Chapter 3

The effect of environmental features in determining patterns in the presence of exotic plants, shrubs and drivers for alpha and beta diversity in metacommunitys of the subtropical grasslands.

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Short title: The effect of environmental features in subtropical grasslands metacommunity.

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Introduction

The metacommunity concept aims at identifying the factors behind changes in composition and richness of communities in space, by explicitly considering how diversity of plants among localities might interact with local environmental conditions to determine variation in community structure among localities (Leibold 2011). The metacommunity perspective explicitly integrates ecological processes that work at different spatial scales, and thus goes beyond classical approaches in Ecology that focus either on local factors, factors working on ecological gradient, or on population- and community-level processes such as dispersal. Empirical tests of the concept in grasslands are still few (Gibson 2009).

The definition of a metacommunity as a "*set of local communities that are linked by dispersal of multiple potentially interacting species*" (Leibold et al. 2004) reflects the view that community structure can be understood in the light of regional dispersal processes. There are, however, different scenarios of how dispersal, local site conditions, and the species' ecological characteristics might actually regulate community patterns. Leibold et al. (2004) and Leibold (2011) formalize four classes of metacommunity models, which differ in the importance they ascribe to dispersal processes, variation in local site factors over a larger region, and species' characteristics as drivers of community assembly Importantly, previous investigations of alpha and beta diversity in fragmented landscapes have shown that diversity patterns reflect past rather than present habitat connectivity (Lindborg & Eriksson 2004; Helm et al. 2006; Purschke et al. 2012). This scenario can thus be considered as a special case of dispersal assembly in which variation in local community structure is explained by past dispersal processes (Fukami 2015) and beta diversity thus related to variation in historical landscape configuration. Mechanisms leading to nestedness and turnover are similar to the dispersal-driven assembly scenario, with the exception that the dispersal processes happened in the past and are no longer occurring in the contemporary landscape.

Even under scenarios that emphasize the role of dispersal, differences in local community structure are determined by interspecific differences in resource requirements and physiological tolerance limits that confine species to certain sections of environmental features and gradients, leading to an important role of environmental variation for explication of beta diversity (Chase & Myers 2011). In fragmented landscapes, environmental sorting might be an important driver of community structure because habitat patches often differ in soil properties due to contrasting land-use histories (Verheyen et al. 1999; Freschet et al. 2013). In the environmental sorting scenario, environmental variation can produce nestedness when soil gradients reach into marginal habitats where only a subset of species can survive. Alternatively, high resource availability may lead to competitive displacement of many species by a subset of few competitive species (Harpole & Tilman 2007). It can also produce spatial turnover when different species replace each other along environmental gradients. When environmental sorting is important, nestedness might also result from variation in soil spatial heterogeneity because of the contrasting numbers of niches provided (Tilman 1982; Adler et al. 2013).

Here, we aim at identifying the direct and indirect effects of environmental features on grassland plant community composition. Specifically, we tested the variation in alpha and better diversity of grassland plant community as well as differences in presence of shrub and exotic species, using 58 grassland sites in the South Brazilian grassland region. As land use change, specifically afforestation by exotic trees, has been strong in the region, we expected that environmental features explained most of the total variation in community composition. Specifically, we tested the following hypotheses: 1) Grasslands situated in less fragmented landscapes show high alpha and beta diversity, and differ in species composition from those of fragmented landscapes with show more shrubs and exotic species; 2) Physical features of the environment, such as soil characteristics (fertility, depth, texture) and topography are drivers that influence changes in structure and composition of grassland plant ; 3) Climatic differences in the region also influence the presence of shrubs, with more humid (more subtropical regions) showing a higher proportion of shrubs in grasslands, which in turn influences alpha and beta diversity negatively.

Materials and methods

Study region

Our study region comprised 58 sites in the Brazilian Pampa Biome, in the Serra do Sudeste mountain range in the extreme south of Brazil, comprising the area between the municipalities of Bagé, Jaguarão and Pelotas (Fig. 1). The region is a conservation priority area in the Pampa Biome by the Brazilian government due to high levels of endemism among herbaceous plant species (MMA, 2000). Geologically the oldest region of southern Brazil, it consists of a mosaic of geological formations with dominance of granitic and magmatic formations. Climate is temperate, with cold winters and hot summer without rainy season, average temperature of the coldest month above 11.3° C, and no dry season (Cfa according to the Koppen-Geigen classification; Alvares et al. 2013). The topography is slightly undulated to strongly accentuated (average altitude 30 to 430 m a. s.) and soils are poor in nutrients, ranging from deep to shallow soils, depending on relief features (Streck et al., 2008). The region is composed of forest-grassland mosaics while forests occur mainly along river valleys, the predominant vegetation is dry grasslands composed of grasses and herbs, with the presence of many shrubs and subshrubs.

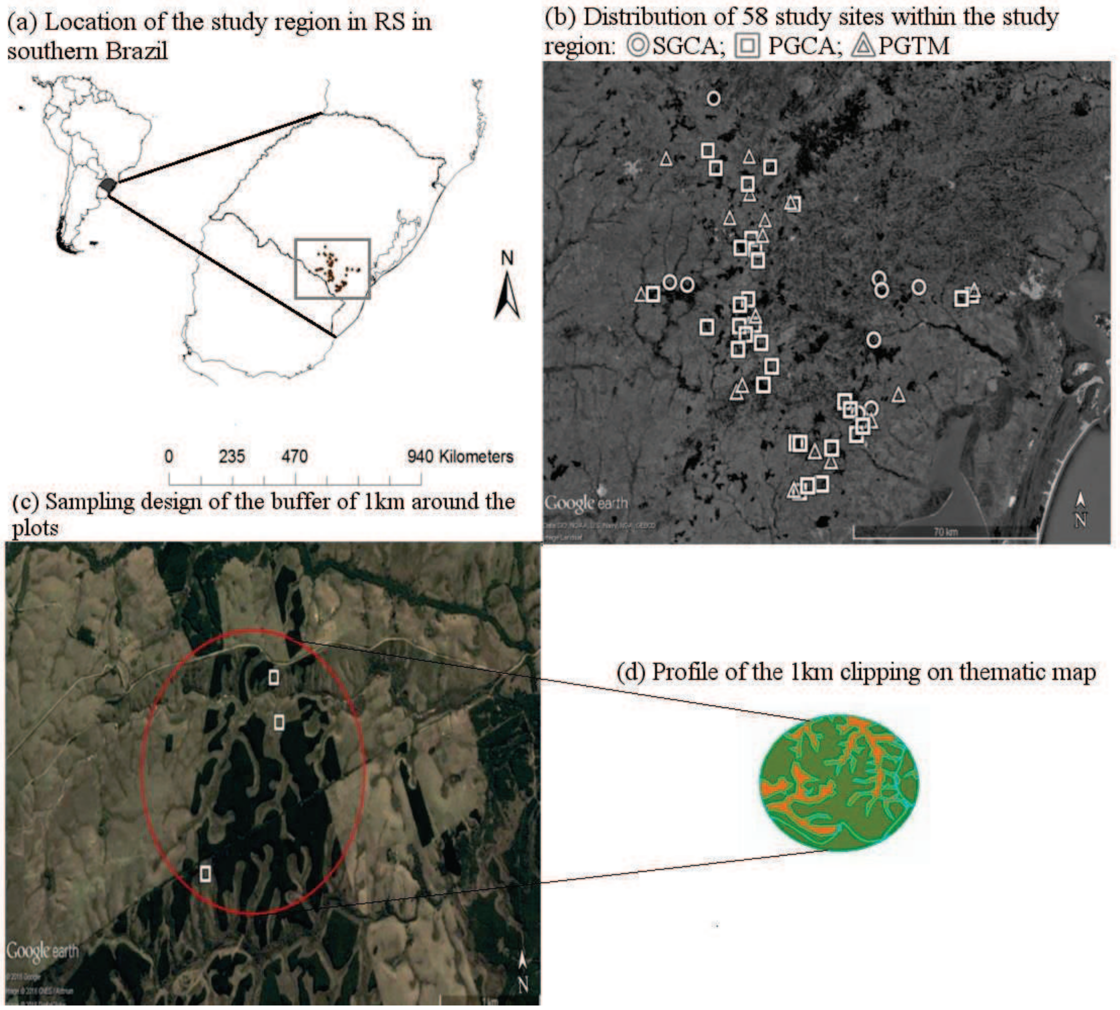


Fig. 1 (a) Location of the study region in the grasslands of Rio Grande do Sul (RS), southern Brazil; (b) distribution of 58 study sites throughout the study region (background map©Google Earth 2015): ⧈ PGCA = primary grasslands in conservation areas; ◎ SGCA = secondary grassland in conservation areas; △ PGTM = primary grassland subjected to the traditionally management; (c) sampling design of the buffer of 1km around the 25 m^2 study sites (plots); and (d) Profile of 1km clipping on thematic map, showing the variations on landscape elements.

Sampling design and vegetation data

The study was conducted at a total of fifty eight sites, each consisting of three distinct types of grasslands with contrasting land use histories and management intensities: 1) primary grasslands in conservation areas (PGCA) without formal management and long history of livestock, located around the eucalyptus plantations; 2) secondary grassland in conservation areas (SGCA), recovering from conversion to arable land with grazing at variable stocking rates, located around the eucalyptus plantations; 3) primary grassland subjected to the traditionally management (PGTM) of the region (extensive livestock: cattle average 0.5-1 animals per hectare). The study was conducted in the spring and summer of the years 2013 and 2014, the eucalypt plantations has been established 7 - 8 years (2006) before our sampling, and tree height varied from 8 to 12 m.

Within the three land-use types 58 sites were selected based on a stratified design (Fig. 1). This design ensured that sampling sites of all land-use types were distributed as randomly on the treatments over the entire study region using as base images of google earth. Criteria for the inclusion of a site in the study are the distance of the 30 m to native forest, eucalyptus plantations, roads and other site. The all sites were located in predominantly dry grasslands

At each site, we established three plots of 25 m^2 per area, allocated randomly In each plot, we randomly selected three plots of 1m^2 and identified all vascular plant species and estimated their cover according to the Londo (1976) scale. Additionally, we recorded vegetation height (measured at 5 points), percentage of plant litter, manure and exposed soil. Vegetation parameters were calculated according to Muller-Dombois & Ellenberg (1974): relative cover (RC), relative frequency (RF), and importance value index (IVI). In the 25 m^2 plots, we recorded identity and height of all shrubs, sub-shrubs and trees. Species were classified regarding their origin (native/exotic; Rolim et al. 2014) and degree of threat of species was checked in the current Red List for the state (Rio Grande do Sul, 2014).

Species and functional diversity

We measure grassland species diversity within and between sample units through Whittaker's components of diversity (Whittaker, 1972). We defined alpha diversity as the local diversity within sample and beta diversity as the variation in community composition among sample units in the study region, i.e., the variation in composition among the pastures constitute our metacommunity. The variable alfa diversity was composed by the effective number of species (Jost et al., 2011). The variable beta diversity was represented by the first axes (r^2= 31.3) of a principal coordinates analysis (PCoA) of vegetation data based on the Chord distance (standardized Euclidean) matrix. The chord distance is a measure of dissimilarity evaluating the values from the Euclidean distance between two sample units (MacCune and Grace, 2002).

Variable exotic plants and shrubs were determined from the average vegetation cover of exotic species (Rolim, 2014) and shrub species. In our sample were recorded 29 exotic species, of which 5 are invasive species. We define as shrub, woody or herbaceous plants with potential to reach more than 1m in height. In our sampling data, 61 species with these characteristics were registered.

Environmental descriptors

Environmental features were grouped by nine blocks of variables: climate, landscape, relief, soil type, fertility, drainage, depth, stoniness and texture. Each block of environmental predictors represents a latent variable (LV) in our path modeling framework. We consider the LV as the variable group observed, containing information which reflect aspects of their latent variable (Grace, 2006; Grace et al., 2010). In our case, the LV consist of representative values of the nature of the direct and indirect effects on the studied metacommunity. For climate, we selected the folloing variables of Worldclim (global climate layers): Annual Mean Temperature, Mean Diurnal Range, Isothermality, Temperature Seasonality, Max Temperature of Warmest Month, Min Temperature of Coldest Month, Annual Precipitation, Precipitation Seasonality (Coefficient of Variation). Latent landscape was built from the Project PROBIO (Plant Cover of the Pampa Biome) shape (UFRGS-IB-Centro de Ecologia 2016), consindering: dry grassland, afforestation, grassland with forest and rocky outcrops, native forests, agriculture, degraded grassland, mixed vegetation, water and roads. Soil data were collected from thematic map with adaptations of Brazilian soil map (Cunha, 2006; Flores, 2009), using the following variables: texture, classified by the percentage of clay, sand and organic matter; effective depth, classified as very deep (> 200 cm), deep (100-200 cm), half shallow (50 - 100 cm), shallow (<50 cm), very shallow (<25 cm); relief was classified according to the steepness of the terrain, such as flat (0-3%), soft wavy (3-8%), wavy (8-20%), strong corrugated (20-45%), mountainous (45-75%), cliff (> 75%); drainage refers to the amount and speed with which the water received by the soil infiltrates and flows thus created were the following classes: heavily and excessively drained, sharply drained, well-drained, moderately drain, imperfectly drained, poorly drained; fertility was classified as the base saturation (V%), determining the following variables: high fertility, medium and low; the stony refers to the portion (%) of rocky outcrops ("boulders"), classified as: absent (0 to 0.1), low (0.1 to 0.3), moderate (3 to 15), abundant (greater than 15). We use the environmental characteristics to evaluate the effect of the variables in the local grassland metacommunity.

Description of the analysis

Principal Components Analysis (PCA)

In order to reduce dimensionality, the environmental variables were submitted to Principal Component Analysis (PCA), with different PCAs for each set of variables. Before running the analysis the data were transformed into "normal scores" to give equal weights and reduce the outliers. The first two principal components (PC) presented greater potential for explanation of the environmental variation (Table 1), therefore the scores of axis 1 and axis 2 were used as explanatory variables of the environmental set.

Table 1 - Pearson correlation of environmental variables with principal component (PC) scores of grasslands in fifty eight landscapes with contrasting in conservation state in southern Brazil. Percentage values below PCs are their explained variance:

Clime	PC1 (38%)	PC2 (28%)
Annual Mean Temperature	0.51	0.02
Mean Diurnal Range	0.01	0.42
Isothermality	-0.17	0.57
Temperature Seasonality	0.21	-0.42
Max Temperature of Warmest Month	0.57	0.1
Min Temperature of Coldest Month	0.38	0.26
Annual Precipitation	-0.45	-0.1
Precipitation Seasonality	0.05	-0.49

Landscape	PC1 (27%)	PC2 (20%)
Grassland	0.32	-0.6
Afforestation	-0.09	0.58
Forest-grassland mosaic	0.46	-0.15

Forest	-0.47	0.37
Crop land	-0.33	0.19
Grassland degraded	-0.01	0.48
Mixed vegetation	-0.04	-0.31
Water	0.05	0.11
Roads	-0.3	0.14

Soil class	PC1 (45%)	PC2 (28%)
Argissolo	0.55	-0.41
Chernossolo	0.49	0.05
Luvissolo	-0.07	-0.53
Neossolo	-0.29	0.38
Planossolo	0.05	0.37
Gleissolo	0.5	0.22
Vertissolo	0.5	0.29

Soil drainage	PC1 (47%)	PC2 (21%)
Markedly drained	-0.59	-0.13
Well drained	0.62	-0.43
Excessively drained	-0.33	-0.02
Heavily drained	-0.34	-0.05
Imperfectly drained	0.11	0.71
Poorly drained	0.16	0.53
Moderately drained	0.07	-0.02

Soil fertility	PC1 (59%)	PC2 (40%)
High fertility	-0.19	0.73
Low fertility	0.89	-0.16
Average fertility	-0.66	-0.42

Depth of soil	PC1 (54%)	PC2 (45%)
Little profound	0.76	-0.16
Deep	0.82	-0.26
Shallow	-0.59	0.56

Boulders	PC1 (43%)	PC2 (34%)
Abundant	-0.54	0.57
Absent	0.69	-0.28
Moderate	0.07	0.46
Few	0.61	-0.23

Relief	PC1 (60%)	PC2 (27%)
Strong wavy	-0.52	0.63
Wavy	0.75	0.0021
Plan	-0.31	-0.55
Soft wavy	-0.27	-0.55

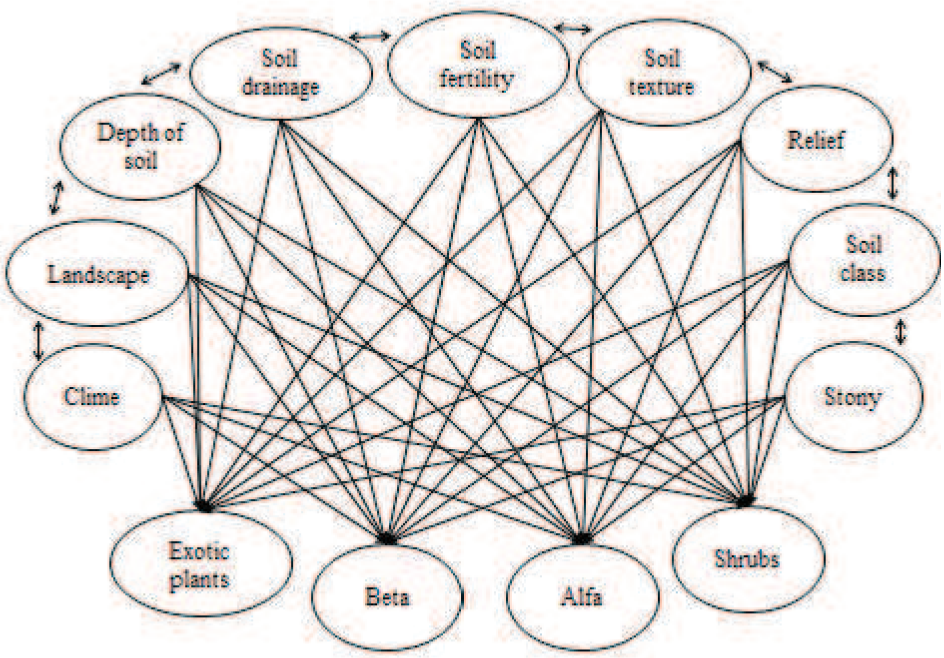
Soil texture	PC1 (94%)	PC2 (6%)
Sandy	-0.34	0.91
Clayey	-0.64	-0.4
Medium texture	0.69	0.08

Path analysis

We used Wright's path analysis (Wright 1921) in order to identify the direct and indirect effects of environmental features on exotic species, abundance of shrubs, alfa and beta diversity of grasslands in the Serra do Sudeste. In this approach, the correlation between predictor (x) and response (y) is partitioned as the sum of two types of effects: the direct effect of x on y (single path) and the indirect effect of x on y through one or more predictor variables (compound path) (McCune and Grace 2002). Thus, the total effect is the sum of all direct and indirect effects of one variable on another. For instance, the partitioning of the correlations between two predictor variables (x_1, x_2) and one response variable (y_1) involves the direct effects estimates of x_1 and x_2 on y_1 and indirect effects of x_1 on y_1 through x_2 and x_2 on y_1 through x_1 (Wright 1934). When x_1 and y_1 are only connected through a single path, the path coefficient for this relationship is equivalent to the bivariate regression coefficient (Grace 2006). On the other hand, when x_1 and y_1 are connected through x_2, the path coefficient corresponds to the partial regression coefficient (Grace 2006). According to Shipley (2000), the partial regression coefficient is a function of the partial correlation coefficient which measures the degree of linear association between two variables after to remove ('partialling out') the effect of one or more variables.

We used the environmental variables as LV (Figure 1), in order to determine the direct and indirect effects in the grasslands. In addition, we tested the environmental variables individually, forming a single set of variables (model 1), this matrix was decomposed into 5 other models determined from the values of correlation between variables, excluding variables with more than three correlations above 70%.

Figure 1 - Conceptual structural model illustrating predictive relationships among predictor and response latent variables (straight arrows) and associative (correlational) relationships among latent predictor variables (small arrows).



Results

Spatial and biogeographical components of species distribution

We sampled a total of 518 species in the 58 grasslands located in the Serra do Sudeste region. The sites were initially separated into three types of grasslands: PGCA with 445 species; SGCA with 238 species; PGTM with 345 species. Differences in structure and composition among these three types are discussed in Torchelsen et al. (in preparation/Chapter 2, this thesis).

Drivers of alpha, beta diversity, exotic species and abundance of shrubs

Overall variation in community composition among natural and semi-natural grasslands resulted mainly from climate, soil and landscape turnover, with 27 significant models (p>0.05; Table 2). After exclusion of variables with more than three variables with high correlation (<70%), there remained 14 LV, as soil texture (texture 1 and 2), relief (relief 2) and climate (climate 2) were removed.

The contrast with more significant variables was driven by environmental factors in the landscape, with turnover between the presence of primary grasslands and transformed landscapes, with direct and indirect effects in the composition of species. A higher proportion of natural ecosystems in LV landscape 1 promotes higher values of alpha and beta diversity, in contrast the effect is negative for the cover of exotic and abundance shrubs. In LV landscape 2, the transformed ecosystems produced positive effects on the abundance of shrubs and the cover of exotic species, in contrast the effect was negative for alpha and beta diversity.

Factors related to environmental filtering also determined structure and composition. The positive values for alpha and beta diversity were determined by direct and indirect effects of the latent variables of climate 1, soil fertility 1, stony 2 and soil class 1 and 2. In contrast, positive values for exotic species and abundance of shrubs were determined by soil drainage 2, depth of soil 2, soil fertility 2.

Table 2 - Direct and total effects of the environmental latent variables for the path modeling. Direct effects are given by the standardized path coefficients and the total effects as the sum of both the direct and indirect effects. Only values of significant variables (P> 0.05) are shown.

LV	Way	Alpha	Beta	Exotic cover	Abundance shrubs
Landscape					
Landscape 1	Direct	0.09	0.42	-0.18	-0.46
r total		0.27	0.45	-0.23	-0.47
Landscape 2	Direct	-0.15	-0.24	0.1	
r total		-0.32	-0.28	0.22	

Climate					
Climate 1	Direct	0.15			
r total		0.29			
Soil drainage					
Soil drainage 2	Direct	-0.01		0.34	
r total		-0.33		0.27	
Soil fertility					
Soil fertility 1	Direct	0.13	0.08		
r total		0.26	0.24		
Soil fertility 2	Direct			0.05	
r total				0.24	
Depth of soil					
Depth of soil 1	Direct	-0.34			
r total		-0.38			
Depth of soil 2	Direct	0.02	0.02	0.19	-0.02
r total		-0.32	-0.31	0.34	0.28
Stony					
Stony 2	Direct	0.37	0.1	0.1	
r total		0.43	0.24	-0.24	
Relief					
Relief 1	Direct				-0.28
r total					-0.23
Soil class					
Stony 1	Direct	0.25			-0.21
r total		0.27			-0.25
Stony 2	Direct	0.11		-0.52	-0.38
r total		0.26		-0.4	-0.22

To determine how the entire set of specific variables influenced species composition in our metacommunity, we assemble the matrix with 48 environmental variables, we excluded the variables with more than three variables with high correlation (<70%), reaching a total of 19 specific variables. We consider all the variables as part of the functioning of the ecosystem under study and influence directly and indirectly the composition of species in the grasslands (Table 3).

Table 3 - Direct and total effects of the specific environmental variables for the path modeling. Direct effects are given by the standardized path coefficients and the total effects as the sum of both the direct and indirect effects. They were only included the values of the significant variables (P> 0.05).

Specific variables	**Way**	**Alpha**	**Beta**	**Exotic cover**	**Abundance shrubs**
Landscape					
Grassland	Direct	0.21	0.15	-0.2	-0.05
r total		0.37	0.51	-0.29	-0.4
Afforestation	Direct		-0.24		0.42
r total			-0.43		0.48
Agriculture	Direct	-0.13	-0.26		
r total		-0.35	-0.28		
Degraded grassland	Direct	0.19	-0.15		
r total		-0.27	-0.22		
Roads	Direct			0.17	
r total				0.24	
Climate					
Annual Mean Temperature	Direct	-0.21	-0.19	0.46	0.33
r total		-0.38	-0.34	0.35	0.27
Annual Precipitation	Direct	0.15			
r total		0.27			
Soil drainage					
Sharply drained	Direct		-0.03		
r total			0.25		
Imperfectly drained	Direct	-0.01		0.33	
r total		-0.29		0.32	
Fertility					
High fertility	Direct			-0.15	
r total				0.26	
Depth of soil					
Deep	Direct		-0.15	0.31	0.18
r total			-0.32	0.33	0.33
Shallow	Direct	0.28		0.18	
r total		0.49		-0.31	
Stony					
Abundant	Direct	0.15			
r total		0.38			
Absent	Direct	-0.36	0.07	-0.12	
r total		-0.36	-0.26	0.28	
Relief					
Strong corrugated	Direct		-0.16		0.02

r total			-0.23		0.25
Soil class					
Chernossolo	Direct	0.09	-0.34	0.05	
r total		-0.24	-0.38	0.23	
Neossolo	Direct	0.43	0.18	-0.3	-0.27
r total		0.36	0.23	-0.32	-0.29
Planossolo	Direct	0.01			-0.13
r total		-0.22			-0.12

Supplementary Table (S1) present the indirect scores of the path coefficient, responsible for the total r of the climate, soil and landscape variables.

The effect of interaction between alpha and beta diversity vs. coverage of exotic species and abundance of shrubs.

The prediction performance of the path modeling was high for the predictive variables, with low correlation between variables, the model showed significance in all interactions (Figure 3). The results show positive relationships in the interaction between alpha and beta diversity, the direct effect of beta diversity (r^2=0.28) in alpha diversity, and alpha diversity in beta diversity (r^2=023) reveals relatively close relationships, however they represent independent components. The best scores obtained in the framework were from indirect results, considering the variables contributed to strengthen the effects of the model. Especially the relations between exotic and shrubs (r^2=0.58), alpha and beta (r^2=0.38) and beta and shrubs (r^2=-0.56).

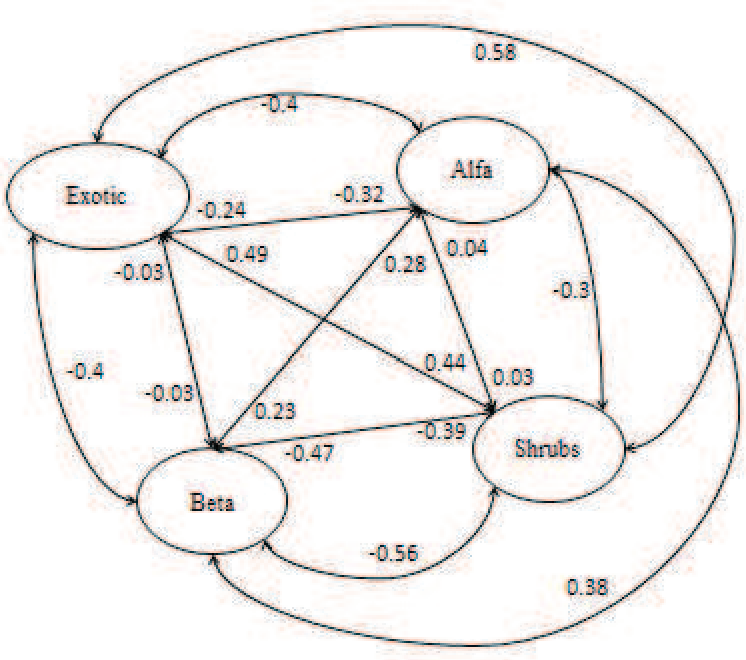


Figure 3 - Path modeling showing the strength and direction of the interaction effect among variables. Direct (straight arrows) and indirect (curved arrows) effects are shown through path coefficients.

Discussion

Environmental drivers for community assembly in a region with recently fragmented grasslands

This study contributes to a better understanding of how different environmental variables, including those related to recent anthropogenic land use, shape alpha and beta diversity in species rich subtropical grasslands. Our method allows us to discriminate between direct and indirect drivers and to identify. Overall, our results indicate that the species-sorting model is useful in understand environmental filtering in grassland communities in our study region.

Natural variation of environmental features – related to climate and soil – but especially factors related to anthropogenic land use change were identified as main drivers for diversity patterns at both the site (alpha diversity) and regional (beta diversity) scales. Specifically, in the case of our study region, we see clear effects of silviculture on grasslands. However, it is important to recognize that the effect of fragmentation per se cannot easily be separated from that of management changes in the context of Eucalypt plantions (see also Chapter 2). Studies with metacommunity in fragmented grasslands are rare, however it has been shown in other studies that the historical presence of grassland influences the current community assembly processes in extant grasslands (Helm et al. 2006; Purschke et al. 2012). In our study a considerable proportion of grasslands directly situated in the context of Eucalypt plantations still present typical communities of the region, as the occupation of the region by afforestation is relatively recent (10 years). Nonetheless, this process leads to changes in management – abandonment of traditional practices – which in turn leads to changes in the plant community, e.g. higher presence of shrubs or invasion of exotic species. Altogether, we can thus see that the intensity of management acts as driver for of the structure and the grasslands, leading to changes from the reference state that can be considered as degradation (Andrade et al. 2015; Koch et al. 2016).

Grassland communities are also directly associated with natural drivers. In our study, community composition and thus alpha and beta diversity varied in relation to environmental filters, specifically climate and soil features. For instance, higher annual temperature and lower rainfall favored alpha diversity. Low soil fertility was positive for alpha and beta diversity. These findings show clear diversity patterns on a regional scale, even though we may not forget the apparent clear filtering at high fertility sites may result from the fact that under these conditions, a relatively small number of widely-distributed plants that are highly competitive may dominate (Zobel 2015).

Drivers of exotic plant invasions and shrub encroachment

At regional scales, climate has been considered the major driver of invasive species occurrence (Ibáñez et al. 2009), as temperature and precipitation are key factors of resource availability, which limits survival, growth and reproduction of plants (Woodward 1987). Our study reveals a positive relationship between the presence of exotic species and annual temperature, but not precipitation. Importantly, the most expressive alien invasive species in the region (Chapter 2) are *Eragrostis plana*, with origin in South Africa, and *Cynodon dactylon*, likely of Mediterranean origin. These species are clearly benefitted from higher temperature, just as the shrub *Ulex europaeus*, especially invading abandoned sites in the context of *Eucalypt* plantations is.

Habitat fragmentation is an important driver of exotic species invasions Elton (1958) and increasing levels of human transformation of ecosystems, such as roads and roadsides (Vilà and Ibañéz 2011) contribute to spread of exotics. This has also been shown for our study region, as shown, for instance, by Guido et al. (2016). In our analysis, better conserved landscapes (landscape 1) negatively influenced the presence of exotic, contrasting fragmented landscape that showed a greater propensity for the establishment of exotic species. We also found a positive relation between the presence of roads and the occurrence of exotic species. In contrast, grasslands situated in less fragmented landscapes showed higher levels of alpha and beta diversity, confirming our hypothesis.

Encroachment of woody species in grasslands and savannas is a process occurring around the world, reflecting ecosystem changes and resulting in negative changes of important ecosystem processes such as carbon storage, water discharge, and biodiversity (Stevens et al. 2016), For South Brazilian grasslands, a number of studies has shown that the absence of disturbances, such as fire and grazing results not only in changes of the dominant grasses (e.g. Boldrini & Eggers 1996, Lezama et al. 2014), but, on a medium or long-term scale, also on succession from grassland to forest (e.g. Oliveira & Pillar, Müller et al. 2012, Blanco et al. 2014). In our study, shrub encroachment is related to a number of natural (climatic and soil related factors), but also the landscapes changes observed. This reflects, principally, the changes in grassland management when traditional grazing management is abandoned (Torchelsen et al. in prep.; Chapter 2), and also seems related to the fact that a changed landscape configuration, with degradation patterns, will also increase the presence of wind-dispersed shrubs, such as species of the *Baccharis* genus, i.e. of a ruderal character.

Alpha and beta diversity in relation to presence of exotic species and shrubs

Martin & Wilsey (2015) present a hierarchical concept of factors influencing alpha and beta diversity of plant communities. According to this concept, community composition changes, first of all, due to species sorting according to abiotic conditions, such as soil types or climates, as shown in our model as well. Assembly may, secondly, depend on dispersal processes that vary in the environment, as also evidenced in our study). Their third level, animal activities, that can alter plant species composition among patches and increase beta diversity (Steinauer and Collins 1995) was only studied indirectly by us, as it relates to land management by grazing. Last, beta diversity needs to be considered in the context of metacommunity theory through current dispersal rates and connectivity of habitat patches.

The introduction of alien plant species, and especially invasive plants, is a factor with considerable potential to change patterns of alpha and beta diversity (Hobbs et al. 2006). However, no general effect of exotic species on beta diversity has been found in a study comparing a large set of grassland vegetation data, over different climate zones and spatial scales (Martin & Wisley 2015). Here, we found that direct negative influence in alpha diversity is clear (r2=-32), but for beta diversity the effect was only slightly negative (r2=-0.04). Based on our data, we thus cannot affirm that exotic plant invasions lead to an overall homogenization and general losses of plant communities when considering a regional scale (beta diversity), even though there are clear effects on a the local (alpha) scale. Possibly, the lack of effects on beta diversity is related to the rather recent landscape changes in the region which still is considered one of the best preserved of the South Brazilian grasslands (Andrade et al. 2015). Shrub encroachment, on the other hand, had a strong negative effect on beta diversity (-0,56), indicating losses of typical grassland species, as discussed above.

Conclusion

The present study provides empirical evidence for the relative contributions of local environmental conditions, contemporary landscape spatial configuration, and historical landscape context for alfa and beta diversity in fragmented grasslands. We show that alpha and beta diversity patterns reflect complex interactions between different sets of variables, and that especially human induced land-use changes, in our case, tree plantations, are important drivers of assembly processes. Importantly, we here only talk of indirect effects, as we do not consider losses of grasslands per se due to expansion of forest plantations, but only changes in remaining grassland fragments. Nonetheless, clear negative effects on alpha and beta diversity were shown. From a theoretical perspective, our results confirm the species sorting model for grassland plant community assembly. From an applied perspective, our results indicate that conservation actions should be coordinated at a regional level, taking into account climatic and soil-related variation, as well as landscape-related processes.

Acknowledgements

We thank the Fundação Grupo Boticário de Proteção à Natureza, Brazil (grant 0950_20122 to GEO) for funding of the research that led to this paper. FPT received a Doctorate grant from CAPES, and GEO receives a CNPq productivity grant (310022/2015-0).

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Conclusão Geral

De forma geral, os estudos presentes na tese abordam diferentes aspectos das mudanças indiretas em comunidades campestres, principalmente em relação aos plantios de eucalipto no bioma Pampa. Os dados levantados demosntram o potencial da vegetação campestre se recuperar mesmo após longos períodos de uso, mas também que as comunidades secundarias diferem das comunidades primarias. No entanto, há evidencias que o manejo tem um papel importante nos processos de manutenção e restauração dos campos, no emtanto, mais estudos são necessários para poder indicar como a restauração da vegetação campestre torna-se mais eficiente. O manejo também foi apontando, na presente tese, como fator principal que define a composição e o estado de conservação de áreas de campo em diferentes contextos ambientais (com ou sem silvicultura no entorno, com ou sem histórico de agricultura), e mudanças no uso, de forma geral, demontram influenciar diretamente a variação na diversidade alfa e beta de comunidades campestres, em conjunto com outras variáveis ambientais. Desta forma, a presente tese evidencia o marcante efeito antrópico para comunidades de plantas campestres, em diversas escalas. Fica evidente que estratégias de conservação tem de considerar estes efeitos, e deverão considerar o manejo como elemento principal na conservação da biodiversidade da região.

Futuros estudos devem buscar interpreter qual a intensidade de manejo adequada para a efetiva conservação de cada fisionomia campestre, considerando indicadores de qualidade ambiental, como por exemplo: a riqueza de espécies, a altura da vegetação, a abundância de arbustos, a presença de espécies invasoras, etc.. Testar práticas como o diferimento (exclusão do gado por determinados períodos) é uma alternativa, visando à heterogeneidade de plantas e habitas em areas de preservação. Implementar a coleta e a introdução de sementes nativas em areas degradadas, manejar os campos secundários, são alguns dos desafios necessários para a manutenção campos, e assim conservar de forma efetiva a biodiversidade e os serviços ambientais prestados pelos campos do bioma Pampa.