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Inductive Approach To Build State-and-Transition Models for Uruguayan Grasslands☆

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ABSTRACT

We report state-and-transition models for Uruguayan grasslands built on a methodological approach that objectively defined states/phases associated, a priori, with rangeland management. Such approach was based on randomly sampled areas corresponding to mapped grassland communities. Each sampled area matched a MODIS pixel. Vegetation structural indicators were recorded in every pixel. After a multivariate analysis, field observations were grouped according to similarities in terms of structure, and different "states" and "phases" were identified. Ecosystem functioning and the supply of regulating ecosystem services were estimated for each grassland state/phase using the normalized difference vegetation index derived from the MODIS sensor. Finally, workshops were held in order to detect local stakeholders' perceptions and discuss the management practices to promote the desired transitions among phases. Results were presented for two vegetation units of the Basaltic "Cuesta" region. The "inductive approach" applied led to not only the description of "states" but also the identification of more subtle changes in vegetation ("phases"). Our approach minimized biases due to personal experience, as well as differences derived from using different observation protocols. The two vegetation units presented an internal heterogeneity associated with changes in basal stratum height, total cover, stratification, frequency of decreasing species due to grazing, and proportion of plant life forms. The ecosystem functioning descriptors of each phase responded to extreme climatic events differently. On the basis of stakeholder's opinions and experiences, stocking rate, sheep/cattle ratio, and grazing method were the main management practices promoting the transition among phases.

Introduction

Uruguay is entirely composed of grassland biome, particularly in the so-called Río de la Plata Grasslands. Lezama et al. (2006, 2011, 2019) presented a synthesis of the floristic heterogeneity of the Uruguayan grasslands based on a wide and comprehensive set of phytosociological relevés. These surveys defined five vegetation units or plant communities, three of them corresponding to densely vegetated grasslands associated with medium and deep soils. The remaining two communities correspond to sparsely vegetated grasslands on shallow soils. The floristic pattern was associated with soil depth, topographical characteristics, and geological substrates (Lezama et al., 2019).

In the past two decades, the grassland area decreased from 80% to 64.3% (DIEA-MGAP, 2000, 2011) due to the expansion of agriculture (that replaced principally densely vegetated grasslands) and tree plantations (Jobbágy et al., 2006; Baeza et al., 2011, 2014; Graesser et al., 2015; Volante et al., 2015). Associated with such changes, livestock production became more intensive, incorporating sowed pastures, fodder supplements, and feedlot systems (Bervejillo, 2013). Probably (there are no trustworthy records at a national level), given that pastoral areas were reduced while the herd number was maintained, the stocking rate on natural

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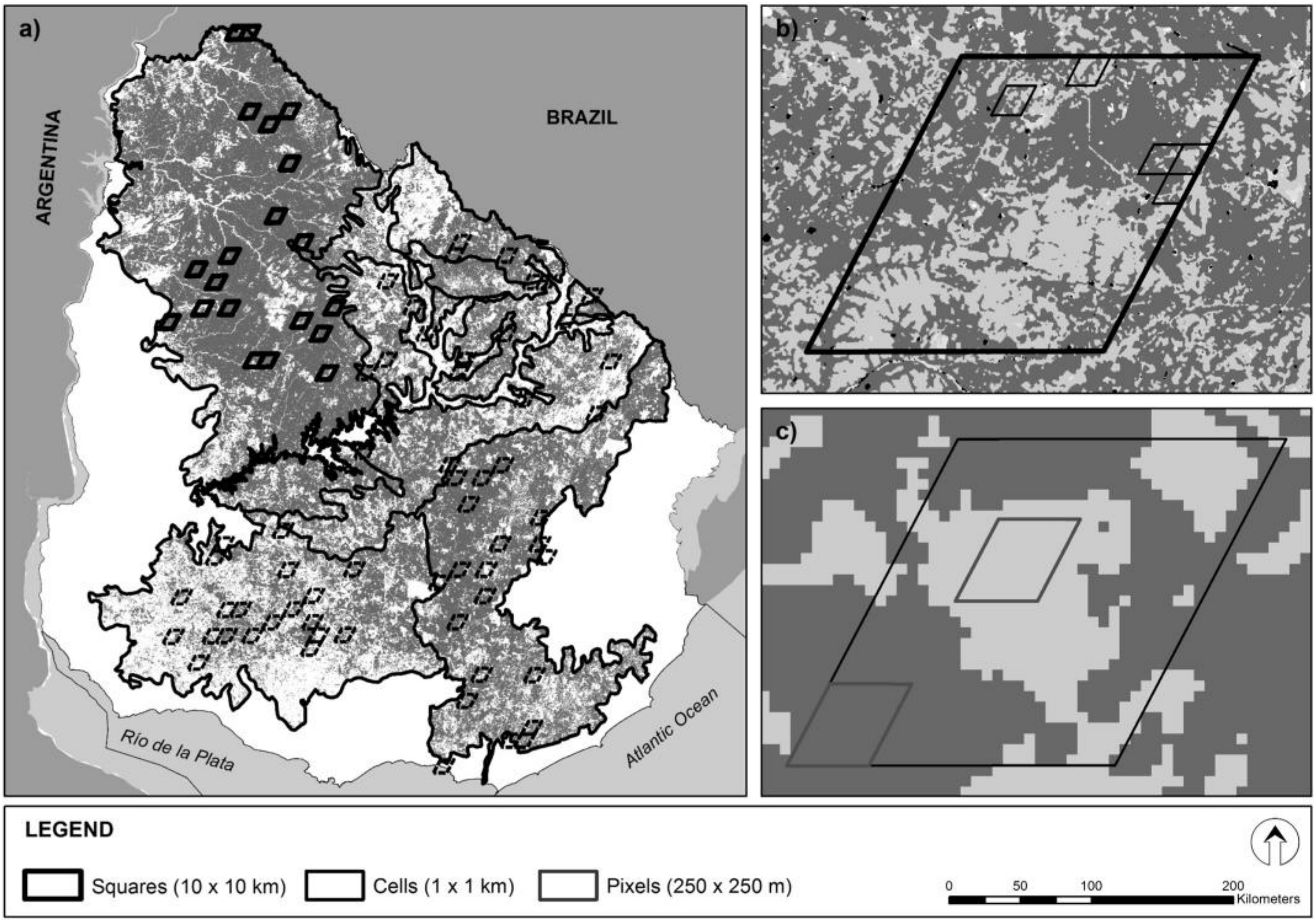


Figure 1. **a,** Land cover map of Uruguay. In gray is shown the area covered by grasslands in the four geomorphological regions. The *solid black line* shows the 10 x 10 km squares randomly selected in the Basaltic Cuesta. The *dotted line squares* corresponded to the remaining regions (Cuenca Sedimentaria del Noreste, Centro-Sur y Sierras del Este). **b,** Within each square, five 1 x 1 km cells were selected randomly. Dark and light gray areas corresponded to densely and sparsely vegetated grasslands respectively. **c,** Detail showing two MODIS pixels (250 x 250 m) of each grassland community.

grasslands increased, too. Experimental evidence from the Uruguayan grasslands showed that excessive grazing modified the structure and functioning of grasslands. Grazing increased species richness and promoted a matrix of prostrate perennial C_4 grasses and rosette forbs with a second group of interstitials, less abundant species of erect grasses, forbs and subshrubs (Rodríguez et al., 2003; Altesor et al., 2005, 2006). The aboveground and belowground primary production also increased in response to grazing (Altesor et al., 2005; López-Mársico et al., 2016).

The state-and-transition model (STM) proposed originally by Westoby et al. (1989) formalized the shift from the equilibrium paradigm to a conceptual model that incorporated multiple successional pathways, alternative stable states, thresholds of change, and discontinuous and irreversible transitions. STMs represent

Table 1
Structural vegetation indicators recorded in field samples.

Structural indicator	Abbreviation
Number of vegetation strata	N° VS
Height of basal vegetation stratum	HBVS
Height of second vegetation stratum	H2°VS
Height of third vegetation stratum	H3°VS
Coverage of basal vegetation stratum	CBVS
Coverage of second vegetation stratum	C2°VS
Coverage of third vegetation stratum	C3°VS
Bare soil	BS
Coverage of grasses in basal stratum	CGBS
Coverage of annual species	CAS
Coverage of alien invasive species (*Lolium multiflorum*, *Cynodon dactylon*, *Eragrostis plana*, *Senecio madagascariensis*, *Ulex europaeus*)	CAIS
Number of dominant species in the basal stratum (species whose coverage combined exceed 50% of the total coverage)	N°DomBS
Number of dominant species in second stratum	N° Dom2°S
Number of decreaser species	N° DecS
Species that become scarce (decreasers) (sensu Dyksterhuis, 1949; Noy-Meir et al., 1989) under herbivory. *Bromus auleticus, Chascolytrum subaristatum, Deyeuxia viridiflavescens, Melica brasiliana, Mnesithea selloana, Nassella megapotamica, Nassella neesiana, Paspalum plicatulum, Piptochaetium stipoides, Poa lanigera* (Cayssials, 2010).	

nonlinear vegetation dynamics as a group of discrete states co-occurring in a given area (ecological site or phytosociological community) and the transitions between such states. When the system remains in the same domain of attraction, the transitions may be reversible and different phases may be identified for a single state (Stringham et al., 2003). The transition to a different state is associated with notorious changes in structure and functioning. STMs became an important conceptual framework that has been widely used for restoration and management in grasslands and woodlands worldwide (Oesterheld and Sala, 1994; Bestelmeyer et al., 2003, 2004, 2009; McIntyre and Lavorel, 2007; Rumpff et al., 2011; Bagchi et al., 2012; Andrade et al., 2015).

Building an STM implies the identification and characterization of different vegetation states and phases through vegetation attributes ("state variables") (Westoby et al., 1989; Knapp et al., 2011). Vegetation attributes can be structural (species richness, total cover, cover of plant functional types, vegetation height, floristic composition, etc.), or functional (aboveground net primary production, evapotranspiration, etc.). The approach to build STMs often relies on compiling the opinion and expertise of range scientists

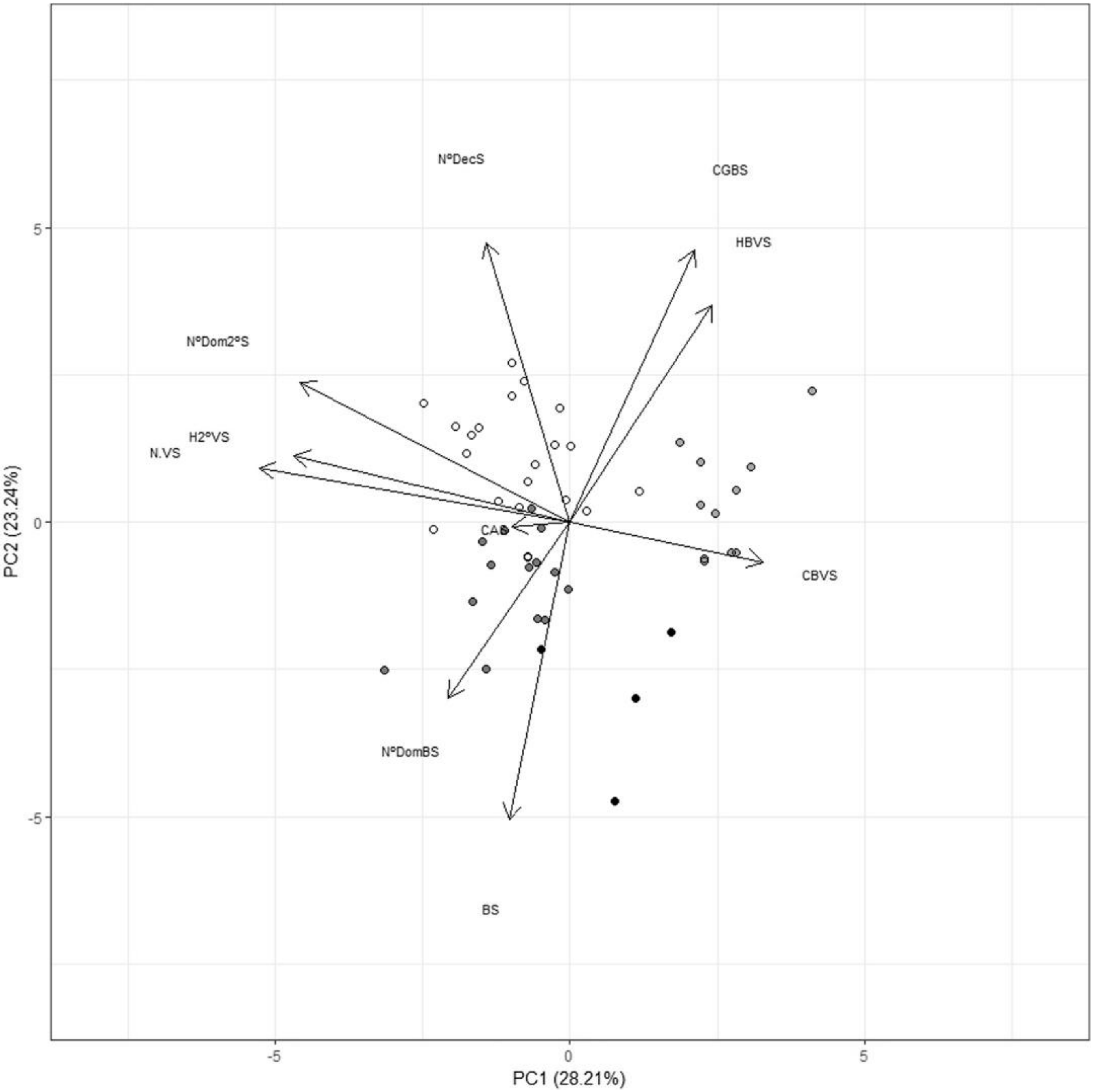


Figure 2. Principal components analysis of the pixels x structural indicators matrix of densely vegetated grasslands of the Basaltic “Cuesta.” The four groups were interpreted as phases (A: *white circles*, B: *light gray circles*, C: *dark gray circles*, D: *black circles*) within a same state. Structural indicators are as follows: Number of vegetation strata (N.VS), Height of the basal vegetation stratum (HBVS), Height of the second vegetation stratum (H2°VS), Coverage of the basal vegetation stratum (CBVS), Bare soil (BS), Coverage of grasses in basal stratum (CGBS), Coverage of annual species (CAS), Number of dominant species in the basal stratum (N°DomBS), Number of dominant species in the second stratum (N° Dom2°S), and Number of decreaser species (N° DecS).

and managers (Bestelmeyer et al., 2003; Briske et al., 2003). Such compilation could be more or less systematic. For example, Paruelo et al. (1993) explicitly recognize that the models presented for several vegetation units of the semiarid steppes of Patagonia are rough hypotheses based on the experience of range scientists. For some areas of the Rio de la Plata Grasslands, Oesterheld and Sala (1994) provide a systematic review of the empirical evidences to support the definitions of the states and transitions. However, those articles (and many others throughout different rangelands worldwide) did not derive states/phases from specific and systematic surveys. Such approaches can be defined as "deductive": States are derived from accumulated knowledge on rangeland structural heterogeneity and hypothesis on the drivers of transitions. States may alternatively define through an "inductive" process from field surveys of a large number of situations and their subsequent clustering according to their similarity. Of course, previous knowledge and experience influence the definition of the structural attributes to be recorded, but states and/or phases would result from the actual combination of such attributes.

An inductive definition of the grassland states/phases would provide an objective description of the structural and functional heterogeneity derived from anthropic activities. The probability of transitions between states, as well as the identification of the factors that promote them, is much more difficult to derive. Usually they result from an integration of knowledge on partial aspects, observational studies, and/or expert opinion (Knapp et al., 2011). The definition of the transitions among phases and states becomes a formalization of the hypotheses on the dynamics of the system, and their evaluation requires further analysis. Adaptive management (Holling, 1973; Berkes et al., 2000) is an ideal framework to evaluate and reformulate such hypotheses.

On the basis of the floristic heterogeneity defined by Lezama et al. (2019) and a detailed land use/cover map of the geomorphological regions with a larger proportion of natural grasslands, we presented an inductive approach to objectively define states/phases associated, a priori, to rangeland management. Specifically, we asked the following questions:

1. Does the heterogeneity within the mapped grassland communities represent alternative states of phases within one state?
2. Will these states and phases relate to their function?
3. Will the outcome of this inductive approach reveal states or phases that are recognizable to range managers?

Methods

Study Area

The Basaltic "Cuesta" region covers approximately 4.4 million ha (25% of the territory), and natural grasslands occupy 74.7% of this region (Baeza, 2017). These grasslands were characterized into two vegetation units (phytosociological communities) with different species composition and physiognomies that occurred on sites with different combinations of topography and soil properties. Sparsely vegetated grasslands (*Selaginella sellowii – Rostraria cristata* community [Lezama et al., 2019]), covering 24.8% of the Basaltic region, showed predominantly a two-layer structure covering around 60%. The upper layer was dominated by grasses and subshrubs and the lower by forbs and grasses. This community occurred mainly on shallow soils or directly above rocky outcrops. The densely vegetated grasslands (*Steinchisma hians-Piptochaetium stipoides* community [Lezama et al., 2019]), covering 49.8% of the area, were a closed-vegetation type, with two layers dominated by grasses and graminoids. This community occurred predominantly on deep soils on gentle low slopes, valleys, and plains. These communities defined on phytosociological inventory are associated with edaphic, topographical, and geomorphological variables, in such a way that they can be associated with the concept of "ecological sites" (Bestelmeyer et al., 2010). All the surveyed sites were under continuous grazing, and their structural conditions reflected both long- and short-term management conditions. Because sites were randomly selected, we did not have a record of past management for these specific areas.

Sampling Design

We used land cover maps and a recent cartography of grassland communities (Baeza et al., 2011; Baeza, 2017). A 10 x 10 km grid was overlapped on the community cartography, and 20 cells were chosen randomly. Within each square, five 1 x 1 km cells were selected randomly. Within each 1 x 1 km cell, two areas, belonging to each vegetation unit, including at least 90% of the same grassland community and corresponding with a MODIS pixel (250 x 250 m), were selected ("pure" pixels, Fig.1). For each pixel a qualitative description of macrotopography (high, medium, and low hillside); slope (pronounced, moderate, slight, null); and percentage of rockiness and stoniness was performed. Structural vegetation indicators were recorded in three 5 x 5 m plots between September and December 2014. Each plot was georeferenced and photographed.

Indicators Selection

The vegetation structural attributes were selected on the basis of the correlation with changes in ecosystem processes or structure, sensitivity to changes, responsiveness to livestock management, and a low cost-effectivity ratio (Table 1).

Structural Data Analysis

We constructed a matrix with average or mode values of the structural attributes for each plant community. We standardized

Table 2
Structural indicators (mode or mean ± standard deviation) of the four phases (A, B, C, and D) identified through principal component analysis and cluster analysis in densely vegetated grasslands of the Basaltic "Cuesta."

	Phase A	Phase B	Phase C	Phase D
N° of vegetation strata (mode)	2.00	1.00	2.00	1.00
Height of basal vegetation stratum (cm)	9.71 ± 4.41	10.75 ± 5.51	5.43 ± 2.16	4.75 ± 0.97
Height of second vegetation stratum (cm)	38.75 ± 19.76	—	33 ± 27.15	—
Coverage of basal vegetation stratum (%)	72.88 ± 18.87	98.61 ± 1.87	89.24 ± 7.6	83.75 ± 10.31
Bare soil (%)	1.28 ± 0.89	1.18 ± 1.06	3.8 ± 3.44	10.29 ± 6.43
Coverage of grasses in basal stratum (%)	90.6 ± 6.94	95.91 ± 4.11	76.11 ± 8.25	66.67 ± 14.14
Coverage of annual species (%)	0.53 ± 1.00	0.35 ± 0.42	0.81 ± 0.97	0.63 ± 0.95
Coverage of alien invasive species (%)	—	—	—	—
N° of dominant species in basal stratum	3.90 ± 0.92	3.64 ± 1.22	5.49 ± 1.16	4.25 ± 1.00
N° of dominant species in second stratum	2.45 ± 0.99	0.30 ± 0.41	2.04 ± 0.63	0.42 ± 0.32
N° of decreaser species	2.45 ± 1.47	1.45 ± 1.22	1.22 ± 1.05	0.17 ± 0.19

the variables and performed principal component analysis (PCA) and a hierarchical clustering analysis using Ward's method (Ward, 1963) (R Core Team, 2016) to group field observations according to their structural similarity and to identify "states" and "phases." The dominant plant species of the basal and second strata were grouped into 15 Plant Life Forms (PLF): Shrubs (S); Erect warm-season grasses (EWSG); Tussock warm-season grasses (TWSG); Prostrated warm-season grasses (PWSG), Cool-season grasses (CSG); Annual cool-season grasses (ACSG); Tussock cool-season grasses (TCSG); Graminoids (sedges and rushes) (Gr); Annual forbs (AF); Erect forbs (EF); Rosette forbs (RF); Legumes (L); Other (algae and mosses) (O); Subshrubs (SS); and *Selaginella sellowii* (Ssel). PLF frequency matrix was built for each phase and state of each community. If a PLF was present in the three quadrants of a pixel, a value 3 was assigned; if it was present in two of the three quadrants, 2; and if it was only represented in one quadrant, the assigned value was 1. We performed Discriminant Analysis (Stat Soft, Inc., 2007) to determine if the PLFs might be used to differentiate phases and states. In addition, a Discriminant Analysis using the environmental variables (position in landscape, slope, rockiness, and stoniness percentage) was carried out to evaluate differences among phases and states within a community.

The distinction between states and phases was based on the magnitude of changes in several structural indicators and on PLFs. Particularly, a state transition will be related to the presence of a third shrub stratum, an increase in the cover of strata 2 and 3, the abundance of alien invasive species, and the increase of bare soil. The transitions between phases would be possible through simple management actions such as alterations in the stocking rate, the sheep/cattle ratio, and/or the method of grazing (Bestelmeyer et al., 2010).

Functional Characterization of States/Phases

The ecosystem functioning of each grassland phase and state was characterized from the seasonal dynamics of the Normalized Difference Vegetation Index (NDVI) provided by the Mod13q1 product of MODIS (Moderate Resolution Imaging Spectroradiometer, collection 6). This product provides an image every 16 d, with a spatial resolution of 250 m (~6 ha). Each image was filtered using the quality band (Roy et al., 2002), and only those pixels without clouds or shadows and with low levels of aerosols in the atmosphere were analyzed. The NDVI values corresponded to the year in which the field samplings were made (23 images), and data were integrated on an annual basis for the period July–June.

The NDVI seasonal dynamics was also used to calculate an index of Ecosystem Services Supply (ESSI). The index was estimated for each field survey as ($NDVI_{average}$* [1-$NDVI_{CV}$]) (Paruelo et al., 2016), where $NDVI_{average}$ and $NDVI_{CV}$ are the annual average NDVI and the intra-annual coefficient of variation (average/STD), respectively. Such index was empirically related to different regulation or support ecosystem services (soil carbon stocks, hydrological yield, biodiversity) (Paruelo et al., 2016).

To analyze the seasonal dynamics for each grassland community phases, an analysis of variance (ANOVA) of repeated measures over time was used, with the phase being the dependent variable and the months of the year the repeated factor. To analyze differences in the NDVI annual average and ESSI among phases and states of each grassland community, a one-factor ANOVA was used, with the phase being the dependent variable. We used a *post hoc* Tukey HSD test to evaluate significant differences among phases of the same community.

We performed the same type of analysis, a structural and functional characterization of phases/states, for all the remaining mapped grasslands communities present in Uruguay. A summary of such information is presented as a supplementary material (Doc. S1, Table S1, Figs. S1, S2, S3, S4, S5; available online at https://doi.org/10.1016/j.rama.2019.06.004).

Management practices to promote transitions

Two workshops were held with ranchers and range extensionists at two different locations of the Basaltic Cuesta, Tacuarembó and Colonia Juan Gutiérrez, Paysandú, with 25 and 30

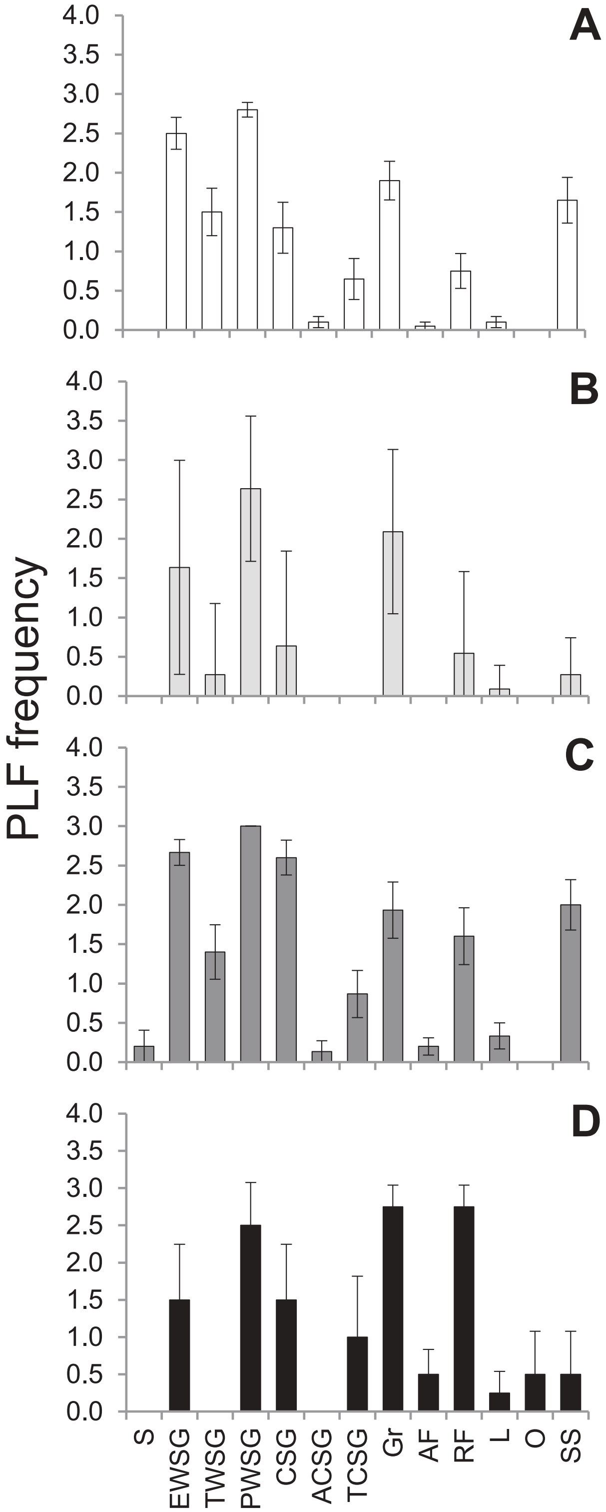


Figure 3. Plant life forms frequency of the four phases (A, B, C, and D) for densely vegetated grasslands of the Basaltic "Cuesta." Shrubs (S), Erect warm-season grasses (EWSG), Tussock warm-season grasses (TWSG), Prostrated warm-season grasses (PWSG), Cool-season grasses (CSG), Annual cool-season grasses (ACSG), Tussock cool-season grasses (TCSG), Graminoids (sedges and rushes) (Gr), Annual forbs (AF), Rosette forbs (RF), Legumes (L), Other (algae and mosses) (O), and Subshrubs (SS).

participants, respectively. The workshops consisted of two parts: an exposition on the characterization of the phases/states of each grassland community and, then, a group discussion. Each group was provided with a protocol including guiding questions and representative photos of each community phases (Doc. S2; available online at https://doi.org/10.1016/j.rama.2019.06.004). Finally, in a plenary session, each group presented the management practices to promote the desired transitions and explain their choice of the phase preferred.

Results

States and Phases Structural Description

Densely Vegetated Grasslands of the Basaltic "Cuesta" (Steinchisma hians-Piptochaetium stipoides community)

We surveyed 48 pixels (250 × 250 m) of this community. Through the PCA and cluster analysis, four groups of pixels were identified with differences in basal stratum height, second stratum

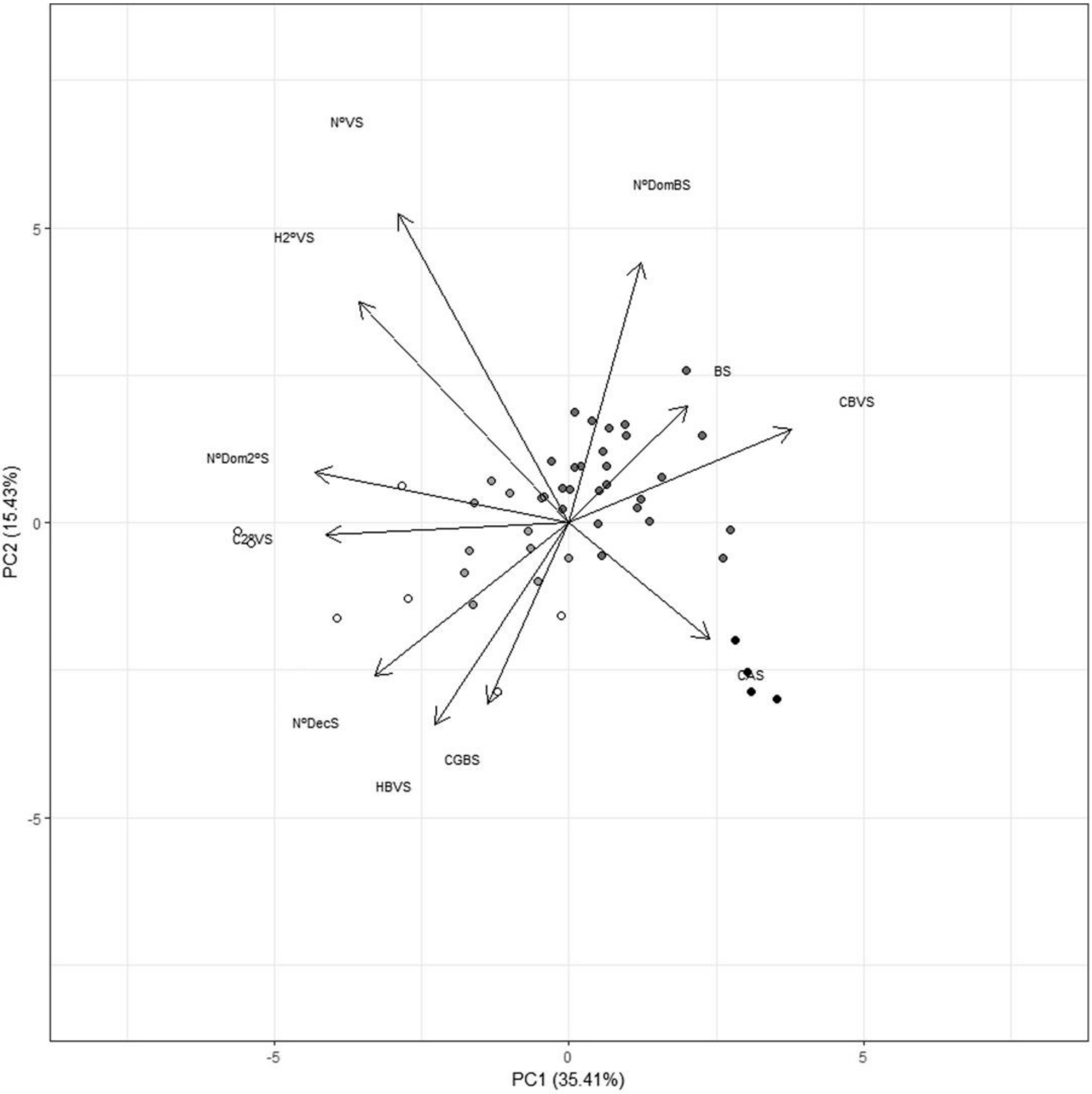


Figure 4. Principal components analysis of the pixels x structural indicators matrix of sparsely vegetated grasslands of the Basaltic "Cuesta." The four groups were interpreted as phases (A: *white circles*, B: *light gray circles*, C: *dark gray circles*, D: *black circles*) within a same state. Structural vegetation indicators are as follows: Number of vegetation strata (N° VS), Height of the basal vegetation stratum (HBVS), Height of the second vegetation stratum (H2°VS), Coverage of the basal vegetation stratum (CBVS), Bare soil (BS), Coverage of grasses in basal stratum (CGBS), Coverage of annual species (CAS), Number of dominant species in the basal stratum (N°DomBS), Number of dominant species in the second stratum (N° Dom2°S), and Number of decreaser species (N° DecS).

Table 3
Structural indicators (mode or mean ± standard deviation) of the four phases (A, B, C, and D) identified through principal component analysis and cluster analysis in sparsely vegetated grasslands of the Basaltic "Cuesta."

	Phase A	Phase B	Phase C	Phase D
N° of vegetation strata (mode)	2.00	2.00	2.00	1.00
Height of basal vegetation stratum (cm)	8.71 ± 1.85	4.88 ± 1.72	4.27 ± 1.62	4.25 ± 2.2
Height of second vegetation stratum (cm)	29.76 ± 2.38	28.33 ± 7.07	24.07 ± 7.48	—
Coverage of basal vegetation stratum (%)	49.86 ± 3.68	63.25 ± 5.37	90.53 ± 1.82	89.83 ± 2.85
Coverage of second vegetation stratum (%)	40.38 ± 1.99	18.64 ± 5.17	5.4 ± 6.13	—
Bare soil (%)	2.17 ± 0.7	3.47 ± 2.16	8.79 ± 7.14	8.17 ± 6.14
Coverage of grasses in basal stratum (%)	70.38 ± 18.8	61.81 ± 13.7	50.33 ± 3.47	62.5 ± 12.87
Coverage of annual species (%)	0.29 ± 0.19	0.54 ± 0.34	1.42 ± 1.56	4.00 ± 3.49
Coverage of alien invasive species (%)	—	—	—	—
N° of dominant species in basal stratum	4.43 ± 1.67	4.00 ± 0.83	5.19 ± 0.86	4.17 ± 1.04
Number of dominant species in second stratum	2.76 ± 1.56	1.36 ± 0.46	1.07 ± 0.54	—
N° of decreaser species	2.24 ± 1.15	1.14 ± 1.2	0.33 ± 0.54	0.42 ± 0.32

cover, grass cover, and number of decreaser species (Fig. 2, Table 2). The first two components accounted for 52.3% of the variance (28.9% and 23.4%, respectively). Due to the low magnitude and type of structural changes observed, the four groups were interpreted as phases within the same state.

Phase A was characterized by having a double stratum. The basal stratum is tall and dominated by grasses, with high cover and the presence of decreaser species. The second stratum, with < 30% of cover, was dominated mainly by tussock grasses (*Paspalum quadrifarium*, *Sporobolus indicus*, *Andropogon lateralis*, *Nassella charruana*) and sometimes with the presence of subshrubs of genus *Baccharis* and *Eryngium horridum*. Phase A was represented in 40% of the surveyed pixels. Phase B corresponds to grasslands with a single and tall vegetation stratum, with high grass cover, and the presence of decreaser species. Phase B was represented in 22% of the surveyed pixels. Pixels corresponding to Phase C have a basal stratum whose height was half of phases A and B, also dominated by grasses, with the presence of decreasers. The second stratum, with very low cover, was dominated by the subshrub *Baccharis trimera* and the grasses *N. charruana* and *S. indicus*. Phase C was represented in 30% of the surveyed pixels. Phase D represents grasslands with a single stratum with low height, dominated by grasses and without the presence of decreasing species. This phase was represented in 8% of the surveyed pixels (see Table 2).

The dominant species were grouped in 13 PLFs (Fig. 3). The Discriminant Analysis indicated significant differences between the PLFs spectra of different phases ($F_{(39,101)} = 2.62$, $P < 0.0001$). The differences are explained by tussock warm-season grasses, rosette forbs, and subshrubs frequencies. The result of the Discriminant Analysis performed with the environmental variables (rockiness, stoniness, position in the landscape, and slope) showed no differences among the phases ($F_{(15,\ 88)} = 1.59$, $P = 0.09$).

Sparsely Vegetated Grasslands of the Basaltic "Cuesta" (Selaginella sellowii – Rostraria cristata community)

The PCA and cluster analysis identified four groups corresponding to phases within the same state (Fig. 4). The first two components of the PCA accounted for 50.8% of the variance (35.4% and 15.4%, respectively). Such phases (A, B, C, and D) defined a gradient in which both the plant basal stratum height and the second highest stratum cover decrease (Table 3). Phase A was characterized by a basal stratum dominated by grasses, with the presence of decreaser species. The cover of the second stratum was variable and was dominated by the subshrub *Baccharis coridifolia*. The percentage of bare soil is low. This phase was represented in 15% of the surveyed sites. Phase B was characterized by a basal stratum with high grass cover, medium height, and the presence of decreaser species. The second stratum with low cover was dominated by *B. coridifolia* and *E. horridum*. The percentage of bare soil is higher than for phase A. This phase was represented in 25% of the surveyed pixels. Phase C presented a low-height basal stratum, with grasses and forbs in similar proportions and almost no decreaser species. Bare soil is also relatively high. In this phase, the second stratum —with 5% average cover—disappears. This is the most frequent phase, present in 52% of the surveyed pixels. Phase D was at the end of the gradient, with clear signs of degradation due to overgrazing. It presented a single, short stratum. This phase was represented in 8% of the surveyed sites (Table 3).

Dominant species were grouped into 14 PLFs (Fig. 5). The Discriminant Analysis indicated significant differences between the PLFs spectra of the different phases ($F_{(42,\ 92)} = 2.82$, $P < 0.0000$). The differences are explained by tussock cool-season grasses, annual cool-season grasses, graminoids, and subshrubs frequencies. The result of the Discriminant Analysis performed with the environmental variables (rockiness, stoniness, position in the landscape, and slope) indicated that there were no differences between the phases ($F_{(4,\ 18)} = 1.48$, $P = 0.25$).

States and Phases Functional Description

Densely Vegetated Grasslands of the Basaltic "Cuesta" (Mnesithea selloana – Piptochaetium stipoides community)

The phases defined for densely vegetated grasslands of the Basaltic "Cuesta" (except phase D, which was eliminated due to lack of replicates) showed significant differences in the annual average NDVI ($F = 8.15$, $DF = 2$, $P < 0.001$) and in NDVI monthly dynamics ($F = 2.81$, $DF = 24$, $P < 0.0001$) (Fig. 6). The Tukey HSD test showed significant differences between the phases for 10 out of 12 months analyzed, with phase B presenting the highest NDVI values throughout the year, followed by phase A and C. Maximum radiation absorption occurred in December in phase B, while in A and C phases occurred in January. On the contrary, the minimum photosynthetic activity coincided among phases (April 2015). The three analyzed phases showed an abrupt fall in the NDVI values in April 2015, the decrease being more pronounced for phase C. Phases B and C of these grasslands showed significant differences ($F = 3.81$, $DF = 2$, $P < 0.05$) in the Ecosystem Services Supply Index (ESSI). Phase B showed the greatest ecosystem service supply (Fig. 7A).

Sparsely Vegetated Grasslands in the Basaltic "Cuesta" (Selaginella sellowii – Rostraria cristata community)

The four defined phases for the sparsely vegetated grasslands of the Basaltic "Cuesta" did not show significant differences in the mean annual NDVI ($F = 1.35$, $DF = 3$, $P = 0.27$), but it did in its monthly dynamics ($F = 1.67$, $DF = 36$, $P < 0.05$) (Fig. 8). The honestly significant difference Tukey test showed significant differences between the phases for 5 out of 12 months analyzed. The maximum peak of photosynthetic activity coincided in all phases and occurred in January 2015. The minimum photosynthetic activity differed between phase A (May 2015) and phases B, C, and D (April 2015) (see Fig. 8). As in densely vegetated grasslands, the four analyzed phases showed an abrupt fall in the index values in April 2015, even more pronounced for phases C and D. No significant differences were found in the index of Ecosystem Services Supply (ESSI) ($F = 1.06$, $DF = 3$, $P = 0.38$) among the phases (see Fig. 7B).

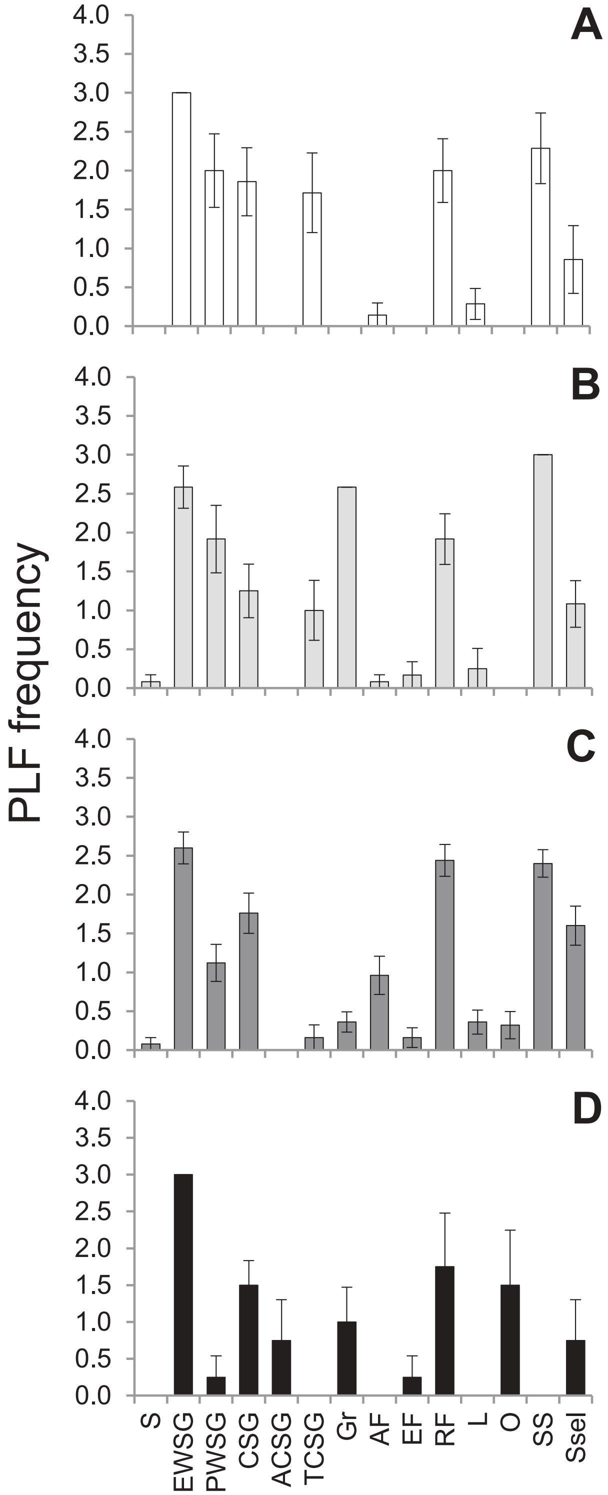


Figure 5. Plant life forms frequency of the four phases (A, B, C, and D) in sparsely vegetated grasslands of the Basaltic “Cuesta.” Shrubs (S), Erect warm-season grasses (EWSG), Prostrated warm-season grasses (PWSG), Cool-season grasses (CSG), Annual cool-season grasses (ACSG), Tussock cool-season grasses (TCSG), Graminoids (sedges and rushes) (Gr), Annual forbs (AF), Erect forbs (EF), Rosette forbs (RF), Legumes (L), Other (algae and mosses) (O), Subshrubs (SS), and *Selaginella sellowii* (Ssel).

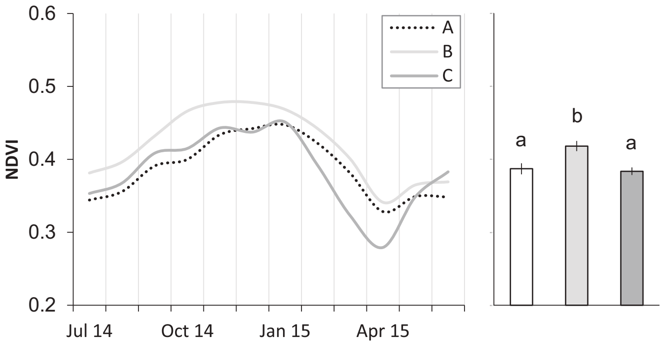


Figure 6. Monthly dynamic and annual average of the normalized difference vegetation index (NDVI) of phases A, B, and C for densely vegetated grasslands of the Basaltic “Cuesta.”

The results corresponding to the grasslands communities of the other geomorphological regions are presented in Table S1, Figs. S1, S2, S3, S4, S5; available online at https://doi.org/10.1016/j.rama.2019.06.004).

Management Practices to Promote Transitions

Densely Vegetated Grasslands in the Basaltic “Cuesta”

In the workshops, ranchers and extensionists recognized, on the basis of pictures and physiognomic descriptions, the phases that

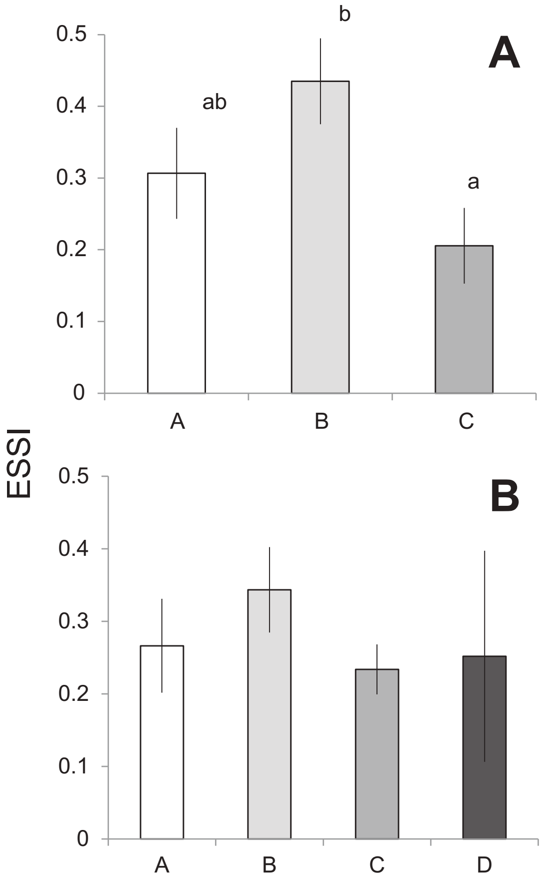


Figure 7. Ecosystem Services Supply Index (ESSI) calculated as ($NDVI_{average}$* [1-$NDVI_{CV}$]), where $NDVI_{average}$ and $NDVI_{CV}$ are the annual average NDVI and the intra-annual coefficient of variation (average/STD), respectively, of **A,** phases A, B, and C for densely vegetated grasslands; **B,** phases A, B, C, and D for sparsely vegetated grasslands of the Basaltic “Cuesta.”

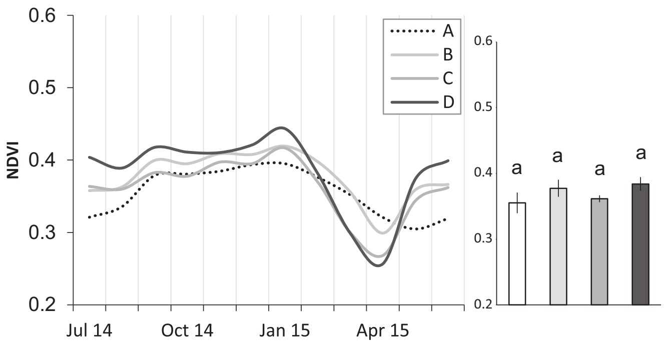


Figure 8. Monthly dynamic and annual average of the normalized difference vegetation index of phases A, B, C, and D for sparsely vegetated grasslands of the Basaltic "Cuesta."

resulted from grouping the field samples. They agreed to propose phase B as the most valued one for this community. Regarding the management practices determining the transitions, it was proposed that transition from phase B to A would result from low stocking rates (lower than a forage demand of 2200 kg dry matter.ha^{-1}.y^{-1}, Pereira, 2002) and a low sheep/cattle ratio (< 1). Transition from A to B requires changes in the grazing method, from continuous to deferred stocking. Transitions from B to C would be determined by higher stocking rates and sheep/cattle ratios > 1. Phase D would result from extreme values in sheep/cattle ratios and even higher stocking rates. Continuous grazing was identified as a factor leading to the transition to phase C and D (Fig. 9A).

Sparsely Vegetated Grasslands of Basaltic "Cuesta"

All ranchers and extensionists groups identified the phases described and agreed on choosing phase B as the most valued one, even though they also value the presence of patches corresponding to phase A. Regarding the management practices determining the transitions, it was proposed that phase A would result from very low stocking rates (< forage demand of 1 380 kg dry matter.ha^{-1}.y^{-1}, Pereira, 2002) and a sheep/cattle ratio < 1. Moderate livestock stocking rates (≈ 1 664 kg dry matter.ha^{-1}.y^{-1} of forage demand, Pereira, 2002) and sheep/cattle ratio close to 1 would determine transitions to phase B. Phase C would result from higher stocking rates and a sheep/cattle ratio > 1. The extreme values of stocking rate and sheep/cattle ratio would lead the system to phase D. Some groups of ranchers and extensionists proposed to incorporate a second state with high coverage of a third shrub stratum into the model, but such a state was not detected in field samplings. In this community the stakeholders did not identify the grazing method as responsible for any phase transition (see Fig. 9B).

Forage supply was the main criteria to select the most valuable phases. Stakeholders based their choice on the quantity and quality in forage production, the magnitude of purchased inputs (the lowest), and the stability under extreme climatic events and management contingencies.

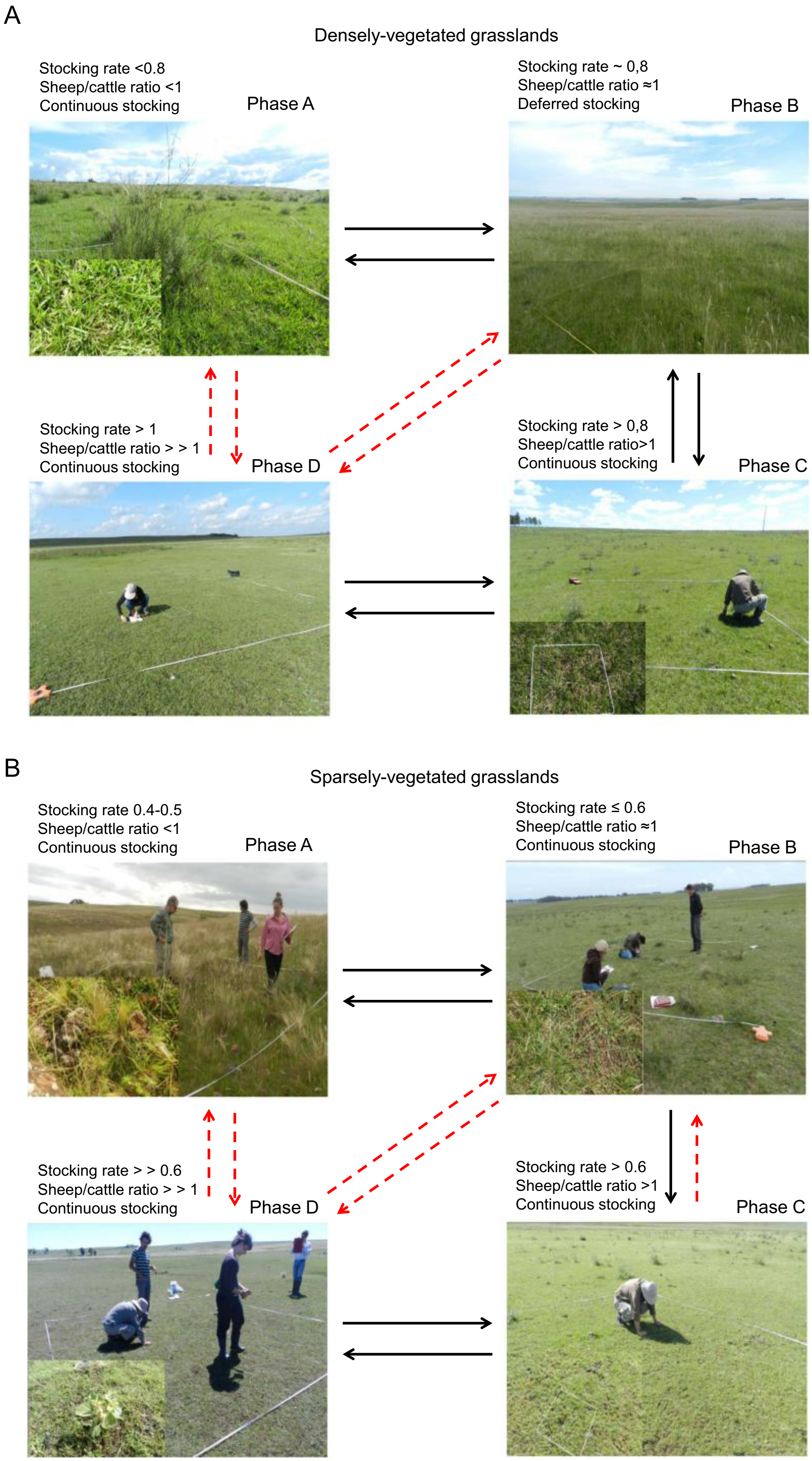
Discussion

1. Does the heterogeneity within the mapped grassland communities represent alternative states of phases within one state?

The two grassland communities studied presented an internal heterogeneity associated with changes in the basal stratum height, total cover, stratification, frequency of decreaser species, and the proportion of different plant life forms. The inductive approach used in this study facilitated an objective description beyond "states," identifying subtle changes in vegetation within them ("phases").The randomly based design of the survey and a priori definition of the attributes to be measured minimized the biases associated with individual experience and the differences derived from different observation protocols. Sampling randomization determined that particular situations (e.g., extreme degradation) were not surveyed; however, it allowed us to quantify the area occupied by the different phases. For the Basaltic "Cuesta" region, on the basis of the criteria defined, we did not identify grasslands in different states. The structural heterogeneity is compatible with a differentiation of phases because we did not detect the occurrence of a third shrub layer with high coverage, the presence of alien invasive species, or areas with a high proportion of bare soil. Different states were identified for other geomorphological regions and communities (Fig. S5; available online at https://doi.org/10.1016/j.rama.2019.06.004). The transitions between phases would be gradual and reversible, and they would result from changes in stocking rate, sheep/cattle ratios, or the grazing system. Grazing prevents competitive exclusion. Even at intermediate stocking rates, grazing promotes the increase of richness and productivity (Altesor et al., 2005, 2006). As the intensity of grazing increases, biomass gets concentrated close to the ground and the percentage of grasses decreases, giving space for the establishment of rosette forbs (Rodríguez et al., 2003). The differential selectivity of sheep and cattle promotes a double stratification of the canopy. At very high stock densities, richness may decrease, facilitating the invasion by exotic species and increasing soil erosion.

This study described the internal heterogeneity of two vegetation units or phytosociological communities (Lezama et al., 2019). Such communities corresponded to the "ecological sites" described in, mainly, the North American literature on STM (Stringham et al., 2003; Bestelmeyer et al., 2003, 2010; Knapp et al., 2011; Bestelmeyer, 2015). A previous definition of phytosociological communities made it possible to minimize the effect of environmental conditions and habitat characteristics as determinants of the observed heterogeneity. The magnitude and hierarchy of the structural and floristic variation observed in our study were smaller than the differences between communities. In all cases, the indicator species of the respective communities were observed (Lezama et al., 2019), confirming than the site corresponds to either one or another vegetation unit. However, from a strictly floristic point of view, the two communities studied are not homogenous. Lezama et al. (2019) identified two subcommunities with their own indicator species. To what extent are the subcommunities associated with the phases described? The characteristics of our survey do not enable us to answer this question since the subcommunities indicator species were not recorded. The question on relationship between the phases described here and the floristic differences among subcommunities is an interesting one, and its answer requires a specific experimental approach.

Having controlled the edaphic and topographic variation, the factor that presents the greatest variation among the studied sites is grazing management. Grazing includes various components such as defoliation, trampling, and fertilization through feces and urine deposition. Such components act simultaneously on vegetation, promoting individual and combined effects on different structural and functional attributes (Lezama and Paruelo, 2016). The characterized phases result from the combined effect of the grazing history of the site. What "memory" does the system have of past grazing conditions? To answer this question, either studies on the vegetation trajectory or an exhaustive record of the grazing syndrome experienced by each particular site will be needed. The combination of experimental manipulative studies—such as Lezama and Paruelo (2016)—with retrospective observational studies and experiences of controlled grazing management lays the basis for the generation of specific hypotheses on structural and functional changes, as well as their reversibility.


A
Densely-vegetated grasslands
Stocking rate <0.8
Sheep/cattle ratio <1
Continuous stocking
Phase A
Stocking rate ~ 0,8
Sheep/cattle ratio ≈1
Deferred stocking
Phase B
Stocking rate > 1
Sheep/cattle ratio > > 1
Continuous stocking
Phase D
Stocking rate > 0,8
Sheep/cattle ratio>1
Continuous stocking
Phase C
B
Sparsely-vegetated grasslands
Stocking rate 0.4-0.5
Sheep/cattle ratio <1
Continuous stocking
Phase A
Stocking rate ≤ 0.6
Sheep/cattle ratio ≈1
Continuous stocking
Phase B
Stocking rate > > 0.6
Sheep/cattle ratio > > 1
Continuous stocking
Phase D
Stocking rate > 0.6
Sheep/cattle ratio >1
Continuous stocking
Phase C

Other factors, besides grazing, could explain in a complementary or alternative way the observed intracommunity heterogeneity. Although the surveys were concentrated over time, the climatic conditions were not homogeneous and may account for part of the differences observed. Moreover, climate can also have a medium and long-term effect (Briske et al., 2005). Differences in the magnitude of summer droughts experienced by the different sites are, clearly, another factor that contributes to generate heterogeneity and interacts with the different dimensions of the grazing syndrome. Finally, legacies (e.g., agricultural history) or particular events (e.g., fires) are potential factors that could generate spatial heterogeneity (Foster et al., 2003).

2. Will these states and phases relate to their function?

Despite the relative physiognomic homogeneity between the phases of the same state and the same grassland community and region, MODIS images allowed us to detect subtle intracommunity differences in carbon gains dynamics and in ecosystem services supply derived a priori from livestock management. The seasonal dynamics of the NDVI for the grassland phases was, in general, similar to the pattern described in other studies (Baeza et al., 2010, 2011; Guido et al., 2014). Each phase responded differently in terms of NDVI dynamics to extreme weather events. During the months of the period February to April 2015, a large part of Uruguay was under a severe water deficit event. The average accumulated rainfall in the February-April period for the past 15 yr, for Basaltic "Cuesta" was 346 mm (INIA, Tacuarembó, 2018). During the analyzed period (February to April 2015), the accumulated precipitation for this region was 92 mm, only 26% of the historical average. Those phases with low height and basal stratum vegetal cover, as well as with low second stratum cover, showed an abrupt fall in NDVI (see phases C and D in dense and sparsely vegetated grasslands) and, therefore, in their productivity (see Figs. 6 and 8).

Our results showed a differential sensitivity of the phases to stress (water deficit) and/or disturbance (grazing) events. This would result in differences in stability and resilience between the different phases. Particularly, phases A and B of both communities of the Basaltic "Cuesta" (densely and sparsely vegetated grasslands) showed a greater capacity to absorb the disturbance associated to the drought event.

Ecosystem services supply, evaluated by means of a synoptic index (ESSI) (Paruelo et al., 2016), showed differences between phases that varied according to the grassland community considered. Low ESSI values were associated with a high proportion of bare soil, which in turn result in lower annual productivity. An annualization of the system or the loss of C_3 species, which in general decreased their cover with grazing, would determine a greater seasonality and a higher coefficient variation reducing the value of the ESSI. In a recent regional study, Texeira et al. (2019) showed that most of the negative trends in C gains observed in the Basaltic Cuesta were associated with seasonality increase and vegetation loss syndromes. Associated with this, a series of final ecosystem services, such as the capacity of C sequestration or soil loss regulation, would be affected, as was empirically shown by Paruelo et al. (2016).

3. Will the outcome of this inductive approach reveal states or phases that are recognizable to range managers?

Both ranchers and range extensionists recognized the phases identified using the inductive approach. Stakeholders value STMs as a management tool that minimize risks and take advantage of opportunities to promote or avoid particular transitions. They identified the stocking rate, sheep/cattle ratio, and grazing method (fundamentally the existence of resting periods in paddocks) as the main management practices that may promote the transition between phases. The design of mensurative experiments in the framework of an adaptive management process will assess the capacity of these factors to modify the portion of the landscape occupied by the different phases and the interaction of livestock management with climatic factors.

Implications

Our results highlighted an important issue related to grassland conservation: Uruguayan rangelands presented a relatively functional conservation status. Our systematic and objective approach identified only reversible phases for the grasslands of a large subregion of the country (the Basaltic Cuesta). This can be a key piece of information to value Uruguayan meat on international markets. Meat production systems based on grasslands can meet high environmental standards on biodiversity conservation and ecosystem services production. Recognizing the heterogeneity derived from management practices within phytosociological units (or ecological sites) is quite important to assess vulnerability. Sparse grasslands, one of the phytosociological units identified in Uruguay, experience a larger level of degradation than the other one (dense grasslands).

The relatively small structural changes observed may induce range managers to ignore grasslands heterogeneity. However, subtle differences in plant life forms composition determine important differences in animal performance. For both grasslands units (phytosociological communities), phases were associated with changes that determine animal performance: proportion of preferred species, forage accessibility, and vulnerability to extreme drought events.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2019.06.004.

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Figure 9. Representative photos of phases A, B, C, and D (insert photos with greater detail) described in **A,** densely vegetated and **B,** Sparsely vegetated grasslands of Basaltic "Cuesta" and the management practices determining the transitions derived from the workshops with ranchers and extensionists. Those transitions among phases belonging to one state that are reversible through changes in the grazing system (stocking rate, sheep/cattle ratio, and grazing method) are indicated by *solid black arrows.* The less frequent and more difficult transitions are indicated by *dashed red lines.*

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