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Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern

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Summary

1. Recent studies have suggested that the simultaneous maintenance of multiple ecosystem functions (multifunctionality) is positively supported by species richness. However, little is known regarding the relative importance of other community attributes (e.g. spatial pattern, species evenness) as drivers of multifunctionality.

2. We conducted two microcosm experiments using model biological soil crust communities dominated by lichens to: (i) evaluate the joint effects and relative importance of changes in species composition, spatial pattern (clumped and random distribution of lichens), evenness (maximal and low evenness) and richness (from two to eight species) on soil functions related to nutrient cycling (β-glucosidase, urease and acid phosphatase enzymes, *in situ* N availability, total N, organic C, and N fixation), and (ii) assess how these community attributes affect multifunctionality.

3. Species richness, composition and spatial pattern affected multiple ecosystem functions (e.g. organic C, total N, N availability, β-glucosidase activity), albeit the magnitude and direction of their effects varied with the particular function, experiment and soil depth considered. Changes in species composition had effects on organic C, total N and the activity of β-glucosidase. Significant species richness × evenness and spatial pattern × evenness interactions were found when analysing functions such as organic C, total N and the activity of phosphatase.

4. The probability of sustaining multiple ecosystem functions increased with species richness, but this effect was largely modulated by attributes such as species evenness, composition and spatial pattern. Overall, we found that model communities with high species richness, random spatial pattern and low evenness increased multifunctionality.

5. *Synthesis*. Our results illustrate how different community attributes have a diverse impact on ecosystem functions related to nutrient cycling, and provide new experimental evidence illustrating the importance of the spatial pattern of organisms on ecosystem functioning. They also indicate that species richness is not the only biotic driver of multifunctionality, and that particular combinations of community attributes may be required to maximize it.

Key-words: biodiversity, biological soil crusts, community attributes, ecosystem functioning, lichens, nutrient cycling, plant–soil (below-ground) interactions, spatial pattern, species evenness

Introduction

During the last two decades, the relationship between biodiversity and ecosystem functioning (biodiversity–function hereafter) has been a core research area in community and ecosystem ecology (see Naeem *et al*. 2009 and Cardinale *et al*. 2011 for recent reviews). Our current understanding primarily results from studies that have focused on the role of species richness and, to a lesser degree, of functional group richness in driving above-ground production in addition to other

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ecosystem functions (e.g. Loreau, Naeem & Inchusti 2002; Hooper *et al.* 2005; Cardinale *et al.* 2011). Most of this research has focused on evaluating only one ecosystem function at a time, such as productivity (e.g. Tilman *et al.* 1997; Montès *et al.* 2008; Hector *et al.* 2011). However, ecosystems are valued primarily for the multiple functions and services they provide, and thus there is a critical need to examine the effects of biodiversity on multiple ecosystem functions simultaneously (multifunctionality; Stachowicz, Bruno & Duffy 2007; Reiss *et al.* 2009; Cardinale *et al.* 2011). While the use of multiple functions in biodiversity–function research started more than 10 years ago (Hooper & Vitousek 1998; Duffy, Richardson & Canuel 2003), the first quantitative tests of multifunctionality have been done much more recently and have been limited to communities constituted by terrestrial plants, bacteria and seagrasses (Hector & Bagchi 2007; Gamfeldt, Hillebrand & Jonsson 2008; He *et al.* 2009; Zavaleta *et al.* 2010; Mouillot *et al.* 2011).

The need to determine the linkages among the different attributes that characterize biotic communities as determinants of ecosystem functioning and stability has been recognized for a long time (Loreau *et al.* 2001). However, little is known regarding the relative importance of species richness against other community attributes as drivers of ecosystem multifunctionality. Species composition and evenness are community attributes that have been shown to affect ecosystem functioning, and are being increasingly considered (Downing 2005; Hillebrand, Bennett & Cadotte 2008; Hector *et al.* 2011). However, the spatial distribution pattern of organisms (hereafter spatial pattern) is also a potentially relevant attribute that has been overlooked by previous biodiversity–function research. Non-random spatial patterns (e.g. clumped or regular) of organisms and ecosystem processes are common in many terrestrial ecosystems (e.g. Klausmeier 1999; Hutchings, John & Stewart 2000; Deblauwe *et al.* 2008). Theoretical and modelling studies highlight the importance of the spatial pattern of organisms for ecosystem functioning, stability and dynamics (Pacala & Deutschman 1995; Tilman & Kareiva 1997; Bolker, Pacala & Neuhauser 2003). However, few studies to date have empirically evaluated the relationship between such patterns and ecosystem processes (Kikvidze *et al.* 2005; Maestre *et al.* 2005; Pringle *et al.* 2010), and thus, the consequences of these patterns for ecosystem functioning remain poorly understood. Pringle *et al.* (2010) showed that the regular spatial pattern of termite mounds typically found in African savannas promotes greater abundance, biomass and fitness of consumers across trophic levels, increasing the productivity of the whole ecosystem. These results illustrate the importance of accounting for the spatial patterns of organisms to understand how natural ecosystems function.

Expanding current biodiversity–function research to consider additional community attributes such as spatial pattern, and to assess ecosystem multifunctionality, can provide important insights to advance this field (Cardinale *et al.* 2011). To our knowledge, no previous study has simultaneously evaluated the relative importance of different biodiversity components and spatial pattern on ecosystem multifunctionality using a manipulative experimental approach. We did so by conducting a series of experiments where we simultaneously manipulated species composition, spatial pattern (clumped and random distribution), evenness (maximal and low evenness) and richness (from two to eight species), and evaluated their relative importance as drivers of multiple ecosystem functions related to nutrient cycling (β-glucosidase, urease and acid phosphatase enzymes, *in situ* N availability, total N, organic C, and N fixation) using biological soil crust (BSC)-forming lichens as a model system. These communities dominate extensive areas of many terrestrial ecosystems worldwide (Belnap & Lange 2003), where they strongly influence key ecosystem processes like infiltration, CO_2 fluxes and nitrogen (N) fixation and transformations (Belnap 2002, 2006; Castillo-Monroy *et al.* 2010, 2011; Eldridge *et al.* 2010). Biological soil crusts are also a good model system for biodiversity–function research (Bowker, Maestre & Escolar 2010) and have also been recently used to conduct quantitative analyses of the functional role of individual species (e.g. Bowker *et al.* 2011; Gotelli, Ulrich & Maestre 2011) and to assess the relative importance of biodiversity and cover as drivers of particular ecosystem functions in the field (Maestre *et al.* 2010). Our main objectives were to: (i) evaluate the joint effects and relative importance of biodiversity (species composition, richness and evenness) and spatial pattern as drivers of ecosystem functions related to nutrient cycling, and (ii) assess how these community attributes affect ecosystem multifunctionality. More specifically, we tested the following hypotheses: (i) species richness will have non-saturating positive effects on ecosystem multifunctionality. We expect such a response because previous observational studies suggest linear relationships between the richness of BSC-forming organisms and different ecosystem functions related to C, N and P cycling (Bowker, Maestre & Escolar 2010); (ii) species richness effects are modulated by species evenness. Given that the effects of lichen species on nutrient cycling should be driven primarily by their traits and the secondary compounds they produce (Cornelissen *et al.* 2007; Bowker, Maestre & Escolar 2010), and that these vary substantially between species (e.g. Palmqvist *et al.* 2002), variations in species abundance at a specific richness level can potentially affect ecosystem multifunctionality; (iii) species composition will significantly affect ecosystem multifunctionality. Strong composition effects are expected because BSC-forming lichens have been found to be highly individualistic in their effects on multiple ecosystem functions linked to the C, N and P cycles (Bowker *et al.* 2011); and (iv) ecosystem multifunctionality will be lower in assemblages with a clumped spatial pattern. Given the strong competition for space typically observed in BSC communities dominated by lichens (Maestre *et al.* 2008; Bowker, Soliveres & Maestre 2010), this interaction should be more intense in assemblages with a clumped spatial pattern (Armstrong & Welch 2007). We hypothesize that competition-induced mortality of the least adapted or poorer competitor species will reduce their effects on the functions evaluated, and thus on the overall multifunctionality of the whole assemblage.

Materials and methods

EXPERIMENTAL DESIGN

To achieve our objectives, two manipulative microcosm experiments were conducted in the plant growth facilities of the Rey Juan Carlos University, in Móstoles (Spain, 40°20′28″N, 3°52′58″O, 650 m a.s.l.). Soil and BSC-forming lichen species for these experiments were collected from gypsum outcrops located about 50 km south of the University. The species used in the experiments were selected among the pool of the ten most common lichen species found in the field (see Appendix S1 in Supporting Information). The basic experimental unit used in both experiments was a microcosm built from PVC pipe (height 8 cm, internal diameter 20 cm) filled to 7 cm of homogenized and nutrient-poor field soil (0.58% organic C; 0.46% total N at the time of setup). Intact lichen pieces were collected from the field in February 2006, transported to the laboratory on the same day they were collected, separated into species and cut into homogeneous 0.25 cm^2 square fragments (Appendix S2), which were sprayed with distilled water twice per week until the setup of the experiment (late May 2006). During the experimental setup, the fragments were placed onto the soil surface to achieve a 60% coverage of each microcosm unit, which is within the range found in the field (39–98%, Maestre *et al.* 2005). The two experiments were conducted under natural light, temperature and rainfall conditions between June 2006 and December 2008 (Appendix S1).

The first experiment (hereafter Composition experiment) was designed to independently test for the effects of species richness, species composition and spatial pattern on ecosystem functioning (Appendix S3). Four unique species composition levels, determined through random draws (Appendix S1), were nested within two species richness levels (four and eight species), which fall within the range found under field conditions in central Spain (Maestre *et al.* 2005, 2008). Each combination of species composition and richness was established under two spatial patterns: clumped and random. We focused on these two patterns because even spatial distributions of BSC-forming lichens are very rare, as revealed by multiple field surveys conducted throughout Spain (Maestre *et al.* 2005, 2008; Bowker, Soliveres & Maestre 2010). In the clumped treatment, the spatial distribution of the lichen fragments was strongly aggregated, while in the random treatment, these fragments were randomly distributed in space (Appendix S4). The cover of each species in the four-species mixtures was 15%, whereas it was 7.5% in the eight-species mixtures. Thus, total biological crust cover across microcosms was maintained at a constant 60% at the time of establishment, and the communities were perfectly even. A significant species composition effect would indicate that a specific assemblage of species has significantly different effects on ecosystem variables than a different assemblage with the same number of species (Schmid *et al.* 2002). All treatment combinations were replicated six times for a total of 96 microcosms. In addition, six control microcosms, containing only soil, were established. These microcosms were used to test the effects of the added soil lichens on the surrogates of ecosystem functioning measured.

The second experiment (hereafter Evenness experiment) was set up to independently test for the effects of species richness (two, four and eight species), species evenness (maximal vs. low evenness communities) and spatial pattern (clumped and random) on ecosystem functioning (Appendix S3). Random draws (six for each of the two, four and eight species richness levels) were made from the ten species pool (Appendix S1). After draws, we randomly assigned the cover of each species to have either maximal evenness (equal distribution of cover among species, 30% each in two-species mixtures, 15% each in four-species mixtures, and 7.5% each in eight-species mixtures) or a more realistically low evenness based on a geometric distribution of abundances among species (Wilsey & Polley 2004). For the latter distribution, we used rank-abundance slopes of approximately -0.26 (39:21 in two-species mixtures, 25:20:11:4 in four-species mixtures, and 24:17:10:4:2:1:1:1 in eight-species mixtures); this value was the average slope found in a survey of BSC communities in 100 30 cm × 30 cm plots located in the area where the soil and lichens for the experiments were collected (Maestre *et al.* 2005). Each combination of species richness and evenness was established under two spatial patterns: clumped and random. All treatment combinations were replicated six times for a total of 72 microcosms. As in the Composition experiment, six control microcosms, containing only soil, were established.

MEASURING ECOSYSTEM FUNCTIONING

We measured the following ecosystem processes and properties in both experiments: *in situ* nitrate (NO_3^-–N) and ammonium (NH_4^+–N) availability, organic carbon (C), total N, N fixation activity and the activity of three extracellular enzymes that are related to the C (β-glucosidase), N (urease) and phosphorus (phosphatase) cycles. For simplicity, all these variables will hereafter named as ecosystem functions (Gamfeldt, Hillebrand & Jonsson 2008). Indicators like these have been employed in previous studies on ecosystem multifunctionality (e.g. Hector & Bagchi 2007; Gamfeldt, Hillebrand & Jonsson 2008), and they either measure 'true' ecosystem functions (*sensu* Reiss *et al.* 2009; e.g. N fixation) or are key properties/processes (*sensu* Jax 2010, e.g. organic C, total N and soil enzymes) that together constitute a good proxy of nutrient cycling, a main determinant of ecosystem functioning in semiarid ecosystems such as those we aim to recreate (Whitford 2002).

The availability of NH_4^+–N and NO_3^-–N was measured in all the microcosms at the end of the experiment using ion-exchange membranes (IEMs; Subler, Blair & Edwards 1995). These membranes (types I-100 and I-200, Electropure Excellion, Laguna Hills, California) were set up as described in Castillo-Monroy *et al.* (2010), and were then inserted into the center of each microcosm at a 0–2.5 cm depth 20 days before the harvest of the experiment (Appendix S2), which occurred a week after the last rainfall registered during the course of the experiment. Just after harvesting the experiment, in December 2008, they were taken to the laboratory, dried at ambient temperature and analysed as described in Castillo-Monroy *et al.* (2010).

Two composite soil samples (0–2 and 2–5 cm depths, surface and subsurface soils hereafter) from the part of the microcosm covered by lichens (60% of the surface) were obtained for each of the microcosms at harvest. By doing so, we aimed to obtain values representative of the whole lichen assemblages created, averaging potentially within-microcosm spatial variability in the ecosystem functions measured associated to particular lichen species (Bowker *et al.* 2011). Prior to soil collection, the lichens were carefully removed with a knife to avoid measuring nutrients incorporated in or adherent to them; soil samples were air-dried in the laboratory prior to analyses. In semi-arid Mediterranean regions, air drying and medium-term storage of soils do not appreciably degrade the ecosystem functions evaluated here (Zornoza *et al.* 2006, 2009). Total N was obtained using a SKALAR San + + Analyzer (Skalar, Breda, The Netherlands) after digestion of the soil samples with sulphuric acid. Urease, phosphatase and β-glucosidase activities were determined as described in Nannipieri *et al.* (1980), Tabatabai & Bremner (1969) and Tabatabai (1982), respectively. Soil organic

C was estimated using the method of Yeomans & Bremmer (1989). Nitrogen fixation was measured on rewetted soil samples as described in Ruiz-Díez *et al.* (2009). Given that gypsum soils from central Spain usually remain dry for long periods (Castillo-Monroy *et al.* 2011) and, therefore, those organisms living on them (including microbial communities forming part of the native BSC) are used to rewetting and drying processes, we considered measuring N fixation on rewetted soils as a valid approximation (Billings, Schaeffer & Evans 2003). N fixation and the urease activity at the 2–5 cm depth could not be measured because the samples had values below the detection limits of the techniques employed.

ASSESSING MULTIFUNCTIONALITY

Given that we used a common, homogenized, and nutrient-poor soil for the experiments and that all the replicates were subjected to the same environmental conditions, higher values of variables like organic C, total N and N fixation in some microcosms compared with others would imply an enhancement of C and N cycling by the different BSC communities created and their associated microbial assemblages (e.g. Johnson *et al.* 2005; Maestre *et al.* 2005). Similarly, soil enzyme activities catalyse limiting steps in organic matter degradation and are often commonly used as indicators of microbial nutrient demand (Sinsabaugh *et al.* 2008). Therefore, increases in these variables would reflect an enhancement of nutrient cycling, and differences between treatments would reflect a differential effect, either direct or indirect, of the experimental lichen assemblages on the functioning of microbial communities. According to this rationale, we assume that the higher the values for the different functions measured in the microcosms, the higher the overall ecosystem functioning is. With this in mind, and for each of the variables measured (eight [including NH_4^+–N and NO_3^-–N] and four for surface and subsurface soils, respectively), we defined the maximum level of functioning as the average of the top-functioning 5% microcosms (i.e. those having the highest values of the variables measured) for each individual function. For each replicated microcosm, we calculated the percentage of the maximum achieved for each function. The average of these percentages for all the functions evaluated was used as an index of ecosystem multifunctionality (Zavaleta *et al.* 2010). While the use of such average may preclude a detailed analysis of how particular species differ in their importance for different functions (see Gotelli, Ulrich & Maestre 2011 for a detailed methodology for assessing this), it provides a straightforward measure of the ability of different communities to sustain multiple functions simultaneously (see Mouillot *et al.* 2011 for a similar approach).

To gain additional insights into the effect of biodiversity and spatial pattern on ecosystem multifunctionality, we also evaluated the ability of the assemblages created to achieve different multifunctionality thresholds (T), which we defined as the 30%, 50% and 70% of the observed maximum value of each function (Gamfeldt, Hillebrand & Jonsson 2008; Zavaleta *et al.* 2010). To achieve this, we tallied the proportion of assemblages of each treatment combination exceeding a multifunctionality threshold for all possible combinations of 1–7 functions. To simplify the presentation of the results, the assessment of these thresholds was carried out using only data from the surface soils, as this is the depth at which the data from the IEMs were gathered.

STATISTICAL ANALYSES

Some mortality of transplanted lichens occurred during the experiment (A. P. Castillo-Monroy and F. T. Maestre, unpublished data), and thus, the species composition at the end of the experiment departed from the initial composition in some microcosms. However, we did not conduct a frequent and repeated monitoring of survival during the experiment, and thus, we do not know the exact date when mortality occurred. Therefore, we analysed the Composition and Evenness experiments using the initial planted composition.

To evaluate the effects of the attributes evaluated on the surrogates of ecosystem functioning measured, and on the multifunctionality index, at the end of the experiment, we used either a three-way nested ANOVA (Composition experiment) or a factorial ANOVA (Evenness experiment). In the Composition experiment, species richness (two levels) and spatial pattern (two levels) were considered fixed factors, while composition (four levels) was a random factor nested within richness. In the Evenness experiment, species richness, spatial pattern and evenness were considered fixed factors. See Appendix S1 for additional details on these models. Data were tested prior to ANOVA analyses for assumptions of normality and homogeneity of variances and were log-transformed when necessary to meet ANOVA assumptions. Where appropriate, the Tukey's HSD test was used for post hoc comparisons.

To facilitate comparison with previous studies conducted with BSCs, which often analyse their effects on soil variables at 0–1 cm depth (e.g. Bowker *et al.* 2006; Bowker *et al.* 2011; Maestre *et al.* 2010), and to evaluate whether the effects of BSCs varied with depth, we analysed the soils from the two depths separately. This approach has limitations, as the data gathered at the two depths are not fully independent of each other; however, incorporating depth in the ANOVAS would lead to very complex models that are difficult to interpret. To overcome this limitation and to determine the relative importance of richness, spatial pattern, evenness and composition, we conducted additional analyses of data from the two depths together using a structural equation modelling approach (SEM, Grace 2006). Prior to modelling, we verified that relationships to be represented by paths were approximately linear by viewing scatterplots. In the case of the Evenness experiment, richness and evenness were expressed as the number of species and the Pielou's evenness index at the beginning of the experiment, respectively. Spatial pattern was represented as a binary variable, inclusive of random patterning and perfectly clumped patterning. We treated species composition as a covariate by creating a non-metric multidimensional scaling (NMDS) ordination of the relative abundances of the 10 possible species; the axis scores of this ordination were used as predictors in our SEM models. In the case of the Composition experiment, composition was nested within richness, and thus, a strong correlation emerged between these two variables. To separate their effects, we constructed one way ANOVAS using richness level as a predictor and composition axis scores from a NMDS ordination as responses. We saved the residuals of these models, creating axis scores that were essentially independent of richness. The models for the Composition experiment used these residuals in place of the axis scores to model the effect of composition. A composite variable was used to compile the effects of the three different axes into a synthetic composition variable. Because several of our function response variables did not follow a normal distribution, we used less-parametric bootstrap-based techniques to parameterize our SEM models, and the Bollen-Stine bootstrap test (Bollen & Stine 1992) to test their overall goodness-of-fit. See Appendix S1 for additional details on the SEM models conducted.

The proportion of microcosms that met or exceeded multifunctionality thresholds (T) of 30–70% were analysed using ANOVAS (Zavaleta *et al.* 2010). In the Composition experiment, the number of functions (all possible combination of 1–7 functions), species richness and spatial pattern were considered fixed factors, while

composition was a random factor nested within richness. In the Evenness experiment, species richness, evenness, spatial pattern and the number of functions were used as fixed factors. We did not perform *post hoc* tests on the results of these ANOVAS (Zavaleta *et al.* 2010). See Appendix S1 for further details on the models employed. The data used for these analyses were arcsine transformed to improve data conformation with the assumptions of ANOVA, but after transformation, they did not follow normality and homogeneity of variances. The results of these tests were the same as those obtained using the semi-parametric ANOVA (PERM ANOVA) method proposed by Anderson (2001), and thus, we report here only those of ANOVAS.

All ANOVA and SEM analyses were carried out using the SPSS 17.0 and Amos 18.0 statistical software, respectively (SPSS Inc., Chicago, IL, USA). The experiment-wide error rate was not adjusted for multiple testing, as this approach is considered overly conservative (Gotelli & Ellison 2004).

Results

At the end of the experiment, the different lichen assemblages created had higher values than the control (soil only) microcosms for most functions evaluated. This was particularly evident for functions like total N and β-glucosidase at the soil surface (Tables 1 and 2), as significant differences ($P < 0.05$) were found between the control microcosms and the different treatments employed at both experiments (Appendix S5). Functions like organic C showed a more variable response, as 38% (Composition experiment) and 42% (Evenness experiment) of the assemblages created had significantly higher values than the control microcosms at the end of the experiment ($P < 0.05$; Appendix S5). Other functions (N fixation and urease activity) did not show significant differences between the treatments and the control at the end of the experiment, but differences were observed among different experimental lichen communities (see below), which was the true focus of our study.

RELATIVE IMPORTANCE OF COMMUNITY ATTRIBUTES

The SEM analyses of all the attributes in the Evenness experiment revealed that the relative importance of each particular attribute varied depending on the ecosystem function considered. When path coefficients of the SEMs are averaged, both species richness and composition were the most important drivers of ecosystem functioning, followed by spatial pattern (Table 3). Species evenness had in all cases the lowest relative importance. Probability tests associated with SEMs also support this assertion, as detectable effects of species richness were at least five times more frequent than would be expected by chance alone and <0.10 in 54% of cases (Table 4). Effects of $P < 0.10$ were positive (i.e. increased richness increased function) in 25% of the cases evaluated, while this percentage was 29% for negative effects (Table 4). Detectable effect of composition and spatial pattern was at least three times and two times more frequent than would be expected by chance. Similar results were yielded by the ANOVAS (Appendices S6 and S7).

EFFECTS OF COMMUNITY ATTRIBUTES ON INDIVIDUAL FUNCTIONS

The effects of the different community attributes evaluated differed in sign and strength for different functions, and between the two depths considered.

In the Composition Experiment, the amount of total N found in subsurface soils at the end of the experiment increased with species richness (SEM results, Tables 1 and 4). Assemblages containing eight species had also significantly higher values of organic C than those with four species ($P = 0.002$, Tables 1 and 4, Appendix S6). Some of these responses were the opposite when surface soils were analysed, as the contents of total N and organic C were reduced as richness increased ($P < 0.037$, Tables 1 and 4; Appendix S6). The SEMs showed that species richness was positively associated with the activity of phosphatase in subsurface soils (Table 4). When analysing surface data from the Evenness experiment, both ANOVA and SEM analyses revealed that organic C and the activity of β-glucosidase decreased as species richness increased ($P < 0.039$, Tables 2 and 4, Appendices S7 and S8). The amount of total N significantly increased with augments in species richness, but the opposite response was found when analying subsurface soils ($P < 0.009$, Table 2, Appendix S7).

Changes in species composition significantly affected the content of organic C at the soil surface and that of both total N and β-glucosidase in subsurface soils (Composition experiment, $P < 0.003$, Table 1, Appendix S6). Variations in this attribute also promoted changes in the activity of phosphatase in subsurface soils (SEM results, Table 4).

In the Composition experiment, assemblages with a clumped pattern had higher total N (surface soils), and lower activities of β-glucosidase (subsurface soils), compared with those randomly patterned ($P < 0.045$, Tables 1 and 4, Appendices S6 and S8). Microcosms with a random pattern had also higher $NO_3^- - N$ values than those with a clumped pattern (SEM results, Tables 2 and 4). In the Evenness experiment, microcosms with this spatial pattern had higher N fixation rates than those with a clumped pattern (SEM results, Tables 2 and 4).

Species evenness by itself did not significantly affect any of the individual functions evaluated, but modulated the effects of other attributes on different functions. In the Evenness experiment, significant ($P < 0.05$) richness × evenness interactions were found when analysing organic C and the activity of phosphatase in subsurface soils (Appendix S7). We investigated this by conducting separate ANOVAS for each evenness level. Assemblages had the highest and lowest organic C values when they contained four species at the maximal and low evenness levels, respectively ($F_{2,30} > 5.6$, $P < 0.009$ in both cases, Appendix S9). No significant effects of species richness on the activity of β-glucosidase were found in uneven assemblages ($F_{2,\ 30} = 1.7$, $P = 0.201$), but this function tended to be higher in those microcosms with the maximal evenness ($F_{2,\ 30} = 3.0$, $P = 0.066$). Species evenness had also a role modulating the effects of spatial pattern, as a significant ($P = 0.012$) pattern × evenness interaction was found when

Table 1. Ecosystem functions measured at harvest in the Composition experiment. Data represent means ± SE at 0–2 cm and 2–5 cm (in parentheses) soil depths, $n = 6$ in all cases. Ri, number of species; Pa, spatial pattern; Co, species composition; OC, organic carbon (%); TN, total nitrogen (mg g^{-1} soil); NH_4^+–N, ammonia availability (μg cm^{-2}); NO_3^-–N, nitrate availability (μg cm^{-2}); Gl, β-glucosidase activity (μmol $g^{-1}h^{-1}$); Ph, phosphatase activity (μmol g^{-1} h^{-1}); U, urease activity (μmol g^{-1} h^{-1}); NF, nitrogen fixation (nm C_2H_4 g $soil^{-1}$ day^{-1}); Cl, clumped; Ra, random. A–D denote the four composition levels evaluated (see Appendix S1 for full details of the species forming them). The values of the microcosms containing only soil (Control) are included as a reference

Ri	Pa	Co	OC	TN	NH_4-N*	NO_3-N*	Gl	Ph	U	NF
4	Cl	A	0.85 ± 0.054 (0.50 ± 0.05)	0.66 ± 0.043 (0.43 ± 0.037)	0.02 ± 0.017	0.02 ± 0.018	0.45 ± 0.05 (0.11 ± 0.02)	0.56 ± 0.06 (0.09 ± 0.03)	0.81 ± 0.07	0.11 ± 0.05
		B	0.83 ± 0.050 (0.48 ± 0.04)	0.72 ± 0.053 (0.45 ± 0.035)	0.01 ± 0.015	0.02 ± 0.019	0.48 ± 0.05 (0.14 ± 0.03)	0.66 ± 0.08 (0.04 ± 0.02)	0.86 ± 0.09	0.10 ± 0.04
		C	0.88 ± 0.047 (0.47 ± 0.06)	0. 68 ± 0.076 (0.35 ± 0.023)	0.01 ± 0.010	0.03 ± 0.016	0.47 ± 0.05 (0.15 ± 0.02)	0.54 ± 0.07 (0.06 ± 0.04)	0.69 ± 0.07	0.19 ± 0.06
		D	0.66 ± 0.044 (0.39 ± 0.09)	0.61 ± 0.040 (0.35 ± 0.050)	0.01 ± 0.012	0.03 ± 0.007	0.47 ± 0.05 (0.13 ± 0.01)	0.59 ± 0.04 (0.05 ± 0.03)	0.61 ± 0.05	0.14 ± 0.04
	Ra	A	0.81 ± 0.046 (0.47 ± 0.05)	0.63 ± 0.038 (0.43 ± 0.037)	0.01 ± 0.012	0.03 ± 0.019	0.43 ± 0.04 (0.13 ± 0.03)	0.77 ± 0.07 (0.09 ± 0.03)	0.92 ± 0.08	0.15 ± 0.05
		B	0.89 ± 0.059 (0.48 ± 0.05)	0.67 ± 0.042 (0.41 ± 0.039)	0.02 ± 0.013	0.03 ± 0.019	0.40 ± 0.04 (0.14 ± 0.02)	0.55 ± 0.06 (0.03 ± 0.02)	1.02 ± 0.13	0.14 ± 0.03
		C	0.79 ± 0.049 (0.39 ± 0.06)	0.57 ± 0.031 (0.38 ± 0.032)	0.01 ± 0.014	0.02 ± 0.019	0.43 ± 0.04 (0.16 ± 0.02)	0.51 ± 0.07 (0.04 ± 0.02)	0.69 ± 0.09	0.18 ± 0.07
		D	0.68 ± 0.078 (0.53 ± 0.08)	0.60 ± 0.054 (0.40 ± 0.025)	0.02 ± 0.014	0.03 ± 0.014	0.48 ± 0.06 (0.13 ± 0.03)	0.65 ± 0.09 (0.04 ± 0.03)	1.09 ± 0.10	0.14 ± 0.04
8	Cl	A	0.73 ± 0.044 (0.72 ± 0.05)	0.58 ± 0.035 (0.40 ± 0.028)	0.01 ± 0.016	0.02 ± 0.020	0.46 ± 0.04 (0.12 ± 0.02)	0.46 ± 0.08 (0.06 ± 0.03)	0.84 ± 0.12	0.15 ± 0.04
		B	0.70 ± 0.030 (0.55 ± 0.03)	0.58 ± 0.045 (0.42 ± 0.025)	0.02 ± 0.015	0.03 ± 0.017	0.37 ± 0.04 (0.12 ± 0.02)	0.44 ± 0.07 (0.03 ± 0.01)	0.73 ± 0.10	0.12 ± 0.04
		C	0.65 ± 0.058 (0.58 ± 0.03)	0.60 ± 0.049 (0.43 ± 0.022)	0.01 ± 0.015	0.03 ± 0.022	0.40 ± 0.05 (0.11 ± 0.01)	0.56 ± 0.06 (0.12 ± 0.06)	0.78 ± 0.08	0.16 ± 0.04
		D	0.67 ± 0.050 (0.55 ± 0.05)	0.58 ± 0.046 (0.41 ± 0.032)	0.02 ± 0.008	0.03 ± 0.014	0.42 ± 0.03 (0.12 ± 0.02)	0.48 ± 0.07 (0.07 ± 0.04)	0.77 ± 0.06	0.15 ± 0.04
	Ra	A	0.69 ± 0.044 (0.64 ± 0.08)	0.56 ± 0.056 (0.44 ± 0.048)	0.01 ± 0.014	0.04 ± 0.023	0.36 ± 0.03 (0.15 ± 0.03)	0.68 ± 0.10 (0.07 ± 0.03)	0.50 ± 0.08	0.14 ± 0.04
		B	0.57 ± 0.060 (0.56 ± 0.03)	0.59 ± 0.032 (0.45 ± 0.031)	0.02 ± 0.009	0.04 ± 0.016	0.47 ± 0.06 (0.12 ± 0.02)	0.71 ± 0.10 (0.17 ± 0.03)	0.77 ± 0.09	0.17 ± 0.03
		C	0.70 ± 0.032 (0.62 ± 0.05)	0.58 ± 0.028 (0.42 ± 0.027)	0.01 ± 0.015	0.03 ± 0.020	0.47 ± 0.04 (0.13 ± 0.01)	0.56 ± 0.04 (0.07 ± 0.04)	0.69 ± 0.08	0.17 ± 0.04
		D	0.70 ± 0.057 (0.64 ± 0.04)	0.59 ± 0.048 (0.42 ± 0.031)	0.02 ± 0.014	0.05 ± 0.024	0.48 ± 0.05 (0.13 ± 0.03)	0.56 ± 0.09 (0.05 ± 0.03)	0.69 ± 0.07	0.10 ± 0.05
Control			0.62 ± 0.04 (0.50 ± 0.03)	0.45 ± 0.008 (0.44 ± 0.009)	0.01 ± 0.003	0.03 ± 0.003	0.17 ± 0.02 (0.10 ± 0.01)	0.34 ± 0.06 (0.08 ± 0.01)	0.60 ± 0.11	0.09 ± 0.02

*Data from ion-exchange membranes (0–2.5 cm depth).

Table 2. Ecosystem functions measured at harvest in the Evenness experiment. Data represent means ± SE at 0–2 cm and 2–5 cm (in parentheses) soil depths, $n = 6$ in all cases. Ri, Number of species; Eve, species evenness; Pa, spatial pattern; OC, organic carbon (%); TN, total nitrogen (mg g^{-1} soil); NH_4^+–N, ammonia availability (μg cm^{-2}); NO_3^-–N, nitrate availability (μg cm^{-2}); Gl, β-glucosidase activity (μmol $g^{-1}h^{-1}$); Ph, phosphatase activity (μmol g^{-1} h^{-1}); U, urease activity (μmol g^{-1} h^{-1}); NF, nitrogen fixation (nm C_2H_4 g $soil^{-1}$ day^{-1}); Ev, maximal evenness; Le, low evenness; Clu, clumped; Ran, random. The values of the microcosms containing only soil (Control) are included as a reference

Ri	Eve	Pa	OC	TN	NH_4-N*	NO_3-N*	Gl	Ph	U	NF
2	Ev	Clu	1.17 ± 0.03 (0.48 ± 0.02)	0.70 ± 0.03 (0.39 ± 0.05)	0.019 ± 0.004	0.026 ± 0.005	0.45 ± 0.04 (0.11 ± 0.01)	0.72 ± 0.10 (0.07 ± 0.01)	0.80 ± 0.08	0.18 ± 0.02
		Ran	1.03 ± 0.05 (0.48 ± 0.02)	0.65 ± 0.01 (0.42 ± 0.01)	0.018 ± 0.001	0.028 ± 0.002	0.45 ± 0.03 (0.12 ± 0.01)	0.70 ± 0.09 (0.07 ± 0.01)	0.88 ± 0.07	0.16 ± 0.01
	Le	Clu	1.05 ± 0.03 (0.56 ± 0.02)	0.65 ± 0.01 (0.40 ± 0.01)	0.019 ± 0.003	0.031 ± 0.008	0.46 ± 0.04 (0.12 ± 0.01)	0.67 ± 0.09 (0.06 ± 0.01)	0.79 ± 0.09	0.17 ± 0.01
		Ran	0.92 ± 0.08 (0.57 ± 0.02)	0.66 ± 0.03 (0.41 ± 0.02)	0.012 ± 0.003	0.026 ± 0.006	0.48 ± 0.04 (0.12 ± 0.01)	0.59 ± 0.08 (0.09 ± 0.02)	0.94 ± 0.13	0.38 ± 0.14
4	Ev	Clu	0.63 ± 0.02 (0.58 ± 0.02)	0.69 ± 0.02 (0.37 ± 0.01)	0.017 ± 0.003	0.031 ± 0.003	0.49 ± 0.02 (0.13 ± 0.01)	0.66 ± 0.08 (0.08 ± 0.01)	0.85 ± 0.07	0.19 ± 0.02
		Ran	0.65 ± 0.04 (0.58 ± 0.06)	0.68 ± 0.02 (0.39 ± 0.01)	0.015 ± 0.002	0.040 ± 0.004	0.42 ± 0.03 (0.12 ± 0.01)	0.85 ± 0.12 (0.08 ± 0.01)	0.93 ± 0.14	0.18 ± 0.03
	Le	Clu	0.72 ± 0.04 (0.43 ± 0.03)	0.73 ± 0.05 (0.41 ± 0.01)	0.017 ± 0.003	0.034 ± 0.006	0.40 ± 0.02 (0.10 ± 0.01)	0.69 ± 0.08 (0.05 ± 0.02)	0.95 ± 0.07	0.21 ± 0.07
		Ran	0.70 ± 0.02 (0.50 ± 0.02)	0.69 ± 0.03 (0.38 ± 0.01)	0.018 ± 0.002	0.037 ± 0.001	0.39 ± 0.01 (0.13 ± 0.01)	0.67 ± 0.04 (0.05 ± 0.01)	0.74 ± 0.09	0.18 ± 0.01
8	Ev	Clu	0.78 ± 0.07 (0.49 ± 0.03)	0.75 ± 0.05 (0.31 ± 0.01)	0.021 ± 0.001	0.031 ± 0.005	0.39 ± 0.04 (0.14 ± 0.02)	0.70 ± 0.11 (0.05 ± 0.02)	0.86 ± 0.05	0.13 ± 0.01
		Ran	0.79 ± 0.05 (0.42 ± 0.06)	0.73 ± 0.04 (0.39 ± 0.02)	0.015 ± 0.003	0.037 ± 0.006	0.40 ± 0.02 (0.13 ± 0.01)	0.87 ± 0.08 (0.06 ± 0.01)	0.80 ± 0.11	0.31 ± 0.10
	Le	Clu	0.83 ± 0.06 (0.52 ± 0.03)	0.76 ± 0.03 (0.38 ± 0.01)	0.020 ± 0.003	0.033 ± 0.006	0.42 ± 0.03 (0.13 ± 0.01)	0.74 ± 0.09 (0.06 ± 0.02)	1.14 ± 0.12	0.16 ± 0.01
		Ran	0.72 ± 0.02 (0.54 ± 0.03)	0.70 ± 0.03 (0.36 ± 0.01)	0.023 ± 0.003	0.027 ± 0.006	0.42 ± 0.03 (0.14 ± 0.01)	0.77 ± 0.12 (0.06 ± 0.01)	0.77 ± 0.12	0.25 ± 0.07
Control			0.57 ± 0.03 (0.61 ± 0.02)	0.53 ± 0.02 (0.30 ± 0.01)	0.015 ± 0.02	0.026 ± 0.0304	0.18 ± 0.01 (0.13 ± 0.008)	0.46 ± 0.06 (0.07 ± 0.01)	1.09 ± 0.10	0.15 ± 0.03

*Data from ion-exchange membranes (0–2.5 cm depth).

Table 3. Summary of the relative importance of community attributes in determining ecosystem functions and multifunctionality in SEM models. Mean path coefficient (λ) is the average standardized effect of a community attribute on the various measured functions in both experiments; because the sign associated with the effects of composition is meaningless, this mean is omitted for composition. The mean absolute value of λ is calculated similarly, except that the sign of the path is ignored; it is an average effect size statistic. The final three columns report the proportion of times a *P*-value associated with the listed path is less than a threshold of $P = 0.10$, $P = 0.05$ and $P = 0.01$. If apparent patterns were due to chance alone, these proportions would be expected to be about 0.10, 0.05 and 0.01; when the actual values are higher, it indicates an increasingly general pattern

	Mean λ	Mean |λ|	$P < 0.10$	$P < 0.05$	$P < 0.01$
Pattern	0.05	0.12	0.21	0.14	0.04
Richness	−0.01	0.21	0.54	0.43	0.14
Evenness	−0.03	0.08	0.00	0.00	0.00
Composition	–	0.22	0.32	0.29	0.21

analysing total N data in subsurface soils (Appendix S7). We investigated this interaction by conducting separate ANOVAS for each spatial pattern level. No significant effects of evenness on total N were found when such pattern was random ($F_{1, 30} = 1.8$, $P = 0.195$), but under a clumped spatial pattern, microcosms had higher total N under low evenness conditions ($F_{1, 30} = 5.0$, $P = 0.032$).

EFFECTS OF COMMUNITY ATTRIBUTES ON MULTIFUNCTIONALITY

When analysing subsurface soils in the Composition experiment, assemblages containing eight species had significantly higher values of the multifunctionality index than those with four species (12% on average; $P = 0.043$, Fig. 1, Appendix S6). A significant richness × evenness interaction ($P = 0.001$) was found in the Evenness experiment when analysing the multifunctionality index at this depth (Fig. 1, Appendix S7). We conducted separate ANOVAS for each evenness level to investigate it. Under maximal evenness, assemblages containing two and four species showed the highest values of the multifunctionality index, while under low evenness, this variable was maximized in microcosms containing two and eight species ($F_{2,30} > 3.7$, $P < 0.035$ in both cases, Appendix S9).

In the Composition experiment, complex variations among treatments in the proportion of assemblages achieving different multifunctionality thresholds (*T*) were found (Fig. 2, Appendices S10 and S11). Species richness had no significant effects on this proportion, albeit its effects were marginally significant ($P = 0.059$) when $T = 70\%$ (Appendices S10 and S11). Significant differences between composition levels were found for *T* values of 30% and 50% ($P < 0.05$, Fig. 2, Appendix S11). When $T = 50\%$, the proportion of assemblages achieving *T* increased under a random spatial pattern ($P = 0.001$, Appendices S10 and S11). Significant spatial pattern × composition and species richness × spatial pattern ×

Table 4. Complete results of structural equation models tabulated by experiment and response variable. Columns tabulate path coefficients (λ) and associated *P*-values for the four community properties (Pa, spatial pattern; Ri, richness; Ev, evenness; Co, composition). For the subsurface (sub) measurements, the influence of the surface (surf) value of the same variable is also listed. All paths in each structural equation model are associated with probability tests, which test the probability that the path estimate differs from zero. *P* values of these tests below 0.05 are in bold. R^2 refers to proportion of variance explained in the listed response. All the structural equation models conducted fitted the data adequately ($\chi^2 < 0.80$, $P > 0.97$, bootstrap $P > 0.98$ in all cases)

Experiment	Response	Pa	*P*	Ri	*P*	Ev	*P*	Co*	*P*	Surf. → sub.†	*P*	R^2
Composition	$Multifunction_{sub}$	0.12	0.220	0.38	**0.001**	–	–	0.16	0.176	0.23	0.090	0.22
Evenness	$Multifunction_{sub}$	0.14	0.229	−0.13	0.398	0.00	0.992	0.30	**0.009**	0.29	0.053	0.20
Composition	$Multifunction_{surf}$	0.18	0.080	−0.17	0.110	–	–	0.15	0.811	–	–	0.08
Evenness	$Multifunction_{surf}$	−0.03	0.960	0.00	0.900	−0.06	0.689	−0.17	0.553	–	–	0.03
Composition	N-fixation	0.05	0.647	−0.03	0.819	–	–	−0.19	0.537	–	–	0.04
Evenness	N-fixation	0.24	**0.023**	−0.03	0.963	−0.01	0.983	0.19	0.609	–	–	0.09
Composition	NH_4^+-N	0.09	0.350	0.07	0.525	–	–	0.20	0.247	–	–	0.05
Evenness	NH_4^+-N	−0.13	0.267	0.11	0.515	−0.19	0.181	−0.16	0.992	–	–	0.10
Composition	NO_3^--N	0.30	**0.003**	0.18	0.076	–	–	0.10	0.716	0.07	0.59	0.14
Evenness	NO_3^--N	0.04	0.720	−0.05	0.873	0.04	0.716	0.47	**0.002**	−0.08	0.524	0.21
Composition	Org C_{sub}	0.06	0.521	0.61	**0.001**	–	–	−0.11	0.852	0.30	0.020	0.28
Evenness	Org C_{sub}	0.01	0.893	−0.32	**0.040**	−0.18	0.203	−0.19	0.465	−0.18	0.263	0.11
Composition	Org C_{surf}	−0.08	0.325	−0.48	**0.001**	–	–	0.37	**0.003**	–	–	0.37
Evenness	Org C_{surf}	−0.14	0.172	−0.24	0.069	0.04	0.742	−0.34	**0.011**	–	–	0.28
Composition	$Phosphatase_{sub}$	0.07	0.550	0.21	**0.025**	–	–	0.29	**0.004**	−0.03	0.809	0.13
Evenness	$Phosphatase_{sub}$	0.06	0.714	−0.04	0.917	0.08	0.544	0.39	**0.011**	0.09	0.408	0.16
Composition	$Phosphatase_{surf}$	0.20	**0.037**	−0.10	0.339	–	–	0.16	0.484	–	–	0.08
Evenness	$Phosphatase_{surf}$	0.09	0.355	0.15	0.405	0.06	0.635	−0.20	0.776	–	–	0.08
Composition	Total N_{sub}	0.13	0.117	0.22	**0.013**	–	–	0.38	**0.006**	−0.04	0.781	0.21
Evenness	Total N_{sub}	0.15	0.152	−0.45	**0.019**	−0.15	0.140	−0.22	0.156	0.05	0.661	0.23
Composition	Total N_{surf}	−0.15	0.091	−0.31	**0.001**	–	–	0.22	0.188	–	–	0.17
Evenness	Total N_{surf}	−0.19	0.104	0.37	**0.026**	0.01	0.977	−0.17	0.699	–	–	0.20
Composition	Urease	0.05	0.651	−0.17	0.095	–	–	0.24	0.082	–	–	0.09
Evenness	Urease	−0.12	0.432	0.08	0.613	−0.11	0.421	−0.15	0.788	–	–	0.05
Composition	$β\text{-}gluc_{sub}$	0.20	**0.027**	−0.24	**0.031**	–	–	−0.42	**0.003**	0.12	0.176	0.29
Evenness	$β\text{-}gluc_{sub}$	0.12	0.238	0.38	**0.037**	0.13	0.387	0.16	0.874	0.35	0.010	0.18
Composition	$β\text{-}gluc_{surf}$	−0.01	0.900	−0.12	0.256	–	–	−0.06	0.612	–	–	0.02
Evenness	$β\text{-}gluc_{surf}$	−0.06	0.599	−0.29	0.059	−0.04	0.749	−0.14	0.802	–	–	0.111

*In the case of composition, the sign of the coefficient does not have meaning; thus, absolute values should be interpreted as an index of effect size.

†In the case of the effect of available N, both forms are measured at the surface only; therefore, the effect of NH_4^+-N on NO_3^--N was modelled and is reported here.

number of functions were also found when $T = 30\%$ (Fig. 2, Appendix S11). When $T = 70\%$, a significant spatial pattern × number of functions was also found ($P = 0.049$, Appendices S10 and S11). In the Evenness experiment, the proportion of assemblages achieving *T* increased with species richness when $T = 30\%$ and $T = 50\%$, albeit in the later case it was modulated by species evenness, as indicated by a significant richness × evenness interaction ($P < 0.025$ in all cases, Fig. 3, Appendix S12). When $T = 30\%$ and $T = 70\%$, the proportion of assemblages achieving *T* was higher under a random spatial pattern ($P < 0.033$, Fig. 3, Appendices S12 and S13). Such proportion increased under low evenness conditions when $T = 50\%$ ($P = 0.012$, Fig. 3, Appendix S12).

Discussion

Understanding how attributes of biotic communities, such as biodiversity, maintain and promote ecosystem functioning has received considerable attention by ecologists (Naeem *et al.* 2009; Cardinale *et al.* 2011). Yet no previous study has evaluated how different biodiversity components and the spatial arrangement of organisms influence multiple ecosystem functions simultaneously. Our results show important main effects and interactions of different community attributes on ecosystem functioning, both when considering particular functions in isolation and when evaluating multifunctionality. They also provide experimental evidence for a strong biotic control on ecosystem functioning in lichen-dominated BSCs, a key, but understudied, community in many terrestrial ecosystems (Belnap & Lange 2003).

When evaluating the results obtained with the different functions evaluated, species richness had the highest relative importance among all the community attributes evaluated (Table 3). These results agree with previous studies suggesting that richness is a key determinant of ecosystem functioning in BSC (Bowker, Maestre & Escolar 2010; Maestre *et al.* 2010) and plant (e.g., Hooper *et al.* 2005; Hector & Bagchi 2007; Zavaleta *et al.* 2010) communities. It must be noted, however, that some studies carried out with plant communities have not found species richness to be a strong predictor of soil functions

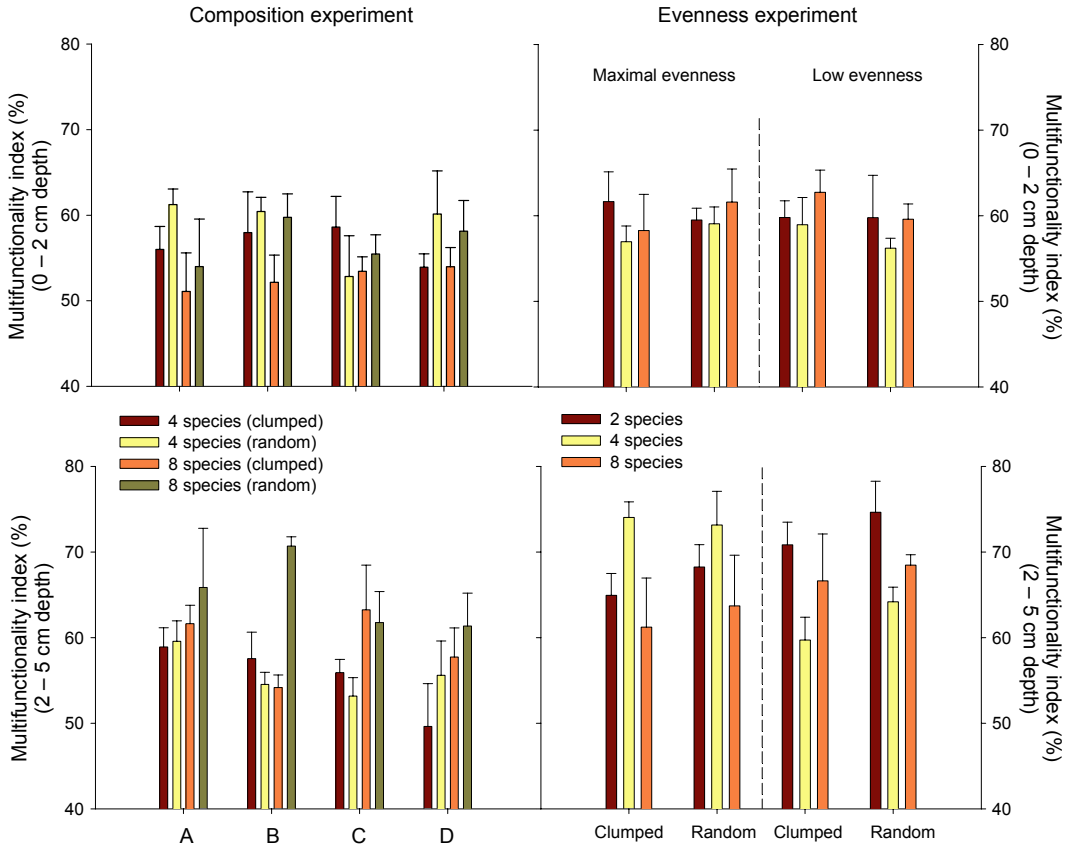

Fig. 1. Multifunctionality index for the Composition and Evenness experiments at the two depths evaluated. A–D in the *x* axis of the left panels denote the four composition levels used in the Composition experiment. Note that these compositions differ between the assemblages containing four and eight species (see Appendix S1 for details on the species forming the compositions used). Data are means ± SE ($n = 6$).

related to C and N cycling (e.g. De Deyn *et al*. 2009), and even when it is, the effects are often linked to the presence of specific plant functional groups (e.g. Fornara & Tilman 2008). In our study, the direction of the effects of species richness was not always consistent, as it ranged from negative to positive depending on the particular function, experiment and soil depth considered. The literature on biodiversity–ecosystem functioning using BSCs is in its infancy, and there are few studies to compare these responses with. However, our results agree with previous observations with BSCs suggesting that the linearity of the biodiversity–function relationship largely depends on the particular function being studied (Bowker, Maestre & Escolar 2010). While the responses observed with individual functions were not always positive, as commonly found with other primary producers (Cardinale *et al*. 2011), we found evidence indicating a positive effect of species richness on ecosystem multifunctionality. While this effect was not found in all the cases, the analyses of the multifunctionality index in the Composition experiment (subsurface soils) and of the proportion of assemblages exceeding different multifunctionality thresholds in the Evenness experiment revealed significant positive effects of species richness on ecosystem multifunctionality (Appendices S6, S7, and S12). Thus, our results provide some experimental evidence for the importance of the highest richness levels evaluated in this study in maintaining multiple ecosystem functions simultaneously and provide partial support for our first hypothesis (i.e. non-linear positive effects of species richness on ecosystem multifunctionality). These results support previous experimental studies using vascular plants and bacteria (Hector & Bagchi 2007; Gamfeldt, Hillebrand & Jonsson 2008; He *et al*. 2009; Zavaleta *et al*. 2010; Mouillot *et al*. 2011) and suggest that the probability of sustaining multiple ecosystem functions is enhanced as the richness of the lichen assemblages increases, at least within the range explored in our experiments.

Species evenness *per se* did not affect any of the functions evaluated and had the lowest relative importance of all the attributes measured when individual functions were considered (Table 3). However, in support of our second hypothesis, species evenness modulated the effects of species richness on important functions, such as organic C. Contrasting effects of species evenness on individual ecosystem functions have previously been reported in BSC (Bowker, Maestre & Escolar 2010) and plant (Wilsey & Polley 2004; Maestre & Reynolds 2006) communities. These results are not fully surprising, as the effects of the richness × evenness interaction on ecosystem functioning will largely be driven by individual species; when a dominant species has a strong influence on a given function, we would expect to see a negative relationship between evenness and this particular function, because evenness is inversely proportional to dominance. Species evenness was also an important driver of ecosystem multifunctionality, as it

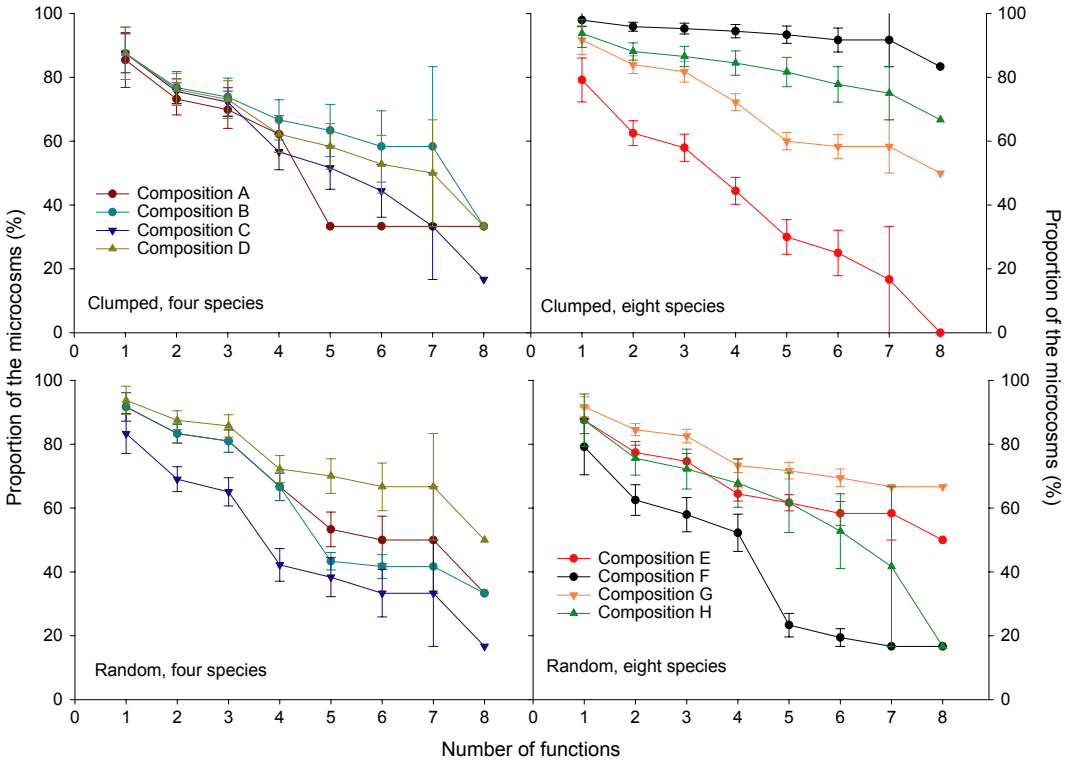

Fig. 2. Effects of composition, species richness and spatial pattern on the proportion of lichen assemblages that achieved a multifunctionality threshold (T) of 30% in the Composition experiment. See Appendix S1 for details on the species forming the eight compositions used in the experiment, and Appendix S9 for the same results when $T = 50\%$ and $T = 70\%$. Data are means ± SE (resulting from all possible combinations of the number of functions indicated in the x axis).

modulated the effects of species richness when evaluating both the multifunctionality index and the proportion of assemblages exceeding a 50% multifunctionality threshold (Appendices S7 and S12). When significant effects of evenness on these variables were found, multifunctionality was maximized in those assemblages with low evenness, particularly at the highest species richness levels evaluated. While the effects of species evenness on ecosystem multifunctionality have not been explored before, our results indicate that particular lichen species can affect multiple functions simultaneously, and thus, increases in their relative abundance compared with other species would promote ecosystem multifunctionality. Our experiments were not specifically designed to test for the effects of particular species, but it is worth highlighting that this idea is supported by a separate analysis of different field studies evaluating species-specific effects of BSC-forming lichens on five of the functions evaluated (total N, organic C, urease, glucosidase and phosphatase; Bowker *et al.* 2011). These authors found that species used in our experiment, such as *Diploschistes diacapsis* and *Squamarina lentigera* can affect all these functions when data from multiple studies are pooled, albeit effects on more than two functions simultaneously in a given site are more difficult to detect (Gotelli, Ulrich & Maestre 2011). While our results cannot provide a fully mechanistic understanding of the effects of species evenness found, they indicate that this attribute has important implications for fully understanding how species richness affects ecosystem multifunctionality, and as such must be explicitly considered in future biodiversity–functioning experiments.

As predicted by our third hypothesis, species composition had important effects on key functions, such as organic C and total N. Indeed, it had the same importance as species richness as a driver of isolated ecosystem functions (Table 3). These results match those of a recent analysis of biodiversity–ecosystem functioning experiments carried out with plants (Hector *et al.* 2011). Changes in species composition also modified substantially the proportion of assemblages exceeding multifunctionality thresholds (Appendix S11), highlighting the importance of this attribute to understand how reductions in biodiversity can affect ecosystem functioning. The effects of species composition could be a result of the unique assemblage of species, or they could indicate that one or a few species are having large effects on ecosystem responses. While the second scenario is often observed in terrestrial plant communities (Fridley 2001; Bruno *et al.* 2005; Downing 2005), a particular species is less likely to affect multiple ecosystem responses simultaneously in our assemblages, given the potentially indirect and complex links between the lichens and the ecosystem functions evaluated (Bowker, Maestre & Escolar 2010). Indeed, recent analyses of field data gathered at different spatial scales indicate that functional redundancy in the lichen species used in our microcosms is very low (Bowker *et al.* 2011). According to these authors, none of the species used in our experiments match the 'functional profile' (i.e. the effects

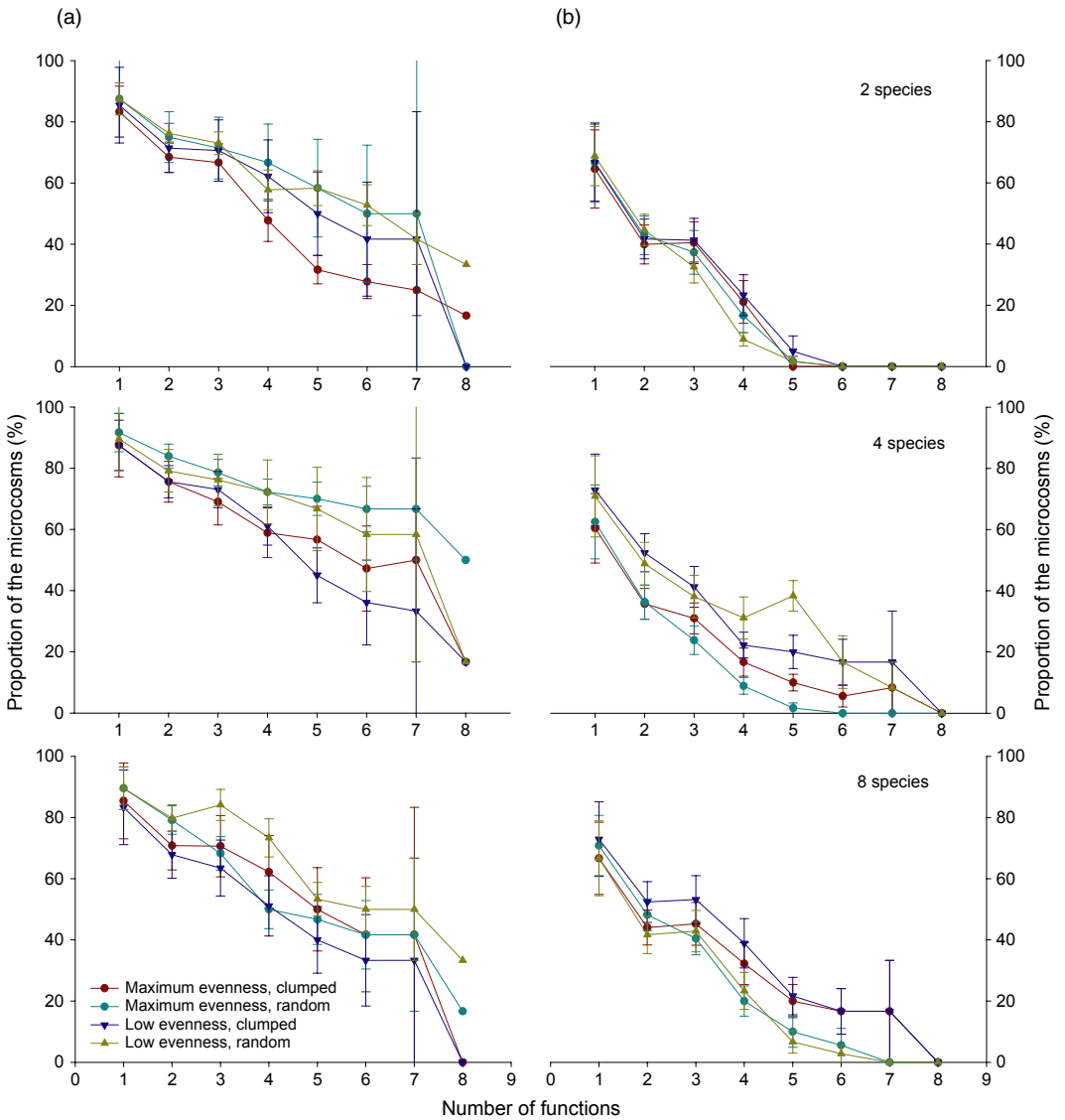

Fig. 3. Effects of species richness, species evenness and spatial pattern on the proportion of lichen assemblages that achieved a multifunctionality threshold (T) of 30% (a) and 50% (b) in the Evenness experiment. See Appendix S12 for the same results when $T = 70\%$. Data are means ± SE (resulting from all possible combinations of the number of functions indicated in the x axis).

of a given species – neutral, positive or negative – on a set of ecosystem functions) of any other species. The strong effects of composition on multifunctionality suggest that particular assemblages with unique suites of species interactions are likely responsible for some of the variation observed in ecosystem functioning.

Spatial pattern significantly affected several of the ecosystem functions assessed and interacted with evenness when evaluating total N in subsurface soils. This attribute was also an important driver of ecosystem multifunctionality, as it had an effect on the proportion of assemblages exceeding different multifunctionality thresholds, either directly or via interactions with other attributes (Appendices S7 and S11). The overall pattern that emerged was that ecosystem multifunctionality was maximized under a random spatial pattern. Our results clearly indicate that the spatial pattern of organisms can have an important role in ecosystem functioning. Previous studies have found that non-random distributions in the spatial distribution of resources (Replansky & Bell 2009; Langenheder *et al.* 2010; García-Palacios *et al.* 2011) and the physical environment (e.g. Griffin *et al.* 2009) can modulate diversity effects, but our experiments were carried out with homogeneous soils. Under these homogenous conditions, the different spatial arrangements created likely modified the degree of intra- and interspecific competition (Armstrong & Welch 2007). Indeed, and in support of our fourth hypothesis, we observed higher lichen mortality in the clumped microcosms (APCM and FTM, unpublished data). Given the lack of functional redundancy between species suggested by our results, it is plausible that competition-induced mortality could be the mechanism underlying the observed effects of spatial pattern. However, we do not yet know the relative importance of traits vs. biomass as determinants of ecosystem functioning in BSC communities, and thus cannot exclude other potential

mechanisms. If biomass plays an important functional role, then the reduced lichen biomass in those microcosms with higher degree of mortality, rather than a reduction in the diversity of traits present, could be responsible for the observed responses. A detailed examination of the dynamics and species interactions of transplanted lichens and the degree to which they may explain additional variation in function will be developed in a separate work. Our results add to the still scarce literature of empirical/experimental studies that have evaluated the functional consequences of the spatial pattern of organisms (Kikvidze *et al*. 2005; Maestre *et al*. 2005; Pringle *et al*. 2010). While the low number of studies available precludes making strong generalizations on such consequences, it is quite likely that particular spatial arrangements may have differential effects on ecosystem functioning depending both on the organisms studied and the ecosystem functions evaluated.

The combinations of species employed are common under field conditions (e.g. Martínez *et al*. 2006; Maestre *et al*. 2008; Bowker *et al*. 2011), and the experiments were carried out under natural conditions. However, our approach is not without limitations. While we defined species richness using clearly defined taxonomic units (lichen species), the transplanted lichen fragments could also add uncontrolled sources of bacteria, soil microfauna and fungi that can potentially mask the effects of the treatments being evaluated. But it must be noted that no species is an island, and the same problem is applicable to many experimental studies carried out with terrestrial and aquatic organisms, which have formed the foundation of our current knowledge on the relationships between biodiversity and ecosystem function. While we developed our experiments during a period long enough to allow the establishment and development of the artificial lichen assemblages created, they may not necessarily function as natural communities where species naturally establish and interact during longer periods to form complex communities. However, some of the patterns observed matched those from observational field studies (e.g. negative relationship between species richness and organic C in surface soils, Maestre *et al*. 2005), and the created assemblages were able to modify the different surrogates of ecosystem functioning evaluated, as indicated by the overall increase in their values compared with the control microcosms in many functions (Appendix S5). These results suggest that the assemblages created may function in a similar way as natural communities in the field.

Our experiments are the first in experimentally evaluating the effects of simultaneous changes in key community attributes (species richness, composition, evenness and spatial pattern) on multiple ecosystem functions and on ecosystem multifunctionality. They show that species richness, composition, evenness and spatial pattern are important drivers of individual functions in model BSC communities and highlight the potential role of species evenness and spatial pattern as key modulators of richness and composition effects on ecosystem multifunctionality. Our results also demonstrate that different biotic attributes impact ecosystem functions related to nutrient cycling and indicate that particular combinations of several of these attributes (e.g. high species richness, random spatial pattern and uneven species abundances) are required to maximize ecosystem multifunctionality. Albeit experimentally challenging, the explicit consideration of attributes such as spatial pattern in future biodiversity–functioning studies offer promise to fully disentangle the effects of biodiversity on ecosystem functioning and to increase our mechanistic understanding on the ecological consequences of its decline.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed materials and methods.

Appendix S2. Pictures of the setting up and harvesting of the microcosms.

Appendix S3. Schematic layout of the two experiments conducted.

Appendix S4. Examples of microcosms showing a random and clumped spatial pattern of biological soil crust-forming lichens.

Appendix S5. Synthesis of the statistical comparisons between the microcosms containing only soil and the different combinations of treatments in the Composition and Evenness experiments.

Appendix S6. Summary results of the ANOVA analyses of ecosystem functions measured in the Composition experiment.

Appendix S7. Summary results of the ANOVA analyses of ecosystem functions measured in the Evenness experiment.

Appendix S8. Selected structural equation models of the main effects of community properties on ecosystem functions in the Composition and Evenness experiments.

Appendix S9. Results of *post hoc* analyses of the species richness × evenness interactions found in the Evenness experiment.

Appendix S10. Proportion of lichen assemblages that achieved multifunctionality thresholds of 50% and 70% in the Composition experiment.

Appendix S11. Summary results of the ANOVA analyses carried out with the proportion of lichen assemblages achieving multifunctionality thresholds in the Composition experiment.

Appendix S12. Summary results of the ANOVA analyses carried out with the proportion of lichen assemblages achieving multifunctionality thresholds in the Evenness experiment.

Appendix S13. Proportion of lichen assemblages that achieved multifunctionality thresholds of 70% in the Evenness experiment.

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