UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

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INFLUÊNCIA DE GRADIENTES AMBIENTAIS NOS PADRÕES DE DIVERSIDADE DAS COMUNIDADES CAMPESTRES NOS CAMPOS DE CIMA DA SERRA, RS, BRASIL.

Porto Alegre
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Tese apresentada como requisito parcial para obtenção do título de Doutor em Ciências com ênfase em Ecologia na Universidade Federal do Rio Grande do Sul.

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CIP - Catalogação na Publicação

Martin, Eduardo Vélez
Influência de gradientes ambientais nos padrões de diversidade das comunidades campestres nos Campos de Cima da Serra, RS, Brasil. / Eduardo Vélez Martin. -- 2012.
135 f.
Orientador: Valério De Patta Pillar.

Tese (Doutorado) -- Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Programa de Pós-Graduação em Ecologia, Porto Alegre, BR-RS, 2012.

1. Vegetação campestre. 2. Campos Sulinos. 3. Diversidade beta. 4. Partição da diversidade. I. De Patta Pillar, Valério, orient. II. Título.

Elaborada pelo Sistema de Geração Automática de Ficha Catalográfica da UFRGS com os dados fornecidos pelo(a) autor(a).

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Aprovada em: 25/09/2012

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Agradecimentos

Inicialmente faço um agradecimento ao Programa de Pós-Graduação em Ecologia da UFRGS pela oportunidade de aperfeiçoamento e qualificação profissional. Em especial, agradeço à Coordenação do PPG-Ecologia pela compreensão dispensada em momentos difíceis.

Ao meu orientador, Valério De Patta Pillar, pela liderança, ensinamentos, exemplo e apoio, e também pela paciência durante a realização deste trabalho.

Ao CNPq pela concessão da bolsa de estudos e da taxa de bancada durante todo o período da tese e também ao *Interamerican Institute for Global Change Research* (IAI) pelo financiamento de boa parte do trabalho através do projeto *From Landscape to Ecosystem: Across-scales Functioning in changing environments (LEAF)* sem o apoio dos quais este trabalho não teria sido possível.

Faço um agradecimento especial à minha família por ter abraçado esta causa junto comigo, em especial a Ivana da Cruz, minha esposa e companheira de todas as horas, a minha mãe Niza Martin de Vélez por continuar sendo uma mão coruja e aos queridos filhotes Pedro, Felipe, Ivo e Ronald.

Também de forma muito especial aos co-autores de capítulos Ilsi Boldrini, Angelo Schneider e Rafael Trevisan, cujos conhecimentos taxonômicos e ensinamentos foram imprescindíveis, e aos colaboradores nas expedições a campo Bruno S.G. Fonseca, Cláudio Reis, Gabriel Specht, Marcel Tust e Tiago Caetano Edruziane.

Aos amigos Heinrich Hasenack, Eliseu Weber e demais integrantes do Laboratório de Geoprocessamento/UFRGS, pelos ensinamentos em geoprocessamento e pela cessão de dados para o desenvolvimento da tese. Também agradeço a Sandra C. Müller do Laboratório de Ecologia Vegetal e à colega Adriane E. Muellbert pelo auxílio em um momento decisivo.

A Tatiana Mora Kuplich, pesquisadora do Centro Regional Sul de Pesquisas Espaciais – CRS/INPE pela amizade, apoio e parceria nos estudos da paisagem na região dos Campos de Cima da Serra e também pela pareceria aos colegas Aline Trentin, Andreise Moreira, Bruno Deprá e Rosana Corazza.

A todos os colegas do Laboratório de Ecologia Quantitativa e dos demais laboratórios do PPG-Ecologia pela parceria, amizade, companheirismo e aprendizado. Não vou citar nomes porque sempre esqueço de alguém e foram muitos os amigos e amigas com quem convivi ao longo desses anos.

Aos demais professores e funcionários do Departamento de Ecologia e do Centro de Ecologia pelo convívio e cooperação e, em especial, a Silvana Barzotto pela pronta atenção em todos os momentos.

Ao apoio da Secretaria Estadual do Meio Ambiente e da Fundação Zoobotânica do Rio Grande do Sul pela cessão de dados do Projeto de Conservação da Mata Atlântica no Rio Grande do Sul.

Resumo

Os Campos de Cima da Serra são uma das principais tipologias dos Campos Sulinos e seus remanescentes ocupavam, em 2002, uma área de 7.653 km^2. Eles coexistem com manchas de floresta com Araucária, sendo que o clima atual gera uma tensão permanente ao favorecer o adensamento com arbustos e o avanço da colonização florestal. Por outro lado, estão sujeitos a um intenso regime de distúrbios (pastejo e queimadas periódicas), que detém a colonização de espécies lenhosas e afeta profundamente a estrutura das comunidades campestres. As consequências destes processos sobre a diversidade dessas comunidades campestres ainda não são totalmente compreendidas. Os principais objetivos do estudo incluíram: a descrição da diversidade florística e da composição funcional, a identificação de tipos de comunidades e de suas espécies indicadoras. Também foi avaliada a influência relativa de um conjunto de variáveis ambientais (clima, solos, geomorfologia da paisagem e topografia local) e de fatores espaciais para modelar a riqueza de espécies e a diversidade β. Além disso, buscou-se identificar as escalas espaciais com as maiores variações na diversidade β. Um estudo regional foi conduzido com amostragem de 320 parcelas em um delineamento aleatório estratificado e aninhado, de forma a incluir gradientes ambientais numa amplitude geográfica de 160 km de latitude e 170 km de longitude. Foi utilizada Análise de Redundância (RDA) e Análise de Redundância parcial (pRDA) para decompor as influências relativas dos fatores ambientais e espaciais sobre a diversidade β e sobre a riqueza de espécies. Os fatores espaciais foram avaliados com base na Análise de Coordenadas Principais de Matrizes Vizinhas (PCNM). Para decompor a diversidade γ nos componentes α e β foi utilizada a partição aditiva da diversidade considerando cinco escalas espaciais: parcelas (320), transecções (64), sítios (16), sub-regiões (8) e regiões (4), seguida de aleatorizações baseadas em modelos nulos para testar se os valores observados foram casuais. A magnitude e a extensão da correlação espacial na composição das espécies foram avaliadas com o correlograma de Mantel. Um total de 390 táxons pertencentes a 53 famílias foi registrado. Quatro tipos de comunidades foram identificados e a alta riqueza de espécie na escala das parcelas, além da alta riqueza de herbáceas não graminóides foram características indicadoras do regime geral de distúrbios. Um total de 41,4 % da variação na composição das comunidades foi explicado pelas variáveis ambientais e espaciais utilizadas. O efeito dos gradientes ambientais representou cerca de um terço da variação total, sendo na maior parte espacialmente estruturado. A fração espacial pura representou apenas 5,7 % da variação total. A fração das variáveis ambientais sem estrutura espacial foi também baixa. As variáveis representando gradientes de clima e tipos de solo sobrepujaram o efeito da topografia local. A temperatura anual média, a sazonalidade da temperatura e o tipo de solo foram as principais variáveis selecionadas para modelar a diversidade β. A partição aditiva da diversidade revelou que a maior proporção da diversidade β ocorreu em escalas mais amplas, com 46,3% da diversidade total representada pela escala de regiões. A alta proporção de espécies pouco frequentes sugere que áreas protegidas de grandes dimensões são necessárias para representar a maioria das espécies, entretanto os resultados de diversidade β demonstraram que sua efetividade para conservar a diversidade seria incrementada se a área a ser conservada fosse dividida entre as quatro regiões amostradas. Um artigo final de opinião complementou o trabalho com o argumento de que os distúrbios são essenciais para conservar a diversidade dos campos e devem ser reintroduzidos nas áreas protegidas que protegem os campos com ações específicas de manejo.

Palavras-chave: Diversidade beta, Partição da diversidade, Comunidades campestres, Análise de Redundância, Campos Sulinos.

Abstract

The *Campos de Cima da Serra* are one of the main physiognomies of the South Brazilian *Campos* with a remnant area of 7.653 km^2 recorded in 2002. They coexist with patches of *Araucaria* forest, but current climate conditions favors encroachment and forest colonization over grasslands. On the other hand, there is a widespread regime of disturbances (grazing and periodic burns) that prevents the colonization by woody plants and deeply affect the structure of grassland communities. The consequences of both processes on the diversity of these grasslands are still not fully understood. Our main objectives included describing their floristic and functional diversity and identifying community types and associated indicator species. We evaluated the relative role of a set of environmental variables (climate, soil, landscape geomorphology and local topography) and of spatial factors to model the grasslands species richness and β diversity. We also searched for the spatial scales with the larger variations in β diversity. A regional survey was designed to sample 320 plots in a random stratified and nested sampling to encompass environmental gradients within an area ranging 160 km of latitude and 170 km of longitude. We used Redundancy Analysis (RDA) and Partial RDA to disentangle the relative role of the environmental and spatial drivers and to model β diversity and species richness. The spatial factors were evaluated using PCNM eigenfunctions. To decompose γ diversity into α and β components we used additive partitioning considering five spatial scales: plots (320), transects (64), sites (16), sub-regions (8) and regions (4) followed by randomization procedures with null models to test if observed values were random. The magnitude and extension of the spatial correlation among species composition were evaluated with a Mantel correlogram. A total of 390 taxa belonging to 53 families was recorded. Four community types were revealed and the high species richness at the plot level and the high forbs richness were indicative of the general disturbance regime. A total of 41.4% of the variation of community composition was explained jointly by the environmental and spatial variables. The environmental effect accounted for nearly one third of total variation, mostly spatially structured. The pure space fraction accounted for only 5.7% of total variation. The fraction of environmental variables not spatially structured was also low. Variables representing regional gradients of climate and soil overwhelmed the effect of local topography. Annual mean temperature, temperature seasonality and soil type were the main selected variables to model β diversity. Species richness showed a different pattern with a lower effect of two variables related to water supply and retention suggesting that different forces drive α and β diversity. The observed patterns indicate that niche processes have a considerable influence on β diversity. Diversity additive partitioning revealed a large proportion of β diversity at broader scales, with 46.3 % of overall diversity at the regions scale. The high proportion of less frequent species suggests that a large protected area would be necessary to represent most species. However, β diversity results showed that their effectiveness to conserve grasslands diversity would be improved by splitting the effort to represent each one of the four sampled geographical regions. A final opinion article complement the work arguing that disturbances are essential to conserve grasslands diversity and shall be reintroduced within grasslands protected areas through specific management actions.

Key words: Beta diversity, Diversity partitioning, Grassland community, Redundancy Analysis, South Brazilian *Campos*.

Lista de Figuras

Introdução Geral

Capítulo 1. The grasslands of the Campos de Cima da Serra region (South Brazilian *Campos*): floristic and functional diversity

Capítulo 2. The role of environmental factors and spatial processes on highland grassland communities of South Brazilian *Campos*

Capítulo 3. Diversity of grasslands across spatial scales in highland Southern Brazil *Campos* and implications for conservation

Lista de Tabelas e Apêndices

Capítulo 1. The grasslands of the *Campos de Cima da Serra* region (South Brazilian *Campos*): floristic and functional diversity

Capítulo 2. The role of environmental factors and spatial processes on highland grassland communities of South Brazilian *Campos*

Capítulo 3. Diversity of grasslands across spatial scales in highland Southern Brazil *Campos* and implications for conservation

SUMÁRIO

Introdução Geral

Apresentação

Os Campos Sulinos são ecossistemas típicos da região sul do Brasil. Desenvolvem-se sob clima temperado e úmido e abrigam uma notável diversidade taxonômica, com cerca de 2.200 espécies de plantas, e com um considerável grau de endemismo (Boldrini 2009). Dentre as diferentes tipologias regionais existentes merecem destaque os campos de altitude localizados no Planalto Meridional, também conhecidos como Campos de Cima da Serra. Estes campos, em 2002, totalizavam 7.653 km^2 (Cordeiro & Hasenack 2009), ocupando grande parte do nordeste do estado do Rio Grande do Sul. Uma característica singular destes campos é a existência de dois processos geradores de tensão ecológica.

O primeiro corresponde ao clima atual, que afeta a coexistência entre os campos com a floresta com Araucária, numa paisagem caracterizada por mosaicos vegetacionais (Rambo 1956a; Teixeira et al. 1986; Leite & Klein 1990) (Fig. 1). Estudos realizados nessa região mostram que há uma permanente tendência ao adensamento de arbustos e ao avanço da colonização florestal sobre os campos (Pillar & Quadros 1997; Machado 2004; Oliveira & Pillar 2004; Duarte et al. 2006).

O segundo corresponde a um regime de distúrbios generalizado, de natureza antrópica, representado pelo pastejo permanente por rebanhos bovinos associado a queimadas periódicas, que são praticadas para renovar as pastagens naturais (Figs. 2-4). Estes distúrbios impedem o domínio da comunidade campestre por espécies competitivamente superiores (Overbeck et al. 2005), favorecem a presença de dicotiledôneas (Fontaneli & Jacques 1988; Eggers & Porto 1994) e detém o avanço das florestas sobre os campos (Pillar & Quadros 1997).

Figura 1. Paisagem dos Campos de Cima da Serra. Matriz campestre com presença de manchas de floresta com Araucária em Bom Jesus, RS, Brasil. Foto: E. Vélez-Martin (Fevereiro 2009).

Figura 2. Fisionomia geral das comunidades campestres nos Campos de Cima da Serra. Caracterizada pelo domínio de espécies cespitosas, pela baixa altura média da vegetação e pelo pouco acúmulo de biomassa no verão em função do tipo de manejo. São Francisco de Paula, RS, Brasil. Foto: E. Vélez-Martin (Fevereiro 2009).

Figura 3. Queimadas nos campos de São Francisco de Paula, RS, Brasil. Os incêndios são geralmente de baixa intensidade por conta do pouco acúmulo de biomassa em função do manejo. Foto: E. Vélez-Martin (Setembro 2008).

Figura 4. Fisionomias dos campos em função das queimadas e do pastejo em São José dos Ausentes, RS, Brasil. No primeiro plano, o tom alaranjado indica campos que foram recentemente queimados; no segundo plano, o tom paleáceo indica campos que não foram queimados; no terceiro plano, o tom verde indica o rebrote dos campos após a queima. Foto: E. Vélez-Martin (Setembro 2008).

Entretanto, as consequências destes processos sobre a estrutura e a dinâmica dessas comunidades campestres ainda não são totalmente compreendidas. Os estudos realizados ao longo do meu doutorado trataram de avaliar, neste contexto ambiental, os padrões de diversidade das comunidades campestres dos Campos de Cima da Serra. Em especial, foram avaliados os efeitos de gradientes ambientais sobre os padrões de diversidade observados e suas contribuições relativas em diferentes escalas espaciais. Como desdobramento do trabalho foram feitas algumas considerações sobre a necessidade de manejo e de conservação da vegetação campestre na região.

Os Campos Sulinos como modelo para estudos de diversidade

Os ecossistemas campestres correspondem a uma das principais fisionomias da vegetação terrestre sendo caracterizados pelo predomínio da vegetação herbácea, principalmente de espécies graminóides, e pela ausência ou apenas uma pequena presença de árvores. Estas formações vegetais, tipicamente abertas, ocupam atualmente cerca de 8,3 % da superfície terrestre. Entretanto, a vegetação herbácea também é encontrada em outras fisionomias vegetais em que o elemento lenhoso tem uma grande presença, como no caso das savanas e outras formações arbustivas, de tal forma que num sentido amplo a vegetação campestre está presente em cerca de 40% da superfície terrestre, excluindo a Groenlândia e a Antártida (White et al. 2000).

As singularidades dos ecossistemas campestres podem ser mais bem compreendidas quando analisadas em contraste com as florestas. De um modo geral, enquanto as espécies florestais preferem ambientes sombreados, as espécies campestres evitam a falta de luz; enquanto as folhas caídas das árvores se decompõem rapidamente, a biomassa campestre se decompõe mais lentamente e o mantilho é frequentemente consumido nas queimadas; enquanto o fogo geralmente destrói a estrutura das florestas, ele é essencial para manter grandes áreas de campos e savanas tropicais (Bond & Parr 2010).

Existem múltiplas definições para os ecossistemas campestres. Uma definição sucinta é dada pelo *Oxford Dictionary of Plant Sciences*: “Os campos ocorrem onde há umidade suficiente para o crescimento das herbáceas, mas onde as condições ambientais, tanto climáticas como antrópicas, impedem o desenvolvimento das árvores. Sua ocorrência, portanto, se correlaciona com uma intensidade de chuvas entre a dos desertos e a das florestas, sendo estendida pelo pastejo ou pelo fogo, formando um plagioclímax em muitas áreas que foram previamente florestadas” (Allaby 1998). Entretanto, os campos também ocorrem em algumas regiões com regimes pluviométricos compatíveis com a presença de florestas, como é o caso dos campos do sul do Brasil.

Esta fisionomia campestre denominada de Campos Sulinos (Eiten 1992; Overbeck et al. 2007; Pillar et al. 2009) distribui-se desde as áreas planálticas da fronteira do estado de São Paulo com o estado do Paraná, onde há uma brusca interrupção da tropicalidade (Ab'Sáber & Marigo 2006), e gradualmente toma conta da paisagem na direção do Rio Grande do Sul, conectando-se, finalmente, aos campos e pampas do Uruguai e da Argentina. Este complexo de formações campestres do cone sul do continente sul americano totaliza aproximadamente um milhão de km^2 e constitui uma das principais formações de campos temperados do planeta (Soriano et al. 1992; Bilenca & Miñarro 2004; Pallarés et al. 2005).

A presença destes campos em áreas passíveis de desenvolvimento florestal tem intrigado naturalistas desde o século XIX (Lindman 1906). No entanto, conforme proposto por Rambo (1956a; 1956b) e por Klein (1975) estes campos correspondem à vegetação mais antiga, constituindo relictos de um clima mais seco, sendo a expansão das florestas um processo recente. Durante o Quaternário (últimos 2,6 milhões de anos) a alternância entre períodos glaciais e interglaciais tem sido determinante no processo de expansão e retração das formações campestres no hemisfério sul (Bredenkamp et al. 2002).

Estudos de perfis palinológicos no sul do Brasil têm permitido elucidar a dinâmica espacial pretérita dos campos e das florestas, detectando uma dominância da vegetação campestre antes e durante o último período glacial, e também entre o início e a metade do Holoceno, em condições de clima seco/frio e seco/quente, respectivamente (Behling et al. 2004; Behling et al. 2005; Behling & Pillar 2007). Além disso, apresentam evidências de expansão florestal sobre os campos, especialmente nos últimos cinco mil e, mais intensamente, desde os últimos 1000 anos, como decorrência do clima úmido e da ausência de uma estação seca marcante.

Portanto, na maior parte dos casos, estes campos não correspondem a ecossistemas secundários, derivados do desmatamento, estando presentes muito antes da chegada dos primeiros grupos humanos na América do Sul, há cerca de doze mil anos. Por outro lado, os impactos das atividades humanas como o desmatamento, as queimadas e a criação de gado têm modificado o curso da história ambiental da região, retardando o avanço das florestas sobre os campos e causando profundas transformações na estrutura das comunidades campestres.

Embora constituam uma unidade do ponto de vista ecológico, os Campos Sulinos apresentam uma diferenciação latitudinal, tanto em termos florísticos, como na sua fisionomia e configuração espacial. Ao norte, estes campos distribuem-se sobre os derrames basálticos do Planalto Meridional, dispostos em grandes manchas espacialmente desconectadas, formando encraves de campos associados principalmente à Floresta com Araucária. Estes campos são também conhecidos como campos de altitude (Behling et al. 2009) e integram a Província do Paraná (Cabrera & Willink 1980) e o Bioma Mata Atlântica (IBGE 2004). Ao sul, os campos distribuem-se sobre planícies e elevações menos pronunciadas, e correspondem à fisionomia predominante da paisagem. Estes campos também denominados de subtropicais (Behling et al. 2009) integram a Província Pampeana (Cabrera & Willink 1980) e o Bioma Pampa (IBGE 2004), sendo também reconhecidos como parte dos *Pastizales del Rio de la Plata* (Soriano et al. 1992).

Em uma escala regional os Campos Sulinos apresentam variações florísticas e fisionômicas associadas ao clima, à topografia e à heterogeneidade dos solos (Boldrini 1997) e aos regimes de distúrbios (Pillar & Quadros 1997). Várias tipologias regionais campestres já foram reconhecidas e descritas para o estado do Rio Grande do Sul com base em diferenças na composição de espécies e famílias botânicas, na presença de espécies endêmicas, nas condições edáficas e na localização geográfica, incluindo: os Campos de Cima da Serra, os Campos de barba de bode, os Campos de solos rasos, os Campos de solos profundos, os Campos dos areais, os Campos do centro do Estado, os Campos litorâneos e os Campos da Serra do Sudeste (Boldrini 1997; 2009).

Entretanto, o conhecimento ecológico de cada um destes tipos campestres ainda permanece bastante limitado, o que subestima a sua diversidade e valor de conservação (Ferreira et al. 2010). A insuficiência de levantamentos florísticos e fitossociológicos tem limitado as estimativas de diversidade, das conexões florísticas entre estas tipologias e do estado atual de ameaça de cada uma delas (Overbeck et al. 2007). Além disso, a falta de conhecimento sobre os padrões espaciais das comunidades campestres e dos seus fatores causais é uma etapa imprescindível para estabelecer hipóteses sobre seu funcionamento ou para avaliar o impacto de distúrbios locais ou globais (Lezama et al. 2006) e compromete a adoção de políticas de conservação, restauração e uso sustentável dos campos.

Tratar de responder parte destas lacunas de conhecimento para os Campos de Cima da Serra foi o objetivo geral deste trabalho. Para tanto, o delineamento amostral teve abrangência regional, incluindo a descrição da composição e da cobertura relativa das espécies campestres em parcelas distribuídas de forma estratificada, a fim de representar a heterogeneidade de condições ambientais. Os estratos para alocação das unidades amostrais foram estabelecidos com base nos principais gradientes ambientais, que reconhecidamente exercem influência sobre as comunidades campestres, incluindo as variações de temperatura e de pluviosidade, os tipos de solo, a orientação solar e a declividade do relevo. A partir daí foram formuladas uma série de questões associadas aos padrões de diversidade biológica.

As questões iniciais que se buscou responder foram as seguintes: É possível identificar dentro dessa região tipos distintos de comunidades campestres? Existem espécies que podem ser consideradas indicadoras dessas comunidades? Os tipos funcionais de plantas (formas de crescimento) apresentam diferenciações entre essas comunidades? Qual o padrão de riqueza de espécies observado em escala local e como ele varia entre os tipos de comunidades? Estas questões são tratadas no Capítulo 1 da tese.

Padrões de Diversidade em Comunidades Campestres

A visão moderna sobre as comunidades biológicas, incluindo as comunidades campestres, integra em grande parte o conceito individualista de Gleason (Gleason 1926), no qual elas não correspondem a superorganismos com fronteiras distintas e rígidas, mas adota também parte do conceito holístico de Clements (Clements 1916), segundo o qual elas não são apenas uma associação fortuita de espécies, mas conjuntos particulares, cuja estrutura e funcionamento são regulados pelas interações interespecíficas (Ricklefs 2010).

De fato, as distribuições das espécies raramente são idênticas, conformando comunidades fechadas, mas ao contrário, apresentam distribuições mais ou menos independentes ou sobrepostas, umas em relação às outras, ao longo dos gradientes ecológicos, revelando estruturas de comunidades abertas. Esta compreensão foi fortalecida com a observação de que cada espécie pode apresentar maior abundância em determinado ponto do gradiente ambiental, conforme descrito no conceito de *continuum* (Whittaker 1956), de tal forma que a distribuição de cada espécie é o resultado das suas adaptações às condições ambientais e das interações com as demais espécies ao longo do gradiente. As comunidades biológicas representam, portanto, grupos de espécies que coexistem, e que conformam arranjos não casuais, complexos e heterogêneos (Quinn & Dunham 1983; Orlóci 1993).

As características do ambiente local e a heterogeneidade da paisagem são fatores que sabidamente influenciam a alocação das espécies potencialmente colonizadoras do *pool* regional em comunidades locais no espaço geográfico (Peres-Neto & Legendre 2010). Entretanto, além do controle ambiental (Hutchinson 1957) e das interações biológicas, outros fatores como as diferenças na capacidade de dispersão entre as espécies (MacArthur & Wilson 1967), a limitação na dispersão (Hubbell 2001), a aleatoriedade demográfica e os distúrbios (Pickett & White 1985) podem também ser responsáveis pelas diferenças observadas no número de espécies em cada comunidade e na variação da sua composição. Portanto, os padrões espaciais observados nas comunidades biológicas são consequência de múltiplos fatores causais, cujas contribuições relativas dependem de cada contexto ambiental (Borcard et al. 1992).

Para decompor o problema e avaliar o grau de influência destes fatores é necessário definir inicialmente um conjunto de descritores dos padrões espaciais da comunidade. A diversidade taxonômica é uma das abordagens mais utilizadas para representar a organização das comunidades biológicas. Sua relação com o espaço foi estabelecida nos conceitos de diversidade gama (γ), alfa (α) e beta (β) (Whittaker 1960; 1972): o conjunto completo de espécies que ocorre em uma região de interesse corresponde à diversidade γ; dentro desta região, o número de espécies em cada sítio particular, cujas dimensões são normalmente arbitrárias, corresponde à diversidade α; e a variação na composição de espécies entre os sítios, dentro dessa região, corresponde à diversidade β.

A diversidade α e a diversidade β têm sido tradicionalmente utilizadas em estudos de ecologia de comunidades sendo tratadas como variáveis resposta que refletem a ação de diferentes fatores geradores e mantenedores destas comunidades (Grace 1999). Na busca desses fatores devemos levar em conta que os processos determinísticos podem não ser a única fonte de variação da diversidade. Se por um lado os gradientes ambientais atuam como um filtro, selecionando espécies de acordo com a suas adaptações fisiológicas ou morfológicas, ou seja, de acordo com seus nichos (Whittaker 1956; Hutchinson 1957; Tilman 2004), por outro lado a composição de espécies também pode variar sob as mesmas condições ambientais. A percepção de que os padrões espaciais na composição das comunidades podem ser gerados pelas próprias espécies, mediante a limitação da dispersão, por exemplo, independente das variações ambientais, trouxe à tona a importância dos processos neutros na estruturação das comunidades biológicas (Hubbell 2001; Adler et al. 2007).

A combinação da teoria do nicho e da teoria neutra em estudos sobre a origem da diversidade β foi sistematizada por Legendre et al. (2005) que propõem como ponto de partida três hipóteses a serem testadas com dados empíricos. A primeira hipótese tem o papel de modelo nulo e propõe que a composição de espécies é uniforme ao longo de extensas áreas. Neste caso a diversidade β é muito baixa, por conta do domínio de um número limitado de espécies competitivamente superiores (Pitman et al. 1999; Pitman et al. 2001). A segunda hipótese alega que a composição de espécies flutua de forma aleatória e autocorrelacionada. Esta hipótese deriva de modelos da teoria neutra que consideram que as espécies são demográfica e competitivamente equivalentes. Neste caso, as diferenças observadas são geradas a partir da dispersão espacialmente limitada das espécies, estabelecidas de forma aleatória a partir do *pool* de espécies da metacomunidade, juntamente com o possível surgimento de novas espécies que evoluem em diferentes áreas (Bell 2001; Hubbell 2001; He 2005). A terceira hipótese baseia-se no controle ambiental e alega que a distribuição das espécies é relacionada com as condições ambientais (Hutchinson 1957; Tuomisto et al. 1995).

As hipóteses que buscam explicar a geração da diversidade β não são mutuamente exclusivas. Estudos recentes têm demonstrado que ambos os processos podem agir ao mesmo tempo, com sua importância relativa variando de acordo com a região, a sazonalidade e a escala espacial (Tuomisto et al. 2003; Chust et al. 2006; Gravel et al. 2006; Laliberté et al. 2009; Rominger et al. 2009; Li et al. 2011).

Uma das abordagens metodológicas mais promissoras para decompor os efeitos dos fatores causais sobre a diversidade β é a partição da variância na composição de espécies entre fatores ambientais e fatores espaciais, combinando Análises de Redundância (RDA) com

Análise de Redundância Parcial (pRDA) para retirar o efeito de covariáveis e avaliar os efeitos compartilhados (Borcard et al. 1992; Legendre et al. 2005). As variações associadas aos fatores ambientais podem ser atribuídas a fatores de nicho e a variação espacial pura tem sido associada a fatores neutros, geradores de autocorrelação espacial na distribuição das espécies (Legendre et al. 2009). Neste caso o espaço não é uma variável *per se*, mas uma expressão de processos neutros sobre a composição da comunidade que não foram diretamente avaliados, ao contrário dos fatores ambientais. A inclusão da variável espacial em modelos canônicos e de regressão tem sido feita com base no método de Análise de Coordenadas Principais de Matrizes Vizinhas (PCNM) (Borcard & Legendre 2002; Borcard et al. 2004) a partir das informações do sistema de coordenadas planas das unidades amostrais. A análise de PCNM gera um conjunto de variáveis espaciais explanatórias que abrange todo o espectro de escalas incluídas na matriz de dados e define com quais delas a variável resposta tem uma relação estatisticamente significativa (Borcard et al. 2004).

Com base neste tipo de abordagem foram formuladas questões adicionais relacionadas com os padrões de diversidade observados nas comunidades dos Campos de Cima da Serra. Quais são as variáveis ambientais mais importantes para explicar as variações observadas na diversidade α e na diversidade β? Os gradientes locais de orientação solar e de declividade são suficientemente fortes para propagar seu efeito sobre a diversidade das comunidades campestres em escalas maiores ou, ao contrário, os gradientes climáticos, geomorfológicos e edáficos regionais são preponderantes? As variáveis ambientais têm efeitos relevantes sobre a diversidade ou são menos importantes do que os fatores supostamente neutros? Estas questões são tratadas no Capítulo 2 da tese.

Diversidade e Conservação dos Campos de Cima da Serra

Os campos figuram entre os ecossistemas mais antropizados (Hannah et al. 1995) e menos protegidos do planeta (Henwood 1998). A preocupação global com a conservação dos campos temperados é ainda incipiente (TGCI 2008). Os campos temperados, juntamente com as savanas, estão entre os biomas terrestres com a situação global mais crítica – cerca de 45,8% de conversão e apenas 4,6% de proteção (Hoekstra et al. 2005). Este panorama é válido para os Campos Sulinos, um bioma negligenciado no Brasil, que detém uma expressiva biodiversidade, mas que se encontra seriamente ameaçado pela intensificação dos sistemas agrícolas (Overbeck et al. 2007).

Nos Campos de Cima da Serra, os atuais remanescentes campestres correspondem a 44% da sua área de distribuição original (Cordeiro & Hasenack 2009) e vêm sendo progressivamente convertidos pela agricultura, pelas pastagens com espécies forrageiras exóticas e pela silvicultura.

O grau de conservação dos Campos Sulinos em áreas protegidas é muito baixo. No estado do Rio Grande do Sul, os campos têm apenas 2,58% dos seus remanescentes em unidades de conservação (Brandão et al. 2007), indicando uma insuficiência de representação nesta modalidade de proteção ambiental.

O conhecimento dos padrões de diversidade campestre pode ser de grande utilidade no estabelecimento de novas áreas protegidas. Independente de quais sejam os seus processos geradores e mantenedores, os padrões de diversidade β podem orientar a tomada de decisões em conservação. A maioria das espécies não está presente em todos os locais e a estrutura espacial das comunidades biológicas não é somente um artefato oriundo de processos aleatórios atuais ou históricos. Na maioria dos casos, ela resulta de diferenças ambientais ou mesmo de processos históricos singulares desenvolvidos em áreas ambientalmente homogêneas. Por conta disso, deve-se preservar essa organização espacial das comunidades biológicas ou as relações espécie-ambiente que são necessárias para recriar e manter a diversidade β (Legendre et al. 2005).

Além disso, deve-se considerar também que os padrões de diversidade e seus fatores causais podem variar em função da escala espacial. Por conta disso, recomenda-se a análise das relações padrão/processo em várias escalas, de forma a detectar a escala onde estas relações são biologicamente mais significativas (Metzger 2003). Numa escala de maior abrangência espacial, os fatores ambientais regionais (e.g., clima e solo), podem se tornar mais fortes que os fatores ambientais locais (e.g., topografia). Por outro lado, as limitações ou fatores ambientais que operam em escala local podem ser tão intensos na determinação de padrões que sobrepujam fatores que variam em escala regional (Peters et al. 2008). O conhecimento sobre quais são as escalas em que a diversidade β é maior não é algo trivial, ele pode ajudar a aperfeiçoar o manejo e as estratégias de conservação (Gering et al. 2003) e também a eficiência de programas de pesquisa e monitoramento da diversidade biológica (Ligeiro et al. 2009).

A combinação de delineamentos amostrais espacialmente aninhados com a partição aditiva da diversidade biológica tem sido uma abordagem metodológica utilizada para decompor a importância relativa da diversidade β em diferentes escalas espaciais (Veech et al. 2002; Crist et al. 2003; Veech 2005; Veech & Crist 2010). Considerando um espectro de escalas espaciais (hábitats, paisagens, regiões, por exemplo) a diversidade α observada na escala mais fina, somada à diversidade β dessa mesma escala, equivale à diversidade α do nível imediatamente superior e assim por diante. Logo, é possível expressar a diversidade γ observada em um delineamento baseado em três escalas espaciais como sendo $\gamma = \alpha 1 + \beta 1 + \beta 2 + \beta 3$. A combinação deste procedimento com aleatorização baseada em diferentes modelos nulos tem também possibilitado quantificar o quanto os padrões observados são casuais ou se estão associados a determinados processos ecológicos subjacentes (Veech et al. 2002).

A partição aditiva da diversidade pode ajudar a definir áreas prioritárias para a conservação ao revelar em quais escalas se observa a maior amplitude de variação na composição de espécies. Este tipo de informação encontra sintonia com o princípio da complementariedade utilizado na biologia da conservação (Kirkpatrick 1983), que trata de resolver o problema do conjunto mínimo, ou seja, como conservar um número maior de alvos de conservação com a menor área possível, de forma a reduzir os custos das ações de conservação e garantir que toda a biodiversidade receba algum nível de investimento de conservação (Wilson et al. 2009).

Esta abordagem foi aplicada no estudo das comunidades dos Campos de Cima da Serra permitindo tratar das seguintes questões: Como se comporta a diversidade β nas diferentes escalas espaciais abrangidas no delineamento amostral utilizado? Em quais destas escalas é possível identificar as maiores contribuições nas variações de composição das espécies? De que modo os desdobramentos destes padrões poderiam guiar a definição de novas unidades de conservação na região? Estas questões foram tratadas no Capítulo 3 da tese.

Os estudos desenvolvidos nos Capítulos 1, 2 e 3, juntamente com o conhecimento produzido em trabalhos anteriores sobre a dinâmica das comunidades campestres na região dos Campos Sulinos permitiram fazer considerações adicionais sobre a conservação dos campos em unidades de conservação. A partir da constatação de que a proteção dos campos, especialmente em áreas de proteção integral, pode resultar na eliminação do regime de distúrbios, cujas consequências podem ser incompatíveis com os objetivos de conservação inicialmente pretendidos, incluindo extinções locais de espécies e em alguns casos, da própria formação campestre, desenvolvemos um conjunto de reflexões com base na visão de que no caso dos campos, a conservação das espécies não pode ser dissociada da conservação dos distúrbios. Este tema foi tratado no Capítulo 4, buscando responder a seguinte questão: a extinção dos Campos Sulinos em unidades de conservação deve ser considerada como um fenômeno natural ou como um problema ético?

A tese foi estruturada na forma de quatro capítulos, com abordagens complementares, e apresentados na forma de artigos científicos. O Capítulo 1 intitula-se “As comunidades campestres na região dos Campos de Cima da Serra (Campos Sulinos, Brasil): diversidade florística e funcional” e está formatado de acordo com as normas do periódico *Biodiversity and Conservation.* O Capítulo 2 intitula-se “A influência de fatores ambientais e de processos espaciais nas comunidades campestres de altitude dos Campos Sulinos” e está formatado de acordo com as normas do periódico *Journal of Vegetation Science.* O Capítulo 3 intitula-se “Diversidade campestre em diferentes escalas espaciais nos Campos Sulinos de altitude e suas implicações para a conservação” e está formatado de acordo com as normas do periódico *Natureza & Conservação*. O Capítulo 4 intitula-se “Extinção dos Campos Sulinos em Unidades de Conservação: um Fenômeno Natural ou um Problema Ético?” e está formatado de acordo com as normas do periódico *Natureza & Conservação.* Este artigo foi publicado numa versão parcialmente reduzida no volume 8 (1), páginas 84-86, em julho de 2010.

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Capítulo 1. (Artigo 1) The grasslands of the Campos de Cima da Serra region (South Brazilian *Campos*): floristic and functional diversity[1]

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Key words: plant communities, *Mata Atlântica* biome, diversity of plants

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[1] Este artigo será submetido ao periódico *Biodiversity and Conservation*

Abstract

This study describes the floristic and functional diversity of the mesic highland grasslands in the northeast of Rio Grande do Sul state, Brazil, one of the physiognomies of South Brazilian *Campos* and regionally known as *Campos de Cima da Serra*. These grasslands have been used for livestock production and frequent fires are used for pasture management. We delimited a region of 18,667 km^2 with 41% of grasslands remnants to conduct a floristic survey in 320 (one square meter) plots placed using a random stratified sampling, considering climate, soil, aspect and relief gradients. Plots with 0.25m^2 were recorded regarding species cover data. A total of 390 taxa belonging to 53 families were recorded. Total richness estimators ranged from 473 (ICE) to 527 (Jackknife 2) species. Asteraceae, Poaceae, Fabaceae and Cyperaceae comprised 59% of total species. Species-abundance distribution included few cover dominant and frequent core species, mostly caespitose graminoids, and a high number of low cover with low frequency satellite species. Four community types were revealed by cluster analysis and corresponding indicator species were established. Communities showed very low proportion of annual species, a high proportion of species with reserve organs and low proportion of hibernal grasses. Environmental regional gradients seem to be more important than local environmental gradients in defining community types. The observed richness confirmed the characteristic high diversity of South Brazilian *Campos*. High species richness at the plot level and the high forbs richness were indicative of the large-scale disturbance regime. We interpret the current composition and structure of these grasslands as an expression of a convergence process, driven by fires and grazing, that selects those disturbance tolerant species and detains the dominance of tall grass species.

Introduction

South Brazilian grasslands constitute one of the main vegetation physiognomies in the region and have been referred as *Campos* (Lindman 1906; Rambo 1956; Boldrini 1997; Pillar & Quadros 1997) or South Brazilian *Campos* (Overbeck et al. 2007; Pillar et al. 2009). Starting at approximately latitude 24.5 S (NE of Paraná state), they extend southward, composing with the *pampas* and *campos* in Argentina and Uruguay the most important temperate grassland zone in South America (Soriano et al. 1992; Bilenca & Miñarro 2004), which originally covered near 1 million km^2. Remarkably features include the high diversity in grasses and a decreasing North-South proportion between macrothermic (C4) and microthermic (C3) grasses (Burkart 1975).

On a continental scale, these grasslands belong to two different biogeographical provinces. The northern portion corresponds to the Paraná province (Cabrera & Willink 1980). It has a smaller area and corresponds to the highland grasslands distributed, in Brazil, in the states of Paraná, Santa Catarina and northern half of Rio Grande do Sul. The southern portion corresponds to the Pampean province and is also known as *Rio de la Plata* Grasslands (Soriano et al. 1992).

On a regional scale these grasslands show floristic and physiognomy variations associated to climate, topographic and soil heterogeneity (Boldrini 1997), but also with disturbance regimes, especially grazing and fires (Pillar & Quadros 1997). In Rio Grande do Sul state, a preliminary classification proposed seven grassland types according to differences in composition of plant species and families, the presence of endemic plant species, soil conditions and geographical location (Boldrini 2009). However, the understanding of the heterogeneity of these grasslands is still limited, which underestimates their diversity and conservational value (Ferreira et al. 2010). Regional floristic and community surveys may provide better estimates of species alpha and beta diversity and a more refined grassland classification, as well as the assessment of community type endangerment in the South Brazilian *Campos* (Overbeck et al. 2007). Furthermore, the lack of knowledge on grassland spatial patterns and their drivers undermines grassland restoration, conservation policies and predictions.

Surveys on the community composition at landscape and regional scales are scarce (Boldrini et al. 2009) and mostly conducted in the Argentinean Pampas (Burkart et al. 1990; Burkart et al. 1998; Perelman et al. 2001; Chaneton et al. 2005) and in the basaltic region of Uruguay (Lezama et al. 2006). We applied a similar approach to study the heterogeneity of the highland basaltic grasslands in the *Campos de Cima da Serra* region (Fortes 1959; Behling et al. 2009). These grasslands occur in the northeast of *Rio Grande do Sul* state, and represent one of the main areas of South Brazilian *Campos* remnants. According to the Brazilian environmental legislation they were recently recognized as *campos de altitude* whose conversion to agriculture/silviculture are restricted under the Atlantic Forest Biome - *Mata Atlântica* federal law nº 11,428 (Brazil´s House of Representatives 2006).

A recent floristic inventory of this region revealed a very high diversity of 1,161 species, 107 of them endemics (Boldrini et al. 2009). The maintenance of this diversity and current physiognomy, especially of mesic grasslands, is dependent on a regime of frequent disturbances combining grazing at medium/low pressure and regular anthropogenic burning (2-3 years interval) that detains the dominance of tall caespitose grasses and woody species encroachment (Pillar & Quadros 1997; Overbeck et al. 2005). Grassland communities in the *Campos de Cima da Serra* show high seasonality in the biomass production. Part of the ungrazed biomass produced in spring and summer remain attached to the plants as senescent leaves and dry with the arrival of cooler winter season and frosts. Despite being controversial, fires in late winter are a traditional practice to eliminate accumulated biomass and to stimulate sprouting of fresh biomass (Pillar and Quadros 1997; Vincent 1935) and therefore the existing grassland communities reflect the long-term effects of such a disturbance regime.

In this paper, based on a regional survey designed to encompass climatic, soil and topographic gradients, we describe the diversity of floristic and functional composition of these mesic grasslands communities under typical grazing/fire disturbance regimes. We identify community types and indicator species and analyze small-scale alpha and beta diversity to gain a better understanding of spatial patterns and possible long-term effects of the disturbance regime.

Material and methods

Study site

The study area comprised 18,667 km^2 in the northeast of Rio Grande do Sul state, southern Brazil (27.48º/29.49ºS;49.7º/52ºW) (Fig.1.). It was delimited based on the physiographic *Campos de Cima da Serra* region proposed by Fortes (1959), shifting political limits to those of equivalent natural landscape units (SEMA et al. 2007).

The region lies on a highland plateau formed by successive flows of basalt and rhiodacyte extrusive volcanic rocks (120-135 My BP) with altitudes ranging from 1,400 to 600m a.s.l., decreasing from east to west (Weber et al. 2004). The relief is smoothly undulate to undulate with some typical conic mammillary shaped hills and frequent rocky outcrops (Almeida 2009; Horbach 1986). Soils in the East belong mainly to cambisols (*Cambissolo Húmico Alumínico)* and in the West to ferralsols (*Latossolo Bruno Aluminoferrico* and *Latossolo Vermelho Aluminoférrico húmico/distroférrico húmico)* according to the Brazilian system of soil classification (EMBRAPA 2006; Streck et al. 2008).

The climate is warm temperate (subtropical) and humid and is classified as “Cfb” (Köppen 1948). Annual precipitation ranges from 1,600 to 2,162 mm and is regularly distributed along the year (IPAGRO 1989), increasing during spring and summer (Matzenauer et al. 2007). Mean annual temperature ranges from 13.6 to 18.6ºC (IPAGRO 1989) and frosts are frequent on winter when sometimes snowfall occur. In the East, fogs are common (92 fog days/year) closer to the scarp (Moreno 1961). Temperature and precipitation are not spatially homogeneous. Annual mean temperature ranges from 12.7 to 18.6 ºC along ESW-WSE direction and annual precipitation ranges from 1,587 to 2,164 mm along N-S direction (Hijmans et al. 2005).

In 2002, the grasslands remnants in the *Campos de Cima da Serra* correspond to 41 % of the region and to 44% of the original estimated grassland cover(14,463 km^2) (Cordeiro & Hasenack 2009). The landscape alternates wide-open areas of mesic grasslands, with narrow hygrophilous patches and mosaics with Araucaria forest (mixed ombrophylous forest) (IBGE 2004). A typical homogeneous appearance is given by large and abundant populations of Poaceae species, mostly with caespitose erect habit and austral summer cycle, like *Andropogon* *lateralis* Nees, which at the end of its annual life cycle gives a yellowish color to the landscape (Boldrini et al. 2009).

These grasslands have continuously been replaced mostly by agriculture, cultivated pastures and exotic trees plantations. In the West, agriculture has expanded over grasslands that remains only in small and isolated patches. In the East, grasslands are still conserved in large and continuous patches corresponding to the landscape matrix. The *Antas* river crosses the central region in the E-W direction and a deep-forested valley divides Western grasslands in the northern half, limited by *Pelotas* river at the North and the southern half, limited by *Caí* river, in the South. Grazing and human-induced fires shape grasslands physiognomy maintaining a homogeneous appearance, with low height, little litter deposit and without shrubs and trees.

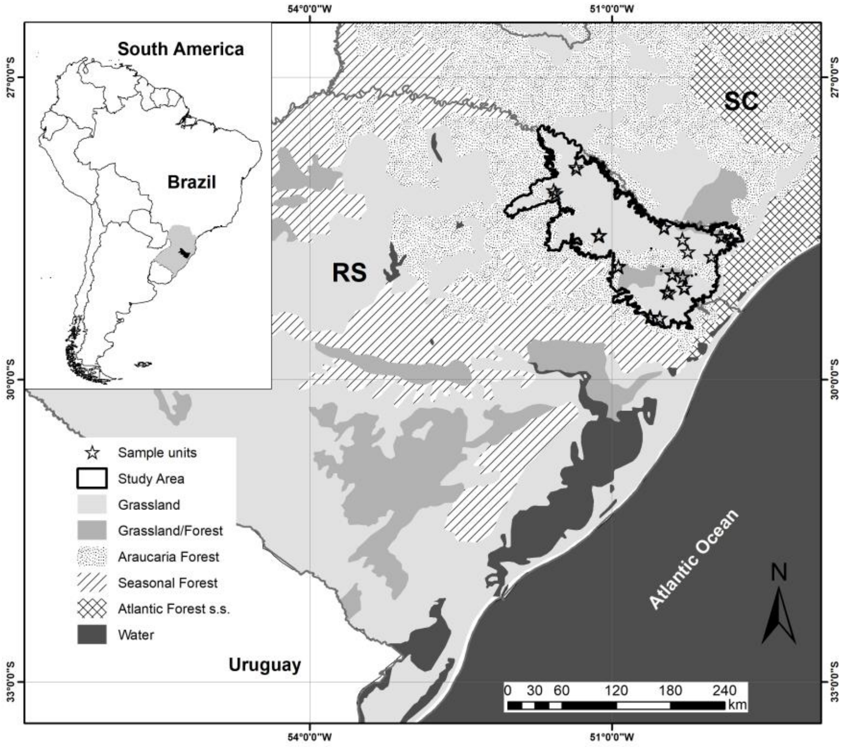

Figure 1. South Brazilian *Campos* and Araucaria forest distribution with spatial location of the study area – the *Campos de Cima da Serra* region. Mapped vegetation is the expected original distribution before the arrival of European settlers (IBGE 2004).

Sampling design and field data collection

We sampled 320 plots within an area ranging 160 km of latitude and 170 km of longitude (Fig. 1). To ensure representativeness of the main climatic, edaphic and topographic gradients, we set a stratified nested design across different spatial scales.

First, we sampled eight climate strata, combining different levels of annual mean temperature (13.6-15, 15.1-16.5, 16.6-18.6 ºC) and annual mean rainfall (1600-1750, 1751-1900, 1901-2050, 2051-2200 mm) based on WorldClim – Global Climate Data (Hijmans et al. 2005). From the twelve strata, we selected only those with the presence of grassland remnants. Within each climate strata, two farms (sites) where chosen by placing random points over mapped grassland remnants accessible by road. Within each farm, a cluster of four relief–aspect strata (northern hillslope, southern hillslope, tophill and lowland) was sampled considering ease of access. Within each relief–aspect strata we set a transect with five 1m^2 plots (20m distant from each other). In each plot we recorded the presence of plant species (presence-absence data). Inside the plot, a 0.25m^2 plot (0.5 x 0.5 m) was set to visually estimate species performance based on the aboveground percentage cover (cover data), considering a scale of 5% intervals and the cover values of 1, 2 and 3% under the 5% limit. Bare soil and rock cover were also recorded. Whenever necessary specimens were collected for further identification. Species and author names are in accordance with The Plant List (www.theplantlist.org) and family circumscription follows APGIII (2009) and Smith et al. (2006).

Field sampling was conducted from December 2008 to February 2009, during austral summer season, when reproductive organs are present allowing reliable species identification. To exclude extreme situations of grassland management, samples were taken excluding those areas with signs of previous burning episodes or without grazing. Peat bogs and permanently wet grasslands were also excluded from sampling. We assumed that with these exclusion criteria the disturbance regime of sampled areas was approximately similar.

Data analysis

Floristic patterns were analyzed by using the presence-absence data. The pattern of species richness increase with additional sampling effort was analyzed with a species accumulation curve using sample based rarefaction (Gotelli and Colwell, 2001) and Mao tau analytical solution to estimate observed mean richness and confidence limits (Colwell *et al*. 2004). Non-parametric total richness estimators Chao 1, Chao 2, Jackknife 1st order and 2nd order were also evaluated (Colwell and Coddington, 1994). Both analyses were performed with EstimateS 8.2 (Colwell, 2009). Each dot in the species accumulation curves of species estimators corresponds to estimated mean after 100 randomizations in sample units order.

For the analysis of functional patterns each species was assigned to a plant functional type (PFT) according to: 1) life forms: chamaephytes/phanerophytes, hemicryptophytes, geophytes (bulbous, rhizomatous or tuberous), therophytes and lianas; 2) growth forms: shrubs, reptant graminoids, caespitose graminoids, reptant forbs, rosulate forbs, erect forbs and lianas and 3) metabolic pathways: C3 and C4. Species assignment took into account Overbeck & Pfadenhauer (2007), Freitas et al. (2009) and Sosinski & Pillar (2004).

For the analysis of community structural patterns, we used the cover data. We calculated, for each species in the raw table (320 plots x 315 species), the following descriptors: absolute (AF) and relative (RF) frequency, absolute (CA) and relative (CR) cover and Importance Value Index (IVI) by adding up RF and CR values.

The cover data for the 320 original plots were merged within each 80m transect resulting in a data matrix of 64 transects and 315 species. This data matrix was subjected to classification and ordination analysis. Species present in less than 10% of the transects were excluded from the analyses. Classification and ordination were based on a dissimilarity matrix of chord distances between plots (Podani 2000). Community types were established by a hierarchical clustering method based on incremental sum of squares between groups (Ward 1963; Orlóci 1967), and submitted to bootstrap analysis to establish cluster groups sharpness (Pillar 1999a; Pillar 1999b). Main gradients in the species composition were evaluated with ordination by Principal Coordinates Analysis (PCoA), and ordination axis stability and sampling sufficiency were evaluated by bootstrap resampling (Pillar 1999a; Pillar 1999b). The same ordination analysis was done using data in which the cover of species belonging to the same PFT, according to growth form, was pooled. These analyses were performed with Multiv Software (Pillar 2008).

For each community type indicator species were identified with the INDVAL method (Dufrene & Legendre 1997) using the “labdsv” library (Roberts 2006) of the R statistical language (R Development Core Team, 2007). Plant community types were named based on indicator species with higher IVI values.

Community types were compared regarding the relative cover of each family and the species richness of each family, using a homogeneity test using chi-square. The internal heterogeneity of community types was explored by examining the sum of squares within the groups generated in the incremental sum of squares clustering process for cover data (Ward 1963; Orlóci 1967) and Sorensen similarity index for presence-absence data.

Species diversity in the plots was characterized using species richness, for 1 m^2 plots, and Shannon diversity index (H’) and Pielou eveness index (J) for 0.25 m^2 plots (Pielou 1966; 1975). Data on species richness at plot level were submitted to ANOVA with randomization test to compare community types (Pillar & Orlóci 1996; Manly 1997). ANOVA was also applied to compare community types regarding the ratio of C3/C4, annuals/perennials and presence/absence of reserve organs, using the ratios calculated with species richness and cover.

To explore the association of community types with some categorical environmental variables we also applied a chi-square test. Environmental variables considered were topographic position (northern hillslope, southern hillslope, tophill and lowland), soil types (cambisol and ferralsol), latitude (North, Center, and South) and longitude (West, Center, and East). The latter two variables were established dividing the North-South range and the West-East range in three equal classes, respectively.

Results

A total of 390 taxa, belonging to 53 families, was recorded in the floristic survey. This includes 23 that could be identified only to the genus level, seven to the family level and five species not identified at all (Appendix 1). Three new species were discovered, including one of the genera *Anagalis* sp., one of the genera *Fimbristylis* sp. and *Chevreulia revoluta* A.A. Schneid. & Trevis. (Schneider et al. 2011).

Four families comprised 59% of total species richness: Asteraceae (94), Poaceae (77), Fabaceae (33), Cyperaceae (26); and 26 families were represented by only one species. The most species rich genera were *Baccharis* (10), *Eupatorium* (11), *Oxalis* (10), *Vernonia* (9), *Polygala* (9), *Eryngium* (8), *Paspalum* (8), *Hypochaeris* (7), *Bulbostylis* (7), *Chascolytrum* (7), *Rhynchospora* (7), *Chaptalia* (6), *Galium* (6), *Aristida* (6) and *Verbena* (6).

Compositional patterns were also analyzed through plant functional types. Hemicryptophytes was the most frequent life form (245 species, 63%), followed by geophytes (72 species, 18%), chamaephytes (44 species, 11%), therophytes (27 species, 7%) and lianas (2 species, 1%). Species distribution within growth forms revealed that erect forbs and caespitose graminoids were dominants, with 35% and 26% of total species, respectively. Other groups included reptant forbs (14%), rosulate forbs (12%), shrubs (11%), reptant graminoids (2%) and lianas (1%).

According to life cycle, 352 (90.3%) species were perennials and 27 (6.9%) were annuals. Within annuals, graminoids were represented by only two species of Poaceae (*Polypogon chilensis* and *Vulpia bromoides)* and forbs by 25 species. Many species (139, 35.6%) presented below-ground reserve organs, especially rhizome and xilopodium but also a variety of other reserve organs like bulbs, corms, tubers, stolons and rhizofore. Within Poaceae, 25 species (32.4%) presented C3 and 52 species (67.5%) presented C4 metabolic pathway.

The species accumulation curve, through sample rarefaction, showed that stability was not achieved. However, the true species richness was estimated using different non-parametric estimators: ICE (473 species ± 0.01 SD), Chao 1 and Chao 2 (478.36 species ± 24.02 SD), Jackknife 1 (483.71 species ± 10.58 SD) and Jackknife 2 (527.59 species). Comparing the observed with the lowest and greatest estimated richness the sampling representativeness ranged from 74 to 82% of total richness (**Figure 2**).

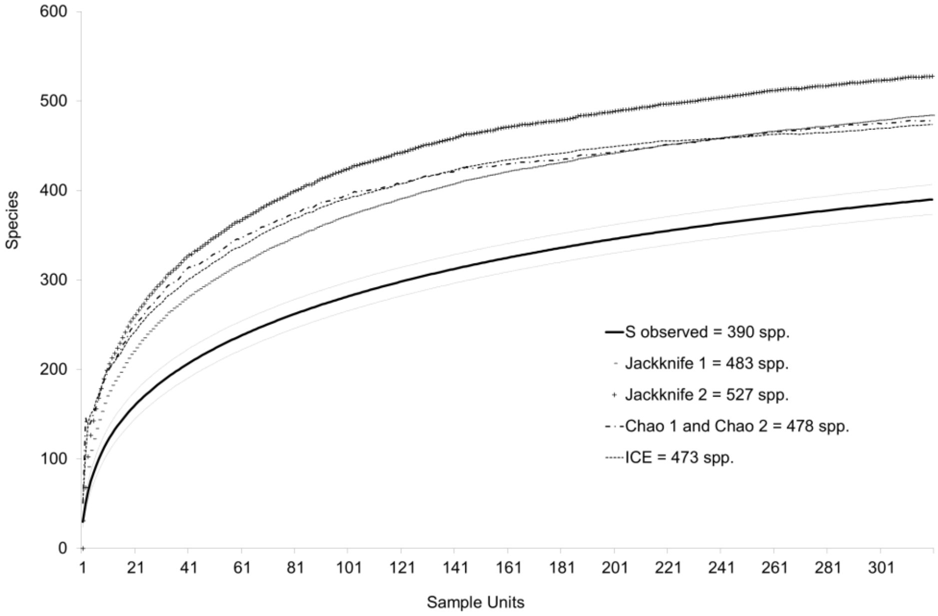

Figure 2. Species accumulation curve considering 320 plots ($1m^2$) and comprising the total area sampled in *Campos de Cima da Serra* region, RS, Brazil. The line is the mean richness calculated through "Mau tau" analytical solution and dotted lines are the 95% confidence intervals. Additional curves correspond to species richness estimators based on incidence data.

Few species presented a wide distribution range and only eleven species were represented in more than 50% of sampled plots of the floristic survey: *Andropogon lateralis, Schizachyrium tenerum, Paspalum plicatulum, Gamochaeta americana, Dichanthelium sabulorum, Piptochaetium montevidense, Eragrostis lugens, Galium humile, Chaptalia integerrima, Baccharis trimera, Axonopus affinis.* A set of 69 species had intermediary frequencies (11-50%) and 310 species (79,5% of all species) were recorded in less than 10% of plots, with 94 found in only one plot (uniques) (**Figure 3a**).

The cover data contained 315 taxa, distributed in 46 families. Combining species constancy with cover, we detected an inversion in the floristic families rank. Poaceae dominated the physiognomy of the community with the highest accumulated IVI (54.8%), followed by Asteraceae (15.8%), Cyperaceae (10.5%) and Fabaceae (5%). Caespitose graminoids were dominants with the highest accumulated IVI (54.3%), followed by erect forbs (13.9%), reptant graminoids (10.9%), rosulate forbs (8.2%), reptant forbs (6.8%), shrubs (5.5%) and lianas (0.3%).

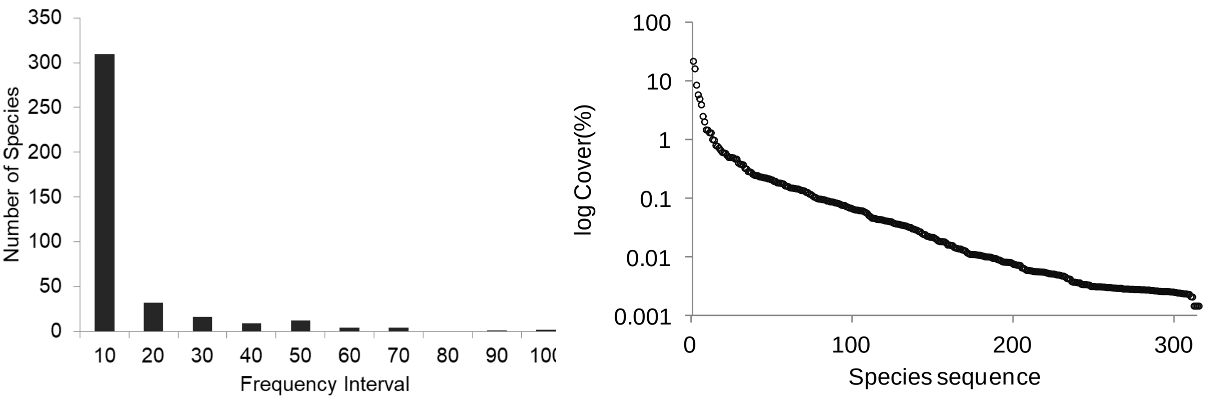

Figure 3. a) Frequency histogram of grassland species, grouped into 10% frequency intervals based on floristic survey of 320 plots (1 m^2 plots) on grassland communities in *Campos de Cima da Serra* region, RS, Brazil. b) Rank abundance plot, based on structural survey, after pooling 320 plots. Cover percentage (y) is plotted on logarithmic scale against a species rank of decreasing cover percentage (x).

The species-abundance distribution was also characterized by a few dominant species and a high percentage of very low cover species. Only 14 dominant species had relative cover values higher than 1%, considering the relative cover after pooling all sample units (**Figure 3b**). The 20 species with the highest IVI included 13 caespitose and reptant graminoids (Poaceae and Cyperaceae). Dominant forbs were represented by the erect forb *Galium humile* (Rubiaceae), the reptant forb *Dichondra sericea* (Convolvulaceae), the rosulate forbs *Chaptalia runcinata* (Asteraceae) and *Gamochaeta americana* (Asteraceae) and the shrubs *Bacharis pentodonta, B. trimera, B. sagittalis (*Asteraceae) (**Table 1**).

Cluster analysis was performed with a 137 species x 64 plots matrix, after removing species present in less than 10% of the plots. Four sharp groups were obtained among sampling units and considered as different communities: (A) *Andropogon lateralis* - *Gamochaeta americana* community, (B) *Rhynchospora flexuosa* – *Axonopus siccus* community (C) *Schizachyrium tenerum* - *Macroptilium prostratum* community (D) *Paspalum notatum* - *Desmodium incanum* community (Appendix 2).

Community A (*Andropogon lateralis-Gamochaeta americana*). This community type was the most frequent and with the highest richness per plot. It occurred only on cambisol zone and geographic distribution included the middle-south and middle-east zones. Six indicator species were selected, with the rosulate forb *Gamochaeta americana* and the caespitose graminoid *Andropogon lateralis* with higher values. Other species included the forbs *Wahlenbergia linarioides*, *Polygala pulchella*, *Stenachaenium adenanthum* and *Plantago australis*.

Table 1. Top 20 IVI valued grassland species sampled in the structural survey. (IVI = importance value index, N = sampling units of occurrence, RF = relative frequency, RC = relative cover).

Family	Species	Growth Form	IVI%	N	RF%	RC%
Poaceae	*Andropogon lateralis*	Caespitose graminoid	13.66	293	4.75	22.57
Poaceae	*Schizachyrium tenerum*	Caespitose graminoid	10.69	283	4.59	16.80
Poaceae	*Paspalum notatum*	Reptant graminoid	5.37	116	1.88	8.85
Poaceae	*Paspalum plicatulum*	Caespitose graminoid	5.06	251	4.07	6.05
Cyperaceae	*Rhynchospora flexuosa*	Caespitose graminoid	3.55	121	1.96	5.14
Poaceae	*Piptochaetium montevidense*	Caespitose graminoid	3.32	158	2.56	4.09
Poaceae	*Axonopus affinis*	Reptant graminoid	2.30	124	2.01	2.60
Poaceae	*Eragrostis lugens*	Caespitose graminoid	1.87	55	2.38	1.36
Poaceae	*Dichanthelium sabulorum*	Reptant graminoid	1.78	76	2.54	1.01
Poaceae	*Axonopus siccus*	Caespitose graminoid	1.75	123	1.99	1.51
Rubiaceae	*Galium humile*	Erect forb	1.64	83	2.59	0.68
Asteraceae	*Gamochaeta americana*	Rosulate forb	1.50	147	2.38	0.62
Poaceae	*Paspalum pumilum*	Reptant graminoid	1.49	104	0.89	2.09
Cyperaceae	*Scleria sellowiana*	Caespitose graminoid	1.38	157	1.23	1.52
Convolvulaceae	*Dichondra sericea*	Reptant forb	1.36	53	1.69	1.04
Cyperaceae	*Rhynchospora barrosiana*	Caespitose graminoid	1.36	102	1.35	1.37
Asteraceae	*Baccharis trimera*	Shrub	1.24	107	1.73	0.75
Asteraceae	*Baccharis pentodonta*	Shrub	1.23	160	1.65	0.80
Asteraceae	*Baccharis sagittalis*	Shrub	1.12	46	1.64	0.61
Asteraceae	*Chaptalia runcinata*	Rosulate forb	1.09	147	1.70	0.48
Total			62.8	-	45.6	79.9

Community B (*Rhynchospora flexuosa-Axonopus siccus*): Also restricted to the cambisol zone and with a middle east occurrence, this community was the most poor in species per plot but showed the highest mean eveness and beta diversity. It presented a higher cover of Cyperaceae in detrimental of Poaceae. Within the seven indicator species the caespitose graminoids *Rhynchospora flexuosa, Scleria sellowiana* (Cyperaceae), *Axonopus siccus* and the reptant graminoids *Paspalum pumilum* (Poaceae) presented notable coverage values. Other indicator species included *Galium humile, Euphorbia peperomioides* and *Chevreulia revoluta.*

Community C (*Schizachyrium tenerum-Macroptilium prostratum):* This community was the least frequent and with the higher homogeneity among plots. It presented a wide distribution and was more frequent in the middle and cambisol zone. Thirteen indicator species was selected and the caespitose graminoid *Schizachyrium tenerum* outperformed *Andropogon lateralis*. Several Fabaceae species were characteristic, including reptant forbs *Macroptilium prostratum, Rhynchosia corylifolia, Aeschynomene falcata* and *Aeschynomene elegans* and the erect forbs *Tephrosia adunca and Galactia pretiosa.* The shrub species *Desmanthus virgatus* and *Baccharis pentodonta* were selected as indicators only in this community type. Other indicator species included *Chaptalia runcinata, Halimium brasiliense, Krapovickasia macrodon* and *Borreria capitata.*

Community D (*Paspalum notatum-Desmodium incanum):* Lowest eveness and main distribution on ferralsol zone featured this community type. It occurred mostly in the northwest zone. Dominance of the reptant grass *Paspalum notatum* was typical. Two species of Fabaceae erect forbs, *Desmodium incanum* and *Trifolium riograndense,* also showed higher indicator values and several Asteracea were selected including *Chevreulia sarmentosa, Chevreulia acuminata, Aspilia montevidensis, Vernonia chamaedrys and Conyza bonariensis.* Other indicator species included *Diodia radula, Steinchisma decipiens, Setaria parviflora, Mnesithea selloana, Aristida spegazzinii, Aristida venustula, Sisyrinchium vaginatum* and *Eryngium pandanifolium.*

The ordination of plots based on species cover data along the two first ordination axes (**Figure 4a**) showed an overlap between communities A and B. Communities C and D were makedly different in relation to them, but community C showed divergence, along de Axis II and community D, along the Axis I. Community D was the less similar in relation to other communities and, like community B, showed higher dispersion among plots. Community C presented the highest internal homogeneity.

The ordination based on cover data of growth forms showed a great overlap of plots from communities A, B and C and a gradual shift to community D, widely spreaded along axis I (**Figure 4b**). The formers were grouped by a very high dominance of caespitose graminoids and the latter showed a gradual shift with increasing ratios between reptant and caespitose graminoids. The second axis was associated with increasing levels of forbs and shrubs. Community B distinguished by a lower presence of these growth forms.

The four communities did not show differences in species richness proportions among dominant families ($\chi^2 = 1.75$, df = 9, p = 0.99). However, differences were significant when considering relative cover of families ($\chi^2 = 37.8$, df = 12, $p < 0.01$) (**Figures 5a** and **5b**). When considering growth forms the communities also did not show differences when considering species richness proportions ($\chi^2 = 3.23$, df = 18, p = 1), but show significant differences in relative cover ($\chi^2 = 78.7$, df = 18, $p < 0.01$) (**Figures 5c** and **5d**).

Plant communities were not associated with topographic position of plots ($\chi^2 = 5.26$, df = 3, p =0,3635). However, distribution of communities showed differences in frequency according to soil types ($\chi^2 = 5.26$, df = 3, $p < 0.01$), latitude ($\chi^2 = 5.26$, df = 3, $p < 0.01$) and longitude ($\chi^2 = 5.26$, df = 3, $p < 0.01$) (**Figure 6**).

Mean species number in the floristic survey (1m^2 plots) was 29.78 species (standard deviation = 7.17), ranging from eight to 54 species. Mean species number in the structural survey (0.25 m^2 plots) was 19.27 species (standard deviation = 5.14), ranging from four to 35 species.

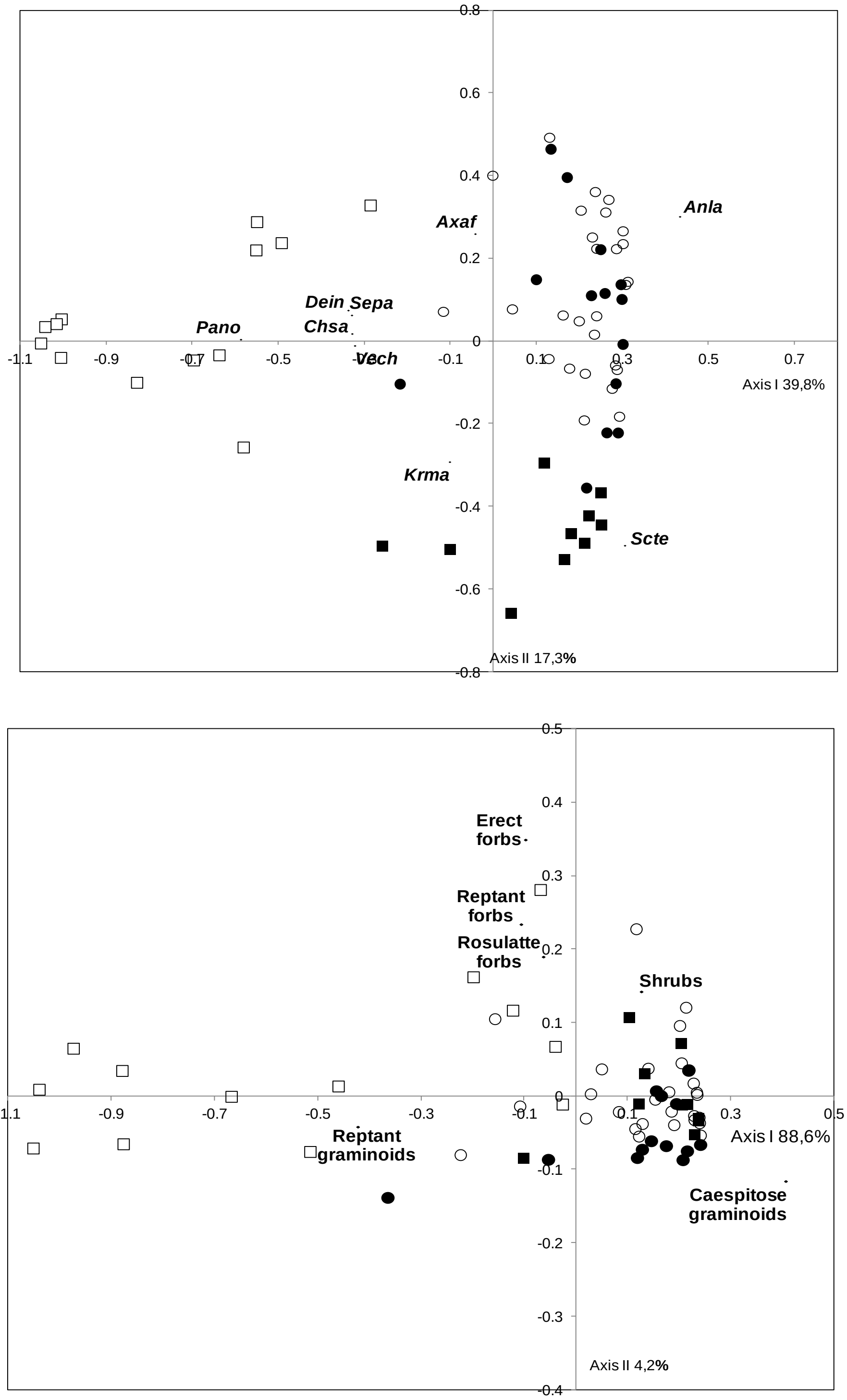

Figure 4. Ordination diagrams (PCoA of the 64 transects; chord distance as dissimilarity measure) of grassland vegetation in *Campos de Cima da Serra* region, RS, Brazil. a) Plots based on species cover data. Axis I showed sample sufficiency and stability for the observed pattern. Anla = *Andropogon lateralis*, Scte = *Schizachyrium tenerum*, Sepa = *Setaria parviflora*, Chsa = *Chevreulia sarmentosa*, Dein = *Desmodium incanum*, Vech = *Vernonia chamaedrys*, Pano = *Paspalum notatum*, Axaf = *Axonopus affinis*, Krma = *Krapovickasia macrodon*; b) Plots based on growth forms cover data. Plot labels are identified according to community types defined through cluster analysis. Species and growth forms correlated more than 0.4 with the ordination axes were plotted in both diagrams. Empty circles = community type A, full circles = community type B, full squares = community type C, empty squares = community type D).

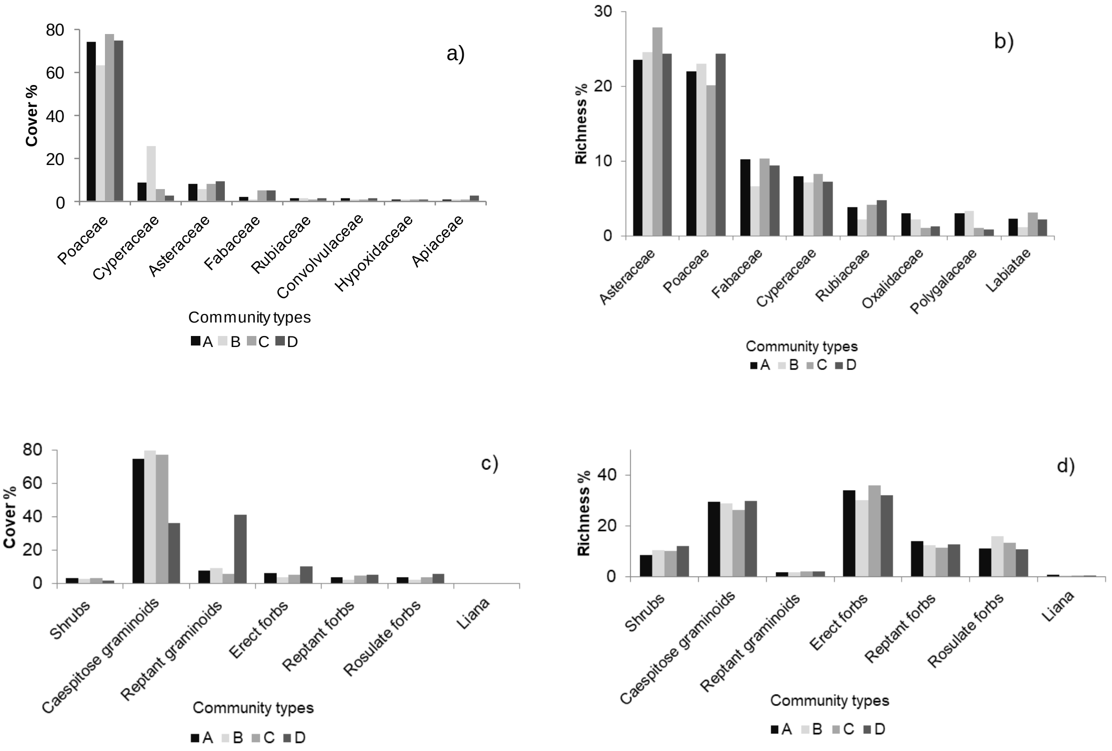

Figure 5. Cover percentage (a) and species richness percentage (b) distribution within main families (a, b) and within growth forms (c, d) for each community type.

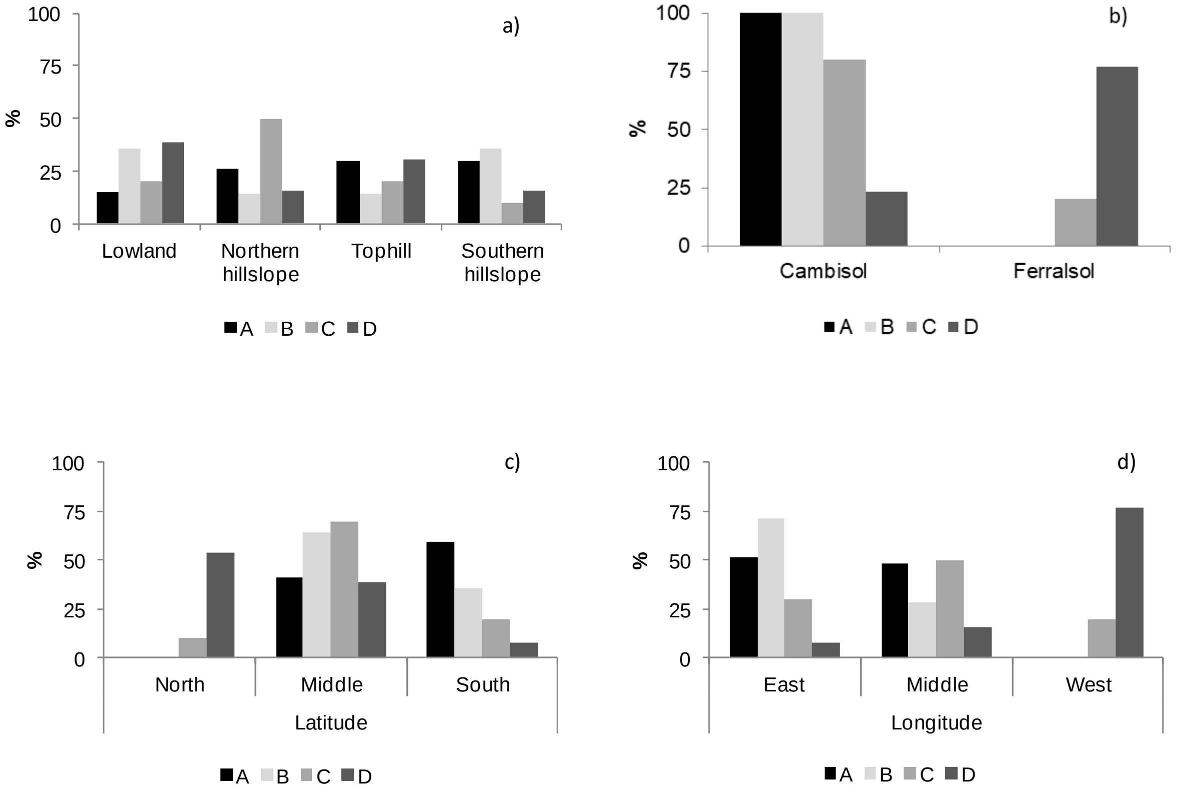

Figure 6. Relative frequency of each community type in relation to: a) topographic position, b) soil type, c) latitude zone and d) longitude zone.

The diversity and evenness indexes obtained for the community, considering jointly the 320 survey plots, were H' = 3.28 nats ind^{-1} and J = 0.57. Shannon diversity at the plot level ranged from 0.31 to 2.63 with a median of 1.97 nats ind^{-1} and Pielou equitability ranged from 0.17 to 0.82, with a median of 0.68. Both indexes presented negative skewed distribution. For differences in diversity and evenness indexes for community types, see **Table 2**.

Table 2. Diversity, similarity and environment descriptors of grassland community types of the *Campos de Cima da Serra* region.

Community type	**A** *Andropogon lateralis-Gamochaeta americana*	**B** *Rhynchospora flexuosa – Axonopus siccus*	**C** *Schizachyrium tenerum-Macroptilium prostratum*	**D** *Paspalum notatum - Desmodium incanum*
N° plots	135	70	50	65
Total richness	264	183	194	234
Mean plot (1m^2) richness (SD)**	32.1 (5) ^{a}	24.7 (6.1) ^{c}	31.2 (6.6) ^{ab}	29.4 (9.5) ^{b}
Max-Min plot richness	21 -49	15 - 39	20 - 49	8 – 54
Mean Shannon diversity (SD)**	2.05 (0.29)^a	1.96 (0.25)^b	1.92 (0.32)^b	1.71 (0.57)^c
Mean Evenness**	0.67 (0.08)^a	0.70 (0.06)^b	0.66 (0.08)^a	0.59 (0.15)^c
Exclusive species	59	31	17	49
Mean similarity (Qualitative)	0,53	0,48	0,54	0,47
Mean SSw (Quantitative)	0.50	0.74	0.25	0.65
Mean Open Soil % (SD)*	9.1 (9.6) ^{ab}	7.1 (10.2) ^{a}	11.8 (11.2) ^{b}	8.3 (10.1)^{ab}
Soils	Cambisol (only)	Cambisol (only)	Cambisol (mainly)	Ferralsol (mainly)

Significant differences of the contrasts between communities A, B, C and D are indicated for some variables (n.s.: non-significant, *: p<0.1, **: p<0.01, ***: p<0.001). Mean similarity: Sorensen similarity index; Mean SSw: mean Sum of Squares within groups, lower values represent higher similarity.

The cover ratio of annuals/perennials species was extremely low and communities means ranged from 0.38 to 0.71%, but without significant differences among community types (Q_b = 0.83, p=0.407). The species richness ratio of annuals/perennials was also low, ranging from 3.8 to 5.2%, and with no significant differences (Q_b = 19.1, p=0.133). The cover ratio of species with presence/absence of reserve organs was similar among the communities A, B and C, with means of 28.8 to 37%, but different in relation to community D with a mean of 299% (Q_b= 0,000073, p=0,001), mostly related to *Paspalum notatum* presence. Otherwise, the richness ratio of species with presence/absence of reserve organs was balanced and a little higher in communities A (89.3%), C (95.1%) and D (82.6%) than in community B (79.3%) (Q_b = 1881.1, p=0.068). The cover ratio of C3/C4 grass species was low and a little higher in communities C (11.5%) and D (22.4%) in relation to communities A (7.8%) and B (2.8%) (Q_b = 2861.7, p=0.001). The mean grass species richness C3/C4 ratio ranged from 30.4 to 46.4% but showed no differences between communities (Q_b = 2512.2, p=0.112).

Discussion

The total sampling effort distributed in the studied region resulted in 390 observed taxa and a total estimated richness ranging from 473 to 527 species. These numbers are lower than the 1,161 taxa previously listed for this region (Boldrini et al. 2009). However, we found 66 new taxa records, expanding the regional known grasslands richness to 1,227 taxa. Our study focused only on grasslands under mesic conditions and submitted to a regular disturbance regime of grazing and fires, while the regional list encompasses species in a wide range of habitats, including xeric and hygrophilous conditions, undisturbed sites and forest border grasslands that were not considered here. Therefore, the species subset limited to mesic grasslands conditions is probably a number closer to our estimates. Regardless of the actual gamma diversity, even the estimated richness for mesic grasslands is higher than the observed in regional surveys performed in the southern Rio de la Plata grasslands with 430 species in 90.000 km^2 of Flooding Pampa (Argentina) (Perelman et al. 2001) and Uruguayan basaltic grasslands (Lezama et al. 2006) with 274 species in 15.000 Km^2.

The floristic and structural results confirm some previous generalizations based on less systematic observations for the grasslands in *Campos de Cima da Serra* region: dominance of erect caespitose grasses with summer cycle; high percentage of bare soil; an expressive floristic diversity of Asteraceae; Fabaceae as the third most diverse family, but with scattered populations and low contribution to physiognomy; abundance of Cyperaceae species even in well drained grasslands (Mohrdieck 1980; Boldrini 1997; Matzenbacher 2003; Boldrini 2006; Boldrini 2009; Boldrini et al. 2009). On the other hand, species associated to well-drained grasslands like *Paspalum maculosum* and *Schizachyrium spicatum* were less frequent than *Paspalum plicatulum*, *Piptochaetium montevidense* and *Eragrostis lugens.*

The great species richness of Asteraceae is a common feature of the highland grasslands of Rio Grande do Sul, Santa Catarina and Paraná (Matzenbacher 2003). Southwards, in the Pampean grasslands of Brazil (Boldrini 2009), Uruguay (Lezama et al. 2006) and Argentina (Burkart et al. 1998) the species richness of Asteraceae decreases and Poaceae becomes the richest. The high diversity of Poaceae species in South Brazilian *Campos* results from the overlap of distribution areas of a larger group of tropical summer cycle species (macrothermic, C4 photosynthetic metabolism) and a lower group of extra-tropical winter-spring cycle species (microthermic, C3). The former are vegetative dormant in winter and flourish in summer and autumn and the latter develops in winter and flourish in spring (Burkart 1975; Longhi-Wagner 2003)

Grasslands physiognomy was characterized by a small group of graminoid core species, mostly Poaceae and some Cyperaceae, with high cover values and high constancy, accompanied by a diverse and variable group of satellite species, mainly forbs. On average, only three species presented cover values higher than 10% at the plot level, and only one species presented cover values higher than 25%. One of the most striking characteristics of these grasslands was the wide distribution of *Andropogon lateralis*, with high cover and present in 91% of the sampled plots. Probably this species benefits from the high regional moisture availability (IPAGRO 1989) combined with its pyrophilous traits, once anthropic burns are common in the region. According to Leite (1995) its distribution is the main distinctive physiognomic characteristic between the northern highland grasslands and the southern Pampean grasslands where its occurrence is limited to lowlands and surrounding wetlands. Northward it decreases gradually throughout Santa Catarina and Paraná states and becomes less common in Central Brazil (Longhi-Wagner 2003). Among satellite species, erect forbs were dominant in cover and number of species when compared to reptant and rosulate forbs, probably as a consequence of being more adaptive to competition with caespitose graminoids.

The four community types identified through cluster analysis showed no association with topography, suggesting that at the regional scale local environmental gradients are less determinant of community composition and structure than regional gradients. However, they also could be associated with differences in the land management history of the sampled grasslands. The community D was the most distinctive, with a two-layer physiognomy set by reptant and caespitose graminoids, and a higher frequency of erect forbs. This community type showed high association with ferralsol, but its distinctiveness seems to be primarily an effect of higher grazing pressure. The landscape context at the western region, where community D was the most frequent, correspond to more isolated patches of remnant grasslands in an agriculture matrix, while in the other regions grasslands are the main matrix and remain little fragmented by other land use types. Once the areas for cattle raising decrease we conjecture that land management becomes less uniform and grazing pressure becomes more intense and frequent, inducing changes in vegetation structure. This could explain the observed increment of *Paspalum notatum* and the decrease in *Schizachyrium tenerum*. In grasslands under higher grazing pressure the aerial biomass of grasses concentrates closer to the ground, and prostate plant types with stolons or rhizomes benefits over taller species (Diaz et al. 1992; Boldrini & Eggers 1996). In communities A, B and C dominance of tall tussocks grasses suggests lower grazing pressures.

Communities A and B showed high similarity and a distribution limited to the eastern zones, where moister conditions and frequent mists may have favored the development of *Andropogon lateralis* and species of Cyperaceae. Differences in communities dominated by *A. laterais* (A and B) and by *Schizachyrium tenerum* (C) have been previously recognized in the region and called as *Palha Grossa* and *Palha Fina* grasslands, respectively (Bradenburg 2001; Boldrini et al. 2009).

High species richness at the plot level, forbs richness and low quantity of litter (field observation) were ubiquitous indicating that these grasslands are under a large-scale disturbance regime. In fact, grasslands in the region are used for cattle grazing since the beginning of the 18th century (Porto 1954) and fires are a common tool in pasture management. Higher seasonality in the biomass production of these grasslands (Pillar & Quadros 1997) results in low forage availability in winter and imposes a low-density of livestock (1 animal per 2-3 ha) (Mohrdieck 1980). Furthermore, the low temperatures and frosts on winter increase standing dead biomass of vegetative dormant tussock grasses (Boldrini 1997). Therefore, ranchers regularly practice burns of low intensity in spring, with 2 to 3 years interval, to eliminate old and dead leaves of grass tussocks that accumulates in winter and are not consumed by ruminants, and to induce resprouting of fresh leaves for cattle feeding (Jacques 2003). Therefore, interaction of grazing, fires and environmental gradients are the main drivers of observed grasslands composition, structure and successional pattern.

Current grazing disturbance can be considered as the reintroduction of a suppressed ecossystemic process previously played by grazing megafauna (Pillar & Vélez 2010). In fact, grass species co-evolved with herbivores in South America since the beginning of the Miocene (MacFadden 1997). Disturbances are known to enhance species richness by lowering dominant species and by increasing spatial heterogeneity (Denslow 1985). Analysis of fine-scale post-fire dynamics on South Brazilian grasslands have shown that fire leads to a short-term increase in species richness and diversity at the plot scale and favors small herbs through removal of dominant tussock grasses. The nearly complete incineration of plant aerial portions increases resource availability of space, light and nutrients and consequently the impact of competitive dominance and thus extinction processes are kept low (Overbeck et al. 2005). Increase in dicotiledons at the expense of grasses after burning events has also been documented in regional studies (Castilhos & Jacques 1984; Fontaneli & Jacques 1988; Eggers & Porto 1994).

The observed cover dominance of caespitose graminoids was not sufficient to eliminate weaker competitors like erect and rosulate forbs and reptant forbs and graminoids and most plots presented a twofold structural pattern with few cover dominant graminoids and many satellite species. The observed life form and growth form community spectra were similar to those of regularly burned grasslands of Morro Santana, a southern granitic hill localized approximately 100 km of the study region with cover dominance by hemicryptophytic caespitose graminoids that resist fires but with a large number of geophytic and hemicryptophytic forbs species that resprout after fires, and a small percentage of species not able to resprout, including therophytes, hemicriptophytes and shrubs (Overbeck & Pfadenhauer 2007). Fires do not totally remove caespitose graminoids, just temporarily reduce their competitive dominance and succession tends towards the domination of the same species (Overbeck et al. 2005). In fact, tussock grasses profit from higher fire frequencies (Uys et al. 2004) and some species have their growth rates increased after burns (Silva et al. 1991; Trindade & Da Rocha 2001).

The current composition and structure of the grassland studied here contrast with expectations of how they would look like in the absence of such disturbances. Studies of excluded areas at grassland-forest boundaries have shown that grasslands are subject to a gradual shrub encroachment and invasion of forests species (Machado 2004; Oliveira & Pillar 2004; Müller 2005). In fact, grasslands in the region have been described as “islands” on the Araucaria forest domain (Leite 1995) and vicinity of forest vegetation represent a permanent source of diaspores and of ecological tension.

However, it also has been stressed that data from exclosures of fire and grazing indicate that not always grasslands inevitably evolve to shrubland or to a forest (Pillar & Quadros 1997) and data from long-term studies on grassland succession far away from the forest border are still not available. At which rate grasslands will evolve to a shrubland or to a forest remains to be investigated. On the one hand, grasslands in the region show low cover of shrubs and of pioneer forest, on the other hand, there is a high frequency of several species of shrubs, that seem not be affected by fires (Fidelis et al. 2012). Regardless the real potential for vegetation encroachment, the fact is that in the absence of such disturbances, grasslands would shift to more homogeneous tall tussocks communities or to patches with an increased density of shrubs and trees. Additionally, a progressive loss of species in the seed and bud bank would be expected in both cases, turning the current landscape physiognomy with great extensions of diverse non-woody grasslands into a mosaic of intermingled patches of shrubby grasslands, shrublands and forests.

Other important known pattern of these grasslands is the absence of major overall compositional changes after burnings - vegetation quickly recover to its pre-burn species composition as the majority of species resprout shortly after the fire (Eggers & Porto 1994; Quadros & Pillar 2001; Overbeck et al. 2005; Overbeck & Pfadenhauer 2007).

This sprouting ability is linked to bud protection and includes resisters - mainly caespitose graminoids with aboveground meristems protection, through basal leafs, and sprouters - with belowground organs, resulting in a community well adapted to the current fire regime (Overbeck & Pfadenhauer 2007).

The community showed a considerable presence of resisters and sprouters suggesting temporal stability in composition. After each new burning episode, vegetation regeneration occurs from different sources. First, occurs the reestablishment of native shrub, forb and graminoid species that were present before burning, through aboveground biomass; dormant seeds in the soil seed bank or buds in the below-ground bud bank (Fidelis et al. 2012), with the local extinction of a low number of fire-sensitive species. Then, a low number of new species colonizes the open microsites through germination of dispersed seeds or directly from the seed bank.

This pattern is reinforced by the lack of a group of fire followers - opportunistic species specialized in colonizing recently open post-fire areas and by the low number of annual species that use to benefit from disturbance events. Therophytes represented only 7% of total species and presented very low cover and frequency. Low number of therophytes seems to be a common ground in South Brazilian grasslands (Boldrini 1993; Garcia et al. 2002; Overbeck & Pfadenhauer 2007). As stated by Overbeck et al. (2005) the high small-scale diversity in these grasslands is due to recurrent disturbances and not to the presence of species that are specialized on different phases in post-fire development. A small number of exotic species was found, including the perennial *Spergularia grandis* and the annuals *Cerastium glomeratum, Sonchus oleraceus* and *Vulpia bromoides* also suggesting that the resprouting pattern of current grassland communities helps to detain strong colonization by outsiders.

Obviously, such a stable composition of species represents a subset of the regional pool of potentially occurring species. Our results showed a proportion of 32% of microthermic species of Poaceae, similar to the 34% found in the floristic regional list (Boldrini et al. 2009), but a very low C3/C4 cover ratio (mean of 10.3%), confirming the lower expression of these species. In addition, these grassland harbor 107 endemic species and several have winter or winter-spring cycle (Boldrini et al. 2009) or may be fire-sensitive. The number of observed endemics was also low, however not all endemic species occur in mesic grasslands and others may not have been recorded simply by insufficient sampling effort.

This survey allowed a comprehensive understanding of the main diversity patterns of *Campos de Cima da Serra* grasslands, considering both geographic amplitude and some environmental gradients. However, these patterns contain an intentional bias, once only mesic grasslands, subject to grazing and anthropic fires, were considered. This grassland type prevails in the region and the results indicate that they harbor a high species diversity, with high species richness mean values at the local scale. In general, the observed patterns suggest that disturbances associated with grazing and man-induced fires are compatible and even necessary to ensure the observed diversity. The dominance of Poaceae is typical of any grassland, but it is remarkable the large proportion of Asteraceae species and the high cover by Cyperaceae species. The fact that several species of the regional pool were not been sampled reveals the need for additional sampling effort but also suggests that this managed mesic grasslands could filter out some species more sensitive to such disturbances, like C3 species. On the other hand, the low number of exotic species also suggests that disturbances do not promote their invasion, demonstrating that current livestock farming practices are compatible with plant biodiversity conservation. Four types of communities were detected, some of them potentially associated with environmental gradients, like soil type, soil moisture, and grazing intensity. Additional efforts are necessary to understand these relationships.

Acknowledgements

We are grateful to Bruno S.G. Fonseca, Claudio Reis, Gabriel Specht Marcel Tust and Tiago Caetano Edruziane for help in field expeditions and Heinrich Hasenack and Eliseu Weber for aid with geoprocessing tools. Part of this work was carried out with the aid of a grant (LEAF) from the Inter-American Institute for Global Change Research (IAI) CRN-2005, which is supported by the US National Science Foundation (grant GEO-0452325). E.V.M received a doctoral CNPq scholarship. V.P. receives support from CNPq (306573/2009-1).

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Appendix 1. Floristic list of grassland communities in *Campos de Cima da Serra*. (FS = Species sampled in floristic and structural survey, F = species sampled only in floristic survey, *exotic species).

Family	Species	Survey	Community type	Life form	Growth form
Acanthaceae	*Carlowrightia sulcata*	FS	D	Hemicryptophyte	Erect forb
	Hygrophila verticillata	FS	C	Hemicryptophyte	Erect forb
	Ruellia bulbifera	FS	B	Geophyte	Erect forb
	Ruellia sp.	FS	A, C, D	Hemicryptophyte	Rosulate forb
	Stenandrium diphyllum	FS	A, B, C, D	Geophyte	Reptant forb
Alliaceae	*Nothoscordum bonariense*	FS	A	Geophyte	Erect forb
	Nothoscordum inodorum	FS	A	Geophyte	Erect forb
Amaranthaceae	*Pfaffia gnaphaloides*	FS	A, D	Geophyte	Erect forb
	Pfaffia tuberosa	FS	A, B, C, D	Geophyte	Erect forb
Apiaceae	*Apium leptophyllum*	FS	D	Therophyte	Erect forb
	Apium sellowianum	FS	D	Hemicryptophyte	Erect forb
	Bowlesia incana	FS	A	Therophyte	Reptant forb
	Centella asiatica	FS	B	Hemicryptophyte	Reptant forb
	Eryngium ciliatum	FS	C	Geophyte	Rosulate forb
	Eryngium ebracteatum	FS	A, B	Geophyte	Rosulate forb
	Eryngium eriophorum	FS	B	Geophyte	Rosulate forb
	Eryngium floribundum	FS	A, B, C, D	Geophyte	Rosulate forb
	Eryngium horridum	FS	A, C, D	Geophyte	Rosulate forb
	Eryngium pandanifolium	FS	B, D	Geophyte	Rosulate forb
	Eryngium sanguisorba	FS	B	Geophyte	Rosulate forb
	Eryngium zozterifolium	FS	B	Geophyte	Rosulate forb
	Hydrocotyle exigua	FS	A, B, C, D	Hemicryptophyte	Reptant forb
Apocynaceae	*Oxypetalum erectum*	F	A, C	Camephyte	Shrub
Aristolochiaceae	*Aristolochia sessilifolia*	F	D	Hemicryptophyte	Erect forb
Asclepidaceae	*Asclepias campestris*	FS	C, D	Camephyte	Shrub
Asteraceae	*Achyrocline satureioides*	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Acmella bellidioides	FS	A, B, C, D	Hemicryptophyte	Reptant forb
	Acmella decumbens	FS	A	Hemicryptophyte	Reptant forb
	Angelphytum oppositifolium	FS	A	Hemicryptophyte	Erect forb

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Aspilia montevidensis	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Asteraceae 01	F	D	-	-
	Asteraceae 02	FS	B	-	-
	Baccharis articulata	FS	D	Camephyte	Shrub
	Baccharis brevifolia	FS	B, C	Camephyte	Shrub
	Baccharis cognata	FS	B	Camephyte	Shrub
	Baccharis coridifolia	F	A, C, D	Camephyte	Shrub
	Baccharis dracunculifolia	FS	C, D	Camephyte	Shrub
	Baccharis erigeroides	FS	A	Camephyte	Shrub
	Baccharis hypericifolia	FS	A	Camephyte	Shrub
	Baccharis pentodonta	FS	A, B, C, D	Camephyte	Shrub
	Baccharis sagittalis	FS	A, B, C, D	Camephyte	Shrub
	Baccharis sp.	F	B, C, D	Camephyte	Shrub
	Baccharis trimera	FS	A, B, C, D	Camephyte	Shrub
	Baccharis uncinella	F	A, B	Camephyte	Shrub
	Calea cymosa	FS	A, D	Geophyte	Erect forb
	Calea phyllolepis	FS	D	Geophyte	Erect forb
	Calea uniflora	F	A	Geophyte	Reptant forb
	Calyptocarpus biaristatus	FS	A	Therophyte	Erect forb
	Chaptalia exscapa	FS	A, B, C, D	Hemicryptophyte	Rosulate forb
	Chaptalia graminifolia	FS	B	Hemicryptophyte	Rosulate forb
	Chaptalia integerrima	FS	A, B, C, D	Hemicryptophyte	Rosulate forb
	Chaptalia mandonii	FS	B	Hemicryptophyte	Rosulate forb
	Chaptalia runcinata	FS	A, B, C, D	Hemicryptophyte	Rosulate forb
	Chaptalia sinuata	FS	A, B, D	Hemicryptophyte	Rosulate forb
	Chevreulia acuminata	FS	A, B, C, D	Hemicryptophyte	Rosulate forb
	Chevreulia sarmentosa	FS	A, C, D	Hemicryptophyte	Rosulate forb
	Chevreulia revoluta	FS	A, B, C	Hemicryptophyte	Rosulate forb
	Conyza bonariensis	FS	A, B, C, D	Therophyte	Erect forb
	Conyza primulifolia	FS	A, B, C, D	Therophyte	Erect forb
	Elephantopus mollis	FS	A, C, D	Hemicryptophyte	Rosulate forb
	Erechthites hieracifolia	FS	A	Therophyte	Erect forb

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Eupatorium ascendens	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Eupatorium candolleanum	FS	A	Hemicryptophyte	Erect forb
	Eupatorium congestum	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Eupatorium laetevirens	FS	A, C, D	Hemicryptophyte	Erect forb
	Eupatorium laevigatum	FS	C, D	Hemicryptophyte	Erect forb
	Eupatorium rufescens	FS	A	Hemicryptophyte	Erect forb
	Eupatorium squarrulosum	FS	C, D	Hemicryptophyte	Erect forb
	Eupatorium tanacetifolium	FS	A, B, D	Hemicryptophyte	Erect forb
	Eupatorium tweedieanum	F	D	Hemicryptophyte	Erect forb
	Eupatorium umbelliforme	FS	C, D	Hemicryptophyte	Erect forb
	Eupatorium sp.	FS	C	Hemicryptophyte	Erect forb
	Facelis retusa	FS	A	Therophyte	Erect forb
	Gamochaeta americana	FS	A, B, C, D	Geophyte	Rosulate forb
	Gamochaeta coarctata	FS	D	Geophyte	Rosulate forb
	Gamochaeta filaginea	FS	B	Geophyte	Rosulate forb
	Hieracium commersonii	FS	A, B, C	Geophyte	Rosulate forb
	Holocheilus illustris	FS	A, C	Hemicryptophyte	Rosulate forb
	Holocheilus sp.	F	C	Hemicryptophyte	Rosulate forb
	Hypochaeris albiflora	FS	C	Hemicryptophyte	Rosulate forb
	Hypochaeris catharinensis	FS	A, B, C, D	Geophyte	Rosulate forb
	Hypochaeris chilensis	FS	A, B, C, D	Hemicryptophyte	Rosulate forb
	Hypochaeris megapotamica	F	A	Hemicryptophyte	Rosulate forb
	Hypochaeris radicata	FS	A	Hemicryptophyte	Rosulate forb
	Hypochaeris sp.	FS	B, D	Hemicryptophyte	Rosulate forb
	Hypochaeris variegata	F	C	Hemicryptophyte	Rosulate forb
	Lucilia acutifolia	FS	A, B, C, D	Geophyte	Erect forb
	Lucilia linearifolia	FS	A, B, D	Geophyte	Erect forb
	Lucilia nitens	F	A, C, D	Geophyte	Erect forb
	Mikania decumbens	F	A	Liana	Liana
	Noticastrum decumbens	FS	A, B, C, D	Hemicryptophyte	Rosulate forb
	Noticastrum sp.	F	D	Hemicryptophyte	Rosulate forb
	Pamphalea smithii	FS	A, B	Hemicryptophyte	Rosulate forb

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Podocoma hirsuta	FS	D	Hemicryptophyte	Rosulate forb
	Pseudognaphalium cheiranthifolium	FS	A, D	Therophyte	Erect forb
	Pterocaulon alopecuroides	FS	A, C, D	Hemicryptophyte	Erect forb
	Senecio brasiliensis var. brasiliensis	F	A, D	Camephyte	Shrub
	Senecio conyzifolius	FS	A, B, C, D	Camephyte	Shrub
	Senecio heterotrichius	F	B	Camephyte	Shrub
	Senecio oleosus	FS	A, B, C, D	Camephyte	Shrub
	Solidago chilensis	F	A, C	Therophyte	Erect forb
	Soliva pterosperma	FS	A, C	Therophyte	Rosulate forb
	*Sonchus oleraceus**	F	B	Therophyte	Erect forb
	Stenachaenium adenanthum	FS	A, B, C, D	Geophyte	Rosulate forb
	Stenachaenium campestre	FS	C, D	Geophyte	Rosulate forb
	Stenachaenium megapotamicum	FS	D	Geophyte	Erect forb
	Stevia lundiana	FS	A, B, C	Hemicryptophyte	Erect forb
	Stevia sp.	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Symphyotrichum graminifolium	FS	B	Hemicryptophyte	Erect forb
	Trichocline catharinensis	FS	A, B, C, D	Hemicryptophyte	Rosulate forb
	Vernonia chamaedrys	FS	C, D	Hemicryptophyte	Erect forb
	Vernonia flexuosa	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Vernonia florida	FS	C, D	Hemicryptophyte	Erect forb
	Vernonia megapotamica	F	A	Hemicryptophyte	Erect forb
	Vernonia nitidula	FS	A, C	Camephyte	Shrub
	Vernonia nudiflora	FS	C, D	Camephyte	Shrub
	Vernonia oligactoides	FS	D	Hemicryptophyte	Erect forb
	Vernonia sellowii	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Vernonia sp.	FS	A, C	Hemicryptophyte	Erect forb
Boraginaceae	*Moritzia dasyantha*	F	A, C, D	Camephyte	Shrub
Brassicaceae	*Lepidium aletes*	F	A	Therophyte	Erect forb
Calyceraceae	*Acicarpha tribuloides*	FS	D	Therophyte	Rosulate forb

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
Campanulaceae	*Lobelia camporum*	FS	B, C	Therophyte	Erect forb
	Lobelia hederacea	FS	A, B, D	Therophyte	Reptant forb
	Wahlenbergia linarioides	FS	A, B, C, D	Therophyte	Erect forb
Caryophyllaceae	*Cerastium commersonianum*	F	A, B, C	Therophyte	Erect forb
	*Cerastium glomeratum**	FS	A	Therophyte	Erect forb
	Paronychia camphorosmoides	FS	A, B, C, D	Hemicryptophyte	Reptant forb
	Paronychia chilensis	FS	A, B, D	Hemicryptophyte	Reptant forb
	Polycarpon tetraphyllum	F	B	Therophyte	Reptant forb
	*Spergularia grandis**	F	A	Hemicryptophyte	Erect forb
Cistaceae	*Halimium brasiliense*	FS	A, B, C, D	Hemicryptophyte	Erect forb
Commelinaceae	*Tradescantia umbraculifera*	FS	A	Hemicryptophyte	Reptant forb
Convolvulaceae	*Dichondra sericea*	FS	A, B, C, D	Hemicryptophyte	Reptant forb
	Evolvulus sericeus	FS	C, D	Hemicryptophyte	Reptant forb
Cyperaceae	*Abildgaardia ovata*	FS	D	Hemicryptophyte	Caespitose graminoid
	Bulbostylis capillaris	FS	A, C, D	Hemicryptophyte	Caespitose graminoid
	Bulbostylis consanguinea	FS	C	Hemicryptophyte	Caespitose graminoid
	Bulbostylis hirtella	FS	A	Hemicryptophyte	Caespitose graminoid
	Bulbostylis juncoides	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Bulbostylis major	FS	C	Hemicryptophyte	Caespitose graminoid
	Bulbostylis sphaerocephala	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Bulbostylis subtilis	FS	A	Hemicryptophyte	Caespitose graminoid
	Carex longii	FS	A, B	Hemicryptophyte	Caespitose graminoid
	Carex phalaroides	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Carex sororia	FS	A, D	Hemicryptophyte	Caespitose graminoid
	Cyperus aggregatus	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Cyperus hermaphroditus	FS	A, D	Hemicryptophyte	Caespitose graminoid
	Cyperus reflexus	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Fimbristylis sp. (new)	F	D	Hemicryptophyte	Caespitose graminoid
	Kyllinga odorata	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Rhynchospora barrosiana	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Rhynchospora flexuosa	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Rhynchospora gollmeri	FS	A	Hemicryptophyte	Caespitose graminoid

Continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Rhynchospora pungens	FS	A, C, D	Hemicryptophyte	Caespitose graminoid
	Rhynchospora rugosa	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Rhynchospora setigera	FS	A, C	Hemicryptophyte	Caespitose graminoid
	Rhynchospora tenuis	FS	A, B, C, D	Hemicryptophyte	Caespitose graminoid
	Scleria balansae	FS	A	Geophyte	Caespitose graminoid
	Scleria distans	FS	B	Geophyte	Caespitose graminoid
	Scleria sellowiana	FS	A, B, C, D	Geophyte	Caespitose graminoid
Dennstaedtiaceae	*Pteridium aquilinum*	FS	A, B, C, D	Geophyte	Erect forb
Droseraceae	*Drosera brevifolia*	F	A	Hemicryptophyte	Rosulate forb
Ericaceae	*Gaylussacia brasiliensis*	FS	A, B	Camephyte	Shrub
Eriocaulaceae	*Eriocaulon modestum*	FS	B	Hemicryptophyte	Rosulate forb
Euphorbiaceae	*Euphorbia papillosa*	FS	D	Camephyte	Shrub
	Euphorbia peperomioides	FS	A, B, C	Hemicryptophyte	Reptant forb
	Euphorbia serpens	FS	D	Hemicryptophyte	Reptant forb
	Euphorbia stenophylla	FS	A, C	Hemicryptophyte	Erect forb
	Euphorbiaceae 01	FS	C	-	-
	Tragia bahiensis	F	D	Camephyte	Shrub
	Tragia uberabana	FS	A, C, D	Camephyte	Shrub
Fabaceae	*Adesmia tristis*	FS	A, D	Hemicryptophyte	Reptant forb
	Aeschynomene elegans	FS	A, B, C, D	Hemicryptophyte	Reptant forb
	Aeschynomene falcata	FS	A, C, D	Hemicryptophyte	Reptant forb
	Clitoria nana	FS	D	Geophyte	Erect forb
	Collaea stenophylla	F	D	Camephyte	Shrub
	Crotalaria hilariana	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Desmanthus virgatus	FS	A, B, C, D	Camephyte	Shrub
	Desmodium craspediferum	FS	A, C	Hemicryptophyte	Erect forb
	Desmodium incanum	FS	A, C, D	Hemicryptophyte	Erect forb
	Desmodium pachyrhizum	F	C	Hemicryptophyte	Erect forb
	Desmodium triarticulatum	FS	A, B, C, D	Therophyte	Erect forb
	Eriosema tacuaremboense	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Fabaceae 01	F	D	-	-
	Galactia gracillima	FS	A, B, C, D	Liana	Liana

Continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Galactia marginalis	F	A, C	Geophyte	Erect forb
	Galactia neesii	FS	A, B, D	Geophyte	Erect forb
	Galactia pretiosa	FS	A, C, D	Geophyte	Erect forb
	Lathyrus linearifolius	FS	A	Hemicryptophyte	Erect forb
	Lathyrus subulatus	F	A	Hemicryptophyte	Erect forb
	Lupinus paraguariensis	F	C	Hemicryptophyte	Erect forb
	Macroptilium prostratum	FS	A, B, C, D	Hemicryptophyte	Reptant forb
	Mimosa dutrae	FS	D	Hemicryptophyte	Reptant forb
	Mimosa myriophylla	F	A	Camephyte	Shrub
	Poiretia latifolia	FS	A	Camephyte	Shrub
	Rhynchosia corylifolia	FS	A, C, D	Hemicryptophyte	Reptant forb
	Rhynchosia diversifolia	F	A	Hemicryptophyte	Reptant forb
	Stylosanthes leiocarpa	F	A	Geophyte	Erect forb
	Stylosanthes montevidensis	FS	A, B, C, D	Geophyte	Erect forb
	Tephrosia adunca	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Trifolium riograndense	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Vigna peduncularis	FS	A, C, D	Hemicryptophyte	Reptant forb
	Zornia orbiculata	FS	A	Hemicryptophyte	Reptant forb
	Zornia ramboiana	FS	A, B, C, D	Hemicryptophyte	Reptant forb
Gentianaceae	*Zygostigma australe*	F	A, B	Hemicryptophyte	Erect forb
Geraniaceae	*Geranium arachnoideum*	FS	A, C	Hemicryptophyte	Erect forb
Hypericaceae	*Hypericum connatum*	FS	A, B, C	Hemicryptophyte	Erect forb
Hypoxidaceae	*Hypoxis decumbens*	FS	A, B, C, D	Geophyte	Erect forb
Iridaceae	*Cypella coelestis*	FS	B	Hemicryptophyte	Erect forb
	Cypella herbertii	F	A	Hemicryptophyte	Erect forb
	Sisyrinchium micranthum	FS	C	Hemicryptophyte	Erect forb
	Sisyrinchium palmifolium	FS	C	Hemicryptophyte	Erect forb
	Sisyrinchium sellowianum	FS	D	Hemicryptophyte	Erect forb
	Sisyrinchium setaceum	F	B	Geophyte	Erect forb
	Sisyrinchium vaginatum	FS	C, D	Geophyte	Erect forb
Juncaceae	*Juncus capillaceus*	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Juncus microcephalus	FS	A	Hemicryptophyte	Erect forb

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Juncus tenuis	F	A, D	Hemicryptophyte	Caespitose graminoid
	Luzula ulei	FS	A	Hemicryptophyte	Caespitose graminoid
Lamiaceae	*Cunila galioides*	FS	A, B, C	Hemicryptophyte	Erect forb
	Glechon ciliata	FS	A, B, C	Hemicryptophyte	Erect forb
	Glechon marifolia	F	A	Hemicryptophyte	Erect forb
	Glechon spathulata	FS	A, C	Hemicryptophyte	Erect forb
	Hyptis sp.	F	A, C	Hemicryptophyte	Erect forb
	Hyptis stricta	FS	D	Hemicryptophyte	Erect forb
	Lamiaceae 01	FS	C, D	-	-
	Peltodon longipes	FS	C, D	Geophyte	Erect forb
	Rhabdocaulon gracilis	FS	A, D	Camephyte	Shrub
	Scutellaria racemosa	F	D	Therophyte	Erect forb
Lentibulariaceae	*Utricularia sp.*	FS	B	Hemicryptophyte	Erect forb
Linaceae	*Cliococca selaginoides*	FS	A, C, D	Hemicryptophyte	Erect forb
Loganiaceae	*Spigelia stenophylla*	FS	D	Hemicryptophyte	Erect forb
Lycopodiaceae	*Lycopodiella alopecuroides*	FS	B	Hemicryptophyte	Reptant forb
Lythraceae	*Cuphea glutinosa*	FS	A, B, C, D	Hemicryptophyte	Erect forb
Malpighiaceae	*Aspicarpa pulchella*	FS	D	Hemicryptophyte	Erect forb
Malvaceae	*Krapovickasia macrodon*	FS	A, C, D	Hemicryptophyte	Reptant forb
	Krapovickasia urticifolia	FS	C, D	Hemicryptophyte	Reptant forb
	Pavonia dusenii	FS	D	Camephyte	Shrub
	Pavonia reticulata	F	D	Camephyte	Shrub
Melastomataceae	*Acisanthera alsinaefolia*	FS	B	Camephyte	Shrub
	Leandra camporum	FS	B	Camephyte	Shrub
	Rhynchanthera sp.	FS	B	Camephyte	Shrub
	Tibouchina gracilis	FS	A, B, C, D	Camephyte	Shrub
	Myrsinaceae	FS	A, B, C	Therophyte	Reptant forb
	Anagallis sp. (new)	FS	A, D	Camephyte	Shrub
Myrtaceae	*Campomanesia aurea*	FS	C, D	Camephyte	Shrub
	Psidium luridum	F	A	Hemicryptophyte	Erect forb
Ochnaceae	*Sauvagesia sp.*	FS	A	Geophyte	Erect forb
Orchidaceae	*Brachystele subfiliformis*	F	A, D	Hemicryptophyte	Caespitouse graminoid

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Habenaria parviflora	FS	A, B, C	Geophyte	Erect forb
Oxalidaceae	*Oxalis bipartita*	FS	A, B	Geophyte	Reptant forb
	Oxalis brasiliensis	F	A, B	Geophyte	Reptant forb
	Oxalis conorrhiza	FS	D	Geophyte	Reptant forb
	Oxalis eriocarpa	F	A, D	Hemicryptophyte	Reptant forb
	Oxalis floribunda	F	A, C	Hemicryptophyte	Reptant forb
	Oxalis hispidula	F	A	Geophyte	Reptant forb
	Oxalis lasiopetala	F	B, C	Geophyte	Reptant forb
	Oxalis perdicaria	F	A	Geophyte	Reptant forb
	Oxalis sp.	FS	A, B, D	Geophyte	Reptant forb
	Oxalis tenerrima	FS	A	Hemicryptophyte	Reptant forb
Plantaginaceae	*Plantago australis*	FS	A, B	Hemicryptophyte	Rosulate forb
	Plantago guilleminiana	FS	A, B	Hemicryptophyte	Rosulate forb
	Plantago tomentosa	FS	A, B, C, D	Hemicryptophyte	Rosulate forb
	Plantago turficola	FS	A, B, D	Hemicryptophyte	Rosulate forb
Poaceae	*Agenium villosum*	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Agrostis montevidensis	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Andropogon lateralis	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Andropogon leucostachyus	FS	A	Hemicryptophyte	Caespitouse graminoid
	Andropogon macrothrix	FS	A, B, D	Hemicryptophyte	Caespitouse graminoid
	Andropogon selloanus	FS	A	Hemicryptophyte	Caespitouse graminoid
	Andropogon virgatus	FS	B, D	Hemicryptophyte	Caespitouse graminoid
	Aristida circinalis	FS	D	Hemicryptophyte	Caespitouse graminoid
	Aristida filifolia	FS	D	Hemicryptophyte	Caespitouse graminoid
	Aristida flaccida	FS	A, B, D	Hemicryptophyte	Caespitouse graminoid
	Aristida laevis	F	D	Hemicryptophyte	Caespitouse graminoid
	Aristida sp.	FS	D	Hemicryptophyte	Caespitouse graminoid
	Aristida spegazzinii	FS	A, C, D	Hemicryptophyte	Caespitouse graminoid
	Aristida venustula	FS	C, D	Hemicryptophyte	Caespitouse graminoid
	Axonopus affinis	FS	A, B, C, D	Geophyte	Reptant graminoid
	Axonopus argentinus	FS	A, B, C, D	Geophyte	Caespitouse graminoid
	Axonopus compressus	F	D	Geophyte	Reptant graminoid

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Axonopus siccus	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Axonopus suffultus	FS	B	Hemicryptophyte	Caespitouse graminoid
	Bothriochloa laguroides	FS	C, D	Hemicryptophyte	Caespitouse graminoid
	Chascolytrum calotheca	FS	B	Hemicryptophyte	Caespitouse graminoid
	Chascolytrum lamarckiana	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Chascolytrum poaemorpha	FS	A, B, D	Hemicryptophyte	Caespitouse graminoid
	Chascolytrum rufa	FS	A, B, D	Hemicryptophyte	Caespitouse graminoid
	Chascolytrum scabra	F	A, C, D	Hemicryptophyte	Caespitouse graminoid
	Chascolytrum subaristata	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Chascolytrum uniolae	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Calamagrostis alba	FS	A, B	Geophyte	Caespitouse graminoid
	Calamagrostis viridiflavescens	FS	A, C, D	Geophyte	Caespitouse graminoid
	Danthonia cirrata	FS	A, B, C, D	Geophyte	Caespitouse graminoid
	Danthonia montana	F	B	Geophyte	Caespitouse graminoid
	Danthonia secundiflora	FS	A, B, D	Geophyte	Caespitouse graminoid
	Dichanthelium sabulorum	FS	A, B, C, D	Geophyte	Reptant graminoid
	Eragrostis airoides	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Eragrostis lugens	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Eragrostis neesii	FS	A, C, D	Hemicryptophyte	Caespitouse graminoid
	Eragrostis polytricha	FS	A, D	Hemicryptophyte	Caespitouse graminoid
	Eustachys uliginosa	FS	A, B, D	Hemicryptophyte	Caespitouse graminoid
	Gymnopogon burchellii	F	C	Geophyte	Caespitouse graminoid
	Gymnopogon grandiflorus	FS	A, C, D	Geophyte	Caespitouse graminoid
	Gymnopogon spicatus	F	A, C	Geophyte	Caespitouse graminoid
	Melica brasiliana	FS	D	Geophyte	Caespitouse graminoid
	Mnesithea selloana	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Panicum bergii	F	D	Hemicryptophyte	Caespitouse graminoid
	Paspalum barretoi	FS	A	Geophyte	Reptant graminoid
	Paspalum dilatatum	FS	A, D	Geophyte	Caespitouse graminoid
	Paspalum maculosum	FS	A, B	Hemicryptophyte	Caespitouse graminoid
	Paspalum notatum	FS	A, C, D	Geophyte	Reptant graminoid
	Paspalum plicatulum	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Paspalum polyphyllum	FS	A, B, C, D	Geophyte	Caespitouse graminoid
	Paspalum pumilum	FS	A, B, C, D	Geophyte	Reptant graminoid
	Paspalum umbrosum	FS	D	Geophyte	Caespitouse graminoid
	Piptochaetium montevidense	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Piptochaetium stipoides	FS	A, C, D	Hemicryptophyte	Caespitouse graminoid
	Poaceae 01	FS	D	-	-
	Poaceae 02	FS	D	-	-
	Polypogon chilensis	FS	A	Therophyte	Caespitouse graminoid
	Saccharum angustifolium	FS	B, D	Hemicryptophyte	Caespitouse graminoid
	Schizachyrium imberbe	FS	A, B	Hemicryptophyte	Caespitouse graminoid
	Schizachyrium microstachyum	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Schizachyrium spicatum	FS	A, C	Hemicryptophyte	Caespitouse graminoid
	Schizachyrium tenerum	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Setaria parviflora	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Sorghastrum albescens	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Sporobolus camporum	FS	A, B	Hemicryptophyte	Caespitouse graminoid
	Sporobolus indicus	F	A, C, D	Hemicryptophyte	Caespitouse graminoid
	Sporobolus multinodis	F	A	Hemicryptophyte	Caespitouse graminoid
	Steinchisma decipiens	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Steinchisma hians	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	Stipa juergensii	FS	A, D	Hemicryptophyte	Caespitouse graminoid
	Stipa melanosperma	FS	A	Hemicryptophyte	Caespitouse graminoid
	Stipa nutans	FS	A	Hemicryptophyte	Caespitouse graminoid
	Stipa planaltina	F	B	Hemicryptophyte	Caespitouse graminoid
	Stipa sp.	FS	A, C	Hemicryptophyte	Caespitouse graminoid
	Stipa vallsii	FS	A, B, D	Hemicryptophyte	Caespitouse graminoid
	Trachypogon montufari	FS	A, B, C, D	Hemicryptophyte	Caespitouse graminoid
	*Vulpia bromoides**	FS	A	Therophyte	Caespitouse graminoid
Polygalaceae	*Polygala brasiliensis*	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Polygala campestris	FS	A	Hemicryptophyte	Erect forb
	Polygala extraaxillaris	F	A	Hemicryptophyte	Erect forb
	Polygala linoides	FS	A, B	Therophyte	Erect forb

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Polygala obovata	FS	A, B	Hemicryptophyte	Erect forb
	Polygala pulchella	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Polygala pumila	F	A, B	Hemicryptophyte	Erect forb
	Polygala sabulosa	FS	B	Hemicryptophyte	Erect forb
	Polygala sp.	FS	A	Hemicryptophyte	Erect forb
Rosaceae	*Agrimonia hirsuta*	FS	C	Geophyte	Rosulate forb
	Rosaceae 01	FS	B, D	-	-
Rubiaceae	*Borreria brachystemonoides*	FS	A, C, D	Hemicryptophyte	Erect forb
	Borreria capitata	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Diodia alata	FS	D	Hemicryptophyte	Reptant forb
	Diodia dasycephala	FS	A	Geophyte	Erect forb
	Diodia radula	FS	A, B, C, D	Hemicryptophyte	Reptant forb
	Diodia saponariifolia	F	C	Hemicryptophyte	Reptant forb
	Galianthe fastigiata	FS	A, C, D	Hemicryptophyte	Erect forb
	Galianthe verbenoides	FS	A, C	Hemicryptophyte	Erect forb
	Galium atherodes	FS	B	Hemicryptophyte	Erect forb
	Galium humile	FS	A, B, C, D	Hemicryptophyte	Erect forb
	Galium hypocarpium	FS	D	Hemicryptophyte	Erect forb
	Galium richardianum	FS	A, C, D	Hemicryptophyte	Erect forb
	Galium sp.	FS	D	Hemicryptophyte	Erect forb
	Galium valantioides	FS	A, D	Therophyte	Erect forb
	Richardia brasiliensis	F	D	Hemicryptophyte	Reptant forb
	Richardia humistrata	FS	A	Hemicryptophyte	Reptant forb
Sellaginellaceae	*Sellaginellaceae 01*	FS	A, B, D	-	-
	Sellaginella sp.	FS	A	Hemicryptophyte	Reptant forb
Solanaceae	*Calibrachoa sellowiana*	FS	D	Hemicryptophyte	Reptant forb
	Nierembergia micrantha	FS	D	Hemicryptophyte	Reptant forb
	Nierembergia sp.	F	A, D	Hemicryptophyte	Reptant forb
	Petunia integrifolia	FS	B, D	Camephyte	Shrub
	Solanum sp.	FS	D	Hemicryptophyte	Erect forb
Turneraceae	*Turnera sidoides*	F	B	Hemicryptophyte	Reptant forb
Verbenaceae	*Glandularia catharinae*	F	A, B	Hemicryptophyte	Erect forb

continue

Continuation

Family	Species	Survey	Community type	Life form	Growth form
	Glandularia marrubioides	FS	A, B, C, D	Hemicryptophyte	Reptant forb
	Glandularia peruviana	FS	C	Hemicryptophyte	Reptant forb
	Glandularia thymoides	FS	A, B, D	Hemicryptophyte	Erect forb
	Verbena ephedroides	F	A	Camephyte	Shrub
	Verbena filicaulis	F	A	Hemicryptophyte	Erect forb
	Verbena hirta	F	B	Camephyte	Shrub
	Verbena montevidensis	F	D	Camephyte	Shrub
	Verbena rigida	FS	C, D	Camephyte	Shrub
	Verbena strigosa	FS	A, B, C, D	Camephyte	Shrub
Undetermined	Undetermined 1	FS	A, B, C, D	-	-
	Undetermined 2	FS	C	-	-
	Undetermined 3	F	A, B, D	-	-
	Undetermined 4	F	A	-	-
	Undetermined 5	FS	A	-	-

Appendix 2. List of grassland species sampled in the structural survey (320 plots with 0.25m^2) in Campos de Cima da Serra. The 64 transects (five plots within each transect) were classified in four community types, each one with a specific number of transects (A = 27, B = 14, C = 10, D = 13). AF (absolute frequency): proportion of transects of a community type with the presence of the species, CA (absolute cover): sum of the proportional cover (0-100%) of a species observed at each one of the transects, IVI% (relative Importance Value Index): AF and AC were converted to relatives values (FR and CR) and summed to calculate IVI, then the values were transformed in relative values for each species. Indicator species (INDVAL method) within each community type are marked with capital letters (A, B, C or D). The top ten values of IVI% within each community type are highlighted in bold.

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
Acanthaceae	*Carlowrightia sulcata*	-	-	-	-	-	-	-	-	-	7.69	0.18	0.10
	Hygrophila verticillata	-	-	-	-	-	-	20.00	0.39	0.24	-	-	-
	Ruellia bulbifera	-	-	-	7.14	0.38	0.11	-	-	-	-	-	-
	Ruellia sp.	-	-	-	-	-	-	10.00	0.17	0.12	7.69	0.17	0.10
	Stenandrium diphyllum	7.41	0.64	0.09	7.14	0.20	0.10	20.00	1.02	0.27	15.38	0.32	0.19
Alliaceae	*Nothoscordum bonariense*	3.70	0.19	0.04	-	-	-	-	-	-	-	-	-
	Nothoscordum inodorum	3.70	0.16	0.04	-	-	-	-	-	-	-	-	-
Amaranthaceae	*Pfaffia gnaphaloides*	11.11	0.60	0.13	-	-	-	-	-	-	7.69	0.18	0.10
	Pfaffia tuberosa	70.37	6.72	0.86	28.57	3.23	0.51	90.00	3.60	1.17	46.15	1.96	0.61
Apiaceae	*Apium leptophyllum*	-	-	-	-	-	-	-	-	-	7.69	0.66	0.11
	Apium sellowianum	-	-	-	-	-	-	-	-	-	15.38	0.31	0.19
	Bowlesia incana	3.70	0.20	0.04	-	-	-	-	-	-	-	-	-
	Centella asiatica	-	-	-	7.14	0.88	0.13	-	-	-	-	-	-
	Eryngium ciliatum	-	-	-	-	-	-	10.00	2.33	0.23	-	-	-
	Eryngium ebracteatum	-	-	-	21.43	0.71	0.32	-	-	-	-	-	-
	Eryngium eriophorum	-	-	-	7.14	0.54	0.12	-	-	-	-	-	-
	Eryngium floribundum	7.41	8.71	0.24	7.14	0.16	0.10	-	-	-	-	-	-
	Eryngium horridum	3.70	2.82	0.09	-	-	-	-	-	-	15.38	9.27	0.54
	Eryngium pandanifolium^{D}	-	-	-	7.14	0.18	0.10	-	-	-	23.08	6.28	0.51
	Eryngium sanguisorba	-	-	-	7.14	0.29	0.11	-	-	-	-	-	-
	Eryngium zozterifolium	-	-	-	7.14	0.17	0.10	-	-	-	-	-	-
	Hydrocotyle exigua	70.37	9.78	0.92	64.29	3.51	1.00	10.00	0.39	0.13	61.54	19.41	1.46
Asclepidaceae	*Asclepias campestris*	-	-	-	-	-	-	10.00	0.23	0.12	7.69	0.18	0.10
Asteraceae	*Achyrocline satureioides*	25.93	2.04	0.31	21.43	0.66	0.32	-	-	-	-	-	-
	Acmella bellidioides	59.26	14.44	0.89	50.00	7.39	0.95	60.00	2.11	0.77	46.15	1.23	0.58
	Acmella decumbens	3.70	0.21	0.04	-	-	-	-	-	-	-	-	-
	Angelphytum oppositifolium	7.41	0.54	0.09	-	-	-	-	-	-	-	-	-
	Aspilia montevidensis^{D}	37.04	4.03	0.46	7.14	0.88	0.13	40.00	1.82	0.53	69.23	6.20	1.04
	Asteraceae 02	-	-	-	7.14	0.19	0.10	-	-	-	-	-	-
	Baccharis articulata	-	-	-	-	-	-	-	-	-	7.69	0.31	0.10

continue

Continuation

Family	Species	Community type A			Community type B			Community type C			Community type D		
		AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
	Baccharis brevifolia	-	-	-	14.29	0.67	0.22	-	-	-	-	-	-
	Baccharis cognata	-	-	-	7.14	0.20	0.10	-	-	-	-	-	-
	Baccharis dracunculifolia	-	-	-	-	-	-	20.00	0.37	0.24	15.38	0.34	0.19
	Baccharis erigeroides	3.70	0.21	0.04	-	-	-	-	-	-	-	-	-
	Baccharis hypericifolia	3.70	0.63	0.05	-	-	-	-	-	-	-	-	-
	Baccharis pentodonta^C	74.07	25.54	1.25	35.71	9.86	0.84	100.00	13.49	**1.78**	38.46	2.25	0.53
	Baccharis sagittalis	74.07	21.53	1.18	50.00	10.03	1.04	60.00	4.70	0.90	61.54	2.56	0.81
	Baccharis trimera	85.19	25.59	**1.37**	64.29	8.42	1.18	40.00	3.77	0.63	69.23	9.96	1.19
	Calea cymosa	7.41	2.35	0.12	-	-	-	-	-	-	7.69	0.18	0.10
	Calea phyllolepis	-	-	-	-	-	-	-	-	-	7.69	0.25	0.10
	Calyptocarpus biaristatus	3.70	0.21	0.04	-	-	-	-	-	-	-	-	-
	Chaptalia exscapa	18.52	1.17	0.22	14.29	0.88	0.23	10.00	0.19	0.12	15.38	0.48	0.20
	Chaptalia graminifolia	-	-	-	7.14	0.19	0.10	-	-	-	-	-	-
	Chaptalia integerrima	81.48	10.25	1.05	85.71	6.08	1.39	90.00	3.77	1.18	46.15	1.49	0.59
	Chaptalia mandonii	-	-	-	7.14	0.17	0.10	-	-	-	-	-	-
	Chaptalia runcinata^C	85.19	11.76	1.11	64.29	3.93	1.02	90.00	14.02	**1.69**	30.77	1.23	0.41
	Chaptalia sinuata	11.11	0.59	0.13	14.29	1.23	0.24	-	-	-	7.69	0.18	0.10
	Chevreulia acuminata^D	62.96	9.89	0.84	28.57	1.29	0.44	70.00	3.00	0.92	92.31	10.56	1.48
	Chevreulia sarmentosa^D	37.04	5.15	0.48	-	-	-	30.00	1.94	0.43	84.62	18.37	**1.69**
	Chevreulia revoluta^B	33.33	4.80	0.44	78.57	3.83	1.21	20.00	1.26	0.28	-	-	-
	Conyza bonariensis^D	22.22	1.87	0.27	7.14	0.18	0.10	-	-	-	53.85	1.90	0.70
	Conyza primulifolia	14.81	0.99	0.17	21.43	0.83	0.32	40.00	1.76	0.53	15.38	0.52	0.20
	Elephantopus mollis	3.70	0.15	0.04	-	-	-	-	-	-	15.38	0.28	0.19
	Erechthites hieracifolia	3.70	0.25	0.04	-	-	-	-	-	-	-	-	-
	Eupatorium ascendens	62.96	7.17	0.79	42.86	3.40	0.71	70.00	5.88	1.07	46.15	2.43	0.63
	Eupatorium candolleanum	3.70	0.19	0.04	-	-	-	-	-	-	-	-	-
	Eupatorium congestum	-	-	-	-	-	-	10.00	0.21	0.12	-	-	-
	Eupatorium laetevirens	3.70	0.17	0.04	-	-	-	10.00	0.18	0.12	7.69	0.15	0.10
	Eupatorium laevigatum	-	-	-	-	-	-	10.00	2.66	0.24	30.77	5.07	0.55
	Eupatorium rufescens	3.70	0.20	0.04	-	-	-	-	-	-	-	-	-
	Eupatorium sp.	-	-	-	-	-	-	10.00	0.19	0.12	-	-	-
	Eupatorium squarrulosum	-	-	-	-	-	-	10.00	0.21	0.12	7.69	0.10	0.09
	Eupatorium tanacetifolium	7.41	0.45	0.09	7.14	0.22	0.11	-	-	-	-	-	-
	Eupatorium umbelliforme	-	-	-	-	-	-	30.00	0.62	0.36	7.69	0.82	0.12

Continue

Continuation

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
	Facelis retusa	3.70	0.18	0.04	-	-	-	-	-	-	-	-	-
	Gamochaeta americana^{A}	100.00	26.07	**1.53**	85.71	5.06	1.35	80.00	3.50	1.06	61.54	4.92	0.90
	Gamochaeta coarctata	-	-	-	-	-	-	-	-	-	7.69	0.24	0.10
	Gamochaeta filaginea	-	-	-	7.14	0.19	0.10	-	-	-	-	-	-
	Hieracium commersonii	18.52	1.85	0.23	7.14	0.97	0.13	10.00	0.20	0.12	-	-	-
	Holocheilus illustris	3.70	0.18	0.04	-	-	-	10.00	0.20	0.12	-	-	-
	Hypochaeris albiflora	-	-	-	-	-	-	10.00	0.25	0.12	-	-	-
	Hypochaeris catharinensis	44.44	3.50	0.53	64.29	2.57	0.97	30.00	0.60	0.36	15.38	0.69	0.21
	Hypochaeris chilensis	14.81	0.77	0.17	7.14	0.81	0.13	20.00	0.55	0.25	7.69	0.18	0.10
	Hypochaeris radicata	3.70	0.18	0.04	-	-	-	-	-	-	-	-	-
	Hypochaeris sp.	-	-	-	7.14	0.39	0.11	-	-	-	-	-	-
	Lucilia acutifolia	18.52	2.64	0.24	35.71	1.79	0.55	20.00	0.51	0.25	38.46	1.91	0.52
	Lucilia linearifolia	14.81	1.16	0.18	14.29	1.01	0.23	-	-	-	15.38	0.30	0.19
	Noticastrum decumbens	7.41	0.55	0.09	-	-	-	10.00	0.39	0.13	23.08	1.00	0.31
	Pamphalea smithii	-	-	-	7.14	0.21	0.10	-	-	-	-	-	-
	Podocoma hirsuta	-	-	-	-	-	-	-	-	-	7.69	0.18	0.10
	Pseudognaphalium cheiranthifolium	-	-	-	-	-	-	-	-	-	7.69	0.19	0.10
	Pterocaulon alopecuroides	7.41	0.36	0.08	-	-	-	30.00	0.86	0.37	30.77	1.21	0.40
	Senecio conyzifolius	18.52	3.57	0.26	14.29	0.35	0.21	10.00	0.28	0.12	-	-	-
	Senecio oleosus	7.41	0.35	0.08	7.14	0.56	0.12	10.00	0.87	0.15	7.69	0.19	0.10
	Soliva pterosperma	3.70	0.17	0.04	-	-	-	-	-	-	-	-	-
	Stenachaenium adenanthum^{A}	40.74	3.35	0.49	-	-	-	20.00	0.52	0.25	7.69	0.20	0.10
	Stenachaenium campestre	-	-	-	-	-	-	10.00	0.29	0.12	7.69	2.60	0.19
	Stenachaenium megapotamicum	-	-	-	-	-	-	-	-	-	15.38	0.34	0.19
	Stevia lundiana	14.81	0.73	0.17	14.29	0.47	0.21	30.00	0.60	0.36	-	-	-
	Stevia sp.	14.81	1.20	0.18	7.14	0.31	0.11	10.00	0.20	0.12	15.38	0.41	0.19
	Symphyotrichum graminifolium	-	-	-	14.29	0.94	0.23	-	-	-	-	-	-
	Trichocline catharinensis	29.63	6.68	0.43	14.29	0.57	0.22	20.00	5.95	0.52	46.15	13.35	1.05
	Vernonia chamaedrys^{D}	-	-	-	-	-	-	10.00	0.20	0.12	38.46	16.01	1.06
	Vernonia flexuosa	11.11	4.61	0.20	-	-	-	20.00	0.34	0.24	30.77	4.84	0.54
	Vernonia florida	-	-	-	-	-	-	-	-	-	7.69	0.10	0.09
	Vernonia nitidula	3.70	0.16	0.04	-	-	-	20.00	0.57	0.25	-	-	-
	Vernonia nudiflora	-	-	-	-	-	-	20.00	1.21	0.28	-	-	-

Continue

Continuation

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
	Vernonia oligactoides	-	-	-	-	-	-	-	-	-	7.69	5.98	0.32
	Vernonia sellowii	25.93	1.76	0.30	28.57	1.44	0.44	10.00	0.18	0.12	-	-	-
	Vernonia sp.	3.70	0.19	0.04	-	-	-	-	-	-	-	-	-
Calyceraceae	*Acicarpha tribuloides*	-	-	-	-	-	-	-	-	-	7.69	0.18	0.10
Campanulaceae	*Lobelia camporum*	-	-	-	14.29	0.53	0.21	10.00	0.16	0.12	-	-	-
	Lobelia hederacea	3.70	0.17	0.04	7.14	0.22	0.11	-	-	-	7.69	0.54	0.11
	Wahlenbergia linarioides^{A}	77.78	9.58	0.99	35.71	1.18	0.53	40.00	1.48	0.52	38.46	2.09	0.53
Caryophyllaceae	*Cerastium glomeratum*	7.41	0.39	0.09	-	-	-	-	-	-	-	-	-
	Paronychia camphorosmoides	18.52	2.94	0.25	7.14	0.53	0.12	20.00	0.47	0.24	7.69	0.14	0.09
	Paronychia chilensis	-	-	-	7.14	0.18	0.10	-	-	-	7.69	0.17	0.10
Cistaceae	*Halimium brasiliense*^{C}	51.85	5.78	0.65	21.43	0.57	0.31	80.00	3.20	1.04	23.08	0.52	0.29
Commelinaceae	*Tradescantia umbraculifera*	3.70	0.17	0.04	-	-	-	-	-	-	-	-	-
Convolvulaceae	*Dichondra sericea*	55.56	35.66	1.24	42.86	3.28	0.70	60.00	6.64	0.99	84.62	21.19	**1.80**
	Evolvulus sericeus	-	-	-	-	-	-	30.00	0.54	0.36	23.08	0.96	0.31
Cyperaceae	*Abildgaardia ovata*	-	-	-	-	-	-	-	-	-	7.69	2.25	0.18
	Bulbostylis capillaris	18.52	1.34	0.22	-	-	-	-	-	-	15.38	5.23	0.38
	Bulbostylis consanguinea	-	-	-	-	-	-	10.00	5.08	0.36	-	-	-
	Bulbostylis hirtella	3.70	0.28	0.04	-	-	-	-	-	-	-	-	-
	Bulbostylis juncoides	25.93	5.84	0.38	28.57	6.03	0.61	40.00	2.63	0.57	7.69	0.35	0.10
	Bulbostylis major	-	-	-	-	-	-	10.00	0.20	0.12	-	-	-
	Bulbostylis sphaerocephala	55.56	18.49	0.93	42.86	6.35	0.81	70.00	7.40	1.14	7.69	0.25	0.10
	Bulbostylis subtilis	3.70	0.19	0.04	-	-	-	-	-	-	-	-	-
	Carex longii	-	-	-	7.14	0.19	0.10	-	-	-	-	-	-
	Carex phalaroides	29.63	3.63	0.38	7.14	1.09	0.14	10.00	0.20	0.12	23.08	1.05	0.31
	Carex sororia	-	-	-	-	-	-	-	-	-	15.38	0.76	0.21
	Cyperus aggregatus	62.96	5.37	0.76	28.57	1.11	0.43	70.00	2.00	0.87	30.77	3.62	0.50
	Cyperus hermaphroditus	3.70	0.19	0.04	-	-	-	-	-	-	7.69	0.96	0.13
	Cyperus reflexus	18.52	1.69	0.23	14.29	0.87	0.23	20.00	3.77	0.41	-	-	-
	Kyllinga odorata	70.37	11.86	0.96	21.43	1.45	0.34	70.00	2.20	0.88	38.46	3.50	0.58
	Rhynchospora barrosiana	51.85	24.73	1.00	57.14	47.57	**2.48**	40.00	10.68	0.98	23.08	4.52	0.44
	Rhynchospora flexuosa^{B}	55.56	82.91	**2.12**	100.00	228.53	**9.53**	50.00	7.37	0.92	15.38	10.41	0.58
	Rhynchospora gollmeri	3.70	4.36	0.12	-	-	-	-	-	-	-	-	-
	Rhynchospora pungens	3.70	0.19	0.04	-	-	-	10.00	2.17	0.22	15.38	0.31	0.19
	Rhynchospora rugosa	40.74	17.02	0.74	42.86	8.70	0.90	50.00	6.21	0.86	30.77	1.07	0.40

Continue

Continuation

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
	Rhynchospora setigera	-	-	-	-	-	-	20.00	0.55	0.25	-	-	-
	Rhynchospora tenuis	11.11	4.62	0.20	7.14	2.94	0.20	20.00	3.75	0.41	15.38	0.39	0.19
	Scleria balansae	3.70	0.86	0.05	-	-	-	-	-	-	-	-	-
	Scleria distans	-	-	-	7.14	1.43	0.15	-	-	-	-	-	-
	Scleria sellowiana^{B}	55.56	43.12	**1.38**	92.86	53.56	**3.18**	10.00	0.35	0.13	7.69	0.55	0.11
Dennstaedtiaceae	*Pteridium aquilinum*	18.52	16.90	0.51	28.57	3.68	0.52	20.00	0.48	0.24	-	-	-
Ericaceae	*Gaylussacia brasiliensis*	3.70	1.04	0.06	7.14	1.85	0.16	-	-	-	-	-	-
Eriocaulaceae	*Eriocaulon modestum*	-	-	-	7.14	0.22	0.11	-	-	-	-	-	-
Euphorbiaceae	*Euphorbia papillosa*	-	-	-	-	-	-	-	-	-	7.69	0.91	0.12
	Euphorbia peperomioides^{B}	40.74	4.78	0.52	64.29	5.39	1.07	20.00	0.36	0.24	-	-	-
	Euphorbia serpens	-	-	-	-	-	-	-	-	-	7.69	0.17	0.10
	Euphorbia stenophylla	7.41	0.40	0.09	-	-	-	10.00	0.19	0.12	-	-	-
	Euphorbiaceae 01	-	-	-	-	-	-	10.00	0.21	0.12	-	-	-
	Tragia uberabana	3.70	0.18	0.04	-	-	-	20.00	0.46	0.24	23.08	0.74	0.30
Fabaceae	*Adesmia tristis*	7.41	0.67	0.09	-	-	-	-	-	-	-	-	-
	Aeschynomene elegans^{C}	11.11	0.91	0.13	-	-	-	30.00	3.42	0.50	7.69	0.20	0.10
	Aeschynomene falcata^{C}	7.41	0.97	0.10	-	-	-	30.00	2.69	0.47	-	-	-
	Clitoria nana	-	-	-	-	-	-	-	-	-	7.69	0.48	0.11
	Crotalaria hilariana	33.33	3.85	0.42	21.43	0.83	0.32	50.00	1.12	0.61	-	-	-
	Desmanthus virgatus^{C}	44.44	4.27	0.55	21.43	1.16	0.33	80.00	2.47	1.01	30.77	1.14	0.40
	Desmodium craspediferum	3.70	0.16	0.04	-	-	-	10.00	0.16	0.12	-	-	-
	Desmodium incanum^{D}	3.70	0.16	0.04	-	-	-	50.00	3.12	0.71	76.92	37.11	**2.32**
	Desmodium triarticulatum	11.11	0.72	0.13	-	-	-	10.00	0.17	0.12	7.69	0.35	0.10
	Eriosema tacuaremboense	22.22	3.83	0.30	7.14	0.25	0.11	30.00	1.86	0.42	15.38	0.36	0.19
	Galactia gracillima	37.04	3.25	0.45	21.43	0.61	0.31	30.00	0.92	0.38	23.08	1.01	0.31
	Galactia neesii	7.41	0.54	0.09	-	-	-	-	-	-	-	-	-
	Galactia pretiosa^{C}	7.41	0.96	0.10	-	-	-	40.00	0.93	0.49	-	-	-
	Lathyrus linearifolius	3.70	0.22	0.04	-	-	-	-	-	-	-	-	-
	Macroptilium prostratum^{C}	59.26	13.31	0.87	7.14	1.02	0.13	80.00	19.48	**1.86**	38.46	1.84	0.52
	Mimosa dutrae	-	-	-	-	-	-	-	-	-	7.69	2.91	0.20
	Poiretia latifolia	3.70	0.48	0.05	-	-	-	-	-	-	-	-	-
	Rhynchosia corylifolia^{C}	29.63	6.11	0.42	-	-	-	60.00	3.91	0.86	23.08	0.66	0.29
	Stylosanthes montevidensis	44.44	4.21	0.54	21.43	1.44	0.34	40.00	1.27	0.51	53.85	8.44	0.95
	Tephrosia adunca^{C}	25.93	5.83	0.38	7.14	0.71	0.12	60.00	7.11	1.02	30.77	1.21	0.40

Continue

Continuation

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
	Trifolium riograndense^{D}	22.22	4.87	0.32	-	-	-	-	-	-	84.62	9.49	1.35
	Vigna peduncularis	18.52	1.28	0.22	-	-	-	10.00	0.85	0.15	7.69	0.15	0.10
	Zornia orbiculata	3.70	0.22	0.04	-	-	-	-	-	-	-	-	-
	Zornia ramboiana	3.70	0.17	0.04	21.43	0.72	0.32	10.00	0.17	0.12	-	-	-
Geraniaceae	*Geranium arachnoideum*	3.70	0.20	0.04	-	-	-	-	-	-	-	-	-
Hypericaceae	*Hypericum connatum*	-	-	-	7.14	0.19	0.10	10.00	0.18	0.12	-	-	-
Hypoxidaceae	*Hypoxis decumbens*	48.15	21.87	0.91	42.86	1.97	0.66	20.00	0.95	0.27	53.85	8.24	0.94
Indeterminada	Indeterminada 01	-	-	-	14.29	0.34	0.21	-	-	-	-	-	-
	Indeterminada 02	3.70	0.19	0.04	-	-	-	-	-	-	-	-	-
	Indeterminada 05	-	-	-	-	-	-	-	-	-	7.69	0.17	0.10
Iridaceae	*Cypella coelestis*	-	-	-	7.14	0.18	0.10	-	-	-	-	-	-
	Sisyrinchium micranthum	40.74	4.37	0.51	35.71	1.50	0.54	10.00	0.16	0.12	7.69	0.17	0.10
	Sisyrinchium palmifolium	3.70	0.16	0.04	-	-	-	-	-	-	-	-	-
	Sisyrinchium sellowianum	44.44	4.04	0.54	14.29	0.35	0.21	20.00	1.32	0.29	-	-	-
	Sisyrinchium vaginatum^{D}	3.70	0.19	0.04	7.14	0.19	0.10	10.00	0.17	0.12	38.46	1.06	0.49
Juncaceae	*Juncus capillaceus*	3.70	1.20	0.06	-	-	-	-	-	-	-	-	-
	Juncus microcephalus	-	-	-	7.14	0.20	0.10	-	-	-	-	-	-
	Luzula ulei	3.70	0.37	0.05	-	-	-	-	-	-	-	-	-
Labiatae	*Cunila galioides*	7.41	1.84	0.11	21.43	0.57	0.31	-	-	-	-	-	-
	Glechon ciliata	7.41	0.44	0.09	7.14	0.29	0.11	10.00	0.19	0.12	-	-	-
	Glechon spathulata	3.70	0.16	0.04	-	-	-	-	-	-	-	-	-
	Hyptis stricta	-	-	-	-	-	-	-	-	-	7.69	0.23	0.10
	Labiatae 01	-	-	-	-	-	-	-	-	-	7.69	0.15	0.10
	Peltodon longipes	-	-	-	-	-	-	-	-	-	15.38	0.49	0.20
	Rhabdocaulon gracilis	3.70	0.20	0.04	-	-	-	-	-	-	7.69	0.17	0.10
Lentibulariaceae	*Utricularia sp.*	-	-	-	7.14	0.17	0.10	-	-	-	-	-	-
Linaceae	*Cliococca selaginoides*	3.70	0.16	0.04	-	-	-	10.00	0.40	0.13	7.69	0.14	0.09
Loganiaceae	*Spigelia stenophylla*	-	-	-	-	-	-	-	-	-	7.69	0.10	0.09
Lycopodiaceae	*Lycopodiella alopecuroides*	-	-	-	7.14	0.20	0.10	-	-	-	-	-	-
Lythraceae	*Cuphea glutinosa*	3.70	0.19	0.04	21.43	1.27	0.34	10.00	0.73	0.15	38.46	2.07	0.53
Malpighiaceae	*Aspicarpa pulchella*	-	-	-	-	-	-	-	-	-	15.38	0.73	0.21
Malvaceae	*Krapovickasia macrodon*^{C}	3.70	0.34	0.05	-	-	-	60.00	1.61	0.74	30.77	0.92	0.39
	Krapovickasia urticifolia	-	-	-	-	-	-	-	-	-	15.38	0.43	0.20
	Pavonia dusenii	-	-	-	-	-	-	-	-	-	7.69	0.22	0.10

Continue

Continuation

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
Melastomataceae	*Acisanthera alsinaefolia*	-	-	-	7.14	0.20	0.10	-	-	-	-	-	-
	Leandra camporum	-	-	-	14.29	0.39	0.21	-	-	-	-	-	-
	Rhynchanthera sp.	-	-	-	7.14	0.18	0.10	-	-	-	-	-	-
	Tibouchina gracilis	44.44	6.32	0.58	78.57	4.20	1.22	50.00	2.33	0.67	46.15	3.35	0.67
Myrsinaceae	*Anagallis* sp. (nova)	22.22	3.40	0.30	35.71	1.71	0.55	10.00	0.19	0.12	-	-	-
Myrtaceae	*Campomanesia aurea*	3.70	0.35	0.05	-	-	-	-	-	-	-	-	-
Ochnaceae	*Sauvagesia* sp.	3.70	0.19	0.04	-	-	-	-	-	-	-	-	-
Orchidaceae	*Habenaria parviflora*	29.63	1.83	0.34	28.57	0.87	0.42	20.00	0.34	0.24	-	-	-
Oxalidaceae	*Oxalis bipartita*	3.70	0.19	0.04	7.14	0.55	0.12	-	-	-	-	-	-
	Oxalis conorrhiza	-	-	-	-	-	-	-	-	-	7.69	0.18	0.10
	Oxalis sp. 01	18.52	0.97	0.21	14.29	0.40	0.21	-	-	-	15.38	0.76	0.21
	Oxalis tenerrima	3.70	0.15	0.04	-	-	-	-	-	-	-	-	-
Plantaginaceae	*Plantago australis*^{A}	18.52	1.45	0.22	-	-	-	-	-	-	-	-	-
	Plantago guilleminiana	7.41	1.60	0.11	7.14	0.19	0.10	-	-	-	-	-	-
	Plantago tomentosa	11.11	0.73	0.13	7.14	1.03	0.13	10.00	0.25	0.12	15.38	0.74	0.21
	Plantago turficola	3.70	0.19	0.04	-	-	-	-	-	-	15.38	0.35	0.19
Poaceae	*Agenium villosum*	18.52	12.55	0.43	-	-	-	10.00	4.48	0.33	-	-	-
	Agrostis montevidensis	14.81	0.75	0.17	14.29	0.38	0.21	10.00	8.35	0.53	7.69	0.17	0.10
	Andropogon lateralis^{A}	100.00	873.31	**17.22**	100.00	289.90	**11.72**	100.00	173.23	**9.77**	84.62	107.97	**5.14**
	Andropogon leucostachyus	7.41	2.81	0.13	-	-	-	-	-	-	-	-	-
	Andropogon macrothrix	-	-	-	14.29	5.10	0.38	-	-	-	7.69	0.34	0.10
	Andropogon selloanus	3.70	0.16	0.04	-	-	-	-	-	-	-	-	-
	Andropogon virgatus	-	-	-	7.14	2.25	0.18	-	-	-	7.69	0.14	0.09
	Aristida circinalis	-	-	-	-	-	-	-	-	-	7.69	0.84	0.12
	Aristida filifolia	-	-	-	-	-	-	-	-	-	7.69	3.23	0.21
	Aristida flaccida	11.11	0.82	0.13	7.14	0.39	0.11	-	-	-	-	-	-
	Aristida sp.	-	-	-	-	-	-	-	-	-	7.69	0.22	0.10
	Aristida spegazzinii^{D}	-	-	-	-	-	-	-	-	-	30.77	8.35	0.68
	Aristida venustula^{D}	-	-	-	-	-	-	10.00	0.91	0.16	30.77	14.24	0.91
	Axonopus affinis	81.48	100.77	**2.72**	64.29	23.23	**1.71**	30.00	1.71	0.42	69.23	40.65	**2.37**
	Axonopus argentinus	-	-	-	14.29	11.05	0.59	10.00	0.25	0.12	7.69	1.68	0.15
	Axonopus siccus^{B}	59.26	29.89	1.18	92.86	57.31	**3.31**	90.00	8.38	1.41	23.08	1.00	0.31
	Axonopus suffultus	-	-	-	7.14	11.90	0.52	-	-	-	-	-	-
	Bothriochloa laguroides	-	-	-	-	-	-	-	-	-	15.38	0.37	0.19

Continue

Continuation

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
	Briza calotheca	-	-	-	7.14	0.16	0.10	-	-	-	-	-	-
	Briza lamarckiana	29.63	3.35	0.37	-	-	-	10.00	1.14	0.17	23.08	0.53	0.29
	Briza poaemorpha	37.04	6.71	0.51	35.71	1.35	0.54	-	-	-	7.69	0.37	0.10
	Briza rufa	14.81	0.77	0.17	-	-	-	-	-	-	7.69	0.19	0.10
	Briza subaristata	44.44	3.48	0.53	21.43	1.94	0.36	20.00	2.63	0.35	23.08	0.98	0.31
	Briza uniolae	29.63	5.12	0.41	14.29	3.51	0.32	20.00	0.37	0.24	15.38	0.61	0.20
	Calamagrostis alba	3.70	0.37	0.05	-	-	-	-	-	-	-	-	-
	Calamagrostis viridiflavescens	-	-	-	-	-	-	-	-	-	7.69	0.16	0.10
	Danthonia cirrata	11.11	0.54	0.13	7.14	0.14	0.10	-	-	-	7.69	4.84	0.28
	Danthonia secundiflora	22.22	1.18	0.26	7.14	0.31	0.11	-	-	-	15.38	1.55	0.24
	Dichanthelium sabulorum	81.48	23.47	1.29	64.29	14.20	1.38	90.00	14.97	**1.74**	92.31	12.27	1.55
	Eragrostis airoides	44.44	5.40	0.57	21.43	0.96	0.33	50.00	1.26	0.62	7.69	0.25	0.10
	Eragrostis lugens	92.59	43.48	**1.78**	57.14	16.50	1.37	80.00	4.61	1.11	69.23	22.15	**1.66**
	Eragrostis neesii	18.52	6.29	0.31	-	-	-	-	-	-	7.69	0.16	0.10
	Eragrostis polytricha	3.70	0.28	0.04	-	-	-	-	-	-	7.69	0.31	0.10
	Eustachys uliginosa	-	-	-	-	-	-	-	-	-	7.69	0.14	0.09
	Gymnopogon grandiflorus	3.70	0.17	0.04	-	-	-	-	-	-	-	-	-
	Melica brasiliana	-	-	-	-	-	-	-	-	-	7.69	0.10	0.09
	Mnesithea selloana^{D}	33.33	3.44	0.41	-	-	-	40.00	1.83	0.53	53.85	5.57	0.84
	Paspalum barretoi	3.70	0.18	0.04	-	-	-	-	-	-	-	-	-
	Paspalum dilatatum	3.70	0.22	0.04	-	-	-	-	-	-	15.38	16.20	0.80
	Paspalum maculosum	25.93	6.62	0.39	28.57	7.30	0.65	-	-	-	-	-	-
	Paspalum notatum^{D}	48.15	46.88	**1.37**	-	-	-	60.00	41.89	**2.76**	100.00	477.65	**19.53**
	Paspalum plicatulum	96.30	171.27	**4.18**	92.86	117.71	**5.47**	100.00	68.13	**4.51**	92.31	30.04	**2.23**
	Paspalum polyphyllum	62.96	16.49	0.97	85.71	8.05	1.46	70.00	5.75	1.06	23.08	0.72	0.30
	Paspalum pumilum^{B}	44.44	40.19	1.21	57.14	90.62	**4.02**	-	-	-	7.69	2.73	0.19
	Paspalum umbrosum	-	-	-	-	-	-	-	-	-	23.08	6.99	0.54
	Piptochaetium montevidense	81.48	91.33	**2.55**	14.29	4.19	0.34	80.00	40.57	**2.91**	100.00	125.46	**5.99**
	Piptochaetium stipoides	-	-	-	-	-	-	-	-	-	7.69	5.05	0.28
	Poaceae 01	-	-	-	-	-	-	-	-	-	7.69	0.33	0.10
	Poaceae 02	-	-	-	-	-	-	-	-	-	7.69	0.18	0.10
	Polypogon chilensis	3.70	0.34	0.05	-	-	-	-	-	-	-	-	-
	Saccharum angustifolium	-	-	-	7.14	0.24	0.11	-	-	-	15.38	5.34	0.38
	Schizachyrium imberbe	3.70	0.28	0.04	7.14	0.38	0.11	-	-	-	-	-	-

Continue

Continuation

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
	Schizachyrium microstachyum	18.52	7.55	0.33	-	-	-	30.00	1.18	0.39	38.46	1.23	0.49
	Schizachyrium spicatum	29.63	3.09	0.37	-	-	-	40.00	1.70	0.53	-	-	-
	Schizachyrium tenerum^{C}	100.00	435.69	**9.12**	100.00	210.08	**8.87**	100.00	373.25	**19.77**	84.62	56.23	**3.15**
	Setaria parviflora^{D}	18.52	0.98	0.21	7.14	0.55	0.12	10.00	0.23	0.12	53.85	2.95	0.74
	Sorghastrum albescens	11.11	6.95	0.25	14.29	3.07	0.30	10.00	1.68	0.19	7.69	0.55	0.11
	Sporobolus camporum	3.70	0.28	0.04	7.14	0.20	0.10	-	-	-	-	-	-
	Steinchisma decipiens^{D}	14.81	2.55	0.20	7.14	0.84	0.13	20.00	0.35	0.24	61.54	5.62	0.93
	Steinchisma hians	7.41	0.83	0.09	-	-	-	10.00	0.23	0.12	-	-	-
	Stipa juergensii	7.41	0.73	0.09	-	-	-	-	-	-	15.38	0.31	0.19
	Stipa melanosperma	3.70	0.37	0.05	-	-	-	-	-	-	-	-	-
	Stipa nutans	3.70	0.19	0.04	-	-	-	-	-	-	-	-	-
	Stipa sp.	7.41	0.35	0.08	-	-	-	10.00	0.20	0.12	-	-	-
	Stipa vallsii	3.70	0.22	0.04	-	-	-	-	-	-	7.69	0.35	0.10
	Trachypogon montufari	51.85	33.83	1.17	21.43	0.60	0.31	50.00	17.39	**1.42**	7.69	1.08	0.13
	Vulpia bromoides	3.70	0.24	0.04	-	-	-	-	-	-	-	-	-
Polygalaceae	*Polygala brasiliensis*	14.81	0.73	0.17	7.14	0.17	0.10	10.00	0.25	0.12	7.69	0.18	0.10
	Polygala campestris	3.70	0.28	0.04	-	-	-	-	-	-	-	-	-
	Polygala linoides	-	-	-	7.14	0.17	0.10	-	-	-	-	-	-
	Polygala obovata	3.70	0.17	0.04	14.29	1.32	0.24	-	-	-	-	-	-
	Polygala pulchella^{A}	70.37	8.77	0.90	57.14	2.84	0.88	30.00	0.56	0.36	30.77	1.52	0.42
	Polygala sabulosa	-	-	-	14.29	0.62	0.22	-	-	-	-	-	-
	Polygala sp.	3.70	0.24	0.04	-	-	-	-	-	-	-	-	-
Rosaceae	*Agrimonia hirsuta*	-	-	-	-	-	-	10.00	0.36	0.13	-	-	-
	Rosaceae 01	-	-	-	-	-	-	-	-	-	7.69	0.17	0.10
Rubiaceae	*Borreria brachystemonoides*	3.70	0.16	0.04	-	-	-	10.00	0.17	0.12	-	-	-
	Borreria capitata^{C}	22.22	1.92	0.27	14.29	0.69	0.22	50.00	1.90	0.65	-	-	-
	Diodia alata	-	-	-	-	-	-	-	-	-	7.69	0.14	0.09
	Diodia dasycephala	3.70	0.19	0.04	-	-	-	-	-	-	-	-	-
	Diodia radula^{D}	25.93	2.54	0.32	7.14	0.17	0.10	40.00	1.09	0.50	69.23	14.48	1.36
	Galianthe fastigiata	7.41	0.34	0.08	-	-	-	20.00	0.57	0.25	23.08	0.69	0.29
	Galianthe verbenoides	7.41	1.05	0.10	-	-	-	-	-	-	-	-	-
	Galium atherodes	-	-	-	7.14	0.21	0.10	-	-	-	-	-	-
	Galium humile^{B}	85.19	25.17	1.36	100.00	15.96	**1.93**	30.00	0.84	0.37	23.08	1.73	0.34
	Galium hypocarpium	-	-	-	-	-	-	-	-	-	7.69	0.17	0.10

Continue

Continuation

		Community type A			Community type B			Community type C			Community type D		
Family	Species	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%	AF	AC	IVI%
	Galium richardianum	22.22	1.92	0.27	-	-	-	30.00	0.68	0.36	30.77	1.59	0.42
	Galium sp.	-	-	-	-	-	-	-	-	-	7.69	0.18	0.10
	Galium valantioides	3.70	0.16	0.04	-	-	-	-	-	-	15.38	0.36	0.19
	Richardia humistrata	3.70	3.82	0.11	-	-	-	-	-	-	-	-	-
Sellaginellaceae	*Sellaginella* sp.	-	-	-	14.29	2.65	0.29	-	-	-	-	-	-
Solanaceae	*Calibrachoa sellowiana*	3.70	0.16	0.04	-	-	-	-	-	-	-	-	-
	Nierembergia micrantha	-	-	-	-	-	-	-	-	-	7.69	0.10	0.09
	Petunia integrifolia	11.11	0.55	0.13	-	-	-	-	-	-	7.69	0.17	0.10
	Solanum sp.	-	-	-	7.14	0.19	0.10	-	-	-	-	-	-
Verbenaceae	*Glandularia marrubioides*	7.41	0.39	0.08	7.14	0.20	0.10	20.00	0.43	0.24	7.69	0.20	0.10
	Glandularia peruviana	-	-	-	-	-	-	10.00	0.20	0.12	-	-	-
	Glandularia thymoides	3.70	0.33	0.05	7.14	0.17	0.10	-	-	-	7.69	0.23	0.10
	Verbena rigida	-	-	-	-	-	-	10.00	0.39	0.13	7.69	0.24	0.10
	Verbena strigosa	14.81	0.98	0.17	14.29	0.51	0.21	10.00	0.18	0.12	-	-	-
totals		4763	2700	100	3664	1400	100	4530	1000	100	4300	1300	100

Capítulo 2. (Artigo 2) The role of environmental factors and spatial processes on highland grassland communities of South Brazilian *Campos*[1]

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[1] Este artigo será submetido ao periódico *Journal of Vegetation Science.*

Abstract

Question: What are the relative roles of environmental variables (climate, soil, landscape geomorphology and local topography) and of spatial factors in defining grasslands species richness and beta diversity in the highland South Brazilian Campos?

Location: Mesic highland grasslands in the *Campos de Cima da Serra* region, northeast of Rio Grande do Sul, Brazil (27.48º/29.49ºS and 49.7º/52ºW), with altitudes ranging from 600 to 1,400 m a.s.l.

Methods: We used Redundancy Analysis (RDA) and Partial RDA to disentangle the relative role of these drivers. The spatial factors were evaluated using PCNM eigenfunctions.

Results: A considerable variation of community composition (41.4%) was explained jointly by the environmental and spatial variables. The environmental effect accounted for nearly one third of total variation and most of it was spatially structured. The pure spatial fraction accounted for 5.7% of total variation. Annual mean temperature, temperature seasonality and soil type were the main selected variables to model beta diversity. Species richness showed a different pattern with a lower effect of the environmental variables and a higher effect of the pure spatial fraction. Only two variables related to water supply and retention were selected to model species richness.

Conclusions: Different forces drive alpha and beta diversity. In the case of beta diversity, neutral factors were less relevant than niche and variables representing regional gradients of climate and soil type overwhelmed the effect of local topography. The high unexplained variation might be consequence of factors that were not considered in the model, such as differences in grassland management.

Keywords: Beta diversity, Environmental control, Niche, Neutral theory, Redundancy Analysis, Variation Partitioning, Scale.

Introduction

The complexity of ecological phenomena, like the variation of species assemblages, stems on non-mutually-exclusive abiotic and biotic processes that overlap in space and time (Quinn & Dunham 1983). Instead of searching for single causes, we are supposed to search for alternative causes in terms of their relative contribution (Borcard et al. 1992).

Moreover, when searching for factors driving the structure of biological communities we should take into account those deterministic processes are not the only source of variation. In one hand the environment acts as a filter, selecting species because of their physiology or morphological adaptations, *i.e* accordingly to their ecological niches (Whittaker 1956; Hutchinson 1957; Tilman 2004), resulting in a non-random set of species. In the other hand, the variation in species composition may be generated by the species assemblages themselves, through contagious processes, like dispersal limitation, irrespective of the environment. This approach has brought the importance of stochastic processes in structuring local communities and has been the basis of neutral models (Hubbell 2001; Adler et al. 2007).

Neutral and deterministic models each make unique predictions regarding spatial patterns of community assembly (Chave 2004; Gilbert & Lechowicz 2004). However, recent studies have shown that both processes may be acting at the same time, with their relative importance changing according to the region, the seasonality and the spatial scale (Tuomisto et al. 2003; Chust et al. 2006; Gravel et al. 2006; Laliberté et al. 2009; Legendre et al. 2009; Rominger et al. 2009; Li et al. 2011).

Accordingly, a first step to understand the underlying causes that structure a biological community is to disentangle the relative importance of deterministic and stochastic processes. One of the most popular methodological approaches has been the partition of variation of community composition between environmental and spatial factors through constrained and partial ordinations (Borcard et al. 1992; Legendre et al. 2005).

In these, the variation associated to environmental factors has been interpreted to be consequence of niche processes and the spatial variation not related with environmental factors has been often attributed to neutral mechanisms, which leads to spatial autocorrelation in the species data (Legendre et al. 2009). In this case, the presence of a spatial effect that is not explained by the environmental factors is not a variable *per se*, but a synthetic expression of possible underlying stochastic processes (including dispersal limitation, historical events, and disturbances) in the data set and that were not directly measured like environmental factors.

A second step is to explore the spatial structure of community at different spatial scales. Most ecological patterns and processes are scale-dependent (Wiens et al. 1986; Levin 1992). Environmental drivers at finer scales can affect broad-scale ecological dynamics and broad-scale drivers can overwhelm local patterns and processes (Peters et al. 2008). This interplay is increasingly being recognized as crucial to understand ecosystem dynamics (Huston 1999), and specific methods to dissect the spatial variability of community data at multiple scales are available (Borcard & Legendre 2002; Borcard et al. 2004).

Among these methods, the principal coordinates of neighbor matrices (PCNM) analysis has been used to decompose the spatial structure of species abundances into additive scale-specific models, with the advantage of modeling spatial structures over a wide range of scales (Borcard & Legendre 2002; Borcard et al. 2004). This procedure is based on the eigenfunctions of spatial configurations matrices, producing spatial predictors that can be used in regression and canonical models (Dray et al. 2006; Griffith & Peres-Neto 2006). In these, those eigenvectors with large eigenvalues correspond to global structures, and those with small ones correspond to local structures (Borcard & Legendre 2002).

Here we combine canonical redundancy analysis with PCNM to explore the role of niche and other spatial processes in the structuring of highland grassland communities located in the northeast of the Rio Grande do Sul state, Brazil, known as *Campos de Cima da Serra* grasslands. For this, we collected data by a regional survey on these grasslands along climate, soil and topographic gradients encompassing an area of 18,667 km^2. Previous studies have elucidated compositional differences among South Brazilian grassland types (Boldrini 2009) but their internal heterogeneity and main drivers remained still poorly understood (Boldrini et al. 2009). Moreover, quantitative data on species composition and distribution patterns in relation to environmental variables are scarce (Overbeck et al. 2007) undermining conservation policies targeting this ecosystem. The knowledge of these grasslands dynamics also has important implications to develop conceptual models of vegetation variation along environmental gradients (Perelman et al. 2001).

In this paper, we answer the following questions: Which are the most important environmental variables to model species richness and beta diversity? Which set of environmental variables show stronger influence on the community structure, the local or the regional ones? Are the selected environmental variables relevant to understand grasslands species richness and beta diversity or their effects are overcome by spatial factors?

Methods

Study area

The study was conducted at the *Campos de Cima da Serra* region (Fortes 1959) in the northeast of Rio Grande do Sul state, southern Brazil (27.48°/29.49°S and 49.7°/52°W) where natural grassland still cover 41 % of the study area (Cordeiro & Hasenack 2009). It lies on the Meridional Plateau, a highland formed by successive flows of basalt and rhiodacyte extrusive volcanic rocks (120-135 My BP). Altitudes range from 600 to 1,400 m a.s.l., decreasing from east to west (Weber et al. 2004). The relief is smoothly undulate with some typical conic mammillary shaped hills and frequent rocky outcrops (Horbach et al. 1986; Almeida 2009). Soils in the central and east sectors belong mainly to cambisol and in the west sector to ferralsol (EMBRAPA 2006; Streck et al. 2008).

The climate is warm temperate (subtropical) and humid. Annual precipitation ranges from 1,600 to 2,162 mm and is regularly distributed along the year (IPAGRO 1989). Mean annual temperature ranges from 13.6 to 18.6ºC (IPAGRO 1989) and frosts are frequent on winter when sometimes snowfall occur. Fogs are common (92 fog days/year) closer to the escarpment at the easternmost limit (Moreno 1961).

Biogeographically, the Southern Brazilian highland grasslands are included in the Paranaense sub-region, *Araucaria angustifolia* Forest province (Morrone 2001). The grassland physiognomy has a homogeneous appearance given by large and abundant populations of Poaceae species, mostly with caespitose erect habit and austral summer cycle. All these grasslands are continuously grazed and subject to frequent anthropogenic burning (2-3 years interval). Shrubs occur mostly in low grazing intensity areas. Floristic diversity is high with more than 1,161 species, 107 of them endemics (Boldrini et al. 2009), with a mixture of tropical and subtropical grasses from the north and temperate grasses from the south (C4 and C3 species, respectively) (Burkart 1975).

Sampling design and data collection

Within an area ranging 160 km of latitude and 170 km of longitude, we sampled 320 plots. These plots were positioned according to a stratified nested design across different spatial scales and considering the main climatic, edaphic and topographic gradients.

First, we set sixteen sites representing eight climate spatial strata, previously defined by the combination of different ranges of annual mean temperature (13.6-15, 15.1-16.5, 16.6-18.6 ºC) and annual mean rainfall (1600-1750, 1751-1900, 1901-2050, 2051-2200 mm). Within each climate strata, two sites (corresponding to different farms) where chosen by random points over mapped grasslands remnants accessible by road. Second, we set a cluster of four relief–aspect strata (northern hillslope, southern hillslope, tophill and lowland) within each site, considering accessibility as the critical selection criteria. Within each relief–aspect strata we set an 80 m transect, resulting in 64 transects. At last, within each transect we sampled five 0.25 m^2 plots (0.5 x 0.5 m), 20 m apart, resulting in a total of 320 plots.

We used available climate data from WorldClim – Global Climate Data, with a resolution of 1 km^2 (Hijmans et al. 2005), and for the relief-aspect data we combined quantitative slope and aspect data from *Topodata*, with a resolution of 0.01 km^2 (Valeriano 2008). Regional soil classes were represented in the final sample by 12 transects on ferralsol and 52 transects on cambisol. The distance between transects at each site ranged from 0.1 to 2 km, and the distance between sites ranged from 10 to 170 km at the broader scale.

Inside each plot, we visually estimated species abundance based on the aboveground percentage cover, considering a scale of 5% intervals and the cover values of 1, 2 and 3% under the 5% limit. Fieldwork was conducted from December 2008 to February 2009, during austral summer season, when reproductive organs are present to allow reliable species identification.

The scope of this study was limited to the dominant mesic grasslands, therefore peat bogs and permanently wet grasslands were excluded from sampling. To avoid extreme situations of grassland management and to ensure areas with approximately similar disturbances regimes, the sampling excluded those areas with signs of previous burning episodes or without grazing.

Environmental and spatial variables

A total of 30 environmental variables were obtained for each transect. Nineteen quantitative climate variables of temperature, precipitation and a combination of both (see Table 1) were extracted from the WorldClim – Global Climate Data (HIJMANS *et al.* 2005), corresponding to monthly values averaged for the 1960-2000 period. From this data we eliminated variables with higher collinearity and as a result we kept four temperature variables (annual mean temperature, mean diurnal range, temperature seasonality, mean temperature of warmest quarter) and three precipitation ones (annual precipitation, precipitation of wettest month, precipitation of warmest quarter). Altitude and seven geomorphometric variables were obtained from *Topodata* database (Valeriano 2008). The geomorphometric variables (slope, aspect, vertical curvature, horizontal curvature and the topographic wetness index) (Dikau 1990; Schmidt & Dikau 1999) correspond to the landscape context surrounding each transect and were extracted using a buffer with radius of 1 km (see Table 1). We transformed circular aspect data to sine and cosine, ranging from -1 to 1, to express Eastness and Northness, respectively, allowing their use in linear models. Horizontal and vertical curvatures are topographic factors that affect the dynamics of overland and intrasoil water. The former is a measure of water flow convergence and divergence and the latter a measure of relative deceleration and acceleration of water flows. Both influence soil moisture, pH, thickness of soil horizons, organic matter and plant cover distribution. The topographic wetness index (TWI) is a ratio of the local upslope contributing area and the local slope, the greater values indicate higher propensity to water saturation. Soil type of each transect was extracted from the *Radambrasil* soils map (IBGE 2003). All data were extracted from shape files using the central coordinates of transects with the software Quantum GIS (Quantum GIS Development Team 2011). This dataset was complemented by local qualitative topographic variables indicating transect aspect (North, South or neutral) and transect slope (hillside, plain) resulting in an environmental matrix with 18 variables.

To detect and quantify spatial patterns at all scales encompassed by the data matrix we generated continuous spatial variables from the UTM x and y coordinates of each of 64 transects through Principal Coordinates Neighbor Matrices (PCNM) (Borcard & Legendre 2002; Dray et al. 2006). The PCNM represents a spectral decomposition of the spatial relationships among the sample units. Its algorithm includes the calculation of a geographical distance matrix between transects, the selection of a truncation value, the building of a truncated connectivity matrix and finally, the eigenvalue decomposition of this matrix through principal coordinate analysis. We obtained 34 PCNM variables for transects, corresponding to those eigenvectors with positive eigenvalues, which were used as spatial descriptors. The truncation value was the largest distance in the minimum spanning tree linking all transects. The axes order represent a gradient from broader to finer scales (Borcard et al. 2004).

Data analysis

Three matrices were used in the statistical analyses: species cover data, environmental variables and spatial variables. The original species cover data of 315 species by 320 plots was converted into a matrix of 137 species by 64 transects by merging the species cover data from the five plots within each transect followed by the exclusion of those species that were present in less than 10% of the transects. The resulting species data matrix was Hellinger-transformed (Legendre & Gallagher 2001).

Environmental variables were standardized to mean = 0 and variance =1 to build the matrix of environmental variables. Qualitative variables (soil type, transect aspect and slope) were converted into dummy variables. The environmental matrix was also split into four matrices to explore the role of different subsets of variables: climate, landscape geomorphology, soil type and local topography on community composition.

To model community composition and species richness and to assess the relative importance of niche processes versus other spatial processes we used canonical redundancy analysis (RDA) and partial RDA (Rao 1964), alternating the environmental and spatial variables (PCNMs) as predictors and covariables (Borcard et al. 1992).

Table 1. Environmental variables evaluated in the 64 transects at the *Campos de Cima da Serra* grasslands, Brazil.

Variable	Label	Unit	Min.	Max.	Median
Annual Mean Temperature$^+$	AMT	ºC	13.6	18.1	15.7
Mean Diurnal Range (Mean of monthly maximum temperature - monthly minimum temperature)	MDR	ºC	9.1	10.7	9.7
Isothermality (Mean Diurnal Range/Annual Range) (* 100)	Isot	%	51.0	55.0	54.0
Temperature Seasonality (stand. deviation *100)$^+$	Tsea	ºC	279.3	314.1	289.8
Maximum Temperature of Warmest Month	MaxTWarm	ºC	22.6	27.5	24.6
Minimum Temperature of Coldest Month	MinTColm	ºC	4.4	8.7	6.8
Temperature Annual Range	TAR	ºC	17.1	19.4	17.9
Mean Temperature of Warmest Quarter	MTWarq	ºC	16.6	21.3	19.1
Mean Temperature of Coldest Quarter	MTColq	ºC	10.0	13.9	11.9
Mean Temperature of Wettest Quarter	MTWetq	ºC	13.4	19.3	16.6
Mean Temperature of Driest Quarter	MTDriq	ºC	10.9	19.4	13.4
Annual Precipitation	AP	mm	1735	2161	1977
Precipitation of Wettest Month	PWetm	mm	168	206	178
Precipitation of Driest Month	PDrim	mm	100	135	126
Precipitation Seasonality (coefficient of variation)	Psea	%	8	16	11
Precipitation of Wettest Quarter	PWetq	mm	469	543	502
Precipitation of Driest Quarter	PDriq	mm	318	465	401
Precipitation of Warmest Quarter	PWarq	mm	438	521	475
Precipitation of Coldest Quarter	Pcolq	mm	322	504	441
Altitude	Alt	m	644	1348	949
Landscape* slope (median)	LSlopem	%	7	18	12
Landscape* slope (coefficient of variation)	LSlopecv	%	45.0	129.2	56.9
Landscape* Aspect Cosine (mean) - Northness	LAspc	-	-0.273	0.249	-0.039
Landscape* Aspect Sine (mean) - Eastness	LAsps	-	-0.418	0.289	-0.079
Landscape* Vertical curvature (mean)	LCurV	m^{-1}	0.4913	0.5051	0.4975
Landscape* Horizontal curvature (mean)	LCurH	m^{-1}	5.88	6.03	5.96
Landscape* Topographic Wetness Index (mean)$^+$	LTWI	-	6.27	7.07	6.54
Soil type**					
Cambisol$^+$	Csoil	-	-	-	-
Ferralsol	Fsoil	-	-	-	-
Transect Aspect**					
North$^+$	NAsp	-	-	-	-
South	SAsp	-	-	-	-
Neutral***	NeAsp	-	-	-	-
Transect Slope**					
Flat terrain***$^+$	Ft	-	-	-	-
Hillside	Hs	-	-	-	-

* within a buffer with radius of 1 km, ** qualitative variables, *** plain surface $^+$ selected variables after forward selection to model β diversity

To achieve models that are more parsimonious and to avoid possible strong linear dependencies among the explanatory variables we applied forward selection for both spatial and environmental data sets. First, we performed separated RDA analyses with all variables of each dataset to calculate the adjusted coefficient of multiple determination (R_a^2) (Peres-Neto et al. 2006) and the significance of the models. The forward selection was applied with the double stopping rule: R_a^2 and α value ($p<0.05$, after 999 random permutations) to prevent the overestimation of the explained variance (Blanchet et al. 2008; Borcard et al. 2011). Then RDA analyses were applied again using only the forward selected variables. For the RDA triplot we choiced the fitted site scores (lc) and the scaling 2 option to display objects and variables. Scaling 2 corresponds to a correlation biplot, where the angles between all vectors reflect linear correlation and the distances between objects are not approximate Euclidean distances (Legendre & Legendre 1998; Borcard et al. 2011).

The variance partitioning results produced independent components including the fraction explained by the pure environmental variables [a], the pure spatial variables [c], the spatial component of environmental influence [b] and the undetermined fraction [d]. Adjustment of explained variation and significance of testable components complemented the analyses (Peres-Neto et al. 2006; Legendre 2008).

All statistical analyses were done with the R statistical language (R Development Core Team, 2012). For RDA analyses, we used the “vegan” library (Oksanen 2011). The function “spacemakeR” (Dray et al. 2006) was used to build PCNM eigenvectors and the function “varpart” (Peres-Neto et al. 2006) to perform variation partitioning with RDA-adjusted R^2 values and to test fractions significance. Forward selection was performed with “packfor” library (Dray et al. 2007).

Results

The survey of grasslands diversity in the 320 sampled plots resulted in 315 taxa, distributed in 46 families: Asteraceae (77), Poaceae (67), Cyperaceae (24), Fabaceae (24), Rubiaceae (14) Apiaceae 13), and another 40 families with lower than 10 taxa each (95).

Considering cover data, Poaceae dominated the physiognomy of the community (72%), followed by Cyperaceae (11%), Asteraceae (8%), and Fabaceae (3%). The species-abundance distribution revealed few dominant species and a high percentage of very low cover species. Only 14 dominant species had relative cover values higher than 1%, considering the relative cover after pooling all sample units: Poaceae (*Andropogon lateralis*, *Axonopus affinis*, *Axonopus siccus*, *Dichanthelium sabulorum*, *Eragrostis lugens*, *Paspalum notatum*, *Paspalum plicatulum*, *Paspalum pumilum*, *Piptochaetium montevidense*, *Schizachyrium tenerum*), Cyperaceae (*Rhynchospora barrosiana*, *Rhynchospora flexuosa*, *Scleria sellowiana*) and Convolvulaceae (*Dichondra sericea*).

Variation of community composition at the transect scale

The original data set with all the environmental variables used for modeling community composition was reduced from 18 to 6 variables after the forward selection procedure. The following variables were selected: annual mean Temperature, temperature seasonality, landscape Topographic Wetness Index, North transect aspect, Flat terrain transect, cambisol soil type.

After forward selection in each data set, the combined explained variation of the selected spatial and environmental variables was of 41.4 % (R_a^2) (Fig. 1a). The environmental variables accounted for 35.7% and most of it was spatially structured. The pure effects of environment and space were significant ($P<0.05$) but with lower expression, corresponding to 7.2% and 5.7% of the total variation, respectively. All fractions resulting from variation partitioning (a+b, b+c, a+b+c, a and c) were significant ($p<0.001$). Fig. 2 show the fitted values of the two most significant canonical axes corresponding to the environmentally explained variation [a+b] and to the pure structured fraction [c].

A second partitioning using only the full dataset of environmental variables, split in four thematic subsets, showed each one of the pure and shared loadings (Fig. 1b). The climate variables accounted for the largest variation 28% (R_a^2). However, only 4.9% of it corresponded to their pure effect. The shared effect of climate with landscape geomorphology and soil type together accounted for 9.8% (R_a^2). The shared effect with soil type only was similar 9.3% (R_a^2) and with landscape geomorphology variables a little smaller 6.1% (R_a^2). The pure effects of landscape geomorphology and soil type were very low (R_a^2<0.01). The local topography variables showed a pure loading of 6% (R_a^2) and very low or even absence of shared effect with the other subsets.

The six selected variables showed the following decreasing loadings to the overall variation in the community composition: annual mean temperature (AMT, $R_a^2 = 0.195$), cambisol (Csoil, $R_a^2 = 0.068$), flat terrain (Ft, $R_a^2 = 0.052$), temperature seasonality (Tsea, $R_a^2 = 0.023$), landscape Topographic Wetness Index (LTWI, $R_a^2 = 0.012$) and North aspect (NAsp, $R_a^2 = 0.006$). By partitioning the variance of each one of this variables with the spatial data set (10 selected PCNMs), only Ft and NAsp showed absence of spatial dependency (b = 0 and 0.004, respectively) and the others showed irrelevant spatial independency.

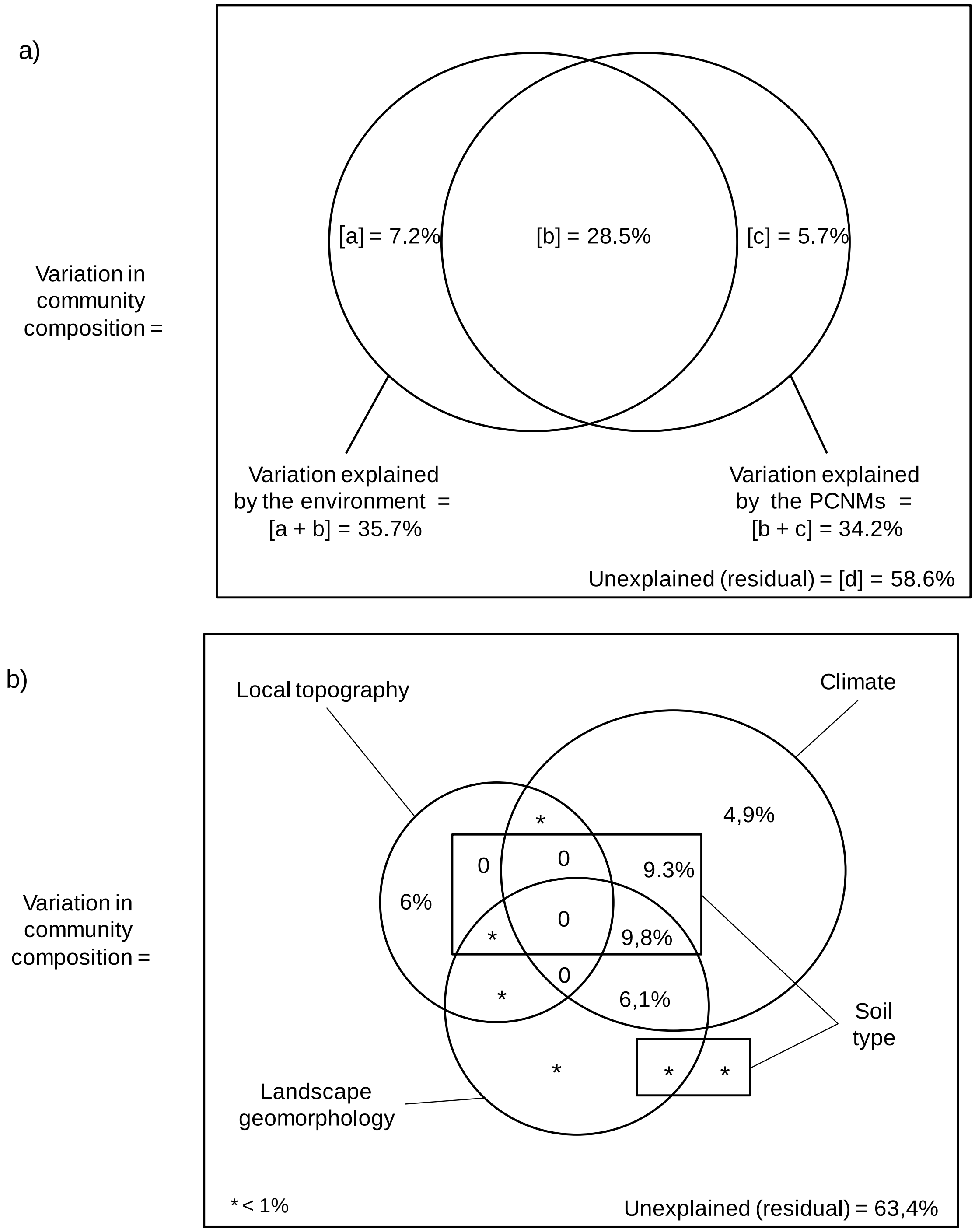
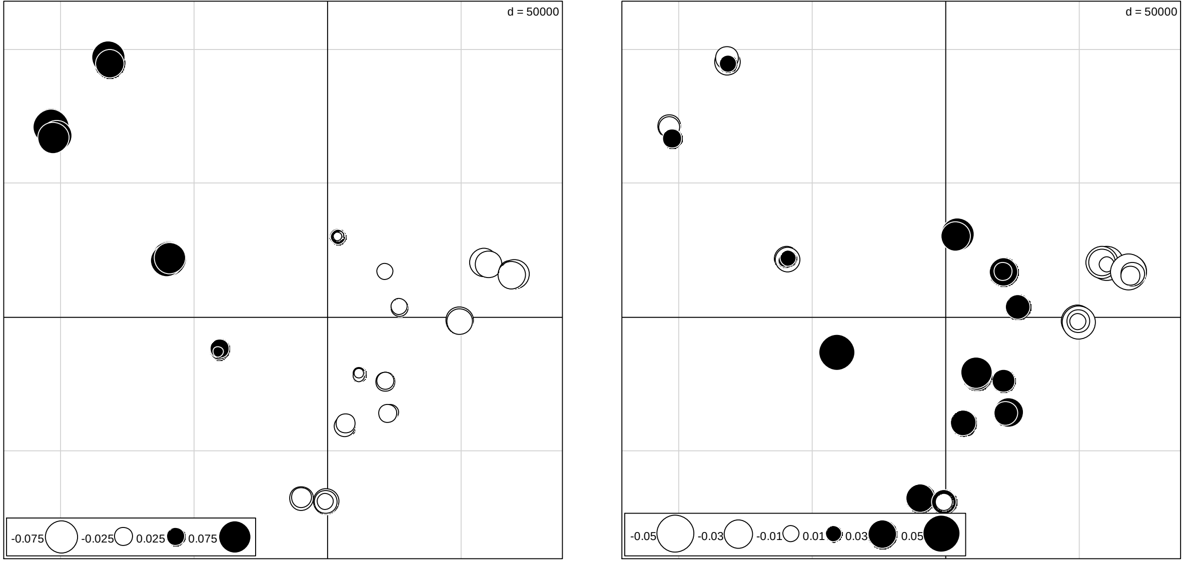


Figure 1. Variation partitioning of community composition based on 64 transects considering (a) the set of environmental variables and the set of PCNM eigenfunctions after forward selection and (b) only the environmental variables considering the different subsets (local topography, climate, landscape geomorphology and soil type). The figures are Venn diagrams where the box represents 100 % of the variation in the response variable. All represented fractions are adjusted R^2 statistics (R_a^2).



a) Canonical axis I of the environmental fraction [a+b]; 25.9% of the species variation (unadjusted R^2).

b) Canonical axis II of the environmental fraction [a+b]; 7.6% of the species variation (unadjusted R^2).

c) Canonical axis I of pure spatial fraction [c]; 7% of the species variation (unadjusted R^2).

d) Canonical axis II of pure spatial fraction [c]; 4.2% of the species variation (unadjusted R^2).

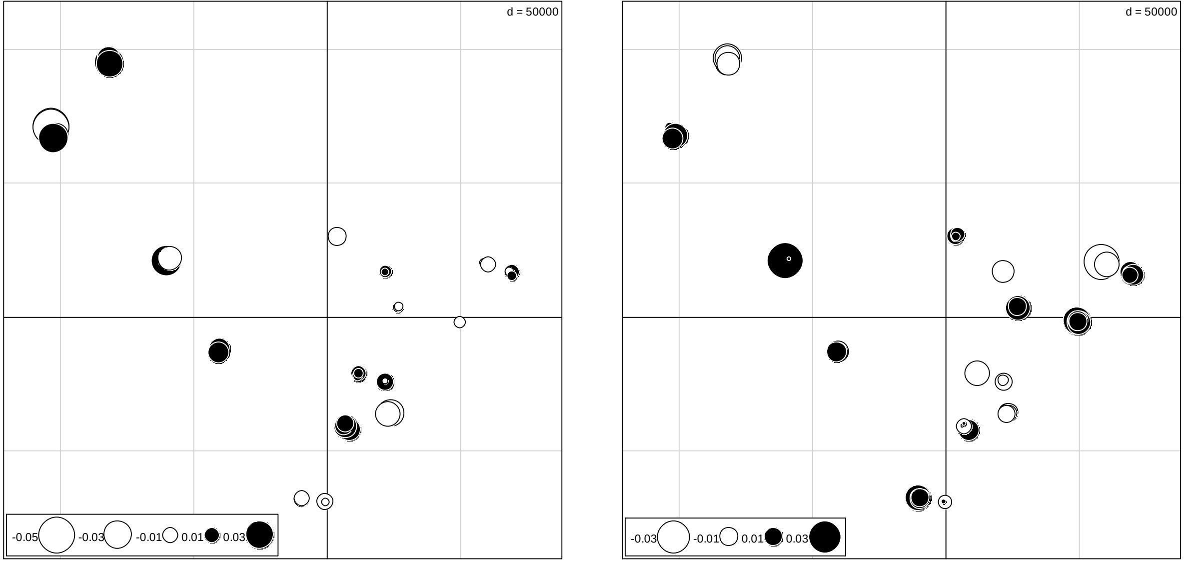


Figure 2. Maps of sampling units (64 transects) in the geographical space with the fitted site scores (circles) of the two more significant canonical axes I and II. Maps a) and b) correspond to the environmental variation [a+b]. Maps c) and d) correspond to the pure spatially structured fraction [c], unexplained by the evaluated environmental dataset. In each map, the horizontal axis corresponds to longitude and the vertical axis to latitude (UTM). Circle size is proportional to each site score value.

The RDA triplot (Fig. 3) shows stronger correlation of axis 1 with cambisol (Csoil, simple $R_a^2 = 0.758$), temperature seasonality (Tsea, simple $R_a^2 = 0.303$) and annual mean temperature (AMT, simple $R_a^2 = 0.158$) and of axis 2 with flat terrain (Ft, simple $R_a^2 = 0.374$), North aspect (Nasp, simple $R_a^2 = 0.236$) and the landscape Topographic Wetness Index (LTWI, simple $R_a^2 = 0.1225$). Among species with the highest scores, *Paspalum notatum* (pano), *Desmodium* *incanum* (dein) and *Chevraeulia sarmentosa* (chsa) were highly associated to ferralsols, and *Andropogon lateralis* (anla), *Paspalum plicatulum* (papl), *Galium humile* (gahu) and *Axonopus siccus* (axsi) with cambisols. Those species negatively correlated with annual mean temperature and temperature seasonality included *Rhynchospora flexuosa* (rhfl), *Paspalum pumilum* (papu), *Scleria sellowiana* (scse), *Rhynchospora barrosiana* (rhba). *Piptochaetium montevidense* (pimo) was positively correlated with temperature. *Baccharis pentodonta* (bape) and *Schizachyrium tenerum* (scte) were positively associated to transects on hillsides.

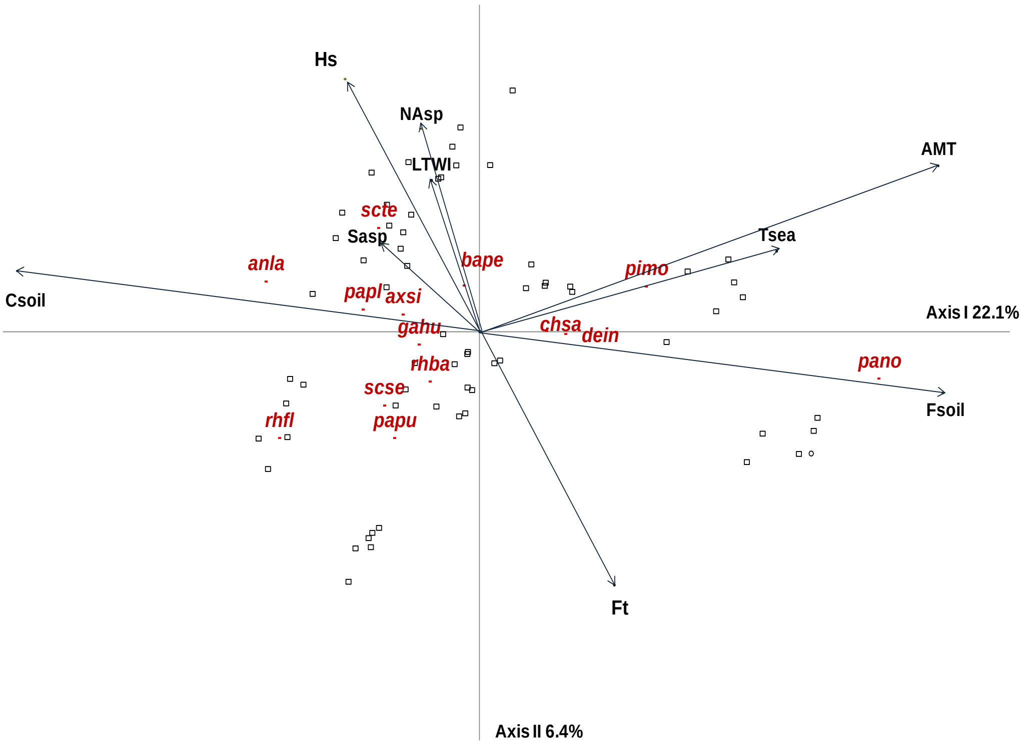


Figure 3. RDA triplot of grassland species composition constrained by the six selected environmental variables, fraction [a +b]. Open squares represent the communities (transects) according to the fitted site scores, arrows correspond to quantitative or to qualitative variables. Csoil = cambisol, Fsoil, ferralsol, Hs = hillslope, Ft = flat terrain (and neutral aspect), NAsp = North aspect, Sasp = South aspect, AMT = annual mean temperature, Tsea = temperature seasonality, LTWI = landscape Topographic Wetness Index. Species composition was previously Hellinger-transformed. Species with higher correlation values (red letters): *Paspalum notatum* (pano), *Desmodium incanum* (dein), *Chevraeulia sarmentosa* (chsa), *Andropogon lateralis* (anla), *Paspalum plicatulum* (papl), *Galium humile* (gahu), *Axonopus siccus* (axsi), *Rhynchospora flexuosa* (rhfl), *Paspalum pumilum* (papu), *Scleria sellowiana* (scse), *Rhynchospora barrosiana* (rhba). *Piptochaetium montevidense* (pimo), *Baccharis pentodonta* (bape), *Schizachyrium tenerum* (scte).

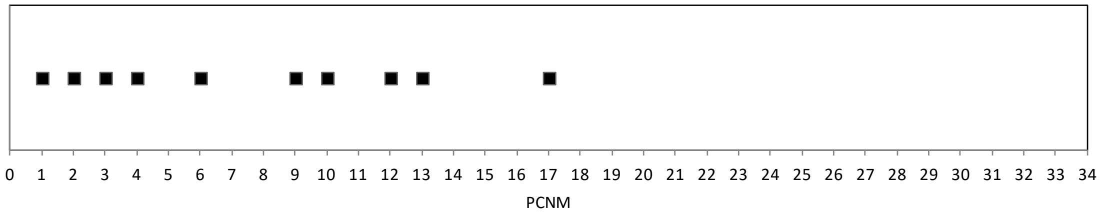
The original set with 34 PCNM eigenfunctions was reduced to 10 variables to best model community composition (R_a^2 = 0.3422, which was similar to the value for all 34 PCNMs without any selection, R_a^2 = 0.3341). The selected PCNMs are within the first PCNMs, and considering that the decreasing variance order of PCNM axes correspond to decreasing spatial scales, they represent mainly broad to medium-scale spatial variation (Fig. 4). However, most of this spatial variation was also related to the selected environmental variables, since the pure spatial component was very low. The maps of the fitted values corresponding only to the spatially structured variation that is not explained by the set of environmental variables, the fraction [c], are presented in Figs. 3 c-d. The fraction [c] correspond mainly to medium spatial scales, since after individually partitioning each one of the selected PCNMs with the environmental data set the highest loadings were obtained by the PCNMs 13, 9 and 17.

Variation of species richness at the transect scale

The mean number of species per transect was 43.9, ranging from 18 to 65. The forward selection procedure to model species richness selected two of the 18 environmental variables (R_a^2 = 0.1882). The landscape Topographic Wetness Index showed the dominant effect accounting for 10.7% (semipartial R_a^2) of the richness variation and Precipitation of Wettest Month for 8.1%. Species richness is positively correlated with both variables (LTWI, r=0.348 and PWetm, r=0.137), suggesting that water availability conditions the number of species. Six PCNM eigenfunctions remained after forward selection for modelling species richness (R_a^2 = 0.417) and most of these represent intermediate-scale variation (Fig. 4b).

The variation partitioning of species richness showed that 49.2% of the total variation was explained by the environmental variables and by the PCNMs. Most of this is spatially structured (41.7%) but only 11.3% is shared with the two environmental variables. The pure effect of environmental variables was low (7.5%) and the pure effect of the PCNMs was high (30.4%) (Fig. 5).

a) The 10 selected PCNM eigenfunctions for the community composition matrix.



b) The six selected PCNM eigenfunctions for the species richness data.

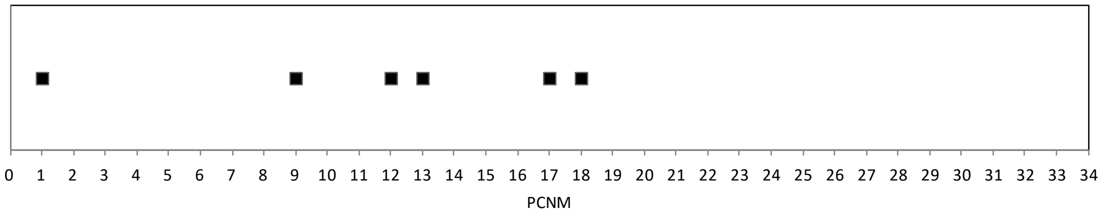


Figure 4. Selected principal coordinates of neighbor matrices (PCNM) eigenfunctions represented by black squares: (a) community composition and (b) species richness.

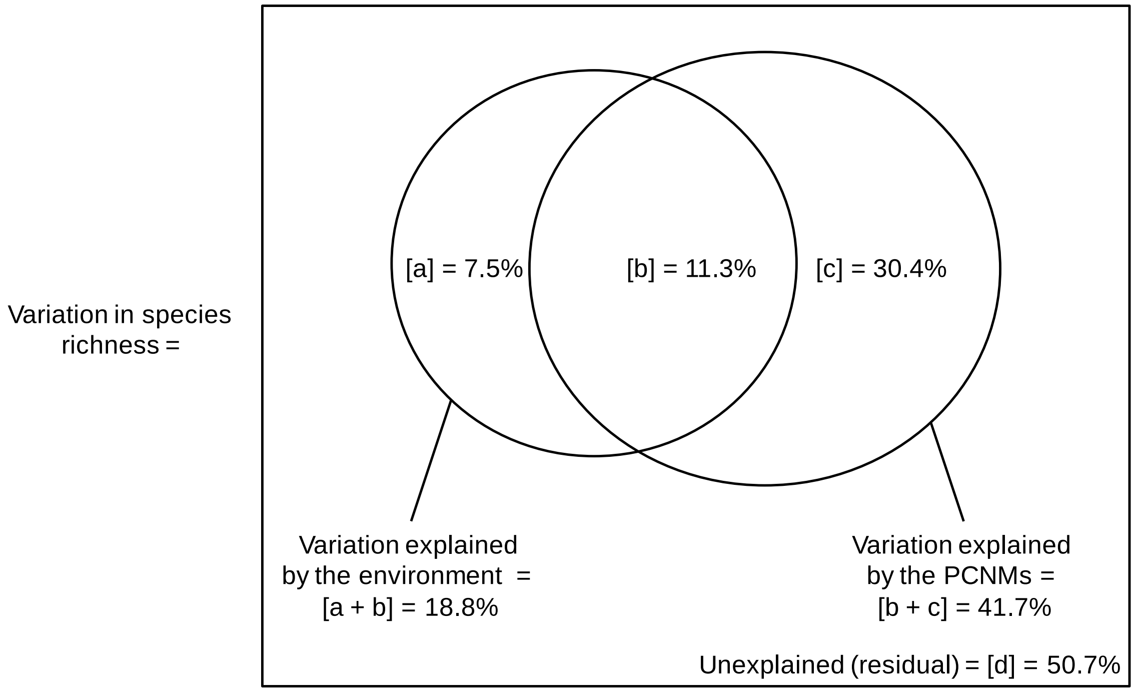


Figure 5. Variation partitioning of species richness based on 64 transects considering the set of environmental variables and the set of PCNM eigenfunctions after forward selection.

Discussion

A considerable portion of the variation in community composition (41.4%) and in species richness (49.3%) was explained by the selected environmental variables and the PCNMs. For community composition, the spatially structured environmental variables loadings suggest an important influence of niche processes at broad scales.

The analysis of the relative contribution of different environmental variables revealed supremacy of the spatially structured variables, with a high-shared effect among climate variables, soil type and landscape geomorphology variables (Fig.1b). This makes it difficult to identify which are the real drivers, but the forward selection procedure retained at least one variable of each one of these datasets suggesting that all are truly important to structure the community composition (Fig. 4).

The pure effect of the environment, not spatially structured, corresponded completely to the local topographic qualitative variables (aspect and slope), with a pure fraction of 6% of the total variation. These variables reflect the environmental effect at a very fine spatial scale, but the effect should be considered indirect, since these are proxy variables that comprehensively characterize the overall quality of the habitat (Legendre et al. 2009). Relief position and aspect have been detected as strong drivers in other studies at local scales in the South Brazilian Campos (Pillar et al. 1992; Focht & Pillar 2003; Overbeck et al. 2006). Both variables were retained in the forward selection and were associated to the second axis of the constrained ordination. Slope (flat/hillside) showed the larger effect and aspect the lower one. However, considering the extent of the study area, these variables showed a secondary role when compared to other variables associated to variation at broader spatial scales.

The three variables mostly associated to the main axis of constrained ordination included two climatic variables (annual mean temperature and temperature seasonality) and soil type. Annual mean temperature showed the strongest effect, indicating that the mean range of 4.5 ºC between sites was enough to explain changes in the composition of species. The effect of temperature was recognized as the main factor driving the north-south floristic differentiation of Atlantic forests in Brazil (Oliveira-Filho & Fontes 2000). In our case, the observed temperature gradient is not completely correlated to latitude, but with a NW-SE orientation, mainly because of regional changes in altitude.

We hypothesize that differences in soil type (ferralsol/cambisol) and temperature have not only a strictly direct effect on the physiology of plant species. They also trigger different regional grassland management regimes, which cause changes in community composition. On the one hand, the cambisol soils are rich in organic matter and strongly acidic, with high saturation of aluminum and clay contents. They suffer high leaching and are nutrient poor (Dümig et al. 2008; Almeida 2009), what makes them less suitable for agriculture and their grasslands are probably less productive. Therefore, they shall support lower cattle stocking rates. On the other hand, the ferralsol soils have high content of oxides of iron and aluminum and are typically deeper, allowing crop farming. Native grasslands on ferralsols have been largely converted into summer crops and winter annual pastures (Pinillos et al. 2009). Because of this, during the crop season cattle that occupy these areas in winter pastures are shifted to the remnant grasslands that temporarily support an increased cattle-stocking rate compared to the cambisol grasslands and are less prone to fires. The strong association of *Paspalum notatum* with ferralsol seems to be an evidence of higher grazing intensity. This reptant grass is characteristic of intensively grazed areas (Boldrini & Eggers 1997).

The landscape Topographic Wetness Index was also selected but with a weak influence on species composition. The selection of this variable suggests that for these grasslands the capacity of water retention associated to the local geomorphology is more important to influence species composition than differences in the rainfall gradient.

The variance partitioning for species richness data showed less effect of the evaluated environmental variables. This pattern was expected since factors of other nature are known to influence species richness, and its variance is often poorly explained by predictor variables. Factors like total community biomass, which conditions the availability of light at the soil surface, the level of disturbance and gradients in the species pool usually are within the main predictors (Grace 1999) but were not evaluated in our work. However, nearly one fifth of the total variation was associated by two variables related to water supply (precipitation of the wettest month) and retention (mean landscape Topographic Wetness Index) and positively related to species richness. The underlying mechanisms of this relationship are still not clear and demand further investigation.

The PCNM results revealed some differences in the patterns of spatial variation of community composition and species richness. In the former, the dominant spatial structure is broad-scaled, as indicated by the selected PCNM eigenfunctions. In the later, the selected PCNMs indicate a tendency to meso-scale spatial structure, since the initial, larger PCNMs were not selected. Further, the set of PCNMs selected for community composition contain the selected PCNMs for species richness, suggesting that some of the unmeasured spatially structured variables contribute to explain species richness and community composition (Legendre et al. 2009).

The pure spatial fraction [c] for community composition was low, suggesting that neutral ecological processes, such as directional dispersal limitation, were less important. It is worth mentioning that these spatial processes that do not covary with the evaluated environmental variables reflected medium scale processes and this information serves as a clue for searching for the corresponding processes. However, we should keep in mind that in observational studies part of the shared fraction [b] that is assigned to the environmental variables could be caused by other spatial processes with a fortuitous correlation with the environment (Bell et al. 2006). Therefore, the relative importance of neutral processes shall not be underestimated based only in the analysis of fraction [c].

In the modeling of community composition and species richness, a large proportion remained unexplained by the predictor variables that were considered. The unexplained fraction [d] may correspond to a variety of factors not evaluated in our study which includes (1) environmental variables and/or (2) biological factors, both not spatially structured, (3) historical events and (4) stochastic processes, like ecological drift and dispersal in the absence of a spatial signature (Legendre et al. 2005). It is probable that with the inclusion of additional environmental variables, we could improve the loading of the fraction [a+b]; however, the great-unexplained fraction suggests that other factors are important drivers for these grasslands. In fact, these grassland are under permanent disturbances, including fires and grazing, whose extension, intensity and frequency are highly variable and are not necessarily spatially structured, causing random elimination of species and changing the structure of these communities.

The observed patterns are not conclusive, but suggest a higher influence of niche processes, which accounted for nearly one-third of the variation in the community composition. The low contribution of the pure spatial component [c] suggests a secondary role for dispersal limitation on shaping these communities. Moreover, the niche effect that was detected indicates that regional climate and soil gradients overwhelm the effect of fine-scale variables related to the local topography.

Acknowledgements. We are grateful to Ilsi Boldrini, Angelo Schneider and Rafael Trevisan for taxonomic identification of grassland species, to Heinrich Hasenack, Eliseu Weber and Tatiana Kuplich for aid with geoprocessing tools and to Bruno S.G. Fonseca, Claudio Reis, Gabriel Specht, Marcel Tust and Tiago Caetano Edruziane for help in field expeditions, Part of this work was carried out with the aid of a grant (LEAF) from the Inter-American Institute for Global Change Research (IAI) CRN-2005 which is supported by the US National Science Foundation (grant GEO-0452325). E.V.M received a doctoral CNPq scholarship. V.P. receives support from CNPq (306573/2009-1).

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Capítulo 3. (Artigo 3) Diversity of grasslands across spatial scales in highland Southern Brazil *Campos* and implications for conservation[1]

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[1] Este artigo será submetido ao periódico *Natureza & Conservação* na secção *Research Letters.*

Abstract

Community patterns are scale dependent and environmental drivers at finer scales may affect broad–scale ecological dynamics as well as broad-scale drivers can overwhelm local patterns and processes. Knowledge about the hierarchical dynamic of grassland species turnover helps to develop conceptual ecological models and to implement conservation, sustainable use and restoration actions. We combined a nested sampling design with additive diversity partition to explore the scale dependent grassland diversity patterns of highland southern Brazil grassland communities, regionally known as *Campos de Cima da Serra*. Our specific objectives were to know how the total community variation can be explained at different scale levels and to identify which ones have stronger influence on the community composition. A total of 320 plots were sampled (five plots x four transects x two sites x two subregions x four regions) within an area ranging 160 km of latitude and 170 km of longitude. To decompose γ diversity into α and β components we used additive partitioning considering the five spatial scales followed by randomization procedures with null models to test if observed values were random. The magnitude and extension of the spatial correlation among species composition was evaluated with a Mantel correlogram. A total of 315 species were identified and four families comprised 61.3% of total species richness: Asteraceae (77), Poaceae (67), Cyperaceae (25) and Fabaceae (24). Most species (264) occurred in less than 10% of the plots and a few group of grass dominant species had higher relative cover values. Additive diversity partitioning revealed a large proportion of beta diversity at broader scales, with 46.3% of overall diversity at scale of region. Variation of species richness among transects and among plots was lower suggesting that regional drivers are more influent on the communities structure. The high proportion of less frequent species suggests that a large protected area would be necessary to represent most species; however, beta diversity results showed that their effectiveness to conserve grasslands diversity would be improved splitting the area effort to represent each one of the four geographical regions.

Key words: Beta diversity, Additive partitioning, Hierarchy

Introduction

The observed spatial patterns of biological communities are a consequence of multiple drivers that may act with different proportions in each environmental context. Local environment and landscape heterogeneity are known to contribute to the sorting of regional pools of potential colonizer species into local communities across space (Peres-Neto & Legendre 2010). Besides environmental niches (Hutchinson 1957), biological interactions, dispersal differences amongst species (MacArthur & Wilson 1967), limited dispersal (Hubbell 2001), population stochasticity and disturbances (Pickett & White 1985) are also responsible for the differences in species number and composition among sites.

For describing the patterns of diversity in space, a set of descriptors of the taxonomic community diversity was proposed with the concepts of gamma (γ), alfa (α) and beta diversity (β) (Whittaker 1960; 1972). The complete set of species occurring in the whole region of interest is termed gamma diversity. Within this region, the number of species within each individual site correspond to the alpha diversity and the variation in species composition among sites within a specific region correspond to beta diversity. Therefore, alpha and beta diversity correspond to the within-habitat and between-habitat concepts (MacArthur 1965), respectively. The knowledge of alpha and betta patterns, independently of which processes create and maintain the observed diversity, are important tools for conservation planning, including application in the establishment of protected areas. Most species are not distributed everywhere and the spatial structure is not only an artifact that results of contemporary and historical random processes. In most of cases, it is the result of differences in the ecosystem or even singular historical processes developed along environmentally equivalent areas. Therefore, we shall preserve this spatial organization or the species-environment relationships necessary for nature to recreate and maintain beta diversity (Legendre et al. 2005).

To understand the spatio temporal dynamic of biological communities we also should take into account that the observed patterns are scale dependent. They change with hierarchies - the grain and extent considered (Hoagland & Collins 1997; Perelman et al. 2001) and are affected by connectivity across scales. Environmental drivers at finer scales can affect broad-scale ecological dynamics and broad-scale drivers can overwhelm local patterns and processes (Peters et al. 2008). This interplay is increasingly being recognized as crucial to understand ecosystem dynamics (Huston 1999). Revealing patterns of scale-dependency increases our capacity to develop conceptual models of vegetation variation along environmental gradients and to implement conservation, sustainable use and restoration actions (Perelman *et al*. 2001). The additive diversity partition has been a methodological approach used to split the relative importance of beta diversity across several spatial scales (Veech et al. 2002; Crist et al. 2003; Veech 2005; Veech & Crist 2010). It decomposes regional diversity into α and β components in a way that both correspond to average values and have the same unit, allowing direct comparison (Crist et al. 2003). The alpha diversity at the first scale plus beta diversity equals to alpha diversity of the next spatial higher level and so on. This allows, for instance, to decompose gamma diversity into components at different scales, such as $\gamma = \alpha 1 + \beta 1 + \beta 2 + \beta 3$, with the advantage of assessing the relative proportions of the total diversity found at each scale (e.g., habitats, landscapes, regions). The combination of this method with randomization routines have allowed to test if observed values departure from expected ones by null models, improving the search for the underlying ecological processes (Veech et al. 2002).

Knowledge on which spatial scale beta diversity is higher is not trivial. Yet, it can help to improve management and strengthen conservation strategies (Gering et al. 2003) and the efficiency of biological diversity research sampling designs and biomonitoring schemes (Ligeiro et al. 2009). Additive partitioning can help conservation biologists to evaluate alpha and beta contributions to overall diversity across scales and to target those scales that concentrate higher beta diversity. When most of beta diversity is at a higher level, the best option is to split the conservation effort in several smaller areas, while when it concentrates at a lower level, to establish one bigger area is more appropriate. Obviously, beta diversity is not the only information to be considered, and a sound reserve design is more complicated than adopting one general principle (Meffe & Carroll 1994, Diniz-Filho et al. 2004, Padua et al. 2008).

The additive diversity partitioning has been applied in several studies of aquatic and terrestrial ecosystems and this approach can help to understand the heterogeneity of grassland communities in southern Brazil. Grasslands are among the most human-modified (Hannah et al. 1995) and less protected (Henwood 1998; Hoekstra et al. 2005) biomes of the world. Global concern with temperate grasslands is recent with few concrete conservation results (TGCI 2008). This is true for the South Brazilian Campos, a neglected biome in Brazil in terms of biodiversity conservation. These grasslands show an expressive biodiversity but are seriously threatened by recent intensification of land use (Overbeck et al. 2007) and have a low degree of protection within protected areas.

In the Rio Grande do Sul state, where most of these grasslands remnain, only a small fraction of 2.58% are conserved in natural reserves (Brandão et al. 2007). Moreover, these grasslands show regional singularities related with differences in composition of species, families and endemic species (Boldrini 2009). Therefore, additive partitioning can help to explore unknown diversity differences within these grasslands and guide the expansion of conservation actions in accordance with the spatial scales that show the widest variation in taxa composition. This approach is consistent with the principle of complementarity used in conservation priorization (Kirkpatrick 1983) to minimize the cost of the conservation and to ensure that all biodiversity features receive some level of conservation investment (Wilson et al. 2009).

In this paper, we combined a nested sampling design with additive diversity partition to explore scale dependent diversity patterns of highland southern Brazil grassland communities, regionally known as *Campos de Cima da Serra*. Our specific objectives are to know the total community variation distribution at different scale levels and to identify which are the spatial scales with a higher influence on the community composition. We expect that differences in relief and aspect could operate as strong environmental constraints propagating a small-scale vegetation pattern over larger spatial extents.

Methods

Study area

The study area comprises an 18,667 km^2 region in the northeast of Rio Grande do Sul state, southern Brazil (27.48º/29.49ºS and 49.7º/52ºW), known as *Campos de Cima da Serra* (Fortes 1959) (Fig.1). It lies on the Meridional Plateau, a highland formed by successive flows of basalt and rhiodacyte extrusive volcanic rocks (120-135 My BP). Altitudes range from 600 to 1,400m a.s.l., decreasing from east to west (Weber et al. 2004). The relief is smoothly undulate to undulate. Soils in the central and east sectors correspond to cambisol and in the west sector to ferralsol. The climate is warm temperate (subtropical) and humid. Mean annual temperature ranges from 13.6 to 18.6ºC (IPAGRO 1989) along ESW-WSE direction and annual precipitation ranges from 1,587 to 2,164 mm along N-S direction (Hijmans et al. 2005) and is regularly distributed along the year (IPAGRO 1989).

Natural grassland still cover 41 % of the study area (Cordeiro & Hasenack 2009) and are at risk mostly by conversion to agriculture, cultivated pastures and exotic trees plantations, which are still increasing in area. All these grasslands are continuously grazed and subject to frequent anthropogenic burnings (2-3 years interval). They show a homogeneous physiognomy, forming mosaics with *Araucaria angustifolia* forest. Floristic diversity is high with 1,161 known species, 107 of them endemics (Boldrini et al. 2009). These grasslands were legally recognized as *Campos de Altitude* within the Atlantic Forest Biome by the so-called *Mata Atlântica* federal law nº 11,428 (Brazil´s House of Representatives 2006), which if enforced would restrict land use conversion.

Sampling design and field data collection

Field sampling was conducted from December 2008 to February 2009, during austral summer season, when reproductive organs are present allowing reliable species identification. Grassland sampling units were selected excluding those areas with less than two years from the last burning episode or without grazing (grassy vegetation height higher than 0.5m). We assumed that with the exclusion criteria adopted the disturbance regime of sampled areas was relatively similar. Peat bogs and permanently wet grasslands were excluded from sampling.

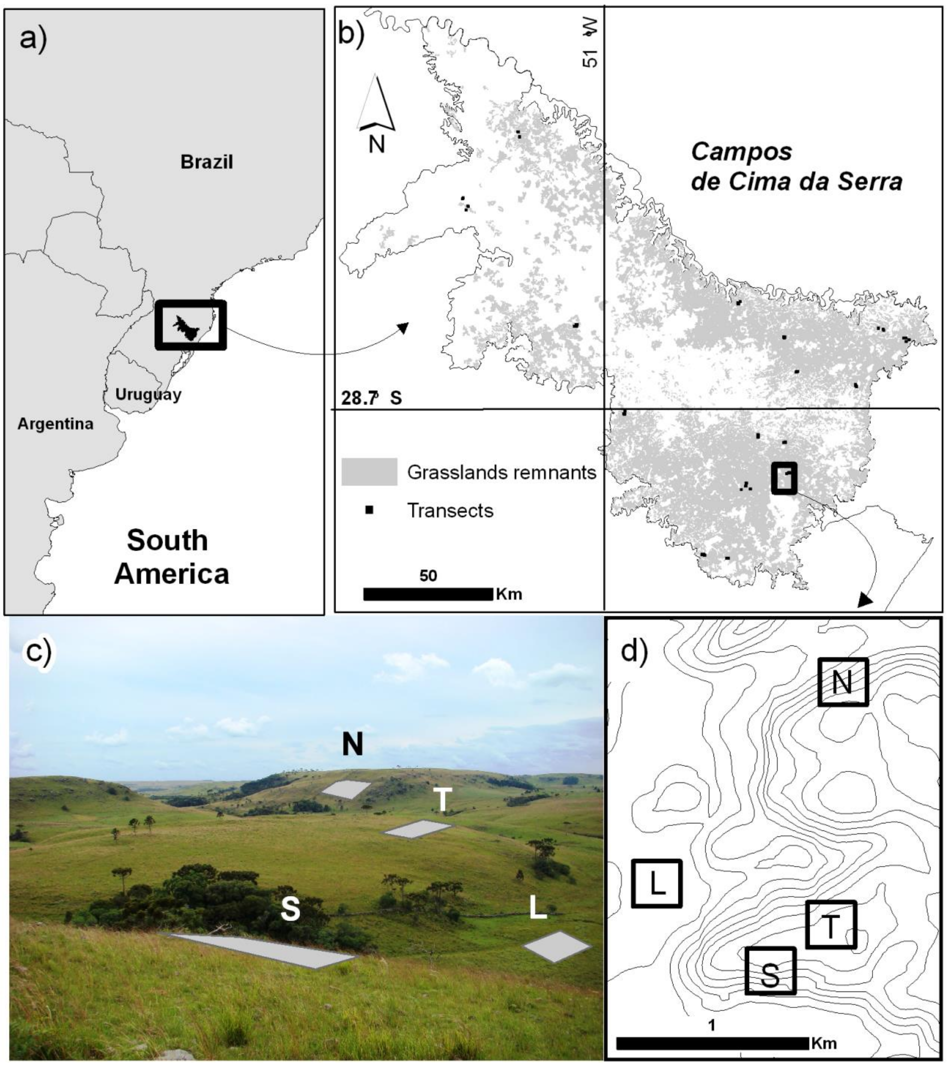

Figure 1. The *Campos de Cima da Serra* region, Rio Grande do Sul, Brazil and the sampling design. a) Location of the study region in Southern Brazil. b) Limits of study area, grassland remnants and sampled transects c) Site with four relief–aspect strata. Within each strata a transect (80 m) with five plots (20 m distant from each other) was set. N = northern hillslope, S = southern hillslope, T = tophill and L = lowland.

To ensure representativeness of the main climatic, edaphic and topographic gradients we set a stratified nested design across different spatial scales, including plots, transects, sites, subregions and regions. The finest spatial scale consisted of 0.25 m^2 plots (0.5 x 0.5 m), used to visually estimate species abundance based on the aboveground percentage cover (0-100% cover data). Subsets of five plots (20 m distant from each other) were nested within 64 transects (80 m). Subsets of four transects were nested within 16 sites. Each site corresponded to a different farm and each one of the four transects correspond to a specific relief–aspect strata (northern hillslope, southern hillslope, tophill and lowland). Sites were nested within eight subregions that were previously defined combining different levels of annual mean temperature (13.6-18.6 ºC) and annual mean rainfall (1600-2200 mm) based on WorldClim – Global Climate Data (Hijmans et al. 2005). Two subregions where identified within each region among four geographical regions.

Therefore, we sampled 320 plots (five plots x four transects x two sites x two subregions x four regions) within an area ranging 160 km of latitude and 170 km of longitude (Fig. 1). Spatial distance between transects within each site ranged from 0.1 to 2 km and distance between farms within each subregion ranged from 10 to 30 km. Distance among sites of different subregions and regions ranged from 30 to 170km.

Data analysis

To describe the species heterogeneity at the plot level we used species richness and Pielou evenness index (Pielou 1975). For the additive partitioning of diversity we adopted the approach described by Veech et al. (2002) and Crist et al. (2003). Total variation in taxonomic composition was decomposed into alpha and beta components. We tested if diversity was uniform at all spatial scales by partitioning the total diversity using species richness as the only metric. The spatial structure of species diversity was assessed by pooling plots from lower to higher levels: plots (320), transects (64), sites (16), sub-regions (8) and regions (4).

Alpha and beta diversity were calculated for each level. At the first level, alpha diversity is the mean of plot diversities, at the second level, alpha diversity is the mean of transects diversities and so on. Beta diversity at a given level *i* is the difference between alpha of the higher level *i*+1 and alpha of level *i*. For species richness, beta diversity represents the mean number of species added up to the community between levels *i* and *i*+1 (Fig.2).

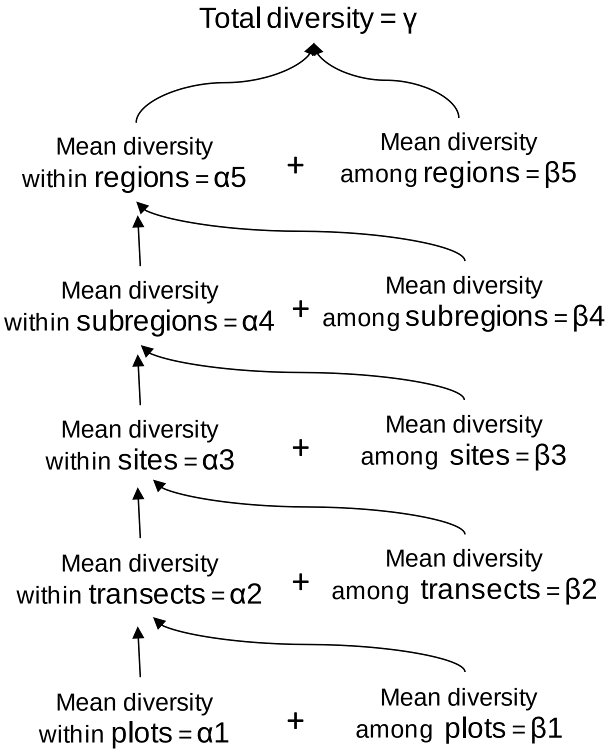

Figure 2. Additive partitioning of total species richness in alpha and beta components over five spatial scales.

At each scale, we tested if the observed diversity was the result of non-random communities or a mere artifact generated by the sampling design (Crist et al. 2003). To evaluate if observed values are larger or smaller than expected by chance, we used a null model to derive the expected values from randomly distributed samples. In sample-based randomization, tests are performed one level at a time. To test each hierarchical level, the samples at level *i*-1 are randomly allocated only to those samples at level *i* that belong to the same sample unit at *i*-1 (Crist et al. 2003). After 1000 permutations, the proportion of values in the null distribution higher than the observed was calculated. We adopted the threshold of $p<0.05$ to conclude that the observed diversity was higher and p>0.95 to conclude that the observed diversity was lower than expected by the null model. In sample-based randomization, the integrity of samples at each hierarchical level is preserved. The only exception was at the plot level; in which sampled species were shuffled among plots within each transect to test for significance of beta at the plot level. An alternative approach, the individual-based randomization, shuffles individuals rather than samples to test if observed values are the result of intraspecific aggregation (Crist et al. 2003). However, our grassland species abundance data are based on the aboveground percentage cover, and not on individuals, precluding the application of this approach. Therefore, species cover matrix was previously converted to a presence-absence data before randomization. To perform the sample-based partitioning we used the function 's.based' (Ribeiro et al. 2008) in the R statistical language (R Development Core Team, 2012).

The magnitude and extent of spatial correlation among the species composition was evaluated and tested by using a Mantel correlogram (Sokal 1986). This test uses a normalized Mantel statistic r_M calculated for different distance classes of the dataset followed by a permutation statistical significance test (Borcard et al. 2011). The Mantel correlogram was performed using R function *mantel.correlog* from vegan package (Oksanen 2011). Community data from plots were previously merged within transects and Hellinger transformed. The matrix of species data was detrended using a third-degree function with the transects geographical coordinates to meet assumption of second-order stationarity and a Holm´s correction was applied for multiple testing of spatial correlation values (Holm 1979).

Results

The total richness observed in the sampled plots was of 315 species. Most species were represented by four families: Asteraceae (77 species), Poaceae (67 species), Cyperaceae (25 species), Fabaceae (24 species). Other 21 families were represented by only one species each. Species richness in 0.25m^2 plots (α1) ranged from four to 35, with a mean value of 19.3 species.

Alpha richness values were normally distributed with low coefficient of variation (CV=26.7%) Evenness values were left skewed with a median of 0.68 and less variable than species richness (CV=15.3%).

Most species were restricted to a small number of sites (satellite species) - 264 species had a frequency below than 10% of the 320 plots, and only few species were found in almost all plots (core species) (Fig.3). This small group of core species was also represented by cover dominant species, principally perennial cespitous grasses. Therefore, grassland physiognomy had a twofold pattern: a homogenous group of core, and biomass expressive, grass species forming the vegetation matrix, and a highly heterogeneous group of rare species, including also grasses, grass-like herbs, forbs, and small shrubs with low cover values distributed in interstitial gaps.

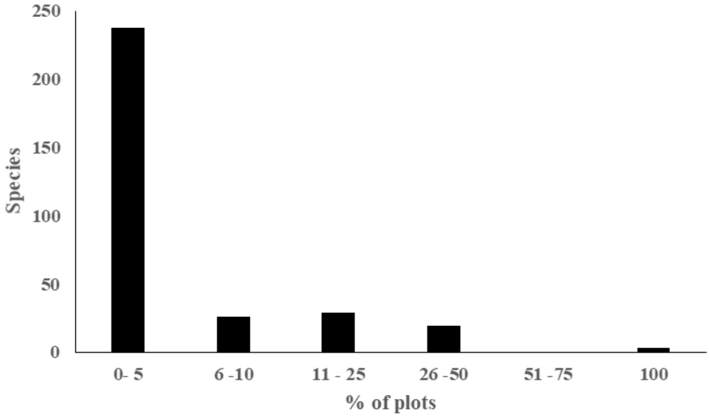

Figure 3. Frequency histogram of grassland species sampled in the regional survey (320 plots, 0.25 m^2) on grassland communities in *Campos de Cima da Serra* region, RS, Brazil.

Additive partitioning of overall diversity (species richness) revealed a heterogeneous distribution of diversity among spatial scales with most of variation lying at the broader scale (Tab.1). Moreover, most of the diversity values were significant, suggesting that they were not sampling artifacts and deserve investigation of their underlying ecological processes. Less than 14% of the total species diversity was due to within and among plots components ($\alpha 1$ and $\beta 1$). The mean species richness in plots ($\alpha 1$ = 19.3) was higher than expected under the null model (p =0.001) Species turnover at the lower spatial scale β1 (among plots of a same transect) was lower than expected by the null model (p = 0.001) contributing with 7.8% of overall diversity. Beta diversity at transects (β2) and sites levels (β3) was higher than expected by the null model (p =0.319) suggesting relevant ecological processes influencing species distribution at these scales.

However, mean beta diversity at subregions level (β4=13.8%) was not different from expected by chance (p = 0.193). The variation in beta diversity recorded at the regional scale (β5) showed the highest proportion, with 46.3% of overall diversity, a value higher than the expected under the null model (p = 0.022). It means that moving across the four regions there is a mean increase of 145.8 species.

Table 1. Additive partitioning of grassland diversity across a hierarchically scaled survey in *Campos de Cima da Serra* region, RS, Brazil.

	Source	***No. samples***	***Species richness***				
			obs	***%***	***exp***	***p***	***obs-exp***
α1	Within plots	320	19.3	6.1	15.85	0.001	+
β1	Among plots	320	24.6	7.8	28.06	0.001	-
β2	Transects	64	46.5	14.8	38.91	0.001	+
β3	sites	16	35.3	11.2	31.95	0.001	+
β4	subregions	8	43.5	13.8	42.75	0.193	ns
β5	regions	4	145.8	46.3	139.1	0.022	+
Y	totals		315	100			

obs: mean observed values, *%*: percentage of total species richness, *exp*: mean expected values from null distributions, *p* = proportion of random values higher than observed, *obs-exp*: + indicates that observed values are significantly higher than expected by chance, - indicates that observed values are significantly lower than expected by chance, ns indicates that observed values are not significantly different from expected values.

The Mantel correlogram revealed that beta diversity was spatially structured within 100 m to 30 km transects interdistance, with low, but significant positive spatial correlation ($0.05<r_M<0.1$) (Fig. 4). It means that under a 30 km threshold, closer communities were more similar, within a distance decay pattern. Beyond this distance, the observed differences in species composition were spatially independent.

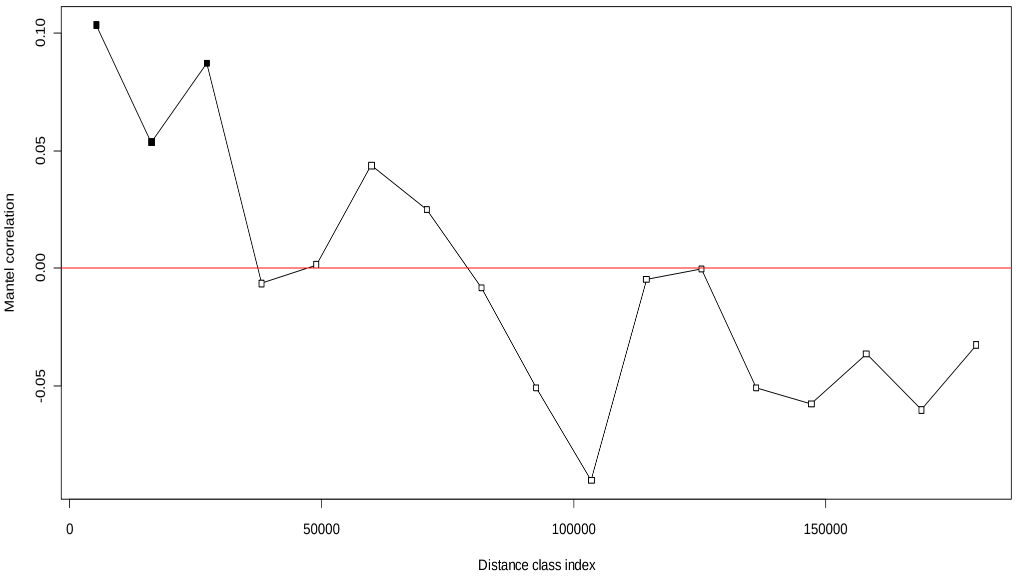

Figure 4. Mantel correlogram of grassland transects in *Campos de Cima da Serra* region, Brazil. Axis X correspond to distance between transects (meters) and axis Y to correlations between the community dissimilarity matrix and geographic coordinate's dissimilarity matrix. Black squares mean significant multivariate spatial correlation after Holm correction for multiple testing.

Discussion

The additive partitioning of species diversity revealed a hierarchical pattern with non-random communities at some specific spatial scales. It also revealed that broadest scale (regions) has largely the most important contribution to overall diversity, since species turnover among regions is 3.1 times higher than turnover among transects and 4.1 times higher than among sites.

The high observed values of $\alpha 1$ at plots scale, and the consequent low $\beta 1$ among plots of a same transect, indicates a low level of species dominance and a high similarity in species composition within each transect. Southern Brazil grasslands usually have dominant core grass species, which compete for light and space with other species reducing the species number at the plot level (Overbeck et al. 2005). On the other hand, disturbances, like grazing and fires, can curb the expression of big sized tussock plants and relax competitive interactions. The observed $\alpha 1$ (19.3) is higher than we should expect for these grasslands in the absence of disturbances

(Boldrini & Eggers 1996; Overbeck et al. 2005; Baldissera et al. 2010) suggesting that continuous grazing by cattle and periodical burns, conditions to which these grasslands are submitted, drive grassland communities with high species diversity and homogeneity among plots.

The observed pattern at plots scale is also in accordance with other studies on grasslands that have found little evidence of niche differentiation at small scales (Mahdi et al. 1989; van der Maarel & Sykes 1993), suggesting coexistence by niche sharing. In fact, grassland satellite species are spatially dynamic at fine scales within the stable matrix of core dominant species (Collins & Glenn 1991) and they disperse around the community in such a way that eventually they could reach every part of the community area.

At transects (β2) and sites (β3) scales, beta diversity was higher than expected by chance. Transects at each site were sampled in different conditions of relief and aspect which could explain the observed pattern. Geomorphology creates gradients of water and nutrient availability, with the lower and concave areas of the relief with higher soil humidity and nutrients in relation to the higher and convex areas. Moreover, the south-facing slopes receive less solar radiation than the north-facing ones, which also creates local gradients of temperature and humidity. Studies in the Rio de la Plata grasslands in Uruguay and Argentina have claim water availability as one of the main drivers of species composition (Perelman et al. 2001, Lezama et al. 2006). On the other hand, the sampled sites correspond to different rural properties. Although the management of livestock is relatively uniform among properties, it is expected that paddocks among farms, or even within a same farm, show differences in the intensity and frequency of disturbances, including cattle grazing and trampling, tall grass mowing, or prescribed fires, to meet livestock farming objectives. Such differences in the disturbance regime among farms could be the main driver of beta diversity at this scale.

Beta diversity at sub-regions scale (β4) was not significantly different from the expected value, indicating that at this spatial level the observed differences in species composition are a sampling artifact. However, at regions scale (β5) the species turnover was higher than expected by chance and higher than on the other spatial scales. The stratified sampling design was purposely established to ensure the representation of regional climatic (temperature and rainfall) and edaphic gradients and the observed beta diversity at this scale is probably an expression of the effect of such drivers. Moreover, beta diversity is negatively related with dispersal ability (Quian 2009) and most of the sampled species showed low frequencies of occurrence, suggesting limited dispersal ability. The high number of species restricted to some of the four sampled regions explains the high turnover at this scale and could be the combination of specific environmental requirements with limited dispersion. At last, it is also important to consider that regional beta diversity may have been somewhat inflated due to limitations of the sampling effort to detect the true occurrence of rare species among the four regions.

The observed results discard our initial hypothesis for the *Campos de Cima da Serra* region, once the species turnover at regions scale is higher than at the transects scale, where topography exerts its effect. Studies of additive partitioning in grasslands communities are still scarce and multi-scale diversity patterns remains little explored. However, some grassland spatial cross-scale patterns have been investigated with other methodologies and different scale ranges. In the North American tall grass prairie the species turnover among sites separated by some degrees of latitude was higher than the observed at finer scales, under the effect of topographic and disturbance gradients (Gibson & Hulbert 1987; Diamond & Smeins 1988), which is similar with our results. Nevertheless, Perelman et al. (2001) found an opposite pattern in the Flooding Pampa, Argentina, with higher species heterogeneity at finer spatial scales (1-10 km^2) associated to topographic and salinity gradients, while latitudinal changes had a secondary role. The heterogeneity of Serengeti grasslands showed a similar pattern, the diversity between community types at finer scales was higher than that observed among landscapes of the region (McNaughton 1983). The predominance of fine scale drivers was also detected in herbaceous layer in semi-arid savanna central Kenya, where topography explained species turnover across distances of 5-45 m and variation in species composition across the rainfall gradient was minimal (Augustine 2003).

The pattern of species distribution for the *Campos de Cima da Serra* grassland, with a high proportion of less frequent species, suggests that a largest extension of conserved grasslands would be necessary to represent most of the species pool. With the aid of information generated by additive partitioning, we could maximize the effectiveness of a grassland reserve design, using the observed beta diversity data across scales. In this case, the best decision would be to split any effort in the *Campos de Cima da Serra* setting protected areas to represent each one of the four sampled regions, instead of concentrating in one specific region.

The grasslands in the *Campos de Cima da Serra* region deserve conservation attention by their high species diversity (1,161 species) and the existence of 107 endemics species (Boldrini et al. 2009). Moreover, the great species richness of Asteraceae is a singular feature of these highland grasslands (Matzenbacher 2003). Currently, they are only partially protected in seven federal and state protected areas (*Serra Geral* National Park, *Aparados da Serra* National Park, *Tainhas* State Park, *Aracurí* Ecological Station, *Aratinga* Ecological Station, *Rota do Sol* Environmental Protected Area and *São Franc*isco National Forest). However, six of these areas are concentrated in the eastern region and were not designed and are not managed to conserve grasslands. Considering that they are include in only one of the four regions of our survey, it is necessary an additional effort to set new conservation units to include the three other unprotected regions. Implementing new protected areas in these grassland landscapes is a priority (Brandão et al. 2007; Overbeck et al. 2007) but needs caution on species persistence in the long run. Complete suppression of the disturbance regime by cattle grazing and fires can undermine species conservation, especially by competitive dominance of tall tussock grasses, risk of fires with high severity, shrubland encroachment and expansion of forest over grasslands. Therefore, to keep targeted species conserved, the implementation of future protected areas shall include active management programs that simulate natural disturbances regimes (Pillar & Vélez 2010) and combine it with the promotion of best management practices in livestock raising activities outside the protected areas.

Acknowledgements

We are grateful to Ilsi Boldrini, Angelo Schneider and Rafael Trevisan for taxonomic identification of grassland species, to Heinrich Hasenack, Eliseu Weber and Tatiana Kuplich for aid with geoprocessing tools and to Bruno S.G. Fonseca, Claudio Reis, Gabriel Specht, Marcel Tust and Tiago Caetano Edruziane for help in field expeditions, Part of this work was carried out with the aid of a grant (LEAF) from the Inter-American Institute for Global Change Research (IAI) CRN-2005 which is supported by the US National Science Foundation (grant GEO-0452325). E.V.M received a doctoral CNPq scholarship. V.P. receives support from CNPq (306573/2009-1).

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Capítulo 4. (Artigo 4) Extinção dos Campos Sulinos em Unidades de Conservação: um Fenômeno Natural ou um Problema Ético?[1]

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[1] Versão integral do artigo publicado em versão reduzida na seção *Fórum* do periódico *Natureza & Conservação* 8(1): 84-86 em Julho de 2010.

Os Campos Sulinos correspondem aos ecossistemas que caracterizam grande parte das paisagens da região sul do Brasil. Sua singularidade frente às demais formações abertas da Região Neotropical vincula-se em grande medida ao clima temperado, sofrendo o efeito de geadas no inverno, e úmido, com pluviosidade elevada e bem distribuída ao longo do ano. Pela classificação do IBGE, incluem-se tanto no bioma Pampa, na porção sul e oeste do Rio Grande do Sul, como no bioma Mata Atlântica, nas partes mais altas do planalto onde estão associados às florestas com Araucária (IBGE 2004).

Abrigam cerca de 2,2 mil espécies vegetais, cujo conhecimento sobre usos potenciais, todavia é incipiente (Boldrini 2009) e uma importante diversidade faunística incluindo espécies ameaçadas de extinção (Bencke 2009). São responsáveis por importantes serviços ambientais, como a conservação de recursos hídricos, além de oferecer beleza cênica com potencial turístico importante. Sua conservação tem implicações no balanço de carbono no solo e nas emissões de gases de efeito estufa, contribuindo assim no esforço de mitigação de mudanças climáticas globais (Klumpp & Soussana 2009; Soussana 2009). Além disso, têm sido a principal fonte forrageira para a atividade pastoril, que no Rio Grande do Sul é um dos principais setores da economia (Pillar et al. 2006; Pillar et al. 2009).

Nas últimas três décadas sua conversão em áreas agrícolas e silviculturais levou a que em 2002 os remanescentes com vegetação campestre natural cobrissem apenas 50% da área original no Rio Grande do Sul (Cordeiro & Hasenack 2009) sem que isto tenha causado qualquer comoção social. Além da perda de hábitat, a conversão gera fragmentação dos ambientes com alteração nos padrões de biodiversidade e incremento nos riscos de extinções de espécies da flora e da fauna silvestre. A invasão de espécies exóticas como a gramínea africana *Eragrostis plana* (Medeiros et al. 2009) e de espécies lenhosas (Guadagnin et al. 2009) também tem sido uma séria ameaça à sua integridade.

A conservação destes campos tem sido negligenciada (Overbeck et al. 2007). Ainda persiste uma visão equivocada sobre a sua natureza. Muitos consideram que os campos, de um modo geral, têm uma origem antrópica, ocupando áreas originalmente florestais e que foram desmatadas, sendo mantidos pela intervenção do homem. No Brasil, isto é bastante evidente já que a preocupação ambiental é flagrantemente enviesada para as florestas, em detrimento de outros tipos de ecossistemas. Não é à toa que o Código Florestal, um dos principais instrumentos de conservação da biodiversidade refere-se apenas às florestas, ainda que outros tipos de formações vegetais, de forma menos explícita, também encontrem nele algum tipo de proteção.

Há também um problema conceitual em considerar os campos como um estágio inicial da sucessão vegetal. Dentro desta visão muito simplificada da dinâmica da vegetação, as áreas de campo sempre estariam sujeitas a um processo unidirecional até um estágio final florestal, de modo que esta seria a única tipologia em equilíbrio com as condições ambientais atuais. Na verdade, os Campos Sulinos correspondem à vegetação primária ou secundária, nos estágios inicial, médio ou avançado de regeneração. Eles estão presentes na região há milhares de anos, muito antes da expansão das formações florestais ocorrida após a metade do Holoceno – nos últimos 4.000 anos (Behling & Pillar 2007; Dümig et al. 2008; Behling et al. 2009). Atualmente, convivem em maior ou menor grau com a vegetação lenhosa apresentando-se em algumas regiões na forma de mosaicos de campo/floresta. Ainda que o clima atual favoreça o desenvolvimento das florestas, em função da disponibilidade de água, vários outros fatores interagem para definir se um determinado sítio será colonizado e ocupado por campos ou florestas. Portanto, neste contexto, os campos e as formações florestais associadas não constituem estágios sucessionais distintos, mas estados ecossistêmicos estáveis que coexistem, com um grau variável de tensão, devendo ambos ser alvo de preocupação conservacionista.

O conceito de estados ecossistêmicos alternativos, no qual mais de uma tipologia vegetacional é esperada para um mesmo conjunto de condições ambientais parecer ser a base conceitual mais adequada para analisar a dinâmica campo/floresta nas regiões tropicais e sub-tropicais, já que seria inapropriado considerar uma vegetação que persiste há milênios como um “estágio sucessional inicial” (Bond & Parr 2010).

A despeito da sua importância histórica e de sua biodiversidade característica o grau de proteção dos Campos Sulinos é muito baixo. Apenas 0,33% dos campos estão atualmente protegidos por unidades de conservação de proteção integral no Rio Grande do Sul (Overbeck et al. 2007). A grande maioria das áreas que ainda hoje mantêm características ecossistêmicas dos campos típicos dessa região encontram-se em áreas privadas, sob manejo tradicional, com uso pastoril (Cordeiro & Hasenack 2009).

Esta realidade não é exclusiva do Brasil, pois os campos encontram-se globalmente ameaçados. Hoekstra et al. (2005) destacam a necessidade de dirigir esforços de conservação para os biomas terrestres sob maior risco em função da disparidade entre a extensão da perda de hábitat e o baixo grau de proteção. Os campos temperados juntamente com as savanas estão na situação mais crítica dentre todos os biomas terrestres com 45,8% de conversão e apenas 4,6% de proteção.

O Brasil como signatário da Convenção da Diversidade Biológica comprometeu-se com as Metas Globais de Biodiversidade para 2010, dentre as quais a de que pelo menos 10% de cada região ecológica do mundo seja efetivamente conservada. Os Campos Sulinos estão muito aquém deste objetivo, portanto, demandam prioridade por partes dos esforços públicos e privados de conservação.

A criação de unidades de conservação constitui um importante instrumento de proteção. No entanto, os campos apresentam particularidades na dinâmica de sua vegetação que devem ser levadas em conta para evitar que iniciativas bem intencionadas não concorram para sua própria extinção, fenômeno que parece estar ocorrendo nas poucas unidades de conservação existentes na região dos Campos Sulinos.

A dinâmica natural dos ecossistemas campestres está associada à ocorrência de determinados níveis de distúrbios naturais, em especial a herbivoria (pastejo animal) e a ocorrência de queimadas. Existem evidências de que grandes herbívoros pastadores co-evoluíram com as espécies de gramíneas na América do Sul desde o início do Mioceno (MacFadden 1997; MacFadden 2005). Além disso, as adaptações morfológicas e fisiológicas de várias espécies herbáceas aos efeitos do fogo (presença de espécies pirófilas) são um indício da ocorrência histórica de queimadas em função do acúmulo de biomassa inflamável. Nos campos do sul do Brasil há evidências de que as queimadas têm ocorrido desde o início do Holoceno, provavelmente de origem antrópica e facilitadas pela extinção dos grandes pastadores nesse período (Behling et al. 2005; Behling & Pillar 2007).

Cada vez que ocorrem distúrbios há uma renovação dos processos sucessionais, impedindo a homogeneização da comunidade por poucas espécies competitivamente superiores. Em determinados níveis, eles promovem a heterogeneidade espacial fazendo com que várias fisionomias campestres coexistam, maximizando a diversidade de espécies na comunidade. Avaliações sobre esses distúrbios para os Campos Sulinos demonstraram sua influência positiva sobre a diversidade de espécies vegetais e, portanto, sua importância para a própria conservação (Boldrini & Eggers 1996; Quadros & Pillar 2001; Overbeck et al. 2005; Overbeck & Pfadenhauer 2007).

No entanto, o regime de distúrbios naturais dos Campos Sulinos foi drasticamente alterado em função da presença humana na região. A pressão natural de herbivoria foi suprimida com a extinção da megafauna durante o início do Holoceno e o regime de incêndios naturais foi praticamente eliminado com a mudança do contexto da paisagem, intensamente ocupada pelo homem e dividida em unidades de manejo independentes - propriedades rurais delimitadas por cercas e com pautas de uso relativamente independentes.

Por outro lado, estes processos naturais foram parcialmente reintroduzidos na região em função do manejo do campo destinado à atividade pastoril. No Rio Grande do Sul, a herbivoria pelo gado doméstico está presente desde sua introdução no século XVII. É plausível a conjectura de que o gado doméstico possa representar a reintrodução de um processo ecossistêmico antes desempenhado por uma megafauna pastadora, mantidas as devidas proporções em termos de densidade populacional. A presença dos animais pastadores modifica a estrutura da vegetação pela seleção entre plantas palatáveis e não palatáveis e também influencia na microvariação topográfica, incrementando a heterogeneidade espacial dos hábitats (Morris 2000). Em algumas regiões, as queimadas têm sido utilizadas como prática tradicional de renovação das pastagens, realizadas no final do inverno e início da primavera. Atualmente as queimadas estão proibidas por lei estadual, no Rio Grande do Sul, embora ainda ocorram anualmente na região dos Campos de Cima da Serra, e seguem sendo praticadas nos estados de Santa Catarina e no Paraná. Não existem estudos detalhados que indiquem as consequências a longo prazo para as comunidades campestres com base na intensidade e frequência com que têm sido praticadas sobre os Campos Sulinos.

Toda vez que uma unidade de conservação é criada e implementada na região dos Campos Sulinos, uma das primeiras iniciativas adotadas é a supressão destes distúrbios antrópicos. Assim com o excesso, a ausência de distúrbios pode representar um problema ecológico, especialmente nos casos em que o regime de distúrbios naturais foi drasticamente alterado. No caso dos campos, verifica-se uma perda da heterogeneidade natural, já que a dinâmica sucessional das comunidades campestres evolui para estágios avançados, caracterizados por um número restrito de espécies dominantes, de hábito cespitoso (touceiras) e arbustivo. A presença destas fisionomias em todas as áreas campestres de uma unidade de conservação resulta na redução da diversidade de espécies campestres. Outro desdobramento disto é o acúmulo de uma grande quantidade de biomassa inflamável, aumentando o risco de incêndios catastróficos, que podem comprometer todos os ecossistemas da unidade de conservação.

Além disso, especialmente nas áreas onde os campos ocorrem conjuntamente com as florestas na forma de mosaicos, a ausência de distúrbios permite o rápido avanço das formações florestais sobre os campos. Sem distúrbios (pastejo ou queimadas), as espécies florestais pioneiras deixam de ser eliminadas, possibilitando o avanço das florestas e a decorrente homogeneização da paisagem por uma única fisionomia.

Em síntese, no contexto atual, a ausência de manejo nas unidades de conservação criadas na região dos Campos Sulinos equivale a uma ação deliberada de extinção local da rica biodiversidade campestre. É inadmissível que as unidades de conservação criadas para conservar a biodiversidade típica da região, o que inclui também, em maior ou menor grau, as florestas, não tenham com um de seus objetivos a manutenção da heterogeneidade das fisionomias campestres e de todas as espécies associadas, com um olhar especial para aquelas que estão ameaçadas de extinção. Logo, manejar as unidades de conservação para assegurar a persistência da diversidade campestre passa a ser um problema de natureza ética.

Os campos temperados estão ameaçados global, regional e localmente. Urge que as poucas unidades de conservação delimitadas em áreas de ocorrência natural de campos tenham como objetivo explícito a sua conservação, com a correspondente definição de ações de manejo específicas de modo a simular os efeitos de distúrbios naturais que têm ocorrido desde milênios, assegurando a sua diversidade fisionômica, os processos ecológicos associados, os requisitos de hábitat das espécies ameaçadas e, também, contribuindo para diminuir os riscos de incêndios indesejados de grandes proporções.

A reintrodução de um nível mínimo de distúrbios nos remanescentes campestres tem como referência a hipótese do distúrbio intermediário (Grime 1973) que preconiza que para muitos sistemas ecológicos a riqueza máxima de espécies ocorre quando submetidos a níveis intermediários de distúrbios, tanto em termos de intensidade como de frequência. O desdobramento espacial desta dinâmica permite que se configure um mosaico sucessional, onde a paisagem se caracteriza pela heterogeneidade de manchas, decorrentes da ação de distúrbios com diferentes intensidades. Isto permite maximizar a coexistência e a persistência das espécies, já que para uma mesma paisagem teremos ao mesmo tempo: as poucas espécies adaptadas a níveis altos de distúrbios (ambientes muito abertos, com baixa estratificação vertical e maior proporção de espécies cespitosas ou prostradas, baixas), as poucas espécies que se tornam dominantes em sistemas com baixo nível de distúrbio (espécies entouceiradas, altas) e as demais espécies que não se enquadram nestas situações extremas.

Todavia, o manejo das áreas campestres em unidades de conservação ainda parece ser um verdadeiro tabu no Brasil. A falta de conhecimento específico de como realizar o manejo pode ser um dos fatores limitantes. Qual manejo? Onde e como? É claro que não existem respostas prontas para estes desafios. No entanto, é da natureza da biologia da conservação atuar com base no conhecimento e nas evidências disponíveis. Cabe aos gestores das unidades de conservação implementar ações de manejo, inicialmente de caráter experimental, com alvos e metas definidas de modo transparente e com a colaboração de instituições de pesquisa, com o monitoramento de indicadores e em sintonia com os objetivos e as particularidades de cada unidade de conservação.

Existem várias possibilidades para a reintrodução de uma dinâmica de distúrbios nas áreas de campo que podem ser aplicadas em cada contexto e que podem incluir o pastejo animal, as roçadas e as queimadas localizadas. A introdução da herbivoria (bovinos, equinos ou ovinos) em determinados locais e períodos, e com intensidades vinculadas ao manejo da própria vegetação campestre, e não da produção animal, evidentemente, parece ser uma medida bastante prática e de menor risco. Estudos sobre as consequências do manejo pastoril na biodiversidade da fauna indicam que a ausência de distúrbios, assim como o seu excesso (e.g. sobrepastejo), são prejudiciais (Bencke 2009). Além disso, áreas manejadas adequadamente com pastejo são menos inflamáveis. Portanto, o manejo pastoril adequado poderia reproduzir um distúrbio natural, alternativo a necessidade de roçadas ou queimadas. Com isso, pode-se moldar as fisionomias campestres existentes e eliminar o excesso de biomassa, diminuindo os riscos de queimadas catastróficas.

Nas últimas décadas a ciência ecológica tem passado por uma mudança de paradigma na compreensão dos fenômenos ecológicos. Não se concebe mais a natureza como um sistema em total equilíbrio, onde os ecossistemas têm um ponto estável, autorregulado, estrutural e funcionalmente completo, sendo possível vislumbrar um estágio de clímax previsível. A realidade demonstra que os ecossistemas sofrem constantemente transformações e raramente há um ponto estável. Os sistemas são abertos à troca de matéria e energia com o entorno, não são internamente autorregulados e são muito influenciados por distúrbios periódicos que afetam sua estrutura interna e seu funcionamento. Esta perspectiva, denominada de paradigma do “não-equilíbrio” enfatiza os processos, as dinâmicas e o contexto dos sistemas naturais ao invés de um ponto final estável, como forma de compreender o funcionamento dos ecossistemas e de como manejá-los (Meffe & Carroll 1994).

De acordo com esta visão dinâmica da natureza, as unidades de conservação não se mantêm estáveis e com uma configuração balanceada. Há sempre uma mudança na composição de espécies, sendo a direção e a intensidade dos processos naturais dependente das influências externas e da ação (ou da supressão) de distúrbios naturais.

O desafio prático disto é que para manter a diversidade de espécies e os processos ecológicos que se pretende conservar em uma determinada unidade de conservação, serão necessárias ações de manejo capazes de lidar com as tendências de mudança do sistema ecológico, cuja magnitude e direção, muitas vezes, são pouco previsíveis. Estas considerações são particularmente importantes para a conservação dos ecossistemas de formações abertas, como os campos. Especialmente em regiões de tensão ecológica com as formações florestais como a verificada nas paisagens da região dos Campos de Cima da Serra, no Rio Grande do Sul e Santa Catarina, caracterizada pelo mosaico de formações florestais e campestres e principalmente, em tempos de mudanças climáticas, onde o aumento de origem antrópica da concentração de CO_2 na atmosfera tende a favorecer ainda mais o avanço da vegetação lenhosa sobre os campos.

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Considerações Finais

As comunidades campestres avaliadas neste estudo correspondem às fisionomias que ocorrem sob condições mésicas e que predominam na paisagem dos Campos de Cima da Serra estão sujeitas a um intenso regime de distúrbios advindos do pastejo do gado e de queimadas periódicas. Os resultados observados de riqueza de espécies corroboram estudos prévios que descrevem a alta diversidade de espécies nos campos do Rio Grande do Sul (Boldrini 2009), sugerindo que os Campos Sulinos devem estar entre as comunidades campestres mais biodiversas do mundo (Overbeck et al. 2007). O caráter regional do estudo também permitiu confirmar algumas generalizações anteriores feitas para estas comunidades com base em observações menos sistemáticas do ponto de vista da abrangência espacial: o domínio das espécies de hábito cespitoso e ereto e de ciclo estival, a expressiva diversidade de espécies nas famílias Asteraceae e Fabaceae, bem como a grande abundância de espécies de família Cyperaceae, mesmo em solos com boas condições de drenagem (Mohrdieck 1980; Boldrini 1997; Matzenbacher 2003; Boldrini 2006; Boldrini 2009; Boldrini et al. 2009).

Entretanto, a principal contribuição deste estudo para a ecologia das comunidades campestres na região dos Campos de Cima da Serra foi revelar que, sob a aparente homogeneidade fisionômica dessa vegetação, há uma grande heterogeneidade que se manifesta em diferentes escalas espaciais. No Capítulo 1, foram apresentados vários resultados que descrevem a diversidade florística e funcional destas comunidades. Foram identificados quatro tipos de comunidades com espécies indicadoras características e diferenças significativas nas coberturas relativas das formas de crescimento e das famílias dominantes.

A alta riqueza de espécies, incluindo muitas herbáceas não graminóides, e a pouca quantidade de serrapilheira foram outro padrão geral observado e que pode ser atribuído ao amplo sistema de distúrbios (pastejo e queimadas) que caracteriza a região, atenuando a dominância competitiva das espécies graminóides, de hábito cespitoso, que têm grande frequência de ocorrência e valores altos de cobertura na maioria dos casos. Outro efeito destes distúrbios observado nos levantamentos realizados foi a baixa riqueza e cobertura de espécies arbustivas.

Embora as queimadas, como um fator de distúrbio, tenham reflexos positivos sobre a diversidade dos campos, seu uso frequente como técnica de manejo da vegetação campestre para fins de renovação da biomassa verde tem gerado muitas controvérsias de ordem técnica, jurídica e social. Estudos sobre seus impactos sobre as espécies e a composição de tipos funcionais das comunidades campestres ainda são escassos (Overbeck et al. 2005; Overbeck & Pfadenhauer 2007) e é provável que apesar da grande diversidade observada, algumas espécies não tolerem este tipo de distúrbio da forma como é praticado, sendo mantidas com populações muito reduzidas ou já tendo sido localmente extintas na região dos Campos de Cima da Serra. Do ponto de vista da produção animal sabe-se que esse regime de queimadas reduz a produção e a qualidade forrageira (Jacques 2003), além de diminuir a fertilidade do solo e a retenção de umidade (Heringer 2000). Além disso, as queimadas comprometem as metas de redução de gases atmosféricos causadores do efeito estufa. Como estes campos constituem sistemas de produção animal, a melhor alternativa para resolver este impasse, e ao mesmo tempo manter um sistema de distúrbios nessa região, alternativo às queimadas, parece ser a adoção de novas práticas de manejo da pecuária que vêm demonstrando resultados benéficos do ponto de vista da estrutura e diversidade da vegetação campestre nos Campos Sulinos (Castilhos et al. 2009; Nabinger et al. 2009). Para que isto fosse efetivamente praticado na região seria mais importante, do ponto de vista da conservação dos campos, implantar uma política de promoção da pecuária sustentável na região, combinada com metas e ações de conservação, ao invés da simples proibição legal das queimadas, atualmente em curso no estado do Rio Grande do Sul.

O Capítulo 2 buscou identificar mecanismos de controle da diversidade beta e da diversidade alfa. As análises revelaram que parte dos gradientes ambientais avaliados exerce um efeito importante sobre a composição de espécies das comunidades campestres e que os fatores neutros, estimados pela contribuição das variações espaciais, após a remoção dos efeitos das variações ambientais, parecem ter um papel acessório. As principais variáveis selecionadas para modelar a diversidade β foram a temperatura média anual, a sazonalidade da temperatura e as diferenças no tipo de solo.

Estas variáveis representam gradientes espacialmente estruturados em escala regional e que, no contexto deste trabalho, tiveram um efeito bastante superior ao dos gradientes locais avaliados, representados pelas diferenças na orientação solar e na declividade do terreno. A resposta das variações nas comunidades a estas duas variáveis revelou diferenças de composição nas áreas de encostas, independente da orientação norte ou sul, em contraste com as áreas planas.

É possível que os tipos de solo e as diferenças de temperatura não exerçam apenas um efeito direto sobre a fisiologia das espécies influenciando desse modo sua distribuição, mas que determinem regimes regionalizados de manejo da vegetação campestre, os quais seriam em última instância responsáveis por parte das variações observadas na diversidade β. Esta hipótese necessita ser investigada, quantificando as possíveis diferenças no manejo para aperfeiçoar a modelagem dos fatores controladores da diversidade na região.

As diferenças no gradiente regional de precipitação que foi incorporado no delineamento amostral não foram selecionadas no processo de modelagem da diversidade β, entretanto, o índice avaliado para medir a retenção de umidade em paisagens com raio de 1 km em torno das unidades amostrais foi selecionado como uma variável importante. Isto sugere que o gradiente pluviométrico não é suficientemente amplo para influenciar a diversidade em termos regionais, porém a capacidade de reter a água das precipitações com base na conformação geomorfológica da paisagem, apresenta diferenças que afetam a composição de espécies.

Os resultados obtidos para a modelagem da riqueza de espécies resultaram num efeito menor das variáveis ambientais, o que em certa medida já era esperado uma vez que esta variável é muito influenciada por fatores que não foram avaliados neste trabalho e que incluem principalmente a biomassa da comunidade, a disponibilidade de luz na superfície do solo, a intensidade dos distúrbios e variações no *pool* de espécies colonizadoras (Grace 1999). Além disso, as variáveis selecionadas (precipitação no mês mais úmido e o índice topográfico de umidade na paisagem) indicaram uma relação principal com o gradiente de umidade.

Grande parte das variações na diversidade β e na riqueza de espécies não foi explicada pelas variáveis preditoras utilizadas, indicando que outras variáveis precisam ser consideradas em estudos adicionais sobre a diversidade campestre na região. Entretanto, deve-se também levar em conta que a extensão, intensidade e frequência dos distúrbios nessa região são muito variáveis, o que provoca a eliminação aleatória de muitas espécies e infla o componente da variação não explicada.

No Capítulo 3, a partição aditiva da diversidade permitiu identificar em qual escala espacial a diversidade beta apresentou a maior variação. O resultado observado corrobora o mesmo padrão identificado com a abordagem metodológica do Capítulo 2, com a preponderância das variações na composição da comunidade relacionadas a gradientes regionais. Embora este resultado possa parecer trivial, muitas formações campestres avaliadas em outras regiões e continentes indicam um padrão oposto, no qual a heterogeneidade ambiental em escalas locais é mais importante na definição da diversidade do que os gradientes regionais.

Embora os objetivos deste trabalho tenham sido eminentemente ecológicos, voltados a detectar padrões de diversidade e seus possíveis fatores preditivos, foi possível a partir do seu enfoque regional e das abordagens metodológicas utilizadas tecer considerações de cunho teórico (Capítulo 4) e de cunho prático (Capítulo 3) sobre a conservação dos ecossistemas campestres. No primeiro caso, foi ressaltada a importância de conservar não apenas a biodiversidade campestre, mas também os distúrbios naturais associados e, na ausência dos mesmos, a necessidade de implantar ações de manejo destinadas a reintroduzi-los de forma alternativa. No segundo caso, os resultados observados da diversidade beta são utilizados como argumento para a criação de três novas áreas protegidas, além das já existentes na região para representar a amplitude de variação geográfica da diversidade dos Campos de Cima da Serra.

A ecologia de comunidades ao elucidar as relações espécie-hábitat e dos fatores geradores de diversidade β tem dado grandes contribuições para a biologia da conservação. Ao mesmo tempo, a preocupação com a conservação dos campos ainda apresenta uma série de particularidades relacionadas com a sua ecologia e dinâmica que não se encontram suficientemente acolhidas nas iniciativas legais e políticas voltadas à conservação da biodiversidade no Brasil.

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