Insights into Ecosystem Composition and Function in a Sequence of Degraded Semiarid Steppes

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Abstract

We evaluated changes in ecosystem function in semiarid *Stipa tenacissima* L. steppes along a degradation gradient in southeast Spain. We used soil surface indicators to obtain surrogates of ecosystem function (resistance to erosion, infiltration, and nutrient cycling) and related these values to the main abiotic and biotic characteristics of the experimental sites. When ranked in an ordered sequence, the trajectory of these indicators showed abrupt changes, providing empirical evidence of discontinuities in ecosystem function along the degradation gradient evaluated. Surrogates of resistance to erosion showed nonlinear relationships with variables defining the spatial structure of patches, the area covered by sprouting shrubs, and species richness. The latter two variables were significantly related to surrogates of nutrient cycling and infiltration. Our results suggest that sprouting shrubs are playing a key role in improving ecosystem function and composition in degraded *S. tenacissima* steppes. The implications of our results for the optimization of restoration procedures in semiarid degraded steppes are discussed.

Key words: **ecosystem functioning, indicator, restoration, semiarid, shrubs, *Stipa tenacissima.***

Introduction

Increasing public concern for the accelerated destruction of ecological systems and the lack of sustainability of modern human societies has led to an unprecedented interest in ecological restoration (Bradshaw 2002). Due to the widespread extent of degraded ecosystems and due to limited funds available for natural resource management, selection of the areas and ecosystem components to be restored is one of the major challenges faced by scientists and practitioners worldwide. Despite being crucial, it is difficult to conduct a practical assessment of whether a particular landscape is in need of restoration, and if so, which ecosystem components or functions should be restored first (Hobbs 2002). The selection of target areas to be restored can be greatly improved if the degradation status of ecosystems can be defined beforehand (Tongway & Hindley 2000). Methods based on indicators of ecosystem function have often been employed due to their compromise between accuracy and affordability, especially in arid and semiarid ecosystems (Whitford 2002). However, they have barely been used to assist in the restoration of degraded areas in the field.

Models describing the recovery of ecosystem function after disturbances recognize that the steps in this trajectory may not be of equal magnitude or importance and that some of them can hardly be reversed spontaneously (Hobbs & Norton 1996; Whisenant 1999). These thresholds are of major importance because they prevent the system from returning to a less-degraded state without external inputs (Whisenant 1999). Despite important theoretical advances on the identification of degradation trajectories and on the development of suitable procedures to monitor them, there is still a clear lack of studies dealing with the determination of thresholds in the field (Krogh et al. 2002). The identification of these thresholds would aid decision-makers when planning land restoration and has also been recognized as a priority within environmental research and policy by authorities like the European Union (European Commission 2002).

Semiarid ecosystems with sparse plant cover are often organized into source-sink systems, where the open areas act as a source of water, sediments, and nutrients for plant patches (Aguiar & Sala 1999). The maintenance of ecosystem function in these areas is highly dependent on the conservation of patch attributes such as number, width, and spatial distribution (Ludwig & Tongway 1995). Soil surface condition in the open areas is also relevant for ecosystem functioning because it may compensate for reduced patchiness (Tongway & Ludwig 1997) and because its degradation may impair source-sink dynamics (Eldridge et al. 2000) and modify ecosystem-level processes like soil respiration (Maestre & Cortina 2003). Thus, understanding those factors affecting the status of soil surface conditions in the interpatch areas can be of great importance when evaluating the functional status of semiarid ecosystems and will improve our understanding of semiarid ecosystem functioning.

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In this study we evaluated the functional status of *Stipa tenacissima* L. steppes using indicators of ecosystem function along a degradation gradient and related these indicators to major abiotic and biotic features of the ecosystem. These steppes are widespread in the driest areas of the Mediterranean Basin and derive from the long-term degradation of open shrublands and woodlands by human activities like fiber cropping, grazing, and repeated burning (Le Houérou 2001). The main objectives of this study were to (1) characterize the functional status of semiarid *S. tenacissima* steppes along a degradation gradient; (2) evaluate the importance of abiotic and biotic features of the ecosystem (plant patch characteristics, climate, soil organic matter, and topographical features) as determinants of ecosystem function; and (3) discuss the implications of our results for the management and restoration of semiarid degraded steppes.

Methods

Study Area

Our study was conducted at 17 experimental sites located in the provinces of Alicante and Murcia, in southeast Spain (Table 1). Because of the complexity of previous land uses in this area and the impossibility of isolating areas affected by a single human disturbance, a chronosequence cannot be implemented. However, we selected a wide range of *Stipa tenacissima* steppes showing a priori contrasting signs of degradation (as suggested by observations of plant cover, erosion features, and abundance of biological soil crusts and late-successional sprouting shrubs). Site selection also aimed at capturing a significant range in the variability in average rainfall in semiarid *S. tenacissima* steppes and at reducing between-site variability associated with vegetation type, slope aspect, and soil type. The climate of the study area is Mediterranean semiarid, with average annual precipitation ranging from 220 to 388 mm, and average annual temperature ranging from 16 to 18°C (1960–1990 period). All sites are located on south-facing slopes, with slope values ranging between 4 and 29°. Soils are loamy-silty loam, Lithic Calciorthid, derived from marls and limestone. Vegetation is an open steppe dominated by *S. tenacissima*, with total cover values ranging between 17 and 51%. The relative percent cover of this species (as related to percentage cover of all vascular plants) varied between 35 and 95%.

Evaluation of Ecosystem Functional Status and Field Survey

We assessed the functional status of each site by using the landscape function analysis (LFA; Tongway & Hindley 1995). Landscape function analysis uses soil surface indicators to assess the status of a given ecosystem in terms of functionality, that is, the degree to which resources tend to be retained, used, and cycled within the system (Tongway & Hindley 2000). It fills the conditions that methods based on indicators should meet to be meaningful in arid and semiarid areas (Whitford 2002): it reflects the status of critical ecosystem processes, it is unambiguous, and it can be used over a wide range of ecosystems. In addition, its use in the field is rapid and inexpensive. Landscape function analysis output is given by three indices (stability, infiltration, and nutrient cycling) that summarize different

Table 1. Main characteristics of the experimental sites.

Site[a]	*ALT*[d]	*RAI*[d]	*AZI*[d]	*SLO*[b,d]	*UTM*[d]		*OMA*[c]	*TCO*[b]
Aguas (Ag)	441	388	168	13.6 ± 0.4	731431 E	4267459 N	5.3 ± 0.2	39.0 ± 6.8
Albatera (Al)	355	277	228	24.8 ± 0.6	683000 E	4235820 N	6.9 ± 0.2	44.6 ± 3.3
Campello (Ca)	349	220	140	14.8 ± 0.8	728411 E	4264059 N	5.6 ± 0.4	50.5 ± 4.2
Colominas (Co)	726	486	198	9.8 ± 0.3	692176 E	4273892 N	4.2 ± 0.3	43.2 ± 1.6
Etasa (Et)	205	386	290	23.5 ± 0.9	720469 E	4261970 N	4.1 ± 0.4	16.6 ± 2.5
Finestrat (Fi)	212	318	160	22.8 ± 0.6	745052 E	4271046 N	6.4 ± 0.3	47.1 ± 2.4
Foncalent1 (Fn)	80	302	220	4.4 ± 0.2	712879 E	4245495 N	7.5 ± 0.3	35.4 ± 3.3
Foncalent2 (Ft)	63	302	100	23.5 ± 0.3	713572 E	4246605 N	4.3 ± 0.2	17.4 ± 3.4
Fortuna (Fo)	99	294	220	14.1 ± 0.7	666166 E	4215166 N	5.6 ± 0.2	35.8 ± 2.5
Jijona (Ji)	240	386	180	24.8 ± 0.3	720312 E	4263831 N	4.4 ± 0.3	18.8 ± 2.2
La Nuza (Ln)	102	220	160	27.8 ± 0.6	730961 E	4260414 N	5.5 ± 0.3	42.0 ± 4.3
Marquesa (Ma)	85	220	178	23.8 ± 0.3	727972 E	4259533 N	6.0 ± 0.3	44.5 ± 3.4
Palomaret (Pa)	540	302	190	23.5 ± 1.8	703116 E	4261639 N	7.5 ± 0.3	37.0 ± 2.2
Peñarrubia (Pe)	769	369	180	22.5 ± 0.3	690160 E	4273578 N	4.5 ± 0.2	44.6 ± 1.0
Relleu (Re)	395	388	125	10.8 ± 0.3	735591 E	4269506 N	6.9 ± 0.2	47.1 ± 1.5
Ventós1 (Ve)	468	302	270	26.3 ± 0.6	707768 E	4259748 N	5.6 ± 0.2	46.4 ± 3.8
Ventós2 (Vn)	550	302	240	24.5 ± 0.3	707506 E	4260684 N	6.2 ± 0.3	37.7 ± 4.1

ALT = altitude (m above sea level), AZI = azimuth (°), OMA = loss-on-ignition organic matter (%), RAI = mean annual rainfall (1960–1990) in the nearest meteorological station, SLO = slope (°), TCO = total patch cover (%), UTM = UTM co-ordinates.
[a]The code in brackets is the name given to the experimental sites in Figure 1.
[b]Mean ± SE ($n = 4$).
[c]Mean ±SE ($n = 12$).
[d]Data come from Maestre (2004).

facets of the functionality of the ecosystem and that are strongly related to more quantitative measures of related ecosystem processes (McR. Holm et al. 2002; Tongway & Hindley 2003). The stability index provides information about the ability of the soil to withstand erosive forces and to recover after disturbance. The infiltration index shows how the soil partitions rainfall into water available for plants to use and run-off water that is lost from the system. The nutrient cycling index provides information about how efficiently organic matter is cycled back into the soil.

Within each site, we established a 30×30–m plot starting on the upper edge of the hillslope. In the upper left corner of the plot, we located one 30 m–long transect downslope for vegetation and soil survey. Three parallel transects of the same length, each 8 m apart across the slope, were added. In each transect, we collected a continuous record of patch and interpatch zones. A patch is defined as a long-lived feature that is able to collect water, sediments, and nutrients coming from run-off—such as perennial plants and shrub branches contacting soil (Tongway & Hindley 1995)—and that is separated by bare soil surface from the next patch. The assessment of LFA indices was performed in both patches and interpatches. With the aim of having good coverage of the entire transect length, we divided it into three intervals (0–10, 10–20, and 20–30 m). Within each of these intervals, we randomly located a 50×50–cm sampling quadrat in the interpatch areas and in each of the different patch types located in the transect. In each quadrat we recorded 11 soil surface features following a semiquantitative scale (Table 2). The combination of the measured soil properties to obtain the LFA indices was performed with a Microsoft Excel template developed by David Tongway (http://www.cse.csiro.au/research/Program3/efa/). Here we present LFA values as percentages: the higher the values obtained, the better the status of the ecosystem for a given function. The LFA values for the whole site were obtained by multiplying the proportion of the transect area covered by each patch/interpatch type by the average index values obtained at that patch/interpatch and then adding them together. Statistical differences between the sites in the LFA indices were assessed with one-way ANOVA. Before these analyses, the stability index data were transformed with an exponential function (X^5) to achieve homogeneity of variances. ANOVA analyses were conducted with the SPSS 9.0 for Windows package (SPSS Inc., Chicago, IL, U.S.A.).

When a patch was located in a transect, we measured its width at right angles to the transect line. Clumps of grasses or of grasses and small shrubs growing closely together or connected with litter bridges were considered a single patch. From the transects we obtained total patch cover, patch width density (m/10 m of transect), mean length of interpatch zones, and number of patches per 10 m of transect. We also used the transects to evaluate perennial plant species diversity (Shannon's H index) by using the line-point sampling method, with a sampling frequency of 50 cm along the 30-m transect. The number of perennial species present within the 30×30–m plot was also evaluated and was used as an estimate of species richness. We evaluated only perennial plant species because the occurrence of annual plants in *S. tenacissima* steppes shows high

Table 2. Soil surface features used to calculate the landscape function analysis indices.

Soil Surface Feature	*Interpretation*	*Maximum Score*	*Index Used*
Soil cover	Assesses vulnerability to physical crust formation	5	Stability
Basal cover of perennial grasses and shrub canopy cover	Assess contribution of root biomass to nutrient cycling processes	4	Infiltration, nutrient cycling
Litter cover and degree of decomposition	Assess the availability of surface organic matter for decomposition and nutrient cycling	30	Infiltration, nutrient cycling
Biological crusts cover	An indicator of surface stability, resistance to erosion, and nutrient availability	4	Nutrient cycling
Crust brokenness	Assesses loose crusted material available for wind ablation or water erosion	4	Stability
Erosion type and severity	Assesses the nature and severity of current soil loss from quadrats	4	Stability
Deposited materials	Assesses the quantity of soil accumulated from upslope sources	4	Infiltration
Microtopography	Assesses surface roughness for water infiltration and flow disruption, seed lodgment	5	Infiltration, nutrient cycling
Surface resistance to disturbance	Assesses likelihood of soil detachment and mobilization by mechanical disturbance	5	Stability
Slake test	Assesses soil stability/dispersiveness when wet	4	Stability, infiltration
Soil texture	Assesses infiltration rate and water storage	4	Infiltration

To obtain the value of a given landscape function analysis (LFA) index, we sum the scores for the different soil surface features involved in the calculation of the index (fourth column). In the manuscript these values are presented as percentages; to obtain them, we divide the LFA value obtained in the previous step by the maximum score that can be obtained for a given LFA index (40, 57, and 40 for the stability, infiltration, and nutrient cycling indices, respectively). See Tongway and Hindley (1995) for a complete description of score assignment and calculations.

interannual variability due to site-specific seasonal conditions. In addition to these measurements, we measured all sprouting shrubs existing in the plots, which may be remnants of mature shrubland vegetation (Rivas Martínez 1987) and estimated the area of each plot covered by them. Other abiotic characteristics (altitude, azimuth, slope, Universal Transverse Mercator Coordinate system (UTM) co-ordinates, mean annual rainfall at the nearest weather station, and soil organic matter at 0–10 cm depth measured by loss on ignition in a furnace for 2 hr at 550°C) were also obtained for all sites.

Relationships Between Ecosystem Function and Abiotic and Biotic Features

We regressed separately the three LFA indices on each of the biotic and abiotic variables measured at the experimental sites using linear and nonlinear regression. We performed separate analyses for the LFA values obtained for the whole ecosystem (patch + interpatch areas) and for interpatch areas only. We fitted the data to linear and nonlinear (sigmoidal, logarithmic, power, exponential, and hyperbolic) functions and selected the model that minimized the Akaike's information criterion (AIC; Akaike 1973) after examining the residuals for normality and homoscedasticity. We used the AIC because it provides a reasonable compromise between goodness of fit and parsimony (Webster & McBratney 1989). When the same function was selected more than once, significance levels ($\alpha = 0.05$) were Bonferroni corrected to reduce the probability of getting a significant result by chance. This adjustment was performed separately for the regression analyses conducted with the data from the whole ecosystem and interpatch areas. Before regression analyses, we evaluated the relationships between the abiotic and biotic variables with the Spearman rank correlation coefficient, adjusting the significant values for the number of paired comparisons with the procedure described in Hochberg (1988). Significant correlations were found between the number of patches and the average distance between them ($r = -0.74$), between their cover and width ($r = 0.89$), between elevation and both the area covered by sprouting shrubs ($r = 0.83$) and species richness ($r = 0.83$), and between the UTM North co-ordinate and rainfall ($r = 0.70$). Thus, we excluded from regression analyses the number of patches, the cover of patches, elevation, and the UTM North co-ordinate. Correlation and regression analyses were conducted with the software SPSS 9.0 for Windows and Sigmaplot 2001, respectively.

Functional Differences Between Plant Patches

We evaluated functional differences between patch types by comparing the values of the LFA indices obtained at four representative patch types of our study area: *S. tenacissima* tussocks, *Brachypodium retusum* (Pers.) P. Beauv. grass patches, sprouting shrubs (*Pistacia lentiscus* L., *Quercus coccifera* L., *Rhamnus lycioides* L., *Ephedra fragilis* L., *Erica multiflora* L., and *Juniperus oxycedrus* L.), and non-sprouting shrubs (*Rosmarinus officinalis* L., *Globularia alypum* L., and chamaephytes). Due to the differences in abundance, and to avoid unequal sample sizes, we randomly selected 20 patches of each type among the pooled

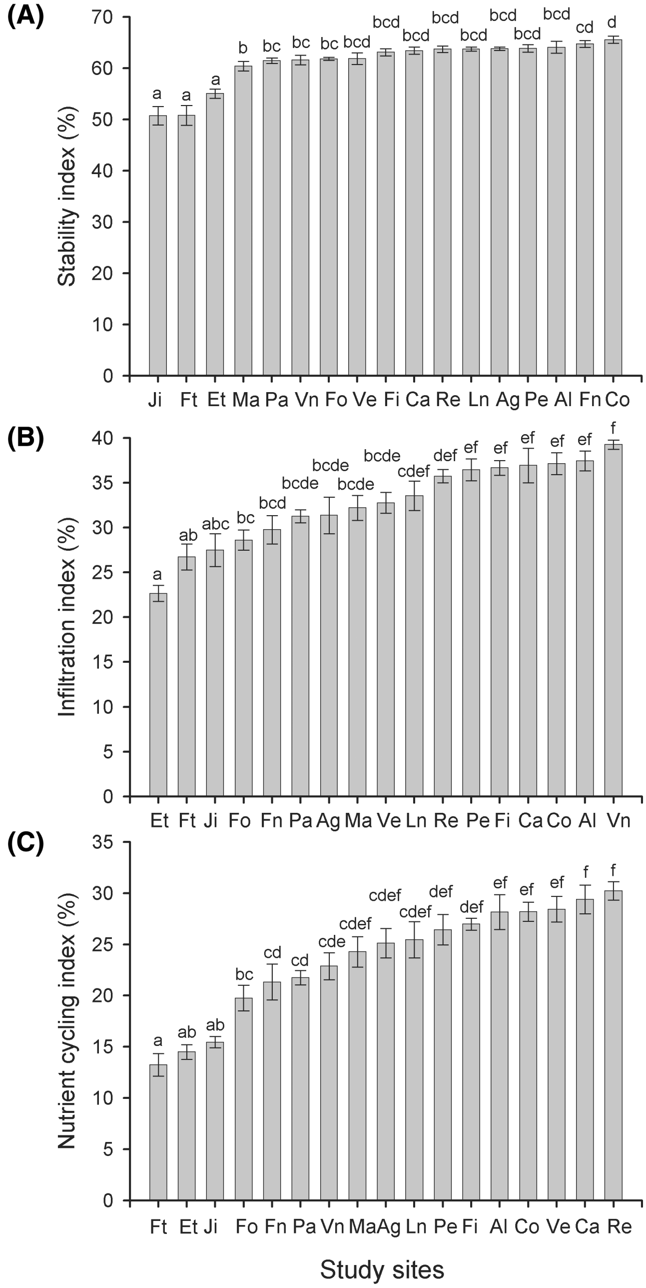

Figure 1. Experimental sites arranged in sequence of landscape function analysis indices. The *y*-axes represent the values of the stability (A), infiltration (B), and nutrient cycling (C) indices, respectively ($\bar{X} \pm SE$; $n = 4$). Different letters indicate significant differences between the sites ($p < 0.05$, Tukey's *b* test after one-way ANOVA; post hoc results for the stability index are shown for data transformed with an exponential function). Note the differences in the scale between the indices. The full name and main characteristics of the experimental sites can be found in Table 1.

Table 3. Regression models fitted to the relationship between the stability index (Y) and measured abiotic and biotic features of the experimental sites (X).

Variable	*Model*	r^2 *(p)*
Interpatch areas		
Distance between consecutive patches (m)	$Y = 55.6 + 13.4X - 11.2X^2$	0.65 (<0.001)
Width of patches (m/10 m of transect)	$Y = (62.9X)/(0.5X)$	0.54 (0.001)
Cover of patches (%)	$Y = 24.4 + 1.8X - 0.02X^2$	0.68 (<0.001)
Whole ecosystem		
Distance between consecutive patches	$Y = 60.4 + 11.3X - 10.5X^2$	0.87 (<0.001)
Width of patches	$Y = 46 + 3.8X - 0.2X^2$	0.79 (<0.001)

Separate analyses were performed for the values of this index obtained for the interpatch areas and for the whole ecosystem (patch + interpatch areas). Only significant relationships (after a Bonferroni adjustment of p values) are shown. In all cases, $n = 17$.

data from all sites. Landscape function analysis data for selected patches did not follow a normal distribution or show homogeneity of variances. To correct for these deviations, we transformed the data to ranks (Conover & Iman 1981). Differences between the patch types in the LFA indices were assessed with one-way ANOVA by using the SPSS 9.0 for Windows package.

Results

The experimental sites differed substantially in their functional status, as described by the landscape function analysis (LFA) indices (Fig. 1). The ordered sequence of LFA indices showed how the steps in this sequence were not equal for the different indices. The stability index showed a clear transition between those sites with values below 60% and the other sites. Changes in the ranked sequence of the infiltration and the nutrient cycling indices were more staggered, but transitions at the lower tail of the ranked sequence can also be observed for those sites with values below 25 and 19% of the infiltration and nutrient cycling indices, respectively.

The stability index measured in the interpatch areas showed nonlinear relationships with surrogates of patch attributes like the distance between consecutive patches and their width (Table 3). These variables, together with the area covered by sprouting shrubs and with species richness, also showed significant relationships with the infiltration index in the same areas (Table 4). The nutrient cycling index in the interpatch areas showed significant relationships with the distance between consecutive patches, species richness, diversity, and the area covered by sprouting shrubs (Table 5). When the LFA values were obtained for the whole ecosystem (patch + interpatch areas), the shape of some relationships varied regarding that observed with the values estimated from the interpatch areas only. The most noticeable changes were found in the relationships between species richness, the distance between consecutive patches and the nutrient cycling index (Table 5), and in the relationship between the width of patches and the infiltration index (Table 4). In these cases, nonlinear and linear relationships were found when using the LFA values obtained in the interpatch areas and in the whole ecosystem, respectively. Abiotic variables such as slope, azimuth, rainfall, and organic matter content did not show significant relationships with any LFA index measured for both the whole ecosystem and the interpatch areas only. Among all evaluated variables, the distance between consecutive patches was the only variable that showed significant relationships with the three LFA indices, but the shape of the relationship varied regarding the index considered.

The stability index did not show significant differences between the evaluated patch types (Fig. 2). This index

Table 4. Regression models fitted to the relationship between the infiltration index (Y) and measured abiotic and biotic features of the experimental sites (X).

Variable	*Model*	r^2 *(p)*
Interpatch areas		
Distance between consecutive patches (m)	$Y = 40.1 - 6.9X$	0.78 (<0.001)
Width of patches (m/10 m of transect)	$Y = 27.2 + 3.9 \ln X$	0.63 (<0.001)
Area covered by sprouting shrubs (%)	$Y = 31.5 + 4.6(1 - \exp[-148.5X])$	0.54 (0.005)
Species richness (n)	$Y = 25.8 + 0.3X$	0.38 (0.009)
Whole ecosystem		
Area covered by sprouting shrubs	$Y = 26.5 + 8.7(1 - \exp[-941.8X])$	0.75 (<0.001)
Distance between consecutive patches	$Y = 41.2 - 9.8X$	0.76 (<0.001)
Width of patches	$Y = 22.7 + 1.5X$	0.85 (<0.001)

Remainder of legend as in Table 3.

Table 5. Regression models fitted to the relationship between the nutrient cycling index (Y) and measured abiotic and biotic features of the experimental sites (X).

Variable	*Model*	r^2 *(p)*
Interpatch areas		
Distance between consecutive patches (m)	$Y = 10.5 + 33.2\exp(-3.8X)$	0.37 (0.041)
Diversity (bits)	$Y = 7.4 + 4.3X$	0.37 (0.010)
Area covered by sprouting shrubs (%)	$Y = 10.4 + 195.3X - 1{,}653.5X^2$	0.61 (0.001)
Species richness (n)	$Y = 10.4 + 5(1 + [X/28.3]^{-26.4})$	0.70 (0.001)
Whole ecosystem		
Area covered by sprouting shrubs	$Y = 16 + 10.7(1 - \exp[-1{,}475.2X])$	0.72 (<0.001)
Distance between consecutive patches	$Y = 34.5 - 12.5X$	0.66 (<0.001)
Species richness	$Y = 6.3 + 0.6X$	0.45 (0.003)

Remainder of legend as in Table 3.

showed high values in all patch types, and only a marginally significant reduction was found for the non-sprouting shrubs. For the infiltration and nutrient cycling indices, sprouting shrubs had higher values than the other patch types. The values found under *Stipa tenacissima* tussocks were also higher than those from *Brachypodium retusum* patches and non-sprouting shrubs.

We found a significant and positive power relationship between the cover of sprouting shrubs and species richness in the steppes studied (Fig. 3).

Discussion

The differences between sites in processes like the duration of active degrading forces, their management regime over time, and past stochastic events—issues that cannot be easily known in the ecosystem studied—did not allow us to follow a chronosequence approach. This precluded the utilization of procedures to numerically detect thresholds in ecosystem function, like those described in Tongway and Hindley (2000), and thus limited the ability of our approach to track them. Despite these limitations, the abrupt changes found in the sequence of ranked landscape function analysis (LFA) indices provided empirical evidence of discontinuities in ecosystem function along the degradation gradient evaluated, especially for the stability index. The differences found in the values and in the trajectory of the LFA indices along the gradient evaluated also suggest that different ecosystem functions may not recover at the same rate after a disturbance in semiarid *Stipa tenacissima* steppes.

The stability index showed significant relationships only with patch features. The infiltration and nutrient cycling indices showed significant relationships with these features, but also with surrogates of biodiversity and sprouting shrub cover. This suggests that, in *S. tenacissima* steppes, the recovery of infiltration and nutrient cycling functions is likely to be coupled to the abundance of late-successional sprouting shrubs. In fact, sprouting shrubs had higher values of the infiltration and nutrient cycling indices than other patch types. These results suggest that these species play a relevant role in structuring the community and improving ecosystem functions in semiarid *S. tenacissima* steppes and that they could be acting as keystone species regarding their role in infiltration and nutrient cycling (sensu Naeem et al. 2002). Differences between sprouting shrubs and *S. tenacissima* may lead to enhanced infiltration and nutrient cycling in semiarid steppes as sprouting shrubs colonize them. These include differential patterns in root growth and size (Puigdefábregas et al. 1999; Archer et al. 2002), improved undercanopy soil properties (Puigdefábregas et al. 1999), and their role as perches for frugivorous birds that may increase nutrient inputs by defecation (Dean et al. 1999). Our results also suggest that, from a functional perspective, *S. tenacissima* steppes are relatively immature as compared with shrublands dominated by sprouting species, which are expected to dominate non-degraded ecosystems in our study area (Rivas Martínez 1987).

The significant relationships found between perennial species richness and LFA indices suggest that biodiversity plays a relevant role in the functioning of *S. tenacissima* steppes. These relationships had higher r^2 values than the relationships between LFA indices and both species diversity and the relative percent cover of *S. tenacissima* (data not shown). This suggests that several aspects of the functionality of the ecosystem, such as nutrient cycling and infiltration, were more affected by the presence of particular species than by the dominance of the most common ones (Troumbis & Memtsas 2000). It is interesting to note the power relationship found between the cover of sprouting shrubs and species richness and the fact that this cover is the most important determinant of the latter in the steppes studied (Maestre 2004). In addition, the logistic model fitted to the relationship between species richness and the nutrient cycling index for the interpatch areas had an inflection point located over 28 species. All our experimental sites having this much, or higher, species richness included from one to six sprouting shrub species. According to the relationships found, we hypothesize that a positive feedback between species richness and ecosystem function, driven by sprouting shrubs, is taking place in

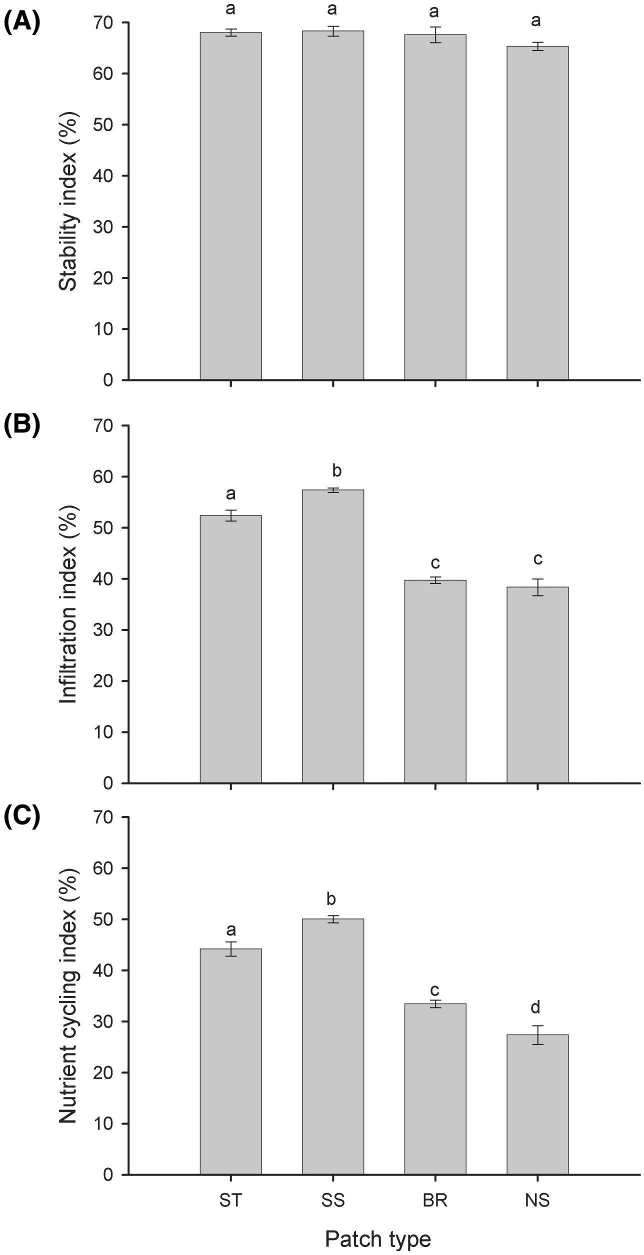

Figure 2. Characterization of major patch types in terms of the landscape function analysis indices. The *y*-axes represent the values of the stability (A), infiltration (B), and nutrient cycling (C) indices, respectively ($\bar{X} \pm SE$; $n = 20$). Different letters indicate significant differences between patch types ($p < 0.05$, Tukey's *b* test after one-way ANOVA with rank-transformed data). BR = *Brachypodium retusum* patch, NS = non-sprouting shrub patch, SS = sprouting shrub patch, ST = *Stipa tenacissima* patch.

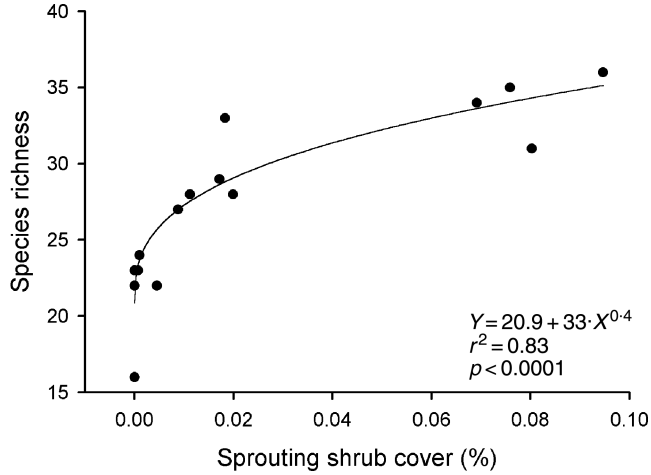

Figure 3. Relationship between the area covered by sprouting shrubs and perennial species richness (number of species per 900 m^2) in the experimental sites.

S. tenacissima steppes. The colonization of degraded steppes by sprouting shrubs would, at the mid- to long term, promote the introduction of more woody species, probably by facilitative processes (Callaway 1995). This increment in species richness would ultimately foster ecosystem function by improving nutrient cycling, infiltration, and other ecosystem processes. Further studies are needed to test this hypothesis and to fully elucidate the mechanisms underlying the relationships between species richness and ecosystem function in *S. tenacissima* steppes.

The relationships between patch attributes and the LFA indices agree with theoretical and empirical work showing the importance of the patchy structure of vegetation for the proper functioning of semiarid ecosystems (Ludwig & Tongway 1995). In *S. tenacissima* steppes, the open areas act as a source of water and sediments for *S. tenacissima* tussocks and other plant patches (Puigdefábregas et al. 1999). These patches have higher infiltration rates, improved soil structure and nutrient content, and higher biological activity (Puigdefábregas et al. 1999; Maestre et al. 2002; Azcón-Aguilar et al. 2003), acting as "resource islands" (Reynolds et al. 1999). The significant relationships found between patch attributes and the LFA indices in the interpatch areas emphasize their importance for ecosystem functioning at scales beyond the individual resource islands. It is interesting to note that all variables significantly related to the stability index were those describing patch attributes. This suggests that resilience against erosive forces is likely to be one of the first ecosystem properties that may be lost when *S. tenacissima* steppes are degraded. Human-induced degradation processes in these ecosystems may destroy or substantially modify both patch number and width, resulting in an increased distance between them. These changes may increase the amount of water, nutrients, and sediments transported during run-off events up to levels that may exceed the ability of existing patches to retain them (Ludwig & Tongway 1995). As a consequence, a greater proportion of resources are exported from the system, the quality of the soil in places once occupied by patches drops, and the overall resilience of the system against further run-off events is reduced, fostering their erosion and degradation.

Implications for Ecosystem Management and Restoration

The evaluation of ecosystem function provides a useful framework for the initial assessment of ecosystem status and the subsequent selection of repair measures (Tongway & Ludwig 1996) and can be used to optimize the restoration of degraded arid and semiarid areas. The output from the LFA methodology can be used to decide which areas are in more need of restoration and which ecosystem functions should be recovered first. However, because this methodology was developed in Australian semiarid ecosystems, it should be used with certain caution in other regions of the world until it becomes more widely validated. Future studies are needed to validate the LFA indices with empirical, experimental data gathered in other semiarid areas and to test whether the LFA indices adequately reflect the processes and functions that they represent in different, despite structural and functionally similar, ecosystems.

Our results have direct implications for the optimization of restoration procedures in *S. tenacissima* steppes. If the target area is very degraded, restoration efforts could be initiated with actions focusing on the recovery of ecosystem structure by increasing the number of patches and reducing the downslope distance between them. This can be done by inserting brush piles parallel to land contours. Experiments conducted in Australia have shown the effectiveness of this technique in creating fertile patches and ultimately rehabilitating degraded landscapes (Ludwig & Tongway 1996; Tongway & Ludwig 1996). Such brush piles would reduce soil and nutrient losses and would act as filters rather than barriers. They would also provide suitable microsites for enhancing the establishment, growth, and survival of perennial plants in the short term (Ludwig & Tongway 1996). Once this intervention has reduced degradation, the next step to restore these systems should be the introduction of seedlings of native sprouting shrubs. The introduction of these species would foster the recovery of nutrient cycling in the long term, increase species richness, and provide suitable habitats for further spontaneous plant and wild animal colonization (López & Moro 1997). Recent studies have shown that *S. tenacissima* facilitates the establishment of sprouting shrubs in semiarid steppes (Maestre et al. 2001). Thus, we recommend that these shrubs should be introduced in the microsites provided by *S. tenacissima* tussocks.

Although methods based on indicators provide easily measurable and interpretable quantitative indices reflecting ecosystem functional status, they have barely been used to assist in the restoration of degraded areas in the field. The LFA methodology can be used over large areas in a ready and inexpensive manner, and data acquisition can be successfully achieved with minimal training. Our results have shown that it characterizes adequately the functional status of semiarid *S. tenacissima* steppes and that this information can be used to design appropriate restoration measures at a landscape scale in this ecosystem. Future studies aiming to validate the LFA indices are, however, needed before incorporating this methodology into routine restoration practices.

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