Austral Ecology A Journal of ecology in the Southern Hemisphere

Austral Ecology (2020) ●●, ●●–●●

Distinct ecosystem types respond differentially to grazing exclosure

FEDERICO GALLEGO,[1]* JOSÉ M. PARUELO,[1,2,3] SANTIAGO BAEZA[4] AND ALICE ALTESOR[1]

[1]*Instituto de Ecología y Ciencias Ambientales, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo, Uruguay (Email: fgallego@fcien.edu.uy);* [2]*Laboratorio de Análisis Regional y Teledetección, Depto. Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía and IFEVA, UBA and CONICET, Buenos Aires, Argentina;* [3]*Instituto Nacional de Investigación Agropecuaria, Montevideo, Uruguay; and* [4]*Departamento de Sistemas Ambientales, Facultad de Agronomía, Universidad de la República, Montevideo, Uruguay*

Abstract Here, we evaluate the ecosystem functioning and the ecosystems services supply of different vegetation types (grasslands, shrublands and woodlands) under contrasting management regimes by comparing a protected area with the surrounding landscape, which has been subjected to human disturbance in the Eastern Hills of Uruguay. We propose, based on functional attributes and vegetation physiognomy, a State and Transition Model for the dynamics of the grassland–woodland mosaic. We used remote sensing techniques to: (i) develop a land-cover map of the study area based on supervised Landsat imagery classification, and (ii) compare attributes of the ecosystem functioning (productivity and seasonality) and service supply derived from the Normalized Difference Vegetation Index (NDVI) images provided by the moderate resolution imaging spectroradiometer (MODIS) sensor. The land-cover map showed that grasslands and shrublands were the most extensive land covers in the study area. These vegetation types presented higher productivity, seasonality and ecosystem service supply, outside the protected area than inside it. On the other hand, woodlands showed higher productivity, ecosystem service supply and lower seasonality inside the protected area than outside of it. Two axes represented the grassland–woodland mosaic dynamic: (i) the mean annual and (ii) the intra-annual coefficient of variation of the NDVI. Our results highlight that conservation of grasslands, shrublands and woodlands require different management strategies based on particular disturbance regimes like moderate grazing and controlled burns. Moderate disturbances may help to preserve ecosystem services provisioning in grasslands and shrublands. On the contrary, woodland conservation requires a more rigorous regime of protection against disturbances.

Key words: ecosystem services, grassland, Normalized Difference Vegetation Index, remote sensing, state and transition model, woodland mosaic ecosystem.

INTRODUCTION

Temperate grasslands, savannas and shrublands exhibit the highest Conservation Risk Index, with 70.5% of the area converted to 3.66% protected (Watson *et al.* 2016). These ecosystems are poorly conserved despite their fauna and flora richness, including many endemics (Henwood 2010; Bond & Parr 2010; Andrade *et al.* 2018). Grassland conservation depends not only on the expansion of the protected areas network but also on defining management strategies based on the understanding of the role of disturbances on the structure, composition, and functioning of these ecosystems.

Disturbances such as grazing or fire are excluded from conservation areas as they are perceived by some land managers as incompatible with the preservation of natural ecosystems. However, this approach has changed in many parts of the world (i.e. Australian and Mediterranean grasslands) and, in many cases, livestock grazing is included as a management tool to achieve a variety of conservation goals (i.e. to maintain biodiversity, to prevent invasion or encroachment by undesirable species, and to provide habitats to rare or endemic species) (Perevolotsky & Seligman 1998; Dorrough & Ash 2003; Lunt *et al.* 2007; Cingolani *et al.* 2008). The use of grazing and fire in protected areas is a controversial issue. Several models can explain the variable effect of disturbances on diversity, floristic composition and ecosystem functioning. These models include different factors like habitat productivity (Milchunas *et al.* 1988), grazing intensity (Connell 1978) and type of herbivore (Olff & Ritchie 1998), among others. Lezama *et al.* (2014) evaluated the grazing effects along a regional productivity gradient

*Corresponding author.

Accepted for publication January 2020.

doi:10.1111/aec.12870

through a comparison of 23 pairs of grazed and ungrazed plots in South American grasslands. Their findings support the idea that the magnitude of grazing effects on vegetation structure (richness and composition of species and plant functional types) increases along the productivity gradient. In Uruguay, which belongs to the Rio de la Plata Grasslands (Soriano 1992), several studies showed that the absence of grazing promoted shrub increase (Altesor *et al.* 2006), reduced species richness (Rodríguez *et al.* 2003) and reduced productivity (Altesor *et al.* 2005).

A central issue in conservation biology is the type of management applied in different protected ecosystems (Pelkey *et al.* 2000; Lunt *et al.* 2007; Cingolani *et al.* 2008). Currently, there is an active debate on the conservation of biodiversity in the grasslands-forest mosaic of South America (Luza *et al.* 2014; Overbeck *et al.* 2016; Carlucci *et al.* 2016). Two different perspectives have been raised on the role of disturbances in conservation. On the one hand, Luza *et al.* (2014) propose the use of passive management (without burning and livestock grazing) and the precautionary principle in the conservation of grasslands-forest mosaic ecosystems. On the other hand, Overbeck *et al.* (2016) support the idea that different types of ecosystems should have different conservation strategies where disturbances (i.e. grazing or fire) play a crucial role.

State and Transition Models (STM; Westoby *et al.* 1989) describe non-equilibrium dynamics derived from disturbances (i.e. grazing and fire) or climatic events. Such a framework may be appropriate to describe the grassland–woodland mosaic dynamics. The different states of the dynamical model would have a differential supply of ecosystem services (ES). The ecosystem services concept allows us to link ecosystem properties with human well-being (Boyd & Banzhaf 2007). Paruelo *et al.* (2016) proposed an index to describe the Ecosystem Services Supply (ESSI) in the Chaco-Pampean Plains of South America. The index is related to biodiversity (avian richness), carbon (soil carbon sequestration) and water dynamics (evapotranspiration and groundwater recharge), and is based on two functional attributes that can be monitored continuously over time and space by remote sensing. These two attributes are derived from the seasonal dynamics of the Normalized Difference Vegetation Index (NDVI): the annual mean, an indicator of light interception and hence of total carbon gains, and the intra-annual coefficient of variation of the NDVI, a descriptor of seasonality. The NDVI is one of the most widely used vegetation indexes and shows a positive relationship with the fraction of photosynthetically active radiation absorbed by green vegetation and hence with productivity (Pettorelli 2013).

In this study, we evaluate the ecosystem functioning and services supply of different vegetation types (grasslands, shrublands and woodlands) under contrasting management regimes by comparing a protected area with the surrounding landscape, which has been subjected to human disturbance. We address the following questions:

1. Does the type of management, applied inside and outside a protected area, modify the structural and functional characteristics and consequently, ecosystem services supply of different vegetation types?
2. Do different structural states of the vegetation differ in functional attributes?
3. What would be the best strategy to preserve grasslands and woodlands in the region?

METHODS

Study area

We conducted the study in the Paisaje Protegido Quebrada de los Cuervos (PPQC) and its buffer area. The protected area is located in the Eastern Hills region, Uruguay (32°46′–33°03′S, 54°36′–54°20′W) measuring a total of 2.5×10^6 ha that includes grasslands, shrublands and woodlands. Grasslands and shrublands cover most of the area and woodlands are arranged in small patches located on rocky slopes and gorges and cover less than 10% of the landscape (Lezama *et al.* 2019; Baeza *et al.* 2019).

The PPQC occupies about 4412 ha, of which 62.5% is public, and 37.5 % is private. The area was formally included in the National System of Protected Areas in 2008; however, most of the area (3100 ha) has been protected since the 1980s (Villalba *et al.* 1998). The protected area includes two levels of protection: an area of 365 ha where anthropic activity has been excluded since 1986 (Exclusion area, EA) and the remaining area whose management plan includes touristic activities and livestock production at low stocking rates (Protected area, PA). The buffer area (BA) is 100% private-owned and totals 36 000 ha (SISNAP 2017). The local climate is temperate with a mean annual precipitation of 1450 mm and a mean annual temperature of 17°C for the period 2000–2016 (INIA meteorological station).

Land-cover map

We constructed a land-cover map for the PPQC and BA based on field samples and remote sensing data. Native land covers were defined in terms of physiognomic units: (i) sparsely vegetated grasslands (characterised by meso-xerophytic species on shallow or very shallow soils), (ii) densely vegetated grasslands (dominated by mesophytic species on medium and deep soils), (iii) tall grasses & shrublands (dominated by mesophytic species associated with moderate or concave slopes) and (iv) woodlands (dominated by

doi:10.1111/aec.12870

woody species occupying valleys and moderate to pronounced rocky slopes) (Gautreau & Lezama 2009; Lezama *et al.* 2019). Two anthropogenic land covers were also present in the area: winter crops and afforestation. One scene (Path: 223; Row: 083) and three dates were used (30 April 2010, 05 September 2010 and 16 December 2010) to detect phenological differences in vegetation (Guerschman *et al.* 2003). Images were radiometrically and atmospherically corrected to make spectral information comparable both in time and space.

A supervised classification of Landsat TM imagery (30×30 m) was performed, and 135 observations (registered with GPS) were collected in the field. Training and control polygons were digitalised to generate and evaluate the map. Afforestation was identified by interpretation of Landsat images (2012–2013) and field observations, and subsequently overlapped on the final map. The spectral information of 18 reflective bands (six bands for each date) of all pixels included in the training polygons and maximum likelihood decision rule were used to classify the pixels. We applied a 3×3 pixel mobile mode filter to the final map to reduce the flecked high-density appearance usually present in this type of classifications. To evaluate the precision of the classification, we calculated the overall accuracy, Kappa coefficient, and producer and user's precisions from a contingency matrix.

Ecosystem Services Supply Index

We compared the ecosystem functioning and ESSI among the buffer area and the two levels of protection, for each land cover. We used NDVI from the MODIS sensor (collection 6, Mod13q1). The NDVI was calculated, taking into account the reflectance in the red (R) and infrared (IR) portions of the electromagnetic spectrum [$\text{NDVI} = (\text{IR} - \text{R})/(\text{IR} + \text{R})$]. NDVI images consisted of a gridded 16-day composite with a 250 m pixel size (~6 ha). We used an NDVI time series covering the period 2001–2015 (345 images). Each NDVI image was filtered using its associated 'per pixel' quality image (Roy *et al.* 2002), and only those pixels without clouds or shadows, and with low levels of aerosols in the atmosphere were analysed. Pixels that did not have the highest quality were discarded and their values replaced by simple linear interpolation from the previous and the following dates of the same pixel.

Based on the NDVI, we estimated two attributes of the ecosystem functioning: the annual NDVI integral (NDVI-I) and the NDVI coefficient of variation (NDVI-CV). Based on these attributes, we calculated the mean ES supply index as [$\text{ESSI} = \text{NDVI}_{\text{mean}} * (1 - \text{NDVI}_{\text{CV}})$] (Paruelo *et al.* 2016). We selected MODIS pixels that included at least 95% of the same land cover. We also checked, based on recent images from Google Earth, that selected pixels had not changed since 2010 when the land-cover map was generated.

The land covers analysed for the comparison between EA and BA were as follows: tall grasses & shrublands (12 pixels) and woodlands (four pixels); and for PA *vs.* BA were as follows: sparsely vegetated grasslands (32 pixels), tall grasses & shrublands (85 pixels) and woodlands (20 pixels). Densely vegetated grasslands were not compared because they cover a small area in PA or EA.

State and transition model

A State and Transition Model (STM) for the grassland–woodland mosaic ecosystem (sparsely vegetated grasslands, tall grasses & shrublands and woodlands) was generated based on functional attributes (NDVI-I and NDVI-CV) and vegetation physiognomy under different management regimes (EA, PA and BA). Also, we illustrated the STM with a sequence of Google Earth images of the EA for the period 1985–2015 (30 years).

Statistical analysis

We compared functional attributes (NDVI-I and NDVI-CV) and ESSI of each land cover through time using a 'factorial repeated measure in time' ANOVA, with one between-subjects factor with two levels (land protection: protected/non-protected) and one within-subjects factor with 15 levels: individual years). Before the test, we checked that the data met the assumptions of normality (Shapiro–Wilk test), homogeneity of variances (Levene's test) and sphericity (Mauchly's test). A Greenhouse–Geisser correction was used when the assumption of sphericity was violated. Finally, we used a post hoc Tukey HSD test (Zar 1996) for pairwise comparisons. Statistical analyses were performed with STATISTICA 6.0. (Statsoft, Inc. Tulsa, OK, USA).

RESULTS

Land-cover map

Natural grasslands covered 49% of the studied area. Of the 100 000 ha classified, approximately 33% corresponded to sparsely vegetated grasslands, 31% to tall grasses & shrublands, 16% to densely vegetated grasslands, 14.5% to afforestation, 4.4% to woodlands and 0.5% to winter crops (Fig. 1). The contingency matrix showed an overall accuracy of the classification of 99.4% and Kappa coefficient value of 0.9 (Table S1). The producer and user's exactitude showed similar levels and high accuracy for all land covers, which indicates robust similarity between the field data and the classification (Table S2).

Ecosystem Services Supply Index

The comparison between the excluded site inside the protected area (EA) and the buffer area (BA) showed significant differences in the ES supply. The ES Supply Index average (2001–2015) for tall grasses & shrublands was 15% higher outside the exclusion area than inside of it (significant interaction $F_{\text{ESSI}} = 46.442$; d.f. = 14; $P < 0.0001$; Table S3). The ESSI showed the opposite pattern for woodlands. The ES Supply was significantly higher inside the exclusion area than in the buffer area

doi:10.1111/aec.12870

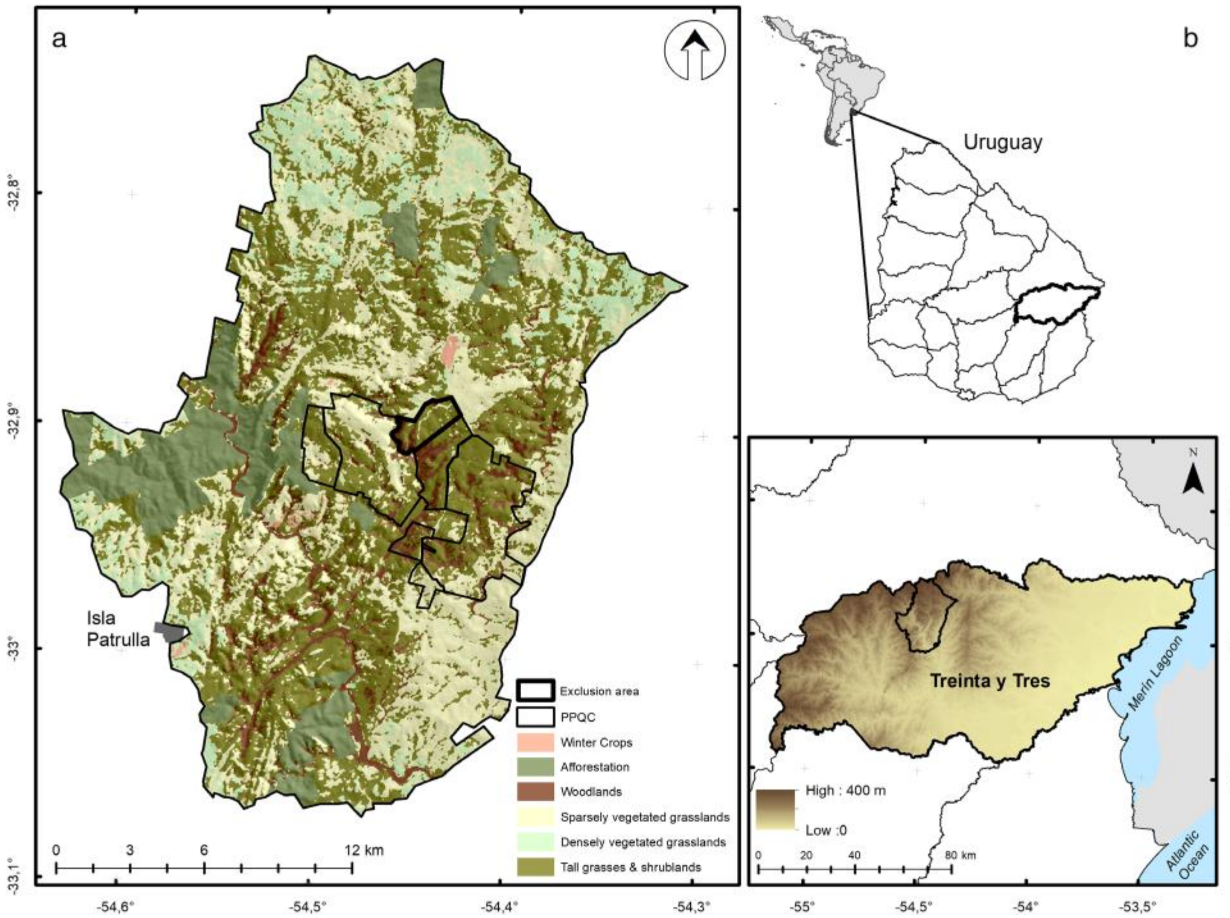

Fig. 1. (a) Land-cover map for the Paisaje Protegido Quebrada de los Cuervos (PPQC) and buffer area (BA). (b) Study area and its location in Uruguayan territory.

for most of the analysed years (significant interaction $F_{ESSI} = 2.577$; d.f. = 14; $P < 0.01$; Table S3) (Fig. 2).

The comparison of the ES Supply Index average (2001–2015) for the three land covers between protected (PA) and buffer area (BA) showed differences. The ES supply of sparsely vegetated grasslands and tall grasses & shrublands was 54% and 8% higher, respectively, outside the protected area than inside of it (significant interaction $F_{ESSI} = 12.149$; d.f. = 14; $P < 0.0001$; $F_{ESSI} = 10.551$; d.f. = 14; $P < 0.0001$, respectively; Table S3). In contrast, the ESSI values for woodlands were higher inside than outside the protected area (significant interaction $F_{ESSI} = 3.148$; d.f. = 14; $P < 0.001$; Table S3) (Fig. 2).

State and transition model

The STM formalised our hypotheses on the land-cover dynamics of the Eastern Hills. The model included three states, each one with two phases (Fig. 3). States differed in two main axes: (i) the mean annual NDVI-I and (ii) the intra-annual NDVI-CV. Sparsely vegetated grasslands (State 1) showed the lowest values of NDVI-I and the highest coefficient of variation. tall grasses & shrublands (State 2) were characterised by intermediate values of mean NDVI-I and NDVI-CV. Woodlands (State 3) presented the highest NDVI-I and the lowest seasonality (significant interaction $F_{NDVI-I} = 24.93$; d.f. = 28; $P < 0.0001$; $F_{NDVI-CV} = 36.57$; d.f. = 14; $P < 0.0001$; Fig. 3). The comparison between inside and outside the protected area allowed us to identify two phases within each state. For sparsely vegetated grasslands, the Phase I (under protection) was characterised by 10% lower NDVI-I values (significant interaction $F = 10.22$; d.f. = 14; $P < 0.0001$; Table S3) and NDVI-CV (significant interaction $F = 8.81$; d.f. = 14; $P < 0.0001$; Table S3) than Phase II (unprotected). For tall grasses & shrublands, Phase I (under protection) was characterised by lower values of NDVI-I (significant interaction $F = 5.6$; d.f. = 14; $P < 0.0001$; Table S3) and NDVI-CV (significant interaction $F = 13.64$; d.f. = 14; $P < 0.0001$; Table S3) than Phase II (unprotected). The phases defined for woodlands

doi:10.1111/aec.12870

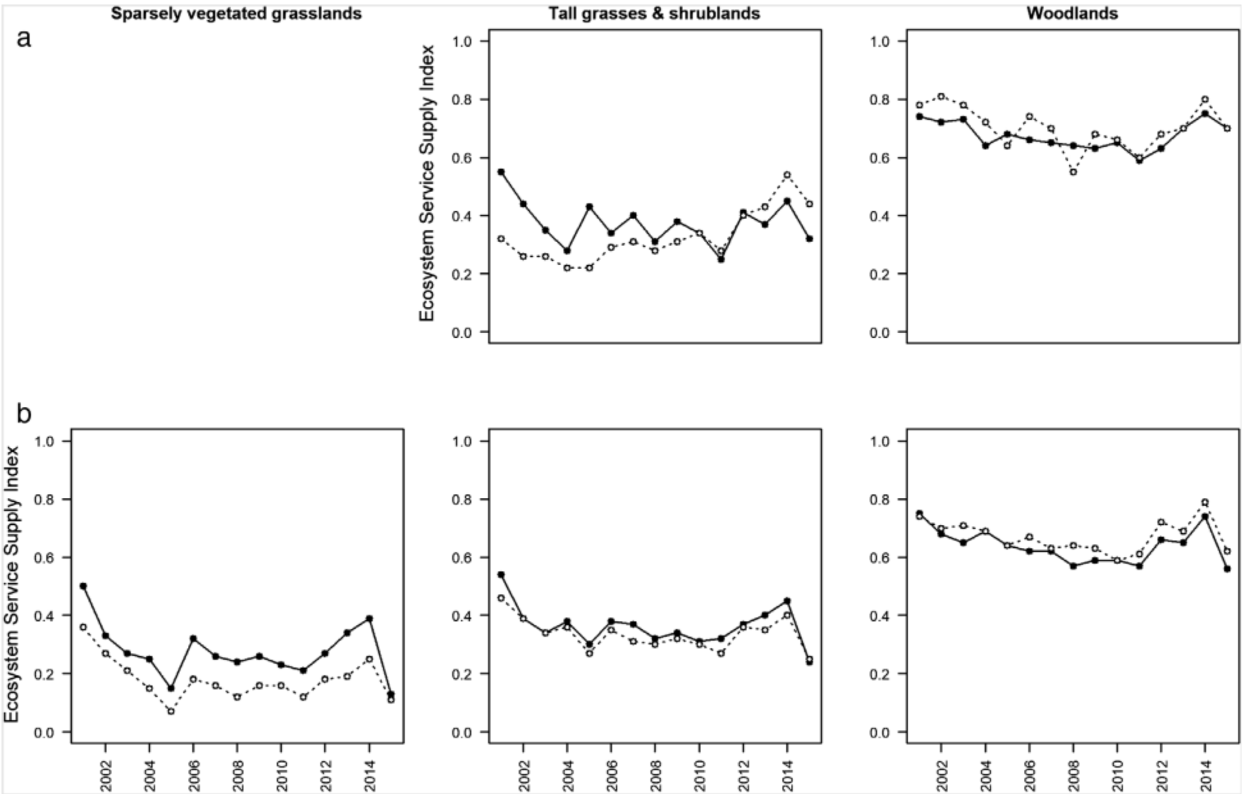

Fig. 2. Annual Ecosystem Service Supply Index dynamic for the land covers in (a) exclusion area (EA, dotted line) *vs.* buffer area (BA, solid line) comparison and (b) protected area (PA, dotted line) *vs.* buffer area (BA, solid line) comparison.

showed the opposite pattern. Phase I (under protection) showed higher productivity (significant interaction $F = 4.36$; d.f. = 14; $P < 0.0001$; Table S3) and less variability in NDVI (significant interaction $F = 2.324$; d.f. = 14; $P < 0.01$; Table S3) than Phase II (unprotected) (Fig. 3).

The evaluation of Google Earth images of the EA showed structural vegetation changes over 30 years (1985–2015) compatible with the proposed STM. The vegetation of the EA changed from sparsely vegetated grasslands to tall grasses & shrublands and finally, woodlands (Fig. 4). These images constitute graphic evidence of the transitions between the states of the model. Transitions can occur between phases within the same state or between states. In the first case (between phases), we hypothesised that transitions are faster and can be in both directions. In the second, transitions may be slower and occur in one direction (grasslands to woodlands). The opposite transition would be less likely.

DISCUSSION

High protection levels, like exclusion areas, may either increase or decrease ecosystem services supply depending on the land-cover type. Ecosystem services supply of sparsely vegetated grasslands and tall grasses & shrublands was higher outside than inside the protected area; in contrast, the ecosystem services supply of woodlands was greater inside than outside the protected area. These results suggest that conservation of grasslands and woodlands requires different management strategies (Overbeck *et al.* 2007, 2015, 2016). Grazing exclusion in protected areas located in temperate and subhumid regions does not necessarily lead to grassland conservation (Lunt *et al.* 2007; Cingolani *et al.* 2008). Grasslands and tall grasses & shrublands require disturbances, such as livestock grazing or burning, to maximise ES supply (Bond & Parr 2010). On the other hand, restricting grazing appears to be the most appropriate management strategy to conserve woodlands (Pelkey *et al.* 2000). For woodland ecosystems, disturbances, particularly grazing, should be considered a threat to the conservation of biodiversity and ecosystem services provision (Overbeck *et al.* 2016).

Woodlands, shrublands and grasslands compose a dynamic mosaic. The proposed STM summarised our hypotheses on the most critical processes determining state and phase transitions. High spatial

doi:10.1111/aec.12870

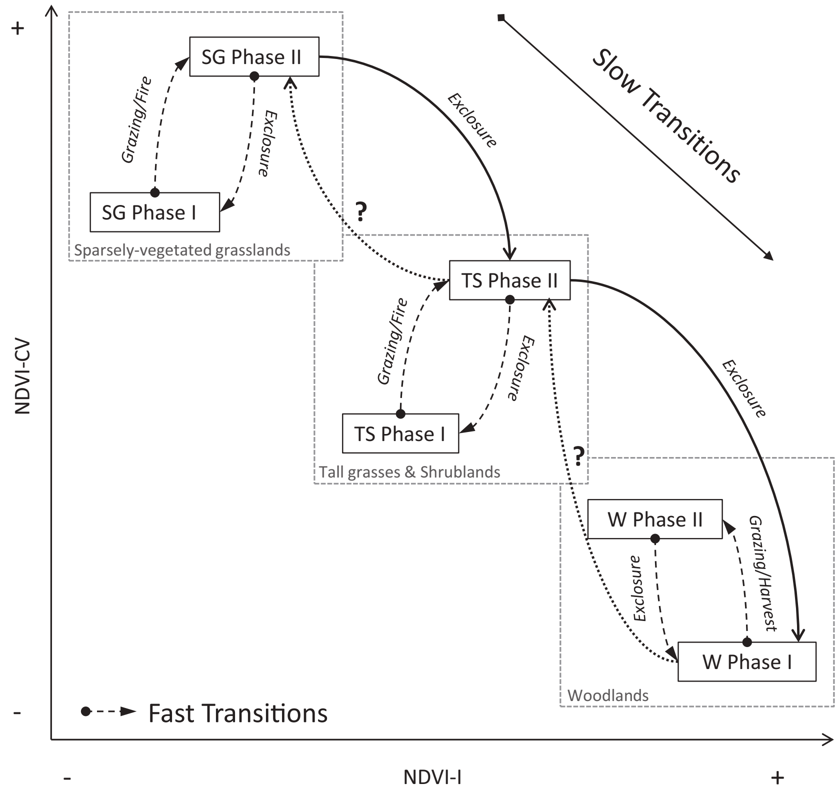

Fig. 3. Representation of the State and Transition Model in the Paisaje Protegido Quebrada de los Cuervos (PPQC) and buffer area (BA). The '*x*'-axis represents the NDVI integral value (NDVI-I) and the '*y*'-axis the NDVI coefficient of variation (NDVI-CV). SG, sparsely vegetated grasslands; TS, tall grasses & shrublands; and W, woodlands. Dotted arrows represent transitions between phases and solid arrows between states. For all land covers, Phase I and Phase II represent the protected and unprotected conditions, respectively.

resolution images provide indirect evidence for our STM model. From 1986 to 2015, domestic herbivory was excluded from a portion of the PPQC. During this period, vegetation physiognomy changed from sparsely vegetated grasslands to tall grasses & shrublands and, finally, to woodlands. Such structural changes were associated with functional changes, basically an increase in productivity and a decrease in seasonality. Transitions from one state to another imply that a threshold value in the state has been reached, resulting in a qualitative shift in vegetation structure and composition that justifies the definition of different states (Bestelmeyer 2006). Sparsely vegetated grasslands (State 1) were characterised by meso-xerophytic species and a double stratum physiognomy: one low stratum of 5 cm dominated by prostrate grasses and forbs, and a 30 cm tall stratum dominated by woody species (Lezama *et al.* 2019). State 1 showed the lowest productivity and highest seasonality (Fig. 3). Grazing exclusion in these temperate subhumid grasslands promoted tall tussock grasses (i.e. *Erianthus angustifolius*) and shrub encroachment (i.e. *Dodonaea viscosa*) (Altesor *et al.* 2006; Lezama *et al.* 2014) (State 2). If grazing exclusion and fire suppression remain, woody species will colonise to the point at which a qualitative shift in vegetation structure may occur (State 3). This state showed the highest values of productivity and seasonality. The reversibility from State 3 to herbaceous dominated ones would be difficult and may require critical anthropogenic inputs.

Within each state, we identified two phases, one inside and the other outside the protected area. Sparsely vegetated grasslands and tall grasses & shrublands showed higher productivity and seasonality in the buffer area. Grazing prevents the accumulation of standing dead biomass, increasing light availability and, hence, the productivity and species richness (Altesor *et al.* 2005 2006; Overbeck *et al.* 2007). The transitions between phases in grasslands and shrublands would be reversible (months for grasslands phases and years for shrublands phases, Altesor *et al.* 2019) and result from changes in stocking rate and burnings (Altesor *et al.* 2019). Woodlands showed the opposite pattern; inside the PPQC, their productivity was greater and less variable than in the buffer area. Several disturbances, like logging, herbivory and trampling, may explain these differences (Etchebarne & Brazeiro 2016).

doi:10.1111/aec.12870

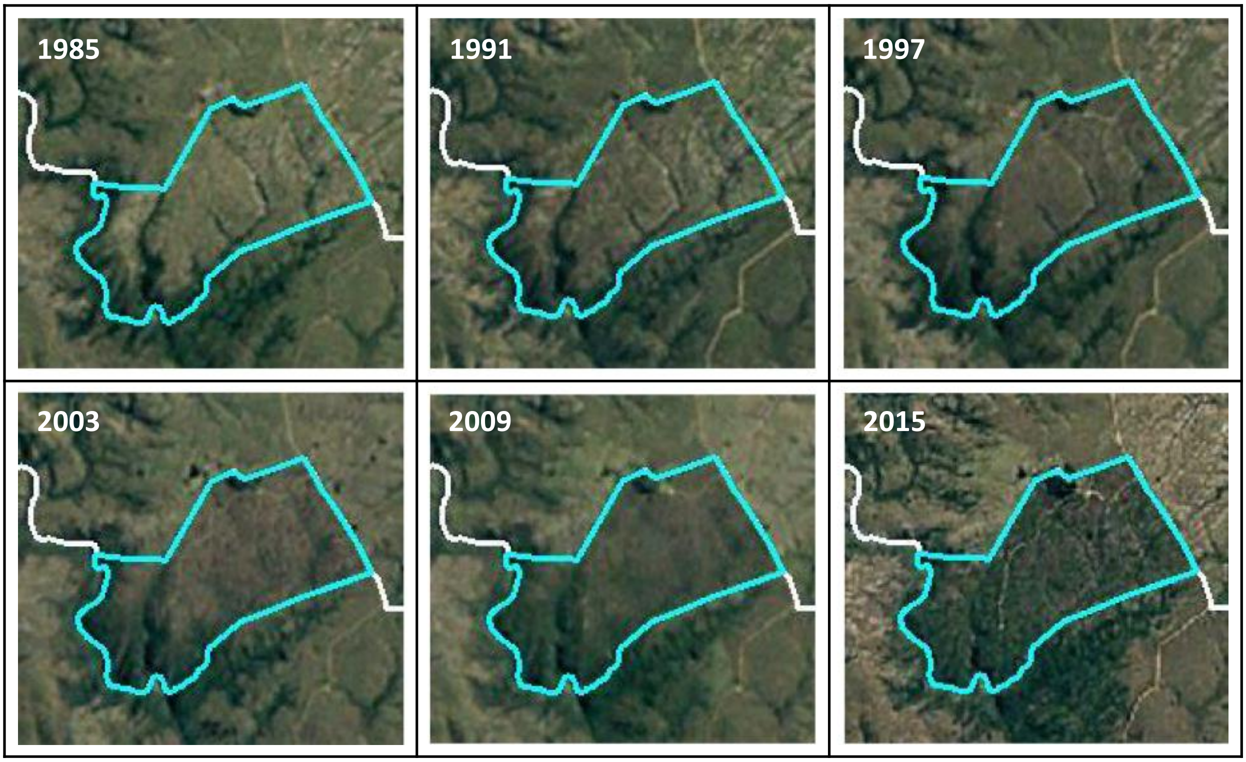

Fig. 4. Sequence of Google Earth images for the exclusion area inside the Paisaje Protegido Quebrada de los Cuervos (PPQC). Changes in the roughness and colour of the image are associated with structural vegetation changes over a period of 30 years (1985–2015). The sequence begins in 1985 with the dominance of sparse vegetated grasslands in the exclusion area. In 1997 and 2003, changes in vegetation are denoted by the presence of tall grasses & shrublands. Finally, at the end of the temporal sequence (2009–2015), the increase of shrublands and tree cover is remarkable in the area.

Disturbances could have severe effects on forest structure and dynamics, generating a decrease in canopy cover (Uhl & Kauffman 1990), lower regeneration rates (Fleischner 1994) and a replacement in species composition (Xiaoming *et al.* 1995). Consequently, woodlands management requires conditions of small or null disturbances to maintain the structure and ES provision (Pelkey *et al.* 2000; Luza *et al.* 2014; Overbeck *et al.* 2015).

The STM proposed could provide a suitable framework to organise and communicate knowledge and to identify management strategies that favour the conservation of vegetation heterogeneity and ecosystem services. The model enhances and extends previous models (Altesor *et al.* 2019), incorporating other ecosystems (shrublands and woodlands). Also, it highlights the importance of the disturbance regime within protected areas, showing thresholds and hysteresis. Consequently, the chance to preserve a given state needs to incorporate disturbances like grazing and fire carefully. Once a threshold is crossed, the opportunity to return to previous conditions may be beyond the logistic possibilities. Moreover, a return may increase the risks of non-intended transitions to more degraded states, that is removing woody components may increase soil erosion risks. Under the current rates of grassland transformation into croplands or tree plantations, adequately managed livestock grazing maybe not only compatible with conservation but also a necessary to preserve grassland structure and ecosystem services supply (Overbeck *et al.* 2007, 2015, 2016). To what extent are transitions possible? The design of an adaptive management scheme based on the STM, such as the one outlined here may contribute to test and redefine the model and to better preserve different ecosystems.

ACKNOWLEDGEMENTS

We specially thank the members of the Quebrada de los Cuervos Agricultural Cooperative for the support and advice offered in the field work. The research was supported by the Comisión Sectorial de Investigación Científica (CSIC) from Uruguay. This work was carried out with the aid of a grant from the Inter-American Institute for Global Change Research (IAI) CRN3095 which is supported by the US National Science Foundation (Grant GEO-1128040).

 doi:10.1111/aec.12870

AUTHOR CONTRIBUTIONS

Conceptualization: F.G. J.M.P., A.A.; Data curation: F.G.; Formal analysis: F.G.; Funding acquisition: J.M.P., A.A.; Investigation: F.G., A.A.; Methodology: F.G. J.M.P., S.B., A.A.; Writing-original draft: F.G., J.M.P., A.A.; Writing-review & editing: S.B.

REFERENCES

Altesor A., Oesterheld M., Leoni E., Lezama F. & Rodríguez C. (2005) Effect of grazing on community structure and productivity of a Uruguayan grassland. *Plant. Ecol.* **179,** 83–91.

Altesor A., Piñeiro G., Lezama F., Jackson R., Sarasola M. & Paruelo J. (2006) Ecosystem changes associated with grazing in subhumid South American grasslands. *J. Veg. Sci.* **17,** 323–32.

Altesor A., Gallego F., Ferrón M. *et al.* (2019) Inductive approach to build state-and-transition models for Uruguayan Grasslands. *Rangeland Ecol. Manag.* **77,** 1005–16.

Andrade B., Marchesi E., Burkart S. *et al.* (2018) Vascular plant species richness and distribution in the Río de la Plata grasslands. *Bot. J. Linn. Soc.* **188,** 250–6.

Baeza S., Rama G. & Lezama F. (2019) Cartografía de los pastizales naturales en las regiones geomorfológicas de Uruguay predominantemente ganaderas. Ampliación y actualización. In: *Bases Ecológicas y tecnológicas para el manejo de pastixales II. Serie FPTA N° 69* (eds A. Altesor, L. López-Mársico & J. M. Paruelo) pp. 27–47. INIA, Montevideo.

Bestelmeyer B. T. (2006) Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Rest. Ecol.* **14,** 325–9.

Bond W. & Parr C. (2010) Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biol. Conserv.* **143,** 2395–404.

Boyd J. & Banzhaf S. (2007) What are ecosystem services? The need for standardized environmental accounting units. *Ecol. Econ.* **63,** 616–26.

Carlucci M., Luza A., Hartz S. *et al.* (2016) Forests shrublands and grasslands in southern Brazil are neglected and have specific needs for their conservation. Reply to Overbeck et al. *Nat. Conserv.* **2,** 155–7.

Cingolani A., Renison D., Tecco P., Gurvich D. & Cabido M. (2008) Predicting cover types in a mountain range with long evolutionary grazing history: a GIS approach. *J. Biogeogr.* **35,** 538–51.

Connell J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science* **199,** 1302–10.

Dorrough J. & Ash J. (2003) The impact of livestock grazing on the persistence of a perennial forb in a temperate Australian grassland. *Pac. Conserv. Biol.* **9,** 120–9.

Etchebarne V. & Brazeiro A. (2016) Effects of livestock exclusion in forests of Uruguay: soil condition and tree regeneration. *For. Ecol. Manag.* **362,** 120–9.

Fleischner T. L. (1994) Ecological costs of livestock grazing in western North America. *Conserv. Biol.* **8,** 629–44.

Gautreau P. & Lezama F. (2009) Clasificación florística de los bosques y arbustales de las sierras del Uruguay. *Ecología Austral* **19,** 81–92.

Guerschman J., Paruelo J., Di Bella C., Giallorenzi M. & Pacín F. (2003) Land cover classification in the Argentine Pampas using multi-temporal Landsat TM data. *Int. J. Remote Sens.* **24,** 3381–402.

Henwood W. D. (2010) Toward a strategy for the conservation and protection of the world's temperate grasslands. *Great Plains Res.* **20,** 121–34.

INIA meteorological station. Available from URL: http://www.inia.uy/gras/Clima/Banco-datos-agroclimatico/ (accessed 30 January 2017).

Lezama F., Baeza S., Altesor A., Cesa A., Chaneton E. J. & Paruelo J. M. (2014) Variation of grazing-induced vegetation changes across a large-scale productivity gradient. *J. Veg. Sci.* **25,** 8–21.

Lezama F., Pereira M., Altesor A. & Paruelo J. M. (2019) Grasslands of Uruguay: classification based on vegetation plots. *Phytocoenologia* **49,** 211–29. Available from URL: https://www.schweizerbart.de/papers/phyto/detail/prepub/90497/Grasslands_of_Uruguay_classification_based_on_vegetation_plots?af=search

Lunt I., Eldridge D., Morgan J. & Witt G. (2007) A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia. *Aust. J. Bot.* **55,** 401–15.

Luza A., Carlucci M., Hartz S. & Duarte L. (2014) Moving from forest vs. grassland perspectives to an integrated view towards the conservation of forest–grassland mosaics. *Nat. Conserv.* **12,** 166–9.

Milchunas D. G., Sala O. E. & Lauenroth W. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.* **132,** 87–106.

Olff H. & Ritchie M. E. (1998) Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* **13,** 261–5.

Overbeck G., Müller S. & Fidelis A. (2007) Brazil's neglected biome: the South Brazilian campos. *Perspec. Plant Ecol. Evol. Syst.* **9,** 101–16.

Overbeck G., Vélez-Martin E., Scarano F. *et al.* (2015) Conservation in Brazil needs to include non-forest ecosystems. *Divers. Distrib.* **21,** 1455–60.

Overbeck G., Abreu P., Pillar V. (2016) Conservation of mosaics calls for a perspective that considers all types of mosaics-patches. Reply to Luza et al. *Nat. Conserv.* **14,** 152–4.

Paruelo J., Texeira M., Staiano L., Mastrangelo M., Amdan L. & Gallego F. (2016) An integrative Index of Ecosystem Services provision based on remotely sensed data. *Ecol. Indic.* **71,** 145–54.

Pelkey N., Stoner C. & Caro T. (2000) Vegetation in Tanzania: assessing long term trends and effects of protection using satellite imagery. *Biol. Conserv.* **94,** 297–309.

Perevolotsky A. & Seligman N. (1998) Role of grazing in Mediterranean rangeland ecosystems. *Bioscience* **48,** 1007–17.

Pettorelli N. (2013) *The Normalized Difference Vegetation Index*. Oxford University Press, Oxford.

Rodríguez C., Leoni E., Lezama F. & Altesor A. (2003) Temporal trends in species composition and plant traits in natural grasslands of Uruguay. *J. Veg. Sci.* **14,** 433–40.

Roy D., Borak J., Devadiga S., Wolfe R., Zheng M. & Descloitres J. (2002) The MODIS Land product quality assessment approach. *Remote Sens. Environ.* **83,** 62–76.

SISNAP (2017) Sistema de Información del Sistema Nacional de Áreas Protegidas. Available from URL: http://www.snap.gub.uy/sisnap/web/mapa_conceptual/nodo/17/informacion_general/aspectos_territoriales (accessed 15 December 2017).

Soriano A. (1992) Río de la plata grasslands. In: *Natural Grasslands. Introduction and Western Hemisphere*(ed. R. T. Coupland) pp. 367–407. Elsevier, Amsterdam.

doi:10.1111/aec.12870

Uhl C. & Kauffman J. B. (1990) Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* **71,** 437–49.

Villalba J., Sans C., Baycé D. *et al.* (1998) *Plan de manejo Paisaje Protegido "Quebrada de los Cuervos"*. Intendencia Municipal de Treinta y Tres, Treinta y Tres, Uruguay.

Watson J., Jones K. R., Fuller R. A. *et al.* (2016) Persistent disparities between recent rates of habitat conversion and protection and implications for future global conservation targets. *Conserv. Lett.* **9,** 413–21.

Westoby M., Walker B. & Noy-Meir I. (1989) Opportunistic management for rangelands not at equilibrium. *J. Range Manag.* **42,** 266–74.

Xiaoming Z., Zucca C., Waide R. & McDowell W. (1995) Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. *For. Ecol. Manage.* **78,** 147–57.

Zar J. H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, NJ.

SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Table S1. Contingency matrix for the land-cover map.

Table S2. Accuracy producer (AP) and user (AU), expressed in percentages.

Table S3. Results of ANOVA analysis with interactions in the ecosystem functioning (NDVI-I and NDVI-CV) and Ecosystem Service Supply Index (ESSI) for: A) Exclusion area *vs.* Buffer area comparison and B) Protected area *vs.* Buffer area comparison.

doi:10.1111/aec.12870