
Volume 41, No. 3, March 2009
ISSN 0929-1393
ELSEVIER
Applied
Soil Ecology

Applied Soil Ecology 41 (2009) 342–350

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Indices based on surface indicators predict soil functioning in Mediterranean semi-arid steppes

Fernando T. Maestre *, María D. Puche

Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, 28933 Móstoles, Spain

ARTICLE INFO

Article history:
Received 18 June 2008
Received in revised form 14 November 2008
Accepted 27 December 2008

Keywords:
Stipa tenacissima
Landscape function analysis
Soil indicators
Soil functioning
Desertification

ABSTRACT

Methodologies based on indicators occupy a prevalent place when assessing ecosystem functioning and monitoring desertification processes because they are affordable yet do not compromise accuracy. The landscape function analysis (LFA), developed in Australia by David Tongway (CSIRO), uses soil surface indicators to assess the condition of a given ecosystem by producing three numerical indices (stability, infiltration and nutrient cycling) reflecting the status of basic soil functions. None of the previous studies aiming to validate the LFA indices have explored how they relate to surrogates of soil functioning using a large number of test sites capturing different climatic and soil conditions. We aimed to do so using data gathered in 29 *Stipa tenacissima* steppes in Spain. The nutrient cycling index was strongly correlated with soil variables related to microbial activity and nutrient cycling, such as soil pH, total soil N and P, soil respiration and phosphatase and β-glucosidase activities. Strong correlations between the infiltration index and both soil compaction and the water holding capacity of soils were found. The stability index was also significantly correlated with most of the soil variables evaluated. These relationships were evident in both gypsum and calcareous soils. Our results indicate that the LFA indices may be employed as surrogates of soil variables related to nutrient cycling and water infiltration in semi-arid *S. tenacissima* steppes. The LFA methodology has an enormous potential to assist land managers and policy makers in the establishment of cost-effective desertification monitoring and restoration programs in semi-arid environments.

1. Introduction

Land degradation in arid, semi-arid and dry sub-humid ecosystems, commonly called desertification, constitutes one of the major environmental problems of the twenty-one century, affecting an estimated population of 250 million worldwide (Reynolds et al., 2007a). The monitoring of desertification processes, and particularly the development of "early warning" systems, i.e. the detection of changes in ecosystem attributes and processes at stages where management actions would be most cost-effective (Fernández et al., 2002), is an increasingly important development in the management of these areas, and a field of active research (Whitford, 2002; Reynolds et al., 2007b). Among the different methodologies being employed for this aim, techniques based on indicators of ecosystem functions occupy a prevalent place because they can provide reasonable accuracy while still being affordable (Whitford, 2002). These methods are based on the collection of basic information on those attributes of vegetation and soils (e.g., cover, spatial pattern, and soil surface attributes) that largely determine the ecosystem's resilience to erosive forces and its ability to retain water and nutrients (Pyke et al., 2002; Tongway and Hindley, 1995, 2004; Herrick et al., 2005).

One of the monitoring methods that has received more attention in recent years is the landscape function analysis (LFA) methodology developed in Australian rangelands by Tongway (1995) and Tongway and Hindley (1995, 2004). LFA uses soil surface indicators to assess the status of a given ecosystem in terms of functionality, i.e. the degree to which resources tend to be retained, used and cycled within the system (Tongway and Hindley, 2000). This methodology satisfies the requirements (proposed by Whitford, 2002) for meaningful indicator-based methods: it reflects the status of critical ecosystem processes, is unambiguous, and can be used over a wide range of ecosystems. In addition, its use in the field is rapid and inexpensive, and thus is particularly suitable for land managers and technicians. The output of LFA is given by three indices (stability, infiltration, and nutrient cycling) that summarize different facets of the functionality of the ecosystem, and that are strongly related to quantitative measures of related ecosystem processes (McR. Holm et al., 2002; Tongway

* *Corresponding author.* Tel.: +34 914888511; fax: +34 916647490.
E-mail address: fernando.maestre@urjc.es (F.T. Maestre).

0929-1393/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.apsoil.2008.12.007

and Hindley, 2003; Ata Rezaei et al., 2006; Bartley et al., 2006). The LFA methodology has been extensively used and tested in semi-arid ecosystems of Australia, where it was developed, to monitor soil functioning at different spatial scales (McR. Holm et al., 2002; Ludwig et al., 2004; Bartley et al., 2006), to study the dynamics of ecosystem recovery after mine site rehabilitation (Tongway and Hindley, 2003), and to explore the relationships between the conditions of the soil surface and the composition and the composition and diversity of biological soil crusts (Thompson et al., 2006).

The LFA methodology is starting to be employed outside the areas where it was developed, and has been successfully used to assess rangeland capacity in Iran (Ata Rezaei et al., 2006), to evaluate the relationships between ecosystem structure and functioning in semi-arid steppes of Spain (Maestre and Cortina, 2004, 2006), to explore the relationships between soil functioning and restorability in these steppes (Maestre et al., 2006; Cortina et al., 2006), and to study the hydrological functioning of the ecosystem at different spatial scales (Mayor, 2008). However, this method has not been fully validated outside Australia, a crucial step to test whether the LFA indices adequately reflect the processes and functions that they aim to represent, and to implement its use as a monitoring tool in other regions. Furthermore, none of the previous studies aiming to validate the LFA indices have explored how they relate to variables used to define soil functioning using a large number of test sites encompassing different climatic and soil conditions. We aimed to do so using a database obtained from 29 *Stipa tenacissima* L. steppes located along a latitudinal gradient in Spain. These steppes are one of the most important vegetation types in the driest areas of the Western Mediterranean Basin, where they cover over 28,000 km^2 in Northern Africa (from Lybia to Morocco) and in the Iberian Peninsula (Le Houérou, 2001), and are often structured in a spotted or banded spatial configuration (Webster and Maestre, 2004; Maestre et al., 2005) with patterns resembling features of the "tiger-bush" vegetation described for semi-arid regions in Australia, the Sahel zone of Africa, Mexico and USA (Valentin et al., 1999). The main objectives of this paper are to: (i) evaluate the relationships between the LFA indices and key variables acting as surrogates of soil functioning (total N and P, K, soil organic carbon, pH, respiration and enzyme activities, soil compaction and water holding capacity), (ii) assess if these relationships change when small-scale (i.e. microsite) data are averaged to obtain plot estimates, and (iii) examine the relationships between the LFA indices and the main biotic and abiotic features of the study sites.

2. Materials and methods

2.1. Study area

Our study was conducted at 29 experimental sites located along a latitudinal gradient spanning from the center to the south-eastern coast of Spain (Appendix A). This gradient matches the core distribution area of *S. tenacissima* steppes in the Iberian Peninsula (Maestre et al., 2007). Site selection aimed to capture the significant range in the variability on average rainfall in semi-arid *S. tenacissima* steppes, and to reduce between-site variability associated with slope aspect and soil type. To achieve this aim, all the sites were located in soils derived from limestone (22 sites; *Lithic Calciorthid*; Soil Survey Staff, 1994) or in gypsum-rich soils (7 sites; *Typic Gypsiorthid*; Soil Survey Staff, 1994), two of the main substrates over which *S. tenacissima* steppes develop (Maestre et al., 2007), and on south-facing slopes, with slope values ranging between 1° and 22°. The climate of the study area is Mediterranean semi-arid, with average annual precipitation ranging from 265 mm to 497 mm, and average annual temperature ranging from 13 °C to 17 °C. Vegetation was in all cases an open grassland dominated by *S. tenacissima*, with total cover values ranging between 31% and 67%. Further details on the characteristics of the experimental sites can be found in Appendix A.

2.2. Assessment of landscape function indices

The assessment of LFA indices was performed in bare ground areas devoid of vascular vegetation and under the canopy of dominant perennial species (*S. tenacissima* and sprouting shrubs). Within each site, we randomly located five 50 cm × 50 cm sampling points in open areas and under the canopy of *S. tenacissima* tussocks for the assessment of the LFA indices (hereafter denoted as "Open" and "Stipa" microsites). Some of the sites had well-developed individuals of sprouting shrubs (mostly *Quercus coccifera* L., *Juniperus oxycedrus* L., *Rhamnus lycioides* L., *Ephedra nebrodensis* Tineo ex Guss, *Rhamnus alaternus* L. and *Pistacia lentiscus* L.); in these sites, five shrub individuals were also randomly selected for the assessment of the LFA indices under their canopies (hereafter denoted as "Shrub" microsite). A total of 350 sampling points were surveyed. In each sampling point, we measured 11 soil surface features following a semi-quantitative scale according to the guidelines of Tongway and Hindley (2004; Table 1). These indicators were further combined to obtain the three LFA indices (stability, infiltration and nutrient cycling) with a Microsoft® Excel template developed by David Tongway (downloaded from http://www.cse.csiro.au/research/efa/). 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 plant-available water, and runoff water that is lost from the system. The nutrient cycling index provides information about how efficiently organic matter is cycled back into the soil. All the LFA assessments were carried out between 20 July and 15 August 2006, when the soil was dry after 1.5–2 months of summer drought.

The LFA and soil data (see below) obtained in the different microsites were scaled up to obtain average estimates for each site. This was done by multiplying the proportion of the area covered by each microsite (Open and Stipa in the plots without shrubs, these two plus Shrub in the plots with shrubs) by the average soil variables and LFA indices obtained at that microsite and then adding them together, an approach followed by previous studies on the topic (McR. Holm et al., 2002; Maestre and Cortina, 2004; Mayor, 2008). The cover values of each microsite were estimated at each plot with the line-intercept method using four 30 m long transects, placed 8 m apart from each other, in the direction of maximum slope (as detailed in Maestre and Cortina, 2004). When a vegetated patch was located in a transect, we measured its width at right angles to the transect line. From the transects we also obtained the following variables: area covered by patches, mean length of inter-patch zones, and number of patches per 10 m of transect.

2.3. Assessment of variables related to soil functioning

The following soil variables were measured as surrogates of soil functioning in all the plots: pH, respiration, organic carbon, total N and P, K, activity of enzymes related to the C (β-glucosidase), N (urease) and P (phosphatase) cycles, soil compaction and water holding capacity. These variables are strongly related to processes such as infiltration and soil water dynamics (compaction and water holding capacity; Forster, 1995; Castellano and Valone, 2007), biological activity (respiration, pH; Kuzyakov, 2006) and nutrient cycling (enzymatic activities, organic carbon, total N and P; Chapin et al., 2002), which are critical determinants of the functioning of arid and semi-arid ecosystems (Whitford, 2002).

Table 1
Brief description and interpretation of soil surface features used to calculate the LFA indices. To obtain the value of a given LFA index, we sum the scores for the different soil surface features involved in the calculation of the index (third 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 43 for the stability, infiltration, and nutrient cycling indices, respectively). See Tongway and Hindley (2004) for a complete description of the soil surface features, score assignment and calculations. Adapted from Tongway and Hindley (2004).

Soil surface feature	Description and interpretation	Maximum score	Index where used
Soil cover	Projected percentage cover of perennial vegetation to a height of 0.5 m, plus rocks > 2 cm and woody material > 1 cm in diameter or other long-lived, immoveable objects. This indicator assesses vulnerability to physical crust formation.	5	Stability
Basal cover of perennial grasses and shrub canopy cover	Basal cover of perennial grass and/or the density of canopy cover of trees and shrubs. The objective of this indicator is to evaluate the contribution of root biomass to nutrient cycling processes.	4	Infiltration Nutrient cycling
Litter cover and degree of decomposition	Amount, origin and degree of decomposition of plant litter. Assesses the availability of surface organic matter for decomposition and nutrient cycling.	30	Stability Infiltration Nutrient cycling
Biological crust cover	Cover of cryptogams (mosses, lichens and cyanobacteria) visible on the soil surface. An indicator of surface stability, resistance to erosion and nutrient availability.	4	Stability Nutrient cycling
Crust broken-ness	A crust is defined as a physical surface layer that overlies sub-crust material. Measures to what extent the surface crust is broken, leaving loosely attached soil material available for erosion.	4	Stability
Erosion type and severity	Erosion in this context refers to accelerated erosion caused by the interaction of management and climatic events, rather than the background levels of geologic erosion. This indicator evaluates the nature and severity of current soil loss from quadrats.	4	Stability
Deposited materials	This indicator assesses the nature and amount of alluvium transported to and deposited on the query zone.	4	Stability
Soil surface roughness	This measurement evaluates the surface roughness for its capacity to capture and retain mobile resources such as water, propagules, topsoil and organic matter.	5	Infiltration Nutrient cycling
Surface resistance to disturbance	Measures the ease with which the soil can be mechanically disturbed to yield material suitable for erosion by wind or water.	5	Stability Infiltration
Slake test	Evaluates the stability of natural soil fragments to rapid wetting.	4	Stability Infiltration
Soil texture	This measurement classifies the texture of the surface soil.	4	Infiltration

We estimated soil surface compaction in all the sampling points placed in the Open microsite immediately after the LFA assessment using a portable penetrometer for top layers (model 06.06, Eijkelkamp, The Netherlands). Due to the high spatial variability of this variable, we took 20 randomly placed measurements within each sampling point, and calculated the average value for subsequent analyses. As the soil surface was dry, and no rainfall was registered during all the survey periods, we did not correct these values for moisture content. These measurements were not carried out in Stipa and Shrub microsites because of the lack of a well-developed physical soil crust in these areas. After soil compaction measurements, we obtained a composite sample from five 145 cm^3 soil cores soil cores (0–7.5 cm depth) for each sampling point (all microsites), bulked and homogenized in the field. Samples were transported to the laboratory, where they were sieved by 2 mm mesh and air dried for two months.

Soil respiration rates were determined by NaOH absorption followed by titration with HCl (Froment, 1972). Total N and P were obtained using a SKALAR San^{++} Analyzer (Skalar, Breda, The Netherlands) after digestion of the soil samples with sulphuric acid. Total P has been found to be positively related to fractions of available P (e.g., van der Zee and van Riemsdijk, 1988; Pautler and Sims, 2000), and has also been employed when evaluating the effects of plant cover on nutrient cycling at spatial scales such as those employed in our study (Krämer and Green, 1999). Soil K was measured with the same analyzer after shaking the soil sample with distilled water (1:5 ratio) for one hour. Water-soluble K is closely and linearly related to other K fractions, such as exchangeable K, in a wide variety of soil types (e.g. Sharpley, 1989; Ghosh and Singh, 2001; López Mateo et al., 2002). This fraction is also related to K uptake by plants and to the K content in foliage (Hood et al., 1956). Urease activity was determined as the amount of NH_4^+ released from 0.5 g soil after incubation for 90 min with urea (6.4%) at 30 °C in phosphate buffer (pH 7; Nannipieri et al., 1980). Phosphatase activity was measured by the determination of the amount of *p*-nitrophenol (PNF) released from 0.5 g soil after incubation at 37 °C for 1 h with the substrate *p*-nitrophenyl phosphate in MUB buffer (pH 6.5; Tabatabai and Bremner, 1969). The activity of β-glucosidase was assayed according to Tabatabai (1982), following the procedure for phosphatase, but using *p*-nitrophenyl-β-D-glucopyranoside as substrate and trishydroxymethyl aminomethane instead of NaOH. Soil organic carbon was estimated using the Walkley-Black method (Nelson and Sommers, 1982). pH was measured with a pH meter, in a 1:2.5 mass:volume soil and water suspension. Water holding capacity was measured as described in Forster (1995). This variable was measured only in two replicates per microsite and site, resulting in 110 and 30 samples in calcareous and gypsum soils, respectively.

2.4. Statistical analyses

As the LFA indices were highly intercorrelated, both in gypsum (Spearman $r > 0.794$, $n = 75$, $P < 0.001$ in all cases) and calcareous (Spearman $r > 0.768$, $n = 275$, $P < 0.001$ in all cases) soils, we used multivariate techniques to explore overall differences among soil types (gypsum/calcareous) and microsites (Open, Stipa and Shrub). To do this, we conducted a canonical discriminant analysis of principal coordinates (CAP; *sensu* Anderson and Willis, 2003). This method is described in detail elsewhere (Anderson and Willis, 2003; Anderson and Robinson, 2003), and only a brief description will be given here. CAP performs a principal-coordinate analysis of a multivariate matrix using a dissimilarity measure of choice to provide a series of m orthonormal axes; a canonical discriminate analysis is then conducted on the first m axes. The canonical axes resulting from this ordination are derived from linear combinations of variables that maximize the differences between the different experimental groups (in our case the 6 groups resulting from each combination of substrate and microsite). CAP conducts a statistical test evaluating the hypothesis of no significant differences in multivariate location among the 6 groups evaluated. This test is carried out by using the trace statistic (sum of canonical eigenvalues = sum of squared canonical correlations; Anderson and Willis, 2003) and obtaining a P value by permutation (e.g., Anderson, 2001). In addition, CAP provides misclassification or residual errors according to the "leave-one-out" approach of Lachenbruch and Mickey (1968). To accomplish this, a single observation was removed and the CAP analysis was conducted without it using the remaining observations; then the withheld observation was classified in the canonical space determined by the rest of the observations, as described in Anderson and Willis (2003).

We conducted correlation analyses between the LFA indices and the different surrogates of soil functioning with the data gathered with the quadrats (50 cm × 50 cm) and with the estimates obtained for whole plots. At the quadrat scale, most of the variables were non-normally distributed (Kolmogorov–Smirnoff test, $P < 0.05$), and thus we used the Spearman correlation coefficient. Separate analyses were conducted for each soil type; when significant correlations were found, the data were further separated into the different microsites studied. As estimates obtained for whole plots were normally distributed (Kolmogorov–Smirnoff test, $P > 0.05$), the relationships between the LFA indices and the different surrogates of soil functioning were evaluated using Pearson correlation analyses. Given the similarity of the relationships found between soil types (see below), and the relatively low number of plots located on gypsum soils, the data from all the plots were pooled to evaluate relationships with the surrogates of soil functioning for these analyses. Given that soil compaction was only measured in the Open microsite, this variable was not correlated with the LFA indices estimated for whole plots.

We used ordination analyses to examine the multivariate relationships between the average values of the LFA indices obtained in the Open microsite (dependent variables; hereafter LFA matrix) and the main biotic and abiotic features of the study sites (independent variables; hereafter environmental matrix). The environmental matrix was formed by the following variables: total plant cover, cover of shrubs, area of plant patches, distance between consecutive patches, number of patches per 10 m of transects, species density (number of perennial plant species per 900 m^2 plot), average annual temperature, rainfall and radiation for the period 1951–2000 (obtained from Ninyerola et al., 2005), elevation, slope, and aspect. We first conducted a Detrended Correspondence Analysis (Hill and Gauch, 1980) with the LFA matrix by detrending by segments and non-linear rescaling of the axes, which has the property that the extracted axes are scaled in units of average standard deviation (Gauch, 1982). As the extracted gradients of the LFA matrix were short (standard deviation units < 1), we conducted a Redundancy Analysis (hereafter RDA). RDA is a constraining ordination technique that assumes linear responses of the LFA matrix with the extracted axes. The total variation explained by the RDA analysis was calculated as the sum of all extracted canonical axes (Borcard et al., 1992). A Monte Carlo permutation test (9999 randomizations) was performed to determine the accuracy of the relationship between the LFA and environmental matrices, using the sum of all canonical eigenvalues or trace to build the F-ratio statistic (Legendre and Anderson, 1999). When the RDA model was significant, a forward stepwise procedure was carried out to select a reduced model including only significant variables. We incorporated explanatory variables one at a time and step by step in the order of their decreasing eigenvalues after partitioning out the variation accounted for the already included variables. The process ended when the new variable entered was not significant ($P > 0.01$ after a multiple comparison correction). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 9999 randomizations. In this analysis, λ for a given independent variable is the increase in the sum of all canonical eigenvalues of the ordination when the variable is added to the environmental variables included already (i.e. provides the additional variance the variable explains, given the variables already included). Before RDA analyses, we checked for collinearity between environmental variables using the variance inflation factor (VIF). VIF was in all cases below 15, suggesting the absence of strong collinearity problems (Chatterjee and Price, 1991).

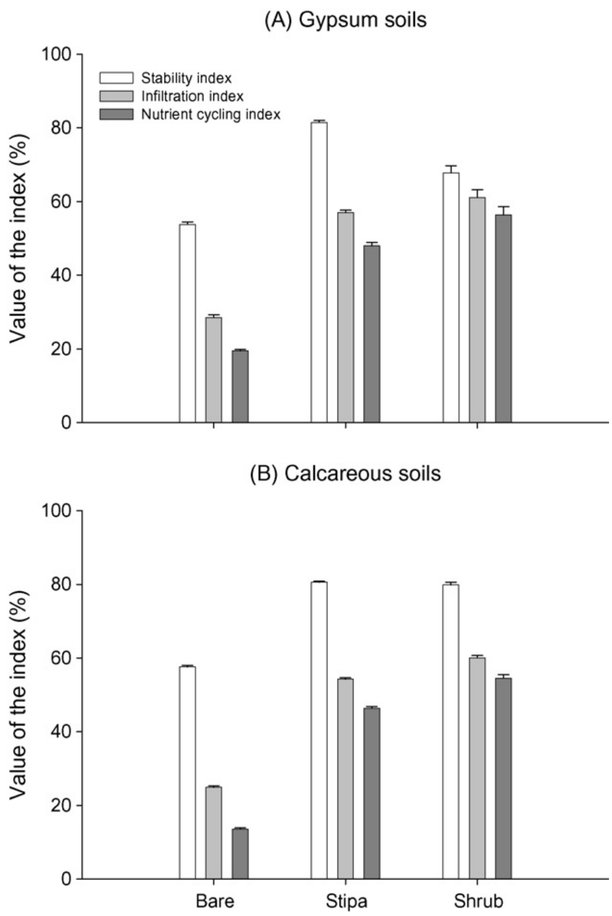

Fig. 1. Summary of the landscape function analysis indices obtained in the different substrates and microsites evaluated. Legend of microsites as follows: Bare = areas devoid of vascular vegetation, Stipa = areas located under the canopy of *Stipa tenacissima* tussocks, and Shrub = areas located under the canopy of sprouting shrubs. Data represents means ± SE (n = 35, 35 and 5 for Bare, Stipa, and Shrub microsites under gypsum soils; n = 110, 110, and 55 for Bare, Stipa, and Shrub microsites under calcareous soils).

CAP analyses were performed with the CAP program (Anderson, 2004), which can be downloaded from http://www.stat.auckland.ac.nz/~cmja/Programs.htm. For these analyses, we used the Euclidean distance and 9999 permutations. RDA analyses were conducted with CANOCO for Windows v. 4.5 (ter Braak and Šmilauer, 1998). All the other statistical analyses were conducted with SPSS for Windows 14.0 (SPSS Inc., Chicago, IL, USA). As suggested by Gotelli and Ellison (2004), the experiment-wide error rate was not adjusted because this approach is overly conservative, and all the interpretations of the statistical analyses were done by evaluating the raw P values.

3. Results

The LFA indices obtained at the different sites are summarized in Fig. 1. Values obtained at Stipa and Shrub microsites were higher than those obtained in open areas, regardless of the substrate considered (see Appendix B for detailed data). The first two CAP axes explained over 99% of the variation observed in the LFA indices, and clearly separated the three microsites evaluated (Fig. 2; trace statistic = 1.43, $P = 0.0001$). The effect of substrate was particularly marked for the LFA indices obtained in both Shrub and Open microsites. Over 71% of all the observations were correctly classified by CAP into their respective groups (Appendix C). This percentage rises up to 100% for the group with the lowest replication level (shrubs on gypsum substrate).

At the quadrat scale, and considering all the microsites together, the three LFA indices were significantly related with most of the surrogates of soil functioning evaluated in both calcareous and gypsum soils (Table 2; Appendices D–I). In calcareous soils, the infiltration index was strongly related to variables such as soil compaction and water holding capacity, in a negative and positive manner, respectively; while the nutrient cycling index was significantly and positively related to all variables related to nutrient cycling excepting the urease activity. The stability index was also related to all the variables measured excepting the urease activity. The relationships found in gypsum soils were very similar, and the only noticeable change is the lack of relationships between any LFA index and soil respiration, and the lack of relationships between the stability index and soil compaction, and between the infiltration and nutrient cycling indices and the water holding capacity of soils. Many of these relationships were maintained when the data of the different microsites were analyzed separately, particularly in the Open microsites (Appendices D–I). It is interesting, however, to note that some relationships that were not significant when analyzing all the

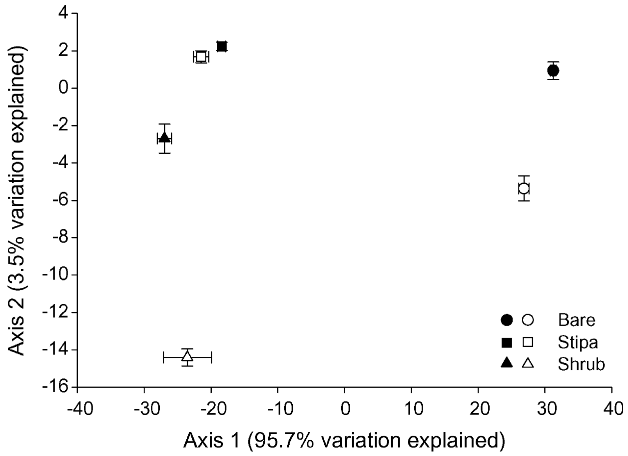

Fig. 2. Canonical analysis of principal coordinates of the landscape function analysis indices obtained at the different soil and microsite types. Black and white symbols represent soils obtained from calcareous and gypsum microsites, respectively. Data represent means ± SE ($n = 35$, 35 and 5 for Bare, Stipa, and Shrub microsites under gypsum soils; $n = 110$, 110, and 55 for Bare, Stipa, and Shrub microsites under calcareous soils).

data together, such as those between the nutrient cycling index and the urease activity, became significant when analyzing the data from the Open microsite in gypsum soils (Spearman $r = 0.422$, $P = 0.012$, $n = 35$) and the data from all the microsites in calcareous soils (Open, Spearman $r = 0.191$, $P = 0.045$; Stipa, Spearman $r = 0.292$, $P = 0.002$; Shrub, Spearman $r = 0.447$, $P = 0.001$; $n = 110$ in all cases). Other relationships shifted in sign when evaluating data for particular microsites, such as the case of K measured in gypsum soils, which showed an overall positive relationship with the three indices when analyzing the data together, but a negative relationship with the infiltration (Spearman $r = -0.422$, $P = 0.012$, $n = 35$) and nutrient cycling (Spearman $r = -0.484$, $P = 0.003$, $n = 35$) indices measured in the Open microsites. Many of the relationships found at the quadrat scale were maintained when the LFA indices were scaled up to whole plots (Table 3; Appendices J–L), albeit some of them, such as those with K and soil pH, became non-significant.

The environmental matrix significantly explained the variation found in the LFA indices obtained in the Open microsite (RDA; first canonical axis, eigenvalue = 0.531, $F = 19.22$, $P < 0.001$; All canonical axes, trace = 0.676, $F = 3.22$, $P < 0.001$). The independent variables that best explained such variation were the average

Table 2
Spearman correlation coefficients between the landscape function analysis indices and the soil variables evaluated. BA = β-glucosidase activity, PA = phosphatase activity, PR = soil compaction, SOC = soil organic carbon, SR = soil respiration TSN = total soil nitrogen, TSP = total soil phosphorus, UA = urease activity, and WHC = water holding capacity. Significance levels as follows: (ns) $P > 0.05$, (*) $P < 0.05$, (**) $P < 0.01$, and (***) $P < 0.001$.

	Calcareous soils			Gypsum soils		
	Stability index	Infiltration index	Nutrient cycling index	Stability index	Infiltration index	Nutrient cycling index
pH[a]	-0.34^{***}	-0.28^{***}	-0.33^{***}	-0.19^{ns}	-0.21^{ns}	-0.23^{*}
SOC[a]	0.44^{***}	0.49^{***}	0.46^{***}	0.54^{***}	0.58^{***}	0.62^{***}
SR[a]	0.51^{***}	0.57^{***}	0.59^{***}	$< 0.01^{ns}$	0.11^{ns}	0.15^{ns}
TSN[a]	0.43^{***}	0.50^{***}	0.46^{***}	0.56^{***}	0.57^{***}	0.61^{***}
TSP[a]	-0.02^{ns}	0.17^{**}	0.14^{*}	0.34^{**}	0.39^{**}	0.44^{***}
K[a]	0.46^{***}	0.55^{***}	0.53^{***}	0.26^{*}	0.29^{*}	0.30^{**}
PA[a]	0.65^{***}	0.57^{***}	0.58^{***}	0.46^{***}	0.46^{***}	0.55^{***}
BA[a]	0.61^{***}	0.60^{***}	0.59^{***}	0.58^{***}	0.55^{***}	0.58^{***}
UA[a]	-0.11^{ns}	0.02^{ns}	0.03^{ns}	0.07^{ns}	0.15^{ns}	0.15^{ns}
PR[b]	0.25^{**}	-0.79^{***}	-0.30^{**}	-0.18^{ns}	-0.62^{***}	-0.64^{***}
WHC[c]	0.27^{**}	0.34^{***}	0.32^{***}	0.41^{*}	0.20^{ns}	0.13^{ns}

[a] $n = 275$ and 75 for calcareous and gypsum soils, respectively.
[b] $n = 110$ and 35 for calcareous and gypsum soils, respectively.
[c] $n = 110$ and 30 for calcareous and gypsum soils, respectively.

Table 3
Pearson correlation coefficients between the plot estimates of the landscape function analysis indices and the soil variables evaluated. $n = 29$ in all cases. Significance levels as follows: (ns) $P > 0.05$, (*) $P < 0.05$, (**) $P < 0.01$, and (***) $P < 0.001$.

	Stability index	Infiltration index	Nutrient cycling index
Soil pH	0.30^{ns}	0.14^{ns}	0.10^{ns}
Soil organic carbon	0.72^{***}	0.43^{*}	0.43^{*}
Soil respiration	0.26^{ns}	0.39^{*}	0.40^{*}
Total soil nitrogen	0.73^{***}	0.42^{*}	0.42^{*}
Total soil phosphorus	0.67^{***}	0.54^{**}	0.52^{**}
Soil potassium	-0.20^{ns}	-0.35^{s}	-0.28^{ns}
Phosphatase activity	0.70^{***}	0.18^{ns}	0.23^{ns}
β-Glucosidase activity	0.62^{***}	0.34^{ns}	0.29^{ns}
Urease activity	-0.48^{**}	0.03^{ns}	$<-0.01^{ns}$
Water holding capacity	0.38^{*}	0.38^{*}	0.44^{*}

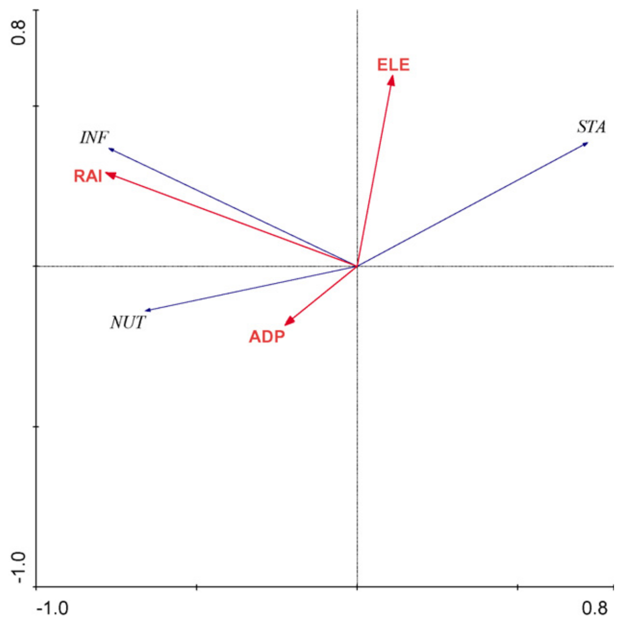

Fig. 3. First two axes of a redundancy analysis (RDA) ordination diagram conducted with the average landscape function analysis (LFA) indices (dependent variables) obtained in the Open microsites and main patch attributes and abiotic factors (independent variables). The first two RDA axes explained 64.3% of the variance found in the LFA indices. Only independent variables that significantly contributed to this variance, as indicated by the forward selection procedure, are presented in the diagram. The abbreviations and results of the forward selection procedure are the following: ELE = elevation ($\lambda = 0.5$, $F = 7.55$, $P < 0.001$), RAI = average rainfall ($\lambda = 0.34$, $F = 13.79$, $P < 0.001$), and ADP = mean length of inter-patch zones ($\lambda = 0.05$, $F = 3$, $P = 0.039$).

precipitation of the sites, their elevation and the mean length of inter-patch zones (Fig. 3).

4. Discussion

4.1. LFA indices as surrogates of soil functioning

Recent recommendations for monitoring systems in arid environments have attempted to identify indices of landscape function that are quantitative, rapid, repeatable and sensitive to change (National Research Council, 1994; Rapport et al., 1995; Whitford, 2002). Significant relationships between plant cover and soil variables related to the functions evaluated by the LFA indices have been demonstrated by many studies (e.g., Martínez-Mena et al., 2002; Bastida et al., 2007; Li et al., 2007). Indeed, this variable is commonly included in protocols for monitoring and assessing land degradation and processes (e.g., Herrick et al., 2005). While acknowledging the key role of total plant cover as a driver of ecosystem functioning, we do not believe that it precludes the use of other valid and alternative indicators of ecosystem functioning, such as those employed by the LFA methodology. Many independent studies have suggested that attributes of soil–surface condition (e.g. soil cover, soil texture, cryptogam cover) may be combined in various ways to provide useful indices of landscape function (Herrick and Whitford, 1995; Tongway, 1995; de Soyza et al., 1997; Whitford, 2002). Indeed, the LFA infiltration index has been found to perform better than total plant cover as a descriptor of infiltration processes under field conditions (Bartley et al., 2006).

In our study, the nutrient cycling index was strongly correlated with variables related with microbial activity and nutrient cycling, such as soil pH, total soil N and P, soil respiration and the activities of phosphatase and β-glucosidase. In the same direction, strong correlations between the infiltration index and both soil compaction and the water holding capacity of soils, two important variables defining the hydrological behavior of a site, were found. The stability index was also significantly correlated with most of the surrogates of soil functioning evaluated. We would like to highlight that the use of a semi-quantitative estimation of resistance to penetration by LFA does not invalidate our quantitative measurements of soil compaction as a functional variable because the LFA indices are built combining many different soil surface indicators. While the test for ease of physical disturbance made by LFA is quite informal, and may not conform to the normal "accuracy" criteria, the indicators are used in a multivariate sense, and the lack of precision in the individual indicators is compensated by the breadth of other relevant information. In this direction, Bartley et al. (2006) found a linear and highly significant ($r^2 = 0.95$) relationship between infiltration (in mm h^{-1}) and the LFA infiltration index, suggesting that this index can predict infiltration across the full range of circumstances they evaluated because of the information contained in the number of indicators making up the calculated indices.

The relationships observed, which were also evident in the two soil types studied and when using both the quadrat data and the plot averages, indicate that the LFA indices can be used as surrogates of variables related to key soil functions in semi-arid Mediterranean steppes. Our results agree with studies conducted in semi-arid environments of Australia and Iran, where the nutrient cycling is positively and significantly correlated to variables such as soil organic C and total N (McR. Holm et al., 2002; Tongway and Hindley, 2003; Ata Rezaei et al., 2006), and with those performed in a semi-arid steppe in SE Spain, where positive and significant relationships between the three LFA indices and both soil organic C and the activities of two of the enzymes evaluated here (phosphatase and β-glucosidase) were found (Mayor, 2008). They also complement results from the later study, which found a negative relationship between the infiltration index and the production of sediments in erosion plots, and a positive relationship between this index and the infiltration rate measured *in situ* when the soil was dry.

Many of the correlations observed at the quadrat scale were maintained when different microsites were analyzed separately, particularly in calcareous soils. These analyses revealed also correlations that were not evident when using data from all the microsites. These results contrast with those of Mayor (2008), who failed to find significant relationships between the LFA indices and both soil organic carbon and enzyme activities when considering the data gathered in Stipa and Open microsites separately in a single steppe from SE Spain. This difference is likely caused by the higher range of variation in the LFA indices used in our study. The variability in the three LFA indices and the surrogates of soil functioning measured, as measured with the coefficient of variation, was always higher in the Open than in the Stipa and Shrub microsites (Appendix M). This may explain why more significant correlations between the LFA indices and the soil variables evaluated were found in this microsite (Appendices D–I). Our results indicate that the LFA indices can be sensitive enough to detect variations in ecosystem processes within particular microsites, at least with variability ranges in both these processes and the LFA indices as large as those found in our study.

4.2. Variation in the LFA indices

As found in other studies conducted in arid and semi-arid areas (McR. Holm et al., 2002; Maestre and Cortina, 2004; Mayor, 2008), the LFA indices were substantially higher under the canopy of plant patches than in open areas devoid of vascular vegetation. These sharp transitions between bare ground and vegetated microsites reflect the nature of the ecosystem studied, where vegetation forms a two-phase mosaic with discrete plant patches surrounded by a matrix of bare ground soil (this vegetation pattern is characteristic of most arid and semi-arid ecosystems; Valentin et al., 1999). Our results highlight the higher potential of such patches to withstand erosive processes, to increase infiltration and to cycle nutrients as compared to bare ground areas, as found by many studies that have used more quantitative measures of these soil functions conducted in arid and semi-arid areas of the world (e.g. Reynolds et al., 1999; Puigdefábregas et al., 1999; Maestre et al., 2002; Bhark and Small, 2003; Thompson et al., 2005). According to what has been previously reported in *S. tenacissima* steppes of SE Spain (Maestre and Cortina, 2004; Mayor, 2008), we also found differences in the LFA indices within the two types of plant patches evaluated, as shrub patches had higher values of the nutrient cycling and infiltration indices than *S. tenacissima* tussocks. Shrub patches also showed the highest values of many of the surrogates of soil functioning evaluated, particularly in calcareous soils (Appendices D–F). These results reinforce the role of shrubs as key species to maintain and improve soil functioning in semi-arid *S. tenacissima* steppes (Cortina et al., 2006; Maestre and Cortina, 2004). Differences between shrub and *S. tenacissima* patches that may lead to enhanced infiltration and nutrient cycling in the former include differential patterns in root growth and size (Puigdefábregas et al., 1999; Archer et al., 2002), increased understorey diversity and biomass under the canopy of shrubs (Maestre, 2004; Maestre and Cortina, 2005), higher litter inputs (Bochet et al., 1998), and availability of avian perch sites that may increase nutrient inputs by defecation (Pausas et al., 2006). Differences among plant patch types in soil properties may also result from contrasting disturbance regimes (e.g., Shrub microsites being less altered by human activity in the past than Stipa microsites). However, this possibility is unlikely because the long-term history of human exploitation in *S. tenacissima* steppes includes collection of shrub wood for fuel (Maestre et al., 2007). As we only sampled shrubs in a single site under gypsum soils, the lower values of the stability index found under shrubs as compared to *S. tenacissima* tussocks should be interpreted with caution, and cannot be generalized.

The results obtained when exploring the relationships between the average LFA indices obtained in the Open microsites and the main biotic and abiotic features of the study sites agree with previous work showing the importance of the spatial distribution of plant patches and adjacent open areas for the proper functioning of semi-arid ecosystems (e.g., Ludwig and Tongway, 1995; Ludwig et al., 2000). They also coincide with the patterns reported by Maestre and Cortina (2004), who evaluated the relationships between the LFA indices and main patch attributes and abiotic factors in *S. tenacissima* steppes from SE Spain. 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 than surrounding bare ground areas (Puigdefábregas et al., 1999; Maestre et al., 2002; Azcón-Aguilar et al., 2003), acting as "resource islands" (*sensu* Reynolds et al., 1999). Human-induced degradation processes in *S. tenacissima* steppes may destroy or substantially modify vegetated patches, resulting in an increased distance between them. These changes may increase the amount of water, nutrients and sediments transported during runoff events up to levels that may exceed the ability of existing patches to retain them (Puigdefábregas et al., 1999). As a consequence, a greater proportion of resources are exported from the system, the quality of the soil in places once occupied by plant patches drops, and the overall resilience of the system against further runoff events is reduced, fostering their erosion and degradation. The characterization of the inter-patch distance forms part of the initial phase of the LFA assessment, where bare ground areas and "patch" zones are identified and mapped at the plot scale using transects (Tongway and Hindley, 2004). Our results highlight the importance of this characterization; by using these data in conjunction with the LFA indices, any bare areas can be assessed in terms of management risk.

4.3. Use of LFA indices in ecological restoration and monitoring

LFA is a monitoring tool developed mainly to advise managers, and does not pretend to replace accurate measurements when these are needed. The cost/benefit of a rapidly deployed monitoring procedure which gives adequate information (no false negatives or positives) to managers is undeniable, and this is one of the main advantages of this methodology. In addition, LFA can be used over large areas in a ready and inexpensive manner, and data acquisition can be successfully achieved with minimal training. Therefore, this methodology has an enormous potential to assist land managers, technicians and policy makers in the establishment of cost-effective ecological monitoring programs.

Our results have shown that the LFA indices can be used as surrogates of key soil variables related to soil stability, nutrient cycling and water infiltration in *S. tenacissima* steppes. Given that the LFA indices in the Open microsite are strongly and positively related to many of the surrogates of soil functioning evaluated (Appendices D–I), we suggest that this microsite should be primarily selected for the establishment of monitoring programs when logistic or monetary constrains limit the total number of sites that can be evaluated. However, it must be emphasized that the accurate estimation of the functional status of a given site will require the information of all their constituent units (both bare ground areas and vegetated patches).

An in-depth consideration of the functional status of ecosystems and its drivers may be of great help to define restoration goals, to prioritize economical investments, and to select the target soil functions and components to recover with the restoration of a given area (Tongway and Hindley, 2000; Hobbs, 2002; Méndez et al., 2008). In this direction, it has been suggested that the restoration of semi-arid *S. tenacissima* steppes should follow a two-step approach according to their functional status and structural attributes (Maestre and Cortina, 2004). When they are highly degraded, restoration efforts should focus on the recovery of ecosystem structure by increasing the number and area of patches. This can be easily done by inserting brush piles parallel to land contours (Ludwig and Tongway, 1996; Tongway and Ludwig, 1996). Such artificially created patches would act as sinks of soil, water, nutrients, and seeds, providing favorable microenvironments for the recovery of vascular plants and biological soil crusts (Aguiar and Sala, 1999; Bowker, 2007). Once this intervention has reduced degradation processes, the next step to restore these systems should be the introduction of seedlings of native sprouting shrubs. This introduction would foster the recovery of nutrient cycling in the long term, increase ecosystem resilience, and provide suitable habitats for further spontaneous plant and wild animal colonization (Trabaud, 1991; López and Moro, 1997; Verdú and García-Fayos, 1996; Maestre, 2004). The LFA indices can be extremely helpful when implementing this restoration procedure in *S. tenacissima* steppes, as they provide an easy and inexpensive manner to assess key soil processes in a given site, and to rank a series of target sites according to their functional status. Depending on such status and the economic resources available, and using the information provided in this study, land managers can prioritize the restoration of particular sites, and decide which components or soil functions should be restored at each particular site.

Acknowledgements

We would like to thank M. Carpio, A.P. Castillo, I. Martínez, A. Sánchez, S. Soliveres, P. García-Palacios, A. López de Luzuriaga, C. de Pablos, R. Romao and A. Escudero for their help during lab and fieldwork, G. González-Barberá and J.A. Navarro for their assistance with the selection of some field sites, C. Guerrero for his invaluable help with all the soil analyses, R. Dick and four reviewers for their constructive comments on an earlier version of this manuscript, and M.A. Bowker for revising the English of the manuscript. FTM was supported by a Ramón y Cajal contract from the Spanish Ministerio de Ciencia e Innovación, co-funded by the European Social Fund, and by the British Ecological Society (ECPG 231/607 and Studentship 231/1975). This research was supported by the projects INTERCAMBIO (BIOCON06/105), CEFEMED (URJC-RNT-063-2) and REMEDINAL (S-0505/AMB/0335), funded by Fundación BBVA, Comunidad de Madrid (CM) and Universidad Rey Juan Carlos and CM, respectively.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.apsoil.2008.12.007.

References

Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends Ecol. Evol. 14, 273–277.
Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Aust. Ecol. 26, 32–46.
Anderson, M.J., 2004. CAP: a FORTRAN computer program for canonical analysis of principal coordinates. Department of Statistics, University of Auckland, New Zealand.
Anderson, M.J., Robinson, J., 2003. Generalised discriminant analysis based on distances. Aust. N.Z. J. Stat. 45, 301–318.
Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525.
Archer, N.A.L., Quinton, J.N., Hess, T.M., 2002. Below-ground relationships of soil texture, roots and hydraulic conductivity in two-phase mosaic vegetation in South-east Spain. J. Arid Environ. 52, 535–553.
Ata Rezaei, S., Arzani, H., Tongway, D., 2006. Assessing rangeland capability in Iran using landscape function indices based on soil surface attributes. J. Arid Environ. 65, 460–473.
Azcón-Aguilar, C., Palenzuela, J., Roldán, A., Bautista, S., Vallejo, R., Barea, J.M., 2003. Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened Mediterranean shrublands. Appl. Soil Ecol. 22, 29–37.
Bartley, R., Roth, C.H., Ludwig, J., McJannet, D., Liedloff, A., Corfield, J., Hawdon, A., Abbott, B., 2006. Runoff and erosion from Australia's tropical semi-arid rangelands: influence of ground cover for differing space and time scales. Hydrol. Proc. 20, 3317–3333.
Bastida, F., Moreno, J.L., Hernández, T., García, C., 2007. Microbial activity in non-agricultural degraded soils exposed to semiarid climate. Sci. Total Environ. 378, 183–186.
Bhark, E.W., Small, E.E., 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. Ecosystems 6, 185–196.
Bochet, E., Rubio, J.L., Poesen, J., 1998. Relative efficiency of three representative matorral species in reducing water erosion at the microscale in a semi-arid climate (Valencia Spain). Geomorphology 23, 139–150.
Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.
Bowker, M.A., 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. Restor. Ecol. 15, 13–23.
Castellano, M.J., Valone, T.J., 2007. Livestock, soil compaction and water infiltration rate: evaluating a potential desertification recovery mechanism. J. Arid Environ. 71, 97–108.
Chapin III, F.S., Matson, P., Money, H.A., 2002. Principles of Terrestrial Ecosystem Ecology. Springer, New York, p. 472.
Chatterjee, S., Price, B., 1991. Regression Analysis by Example, 2nd edn. John Wiley & Sons, New York, p. 304.
Cortina, J., Maestre, F.T., Vallejo, R., Baeza, M.J., Valdecantos, A., Pérez-Devesa, M., 2006. Ecosystem structure, function, and restoration success: are they related? J. Nat. Conserv. 14, 152–160.
de Soyza, A.G., Whitford, W.G., Herrick, J.E., 1997. Sensitivity testing of indicators of ecosystem health. Ecosyst. Health 3, 44–53.
Fernández, R.J., Archer, E.R.M., Ash, A.J., Dowlatabadi, H., Hiernaux, P.H.Y., Reynolds, J.F., Vogel, C.H., Walker, B.H., Wiegand, T., 2002. Degradation and recovery in socio-ecological systems: a view from the household/farm level. In: Reynolds, J.F., Stafford Smith, M. (Eds.), Do Humans Create Deserts? The Ecological, Meteorological, and Human Dimensions of Global Desertification. Dahlem University Press, Berlin, pp. 297–324.
Forster, J.C., 1995. Soil physical analysis. In: Alef, K., Nannipieri, P. (Eds.), Methods in Applied Soil Microbiology and Biochemistry. Academic Press Inc., San Diego, pp. 106–111.
Froment, A., 1972. Soil respiration in a mixed oak forest. Oikos 23, 273–277.
Gauch, H.G., 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge, p. 298.
Ghosh, B.N., Singh, R.D., 2001. Potassium release characteristics of some soils of Uttar Pradesh hills varying in altitude and their relationship with forms of soil K and clay mineralogy. Geoderma 104, 135–144.
Gotelli, N.J., Ellison, A.M., 2004. A Primer of Ecological Statistics. Sinauer Associates, Sunderland, p. 280.
Herrick, J.E., Van Zee, J.W., Havstad, K.M., Whitford, W.G., 2005. Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems. Volume II: Design Supplementary Methods and Interpretation. USDA-ARS, Las Cruces.
Herrick, J.E., Whitford, W.G., 1995. Assessing the quality of rangeland soils: challenges and opportunities. J. Soil Water Conserv. 50, 237–242.
Hill, M.O., Gauch, H.G., 1980. Detrended Correspondence Analysis: an improved ordination technique. Vegetatio 42, 47–58.
Hobbs, R.J., 2002. The ecological context: a landscape perspective. In: Perrow, M.R., Davy, A.J. (Eds.), Handbook of Ecological Restoration 1., Cambridge University Press, Cambridge, pp. 24–46.
Hood, J.T., Brady, N.C., Lathwell, D.J., 1956. The relationship of water soluble and exchangeable potassium to yield and potassium uptake by ladino clover. Soil Sci. Soc. Am. J. 20, 228–231.
Krämer, S., Green, D.M., 1999. Phosphorus pools in tree and intercanopy microsites of a Juniper-Grass ecosystem. Soil Sci. Soc. Am. J. 63, 1901–1905.
Kuzyakov, Y., 2006. Sources of CO_2 efflux from soil and review of partitioning methods. Soil Biol. Biochem. 38, 425–448.
Lachenbruch, P.A., Mickey, M.R., 1968. Estimation of error rates in discriminant analysis. Technometrics 10, 1–11.
Le Houérou, H.N., 2001. Biogeography of the arid steppeland north of the Sahara. J. Arid Environ. 48, 103–128.
Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1–24.
Li, J., Okin, G.S., Alvarez, L., Epstein, H., 2007. Quantitative effects of vegetation cover on wind erosion and soil nutrient loss in a desert grassland of southern New Mexico, USA. Biogeochemistry 85, 317–332.
López, G., Moro, M.J., 1997. Birds of Aleppo pine plantations in south-east Spain in relation to vegetation composition and structure. J. Appl. Ecol. 34, 1257–1272.
López Mateo, C., Álvarez, E., Fernández Marcos, M.L., 2002. Potasio en suelos de Galicia y su relación con la mineralogía. Edafología 9, 305–312.
Ludwig, J.A., Tongway, D.J., 1995. Spatial organization of landscapes and its function in semi-arid woodlands, Australia. Landscape Ecol. 10, 51–63.
Ludwig, J.A., Tongway, D.J., 1996. Rehabilitation of semiarid landscapes in Australia. II. Restoring vegetation patches. Restor. Ecol. 4, 398–406.
Ludwig, J.A., Tongway, D.J., Bastin, G.N., James, C.D., 2004. Monitoring ecological indicators of rangeland functional integrity and their relation to biodiversity at local to regional scales. Aust. Ecol. 29, 108–120.
Ludwig, J.A., Wiens, J.A., Tongway, D.J., 2000. A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. Ecosystems 3, 84–97.
Maestre, F.T., 2004. On the importance of patch attributes, environmental factors and past human impacts as determinants of perennial plant species richness and diversity in Mediterranean semi-arid steppes. Divers. Distrib. 10, 21–29.
Maestre, F.T., Cortina, J., 2004. Insights into ecosystem composition and function in a sequence of degraded semiarid steppes. Restor. Ecol. 12, 494–502.

Maestre, F.T., Cortina, J., 2005. Remnant shrubs in Mediterranean semi-arid steppes: effects of shrub size, abiotic factors and species identity on understorey richness and occurrence. Acta Oecol. 27, 161–169.

Maestre, F.T., Cortina, J., 2006. Ecosystem structure and soil surface conditions drive the variability in foliar $\delta^{13}C$ and $\delta^{15}N$ of *Stipa tenacissima* in semiarid Mediterranean steppes. Ecol. Res. 21, 44–53.

Maestre, F.T., Cortina, J., Vallejo, R., 2006. Are ecosystem composition, structure and functional status related to restoration success? A test from semiarid Mediterranean steppes. Restor. Ecol. 14, 258–266.

Maestre, F.T., Huesca, M.T., Zaady, E., Bautista, S., Cortina, J., 2002. Infiltration, penetration resistance and microphytic crust composition in contrasted microsites within a Mediterranean semi-arid steppe. Soil Biol. Biochem. 34, 895–898.

Maestre, F.T., Ramírez, D.A., y Cortina, J., 2007. Ecología del esparto (*Stipa tenacissima* L.) y los espartales en la Península Ibérica. Ecosistemas 16, 116–135.

Maestre, F.T., Rodríguez, F., Bautista, S., Cortina, J., Bellot, J., 2005. Spatial associations and patterns of perennial vegetation in a semi-arid steppe: a multivariate geostatistics approach. Plant Ecol. 179, 133–147.

Martínez-Mena, M., Alvarez Rogel, J., Castillo, V., Albaladejo, J., 2002. Organic carbon and nitrogen losses influenced by vegetation removal in a semiarid mediterranean soil. Biogeochemistry 61, 309–321.

Mayor, A.G., 2008. El papel de la dinámica fuente-sumidero en la respuesta hidrológica, a varias escalas, de una zona mediterránea semiárida. Ph.D. Thesis. University of Alicante, 173 pp.

McR. Holm, A., Bennet, L.T., Loneragan, W.A., Adams, M.A., 2002. Relationships between empirical and nominal indices of landscape function in the arid shrubland of Western Australia. J. Arid Environ. 50, 1–21.

Méndez, M., García, D., Maestre, F.T., Escudero, A., 2008. More ecology is needed to restore Mediterranean ecosystems. A reply to Valladares & Gianoli. Restor. Ecol. 16, 210–216.

Nannipieri, P., Ceccanti, B., Cervelli, S., Matarese, E., 1980. Extraction of phosphatase, urease, protease, organic carbon and nitrogen from soil. Soil Sci. Soc. Am. J. 44, 1011–1016.

National Research Council, 1994. Rangelands Health. New Methods to Classify Inventory and Monitor Rangelands. National Academy Press, Washington DC.

Nelson, R.E., Sommers, L.E., 1982. Total carbon, organic carbon, and organic matter. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of soil analysis., Part 2. Chemical and microbiological properties. American Society of Agronomy and Soil Science Society of America, Madison, pp. 539–580.

Ninyerola, M., Pons, X., Roure, J.M., 2005. Atlas climático digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Barcelona. Maps available online: http://www.opengis.uab.es/wms/iberia/mms/index.htm

Pausas, J.G., Bonet, A., Maestre, F.T., Climent, A., 2006. The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. Acta Oecol. 29, 346–352.

Pautler, M.C., Sims, J.T., 2000. Relationships between soil test phosphorus, soluble phosphorus, and phosphorus saturation in Delaware soils. Soil Sci. Soc. Am. J. 64, 765–773.

Puigdefábregas, J., Solé-Benet, A., Gutierrez, L., Del Barrio, G., Boer, M., 1999. Scales and processes of water and sediment redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. Earth-Sci. Rev. 48, 39–70.

Pyke, D.A., Herrick, J.E., Shaver, P.L., Pellant, M., 2002. Rangeland health attributes and indicators for qualitative assessment. J. Range Manage. 55, 584–597.

Rapport, D.J., Gaudet, C.L., Calow, P., 1995. Evaluating and Monitoring the Health of Large-scale Ecosystems. Springer-Verlag, Montebello, Quebec, p. 454.

Reynolds, J.F., Stafford Smith, D.M., Lambin, E.F., Turner rII, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., Huber-Sannvald, E., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007a. Global desertification: building a science for dryland development. Science 316, 847–851.

Reynolds, J.F., Maestre, F.T., Kemp, P.R., Stafford-Smith, D.M., Lambin, E., 2007b. Natural and human dimensions of land degradation in drylands: causes and consequences. In: Canadell, J., Pataki, D., Pitelka, L.F. (Eds.), Terrestrial Ecosystems in a Changing World. Springer-Verlag, Berlin, pp. 247–258.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., De Soyza, A.G., Tremmel, D.C., 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecol. Monogr. 69, 69–106.

Sharpley, A.N., 1989. Relationship between soil potassium forms and mineralogy. Soil Sci. Soc. Am. J. 53, 1023–1028.

Soil Survey Staff, 1994. Keys to Soil Taxonomy, 6th edn. USDA Soil Conservation Service, Pocahontas Press, Blacksburg, p. 524.

Tabatabai, M.A., 1982. Soil enzymes. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. Part 2. Agronomical Monograph No. 9. 2nd ed. American Society of Agronomy and Soil Science of America, Madison, pp. 501–538.

Tabatabai, M.A., Bremner, J.M., 1969. Use of p-nitrophenyl phosphate in assay of soil phosphatase activity. Soil Biol. Biochem. 1, 301–307.

ter Braak, C.J.C., Šmilauer, P., 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Microcomputer Powever, Ithaca.

Thompson, D.B., Walker, L.R., Landau, F.H., Stark, L.R., 2005. The influence of elevation, shrub species, and biological soil crust on fertile islands in the Mojave Desert, USA. J. Arid Environ. 61, 609–629.

Thompson, W.A., Eldridge, D.J., Bonser, S.P., 2006. Structure of biological soil crust communities in *Callitris glaucophylla* woodlands of New South Wales, Australia. J. Veg. Sci. 17, 271–280.

Tongway, D.J., 1995. Monitoring soil productive potential. Environ. Monit. Assess. 37, 303–318.

Tongway, D.J., Hindley, N., 1995. Assessment of Soil Condition of Tropical Grasslands. CSIRO Ecology and Wildlife, Canberra, p. 60.

Tongway, D.J., Hindley, N., 2000. Assessing and monitoring desertification with soil indicators. In: Arnalds, O., Archer, S. (Eds.), Rangeland Desertification. Kluwer Academic Publishers, Dordrecht, pp. 89–98.

Tongway, D.J., Hindley, N., 2003. Indicators of ecosystem rehabilitation success. Unpublished report. Available from http://www.cse.csiro.au/publications/2003/IndicatorsOfMinesiteRehabilitationSuccessStage2-100703.pdf.

Tongway, D.J., Hindley, N., 2004. Landscape Function Analysis: Procedures for Monitoring and Assessing Landscapes. CSIRO Publishing, Brisbane, p. 82.

Tongway, D.J., Ludwig, J.A., 1996. Rehabilitation of semiarid landscapes in Australia I. Restoring productive soil patches. Restor. Ecol. 4, 388–397.

Trabaud, L., 1991. Fire regimes and phytomass growth dynamics in a *Quercus coccifera* garrigue. J. Veg. Sci. 2, 307–314.

Valentin, C., d Herbes, J.M., Poesen, J., 1999. Soil and water components of banded vegetation patterns. Catena 37, 1–24.

van der Zee, S.E.A.T.M., van Riemsdijk, W.H., 1988. Model for long-term phosphate reaction kinetics in soil. J. Environ. Qual. 17, 35–41.

Verdú, M., García-Fayos, P., 1996. Nucleation processes in a Mediterranean bird-dispersed plant. Funct. Ecol. 10, 275–280.

Webster, R., Maestre, F.T., 2004. Spatial analysis of semi-arid patchy vegetation by the cumulative distribution of patch boundary spacings and transition probabilities. Environ. Ecol. Stat. 11, 257–281.

Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press, London.