



Grasslands of Uruguay: classification based on vegetation plots

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Abstract

Aims: The Rio de la Plata grasslands are one of the largest areas of temperate humid and sub-humid grasslands of the world. A substantial fraction of these natural grasslands are preserved in Uruguay, occupying more than 60% of the country. So far, Uruguayan grasslands have been indirectly classified using only geomorphological and edaphic criteria. An adequate description of vegetation heterogeneity is a prerequisite to study ecosystem function and to design management and conservation strategies for this region. To this end, we present a classification of the natural grassland communities of Uruguay based on a wide and comprehensive set of phytosociological relevés. Study area: Uruguay. **Methods:** Three hundred eight grassland relevés were utilized for classification and ordination multivariate analyses. Agglomerative clustering based on the flexible Beta linkage method and Sørensen distance measure were employed to identify relevé groups. Indicator species analysis was also performed to identify diagnostic species. We used Non-metric multidimensional scaling to determine the main floristic gradients. **Results:** Five communities and 14 sub-communities were identified. Two of the communities were restricted to the “Basaltic” region of central and northern Uruguay, while the other three were distributed through the Eastern Hills, North Eastern Sedimentary Basin and the South Central regions. Three of the communities correspond to densely-vegetated grasslands associated with medium and deep soils. The remaining two communities correspond to sparsely-vegetated grasslands on shallow soils. The main floristic gradient separated sparsely-vegetated grasslands from densely-vegetated ones, and was related to soil and topographical characteristics. The second floristic gradient separated grasslands by their different geological substrates. **Conclusions:** In this study, we present the first attempt to conduct a vegetation classification of Uruguayan grasslands based on floristic composition. Vegetation typologies, like the one we propose, can be used as a framework to extrapolate point information on grassland management and vulnerability.

Keywords: Campos; cool-season grass; grassland; Indicator Species Analysis; phytosociological relevé; species richness; soil depth; South America; Uruguay; vegetation classification; warm-season grass.

Taxonomic reference: IBODA (2018).

Abbreviations: CSG = cool-season grasses; IndVal = Indicator Value; MAP = Mean Annual Precipitation; MAT = Mean Annual Temperature; NMDS = Non-metric Multidimensional Scaling; PFT = Plant Functional Types; RPG = Rio de la Plata grasslands; WSG = warm-season grasses.

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Introduction

The Rio de la Plata grasslands (RPG), which extend through southern Brazil, Uruguay and eastern Argentina, are one of the largest areas of the temperate humid and sub-humid grasslands biome of the world (Soriano 1992). The mix of sub-tropical grasses, with C4 metabolism and warm-season growth, and temperate grasses,

with C3 metabolism and cool-season growth, present in the regional flora classifies the RPG as mixed grasslands, a particularity among grasslands worldwide (Gibson 2009).

An abundant megafauna of vertebrate herbivores occupied southern South America until Late Pleistocene extinctions (McFadden 1997), but there is scarce evidence on the evolutionary history of grazing for the study re-

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gion since then (Oesterheld & Semmartin 2011). Prior to livestock introduction by European settlers, the main native grazer seems to have been *Ozotoceros bezoarticus* (pampas deer), nowadays reduced to small, protected populations in the RPG. Our knowledge of fire history is even scarcer, and except for isolated evidence from the northern part of the region, little is known (Behling et al. 2007). Closer in time, the whole region has been grazed by domestic herbivores for more than 300 years, while fire importance is restricted to marginal areas (Soriano 1992). Currently, the RPG are severely threatened by land use change (i.e. cropping, forestry), a scenario similar to the rest of the biome in the world (Hoekstra et al. 2005; Baldi & Paruelo 2008).

Soriano (1992) divided the RPG into two sub-regions: *Campos* and *Pampas* (Fig. 1), mainly based on geomorphological and geological criteria. The first region corresponds to Brazil, Uruguay and a small portion of eastern Argentina, while the second region occurs exclusively in the Argentinean territory. From a physiognomical point of view, Soriano (1992) noted the *Campos* includes gallery forests along rivers and woodlands dispersed on hilly areas, a feature absent in the *Pampas*. Furthermore, Soriano (1992) divided the *Campos* into Northern and Southern *Campos*, based on partial data from local studies that suggest a northern region enriched by tropical grasses and a southern one with the temperate species at the limit of their distribution. In this scheme, Northern *Campos* included the areas corresponding to Brazil and Argentina and the northern half of Uruguay, while Southern *Campos* included the southern half of Uruguay (Fig. 1).

Despite the pronounced land use changes of the last decades, a substantial fraction of natural grasslands are still preserved in Uruguay, where approximately 60% of the territory is covered by this vegetation type (Baeza et al. 2014). An adequate design of management and conservation strategies for these grasslands requires a thorough description of the heterogeneity of vegetation in the region (Paruelo et al. 2004). The current lack of regional descriptions restricts extrapolation of experimental results and observations made at specific localities. From an applied point of view, Golluscio et al. (1998) identify the neglect of vegetation heterogeneity as one of the main drivers of degradation in pastoral systems. Even though several studies analysed floristic aspects of Uruguayan grasslands, particularly issues related to grazing effects conducted at a local scale (i.e. Rodríguez et al. 2003), regional floristic studies are scarce (but see Lezama et al. 2006). Instead, Uruguayan grasslands have been indirectly classified using geomorphological and edaphic criteria without support from floristic data (Rosengurt 1944; Soriano 1992). The phytosociological approach, oriented to the recognition and characterization of plant communities through the study of the co-occurrence of species, represents a useful approximation to describe the

vegetation at regional scale (Ewald 2003). In the RPG there are antecedents of its use in the *Pampas* sub-region (León et al. 1979; Batista et al. 1988; Burkart et al. 1990, 1998). In Uruguay, Lezama et al. (2006) used this approach to characterize the plant communities of a sub-region in the northwest part of the country. The present study extends the phytosociological analysis of plant communities to the natural grasslands of the main pastoral regions of Uruguay.

In this study, we present a floristic classification of Uruguayan grasslands based on a wide and comprehensive set of phytosociological relevés. Our objectives were: a) to identify the grassland communities and their diagnostic species, and to characterize the structure and environment of the resulting defined communities, and b) to describe the main floristic gradients and their relationship with environmental variables.

Study area

The Uruguayan territory is entirely in the *Campos* region of the Rio de la Plata grasslands (Fig. 1). The climate is temperate; the mean annual rainfall varies from south to north, from 1,098 mm to 1,639 mm, and the annual mean temperature ranges from 16.5 °C to 18.1 °C (www.world.clim.org). Four among nine geomorphological regions within the Uruguayan territory still present high percentages of natural grasslands (greater than 50%): the Basaltic “*Cuesta*”, the Eastern Hills, the North Eastern Sedimentary Basin and the South Central region (Fig. 2) (Baeza et al. 2014; Panario et al. 2015). The remaining regions, whose total area is smaller than the pastoral regions, are mostly covered by sowed pastures, croplands and forest plantations. The Basaltic “*Cuesta*” region covers approximately 4.4 million hectares (25% of the territory), containing mainly hills. The Eastern Hills region consists of a set of elevations with a SW-NE direction and represents the region with the highest relief energy of the Uruguayan territory. It occupies 2.5 million hectares, and comprises a wide variety of geological substrata (ectonites, migmatites, granites, among others) (Bossi & Navarro 1988). The North Eastern Sedimentary Basin comprises approximately 2.5 million hectares of gentle hills, where diverse sedimentary rocks and a great variety of soils occur (from sandy to clayey) (Bossi & Navarro 1988). The South Central region, with 2.3 million hectares, is characterized by gentle hills with soils originated from granitic bedrock and quaternary sediments (Panario et al. 2015). The Basaltic “*Cuesta*” and the North Eastern Sedimentary Basin are entirely included in the Northern *Campos*, the South Central region in the Southern *Campos*, while the Eastern Hills cross both regions. A total of 11.7 million hectares (66.4% of the entire country) were included in our survey.

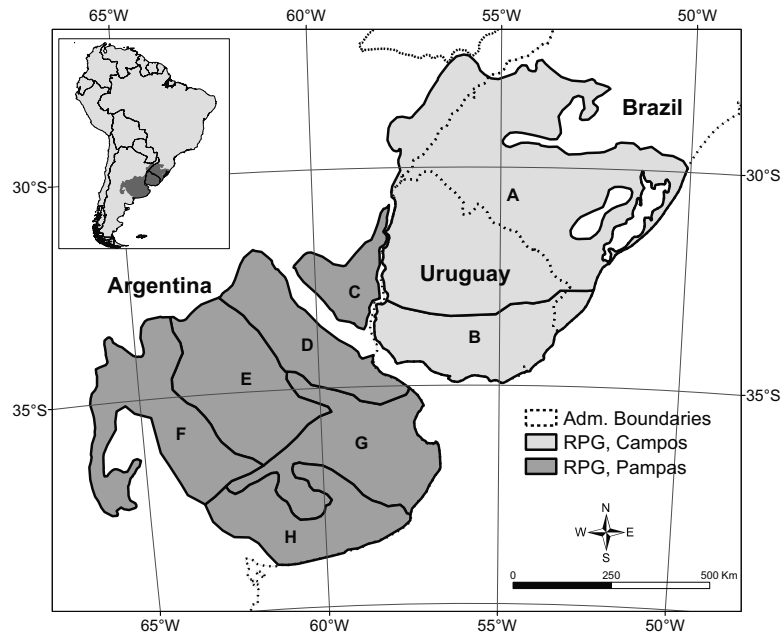


Fig. 1. Location of study area in Rio de la Plata grasslands and its sub-regions. *Campos*: A) northern *Campos*, B) southern *Campos*; *Pampas*: C) mesopotamic *Pampa*, D) rolling *Pampa*, E) flat inland *Pampa*, F) west inland *Pampa*, G) flooding *Pampa* and H) southern *Pampa* (Soriano 1992).

Methods

Data collection

Vegetation data were obtained by the phytosociological method (Dengler et al. 2008), during late spring and early summer, when the majority of species can be easily identified. Surveys were based on soil maps at 1:1,000,000 and 1:50,000 scale (Altamirano et al. 1976), encompassing the most representative soil units of each region in terms of occupied area. Stands were preferentially selected to encompass the whole range of physiognomic variability perceived (i.e. all physiognomic grassland types were sampled). At least three stands for each combination of soil type and physiognomic type were selected, but only one relevé per stand was performed, always in grazed paddocks although we avoided areas with a high degree of disturbance (e.g. cattle resting areas). Relevés were sampled in 5 m × 5 m quadrats located in the center of the selected stands. We recorded all vascular plants species and visually estimated percentage aerial cover of each individual species following the Braun-Blanquet abundance scale for values under 5%, and in steps of 5% for higher values. A raw matrix with 314 relevés and 445 species was constructed from field data collected between 2001 and 2009. Relevés were compiled in a vegetation-plot database (GIVD ID: SA-UY-001; www.givd.info). A subset of the relevés was previously used in the description of a sub-region of the Basaltic “Cuesta” (Lezama et

al. 2006), and the complete set has been used to explore patterns of invasions by exotic species (Bresciano et al. 2014). Additionally, each stand was characterized in terms of physiognomy (stratification, height and plant cover), and environmental variables (slope, rock cover, stone and pebble cover and climate). Slope was ranked from 1 to 4 (plane to pronounced), and plant, rock and stone and pebble cover were recorded as percentage cover values after a quick visual estimation. WorldClim database (www.world.clim.org) provided information about mean annual temperature (MAT) and mean annual precipitation (MAP) for each relevé. Latitude and longitude were also recorded. Species were classified into seven plant functional types (PFT): forbs, cool-season grasses (CSG), warm-season grasses (WSG), graminoids (sedges and rushes), succulents (*Cactaceae*), *Selaginella sellowii*, subshrubs and shrubs (a classification following mainly Altesor et al. 2006). In addition, WSG/CSG ratio was calculated for each relevé.

Data analysis

The multivariate analysis only included those species that were present in more than 1% of the relevés, since infrequent species of random occurrence can generate spurious results (McCune & Mefford 2011). After this filtering, the number of species was 333. In addition, multivariate analysis identified six relevés as outliers (> 2 standard devia-

tions from the mean of distances among relevés) that were then excluded from further analysis (McCune & Mefford 2011).

A combination of agglomerative hierarchical clustering and indicator species analysis (indicator value, IndVal, Dufrêne & Legendre 1997) was used to identify clusters of relevés. On the one hand, Sørensen distance and the Beta flexible method calculated from presence/absence data of 308 relevés were used for clustering (McCune & Mefford 2011). On the other hand, IndVal calculated from species cover-abundance data (transformed to percentage values) were used to identify diagnostic species for relevé clusters. Additionally, the sum of significant IndVals for each level ($p < 0.05$) allowed identifying the two most informative levels of the dendrogram (Dufrêne & Legendre 1997). Relevé clusters resulting from the highest hierarchical level were named as communities, while the clusters from the subsequent level were named as sub-communities.

To identify the main floristic gradients, we used Non-metric Multidimensional Scaling (NMDS), with a distance matrix based on Jaccard distance calculated from presence/absence data. Autopilot mode was selected to make multiple runs, choose the best solution at each dimensionality, and for a significance test (McCune & Mefford 2011). Percent of variation in the original data that was explained by the ordination was calculated through Pearson r^2 , correlating the distance between the plot scores in ordination space and the distance in the original matrix (McCune & Mefford 2011). To explore the relationship between the ordination and environmental variables and PFT cover, we computed correlations between the scores of each relevé in the first two axes of the NMDS ordination and the corresponding values for each variable, using Pearson's r correlation coefficient. Frequently many explanatory variables are intercorrelated, thus, to facilitate interpretation; we performed a correlation analysis between these variables. Indicator species analysis, agglomerative clustering and NMDS were run in the PC-ORD package (version 6, MjM Software Design, Gleneden Beach, Oregon, US).

Sub-communities were characterized in terms of indicator species, physiognomy, environmental variables and PFT composition. PFT cover and species richness values per plot were compared among clusters using ANOVA and a Tukey test. Homogeneity of variances was tested using Levene's test and, if necessary, a square root transformation was applied to the response variable. Even after transformations, however, homogeneity of variances could not be reached for succulents, *Selaginella sellowii* and shrubs. The variance analyses were performed using SPSS (SPSS, Chicago, IL, US).

Species accumulation curves for each community were constructed by plotting the average number of species against the total number of samples. This graph provides a measure of the rate of accumulation of different species

as the sampled area increases. The analysis was performed using PAST 1.89 software (Hammer et al. 2008). Geographical distributions of species were obtained from herbaria lists (Herbario Bernardo Rosengurtt, Facultad de Agronomía, Montevideo, Uruguay) and regional catalogues (IBODA 2018). In most cases, species distributions could not be assigned to specific geomorphological regions due to the lack of precision. Instead, we used a coarse division of the territory: Northern, Southern, Eastern, Western and wide. In this way, the contribution of species of restricted distribution to the lists of the different regions was evaluated.

Results

General floristic features of grasslands

The 445 species found in the complete set of relevés belong to 264 genera and 55 families. The families with the highest representation at the species level were *Poaceae* (156 spp.) and *Asteraceae* (131 spp.) (Supplement S1). *Paspalum notatum*, *Piptochaetium montevidense* and *Dichondra sericea* were the most frequent species, each with frequency values above 80%. Within the grasses, we found a greater number of warm-season grasses than cool-season grasses (113 *versus* 43 species). The WSG genus and the CSG genus with the most taxa were *Paspalum* (10 spp.) and *Nassella* (15 spp.), respectively. We found 14 species reported as endemic of the *Campos* sub-region, and 38 exotic species, mostly from Europe and Asia. The registered species are in general widely distributed in Uruguayan territory (around 92%); in accordance, few species were exclusively registered in one region (Supplement S1).

Community classification

The relevé classification yielded a structure of five principal grassland community types, called I–V (Fig. 3). The communities can be physiognomically distinguished based on the density and height of the vegetation (Fig. 4), and according to the geomorphological regions in which they are distributed. Four of the communities were divided into sub-communities. The communities and sub-communities were named based on the species with the highest indicator value. The analytical tables are presented in Supplement S2 (Tables 1–14) and the synoptic tables at the sub-community and community levels in Table 1 and Supplement S3, respectively. Structural characteristics of the sub-communities are available in Table 2.

I. Sparsely-vegetated grasslands of the Basaltic “Cuesta”. *Selaginella sellowii*-*Rostraria cristata* community
Overall, this community was characterized by meso-xerophytic species (Supplement S3). It includes stands lo-

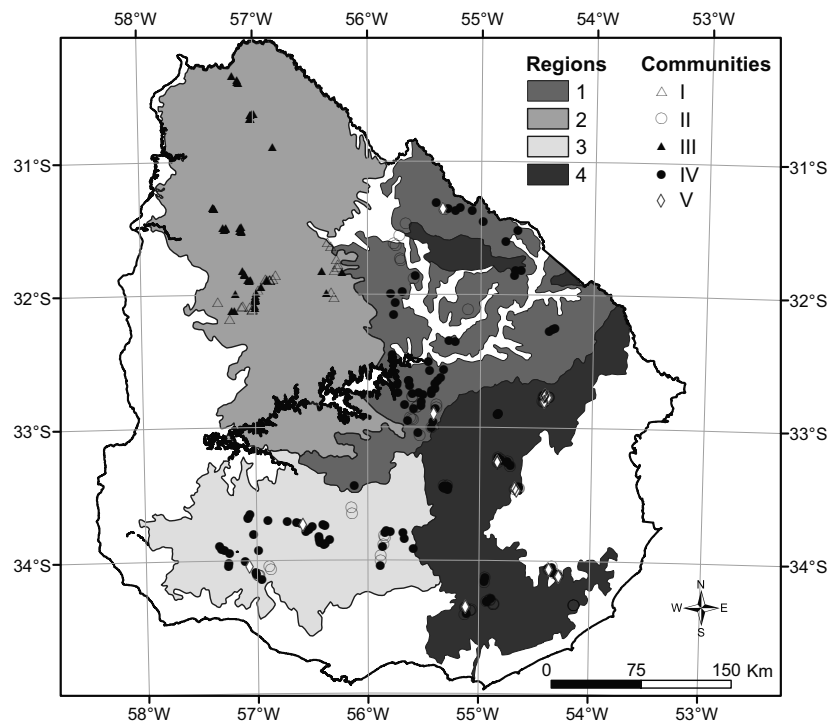


Fig. 2. Distribution of the five main types of Uruguayan grasslands in the surveyed geomorphological regions of Uruguay: 1) North Eastern Sedimentary Basin, 2) Basaltic “Cuesta”, 3) South Central region and 4) Eastern Hills (Panario et al. 2015). Names of communities I-V are given in Fig. 3.

cated upon shallow soils or directly above rocky outcrops of the Basaltic “Cuesta” region. This unit encompasses two physiognomically distinct sub-communities.

Ia *Portulaca papulosa*-*Selaginella sellowii* sub-community

The three most diagnostic species are typical from dry habitats. *Portulaca papulosa* is a succulent species, *Selaginella sellowii* a resurrection spike moss and *Hordeum euclaston* an ephemeral annual grass (Table 1). *Nassella longicoronata* and *Guilleminea densa*, both indicator species of this unit, are reported as exclusive of the Basaltic “Cuesta” region.

Excluding *Selaginella sellowii*, warm-season grasses were the main PFT (Fig. 5). The physiognomy was defined by only one stratum, 2 to 5 cm tall, distributed as an intricate mosaic of vegetal and rocky patches. This sub-community occupied plane and convex-plane rocky outcrops, at medium and high topographical positions (Table 2).

Ib *Lippia coarctata*-*Oenothera parodiana* sub-community

The main indicator species are forbs, a perennial (*Lippia coarctata*) and a biennial (*Oenothera parodiana*) (Table 1). *Lippia coarctata* is exclusive of the Basaltic “Cuesta”. Warm-season grasses, firstly, and cool-season grasses se-

condly, dominated this sub-community (Fig. 5). A double stratum physiognomy is typical of this unit, with the lower stratum, 5 to 10 cm tall, constituted by prostrate grasses and forbs, and the taller stratum, 11 to 30 cm tall, of erect grasses and subshrubs. This sub-community occupied shallow soils located mostly on convex moderate and pronounced slopes. It usually presents moderate values of stoniness in surface, and, in some cases, rockiness (Table 2).

II. Sparsely-vegetated grasslands of Eastern Hills, North Eastern Sedimentary Basin and the South Central region. *Trachypogon spicatus*-*Crocantemum brasiliense* community

This community was characterized by meso-xerophytic species (Supplement S3), and includes stands that occupied shallow or very shallow soils. Community II was divided into five sub-communities, two of them distributed across the three regions, two restricted to Eastern Hills and one to North Eastern Sedimentary Basin.

IIa *Glechon marifolia*-*Jarava filifolia* sub-community

Glechon marifolia is a perennial forb widely distributed in Uruguay, while *Jarava filifolia* is a perennial grass also with a wide distribution, but without reports for Basaltic “Cuesta” region (Table 1) (Supplement S1). Warm-season grasses were the dominant PFT component of plant

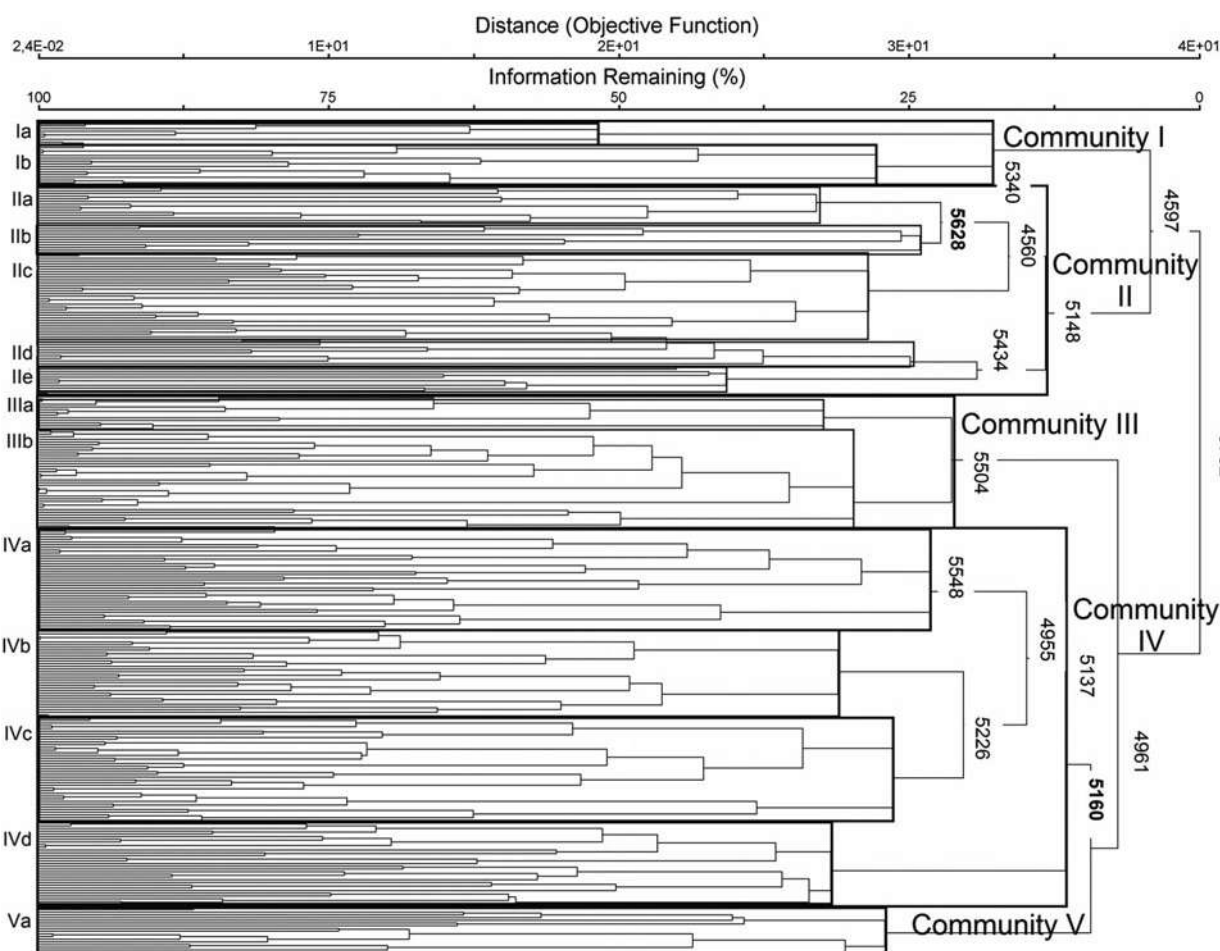


Fig. 3. Dendrogram resulting from the cluster analysis of 308 relevés and 333 species of Uruguayan grasslands. The five communities and the 14 sub-communities are indicated by the codes used in the main text. The sum of significant indicator values for each level is shown in the respective level. The sums corresponding to the identified main steps of the clustering procedure are highlighted in bold. I = *Selaginella sellowii*-*Rostraria cristata* comm., II = *Trachypogon spicatus*-*Crocanthemum brasiliense* comm., III = *Steinchisma hians*-*Piptochaetium stipoides* comm., IV = *Eryngium horridum*-*Juncus capillaceus* comm., and V = *Chascolytrum poomorphum*-*Paspalum pumilum* comm.

cover, followed by forbs and cool-season grasses, in second and third place, respectively (Fig. 5). The sub-community presented low plant cover, around 60%, generally with an upper stratum (30 cm tall) of subshrubs (*Baccharis* spp.) and bunch grasses (*Aristida filifolia* or *Jarava filifolia*) and a lower stratum (5 cm), dominated by prostrate grasses and forbs (Table 2).

The surface of this sub-community in general is comprised of stones and occasionally rocks (Table 2). It was found exclusively on the Eastern Hills region, where it occupied moderate to pronounced slopes with soils originated from metamorphic and sedimentary rocks.

IIb *Oxalis conorrhiza*-*Chascolytrum erectum* sub-community

A perennial forb and a perennial grass, *Oxalis conorrhiza* and *Chascolytrum erectum* respectively, both with a wide

geographical distribution in Uruguay, were the main indicator species. The following two species with the third and fourth highest indicator value are typical subshrubs of the Eastern Hills region: *Baccharis crispa* and *B. ochracea* (Table 1).

The woody component reached important cover values in this subunit (Fig. 5). Sub-community IIb had the particularity of presenting slightly higher percentages of cool-season than warm-season grasses (19.3 versus 17.3). A double stratum physiognomy was typical, one low of 5 cm dominated by prostrate grasses and forbs, and a 30 cm tall stratum dominated by woody species. Sub-community IIb occupied moderate to pronounced slopes of Eastern Hills with stony and rocky soils originated from sedimentary rocks (Table 2).

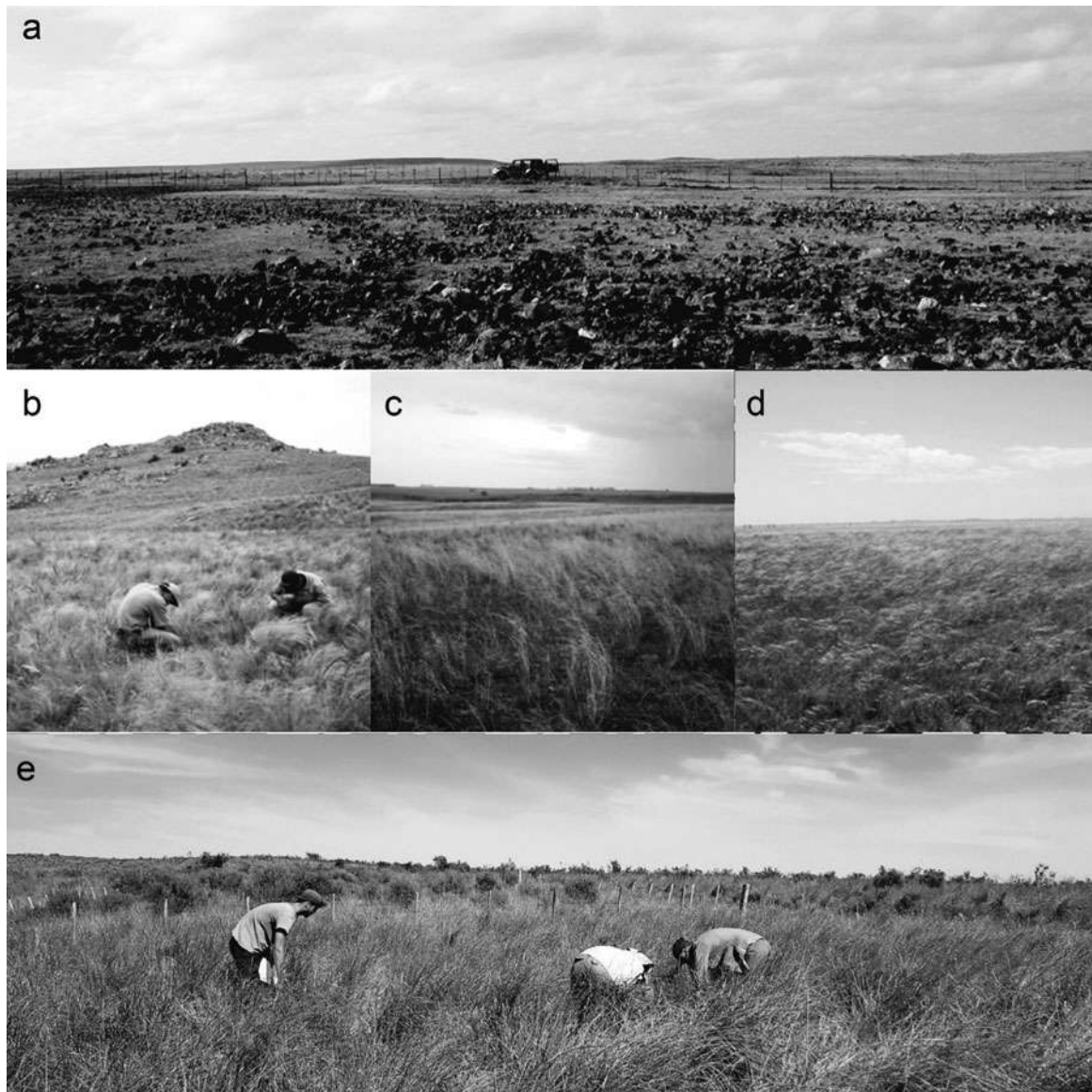


Fig. 4. Photographs of representative stands of the five communities of Uruguayan grasslands. a) *Selaginella sellowii*-*Rostraria cristata* comm.; b) *Trachypogon spicatus*-*Crocianthemum brasiliense* comm.; c) *Eryngium horridum*-*Juncus capillaceus* comm.; d) *Steinchisma hians*-*Piptochaetium stipoides* comm.; e) *Chascolytrum poomorphum*-*Paspalum pumilum* comm.

IIC *Stenachaenium campestre*-*Andropogon ternatus* sub-community

Among the subdivisions of community II, this one presented the lowest number of indicator species. It represents, therefore, the poorest defined unit within the community. The main indicator species were a forb and a perennial grass (*Stenachaenium campestre* and *Andropogon ternatus* respectively), both reported as widely distributed in Uruguay (Table 1). Warm-season grasses were the dominant PFT, followed by cool-season grasses (Fig. 5). Sub-community IIC presented, in general, a double stratum physiognomy, a low one 5 cm tall constituted by prostrate grasses and forbs, and a 30 cm tall stratum of erect grasses and subshrubs (Table 2).

Sub-community IIC, with 28 relevés, was the most common subdivision of community II, occurring on Eastern Hills, North Eastern Sedimentary Basin and the South Central regions. It occurred on convex, slight to moderate slopes, mostly without stones or rocks on the surface (Table 2).

IId *Aira elegantissima*-*Micropsis spathulata* sub-community

The three species with the highest indicator value in this unit were cool-season annual species, two forbs (*Micropsis spathulata* and *Facelis retusa*), and one grass (*Aira elegantissima*), all with a wide distribution in Uruguay. The presence of these species indicates the unit is associated

Table 1. Synoptic table of grassland vegetation in Uruguay at sub-community level. Species values are percentage frequencies in the sub-community types. Only the taxa with significant indicator values (IndVal) larger than 0.2 are shown ($p < 0.05$), ordered according to decreasing IndVal. Indicator values are indicated by grey frames of different intensity: dark grey: 0.8–1, grey: 0.5–0.8, light grey: < 0.5 . Exotic species are indicated by asterisk. For the geographical location of plots and other explanations see analytical tables in Supplement S2.

Community	I				II				III		IV			V
Sub-community	Ia	Ib	Ila	Ilb	Ilc	Ild	Ild	IIla	IIlb	IVa	IVb	IVc	IVd	Va
Number of relevés	7	17	14	10	28	16	8	14	39	35	31	40	33	16
Ia <i>Portulaca papulosa</i>-<i>Selaginella sellowii</i> subcomm.														
<i>Portulaca papulosa</i>	86
<i>Selaginella sellowii</i>	100	82	.	.	7	25	.	.	.	3	.	.	3	.
<i>Hordeum euclaston</i>	100	41	.	.	.	13	.	64	15	.	.	3	.	.
<i>Tripogon spicatus</i>	100	41	7	.	.	19
<i>Euphorbia pampeana</i>	71	6
<i>Paronychia brasiliiana</i>	71	65	.	.	.	13	.	.	.	6
<i>Microchloa indica</i>	100	53	21	.	4	69
<i>Nassella longicoronata</i>	57
<i>Perezia multiflora</i>	86	47	7	3
<i>Chloris grandiflora</i>	100	71	14	.	.	.	5	6	.
<i>Aristida teretifolia</i>	86	29	3
<i>Rostraria cristata</i> *	100	82	.	.	.	6	.	21	23	.	.	10	3	.
<i>Crassula peduncularis</i>	43
<i>Guilleminea densa</i>	43	3
<i>Stemodia verticillata</i>	43	7
<i>Eleusine tristachya</i>	57	35	.	.	.	13	.	7	3	.	3	3	.	.
<i>Richardia stellaris</i>	100	65	29	.	57	56	13	71	92	11	19	90	45	6
<i>Hypochaeris tropicalis</i>	71	35	21
<i>Notocactus</i> sp	43	12
<i>Spergularia</i> sp	43	35	.	.	.	6	13	7	.	6	3	.	3	.
<i>Polycarpon tetraphyllum</i> *	57	35	21	.	4	19	13	.	3	.	.	.	3	.
<i>Plantago myosuroides</i>	100	82	29	.	39	31	13	86	79	37	55	80	33	31
Ib <i>Lippia coarctata</i>-<i>Oenothera parodiana</i> subcomm.														
<i>Lippia coarctata</i>	.	59	3
<i>Oenothera parodiana</i>	14	76	15	3	6	5	3	.
<i>Ayenia mansfeldiana</i>	.	71	71	10	.	13	.	.	3
<i>Melica brasiliiana</i>	14	71	36	40	18	38	13	64	56	86	84	63	67	38
<i>Eragrostis lugens</i>	100	82	29	.	32	19	.	57	69	9	16	35	12	.
<i>Wahlenbergia linarioides</i>	14	94	50	20	39	56	25	14	28	29	23	18	36	6
<i>Nassella filiculmis</i>	.	47	43	60	7	6	.	.	5	17
<i>Euphorbia serpens</i>	43	65	7	13
<i>Aristida echinulata</i>	57	47	.	.	.	13
<i>Schizachyrium spicatum</i>	29	94	64	30	61	19	.	43	46	6	6	30	9	.
<i>Convolvulus laciniatus</i>	.	41
<i>Sida dubia</i>	14	41	7
<i>Aristida venustula</i>	14	76	71	60	93	81	25	.	18	26	29	50	3	6
<i>Tragia geraniifolia</i>	14	65	14	50	7	.	.	14	8	20	.	5	3	.
<i>Oxypetalum microphyllum</i>	.	29
<i>Baccharis coridifolia</i>	14	94	79	.	54	50	50	43	54	71	55	33	61	.
<i>Krapovickasia flavescens</i>	.	65	50	40	36	38	13	.	5	40	16	8	6	.
<i>Lathyrus subulatus</i>	.	29	14	.	4
<i>Bouteloua megapotamica</i>	57	41	14	3	.	.	.	6	.

Table 1. cont.

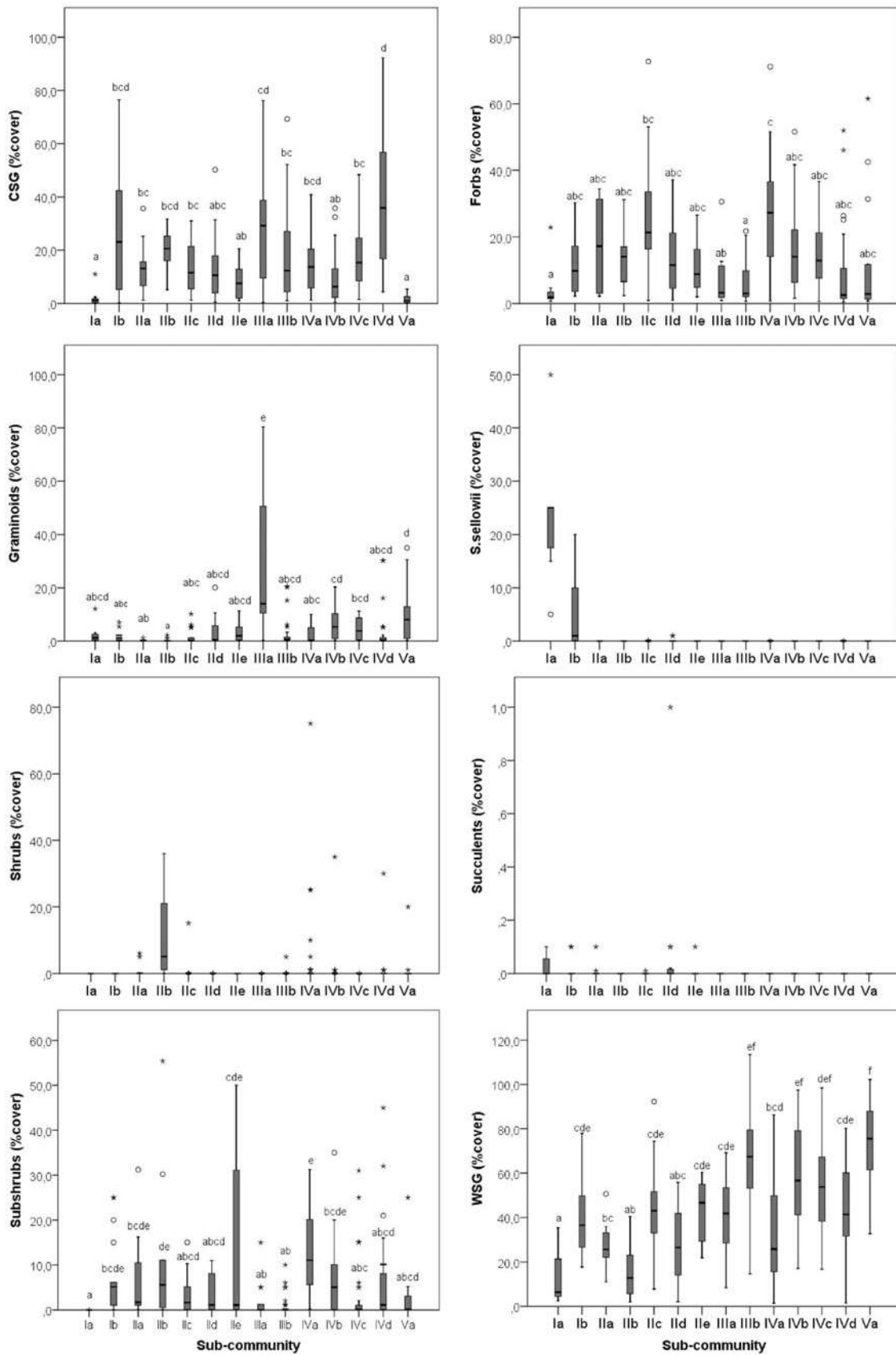
Community Sub-community Number of relevés	I		II				III		IV				V	
	Ia	Ib	Ila	Ilb	Ilc	IId	IIId	IIIa	IIIb	IVa	IVb	IVc	IVd	Va
	7	17	14	10	28	16	8	14	39	35	31	40	33	16
<i>Senna nana</i>	14	29	.	.	4	.	.	.	3
<i>Wissadula glechomaefolia</i>	.	24
<i>Dichondra sericea</i>	71	100	79	70	68	63	75	93	87	97	97	70	94	56
<i>Daucus pusillus</i>	.	24	3	.	.	3	.
Ila Glechon marifolia-Jarava filifolia subcomm.														
<i>Glechon marifolia</i>	.	.	57	10	4
<i>Jarava filifolia</i>	.	.	64	20	7	31	.	.	.	11	.	.	.	6
<i>Aristida filifolia</i>	.	6	71	.	14	19	.	.	.	11	.	3	.	.
<i>Lucilia acutifolia</i>	.	.	71	50	4	6	.	.	.	3	.	.	6	.
<i>Trachypogon spicatus</i>	.	41	100	100	57	81	25	.	5	14	23	5	.	.
<i>Achyrocline satureioides</i>	.	.	36	10	7	6	13	.	.	3	3	.	3	13
<i>Crocantemum brasiliense</i>	.	35	93	70	64	75	38	.	.	14	3	10	3	.
<i>Oxalis eriocarpa</i>	.	.	64	20	14	19	38	.	.	54	3	8	.	.
<i>Galianthe fastigiata</i>	.	.	71	50	43	13	.	.	3	31	3	5	.	13
<i>Paronychia setigera</i>	.	.	29	.	.	6	.	.	.	6
Ilb Oxalis conorrhiza-Chascolytrum erectum subcomm.														
<i>Oxalis conorrhiza</i>	.	.	29	90	9
<i>Chascolytrum erectum</i>	.	.	14	80	6
<i>Baccharis crispa</i>	.	.	29	60	3	.	.	.	6
<i>Baccharis ochracea</i>	.	.	57	90	11	43	.	.	.	6
<i>Hysterionica filiformis</i>	.	.	.	50
<i>Macroptilium psammodes</i>	.	.	.	50
<i>Panphalea commersonii</i>	.	.	.	50	3
<i>Grazielia serrata</i>	.	.	.	40	3
<i>Poa ligularis</i>	.	.	.	40
<i>Danthonia cirrata</i>	.	53	93	80	64	69	.	.	15	34	3	23	6	.
<i>Chrysoleaena flexuosa</i>	.	.	7	70	43	.	.	.	10	14	3	5	12	.
<i>Euphorbia stenophylla</i>	.	.	14	40
<i>Galianthe centranthoides</i>	.	.	29	50	9
<i>Agenium villosum</i>	.	6	36	50	25	6	.	.	5	20	.	3	.	.
<i>Lantana montevidensis</i>	.	.	7	30
<i>Piptochaetium montevidense</i>	57	100	100	100	96	100	100	29	87	97	84	98	52	38
<i>Turnera sidoides</i>	.	12	43	50	21	6	13	.	5	20	6	8	.	.
<i>Chromolaena squarrolosa</i>	.	.	14	30	.	6	.	.	.	9
Ilc Stenachaenium campestre-Andropogon ternatus subcomm.														
<i>Stenachaenium campestre</i>	.	12	43	20	75	6	25	.	3	20	16	23	.	.
<i>Andropogon ternatus</i>	.	65	86	50	93	56	50	57	72	51	42	85	30	.
<i>Aristida murina</i>	.	82	36	30	82	56	.	21	13	43	26	70	21	6
<i>Richardia humistrata</i>	29	94	100	100	96	100	100	14	15	91	77	85	70	63
IId Aira elegantissima-Micropsis spathulata subcomm.														
<i>Aira elegantissima*</i>	.	.	50	10	46	100	50	.	.	17	13	30	6	6
<i>Micropsis spathulata</i>	43	35	.	.	11	75	.	64	23	3	13	30	6	.
<i>Facelis retusa</i>	14	41	57	50	29	63	88	14	5	43	48	28	21	13
<i>Evolvulus sericeus</i>	100	88	93	70	71	100	63	43	67	86	35	65	39	.
<i>Galactia marginalis</i>	.	47	93	40	79	69	.	7	59	63	52	52	6	.
<i>Hypochaeris glabra*</i>	.	.	7	10	.	38	.	.	.	3

Table 1. cont.

Community Sub-community Number of relevés	I		II				III		IV			V		
	Ia	Ib	IIa	IIb	IIc	IId	IId	IIIa	IIIb	IVa	IVb	IVc	IVd	Va
	7	17	14	10	28	16	8	14	39	35	31	40	33	16
<i>Eragrostis neesii</i>	86	82	29	10	82	94	88	7	26	26	45	88	27	6
<i>Bulbostylis</i> sp.	100	53	71	30	43	94	13	.	.	11	3	20	.	.
<i>Cardionema ramosissima</i>	.	6	.	.	.	31
<i>Silene gallica</i> *	.	.	21	10	11	38	.	.	.	6	3	.	15	.
<i>Aira caryophyllea</i> *	.	.	7	.	4	25	13	.	.	.	6	5	6	.
<i>Galium ericoides</i>	.	6	.	.	.	25	.	.	.	3
Ile <i>Paspalum leptum</i>-<i>Hypoxis decumbens</i> subcomm.														
<i>Paspalum leptum</i>	.	.	.	10	.	.	100	.	.	11	23	18	.	13
<i>Hypoxis decumbens</i>	.	.	7	30	14	.	88	.	.	37	74	33	3	75
<i>Mimosa flagellaris</i>	4	.	50
<i>Vernonanthura nudiflora</i>	4	.	38	.	.	.	16	3	3	.
<i>Axonopus argentinus</i>	.	.	50	30	54	50	63	.	3	31	42	33	3	19
<i>Aristida laevis</i>	4	.	25	.	.	3	.	3	.	6
IIIa <i>Mecardonia procumbens</i>-<i>Eleocharis dunensis</i> subcomm.														
<i>Mecardonia procumbens</i>	29	13	93	46	6	3	30	6	6
<i>Eleocharis dunensis</i>	7	.	.	86	15	3	13	5	3	88
<i>Poa lanigera</i>	64	21	.	.	.	3	.
<i>Adesmia bicolor</i>	79	28	6	3	15	3	6
<i>Chascolytrum subaristatum</i>	57	82	64	60	68	50	50	86	77	80	87	80	76	38
<i>Juncus pallescens</i>	11	6	.	64	10	6	35	35	30	44
<i>Cyperus sesquiflorus</i>	29	18	7	10	.	6	50	79	15	.	32	8	6	25
<i>Juncus imbricatus</i>	86	24	.	.	4	.	.	86	69	9	16	25	61	44
<i>Verbena gracilescens</i>	50	13
<i>Bromidium tandilense</i>	43	18	7	.	4	38	13	50	10	.	.	3	3	.
<i>Piptochaetium uruguense</i>	36
<i>Polygala Duarteana</i>	36
<i>Stemodia palustris</i>	36
<i>Nierembergia calycina</i>	50	5	.	.	.	12	.
<i>Chaptalia piloselloides</i>	29	24	14	20	39	13	13	79	74	31	23	52	27	44
<i>Poa annua</i> *	57	13	43	.	3	6	3	.	19
<i>Acmella decumbens</i>	.	29	29	40	29	.	13	86	49	40	26	45	21	31
<i>Centunculus minimus</i> *	14	24	.	.	14	13	25	64	15	3	29	20	6	50
<i>Eleocharis montana</i>	29
<i>Nassella longiglumis</i>	29
<i>Acicarpa tribuloides</i>	14	12	36	5
<i>Trifolium polymorphum</i>	.	41	7	.	7	6	75	64	51	31	65	43	9	38
<i>Scutellaria racemosa</i>	.	6	38	79	46	3	16	13	9	38
<i>Ranunculus platensis</i>	29	5	.	3	3	.	.
<i>Piptochaetium bicolor</i>	.	41	.	.	7	6	.	29	21	31	6	15	48	.
<i>Bromus auleticus</i>	.	6	.	20	.	.	.	21	10	3	.	.	6	.
<i>Linum littorale</i>	.	.	7	36	5
IIIb <i>Ruellia morongii</i>-<i>Steinchisma hians</i> subcomm.														
<i>Ruellia morongii</i>	29	64
<i>Steinchisma hians</i>	43	47	7	.	29	6	100	93	92	51	81	88	61	94
<i>Mnesithea seloana</i>	14	59	7	.	71	38	50	100	97	69	100	100	76	88
<i>Piptochaetium stipoides</i>	.	76	14	40	54	19	.	100	92	71	61	75	73	6

Table 1. cont.

Community Sub-community Number of relevés	I		II				III		IV				V	
	Ia	Ib	IIa	IIb	IIc	IId	IIId	IIIa	IIIb	IVa	IVb	IVc	IVd	Va
	7	17	14	10	28	16	8	14	39	35	31	40	33	16
<i>Schizachyrium microstachyum</i>	.	.	.	10	14	6	38	7	49	11	48	30	6	31
<i>Eryngium echinatum</i>	43	36	.	23	30	18	6
<i>Nassella neesiana</i>	.	53	7	40	25	.	.	79	82	86	45	52	55	6
<i>Verbena montevidensis</i>	.	29	.	10	7	6	13	57	72	49	77	43	79	31
<i>Eustachys paspaloides</i>	14	71	.	.	4	13	13	36	56	9	6	18	9	.
<i>Sporobolus indicus</i>	43	24	.	.	7	25	88	86	72	6	45	60	36	6
<i>Phalaris platensis</i>	14	6	13	57	59	6	.	5	15	6
<i>Aristida uruguayensis</i>	.	29	.	.	7	.	.	93	77	.	.	23	27	25
IVa Eryngium horridum-Danthonia rhizomata subcomm.														
<i>Eryngium horridum</i>	.	41	36	90	57	38	13	21	26	89	87	48	70	31
<i>Danthonia rhizomata</i>	.	.	64	20	61	50	.	.	5	77	6	33	6	6
<i>Piptochaetium lasianthum</i>	.	.	.	40	7	6	.	.	.	43	6	3	3	6
IVb Senecio selloi-Nassella pauciciliata subcomm.														
<i>Senecio selloi</i>	.	.	14	.	7	6	.	.	.	11	48	18	12	44
<i>Nassella pauciciliata</i>	.	.	21	50	46	69	52	25	6	19
<i>Hypochaeris megapotamica</i>	4	.	.	14	.	.	39	15	6	6
<i>Juncus capillaceus</i>	14	12	29	20	39	63	75	36	36	71	90	63	79	38
IVc Chevreulia sarmentosa-Danthonia montevidensis subcomm.														
<i>Chevreulia sarmentosa</i>	57	82	93	70	89	44	50	43	74	71	94	95	33	69
<i>Danthonia montevidensis</i>	.	18	57	26	20	42	55	33	69
<i>Bothriochloa laguroides</i>	.	82	50	30	82	31	13	43	92	97	90	85	88	50
<i>Chaptalia exscapa</i>	.	29	21	40	36	6	.	64	21	17	26	75	30	19
IVd Lolium multiflorum-Nassella charruana subcomm.														
<i>Lolium multiflorum*</i>	4	.	.	50	46	23	26	23	85	6
<i>Nassella charruana</i>	.	6	.	.	7	6	.	71	46	29	26	63	97	.
<i>Centaurium pulchellum*</i>	14	12	21	5	.	6	23	67	.
<i>Paspalum dilatatum</i>	7	.	.	93	90	77	87	65	85	69
<i>Lotus suaveolens*</i>	14	13	.	.	3	3	3	15	30	.
<i>Bromus commutatus*</i>	24	.
<i>Cynodon dactylon*</i>	.	.	29	.	7	44	50	14	3	60	65	10	67	38
<i>Anagallis arvensis*</i>	3	.	21	.
Va Paspalum pumilum-Chascolytrum poomorphum subcomm.														
<i>Paspalum pumilum</i>	7	.	.	.	3	17	6	.	.	81
<i>Chascolytrum poomorphum</i>	18	.	25	.	.	17	42	28	9	81
<i>Eragrostis bahiensis</i>	15	.	19	10	3	50
<i>Lobelia hederacea</i>	3	.	44
<i>Centella asiatica</i>	3	.	.	.	44
<i>Axonopus fissifolius</i>	.	12	21	40	75	25	50	71	82	80	97	93	76	100
<i>Oldenlandia salzmannii</i>	31
<i>Dichantherium sabulorum</i>	.	.	14	50	29	25	88	.	.	71	71	35	6	94
<i>Eryngium eburneum</i>	.	.	7	10	3	.	.	.	31
<i>Gratiola peruviana</i>	14	29	.	.	19	15	15	75
<i>Paspalum quadrifarium</i>	.	.	7	20	14	6	.	7	.	29	6	.	9	38
<i>Hypochaeris microcephala</i>	.	6	.	.	7	.	13	43	5	3	32	23	18	63
<i>Chascolytrum lamarckianum</i>	.	.	7	30	21	.	38	.	.	37	32	28	.	69



dium and deep soils of the Basaltic “Cuesta” region. Two sub-communities could be distinguished:

IIIa *Mecardonia procumbens-Eleocharis dunensis* sub-community

Both main indicator species have a wide geographical distribution and are associated with humid conditions, especially *Eleocharis dunensis* (Table 1). Warm-season grasses, cool-season grasses and graminoids were codominants (Fig. 5). This was the unit with the highest cover of graminoids. Two grassy strata characterize the community, one 5–10 cm tall and the other approximately 30 cm (Table 2).

Sub-community IIIa occupied plane areas, sometimes slightly concave, located in interfluves and valleys. It presented high plant cover values, while stones rarely occurred on the surface (Table 2).

IIIb *Ruellia morongii-Steinchisma hians* sub-community

Ruellia morongii, the main indicator species, is a perennial forb, and its distribution is restricted to the Basaltic “Cuesta” region. The other indicator species have wide distributions in Uruguay (Table 1). Sub-community IIIb was clearly dominated by warm-season grasses (Fig. 5), being physiologically very similar to sub-community IIIa.

It occupied plane interfluves and gentle slopes, both in high as in low positions of the landscape. It presented generally a high plant cover of the soil, nevertheless in some stands low percentages of stones and/or rocks on surface occurred (Table 2).

IV. Densely-vegetated grasslands of the Eastern Hills, North Eastern Sedimentary Basin and the South Central region. *Eryngium horridum-Juncus capillaceus* community

Community IV was dominated by mesophytic species (Supplement S3), encompassing stands with high plant cover values (near 100%) that occupied medium and deep soils of the Eastern Hills, North Eastern Sedimentary Basin and the South Central region. Four sub-communities can be distinguished within this community, and though there were some geographical overlaps, many were linked to specific geomorphological regions.

IVa *Eryngium horridum-Danthonia rhizomata* sub-community

This sub-community is characterized by few species with low indicator values (Table 1). *Eryngium horridum*, the main indicator species, is considered one of the most problematic rangeland weeds of the region. Warm-season grasses dominated the plant cover, followed by forbs (Fig. 5). The latter life form reached its highest relative cover in this unit, mainly due to the high cover values of *Eryngium horridum*. Woody species (subshrubs and shrubs) also showed high covers (Fig. 5). Physiologically, in general it presented two strata, al-

though occasionally an additional 1 m stratum of shrubs was present.

Almost all the relevés of this unit belonged to the Eastern Hills region, and they were mostly located on convex moderate slopes. It was associated to soils originated from metamorphic rocks (mainly gneisses). Although it generally presented high plant cover values, rocks and stones may also be found on the surface (Table 2).

IVb *Senecio selloi-Nassella pauciciliata* sub-community

As well as sub-community IVa, this sub-community was indicated by few species (Table 1). Intriguingly, *Senecio selloi* is a subshrub, rejected by cattle, while in contrast, *Nassella pauciciliata* is a palatable erect grass, little resistant to grazing. Warm-season grasses are widely dominant (Fig. 5). It presented the same physiognomical characteristics as sub-community IVa (Table 2).

Sub-community IVb stands were located predominantly in the North Eastern Sedimentary Basin, on soils developed from diverse geological materials, from limestone to sandstones or gneisses. It occupied, in general, high slopes and convex areas with slight slope, without stones, and exceptionally with rocks, on the surface (Table 2).

IVc *Chevreulia sarmentosa-Danthonia montevidensis* sub-community

Sub-community IVc had only four indicator species (Table 1): *Chevreulia sarmentosa*, *Bothriochloa laguroides*, *Chaptalia exscapa* and *Danthonia montevidensis*, the first three characterized by prostrate growth. Warm-season grasses were the dominant PFT, followed, in order of importance, by forbs and cool-season grasses (Fig. 5). From a physiognomic point of view, it presented either a single stratum 5 cm in height, dominated by forbs and prostrate grasses, or a double strata, that included, in addition to the low stratum, a 30 cm tall stratum dominated by subshrubs (Table 2).

Sub-community IVc was the largest cluster of community IV, including 40 stands, distributed throughout the Eastern Hills, the North Eastern Sedimentary Basin and the South Central region. It occupied diverse topographical positions, but generally, it was associated to hillsides with slight to moderate slope, and without rocks on the surface (Table 2).

IVd *Lolium multiflorum-Nassella charruana* sub-community

Sub-community IVd was the subdivision of community IV with the most indicator species (Table 1). The main diagnostic species were cool-season grasses, one annual (*Lolium multiflorum*, an alien species widely used for forage production) and the other perennial (*Nassella charruana*). A high number of exotic species occurred among the indicator species (6 spp.) (Supplement S1). A remarkable feature of this sub-community was the high

values of cool-season grasses cover (Fig. 5). It presented, in general, two strata, one low (5 cm), conformed by prostrated grasses, and one tall (30 cm) defined mainly by bunches of *N. charruana* (Table 2).

The majority of the relevés were made in Central South region, on soils originated on fine sedimentary rocks. Topographically, it occupied mostly high flat areas and high gentle slopes, without stones and very exceptionally with rocks on the surface (Table 2).

V. Tall and densely-vegetated grasslands of the Eastern Hills, North Eastern Sedimentary Basin and the South Central region. *Chascolytrum poomorphum*-*Paspalum pumilum* community

Community V comprised dense stands with a high stratum of tall grasses (*Paspalum quadrifarium*, *Andropogon lateralis* or *Erianthus angustifolius*), and was characterized by mesophytic and hygrophytic species (Table 1). It was observed across different geomorphological units (Eastern Hills, North Eastern Sedimentary Basin and the South Central regions). It included only one sub-community.

Va *Paspalum pumilum*-*Chascolytrum poomorphum* sub-community

A great number of species indicated this unit, of which the majority were hygrophytes (i.e. *Lobelia hederacea*, *Centella asiatica*, *Oldenlandia salzmännii* and *Gratiola peruviana*) (Table 1). Warm-season grasses were the dominant PFT, followed by forbs (Fig. 5). It was located on humid or temporarily inundated soils associated with concave slopes and river plains (Table 2).

Species richness across the main communities

Mean species richness at the plot level was lowest in Community V (43.2 spp./relevé), while the remaining communities did not significantly differ among each other, with values ranging between 49.6 (Community II) and 57.3 (Community I) ($F_{4,303} = 7.3$, $p < 0.01$) (Supplement S3). Accumulated species curves suggested greater large-scale diversity in communities II and IV than in I and III, because species accumulated more rapidly with increasing sample size (Fig. 6).

Floristic and environmental gradients

A three-axis ordination with a final stress value of 15.2 emerged as the best solution from the NMDS analysis. The first two axes extracted represented 69.7% of community variation (Fig. 7). The distribution of the communities suggests the main axis differentiated sparsely from densely vegetated grasslands, while the second axis discriminated Basaltic “Cuesta” relevés from the rest.

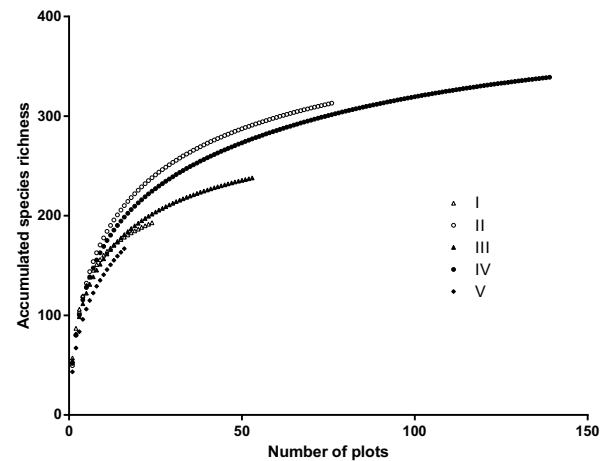


Fig. 6. Species accumulation curves for the five main communities of Uruguayan grasslands. I = *Selaginella sellowii*-*Rostraria cristata* comm., II = *Trachypogon spicatus*-*Crocantemum brasiliense* comm., III = *Steinchisma hians*-*Piptochaetium stipoides* comm., IV = *Eryngium horridum*-*Juncus capillaceus* comm. and V = *Chascolytrum poomorphum*-*Paspalum pumilum* comm.

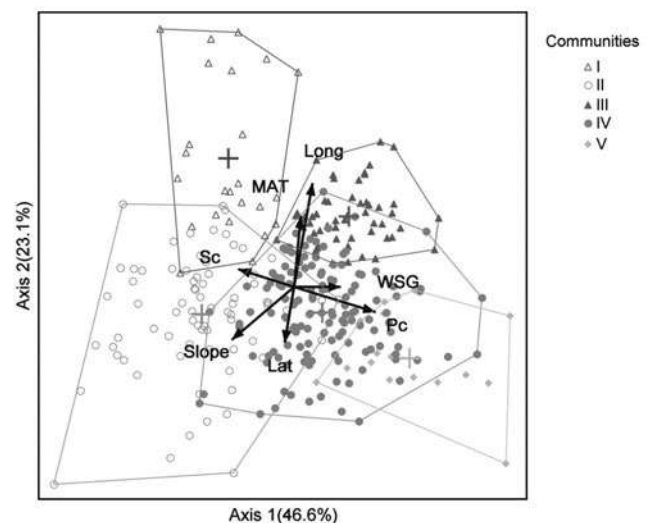


Fig. 7. Diagram of the first two axes of the NMDS analysis of relevés of Uruguayan grasslands classified at community level. The boundaries of the five communities are represented by lines and the centroids by crosses. The relationships between explanatory variables and ordination scores are indicated by arrows (only variables from the secondary matrix with an r^2 value larger than 0.2 are plotted). MAT = Mean Annual Temperature, Pc = plant cover, Sc = stone cover, Lat = latitude, Long = longitude, WSG = warm-season grasses. Names of communities are given in Fig. 6.

Axis 1 was positively correlated with warm-season grass cover and plant cover, and negatively correlated with stone cover and slope. Axis 2 was positively correlated with longitude and mean annual temperature. Con-

versely, Axis 2 was negatively correlated to latitude and slope (Fig. 7).

Some explanatory variables were strongly correlated among themselves. Both mean annual temperature and mean annual precipitation were negatively correlated to latitude ($r = -0.95$ and $r = -0.73$, respectively). Mean annual temperature and mean annual precipitation were moderately and positively correlated ($r = 0.64$). Plant cover showed a negative correlation with rockiness ($r = -0.72$).

Discussion

The studied grasslands, though physiognomically fairly uniform, showed a marked floristic heterogeneity. We recognized five main grassland communities and fourteen sub-communities based on an extensive number of systematic observations made in a large portion of the Uruguayan territory. Two out of five communities were restricted to the Basaltic “*Cuesta*” region of central and northern Uruguay while the other three were distributed through the Eastern Hills, North Eastern Sedimentary Basin and the South Central regions. Three of the communities correspond to densely-vegetated grasslands associated to medium and deep soils. The remaining two communities correspond to sparsely-vegetated grasslands on shallow soils.

Our results indicate the main floristic gradient is associated with edaphic and topographical variables that control water availability (slope and stone cover), and thus plant cover, and operates at the scale of the landscape. We also found that the increase of water availability is mostly capitalized by WSG (see the correlation between Axis 1 and WSG cover in Fig. 7), but nevertheless, the ratio of WSG/CSG cover did not show a pattern across the floristic gradient. No relationship between WSG cover and neither latitude nor MAT was found as expected based on the optimum temperatures of WSG for photosynthesis (Ehleringer & Monson 1993). The relatively small latitude and MAT gradient may obscure a potential relationship with WSG cover. An additional aspect to be considered in relation to this point is the eventual influence of grazing. Several studies have reported a positive effect of grazing on WSG cover and, in return, a negative effect on CSG cover (Rodríguez et al. 2003; Altesor et al. 2006), explained on the basis of the presence of prostrate growth habit exclusively among WSG in the Uruguayan grass flora (Cayssials & Rodríguez 2018).

The second floristic gradient is more difficult to interpret given that a set of intricate factors operating at the regional scale (longitude, MAT, and latitude) were correlated to axis 2. Moreover, some of these factors were correlated among themselves, as is the case of MAT and latitude. In spite of this difficulty, the fact that it discriminates the Basaltic “*Cuesta*” relevés from the all else

suggests the gradient represents a bedrock gradient. The relationship between axis 2 and longitude and latitude (and therefore MAT) may be collateral and can be explained by the fact that the Basaltic “*Cuesta*” is located at the north-western part of the study area.

The environmental factors identified as the main controls of vegetation heterogeneity, water availability and soil parent material, were also identified as the main controls by Batista et al. (2014) for Entre Rios palm savannas and by Gautreau & Lezama (2009) for Eastern Hill’s woody vegetation, both minor vegetation types occurring within the *Campos*. Our results modify the current description of Uruguayan grasslands that simply separated Northern and Southern *Campos* through an east-west boundary across the middle of the country (Soriano 1992) (Fig. 1). The overriding effects of geomorphology suggest that the *Campos* region within Uruguay should rather be divided into two regions, the Basaltic “*Cuesta*” on the Northwest, on one hand, and the rest of the territory on the other hand. Interestingly, our data analysis suggests an interaction between water availability and soil parent material given that the floristic differences between regions were more marked among sparsely-vegetated grasslands. According to our data, the well-developed soils (zonal), despite being originated from different geologies, share a great number of species, while the poorly developed soils provide habitat for specialist species. Anyway, it is remarkable that the communities and sub-communities were mostly defined on the basis of species with broad geographical distribution inside Uruguay (but with variable abundance and frequency among regions); in fact, few species of restricted distribution were recorded in the total set of relevés (Supplement S1).

Several studies performed in the RPG region indicate that domestic herbivores dramatically affect the structure of the grasslands (i.e. Altesor et al. 2006; Lezama et al. 2014; Batista et al. 2018). Few studies show the effects of grazing regime including intensity and frequency of grazing or the sheep/cattle ratio (but see Pizzio et al. 2016). All our relevés were performed on grazed stands, consequently, there may be an uncontrolled variation associated with current and past livestock management. Despite this source of variation, major communities are clearly associated with abiotic characteristics. Nevertheless, at the sub-community level, the differentiation of densely-vegetated grasslands IVa, IVb and IVc could correspond to different successional states in the same habitat according to their high floristic overlap. The fact that many of the indicator species of IVc have been reported as grazing increasers (species significantly more frequent in grazed than abandoned sites) would indicate that this sub-community represents a state associated to overgrazing (see Burkart et al. 1990 for a discussion of this point in *Pampa* grasslands). In any case, the question about the importance of disturbance regime generated by domestic

herbivores as a control of the grassland composition at the regional scale requires further analyses.

Diversity, in terms of communities and sub-communities, among regions highlight the role of geomorphology as a control of floristic heterogeneity (Swanson et al. 1988). At one extreme, the Eastern Hills appeared as the most diverse region with three communities and nine sub-communities, while at the other extreme, the Basaltic “*Cuesta*” region presented two communities and four sub-communities. This is consistent with the hypothesis that community diversity is related to topographic and geological variability, since the Eastern Hills are the most variable region and the Basaltic “*Cuesta*” region is the most uniform. Likewise, the fact that the South Central region does not have exclusive sub-communities provides further support to the hypothesis, since this region does not have any unique geological formations either. Previously, Lezama et al. (2006) classified the grasslands of the Basaltic “*Cuesta*” region into three main units according to their position along a major environmental gradient: xerophytic steppes, meso-xerophytic grasslands and humid mesophytic grasslands. The classification proposed in this paper simplifies their scheme, grouping the first two units into the sparsely-vegetated grasslands community (I) while the humid mesophytic grasslands correspond to our densely-vegetated grasslands (III).

The comparison of the classification of the Uruguayan grasslands presented here with that proposed for the *Pampa* grasslands (León et al. 1979; Perelman et al. 2001) (based on the same methodological approach), can be performed only for those units located on deep soils given that shallow soils are scarce in the *Pampas*, while wetlands and saline soils, abundant in the *Pampas*, are not frequent in the geomorphological regions covered in this study (Soriano 1992). If we restrict our comparison to the phytosociological inventory of the northernmost part of the flooding *Pampa* (León et al. 1979), the diagnostic species suggest that the major similarities are between the densely-vegetated grassland community of Eastern Hills, North Eastern Sedimentary Basin and the South Central region with the *Pampa*'s mesophytic grasslands associated with deep, well drained soils of convex landscape positions (León et al. 1979; Perelman et al. 2001). Among others, they share the following diagnostic species: *Nassella charruana*, *Borreria dasycephala* and *Paspalum dilatatum*. It is difficult to establish comparisons with studies carried out in Southern Brasil where the emphasis of the vegetation descriptions at the regional scale are based on physiognomy and dominant species (Boldrini 1997). We expect continuity of the units over the Uruguayan-Brazilian border, as the geomorphological units crosses the frontier and the main identified factors remain the same.

Only tall densely-vegetated grasslands differed from the rest of the communities in terms of species richness at the plot level, showing a lower richness probably because of the greater size of individual plants (Crawley 1997).

Interestingly, even the low species richness registered in the tall densely-vegetated grasslands (43.2) was greater than the highest mean plot richness reported for the mesophytic community in *Pampas* grasslands (42.2 spp.) (Perelman et al. 2001). This could be associated with differences in the regional species pool sizes and in landscape configuration (Jobbágy et al. 1996) between the *Pampas* and the *Campos*. The *Pampas* region shows a clearly lower diversity compared to *Campos* according to regional catalogues (Rapoport 1996). Additionally the hills and plains of *Campos* provide a more heterogeneous landscape, and therefore more favourable to the occurrence of “spatial mass effects” (Shmida & Wilson 1985), than the flat landscape of the flooding *Pampa*. This term, i.e. “spatial mass effects”, is applied to the phenomenon of species enrichment of heterogeneous landscapes by species that occur in an unfavourable habitat due to influx of propagules from a nearby favourable habitat. Species accumulation curves indicated that grasslands communities from the Eastern Hills, the North Eastern Sedimentary Basin and the South Central regions were richer at a large scale compared to the grasslands from the Basaltic “*Cuesta*”. As in the case of sub-community diversity, this can be related to the greater geomorphological variability of these regions compared to the Basaltic “*Cuesta*”.

Conclusions

An appropriate vegetation description provides a contextualization on an objective basis (Ewald 2003). In this study, we conducted the first comprehensive plot-based classification for Uruguayan grasslands. Vegetation typologies, like the one we propose, provide the framework to extrapolate point information on grassland management and vulnerability. Moreover, our description of grassland units forms the basis for mapping plant communities over the region, a precondition of its rational use and conservation. Some basic questions arise at this point: Do the defined communities differ in their response to grazing? How does the herbivore carrying capacity differ among communities or sub-communities?

Despite being the main vegetation type in Uruguay, only 0.4% of the grasslands are nowadays protected by some type of legal instrument (DINAMA 2014). Indeed, the selection of protected areas has been fundamentally opportunistic, based on preexisting and low cost public areas (Baldi et al. 2017). In this context, our results provide a guide for planning and designing protected areas. Undoubtedly, the availability of a red list of grassland communities (Berg et al. 2014; Janssen et al. 2016) would significantly complement this approach.

Author contributions

F.L. led and conducted the field sampling, made the analysis and led the writing. A.A. and J.M.P. planned the research, and all authors participated in field work and wrote and revised the manuscript.

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Supplement S1. List of species recorded in the relevés of Uruguayan grasslands.

Supplement S2. Relevé tables of Uruguayan grasslands.

Supplement S3. Synoptic table of grassland vegetation in Uruguay at community level.

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