



Spatial patterns of surface soil properties and vegetation in a Mediterranean semi-arid steppe

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Abstract

In arid and semi-arid areas with sparse vegetation cover, the spatial pattern of surface soil properties affects water and nutrient flows, and is a question of considerable interest for understanding degradation processes and establishing adequate management measures. In this study, we investigate the spatial distribution of vegetation and surface soil properties (biological crusts, physical crusts, mosses, rock fragments, earthworm casts, fine root accumulation and below-ground stones) in a semi-arid *Stipa tenacissima* L. steppe in SE Spain. We applied the combination of spatial analysis by distance indices (SADIE) and geostatistics to assess the spatial pattern of soil properties and vegetation, and correlation analyses to explore how these patterns were related. SADIE analysis detected significant clumped patterns in the spatial distribution of vegetation, mosses, fine root accumulation and below-ground stone content. Contoured SADIE index of clustering maps suggested the presence of patchiness in the distribution of earthworm casts, fine roots, below-ground stone content, mosses and biological crusts. Correlation analyses suggested that spatial pattern of some soil properties such as biological crusts, moss cover, surface rock fragments, physical crusts and fine roots were significantly related with above-ground plant distribution. We discuss the spatial arrangement of surface soil properties and suggest mechanistic explanations for the observed spatial patterns and relationships.

Abbreviations: SADIE – Spatial Analysis by Distance Indices

Introduction

Arid and semi-arid ecosystems throughout the world are characterized by a sparse vegetation cover, which is often arranged as a two-phase mosaic of vegetated and bare ground patches (Valentin et al., 1999). The formation, maintenance and dynamics of vegetated patches in these areas are strongly dependent on water, sediment, nutrient and seed fluxes from open areas to vegetated patches (Aguiar and Sala, 1999). The presence in the surface soil of physical crusts, earthworm casts, biological crusts, rock fragments, and roots can be of major relevance for water and nutrient flows at

several scales, influencing ecosystem structure and dynamics (Casper and Jackson, 1997; Poesen and Lavee, 1994; Seghieri et al., 1997; West, 1990). In addition, it has been suggested that an increase in the degree of patchiness in soil nutrients and vegetation may be linked with desertification processes (Schlesinger et al., 1990). As vegetation patchiness increases, so does run-off from bare ground areas (Abrahams et al., 1994), leading to nutrient and sediment losses (Schlesinger et al., 1999). Thus, spatial patterning of surface attributes and soil properties can be a key element in shaping water and nutrient flows in semi-arid ecosystems, and its identification is relevant for understanding degradation processes in these areas, and to establishing adequate management measures (Schlesinger et al., 1990).

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In the Mediterranean Basin, semi-arid areas are frequently covered by open steppe of the tussock grass *Stipa tenacissima* L. (Le Houérou, 1986). Several studies have described the sensitive relationships between *S. tenacissima* tussocks and some soil properties. Soils under this grass commonly show higher organic matter and nutrient contents than inter-tussock areas (Puigdefábregas and Sánchez, 1996), as well as improved physical soil properties such as lower surface compaction (Bochet et al., 1999), and higher infiltration rates (Cerdà, 1997) and water retention capacities (Maestre et al., 2001). On the other hand, inter-tussock areas, frequently referred as 'bare' areas, are far from being passive surfaces. It has been suggested that run-off generated in these areas may be essential for the maintenance of established *S. tenacissima* individuals (Puigdefábregas and Sánchez, 1996). However, the role of surface soil properties in the generation of these fluxes is still poorly known.

Despite the apparent importance that the spatial distribution of surface soil properties has in ecosystem functioning, few studies so far have described small-scale spatial patterns of these properties and their relationship with vegetation in semi-arid areas (Eldridge, 1999; Malam Issa et al., 1999; Seghieri et al., 1997). In this study, we investigate the spatial pattern of some surface soil properties and their relationships with the above-ground pattern of perennial vegetation in a relatively undisturbed *S. tenacissima* steppe using the combination of a novel approach (Spatial Analysis by Distance IndicEs or SADIE) and geostatistics. Geostatistics has been widely used during the last two decades to characterize and model spatial heterogeneity of soil properties at various scales (e.g. Robertson and Freckman, 1995; Webster, 1985; White et al., 1997). More recently, this technique has been used to explore the fine-scale spatial patterns of soil nutrients around individual plants (Halvorson et al., 1995; Jackson and Caldwell, 1993; Schlesinger et al., 1996). In recent years, SADIE has been developed to detect and to measure the degree of non-randomness in discrete variables (Perry, 1998; Perry et al., 1999). This technique has been used to characterize the spatial pattern of insects (Perry et al., 1996), plant pathogens (Turecheck and Madden, 1998), weeds (Perry, 1995) and soil nematodes (Perry, 1998). To our knowledge, it has never been applied to the study of the distribution of surface soil properties.

The main objectives of this paper are: (i) to explore the spatial patterns of surface soil properties; (ii) to relate these patterns with the spatial pattern of

vegetation; (iii) to discuss the implications and underlying mechanisms of the spatial patterns found; and (iv) to discuss the potential and idoneity of SADIE for the joint spatial analysis of surface soil properties and vegetation.

Materials and Methods

Study site

The research site is located close to Aigües de Busot (38° 21' N, 0° 21' W; SE Spain), at an altitude of 460 m a.s.l., and 12° slope facing SE. We chose it because the relatively low impacts of recent human disturbance, as revealed by visual observations of the intact biological and physical surface crusts, and by interviews with local inhabitants. The climate is semi-arid with mean annual precipitation 388 mm in the nearest meteorological station (Relleu, 10 km north), and a mean annual temperature of 15.8 °C (Jaén, 1996). The vegetation is spatially discontinuous with a total cover of 45%. Vegetated patches occur within large areas of bare soil, and the main species present are the tussock grass *S. tenacissima*, and the perennial grass *Brachypodium retusum* (Pers.) P. Beauv. Soils are silty (26% clay, 54% silt and 20% sand, Maestre et al., 2001), Lithic Calciorthid (Soil Survey Staff, 1994), and have been developed from marl and limestone.

Soil and vegetation sampling

We located a 50×50 m plot in the study area and collected soil surface data in autumn 1998, using a stratified random sampling procedure. We randomly located 294 points in two representative situations: close to the canopy of *S. tenacissima* tussocks and in open areas with sparse vegetation cover. At each point, we placed a 25×25 cm quadrat, and evaluated the following soil surface properties: pavement of surface rock fragments, physical crusts (surface sealing promoted by the destruction of surface soil structure), earthworm casts, biological crusts (cyanobacteria and soil lichen crusts) and mosses. We assigned a semi-quantitative value ranging from 0 to 4 for the evaluation of earthworm casts cover (0=0%; 1=1–25%; 2=26–50%; 3=51–75%; 4=76–100%). For the other variables, we recorded their presence (1) or absence (0) within each quadrat. After this, we dug a 25×25×25 cm hole at each sampling point, and we determined the percentage of fine roots and the below-ground stone content using a semi-quantitative

scale ranging from 1 to 3 (1=0–25%; 2=26–50%; 3=51–100%).

In spring 1999, we accurately mapped all perennial vegetation inside the plot, digitized the data, and translated them into a GIS, the Idrisi system (Eastman, 1997). We then divided the map into 400 2.5×2.5 m quadrats, and computed the cover of each single species in each quadrat with the aid of the GIS. In this study, we present results for the grasses *S. tenacissima* and *B. retusum*. They represent more than 73% of total perennial vegetation cover.

Spatial analysis of soil properties and vegetation

Spatial patterns of both soil properties and vegetation were analysed using SADIE (Perry, 1998; Perry et al., 1999). The key concept behind this method is the distance to regularity (D), which measures the total distance involved in passing from the observed spatial arrangement of counts (we refer here to count as the measured discrete value of the variable under study) to move to a regular arrangement where all units have the same value of the variable under study. To calculate D , SADIE uses the transportation algorithm from the linear programming literature (Kennington and Heldason, 1980). Usually, the larger D is, the more spatially aggregated are the data. To assess the magnitude of D , we compare it with the corresponding values from randomizations where the counts are arranged randomly amongst the sample units. Division of the observed value of D by the mean value from randomizations gives an index of aggregation, I_a . Usually, an aggregated sample has an $I_a > 1$, a spatially random sample has a $I_a = 1$ and a regular distributed sample has a $I_a < 1$. A formal randomization test where the counts are randomly arranged is done by calculating what proportion of values in the frequency distribution are as large or larger than the observed value of D . Using the usual two-tailed test and a value of $\alpha = 0.05$, a data set will have an aggregated pattern if $P < 0.05$, a random pattern if P is between 0.05 and 0.95, and a regular pattern if $P > 0.95$.

Another index provided by SADIE is the dimensionless index of clustering (v) that specifically measures the degree of clustering of the data into patches (areas with above-average density) or gaps (areas with below-average density). This index quantifies the degree to which each sample contributes to the overall clustering of the data. For a donor unit i (sampling point with above-average abundance) that has a flow

of counts to n_j receiver units (sampling points with below-average abundance), the average distance of outflow is computed as follows (nomenclature and formulae following Perry et al., 1999):

$$Y_i = \sum_j d_{ij} v_{ij} / \sum_i v_{ij}, \quad (1)$$

where v_{ij} is the outflow to the j th of n_i receiver units, and d_{ij} is the distance of this flow $[(x_i - x_j)^2 + (y_i - y_j)^2]^{1/2}$. Hence, there is an average outflow distance for each of the donor units. The reason that the numerical value of Y_i is a good indicator of clustering is that it tends to be larger for a unit that is part of a patch than for one with an isolated large count with relatively small neighbours. However Y_i depends on three things; the scale on which distances are measured, the count in the sample unit considered, and its location with respect to other units. To allow for these dependencies, we standardize the degree of clustering for each unit to form a dimensionless index, v , by multiplying Y_i by $({}_o Y_i Y_c Y)$, where ${}_o Y$ is the overall average absolute flow distance for all units and counts in the randomizations, ${}_c Y$ is the average flow distance for the observed count in i under randomizations of the observed counts among the sampling units, and Y is the average absolute flow distance of all the counts that were allocated to i during randomizations. For receiver units, the calculations are the same with the convention that the index is negative in sign.

Sampling points within patches have large values of v (by convention v_i), i.e. greater than 1.5, while units located within gaps have large and negative values of v (by convention v_j), i.e. below -1.5; values close to unity indicate a random placement of that unit. To test the overall degree of clustering of the entire data, we perform two permutation tests for donor and receiver units, respectively. In each case, the mean values of v , V_i and V_j respectively, are compared with corresponding values for randomizations in the same way as with I_a . One interesting property of v is that it is a continuous variable (Perry et al., 1999), and when plotted on a map, it can show the location and size of patches and gaps in the data.

We performed SADIE analysis separately for each soil variable and plant species with the software described in Perry et al. (1999). Cover data of *S. tenacissima* and *B. retusum* were categorized using decile distribution (10 classes) before SADIE analyses. We used 5967 randomizations in the permutation tests, the maximum allowed by the program. Contour maps of v were produced with the package SURFER (Golden software, Colorado, U.S.A.).

Evaluating spatial association

A measure of spatial association should have two desirable features: (i) be based on a clear comparison of the spatial properties of each set; and (ii) in these comparisons, take into account the spatial pattern of each of the individual sets (Perry and Dixon, 2002). To assess the spatial relationship between plant species, between soil properties, and between soil properties and vegetation, we compared the values of v using Pearson correlation coefficient. This approach satisfies (i) because units where both sets show a patch or a gap will contribute strongly and positively, and units where one set shows a patch and the other a gap will contribute strongly and negatively. However, units with small absolute values of the clustering index will contribute weakly to the correlation. It also satisfies (ii) because the spatial pattern has already been assessed in the formation of the index (Perry and Dixon, 2002). As values of v were non-normally distributed (Kolmogorov–Smirnov test, $P < 0.05$), significance of the correlation coefficient was determined using a permutation test, and the significance obtained with this test was later corrected for the presence of autocorrelation (Perry and Dixon, 2002; Winder et al., 2001). This was performed as follows. After calculation of correlation coefficient (r), a randomization distribution of r is formed from values of this measure derived from fully permuted sets of data, and 95% confidence intervals are obtained. Following that, the trend existing in the two original sets of v values is removed using trend surface analysis (Legendre and Legendre, 1998). This was achieved by replacing the original data of v by the residuals from ordinary least squares regression of v against the nine monomials resulting from a cubic combination of geographic coordinates centered on their means. These residuals are submitted to the Dutilleul (1993) adjustment procedure, and an effective sample size that takes into account the degree of autocorrelation in data is calculated. The confidence intervals obtained are then inflated by a scale factor of $[(M - 3)/(N - 3)]^{-1/2}$, where N and M are the original and the effective sample size, respectively, and the randomization tests adjusted accordingly (Perry and Dixon, 2002). Significance levels were also Bonferroni-corrected for the number of paired comparisons.

As the data for vegetation were collected with sampling units of different size and shape than those used for collecting soil properties data, we used estimates for v for the latter by using geostatistics. We

estimated the experimental omnidirectional semivariogram (γ) from the values of v for soil properties ($n = 294$). We used a lag interval of 2.9 m, which resulted in a minimum of 106 pairs at the shortest lag. We fitted the experimental semivariograms to spherical, pentaspherical, circular, exponential, and nested-spherical functions (Webster, 1985) following a weighted least-squares approximation (Cressie, 1985). We assigned weights according to the number of paired comparisons in the estimates, and selected the models with the smallest residual mean square (Webster and Oliver, 1990). Values between sampling points were interpolated using ordinary block kriging (Deutsch and Journel, 1998) with an elementary block size of 2.5×2.5 m, resulting in a square grid of 400 cells. Experimental semivariograms were computed with the Variowin 2.2 software (Pannatier, 1997), and the models were fitted using the MLP program (Ross, 1987). Kriging analyses were performed using the GSLIB software library (Deutsch and Journel, 1998). Correlation analyses were performed using 10 000 randomizations with the software described in Perry and Dixon (2002).

Results

S. tenacissima and *B. retusum* were widely distributed throughout the experimental plot, covering 16.5 and 17.4% of the total surface area, respectively (Figure 1). Both species showed a clumped pattern, as reflected by the significant values of all SADIE indices (Table 1). Maps of v showed the presence of complex spatial patterns in both species (Figure 2). *S. tenacissima* showed a clumped distribution throughout the plot, with a major degree of clustering in the middle of the plot. This species shows a general trend to form stripes of vegetated and bare patches in the NW–SE direction, as suggested by the presence of alternating patches and gaps in this direction. *B. retusum* also showed a strong degree of clustering throughout the plot. Despite not being so evident as in the former species, *B. retusum* showed a sequence of patches and gaps in the same direction as *S. tenacissima*. We found a negative relationship between the values of v for the two species ($r = -0.16$, $n = 400$, $P = 0.005$ after adjustment for autocorrelation) suggesting the presence of a negative association between them at the scale of this study.

SADIE analysis detected departures from randomness in the overall pattern of biological crusts, fine root accumulation, and below-ground stone content (Table 1). Both v_i and v_j were statistically significant in

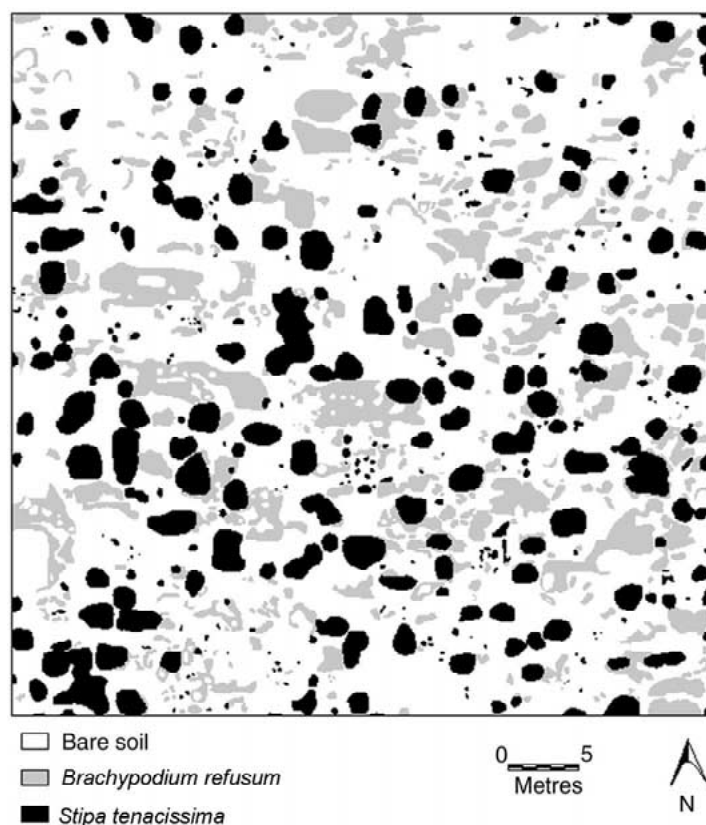


Figure 1. Distribution of *Stipa tenacissima* and *Brachypodium retusum* patches in the steppe studied.

these cases, indicating the presence of clustering into patches and gaps. The overall random pattern could not be rejected for mosses, and the associated probability value of v_i indicated the presence of clumped patches beyond what would be expected from random arrangements. Physical crusts showed a trend towards a regular distribution, as suggested by the small I_a and v_j absolute values, significantly below expectation in the last case. The distribution of earthworm casts and surface rock fragments did not significantly depart from randomness.

Semivariograms of v showed differences in the scale of patterning for the different soil properties (Figure 3). Patterns of mosses and earthworm casts showed two ranges of autocorrelation, suggesting that patches and gaps were autocorrelated at two spatial scales (Table 2). Physical crusts showed autocorrelation up to 5 m distances. All other variables were autocorrelated up to 17–36 m. These differences were clearly reflected in the contour maps, suggesting the presence of complex spatial distributions within the steppe (Figure 4). We observed an overall strong clus-

tering of biological crusts, fine root accumulation and below-ground stone content that was especially evident in the bottom of the plot. We observed some clustering in the distribution of physical crusts and mosses following NW to SE stripes. Surface rock fragments showed virtually no patches, with only a big gap close to the NW corner of the plot. Despite its overall spatial pattern was random, the distribution of earthworm casts also showed a certain degree of clustering in the NW corner of the plot.

Correlation analyses indicated the relationship between the spatial pattern of some soil properties (Table 3), and between soil properties and vegetation (Table 4). The spatial pattern of fine root accumulation showed a positive relationship with that of mosses, and a negative relationship with that of physical crusts. Spatial distribution of mosses was positively related with that of the biological crust, and showed a negative relationship with the spatial pattern of physical crusts. Earthworm casts distribution was negatively related with that of biological crusts. The remaining relationships were not statistically significant. Biological

Table 1. Summary of SADIE analysis of vegetation ($n=400$) and soil properties ($n=294$). P values derived from randomization tests statistics (5967 randomizations) are shown in brackets. I_a =index of aggregation, V_j =mean index of clustering for gaps, and V_i =mean index of clustering for patches

Variable	I_a	V_i	V_j
<i>Stipa tenacissima</i>	2.15 (<0.001)	2.04 (<0.001)	-1.93 (<0.001)
<i>Brachypodium retusum</i>	1.57 (0.001)	1.45 (0.008)	-1.51 (0.003)
Fine root accumulation	1.62 (0.003)	1.68 (<0.001)	-1.60 (0.002)
Mosses	1.25 (0.071)	1.34 (0.033)	-1.23 (0.086)
Earthworm casts	1.17 (0.126)	1.20 (0.095)	-1.14 (0.159)
Biological crusts	1.75 (<0.001)	1.85 (<0.001)	-1.74 (<0.001)
Below-ground stone content	1.57 (0.005)	1.62 (0.004)	-1.54 (0.006)
Surface rock fragments	0.89 (0.721)	0.89 (0.701)	-0.88 (0.712)
Physical crusts	0.82 (0.934)	0.81 (0.925)	-0.83 (0.959)

Table 2. Parameters of the models fitted to the semivariograms of index of clustering for soil properties. C_0 =nugget variance, C =still, a =range (m), SPD=spatial dependence or ratio of structural to population variance (%). In nested models, C_1 and C_2 indicates the still value for the short (A_1) and long (A_2) range structures, respectively. See footnotes for explanations of the various models and parameters

Variable	Model	C_0	C_1	C_2	a_1	a_2	SPD†
Fine root accumulation	Spherical††	2.59	4.04	-	25.79	-	36.05
Mosses	Nested spherical‡	0.46	1.78	2.09	4.94	35.34	81.96
Earthworm casts	Nested spherical	0.08	1.48	2.10	3.80	25.84	96.19
Biological crusts	Exponential‡‡	2.79	5.18	-	17.49	-	46.14
Below-ground stone content	Exponential	1.01	3.31	-	17.33	-	69.49
Surface rock fragments	Spherical	0.04	0.38	-	35.57	-	89.47
Physical crusts	Spherical	0.60	0.75	-	5.49	-	21.35

†The proportion of sample variance explained by the model, $[C/(C_0 + C)] * 100$.

††For $h \leq a$, $\gamma(h) = C_0 + C[(1.5(h/a)) - (0.5(h/a)^3)]$; $h > a$, $\gamma(h) = C$.

‡For $h \leq a_1$, $\gamma(h) = C_0 + C_1[(1.5(h/a_1)) + C_2(1.5(h/a_2) - (0.5(h/a_2)^3)]$; $a_1 < h \leq a_2$, $\gamma(h) = C_1 + C_2[(1.5(h/a_2)) - (0.5(h/a_2)^3)]$; $h > a_2$, $\gamma(h) = C_2$.

‡‡ $\gamma(h) = C_0 + C[1 - \exp(h/a)]$; the range for the experimental model is defined as the distance at which the variogram value of 95% of $(C - C_0)$.

Table 3. Correlation matrix showing the comparison of the index of clustering between different soil properties ($n=294$). Significance was assessed using a randomization test with 10 000 randomizations, and a correction for the degree of autocorrelation. See text for details. Fr=fine root accumulation, Ms=mosses, Ec=earthworm casts, Bc=biological crusts, Bs=below-ground stone content, Sr=surface rock fragments, and Pc=physical crusts

	Fr	Ms	Ec	Bc	Bs	Sr	Pc
Fr							
Ms	0.303*						
Ec	-0.090	0.067					
Bc	0.167	0.325*	-0.173				
Bs	0.060	0.037	-0.094	0.085			
Sr	0.205	0.085	-0.306*	0.122	0.090		
Pc	-0.321*	-0.401*	-0.085	-0.150	0.070	-0.067	

*Significant at the Bonferroni corrected level ($P < 0.0024$).

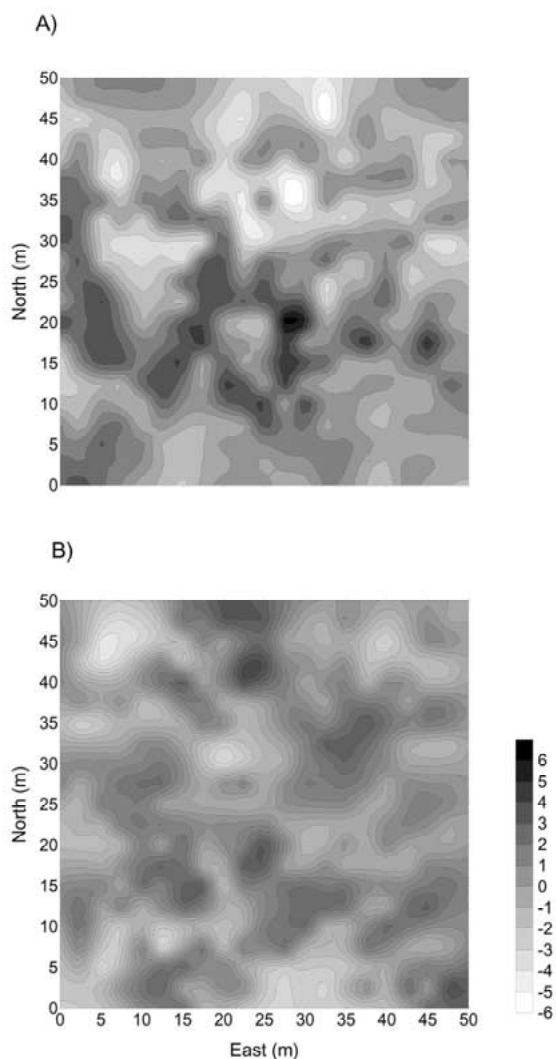


Figure 2. Maps of SADIE index of clustering for *Stipa tenacissima* (A) and *Brachypodium retusum* (B) across the steppe studied. Key scale of maps has no units. See text for details.

crusts, surface rock fragments and fine root accumulation were positively associated with the spatial pattern of *S. tenacissima*. The spatial pattern of physical crusts showed a negative relationship with this species. The distribution of mosses, biological crusts and below-ground stone content was negatively related with that of *B. retusum*.

Table 4. Correlation matrix showing the comparison of the index of clustering between kriged values of soil properties and vegetation ($n=400$). Fr=Fine root accumulation, Ms=mosses, Ec=earthworm casts, Bc=biological crusts, Bs=below-ground stone content, Sr=surface rock fragments, and Pc=physical crusts

	<i>Stipa tenacissima</i>	<i>Brachypodium retusum</i>
Fr	0.366*	-0.103
Ms	0.101	-0.186*
Ec	-0.151	0.089
Bc	0.196*	-0.191*
Bs	-0.102	-0.200*
Sr	0.201*	0.014
Pc	-0.175	0.075

*Significant at the Bonferroni corrected level ($P<0.0036$).

Discussion

Suitability of SADIE indices for soil surface properties

SADIE analysis successfully detected significant departures from randomness in both vegetation and soil surface properties. This technique is able to detect not only a general departure from randomness in the distribution of the data, but also the presence of gaps and patches, providing several indices that can be used to make formal statistical tests. In addition to these tests, maps of v reflect the two-dimensional location and extension of clusters in the data, providing additional information that can be used as a visual aid for interpretation (Diggle, 1983). The spatial relationship between soil properties and vegetation has been assessed using different approaches, such as geostatistics (Schlesinger et al., 1996), Mantel test (Daiyuan et al., 1998), and constrained ordinations (Rubio and Escudero, 2000). Both geostatistical methods and Mantel test approaches are designed for the analysis of variables measured in continuous scales that display a stationary covariance structure over a wide area (Legendre and Legendre, 1998), and its application to count data, data recorded in semi-quantitative scales, and data with a majority of zero values is often not appropriate (Perry et al., 1999). The use of ordination techniques is based on the assumption of linear or unimodal relationships between plant and soil distributions (Legendre and Legendre, 1998). In contrast, no assumptions in the distribution of data are required to SADIE, as results are specifically conditioned by the heterogeneity of the data set (Bell,

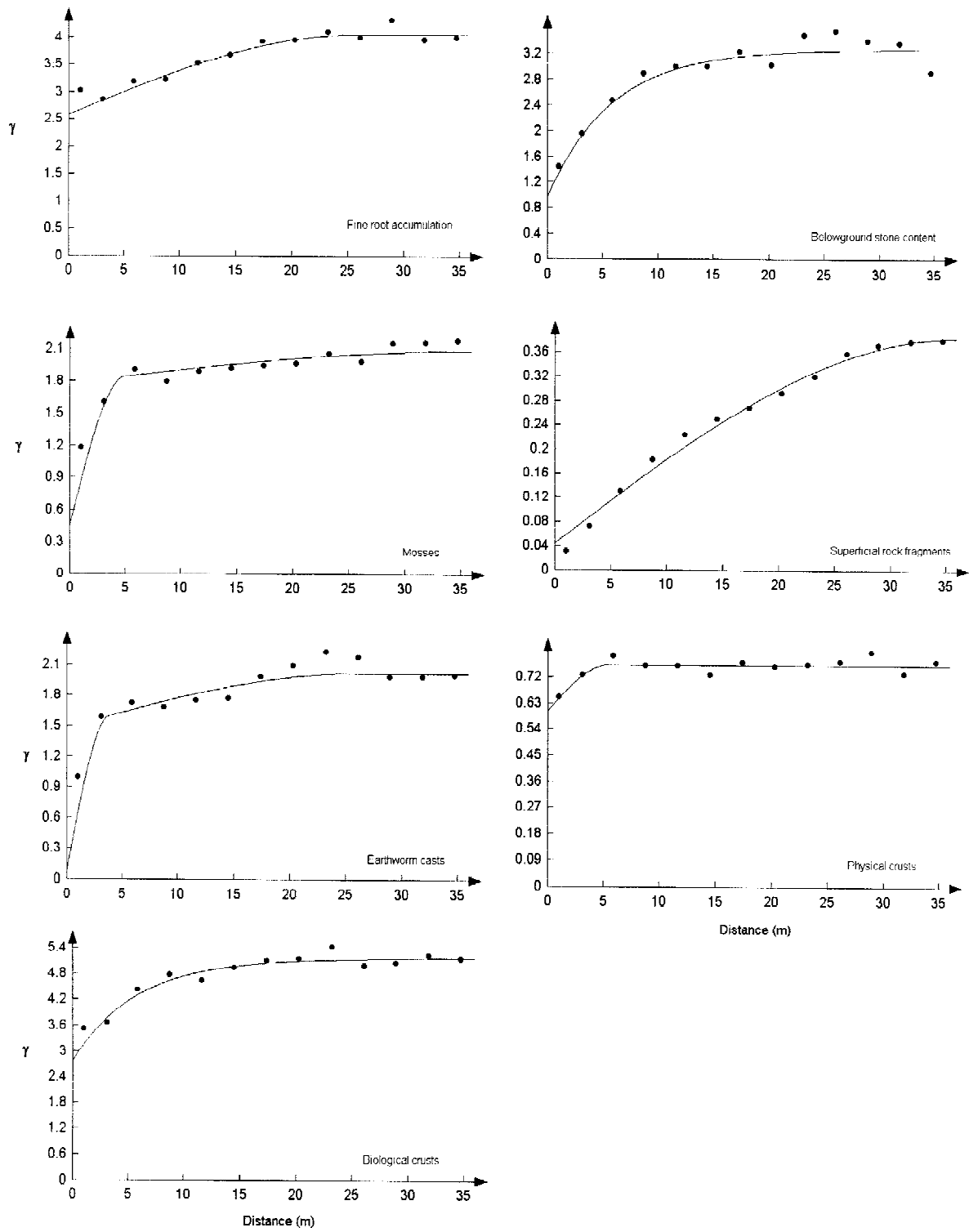


Figure 3. Semivariograms of SADIE index of clustering for soil properties in the steppe studied. γ =semivariance.

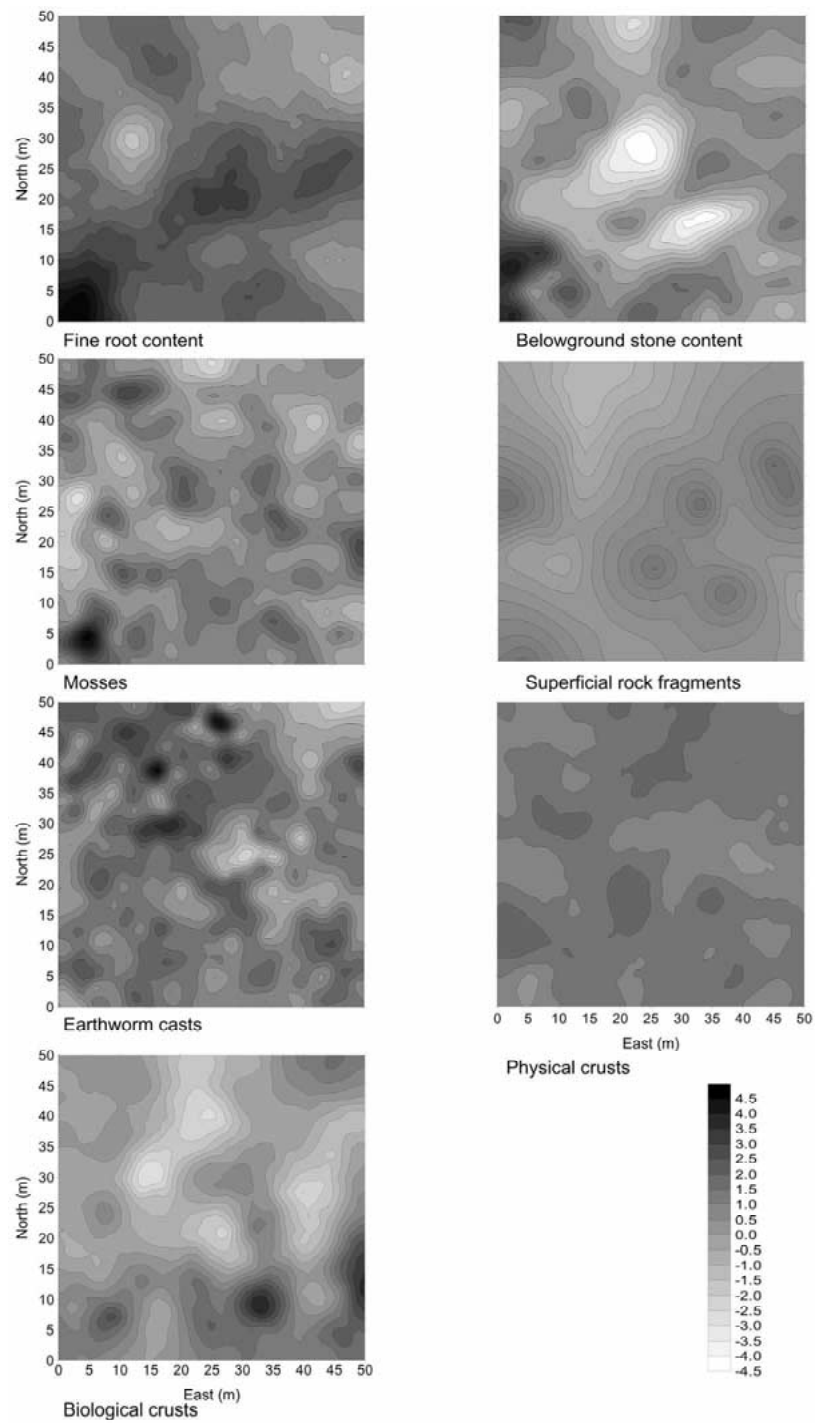


Figure 4. Maps of SADIE index of clustering for soil properties across the steppe studied. Key scale of maps has no units. See text for details.

1998). In addition, SADIE can handle count data, binary data, semi-quantitative data and continuous data if categorized previously (Perry et al., 1999).

The combination of SADIE analysis and geostatistics allowed us to compare the spatial pattern of data obtained with different sampling schemes. The use of kriged estimates for comparison purposes has not been extensively used. Stein et al. (1997) and Van Groeningen (1999) related yield crop variability resulting from kriged estimates with measured soil characteristics, while Ettema et al. (1998) used this approach to relate spatiotemporal distributions of nematodes to soil resources. The approach we follow in this study shows promise for the spatial analysis of soil biotic and abiotic data taken in the form of counts, binary and semi-quantitative scales.

Spatial patterns of vegetation

Steppe of *S. tenacissima* are often structured in a spotted or banded spatial configuration (Puigdefábregas and Sánchez, 1996) with patterns resembling those of the patterned or banded vegetation described for semi-arid regions throughout the world (Valentin et al., 1999). At the study site, the spatial pattern of vegetation showed a complex distribution of patches and gaps, suggesting the presence of a banded pattern in the NW–SE direction. This was confirmed by an analysis of anisotropy in the spatial distribution of v (data not shown), indicating that patches of *S. tenacissima* and *B. retusum* are greater in this direction. Despite the improvement of environmental conditions in the environment of the tussocks (Maestre et al., 2001), *S. tenacissima* showed a negative relationship with *B. retusum* at the scale of this study. This lack of spatial affinity could be related to the functional types of these species, as positive interactions associated with ‘fertile islands’ in semi-arid areas commonly involve two different functional types, such as shrubs and grasses (Callaway, 1995). It is also possible that the scale of the positive interactions defined by the fertile island around *S. tenacissima* tussocks may be smaller than the scale considered in this study. It is not uncommon to observe sparse *B. retusum* tillers beneath *S. tenacissima* tussocks (Maestre et al., unpublished data), a fact that was overlooked by the sampling scheme used in this study.

Spatial patterns of soil properties and their relationship with those of vegetation

Spatial distribution of surface rock fragments did not show any spatial structure. This may be due to the sampling scheme used, which failed to detect small-scale patterns within the study site. In contrast, below-ground stone content showed a patchy distribution. Higher values of stone content in the SW corner of the plot were probably associated with changes in bedrock composition (e.g. hard limestone layers). Spatial pattern of surface rock fragments was related to that of *S. tenacissima*, probably because tussocks of this species act as sediment and rock traps. SADIE analysis showed a negative relationship between physical crusts and *S. tenacissima* tussocks. This result was expected since the formation of physical crusts is favoured by the direct impact of raindrops (Morin and Winkel, 1996), and rainfall intensity and kinetic energy of raindrops can be reduced by more than 50% by the canopies of patchy semi-arid vegetation (Wainwright et al., 1999). The lack of a negative relationship with the spatial pattern of *B. retusum* may be related to the fact that the canopies of this grass were too sparse to avoid the formation of physical crusts. The negative relationship found between the spatial pattern of physical crusts and fine root accumulation suggest the presence of a positive association between physical crusts, gaps and root patches. It is possible that this relationship is mediated by higher water availability in areas where physical crusts are absent and infiltration is higher. Further manipulative experiments are needed to clarify the implications of physical crust distribution in root dynamics.

The spatial distribution of earthworm casts did not deviate from random, and was not related with that of *S. tenacissima* tussocks. This was rather surprising because tussock microsites should be preferentially selected by earthworms due to higher resource availability and buffered climatic conditions (Buck et al., 2000). In addition, earthworm casts deposited in open areas should be more easily disrupted by rainsplash and surface run-off (Binet and Le Bayon, 1999). SADIE revealed the absence of an overall clumped or regular pattern in the distribution of mosses, but the statistically significant V_i reflected the presence of patchiness. The lack of a significant relationship between its spatial distribution and *S. tenacissima* distribution was unexpected, due to the improvement of microclimatic conditions beneath the tussocks as compared with open areas (Maestre et al., 2001). This

result is in contrast with other studies that report a positive association between *S. tenacissima* tussocks and mosses at smaller scales (Maestre et al., 2001; Martínez-Sánchez et al., 1994).

We found a positive relationship between the spatial pattern of biological crusts and that of *S. tenacissima*, which suggests the presence of facilitation between *S. tenacissima* and these crusts. This is in agreement with other studies showing a positive relationship between vascular plant cover and that of biological crusts in semi-arid sites (Eldridge and Tozer, 1997). *S. tenacissima* forms high roughness tussocks that enhance sedimentation on slope, leading to the formation of small terraces (Bochet et al., 1999), and to local enrichment with organic debris (Puigdefábregas and Sánchez, 1996). This local modification of soil properties, together with an improvement of microclimate, may favour the formation of suitable microsites for the development of biological crusts. Our results agree with Martínez-Sánchez et al. (1994), who reported an increase in the number of species and cover of lichens under the canopy of *S. tenacissima* tussocks as compared to open areas in semi-arid sites of SE Spain. Biological crusts may affect the establishment (Zaady et al., 1997), survival (Eckert et al., 1986) and nutrient status (Belnap and Harper, 1995) of vascular plants. Thus, a positive interaction between biological crusts and *S. tenacissima* tussocks is likely to occur, but our study can not provide evidence for this. The importance of biological crusts for semi-arid ecosystem functioning (West, 1990), and their sensitivity to mechanical disturbances (Evans and Belnap, 1999) are strong reasons to recommend further research on the role of these crusts on soil and vegetation dynamics in *S. tenacissima* communities. Fine root accumulation presented a strong clumped pattern that was positively related to the spatial pattern of *S. tenacissima*. This is in agreement with other studies performed in SE Spain (Puigdefábregas and Sánchez, 1996). These authors observed that root accumulation was four- to five-fold higher beneath the tussocks than in open areas.

Conclusion

The lack of a clear spatial pattern of properties that have a strong influence on water and infiltration dynamics, such as physical crusts and surface rock fragments, may have strong implications in the hydrology of the site. It has been suggested that in degraded semi-arid areas, differential rainsplash, in-

filtration and water flow dynamics between vegetated and open areas lead to the formation of gravel-covered surfaces in the open areas (Abrahams et al., 1994). Surface rock fragments may promote run-off, soil and nutrient losses (Abrahams et al., 1994; Schlesinger et al., 1999), and these losses are important steps towards desertification (Schlesinger et al., 1990). The organic matter content of the study site ($46.3 \pm 5.0 \text{ mg g}^{-1}$ in tussock vs. $37.7 \pm 1.9 \text{ mg g}^{-1}$ in open areas, $\text{mean} \pm \text{SE}$, $n = 5$, Maestre et al., 2001) was relatively high as compared to other degraded soils under similar climatic conditions and on similar bedrock types (García and Hernández, 1996). This, together with the spatial patterns found, suggests that the soil in the *S. tenacissima* steppe is not as heavily degraded as could be expected from the patchiness in the distribution of above-ground biomass. Our study reveals the presence of complex spatial patterns in both soil properties and vegetation in the study site. The spatial patterns of surface soil properties were apparently related to the spatial distribution of *S. tenacissima* tussocks. These patterns could be crucial for the nutrient, hydrological and vegetation dynamics in these semi-arid ecosystems. Further research is needed to explore the ecological implications of these spatial arrangements and to incorporate these findings into the management of *S. tenacissima* steppe.

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References

- Abrahams A D, Parsons A J and Wainwright J 1994 Resistance to overland flow on semi-arid grassland and shrubland hillslopes Walnut Gulch, Southern Arizona. *J. Hydrol.* 156, 431–446.
- Aguiar M R and Sala O E 1999 Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends Ecol. Evol.* 14, 273–277.
- Bell E D 1998 Spatio-Temporal Dynamics of U.K. Moths. Ph.D., University of Leicester, Leicester, U.K.
- Belnap J and Harper K T 1995 Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. *Arid Soil Res. Rehab.* 9, 107–115.
- Binet F and Le Bayon R C 1999 Space-time dynamics *in situ* of earthworm casts under temperate cultivated soils. *Soil Biol. Biochem.* 31, 85–93.
- Bochet E, Rubio J L and Poesen J 1999 Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. *Catena* 38, 23–44.
- Buck C, Langmaack M and Schrader S 2000 Influence of mulch and soil compaction on earthworm cast properties. *Appl. Soil Ecol.* 14, 223–229.
- Callaway R M 1996 Positive interactions among plants. *Bot. Rev.* 61, 306–349.
- Casper B B and Jackson R B 1997 Plant competition underground. *Ann. Rev. Ecol. Syst.* 28, 545–570.
- Cerdà A 1997 The effect of patchy distribution of *Stipa tenacissima* L. on run-off and erosion. *J. Arid Environ.* 36, 37–51.
- Cressie N E 1985 Fitting variogram models by weighted least squares. *Math. Geol.* 17, 563–586.
- Daiyuan P, Bouchard A, Legendre P and Gérald D 1998 Influence of edaphic factors on the spatial structure of inland halophytic communities: a case study in China. *J. Veg. Sci.* 9, 797–804.
- Deutsch C V and Journel A G 1998 *GSLIB. Geostatistical Software Library and User's Guide*. Oxford University Press, New York, U.S.A. 369 pp.
- Diggle P J 1983 *Statistical Analysis of Spatial Point Patterns*. Academic Press, London, U.K. 127 pp.
- Dutilleul P 1993 Modifying the t test for assessing the correlation between two spatial processes. *Biometrics* 49, 305–314.
- Eastman J R 1997 *Idrisi for Windows User's Guide, Version 2.0*. Clark University, Worcester, Canada. 331 p.
- Eckert R E, Peterson E F, Meurisse M S and Stephens J L 1986 Effects of soil–surface morphology on emergence and survival of seedlings in big sagebrush communities. *J. Range Manage.* 39, 414–420.
- Eldridge D J 1999 Distribution and floristics of moss- and lichen-dominated soil crusts in a patterned *Callitris glaucophylla* woodland in eastern Australia. *Acta Oecol.* 20, 159–170.
- Eldridge D J and Tozer M E 1997 Environmental factors relating to the distribution of terricolous bryophytes and lichens in semi-arid eastern Australia. *Bryologist* 100, 28–39.
- Ettema C H, Coleman D C, Vellidis G, Lowrance R and Rathbun S L 1998 Spatiotemporal distribution of bacterivorous nematodes and soil resources in a restored riparian wetland. *Ecology* 79, 2721–2734.
- Evans R D and Belnap J 1999 Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology* 80, 150–160.
- García C and Hernández T 1996 Organic matter in bare soils of the Mediterranean region with semi-arid climate. *Arid Soil Res. Rehab.* 10, 31–41.
- Halvorson J J, Smith J L, Bolton H, Rossi R E 1995 Evaluating shrub-associated spatial patterns of soil properties in a shrub-steppe ecosystem using multiple-variable geostatistics. *Soil Sci. Soc. Am. J.* 59, 1476–1487.
- Jackson R B and Caldwell M M 1993 Geostatistical patterns of soil heterogeneity around individual perennial plants. *J. Ecol.* 81, 683–692.
- Jaén G, 1996 *Índices Bioclimáticos de la Provincia de Alicante*. Herbario de Jaén, Spain. 116 pp.
- Kennington J L and Helgason R V 1980 *Algorithms for Network Programming*. John Wiley & Sons Ltd., New York, U.S.A.
- Legendre P and Legendre L 1998 *Numerical Ecology*. Second English Edition. Elsevier Publishers, Amsterdam, The Netherlands. 853 pp.
- Le Houérou H N 1986 The desert and arid zones of Northern Africa. *In The Ecosystems of the World. Hot Deserts and Arid Shrublands*, Vol. 12 B. Ed. M Evenari, I Noy-Meir and D W Goodall. pp 104–147. Elsevier Science, Amsterdam.
- Maestre F T, Bautista S, Cortina J and Bellot J 2001 Potential of using facilitation by grasses to establish shrubs on a semi-arid degraded steppe. *Ecol. Appl.* 11, 1641–1655.
- Malam Issa O, Trichet J, Défarge C, Couté A and Valentin C 1999 Morphology and microstructure of microbiotic soil crusts on a tiger bush sequence (Niger, Sahel). *Catena* 37, 175–196.
- Martínez-Sánchez J J, Casares-Porcel M, Guerra J, Gutiérrez-Carretero L, Ros R M, Hernández-Bastida J and Cano M J 1994 A special habitat for bryophytes and biological crusts in the arid zones of Spain. *Lindbergia* 19, 116–121.
- Morin J and Winkel J V 1996 The effect of raindrop impact and sheet erosion on infiltration rate and crust formation. *Soil Sci. Soc. Am. J.* 60, 1223–1227.
- Pannatier Y 1997 *Variowin Software for Spatial Data Analysis in 2D*. Springer Verlag, New York, U.S.A. 104 pp.
- Perry J N 1995 Spatial aspects of animal and plant distribution in patchy farmland habitats. *In Ecology and Integrated Farming Systems*. Ed. D M Glen, M P Greaves and H M Anderson. pp 221–242. John Wiley & Sons Ltd., Bristol.
- Perry J N 1998 Measures of spatial pattern for counts. *Ecology* 79, 1008–1017.
- Perry J N, Bell E D, Smith R H and Woiwod I P 1996 SADIE: software to measure and model spatial pattern. *Aspects Appl. Biol.* 46, 95–102.
- Perry J N and Dixon P 2002 A new method to measure spatial association for ecological count data. *Ecoscience* (in press).
- Perry J N, Winder L, Holland J M and Alston R D 1999 Red–blue plots for detecting clusters in count data. *Ecol. Lett.* 2, 106–113.
- Poesen J, Lavee H 1994 Rock fragments in top soils: significance and processes. *Catena* 23, 1–28.
- Puigdefábregas J and Sánchez G 1996 Geomorphological implications of vegetation patchiness on semi-arid slopes. *In Advances in Hillslope Processes*, Vol. 2. Ed. M G Anderson and S M Brooks. pp 1027–1060. John Wiley & Sons Ltd., London.
- Robertson G P and Freckman D W 1995 The spatial distribution of nematode trophic groups across a cultivated ecosystem. *Ecology* 76, 1425–1432.
- Ross G J S 1987 *Maximum Likelihood Program*. Numerical Algorithms Group, Oxford, U.K.
- Rubio A and Escudero A 2000 Small-scale spatial soil–plant relationship in semi-arid gypsum environments. *Plant Soil* 220, 139–150.
- Schlesinger W H, Raikes J A, Hartley A E and Cross A F 1996 On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77, 364–374.
- Schlesinger W H, Reynolds J F, Cunningham G L, Huenneke L F, Jarrell W M, Virginia R A and Whitford W G 1990 Biological feedbacks in global desertification. *Science* 247, 1043–1048.

- Schlesinger W H, Abrahams A D, Parsons A J and Wainwright J 1999 Nutrient losses in run-off from grassland and shrubland habitats in Southern New Mexico: I. rainfall simulation experiments. *Biogeochemistry* 45, 21–34.
- Seghieri J, Galle S, Rajot J L and Ehrmann M 1997 Relationships between soil moisture and growth of herbaceous plants in a natural vegetation mosaic in Niger. *J. Arid Environ.* 36, 87–102.
- Soil Survey Staff 1994 Keys to Soil Taxonomy, Sixth Edition. USDA Soil Conservation Service, Pocahontas Press, Blacksburg, U.S.A. 524 pp.
- Stein A, Brouwer J and Bouma J 1997 Methods for comparing spatial variability patterns of millet yield and soil data. *Soil Sci. Soc. Am. J.* 61, 861–870.
- Turecheck W W and Madden L V 1999 Spatial pattern of strawberry leaf blight in perennial production systems. *Phytopathology* 89, 421–433.
- Valentin C, d'Herbès J M and Poesen J 1999 Soil and water components of banded vegetation pattern. *Catena* 37, 1–24.
- Van Groeningen J W 1999 Constrained optimisation of spatial sampling. A geostatistical approach. ITC Publication Series, Enschede, The Netherlands. 143 pp. Wainwright J, Parsons A J and Abrahams A D 1999 Rainfall energy under creosotebush. *J. Arid Environ.* 43, 111–120.
- Webster R 1985 Quantitative spatial analysis of soil in the field. *Adv. Soil Sci.* 3, 1–70.
- Webster R and Oliver M A 1990 *Statistical Methods for Land Resource Survey*. Oxford University Press, Oxford. 316 pp.
- West N E 1990 Structure and function of mycophytic soil crusts in wildland ecosystems of arid to semi-arid regions. *Adv. Ecol. Res.* 20, 179–223.
- White J G, Welch R M and Norvell W A 1997 Soil zinc map of the U.S.A. using Geostatistics and Geographic Information Systems. *Soil Sci. Soc. Am. J.* 61, 185–194.
- Winder L, Alexander C, Holland J M, Woolley and Perry J N 2001 Modelling the dynamic spatio-temporal response of predators to transient prey patches in the field. *Ecol. Lett.* 4, 568–576.
- Zaady E, Gutterman Y and Boeken B 1997 The germination of mucilaginous seeds of *Plantago coronopus*, *Reboudia pinnata* and *Carrichtera annua* on cyanobacterial soil crust from the Negev Desert. *Plant Soil* 190, 247–252.

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