.org/10.1556/ComEc.8.2007.1.8>

619 Boldrini, I.I., Overbeck, G.E., Trevisan, R., 2015. Biodiversidade de plantas, in: Pillar,
620 V.D., Lange, O. (Eds.), *Os Campos Do Sul. Rede Campos Sulinos*, Porto Alegre, pp.
621 53–58.

622 Chave, J., 2013. The problem of pattern and scale in ecology: what have we learned in
623 20 years? *Ecol. Lett.* 16 Suppl 1, 4–16. <https://doi.org/10.1111/ele.12048>

624 Conradi, T., Temperton, V.M., Kollmann, J., 2017. Beta diversity of plant species in
625 human-transformed landscapes: Control of community assembly by regional
626 productivity and historical connectivity. *Perspect. Plant Ecol. Evol. Syst.* 24, 1–10.
627 <https://doi.org/10.1016/j.ppees.2016.10.001>

628 Dixon, A.P., Faber-Langendoen, D., Josse, C., Morrison, J., Loucks, C.J., 2014.
629 Distribution mapping of world grassland types. *J. Biogeogr.* 41, 2003–2019.
630 <https://doi.org/10.1111/jbi.12381>

631 Dobrovolski, R., Melo, A.S., Cassemiro, F.A.S., Diniz-Filho, J.A.F., 2012. Climatic history
632 and dispersal ability explain the relative importance of turnover and nestedness
633 components of beta diversity. *Glob. Ecol. Biogeogr.* 21, 191–197.
634 <https://doi.org/10.1111/j.1466-8238.2011.00671.x>

635 Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Larocque, G., Legendre, P.,
636 Madi, N., Wagner, H.H., 2017. adespatial: Multivariate Multiscale Spatial Analysis.
637 R Packag. version 0.0-8 R package. [https://doi.org/http://cran.r-](https://doi.org/http://cran.r-project.org/package=adespatial)
638 [project.org/package=adespatial](https://doi.org/http://cran.r-project.org/package=adespatial)

639 Dray, S., Péliissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P.R., Bellier,
640 E., Bivand, R., Blanchet, F.G., De Cáceres, M., Dufour, A.-B., Heegaard, E., Jombart,
641 T., Munoz, F., Oksanen, J., Thioulouse, J., Wagner, H.H., 2012. Community ecology
642 in the age of multivariate multiscale spatial analysis. *Ecol. Monogr.* 82, 257–275.

643 Fidelis, A., Blanco, C.C., Müller, S.C., Pillar, V.D., Pfoadenhauer, J., 2012. Short-term
644 changes caused by fire and mowing in Brazilian Campos grasslands with different
645 long-term fire histories. *J. Veg. Sci.* 23, 552–562. <https://doi.org/10.1111/j.1654->
646 1103.2011.01364.x

647 Garzon-Lopez, C.X., Jansen, P. a., Bohlman, S. a., Ordonez, A., Olff, H., 2014. Effects of

648 sampling scale on patterns of habitat association in tropical trees. *J. Veg. Sci.* 25,
649 349–362. <https://doi.org/10.1111/jvs.12090>

650 Gianuca, A.T., Declerck, S.A.J., Lemmens, P., De Meester, L., 2017. Effects of dispersal
651 and environmental heterogeneity on the replacement and nestedness
652 components of B-diversity. *Ecology* 98, 525–533.
653 <https://doi.org/10.1002/ecy.1666>

654 Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M.,
655 Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B.,
656 Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro,
657 E., Wheeler, I., Mantel, S., Kempen, B., 2017. SoilGrids250m: Global gridded soil
658 information based on machine learning, *Plos One*.
659 <https://doi.org/10.1371/journal.pone.0169748>

660 Jewitt, D., Goodman, P.S., O'Connor, T.G., Erasmus, B.F.N., Witkowski, E.T.F., 2016.
661 Mapping landscape beta diversity of plants across KwaZulu-Natal, South Africa,
662 for aiding conservation planning. *Biodivers. Conserv.* 25, 2641–2654.
663 <https://doi.org/10.1007/s10531-016-1190-y>

664 Keil, P., Schweiger, O., Kühn, I., Kunin, W.E., Kuussaari, M., Settele, J., Henle, K.,
665 Brotons, L., Pe'er, G., Lengyel, S., Moustakas, A., Steinicke, H., Storch, D., 2012.
666 Patterns of beta diversity in Europe: The role of climate, land cover and distance
667 across scales. *J. Biogeogr.* 39, 1473–1486. <https://doi.org/10.1111/j.1365-2699.2012.02701.x>

669 Legendre, P., 2014. Interpreting the replacement and richness difference components
670 of beta diversity. *Glob. Ecol. Biogeogr.* 23, 1324–1334.
671 <https://doi.org/10.1111/geb.12207>

672 Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
673 <https://doi.org/10.2307/1941447>

674 Magnusson, W.E., Lima, A.P., Luizão, R., Luizão, F., Costa, F.R.C., Castilho, C. V., Kinupp,
675 V.F., 2005. RAPELD: A modification of the Gentry Method for biodiversity surveys
676 in long-term ecological research sites. *Biota Neotrop.* 5, 19–24.

677 Melchior, L.G., Rossa-Feres, D.D.C., Silva, F.R., 2017. Evaluating multiple spatial scales
678 to understand the distribution of anuran beta diversity in the Brazilian Atlantic
679 Forest. *Ecol. Evol.* 7, 2403–2413. <https://doi.org/10.1002/ece3.2852>

680 Menezes, L. da S., Müller, S.C., Overbeck, G.E., 2016. Scale-specific processes shape
681 plant community patterns in subtropical coastal grasslands. *Austral Ecol.* 41, 65–
682 73. <https://doi.org/10.1111/aec.12299>

683 Menezes, L. da S., Vogel Ely, C., Lucas, D.B., Minervini Silva, G.H., Boldrini, I.I.,
684 Overbeck, G.E., 2018. Plant species richness record in Brazilian Pampa grasslands
685 and implications. *Rev. Bras. Bot.* 41, 817–823. <https://doi.org/10.1007/s40415-018-0492-6>

687 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L.,
688 Solymos, P., Stevens, M.H.H., Wagner, H., 2012. *vegan: Community Ecology*
689 *Package*. R Packag. version.

690 Overbeck, G.E., Müller, S.C., Fidelis, A., Pfadenhauer, J., Pillar, V.D., Blanco, C., Boldrini,
691 I.I., Both, R., Forneck, E., 2007. Brazil's neglected biome: The South Brazilian
692 Campos. *Perspect. Plant Ecol. Evol. Syst.* 9, 101–116.
693 <https://doi.org/10.1016/j.ppees.2007.07.005>

694 Overbeck, G.E., Müller, S.C., Pillar, V.D., Pfadenhauer, J., 2005. Fine-scale post-fire

695 dynamics in southern Brazilian subtropical grassland. *J. Veg. Sci.* 16, 655–664.
696 <https://doi.org/10.1111/j.1654-1103.2005.tb02408.x>

697 Podani, J., Schmera, D., 2016. Once again on the components of pairwise beta
698 diversity. *Ecol. Inform.* 32, 63–68. <https://doi.org/10.1016/j.ecoinf.2016.01.002>

699 Segre, H., Ron, R., De Malach, N., Henkin, Z., Mandel, M., Kadmon, R., 2014.
700 Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of
701 community assembly. *Ecol. Lett.* 17, 1400–1408.
702 <https://doi.org/10.1111/ele.12343>

703 Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How Should Beta-Diversity
704 Inform Biodiversity Conservation? *Trends Ecol. Evol.* 31, 67–80.
705 <https://doi.org/10.1016/j.tree.2015.11.005>

706 Soininen, J., Heino, J., Wang, J., 2018. A meta-analysis of nestedness and turnover
707 components of beta diversity across organisms and ecosystems. *Glob. Ecol.*
708 *Biogeogr.* 27, 96–109. <https://doi.org/10.1111/geb.12660>

709 Staude, I.R., Vélez-Martin, E., Andrade, B.O., Podgaiski, L.R., Boldrini, I.I., Mendonça,
710 M., Pillar, V.D., Overbeck, G.E., 2018. Local biodiversity erosion in South Brazilian
711 grasslands under moderate levels of landscape habitat loss. *J. Appl. Ecol.* 55,
712 1241–1251. <https://doi.org/10.1111/1365-2664.13067>

713 Steinbauer, M.J., Dolos, K., Reineking, B., Beierkuhnlein, C., 2012. Current measures for
714 distance decay in similarity of species composition are influenced by study extent
715 and grain size. *Glob. Ecol. Biogeogr.* 21, 1203–1212.
716 <https://doi.org/10.1111/j.1466-8238.2012.00772.x>

717 Stuart, C.T., Brault, S., Rowe, G.T., Wei, C.L., Wagstaff, M., McClain, C.R., Rex, M.A.,
718 2017. Nestedness and species replacement along bathymetric gradients in the
719 deep sea reflect productivity: a test with polychaete assemblages in the
720 oligotrophic north-west Gulf of Mexico. *J. Biogeogr.* 44, 548–555.
721 <https://doi.org/10.1111/jbi.12810>

722 Tedesco, M.J., Gianello, C., Bissani, C.A., Bohnen, H., 1995. Análises de solo, plantas e
723 outros materiais, 2nd ed. Departamento de Solos da UFRGS, Porto Alegre.

724 Velázquez, E., Martínez, I., Getzin, S., Moloney, K.A., Wiegand, T., 2016. An evaluation
725 of the state of spatial point pattern analysis in ecology. *Ecography (Cop.)* 39,
726 1042–1055. <https://doi.org/10.1111/ecog.01579>

727 Vitousek, P.M., Porder, S., Houlton, B.Z., Oliver, A., Vitousek, P.M., Porder, S., Houlton,
728 B.Z., Chadwick, O. a, 2010. Terrestrial phosphorus limitation: mechanisms,
729 implications, and nitrogen-phosphorus interactions. *Ecol. Appl.* 20, 5–15.

730 Weber, E.J., Hoffmann, G.S., Oliveira, C. V., Hasenack, H., 2016. *Uso e cobertura*
731 *vegetal do Estado do Rio Grande do Sul – situação em 2009*, 1st ed. UFRGS IB
732 *Centro de Ecologia, Porto Alegre.*
733

734 **Supplementary material:**

735

736 **Supplementary table 1:** List of environmental and spatial variables selected to explain737 nestedness and turnover variation in the entire *Campos Sulinos* grasslands (full extent).

		Variables selected:				Selection criteria:			
		Nestedness		Turnover		Nestedness		Turnover	
		r ²	p	r ²	p	alpha	r ²	alpha	r ²
<i>Environment</i>	K	0.24	0.06	-	-	0.2	0.93	0.2	0.74
	Tmax	0.45	<0.01	-	-				
	Al	0.12	0.04	-	-				
	%Sand	0.06	0.05	-	-				
	%Grass	0.05	0.07	-	-				
	N	0.02	0.12	-	-				
	%BareSoil	-	-	0.25	0.05				
	Tmin	-	-	0.23	0.04				
<i>Space</i>	MEM2	0.24	0.07	-	-	0.2	0.12	0.2	0.58
	MEM4	-	-	0.43	<0.01				
	MEM6	-	-	0.13	0.07				
	MEM8	-	-	0.11	0.1				

738

739 **Supplementary table 2:** List of environmental and spatial variables selected to explain

740 nestedness and turnover variation in the two regions (regional extent).

		Variables selected:				Selection criteria:				
		Nestedness		Turnover		Nestedness		Turnover		
		r ²	p	r ²	p	alpha	r ²	alpha	r ²	
Pampa	<i>Environment</i>	%Grass	0.14	<0.01	-	-	0.2	0.15	0.2	0.1
		Clay	0.05	0.03	-	-				
		K	-	-	0.13	0.01				
<i>Space</i>	MEM2	0.24	<0.01	0.27	<0.01	0.2	0.35	0.2	0.56	
	MEM13	0.19	0.01	0.16	<0.01					
	MEM5	-	-	0.07	<0.01					
	MEM24	-	-	0.05	0.01					
	MEM35	-	-	0.02	0.05					
Atlantic Forest	<i>Environment</i>	Clay	0.08	0.05	-	-	0.2	0.2	0.2	0.36
		P	0.18	0.08	0.03	0.11				
		N	-	-	0.31	<0.01				
		%Grass	-	-	0.04	0.09				
<i>Space</i>	MEM4	0.11	0.02	-	-	0.2	0.48	0.2	0.7	
	MEM19	0.04	0.12	-	-					
	MEM23	0.02	0.18	-	-					
	MEM1	-	-	0.2	<0.01					
	MEM15	-	-	0.09	0.03					
	MEM9	-	-	0.05	0.07					
	MEM13	-	-	0.02	0.14					
	MEM12	-	-	0.02	0.19					
	MEM2	-	-	0.02	0.17					

741

742 **Supplementary table 3:** List of environmental and spatial variables selected to explain
 743 nestedness and turnover variation in each landscape unit (medium grain and local extent).

		Variables selected:				Selection criteria:			
		Nestedness		Turnover		Nestedness		Turnover	
		r ²	p	r ²	p	alpha	r ²	alpha	r ²
Palmas									
<i>Environment</i>	K	0.2	0.12	0.22	0.1	0.2	0.51	0.2	0.45
	N	-	-	0.41	0.01				
<i>Space</i>	MEM5	-	-	0.59	0.02	0.2	0.28	0.2	0.72
	MEM2	-	-	0.13	0.09				
Painel									
<i>Environment</i>	P	0.67	<0.01	-	-	0.2	0.97	0.2	0.83
	%Grass	0.21	<0.01	0.21	0.09				
	%Bare Soil	0.07	0.02	0.14	0.07				
	Sand	0.01	0.13	-	-				
	Al	0.02	0.15	0.04	0.2				
	K	-	-	0.55	0.01				
<i>Space</i>	MEM1	0.51	0.03	0.26	0.09	0.2	0.36	0.2	0.55
Soledade									
<i>Environment</i>	K	0.63	0.02	-	-	0.2	0.65	0.2	0.69
	N	-	-	0.54	0.01				
	P	-	-	0.12	0.11				
	Al	-	-	0.13	0.09				
<i>Space</i>	MEM3	0.24	0.09	-	-	0.2	0.75	0.2	0.14
	MEM4	0.31	0.05	-	-				
	MEM2	0.16	0.09	-	-				
	MEM5	0.08	0.13	-	-				
	MEM1	-	-	0.24	0.09				
Vacaria									
<i>Environment</i>	%Grass	0.27	0.09	-	-	0.2	0.81	0.2	0.47
	%Bare Soil	0.51	<0.01	-	-				
	K	0.08	0.11	-	-				
	P	-	-	0.15	0.18				
<i>Space</i>	MEM4	-	-	0.1	0.17	0.2	0.48	0.2	0.2
Alegrete									
<i>Environment</i>	K	0.51	0.02	-	-	0.2	0.97	0.2	0.77
	Clay	0.3	0.02	-	-				
	N	0.1	0.07	-	-				
	%Grass	0.06	0.02	-	-				
	Sand	-	-	0.31	0.1				
<i>Space</i>	MEM3	0.3	0.07	-	-	0.2	0.24	0.2	0.7
	MEM1	-	-	0.79	<0.01				
Lavras do Sul									
<i>Environment</i>	%Grass	0.09	0.2	-	-	0.2	0.74	0.2	0.6
	%BareSoil	-	-	0.23	0.12				
	N	-	-	0.15	0.15				
<i>Space</i>	MEM2	0.67	<0.01	-	-	0.2	0.98	0.2	0.73
	MEM4	0.26	<0.01	-	-				
	MEM6	0.05	0.01	-	-				
	MEM5	0.01	0.07	-	-				
Jaguarão									
<i>Environment</i>	N	0.27	0.09	0.34	0.03	0.2	0.72	0.2	0.83
	K	0.26	0.06	0.26	0.05				
<i>Space</i>	MEM3	0.19	0.14	0.28	0.08	0.2	0.44	0.2	0.55
Quaraí									
<i>Environment</i>	%Grass	0.32	0.05	-	-	0.2	0.87	0.2	0.88
	K	0.14	0.16	-	-				
	Clay	0.2	0.06	-	-				
	%BareSoil	-	-	0.73	<0.01				
	N	-	-	0.07	0.11				
	Al	-	-	0.04	0.16				
	Sand	-	-	0.06	0.11				

Space	MEM1	0.42	0.04	-	-	0.2	0.68	0.2	0.49
	MEM2	0.31	0.02	-	-				
	MEM5	-	-	0.21	0.13				
	MEM6	-	-	0.16	0.15				
São Gabriel									
Environment	%BareSoil	0.13	0.18	0.09	0.17	0.2	0.31	0.2	0.77
	Clay	-	-	0.31	0.09				
	K	-	-	0.31	0.05				
	P	-	-	0.06	0.16				
Space	MEM2	0.29	0.07	-	-	0.2	0.73	0.2	0.54
	MEM4	0.25	0.09	-	-				
	MEM1	0.24	0.05	0.28	0.07				
Tavares									
Environment	Clay	0.4	0.06	0.3	0.09	0.2	0.72	0.2	0.69
Space	MEM2	0.77	<0.01	0.84	<0.01	0.2	0.7	0.2	0.78
Santo Antônio das Missões									
Environment	%BareSoil	0.4	0.03	-	-	0.2	0.4	0.2	0.58
	P	-	-	0.06	0.2				
Space	MEM6	0.29	0.05	0.16	0.14	0.2	0.63	0.2	0.64
	MEM3	-	-	0.38	0.04				
	MEM4	-	-	0.1	0.17				
	MEM1	-	-	0.14	0.12				
Santana da Boa Vista									
Environment	K	0.18	0.16	-	-	0.2	0.65	0.2	0.82
	Al	0.48	0.04	-	-				
	N	-	-	0.3	0.06				
Space	MEM1	0.61	0.01	-	-	0.2	0.97	0.2	0.46
	MEM6	0.2	0.02	-	-				
	MEM4	0.1	0.05	0.48	0.15				
	MEM3	0.05	0.07	-	-				
	MEM5	-	-	0.35	0.06				

744

745 **Supplementary material**

746

747 **Supplementary table 1:** List of environmental and spatial variables selected to explain748 nestedness and turnover variation in the entire *Campos Sulinos* grasslands (full extent).

		Variables selected:				Selection criteria:			
		Nestedness		Turnover		Nestedness		Turnover	
		r ²	p	r ²	p	alpha	r ²	alpha	r ²
Environment	K	0.24	0.06	-	-	0.2	0.93	0.2	0.74
	Tmax	0.45	<0.01	-	-				
	Al	0.12	0.04	-	-				
	%Sand	0.06	0.05	-	-				
	%Grass	0.05	0.07	-	-				
	N	0.02	0.12	-	-				
	%BareSoil	-	-	0.25	0.05				
Space	Tmin	-	-	0.23	0.04	0.2	0.12	0.2	0.58
	MEM2	0.24	0.07	-	-				
	MEM4	-	-	0.43	<0.01				
	MEM6	-	-	0.13	0.07				
	MEM8	-	-	0.11	0.1				

749

750 **Supplementary table 2:** List of environmental and spatial variables selected to explain

751 nestedness and turnover variation in the two regions (regional extent).

		Variables selected:				Selection criteria:			
		Nestedness		Turnover		Nestedness		Turnover	
Pampa		r ²	p	r ²	p	alpha	r ²	alpha	r ²

<i>Environment</i>	%Grass	0.14	<0.01	-	-	0.2	0.15	0.2	0.1
	Clay	0.05	0.03	-	-				
	K	-	-	0.13	0.01				
<i>Space</i>	MEM2	0.24	<0.01	0.27	<0.01	0.2	0.35	0.2	0.56
	MEM13	0.19	0.01	0.16	<0.01				
	MEM5	-	-	0.07	<0.01				
	MEM24	-	-	0.05	0.01				
	MEM35	-	-	0.02	0.05				
Atlantic Forest									
<i>Environment</i>	Clay	0.08	0.05	-	-	0.2	0.2	0.2	0.36
	P	0.18	0.08	0.03	0.11				
	N	-	-	0.31	<0.01				
	%Grass	-	-	0.04	0.09				
<i>Space</i>	MEM4	0.11	0.02	-	-	0.2	0.48	0.2	0.7
	MEM19	0.04	0.12	-	-				
	MEM23	0.02	0.18	-	-				
	MEM1	-	-	0.2	<0.01				
	MEM15	-	-	0.09	0.03				
	MEM9	-	-	0.05	0.07				
	MEM13	-	-	0.02	0.14				
	MEM12	-	-	0.02	0.19				
	MEM2	-	-	0.02	0.17				

752

753 **Supplementary table 3:** List of environmental and spatial variables selected to explain
 754 nestedness and turnover variation in each landscape unit (medium grain and local extent).

		Variables selected:				Selection criteria:			
		Nestedness		Turnover		Nestedness		Turnover	
		r ²	p	r ²	p	alpha	r ²	alpha	r ²
Palmas									
<i>Environment</i>	K	0.2	0.12	0.22	0.1	0.2	0.51	0.2	0.45
	N	-	-	0.41	0.01				
<i>Space</i>	MEM5	-	-	0.59	0.02	0.2	0.28	0.2	0.72
	MEM2	-	-	0.13	0.09				
Painel									
<i>Environment</i>	P	0.67	<0.01	-	-	0.2	0.97	0.2	0.83
	%Grass	0.21	<0.01	0.21	0.09				
	%Bare Soil	0.07	0.02	0.14	0.07				
	Sand	0.01	0.13	-	-				
	Al	0.02	0.15	0.04	0.2				
	K	-	-	0.55	0.01				
<i>Space</i>	MEM1	0.51	0.03	0.26	0.09	0.2	0.36	0.2	0.55
Soledade									
<i>Environment</i>	K	0.63	0.02	-	-	0.2	0.65	0.2	0.69
	N	-	-	0.54	0.01				
	P	-	-	0.12	0.11				
	Al	-	-	0.13	0.09				
<i>Space</i>	MEM3	0.24	0.09	-	-	0.2	0.75	0.2	0.14
	MEM4	0.31	0.05	-	-				
	MEM2	0.16	0.09	-	-				
	MEM5	0.08	0.13	-	-				
	MEM1	-	-	0.24	0.09				
Vacaria									
<i>Environment</i>	%Grass	0.27	0.09	-	-	0.2	0.81	0.2	0.47
	%Bare Soil	0.51	<0.01	-	-				
	K	0.08	0.11	-	-				
	P	-	-	0.15	0.18				
<i>Space</i>	MEM4	-	-	0.1	0.17	0.2	0.48	0.2	0.2
Alegrete									
<i>Environment</i>	K	0.51	0.02	-	-	0.2	0.97	0.2	0.77
	Clay	0.3	0.02	-	-				
	N	0.1	0.07	-	-				
	%Grass	0.06	0.02	-	-				
	Sand	-	-	0.31	0.1				
<i>Space</i>	MEM3	0.3	0.07	-	-	0.2	0.24	0.2	0.7
	MEM1	-	-	0.79	<0.01				
Lavras do Sul									
<i>Environment</i>	%Grass	0.09	0.2	-	-	0.2	0.74	0.2	0.6
	%BareSoil	-	-	0.23	0.12				
	N	-	-	0.15	0.15				
<i>Space</i>	MEM2	0.67	<0.01	-	-	0.2	0.98	0.2	0.73
	MEM4	0.26	<0.01	-	-				
	MEM6	0.05	0.01	-	-				
	MEM5	0.01	0.07	-	-				
Jaguarão									
<i>Environment</i>	N	0.27	0.09	0.34	0.03	0.2	0.72	0.2	0.83
	K	0.26	0.06	0.26	0.05				
<i>Space</i>	MEM3	0.19	0.14	0.28	0.08	0.2	0.44	0.2	0.55
Quaraí									
<i>Environment</i>	%Grass	0.32	0.05	-	-	0.2	0.87	0.2	0.88
	K	0.14	0.16	-	-				
	Clay	0.2	0.06	-	-				
	%BareSoil	-	-	0.73	<0.01				
	N	-	-	0.07	0.11				
	Al	-	-	0.04	0.16				
	Sand	-	-	0.06	0.11				

<i>Space</i>	MEM1	0.42	0.04	-	-	0.2	0.68	0.2	0.49
	MEM2	0.31	0.02	-	-				
	MEM5	-	-	0.21	0.13				
	MEM6	-	-	0.16	0.15				
São Gabriel									
<i>Environment</i>	%BareSoil	0.13	0.18	0.09	0.17	0.2	0.31	0.2	0.77
	Clay	-	-	0.31	0.09				
	K	-	-	0.31	0.05				
	P	-	-	0.06	0.16				
<i>Space</i>	MEM2	0.29	0.07	-	-	0.2	0.73	0.2	0.54
	MEM4	0.25	0.09	-	-				
	MEM1	0.24	0.05	0.28	0.07				
Tavares									
<i>Environment</i>	Clay	0.4	0.06	0.3	0.09	0.2	0.72	0.2	0.69
<i>Space</i>	MEM2	0.77	<0.01	0.84	<0.01	0.2	0.7	0.2	0.78
Santo Antônio das Missões									
<i>Environment</i>	%BareSoil	0.4	0.03	-	-	0.2	0.4	0.2	0.58
	P	-	-	0.06	0.2				
<i>Space</i>	MEM6	0.29	0.05	0.16	0.14	0.2	0.63	0.2	0.64
	MEM3	-	-	0.38	0.04				
	MEM4	-	-	0.1	0.17				
	MEM1	-	-	0.14	0.12				
Santana da Boa Vista									
<i>Environment</i>	K	0.18	0.16	-	-	0.2	0.65	0.2	0.82
	Al	0.48	0.04	-	-				
	N	-	-	0.3	0.06				
<i>Space</i>	MEM1	0.61	0.01	-	-	0.2	0.97	0.2	0.46
	MEM6	0.2	0.02	-	-				
	MEM4	0.1	0.05	0.48	0.15				
	MEM3	0.05	0.07	-	-				
	MEM5	-	-	0.35	0.06				



CAPÍTULO 4

Functional beta diversity reveals hidden interactions: shrubs as keystone features for spiders

Luciana da Silva Menezes, Kimberly da Silva Marta, Luciana Regina Podgaiski e
Gerhard Ernst Overbeck.

Manuscrito formatado nas normas do periódico *Journal of Biogeography*, ainda não submetido.

1 **Title**

2

3 Functional beta diversity reveals hidden interactions: shrubs as keystone features for
4 spiders

5

6 **Short running title**

7

8 Shrubs as keystone features for spiders

9

10 **Authors**

11

12 Luciana da Silva Menezes^{a*}, Kimberly da Silva Marta^b, Luciana Regina Podgaiski^c and
13 Gerhard Ernst Overbeck^{a,d}

14 ^aPrograma de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul.

15 ^bPrograma de Pós-Graduação em Biologia Animal, Universidade Federal do Rio Grande
16 do Sul.

17 ^cDepartamento de Ecologia, Universidade Federal do Rio Grande do Sul.

18 ^dDepartamento de Botânica, Universidade Federal do Rio Grande do Sul.

19

20 **Correspondence**

21

22 Instituto de Biociências, Laboratório de Estudos em Vegetação Campestre, 9500 Bento
23 Gonçalves Av., CEP 91501-970, Porto Alegre, Brazil. E-mail: luciana.menezes@ufrgs.br

24

25 **Acknowledgements**

26

27 The authors thank the more than 50 land owners that allowed to work on their lands.

28 Special thanks to the field work team of the UFRGS Laboratory of Grassland Vegetation
29 Studies for data collection. LSM and KSM were supported by CAPES, LRP and GEO were
30 supported by CNPq. This study was developed within the PPBio Campos Sulinos

31 network, financed by MCTIC through grant CNPq 457447/2012-5 to GEO.

32 **Abstract**

33

34 **Aim:** Understand how plants and spiders interact, considering alpha, beta and gamma
35 diversity levels in a mesic grassland under traditional management. Additionally, we
36 investigated which functional plant groups explained the spider diversity patterns.

37 **Location:** South American Campos Sulinos grasslands.

38 **Taxon:** plants and spiders.

39 **Methods:** Plants and spiders were sampled in eight grids (5x5 Km), each grid with nine
40 plots (250x1 m). Plants were classified into nine functional groups, reflecting above
41 ground structure, and spiders were classified into six foraging guilds. Functional
42 diversity was calculated with Rao index and partitioned with the multiplicative method
43 ($\beta = \gamma / \alpha$). Linear models were applied to investigate relationships between
44 same diversity levels. Plant trait that better explained spider diversity patterns were
45 selected through variable selection procedure.

46 **Results:** Alpha and gamma diversities of the two species groups behaved alike, which is
47 in accordance with habitat heterogeneity theory that predicts that the more complex
48 habitats (higher plant alpha or gamma functional diversity) supports higher animal
49 species diversity (higher spider alpha or gamma functional diversity). Beta functional
50 diversity showed a contrasting pattern: Plant and spider beta diversity were negatively
51 correlated, which was related to the proportional abundance of shrubs within the
52 grids. Shrubs abundance explained spider alpha and beta diversity.

53 **Main conclusion:** Our results support the habitat heterogeneity theory, even in rather
54 mesic grasslands. We also highlighted the importance of shrubs in these environments
55 to the maintenance of spider functional diversity and ecosystem services provided by
56 them. Shrubs act as keystone features, providing good habitat conditions and
57 consequently promoting spider alpha and beta diversity. Abundance of shrubs might
58 also be indicative of lower grazing pressure, absence of chemical or mechanical
59 mowing and overall better habitat conditions.

60

61 **Keywords**

62

63 Arthropod, functional diversity partition, grassland, habitat heterogeneity, interaction,
64 keystone features.

65

66 **1. Introduction**

67

68 Interactions among species of distinct trophic levels are complex and often need
69 to be studied at more than one spatial scale to be fully understood. Diversity
70 decomposition into alpha (local scale), beta (among local units) and gamma (regional
71 scale) diversities is an interesting approach when working with species interactions. It
72 not only provides diversity measures at different spatial extents, but can also reveal
73 how local and regional species pools interact (Anderson et al., 2011; de Bello,
74 Lavergne, Meynard, Lepš, & Thuiller, 2010). This is especially interesting when the
75 functional dimension of biodiversity is considered, i.e. when discussion species'
76 characteristics that drive the interaction with other species and with the environment
77 (Petchey, O'Gorman, & Flynn, 2009).

78 Human well-being relies on the ecosystem services provided by interactions
79 among species (e.g. pollination) and interactions of species with the environment itself
80 (e.g. carbon storage). The maintenance of high functional diversity levels seems to be
81 the best way to conserve a wide variety of ecosystem services (Diaz & Cabido, 1997).
82 Functional diversity (FD), defined as the variation of functional traits of an ecological
83 unit (organism, population, or community) (Carmona, de Bello, Mason, & Lepš, 2016),
84 is considered to be much more related to ecosystem services than other dimensions of
85 biodiversity. However, the spatial scaling of FD is crucial: for example, FD may be low
86 at the local scale (alpha), but if functional characteristics vary through the landscapes
87 (high beta diversity), ultimately, we will have more functional diversity in the regional
88 scale (gamma diversity). This way, overall provisioning of ecosystem services in a
89 region can be regionally guaranteed, even accounting for areas with low functional
90 alpha diversity.

91 Arthropods play an important role in provisioning of several crucial ecosystem
92 services, such as pollination (Williams et al., 2015) and biological control (Bianchi,
93 Schellhorn, Buckley, & Possingham, 2010; Perović et al., 2017). They also are an
94 important component in food webs, sustaining higher trophic levels and can also
95 improve plant productivity (e.g. Classen *et al.* 2014). Understanding how arthropods
96 and plants interact has been a major research field in ecology (see e.g. Joern and Laws
97 2013 for a recent review in grasslands). The habitat heterogeneity theory predicts that
98 changes in the habitat characteristics, or diversity of habitats (plants), will provide
99 more niches and lead to an increase in species diversity (Tews et al., 2004). In
100 grasslands, several features of vegetation are known to influence arthropod
101 communities, such as plant species richness, structural complexity, nutritional quality
102 of plants and above-ground productivity, and a number of experimental studies has
103 revealed details about the interactions between trophic levels (Gomez, Lohmiller, &
104 Joern, 2016; Rouabah, Villerd, Amiaud, Plantureux, & Lasserre-Joulin, 2015; Schirmel,
105 Thiele, Entling, & Buchholz, 2016). Additionally, studies interested in disentangling the
106 relationship among plants and arthropods have focused on comparing grassland
107 management practices (e.g. effects of burning, mowing, different grazing intensities)
108 (Jonas & Joern, 2007; Morris, 2000). A recent overview pointed to the diversification of
109 management practices as the best alternative to conserve plants, arthropods and
110 other groups diversities (Allan et al., 2014).

111 Brazil's 'Southern grasslands' (Fig. 1a; Campos Sulinos in Portuguese) are
112 composed of two grassland regions that lie in distinct biogeographical domains: the
113 grasslands of the Pampa region, and the highland grasslands that are situated within
114 the Atlantic Forest region (Overbeck et al., 2007). In this region, livestock production is
115 one of the main economic activity, although grasslands have been losing space to
116 agriculture, mainly soybean, and exotic tree plantation (Andrade et al., 2015).
117 Furthermore, overgrazing constitutes a major problem in the entire region (Carvalho &
118 Batello, 2009). Habitat loss and degradation are a major risk for biodiversity, including
119 plants and arthropods (Gossner et al., 2016; Staude et al., 2018), and so is degradation
120 due to management (Leidinger et al., 2017).

121 In this research, we investigated correlations between FD patterns of plants and
122 spiders, in mesic grasslands of Campos Sulinos. Spiders are resourceful predators that
123 feed primarily on other small invertebrates, including others spiders (Perkins, Inger,
124 Bearhop, & Sanders, 2018; Wise, 2006). Interactions among spiders and plants are

125 driven mostly by physical structure of vegetation. For example, web-building spiders
126 need the vegetation to be complex enough for anchoring webs (Gomez et al., 2016).
127 An study in a small-scale fire experiment at the Campos Sulinos region has already
128 shown that spiders inhabiting more functionally diverse plant communities were also
129 more diverse in their functional traits (Podgaiski et al., 2013). Here we are interested in
130 exploring the FD patterns at the scales alpha, gamma and beta, in sites spread in the
131 entire region in grasslands under typical grazing management. We investigated plant
132 and spider communities in eight distinct landscapes using a nested sampling design
133 (Fig. 1a). Following the habitat heterogeneity theory, we hypothesized that as plant FD
134 increases, spider FD would also increase (Tews et al., 2004). This positive relationship
135 should be weaker at the alpha scale, where habitat conditions of the grasslands (plants
136 diversity) will not be as important as the local species pool (i.e. spider species
137 richness). At the gamma scale, here defined as the landscape level, FD of both groups
138 will be allowed to vary greatly due to the larger species pool and wider environmental
139 gradient. Therefore, our second hypothesis is that the positive relationship between
140 plants FD and spiders FD will be correlated to the species pool size, especially at the
141 alpha scale, where the species pool is limited and slightly increases or decreases may
142 cause substantial influence over FD. As to functional beta diversity we also expected a
143 positive relationship, because higher levels of plants functional beta diversity
144 represent changes in habitat characteristics for spiders, which would be followed by
145 changes in spider functional composition.

146 Previous studies in the Campos Sulinos region pointed that, not only the plant
147 functional diversity per se, but also specific functional groups of plants may have great
148 influence on spider community patterns. For example, rigid rosette species, especially
149 from the genus *Eryngium*, seem to play an important role in providing vertical
150 structure to orbicular web-builders, while tussock grasses provide buffered habitats for
151 the ground hunters (Podgaiski et al., 2013). Based on this, we explored the
152 relationships between functional composition of plants and spiders, testing if specific
153 plant functional types affect spider alpha, beta and gamma functional diversities in the
154 grassland landscape.

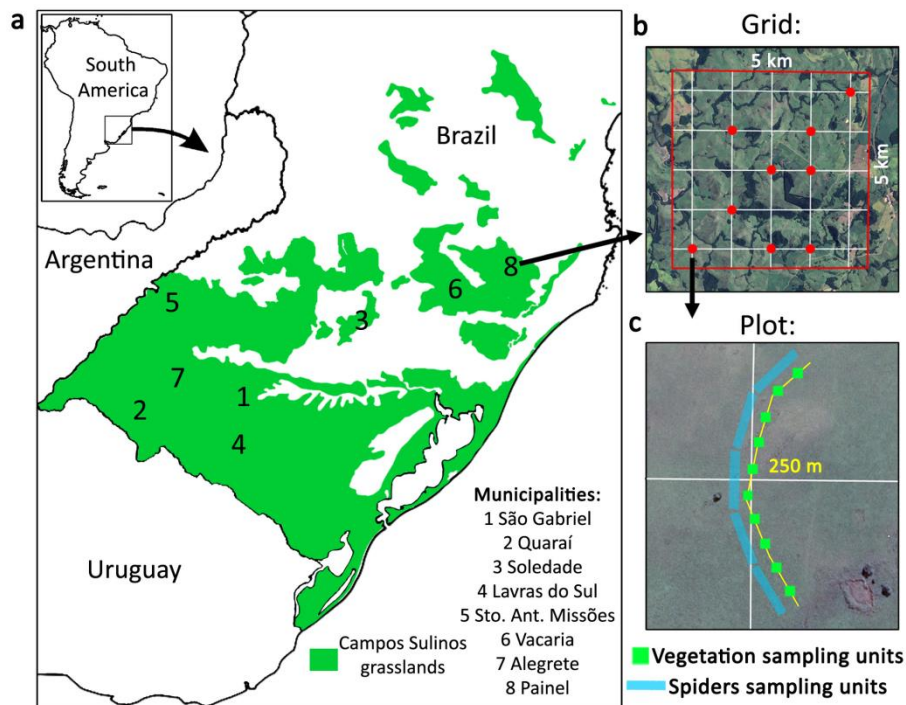
155

156 **2. Material and methods**

157

158 Based on Landsat satellite images with high resolution (1:250,000), we selected
159 Campos Sulinos landscapes where natural grasslands were the dominant formation,
160 i.e. with little percentage of agriculture and tree plantations. In an adaption of the
161 standardized RAPELD protocol (Magnusson et al., 2005), we delimited, in each
162 landscape, one grid of 5 x 5 kilometers (Fig. 1b). Inside the grids, starting 500 meters
163 distant from the border, five horizontal and five vertical lines were draw (equidistant
164 1 km). From the 25 intersection points of those lines, nine were randomly selected for
165 plant and spider sampling. Sampling took place in a 250 m long and 1 m wide plot (Fig.
166 1c), placed along the isocline (i.e. no topographic variation), and sub-sampled with
167 different methods for spiders and plants. All areas were sampled only once for spiders
168 and plants, from October to March in years of 2014 and 2015. In one of the grids (nº 2,
169 Quaraí) only seven of the nine plots could be sampled.

170



171
 172
 173
 174
 175
 176
 177
 178
 179
 180
 181
 182
 183
 184
 185
 186
 187
 188
 189
 190
 191
 192
 193
 194
 195
 196
 197
 198
 199
 200

Figure 1: (a) Distribution of the eight grids in the Campos Sulinos grasslands; (b) representation of the 25 km² grid, red dots are the location of the nine plots in this grid; (c) Plot of 250 x 1 m long where ten square sampling units of vegetation (1 x 1 m) and five transect sampling units of spiders (50 x 1 m) were placed, side-by-side.

2.1. Vegetation sampling and plant traits

Along the plot we placed, equally distributed, ten sampling units of 1 m² (Fig. 1c, light green squares). Inside each sampling unit all visually detected plant species were identified and their cover estimated according to Londo’s decimal scale (Londo, 1976). Most species were identified in the field, whenever necessary the plants were collected and herborized for posterior identification in the laboratory, with help of specific literature and specialists in taxonomy of the respective group.

We classified the plant species into nine categories of morphological traits that represented plants above ground vertical structure, which we assumed that potentially represented important structural features to spider communities (Tab. 1). Those effect traits were specifically chosen to reflect “the effects of a plant on environmental conditions; community or ecosystem properties”, as defined by Violle *et al.* (2007). As the vertical structure of plants is important to spiders (Gomez *et al.*, 2016), our classification was, first of all, based on the division of grasslands plants into: grasses and grass-like plants, herbs and shrubs, reflecting general patterns of aboveground plant structure and complexity. Secondly, we considered differences in the way different species spread their leaves, i.e. closer to ground (like rosette herbs and prostrate grasses) or vertically (along a stem like erect herbs or caespitose grasses). A more detailed explanation of each of the nine morphological categories is given in Table 1.

2.2. Spider sampling and traits

201 For spider sampling, the plot was subdivided into five segments of 50 meters
 202 each (Fig. 1c, blue segments). We used a D-Vac vacuum sampler (Eccho ES250)
 203 equipped with a fine net (0.5 mm), adapted in a backpack, to sample spiders while
 204 walking through the first 20 m of each segment. The sampling in each segment
 205 included both vegetation and ground strata, and occurred from 3 to 5 minutes, varying
 206 according the habitat complexity of each site.

207 Spiders were separated from the rest of the content from the vacuum net and
 208 preserved in 70% ethanol. Adult individuals were identified to the species level, or
 209 whenever not possible, in morphospecies, and deposited at the Spider Collection of
 210 the Museu de Ciências Naturais do Rio Grande do Sul (MCN/FZB-RS). Based on family
 211 and/or generic affiliation, we classified spiders into six functional groups representing
 212 different foraging guilds: three of web-builders, and three of cursorial or non-web-
 213 building spiders (Tab. 1) adapted according to Uetz *et al.* (1999), Dias *et al.* (2010),
 214 Cardoso *et al.* (2011), and to specialists knowledge.

215 By separating spiders into three web-builders and three non-web-building guilds
 216 we are assuming that species from those groups interact differently with the grassland
 217 vegetation structure, and their preys. For example, spiders that build orbicular webs
 218 (e.g. Araneidae family) are more prone to catch flying preys by the preferred vertical
 219 structure of their webs, which demands a more vertical and open structure of the
 220 vegetation. Sheet web-builders (e.g. Linyphiidae family), otherwise, are more likely to
 221 capture falling preys by the horizontal arrangement of their webs. These horizontal
 222 webs close to the ground also facilitate the capture of ground-walking preys. Those
 223 spiders will not require such vertical/open structure of the vegetation, but the
 224 existence of some canopy is important so that preys can fall down to their webs.
 225 Three-dimensional web-builders (e.g. Theridiidae family) are sometimes referred as
 226 space-web builders (Dias et al., 2010) by the scattered design of their webs, with no
 227 preferential spatial arrangement. Those spiders do not rely on the web architecture to
 228 catch preys, but in other characteristics, as Theridiidae family that produce sticky lines
 229 of silk (World Spider Catalog, 2018). This way, habitat characteristics that affect three-
 230 dimensional web-builders distribution might be more related to overall habitat
 231 features that provide more abundant preys.

232 As to the non-web-building guilds, or hunters, we could recognize at least three
 233 kinds of activities: runners are spiders that wait the best moment to run short
 234 distances towards their preys (e.g. Lycosidae family, wolf spiders); ambushers are
 235 spiders that sit and wait for their preys to reach closer, some individuals can mimicry
 236 flower colors, hiding and waiting for pollinizer insects (e.g. Thomisidae family, crab
 237 spiders); stalker spiders are active predators that pursue and assault their preys, for
 238 example, jumping on them (e.g. Salticidae family, jumping spiders).

239
 240 **Table 1:** Description of the binary morphological traits selected for plants and binary foraging traits
 241 selected for spiders. For complete classifications see supplementary material (Suppl. 1 and 2).

Group	Trait (acronym)	Definition
Plants	Erect herb (EH)	Plants without aboveground lignified structures, usually branched, with average height <50cm
	Prostrate herb (PH)	Non-woody plant, with aboveground structures close to the ground
	Rosette herb (RH)	Non-woody plant, with aboveground structures (excluding inflorescences) organized in a basal rosette prostrate leaves (includes species of <i>Eryngium</i> (Apiaceae) without rigid leaves)

Rigid rosette (RR)	Non-woody plant, with aboveground structures (excluding inflorescences) organized in a basal rosette with rigid leaves (like some species of <i>Eryngium</i> (Apiaceae) and Bromeliaceae)
Voluble herb (VH)	Plants without aboveground lignified structures that use other plants as physical support
Shrub (SH)	Plants with aboveground lignified structures, at least at the base, usually strongly branched, with average height >50cm
Caespitose grass (CG)	Grass or grass-like plant, grows preferentially vertically, few or none lateral shoots, does not form dense tufts
Tussock grass (TG)	Plant with grass like leaves, growing in dense tufts by the production of many short lateral shoots, often with accumulation of dead leaves at the basis
Prostrate grass (PG)	Grass or grass-like plant, with vertical spreading by rhizome or stolones, low height, produces many long lateral shoots
Spiders Runners (ruhu)	Spiders that hunt moving actively towards their prey (Lycosidae, Anyphaenidae and Gnaphosidae).
Ambushers (amhu)	Spiders that hunt ambushing their prey (Thomisidae, Sparassidae, Pisauridae, Philodromidae, Corinnidae, Trachelidae and Phrurolithidae)
Stalkers (sthu)	Spiders that hunt like stalkers (Salticidae and Oxyopidae)
Orbicular web-builders (orwe)	Spiders that build orbicular webs (Araneidae, Tetragnathidae, and Mysmeniidae)
Three-dimensional web-builders (tdwe)	Spiders that build three-dimensional webs (Pholcidae, and Theridiidae)
Sheet web-builders (shwe)	Spiders that build sheet webs (Linyphiidae, and Hahniidae)

242

243

2.3. Statistical analysis

244

245

246

247

248

249

250

251

Functional diversity (FD) was partitioned into alpha, beta and gamma by the multiplicative method ($\beta = \gamma / \alpha$), with alpha and gamma diversities based on the Rao index (de Bello et al., 2010). Local scale functional diversity (alpha) was calculated for each plot (i.e., by pooling plant cover from the 10 sampling units and spider abundance of the five segments). Functional gamma diversity was calculated for each grid (i.e., pooling the nine plots of each grid). Functional beta diversity was calculated comparing the nine plots of each grid.

252

253

254

255

256

257

258

259

260

The Rao diversity index can be defined as a measure of expected dissimilarity between randomly selected species (Ricotta & Szeidl, 2009). It takes into account the species' relative abundances and the pairwise species dissimilarities, on the basis of taxonomic identity, traits or phylogeny. At the alpha scale, Rao index is calculated as the sum of the functional dissimilarity between all possible pairs of species, weighted by the product of species relative abundances (proportional coverage of each plant or proportional abundance of each spider) (de Bello et al., 2010). As dissimilarity measure, we used the adapted version of the Gower index to binary data, available in the "vegdist" function of the "vegan" package in R (Oksanen et al., 2012).

261

262

263

264

265

266

267

To calculate functional gamma diversity, using the Rao index, we need to pool local communities (alpha units) together. One simple approach is to consider average species coverage/abundance in the alpha units as representative of the gamma scale. However, when alpha units do not have the same number of individuals, diversity partition may return misleading values (Villéger & Mouillot, 2008). To solve this, we applied a weighting factor to the average local species coverage/abundance (see de Bello et al. 2010 for further details and Suppl. 3).

268 Functional beta diversity is obtained by the classic formula of multiplicative
269 partitioning: $\beta = \gamma / \alpha$. However, it is important to point that even with
270 standardization and weighting in alpha and gamma scales, diversity partitioning may
271 return lower beta diversity values than expected (de Bello et al., 2009). This problem is
272 solved by applying a correction based on equivalent numbers (Jost, 2007), which is
273 based on the true diversity, or the number of equivalent elements within a community
274 needed to produce the given diversity value (i.e. species richness). Finally, based on
275 Josts' corrected beta diversity values, proportional beta diversity was derived,
276 representing the proportion of diversity that differs between communities. All
277 procedures described here, needed to properly partition diversity into meaningful
278 alpha, beta and gamma fractions, were implemented by de Bello *et al.* (2010) in the
279 function "Rao" on the R platform.

280 After calculating alpha, beta and gamma FDs to plant and spider communities we
281 applied linear models to verify the relationship among the pairs from the same
282 diversity scale. To test for our second hypothesis about the richness influence on FD,
283 we added species richness of plants and spiders to the models in the scales alpha and
284 gamma.

285 We looked for traits of plants that better explained the patterns of spider
286 functional alpha, beta and gamma diversities. We performed forward selection
287 procedures (Blanchet, Legendre, & Borcard, 2008) testing all plant functional types as
288 predictive variables of spider FD in the different scales. Forward selection adds
289 predictive variables to the model until one of the two stop criteria is reached:
290 minimum p-value or maximum R^2 . Minimum p-value adopted for all procedures was
291 0.05 and the maximum R^2 must corresponds to the R^2 of the global model (i.e. model
292 including all predictive variables), this way, forward selection avoids that a subset of
293 selected variables will have higher R^2 than the full model (inflation effect). The R^2
294 threshold applied to the model explaining spiders alpha diversity was 0.17, beta
295 diversity 0.75 and gamma diversity 0.006.

296 In the variable selection, spider functional diversity in the different scales were
297 used as response variables and plant functional composition (or community weighted
298 mean trait – CWM trait, sensu Lavorel *et al.* 2008) as predictive variables. Functional
299 composition is calculated with two matrices: species described by functional traits and
300 communities described by species coverage. At the gamma and beta scales we used as
301 community data the average plant species cover for each grid, at the alpha scale the
302 average plant species cover for each plot. Here, as we used only binary traits, the
303 resultant CWM matrix contains the abundance of each individual class in each grid or
304 plot. CWM matrix were calculate with help of "functcomp" function of "FD" package in
305 R (Laliberté, Legendre, & Shipley, 2014) and forward selection was made with function
306 "forward.sel" implemented in "adespatial" R package (Dray et al., 2017).

307 We calculated CWM traits for spiders to explore further relationships between
308 plants CWM traits and spiders CWM traits using co-inertia analysis (COIA) (Dray,
309 Chessel, & Thioulouse, 2003). COIA analysis reduces CWM traits dimensionality by
310 performing PCA ordination for each CWM matrix. We extracted the first two axes of
311 each PCA, the two ordination spaces formed by those axes were routed until maximum
312 correlation is reached, generating new axis. The significance of this correlation was
313 tested by 1000 permutations. Finally, we performed Pearson pairwise correlations to
314 test for CWM traits relationship.

315

316 3. Results

317

318

319

320

321

322

323

324

325

326

327

328

329

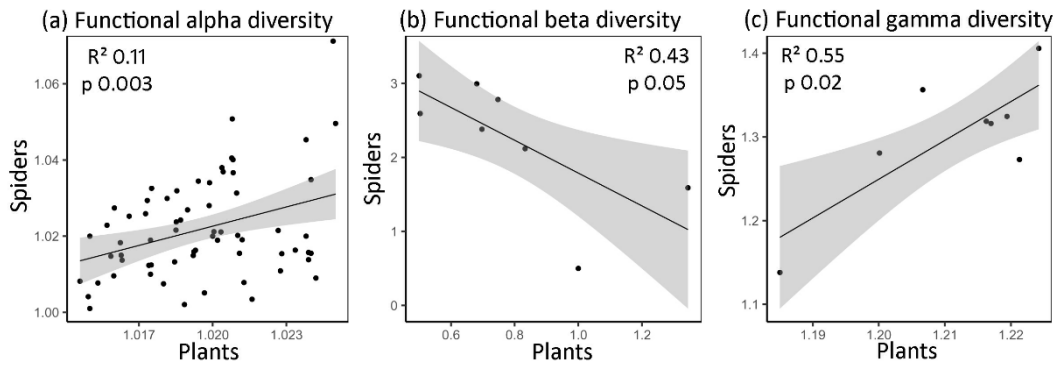
330

331

332

A total of 203 species or morphospecies of spiders were recognized. The most abundant functional guild was sheet web-builders, with 45% of the total abundance, followed by three-dimensional web-builders (22%) and stalker hunters (18%). As to the vegetation, 647 species of plants were identified. The most abundant plant life form, as expected for grasslands, were the caespitose, prostrate and tussock grasses, representing, respectively, 32%, 22% and 17% of total vegetation cover.

We found a significant relationship between plant and spider FD at the three scales of diversity: alpha, beta and gamma (Fig. 2). For alpha and gamma, FD of spiders and plants were positively related, i.e. when plant alpha diversity increased, spider alpha diversity increased as well. Beta diversity, on the other hand, showed the opposite pattern, with spider beta diversity decreasing with the increase in beta plant diversity (Fig. 2b). Spider species richness had a significant influence over spider alpha FD (Tab. 2), but we did not observe a significant relationship between spider species richness and FD at the gamma scale (results not shown).



333

334

335

336

Figure 2: Linear models relating functional alpha, gamma and beta functional diversities among spiders and plants.

337

338

339

Table 2: Linear model with spider alpha functional diversity (FD) as dependent variable and plant alpha FD, plant richness and spider richness as explanatory variables. The complete model had R^2 0.34 and $p < 0.01$. Confidence interval accepted as significant is $p < 0.05$.

	Estimate	Std. Error	p
Plant alpha FD	2.3720	0.6247	0.0003
Plant richness	-0.0001	0.0001	0.5286
Spider richness	0.0011	0.0002	<0.0001
Intercept	-1.4040	0.6326	0.0301

340

341

342

343

344

345

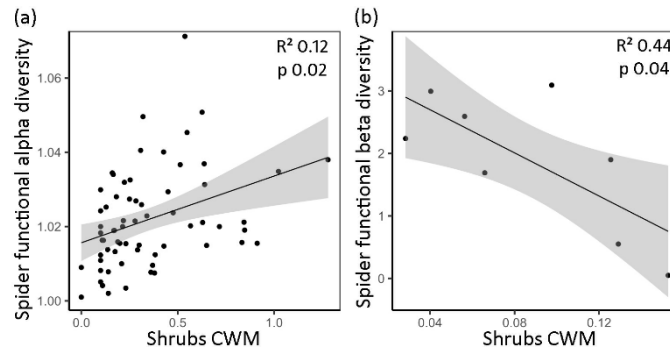
346

347

348

349

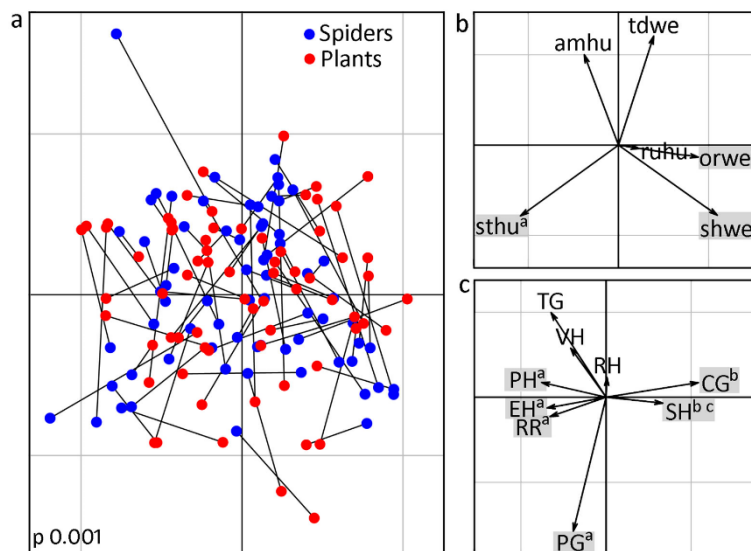
Forward selection of plant CWM traits selected shrubs as significantly correlated to spider alpha and beta FD patterns (Fig. 3). Shrubs presented a positive, but weak correlation with spider functional alpha diversity (i.e. when shrubs are proportionally more abundant in the community, spider functional alpha diversity increase) (Fig. 3a). In contrast, the correlation was negative with spider beta diversity (Fig. 3b): the higher the proportional abundance of shrubs in the landscape, the lesser the spider functional beta diversity. No plant CWM traits significantly explained spider functional gamma diversity.



350
351
352
353
354
355
356
357
358
359
360
361

Figure 3: Relationship of shrubs coverage and spider functional alpha and beta diversities. Shrub was the functional group selected through forward selection as the variable that better explained patterns of functional alpha and beta diversities of spiders.

In fact, shrub was the only functional group that showed significant positive correlations with more than one spider functional guild (i.e. positive relationship with orbicular-web r^2 0.39 and sheet-web r^2 0.2), as illustrated in the coinertia analysis (Fig. 4). Positive correlations were also found between sheet web spiders and caespitose grasses, and between stalker hunter spiders and herbs (prostrate and erect), prostrate grasses and rigid/spiny rosettes.



362
363
364
365
366
367
368
369
370
371
372

Figure 4: Coinertia analysis showing (a) position of sampling units described by plant CWM traits (red dots) and spider CWM traits (blue dots) in an ordination space. Distance among pairwise sampling units (lines connecting dots) represent how far they are from each other in the routed ordinations. Rotation of the two CWM matrices resulted in a significant relationship (p 0.001). (b) PCA ordination for spiders CWM trait matrix, axis represent $x = 37.9\%$ and $y = 22.8\%$ of data variation. (c) PCA ordination for plant CWM trait matrix, axis represent $x = 23.2\%$ and $y = 21.1\%$ of data variation. Functional traits with significant and higher pairwise correlation ($p < 0.05$ and $r^2 > 0.2$) are highlighted (grey boxes) and indicated by same letters. All pairwise correlations between CWM traits are presented in supplementary material (Suppl. 4).

4. Discussion

373
374
375
376
377

Here we investigated plant and spider FD relationships in their alpha, beta and gamma components in mesic grasslands under traditional management in South Brazil. Especially based on the habitat heterogeneity principles (Tews et al., 2004), we had

378 hypothesized that (i) FD of plants and spiders would be positively related at the three
379 scales, alpha, beta and gamma, and that (ii) the size of the species pool (species
380 richness) would constrain alpha diversities, while gamma diversities would be free to
381 vary independently due to the larger species pool. We also hypothesized that (iii) plant
382 functional types responsible for providing vertical structure and good habitat
383 conditions to spiders, as tussock grasses and rigid rosettes, would be correlated to
384 spider FD at the three scales. Our general results confirmed the habitat heterogeneity
385 theory, even though with some unexpected results of different signs of the
386 relationship between spider and plant FD at different spatial scales.

387

388 *Functional diversity at alpha and gamma scales*

389

390 The habitat heterogeneity hypothesis predicts that changes in habitat structural
391 characteristics will diversify niches, and that this will increase species diversity. The
392 majority of research testing this theory found positive relationships among habitat
393 features measured and biodiversity metrics tested (richness, diversity) (Tews et al.,
394 2004). Here, we observed that when plant FD is higher, spider FD increases. This
395 relationship was significant for the levels alpha and gamma, although much weaker at
396 the alpha level (R^2 0.11) than at the gamma level (R^2 0.55).

397

398 For animal species, habitat characteristics are often determined by the plant
399 community. Thereby, plant species richness, vegetation composition and habitat
400 diversity explain community structure and diversity of many arthropods (S. Liu et al.,
401 2015; Schaffers, Raemakers, Sýkora, & ter Braak, 2008; Schirmel et al., 2016). In the
402 case of spiders, properties of the physical vegetation structure seem especially
403 important, as they are decisive for the potential to anchor webs. Additionally, it is
404 important to recognize that within the 'habitat heterogeneity' concept we should not
405 consider only providing of shelter by vegetation, but also indirect effects. For instance,
406 the diversity of preys (Finke & Denno, 2002) is important for spiders since they are
407 predators.

407

408 *Alpha diversity dependent, not only, of the specie pool*

409

410 In the Campos Sulinos, spider functional alpha diversity was positively related to
411 plant functional alpha diversity, as discussed above, and to spider species pool. This
412 means that, at the local scale, adding new species to the pool will significantly increase
413 FD. Cadotte *et al.* (2011) claimed that we still have not fully understood how FD and
414 species pool (richness) interact: indeed, minimal changes in species pool can cause
415 both high or low changes in FD. Indeed, species richness and FD are not independent
416 (Díaz & Cabido, 2001), and some other studies have already indicated a positive
417 relationship among them (Bihn, Gebauer, & Brandl, 2010).

418

419 Here we call attention to how the species pool size had different importance to
420 FD according to the spatial scale addressed: it was important only at the local scale.
421 However, despite the significant relationship found here, species richness should not
422 be always considered an adequate surrogate for functional richness or diversity (Díaz &
423 Cabido, 2001). This is especially so because species richness and FD relationship might
424 be an effect of the number of traits used to calculate FD (Dalerum, Cameron, Kunkel, &
Somers, 2012; Petchey & Gaston, 2002). In our study case, though, the comparison

425 between scales should be valid as the same number of traits were used at both spatial
426 scales.

427

428 *Functional beta diversity and shrubs influence*

429

430 We observed that areas with higher plant functional beta diversity presented
431 lower spider functional beta diversity. Further analyses revealed that this is principally
432 related to the proportional abundance of shrubs. The increase in proportional
433 abundance of shrubs allowed that two functional guilds of spiders (orbicular-web and
434 sheet-web builders) increased their proportional abundance too. The increase in cover
435 of other plant functional types, like prostrate or erect herbs, prostrate grasses and rigid
436 rosettes, in contrast, only favoured one functional guild of spider: stalker hunters (Fig.
437 4). As shrubs increased the proportional abundance of two spider functional guilds,
438 while several other grassland vegetation types favours only one spider guild, we
439 assumed that two possible situations might be occurring to explain the extreme
440 opposites of the observed beta diversity patterns:

441 *(a) High grazing pressure:* The establishment and frequency of shrubs in grassland
442 landscapes can be highly correlated with the grassland management. For example,
443 heavily grazed grasslands tend to have low abundance and richness of shrubs (Lezama
444 et al., 2014), and, in general, vegetation is rather homogenous, dominated by
445 prostrate grasses, prostrate herbs and rosettes (Fedrigo et al., 2017). As shrubs
446 positively influence spider alpha diversity, with lower shrubs proportional abundance
447 mostly sites will have lower alpha diversity of spiders. In this case, with higher grazing
448 pressure and consequently lower shrubs abundance, the remaining shrubs would act
449 as habitat 'islands' for spiders (R. Liu, Pen-Mouratov, & Steinberger, 2016). This way,
450 the low abundance of shrubs generates a scatter matrix of favourable habitats,
451 promoting higher beta diversity of spiders through species loss from richer sites to
452 poorer ones.

453 *(b) Low grazing pressure:* In areas where shrubs are proportionally more abundant,
454 due to less intensive grassland management, the vegetation matrix would be more
455 favourable for the maintenance of high levels of spider functional alpha diversity. With
456 spider alpha diversity stabilized in higher levels we did not observed considerable
457 variation in spider FD between plots (i.e. low spider beta diversity). Also, arthropods
458 communities associated to shrubs are highly influenced by the surrounding habitat
459 (Lanta, Norrdahl, Gilbert, Söderman, & Rinne, 2018). So, this pattern of high overall
460 alpha diversity might be related not only to shrubs itself, but indirectly to the entire
461 surrounding with good habitat conditions for spiders.

462 Shrubs are highly correlated to arthropod diversity, especially if the surrounding
463 habitat is rather homogenous (R. Liu et al., 2016). In the Campos Sulinos, shrubs have
464 previously been shown to be positively related to spider alpha and beta diversities, and
465 this relationship can be due to the vertical structure provided by them (Gomez et al.,
466 2016). However, the most abundant sheet-web spider genus found in Campos Sulinos,
467 *Meioneta* sp. (Linyphiidae family), is known to build webs near the ground, which
468 would require a less complex vegetation stratum. This indicates that the most
469 important feature provided by shrubs might not be the vertical structure, but a
470 canopy, that means protection against light and also predators (Hassall & Tuck, 2007;
471 Podgaiski et al., 2013). Also, shrubs in the Campos Sulinos are mostly from Asteraceae

472 family, from genus *Braccharis* sp., which are very attractive for pollinating insects
473 (Oleques, Overbeck, & de Avila, 2017), which are potential prey for spiders.

474 Similar to previous studies, we found specific relationships between specific
475 plant life forms and spider functional diversities (Podgaiski et al., 2013), but our
476 analyses clearly reveal the important role of shrubs that we can thus consider to be
477 indicators for good habitat conditions for spiders. However, from a production
478 perspective, shrubs are not generally seen as beneficial in grasslands. Woody plant
479 expansion over grasslands, or shrub encroachment, is a growing concern among
480 grassland managers (Archer et al., 2017; Bond & Parr, 2010). Since shrubs are of little
481 interest for cattle grazing, ranchers developed management techniques to mechanic or
482 chemical removal of shrubs, also called brush management (Archer et al., 2017;
483 Fulbright, Davies, & Archer, 2018). Shrubs removal intends to improve grasses biomass
484 productivity and grassland habitat quality by reducing competition and shadow.
485 However, as highlighted by Fulbright *et al.* (2018), habitat quality is a species specific
486 concept. Just as we found shrubs to be an important feature for spider habitats in the
487 Campos Sulinos, their removal can improve habitat for north American birds
488 community (Reinkensmeyer, Miller, Anthony, & Marr, 2007) and benefit other
489 arthropods communities in the Patagonian scrublands (Sola, Peri, Huertas, Martínez
490 Pastur, & Lencinas, 2016).

491 Our results do not allow us to infer about the exact mechanisms of the
492 interactions. Shrubs can provide several resources for spiders, as shelter and vertical
493 structure for webs, but also indirectly for providing shelter and resources for other
494 invertebrates that then will be prey of spiders. Although the keystone concept (Tews *et al.*
495 2004) was first described referring to features that benefit several species groups, it
496 has already been used in reference to characteristics that promote single group's
497 diversity (Parmain & Bouget, 2018). As spiders are generalist predators that occupy
498 different positions in the trophic cascade (Sanders, Vogel, & Knop, 2015), features that
499 influence their diversity will probably influence other groups. Therefore, the concept of
500 shrubs as keystone features in grasslands applies and can probably be extended to
501 other groups, which deserves further attention by research.

502 Spiders are predators that feed on other smaller arthropods, including those
503 considered as agriculture pests, providing an essential service of biological control
504 (Bianchi et al., 2010; Perović et al., 2017). The wide conversion of natural grasslands
505 into extensive croplands may be depleting this ecosystem service. Conserved areas in
506 mosaics with croplands can harbor great arthropods richness and diversity (Schirmel et
507 al., 2016), which contribute to improving the biological control of pests and promote
508 connections, as corridors, in highly converted, fragmented landscapes.

509 Here, we were able to observe the relationship among shrubs and spider FD only
510 by exploring functional diversity patterns of plants and spiders at different scales.
511 Functional beta diversity could detect an interesting relationship of the functional
512 diversity of spiders with shrubs, which very much improved our understanding about
513 the ecological interactions that occur in Campos Sulinos grasslands. Further studies on
514 spider/plant interactions in the Campos Sulinos should focus on deepening our
515 knowledge about how shrub structure influences spider communities. Also, different
516 brush management technics (chemical or mechanic) seems to have different impact in
517 plant associated communities (Fulbright et al., 2018), which needs to be better

518 understood in order to inform managers about ways to manage grassland that also
519 protect arthropod diversity and its benefits.

520

521 **References**

522

- 523 Allan, E., Bossdorf, O., Dormann, C. F., Prati, D., Gossner, M. M., Tschardtke, T., ... Fischer, M. (2014).
524 Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the*
525 *National Academy of Sciences*, *111*(1), 308–313.
- 526 Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., ... Swenson, N. G.
527 (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist.
528 *Ecology Letters*, *14*(1), 19–28.
- 529 Andrade, B. O., Koch, C., Boldrini, I. I., Vélez-Martin, E., Hasenack, H., Hermann, J. M., ... Overbeck, G. E.
530 (2015). Grassland degradation and restoration: A conceptual framework of stages and thresholds
531 illustrated by southern Brazilian grasslands. *Natureza E Conservacao*, *13*(2), 95–104.
- 532 Archer, S. R., Andersen, E. M., Predick, K. I., Schwinning, S., Steidll, R. J., & Woods, S. R. (2017). Woody
533 Plant Encroachment: Causes and Consequences. In D. D. Briske (Ed.), *Rangeland Systems,*
534 *processes, Management and challenges* (pp. 25–84). New York: Springer.
- 535 Bianchi, F. J. J. A., Schellhorn, N. A., Buckley, Y. M., & Possingham, H. P. (2010). Spatial variability in
536 ecosystem services: Simple rules for predator-mediated pest suppression. *Ecological Applications*,
537 *20*(8), 2322–2333.
- 538 Bihn, J. H., Gebauer, G., & Brandl, R. (2010). Loss of functional diversity of ant assemblages in secondary
539 tropical forests. *Ecology*, *91*(3), 782–792. doi:doi:10.1890/08-1276.1
- 540 Blanchet, F. G., Legendre, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology*,
541 *89*(9), 2623–2632.
- 542 Bond, W. J., & Parr, C. L. (2010). Beyond the forest edge: Ecology, diversity and conservation of the
543 grassy biomes. *Biological Conservation*, *143*(10), 2395–2404.
- 544 Cadotte, M. W., Carscadden, K., & Mirotnick, N. (2011). Beyond species: Functional diversity and the
545 maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*(5), 1079–1087.
- 546 Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global patterns of guild composition and
547 functional diversity of spiders. *PLoS ONE*, *6*(6).
- 548 Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2016). Traits Without Borders: Integrating
549 Functional Diversity Across Scales. *Trends in Ecology and Evolution*, *31*(5), 382–394.
- 550 Carvalho, P. C. de F., & Batello, C. (2009). Access to land, livestock production and ecosystem
551 conservation in the Brazilian Campos biome: The natural grasslands dilemma. *Livestock Science*,
552 *120*(1–2), 158–162.
- 553 Classen, A., Peters, M. K., Ferger, S. W., Helbig-Bonitz, M., Schmack, J. M., Maassen, G., ... Steffan-
554 Dewenter, I. (2014). Complementary ecosystem services provided by pest predators and
555 pollinators increase quantity and quality of coffee yields. *Proceedings of the Royal Society B:*
556 *Biological Sciences*, *281*, 20133148.
- 557 Dalerum, F., Cameron, E. Z., Kunkel, K., & Somers, M. J. (2012). Interactive effects of species richness
558 and species traits on functional diversity and redundancy. *Theoretical Ecology*, *5*(1), 129–139.
- 559 de Bello, F., Lavergne, S., Meynard, C. N., Lepš, J., & Thuiller, W. (2010). The partitioning of diversity:
560 Showing Theseus a way out of the labyrinth. *Journal of Vegetation Science*, *21*(5), 992–1000.
- 561 de Bello, F., Thuiller, W., Lepš, J., Choler, P., Clément, J.-C., Macek, P., ... Lavorel, S. (2009). Partitioning of
562 functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of*
563 *Vegetation Science*, *20*(3), 475–486.
- 564 Dias, S. C., Carvalho, L. S., Bonaldo, A. B., & Brescovit, A. D. (2010). Refining the establishment of guilds
565 in Neotropical spiders (Arachnida: Araneae). *Journal of Natural History*, *44*(3–4), 219–239.
- 566 Diaz, S., & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change.
567 *Journal of Vegetation Science*, *8*, 463–474.
- 568 Díaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem
569 processes. *Trends in Ecology & Evolution*, *16*(11), 646–655.
- 570 Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Larocque, G., ... Wagner, H. H. (2017).
571 adespatal: Multivariate Multiscale Spatial Analysis. *R Package Version 0.0-8, R package*.
- 572 Dray, S., Chessel, D., & Thioulouse, J. (2003). Co-Inertia Analysis and the Linking of Ecological Data
573 Tables. *Ecology*, *84*(11), 3078–3089.

574 Fedrigo, J. K., Ataíde, P. F., Filho, J. A., Oliveira, L. V., Jaurena, M., Laca, E. A., ... Nabinger, C. (2017).
575 Temporary grazing exclusion promotes rapid recovery of species richness and productivity in a
576 long-term overgrazed Campos grassland. *Restoration Ecology*, 1–9.

577 Finke, D. L., & Denno, R. F. (2002). Intraguild predation diminished in complex-structured vegetation:
578 Implications for prey suppression. *Ecology*, 83(3), 643–652.

579 Fulbright, T. E., Davies, K. W., & Archer, S. R. (2018). Wildlife Responses to Brush Management: A
580 Contemporary Evaluation. *Rangeland Ecology and Management*, 71(1), 35–44.

581 Gomez, J. E., Lohmiller, J., & Joern, A. (2016). Importance of vegetation structure to the assembly of an
582 aerial web-building spider community in North American open grassland. *Journal of Arachnology*,
583 44(1), 28–35.

584 Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein, F., Boch, S., Prati, D., ... Allan, E. (2016). Land-use
585 intensification causes multitrophic homogenization of grassland communities. *Nature*, 540(7632),
586 266–269.

587 Hassall, M., & Tuck, J. M. (2007). Sheltering behavior of terrestrial isopods in grasslands. *Invertebrate*
588 *Biology*, 126(1), 46–56.

589 Joern, A., & Laws, A. N. (2013). Ecological Mechanisms Underlying Arthropod Species Diversity in
590 Grasslands. *Annual Review of Entomology*, 58(1), 19–36.

591 Jonas, J. L., & Joern, A. (2007). Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison
592 grazing and weather in North American tallgrass prairie: A long-term study. *Oecologia*, 153(3),
593 699–711.

594 Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88(10),
595 2427–2439.

596 Laliberté, A. E., Legendre, P., & Shipley, B. (2014). FD: measuring functional diversity from multiple traits,
597 and other tools for functional ecology. *R Package Version 1.0-12*, R package.

598 Lanta, V., Norrdahl, K., Gilbert, S., Söderman, G., & Rinne, V. (2018). Biotic filtering and mass effects in
599 small shrub patches: is arthropod community structure predictable based on the quality of the
600 vegetation? *Ecological Entomology*, 43(2), 234–244.

601 Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrough, J., ... Bonis, A. (2008).
602 Assessing functional diversity in the field - Methodology matters! *Functional Ecology*, 22(1), 134–
603 147.

604 Leidinger, J. L. G., Gossner, M. M., Weisser, W. W., Koch, C., Cayllahua, Z. L. R., Podgaiski, L. R., ... Meyer,
605 S. T. (2017). Historical and recent land use affects ecosystem functions in subtropical grasslands in
606 Brazil. *Ecosphere*, 8(12), e02032.

607 Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, E. J., & Paruelo, J. M. (2014). Variation of grazing-
608 induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation*
609 *Science*, 25(1), 8–21.

610 Liu, R., Pen-Mouratov, S., & Steinberger, Y. (2016). Shrub cover expressed as an “arthropod island” in
611 xeric environments. *Arthropod-Plant Interactions*, 10(5), 393–402.

612 Liu, S., Chen, J., Gan, W., Schaefer, D., Gan, J., & Yang, X. (2015). Spider foraging strategy affects trophic
613 cascades under natural and drought conditions. *Scientific Reports*, 5, 1–9. doi:10.1038/srep12396

614 Londo, G. (1976). The decimal scale for relevés of permanent quadrats. *Vegetatio*, 33(1), 61–64.

615 Magnusson, W. E., Lima, A. P., Luizão, R., Luizão, F., Costa, F. R. C., Castilho, C. V. de, & Kinupp, V. F.
616 (2005). RAPELD: a modification of the Gentry method for biodiversity surveys in long-term
617 ecological research sites. *Biota Neotropica*, 5(2), 21–26.

618 Morris, M. G. (2000). The effects of structure and its dynamics on the ecology and conservation of
619 arthropods in British grasslands. *Biological Conservation*, 95(2), 129–142.

620 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O’Hara, R. B., Simpson, G. L., ... Wagner, H. (2012).
621 vegan: Community Ecology Package. *R Package Version*. Retrieved from [http://cran.r-](http://cran.r-project.org/package=vegan)
622 [project.org/package=vegan](http://cran.r-project.org/package=vegan)

623 Oleques, S. S., Overbeck, G. E., & de Avila, R. S. (2017). Flowering phenology and plant-pollinator
624 interactions in a grassland community of Southern Brazil. *Flora*, 229, 141–146.

625 Overbeck, G. E., Müller, S. C., Fidelis, A., Pfadenhauer, J., Pillar, V. D., Blanco, C., ... Forneck, E. (2007).
626 Brazil’s neglected biome: The South Brazilian Campos. *Perspectives in Plant Ecology Evolution and*
627 *Systematics*, 9(2), 101–116.

628 Parmain, G., & Bouget, C. (2018). Large solitary oaks as keystone structures for saproxylic beetles in
629 European agricultural landscapes. *Insect Conservation and Diversity*, 11(1), 100–115.

630 Perkins, M. J., Inger, R., Bearhop, S., & Sanders, D. (2018). Multichannel feeding by spider functional

- 631 groups is driven by feeding strategies and resource availability. *Oikos*, 127(1), 23–33.
- 632 Perović, D. J., Gámez-Virués, S., Landis, D. A., Wäckers, F., Gurr, G. M., Wratten, S. D., ... Desneux, N.
- 633 (2017). Managing biological control services through multi-trophic trait interactions: Review and
- 634 guidelines for implementation at local and landscape scales. *Biological Reviews*, 93, 306–321.
- 635 Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community
- 636 composition. *Ecology Letters*, 5(3), 402–411.
- 637 Petchey, O. L., O’Gorman, E. J., & Flynn, D. F. B. (2009). A functional guide to functional diversity
- 638 measures. In S. Naeem, D. E. Bunker, A. Hector, M. Loreau, & C. Perrings (Eds.), *Biodiversity,*
- 639 *Ecosystem Functioning and Human Wellbeing: An Ecological and Economic Perspective* (pp. 49–
- 640 60). Oxford: Oxford University Press.
- 641 Podgaiski, L. R., Joner, F., Lavorel, S., Moretti, M., Ibanez, S., Mendonça, M. D. S., & Pillar, V. D. (2013).
- 642 Spider Trait Assembly Patterns and Resilience under Fire-Induced Vegetation Change in South
- 643 Brazilian Grasslands. *PLoS ONE*, 8(3).
- 644 Reinkensmeyer, D. P., Miller, R. F., Anthony, R. G., & Marr, V. E. (2007). Avian community structure
- 645 along a mountain big sagebrush successional gradient. *Journal of Wildlife Management*, 71(4),
- 646 1057–1066.
- 647 Ricotta, C., & Szeidl, L. (2009). Diversity partitioning of Rao’s quadratic entropy. *Theoretical Population*
- 648 *Biology*, 76(4), 299–302.
- 649 Rouabah, A., Villerd, J., Amiaud, B., Plantureux, S., & Lasserre-Joulin, F. (2015). Response of carabid
- 650 beetles diversity and size distribution to the vegetation structure within differently managed field
- 651 margins. *Agriculture, Ecosystems and Environment*, 200, 21–32.
- 652 Sanders, D., Vogel, E., & Knop, E. (2015). Individual and species-specific traits explain niche size and
- 653 functional role in spiders as generalist predators. *Journal of Animal Ecology*, 84(1), 134–142.
- 654 Schaffers, A. P., Raemakers, I. P., Sýkora, K. V., & ter Braak, C. J. F. (2008). Arthropod assemblages are
- 655 best predicted by plant species composition. *Ecology*, 89(3), 782–794.
- 656 Schirmel, J., Thiele, J., Entling, M. H., & Buchholz, S. (2016). Trait composition and functional diversity of
- 657 spiders and carabids in linear landscape elements. *Agriculture, Ecosystems and Environment*, 235,
- 658 318–328.
- 659 Sola, F. J., Peri, P. L., Huertas, L., Martínez Pastur, G. J., & Lencinas, M. V. (2016). Above-ground
- 660 arthropod community structure and influence of structural-retention management in southern
- 661 Patagonian scrublands, Argentina. *Journal of Insect Conservation*, 20(6), 929–944.
- 662 Staude, I. R., Vélez-Martin, E., Andrade, B. O., Podgaiski, L. R., Boldrini, I. I., Mendonça, M., ... Overbeck,
- 663 G. E. (2018). Local biodiversity erosion in South Brazilian grasslands under moderate levels of
- 664 landscape habitat loss. *Journal of Applied Ecology*, 55(3), 1241–1251.
- 665 Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004).
- 666 Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone
- 667 structures. *Journal of Biogeography*, 31(1), 79–92.
- 668 Uetz, G. W., Halaj, J., & Cady, A. B. (1999). Guild Structure of Spiders in Major Crops. *The Journal of*
- 669 *Arachnology*, 27(1991), 270–280.
- 670 Villéger, S., & Mouillot, D. (2008). Additive partitioning of diversity including species differences: A
- 671 comment on Hardy & Senterre (2007). *Journal of Ecology*, 96(5), 845–848.
- 672 Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the
- 673 concept of trait be functional! *Oikos*, 116(5), 882–892.
- 674 Williams, N. M., Ward, K. L., Pope, N., Isaacs, R., Wilson, J., May, E. A., ... Peters, J. (2015). Native
- 675 wildflower plantings support wild bee abundance and diversity in agricultural landscapes across
- 676 the United States. *Ecological Applications*, 25(8), 2119–2131.
- 677 Wise, D. H. (2006). Cannibalism, Food Limitation, Intraspecific Competition, and the Regulation of Spider
- 678 Populations. *Annual Review of Entomology*, 51(1), 441–465.
- 679 World Spider Catalog. (2018). World Spider Catalog version 19.0. Retrieved from <http://wsc.nmbe.ch>
- 680

681 Biosketch

- 682 L.S.M. is interested in grassland ecology, diversity patterns and functional ecology,
- 683 K.S.M. works with spider functional ecology and species distribution, L.R.P. is
- 684 interested in arthropod diversity patterns, functional ecology and interactions, G.E.O.
- 685 works with grassland ecology, restoration, functional and taxonomic diversities.

686 **Supplementary material**

687

688 **Supplement 1:** Spider classification into foraging guilds, all morphospecies within the same family
 689 received the same foraging guild classification. Foraging guild categories are: runner hunter (ruhu),
 690 ambush hunters (amhu), stalker hunters (sthu), orbicular web-builders (orwe), three-dimensional web-
 691 builders (tdwe) and sheet web-builders (shwe). Also showing the number of morphospecies in each
 692 family and the family abundance (all sampling sites added up).

Family	Foraging guild	Morphospecies richness	Total abundance
Anyphaenidae	ruhu	50	63
Araneidae	orwe	79	94
Corinnidae	amhu	29	34
Gnaphosidae	ruhu	4	5
Hahniidae	shwe	38	59
Linyphiidae	shwe	588	1239
Lycosidae	ruhu	28	29
Mysmenidae	orwe	5	5
Oxyopidae	sthu	130	292
Philodromidae	amhu	36	46
Pholicidae	tdwe	1	1
Phrurolithidae	amhu	9	10
Pisauridae	amhu	2	2
Salticidae	sthu	183	237
Sparassidae	amhu	1	1
Tetragnathidae	orwe	5	5
Theridiidae	tdwe	313	632
Thomisidae	amhu	63	80
Trachelidae	amhu	24	27

693

694 **Supplement 2:** Plants classification into aboveground structural forms: Erect herb (EH), prostrate
 695 herb (PH), rosette herb (RH), rigid rosette (RR), voluble herb (VH), shrub (SH), caespitose grass
 696 (CG), tussock grass (TG) and prostrate grass (PG).

Family/Species	Life forms									
	EH	PH	RH	RR	VH	SH	CG	TG	PG	
Acanthaceae										
<i>Dyschoriste humilis</i> Lindau	1									
<i>Justicia axillaris</i> (Nees) Lindau	1									
<i>Ruellia brevicaulis</i> (Nees) Lindau	1									
<i>Ruellia bulbifera</i> Lindau	1									
<i>Ruellia geminiflora</i> Kunth	1									
<i>Ruellia hypericoides</i> (Nees) Lindau	1									
<i>Ruellia morongii</i> Britton			1							
<i>Stenandrium dulce</i> (Cav.) Nees			1							
Amaranthaceae										
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	1									
<i>Gomphrena perennis</i> L.	1									
<i>Pfaffia gnaphaloides</i> (L.f.) Mart.	1									
<i>Pfaffia tuberosa</i> (Spreng.) Hicken	1									
Amaryllidaceae										
<i>Nothoscordum bivalve</i> (L.) Britton							1			
<i>Nothoscordum bonariense</i> (Pers.) Beauverd							1			
<i>Nothoscordum gaudichaudianum</i> Kunth							1			
<i>Nothoscordum gracile</i> (Aiton) Stearn							1			
<i>Nothoscordum montevidense</i> Beauverd							1			
Anacardiaceae										
<i>Schinus lentiscifolius</i> Marchand						1				
<i>Schinus weinmannifolius</i> Engl.						1				
Apiaceae										
<i>Bowlesia incana</i> Ruiz & Pav.			1							
<i>Centella asiatica</i> (L.) Urb.		1								
<i>Cyclospermum leptophyllum</i> (Pers.) Sprague ex Britton & P.Wilson	1									
<i>Eryngium ciliatum</i> Cham. & Schldl.				1						
<i>Eryngium ebracteatum</i> Lam.				1						
<i>Eryngium echinatum</i> Urb.			1							
<i>Eryngium elegans</i> Cham. & Schldl.				1						
<i>Eryngium horridum</i> Malme				1						
<i>Eryngium junceum</i> Cham. & Schldl.				1						
<i>Eryngium nudicaule</i> Lam.			1							
<i>Eryngium sanguisorba</i> Cham. & Schldl.				1						
<i>Lilaeopsis brasiliensis</i> (Glaz.) Affolter		1								
<i>Lilaeopsis carolinensis</i> J.M.Coult. & Rose		1								
Apocynaceae										
<i>Mandevilla coccinea</i> (Hook. & Arn.) Woodson	1									
<i>Oxypetalum crispum</i> Wight ex Hook. & Arn.	1									
<i>Oxypetalum dusenii</i> Malme	1									
<i>Oxypetalum tomentosum</i> Wight ex Hook. & Arn.					1					
Araliaceae										
<i>Hydrocotyle bonariensis</i> Lam.	1									

<i>Dimerostemma arnottii</i> (Baker) M.D.Moraes	1	
<i>Disynaphia spathulata</i> (Hook. & Arn.) R.M.King & H.Rob.		1
<i>Elephantopus mollis</i> Kunth	1	
<i>Erechtites hieracifolius</i> (L.) Raf. ex DC.		1
<i>Facelis retusa</i> (Lam.) Sch.Bip.	1	
<i>Galinsoga parviflora</i> Cav.	1	
<i>Gamochaeta americana</i> (Mill.) Wedd.		1
<i>Gamochaeta argentina</i> Cabrera		1
<i>Gamochaeta coarctata</i> (Willd.) Kerguélen		1
<i>Gamochaeta filaginea</i> (DC.) Cabrera		1
<i>Gamochaeta stachydifolia</i> (Lam.) Cabrera		1
<i>Gamochaeta simplicicaulis</i> (Willd. ex Spreng.) Cabrera		1
<i>Grazielia gaudichaudeana</i> (DC.) R.M.King & H.Rob.	1	
<i>Grazielia intermedia</i> (DC.) R.M.King & H.Rob.	1	
<i>Gyptis crassipes</i> (Hieron.) R.M.King & H.Rob.		1
<i>Gyptis tanacetifolia</i> (Gillies ex Hook. & Arn.) D.J.N.Hind & Flann	1	
<i>Hieracium commersonii</i> Monnier		1
<i>Holocheilus illustris</i> (Vell.) Cabrera		1
<i>Hypochaeris albiflora</i> (Kuntze) Azevêdo-Gonç. & Matzenb.		1
<i>Hypochaeris catharinensis</i> Cabrera		1
<i>Hypochaeris chillensis</i> (Kunth) Britton		1
<i>Hypochaeris glabra</i> L.		1
<i>Hypochaeris lutea</i> (Vell.) Britton		1
<i>Hypochaeris megapotamica</i> Cabrera		1
<i>Hypochaeris neopinnatifida</i> Azevêdo-Gonç. & Matzenb.		1
<i>Hypochaeris tropicalis</i> Cabrera		1
<i>Leptostelma tweediei</i> (Hook. & Arn.) D.J.N.Hind & G.L.Nesom		1
<i>Lessingianthus hypochaeris</i> (DC.) H.Rob.		1
<i>Lessingianthus plantaginodes</i> (Kuntze) H.Rob.	1	
<i>Lessingianthus rubricaulis</i> (Humb. & Bonpl.) H.Rob.	1	
<i>Lucilia linearifolia</i> Baker	1	
<i>Lucilia acutifolia</i> (Poir.) Cass.	1	
<i>Lucilia nitens</i> Less.	1	
<i>Micropsis dasycarpa</i> (Griseb.) Beauverd		1
<i>Micropsis spathulata</i> (Pers.) Cabrera		1
<i>Noticastrum calvatum</i> (Baker) Cuatrec.		1
<i>Noticastrum decumbens</i> (Baker) Cuatrec.		1
<i>Orthopappus angustifolius</i> (Sw.) Gleason		1
<i>Pamphalea bupleurifolia</i> Less		1
<i>Pamphalea heterophylla</i> Less.		1
<i>Perezia multiflora</i> Less.		1
<i>Picrosia longifolia</i> D.Don		1
<i>Pluchea laxiflora</i> Hook. & Arn. ex Baker		1
<i>Pluchea sagittalis</i> Less.		1
<i>Podocoma hieraciifolia</i> (Poir.) Cass.	1	
<i>Pseudognaphalium cheiranthifolium</i> (Lam.) Hilliard & B.L.Burt		1
<i>Pterocaulon alopecuroides</i> (Lam.) DC.	1	

<i>Pterocaulon angustifolium</i> DC.	1								
<i>Pterocaulon lorentzii</i> Malme	1								
<i>Pterocaulon rugosum</i> (Vahl) Malme	1								
<i>Senecio brasiliensis</i> (Spreng.) Less.								1	
<i>Senecio conyzifolius</i> Baker								1	
<i>Senecio heterotrichius</i> DC.								1	
<i>Senecio leptolobus</i> DC.								1	
<i>Senecio oxyphyllus</i> DC.								1	
<i>Senecio selloi</i> (Spreng.) DC.								1	
<i>Solidago chilensis</i> Meyen								1	
<i>Soliva sessilis</i> Ruiz & Pav.									1
<i>Sommerfeltia spinulosa</i> (Spreng.) Less.									1
<i>Stenachaenium campestre</i> Baker									1
<i>Stenachaenium megapotamicum</i> (Spreng.) Baker									1
<i>Stenachaenium riedelli</i> Baker									1
<i>Stenocephalum megapotamicum</i> (Spreng.) Sch.Bip.	1								
<i>Stevia alternifolia</i> Hieron.	1								
<i>Stevia cinerascens</i> Sch.Bip. ex Baker	1								
<i>Stevia selloi</i> (Spreng.) B.L.Rob.	1								
<i>Symphyotrichum squamatum</i> (Spreng.) G.L.Nesom	1								
<i>Trichocline catharinensis</i> Cabrera									1
<i>Vernonanthura beyrichii</i> (Less.) H. Rob.									1
<i>Vernonanthura catharinensis</i> (Cabrera) H.Rob.									1
<i>Vernonanthura chamaedrys</i> (Less.) H. Rob.									1
<i>Vernonanthura discolor</i> (Spreng.) H.Rob.									1
<i>Vernonanthura nudiflora</i> (Less.) H. Rob.									1
<i>Vernonanthura phosphorica</i> (Vell.) H.Rob.									1
Begoniaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Begonia cucullata</i> Willd.	1								
Boraginaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Moritzia dusenii</i> I.M. Johnst.				1					
Brassicaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Lepidium auriculatum</i> Regel & Körn.								1	
<i>Lepidium bonariense</i> L.								1	
<i>Lepidium ruderae</i> L.								1	
Cactaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Parodia ottonis</i> (Lehm.) N.P. Taylor					1				
Calyceraceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Acicarpa procumbens</i> Less.					1				
Campanulaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Lobelia camporum</i> Pohl					1				
<i>Lobelia hederacea</i> Cham.					1				
<i>Triodanis perfoliata</i> (L.) Nieuwl.	1								
<i>Wahlenbergia linarioides</i> (Lam.) A.DC.	1								
Caprifoliaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Valeriana salicariifolia</i> Vahl	1								
Caryophyllaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Cardionema ramosissima</i> (Weinm.) A. Nelson & J.F.Macbr					1				

<i>Cerastium commersonianum</i> Ser.	1									
<i>Cerastium dicotrichum</i> Fenzl ex Rohrb.		1								
<i>Cerastium glomeratum</i> Thuill.		1								
<i>Cerastium rivulare</i> Cambess.		1								
<i>Paronychia brasiliana</i> A.DC.		1								
<i>Paronychia camphorosmoides</i> Cambess.		1								
<i>Paronychia chilensis</i> DC.		1								
<i>Paronychia communis</i> Cambess.	1									
<i>Polycarpon tetraphyllum</i> (L.) L.		1								
<i>Spergularia grandis</i> (Pers.) Cambess.	1									
<i>Stellaria media</i> (L.) Vill.		1								
Cistaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Crocanthemum brasiliensis</i> Spach		1								
Commelinaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Commelina diffusa</i> Burm.f.		1								
<i>Commelina erecta</i> L.		1								
<i>Commelina platyphylla</i> Klotzsch ex Seub.		1								
Convolvulaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Convolvulus bonariensis</i> Cav.						1				
<i>Dichondra microcalyx</i> (Hallier f.) Fabris	1									
<i>Dichondra sericea</i> Sw.	1									
<i>Evolvulus sericeus</i> Sw.	1									
Cyperaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Abildgaardia ovata</i> (L.) Vahl							1			
<i>Ascolepis brasiliensis</i> (Kunth) Benth. ex C.B. Clarke							1			
<i>Bulbostylis</i> aff. <i>juncooides</i>							1			
<i>Bulbostylis capillaris</i> (L.) C.B. Clarke							1			
<i>Bulbostylis communis</i> M.G. López & D.A. Simpson							1			
<i>Bulbostylis consanguinea</i> (Kunth) C.B. Clarke							1			
<i>Bulbostylis contracta</i> (Kük. ex Osten) M.G. López & D.A. Simpson							1			
<i>Bulbostylis glaziovii</i> (Boeckeler) C.B. Clarke							1			
<i>Bulbostylis hirtella</i> (Schrad.) Urb.							1			
<i>Bulbostylis juncooides</i> (Vahl) Kük. ex Osten							1			
<i>Bulbostylis scabra</i> (J. Presl & C. Presl) C.B. Clarke							1			
<i>Bulbostylis sphaerocephala</i> (Boeckeler) C.B. Clarke							1			
<i>Bulbostylis sphaerolepis</i> (Boeckeler) C.B. Clarke							1			
<i>Bulbostylis subtilis</i> M.G. López							1			
<i>Carex bonariensis</i> Desf. ex Poir.							1			
<i>Carex phalaroides</i> Kunth							1			
<i>Carex sororia</i> Kunth							1			
<i>Cyperus aggregatus</i> (Willd.) Endl.							1			
<i>Cyperus brevifolius</i> (Rottb.) Endl. ex Hassk.							1			
<i>Cyperus haspan</i> L.							1			
<i>Cyperus hermaphroditus</i> (Jacq.) Standl.							1			
<i>Cyperus obtusatus</i> (J. Presl & C. Presl) Mattf. & Kük.							1			
<i>Cyperus reflexus</i> Vahl							1			
<i>Cyperus rigens</i> C. Presl							1			

<i>Cyperus sesquiflorus</i> (Torr.) Mattf. & Kük.	1
<i>Eleocharis bonariensis</i> Nees	1
<i>Eleocharis contracta</i> Maury	1
<i>Eleocharis dunensis</i> Kük.	1
<i>Eleocharis montana</i> (Kunth) Roem. & Schult.	1
<i>Eleocharis quinquangularis</i> Boeckeler	1
<i>Eleocharis sellowiana</i> Kunth	1
<i>Eleocharis viridans</i> Kük. ex Osten	1
<i>Fimbristylis autumnalis</i> (L.) Roem. & Schult.	1
<i>Fimbristylis complanata</i> (Retz.) Link	1
<i>Fimbristylis dichotoma</i> (L.) Vahl	1
<i>Lipocarpa chinensis</i> (Osbeck) J.Kern	1
<i>Pycreus flavescens</i> (L.) Rchb.	1
<i>Pycreus niger</i> (Ruiz & Pav.) Cufod.	1
<i>Pycreus polystachyos</i> (Rottb.) P.Beauv.	1
<i>Pycreus unioloides</i> (R.Br.) Urb.	1
<i>Rhynchospora barrosiana</i> Guagl.	1
<i>Rhynchospora brittonii</i> Gale	1
<i>Rhynchospora corymbosa</i> (L.) Britton	1
<i>Rhynchospora crinigera</i> Boeckeler	1
<i>Rhynchospora edwalliana</i> Boeckeler	1
<i>Rhynchospora holoschoenoides</i> (Rich.) Herter	1
<i>Rhynchospora marisculus</i> Lindl. & Nees	1
<i>Rhynchospora megapotamica</i> (A.Spreng.) H.Pfeiff.	1
<i>Rhynchospora praecincta</i> Maury ex Micheli	1
<i>Rhynchospora rugosa</i> (Vahl) Gale	1
<i>Rhynchospora scutellata</i> Griseb.	1
<i>Rhynchospora setigera</i> (Kunth) Griseb.	1
<i>Rhynchospora tenuis</i> Link	1
<i>Scleria distans</i> Poir.	1
<i>Scleria sellowiana</i> Kunth	1
<i>Scleria spicata</i> (Spreng.) J.F.Macbr.	1
Dennstaedtiaceae	EH PH RH RR VH SH CG TG PG
<i>Pteridium arachnoideum</i> (Kaulf.) Maxon	1
Droseraceae	EH PH RH RR VH SH CG TG PG
<i>Drosera brevifolia</i> Pursh	1
Equisetaceae	EH PH RH RR VH SH CG TG PG
<i>Equisetum giganteum</i> L.	1
Escalloniaceae	EH PH RH RR VH SH CG TG PG
<i>Escallonia bifida</i> Link & Otto	1
Euphorbiaceae	EH PH RH RR VH SH CG TG PG
<i>Acalypha communis</i> Müll. Arg.	1
<i>Croton didrichsenii</i> G.L.Webster	1
<i>Croton heterodoxus</i> Baill.	1
<i>Croton lanatus</i> Lam.	1
<i>Euphorbia papillosa</i> A.St.-Hil.	1
<i>Euphorbia peperomioides</i> Boiss.	1
<i>Euphorbia selloi</i> (Klotzsch & Garcke) Boiss.	1

<i>Euphorbia spathulata</i> Lam.	1								
<i>Euphorbia stenophylla</i> (Klotzsch & Garcke) Boiss.	1								
<i>Tragia bahiensis</i> Müll. Arg.		1							
<i>Tragia uberabana</i> Müll.Arg.		1							
Fabaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Adesmia bicolor</i> (Poir.) DC.		1							
<i>Adesmia ciliata</i> Vogel		1							
<i>Adesmia incana</i> Vogel		1							
<i>Adesmia latifolia</i> (Spreng.) Vogel		1							
<i>Adesmia tristis</i> Vogel		1							
<i>Aeschynomene falcata</i> (Poir.) DC.		1							
<i>Ancistrotropis peduncularis</i> (Kunth) A. Delgado						1			
<i>Arachis burkartii</i> Handro		1							
<i>Clitoria nana</i> Benth.	1								
<i>Crotalaria hilariana</i> Benth.		1							
<i>Crotalaria incana</i> L.		1							
<i>Desmanthus tatuhyensis</i> Hoehne		1							
<i>Desmanthus virgatus</i> (L.) Willd.		1							
<i>Desmodium adscendens</i> (Sw.) DC.	1								
<i>Desmodium affine</i> Schltld.	1								
<i>Desmodium barbatum</i> (L.) Benth.		1							
<i>Desmodium incanum</i> (Sw.) DC.	1								
<i>Desmodium uncinatum</i> (Jacq.) DC.	1								
<i>Eriosema campestre</i> Benth.	1								
<i>Eriosema tacuareboense</i> Arechav.	1								
<i>Galactia benthamiana</i> Micheli		1							
<i>Galactia gracillima</i> Benth.		1							
<i>Galactia marginalis</i> Benth.						1			
<i>Galactia neesii</i> DC.		1							
<i>Indigofera asperifolia</i> Bong. ex Benth.		1							
<i>Lathyrus crassipes</i> Gillies ex Hook. & Arn.						1			
<i>Leptospron adenanthum</i> (G. Mey.) A. Delgado						1			
<i>Lupinus magnistipulatus</i> Burkart ex Planchuelo & D.B.Dunn							1		
<i>Macroptilium prostratum</i> (Benth.) Urb.	1								
<i>Mimosa cruenta</i> Benth.							1		
<i>Mimosa flagellaris</i> Benth.		1							
<i>Mimosa paupera</i> Benth.		1							
<i>Poiretia tetraphylla</i> (Poir.) Burkart		1							
<i>Pomaria pilosa</i> (Vogel) B.B.Simpson & G.P.Lewis		1							
<i>Rhynchosia corylifolia</i> Mart. ex Benth.		1							
<i>Rhynchosia diversifolia</i> Micheli		1							
<i>Rhynchosia senna</i> Gillies ex Hook.		1							
<i>Stylosanthes leiocarpa</i> Vogel		1							
<i>Stylosanthes montevidensis</i> Vogel	1								
<i>Tephrosia adunca</i> Benth.		1							
<i>Trifolium argentinense</i> Speg.	1								
<i>Trifolium polymorphum</i> Poir.	1								
<i>Trifolium repens</i> L.	1								

<i>Trifolium riograndense</i> Burkart	1								
<i>Vachellia caven</i> (Molina) Seigler & Ebinger								1	
<i>Vicia graminea</i> Sm.								1	
<i>Zornia burkartii</i> Vanni	1								
<i>Zornia cryptantha</i> Arechav.	1								
<i>Zornia multinervosa</i> Burkart ex N.M.Bacigal.	1								
<i>Zornia orbiculata</i> Mohlenbr.	1								
<i>Zornia pardina</i> Mohlenbr.	1								
Gentianaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Cicendia quadrangularis</i> (Lam.) Griseb.	1								
<i>Zygostigma australe</i> (Cham. & Schltdl.) Griseb.	1								
Geraniaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Geranium albicans</i> A.St.-Hil.	1								
Hypericaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Hypericum brasiliense</i> Choisy	1								
<i>Hypericum connatum</i> Lam.	1								
<i>Hypericum mutilum</i> L.	1								
Hypoxidaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Hypoxis decumbens</i> L.								1	
Iridaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Calydorea crocoides</i> Ravenna	1								
<i>Cypella discolor</i> Ravenna	1								
<i>Cypella hauthalii</i> (Kuntze) R.C.Foster	1								
<i>Cypella herbertii</i> (Lindl.) Herb.	1								
<i>Herbertia furcata</i> (Klatt) Ravenna	1								
<i>Herbertia lahue</i> (Molina) Goldblatt	1								
<i>Herbertia pulchella</i> Sweet	1								
<i>Herbertia quareimana</i> Ravenna	1								
<i>Kelissa brasiliensis</i> (Baker) Ravenna	1								
<i>Sisyrinchium hoehnei</i> I.M.Johnst.								1	
<i>Sisyrinchium megapotamicum</i> Malme								1	
<i>Sisyrinchium micranthum</i> Cav.								1	
<i>Sisyrinchium minutiflorum</i> Klatt								1	
<i>Sisyrinchium pachyrhizum</i> Baker								1	
<i>Sisyrinchium palmifolium</i> L.								1	
<i>Sisyrinchium scariosum</i> I.M.Johnst.								1	
<i>Sisyrinchium sellowianum</i> Klatt								1	
<i>Sisyrinchium setaceum</i> Klatt								1	
<i>Sisyrinchium vaginatum</i> Spreng.								1	
Juncaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Juncus bufonius</i> L.								1	
<i>Juncus capillaceus</i> Lam.								1	
<i>Juncus capitatus</i> Weigel								1	
<i>Juncus imbricatus</i> Laharpe								1	
<i>Juncus microcephalus</i> Kunth								1	
<i>Juncus scirpoides</i> Lam.								1	
<i>Juncus tenuis</i> Willd.								1	
Lamiaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG

<i>Cantinoa mutabilis</i> (Rich.) Harley & J.F.B. Pastore	1									
<i>Cunila galioides</i> Benth.	1									
<i>Cunila spicata</i> Benth.	1									
<i>Glechon marifolia</i> Benth.	1									
<i>Glechon spathulata</i> Benth.	1									
<i>Hyptis stricta</i> Benth.	1									
<i>Ocimum nudicaule</i> Benth.									1	
<i>Ocimum ovatum</i> Benth.	1									
<i>Rhabdocaulon gracile</i> (Benth.) Epling	1									
<i>Rhabdocaulon stenodontum</i> (Briq.) Epling	1									
<i>Salvia ovalifolia</i> A.St.-Hil. ex Benth.	1									
<i>Salvia procurrens</i> Benth.	1									
<i>Salvia uliginosa</i> Benth.	1									
<i>Scutellaria racemosa</i> Pers.	1									
Lentibulariaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Utricularia subulata</i> L.	1									
<i>Utricularia tridentata</i> Sylvén	1									
Linaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Cliococca selaginoides</i> (Lam.) C.M. Rogers & Mildner										1
Loganiaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Spigelia stenophylla</i> Progel	1									
Lycopodiaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Lycopodiella alopecuroides</i> (L.) Cranfill										1
Lythraceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Cuphea calophylla</i> Cham. & Schltld.	1									
<i>Cuphea campylocentra</i> Griseb.	1									
<i>Cuphea glutinosa</i> Cham. & Schltld.	1									
<i>Cuphea linarioides</i> Cham. & Schltld.	1									
<i>Cuphea racemosa</i> (L.f.) Spreng.	1									
<i>Heimia apetala</i> (Spreng.) S.A.Graham & Gandhi	1									
Malpighiaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Aspicarpa pulchella</i> O'Donell & Lourteig	1									
<i>Galphimia australis</i> Chodat	1									
<i>Janusia guaranitica</i> (A.St.-Hil.) A.Juss.	1									
Malvaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Ayenia mansfeldiana</i> (Herter) Herter ex Cristóbal	1									
<i>Byttneria scabra</i> L.	1									
<i>Krapovickasia flavescens</i> (Cav.) Fryxell										1
<i>Krapovickasia macrodon</i> (A.DC.) Fryxell										1
<i>Melochia chamaedrys</i> A.St.-Hil.	1									
<i>Melochia hermannioides</i> A.St.-Hil.	1									
<i>Melochia pyramidata</i> L.	1									
<i>Modiola caroliniana</i> (L.) G.Don										1
<i>Modiolastrum malvifolium</i> (Griseb.) K. Schum.										1
<i>Pavonia dusenii</i> Krapov.										1
<i>Pavonia glechomoides</i> A.St.-Hil.										1
<i>Pavonia hastata</i> Cav.										1
<i>Pavonia reticulata</i> Garcke										1

<i>Rhynchosida physocalyx</i> (A.Gray) Fryxell	1									
<i>Sida potentilloides</i> A.St.-Hil.	1									
<i>Sida rhombifolia</i> L.	1									
<i>Sida spinosa</i> L.	1									
<i>Sida tuberculata</i> R.E.Fr.	1									
<i>Sida viarum</i> A.St.-Hil.	1									
<i>Waltheria communis</i> A.St.-Hil.	1									
Melastomataceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Chaetogastra gracilis</i> (Bonpl.) DC.	1									
<i>Tibouchina cerastifolia</i> Cogn.	1									
<i>Tibouchina rupestris</i> Cogn.	1									
Menyanthaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Nymphoides indica</i> (L.) Kuntze	1									
Moraceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Dorstenia brasiliensis</i> Lam.	1									
Myrtaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Campomanesia aurea</i> O.Berg						1				
<i>Psidium salutare</i> (Kunth) O.Berg						1				
Onagraceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Ludwigia hookeri</i> (Micheli) H.Hara	1									
<i>Ludwigia sericea</i> (Cambess.) H.Hara						1				
<i>Oenothera affinis</i> Cambess.	1									
Ophioglossaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Ophioglossum nudicaule</i> L.f.	1									
Orchidaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Brachystele camporum</i> (Lindl.) Schltr.	1									
<i>Habenaria macronectar</i> (Vell.) Hoehne	1									
<i>Habenaria parviflora</i> Lindl.	1									
<i>Sacoila lanceolata</i> (Aubl.) Garay	1									
Orobanchaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Agalinis communis</i> (Cham. & Schltdl.) D'Arcy	1									
<i>Agalinis linarioides</i> (Cham. & Schltdl.) D'Arcy	1									
<i>Buchnera longifolia</i> Kunth	1									
<i>Castilleja arvensis</i> Schltdl. & Cham.	1									
Oxalidaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Oxalis articulata</i> Savigny	1									
<i>Oxalis bipartita</i> A.St.-Hil.	1									
<i>Oxalis brasiliensis</i> G.Lodd.	1									
<i>Oxalis conorrhiza</i> Jacq.		1								
<i>Oxalis eriocarpa</i> DC.		1								
<i>Oxalis floribunda</i> Lehm.	1									
<i>Oxalis hispidula</i> Zucc.	1									
<i>Oxalis lasiopetala</i> Zucc.	1									
<i>Oxalis paludosa</i> A.St.-Hil.	1									
<i>Oxalis tenerrima</i> Knuth	1									
Plantaginaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Gratiola peruviana</i> L.	1									
<i>Mecardonia procumbens</i> (Mill.) Small	1									

<i>Mecardonia procumbens</i> var. <i>flagellaris</i> (Cham. & Schltld.) V.C.Souza	1									
<i>Mecardonia procumbens</i> var. <i>herniarioides</i> (Cham.) V.C.Souza	1									
<i>Mecardonia procumbens</i> var. <i>tenella</i> (Cham. & Schltld.) V.C.Souza	1									
<i>Plantago australis</i> Lam.		1								
<i>Plantago guilleminiana</i> Decne.		1								
<i>Plantago myosuroides</i> Lam.		1								
<i>Plantago napiformis</i> (Rahn) Hassemer		1								
<i>Plantago penantha</i> Griseb.		1								
<i>Plantago tomentosa</i> Lam.		1								
<i>Scoparia dulcis</i> L.	1									
<i>Scoparia hassleriana</i> Chodat	1									
<i>Scoparia montevidensis</i> (Spreng.) R.E.Fr.	1									
<i>Stemodia lanceolata</i> Benth.		1								
<i>Stemodia verticillata</i> (Mill.) Hassl.		1								
<i>Veronica arvensis</i> L.	1									
<i>Veronica persica</i> Poir.		1								
Poaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG	
<i>Agenium villosum</i> (Nees) Pilg.							1			
<i>Agrostis montevidensis</i> Spreng. ex Nees								1		
<i>Agrostis tandilensis</i> (Kuntze) Parodi									1	
<i>Andropogon lateralis</i> Nees								1		
<i>Andropogon leucostachyus</i> Kunth							1			
<i>Andropogon macrothrix</i> Trin.							1			
<i>Andropogon selloanus</i> (Hack.) Hack.							1			
<i>Andropogon ternatus</i> (Spreng.) Nees							1			
<i>Anthraenantia lanata</i> (Kunth) Benth.							1			
<i>Anthoxanthum odoratum</i> L.							1			
<i>Aristida circinalis</i> Lindm.									1	
<i>Aristida filifolia</i> (Arechav.) Herter									1	
<i>Aristida flaccida</i> Trin. & Rupr.							1			
<i>Aristida jubata</i> (Arechav.) Herter									1	
<i>Aristida laevis</i> (Nees) Kunth									1	
<i>Aristida megapotamica</i> Spreng.							1			
<i>Aristida murina</i> Cav.							1			
<i>Aristida spagazzinii</i> Arechav.							1			
<i>Aristida venustula</i> Arechav.							1			
<i>Axonopus affinis</i> Chase										1
<i>Axonopus argentinus</i> Parodi									1	
<i>Axonopus compressus</i> (Sw.) P. Beauv.										1
<i>Axonopus fissifolius</i> (Raddi) Kuhlmann										1
<i>Axonopus obtusifolius</i> (Raddi) Chase										1
<i>Axonopus siccus</i> (Nees) Kuhlmann									1	
<i>Axonopus suffultus</i> (Mikan ex Trin.) Parodi									1	
<i>Bothriochloa laguroides</i> (DC.) Herter							1			
<i>Bouteloua megapotamica</i> (Spreng.) Kuntze							1			
<i>Briza minor</i> L.									1	
<i>Bromidium hygrometricum</i> (Nees) Nees & Meyen										1

<i>Calamagrostis rupestris</i> Trin.	1	
<i>Calamagrostis viridiflavescens</i> (Poir.) Steud.		1
<i>Cenchrus clandestinus</i> (Hochst. ex Chiov.) Morrone		1
<i>Chascolytrum lamarckianum</i> (Nees) Matthei	1	
<i>Chascolytrum poomorphum</i> (J. Presl) Essi, Longhi-Wagner & Souza-Chies	1	
<i>Chascolytrum rufum</i> J.Presl	1	
<i>Chascolytrum subaristatum</i> (Lam.) Desv.	1	
<i>Chascolytrum uniolae</i> (Nees) Essi, Longhi-Wagner & Souza-Chies	1	
<i>Cynodon dactylon</i> (L.) Pers.		1
<i>Danthonia cirrata</i> Hack. & Arechav.	1	
<i>Danthonia montana</i> Döll	1	
<i>Danthonia secundiflora</i> J.Presl	1	
<i>Dichantherium sabulorum</i> (Lam.) Gould & C.A.Clark	1	
<i>Digitaria violascens</i> Link		1
<i>Eleusine indica</i> (L.) Gaertn.	1	
<i>Eleusine tristachya</i> (Lam.) Lam.		1
<i>Elionurus muticus</i> (Spreng.) Kuntze		1
<i>Eragrostis airoides</i> Nees		1
<i>Eragrostis bahiensis</i> Roem. & Schult.	1	
<i>Eragrostis lugens</i> Nees	1	
<i>Eragrostis neesii</i> Trin.	1	
<i>Eragrostis pilosa</i> (L.) P.Beauv.	1	
<i>Eragrostis plana</i> Nees		1
<i>Eragrostis polytricha</i> Nees	1	
<i>Eriochrysis cayennensis</i> P.Beauv.		1
<i>Eustachys retusa</i> (Lag.) Kunth	1	
<i>Eustachys uliginosa</i> (Hack.) Herter	1	
<i>Gymnopogon grandiflorus</i> Roseng., B.R.Arrill. & Izag.	1	
<i>Gymnopogon spicatus</i> (Spreng.) Kuntze	1	
<i>Holcus lanatus</i> L.	1	
<i>Ichnanthus procurrans</i> (Nees ex Trin.) Swallen	1	
<i>Ischaemum minus</i> J. Presl		1
<i>Jarava megapotamica</i> (Spreng.) Peñail.	1	
<i>Leersia hexandra</i> Sw.		1
<i>Leptocoryphium lanatum</i> (Kunth) Nees	1	
<i>Lolium multiflorum</i> Lam.	1	
<i>Luziola peruviana</i> Juss. ex J.F. Gmel.	1	
<i>Melica hyalina</i> Döll	1	
<i>Melica macra</i> Nees		1
<i>Melica rigida</i> Cav.	1	
<i>Microchloa indica</i> (L.f.) P. Beauv.	1	
<i>Mnesithea selloana</i> (Hack.) de Koning & Sosef	1	
<i>Nassella airoides</i> (E.Ekman) Barkworth	1	
<i>Nassella hyalina</i> (Nees) Barkworth	1	
<i>Nassella juergensii</i> (Hack.) Barkworth	1	
<i>Nassella megapotamia</i> (Spreng. ex Trin.) Barkworth	1	
<i>Nassella melanosperma</i> (J. Presl) Barkworth	1	

<i>Nassella neesiana</i> (Trin. & Rupr.) Barkworth	1	
<i>Nassella nutans</i> (Hack.) Barkworth		1
<i>Nassella tenuiculmis</i> (Hack.) Peñail.		1
<i>Panicum aquaticum</i> Poir.	1	
<i>Panicum bergii</i> Arechav.	1	
<i>Paspalum compressifolium</i> Swallen		1
<i>Paspalum conduplicatum</i> Canto-Dorow, Valls & Longhi-Wagner		1
<i>Paspalum dilatatum</i> Poir.	1	
<i>Paspalum glaucescens</i> Hack.		1
<i>Paspalum indecorum</i> Mez		1
<i>Paspalum leptum</i> Schult.	1	
<i>Paspalum maculosum</i> Trin.	1	
<i>Paspalum notatum</i> Flüggé		1
<i>Paspalum pauciciliatum</i> (Parodi) Herter	1	
<i>Paspalum paucifolium</i> Swallen		1
<i>Paspalum plicatulum</i> Michx.	1	
<i>Paspalum polyphyllum</i> Nees ex Trin.	1	
<i>Paspalum pumilum</i> Nees		1
<i>Paspalum umbrosum</i> Trin.	1	
<i>Paspalum urvillei</i> Steud.		1
<i>Phalaris angusta</i> Nees ex Trin.	1	
<i>Phalaris platensis</i> Henrard ex Wacht.	1	
<i>Piptochaetium bicolor</i> (Vahl) Desv.	1	
<i>Piptochaetium lasianthum</i> Griseb.	1	
<i>Piptochaetium montevidense</i> (Spreng.) Parodi	1	
<i>Piptochaetium ruprechtianum</i> Desv.	1	
<i>Piptochaetium stipoides</i> (Trin. & Rupr.) Hack. ex Arechav.	1	
<i>Piptochaetium uruguense</i> Griseb.	1	
<i>Poa annua</i> L.	1	
<i>Saccharum angustifolium</i> (Nees) Trin.		1
<i>Saccharum villosum</i> Steud.		1
<i>Sacciolepis vilvoides</i> (Trin.) Chase	1	
<i>Schizachyrium bimucronatum</i> Roseng., B.R. Arrill. & Izag.	1	
<i>Schizachyrium condensatum</i> (Kunth) Nees	1	
<i>Schizachyrium gracilipes</i> (Hack.) A. Camus	1	
<i>Schizachyrium hatschbachii</i> Peichoto	1	
<i>Schizachyrium imberbe</i> (Hack.) A. Camus		1
<i>Schizachyrium microstachyum</i> (Desv. ex Ham.) Roseng., B.R. Arrill. & Izag.		1
<i>Schizachyrium plumigerum</i> (Ekman) Parodi	1	
<i>Schizachyrium spicatum</i> (Spreng.) Herter	1	
<i>Schizachyrium tenerum</i> Nees	1	
<i>Setaria parviflora</i> (Poir.) M. Kerguelen	1	
<i>Setaria vaginata</i> Spreng.	1	
<i>Sorghastrum pellitum</i> (Hack.) Parodi		1
<i>Sorghastrum setosum</i> (Griseb.) Hitchc.		1
<i>Sporobolus aeneus</i> var. <i>angustifolius</i> (Doll) S. Denham & Aliscioni	1	
<i>Sporobolus indicus</i> (L.) R.Br.		1

<i>Sporobolus pseudairoides</i> Parodi	1
<i>Steinchisma decipiens</i> (Nees ex Trin.) W.V.Br.	1
<i>Steinchisma hians</i> (Elliott) Nash	1
<i>Trachypogon montufarii</i> (Kunth) Nees	1
<i>Trachypogon spicatus</i> (L.f.) Kuntze	1
<i>Trichantheium schwackeanum</i> (Mez) Zuloaga & Morrone	1
<i>Urochloa decumbens</i> (Stapf) R.D.Webster	1
<i>Vulpia bromoides</i> (L.) Gray	1
<i>Vulpia myuros</i> (L.) C.C.Gmel.	1

Polygalaceae	EH PH RH RR VH SH CG TG PG
---------------------	-----------------------------------

<i>Polygala adenophylla</i> A.St.-Hil. & Moq.	1
<i>Polygala aphylla</i> A.W.Benn.	1
<i>Polygala australis</i> A.W.Benn.	1
<i>Polygala bonariensis</i> Grondona	1
<i>Polygala brasiliensis</i> L.	1
<i>Polygala campestris</i> Gardner	1
<i>Polygala duarteana</i> A.St.-Hil. & Moq.	1
<i>Polygala extraaxillaris</i> Chodat	1
<i>Polygala linoides</i> Poir.	1
<i>Polygala molluginifolia</i> A.St.-Hil. & Moq.	1
<i>Polygala paniculata</i> L.	1
<i>Polygala pulchella</i> A.St.-Hil. & Moq.	1

Polygonaceae	EH PH RH RR VH SH CG TG PG
---------------------	-----------------------------------

<i>Persicaria punctata</i> (Elliott) Small	1
--	---

Primulaceae	EH PH RH RR VH SH CG TG PG
--------------------	-----------------------------------

<i>Lysimachia arvensis</i> (L.) U. Manns & Anderb.	1
<i>Lysimachia filiformis</i> (Cham. & Schltdl.) U. Manns & Anderb.	1
<i>Lysimachia minima</i> (L.) U. Manns & Anderb.	1

Pteridaceae	EH PH RH RR VH SH CG TG PG
--------------------	-----------------------------------

<i>Adiantopsis chlorophylla</i> (Sw.) Fée	1
<i>Adiantopsis perfasciculata</i> Sehnem	1

Ranunculaceae	EH PH RH RR VH SH CG TG PG
----------------------	-----------------------------------

<i>Ranunculus flagelliformis</i> Sm.	1
<i>Ranunculus platensis</i> Spreng.	1

Rhamnaceae	EH PH RH RR VH SH CG TG PG
-------------------	-----------------------------------

<i>Discaria americana</i> Gillies & Hook.	1
---	---

Rosaceae	EH PH RH RR VH SH CG TG PG
-----------------	-----------------------------------

<i>Acaena eupatoria</i> Cham. & Schltdl.	1
<i>Agrimonia hirsuta</i> Bong. ex C.A.Mey.	1
<i>Aphanes arvensis</i> L.	1
<i>Aphanes parodii</i> (I.M.Johnst.) Rothm.	1
<i>Margyricarpus pinnatus</i> (Lam.) Kuntze	1

Rubiaceae	EH PH RH RR VH SH CG TG PG
------------------	-----------------------------------

<i>Borreria brachystemonoides</i> Cham. & Schltdl.	1
<i>Borreria capitata</i> (Ruiz & Pav.) DC.	1
<i>Borreria dasycephala</i> (Cham. & Schltdl.) Bacigalupo & E.L.Cabral	1
<i>Borreria latifolia</i> (Aubl.) K.Schum.	1

<i>Borreria poaya</i> (A.St.-Hil.) DC.	1								
<i>Borreria tenella</i> (Kunth) Cham. & Schltdl.		1							
<i>Borreria verticillata</i> (L.) G.Mey.		1							
<i>Galianthe fastigiata</i> Griseb.	1								
<i>Galium equisetoides</i> (Cham. & Schltdl.) Standl.						1			
<i>Galium ericoides</i> Lam.	1								
<i>Galium hirtum</i> Lam.	1								
<i>Galium humile</i> Cham. & Schltdl.	1								
<i>Galium hypocarpium</i> (L.) Endl. ex Griseb.	1								
<i>Galium noxium</i> (A.St.-Hil.) Dempster	1								
<i>Galium richardianum</i> (Gillies ex Hook. & Arn.) Endl. ex Walp.	1								
<i>Galium uruguayense</i> Bacigalupo							1		
<i>Galium vile</i> (Cham. & Schltdl.) Dempster	1								
<i>Oldenlandia salzmannii</i> (DC.) Benth. & Hook. f. ex B.D. Jacks.		1							
<i>Richardia brasiliensis</i> Gomes	1								
<i>Richardia grandiflora</i> (Cham. & Schltdl.) Steud.	1								
<i>Richardia humistrata</i> (Cham. & Schltdl.) Steud.		1							
<i>Richardia stellaris</i> (Cham. & Schltdl.) Steud.		1							
<i>Spermacoce eryngioides</i> (Cham. & Schltdl.) Kuntze	1								
Selaginellaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Selaginella sellowii</i> Hieron.		1							
<i>Selaginella tenuissima</i> Fée		1							
Smilacaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Smilax campestris</i> Griseb.					1				
Solanaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Calibrachoa ovalifolia</i> (Miers) Stehmann & Semir		1							
<i>Calibrachoa sellowiana</i> (Sendtn.) Wijsman		1							
<i>Nicotiana bonariensis</i> Lehm.	1								
<i>Petunia integrifolia</i> (Hook.) Schinz & Thell.		1							
<i>Solanum aculeatissimum</i> Jacq.						1			
<i>Solanum commersonii</i> Dunal	1								
Turneraceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Turnera sidoides</i> L.	1								
Urticaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Urtica circularis</i> (Hicken) Sorarú	1								
Verbenaceae	EH	PH	RH	RR	VH	SH	CG	TG	PG
<i>Aloysia gratissima</i> (Gillies & Hook.) Tronc.						1			
<i>Glandularia balansae</i> (Briq.) N.O'Leary	1								
<i>Glandularia catharinae</i> (Moldenke) N.O'Leary & P.Peralta		1							
<i>Glandularia marrubioides</i> (Cham.) Tronc.		1							
<i>Glandularia peruviana</i> (L.) Small		1							
<i>Glandularia selloi</i> (Spreng.) Tronc.		1							
<i>Lantana montevidensis</i> (Spreng.) Briq.	1								
<i>Lippia asperrima</i> Cham.	1								
<i>Lippia coarctata</i> Tronc.	1								
<i>Lippia turnerifolia</i> Cham.	1								
<i>Verbena gracilescens</i> (Cham.) Herter	1								
<i>Verbena intermedia</i> Gillies & Hook. ex Hook.	1								

<i>Verbena litoralis</i> Kunth	1
<i>Verbena montevidensis</i> Spreng.	1
<i>Verbena rigida</i> Spreng.	1
Violaceae	EH PH RH RR VH SH CG TG PG
<i>Pombalia bicolor</i> (A.St-Hil.) Paula-Souza	1
<i>Pombalia parviflora</i> (Mutis ex L.f.) Paula-Souza	1
Vivianiaceae	EH PH RH RR VH SH CG TG PG
<i>Viviania albiflora</i> (Cambess.) Reiche	1

697

698 **Supplement 3:** Weighting factors applied to each local community (alpha units) accounting for
 699 differences in numbers of individuals. This correction allowed for correct calculation of gamma FD.

Municipality	Plot	Spiders weighting factor	Plants weighting factor
Alegrete	1	0.012	0.111
	2	0.024	0.113
	3	0.091	0.112
	4	0.006	0.102
	5	0.366	0.115
	6	0.250	0.122
	7	0.012	0.099
	8	0.128	0.108
	9	0.110	0.117
Quaraí	1	0.105	0.127
	2	0.077	0.144
	3	0.061	0.136
	4	0.223	0.155
	5	0.140	0.158
	6	0.317	0.148
	7	0.077	0.133
São Gabriel	1	0.099	0.095
	2	0.051	0.098
	3	0.079	0.121
	4	0.211	0.112
	5	0.122	0.102
	6	0.071	0.132
	7	0.097	0.096
	8	0.157	0.130
	9	0.114	0.114
Sto. Ant. Missões	1	0.031	0.134
	2	0.174	0.121
	3	0.330	0.081
	4	0.080	0.128
	5	0.108	0.085
	6	0.059	0.125
	7	0.035	0.083
	8	0.073	0.135
	9	0.111	0.107
Lavras do Sul	1	0.122	0.094
	2	0.094	0.127
	3	0.113	0.108
	4	0.164	0.093
	5	0.085	0.100
	6	0.155	0.128
	7	0.108	0.106
	8	0.075	0.117
	9	0.085	0.126
Painel	1	0.052	0.106
	2	0.077	0.108
	3	0.097	0.113
	4	0.223	0.112
	5	0.150	0.120
	6	0.044	0.116
	7	0.111	0.116
	8	0.090	0.107
	9	0.156	0.101
Soledade	1	0.152	0.118

	2	0.025	0.104
	3	0.037	0.118
	4	0.156	0.114
	5	0.152	0.107
	6	0.082	0.111
	7	0.156	0.110
	8	0.148	0.112
	9	0.094	0.106
	<hr/>		
	1	0.122	0.111
	2	0.127	0.102
	3	0.087	0.104
	4	0.162	0.126
Vacaria	5	0.114	0.097
	6	0.087	0.111
	7	0.052	0.119
	8	0.140	0.109
	9	0.109	0.121
	<hr/>		

700

701 **Supplement 4:** Pairwise correlations between CWM traits of plants and spiders.

	PG	CG	TG	PH	RH	EH	VH	RR	SH
ruhu	-0.04	0.05	-0.02	0.00	0.16	-0.09	-0.24*	-0.07	0.03
amhu	-0.16	-0.10	0.20	0.18	-0.03	0.21	0.06	-0.08	-0.14
sthu	0.34*	-0.51*	0.18	0.28*	-0.05	0.33*	0.16	0.36*	-0.22
orwe	-0.10	0.22	-0.20	-0.23	-0.03	-0.21	-0.12	-0.22	0.39*
tdwe	-0.27*	0.18	0.06	-0.14	0.03	-0.22	0.12	0.02	0.11
shwe	0.00	0.51*	-0.39*	-0.35*	-0.07	-0.30*	-0.22	-0.28*	0.20*

702

CONSIDERAÇÕES FINAIS

Quem vê o monótono horizonte da paisagem campestre não imagina a riqueza e a diversidade sob seus pés. Nesta tese exploramos um pouco mais a fundo a biodiversidade dos Campos Sulinos. Esperamos, nesses poucos capítulos, ter contribuído para o entendimento dos padrões de diversidade da vegetação campestre, sua relação com clima, solo e outros grupos biológicos em diferentes escalas espaciais. Nesta tese procuramos, sempre que possível, caminhar pela fronteira do conhecimento científico ecológico e botânico explorando os métodos científicos mais recentes e dando um passo além, incorporando a complexidade das diferentes escalas espaciais ou o desafio de visualizar padrões nos táxons super diversos dos Campos Sulinos.

Tenho certeza que uma das grandes contribuições dessa tese para os Campos Sulinos, e para ciência de forma geral, foi a geração do banco de dados da vegetação campestre. Registramos ocorrência e cobertura para 759 espécies de plantas e mais atributo morfológico (forma de crescimento acima do solo) para 654 dessas. Foram ao todo 1.170 parcelas de 1 m² de vegetação campestre. Todos esses dados são públicos e estarão disponíveis para quem quiser usá-los.

Além disso, também tivemos a oportunidade de integrar dados de comunidades vegetais com comunidades de aranhas, em uma ampla escala espacial. Esses resultados foram muito enriquecedores para que pudéssemos compreender melhor como a vegetação campestre é utilizada pela fauna nativa de aranhas. Pesquisas integradoras desse tipo, em amplas escalas espaciais, são difíceis de serem realizadas por seu alto custo e necessidade de articulação entre diferentes especialistas. O projeto PPBio Campos Sulinos foi uma ótima oportunidade para realização desse tipo de pesquisa e com certeza os dados biológicos trabalhados pelos diferentes grupos envolvidos no projeto ainda possuem muito potencial para responder novas perguntas.