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Fragment size, vegetation structure and physical environment control grassland functioning: a test based on artificial neural networks

Lorena P.Herrera, M. Texeira & J.M. Paruelo

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Enhanced vegetation index; Fragmentation; Landscape structure; MODIS data; Neural networks; *Paspalum quadrifarium*; Tall-tussock grassland

Nomenclature
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Herrera, L.P. (corresponding author, lherrera@mdp.edu.ar): FCA, UNMdP and CONICET. EEA Balcarce, INTA,
CC 276, Ruta 226, Km 73.5, 7620, Balcarce, Argentina
Texeira, M. (mtexeira@agro.uba.ar) &
Paruelo, J.M. (paruelo@agro.uba.ar):
Departamento de Métodos Cuantitativos y Sistemas de Información, Laboratorio de Análisis Regional y Teledetección, IFEVA, FAUBA-CONICET, Buenos Aires, Argentina

Abstract

Questions: How do fragment-level characteristics affect remnant grassland functioning in a highly transformed landscape? Are artificial neural networks (ANNs) a better statistical tool to model variations in grassland functioning compared to linear regression models (LRMs)?

Location: Tandilia Range, Southern Pampa, Buenos Aires Province, Argentina.

Methods: We characterized the dynamics of the vegetation functioning in 60 remnant grasslands using enhanced vegetation index (EVI) data provided by MODIS/Terra images from July 2000 to June 2005. First, we performed a principal components analysis (PCA) on the fragment mean monthly values of EVI in order to obtain synthetic measures (i.e. the PCA axes) of grassland functioning. Grassland fragments were also characterized by size, vegetation structure (abundance of the tall-tussock grass *Paspalum quadrifarium*) and physical environment (soil type – abundance of litholitic soils – elevation, aspect and slope). The relationship between grassland functioning and these explanatory variables was explored using linear regression models (LRMs) and artificial neural networks (ANNs).

Results: The first and second PCA axes were related to the annual integral of EVI (EVI-I) and EVI seasonality (EVI-S), respectively; these explained jointly ca. 80% of total variability in mean EVI values. ANNs captured better than regression models the relationships among the proposed controls and the spatial variability of grassland functioning in Southern Pampa. Results showed that EVI-I variability was related to all independent variables except aspect. While fragment size, litholitic soils and slope were negatively related to EVI-I, the abundance of *P. quadrifarium* had a positive effect on the spectral index. Grasslands with high seasonality were large and had high slope and aspect, low abundance of *P. quadrifarium* and increased abundance of litholitic soils.

Conclusions: Our results showed that grassland functioning in Southern Pampa, as estimated by EVI, depends on fragment size, vegetation structure and physical factors (soil type, aspect and slope). *Paspalum quadrifarium* may have an important functional role in this grassland system.

Introduction

Grassland conversion into cropland and afforestation are the major threats to South American grasslands (Baldi & Paruelo 2008). The extensive plains occupied by the Rio de la Plata grasslands have suffered profound transformations since European settlement in the first half of the 16th century (Soriano et al. 1991), when grasslands began to be replaced by annual crops and cultivated pastures. Nowadays, the original vegetation (prairies and grass steppes) has been highly modified and restricted to small patches, railroads, wire fencerows and roadside verges, often embedded in an intensively used agricultural matrix (León et al. 1984; Herrera et al. 2009; Herrera & Laterra 2011). In the southernmost unit of the region, the Southern Pampa, the remaining tallgrass prairies (dominated by the

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native tall-tussock grass, *Paspalum quadrifarium*) are mostly associated with rocky outcrops and shallow soils, making it impossible to plough and sow crops. Thus, in this area, natural or semi-natural grasslands still persist, confined to remnant hills and small rocky outcrops, surrounded by an agricultural matrix. These remnants represent a valuable refuge for native flora (Herrera & Laterra 2011) and fauna (Comparatore et al. 1996; Isacch & Martínez 2001), and may provide a wide range of ecosystem services (below-ground carbon sequestration, plant–pest–beneficial insect interactions, etc.).

Many studies have shown that agricultural practices modify annual above-ground net primary production (ANPP) and its seasonal dynamics, relative to the original vegetation and land uses (Paruelo et al. 2001; Guerschman et al. 2003; Guerschman & Paruelo 2005). ANPP is an integrative measure of the ecosystem function, and determines the availability of energy for upper trophic levels (McNaughton et al. 1989). At regional scales, ANPP is mainly associated with mean annual precipitation (Lauenroth 1979; Sala et al. 1988), the main control of water availability. At local scales, soil depth and topography become the dominant controls of the ANPP spatial variability, mainly through their effects on soil water availability. These effects are sometimes modulated by disturbances that remove large amounts of biomass that alter the nutrient cycle, such as grazing and fire (Oesterheld et al. 1999). In fragmented landscapes ANPP may be controlled by patch size and isolation, because these factors affects processes of colonization and extinction of species as a result of changes in habitat quality (Hanski 1991; Thomas et al. 2001; Adriaens et al. 2009), and could have an effect on the redistribution of matter and energy. The influence of fragment size and changes in community structure and resource availability on ecosystem functioning has been poorly studied.

Remote sensing is being widely used to estimate ANPP and to describe the spatial and temporal heterogeneity of ecosystem functioning at different scales (Alacaraz-Segura et al. 2006; Baeza et al. 2010). The fraction of photosynthetically active radiation absorbed by the canopy (*f*PAR), a major control of ANPP, may be readily estimated from spectral data, allowing description of both its seasonal and inter-annual variation (Paruelo et al. 1997; Piñeiro et al. 2006). Vegetation indices derived from the red and near-infrared reflectance are good estimators of *f*PAR (Sellers et al. 1992) and thus of ANPP (Piñeiro et al. 2006).

Understanding of the influence of environmental and management factors on ecosystem functioning has been limited by both data availability and analytical tools. Remotely sensed data provide an opportunity to expand both the spatial and temporal coverage of data describing different aspects of ecosystem functioning. Paruelo & Tomasel (1997) showed that traditional analytical approaches (i.e. multiple regressions) provide a poor description of the relationships between environmental variables and ecosystem functioning attributes due to the low capacity of these techniques to capture non-linearity and the strong assumption of normality of the dependent variable.

In this article, we explored the influence of fragment-level characteristics (size, vegetation structure and physical environment factors) on the functioning of remnant grasslands embedded in an agricultural matrix in the Southern Pampa, Argentina. We compared the performance of artificial neural networks (ANNs), one of the simplest forms of generalized regression (Faraway 2006), and linear regression models (LRMs) to understand the influence of fragment-level characteristics on grassland functioning. Specifically, we sought to answer the following questions: how do fragment-level characteristics affect remnant grassland functioning in a highly transformed landscape; and are ANNs a better statistical tool to model variations in grassland functioning compared to LRMs?

Methods

Study area

The study area is located in the Southern Pampa region of Argentina within the Tandilia Range (38°01′–36°54′S, 60°14′–57°32′W; Fig. 1). The climate of the region is sub-humid– humid mesothermal with no or a small water deficiency, with a noticeable seasonal variation in temperature, with a short cold period. Mean annual precipitation is 800 mm (Burgos & Vidal 1951). Soils are typical Argiudoll and Hapludoll developed from loessic deposits over cuarcitic rocks (INTA 1989).

Remnant grasslands (hereafter fragments) primarily occur on sites where ploughing is prevented because of rocky outcrops and shallow soils, so the dominant landscape is a cropland matrix with scattered fragments of variable size (hills and small rock patches; Fig. 1). Vegetation of the studied fragments consists of a mosaic of two plant community types that differ in their physiognomy and species composition: tall-tussock grass patches of 5–50 m in diameter (locally known as 'pajonal') dominated by the native grass *P. quadrifarium*, characterized by a low species richness and turf patches ('flechillar') dominated by a high number of short grasses in the genera *Stipa*, *Piptochaetium*, *Aristida*, *Melica*, *Briza*, *Bromus*, *Eragrostis* and *Poa*, among others (Frangi 1975; Soriano et al. 1991; Herrera & Laterra 2011) (Fig. 1). *Paspalum quadrifarium* is a perennial bunch grass that forms dense and compact tussocks characterized by a tall canopy (up to 1.5 m) and flowering stalks up to 2-m tall, a high ratio of dead to living standing biomass, and a thick litter layer (Laterra et al. 2003). The pajonal is a

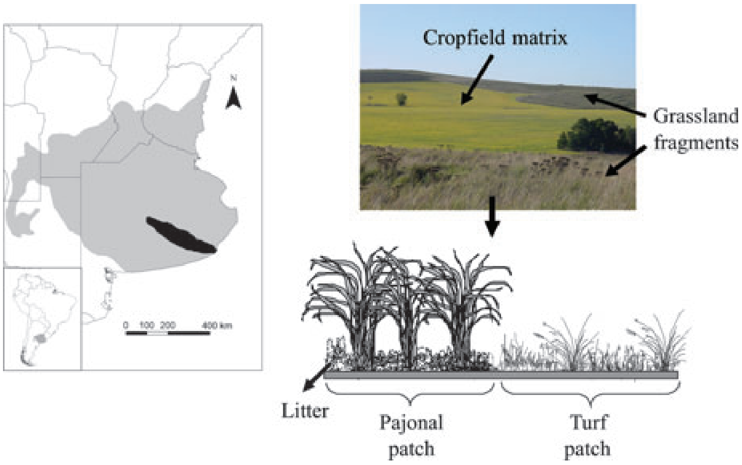

Fig. 1. Left: the Tandilia's Range (black area) in the Pampa region (grey area) where the studied grasslands have scattered distribution. Upper right: a typical landscape of the region where hills and rocky patches of grasslands have scattered distribution in a cropfield matrix. Lower right: a mosaic of pajonal and flechillar patches.

fire-prone grassland, and current grazing management requires occasional burning to improve forage production and quality. Domestic herbivores (cattle) graze mainly on the short-grass matrix and on pajonal patches only for a short period during post-fire resprout of *Paspalum* tussocks (Laterra et al. 2003). As a consequence of the cumulative effects of burning and subsequent grazing, canopy height and litter thickness of pajonal patches are reduced, and complete recovery of the patch in the absence of disturbances may take several years (Laterra et al. 2003; Vignolio et al. 2003). Disturbances promote colonization by exotic species, which has important consequences for plant community structure (Laterra et al. 2003, 2006; Ortega & Laterra 2003; Perelman et al. 2003; Herrera & Laterra 2009).

Fragments characteristics

Characterization of grassland fragments was based on both fieldwork and ancillary data. On Landsat 5 TM images (Path/Row: 224/86, 24 February 2007; Path/Row: 225/86, 3 March 2007) we located potential grassland fragments to be included in this study. We visited the ranches that included these sites and performed a brief interview with land managers on grassland management history during the last 15 yrs. We visited the 60 selected fragments and throughout one transect 2-m wide we visually determined *P. quadrifarium* cover, which was grouped into three broad categories (see below). We discarded from the analysis those fragments in which the information provided by the manager was vague or confusing.

We selected six independent variables to characterize the studied grasslands:

1. Size of fragment: studied fragments were digitized from the Landsat 5 TM satellite images mentioned above; and fragment areas were calculated with the 'Calculate Geometry' tool of ArcGIS 9.2. We selected this variable because it represents an important feature of fragmented landscapes clearly associated with the dynamics of colonization and local extinctions (MacArthur & Wilson 1967). Its effects on grassland carbon gain have not been previously taken into account.
2. Vegetation structure characterized by the abundance (percentage cover) of the tall-tussock *P. quadrifarium* (Pq). Three categories of fragment were defined: 0 = fragments without Pq and 100% of the fragment cover by turf patches; 1 = 50% covered by Pq and 50% covered by turf patches; 2 = >50% covered by mature Pq tussocks. *Paspalum quadrifarium* is a key species of the original grassland vegetation because its presence defines critical aspects of community structure (e.g. strata, height, litter accumulation and species diversity patterns; Perelman et al. 2003).
3. Abundance of litholitic soils: 0 = non-rocky soils, 1 = soils with calcareous layers, 2 = soils with rock outcrops, 3 = rocky soils.
4. Elevation in meters above sea level.
5. Aspect (direction in degrees measured clockwise from N).
6. Slope (%).

Items 3 and 4 were characterized at the resolution of the MODIS pixel (250 m × 250 m). The aspect and slope variables were obtained from a 90-m digital elevation model downloaded from http://srtm.csi.cgiar.org/.

Spectral information

In order to describe grassland functional heterogeneity, we used enhanced vegetation index (EVI) data provided in MODIS/Terra images from July 2000 to June 2005.

Spectral indices such as EVI or NDVI (normalized difference vegetation index) are estimators of the fraction of the photosynthetic active radiation absorbed by green tissues (fPAR) (Di Bella et al. 2004). fPAR is the most important determinant of ANPP in grassland areas on an annual basis (Paruelo et al. 1997; Piñeiro et al. 2006). In this paper we used the EVI annual integral as a surrogate of ANPP and, hence, of grassland functioning. EVI seems to perform relatively better than other indices because of its lower saturation at high vegetation density and less sensitivity to background reflectance (Huete et al. 2002). Thus, EVI calculates the reflectance normalized difference between these two wavelengths (red and near infrared), and incorporates a third wavelength (blue) that minimizes the influence of soil and air (Glenn et al. 2008). We used the EVI Quality 'QA' product of the MODIS to extract information on cloud, aerosols and shade.

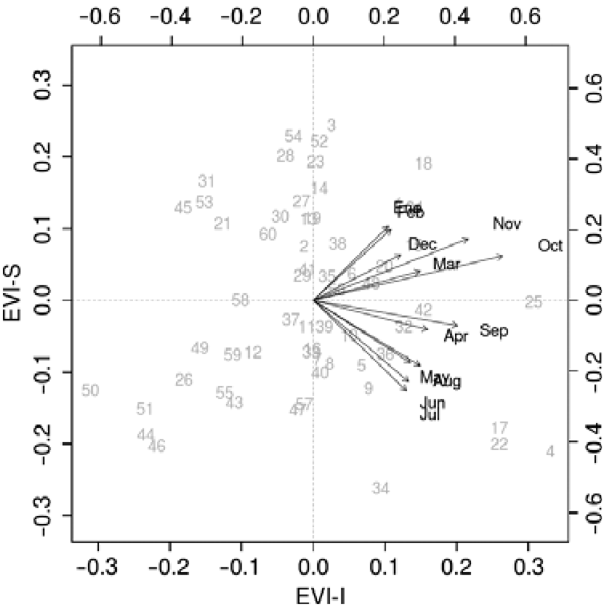

Fig. 2. Principal components analysis ordination of the grassland fragments in terms of mean monthly EVI values for 2000–2005. Each number represents a grassland fragment, and the direction of the arrows shows the relative loadings of the mean EVI on the first and second principal components (PC1 = EVI-I and PC2 = EVI-S). PC1 explains 62.8% of variance and PC2 explains 16.9% of variance.

Data analysis

In order to reduce the dimensionality of the dependent data set (mean monthly EVI values for the years 2000–2005), we applied PCA to the covariance matrix. The first two axes of the PCA explained 80% of the variation in EVI data. The first component (PC1) correlated positively and significantly with all mean monthly EVI values, while the second component (PC2) correlated positively and significantly with November, December, January and February (late spring and summer) mean EVI values; and negatively and significantly with May, June, July and August (autumn–winter) mean EVI values. Thus, we decided to work with the first two principal components as dependent variables: PC1 was interpreted as an indicator of the annual integral of EVI, calculated as growing season (July–June) average of monthly values (Paruelo et al. 1997) (EVI-I=a surrogate of ANPP), and PC2 as an indicator of seasonality, the intra-annual variation of photosynthetic activity (EVI-S=seasonality of grassland ANPP; Fig. 2). Guerschman et al. (2003) showed that ANPP seasonality is one of the more sensitive ecosystem function attributes for land-uses changes. The univariate relationship between the two PC axes and each explanatory variable was explored using scatter-plots, box-plots, additive models and Kruskall–Wallis tests.

Linear regression models (LRMs)

We analysed the controls of PC1 (hereafter EVI-I) and PC2 (hereafter EVI-S) using multiple linear regression (Faraway 2004). Before performing any analysis, we explored the correlation matrix among independent variables in order to identify redundant covariates. Given that elevation was strongly correlated with the size of the grassland fragment ($r = 0.5441$, $P < 0.001$), we removed it from the set of explanatory variables.

A full model with all independent variables was constructed for each dependent variable. We did not find evidence of spatial autocorrelation; instead we found that model residuals were associated with some independent variables. Thus, we adjusted models with variance covariates. For this reason, we modelled the errors as a function of these independent variables (variance covariates; Zuur et al. 2009). Different forms of variance structure of the errors were tried and the optimal ones were selected using the Akaike information criterion and Akaike weights (AIC and W_{AIC}; Zuur et al. 2009). After finding the 'best' general model we proceeded to find an adequate reduced model using deletion tests (Faraway 2006; Crawley 2007; Zuur et al. 2009). These models were fitted by generalized least squares with the *nlme* package in the R software (R Foundation for Statistical Computing, Vienna, AT).

Artificial neural networks (ANNs)

We also analysed our data set using ANNs (Smith 1994; Haykin 1999). ANNs are a flexible kind of generalized non-linear regression that overcomes some of the drawbacks of classical statistical methods (i.e. linear models). We used a multi-layer feed-forward network (multi-layer perceptron, MLP), one of the most popular architectures for generalized regression problems and statistical pattern recognition (Faraway 2006). In this kind of network the processing units ('neurons') are organized in layers. We considered fully connected networks in which all neurons in a given layer are connected to all neurons in adjacent layers. The networks were trained (i.e. estimating values of the parameters that relate values of the dependent variables to the independent variables) using the Levenberg Marquardt (LM) training algorithm (Demuth & Beale 2001). We constructed our network with five neurons in the input layer, corresponding to the five explanatory variables considered: fragment size, *P. quadrifarium* abundance, abundance of litholitic soils, slope and aspect. The output layer consisted of two neurons, one associated with EVI-I and the other associated with EVI-S. The number of neurons in the hidden layer controls the complexity of the relationship that can be approximated, and was selected by training networks with different numbers of neurons in that layer, and testing the performance in terms of R^2 between the observed values of the dependent variables (observed EVI-I and EVI-S) and those produced by the network (values produced by the neurons in the output layer). Once we determined the number of neurons in the hidden layer, we searched for values of the initial connection weights that produced the highest R^2. The predictive performance of this network (as well as performance of the reduced linear model) was evaluated with Jackknife validation. The significance of the effect of the independent variables was assessed by bootstrap (Olden & Jackson 2002). This technique permutes the dependent variables (9999 times) and retrains the network with the same initial connection weights established previously. In this way, we generated the empirical distribution of the overall

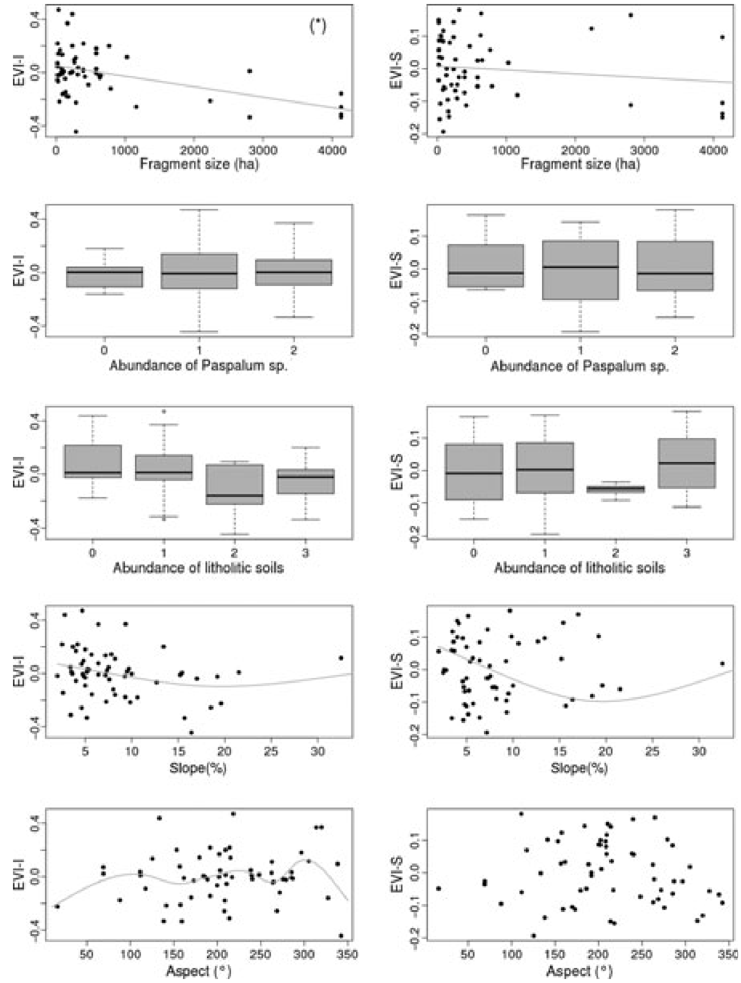

Fig. 3. Univariate relationships among the first two principal components (PC1 = EVI-I and PC2 = EVI-S) and the independent variables considered. In the case of continuous independent variables, an additive model fit is shown. The figures marked with an asterisk represent significant terms at a significance of $\alpha = 0.05$ in the additive model or Kruskal–Wallis tests.

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connection weights (a measure of the marginal effect of each independent variable on the dependent variables obtained as a combination of the weights that connect the input nodes with the hidden nodes and the weights that connect hidden nodes with the output nodes) under the null hypothesis of randomly connected networks (Olden & Jackson 2002). With these null distributions, we tested the significance of effect of the independent variables in the network. We retained only significant variables at a 0.05 significance level.

Results

Univariate analysis showed that fragment size was negatively correlated with EVI-I, while seasonality did not show a significant relationship with any of the studied independent variables (Fig. 3).

Linear regression models (LRMs)

The best LRM for EVI-I included as independent variables the size of the fragment and the abundance of litholitic soils, and modelled the errors as an exponential function of the topographic slope (Table 1). In this model, the dependent variable was related negatively to both independent variables (Table 2). For seasonality, we could not obtain a reduced model with error covariates as a consequence of convergence problems in the *gls* routine in R. Hence only the general model with error covariates is shown (Table 3). In this model none of the terms was significant ($P > 0.05$). Models for both dependent variables had very poor fits and explanatory power (Fig. 4).

Artificial neural networks (ANNs)

The ANNs showed that all independent variables except aspect had significant effects on EVI-I variability. Overall connection weights show that while fragment size, litholitic soils and slope were negatively related with EVI-I, the abundance of *P. quadrifarium* showed a positive relationship with EVI-I, our estimate of ANPP (Fig. 5). Grasslands with high seasonality were larger, had higher slope, aspect, proportion of litholitic soils and lower abundance of *P. quadrifarium* than those with low intra-annual seasonality (Fig. 5). The fits and the explanatory power of ANNs for both dependent variables were much higher than those of the LRMs (Fig. 6).

Table 1. The linear models fitted to the principal components (PC1 = EVI-I and PC2 = EVI-S) of the PCA. Variables, are the independent variables entered in the model; errors are the error covariates; AIC is the Akaike information criterion; W_{AIC} is the Akaike weights of the best model; 2nd W_{AIC} represents the second-best model Akaike weights. In the case of the reduced models, Akaike weights were not computed because these models were derived from the general model with error covariates by deletion tests.

	Variables	Errors	AIC	W_{AIC}	2nd W_{AIC}
EVI-I					
General model	All	–	23.6	0.998	0.002
General model with error covariates	All	Slope	20.397	0.100	0.079
Reduced model	Fragment size, Slope *Paspalum* abundance, Litholitic soils	Slope	−11.384	–	–
EVI-S					
General model	All	–	21.791	0.999	0.001
General model with error covariates	All	Slope	21.563	0.122	0.109
Reduced model	Did not converge	Litholitic soils	−36.502	–	–

Table 2. The best reduced model coefficients, standard errors (SE), *t*-values and significance values (*P*-values) for the first principal component (PC1 = EVI-I).

	Coefficient	SE	*t*-value	*P*-value
Intercept	0.2212	0.0623	3.5475	0.0008
Fragment size	8×10^{-5}	2×10^{-5}	−5.7362	<0.0001
Litholitic soils level 1	−0.1132	0.0495	−2.2833	0.0265
Litholitic soils level 2	−0.2105	0.0813	−2.5905	0.0124
Litholitic soils level 3	−0.2464	0.0545	−4.5218	<0.0001
Slope	−0.0096	0.0046	−2.0826	0.0422
Paspalum level 1	0.1257	0.0560	2.2448	0.0291
Paspalum level 2	0.0407	0.0481	0.8458	0.4015

Table 3. The best reduced model coefficients, SE, *t*-values and significance (*P*-values) for the second principal component (PC2 = EVI-S).

	Coefficient	SE	*t*-value	*P*-value
Intercept	0.1056	0.0432	2.4445	0.0177
Litholitic soils level 1	−0.1517	0.0495	−3.0616	0.0034
Litholitic soils level 2	−0.1397	0.0803	−1.7386	0.0876
Litholitic soils level 3	−0.1057	0.0547	−1.9318	0.0584

Discussion

Our results show evidences of the influence of fragment-level characteristics on the spatial variability of grassland functioning in the Southern Pampa. While the univariate analysis did not provide relevant clues on the controls of EVI-I and EVI-S (Fig. 3), the joint effects of the independent variables in LRMs increased the predictive capacity

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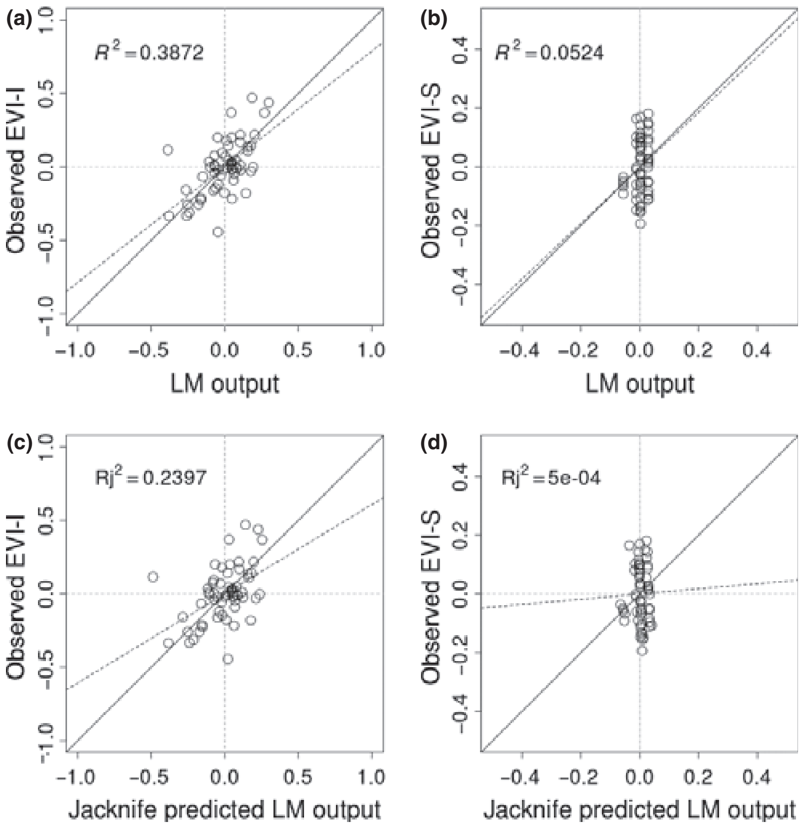
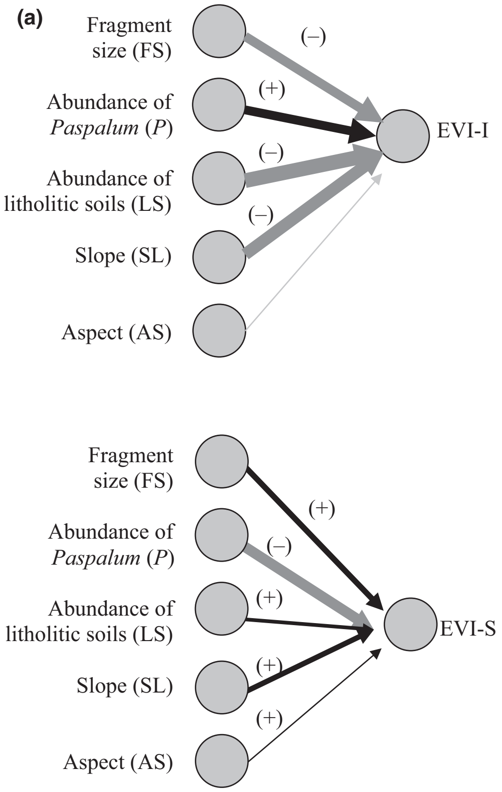


Fig. 4. Values of the first principal component (observed EVI-I) (**a**) and the second principal component (observed EVI-S) (**b**) vs. values predicted by the best linear regression models fitted. The Jackknife validated linear models (LM) are also shown for EVI-I (**c**) and EVI-S (**d**). The dark filled line represents the 1:1 line, whereas the light dotted line represents the observed vs. predicted regression fit.

for EVI-I 25%, while for EVI-S only 0.05% (Fig. 4). ANNs made better predictions than LRMs, explaining 75% and 50% of the variability of total primary production (EVI-I) and seasonality (EVI-S), respectively (Fig. 6). The better performance of ANNs is mainly a consequence of their ability to capture non-linearities. Their intrinsic non-linear structure makes them particularly suitable as fitting tools.

According to the ANNs, fragment size, vegetation structure and physical factors (soil type, aspect and slope) were associated with the spatial variability of our descriptors of grassland functioning (EVI-I and EVI-S). Several studies have analysed the impact of fragment size on plant community structure (Kemper et al. 1999; Cully et al. 2003; Cagnolo et al. 2006) but, to our knowledge, no one has studied its impact on plant community functioning. Many studies have shown that fragments of natural vegetation, in particular the smaller ones, embedded in an agricultural matrix are threatened by weed invasion, agrochemical drift and introduced species affecting vegetation structure and thus habitat quality (Kemper et al. 1999; Cully et al. 2003). This may be reflected in a decrease in carbon inputs to the system. However, contrary to this expectation, we found that smaller fragments had high EVI-I values than larger ones (Fig. 5). Although we did not have quantitative data, larger fragments are usually heavily grazed and more frequently burned and treated with herbicides than the smaller ones (L.P. Herrera pers. obs.). A combination of intensive grazing and management can lead to soil degradation and invasion by exotic species, which may negatively affect carbon inputs of large fragments. Previous studies in Rio de la Plata grasslands showed that grazing reduces the contribution of the dominant grasses, increases the abundance of subordinate grasses and promotes the invasion of dicotyledonous exotic species, many of them from Asia and Europe (Sala et al. 1986; Rusch & Oesterheld 1997; Jacobo et al. 2006). As a result of these floristic changes, ANPP is significantly reduced under continuous grazing (Rusch & Oesterheld 1997).

Despite the low explained variance of EVI-S (16.9%, as derived from PCA), a general trend shows that larger fragments have higher seasonality associated with large EVI values in spring–summer and low EVI values in autumn–winter (Fig. 5). This pattern may also result from grazing management practices because the studied grasslands are



(b)

	OCW	Val p (boot)
FS	–0.5842	<0.001 *
P	0.5143	<0.001 *
LS	–1.3932	<0.001 *
SL	–0.7208	<0.001 *
AS	–0.0229	0.4528

	OCW	Val p (boot)
FS	0.3923	<0.001*
P	–0.6664	<0.001*
LS	0.2293	<0.001*
SL	0.3452	<0.001*
AS	0.1441	<0.001*

Fig. 5. Simplified neural interpretation diagrams associated with the artificial neural network fitted to the first two principal components (PC1 = EVI-I and PC2 = EVI-S). The thickness of the arrows is proportional to the overall connection weight (OCW) associated with it. Dark arrows represent significant positive OCWs, grey arrows represent significant negative OCWs, and light grey arrows represent non-significant OCWs (**a**). Overall connection weights and bootstrap *P*-values associated with the independent variables in the artificial neural network (**b**).

mainly used as a winter forage resource (Cid & Brizuela 2009, 2010) and probably receive heavy grazing pressure at this time of year, affecting ANPP and thus grassland functioning, as explained previously.

A recent work in the same study system showed that fragment size did not affect grassland structure (i.e. species richness, floristic composition and functional groups; Herrera & Laterra 2011). Thus, for these grasslands, functioning would have a shorter response time than structure (Malingreau 1986; Myneni et al. 1997). The faster response of functional attributes represents an important advantage with respect to structural approaches in devising more sensitive monitoring programmes.

Surprisingly, grasslands with high cover of the tall-tussock *P. quadrifarium* were associated with high EVI-I. We expected the opposite pattern, since *P. quadrifarium* in its mature state accumulates large quantities of dead material (Fig. 1) that reduces light interception (Laterra et al. 1998). Posse & Cingolani (2004) found a similar result in Magellanic steppe of Tierra del Fuego (Argentina), where vegetation is dominated by tussock grasslands of *Festuca gracillima* of low palatability, while inter-tussock vegetation is mainly composed of short graminoids and forbs, which are the most consumed and nutritious food items. These authors found that low quality in a low productivity community was not correlated with spectral indices (NDVI in this case) as expected; and explained that the perennial character masked the low productivity during particular seasons, resulting in a large annual integral of the spectral NDVI-I value. According to Tongway & Hindley (2004), tall grass patches may have additional effects on the short-grass matrix. These authors found that dense patches of perennial grasses cause overland water flow to become tortuous, with clumps of plants obstructing and diverting water flow and ‘sieving out’ topsoil, litter and seeds. Patches are richer in resources and have enhanced soil properties, such as infiltration, nutrient concentration and stability. In addition, *P. quadrifarium* has a more extensive root system that explores a large soil volume and would increase access to soil water, increasing its performance under drought (Sakalauskas et al. 2001). On the other hand, grazing, both by removing biomass or trampling, would reduce standing dead biomass accumulation and, hence, the effect of large tussocks on the light interception by green tissues.

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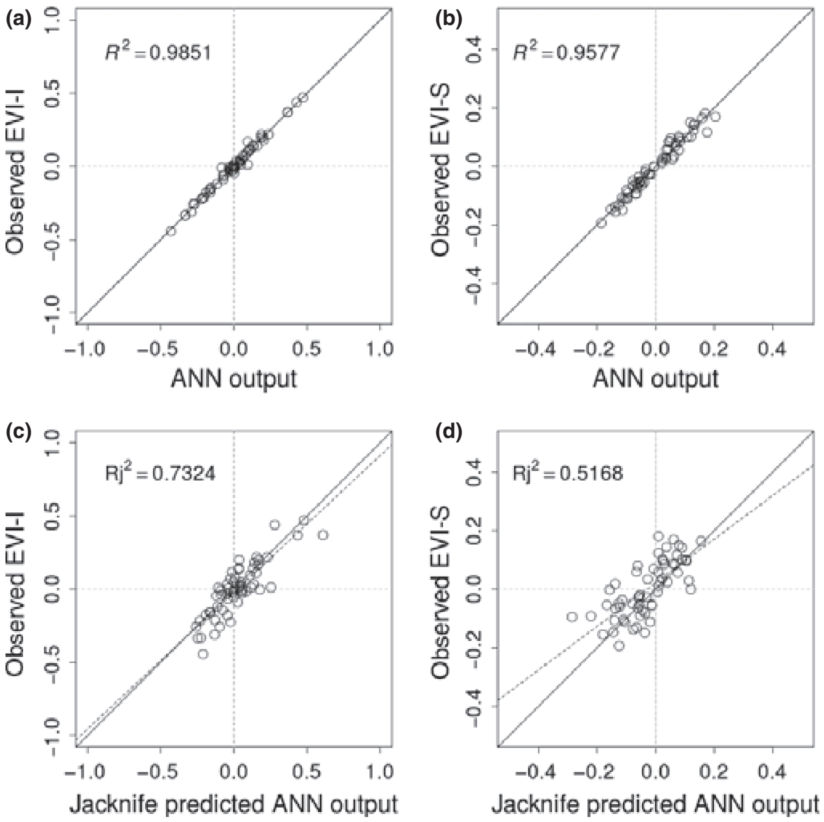

Fig. 6. Values of the first principal component (observed EVI-I) (**a**) and the second principal component (observed EVI-S) (**b**) vs. values predicted by the artificial neural network models fitted. The Jackknife validated models are also shown for EVI-I (**c**) and EVI-S (**d**). The dark dotted line represents the 1:1 line, whereas the light dotted line represents the observed vs predicted regression fit.

Even though *P. quadrifarium* has higher summer forage productivity, we found that grasslands with high cover of *Paspalum* have low seasonality associated with large EVI values in autumn–winter with respect to EVI values in spring–summer (Fig. 5). Although this unexpected result must be carefully considered because of the low explained variance of EVI-S, it can demonstrate the positive functional role of *Paspalum* clumps on overall productivity at times of the year with heavy grazing pressure on the short-grass matrix, as explained above.

Soil type seems to exert an important control on grassland functioning in this area. Grassland areas with high abundance of litholitic soils had low EVI-I and high seasonality associated with high EVI values in the spring–summer months (Fig. 5). The negative relationship between soil characteristics and EVI-I may be associated with a reduction in the soil volume explored by roots due to rock outcrops or the presence of a calcareous layer close to the surface; factors that affect water and nutrient capture, reducing carbon gain (Passioura 2002) and thus grassland functioning.

Steeper fragments had low EVI-I and high seasonality associated with high EVI values in the spring–summer months (Fig. 5). This result can be related to either low soil water availability due to higher run-off or to erosion. It is well known from the literature that erosion and mass movement have serious impacts on land productivity (Blaschke et al. 2000).

Grasslands with a high slope aspect (north-facing slopes) had high seasonality related to high EVI values in the spring–summer months (Fig. 5). The influence of slope aspect has an important effect on the spatial distribution and dynamics of the vegetation (Kutiel 1992). In the present study, grasslands with higher aspects should receive higher solar radiation, promoting species growth, in particular of C4 grasses, and increasing EVI values in warmer periods; while grasslands on south-facing slopes generally receive a lower solar radiation flux density.

Our approach, although not manipulative, provides some surprising and interesting results to derive quantitative hypotheses on landscape controls on ANPP. Specifically, we found that the abundance of *P. quadrifarium* would have an important functional role in these remnant grasslands. Traditionally, ranchers try to eliminate patches of this tall-tussock grass, applying herbicides and sowing exotic pastures. This practice is intended to increase productivity, but produces important structural and functional changes that result in losses of ecosystem services, such as the control of soil erosion by above- and belowground biomass accumulated in *P. quadrifarium* patches (Cauhépé 1990), the provision of wildlife habitat and carbon sequestration, among others. Finally, our study highlights the importance of landscape structure as a control on ecosystem functioning, an aspect seldom considered in the literature.

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References

Adriaens, D., Jacquemyn, H., Honnay, O. & Hermy, M. 2009. Conservation of remnant populations of *Colchicum autumnale*: the relative importance of local habitat quality and habitat fragmentation. *Acta Oecologica* 35: 69–82.

Alacaraz-Segura, D., Paruelo, J.M. & Cabello, J. 2006. Identification of current ecosystem functional types in the Iberian Peninsula. *Global Ecology and Biogeography* 15: 200–212.

Baeza, S., Lezama, F., Piñeiro, G., Altesor, A. & Paruelo, J.M. 2010. Spatial variability of above-ground net primary production in Uruguayan grasslands: a remote sensing approach. *Applied Vegetation Science* 13: 72–85.

Baldi, G. & Paruelo, J.M. 2008. Land-use and land cover dynamics in South American temperate grasslands. *Ecology and Society* 13: 6 [online].

Blaschke, P.M., Trustrum, N.A. & Hicks, D.L. 2000. Impacts of mass movement erosion on land productivity: a review. *Progress in Physical Geography* 24: 21–52.

Burgos, J.J. & Vidal, A.L. 1951. Los climas de la república Argentina según la nueva clasificación de Thornthwaite. *Meteoros* 1: 3–32.

Cagnolo, L., Cabido, M. & Valladares, G. 2006. Plant species richness in the Chaco Serrano Woodland from central Argentina: ecological traits and habitat fragmentation effects. *Biological Conservation* 132: 510–519.

Cabrera, A.L. 1970. Flora de la Provincia de Buenos Aires. Gramíneas. Colección Científica de INTA, Buenos Aires, AR.

Cauhépé, M.A. 1990. Manejo racional de paja colorada. *Revista CREA (Argentina)* 143: 62–69.

Cid, M.S. & Brizuela, M.A. 2009. Variabilidad estacional en el uso de un pastizal serrano de Balcarce por vacunos. *Revista Argentina de Producción Animal* 29: 429–430.

Cid, M.S. & Brizuela, M.A. 2010. Valor nutritivo del forraje de la intermata del pastizal serrano de paja colorada (*Paspalum quadrifarium*) de Balcarce. *Revista Argentina de Producción Animal* 30: 241–242.

Comparatore, V., Martinez, M., Vassallo, A., Barg, M. & Isacch, J. 1996. Abundancia y relaciones con el hábitat de aves y mamíferos en pastizales de *Paspalum quadrifarium* (Paja Colorada) manejados con fuego (Provincia de Buenos Aires, Argentina). *Interciencia* 21: 228–237.

Crawley, M.J. 2007. *The R book*. John Wiley & Sons, Sussex, UK.

Cully, A.C., Cully., J.F. Jr & Hiebert, R.D. 2003. Invasion of exotic plant species in tallgrass prairie remnants. *Conservation Biology* 17: 990–998.

Demuth, H. & Beale, M. 2001. *Neural network toolbox for use with Matlab. Users guide*. The MathWorks, Natick, MA, US.

Di Bella, C., Paruelo, J., Becerra, J., Bacour, C. & Baret, F. 2004. Effect of senescent leaves on NDVI-based estimates of fAPAR: experimental and modelling evidence. *International Journal of Remote Sensing* 25: 5415–5427.

Faraway, J. 2004. *Linear models with R*. CRC Press, London, UK.

Faraway, J. 2006. *Extending the linear model with R*. CRC Press, London, UK.

Frangi, J. 1975. Sinopsis de las comunidades vegetales. *Boletín de la Sociedad Argentina de Botánica* 16: 29–319.

Glenn, E.P., Huete, A.R., Nagler, P.L. & Nelson, S.G. 2008. Relationship between remotely sensed vegetation indices, canopy attributes and plant physiological processes: what vegetation indices can and cannot tell us about the landscape. *Sensors* 8: 2136–2160.

Guerschman, J.P. & Paruelo, J.M. 2005. Agricultural impacts on ecosystem functioning in temperate areas of North and South America. *Global and Planetary Change* 47: 170–180.

Guerschman, J.P., Paruelo, J.M., Di Bella, C.M., Giallorenzi, M. C. & Pacin, F. 2003. Land cover classification in the Argentine Pampas using multi-temporal Landsat TM data. *International Journal of Remote Sensing* 24: 3381–3402.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* 42: 17–38.

Haykin, S. 1999. *Neural networks: a comprehensive foundation*. Prentice-Hall, Upper Saddle River, NJ, US.

Herrera, L. & Laterra, P. 2009. Do seed and microsite limitations interact with species seed size in determining Flooding Pampa grasslands colonization? *Plant Ecology* 201: 457–469.

Herrera, L. & Laterra, P. 2011. Relative influence of size, connectivity and disturbance history on plant species richness and assemblages in fragmented grasslands. *Applied Vegetation Science* 14: 181–188.

Herrera, L., Laterra, P., Maceira, N.O., Zelaya, K.D. & Martínez, G.A. 2009. Fragmentation status of tussock grasslands relicts in Flooding Pampas, Argentina. *Rangeland Ecology and Management* 62: 73–82.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X. & Ferreira, L.G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83: 195–213.

INTA. 1989. Cartas de suelo de la República Argentina, E 1:50000, INTA, AR.

Isacch, J.P. & Martínez, M.M. 2001. Estacionalidad y relaciones con la estructura del hábitat de la comunidad de aves de pastizal de paja colorada (*Paspalum quadrifarium*) manejados con fuego en la provincia de Buenos Aires, Argentina. *Ornitología Neotropical* 12: 345–354.

Jacobo, E., Rodríguez, A., Bartoloni, N. & Deregibus, V.A. 2006. Rotational grazing effects on rangeland vegetation at a farm scale. *Rangeland Ecology and Management* 59: 249–257.

Kemper, J., Cowling, R.M. & Richardson, D.M. 1999. Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biological Conservation* 90: 103–111.

Kutiel, P. 1992. Slope aspect effect on soil and vegetation in a Mediterranean ecosystem. *Israel Journal of Botany* 41: 243–250.

Laterra, P., Vignolio, O.R., Hidalgo, L.G., Fernández, O.N., Cahuépé, M.A. & Maceira, N.O. 1998. Dinámica de pajonales de paja colorada (*Paspalum* spp.) manejados con fuego y pastoreo en la Pampa Deprimida Argentina. *Ecotrópicos* 11: 41–149.

Laterra, P., Vignolio, O., Linares, P., Giaquinta, A. & Maceira, N. 2003. Cumulative effects of fire on the structure and function of a tussock Pampa grassland. *Journal of Vegetation Science* 14: 43–54.

Laterra, P., Ortega, E.Z., Ochoa, M.D.C., Vignolio, O.R. & Fernández, O.N. 2006. Interactive influences of fire intensity and vertical distribution of seed-banks on postfire recolonization of a tall-tussock grassland in Argentina. *Austral Ecology* 31: 608–622.

Lauenroth, W.K. 1979. Grassland primary production: North American Grasslands in perspective. In: French, N.R. (eds.) *Perspectives in grassland ecology*. pp 3–24. Ecological Studies. Springer, Heidelberg, DE.

León, R.J., Rusch, G.M. & Oesterheld, M. 1984. Pastizales pampeanos, impacto agropecuario. *Phytocoenologia* 12: 201–218.

MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ, US.

Malingreau, J.P. 1986. Global vegetation dynamics, satellite observations over Asia. *Journal of Remote Sensing* 7: 1121–1146.

McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341: 142–144.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. 1997. Increased plant growth in the northern high latitudes from 1981–1991. *Nature* 386: 698–702.

Oesterheld, M., Loreti, J., Semmartin, M. & Paruelo, J.M. 1999. Grazing, fire, and climate effects on primary productivity of grasslands and savannas. In: Walker, L.R. (ed.) *Ecosystems of disturbed ground*. pp. 288–306. Elsevier, Las Vegas, NV, US.

Olden, J.D. & Jackson, D.A. 2002. Illuminating the "black box": a randomization approach for understanding variable contributions in artificial neural networks. *Ecological Modelling* 154: 135–150.

Ortega, E. & Laterra, P. 2003. Fire-cued colonization of a Flooding Pampa grassland by thistle species: remnant litter and interference effects. *Applied Vegetation Science* 6: 35–44.

Paruelo, J.M. & Tomasel, F. 1997. Prediction of functional characteristics of ecosystems: a comparison of artificial neural networks and regression models. *Ecological Modelling* 98: 173–186.

Paruelo, J.M., Epstein, H.E., Lauenroth, W.K. & Burke, I.C. 1997. ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* 78: 953–958.

Paruelo, J.M., Jobbágy, E.G. & Sala, O.E. 2001. Current distribution of ecosystem functional types in temperate South America. *Ecosystems* 4: 683–698.

Passioura, J.B. 2002. Soil conditions and plant growth. *Plant, Cell and Environment* 25: 311–318.

Perelman, S.B., Burkart, S.E. & León, R.J.C. 2003. The role of a native tussock grass (*Paspalum quadrifarium* Lam.) in structuring plant communities in the flooding Pampa grasslands, Argentina. *Biodiversity and Conservation* 12: 225–238.

Piñeiro, G., Oesterheld, M. & Paruelo, J.M. 2006. Seasonal variation in aboveground production and radiation use efficiency of temperate rangelands estimated through remote sensing. *Ecosystems* 9: 357–373.

Posse, G. & Cingolani, A.M. 2004. A test of the use of NDVI data to predict secondary productivity. *Applied Vegetation Science* 7: 201–208.

Rusch, G.M. & Oesterheld, M. 1997. Relationship between productivity, and species and functional group diversity in grazed and non-grazed Pampas grasslands. *Oikos* 78: 519–526.

Sakalauskas, K.M., Costa, J.L., Laterra, P., Hidalgo, L. & Aguirrezabal, L. 2001. Effects of burning on soil-water content and water use in a *Paspalum quadrifarium* grassland. *Agricultural Water Management* 50: 97–108.

Sala, O.E., Oesterheld, M., León, R.J.C. & Soriano, A. 1986. Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio* 67: 27–32.

Sala, O.E., Parton, J.W., Joyce, L.A. & Lauenroth, W.K. 1988. Primary production of the central grassland region of the United States. *Ecology* 69: 40–45.

Sellers, P.J., Berry, J.A., Collatz, G.J., Field, C.B. & Hall, F.G. 1992. Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of Environment* 42: 187–216.

Smith, M. 1994. *Neural networks for statistical modeling*. International Thompson Publishing, London, UK.

Soriano, A., León, R.J.C., Sala, O.E., Lavado, R.S., Deregibus, V. A., Cauhépé, M.A., Scaglia, O.A., Velázquez, C.A. & Lemcoff, J.H. 1991. Río de la Plata Grasslands. In: Coupland, R.T. (ed.). *Natural grasslands. Introduction and Western Hemisphere. Ecosystems of the world*. pp. 367–407. Elsevier, New York, NY, US.

Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R. & Goodger, B. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London, Series B* 268: 1791–1796.

Tongway, D.J. & Hindley, N.L. 2004. *Landscape function analysis. Procedures for monitoring and assessing landscapes*. CSIRO Sustainable Ecosystems, Canberra, ACT, AU.

Vignolio, O.R., Laterra, P., Fern'andez, O.N., Linares, M.P., Maceira, N.O. & Giaquinta, A. 2003. Effects of fire frequency on survival, growth and fecundity of *Paspalum quadrifarium* (Lam.) in a grassland of the Flooding Pampa (Argentina). *Austral Ecology* 28: 263–270.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G. M. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, NY, US.

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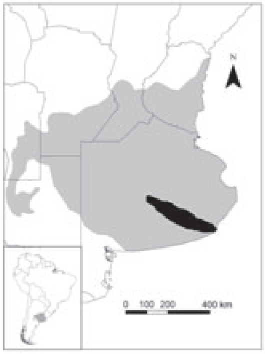

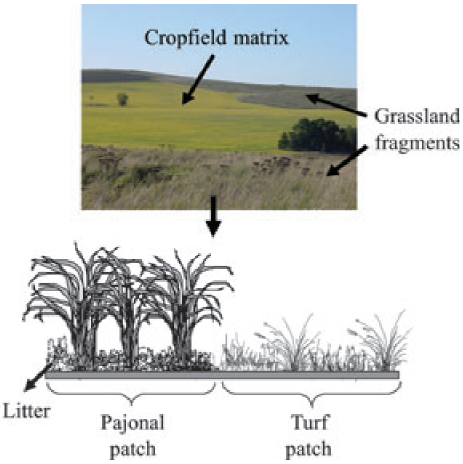

Through artificial neural networks we showed that the temporal dynamics of remnant grasslands in Southern Pampa (Argentina) is controlled by the size of fragments, the vegetation structure (abundance of native grass *Paspalum quadrifarium*) and physical environment (soil, aspect and slope). We highlight the importance of landscape structure as a key control of ecosystem functioning, an aspect seldom considered in the literature.