

Are soil lichen communities structured by biotic interactions? A null model analysis

Author(s) :Fernando T. Maestre, Cristina Escolar, Isabel Martínez, and Adrián Escudero

Source: Journal of Vegetation Science, 19(2):261-266. 2008.

Published By: International Association of Vegetation Science

DOI: 10.3170/2007-8-18366

URL: <http://www.bioone.org/doi/full/10.3170/2007-8-18366>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Are soil lichen communities structured by biotic interactions? A null model analysis

Maestre, Fernando T.^{1,*}; Escolar, Cristina^{1,2}; Martínez, Isabel^{1,3} & Escudero, Adrián^{1,4}

¹Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, 28933 Móstoles, Spain; ²E-mail: c.escolar@alumnos.urjc.es;

³E-mail: isabel.martinez@urjc.es; ⁴E-mail: adrian.escudero@urjc.es;

*Corresponding author; Tel. +34 914888511; Fax +34 916647490; E-mail fernando.maestre@urjc.es;

Web page: http://www.escet.urjc.es/biodiversos/espapersonal/fernandofernando_e.htm

Abstract

Question: Are soil lichen communities structured by biotic interactions?

Location: Gypsum outcrops located next to Belmonte del Tajo, central Spain.

Methods: We sampled a total of 68 (50 cm × 50 cm) plots in gypsum outcrops from central Spain. Each plot was divided into 100 (5 cm × 5 cm) sampling quadrats, and the presence of all lichen species in every quadrat was recorded (6800 quadrats in total). We used two realistic null models to generate random communities unstructured by biotic interactions, and used them to test the hypothesis that soil lichen species co-occur less often than expected by chance.

Results: We found fewer species combinations and less co-occurrence than expected by chance. However, the latter result was dependent on the null model selected. The number of checkerboard pairs did not differ significantly from the null expectation.

Conclusions: Overall, our results suggest that gypsiferous soil lichen communities are structured by competitive interactions. They are consistent with studies conducted with a wide variety of taxa, and fill a gap in our knowledge of the factors driving the small-scale distribution of these important organisms.

Keywords: Biological soil crust; Community assembly rule; Null model analysis; Semi-arid; Species co-occurrence.

Nomenclature: Tutin et al. (1964–1980) for vascular plants; Hladun & Llimona (2002–2007) and Breuss (1996) for lichens.

Abbreviations: BSC = Biological soil crust; SES = Standardized effect size.

Introduction

The structure of biotic communities has important implications for ecosystem functioning and stability (Pimm 1984; Wilsey & Potvin 2000; Maestre et al. 2005a). Thus, it is not surprising that an important part of ecological research has been devoted to understanding how communities are structured and to developing general assembly rules to describe this structure (Diamond 1975; Connor & Simberloff 1979; Weiher & Keddy 1999). Among those developed so far, Diamond's (1975) assembly rules model, which predicts that species should co-occur less often than expected by chance because of competitive interactions, has been one of the most influential and hotly debated (Gotelli 2000). Even if facilitation has been found to be a prevalent force shaping the structure of communities in a wide variety of environments (Castellanos et al. 1994; Armas & Pugnaire 2005; van de Koppel et al. 2006), results of recent studies suggest that Diamond's (1975) predictions hold for most natural plant communities and non-parasitic animals (Gotelli & McCabe 2002; Gotelli & Rohde 2002).

Surprisingly, assembly rules have seldom been employed to describe co-occurrence patterns in moss and lichen communities (Wilson et al. 1995). Such communities are key biotic components of a wide range of ecosystems, including cold and hot deserts, boreal forests and the arctic tundra (Hahn et al. 1996; Belnap & Lange 2001; Nilsson & Wardle 2005). Several authors have suggested that, contrary to Diamond's (1975) predictions, these communities are not structured by biotic interactions such as competition (Watson 1980; Slack 1990; but see Wilson et al. 1995). We used null model analyses (Gotelli 2000) to test for patterns of co-occurrence of lichens forming biological soil crusts (BSC). Soil lichens are an important constituent of BSC in arid and semi-arid environments throughout the globe, and usually represent a later stage in its development (Lange et al. 1997). These organisms exert a great influence on ecosystem functioning by affecting nutrient cycling, soil

stability and infiltration (Evans & Ehleringer 1993; Belnap & Gillette 1998; Maestre et al. 2002), by influencing the establishment and performance of vascular plants (Eckert et al. 1986; DeFalco et al. 2001; Escudero et al. 2007), and by serving as habitat for a large number of arthropods and micro-organisms (Belnap 2001; Shepherd et al. 2002). Despite their importance, null models and assembly rules have not previously been used to evaluate co-occurrence patterns in BSC forming lichens. The main objective of this study was to test the hypothesis that these organisms co-occur less often than expected by chance (Diamond 1975), and thus are likely to be structured by competition. The role of competition for space as a main driver of community structure has been largely recognized in saxicolous lichen communities (e.g. Pentecost 1980; John 1989) and we predict that a similar result may be expected in BSC forming lichen communities because of their morphology, growth habit and substrate requirements (Belnap & Lange 2001).

Material and Methods

Study area and sampling

The study was conducted in gypsum outcrops near Belmonte del Tajo, central Spain (40°7'3" N, 3°18'30" W, 686 m a.s.l.; 8° slope; 220° SW aspect). The climate is mediterranean semi-arid, with a mean annual temperature of 14 °C and mean annual rainfall of 452 mm. The outcrops are surrounded by a well developed forest of *Quercus ilex* and *Pinus halepensis* (App. 1), but perennial plant cover within them remains below 20%. It is patchily distributed and dominated by species such as *Stipa tenacissima*, *Helianthemum squamatum* and *Lepidium subulatum*.

A total of 68 plots (50 cm × 50 cm), spreading over a homogeneous area of 1.3ha, were placed non-randomly on bare ground areas with well developed BSC located in the spaces between perennial plants (App. 1). In order to minimize the variability associated with small-scale differences in topography and to capture the greatest possible contrast in lichen community composition and structure, these plots were placed non-randomly in areas with well developed BSC (Bowker et al. 2002; Maestre et al. 2005a). However, a minimum separation distance between plots of 0.7 m was ensured to minimize the risk of sampling non-independent areas due to the spatial structure of BSC. Much of the spatial variation in the cover of BSC organisms in semi-arid mediterranean areas occurs at spatial scales smaller than the 50 cm × 50 cm quadrats used (Maestre 2003), and with this separation distance we aimed to remove potential sources of non-independence between sampling quadrats. Each plot was divided into 100 (5 cm × 5 cm) sampling quadrats,

and the presence of all lichen species in every quadrat was recorded (6800 quadrats). None of the sampling quadrats was fully covered by thalli of a single species (App. 2). Therefore, we believe that the scale used is appropriate to meet the objectives of the study (Maestre et al. 2005b). We focused only on lichens because they are the dominant component of BSC in gypsum outcrops of our study area (the cover of mosses is usually below 1%; Martínez et al. 2006). For each plot, the data were organized as a presence-absence matrix, where each row and column represents a different species and sampling quadrat, respectively.

Quantification of community structure

We used three indices to quantify patterns of lichen community structure: the number of species pairs forming checkerboard distributions, the C-score and the number of species combinations (see Gotelli 2000 for details on the statistical properties of these indices and on their performance in null model analyses). The first index is calculated by counting the number of unique pairs of species that never co-occur. The C-score is calculated for each pair of species as $(R_i - S)(R_j - S)$, where R_i and R_j are the matrix row totals for species i and j , and S is the number of squares in which both species occur; this score is then averaged over all possible pairs of species in the matrix. The number of species combinations was counted by checking the columns of each matrix for distinct arrangements. If a community is structured by competitive interactions, there should be more checkerboard species pairs than expected by chance, the C-score should be significantly larger than expected by chance and the number of species combinations will be smaller than expected by chance (Diamond 1975; Gotelli 2000; Gotelli & McCabe 2002).

The indices obtained from each matrix were compared with those derived from 10 000 randomly assembled 'null' matrices. Their statistical significance was calculated as the frequency of simulated matrices that had indices that were equal to or more extreme to them (Manly 1995). We used two null models for each comparison: (1) fixed-fixed and (2) fixed-equiprobable (Gotelli 2000). In both cases, species frequencies are retained in random matrices (i.e. rare species remain rare and common species remain common). The fixed-fixed method also keeps constant the number of species in each sample unit, while the fixed-equiprobable method allows any number of species from zero to the total number of species encountered. The performance of both null models with the indices employed has been extensively tested and both have good statistical properties (low Type I error and good power to detect nonrandomness; Gotelli & Entsminger 2003). They also share two characteristics that make them appropriate for the objective of this study (Gotelli 2000): (1) they

maintain the observed species occurrence frequencies, a conceptually satisfying assumption corresponding to a colonization model in which species colonize a given plot randomly with respect to one another and (2) the species occurrences are random with respect to one another, which is an appropriate null model for detecting patterns caused by species interactions.

We created null matrices with a sequential swap algorithm by repeatedly swapping randomly selected submatrices of the form 01/10 (see Gotelli & Entsminger 2006 for details). Although some aspects of this algorithm have been criticized (Sanderson et al. 1998), extensive simulation analyses have shown that it is statistically appropriate (Gotelli & Entsminger 2003).

Statistical analyses

To facilitate comparison with previous studies, a standardized effect size (SES) was calculated for each matrix as $(I_{\text{obs}} - I_{\text{sim}})/S_{\text{sim}}$, where I_{obs} is the observed value of a given index of lichen community structure and I_{sim} and S_{sim} are the mean and standard deviation, respectively, of the index obtained from the 10000 null communities (Gotelli & McCabe 2002). A one-sample t -test was used to test the null hypothesis that the mean SES measured for the 68 presence-absence matrices did not differ from zero (Gotelli & Rohde 2002). We performed six such tests (three indices \times two null models), so we used the Bonferroni procedure to correct the individual tail probabilities of these tests. Null model analyses and t -tests were conducted with Ecosim 7.22 (Gotelli & Entsminger 2006) and SPSS 13.0 (SPSS Inc. Chicago, IL) respectively.

Results and Discussion

The SES of the number of species pairs forming checkerboard distributions did not differ significantly from 0 when using the fixed-fixed null model (Fig. 1A, Table 1). With the fixed-equiprobable null model, the corresponding SES was lower than expected, although the effect was not significant after Bonferroni correction (Table 1). The mean SES obtained with the C-score was greater than 0 for both null models employed, but this departure was significant only for the fixed-fixed algorithm (Fig. 1B, Table 1). For both null models employed, the mean SES of the number of species combinations was significantly lower than 0 (Fig. 1C, Table 1).

According to our working hypothesis, we found evidence that BSC forming lichen communities were mainly structured by competitive interactions. The underlying rationale of this hypothesis was based on the widespread evidence of competition in lichen communities, and on

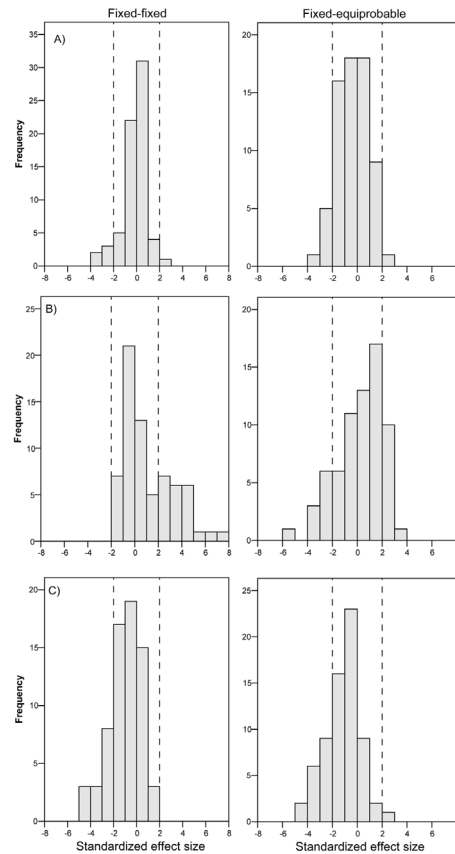


Fig. 1. Frequency histograms for standardized effect sizes measured in biological soil crusts presence-absence matrices. **A.** Number of species pairs forming checkerboard distributions; **B.** C-score; **C.** Number of species combinations. The null hypothesis is that the mean effect size equals 0. Dotted lines indicate 95% confidence intervals for this hypothesis.

the morphological and ecological characteristics of the lichens studied, which probably share the same niche requirements (Martínez et al. 2006). The clearest pattern that emerged from our analyses was that there were fewer species combinations than expected by chance. In addition, results from the C-score when using the fixed-fixed algorithm showed that soil lichens tended to co-occur less often than expected by chance. These results are in agreement with Diamond's (1975) assembly rules model and indicate that competition is the driving biotic force structuring soil lichen communities. In contrast, when empty sampling squares were included in the analyses (fixed-equiprobable model), we found a trend towards finding fewer checkerboard distributions than expected by chance, a result suggesting that facilitation, and not competition, is prevalent in the studied communities. It must be noted, however, that the effect size of this statistic

Table 1. Summary of null model analyses of biological soil crusts matrices. Significant *P*-values (after Bonferroni correction for multiple testing) are in bold.

Index	Null model	Average SES (unitless)	<i>t</i>	<i>P</i>
Checkerboard*	Fixed-fixed	-0.22	-1.67	0.101
Checkerboard*	Fixed-equiprobable	-0.34	-2.19	0.032
C-score	Fixed-fixed	1.16	4.46	< 0.001
C-score	Fixed-equiprobable	0.27	1.20	0.235
Number of species combinations	Fixed-fixed	-1.03	-6.22	< 0.001
Number of species combinations	Fixed-equiprobable	-1.16	-6.81	< 0.001

* Number of species pairs forming checkerboard distributions.

was small and non-significant after Bonferroni correction. Therefore, it is likely ecologically unimportant compared to the results in the other tests (number of species combinations and C-score from the fixed-fixed null model).

It has been argued that the presence of fewer species combinations than expected by chance not only arises as a result of competitive interactions, but can also be generated if the species differ in their affinities for non-overlapping habitats or in their potential for colonizing available habitats within the area studied (Pielou & Pielou 1968; Gotelli & McCabe 2002). Our observational approach does not allow us to distinguish between these hypotheses. However, we believe that differences in habitat suitability between plots and in colonization potential between the species studied are unlikely to explain our results because of three major reasons: (1) the relatively small dimensions of our study area; (2) the dispersal mode of the species found – through spores in most cases (App. 3; Clauzade & Roux 1985) and (3) the fact that all the species are common in well preserved gypsiferous outcrops from the Iberian Peninsula (Crespo 1973; Martínez et al. 2006). Further evidence is provided by the lack of relationship between the roughness of the soil surface, an important factor in determining small-scale differences in BSC composition (Bowker et al. 2006), and the number of species present in each plot (see App. 4). Thus, we believe that competitive interactions, rather than differences in habitat suitability between plots, were the main drivers of our results.

Our findings are consistent with widespread evidence showing interspecific competition among lichen species for space and nutrients (e.g. Armstrong 1991; Stone 1989; Shimizu 2004), and with studies emphasizing the importance of this biotic interaction as a driver of the structure of lichen communities developed over hard substrates (Pentecost 1980; John 1989). They also agree with Wilson et al. (1995), who found that competitive interactions were a key driver of the structure of soil bryophyte communities in New Zealand lawns, and with the results from a recent synthesis of presence-absence matrices from a wide variety of taxa, which suggest that observed co-occurrence in most natural communities was less than expected by chance (Gotelli & McCabe 2002).

The magnitude of the SES obtained varied with the choice of the co-occurrence index and type of null model. Similar results have been found in studies using different indices of community structure and/or null models to analyse the same data set (Gotelli & Rohde 2002; Gotelli & Ellison 2002; Tirado & Pugnaire 2005; see also Gotelli 2000 for a thorough discussion on the effect of null model type and index on the outcome of co-occurrence analyses). In addition to the suitability of the null models selected in our study, it must be highlighted that they have often been used with a wide variety of taxa (e.g. Connor & Simberloff 1979; Winemiller & Pianka 1990; Gotelli & Rohde 2002; Gotelli & McCabe 2002) and that the use of multiple, but conceptually and statistically plausible, null models has been recommended when evaluating co-occurrence patterns with presence-absence matrices (Gotelli 2000).

Our results represent, to our knowledge, the first empirical evidence of non-random species co-occurrence in BSC forming lichen communities. They fill a gap in our knowledge of the ecology of these important organisms and add to available evidence of the dominance of non-random patterns in natural communities (Gotelli & McCabe 2002). It has been recently shown that attributes of BSC, such as diversity and spatial pattern, directly influence ecosystem functioning in gypsiferous semi-arid environments (Maestre et al. 2005a). However, the influence of the documented co-occurrence patterns on key functional processes affected by soil lichens, such as nutrient cycling, remains virtually unknown. Facilitative/competitive processes among BSC components can be potentially relevant for ecosystem functioning if, for instance, they promote changes in the performance and dominance of N-fixing species such as *Collema* spp. (Davidson et al. 2002). Future studies focusing on how abiotic factors such as soil nutrients and microclimate modify observed co-occurrence patterns among soil lichens, as well as on the consequences of these patterns for processes such as nitrogen fixation and nutrient cycling, will undoubtedly improve our understanding of the functioning of arid and semi-arid ecosystems.

Acknowledgements. We thank the owners of La Encomienda

Mayor de Castilla estate for allowing us to work on their property, Mónica García and Marta Carpio for help during fieldwork and Exequiel Ezcurra, Akira Shimizu, Kevin Burns, Matthew Bowker and an anonymous referee for comments on previous versions of the manuscript. FTM was supported by a Ramón y Cajal contract from the Spanish Ministerio de Educación y Ciencia. This research was supported by an Early Career Project Grant from the British Ecological Society (ECPG 231/607) and by the Comunidad de Madrid-funded projects GR/AMB/0932/2004, REMEDINAL (S-0505/AMB/0335) and CEFEMED (URJC-RNT-063-2). The latter was also funded by Universidad Rey Juan Carlos.

References

- Armas, C. & Pugnaire, F.I. 2005. Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology* 93: 978-989.
- Armstrong, R.A. 1991. Competitive interactions between 4 foliose lichens on North and South facing rock surfaces. *Environmental and Experimental Botany* 31: 51-58.
- Belnap, J. 2001. Microbes and microfauna associated with biological soil crusts. In: Belnap, J. & Lange, O.L. (eds.) *Biological soil crusts: Structure, function, and management*, pp. 167-174. Springer Verlag, Berlin, DE.
- Belnap, J. & Gillette, D.A. 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture and disturbance. *Journal of Arid Environments* 39: 133-142.
- Belnap, J. & Lange, O.L. (eds.) 2001. *Biological soil crusts: Structure, function, and management*. Springer Verlag, Berlin, DE.
- Bowker, M.A., Reed, S.C., Belnap, J. & Phillips, S.L. 2002. Temporal variation in community composition, pigmentation, and Fv/Fm of desert cyanobacterial soil crusts. *Microbial Ecology* 43: 13-25.
- Bowker, M.A., Belnap, J., Davidson, D.W. & Goldstein, H. 2006. Correlates of biological soil crust abundance across a continuum of spatial scales: support for a hierarchical conceptual model. *Journal of Applied Ecology* 43: 152-163.
- Breuss, O. 1996. Studien über die Flechtengattung *Catapyrenium* (Verrucariaceae) VIII. Eine übersehene Art aus den Alpen und bemerkenswerte Einzelfunde aus Europa (mit Makaronesien). *Linzer Biologische Beiträge* 28: 529-533.
- Castellanos, E.M., Figueroa, M.E. & Davy, A.J. 1994. Nucleation and facilitation in saltmarsh succession: Interactions between *Spartina maritima* and *Arthrocnemum perenne*. *Journal of Ecology* 82: 239-248.
- Clauzade, G. & Roux, C. 1985. Likenoj de Okcidenta Europo. Ilustrita determinlibro. *Bulletin de la Société Botanique du Centre-Ouest*, Numero spécial 7: 1-893.
- Connor, E.F. & Simberloff, D. 1979 The assembly of species communities: chance or competition? *Ecology* 60: 1132-1140.
- Crespo, A. 1973. Composición florística de la costra de líquenes del Herniario-Teucrietum pumili de la provincia de Madrid. *Anales del Instituto Botánico A.J. Cavanilles* 30: 57-68.
- Davidson, D.W., Bowker, M., George, D., Phillips, S.L. & Belnap, J. 2002. Treatment effects on performance of N-fixing lichens in disturbed soil crusts of the Colorado Plateau. *Ecological Applications* 12: 1391-1405.
- DeFalco, L.A., Detling, J.K., Richard Tracy, C. & Warren, S.D. 2001. Physiological variation among native and exotic winter annual plants associated with microbiotic crusts in the Mojave Desert. *Plant and Soil* 234: 1-14.
- Diamond, J.M. 1975. Assembly of species communities. In: Cody, M.L. & Diamond, J.M. (eds.) *Ecology and evolution of communities*, pp. 342-444. Harvard University Press, Cambridge, MA, US.
- Eckert, R.E., Peterson, E.F., Meurisse, M.S. & Stephens, J.L. 1986. Effects of soil surface morphology on emergence and survival of seedlings in big sagebrush communities. *Journal of Range Management* 39: 414-420.
- Escudero, A., Martínez, I., de la Cruz, A., Otálora, M.A.G. & Maestre, F.T. 2007. Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species. *Journal of Arid Environments* 70: 18-28.
- Evans, R.D. & Ehleringer, J.R. 1993. A break in the nitrogen cycle in aridlands? Evidence from $\delta^{15}N$ of soils. *Oecologia* 94: 314-317.
- Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606-2621.
- Gotelli, N.J. & Ellison, A.M. 2002. Assembly rules for New England ant assemblages. *Oikos* 99: 591-599
- Gotelli, N.J. & Entsminger, G.L. 2003. Swap algorithms in null model analysis. *Ecology* 84: 532-535.
- Gotelli, N.J. & Entsminger, G.L. 2006. *EcoSim: Null models software for ecology. Version 7*. Acquired Intelligence Inc. and Kesey-Bear, Jericho. <http://garyentsminger.com/ecosim.htm>
- Gotelli, N.J. & McCabe, D.J. 2002. Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* 83: 2091-2098.
- Gotelli, N.J. & Rohde, K. 2002. Co-occurrence of ectoparasites of marine fishes: a null model analysis. *Ecology Letters* 5: 86-94.
- Hahn, S.C., Oberbauer, S.F., Gebauer, R., Grulke, N.E., Lange, O.L. & Tenhunen, J.D. 1996. Vegetation structure and aboveground carbon and nutrient pools in the Imnavait Creek Watershed. In: Reynolds, J.F. & Tenhunen, J.D. (eds.) *Landscape function and disturbance in Arctic tundra*, pp. 109-128. Springer, Berlin, DE.
- Hladun, N. & Llimona, X. 2002-2007. *Checklist of the Lichens and lichenicolous Fungi of the Iberian Peninsula and Balearic Islands*. <http://botanica.bio.ub.es/checklist/checklist.htm>
- John, E.A. 1989. An assessment of the role of biotic interactions and dynamic processes in the organization of species in a saxicolous lichen community. *Canadian Journal of Botany* 67: 2025-2037.
- Lange, O.L., Belnap, J., Reichenberger, H. & Meyer A. 1997. Photosynthesis of green algal soil crust lichens from arid lands in southern Utah, USA: Role of water content on light and temperature response of CO_2 exchange. *Flora* 192: 1-15.
- Maestre, F.T. 2003. Small-scale spatial patterns of two soil

- lichens in semi-arid Mediterranean steppe. *Lichenologist* 35: 71-81.
- 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 Biology and Biochemistry* 34: 895-898.
- Maestre, F.T., Escudero, A., Martínez, I., Guerrero, C. & Rubio, A. 2005a. Does spatial pattern matter to ecosystem functioning? Insights from biological soil crusts. *Functional Ecology* 19: 566-573.
- Maestre, F.T., Rodríguez, F., Bautista, S., Cortina, J. & Bellot, J. 2005b. Spatial associations and patterns of perennial vegetation in a semi-arid steppe: a multivariate geostatistics approach. *Plant Ecology* 179: 133-147.
- Manly, B.J. 1995. A note on the analysis of species co-occurrences. *Ecology* 76: 1109-1115.
- Martínez, I., Escudero, A., Maestre, F.T., de la Cruz, A., Guerrero, C. & Rubio, A. 2006. Small-scale patterns of abundance of mosses and lichens forming biological soil crusts in two semi-arid gypsum environments. *Australian Journal of Botany* 54: 339-348.
- Nilsson, M.C. & Wardle, D.A. 2005. Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment* 3: 421-428.
- Pentecost, A. 1980. Aspects of competition in saxicolous lichen communities. *Lichenologist* 12: 135-144.
- Pielou, P.P. & Pielou, E.C. 1968. Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *Journal of Theoretical Biology* 21: 202-216.
- Pimm, S.L. 1984. The complexity and stability of ecosystems. *Nature* 307: 321-326.
- Sanderson, J.G., Moulton, M.P. & Selfridge, R.G. 1998. Null matrices and the analysis of species co-occurrences. *Oecologia* 116: 275-283.
- Shepherd, U.L., Brantley, S.L. & Tarleton, C.A. 2002. Species richness and abundance patterns of microarthropods on cryptobiotic crusts in a pinyon-juniper habitat: a call for greater knowledge. *Journal of Arid Environments* 52: 349-360.
- Shimizu, A. 2004. Community structure of lichens in the volcanic highlands of Mt. Tokachi, Hokkaido, Japan. *Bryologist* 107: 141-151.
- Slack, N.G. 1990. Bryophytes and ecological niche theory. *Botanical Journal of the Linnean Society* 104: 187-213.
- Stone, D.F. 1989. Epiphyte succession on *Quercus garryana* branches in the Willamette Valley of western Oregon (USA). *Bryologist* 92, 81-94.
- Tirado, R. & Pugnaire, I. 2005. Community structure and positive interactions in constraining environments. *Oikos* 111: 437-444.
- Tutin, G.T., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.). 1964-1983. *Flora Europaea*. Cambridge University Press, Cambridge, UK.
- van de Koppel, J., Altieri, A.H., Silliman, B.R., Bruno, J.F. & Bertness, M.D. 2006. Scale-dependent interactions and community structure on cobble beaches. *Ecology Letters* 9: 45-50.
- Watson, M.A. 1980. Patterns of habitat occupation in mosses – relevance to considerations of the niche. *Bulletin of the Torrey Botanical Club* 107: 346-372.
- Weiher, E. & Keddy, P. (eds.) 1999. *Ecology assembly rules: Perspectives, advances, retreats*. Cambridge University Press, New York, NY, US.
- Wilsey, B.J. & Potvin, C. 2000. Biodiversity and ecosystem functioning: Importance of species evenness in an old field. *Ecology* 81: 887-892.
- Wilson, J.B., Steel, J.B., Newman, J.E. & Tangney, R.S. 1995. Are bryophyte communities different? *Journal of Bryology* 18: 689-705.
- Winemiller, K.O. & Pianka, E.R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60: 27-55.

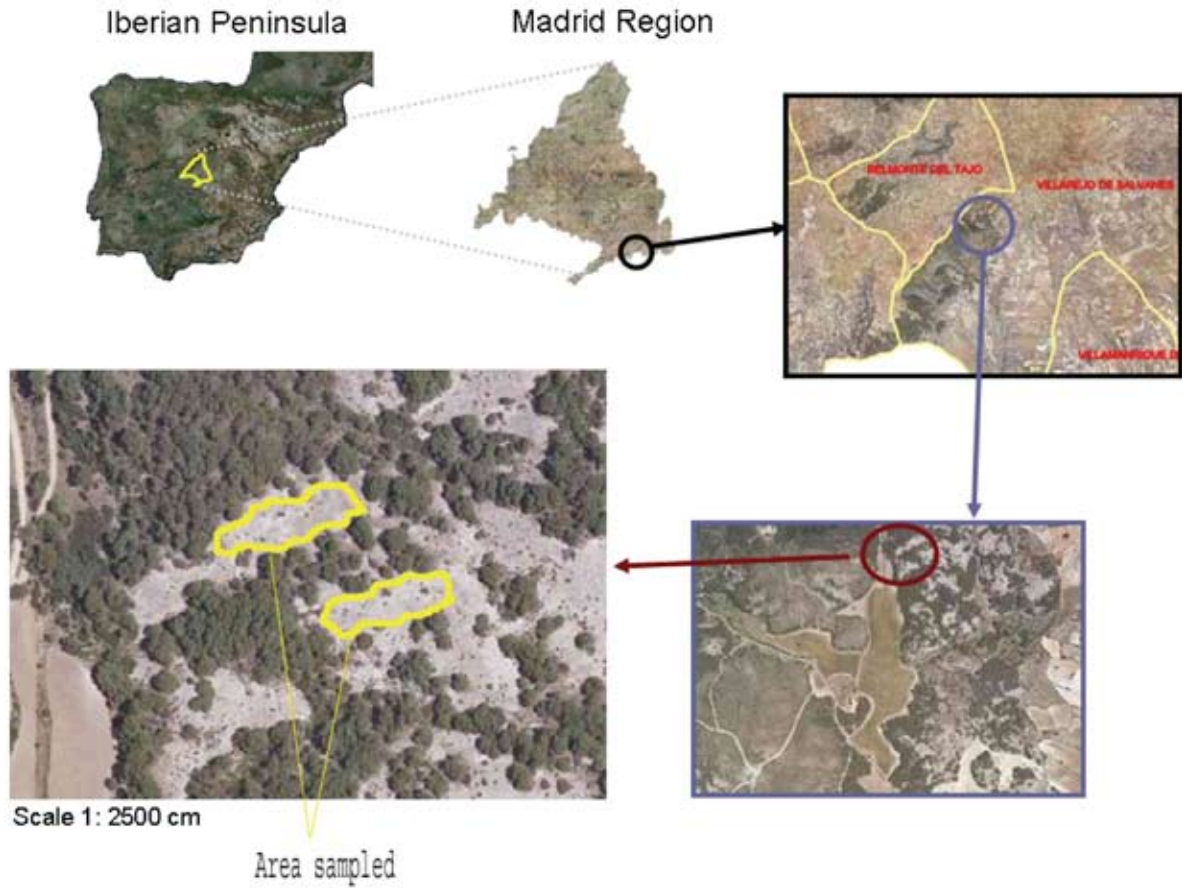
Received 19 March 2007;

Accepted 26 July 2007;

Co-ordinating Editor: E. Ezcurra.

For App. 1-4, see below (online version)
also available at JVS/AVS Electronic Archives;
www.opuluspress.se/

App. 1. Location of the study area in central Spain and view of the area where the sampling quadrats were established (area sampled).

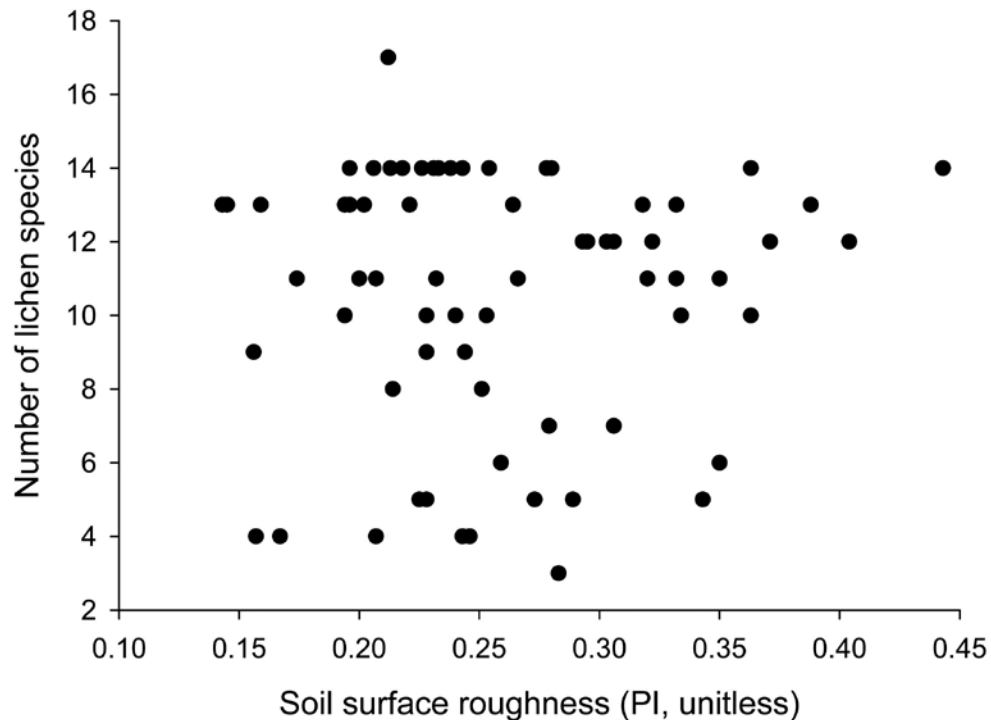


App. 2. A. View of the sampling grid used in each of the plots laid out; **B.** Close-up picture of a typical BSC forming lichen community in the study area. The size of each sampling square in (A) is 5 cm × 5 cm. As can be seen in this photograph, none of the individual thalli exceed the size of a sampling quadrat. Vegetation inside the sampling quadrats was, in all cases, formed by annual plants. Credit of the pictures: Isabel Martínez (A) and Fernando T. Maestre (B).



App. 3. Frequency (proportion of quadrats where the species is present) and cover (number of 5 cm × 5 cm cells occupied within each 50 cm × 50 cm plot) of lichens forming biological soil crusts in the study area. Cover data represent means ± SD ($n = 68$).

Species	Frequency (%)	Cover (%)
<i>Acarospora nodulosa</i>	94	28.76 ± 18.16
<i>Cladonia convoluta</i>	97	32.71 ± 27.41
<i>Collema crispum</i>	79	23.28 ± 22.84
<i>Diploschistes diacapsis</i>	100	73.60 ± 26.68
<i>Endocarpon pusillum</i>	49	3.79 ± 6.58
<i>Fulgensia subbracteata</i>	75	32.51 ± 30.43
<i>Lepraria crassissima</i>	40	3.94 ± 10.83
<i>Placidium pilosellum</i>	44	3.63 ± 7.64
<i>Placidium squamulosum</i>	29	2.29 ± 6.22
<i>Psora decipiens</i>	79	27.68 ± 28.04
<i>Psora globifera</i>	21	1.81 ± 5.59
<i>Psora saviczii</i>	72	3.90 ± 4.63
<i>Squamarina cartilaginea</i>	85	22.13 ± 23.20
<i>Squamarina lentigera</i>	96	42.07 ± 28.73
<i>Toninia albilabra</i>	47	3.31 ± 6.19
<i>Toninia sedifolia</i>	41	5.13 ± 10.53
<i>Toninia toniniana</i>	6	0.07 ± 0.31



App. 4. Relationship between soil surface roughness and the number of species present in each 50 cm × 50 cm plot. Soil surface roughness was estimated in each plot with the roller chain method as described in Jester & Klik (2005). According to these authors, a dimensionless profile index (PI) was obtained as [(measured profile length / projected length) - 1]. The PI value of each plot represents the mean PI obtained from five transects, placed 10 cm apart from each other.

Jester, W. & Klik, A. 2005. Soil surface roughness measurement-methods, applicability, and surface representation. *Catena*, 64: 174-192.

App. 1-4. Internet supplement to: Maestre, F.T.; Escolar, C.; Martínez, I. & Escudero, A. 2008.

Are soil lichen communities structured by biotic interactions? A null model analysis.

J. Veg. Sci. 19: 261-266. doi: 10.3170/2007-8-18366