Does spatial pattern matter to ecosystem functioning? Insights from biological soil crusts

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Summary

1. Theoretical and modelling studies highlight the importance of the spatial patterns
of organisms for ecosystem functioning, stability and dynamics. However, there is little
empirical evidence as to their importance as drivers of such ecosystem attributes.

2. We evaluated the relationships between different biological soil crust attributes
(spatial pattern, cover and diversity) and ecosystem functioning in two semiarid areas
differing in the developmental stage of these crusts.

3. We found a significant direct relationship between spatial pattern and both soil bulk
density and respiration (surrogates of ecosystem infiltration and nutrient cycling,
respectively) at one of our study sites. However, the strength of such a relationship was
lower than that found between attributes such as cover and evenness and the same
ecosystem functioning surrogates.

4. Our results represent, to our knowledge, some of the first empirical evidence linking
the spatial pattern of a community and ecosystem functioning. They also suggest that
the importance of spatial pattern as a driver of ecosystem functioning may depend on
community attributes such as cover and diversity, and that its importance may be lower
than that of these attributes.

Key-words: community attributes, lichens, mosses, heterogeneity

Introduction

Ecologists have long been interested in understanding
how the structure and composition of communities affect
ecosystem processes, functioning and stability (Pimm
1984). A large set of experimental, observational and
modelling studies have shown that attributes such as
the number, relative abundance and identity of species
forming a community have the potential to influence
these ecosystem features (Jones & Lawton 1995; Grime
2001; Loreau, Naeem & Inchausti 2002). Studies con-
ducted so far on this topic have, however, typically focused
on evaluating the effect of a single community attribute
(e.g. species richness) on a given ecosystem feature (e.g.
productivity). Thus little is known about the relative
importance of different co-occurring community attributes
as drivers of ecosystem functioning and stability (Tilman
2001).

Among the community attributes that may be relevant
when explaining observed patterns in ecosystem
functioning and stability, spatial pattern merits special
attention. The presence of non-random patterns in the
spatial distribution of plants, animals and soil organ-
isms is the norm, rather than the exception, in most
ecosystems (Webster & Boag 1992; Perry 1995; Dale
1999). Theoretical and modelling studies highlight the
importance of these patterns for ecosystem functioning,
stability and dynamics (Pacala & Deutschman 1995;
Tilman & Kareiva 1997; Bolker, Pacala & Neuhauser
2003). There is also a growing set of empirical studies
showing that the spatial pattern of organisms alters
phenomena such as population dynamics, species coexis-
tence and community structure (Bergelson 1990; Stoll
& Prati 2001; Tirado & Pugnaire 2003). However, few
studies have evaluated how changes in the spatial
patterns of a community *per se* (independently of other
co-occurring community attributes) are directly related
to ecosystem functioning. Furthermore, to our knowledge
none of the studies on this topic have been conducted

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with organisms other than vascular plants and bacteria (Bolker, Pacala & Neuhauser 2003).

We evaluated the relationships between the spatial pattern of a community and ecosystem functioning using biological soil crusts as a model system. These crusts, composed of eukaryotic algae, cyanobacteria, mosses, liverworts, fungi and lichens, cover the first millimetre of the soil surface in arid and semiarid ecosystems throughout the globe, and are one of the most important biotic components of these areas (West 1990). They exert a great influence on ecosystem functioning by affecting soil nutrient cycling, stability and infiltration; by influencing the establishment and performance of vascular plants; and by serving as habitats for a large number of arthropods and microorganisms (West 1990; Eldridge & Greene 1994; Belnap & Lange 2001). Despite important advances in our knowledge of the structure, composition, physiology and biogeography of biological soil crusts (reviewed by Belnap & Lange 2001), little is known of the effects of small-scale habitat variation on the spatial patterns of their components, and of the influence of these patterns on ecosystem processes (Maestre 2003).

The objectives of this study were twofold: (i) to evaluate the relationship between the spatial pattern of biological crusts and ecosystem functioning; and (ii) to assess the relative importance of these patterns against other community attributes that are likely to play an important role in ecosystem functioning. To achieve these objectives, we quantified the spatial pattern, cover and diversity (species richness and evenness) of biological soil crusts in two semiarid areas, and related them to different surrogates of ecosystem functioning using structural equation modelling. Due to the importance and ubiquity of these crusts, increasing our knowledge on the relationships between their spatial patterns and ecosystem functioning will probably lead to improved understanding on the functioning of arid and semiarid environments. More generally, it may be an important contribution to 'spatial theory', i.e. the importance of spatial patterns in ecological phenomena (Tilman & Kareiva 1997).

Methods

STUDY SITES

Two sites sharing soil characteristics, but differing in their disturbance history and in the developmental stage of their biological soil crusts, were selected for this study. The first site, named El Plano, is located close to Sax (38°32′ N, 0°49′ W, 500 m a.s.l.) in the province of Alicante (south-east Spain). The second site, named Belinchón, is located near to Tarancón (40°30′ N, 3°1′ W, 710 m a.s.l.) in the province of Cuenca (central Spain). The climate is Mediterranean semiarid at the El Plano site, with a mean annual temperature and rainfall of 17 °C and 315 mm, respectively; and Mediterranean dry in the Belinchón site, with a mean

annual temperature and rainfall of 14 °C and 525 mm, respectively. The soil in both cases is a Typic Gypsiorthid (Soil Survey Staff 1994). Natural perennial plant cover is very low at both sites, below 30%, and is dominated by specialized gypsophytes including *Helianthemum squamatum* (L.) Dum.-Cours. and *Herniaria fruticosa* L. The El Plano site also has a very open tree layer of pines (*Pinus halepensis* Miller) coming from a uniform plantation initiated 60 years ago. After the plantation, no further major anthropogenic perturbances occurred at this site. The Belinchón site presents evidence of recent grazing and trampling by sheep.

FIELD SURVEY

In each of the two study sites, 100 30 × 30 cm quadrats were placed on bare ground located in the spaces between plants. In order to minimize the variability associated with small-scale differences in topography, these quadrats were placed non-randomly in flat areas with well developed biological soil crusts. However, a minimum separation distance between quadrats of 1·5 m was established to minimize the risk of sampling non-independent areas due to the spatial structure of both biological soil crusts and the surrogates of ecosystem functioning evaluated (see below). The visible components of biological crusts (lichens and mosses) were sampled at the two sites between August and September 2003 by point sampling (2·5 × 2·5 cm grid; 169 points per 30 × 30 cm quadrat). At each quadrat, total cover was estimated as the proportion of the 169 points occupied by mosses and lichens. This survey was also used to estimate species richness and evenness, calculated as the number of moss and lichen species identified within the grid, and as the ratio of observed to maximum diversity (Magurran 1988). To estimate the spatial pattern of the biological crust community (see below), the spatial co-ordinates (x, y) and the presence/absence of lichen and mosses in each point of the sampling grid were used as raw data. Thus the spatial resolution and the size of area sampled were 2·5 and 30 cm, respectively.

SPATIAL PATTERN ANALYSIS

Spatial pattern analyses were conducted using the spatial analysis by distance indices (SADIE) methodology (Perry *et al.* 1999). SADIE is based on the distance to regularity (D), which measures the total distance in the space that the variable under study (presence/absence of mosses and lichens) would need to move to achieve an arrangement where all the sampling points in a quadrat have the same value (see Appendix S1 in Supplementary Material). Division of D by the average value obtained from permutations where the values of the variable under study are randomly arranged among the sampling locations gives an index of aggregation, I_a, which quantifies the spatial pattern. An aggregated sample has an $I_a > 1$; a random sample has an $I_a = 1$; and a regularly distributed sample has an $I_a < 1$. The higher the I_a, the more
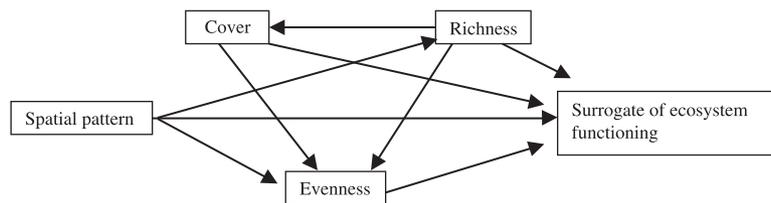
Fig. 1. Hypothetical structural model showing the postulated relationships between biological soil crust attributes and the surrogates of ecosystem functioning. The same model was used for all surrogates evaluated (aggregate stability, total nitrogen, total carbon, soil respiration).

ASSESSMENT OF ECOSYSTEM FUNCTIONING

At both study sites, the following soil variables were measured as surrogates of ecosystem functioning: respiration, total organic carbon and total nitrogen content, bulk density and aggregate stability. These variables act as surrogates of processes such as resistance against erosive forces (aggregate stability), infiltration (bulk density), biological activity and nutrient cycling (respiration, C and N content), which are crucial for the functioning of semiarid ecosystems (Whitford 2002).

Soil sampling was conducted in September 2003, when the soil was dry after a pronounced summer drought. Twelve randomly placed 19.63 cm^2 circular soil cores (5 cm diameter × 1 cm depth) were sampled in each of the 100 quadrats, bulked and homogenized in the field. Prior to sampling, the first 1 mm of the soil surface was removed with a knife. Samples were air-dried for 2 months in the laboratory and weighed after that period. The samples were then sieved through 2 mm mesh, and the two resulting fractions were weighed. The moisture contents of the air-dried samples were gravimetrically assessed, but samples were dried at temperatures below 50 °C to avoid the loss of water molecules from gypsum, which is a hydrous compound (Porta 1998). Soil respiration rates were determined by NaOH absorption followed by titration with HCl (Froment 1972). Total organic C and total N were determined on finely powdered aliquots of the samples by dry combustion followed by gas chromatography using a CN elemental analyser (EuroEA3000, Eurovector, Milan, Italy) after carbonates of these aliquots were removed with diluted HCl. Aggregate stability was assessed on $0.25-2$ mm aggregates by the method of Lax *et al.* (1994).

STATISTICAL ANALYSES

The relationships between the community attributes and the surrogates of ecosystem functioning were evaluated by using structural equation modelling (SEM). Details of this statistical approach can be found

elsewhere (Bollen 1989; Mitchell 1992; Shipley 2000; Iriondo, Albert & Escudero 2003), and only a brief description is given here. In brief, a SEM analysis comprises three main steps: (i) model specification; (ii) parameter estimation; (iii) model testing. Step (i) involves postulating a working model, which represents a hypothesis about essential causal mechanisms among a set of variables as a path diagram. In this diagram, arrows indicate putative causal relationships among the variables. The initial hypothesis used in this study (Fig. 1) predicts that ecosystem functioning depends on both direct and indirect relationships among the community attributes. The relative effect of a variable on another, indicated by an arrow (or path) in the path diagram, is evaluated through standardized path coefficients, which are equivalent to standardized partial regression coefficients. Step (ii) estimates these coefficients by optimally adjusting the observed variance–covariance matrix to the path diagram. As recommended for our sample size ($n = 100$), the maximum likelihood method was used to estimate the standardized path coefficients in our model (see Shipley 2000 for a detailed explanation of how this estimation is conducted). The significance of these coefficients was assessed using multivariate Wald tests (Bentler 1989). Step (iii) tests statistically whether the initial hypothesis fits the data. This is accomplished with a goodness-of-fit (GFI) test that compares the covariance in the observed data with that expected if the working model is true. The test statistic is asymptotically distributed as a χ^2. A non-significant value indicates that the pattern of covariance predicted by the hypothesis is not distinguishable from that observed (Iriondo, Albert & Escudero 2003). In this study, the Bentler and Bonett's normed-fit index (NFI) and the GFI were used here as additional measures of the goodness of fit of the working model (Iriondo, Albert & Escudero 2003). SEM analyses were conducted separately for each site and surrogate of ecosystem functioning. Variance inflation factors (Petraitis, Dunham & Niewiarowski 1996) were in all cases <10, suggesting the absence of collinearity (Iriondo, Albert & Escudero 2003). All SEM analyses were performed with the CALIS procedure of SAS (SAS Institute, Cary, NC, USA).

Results

The proportion of the different mosses and lichens forming biological soil crusts differed substantially

Table 1. Summary statistics of biological soil crust attributes and surrogates of ecosystem functioning evaluated

	Study site	
Variable	El Plano	Belinchón
Cover (%)	65·32 ± 1·78	79·54 ± 1·14
	(9·03 − 94·44)	(39·05 − 98·22)
Species richness	5·39 ± 0·13	6·71 ± 0·15
(number of moss and lichen species)	(2 − 8)	(4 − 11)
Species evenness (no units)	0·65 ± 0·01	0·69 ± 0·01
	(0·24 − 0·92)	(0·36 − 0·90)
Spatial pattern (SADIE's I_a, no units)	1·40 ± 0·03	1·64 ± 0·04
	(0·85 − 2·48)	(0·89 − 2·96)
Bulk density (g cm^{-3})	1·01 ± 0·01	0·91 ± 0·01
	(0·77 − 1·33)	(0·77 − 1·15)
Respiration (mg C-CO$_2$ kg^{-1} h^{-1})	5·51 ± 0·24	3·46 ± 0·11
	(1·07 − 16·99)	(1·08 − 6·63)
Total organic carbon (%)	1·83 ± 0·07	1·38 ± 0·03
	(0·47 − 4·04)	(0·54 − 2·34)
Total nitrogen (%)	0·14 ± 0·004	0·15 ± 0·004
	(0·05 − 0·32)	(0·03 − 0·25)
Aggregate stability (%)	72·28 ± 0·63	55·92 ± 1·15
	(56·01 − 86·72)	(32·47 − 82·25)

In all cases $n = 100$. Data are mean ± SE; range in parentheses.

between the study sites (Appendix S2). The cover of mosses was much higher in the El Plano site, as was the cover of N-fixing lichens of the genus *Collema*. Higher values of total cover and species richness, and of SADIE's I_a, were found in the Belinchón site (Table 1). Important differences were also found in the surrogates of ecosystem functioning measured; excepting total N, all the surrogates of ecosystem functioning evaluated showed higher values in the El Plano site (Table 1).

The hypothetical model created was satisfactorily fitted to our data, as suggested by non-significant χ^2 values ($P > 0.39$ in all cases) and by values of NFI and GFI higher than 0·98 and 0·99, respectively (data not shown). However, the relationships between the different biological soil crust attributes and the surrogates of ecosystem functioning differed between the two study sites. In the El Plano site (Fig. 2), species richness was not directly related to any of these surrogates, but indirectly influenced both bulk density and soil respiration via its influence on total cover. Spatial pattern was positively related to respiration, and negatively related to soil bulk density. Total cover had a direct positive and negative relationship with respiration and bulk density, respectively, and an indirect relationship to total organic C and N via its influence on species evenness. The latter was positively related to bulk density, and negatively related to respiration, total organic C and N. The picture obtained at the Belinchón site was quite different (Fig. 3). Spatial pattern and evenness were not significantly related to any of the surrogates of ecosystem functioning evaluated. Species richness was positively related to aggregate stability, and negatively related to soil organic C, total N and respiration. Total cover was positively related

to soil respiration, but showed no significant relationships with the other surrogates of ecosystem functioning evaluated.

Discussion

The results obtained in the El Plano site represent, to our knowledge, some of the first empirical evidence for a direct relationship between the spatial pattern of a community and surrogates of ecosystem functioning. Previous modelling studies have shown that spatial pattern may be crucial for ecosystem functioning. Pacala & Deutschman (1995) found that the spatial pattern of trees in hardwood forests affected the ecosystem's ability to fix atmospheric CO$_2$. Simioni, Gignoux & Le Roux (2003) demonstrated that the spatial structure of the tree layer influenced both net primary production and water fluxes in a savanna ecosystem. Guo, Gan & Li (2003) found that changes in the spatial pattern of tree patches led to changes in the ecosystem's capacity to retain water in a forest. A large set of field studies conducted in arid and semiarid areas have also demonstrated that the spatial patterns of vegetation influence ecosystem functioning through the formation of 'resource islands' underneath the canopy of plant patches (Whitford 2002). However, the relative importance of spatial pattern against other co-occurring community attributes as a driver of ecosystem functioning in these ecosystems is largely unknown. Our results add new empirical evidence on the importance of the spatial pattern of a community as a driver of ecosystem functioning. They also suggest that this importance may depend on co-occurring community attributes such as total cover and diversity, and that it can be lower than that of those attributes. The mechanisms underlying the relationships found between the spatial pattern of the biological soil crusts and the surrogates of ecosystem functioning cannot be elucidated from our study, and there is also little available evidence on which to build plausible hypotheses to explain them. Further studies are needed to advance our understanding of such relationships.

We found a positive relationship between total cover and soil respiration at both study sites. As much of the C fixed by biological crust organisms is released into the soil (Lewin 1956), augmenting the cover of biological crusts would increase this release and stimulate microbial activity, which is often C-limited in arid and semiarid environments (Gallardo & Schlesinger 1992). However, cover was not related to total soil organic C content in any of the study sites, and only negative relationships between soil respiration and both species richness and evenness were found. These results suggest that species-specific effects on soil organic C content and quality and on microbial populations, rather than total C inputs, could be driving soil respiration in the ecosystem studied. At larger spatial scales than those studied here, it has been shown that shifts in the composition and relative abundance of biological crust
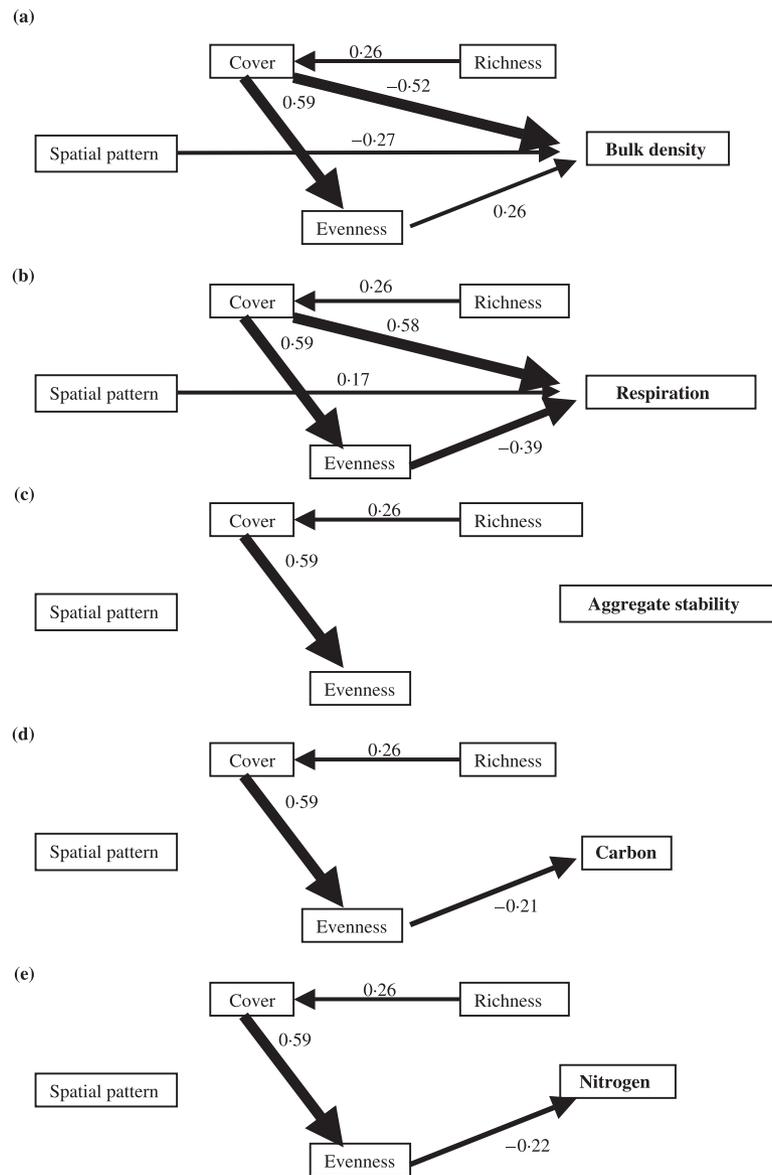
Fig. 2. Results of structural equation modelling for data obtained from the El Plano site. (a) Bulk density; (b) respiration; (c) aggregate stability; (d) total organic carbon; (e) total nitrogen. Only significant paths are shown. The breadth of the arrow is proportional to the standardized path coefficient, which is indicated by the corresponding number.

components such as mosses and lichens lead to substantial changes in soil respiration rates within a given ecosystem (Zaady *et al.* 2000).

Species richness and evenness were directly and negatively related to total N content at the Belinchón and El Plano sites, respectively. These relationships suggest that differences in the composition of mosses and lichens are in some way driving N inputs into the studied system. The cover of the N-fixing lichen *Collema crispum* was not related to N content in any of the sites (data not shown), however, suggesting that N fixation by this species may not be the main input source of N in the system. We speculate that other biological crust constituents that are able to fix N, such as free-living bacteria and cyanobacteria, are the main N inputs in the study system (Zaady *et al.* 1998). Cyanobacteria and free-living bacteria commonly grow epiphytically

on soil mosses and lichens (Belnap & Lange 2001), and their abundance and activity patterns are often linked to particular moss and lichen species (Redfield *et al.* 2002; Hu *et al.* 2003). If this is happening in our study sites, changes in moss and lichen richness and evenness could influence N inputs into the soil.

The lack of a significant relationship between total cover and soil aggregate stability was unexpected because the anchoring structures of mosses and lichens appear likely to contribute to the internal structure and stability of the upper centimetre of soil (Belnap & Lange 2001). However, in the carbonate-rich soils of our study areas, soil particles were perhaps aggregated instead by carbonate concretions (Kemper & Rosenau 1986). Additionally, unmeasured variation in filamentous cyanobacteria, which are likely to be ubiquitous in our study sites (Belnap & Lange 2001), may also have
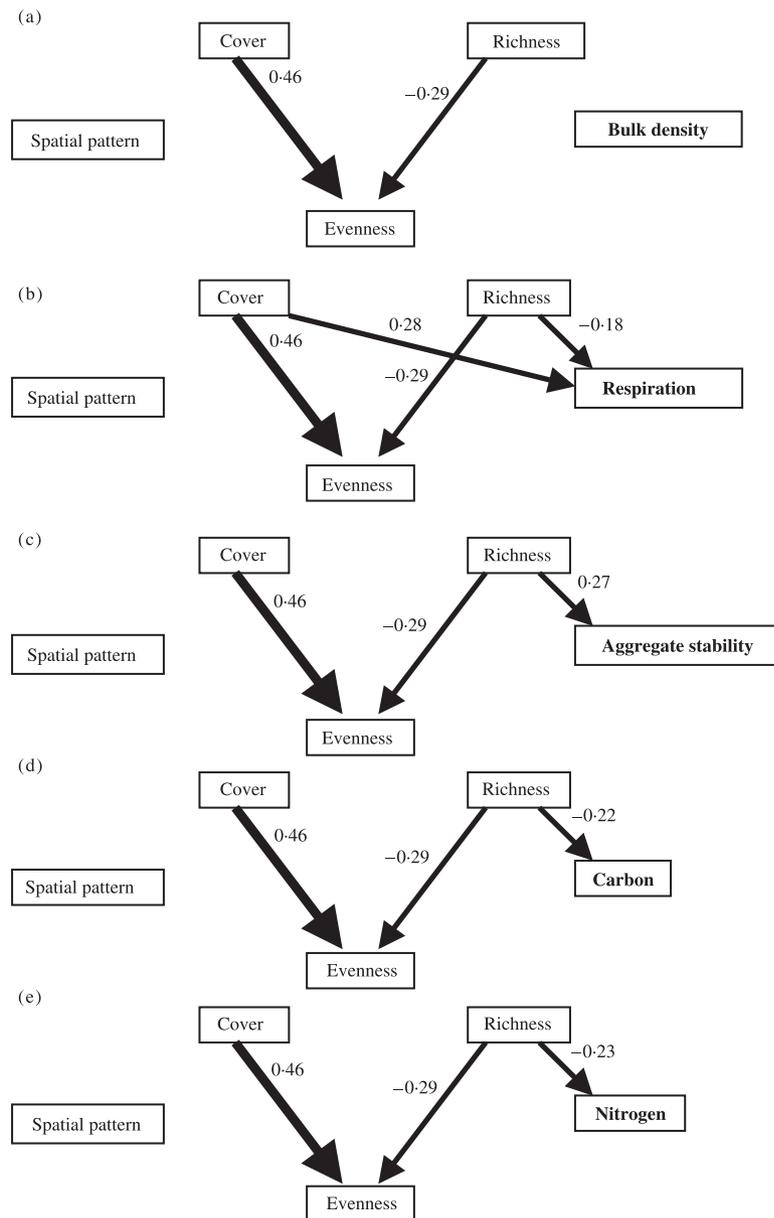
Fig. 3. Results of structural equation modelling for data obtained from the Belinchón site. (a) Bulk density; (b) respiration; (c) aggregate stability; (d) total organic carbon; (e) total nitrogen. Only significant paths are shown. The breadth of the arrow is proportional to the standardized path coefficient, which is indicated by the corresponding number.

influenced soil stability (Belnap & Lange 2001). We speculate that the positive relationship between species richness and aggregate stability found at the Belinchón site may have been caused by shifts in the abundance and activity of cyanobacteria associated with mosses and lichens (Redfield *et al.* 2002; Hu *et al.* 2003).

Our observational approach has limitations. We can only postulate that the variation in the surrogates of ecosystem functioning measured was caused by biological soil crust attributes. We did, however, attempt to eliminate the potential, confounding influence of spatial heterogeneity in the distribution of soil properties (Rubio & Escudero 2000) by selecting our sampling quadrats in a non-random way, and by measuring a large number of them. Additionally, we sampled only the first centimetre of the soil surface, where soil

processes are strongly influenced by biological crusts (Whitford 1996). It is also possible that the spatial patterns of microorganisms such as bacteria and fungi may have caused our results. However, these patterns are controlled by variables including soil moisture, temperature and organic matter content (Parkin 1987; Ronn *et al.* 1996; Nunan *et al.* 2002), all of which are strongly influenced by the composition and abundance of biological soil crusts (Whitford 1996; Belnap & Lange 2001).

Eventually, observations should be reinforced by experimental studies, although manipulating biological soil crusts in the field would require considerable time and effort. Nevertheless, and despite its limitations, our study has presented empirical evidence that the spatial pattern of a biological soil crust community

may influence ecosystem functioning at small spatial scales, and provides valuable insights about its relative importance against other co-occurring community attributes.

Acknowledgements

Supplementary material

The following supplementary material is available for this article online:

Appendix S1. Description of the calculation of SADIE's index of aggregation (I_a).

Fig. S1. Graphical representation of how SADIE estimates the distance to regularity (D) in an hypothetical example.

Appendix S2. Frequency (proportion of quadrats where the species is present) and cover (mean ± SD, $n = 100$) of sampled lichen and moss species at the two study sites.

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