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RESEARCH PAPER

Regional scale relationships between ecosystem structure and functioning: the case of the Patagonian steppes

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ABSTRACT

Aims 1. To characterize ecosystem functioning by focusing on above-ground net primary production (ANPP), and 2. to relate the spatial heterogeneity of both functional and structural attributes of vegetation to environmental factors and landscape structure. We discuss the relationship between vegetation structure and functioning found in Patagonia in terms of the capabilities of remote sensing techniques to monitor and assess desertification.

Location Western portion of the Patagonian steppes in Argentina (39°30′ S to 45°27′ S).

Methods We used remotely-sensed data from Landsat TM and AVHRR/NOAA sensors to characterize vegetation structure (physiognomic units) and ecosystem functioning (ANPP and its seasonal and interannual variation). We combined the satellite information with floristic relevés and field estimates of ANPP. We built an empirical relationship between the Landsat TM-derived normalized difference vegetation index (NDVI) and field ANPP. Using stepwise regressions we explored the relationship between ANPP and both environmental variables (precipitation and temperature surrogates) and structural attributes of the landscape (proportion and diversity of different physiognomic classes (PCs)).

Results PCs were quite heterogeneous in floristic terms, probably reflecting degradation processes. Regional estimates of ANPP showed differences of one order of magnitude among physiognomic classes. Fifty percent of the spatial variance in ANPP was accounted for by longitude, reflecting the dependency of ANPP on precipitation. The proportion of prairies and semideserts, latitude and, to a lesser extent, the number of PCs within an 8 × 8 km cell accounted for an additional 33% of the ANPP variability. ANPP spatial heterogeneity (calculated from Landsat TM data) within an 8 × 8 km cell was positively associated with the mean AVHRR/NOAA NDVI and with the diversity of physiognomic classes.

Main conclusions Our results suggest that the spatial and temporal patterns of ecosystem functioning described from ANPP result not only from water availability and thermal conditions but also from landscape structure (proportion and diversity of different PCs). The structural classification performed using remotely-sensed data captured the spatial variability in physiognomy. Such capability will allow the use of spectral classifications to monitor desertification.

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Above-ground net primary production, AVHRR/NOAA, classification, Landsat TM, NDVI, Patagonia, regional analysis, remote sensing, vegetation physiognomy.

INTRODUCTION

A description of the spatial and temporal heterogeneity of natural resources is a prerequisite of any management plan. The design of sustainable strategies of use or conservation in a given area must be based on an integrated assessment of both structural and functional aspects of its main ecosystems. The correspondence between structure (the distribution of biomass in space and among physiognomic entities) and functioning (the exchange of matter and energy of an ecosystem) is often assumed, but it has seldom been tested (Paruelo & Lauenroth, 1995). The structural features that may influence functioning include total cover, stratification, composition of species and plant functional types, but also biodiversity at different levels (species and landscapes) (Burke & Lauenroth, 1995). Geographic information systems (GIS) provide the operational framework to integrate not only biophysical but also socio-economic information over extensive areas. The integration of information is not only a fundamental tool from an applied perspective (design of grazing management strategies, conservation plans, etc.), but it also provides a way to derive and evaluate ecological hypotheses. GIS allow one to evaluate hypotheses related to, for example, the relationship among structural and functional attributes of the ecosystem or the relative importance of environmental and human controls on ecological patterns or processes.

Extractive activities (mainly oil exploitation) and sheep grazing have generated many areas of desertification across Patagonia, a vast area in southern South America (Soriano & Movia, 1986; Ares *et al.*, 1990; Soriano & Paruelo, 1990; Paruelo & Aguiar, 2003). During the last decades, the reduction of wool prices, the lack of productive alternatives, and the absence of an environmental policy from federal and/or state agencies and governments, induced an increase in the pressure on natural resources, mainly through overgrazing. A poor understanding of the spatial heterogeneity of vegetation and its response to environmental stresses and disturbances is behind the degradation processes.

Previous regional studies in Patagonia have focused on the description of the floristic heterogeneity of different areas of the region. Some of these studies defined a number of phytogeographical districts based on the physiognomy of the vegetation and dominant species (Soriano, 1956) or described the structural heterogeneity of the whole region (Soriano, 1983; Paruelo *et al.*, 1991; León *et al.*, 1998). More detailed studies have provided useful insights on the characteristics of the main plant communities (Golluscio *et al.*, 1982) and their floristic change across the precipitation (León & Facelli, 1981; Jobbágy *et al.*, 1996) and grazing gradients (León & Aguiar, 1985; Bertiller *et al.*, 1995; Perelman *et al.*, 1997). The degradation processes induced by sheep grazing lead to profound changes in total cover and in the relative abundance of plant functional types (PFT) (León & Aguiar, 1985; Bertiller *et al.*, 1995; Perelman *et al.*, 1997). Such changes include shrub encroachment in the grass steppes (León & Aguiar, 1985; Bertiller *et al.*, 1995) or increases of xerophytic grasses (mainly *Stipa speciosa*) in the more arid vegetation units (Aguiar & Sala, 1998). To date, no integrative descriptions or maps of the structure and functioning of the Patagonian ecosystems have been generated.

Our goal was to understand the relationships between environmental factors, vegetation structure and ecosystem functioning in north-west Patagonia. This area concentrates a large diversity of environments and physiognomic types in a relatively small area representing an ideal system for the study of such relationships. After describing the structure of the vegetation at the regional scale our specific objectives were:

1 To characterize ecosystem functioning, focusing on descriptors of the above-ground net primary production and its seasonal dynamics;

2 To relate the spatial heterogeneity of both functional and structural attributes to environmental factors, in order to derive quantitative hypotheses regarding the environmental controls of vegetation structure and functioning.

As a first step, we performed a supervised classification of Landsat TM imagery to derive maps of the most conspicuous physiognomic classes (PC) within the area. Regarding the first objective, we built an empirical relationship between the Landsat TM-derived normalized difference vegetation index (NDVI) and annual net primary production (ANPP). In addition, we characterized the ANPP seasonality of the different physiognomic classes at an 8 × 8 km spatial resolution. Finally (second objective), we analysed the relationships between ANPP and several climate surrogates and structural attributes of the vegetation and the landscape. We discuss the relationship between vegetation structure and functioning found in Patagonia in terms of the capabilities of remote sensing techniques to monitor and assess desertification.

MATERIALS AND METHODS

Study area

The study area (more than 85,000 km^2) includes the western portion of the extra-Andean Patagonian steppes in Argentina (Fig. 1). The area ranges from 39°30′ S to 45°27′ S. The western border is located at approximately 71°30′ W. Towards the east, the area extends 100 km until the meridian 70°23′ W. The area includes the eastern foothills of the Andes Mountains, extra-Andean Sierras, basaltic plateaus, alluvial and glacier valleys and hills.

The area corresponds to one of the least modified regions of the world. The region displays a cold temperate climate, humid towards the Andes (more than 1000 mm of annual precipitation) and arid at the eastern extreme (less than 150 mm of precipitation) (Jobbagy *et al.*, 1995; Paruelo *et al.*, 1998). Precipitation is concentrated during the coldest months of the year, which leads to an asynchrony between the wet and the dry growing seasons (Paruelo *et al.*, 2000). The study area includes the eastern border of the Sub-Antarctic forests (not included in our analysis), and the Sub-Andean and Occidental district of the Patagonian phytogeographical region (Soriano, 1956; León *et al.*, 1998).

Vegetation structure data

We generated a database of 299 floristic relevés composed of 211 species. Vegetation data were collected in late spring and early summer during the period 1995–2000. No major changes in vegetation structure were observed during this period. Relevés were located preferentially in four areas of intensive sampling, corresponding to steppes with relatively easy access and displaying a high physiognomic diversity (Fig. 1). Each relevé was undertaken in a stand (i.e. a physiognomically homogeneous spatial unit)

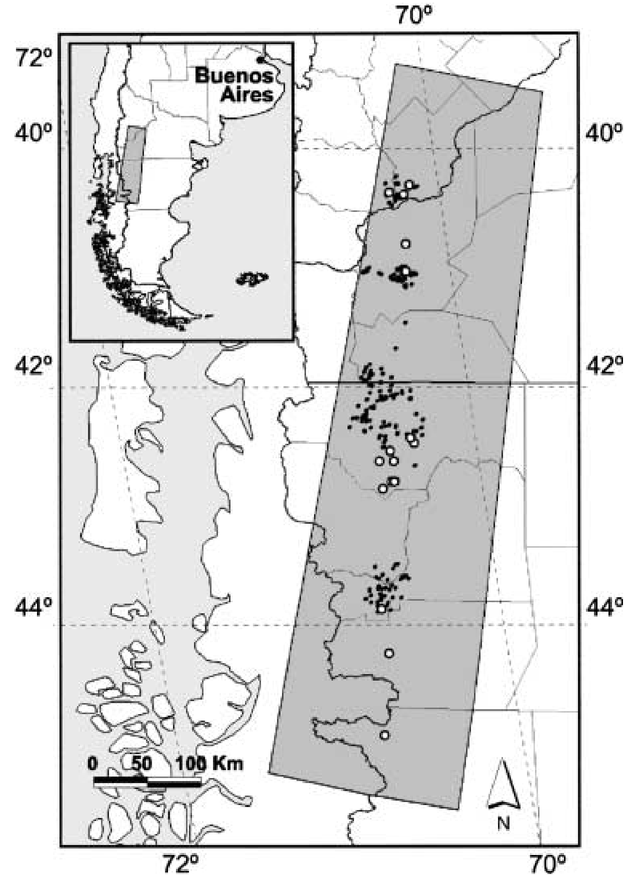

Figure 1 Study area in north-west Patagonia. The shadowed strip corresponds to the mosaic of four Landsat TM scenes (path 231, rows 88, 89, 90 and 91). Black dots correspond to the floristic relevés and white dots to the sites where above-ground net primary production was determined.

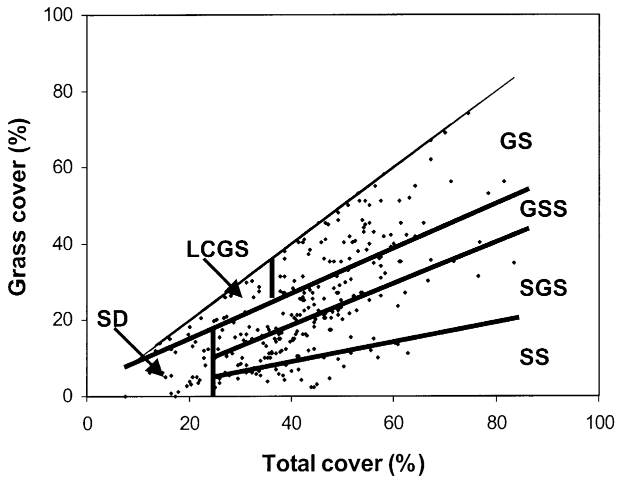

Figure 2 Distribution of the relevés in the space defined by the total cover and the cover of grass species. The lines divided the space in order to define physiognomic classes: semideserts (SD), 'low-covered' grass steppes (LCGS), shrub steppes (SS), shrub-grass steppes (SGS), grass-shrub steppes (GSS), grass steppes (GS).

larger than 1 ha, and all the species present in an area of 500 m^2 were recorded. Each species was visually assigned to a class of cover abundance following the scale proposed by Braun-Blanquet (1932). Most of the relevés (255) were georeferenced using a handheld global positioning system (GPS) device (Garmin II Plus). Geographic coordinates corresponded to the centre of the stand. The GPS error (15–70 m) was relatively small compared to the size of the stand (> 1 ha). The remaining relevés were not included in the GIS but were used to study the structure of the floristic data. Detrended correspondence analysis (DCA) (Hill & Gauch, 1980) was used to describe the structure of the floristic data. The analysis was based on the species that appeared in more than 3% and less than 75% of the relevés (90 species). We discarded not only the extremely rare species but also those present in almost every site. The criteria to discard species for the DCA was based on previous vegetation analyses that showed that those species were not able to discriminate among floristic units (Golluscio *et al.*, 1982; Jobbágy *et al.*, 1996). We also georeferenced and visually registered the physiognomy of additional sites (other than the 299 relevés) corresponding not only to grass and shrub steppes, but also to forests, scrubland and prairie stands. These sites are here referred to as 'observations'. Such observations allowed us to evaluate how well our relevés were capturing the environmental heterogeneity of the area.

We defined 9 physiognomic classes (PC) based on the total cover and the relative proportion of plant functional types (PFT) (grasses, shrubs and trees): forests (FO), scrublands (SC), prairies (PR) (meadows), grass steppes (GS), grass-shrub steppes (GSS), shrub-grass steppes (SGS), shrub steppes (SS), semideserts (SD) and 'low-covered' grass steppes (LCGS). Forests and scrublands corresponded to units dominated by trees and tall shrubs (greater than 1.5 m height). Prairies showed a total cover greater than 80% and were dominated by mesophytic grasses. The 'steppe' classes were defined based on total cover and the proportion of shrubs and grasses (Fig. 2). The changes among steppe units were not discrete, and there was an ample ecotone between all of them. Every relevé was assigned to a single physiognomic class.

Mapping vegetation physiognomy

Pre-processing

We mapped vegetation at the physiognomic level by performing a supervised classification of Landsat 5 TM scenes. We constructed a mosaic of four TM scenes (path 231, rows 88, 89, 90 and 91) corresponding to the same date (30th December 1997). These images were completely cloud free. We georeferenced the mosaic using 60 ground control points obtained from topographic maps, achieving a root mean square error lower than 60 metres (two pixels). The georeferenced mosaic was calibrated to obtain radiance and top-of-atmosphere reflectance values for each pixel using the gain and bias information provided in the image headers. We did not perform atmospheric corrections. The strip analysed is a subset of the constructed mosaic because we discarded part of the western border dominated by forests.

Classification

We selected areas of uniform structure as training areas to avoid contamination from other physiognomies. Spectral signatures were defined for 36 areas including more than 100 pixels each. Such areas corresponded to the main physiognomic classes and to additional covers such as water, snow, rock and bare soil. The sites used for training corresponded to a subset of the relevés and observations performed, and they were independent of those used to evaluate the classification. A supervised classification was performed on the seven bands of the TM mosaic using the maximum likelihood algorithm as a decision rule to assign a pixel into a class. The Landsat TM bands covered the visible part of the spectrum (bands 1, 2 and 3), the near-infrared (band 4), the mid-infrared (bands 5 and 7) and the thermal infrared (band 6) (Lillesand & Kiefer, 1997). The maximum likelihood classification method is based on a parametric algorithm that quantifies the probability that a pixel belongs to a particular class. Band 6 of the TM sensor was transformed to 30-m resolution in order to be used with bands 1–5 and 7. We performed a univariate analysis for testing the contribution of each individual band to the separation among land cover classes. All bands were significant, meaning that each individual band is capable of discriminating among at least two land cover classes.

Classification evaluation

We evaluated the classification using a subset of 48 points located in prairie and steppe units and presenting the same vegetation unit (as defined by the classification) within 80% of the area of a plot with radius of three pixels. A source of misclassification was the diffuse boundaries among classes (Fig. 2). Because of this, instead of computing a confusion matrix and calculating the overall user's and producer's accuracies (Congalton, 1991), we performed a correlation analysis between the number assigned to each physiognomic class according to their cover and proportion of grasses (1 for semideserts and 6 to prairies) as observed in the field and the number of the class that corresponded to this area on the classified image.

Summarizing the information

The information was summarized and aggregated at the level of 8 × 8 km cells, the resolution of the Pathfinder AVHRR Land database used to characterize some functional attributes (see below). We computed the proportion of each physiognomic unit, the number of classes per cell, and its diversity (measured by the Shannon index, Greig-Smith (1983)) within the 8 × 8 km pixel.

Primary production data

We estimated ANPP and its seasonal and interannual dynamics from a spectral index derived from satellite data, the NDVI, where NDVI = (NIR − R)/(NIR + R), where R and NIR are the reflectances in the red and the near-infrared portions of the electromagnetic spectrum, respectively. The NDVI shows a positive and linear relationship with the fraction of photosynthetically active radiation intercepted by the plant canopy (Sellers *et al.*, 1992), and hence with primary production (Prince, 1991).

We used two sources of satellite data that differ in their grain and extent both in space and time. A NDVI layer with a spatial resolution of 30 × 30 m was derived from bands 3 and 4 of the Landsat TM imagery described above to quantify the ANPP-NDVI relationship at a fine scale. The date of these images (30th December) corresponds roughly to the peak of productivity of the steppes (Jobbágy *et al.*, 2002). We calibrated the NDVI-ANPP relationship using field estimates of ANPP for 18 sites distributed over the area (Fig. 1) (data from Jouve, 2003). The sites corresponded to the different physiognomies (2 SD, 3 SS, 5 GSS, 5 SGS, 2 GS and 1 PR sites). ANPP values were calculated from peak biomass (Lauenroth *et al.*, 1986; Scurlock *et al.*, 2002) for the same growing season as the Landsat images (December 1997–January 1998). Grasses, shrubs and forbs were harvested along five transects, randomly distributed over a homogeneous area in terms of physiognomy and topography, greater than 100 ha. Each transect was 10 m long and 20 cm wide. Samples were oven dried and weighed in the laboratory. Peak biomass of grasses and forbs included all green tissue, and for shrubs it included current year twigs (Jobbágy & Sala, 2000). All species were included. Peak biomass is a reliable estimator of ANPP in Patagonia due to the clear seasonality of carbon uptake (Paruelo *et al.*, 1998; Jobbágy & Sala, 2000; Jobbágy *et al.*, 2002). For the same reason, the mean annual and the maximum annual NDVI are highly correlated (Jobbágy *et al.*, 2002). We therefore used the NDVI derived from the Landsat TM scenes of 30th December as an indicator of ANPP.

We used NDVI data from the NOAA Pathfinder AVHRR Land (PAL) database compiled by NASA (James & Kalluri, 1994) to quantify the ANPP-NDVI relationship at a coarser scale. This database has a coarser spatial but finer temporal resolution than the Landsat-derived data. The spatial resolution of the PAL database is 8 × 8 km and covers the period 1981–2000, with one maximum composite image available every 10 days. Although many of the problems of previous global AVHRR products were corrected within the PAL database, we carefully checked the performance of the database for Patagonia by inspecting non-vegetated areas where no seasonal changes or trends were expected in the NDVI (e.g. continental ice fields in Santa Cruz or extreme desert areas in northern Chile). The evidence available for similar areas indicates that the mean annual NDVI derived from AVHRR/NOAA data is a reliable linear estimator of ANPP (Prince, 1991; Paruelo *et al.*, 1997, 2000). We produced monthly averages of NDVI for the 19 years of data. We characterized the temporal variability from the monthly coefficient of variation (CV = SD/Mean). However, because we did not have seasonal ANPP data we did not transform monthly NDVI into production data. We related, using linear regression, the ANPP estimates generated from the Landsat TM calibration, to the annual NDVI integral derived from PAL data, by aggregating the Landsat information to the spatial resolution of the PAL database (8 × 8 km).

Abiotic environmental data

Although precipitation data were available for 11 sites within the study area, we did not interpolate them because their number and spatial distribution were not appropriate to generate a reliable cover (Paruelo *et al*., 1998, 2000). Also, all the weather stations corresponded to sites located at low elevations, and we did not have a model to account for the influence of altitude on precipitation within this area. We therefore used two variables that are closely related to precipitation in the study area: longitude (Jobbágy *et al*., 1995) and altitude. Altitude was derived from a 1 × 1 km database compiled by the US Geological Survey (http://edcdaac.usgs.gov/gtopo30/gtopo30.html). We did not attempt to examine the temporal relationship between ANPP and climatic data, because we do not yet have a consistent precipitation database for the period during which AVHRR data are available. Even though the longitudinal range is small (just one degree), the precipitation gradient is very well defined, with values decreasing from > 1000 mm at 71°30′ to < 200 mm at 70°30′ (Jobbágy *et al*., 1995).

We also used surface temperature data derived from the thermal infrared bands of AVHRR/NOAA satellites (bands 4 and 5). At-sensor radiance in the thermal infrared portion of the electromagnetic spectrum is predominantly due to surface and atmospheric emittance. This emittance is proportional to the fourth power of the temperature of the emitting body (Stefan-Boltzman's Law). Split-window techniques were used to model surface temperature based on data from bands 4 (10.3–11.3 μm) and 5 (11.5–12.5 μm) of the AVHRR/NOAA sensor (Sobrino *et al*., 1991). The relationships of the ANPP estimates derived from the Landsat TM imagery with abiotic and physiognomic variables were analysed using simple and multiple linear regressions. The independent variables included in the analyses were latitude, longitude, mean surface temperature, the proportion of prairies and semideserts, and the richness and diversity of physiognomic units. All variables were aggregated to the level of the 8 × 8 pixel. Stepwise multiple regression has been criticized because it has severe problems in the presence of collinearity of independent variables. To minimize these problems, we took a series of precautions: we set the F-to-enter to a value that produced a P level less than 0.01 (i.e. all the independent variables must have been significant to enter the model). We also tested the significance of the variables in the model by including a random variable among the independent variables and checking whether this variable was included in the final model. We stopped the stepwise process when the increase in r-square was less than 0.02, to keep the model as simple (i.e. few variables) as possible. We compared the model obtained with all possible alternative models with the same number of independent variables. In such a way, we explored if the model obtained using the stepwise procedure was the 'best' model. In all cases we found that the model reported was the best among those evaluated. The satellite-derived information and the environmental variables were integrated into a GIS using ArcView 3.2. Statistical analyses were performed in SAS and PCOrd.

RESULTS

The classification performed on the spectral data allowed us to map the physiognomic heterogeneity of the area (Fig. 3a). The classes observed in the field and those predicted by the classification were highly correlated ($r = 0.81$, $n = 48$, $P < 0.01$). Most of the discrepancies were related to the similarities between contiguous classes in terms of total cover or shrub/grass cover ratio. A non-quantitative evaluation based on extensive field observations provided additional support to the classification performed, particularly for forests and scrubland areas (not included in the formal evaluation).

The plot of the first two axes of the DCA performed on the matrix of floristic data (299 relevés × 90 species) displayed the distributions of the relevés based on their floristic similarities (Fig. 4). As has been shown in previous studies for this area (Jobbágy *et al*., 1996), characteristic species of the *Festuca pallescens*, *Rhytidosperma picta* and *Lathyrus magellanicus* grass steppes (Golluscio *et al*., 1982) dominate one extreme of the axis that captures most of the variability (details of the species scores are provided as Supplementary Material). The species exhibiting the extreme values at the other end of axis 1 (Fig. 4) characterize the shrub steppes that dominate the transition towards the central district of the Patagonian province (León & Facelli, 1981; Golluscio *et al*., 1982; Jobbágy *et al*., 1996; León *et al*., 1998). The sites were not clustered according to their physiognomy within the space of the first two axes (Fig. 4). The space occupied by the relevés for the most extreme steppe physiognomies (semideserts and grass steppes) strongly overlapped within the space defined by the first two axes (Fig. 4).

The classes showed different patterns of association at the grain of a NOAA PAL pixel (64 km^2). At this scale, the distribution of prairies was positively associated with forests, scrublands and, to a lesser extent, grass steppes (Table 1). The proportion of grass steppes was positively correlated with that of grass-shrub steppes and negatively correlated with the proportion of semideserts. The proportion of scrublands was negatively associated with those of semideserts, shrub and shrub-grass steppes, and positively associated with those of forests and prairies (Table 1). The proportions of shrub and shrub-grass steppes were also positively correlated, reflecting the fuzzy boundary between these classes. On average, a 64 km^2 cell contained 6.31 (± 1.34) classes (maximum 9), with 21% of the cells having 8 or 9 classes. The Shannon diversity index, which also took into consideration the relative abundance of the classes within the cell, was on average 1.30 (± 0.34).

The linear model describing the relationship between ANPP and the Landsat TM-derived NDVI explained 84% of the variance ($r^2 = 0.84$, $n = 15$, $P < 0.01$) (Fig. 5). Part of the unexplained variance should be associated with differences in light use efficiency among structural classes or with the influence of different soil backgrounds. The site displaying the greatest NDVI and ANPP was not influential in the calibration (r student = 0.2521, d.f. fits = 0.5812). The scaled change in the model parameters when this site was excluded did not exceed the cutoff values proposed by Belsley *et al*. (1980) (DFBETA intercept = –0.4705,

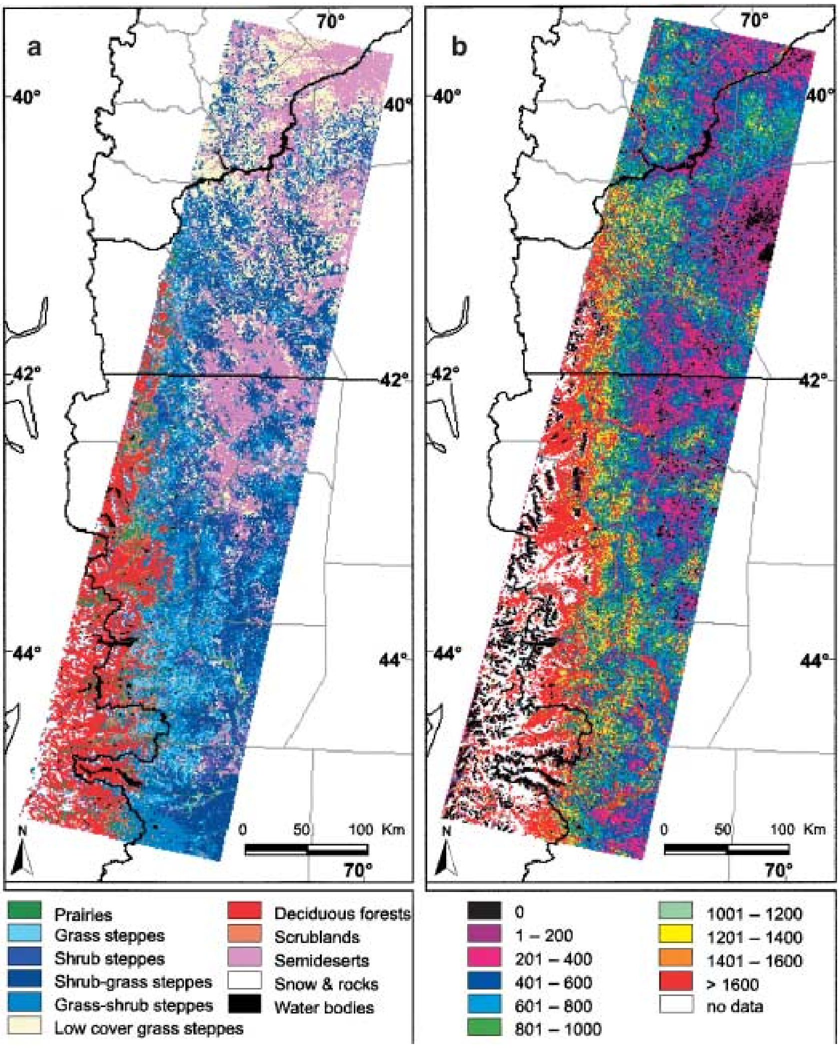

Figure 3 Spatial patterns of vegetation structure (physiognomic classes) (a) and above-ground net primary production (ANPP) (b). ANPP units are kg of dry matter ha^{-1} $year^{-1}$. The physiognomy map was produced from a supervised classification of Landsat TM imagery. ANPP was derived from the Normalized Difference Vegetation Index (NDVI) and the empirical model presented in Figure 5. The deciduous forests and scrublands classes shown in (a) were masked in (b), because the ANPP/NDVI model used did not hold for these classes.

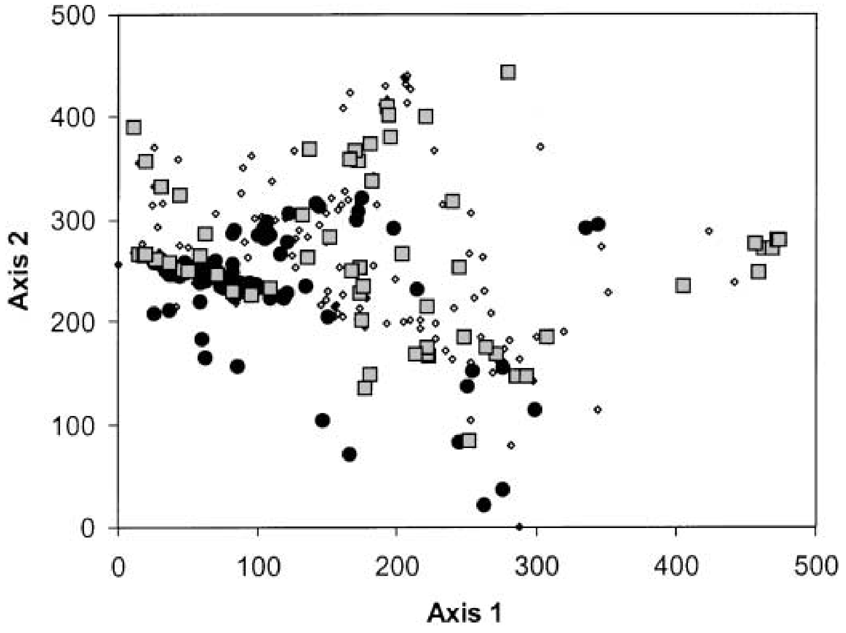

Figure 4 Distribution of the 299 relevés in the space of the first two axes of the Detrended Correspondence Analysis (DCA). The analysis was based on the species that appeared in > 3% and < 75% of the relevés (90 species). Black dots and grey squares correspond to sites characterized, according to the criteria presented in Figure 2, as grass steppes and semideserts, respectively. The small dots correspond to the remaining physiognomic classes.

Table 1 Correlations between the proportions of the different physiognomic classes at the scale of an AVHRR/NOAA pixel (64 km^2) ($n = 1099$). Numbers in bold indicate $P < 0.01$

Physiognomic classes	FO	SC	PR	GS	GSS	SGS	SS	SD	LCGS
Forests (FO)		**0.39**	**0.31**	**−0.22**	**−0.16**	**−0.38**	**−0.36**	**−0.28**	**−0.32**
Scrublands (SC)			**0.71**	**0.07**	**0.15**	**−0.40**	**−0.37**	**−0.34**	**−0.37**
Prairies (PR)				**0.13**	**0.06**	**−0.33**	**−0.28**	**−0.31**	**−0.31**
Grass steppes (GS)					**0.45**	**−0.21**	−0.05	**−0.32**	**−0.24**
Grass-shrub steppes (GSS)						**−0.16**	**−0.23**	**−0.50**	**−0.41**
Shrub-grass steppes (SGS)							**0.22**	**−0.14**	**0.13**
Shrub steppes (SS)								0.02	**0.20**
Semi-deserts (SD)									**0.26**
Low covered grass steppes (LCGS)									

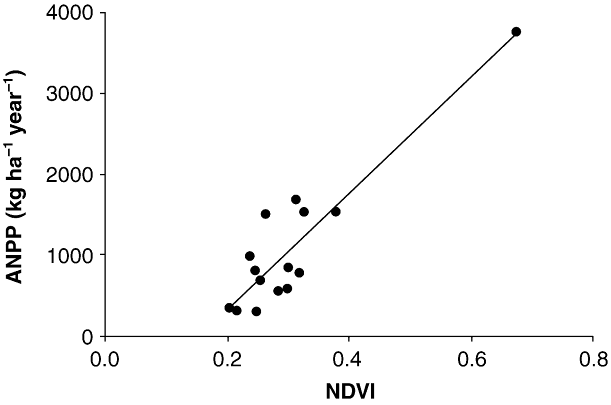

Figure 5 Relationship between the Normalized Difference Vegetation Index (NDVI) derived from the Landsat TM images and above-ground net primary production (ANPP). ANPP = 7951.5 *NDVI – 1088.4 ($r^2 = 0.84$, $n = 15$, $P < 0.001$).

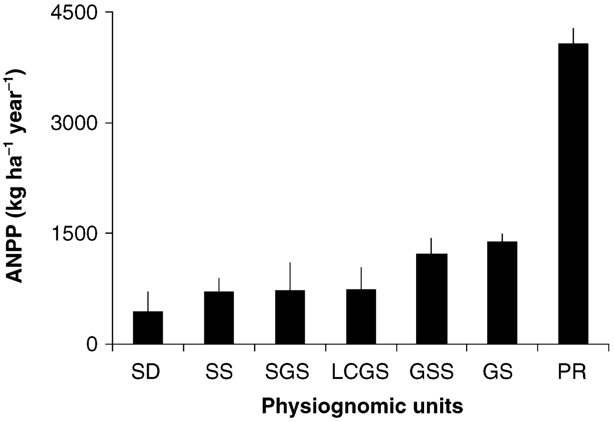

Figure 6 Mean above-ground net primary production (ANPP) for the different physiognomic classes: semideserts (SD), 'low-covered' grass steppes (LCGS), shrub steppes (SS), shrub-grass steppes (SGS), grass-shrub steppes (GSS), grass steppes (GS) and prairies (PR). The lines on the bars correspond to one standard deviation.

Table 2 Coefficients, standard error, cumulative r^2, partial r^2, and F Snedecor corresponding to the multiple regression models fitted for the average ANPP of a 64-km^2 cell (dependent variable) and the longitude, proportion of prairies, proportion of semideserts, latitude and the richness of physiognomic classes (PC richness) (independent variables). $N = 829$, P-values were always < 0.01

	Coefficient	Std error	r^2	partial r^2	F
Y-intercept	−25723	1191.4			
Longitude	−408	18.0	0.51	0.51	512
Prop. Prairies	5641	214.2	0.69	0.18	693
Prop. Semi-deserts	−579	30.0	0.78	0.09	360
Latitude	59	5.5	0.82	0.03	114
PC richness	50	5.5	0.83	0.02	83

DFBETA slope = 0.5577). However, excluding this site from the calibration decreased the r^2 to 0.43. Even though the relationship between NDVI and ANPP showed only moderate r^2 values, the uncertainty of the predictions was similar to the spatial heterogeneity found in each particular site (Jouve, 2003). We applied this relationship to the NDVI layer to generate an estimation of ANPP for the entire study area (Fig. 3b).

We observed a west-east reduction in ANPP that mirrors changes in precipitation (Fig. 3b). Prairies showed the greatest ANPP (4000 kg ha^{-1} year^{-1}), and semideserts the least (500 kg ha^{-1} year^{-1}) (Fig. 6). The ANPP of the 64 km^2 cells showed a negative correlation with longitude (an eastward decrease), a surrogate for mean annual precipitation ($r = -0.71$, $n = 829$, $P < 0.001$). ANPP showed a positive relationship with the proportion of prairies and the richness of physiognomic classes ($r = 0.67$ and r = 0.60, respectively, $n = 829$, $P < 0.001$), and a negative correlation with the proportion of semideserts within the cell ($r = -0.61$, $n = 829$, $P < 0.001$).

A stepwise regression analysis showed that environmental variables and the physiognomy of the cell explained 83% of the spatial variability of ANPP (Table 2). Fifty-one percent of the variance was accounted for by longitude (Table 2). The proportion of prairies and semideserts explained 18% and 9% of the variance, respectively (Table 2). Latitude (mainly through its effect on temperature) accounted for 3% of the variability. A descriptor of landscape diversity, the richness of physiognomic classes, explained a small but significant fraction of the spatial variability of ANPP (Table 2). The variables describing landscape structure (proportion of prairies and semideserts and PC richness) explained together 29% of the regional variability in ANPP.

The spatial heterogeneity of ANPP within an 8 × 8 km cell (calculated from Landsat TM data) was positively associated with the mean NDVI (derived from AVHRR/NOAA data) and with the diversity of physiognomic classes. Both variables accounted for 43% of the spatial variability in ANPP ($n = 829$, $P < 0.001$). ANPP spatial heterogeneity within a cell was greater for the most productive areas and for the more diverse cells ($F_{\text{partial NDVI}} = 467$, $F_{\text{partial PC diversity}} = 27$, $n = 829$, $P < 0.001$).

The average ANPP calculated from Landsat TM data for cells with less than 1% of forests was highly correlated with the mean annual NDVI derived from NOAA PAL data (MEAN PAL NDVI = 0.095 + 0.000131 × ANPP Landsat TM, $r^2 = 0.76$, $n = 829$, $P < 0.001$). We were then able to analyse the average annual seasonal dynamics of the NDVI, as a descriptor of light interception and hence of productivity, for cells dominated by a single class (greater than 80% for forests and semideserts and greater than 60% for the other classes). The low-covered grass steppe class was not abundant enough to be considered dominant in any cell. Forests and prairies showed similar NDVI averages over the year, but had quite different dynamics (Fig. 7a). Forests were more seasonal than prairies, reaching more extreme values both in winter and summer. Forests also maintained greater values of light interception during late summer, while prairies reached a peak in November–December. Grass steppes and grass-shrub steppes showed similar NDVI dynamics (Fig. 7a), differing only in the magnitude of the NDVI peak (and hence in the annual average), which was slightly greater in the GS than in the GSS. Both classes peaked in December and had greater rates of increase of light interception during spring than rates of decrease in summer and fall (Fig. 7a). The less productive classes, semideserts and shrub steppes, showed earlier NDVI peaks (November) and much less seasonal variation than the other classes. Both classes presented a secondary peak of NDVI during fall. The main differences between these classes occurred after the November peak, when shrub steppes maintained NDVI values around 0.05 greater than semideserts (Fig. 7).

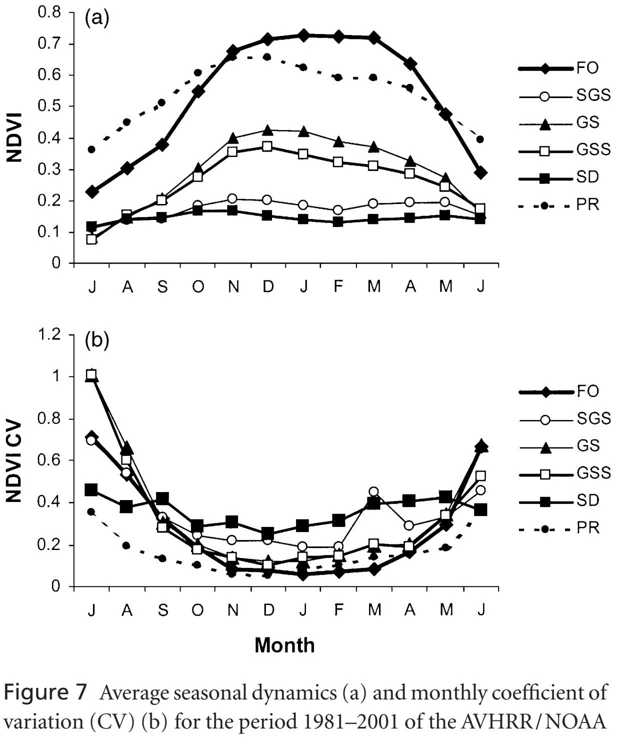

Figure 7 Average seasonal dynamics (a) and monthly coefficient of variation (CV) (b) for the period 1981–2001 of the AVHRR/NOAA NDVI for the main physiognomic classes: forests (FO), prairies (PR), grass steppes (GS), shrub-grass steppes (SGS), grass-shrub steppes (GSS) and semideserts (SD). For the remaining classes, it was not possible to derive the seasonal dynamics because these classes were not dominant (greater than 60%) in any 8 × 8 km cells.

The interannual variability of monthly NDVI derived from NOAA PAL varied both seasonally and among physiognomic classes (Fig. 7b). For all the physiognomic classes, variability increased during the coldest months of the year. Prairies were the least variable class. The driest classes (semideserts and shrub-grass steppes) showed the greatest CV during the growing season. During winter months grass steppes and grass-shrub steppes showed the greatest relative variability (Fig. 7b).

DISCUSSION

Spectral data provided by Landsat TM imagery allowed us to generalize field information for both structural (vegetation physiognomy) and functional (ANPP) characteristics of the ecosystems of an extensive area of Patagonia. From spatially explicit information on vegetation structure, ecosystem functioning and abiotic factors, we were able to describe regional patterns and to generate quantitative hypotheses regarding the abiotic and biotic controls of ecological attributes. Spectral information was able to discriminate land cover among physiognomic classes. A statistical evaluation of the classification, performed using field data independent of those utilized to derive the spectral signatures, provided empirical support for the spatial patterns of physiognomy (Fig. 3a).

The floristic and physiognomic (proportion of plant functional types) structure of the vegetation of the Patagonian steppes were not related (Fig. 4). The floristic composition can vary widely within a physiognomic class, as became evident from the wide distribution of single physiognomic classes in the space of the first two axes of the DCA (Fig. 4). Many of the grass-shrub steppes, low-covered grass steppes and semideserts mapped in our analysis corresponded to degraded states of grass steppes, either by overgrazing (León & Aguiar, 1985) or by accidental fires. Despite the changes in PFT abundance or total cover, many of the species of the original plant community remain in the degraded states. For instance semideserts, which covered 10% of the area, occurred as large patches towards the east, in the driest environments of the region. The typical community of this physiognomic unit has been defined by Golluscio *et al.* (1982), and *Nassauvia glomerulosa* ('colapiche') is the dominant dwarf shrub. However, small patches of semideserts were also common towards the west, which would, again, correspond to cases of extreme degradation of grass steppes or even prairies. The species list in these areas resemble more a grass steppe than a typical plant community of this unit, as became evident from the overlap of grey squares (semideserts) and black dots (grass steppes) in Fig. 4. In the DCA, the distribution of the sites in the space of the first two axes is solely based on floristic similarity. The low correlation between changes in physiognomy and species composition clearly reduces the possibilities of mapping the floristic heterogeneity of the region in terms of plant communities.

The ANPP, derived from Landsat TM NDVI and an empirical model based on field data, differed among physiognomic classes (Fig. 5). Among steppe units, ANPP differed by a factor of three. Prairies, covering only 3.3% of the area, contributed more than 12% of the total ANPP of the study area. Grass steppes and grass-shrub steppes, occupying 34% of the area, accounted for more than 38% of the biomass production. The use of AVHRR/NOAA-derived NDVI allowed us to describe the temporal dynamics of production, both intra- and interannually, of 64 km^2 cells dominated by a single physiognomic class. The main vegetation units differed in the timing of maximum NDVI and hence radiation interception, which occurred later in the most productive units (forests, prairies). Prairies exhibited the least seasonality compared to other physiognomic classes. Such areas present a different water regime than the steppes due to lateral inflows of water almost year round (Paruelo *et al*., 2000). The lack of a clear dry season explains the differences within the steppe units. On the other hand, the dominance of mesophytic grasses that remain green almost year-round account for the difference with forests dominated by deciduous species of *Nothofagus*. In the valleys and low altitude plateaus occupied by such prairies, average monthly temperatures during winter months may remain well above 0 °C. Winters are not as extreme in Patagonia as in the Northern Hemisphere due to the low continentality of climate (Paruelo *et al*., 1998).

Most of the spatial variance of the ANPP among 64 km^2 cells was associated with longitude, a surrogate for precipitation in the study area (Jobbágy *et al*., 1995). The relationship between ANPP and precipitation has been described for Patagonia (Jobbágy & Sala, 2000) and elsewhere for grasslands and shrublands (McNaughton *et al*., 1993). The proportion of the variance explained by this variable (51%) was similar to the values reported in the literature for specific regional studies (e.g. Sala *et al*., 1988; Paruelo & Lauenroth, 1995; Epstein *et al*., 1997). As in the study by Epstein *et al.* (1997), temperature (represented in our analysis by the latitude) accounted for a relatively small proportion of the variability. In our analysis, the variability in ANPP not accounted for by abiotic factors was significantly associated with the proportion of different physiognomic classes present within the cell. Even though the proportion of the physiognomic classes is related to water availability (and hence to longitude and altitude), it depends also on the structure of the landscape. Landscape structure affects water redistribution and the subsequent generation of meadows and prairies (Paruelo *et al*., 2000). Soils and geological substrate also influence (within a given precipitation level) the proportion of certain physiognomic classes. For example, the distribution of semideserts of *Nassauvia glomerulosa* is associated not only with aridity but also with soil texture (Jobbágy *et al*., 1996). As we mentioned above, grazing-mediated degradation of the vegetation transforms a grass steppe (or even a prairie) into a semidesert dominated by dwarf shrubs and having a total cover less than 25%. The relationship of the proportion of physiognomic classes and ANPP would reflect, at least partially, the impact of desertification on total carbon uptake. Further analyses are needed to isolate properly the effects of degradation on ANPP.

The relationship between biodiversity and ANPP has been the subject of intense debate (Schulze & Mooney, 1993; Naeem *et al*., 1994; Tilman *et al*., 1996; Chapin *et al*., 1997, 1998), focused on species and plant functional diversity. The importance of landscape diversity has been pointed out (Burke & Lauenroth, 1995), but no empirical evidence is available. Our results showed a significant relationship between landscape-type richness and ANPP. The mechanisms that underlie this relationship are not clear, but they may be associated again with greater water redistribution in the wettest compared to the driest sites. Grazing may also play an important role in shaping the relationship between ANPP and landscape heterogeneity. The structure of the landscape could control grazing patterns and hence the risk of degradation. Most of the proposed paths of degradation of the different physiognomic classes result in semideserts or shrub steppes (León & Aguiar, 1985; Bertiller *et al*., 1995). Desertification will then promote a homogenization of the landscape unlike the increase in intrastand spatial heterogeneity caused by selective grazing in many arid ecosystems (Schlesinger *et al*., 1990; Adler *et al*., 2001). This grazing-driven landscape homogenization can have profound impacts on the dynamics of the desertification process. As the different physiognomic classes turn into less productive semideserts, the grazing pressure on the remaining (more productive) classes would increase. This process results in a positive feedback between grazing and the increase of semideserts, with very negative consequences for the ecological sustainability of the entire ecosystem. The consideration of such landscape-scale degradation processes can aid in understanding the severe desertification that remains unexplained at the stand scale (van de Koppel *et al*., 2002).

CONCLUSIONS

The floristic and the physiognomic structure of the Patagonian vegetation are loosely related. Remotely-sensed data were able to describe the structural heterogeneity of the steppes at the physiognomic but not at the floristic level. The ability of spectral data to describe the physiognomic spatial heterogeneity opens, however, the possibility of tracking degradation changes in time as they involve changes in total cover and PFT abundance. Combining the state-and-transition models proposed by Westoby *et al.* (1989) with descriptions of physiognomic changes through time derived from Landsat TM seems to be a promising approach for characterizing and mapping desertification in Patagonia.

The ANPP, described by empirical models based on field data and the NDVI derived from Landsat imagery, showed differences of up to 300% among physiognomic classes. Most of the spatial variance in ANPP was associated with climate factors (precipitation and temperature). However, the structure of the landscape was an important control on the total amount and interannual variability of carbon uptake.

ANPP was positively related to the diversity of physiognomic classes. The homogenization of the landscape associated with degradation processes induced by overgrazing of the steppes therefore will enhance the reduction in productivity in desertified areas. A more detailed analysis of the effect of landscape diversity on ANPP would help to disentangle an important ecological point: the relationship between ecosystem functioning and biodiversity at higher levels (landscapes) than species composition. Experimental and modelling studies will allow us to understand the mechanisms of the effects of landscape diversity on ecosystem functioning.

Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/GEB/GEB118/GEB118sm.htm

Appendix S1: Scores of the species of intermediate constancy (higher than 3% and lower than 75%) in a Detrended Correspondence Analysis based on 299 relevés.

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