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Variação na composição de comunidades vegetais campestres ao longo do litoral sul do Brasil

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“*O quadro do litoral não seria perfeito, se não levássemos em conta as variações do firmamento. O céu totalmente coberto de nuvens baixas deprime todas as tintas e avoluma o peso das formas; a atmosfera poeirenta e brumosa dos dias de verão, dilui os contrastes e desorienta o espírito; os bulcões da tempestade unilaterizam a iluminação e, pelos fenômenos impressionantes, deslocam a sensação do belo aprazível para o belo grandioso; é nos dias claros, estando o sol perto do meridiano, que aquelas paisagens encontram a sua mais legítima expressão: então um olhar por entre duas séries de dunas vegetadas sobre uma nesga do oceano azul marinho tocando no azul pálido do firmamento – ou uma observação aérea pairando sobre todo aquele imenso painel de água, areia e vegetação – conduzem o mais perto possível daquilo que se chama a beleza do litoral, atrativo invencível, enquanto houver homens de espírito simples e natura*l.”

Pe. Balduíno Rambo (1974)

A Fisionomia do Rio Grande do Sul

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RESUMO GERAL

A região costeira do sul do Brasil está inserida no bioma Pampa e sua vegetação natural apresenta um mosaico de formações, incluindo áreas de campos utilizadas para pastejo bovino. Os campos do litoral representam uma das fisionomias do bioma Pampa mais convertida para outros usos. Nessa região poucos estudos florísticos isolados foram realizados recentemente, enquanto estudos ecológicos sobre a interação da vegetação campestre com variáveis ambientais e espaciais são ainda mais escassos. Buscamos realizar um amplo estudo descritivo e ecológico da vegetação dos campos arenosos costeiros ao longo de 536 km no sul do Brasil. Amostramos 16 áreas distribuídas ao longo da planície costeira, com 15 parcelas de 1 m² por área. As espécies foram classificadas segundo suas formas de crescimento, origem e grau de ameaça. Também variáveis climáticas, edáficas e as coordenadas geográficas para cada área foram observadas. Através de análises multivariadas (ordenações e partição de variância) verificamos a contribuição relativa do ambiente e do espaço para variação na composição de espécies entre áreas. Foram encontradas 221 espécies, 14 eram exóticas e duas ameaçadas. *Axonopus* aff. *affinis*, *Paspalum notatum* e *Paspalum pumilum* foram algumas das espécies mais importantes caracterizando as áreas. A maior parte da cobertura vegetal é por espécies de gramíneas prostradas, que está relacionado com a presença de pastejo em todas as áreas. A mudança na composição das comunidades entre áreas está relacionada, em sua maior parte, à mudança de variáveis climáticas, como também ao espaço, já que ambos variam juntamente. Observamos que apesar da homogeneidade nas condições edáficas, em escala refinada pudemos observar a influência do solo na variação da comunidade. Os campos da planície costeira possuem uma fisionomia ímpar, porém as áreas remanescentes estão vulneráveis, principalmente pela fragmentação da paisagem. Práticas de manejo, principalmente pecuária, deveriam considerar a fragilidade do solo dessa região, adotando níveis mais baixos de carga animal para contribuir com a preservação dos últimos fragmentos desta formação.

Palavras-chave: bioma Pampa; campos litorâneos; diversidade beta; partição de variância; conservação.

GENERAL ABSTRACT

The coastal region of southern Brazil is inserted into the Pampa biome and its natural vegetation presents a mosaic of formations, including areas of grasslands used for cattle grazing. The coastal grasslands represent one of the Pampa biome physiognomies most converted to other uses. In this region a few floristic isolated studies were recently conducted, while ecological studies about the interaction of vegetation with environmental and spatial variables are even rarer. We aimed to realize a broad descriptive and ecological study of the vegetation of the coastal sandy grasslands along 536 km in southern Brazil. We sampled 16 areas distributed along the coastal plain, with 15 plots of 1 m² per area. The species were classified according to their growth forms, origin and degree of threat. Also climate, soil characteristics and geographic coordinates for each area were observed. By using multivariate analyzes (ordination and variation partitioning) we verified the relative contribution of environment and space for variation in species composition between areas. We found 221 species, from which 14 were exotic and two threatened. *Axonopus* aff. *affinis*, *Paspalum notatum* and *Paspalum pumilum* were some of the most important species characterizing the areas. Most of the vegetation cover is by prostrate species of grasses, which is related to the presence of grazing in all areas. The change in community composition between areas is mostly related, to changing in climatic variables, as well as to space, since both vary together. We observed that despite the homogeneity in the soil conditions, in fine scale we could observe the influence of the soil in community variation. The coastal grasslands have a unique physiognomy, but the remnant areas are vulnerable, mainly by landscape fragmentation. Management practices, especially livestock, should consider the fragility of the soil of this region, adopting lower stocking levels to contribute to the preservation of the last fragments of this formation.

Key-words: Pampa biome; coastal grasslands; beta diversity; variation partitioning; conservancy.

INTRODUÇÃO GERAL

A vegetação do litoral sul brasileiro já foi descrita como um “complexo” de diferentes formações vegetais ocorrendo sobre uma região muito restrita. A chamada vegetação de restinga, ou “complexo de restinga” (Waechter 1985), ocorre principalmente sobre depósitos arenosos provenientes do período quaternário, frequentes no litoral sul e sudeste brasileiro (Suguio & Martin 1990). A vegetação litorânea foi reconhecida como um complexo pela alta variabilidade de formações, compreendendo formações campestres, áreas pantanosas, matas arenosas e paludosas até trechos desprovidos de vegetação (Dillenburg 1986). Diferenças nas condições locais de drenagem do solo já foram apontadas como as principais características ambientais que podem alterar a composição de espécies entre as diferentes formações (Waechter 1985). Contudo, entre locais que apresentam características edáficas semelhantes e, portanto, seriam enquadrados dentro da mesma formação, também se observa variação na composição de espécies. Por quê?

De fato a variação espacial na distribuição das espécies é uma das características mais fundamentais e evidentes do mundo natural (Legendre & De Cáceres 2013). O estudo da variação na distribuição das espécies ao longo da paisagem iniciou com o trabalho de Clements (1916), onde ele dizia que as espécies se organizam em unidades discretas (comunidades nítidas) que se repetem ao longo da paisagem. Dessa forma as comunidades seriam como “super organismos” que nascem, crescem e morrem em uma trajetória definida de sucessão. As ideias de Clements foram contestadas por Gleason (1926), que dizia que as comunidades eram abertas e não unidades discretas e as espécies sofriam alterações ao longo de contínuos, ou gradientes ambientais.

O paradigma Gleasoníano, dominante até hoje, foi confirmado pelos estudos de Whittaker (1960, 1972), em gradientes de vegetação em montanhas. Whittaker definiu conceitos sobre diversidade amplamente aceitos até hoje, dizendo que a diversidade de espécies no ambiente pode ser definida em três níveis: alfa, beta e gamma. Diversidade Alfa (α) é a diversidade de espécies em um local, ou uma unidade amostral; diversidade beta (β) descreve a variação na composição de espécies entre áreas (entre unidades amostrais) ou ao longo de um gradiente na região de interesse; e a diversidade gamma (γ) é a diversidade de espécies de um número de comunidades (da metacomunidade), ou de várias unidades amostrais, de modo que o valor desta é uma resultante de ambas alfa e beta. A partir dos estudos de Whittaker especialmente a diversidade beta ganhou o interesse dos ecólogos como uma forma de quantificar a variação na composição de espécies ao longo dos gradientes, sendo assim uma ferramenta muito útil para desvendar quais são os fatores geradores desta variação.

A ideia de que alguns fatores seriam os principais responsáveis por gerar a diversidade beta levou ao desenvolvimento de teorias ecológicas que buscam explicar como as comunidades são formadas. Entre elas a mais reconhecida, a teoria do Nicho (MacArthur & Levins 1964), diz que fatores ambientais e a interação entre espécies são os principais filtros responsáveis pela organização das comunidades. Mais recentemente a teoria Neutra (Hubbell 2001) buscou explicar o que não poderia ser explicado somente pelas diferenças de nicho entre espécies. Segundo a teoria Neutra as espécies são ecologicamente ou funcionalmente equivalentes e são principalmente processos estocásticos, demográficos e biogeográficos (por exemplo, nascimento e morte, imigração e extinção local, especiação e extinção) que definem a composição das comunidades. Atualmente ambas as teorias são vistas como complementares (Gravel et al. 2006).

Visualizar a ação de processos específicos e mensurar a magnitude de cada um deles é uma tarefa complicada, ainda mais porque nosso objeto de observação são ‘pistas’ deixadas por processos históricos nas comunidades atuais, que podem ser ambíguas. O mesmo padrão encontrado em uma comunidade pode ser devido à ação de dois (ou mais) processos distintos. Além disto, a ação de processos só pode ser verificada quando abordamos a escala específica em que o mesmo atua. Não podemos esperar, por exemplo, que processos relacionados ao macro clima estejam refletidos em padrões observados em unidades amostrais com poucos metros de distância espacial entre si, uma vez que o clima varia significativamente a partir de distâncias maiores.

Neste estudo utilizamos a vegetação dos campos arenosos no litoral sul brasileiro como modelo para compreender os processos atuantes sobre a montagem das comunidades. A planície costeira sul brasileira foi formada durante o período geológico do quaternário (Villwock & Tomazelli 1998). Esta região de formação e colonização recente possui cerca de 620 km de extensão e 80 km de largura, com solo predominantemente arenoso. A vegetação campestre litorânea está compreendida pelo bioma Pampa e representa uma das formações com maior porcentagem de áreas campestres transformadas para outros usos dos Campos Sulinos. Desta forma compreendemos que este estudo, além de investigar os processos ecológicos atuantes em uma região com características ambientais peculiares, também é relevante para o conhecimento e a conservação da vegetação dos remanescentes dos campos litorâneos.

O trabalho aqui apresentado tem os seguintes objetivos e hipóteses:

Objetivo geral

Analisar a diversidade florística existente nos campos arenosos da planície costeira sul brasileira, abordando padrões espaciais na distribuição das espécies ao longo do gradiente latitudinal e também avaliar a relação desses padrões com seus possíveis processos geradores, ambientais e espaciais.

Objetivos específicos e hipóteses

1 Contribuir para o conhecimento florístico da vegetação dos campos litorâneos no sul do Brasil.

2 Analisar a estrutura da vegetação nas áreas campestres do litoral, contribuindo para o conhecimento do estado de conservação desta formação.

3 Explicar a variação na composição de espécies vegetais dos campos litorâneos por diferentes grupos de variáveis (ambientais e espaciais).

Hipótese: A maior parte da variação será explicada por variáveis espaciais, devido à homogeneidade de solo (variável ambiental) no litoral.

4 Explicar a variação das comunidades pela ação de filtros específicos: ambientais (clima e solo) e espaciais (escala ampla e escala refinada).

Hipótese: Clima será mais importante que solo, porque é a variável que vai apresentar maiocr variação neste gradiente.

Hipótese: Espaço em escala ampla terá maior explicação que espeço em escala refinada, pois as espécies são boas dispersoras.

5 Verificar a explicação relativa de variáveis ambientais sobre a variação das comunidades em escalas específicas.

Hipótese: Em escala ampla as variáveis ambientais, principalmente o clima terão maior influência.

Hipótese: Em escala refinada detectaremos maior ação de variáveis edáficas, que agem em escala local.

6 Verificar se a variação de grupos de espécies (no nível de famílias botânicas), por possuírem características semelhantes, principalmente, no que diz a respeito da sua capacidade de dispersão, se comporta de forma semelhante com relação às variáveis ambientais e à distância espacial;

Hipótese: Poaceae: por possuírem dispersão pouco efetiva as espécies desta família apresentarão maior relação com variáveis espaciais, indicando limitação de dispersão.

Hipótese: Asteraceae: a dispersão anemocórica, características das asteráceas é mais efetiva, desta forma estas espécies serão somente limitadas por características ambientais.

Estrutura da dissertação

Esta dissertação é apresentada na forma de dois artigos, com indicação de um possível periódico ao qual serão submetidos.

O primeiro capítulo busca responder aos objetivos específicos 1 e 2. Nele apresentamos um panorama geral sobre o estado de conservação dos campos litorâneos, com ênfase para a composição e estrutura da vegetação.

No segundo capítulo buscamos responder aos objetivos específicos 3, 4, 5 e 6 com um enfoque voltado para as teorias ecológicas que procuram explicar a organização das comunidades.

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CAPÍTULO 1[1]

Campos of the southern coastal plain in Brazil: a broad floristic and ecologic survey

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Campos of the southern coastal plain in Brazil: a broad floristic and ecologic survey

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ABSTRACT

Coastal environments are among the most degraded in the world. The natural vegetation of the South Brazilian coastal region includes grasslands, used for livestock grazing, that are poorly considered in conservation policy. This study reports results from a regional-scale survey of fragments of coastal grasslands vegetation along a gradient of 536 km on southern Brazil. We sampled 16 sites distributed along the coastal plain, with 15 plots of 1 m² per site, where we observed species cover, vegetation height, percentage of bare soil, plant litter and manure. The species were classified according to their growth forms. We also registered the occurrence of exotic, naturalized and threatened species. We found 221 species, 14 of which exotic and two threatened. *Axonopus* aff. *affinis*, *Paspalum notatum* and *Paspalum pumilum*, all of them prostrate grases, were among the most important species characterizing the areas. Vegetation height, bare soil, litter and manure were similar in all areas highlighting the homogeneity of sampling sites due to the presence of cattle grazing in all areas. Prostrate graminoids species were most important in terms of vegetation cover, followed by tussock grasses. Our study shows that the coastal grasslands differ substantially from other grasslands formations in southern Brazil in terms of vegetation physiognomy and structure. The presence of ruderal species as well as the presence of high values for bare soil at all sampling sites indicate the necessity to discuss management practices in the region, especially intensity of livestock grazing. The fragility of the soil of this region should be considered, adopting lower stocking levels to contribute to the preservation of fragments of this formation.

Key-words: Pampa biome, coastal grasslands, conservation, grazing, sandy soil.

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INTRODUCTION

Coastal landscapes currently are among the most degraded environments in the world (UNEP, 2006). This degradation is related to the fact that most of the population worldwide lives close to the coastline and explores natural resources from coastal environments. This is also true for Brazil, where about 74 million people, or 40% of the population, lives in coastal zones (Marroni & Asmus, 2013). The Brazilian shoreline reaches 7500 km in length and encompasses very distinct environments. Throughout this region, conservation problems have been pointed out for a large diversity of ecosystems, such as mangroves (Santos et al., 2014), saltmarshes (Isacch et al., 2006), foredunes (Seeliger, 2003), wetlands (Diegues, 1999), Atlantic forest (Rigueira, Rocha, & Mariano-Neto, 2013) and Restinga forest (Rocha, Bergallo, Van Sluys, Alves, & Jamel, 2007). However, little or no attention has been directed to the grassland landscapes. In the coastal plain of Rio Grande do Sul state, in the South of Brazil, about 5700 km² of grasslands remain, distributed in a strip of 622 km in length and 80 km in width along the coastline, equivalent to 13% of grasslands that still are present in the state (Cordeiro & Hasenack, 2009).

As pointed by Overbeck et al. (2007, 2013), grasslands have not been considered priority for conservation in southern Brazil, despite losses in cover of more than 50%, high biodiversity (concerning plants and animals, see e.g. Boldrini, 2009 and Bencke, 2009) and important ecosystem services offered by them. The situation of costal grasslands is not different. The National Coastal Management Program (GERCO, acronym in Portuguese) is the principal political basis for protection of the coastal environments in Brazil (Marroni & Asmus, 2013; Silva & Tagliani, 2012). However, it is mostly focused on management of water resources such as lagoons, rivers and wetlands, especially those located in the northern part of Brazil, where most research is performed (Diegues, 1999). No policies for protecting coastal grasslands have been developed by GERCO or other instances so far. Furthermore, the management guidelines in the conservation units that exist in the region (National Park of Lagoa do Peixe, State Park of Itapeva and Ecological Station Taim) focus mainly on wetlands, sand dunes and Restinga forest, and do not aim at conservation of grasslands, and even less so on processes that shape them, e.g. cattle grazing (see also Pillar & Vélez, 2010). In fact, at the moment the small number of studies and the lack of data impede the evaluation of the conservation state of the costal grasslands.

Here we discuss results from a regional-scale survey of grassland fragments in the coastal plain of southern Brazil, providing for the first time a more comprehensive knowledge of this vegetation type in the coastal landscape. We explore the vegetation structure and diversity of coastal grasslands, in terms of species richness, composition and growth forms, also identifying exotic and threatened species. With this we aimed to provide a basis for management decisions and conservation politics.

MATERIAL AND METHODS

Study region

The survey was carried out at 16 sites distributed along a 536 km gradient along Brazil's southern coast (Fig. 1), from latitude 28°S to 33°S. Sample sites had an average size of 3.3 ha. Main criteria for selection were presence of natural grasslands with similar management, i.e. cattle grazing, and without influence of high water levels in the soil (i.e., wetlands were excluded).

Soils in the region were formed in the Quaternary and are composed predominantly of sandy sediments (Villwock & Tomazelli, 1995, 1998). However, the influence of different sedimentary depositional environments caused the formation of differents soil types in the region, both with predominance of clay and organic matter (i.e. Organosoil, Gleysoil and Planossoil) formed mainly by Lagoonal deposition processes, or predominance of sand (i.e. Plinthosoil, Spodosoil and Neosoil) formed by Aeolian deposition processes (soil classifications following Brazilian Soil Classification System, Santos, 2013).

The 16 sites were allocated into four subregions in the coastal plain region in southern Brazil (Rio Grande do Sul state: three subregions; southern part of Santa Catarina: one subregion), based on similarity of climatic conditions (Tab. 1). Climate in the region is Cfa subtropical humid (Peel, Finlayson, & Mcmahon, 2007), with average precipitation varying from 1343 mm in the north and 1220 mm in the south and mean temperature varying from 19.1°C in the northern part of the gradient and 17.6°C at the extreme south (data from WorldClim database, Hijmans et al., 2005).

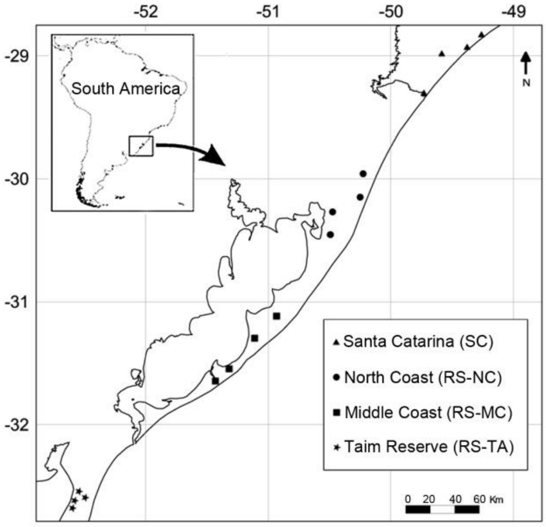

Figure 1: Location of the 16 sampling sites and classification into four climatically defined subregions in the South Brazilian coastal plain.

Table 1: Geographical location and main climatic variables for each of the 16 sample sites in the South Brazilian coastal plain. Precipitation and temperature are annual averages for a series of 50 years (Hijmans et al., 2005).

Subregion	Site	Latitude(S)	Longitude(W)	Municipality	Precip.(mm)	Temp. (°C)
SC	SC1	28°49'49.0"	49°15'48.2"	Balneário Rincão	1341	19.4
	SC2	28°55'55.6"	49°22'50.5"	Conventos	1313	19.2
	SC3	28°59'11.7"	49°35'14.8"	Araranguá	1321	19.1
	SC4	29°18'19.3"	49°43'56.2"	Passo de Torres	1397	18.8
NC	NC1	29°57'20.7"	50°13'40.4"	Osório	1499	18.8
	NC2	30°08'55.3"	50°15'09.3"	Cidreira	1487	18.8
	NC3	30°16'00.8"	50°28'33.9"	Palmares do Sul	1484	18.8
	NC4	30°27'08.5"	50°29'46.0"	Palmares do Sul	1462	18.7
MC	MC1	31°06'52.3"	50°56'00.4"	Mostardas	1381	18.5
	MC2	31°17'40.5"	51°06'40.6"	Tavares	1360	18.5
	MC3	31°32'37.2"	51°19'11.8"	Bojuru	1326	18.4
	MC4	31°38'37.7"	51°25'53.3"	Bojuru	1308	18.4
TA	TA1	32°32'27.3"	52°32'36.8"	Sta. Vitória do Palmar	1227	17.7
	TA2	32°35'31.7"	52°29'33.9"	Sta. Vitória do Palmar	1220	17.7
	TA3	32°36'54.1"	52°34'43.0"	Sta. Vitória do Palmar	1220	17.7
	TA4	32°40'42.2"	52°35'40.5"	Sta. Vitória do Palmar	1216	17.6

Vegetation sampling

Sampling was performed during southern hemisphere spring and summer in 2012 and 2013, when a large percentage of the plants are flowering. Species composition data was obtained in 15 plots of one square meter per site, distributed randomly. In each plot, all vascular plant species were identified and had their cover estimated according to Londo's decimal scale (Londo, 1976), then the mean cover value of plant species across 15 plots was used for the characterization of the species composition at each site. Plant samples were collected for posterior taxonomic identification whenever necessary. Classification of species into families followed the APG III (2009); nomenclature of species follows Boyle et al. (2013). In addition to estimation of species cover, we measured vegetation height and estimated the cover of litter, manure and bare soil.

Data analysis

Species richness of grasslands was explored using average species richness per site, considering shared and exclusive species, and species richness per plot (1 m²). For exploration of general patterns of species composition of the sites we calculated a principal coordinate analysis (PCoA), based on chord distance, using the matrix of species mean cover per site. Due to the high dominance of few species and high importance of bare soil, only species with relative cover higher than 1% were considered for the ordination analysis. Additionally, we tested the difference in species composition between subregions by randomization testing (Pillar & Orlóci, 1996), using chord distance as resemblance measure. Subregions were also compared regarding the parameters vegetation height, total vegetation cover, bare soil, litter and manure by help of randomization tests, using Euclidian distance and 999 permutations. All analyses were performed by the software MULTIV (Pillar, 1997).

For each subregion, vegetation parameters were calculated according to Mueller-Dombois & Ellenberg (1974): relative cover (RC), relative frequency (RF) and the importance value index (IVI). The IVI takes into account relative frequency and relative cover of species, the balance of those two principal descriptors of species importance to community composition is what makes this index so widespread.

Species growth form were characterized using a modified classification from Setubal (2010), resulting in 13 growth form classes: graminoid cespitose herb (GCH), graminoid prostrate herbs (GPH), erect herb (ERH), prostrate herb

(PTH), prostrate herb with stolon (PSH), voluble herb (VOH), rosettes of the genus *Eryngium* and morphologically similar herbs (spiny and rather fibrous rosettes) (EYH), rosulate herb (ROH), shrubs (SHR), erect subshrub (ERS), prostrate subshrub (PTS), non-graminoid creeping species (CRE) and succulent plants (CRA).

We also identified naturalized or exotic species, according to the checklist of exotic species for the Pampa biome (Fonseca et al., 2013) and the list of Brazilian flora website (http://floradobrasil.jbrj.gov.br/). Extinction risk and vulnerability of the species was checked in the current Red List of Threatened Plant Species for the state (Rio Grande do Sul, 2003). The complete list of species with occurrence, growth forms and endangerment status is presented in the supporting material.

RESULTS

A total of 221 taxa of vascular plants were identified to the species level, four individuals could only be identified to the genus or family level. Of the total 225 records, 23.5% belonged to Poaceae family, 20% to Asteraceae, 9.7% to Cyperaceae and 8.9% to Fabaceae family (Fig. 2). Even though other families also presented high richness, most of the plant cover was formed by species from the Poaceae family. The relatively high absolute cover of Verbenaceae in partly is consequence of a specific situation at one of the TA sites. This site, TA3, seems be altered by past agricultural use, where the cover of *Phyla nodiflora* (L.) Greene (Verbenaceae) accounted for about 20% of total vegetation cover.

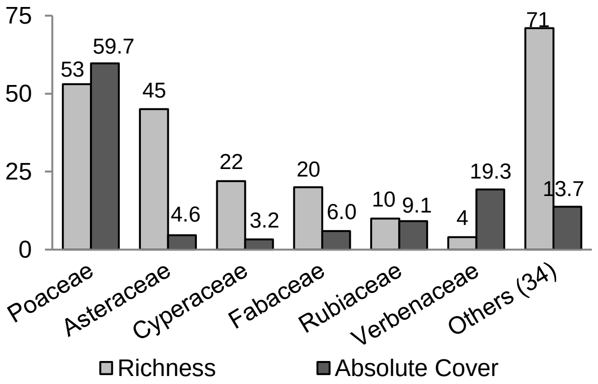

Figure 2: Richness of species and total vegetation cover per family, recorded in 16 sites distributed in four subregions in grasslands of the South Brazilian coastal plain.

The highest species richness was found for the subregion NC, where we recorded 137 species (Fig. 3). Most of the species were shared between one or more subregion. A total of 39 species (18% of total species number) were common to all subregions. Poaceae contributed most to this number, with 12 species, followed by Asteraceae and Cyperaceae. Both with five species common species to all subregions. Average species number per plot (1 m^2) was 13.5, and the highest value was at site NC3, with 22 species per plot, lowest mean value was at SC3, with 7.9 species per plot.

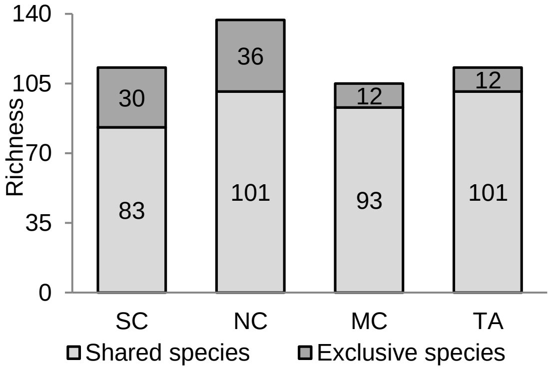

Figure 3: Species richness per subregion registered to the grasslands of southern Brazilian coastal plain, indicating the number of exclusive species and number of species that were shared between two or more subregions.

The first two axes of the PCoA (Fig. 4) together explained 60% of the variation in the data. The first ordination axis separated sites with high cover of *Axonopus* aff. *affinis* Chase and *Andropogon lateralis* Ness, at the left side, from areas with high coverage of *Paspalum notatum* Alain ex Flüggé and *Paspalum pumilum* Nees at the right side. Along the second axis, sites with the presence of the exotic species *Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf. and the ruderal species *P. nodiflora* (in the positive portion) were separated from sites with the presence of the tussock species *Sorghastrum setosum* (Griseb.) Hitchc. and *Andropogon selloanus* Hack (in the negative portion).

Sites belonging to the subregions LN and LM did not present significant differences in species composition (ρ=0.2), which might be expected by their geographical proximity; all sites in these two groups were situated close together in the ordination diagram, i.e. were quite similar in terms of composition and structure. Nonetheless, the sites of SC and TA subregions also did not present significant difference in species composition (ρ=0.09), despite their geographical distance. The subregions LN and LM, however, differed from both SC and TA, resulting in two groups of sites clearly separated along the first ordination axis (Fig. 4)

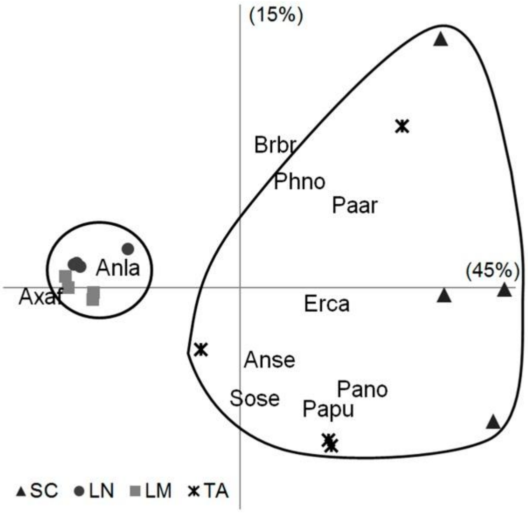

Figure 4: Principal coordinate ordination diagram, based on chord distance, showing the first two axes. Only species with high correlations to the axes are shown (corr.>0.4). Symbols represent the subregions and continuous lines delimit groups of sampling units that were similar in species composition (ρ<0.05). Axaf: *Axonopus* aff. *affinis*; Anla: *Andropogon lateralis*; Anse: *A. selloanus*; Brbr: *Brachiaria brizantha*; Erca: *Eragrostis cataclasta*; Paar: *Paspalum arenarium*; Pano: *P. notatum*; Papu: *P. pumilum*; Phno: *Phylla nodiflora*; Sose: *Sorghastrum setosum*.

The structural parameters of coastal grasslands vegetation were quite similar among areas (Tab. 2). Only two parameters presented differences: mean vegetation cover was significantly higher in LM subregion, when compared to SC subregion, and litter cover was higher at SC and TA subregions when compared to LM subregion.

Table 2: Structural parameters of coastal grasslands sampled in four different regions in the South Brazilian coastal plain. Given are mean values of the 60 plots per subregion and the respective standard deviation. Different letters represent significant difference between subregions (ρ<0.05).

	SC	LN	LM	TA
Vegetation height (cm)	5.8 (±1.2)	6.3 (±1.6)	6.0 (±1.3)	6.3 (±2.4)
Vegetation cover (%)	62.8 (±11.9)^{a}	73.0 (±17.6)^{ab}	79.8 (±5.6)^{b}	78.5 (±11.3)^{ab}
Bare soil cover (%)	19.9 (±13.6)	19.0 (±13.4)	13.7 (±5.4)	7.8 (±9.2)
Litter cover (%)	18.9 (±5.7)^{a}	8.9 (±3.3)^{ab}	7.7 (±1.1)^{b}	14.0 (±5.0)^{a}
Manure cover (%)	0.7 (±0.7)	0.9 (±0.6)	1.4 (±0.6)	2.2 (±1.0)

The five most important species (highest IVI values) registered for each subregion are shown in Tab. 3. *Axonopus* aff. *affinis* is the most important species for the major part of the areas, representing almost half of total cover at MC sites. *P. notatum* also has an important role in species composition of the coastal grasslands, together with other species of the genus Paspalum, such as *Paspalum arenarium* Schrad., *P. pumilum* and *Paspalum lepton* Schult..

Table 3: Grassland vegetation parameters of the five most important species (higher IVI) of the four subregions in the southern Brazilian coastal plain. RF: relative frequency of species in 60 plots (1m²) per subregion; RC: relative cover of species in 60 plots (1m²) per subregion; and IVI: importance value index, average of RF plus RC.

Species	RF(%)	RC(%)	IVI
Subregion SC			
Paspalum notatum Alain ex Flüggé	68.3	29.5	48.9
Paspalum arenarium Schrad.	65.0	9.5	37.3
Desmodium incanum DC.	48.3	1.1	24.7
Cardionema ramosissima (Weinm.) A.Nelson & J.F.Macbr.	48.3	0.7	24.5
Richardia humistrata (Cham. & Schltdl.) Steud.	45.0	1.5	23.2
Subregion NC			
Axonopus aff. *affinis* Chase	95.0	41.8	68.4
Croton lanatus Lam.	63.3	4.2	33.7
Eryngium nudicaule Lam.	60.0	2.3	31.1
Paspalum lepton Schult.	53.3	5.9	29.6
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	51.7	1.9	26.8
Subregion MC			
Axonopus aff. *affinis* Chase	100.0	47.9	73.9
Centella asiatica (L.) Urb.	85.0	3.5	44.3
Andropogon lateralis Nees	66.7	13.7	40.2
Sisyrinchium micranthum Cav.	71.7	1.1	36.4
Kyllinga odorata Vahl	56.7	1.7	29.2
Subregion TA			
Axonopus aff. *affinis* Chase	75.0	15.4	45.2
Paspalum notatum Alain ex Flüggé	71.7	12.2	41.9
Eragrostis cataclasta Nicora	71.7	7.3	39.5
Centella asiatica (L.) Urb.	71.7	3.8	37.7
Gamochaeta americana (Mill.) Wedd.	53.3	0.6	26.9

Only two species listed as threatened for Rio Grande do Sul state were recorded in the sampling. *Gomphrena perennis* L., classified as vulnerable (VU), was registered on five sites (NC1, SC1, SC4, LN1 and TA2). *Laurembergia tetrandra* (Schott ex Spreng.) Kanitz, considered as endangered (EN) had only one individual registered at area TA2.

We registered 14 exotic/naturalized species that together accounted about 6% of total species cover for the entire survey. Among these there are some species with invasive potential as *Eragrostis plana* Nees, *Cynodon dactylon* (L.) Pers. and *B*. *brizantha. C. dactylon* was widely widespread especially in the southern areas (TA), occurring on 22 of the 60 plots and covering about 4.5% of the four TA areas. Also many ruderal species, characteristic for disturbed environments, were recorded, such as *Digitaria connivens* (Trin.) Henrard, *Cenchrus echinatus* L., *Cardionema ramosissima* (Weinm.) A.Nelson & J.F.Macbr. and *Phyla nodiflora*. Particularly very frequent, *C. ramosissima*, was registered occurring in 10 of the 16 sites.

As to growth forms, the grasslands in all four subregions were dominated by graminoid prostrate herbs (Fig. 5), which include the species *A.* aff. *affinis*, *P. notatum*, *P. arenarium*, *P. pumilum* and *P. lepton*. Caespitose grasses (GCH) also played an important role in the communities, whith high importance especially of *Eragrostis cataclasta* Nicora, *A*. *lateralis* and *S*. *setosum*.

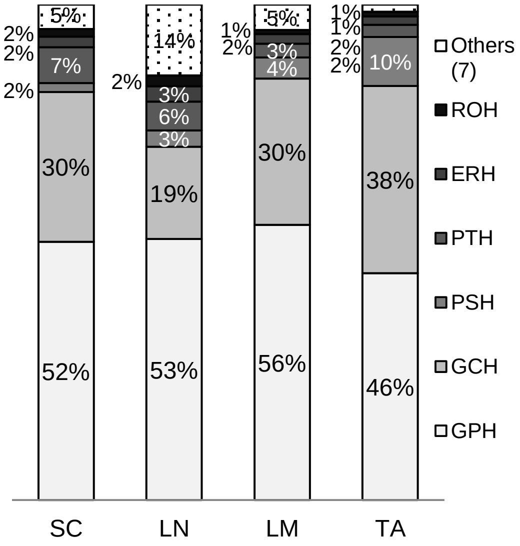

Figure 5: Percentage of cover of species growth form in the four subregions. Growth forms are: GCH - graminoid cespitose herb; GPH - graminoid prostrate herb; ERH – erect herb; PTH - prostrate herb; ROH - rosulate herb; PSH - prostrate herb with stolon. ‘Others’ represent the sum of coverage of: VOH - voluble herb; EYH - Eryngium genus and similar herbs; SHR – shrubs; ERS - erect subshrub; PTS - prostrate subshrub; CRE - creeping species; and CRA - succulent plants.

DISCUSSION

We sampled 16 areas of grassland vegetation along a latitudinal gradient in the South Brazilian coast, where we recorded 221 species distributed in 40 botanical families. The most important families were Poaceae, Asteraceae, Cyperaceae and Fabaceae, which corresponds partly to the general pattern of the South Brazilian grasslands. The high importance of Cyperaceae as the third family in terms of species number is characteristic for the coastal grasslands (Boldrini, 2009) in contrast to other regions in the state, where Fabaceae takes this position. Although Cyperaceae do not present endemism in this region, the species of this family have characteristics that favor their establishment in these areas, such as the presence of well-developed underground structures (Boldrini, 2009). Also, the species of Cyperaceae family are known to establishing well in humid areas and act as weeds invaders of crops (Simpson, Yesson, Culham, Couch, & Muasya, 2011). Those characteristics may facilitate their establishment and spread in coastal grasslands due to the high percentage of bare soil and abundance of wetlands in this region.

When compared to other grasslands formations in the region, in addition to the difference in the third dominant botanic family, the strikingly lower plant species richness in the South Brazilian coastal grasslands becomes obvious. We found, on average, 13.5 species per plot ($1m^2$). For grasslands on the granitic hills in Porto Alegre, in contrast, different studies account for, respectively: 20.7 spp/m^2 (Setubal & Boldrini, 2012), 27 spp/m^2 (Dresseno & Overbeck, 2013), 27.1 spp/m^2 (Ferreira, Müller, Boldrini, & Eggers, 2010) and 33.9 spp. per plot of $0.75m^2$ (Overbeck, Müller, Pillar, & Pfadenhauer, 2006), i.e. considerably higher numbers.

However, considering comparisons with previous studies conducted at single locations of the coastal plain we observe similar richness values as we recorded per subregion. For example, 138 spp. (Garcia & Boldrini, 2007) and 123 spp. (Ferreira & Setubal, 2009), and an average 117 spp. recorded in our survey per subregion. The lower plant species richness of the coastal grasslands is related to the very recent geological formation of this environment (Villwock & Tomazelli, 1998) and the nature of the substrate (sand depositions, i.e. rather limiting conditions), that are responsible for a low rate of endemism in the region and the rather open grassland vegetation, with high percentage of bare soil. Boldrini (2009) point out only six endemic species in the coastal grasslands, while the highlands grasslands, for example, account for 296 cases of endemism (Iganci, Heiden, Miotto, & Pennington, 2011). The recent geological formation of the coastal plain and thus the likewise recent colonization by grassland species in comparison to other grasslands regions in southern Brazil also explains the fact that most species registered in our study were shared between two or more subregions, emphasizing their generally ample distribution and their high capacity for long distance dispersal.

Nonetheless, species with high potential of vegetative spread and a prostrate habitus covered most of the sampling sites, such as the grasses *Axonopus* aff. *affinis* and *Paspalum notatum*. Those two species have already been mentioned as representative of coastal grasslands especially in drier areas (Boldrini, Trevisan, & Schneider, 2008; Ferreira & Setubal, 2009). *Ischaemum minus* and *Paspalum pumilum*, also characterized by vegetative spread, were also found with high coverage in our survey. These species have been pointed out as important species in more humid areas in the coastal grasslands (Caetano, 2003; Canto-Dorow, Longhi-Wagner, & Valls, 1996; Garcia & Boldrini, 2007).

Prostrate species generally have structures adequate for colonization of open soil, such as rhizome and stolons, and can cover this type of environment relatively easily. The limiting availability of resources in the coastal environments provide conditions to which few species are well adapted (Crawford, 2008), and these well adapted species seem to be quite successful in colonizing those environments. Clonal spread, i.e. production of new individuals by the growing of new ramets, has been suggested as particularly advantageous in less favorable environments (Eckert, 1999; Honnay & Bossuyt, 2005). Additionally, high cover of prostrate grasses is also a consequence of high levels of cattle grazing: these plants, characterized by rapid resource acquisition and fast substitution of leaves consumed by cattle, can be considered as indicative of high grazing pressure (Cruz et al., 2010), and at high grazing pressure, it is the dominance of grasses with this strategy that leads to the relatively homogenous vegetation structure (Nabinger, Ferreira, Freitas, Carvalho, & Sant’Anna, 2009).

Tussock species had the second largest percentage of cover among the growth forms, and had particularly high values in the Taim (TA) subregion, in the extreme south of the coastal plain. This region presents high cover of *Sorghastrum setosum*, an important tussock species found in many sites in this survey, while the tussock specie dominant at northern areas is *A. lateralis*. Indeed, *A. lateralis* is one of the main tussock species present in Brazilian grasslands, but Zanin & Longhi-Wagner (2011) pointed out to the decrease in *A. lateralis* presence with higher latitudes, as observed here.

The dominant species were the main responsible for characterizing, in local scale, the grasslands of the coastal plain. The ordination analysis showed the division of the sampling sites among two groups of sites: areas mostly covered by *A.* aff. *affinis* and *A. lateralis*; and areas with higher coverage of *P. notatum* and *P. pumilum*. Also, two sites from TA and SC subregions presented conspicuously different floristic and structural compositions, with presence of exotic and ruderal species like: *B. brizantha* and *P. nodiflora*. This situation seems to be responsible for the grouping of SC and TA sites in the ordination, as the two subregions share sites with degraded characteristics (i.e, high percentage of bare soil and presence of exotic/ruderal species).

The number of exotic species found in our study was rather low, and none of the species reached high abundances, with the exception of *Cynodon dactylon*. Many of the exotic species deliberately introduced in the Pampa biome are for forage use (Fonseca et al., 2013). In our study, this is the case of *Melinis minutiflora* P.Beauv. and *B. brizantha*. *Eragrostis plana* is a Poaceae species that has high invasive capacity, can reach dominance and reduce local biodiversity as well as grassland productivity (Reis & Coelho, 2000). In our survey, *E. plana* was found only at one site in the northernmost subregion, but all the costal grasslands has been considered as vulnerable environment for the invasion of this species (Barbosa, Pillar, Palmer, & Melo, 2013) which can be found along roadsides practically along the entire gradient, making monitoring of the possible spread of this exotic invasive species important.

A comparatively low plant species richness, presence of a large percentage of bare soil, high dominance and high coverage of prostrate species are inherent characteristics of the coastal grasslands on southern Brazil. In other formations of the Brazilian Campos, these features would be interpreted as signs of degradation – for the coastal grasslands, they are typical and a consequence of the limiting characteristics of marginal environments, in consequence of the soil features in the region. However, we should keep in mind that the management of grassland, e.g. high cattle loads, as well as past agricultural use can cause changes in grassland structure. In the case of two sites, one in the SC subregion and other in TA subregion, a legacy of former agricultural use is evident by conspicuously different floristic and structural characteristics of the vegetation, which might be interpreted as low resilience of these grasslands to severe disturbances like land use change. Overgrazing has been identified as a major cause of degradation in grasslands around the world (D'Odorico, Bhattachan, Davis, Ravi, & Runyan, 2013).

From the data of our survey we can conclude that the remaining areas of coastal grassland vegetation preserve their characteristic floristic composition and structure. Nonetheless, just as in other regions of the South Brazilian grasslands, it seems necessary to set more appropriate management goals for coastal grasslands vegetation, e.g. lower stocking rates of cattle (Carvalho & Batello, 2009). On the other hand, in conservation units, maintenance of management is necessary for maintenance of grasslands and thus of the typical ecosystems in the region, the conversion of natural grasslands to other uses is the factor that most threatens this formation. Preservation of the remaining fragments of this landscape, i.e. prevention of their transformation to other land use, thus should be the core of a conservation strategy for grasslands in the South Brazilian coastal plain. A basis for this would be a zoning plan for different types of land use that could be developed in the course of the National Coastal Management Plan (Brasil, 1988).

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ANNEXES

Table 1: Species list with information on presence for subregions. Growth forms are: GCH graminoid cespitose herb; GPH graminoid prostate herbs; ERH erect herb; PTH prostrate herb; ROH rosulate herb; PSH prostrate herb with stolon; VOH voluble herb; EYH eryngium genus/similar herbs; SHR shrubs; ERS erect subshrub; PTS prostate subshrub; CRE creeping species and CRA crass leaves plants. Origin refers to exotic species (E) or naturalized (N), as in the list of [1]Brazilian flora checklist and [2]Pampa exotic species checklist. Threatened species, following the list for the state (Rio Grande do Sul, 2003) are identified with *.

Families / Species	SC	NC	MC	TA	Growth form	Origin
Amaranthaceae						
Chenopodium ambrosioides L.	X				ERH	
Gomphrena perennis L.*	X	X		X	ERH	
Pfaffia tuberosa (Spreng.) Hicken	X	X		X	ERH	
Amaryllidaceae						
Nothoscordum bivalve (L.) Britton		X			ERH	E[1]
Apiaceae						
Centella asiatica (L.) Urb.	X	X	X	X	PSH	N[1] / E[2]
Cyclospermum leptophyllum (Pers.) Sprague ex Britton & P. Wilson	X	X	X	X	ERH	
Eryngium horridum Malme		X			EYH	
Eryngium nudicaule Lam.	X	X	X	X	EYH	
Eryngium sanguisorba Cham. & Schltdl.		X	X	X	EYH	
Apocynaceae						
Asclepias mellodora A.St.-Hil.	X			X	ERH	
Mandevilla pinifolia (A.St.-Hil.) Miers		X			ERH	
Oxypetalum arnottianum H. Buek	X				PTH	
Araliaceae						
Hydrocotyle bonariensis Lam.	X	X	X	X	PSH	
Hydrocotyle exigua Malme	X	X	X	X	PSH	
Hydrocotyle ranunculoides L.f.	X		X		PSH	
Asteraceae						
Acanthospermum australe (Loefl.) Kuntze	X	X			PTH	
Ambrosia artemisiaefolia L.				X	ERS	
Aspilia montevidensis (Spreng.) Kuntze	X			X	PTH	
Baccharis articulata (Lam.) Pers.		X			ERS	
Baccharis gnaphalioides Spreng.				X	ROH	
Baccharis leucopappa DC.				X	SHR	
Baccharis megapotamica Spreng.		X			SHR	
Baccharis spicata (Lam.) Baill.	X			X	SHR	
Baccharis trimera (Less.) DC.		X	X	X	ERS	
Chaptalia piloselloides (Vahl) Baker		X	X		ROH	
Chaptalia runcinata Kunth	X		X	X	ROH	
Chaptalia sinuata (Less.) Baker	X				ROH	
Chevreulia acuminata Less.		X			PTH	
Chevreulia sarmentosa (Pers.) Blake	X	X	X	X	PTH	

[1]Available at: http://floradobrasil.jbrj.gov.br/; [2]Fonseca et al. (2013)

(sequence)

Families / Species	SC	NC	MC	TA	Growth form	Origin
Chrysolaena flexuosa (Sims) H.Rob.		X	X		ROH	
Conyza bonariensis (L.) Cronquist	X	X	X		ERS	
Conyza primulifolia (Lam.) Cuatrec. & Lourteig	X	X	X	X	ERS	
Elephantopus mollis Kunth	X				ERH	
Eupatorium ascendens Sch. Bip. ex Baker	X				ERS	
Facelis retusa (Lam.) Sch. Bip.	X	X		X	ROH	
Gamochaeta americana (Mill.) Wedd.	X	X	X	X	ROH	
Gamochaeta coarctata (Willd.) Kerguélen		X	X		ROH	
Hypochaeris lutea (Vell.) Britton		X	X		ROH	
Hypochaeris megapotamica Cabrera		X			ROH	
Lucilia acutifolia (Poir.) Cass.	X			X	ERH	
Lucilia nitens Less.	X	X			ERH	
Micropsis spathulata (Pers.) Cabrera		X			ERH	
Noticastrum calvatum (Baker) Cuatrec.	X	X	X	X	ROH	
Noticastrum gnaphalioides (Baker) Cuatrec.	X	X		X	ROH	
Orthopappus angustifolius Gleason	X				ROH	
Pterocaulon angustifolium DC.		X			ERH	
Pluchea oblongifolia DC.				X	ERS	
Pterocaulon alopecuroides (Lam.) DC.			X		ERH	
Pterocaulon lorentzii Malme	X	X	X		ERS	
Senecio brasiliensis (Spreng.) Less.	X				ERS	
Senecio crassiflorus (Poir.) DC.	X	X	X		CRA	
Senecio leptolobus DC.	X	X			ERS	
Senecio selloi (Spreng.) DC.			X	X	ERS	
Soliva sessilis Ruiz et Pavón	X	X	X		ROH	
Sommerfeltia spinulosa (Spreng.) Less.	X	X			ROH	
Stenachaenium campestre Baker				X	ROH	
Stenachaenium megapotamicum (Spreng.) Baker	X	X		X	ROH	
Symphyotrichum squamatum (Spreng.) G.L.Nesom				X	ERH	
Tanacetum vulgare L.	X				ERS	
Vernonanthura nudiflora (Less.) H.Rob.	X	X	X	X	ERS	
Boraginaceae						
Varronia curassavica Jacq.	X				ERS	
Brassicaceae						
Lepidium auriculatum Regel & Körn.		X			ERH	
Calyceraceae						
Acicarpha procumbens Less.	X	X			ROH	E[1]
Campanulaceae						
Lobelia hederacea Cham.			X	X	PTH	
Wahlenbergia linarioides (Lam.) A.DC.	X				ERH	
Caryophyllaceae						
Cardionema ramosissima (Weinm.) A.Nelson & J.F.Macbr.	X	X	X	X	PTH	N[1]
Cerastium glomeratum Thuill.	X	X	X		ERH	N[1] / E[2]
Drymaria cordata (L.) Willd. ex Roem. & Schult.	X				PTH	N[1]
Spergula arvensis L.		X			ERH	N[1] / E[2]

[1] Available at: http://floradobrasil.jbrj.gov.br/; [2] Fonseca et al. (2013)

(sequence)

Families / Species	SC	NC	MC	TA	Growth form	Origin
Cistaceae						
Helianthemum brasiliense (Lam.) Pers.	X	X	X		ERH	
Commelinaceae						
Commelina diffusa Burm.f.	X	X		X	GPH	
Convolvulaceae						
Dichondra macrocalyx Meisn.		X	X		PSH	
Dichondra sericea Sw.		X	X	X	PSH	
Evolvulus sericeus Sw.		X	X	X	PTH	
Cyperaceae						
Bulbostylis capillaris (L.) C.B. Clarke	X	X	X	X	GCH	
Bulbostylis juncoides (Vahl) Kük.	X	X			GCH	
Carex phalaroides Kunth		X			GCH	
Cyperus aggregatus (Willd.) Endl.	X	X	X	X	GCH	
Cyperus hermaphroditus (Jacq.) Standl.		X			GCH	
Cyperus intricatus Schrad. ex Schult.			X		GCH	
Cyperus reflexus Vahl		X	X	X	GCH	
Eleocharis bonariensis Nees				X	GCH	
Eleocharis flavescens (Poir.) Urb.				X	GCH	
Eleocharis maculosa (Vahl) Roem. & Schult.			X		GCH	
Fimbristylis autumnalis (L.) Roem. & Schult.			X	X	GCH	
Fimbristylis dichotoma (L.) Vahl				X	GCH	
Fimbristylis spadicea (L.) Vahl			X		GCH	
Isolepis cernua (Vahl) Roem. & Schult.			X		GCH	
Kyllinga brevifolia Rottb.	X	X	X	X	GCH	
Kyllinga odorata Vahl	X	X	X	X	GCH	
Kyllinga vaginata Lam.			X	X	GCH	
Pycreus polystachyos (Rottb.) P.Beauv.	X		X		GCH	
Rhynchospora barrosiana Guagl.		X	X	X	GCH	
Rhynchospora brittonii Gale	X		X		GCH	
Rhynchospora tenuis Link	X	X	X	X	GCH	
Scleria distans Poir.		X	X	X	GCH	
Droseraceae						
Drosera brevifolia Pursh.		X			ROH	
Eriocaulaceae						
Eriocaulon modestum Kunth		X			ROH	
Euphorbiaceae						
Croton lanatus Lam.		X			ERS	
Dalechampia micromeria Baill.	X				PTH	
Euphorbia papillosa A.St.-Hil.	X	X			ERS	
Euphorbia selloi (Klotzsch & Garcke) Boiss.				X	PTS	
Fabaceae						
Aeschynomene falcata (Poir.) DC.	X	X	X		PTH	
Arachis burkartii Handro		X			PTH	
Chamaecrista nictitans (L.) Moench	X				PTH	
Desmodium barbatum (L.) Benth.		X			ERH	
Desmodium incanum DC.	X	X	X		ERS	
Galactia gracillima Benth.		X			VOH	

^{1}Available at: http://floradobrasil.jbrj.gov.br/; ^{2}Fonseca et al. (2013)

(sequence)

Families / Species	SC	NC	MC	TA	Growth form	Origin
Galactia marginalis Benth.		X			VOH	
Macroptilium prostratum (Benth.) Urb.		X	X		PTH	
Macroptilium psammodes (Lindm.) S.I. Drewes & R.A. Palacios		X			VOH	
Mimosa sp.	X				SHR	
Sesbania punicea (Cav.) Burkart	X				SHR	
Stylosanthes leiocarpa Vogel	X	X	X	X	PTH	
Stylosanthes montevidensis Vogel		X		X	PTH	
Stylosanthes viscosa (L.) Sw.	X				PTH	
Vigna luteola (Jacq.) Benth.				X	PTH	
Zornia cryptantha Arechav.		X			PTH	
Zornia orbiculata Mohlenbr.		X	X		PTH	
Zornia reticulata Sm.	X	X	X	X	PTH	
Haloragaceae						
Laurembergia tetrandra (Schott ex Spreng.) Kanitz*				X	ERH	
Hypoxidaceae						
Hypoxis decumbens L.	X	X	X	X	ROH	
Iridaceae						
Cypella coelestis (Lehm.) Diels		X			ERH	
Sisyrinchium micranthum Cav.	X	X	X	X	ERH	
Sisyrinchium palmifolium L.	X				ERH	
Sisyrinchium setaceum Klatt			X		ERH	
Juncaceae						
Juncus capillaceus Lam.			X	X	GCH	
Juncus dichotomus Elliott	X		X	X	GCH	
Juncus microcephalus Kunth		X	X		GCH	
Lamiaceae						
Hyptis brevipes Poit.		X			ERS	
Scutellaria racemosa Pers.			X		ERH	
Linaceae						
Cliococca selaginoides (Lam.) C. M. Rogers & Mild		X			ERH	
Lythraceae						
Cuphea carthagenensis (Jacq.) J.Macbr.				X	ERH	
Cuphea glutinosa Cham. & Schltdl.	X				ERS	
Malvaceae						
Krapovickasia flavescens (Cav.) Fryxell		X			PTH	
Sida rhombifolia L.	X				ERS	
Sida viarum A.St.-Hil.	X				ERS	
Melastomataceae						
Tibouchina gracilis (Bonpl.) Cogn.	X	X	X	X	ERH	
Tibouchina versicolor (Lindl.) Cogn.	X	X		X	ERH	
Menyanthaceae						
Nymphoides indica (L.) Kuntze			X	X	PTH	
Orchidaceae						
Habenaria parviflora Lindl.			X	X	ERH	
Orobanchaceae						
Agalinis communis (Cham. & Schltdl.) D'Arcy			X	X	ERS	

[1]Available at: http://floradobrasil.jbrj.gov.br/; [2]Fonseca et al. (2013)

(sequence)

Families / Species	**SC**	**NC**	**MC**	**TA**	**Growth form**	**Origin**
Oxalidaceae						
Oxalis conorrhiza Jacq.	X				PSH	
Oxalis eriocarpa DC.		X			PSH	
Oxalis lasiopetala Zucc.		X			PSH	
Plantaginaceae						
Bacopa monnieri (L.) Wettst.				X	PSH	
Gratiola peruviana L.			X	X	ERH	
Mecardonia tenella (Cham. & Schltdl.) Pennell		X	X	X	PSH	
Nuttallanthus canadensis (L.) D.A.Sutton	X				ERH	E^{1}
Plantago tomentosa Lam.	X	X	X	X	ROH	
Scoparia ericacea Cham. & Schltdl.			X		ERS	
Poaceae						
Agrostis montevidensis Spreng. ex Nees				X	GCH	
Andropogon lateralis Nees		X	X	X	GCH	
Andropogon selloanus Hack.		X		X	GCH	
Andropogon ternatus (Spreng.) Nees				X	GCH	
Aristida circinalis Lindm.		X			GCH	
Aristida laevis (Nees) Kunth	X				GCH	
Axonopus aff. *affinis* Chase	X	X	X	X	GPH	
Brachiaria brizantha (Hochst. ex A. Rich.) Stapf	X	X			GCH	N^{1} / E^{2}
Briza minor L.			X		GCH	N^{1} / E^{2}
Calamagrostis viridiflavescens (Poir.) Steud.		X		X	GCH	
Cenchrus echinatus L.	X				GCH	
Chascolytrum poomorphum (J. Presl) Essi, Longhi-Wagner & Souza-Chies		X			GCH	
Chascolytrum subaristatum (Lam.) Desv.	X	X	X		GCH	
Chascolytrum uniolae (Nees) Essi, Longhi-Wagner & Souza-Chies	X	X	X		GCH	
Cynodon dactylon (L.) Pers.			X	X	GPH	E^{12}
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	X	X	X	X	GCH	
Digitaria connivens (Trin.) Henrard	X	X		X	GPH	
Eragrostis bahiensis Schrad. ex Schult.				X	GCH	
Eragrostis cataclasta Nicora	X	X	X	X	GCH	
Eragrostis lugens Nees				X	GCH	
Eragrostis plana Nees		X			GCH	E^{12}
Eragrostis trichocolea Hack. & Arech.	X				GCH	
Eustachys uliginosa (Hack.) Herter	X				GCH	
Gymnopogon legrandii Roseng., B.R. Arrill. & Izag.		X			GCH	
Ischaemum minus J. Presl	X		X	X	GPH	
Leptocoryphium lanatum (Kunth) Nees		X	X		GCH	
Melinis minutiflora P.Beauv.	X				GCH	N^{1} / E^{2}
Mnesithea selloana (Hack.) de Koning & Sosef	X	X	X	X	GCH	
Panicum aquaticum Poir.	X	X	X	X	GCH	
Panicum dichotomiflorum Michx.	X		X	X	GCH	
Panicum racemosum (P. Beauv.) Spreng.	X	X		X	GCH	
Paspalum arenarium Schrad.	X	X			GPH	
Paspalum dilatatum Poir.				X	GPH	

^{1}Available at: http://floradobrasil.jbrj.gov.br/; ^{2}Fonseca et al. (2013)

(final part)

Families / Species	SC	NC	MC	TA	Growth form	Origin
Paspalum distichum L.				X	GPH	
Paspalum lepton Schult.	X	X	X	X	GPH	
Paspalum notatum Alain ex Flüggé	X	X	X	X	GPH	
Paspalum plicatulum Michx.	X	X	X	X	GCH	
Paspalum pumilum Nees	X	X	X	X	GCH	
Paspalum umbrosum Trin.	X	X	X		GCH	
Paspalum vaginatum Sw.		X	X	X	GPH	
Piptochaetium montevidense (Spreng.) Parodi	X	X	X	X	GCH	
Poaceae sp2	X				GCH	
Poaceae sp3				X	GCH	
Poaceae sp4				X	GCH	
Schizachyrium spicatum (Spreng.) Herter		X	X	X	GCH	
Setaria parviflora (Poir.) Kerguélen	X	X	X	X	GCH	
Setaria setosa (Sw.) P. Beauv.	X				GCH	
Sorghastrum setosum (Griseb.) Hitchc.		X	X	X	GCH	
Sporobolus indicus (L.) R.Br.	X	X	X	X	GCH	
Steinchisma hians (Elliott) Nash.		X	X	X	GCH	
Stenotaphrum secundatum (Walter) Kuntze	X	X		X	GPH	
Trachypogon spicatus (L. f.) Kuntze		X			GCH	
Vulpia bromoides (L.) Gray		X	X	X	GCH	E[1,2]
Polygalaceae						
Monnina cardiocarpa A.St.-Hil. & Moq.		X		X	ERH	
Polygala linoides Poir.				X	ERH	
Primulaceae						
Lysimachia filiformis (Cham. & Schltdl.) U. Manns & Anderb.				X	ERH	
Rubiaceae						
Borreria capitata (Ruiz & Pav.) DC.			X		PTH	
Borreria eryngioides Cham. & Schltdl.			X		PTH	
Diodia saponariifolia (Cham. & Schltdl.) K. Schum.		X			PTH	
Galium hirtum Lam.		X			ERS	
Galium humile Cham. & Schltdl.			X		ERH	
Galium richardianum (Gillies ex Hook. & Arn.) Endl. ex Walp.	X	X	X	X	ERH	
Oldenlandia salzmannii (DC.) Benth. & Hook. f. ex B.D. Jacks.		X	X	X	PTH	
Richardia humistrata (Cham. & Schltdl.) Steud.	X	X	X	X	PTH	
Richardia stellaris (Cham. & Schltdl.) Steud.	X	X	X	X	PTH	
Spermacoce verticillata L.	X	X			PTH	
Smilacaceae						
Smilax cognata Kunth	X				CRE	
Solanaceae						
Petunia integrifolia (Hook.) Schinz & Thell.	X	X		X	PTH	
Verbenaceae						
Glandularia peruviana (L.) Small	X	X		X	PTH	
Glandularia selloi (Spreng.) Tronc.	X	X	X	X	PTH	
Lippia turnerifolia Cham.		X			ERH	
Phyla nodiflora (L.) Greene			X	X	PSH	

[1]Available at: http://floradobrasil.jbrj.gov.br/; [2]Fonseca et al. (2013)

CAPÍTULO 2[1]

Scale-specific processes shape plant community patterns in subtropical coastal grasslands

Luciana da S. Menezes; Sandra C. Müller; Gerhard E. Overbeck.

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Scale-specific processes shape plant community patterns in subtropical coastal grasslands

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ABSTRACT

Questions What is the relative contribution of environmental and spatial processes in explaining beta diversity in grassland communities? How does relative contribution of either group of processes change with changes in spatial scales? Do these patterns differ between plant families with distinct general dispersal types?

Location 16 sample sites in coastal grasslands in southern Brazil, between 28°49'47.4"S and 32°40'45.3"S.

Methods Species composition and cover were sampled in 15 plots per site. Spatial structure was synthesized using the Moran Eigenvectors Map (MEM) method and climate and soil variables were summarized by PCA analysis. Explanatory variables were then selected with forward selection procedure. The scale-specific relationship of species composition with explanatory variables was explored using scale-specific additive spatial models. Then, variation partitioning procedures were used to verify the influence of each explanatory matrix on the response matrix (total species composition; species composition weighted by specific spatial scales; only composition of Poaceae and Asteraceae).

Results We found that the greatest part of beta diversity in coastal grasslands vegetation is explained by environmental variables structured in space. When considering different spatial scales, climatic variables were of high importance at the broad scale, and edaphic variables act at the fine scale. Species with most effective dispersal (Asteraceae) were less related to spatial variables, than species with low dispersal capability (Poaceae).

Conclusions Our study highlighted the importance of exploring beta diversity at different spatial scales to evaluate the magnitude of effects of different drivers for plant community assembly. The separate consideration of different groups of species will further improve our understanding assembly patterns.

Keywords: Beta diversity; latitudinal gradient; Pampa; Niche; Neutral; MEM; variation partitioning; dispersal limitation.

INTRODUCTION

Understanding the processes responsible for structuring communities is one of the major challenges of ecology (Ricklefs & Schluter 1993; Barot & Gignoux 2004). Today, many ecologists agree that communities are not formed by a subset of individuals randomly selected from a regional pool of species, but that interactions of individuals with the environment and between individuals (e.g. competition) are the main factors responsible for structuring communities. This is expected under the perspective of the Niche theory, where different environmental processes, for example, climatic and edaphic variables, as well as interactions between species, act as filters, selecting the species adapted to the conditions given at a specific site (e.g. MacArthur & Levins 1964; Diamond 1975; Keddy 1992). In contrast, the Neutral theory considers the species as ecologically or functionally equivalents (Bell 2001; Hubbell 2001) and stochastic, demographic and biogeographic processes (e.g. birth and death, immigration and local extinction, speciation and extinction) are the principal factors responsible for defining community composition. Currently, both theories are seen as complementary, or as extreme points of a ‘gradient’ of factors that shape the composition of communities, acting at different spatial scales (Gravel et al. 2006; Legendre et al. 2009; Lindo & Winchester 2009).

Beta diversity (Whittaker 1960, 1972), i.e. the variation in species composition between communities, can be analyzed in relation to environmental factors or in relation to space itself (Borcard & Legendre 2002; Dray et al. 2006). However, the understanding of the relative contribution of each set of variables that might be responsible for generating beta diversity is complicated by the fact that different environmental and spatial processes can produce the same patterns in communities, especially as the environment is often structured in space (Borcard et al. 1992; Veech & Crist 2007). Additionally, changes in spatial scale can alter the perception of the processes related to community assembly (Laliberté et al. 2009; Carvalho et al. 2011; Lewis et al. 2014). Thus, to evaluate the relative contribution of processes determining beta diversity related to the Niche and to the Neutral theory for species assembly, diversity has to be studied at different scales.

Grasslands are a very useful model system to study community assembly patterns (Öpik et al. 2014). Both disturbances (such as fire and grazing, e.g. Overbeck et al. 2005) and environmental conditions (such as climatic factors, soil properties and topography, e.g. Anderson et al. 2007) have been identified as drivers of differences in species composition, on different spatial scales. Here, we used grasslands communities in the coastal plain in southern Brazil as a model system to investigate the relative importance of environmental and spatial processes at different spatial scales. The South Brazilian coastal grasslands are one of the most threatened formations of the Pampa biome: today they cover only 11% of their original extension (Cordeiro & Hasenack 2009). Coastal grasslands extend over a continuous region characterized by predominantly sandy soils, spanning over more than 500 km along the South Brazilian coastline. The coastal plain has been formed by geologic events of forward and regression movements of the ocean (Villwock & Tomazelli 1998) and formed a region with grasslands interspersed with lagoons, wetlands and forest patches. The relatively uniform edaphic characteristic of the grasslands makes the region an especially interesting area for analyses of community assembly rules. Changes in floristic composition can be perceived along the latitudinal gradient, despite the almost lack of variation in soils related to the geological matrix. Based on this, we hypothesized that spatial variables would be the most important factors shaping grasslands communities at the coastal plain. However, we did expect to be able to also detect effects of variation in local soil conditions on vegetation composition at a finer scale.

In species rich plant communities, such as subtropical grasslands, we can expect that different species, or species groups, react to environmental filters in different ways. Also, species distribution in space may vary in consequence of differences in dispersal ability (Levine & Murrell 2003). In addition to the principal objective stated above, we were interested in testing if and to what extent different species groups showed different responses to spatial and environmental factors when compared to the entire community. We investigated the relationship between spatial patterns observed for species with effective (i.e. long distance) dispersal, such as anemochory (Thomson et al. 2010), and not very effective dispersal (e.g. autochory) in relation to spatial and environmental variables. We hypothesized to find a higher relationship of species with good dispersal mechanisms to environmental variables, as the establishment of these would be limited only by the action of climate or soil conditions, while species with low dispersive ability should be more related to spatial variables, as an effect of dispersal limitation.

MATERIAL AND METHODS

Study area

We sampled 16 grassland sites distributed along a 536 km gradient at Brazilian's southern coast (Fig. 1), in the states of Santa Catarina (SC, 4 sites) and Rio Grande do Sul (RS, 12 sites). Sample sites had an average size of 3.3 ha. Main criteria for selection were presence of natural grasslands, without influence of higher soil water levels (i.e., wetlands were excluded). Climate of the region varies with mean precipitation of 1343 mm and mean temperature of 19.1° C in the northern part of the gradient and mean precipitation of 1220 mm and mean temperature of 17.6° C in the extreme south (Hijmans et al. 2005).

It is well known that current and past management, such as grazing intensity, fire and past agricultural uses also contribute to community assembly in grasslands, however our main objective was not to test the influence of management, but the action of environmental and spatial variables. Therefore, we selected areas under similar management, i.e. cattle grazing at similar intensity, and avoided areas where vegetation patterns were conspicuously different due to differences in management.

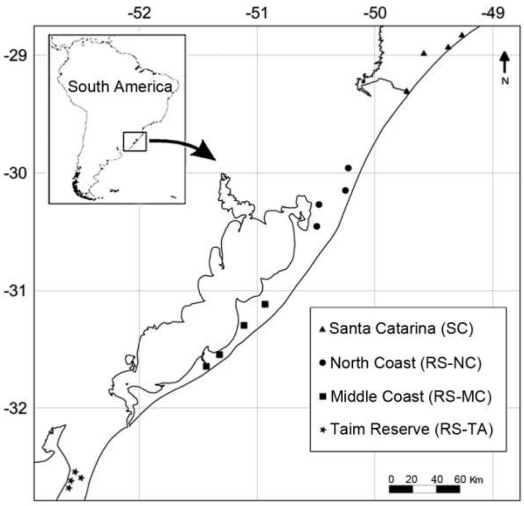

Figure 1: Location of the 16 sampling sites of grassland vegetation in the coastal plain in southern Brazil. The four sampling zones delimitated for this study are indicated by different symbols.

Vegetation sampling

Sampling was performed during southern hemisphere spring and summer in 2012 and 2013, when a large percentage of the plants are flowering. Species composition data was obtained in 15 plots of one square meter per site, distributed randomly. In each plot, all vascular plant species were identified and had their cover estimated by Londo's (1976) decimal scale. When necessary, samples were collected for posterior identification. Morphospecies that could not be identified to the species level (less than 1% of total species) and exotic species that are commonly planted to feed cattle (less than 0.02% of total species and 0.01% of relative cover), were removed from the matrix for the statistical analysis. Mean cover values of species per site were used for all statistical analysis, composing the response matrix Y.

Environmental variables

Climate data was obtained from the WorldClim database (Hijmans et al. 2005). The variables were: annual mean temperature; mean diurnal range of temperature; isothermality; temperature seasonality; max temperature of warmest month; min temperature of coldest month; temperature annual range; mean temperatures of wettest and driest quarters; mean temperatures of warmest and coldest quarters; annual precipitation; precipitations of wettest and driest months; precipitation seasonality; precipitation of wettest and driest quarters; and precipitation of warmest and coldest quarter. One value of each variable was taken per site to compose the explanatory matrix of climate variables, henceforward called '*Clim*'.

Four random samples of soil (depth: 20 cm) were collected per site and mixed together to one composed soil sample used for chemical and physical analysis, following methods described in Tedesco et al. (1995). Analyzed variables of soil were: clay (%); organic matter (%); SMP index; pH; phosphorus (mg/dm^3); potassium (mg/dm^3); sodium (mg/dm^3); zinc (mg/dm^3); copper (mg/dm^3); boron (mg/dm^3); manganese (mg/dm^3); exchangeable aluminum (cmol$_c$/dm^3), calcium (cmol$_c$/dm^3) and magnesium (cmol$_c$/dm^3); aluminum + hydrogen (cmol$_c$/dm^3); cation exchange capacity (cmol$_c$/dm^3); saturations of bases and aluminum (%); and the ratios calcium/magnesium, potassium/calcium, magnesium/potassium. At each site, 30 measures of soil bulk density were taken (sampled along three parallel transects of 100 m, with one measuring point at every 10), by help of an impact penetrometer. The mean value of all 30 measures was used as representative of soil bulk density for the area. Together, mean values for each of the total 22 soil variables made up the explanatory matrix of soil data, called '*Soil*'.

Spatial variables

Spatial structure was explored using principal coordinates of neighbor matrices (PCNM) (Borcard & Legendre 2002), now called Moran's Eigenvector Maps (MEM) (Borcard et al. 2011). MEM variables are well known for their capability to capture spatial trends at different range of scales (Borcard & Legendre 2002; Dray et al. 2006). For producing the MEM variables, we constructed a matrix of UTM coordinates of the sites, which was used to build a Euclidean distance matrix truncated at the smallest distance that keeps all points connected in a single network. Then a principal coordinate analysis was carried out, and the eigenvectors associated with positive eigenvalues were retained as spatial variables, composing the matrix here called '*MEM*'.

Analytical procedures

The response matrix of mean cover of species per area (Y) was Hellinger transformed (Y_H) (Legendre & Gallagher 2001). In addition to using the full Y_H

matrix, we also built matrices with species belonging only to Asteraceae (good long distance dispersal) and Poaceae (poor long distance dispersal) families, composing Y_{Poa} and Y_{Ast} matrices, also Hellinger transformed.

For summarizing the information contained in climate and soil matrices (*Clim* and *Soil*), we ran principal components analysis (PCA) for each matrix. The axes produced at ordination that added up more than 70% of variation in each data were extracted to compose matrices PC_{Clim} and PC_{Soil}.

To select only the most correlated and significant variables that better explained variation in the response data we ran forward selection procedures on the explanatory matrices (PC_{Clim}, PC_{Soil} and *MEM*) (Blanchet et al. 2008). This proceeding uses two stopping criteria, alpha and R^2. For all proceedings we adopted the criteria alpha=0.1, while the R^2 threshold varied according to the response matrix: Y_H=0.54, Y_{Ast}=0.60 and Y_{Poa}=0.50. The value of R^2 adopted corresponds to the R^2 of the global model (i.e. model with all explanatory variables) to each response matrix. The selected variables were used to compose the final explanatory matrices of environmental variables (X_{Soil} and X_{Clim}) that together compose the complete environmental matrix (X_{Env}). The final explanatory matrix of spatial variables (X_{MEM}) was discriminated into the three first MEMs representing the spatial variation in broad scale ($X_{MEMbroad}$), and the one last vector representing the spatial variation in fine scale ($X_{MEMfine}$).

Variation partitioning procedures (Legendre & Legendre 2012) were used to verify the magnitude of influence of each set of explanatory variables on the variation of the response data. Fractions produced by variation partitioning represent specifically: [a] explanation of the first explanatory matrix introduced in the analysis; [c] explanation of the second explanatory matrix; [b] joint effect of both explanatory matrices; [a+b] total variance explained by first explanatory matrix plus the joint effect; [c+b] total variance explained by second explanatory matrix plus the joint effect; [a+b+c] total variance explained; and [NE] variance that could not be explained. Significance level of all fractions can be tested, except for fractions [b] and [NE] (Peres-Neto et al. 2006).

We ran three variation partitioning procedures on the total community matrix (Y_H): first to discern between the influence of environment (X_{Env}) and space (X_{MEM}); second to specify the influence of discriminated environmental variables (X_{Clim} and X_{Soil}); and last to specify the influence of broad-scale ($X_{MEMbroad}$) and fine-scale ($X_{MEMfine}$) spatial variables.

Additionally, in order to ascertain the relative importance of specific environmental variables (soil and climate) on the variation in vegetation composition on broad and fine spatial scales, we build scale-specific additive spatial models (Laliberté et al. 2009). The scale-specific additive spatial models were obtained by first conducting two simple RDA between the species matrix (Y_H) and the spatial scale-specific matrices ($X_{MEMbroad}$ and $X_{MEMfine}$). The axes of these canonicals ordinations were then extracted to compose matrices that contain the information of species composition weighted by the specific spatial scale (Y_{broad} and Y_{fine}). Then, two new variation partitioning procedures were made involving X_{Clim} and X_{Soil} as explanatory matrices, to verify the influence of climate and soil on species variation at broad and fine spatial scales.

To test our hypothesis that high dispersal species are more limited by environmental factors, while low dispersal species are mostly related to spatial variables, we used Asteraceae and Poaceae families composition matrices (Y_{Ast} and Y_{Poa}) as a proxy for the high and low dispersal capability, respectively. To infer the relative contribution of environmental and spatial processes to the patterns in Y_{Ast} and Y_{Poa} we ran another two variation partitioning procedures.

Ordinations of environmental variables for producing the axes used as explanatory variables were performed in Multiv (Pillar 1997). Variation partitioning and MEM analysis were performed in R platform (R Core Team, 2013), using package ‘vegan’ (Oksanen et al. 2012). Package ‘packfor’ (Blanchet et al. 2008) was used to perform the forward selection. A scheme of the matrices used for which analyses can be found in supporting material Fig.1.

RESULTS

A total of 221 species of phanerogams from 40 families were identified until the species level. Poaceae was the most abundant family (53 species), followed by Asteraceae (45 species). Three exotic Poaceae were removed from the matrix (*Brachiaria brizantha*, *Melinis minutiflora* and *Eragrostis plana*), as they are introduced for forage use in the region. Detailed information on species composition and overall floristic patterns is given in Menezes et al. (unpubl., see also Tab. 5 in supporting material).

The first six axes of the ordination of climatic variables accounted for about 95% of the variation in the data and the first seven soil PCA axes for over 75%. These variables were subjected to forward selection, resulting in the selection of axes 1, 2 and 3 of climate and soil axis 1 (Tab. 1), representing more than 90% of climate variation and about 49% of soil variation. Together, the four selected environmental axes composed the matrix of environmental explanatory variables (PC_{Env}). Sixteen positive eigenvectors of MEMs were produced, from which forward selection for Y_H choose vectors 1, 2, 3, composing the matrix of broad spatial scale ($X_{MEMbroad}$), and vector 11 which represents the spatial variation on a fine scale ($X_{MEMfine}$).

Table 1: Environmental and spatial axes selected by forward selection (response matrix: the total community composition Y_H). Variables with highest correlation with each axis are given. Axes have been selected after 999 permutations, with criteria: $R^2>0.54$ and not exceeding alpha=0.1. Graphical representation of each selected explanatory variable is presented in supporting material Fig. 2. ‘***’p<0.001; ‘**’p<0.01; ‘*’p<0.05; ‘·’p<0.1.

Selected axes	Correlated variables (r^2)	Adjusted R^2
PCclim1	Temp. coldest quarter(0.98) Mean temp.(0.97) Precip. warmest quarter(0.95) Precip. wettest month(0.94) Precip. wettest quarter(0.91)	0.08**
PCclim2	Temp. range diurnal (-0.88) Precip. seasonality (-0.86) Precip. coldest quarter (0.85) Precip. driest quarter (0.78) Isotermality (-0.69)	0.12**
PCclim3	Temp. max month(-0.75) Temp. warmest quarter(-0.71) Temp. annual range (-0.48) Precip. coldest quarter(-0.43) Temp. seasonality(-0.40)	0.07*
PCsoil1	Cation exchange capacity(-0.98) Ca-0.97) Mg(-0.95) Base saturation(-0.93) Organic matter(-0.89)	0.08*
MEM1	Broad scale	0.08***
MEM2	Broad scale	0.16***
MEM3	Broad scale	0.03 ·
MEM11	Fine scale	0.06 *

Climatic axes presented a latitudinal structure, especially PCclim2 and PCclim3. PCclim2 represented an inverse gradient of climatic seasonality, with less seasonal areas in the North and more seasonal areas in the South. PCclim3 showed a gradient of maximum temperature, with higher values in the North and lower values in South. PCclim1 captured the variance of winter temperatures, higher at the northern part of the gradient, and the stronger seasonality of temperatures in the South. PCsoil1 was able to capture pronounced differences regarding some of the soil variables in two sample units in the South. When compared to the other sampling areas this strong variance lead us to believe that those areas may have some history of agricultural use (see details of soil variables in supporting material Tab. 6). Spatial vectors 1, 2 and 3 captured the spatial variation along the entire gradient, or broad scale, while MEM 11 captured specifically local spatial variance at the south part of the gradient, or fine scale.

The biggest part of the variation that could be explained in the species composition matrix (Y_H) was related to the shared effect of environment (X_{Env}) and space (X_{MEM}) (22%, Fig. 2A). Percentage of variation explained by environmental factors alone was little higher than that explained by spatial variables alone (13% and 11%, respectively). The total environmental fraction ([a+b], 35%), when discriminated between climate (X_{Clim}) and soil (X_{Soil}), showed that the biggest part of the species variation (28%) was related to climatic factors (Fig. 2B). Also, most of the species composition variation was related to broad-scale spatial factors (29%, Fig. 2C).

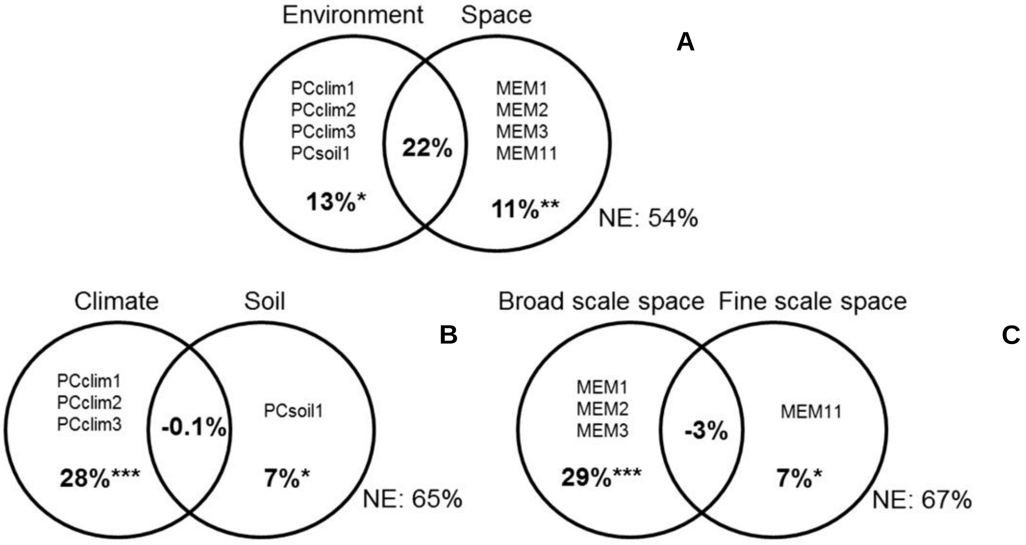

Figure 2: Variation partitioning procedures explaining the variance in the entire community data table (Y_H) by: (A) environment (X_{Env}) and space (X_{MEM}); (B) climate (X_{Clim}) and soil (X_{Soil}); (C) specific-scale spatial variables ($X_{MEMbroad}$ and $X_{MEMfine}$). Complete variation partitioning table are presented in supporting material Tab. 1. '***'p<0.001; '**'p<0.01; '*'p<0.05.

When dissecting the environmental variables on species composition constrained in each spatial scale, we could observe that most variation at the broad scale was related to climatic factors (51%) (Fig. 3), while the variance at the fine scale was more strongly related to changes in edaphic characteristics (87%).

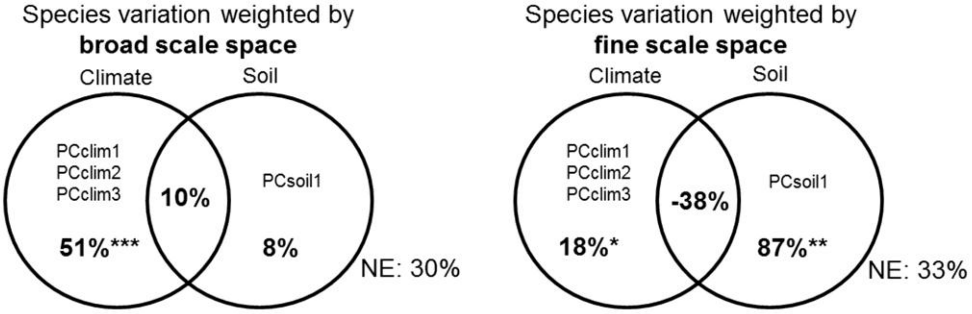

Figure 3: Relative contribution of climate (X_{Clim}) and soil (X_{Soil}) to the variation of grassland vegetal community weighted by scale-specific spatial variables (Y_{broad} and Y_{fine}). Complete variation partitioning table are presented in supporting material Tab. 2. ‘***’p<0.001; ‘**’p<0.01; ‘*’p<0.05.

The forward selection procedure for specific families as response matrices resulted in the selection of four environmental variables and four spatial variables for Poaceae, and five environmental variables and three spatial variables for Asteraceae (Tab. 2). PCsoil5 captured mainly variation in phosphor content in the soil along the gradient (corr. -0.86), and PCsoil6 was mainly related to variance in soil bulk density (corr. 0.46).

Table 2: Environmental and spatial axis selected by forward selection for Poaceae and Asteraceae families. Axes have been selected after 999 permutations, with criteria: $R^2>0.5$ for Y_{Poa} and $R^2>0.6$ for Y_{Ast}, and don't exceeding alpha=0.1. Graphical representation of each selected explanatory variable is presented in supporting material Fig.2 and Fig.3. ‘***’p<0.001; ‘**’p<0.01; ‘*’p<0.05; ‘·’p<0.1.

Poaceae		Asteraceae	
Selected axis	**Adjusted R²**	**Selected axis**	**Adjusted R²**
PCclim1	0.10 **	PCclim1	0.07 **
PCclim2	0.17 **	PCclim2	0.04 ·
PCclim3	0.09 **	PCsoil1	0.05 *
PCsoil1	0.09 **	PCsoil5	0.06 *
MEM1	0.08 **	PCsoil6	0.04 ·
MEM2	0.23 ***	MEM1	0.06 ·
MEM3	0.03 ·	MEM2	0.04 ·
MEM11	0.06 *	MEM3	0.04 ·

The major part of variation in Poaceae species composition was explained by the shared effect of environment and space (30%, Fig. 4), followed by the pure environmental effect, explaining 14%. The variation in Asteraceae species composition was explained mostly by environmental variables (13%), while there was no significant explanation by spatial variables alone to the species composition of this family.

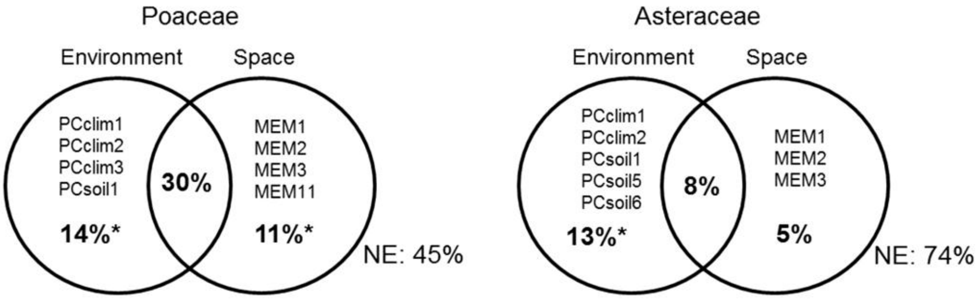

Figure 4: Relative contribution of environmental and spatial variables to the variation in the specific families' species composition matrices: Poaceae (Y_{Poa}) and Asteraceae (Y_{Ast}). Complete variation partitioning table are presented in supporting material Tab. 3 '*'p<0.05.

DISCUSSION

This study aimed to investigate the determinants of beta diversity patterns in coastal grassland vegetation along a latitudinal gradient in southern Brazil, by partitioning the variation of total plant community composition and of two specific groups of species with different dispersal characteristics (Asteraceae and Poaceae) between environmental and spatial factors. Our results showed that almost half of the variation in the entire community of coastal grassland vegetation could be explained by environmental and spatial variables (46%). The major proportion was explained by the shared component (22%), which is not surprising since environmental variables are typically space structured (Bell et al. 1993), making it in fact difficult to discern between effects of niche processes (environmental explanation) and spatial processes (Gilbert & Lechowicz 2004; Bell et al. 2006).

The structuring of environment on space is even more outstanding when we see the similarity in percentage of variance explained specifically by climate (28%) and explained by the broad-scale space (29%). We tested, separately, how much of climatic explanation and broad-scale space explanation were shared (see this additional result in supporting material, Tab. 4), and we found that a great proportion of the explanation (20%, from total 33% explained) was due to the shared component. This means that the climatic gradient clearly seems to be one of the main factors responsible for generating spatial trends in our data (or vice versa), even though the latitudinal structure does not apply to all climatic variables or axes extracted by PCA.

Predominance of niche processes, related to environmental variables, has previously been pointed out for assembly of plant communities (Gilbert & Lechowicz 2004; Anderson et al. 2007; Laliberté et al. 2009). However, in our study, we found little difference between the pure environmental explanation and pure spatial explanation, with values of 13% and 11% respectively. It is important to highlight that the spatially-structured environment fraction might contain the effect of some spatial processes that show random correlation with the environment (Bell et al. 2006), while spatial explanation alone might contain the effect of some unmeasured environmental variables (Borcard & Legendre 1994). Due to the very small difference between pure environmental and pure spatial explanation it is not possible to conclude that either niche or spatial processes are of predominance for the entire community assembly.

We observed much clearer and stronger patterns when we partitioned the variance of species composition matrices weighted by specific-scale spatial variables, i.e. used scale-specific additive spatial models, with the climate and soil matrices as explanatory matrices. On the broad scale, climate was responsible for 51% of the variation. Soil did not exercise much influence on the vegetation of coastal grasslands at the broad scale (only 8%), which is a consequence of the geological homogeneity of the entire region. At the finer spatial scale, we observed exactly the opposite: soil presented a very high explanation, 87% of total explained. This is related to the differences in edaphic characteristics captured by PCsoil1, since the correlation between MEM11, that represented the fine spatial scale, and PCsoil1 was quite high (0.60). This highlights the importance of soil variables on distribution of plant species and thus diversity patterns at finer scales (e.g. Janssens et al. 1998).

Altogether, the assembly of the entire community could be explained mainly by spatially structured environmental variables and by climatic processes at the broad scale and by edaphic variables at the fine scale, i.e. by a combination of different processes at different spatial scales. However, we know that species differ in their reaction to environmental and spatial processes as a consequence of their specific biological adaptations, i.e. they will differ in regard to their capacities to overcome some of these filters, and different species will be more (or less) efficient in this than others, depending on the specific filter (trade-off features) (Grime 2001). Likewise, spatial processes, as dispersal limitation and stochastic colonization (or mortality), can affect different species more or less depending on their biological attributes, thus generating different patterns of beta diversity for different groups of species. Taxonomically closely related species often show similar functional characteristics and thus respond in similar ways to specific processes or factors, even more so when considered traits that are related to reproduction and dispersal, i.e. phylogenetically conserved (Chazdon et al. 2003; Donoghue 2008), making plant family membership a good proxy for studies on dispersal limitation (Gilbert & Lechowicz 2004).

Based on this, we tested the relative importance of the same underlying processes and factors analyzed on the total community for two families with distinct dispersal abilities, Asteraceae and Poaceae. As hypothesized, the assembly of Asteraceae species, which mostly have an efficient dispersal by anemochory, can reach sites along the entire gradient. Only a rather small fraction of total variation was explained by environmental characteristics (13%). The assembly of Poaceae species, in contrast, showed a higher pure spatial explanation than Asteraceae (11% and 5%, respectively), which can be explained by some more limited dispersal of the species from Poaceae family, generating more perceptible spatial patterns. In fact, besides the dispersal by seeds, the production of new tillers in tussock species and the expansion by rhizomes are important mechanisms for local maintenance and growth of populations of grass species (Williams & Cheplick 1999). Once dispersed and established, species with such similar traits seems to stay on the site by being highly competitive at local scale, which results in a spatially structured pattern.

Approaches that consider the entire community composition and thus contribute to disentangling community assembly processes will, in fact, only obtain a general response that is mainly influenced by the dominant species or species groups in the community. This last point becomes clear when we observe the similar responses obtained when partitioning the entire community variation and when using only species from the Poaceae family, as Poaceae is the dominant group in terms of plant cover in our survey. Accessing the processes acting on different components of the community, i.e. different groups of species that may respond similarly to these processes, likely will increase our understanding on community assembly.

In some of the variation partitioning procedures realized in this study, a great part of the variation in composition could not be explained, which is quite common in studies of this kind, irrespective the organisms of interest (Carvalho et al. 2011). In the case of grassland vegetation, especially management and management history are known to be important in assembly of plant communities, such as fire and grazing regimes (Overbeck et al. 2005; Lewis et al. 2014), but were not included in this study. Minor differences among the management history of the sites might contribute to the unexplained variation, however, due to both relatively similar soil conditions and colonization history of the region, we do not expect that the management history of our sites varied greatly, with the exception of two sites that may have had some history of agricultural use. Additionally, other unmeasured environmental variables, or the effect of species interaction may be some reasons for the large proportion of the unexplained variation.

Altogether, we were able to explain a high proportion of the variation in plant species composition of the studied coastal grasslands. Structuring of the environmental variables in space was quite evident, as well as the similar explanation of climate and large-scale spatial factors. The approach of scale-specific additive spatial models proved to be effective and allowed us to detect the effect of an anthropogenic change at two sites in the southern part of the gradient, in fine scale. We also observed that groups of species with different ecological characteristics show contrasting patterns in relation to the investigated factors. Future studies that seek to explain changes in diversity (i.e. beta diversity) along gradients thus should work with combinations of different spatial scales and different species groups in order to rightly ascertain the magnitude of processes that shape extant communities.

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List of Supporting Material with shortened captions:

Figure 1: Scheme of the statistical procedure realized for obtain the matrices used for which analyses.

Figure 2: Distribution of values of environmental and spatial axes selected through forward selection.

Figure 3: Distribution of values of environmental axes selected through forward selection using as response matrices Y_{Poa} and Y_{Ast}.

Table 1: Adjusted R² value and p significance interval for the fractions produced at the variation partitioning procedures for the entire community response matrix (Y_H). Letters codes ‘A’, ’B’ and ‘C’ follow Fig. 3 in text.

Table 2: Adjusted R² value and p significance interval for the fractions produced at the variation partitioning procedures for the scale-specific additive models (Y_{broad} and Y_{fine}).

Table 3: Adjusted R² value and p significance interval for the fractions produced at the variation partitioning procedures of Poaceae and Asteraceae (Y_{Poa} and Y_{Ast}).

Table 4: Adjusted R² value and p significance interval for the fractions produced at the variation partitioning procedures for the entire community response matrix (Y_H), considering the effects climate (X_{Clim}) and broad scale space ($X_{MEMbroad}$). **Table 5:** Species primary data.

Table 6: Soil primary data.
Table 7: Climatic primary data.

Supporting Material to the paper Menezes, L.S.; Muller, S.C.; Overbeck, G.E. Scale-specific processes shape plant community patterns in subtropical coastal grasslands. Journal of Vegetation Science.

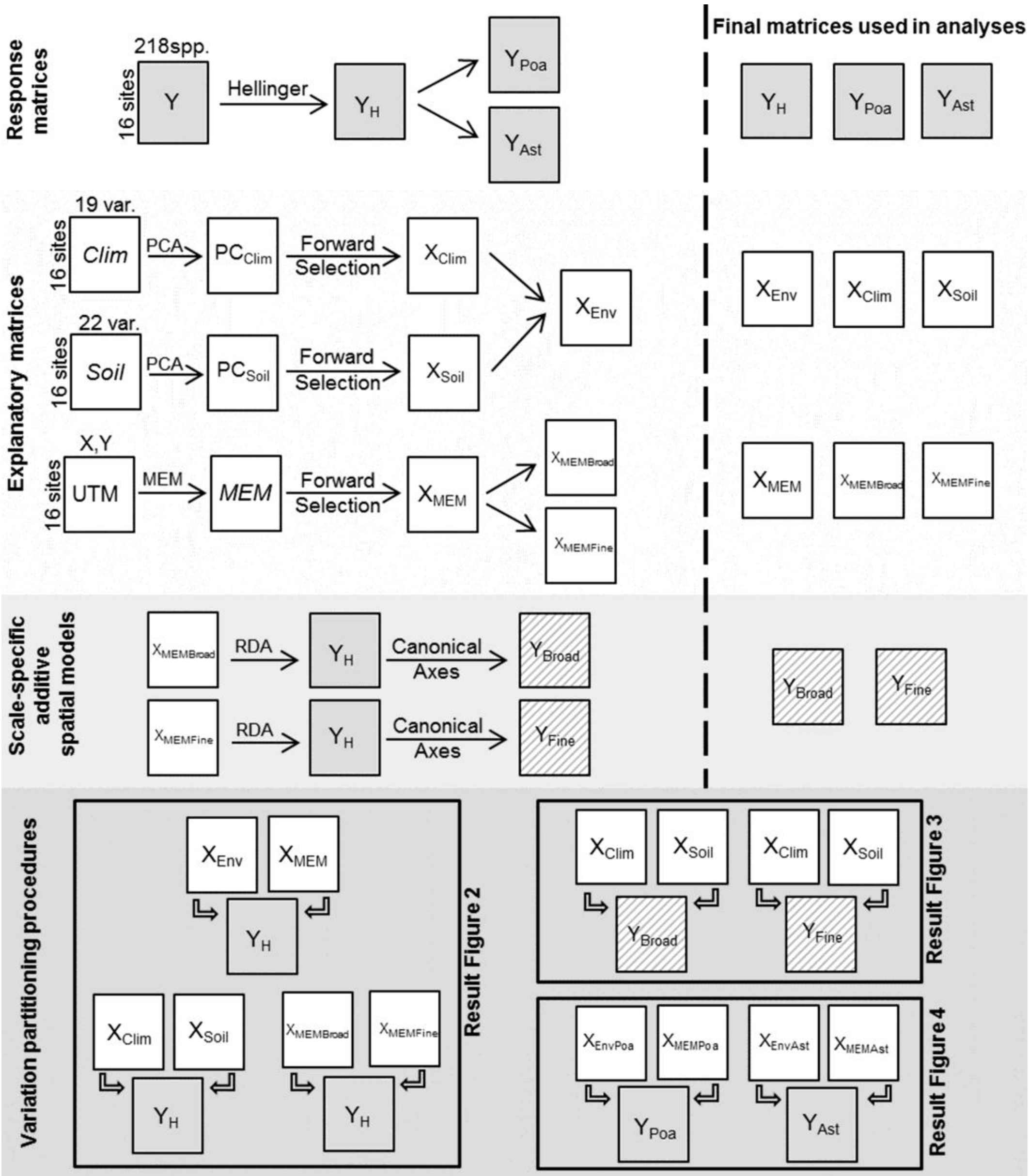

Figure 1: Scheme of the statistical procedure realized for obtain the matrices used for which analyses, including indication of the figures (in the text) that present the result of the analyses.

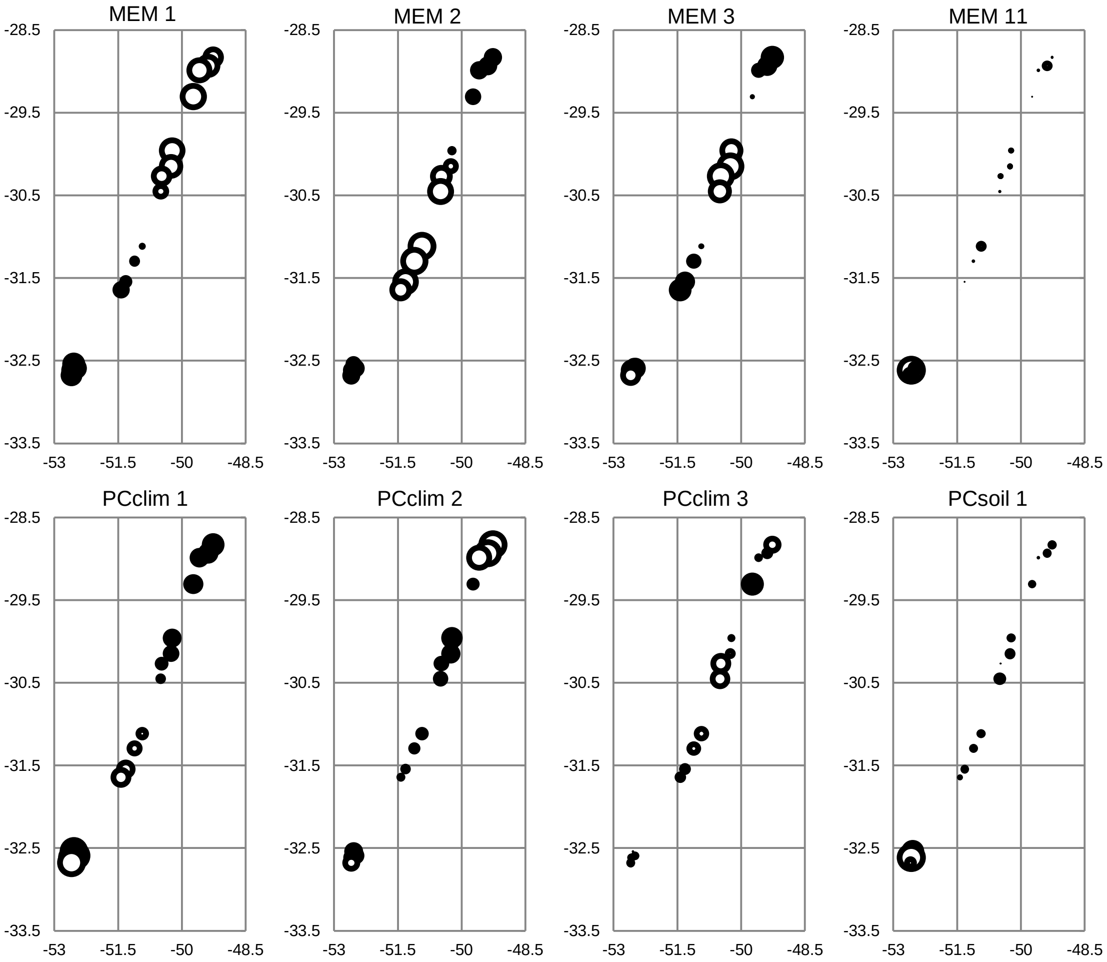

Figure 2: Distribution of values of environmental and spatial axes selected through forward selection. Numbers are the true geographical coordinates, in decimal degrees. Black circles represent positive values, hollow circles represent negative values. Sizes of the circles indicate the magnitude of the variable.

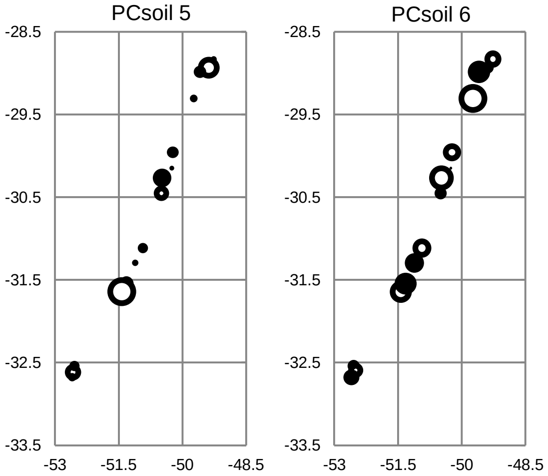

Figure 3: Distribution of values of environmental axes selected through forward selection using as response matrices Y_{Poa} and Y_{Ast}. Numbers are the true geographical coordinates, in decimal degrees. Black circles represent positive values, hollow circles represent negative values. Sizes of the circles indicate the magnitude of the variable.

Table 1: Adjusted R^2 value and p significance interval for the fractions produced at the variation partitioning procedures for the entire community response matrix (Y_H). Letters codes ‘A’, ’B’ and ‘C’ follow Fig. 3 in text. Fractions represent: [a] percentage of explanation of first explanatory matrix; [c] percentage of explanation of second explanatory matrix; [b] joint effect; [a+b] total variance explained by first explanatory matrix plus the joint effect; [c+b] total variance explained by second explanatory matrix plus the joint effect; [a+b+c] total variance explained; and [NE] variance that could not be explained. [1]Fractions cannot be tested. ***p<0.001; **p<0.01; *p<0.05; ‘·’p<0.1.

	[a]	**[c]**	**[b][1]**	**[a+b]**	**[c+b]**	**[a+b+c]**	**NE[1]**
A: X_{Env}[a] X_{MEM}[c]	0.13 *	0.11 **	0.22	0.35 ***	0.33 ***	0.46 ***	0.54
B: X_{Clim}[a] X_{Soil}[c]	0.28 ***	0.07 *	-0.001	0.27 ***	0.07 *	0.35 ***	0.65
C: $X_{MEMbroad}$[a] $X_{MEMfine}$[c]	0.29 ***	0.07 *	-0.03	0.26 ***	0.04	0.33 ***	0.67

Table 2: Adjusted R^2 value and p significance interval for the fractions produced at the variation partitioning procedures for the scale-specific additive models (Y_{broad} and Y_{fine}). Fractions represent: [a] percentage of explanation of first explanatory matrix; [c] percentage of explanation of second explanatory matrix; [b] joint effect; [a+b] total variance explained by first explanatory matrix plus the joint effect; [c+b] total variance explained by second explanatory matrix plus the joint effect; [a+b+c] total variance explained; and [NE] variance that could not be explained. [1]Fractions cannot be tested. ***p<0.001; **p<0.01; *p<0.05; ‘·’p<0.1.

	[a]	**[c]**	**[b][1]**	**[a+b]**	**[c+b]**	**[a+b+c]**	**NE[1]**
Broad: X_{Clim}[a] X_{Soil}[c]	0.51 ***	0.08 ·	0.10	0.61 ***	0.18 ***	0.70 ***	0.30
Fine: X_{Clim}[a] X_{Soil}[c]	0.18 *	0.87 **	-0.38	-0.19	0.49 *	0.67 *	0.33

Table 3: Adjusted R^2 value and p significance interval for the fractions produced at the variation partitioning procedures of Poaceae and Asteraceae (Y_{Poa} and Y_{Ast}). Fractions represent: [a] percentage of explanation of environment alone; [c] percentage of explanation space alone; [b] joint effect; [a+b] total variance explained by environment plus the joint effect; [c+b] total variance explained by space plus the joint effect; [a+b+c] total variance explained; and [NE] variance that could not be explained. [1]Fractions cannot be tested. ***p<0.001; **p<0.01; *p<0.05; ‘·’p<0.1.

	[a]	**[c]**	**[b][1]**	**[a+b]**	**[c+b]**	**[a+b+c]**	**NE[1]**
Poaceae	0.14 *	0.11 *	0.30	0.44 ***	0.41 ***	0.55 ***	0.45
Asteraceae	0.13 *	0.05	0.08	0.21 ***	0.13 **	0.26 ***	0.74

Table 4: Adjusted R^2 value and p significance interval for the fractions produced at the variation partitioning procedures for the entire community response matrix (Y_H), considering the effects climate (X_{Clim}) and broad scale space ($X_{MEMbroad}$). Fractions represent: [a] percentage of explanation of climate alone; [c] percentage of explanation broad scale space alone; [b] joint effect; [a+b] total variance explained by climate plus the joint effect; [c+b] total variance explained by broad scale space plus the joint effect; [a+b+c] total variance explained; and [NE] variance that could not be explained. [1]Fractions cannot be tested. ***p<0.001; **p<0.01; *p<0.05; ‘·’p<0.1.

	[a]	**[c]**	**[b][1]**	**[a+b]**	**[c+b]**	**[a+b+c]**	**NE[1]**
X_{Clim}[a] $X_{MEMbroad}$[b]	0.07 ·	0.06 ·	0.20	0.27 ***	0.26 ***	0.33 ***	0.67

Table 5: Matrix of species mean cover per site (Y) utilized in variation partitioning procedures. Species deliberately introduced for cattle grazing (*Brachiaria brizantha*, *Melinis minutiflora* and *Eragrostis plana*) were removed, as we understood that their distribution is much more strongly influenced by human action than that of the other species.

Families / Species	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Amaranthaceae																
Chenopodium ambrosioides L.	0.007															
Gomphrena perennis L.	0.007			0.067	0.027									0.007		
Pfaffia tuberosa (Spreng.) Hicken				0.047			0.007							0.007		
Amaryllidaceae																
Nothoscordum bivalve (L.) Britton							0.013									
Apiaceae																
Centella asiatica (L.) Urb.		0.080		0.073	0.207	0.200	0.053	0.033	0.280	0.607	0.187	0.240	0.040	0.080	1.093	0.140
Cyclospermum leptophyllum (Pers.) Sprague ex Britton & P. Wilson		0.007	0.007					0.020		0.007			0.013		0.013	
Eryngium horridum Malme							0.013	0.020								
Eryngium nudicaule Lam.			0.013			0.120	0.333	0.227	0.060		0.033	0.020		0.013		0.060
Eryngium sanguisorba Cham. & Schltdl.							0.013	0.007	0.153	0.060		0.033		0.040		
Apocynaceae																
Asclepias mellodora A.St.-Hil.	0.013												0.007			
Mandevilla pinifolia (A.St.-Hil.) Miers					0.007		0.007									
Oxypetalum arnottianum H. Buek	0.007			0.007												
Araliaceae																
Hydrocotyle bonariensis Lam.		0.293		0.013		0.020		0.013	0.027	0.013	0.013	0.067	0.033			0.033
Hydrocotyle exigua Malme		0.007				0.053	0.040		0.033	0.007	0.007	0.013	0.007			0.047
Hydrocotyle ranunculoides L.f.			0.020						0.013							

(sequence)

Families / Species	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Asteraceae																
Acanthospermum australe (Loefl.) Kuntze	0.027	0.007			0.007											
Ambrosia artemisiaefolia L.													0.013			
Aspilia montevidensis (Spreng.) Kuntze	0.007													0.013		
Baccharis articulata (Lam.) Pers.					0.007	0.007										
Baccharis gnaphalioides Spreng.														0.013		
Baccharis leucopappa DC.														0.007		
Baccharis megapotamica Spreng.							0.013									
Baccharis spicata (Lam.) Baill.				0.027									0.007			
Baccharis trimera (Less.) DC.					0.040	0.160	0.060	0.007	0.087	0.207	0.007		0.020	0.013		0.113
Chaptalia piloselloides (Vahl) Baker								0.007		0.027						
Chaptalia runcinata Kunth		0.013	0.007							0.013	0.013					0.013
Chaptalia sinuata (Less.) Baker		0.013	0.007													
Chevreulia acuminata Less.						0.013	0.007									
Chevreulia sarmentosa (Pers.) Blake			0.007			0.047	0.047			0.013	0.027	0.020	0.020		0.007	
Chrysolaena flexuosa (Sims) H.Rob.								0.013		0.020						
Conyza bonariensis (L.) Cronquist	0.013	0.007	0.007			0.020	0.040		0.013	0.013		0.007				
Conyza primulifolia (Lam.) Cuatrec. & Lourteig			0.020		0.013	0.047	0.020	0.007		0.013	0.013					0.013
Elephantopus mollis Kunth			0.007													
Eupatorium ascendens Sch. Bip. ex Baker		0.007														
Facelis retusa (Lam.) Sch. Bip.			0.040					0.007							0.007	
Gamochaeta americana (Mill.) Wedd.	0.040	0.040	0.033	0.033	0.013	0.067	0.027	0.067	0.053	0.033	0.033	0.047	0.093	0.027	0.053	0.060
Gamochaeta coarctata (Willd.) Kerguélen					0.013							0.013				

(sequence)

Families / Species	**SC1**	**SC2**	**SC3**	**SC4**	**NC1**	**NC2**	**NC3**	**NC4**	**MC1**	**MC2**	**MC3**	**MC4**	**TA1**	**TA2**	**TA3**	**TA4**
Hypochaeris lutea (Vell.) Britton								0.020				0.007				
Hypochaeris megapotamica Cabrera								0.013								
Lucilia acutifolia (Poir.) Cass.	0.013			0.013										0.020		0.007
Lucilia nitens Less.	0.073					0.027	0.007									
Micropsis spathulata (Pers.) Cabrera							0.027	0.040								
Noticastrum calvatum (Baker) Cuatrec.	0.007	0.020				0.007		0.067			0.007	0.007		0.020	0.033	
Noticastrum gnaphalioides (Baker) Cuatrec.	0.020			0.013			0.013						0.007			
Orthopappus angustifolius Gleason		0.027	0.020													
Pterocaulon angustifolium DC.					0.067											
Pluchea oblongifolia DC.													0.013			
Pterocaulon alopecuroides (Lam.) DC.									0.020							
Pterocaulon lorentzii Malme	0.067	0.107		0.027	0.020	0.073	0.007			0.013						
Senecio brasiliensis (Spreng.) Less.				0.067												
Senecio crassiflorus (Poir.) DC.	0.220				0.007	0.013				0.020						
Senecio leptolobus DC.				0.013	0.007											
Senecio selloi (Spreng.) DC.									0.007				0.007			0.053
Soliva sessilis Ruiz et Pavón			0.007				0.013	0.013			0.007					
Sommerfeltia spinulosa (Spreng.) Less.				0.007		0.040	0.053	0.040								
Stenachaenium campestre Baker														0.007		
Stenachaenium megapotamicum (Spreng.) Baker		0.007				0.013							0.007			
Symphyotrichum squamatum (Spreng.) G.L.Nesom													0.007		0.067	0.013
Tanacetum vulgare L.		0.013														
Vernonanthura nudiflora (Less.) H.Rob.			0.013		0.027	0.147	0.893	0.007	0.020		0.007			0.013		0.013

(sequence)

Families / Species	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Boraginaceae																
Varronia curassavica Jacq.				0.013												
Brassicaceae																
Lepidium auriculatum Regel & Körn.							0.013	0.020								
Calyceraceae																
Acicarpha procumbens Less.	0.027	0.007		0.007	0.013			0.033								
Campanulaceae																
Lobelia hederacea Cham.									0.007	0.013		0.033	0.053		0.200	0.060
Wahlenbergia linarioides (Lam.) A.DC.	0.007															
Caryophyllaceae																
Cardionema ramosissima (Weinm.) A.Nelson & J.F.Macbr.	0.053	0.033	0.020	0.100	0.033	0.007	0.007	0.080			0.013			0.007		
Cerastium glomeratum Thuill.				0.007		0.040	0.073	0.027	0.007			0.007				
Drymaria cordata (L.) Willd. ex Roem. & Schult.			0.007													
Spergula arvensis L.								0.007								
Cistaceae																
Helianthemum brasiliense (Lam.) Pers.				0.007	0.027	0.007				0.053	0.020	0.007				
Commelinaceae																
Commelina diffusa Burm.f.				0.007			0.013							0.007		
Convolvulaceae																
Dichondra macrocalyx Meisn.						0.007			0.007							
Dichondra sericea Sw.						0.020	0.160	0.007	0.007				0.007			0.013
Evolvulus sericeus Sw.						0.020	0.027	0.007		0.013		0.007		0.007		
Cyperaceae																
Bulbostylis capillaris (L.) C.B. Clarke	0.067	0.033		0.020	0.027	0.060		0.040		0.020	0.027	0.007		0.093	0.127	

(sequence)

Families / Species	**SC1**	**SC2**	**SC3**	**SC4**	**NC1**	**NC2**	**NC3**	**NC4**	**MC1**	**MC2**	**MC3**	**MC4**	**TA1**	**TA2**	**TA3**	**TA4**
Bulbostylis juncoides (Vahl) Kük.		0.013			0.013											
Carex phalaroides Kunth							0.020									
Cyperus aggregatus (Willd.) Endl.	0.027	0.040		0.060	0.073	0.033			0.007	0.007	0.013			0.007		0.013
Cyperus hermaphroditus (Jacq.) Standl.							0.007	0.007								
Cyperus intricatus Schrad. ex Schult.									0.027							
Cyperus reflexus Vahl					0.007							0.020	0.013			0.040
Eleocharis bonariensis Nees															0.720	
Eleocharis flavescens (Poir.) Urb.															0.067	0.013
Eleocharis maculosa (Vahl) Roem. & Schult.									0.007	0.007	0.040					
Fimbristylis autumnalis (L.) Roem. & Schult.									0.013		0.007		0.013			0.007
Fimbristylis dichotoma (L.) Vahl													0.007			
Fimbristylis spadicea (L.) Vahl											0.013	0.007				
Isolepis cernua (Vahl) Roem. & Schult.											0.007					
Kyllinga brevifolia Rottb.		0.060	0.053	0.020		0.020	0.007	0.047	0.027	0.027	0.033	0.033	0.047			
Kyllinga odorata Vahl	0.007	0.193	0.187	0.033		0.020		0.047	0.107	0.173	0.073	0.273	0.033			0.073
Kyllinga vaginata Lam.									0.007				0.060			0.020
Pycreus polystachyos (Rottb.) P.Beauv.		0.027									0.007	0.007				
Rhynchospora barrosiana Guagl.					0.007	0.020			0.027	0.067	0.307			0.113		0.067
Rhynchospora brittonii Gale		0.007										0.007				
Rhynchospora tenuis Link		0.187			0.053	0.053		0.013	0.040	0.027	0.240			0.353		0.053
Scleria distans Poir.					0.007	0.033					0.047	0.007	0.013			
Droseraceae																
Drosera brevifolia Pursh.					0.007											

(sequence)

Families / Species	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Eriocaulaceae																
Eriocaulon modestum Kunth					0.067											
Euphorbiaceae																
Croton lanatus Lam.					0.333	0.173	0.727									
Dalechampia micromeria Baill.				0.007												
Euphorbia papillosa A.St.-Hil.				0.047	0.007	0.020	0.027	0.007								
Euphorbia selloi (Klotzsch & Garcke) Boiss.															0.047	
Fabaceae																
Aeschynomene falcata (Poir.) DC.	0.033	0.167				0.067		0.007	0.007							
Arachis burkartii Handro							0.053									
Chamaecrista nictitans (L.) Moench		0.007														
Chamaecrista rotundifolia (Pers.) Greene						0.013				0.007						
Desmodium adscendens (Sw.) DC.		0.080			0.027	0.073	0.067		0.147	0.107		0.107				0.020
Desmodium barbatum (L.) Benth.						0.047										
Desmodium incanum DC.		0.093	0.113	0.093	0.053	0.160	0.040		0.527	0.047		0.127				
Galactia gracillima Benth.						0.007										
Galactia marginalis Benth.							0.007									
Macroptilium prostratum (Benth.) Urb.						0.067					0.020	0.007				
Macroptilium psammodes (Lindm.) S.I. Drewes & R.A. Palacios					0.013	0.040										
Sesbania punicea (Cav.) Burkart		0.007														
Stylosanthes leiocarpa Vogel	0.560				0.013			0.007	0.100	0.100	0.147	0.053		0.053		0.027
Stylosanthes montevidensis Vogel					0.127	0.020	0.160									0.007
Stylosanthes viscosa (L.) Sw.	0.087															
Vigna luteola (Jacq.) Benth.																0.033

(sequence)

Families / Species	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Zornia cryptantha Arechav.						0.013										
Zornia orbiculata Mohlenbr.							0.020	0.020	0.073							
Zornia reticulata Sm.	0.007			0.013	0.027	0.007					0.020			0.007		
Haloragaceae																
Laurembergia tetrandra (Schott ex Spreng.) Kanitz														0.007		
Hypoxidaceae																
Hypoxis decumbens L.		0.013	0.007		0.007		0.007			0.007		0.007	0.007	0.007		0.007
Iridaceae																
Cypella coelestis (Lehm.) Diels							0.007									
Sisyrinchium micranthum Cav.		0.027	0.080	0.020		0.013	0.033	0.067	0.073	0.080	0.200	0.060		0.027	0.020	0.007
Sisyrinchium palmifolium L.				0.013												
Sisyrinchium setaceum Klatt												0.007				
Juncaceae																
Juncus capillaceus Lam.									0.047	0.047	0.040	0.167	0.100			0.300
Juncus dichotomus Elliott		0.020							0.053	0.007		0.040	0.040			
Juncus microcephalus Kunth					0.027	0.007			0.020	0.027	0.007	0.007				
Lamiaceae																
Hyptis brevipes Poit.					0.047	0.013										
Scutellaria racemosa Pers.									0.007	0.013		0.013				
Linaceae																
Cliococca selaginoides (Lam.) C. M. Rogers & Mild					0.027											
Lythraceae																
Cuphea carthagenensis (Jacq.) J.Macbr.															0.007	
Cuphea glutinosa Cham. & Schltdl.		0.013														

(sequence)

Families / Species	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Malvaceae																
Krapovickasia flavescens (Cav.) Fryxell							0.007									
Sida rhombifolia L.		0.007	0.007													
Sida viarum A.St.-Hil.		0.013														
Melastomataceae																
Tibouchina gracilis (Bonpl.) Cogn.		0.127			0.147		0.013		0.007	0.047				0.033		
Tibouchina versicolor (Lindl.) Cogn.		0.007			0.040									0.133		
Menyanthaceae																
Nymphoides indica (L.) Kuntze											0.013				0.040	
Orchidaceae																
Habenaria parviflora Lindl.									0.007	0.007	0.007			0.020		
Orobanchaceae																
Agalinis communis (Cham. & Schltdl.) D'Arcy									0.007						0.013	
Oxalidaceae																
Oxalis conorrhiza Jacq.				0.007												
Oxalis eriocarpa DC.							0.060									
Oxalis lasiopetala Zucc.							0.047									
Plantaginaceae																
Bacopa monnieri (L.) Wettst.													0.007		0.400	
Gratiola peruviana L.										0.007		0.007	0.013		0.020	
Mecardonia tenella (Cham. & Schltdl.) Pennell					0.053			0.013	0.020			0.033				0.013
Nuttallanthus canadensis (L.) D.A.Sutton				0.007												
Plantago tomentosa Lam.	0.027					0.007	0.007	0.013	0.007							0.007

(sequence)

Families / Species	**SC1**	**SC2**	**SC3**	**SC4**	**NC1**	**NC2**	**NC3**	**NC4**	**MC1**	**MC2**	**MC3**	**MC4**	**TA1**	**TA2**	**TA3**	**TA4**
Scoparia ericacea Cham. & Schltdl.										0.007						
Poaceae																
Agrostis montevidensis Spreng. ex Nees																0.013
Andropogon lateralis Nees					0.067		1.707	0.040	0.667	1.547	1.367	1.507		0.160		
Andropogon selloanus Hack.					0.080	0.247								0.907		0.147
Andropogon ternatus (Spreng.) Nees													0.013			
Aristida circinalis Lindm.					0.033											
Aristida laevis (Nees) Kunth				0.027												
Axonopus aff. *affinis* Chase		0.087		0.040	2.607	2.693	3.213	3.873	5.400	3.600	4.200	4.533	3.133	0.987	0.020	1.413
Briza minor L.											0.013	0.007				
Calamagrostis viridiflavescens (Poir.) Steud.							0.013						0.007			
Cenchrus echinatus L.	0.013			0.107												
Chascolytrum poomorphum (J. Presl) Essi, Longhi-Wagner & Souza-Chies							0.047									
Chascolytrum subaristatum (Lam.) Desv.		0.013				0.047			0.033	0.027	0.013	0.047				
Chascolytrum uniolae (Nees) Essi, Longhi-Wagner & Souza-Chies		0.027				0.027		0.007	0.140	0.093	0.013	0.020				
Cynodon dactylon (L.) Pers.										0.007			0.973		0.347	0.300
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	0.047	0.067	0.027	0.600	0.073	0.367	0.113	0.013	0.013	0.107	0.047	0.107	0.020	0.233	0.007	0.020
Digitaria connivens (Trin.) Henrard	0.733				0.027	0.067		0.007							0.020	
Eragrostis bahiensis Schrad. ex Schult.													0.073	0.093	0.020	0.080
Eragrostis cataclasta Nicora		0.613		0.480	0.013	0.020		0.060	0.040	0.007	0.027	0.347	1.020	0.133	0.747	0.733
Eragrostis lugens Nees													0.013			
Eragrostis trichocolea Hack. & Arech.				0.233												

(sequence)

Families / Species	**SC1**	**SC2**	**SC3**	**SC4**	**NC1**	**NC2**	**NC3**	**NC4**	**MC1**	**MC2**	**MC3**	**MC4**	**TA1**	**TA2**	**TA3**	**TA4**
Eustachys uliginosa (Hack.) Herter		0.127		0.013												
Gymnopogon legrandii Roseng., B.R. Arrill. & Izag.						0.007										
Ischaemum minus J. Presl		1.340	0.027						0.267		0.280	0.040	1.020	0.613		0.213
Leptocoryphium lanatum (Kunth) Nees						0.013				0.007						
Mnesithea selloana (Hack.) de Koning & Sosef		0.007					0.020				0.007	0.040		0.007		0.020
Panicum aquaticum Poir.	0.027	0.473			0.013					0.013	0.013		0.007		0.007	
Panicum dichotomiflorum Michx.		0.060		0.013					0.033	0.007	0.147		0.500		0.060	0.047
Panicum racemosum (P. Beauv.) Spreng.		0.007			0.007	0.007	0.007	0.140					0.007			
Paspalum arenarium Schrad.	0.727	0.380	0.060	1.453	0.127	0.027	0.093	0.387								
Paspalum dilatatum Poir.													0.013	0.020	0.027	0.020
Paspalum distichum L.															0.087	
Paspalum lepton Schult.	0.100	0.773		0.007	0.487	1.087	0.147	0.027	0.280	0.040	0.087	0.067	0.013	0.200	0.007	0.460
Paspalum notatum Alain ex Flüggé	0.153	0.580	5.333	2.053	0.033	0.413	0.133	0.220	0.060	0.647	0.020	0.880	1.640	1.093	0.133	1.533
Paspalum plicatulum Michx.		0.013		0.107	0.027	0.147	0.053	0.080	0.007	0.033		0.020	0.013	0.007		0.007
Paspalum pumilum Nees		0.427	1.340		0.073				0.020	0.040	0.393	0.120	0.027	0.467		1.740
Paspalum umbrosum Trin.				0.007				0.013			0.007					
Paspalum vaginatum Sw.					0.013			0.013		0.080	0.013	0.047		0.013	0.367	
Piptochaetium montevidense (Spreng.) Parodi				0.007			0.227	0.020	0.027	0.060	0.087	0.073		0.007		
Schizachyrium spicatum (Spreng.) Herter						0.013			0.013			0.027		0.400		
Setaria parviflora (Poir.) Kerguélen			0.020	0.053		0.073	0.027					0.007	0.120	0.007	0.073	
Setaria setosa (Sw.) P. Beauv.		0.007														
Sorghastrum setosum (Griseb.) Hitchc.					0.007		0.013		0.833	0.253		0.033		1.900	0.067	1.233
Sporobolus indicus (L.) R.Br.		0.013		0.007		0.007				0.013		0.020	0.213			0.407

(sequence)

Families / Species	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Steinchisma hians (Elliott) Nash.						0.013		0.007			0.007	0.100		0.013		0.013
Stenotaphrum secundatum (Walter) Kuntze		1.213						0.027								0.200
Trachypogon spicatus (L. f.) Kuntze							0.040									
Vulpia bromoides (L.) Gray						0.013	0.020	0.040	0.033	0.007	0.040	0.047				0.007
Polygalaceae																
Monnina cardiocarpa A.St.-Hil. & Moq.							0.007							0.013	0.007	
Polygala linoides Poir.															0.013	
Primulaceae																
Lysimachia filiformis (Cham. & Schltdl.) U. Manns & Anderb.														0.007		
Rubiaceae																
Borreria capitata (Ruiz & Pav.) DC.										0.013						
Borreria eryngioides Cham. & Schltdl.										0.007						
Diodia saponariifolia (Cham. & Schltdl.) K. Schum.						0.007	0.007									
Galium hirtum Lam.						0.007										
Galium humile Cham. & Schltdl.												0.007				
Galium richardianum (Gillies ex Hook. & Arn.) Endl. ex Walp.				0.020		0.007	0.007		0.013							0.093
Oldenlandia salzmannii (DC.) Benth. & Hook. f. ex B.D. Jacks.					0.007				0.007		0.020	0.007		0.007	0.127	0.040
Richardia humistrata (Cham. & Schltdl.) Steud.	0.220	0.027	0.047	0.113	0.047	0.080	0.060	0.080	0.100	0.047	0.067	0.007	0.013	0.087		0.020
Richardia stellaris (Cham. & Schltdl.) Steud.	0.040	0.013		0.007	0.020	0.013	0.087	0.020				0.060		0.007		0.007
Spermacoce verticillata L.	0.207	0.007	0.013	0.033		0.013		0.013								
Smilacaceae																
Smilax cognata Kunth				0.147												

(final part)

Families / Species	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Solanaceae																
Petunia integrifolia (Hook.) Schinz & Thell.				0.007				0.013						0.007		
Verbenaceae																
Glandularia peruviana (L.) Small	0.027	0.040		0.020	0.060		0.187							0.013		
Glandularia selloi (Spreng.) Tronc.				0.013		0.080						0.007				0.020
Lippia turnerifolia Cham.							0.007									
Phyla nodiflora (L.) Greene										0.007			0.047		1.453	

Table 6: Soil variables of the sampling units, used as explanatory variables in the variation partitioning procedures.

Soil variables	**SC1**	**SC2**	**SC3**	**SC4**	**NC1**	**NC2**	**NC3**	**NC4**	**MC1**	**MC2**	**MC3**	**MC4**	**TA1**	**TA2**	**TA3**	**TA4**
Soil bulk density (kg/cm^2)	3.14	3.97	4.59	2.44	3.47	3.30	3.06	3.44	4.45	4.94	4.39	4.03	6.72	3.33	2.92	4.37
Clay (%)	7	7	8	15	6	7	6	6	7	7	7	7	16	6	24	6
pH (H_2O)	5	5	5.1	5.2	4.9	5	5.3	5	4.7	4.9	5.1	5.1	5.3	5.2	5.8	5.2
SMP index	6.8	6.7	6.8	6.6	6.4	6.4	6.7	6.8	6	6.4	6.8	6.4	5.9	6.4	6.5	6.2
Phosphorus (mg/dm^3)	3.3	16	3.5	4.3	4	3.9	3.2	3.4	7	2.9	7.8	22	5.6	8.6	4.2	7.9
Potassium (mg/dm^3)	21	34	45	23	30	19	46	15	37	17	20	24	60	35	230	100
Organic matter (%)	1.1	1.1	1.4	1	0.9	1	1	0.5	2.5	1.6	0.9	1.4	3.2	1.7	4.1	2.3
Exchangeable aluminum (cmol$_c$/dm^3)	0.3	0.3	0.2	0.4	0.5	0.5	0.1	0.4	0.9	0.6	0.3	0.4	0.1	0.3	0	0.4
Exchangeable calcium (cmol$_c$/dm^3)	0.5	0.5	1.2	0.4	0.5	0.3	0.9	0.2	0.4	0.5	0.5	0.9	6.9	1.2	13	1.2
Exchangeable magnesium (cmol$_c$/dm^3)	0.2	0.2	0.7	0.2	0.3	0.2	0.5	0.1	0.3	0.3	0.3	0.3	2.1	0.5	5.9	0.7
Aluminum + hydrogenous (cmol$_c$/dm^3)	1.7	2	1.7	2.2	2.8	2.8	2	1.7	4.4	2.8	1.7	2.8	4.9	2.8	2.5	3.5
Cation exchange capacity (cmol$_c$/dm^3)	2.47	2.8	3.74	2.88	3.7	3.36	3.56	2.04	5.21	3.65	2.56	4.06	14.1	4.6	22	5.6
Base saturation (%)	31	28	54	23	24	16	43	17	15	23	33	31	65	39	89	38
Aluminum saturation (%)	27.8	27.1	8.9	36.9	35.6	47.1	6	53.5	52.4	41.2	25.8	24	1.1	14.2	0	15.5
Calcium/magnesium ratio	2.5	2.5	1.7	2	1.7	1.5	1.8	2	1.3	1.7	1.7	3	3.3	2.4	2.2	1.7
Calcium/potassium ratio	9	6	10	7	7	6	8	5	4	11	10	15	45	13	22	4.7
Magnesium/potassium ratio	3.7	2.3	6	3.4	3.9	4.1	4.2	2.6	3.2	7	6	4.9	14	6	10	2.7
Sodium (mg/dm^3)	2.6	2.2	2.6	5.8	6.4	3.7	6.2	2.6	8.6	4	1.9	3.8	6	3.3	24	6.6
Zinc (mg/dm^3)	1	1.9	1.1	0.6	1	0.5	1	0.4	0.7	0.2	0.7	0.4	0.8	1.3	1.7	2.6
Copper (mg/dm^3)	0.2	0.7	0.3	0.1	0.4	0.2	0.3	0.1	0.5	0.3	0.1	0.3	1.4	11	5	10
Boron (mg/dm^3)	0.1	0.1	0.1	0.1	0.3	0.2	0.2	0.2	0.4	0.3	0.2	0.3	0.2	0.1	0.8	0.3
Manganese (mg/dm^3)	14	10	14	14	15	7	27	5	13	8	7	4	21	14	9	12

Table 7: Climatic variables of the sampling units, data from WorldClim database, values are an average for a 50 year series.

Climatic variables	SC1	SC2	SC3	SC4	NC1	NC2	NC3	NC4	MC1	MC2	MC3	MC4	TA1	TA2	TA3	TA4
Temperature																
Annual mean (°C)	19.4	19.2	19.1	18.8	18.8	18.8	18.8	18.7	18.5	18.5	18.4	18.4	17.7	17.7	17.7	17.6
Mean diurnal range (°C)	9.7	9.7	9.5	7.3	7.7	7.9	8.5	8.3	8	7.9	7.8	7.7	8.9	8.7	8.8	8.8
Isothermality	51	51	51	46	45	45	46	45	43	43	42	42	45	44	45	45
Seasonality	3001	2983	2944	2797	3184	3269	3435	3435	3441	3506	3532	3582	3608	3600	3584	3549
Max of warmest month (°C)	28.6	28.3	28	26.9	27.3	27.6	28.2	28.2	28	28	27.9	27.9	28.2	28	28	28.1
Min of coldest month (°C)	9.7	9.6	9.6	11.3	10.5	10.2	9.8	9.8	9.8	9.8	9.7	9.6	8.5	8.6	8.5	8.6
Annual range (°C)	18.9	18.7	18.4	15.6	16.8	17.4	18.4	18.4	18.2	18.2	18.2	18.3	19.7	19.4	19.5	19.5
Mean of wettest quarter (°C)	23.3	23.1	22.8	19.5	16.6	16.5	14.5	14.5	14.2	14.6	14.5	14.3	13.8	13.8	13.9	13.9
Mean of driest quarter (°C)	16.1	15.9	15.6	15.4	19.9	19.9	20	21.9	21.8	21.7	21.7	21.7	21.2	21.1	21.1	21.1
Mean of warmest quarter (°C)	23.3	23.1	22.8	22.3	23	23.1	23.3	23.2	23	23	23	23	22.4	22.3	22.3	22.2
Mean of coldest quarter (°C)	15.6	15.4	15.3	15.4	14.8	14.7	14.5	14.5	14.2	14.1	13.9	13.9	13.1	13.1	13.1	13.2
Precipitation																
Annual mean (mm)	1341	1313	1321	1397	1499	1487	1484	1462	1381	1360	1326	1308	1227	1220	1220	1216
Mean of wettest month (mm)	151	146	146	137	146	144	146	144	137	135	133	132	122	121	121	120
Mean of driest quarter (mm)	81	82	81	87	107	103	97	95	86	82	77	75	73	73	74	74
Seasonality	20	19	17	12	9	10	11	12	14	14	15	16	14	14	13	13
Mean of wettest quarter (mm)	430	411	401	384	404	401	404	403	393	390	383	378	348	346	346	344
Mean of driest quarter (mm)	257	258	265	299	347	338	330	320	285	276	264	258	251	251	252	253
Mean of warmest quarter (mm)	430	411	401	376	378	370	365	358	337	333	328	324	312	310	309	308
Mean of coldest quarter (mm)	275	279	290	299	391	396	404	403	393	389	380	374	342	340	340	339

CONSIDERAÇÕES FINAIS E PERSPECTIVAS FUTURAS

O primeiro capítulo dessa dissertação apresentou uma síntese sobre a composição florística e a estrutura da vegetação dos campos litorâneos sul brasileiros. A partir dos resultados encontrados pudemos observar um padrão geral de vulnerabilidade das áreas, suportado principalmente pela presença de muito solo descoberto e espécies exóticas com potencial invasor.

Poucas conclusões puderam ser obtidas com base no manejo das áreas, a não ser por duas áreas na região do Taim que apresentaram histórico agrícola. Por todas as áreas possuírem pastejo não pudemos concluir se o baixo porte da vegetação e o solo descoberto são oriundos do sobre pastejo. Contudo, evidencias da literatura apontam efeitos negativos do pastejo em áreas pouco produtivos com solos pouco consolidados (arenosos).

Em áreas de reserva, como no Parque Nacional da Lagoa do Peixe, gestores pretendem retirar o gado das áreas de campo assim que os conflitos de desapropriação das áreas particulares forem resolvidos (com. pess.). Visto que a pecuária é uma das principais atividades econômicas em áreas de campo, e a interação do pastejo com a vegetação é um dos principais fatores responsáveis pela manutenção dos campos em outras formações do estado, futuros estudos deveriam concentrar esforços em buscar entender a relação da vegetação com o pastejo nesse tipo de solo.

No segundo capítulo abordamos os processos determinantes da variação na composição de espécies (diversidade beta) dos campos litorâneos. A maior parte da variação total na composição de espécies foi relacionada com variáveis ambientais estruturadas no espaço, em escala refinada pudemos detectar a ação das mudanças nas variáveis edáficas alterando a composição das comunidades. Quando utilizamos grupos de espécies com características funcionais semelhantes obtivemos respostas mais refinadas sobre os processos que atuam na montagem da comunidade. Observamos que espécies com alta capacidade de dispersão são mais relacionadas com variáveis ambientais e pouco relacionadas com o espaço, enquanto espécies com baixa capacidade de dispersão foram mais relacionadas com o espaço do que as anteriores, indicando maior limitação de dispersão.

Uma simples abordagem baseada em grupos de espécies morfologicamente semelhantes revelou padrões interessantes na montagem das comunidades. Esperamos que futuras abordagens baseadas nos atributos funcionais destas espécies possam nos dizer muito mais sobre quais são os processos históricos que atuaram na montagem das comunidades atuais, uma vez que os atributos são as características que são diretamente selecionadas por estes filtros. A utilização principalmente de atributos relacionados com a dispersão das espécies deve melhorar nosso entendimento sobre a ação dos processos neutros, que atualmente são pouco entendidos devido a maior parte da variação espacial ser compartilhada com a variação climática.