

Functional profiles reveal unique ecological roles of various biological soil crust organisms

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Summary

1. At the heart of the body of research on biodiversity effects on ecosystem function is the debate over whether different species tend to be functionally singular or redundant. When we consider ecosystem multi-function, the provision of multiple ecosystem functions simultaneously, we may find that seemingly redundant species may in fact play unique roles in ecosystems.
2. Over the last few decades, the significance of biological soil crusts (BSCs) as ecological boundaries and ecosystem engineers, and their multi-functional nature, has become increasingly well documented. We compiled 'functional profiles' of the organisms in this understudied community, to determine whether functional singularity emerges when multiple ecosystem functions are considered.
3. In two data sets, one representing multiple sites around the semi-arid regions of Spain (regional scale), and another from a single site in central Spain (local scale), we examined correlations between the abundance or frequency of BSC species in a community, and multiple surrogates of ecosystem functioning. There was a wide array of apparent effects of species on specific functions.
4. Notably, in gypsiferous soils and at regional scale, we found that indicators of carbon (C) and phosphorus cycling were apparently suppressed and promoted by the lichens *Diploschistes diacapsis* and *Squamarina lentigera*, respectively. The moss *Pleurochaete squarrosa* appears to promote C cycling in calcareous soils at this spatial scale. At the local scale in gypsiferous soils, *D. diacapsis* positively correlated with carbon cycling, but negatively with nitrogen cycling, whereas numerous lichens exhibited the opposite profile.
5. We found a high degree of functional singularity, i.e. that species were highly individualistic in their effects on multiple functions. Many functional attributes were not easily predictable from existing functional grouping systems based primarily on morphology.
6. Our results suggest that maintaining species-rich BSC communities is crucial to maintain the overall functionality of ecosystems dominated by these organisms, and that dominance and the outcome of competition could be highly influential in the determination of such functionality.

Key-words: arid and semi-arid, bryophytes, ecosystem function, enzyme activities, lichens, trait diversity

Introduction

Despite their origins as a single discipline, the gap between community and ecosystem ecology has grown consistently wider. Community ecology tends to focus on the structure

of ecological communities (encompassing species interactions, assembly rules, succession), whereas ecosystem ecology focuses on the net function of biological organisms upon the storage, transformation and emission of energy and matter (e.g. production, N-fixation, erosion). This dichotomy is false because community structure can be an important determinant of ecosystem function. This assertion is bolstered by the recent line of work linking the competitive or facilitative interactions of species to their net contributions to ecosystem functioning (Kéfi *et al.* 2007;

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Scanlon *et al.* 2007; Maestre *et al.* 2010), and about 20 years of research examining the effects of biodiversity on such functioning (Naeem *et al.* 1994; Tilman *et al.* 1997; Naeem, Loreau & Inchausti 2002). Additionally, species interactions have long been proposed to be a mechanism which underlies the hump-shaped biodiversity–productivity relationship (Grime 1973; Michalet *et al.* 2006; Yachi & Loreau 2007). Thus far, the large majority of this work has focused upon plant communities and one ecosystem function, productivity (but see Hector & Bagchi 2007; Zavaleta *et al.* 2010). Here, we seek to expand our knowledge of the species-specific traits of biological soil crusts (BSCs), a community active in multiple ecosystem functions that is a major biotic component in cold and hot deserts and semi-arid areas world-wide (see Belnap & Lange 2003 for a review).

Within the biodiversity-function literature, much debate has occurred regarding which aspect or measure of biodiversity is most relevant in the determination of the net functional attributes of communities and ecosystems. It has been argued for some time that functional diversity, rather than taxonomic diversity is the metric of interest (Tilman *et al.* 1997). This idea is appealing, but belies the difficulty of defining what ‘units’ are enumerated by functional diversity, and solutions have run the gamut from the number of functional groups present (Tilman *et al.* 1997) to multivariate functional trait diversity (Cadotte *et al.* 2009). Putting these ideas into practice can be quite difficult because our *a priori* conceptions of functional groups and traits may be inadequate, and because we lack measurement of functional traits for the majority of organisms, although data basing efforts are underway (Naeem & Bunker 2009). The concept of ecosystem multi-functionality further complicates the matter, because ecosystem functioning is really composed of multiple distinct functions conducted simultaneously (Hector & Bagchi 2007; Zavaleta *et al.* 2010). Identifying the large number of traits that must be required to maintain multiple functions is a large task, especially in communities where there is a lack of published information. Here, we attempt a ‘functional profiling’ exercise, wherein the direct and indirect contributions of multiple species to multiple ecosystem functions are estimated and compiled. We consider this as an aid in identifying functional traits, and apply it to the understudied BSC community.

Biological soil crusts are composed of a disparate and intriguing group of organisms. They are present in the dry and/or extremely cold portions of all seven continents, where physiological barriers constrain vascular plant production (Belnap & Lange 2003). Collectively, BSC communities are unusually multi-functional (Bowker *et al.* 2008; Bowker, Maestre & Escolar 2010a), contributing to carbon fixation (Lange *et al.* 1992), nitrogen fixation (Belnap 2002) and mineralization (Castillo-Monroy *et al.* 2010), soil stabilization (Chaudhary *et al.* 2009), infiltration or runoff processes (Eldridge *et al.* 2010) and dust trapping (Reynolds *et al.* 2001). In addition, they exert a strong influence on other associated communities such as soil bacteria and fungi (Bates & Garcia-Pichel 2009), vascular plants (Green, Porrás-Alfaro & Sinsabaugh 2008) and microfauna (Neher *et al.* 2009). Bowker,

Maestre & Escolar (2010a) identified the need to define and measure functional traits of species in the BSC system. Despite that hundreds of papers exist on the potential contribution of BSC organisms to different ecosystem functions (e.g. Lange *et al.* 1992; Bowker *et al.* 2008), few have taken a community perspective and attempted to partition the relative influence of various species upon particular functions.

Using data from semi-arid natural ecosystems in Spain, we sought to determine if the species composing BSC exhibited contrasting functional profiles. We asked to what degree the nutrient cycling activity of a whole community is related to the prevalence of individual species within the community. We also combined our data with other recent data, and investigated the degree to which bryophyte and lichen species exert a unique set of influences upon ecosystem multi-functionality. Documenting the functional profiles of BSC species may be a useful step towards extending biodiversity-function theory to soil ecosystems using a novel model community (Bowker, Maestre & Escolar 2010a).

Materials and methods

STUDY SYSTEM

We analysed data from two studies, one conducted at multiple sites, and another within a single site. The multi-site study was conducted at 20 sites, including 12 sites with gypsiferous soils and eight sites with soils derived from limestones or calcareous marls. Our sampling in both soil types encompassed an environmental gradient spanning about 112 400 km² over central, southern, and eastern Spain, and represents the range of conditions under which BSCs are a prevalent type of ground cover in this country. Among the sites, average annual precipitation and average annual temperatures ranged from 334 to 632 mm, and from 13 to 18 °C, respectively (Ninyerola, Pons & Roure 2005). The single-site study was conducted on gypsum outcrops located near Belmonte del Tajo in Central Spain. The climate is Mediterranean semi-arid, with a mean annual temperature and rainfall of 14 °C and 452 mm, respectively (Ninyerola, Pons & Roure 2005). Key characteristics and locations of all sites are provided in Table A1-1, Appendix S1, Supporting information.

FIELD METHODS

Multi-site study

Within most sites, ten 1.5 m line intercept transects were sampled for percent cover at a species resolution. Transects were non-randomly placed across well developed, multi-specific BSC. We intentionally sampled transects with a wide variety in richness, cover and dominance within each site. We preferred this sampling to a traditional random sampling because such sampling would decrease our ability to locate particular species growing in near isolation or at least in high abundance. By ensuring that we sampled transects rich in the most abundant species, and containing a variety of species mixtures with different abundances, we can better isolate the effects of the different species present in the sampled sites. Transect placement was in all cases greater than 30 cm from the nearest perennial shrub or grass. In a few cases, small interspace size made it difficult to place 1.5 m transects, thus two parallel transects of 75 cm, and spaced 30 cm apart were sampled. Along the length of each transect the beginning and

end of every interception of a BSC moss, lichen, rock or bare patch was recorded to a 1 mm resolution. Whenever possible, mosses and lichens were identified to a species-level in the field, otherwise they were ascribed to genera.

After the percent cover sampling, we collected soil to a depth of 0–1 cm at ≥ 10 regularly spaced locations along each transect. We used either a shallow coring device or a wide-bladed putty knife to collect soil, depending on the effectiveness in the field, which was determined by soil moisture and rock content. Sampling was conducted from May to September 2008 and from May to August 2009. Samples were air-dried and stored in this condition for 1–6 months at room temperature until analyses could be completed. In semi-arid Mediterranean regions, air drying and medium-term storage of soils for up to 9 months does not appreciably degrade the soil biochemical properties of interest in this study (Zornoza *et al.* 2006, 2009). Indeed, this storage approach is commonly used when analysing these properties in arid and semi-arid environments world-wide (e.g., Jin *et al.* 2010; Maestre *et al.* 2010; Hbirkou *et al.* 2011; Zedda *et al.* 2011).

Single-site study

A total of 63 50 × 50 cm plots, spread over an homogeneous area of 1.3 ha, were placed non-randomly on areas with well-developed BSC located in the spaces between perennial plants (see Maestre *et al.* 2008 for details). 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. However, a minimum separation distance between plots of 0.7 m was established. Each plot was divided into 100 5 × 5 cm sampling quadrats, and the presence of all lichen species in every quadrat was registered (6300 quadrats were sampled in total). Bryophytes were not enumerated in this study. From these data, we calculated frequency of occurrence for each lichen species in the 50 × 50 cm plots.

Soil samples were obtained from all of the plots for the assessment of different surrogates of ecosystem functioning. Sampling was conducted in late September 2006, when the soil was dry after a pronounced summer drought. Twelve randomly placed 19.6 cm² circular soil cores were sampled to a 1 cm depth in each plot, then bulked and homogenized in the field. Samples were air-dried and stored in this condition for a month in the laboratory before analyses (Zornoza *et al.* 2006, 2009).

SOIL ANALYSES

In the soil underlying the BSC layer of each transect, we measured several indicators of nutrient cycling and stocks. In the multi-site study, we measured soil respiration, organic C, total N, and activity of three enzymes (phosphatase, urease, β -glucosidase). Soil respiration measures C-mineralization, and is a key indicator of decomposition rates and an overall relative index of total microbial activity (Kuzakov 2006). β -glucosidase provides another measure related to the processing of organic C, and the measurement of organic C provides a measure of soil C stocks. Likewise, urease is related to N-mineralization, and total N measures N stocks in the soil. Phosphatase activity is indicative of the mineralization of phosphorous. In the single-site study, organic C and soil respiration were not measured.

Respiration rates were determined by NaOH absorption followed by titration with HCl (Froment 1972). To do so, homogenized soils

were watered to 80% of a pre-determined field capacity, and incubated in sealed containers in a dark growth chamber at 22 °C for 4–5 days. Organic C was estimated by the Yeomans & Bremner (1989) method after the destruction of inorganic C (carbonates) in H₂SO₄. Total N and P were obtained on a SKALAR San⁺⁺ Analyzer (Skalar, Breda, The Netherlands) after digestion with sulphuric acid. Urease activity was determined as the amount of NH₄⁺ released from 0.5 g soil after incubation for 90 min with urea (6.4%) at 30 °C in phosphate buffer (pH 7) (Nannipieri *et al.* 1980). Phosphatase activity was measured by determination of the amount of *p*-nitrophenol released from 0.5 g soil after incubation at 37 °C for 1 h with the substrate *p*-nitrophenyl phosphate in MUB buffer (pH 6.5) (Tabatabai & Bremner 1969). The activity of β -glucosidase was assayed according to Tabatabai (1982), following the procedure for phosphatase, but using *p*-nitrophenyl- β -D-glucopyranoside as substrate and Trishydroxymethyl aminomethane instead of NaOH when preparing the buffer.

STATISTICAL ANALYSES

We used an ordination-based approach to determine if particular moss and lichen species have an especially important effect on the indicators of nutrient cycling and stocks measured. Because there are a large number of possible pairwise correlation tests among BSC species and ecosystem functions, this approach is more efficient than conducting univariate tests. We created a non-metric multidimensional scaling (NMDS) ordination of the BSC community data, using Bray-Curtis distance. The NMDS technique ordines data points which are associated with multivariate data, e.g. abundance of species in a community, based upon a user-chosen distance measure making it less strict regarding data distribution assumptions than many other techniques such as Principal Components Analysis and its derivatives. From a starting point of a random spherical ordination, single points are iteratively moved to reduce stress, which is disagreement between the distance between samples and their distance in the ordination space. This procedure continues until the user-set iteration limit is reached. Bray-Curtis distance is a useful distance measure with community data primarily because shared zeros among samples is not interpreted as similarity, as it is using linear distance measures. Dimensionality was determined by Monte Carlo tests, resulting in three dimensions in all cases. This ordination technique creates a multidimensional (three in our case) constellation of points; wherein points refer to samples and their degree of proximity indicates community similarity. It can be rotated in any direction without altering the spatial proximity of the points relative to one another. Information from a second data matrix can be overlaid in this ordination space by creating a joint biplot, wherein vectors are added to the ordination representing the correlation of variables from the second matrix (in our case, ecosystem function indicators) to the lichen-bryophyte ordination. For each of these cases, one at a time, we rotated the lichen-bryophyte ordination to maximize correlation with a given function vector. In this procedure, the first axis of the ordination is realigned so that it parallels the functional vector being considered (McCune & Grace 2002). After the rotation we obtained the Pearson correlations between the lichen species and this axis. This exercise was repeated for all function indicators. In the multi-site data set, we analysed gypsiferous and calcareous soils separately because of their different species composition, and likely inherent differences in the different soil variables measured. Results are referred to as very strong when $P < 0.01$, strong when $P < 0.05$, and moderate when $P < 0.10$.

SYNTHESIZING FUNCTIONAL PROFILES

We compiled the results of the two present studies with those of three other studies conducted at small scales in single sites from central Spain (Martínez *et al.* 2006; Eldridge *et al.* 2010; Castillo-Monroy *et al.* 2011). Castillo-Monroy *et al.* (2011) examined the apparent antibiotic effects of some lichen species upon soil bacteria. Eldridge *et al.* (2010) measured steady state infiltration on surfaces crusted by mosses and lichens. Martínez *et al.* (2006) measured soil respiration in soils associated with lichen-dominated BSC. We simply tabulated any moderate or stronger effects from this study along with species-level correlations reported from the other studies. We considered a row of such data to be a 'functional profile', and the degree to which a given species' functional profile differs from other species is its 'functional singularity'. These profiles include both direct effects of a species on a given ecosystem function or property, and its indirect effects mediated by interactions with other species.

Results

MULTI-SITE DATA SET

In gypsiferous soils, phosphatase activity was very strongly negatively related to *Diploschistes diacapsis*, and very strongly positively related to *Squamarina lentigera* (Fig. 1a, Table A2-1, Supporting information). The other enzyme activities, β -glucosidase and urease were less responsive to crust community structure (Table A2-1), with the strongest relationship being a strong negative relationship between the former and *D. diacapsis* (Fig. 1a). Total C and N pools were similarly affected, both being positively and at least strongly correlated with *S. lentigera* and negatively related with *D. diacapsis* (Fig. 1a, Table A2-1).

In calcareous soils, phosphatase activity, urease activity, total N and soil respiration were all generally unaffected by the relative abundance of BSC mosses and lichens (Table A2-2). The variables related to C-cycling were much more related. Both β -glucosidase and organic C were most strongly, positively affected by *Pleurochaete squarrosa* (Fig. 1b). Ten additional species also were related to organic C, including a very strong negative correlation with *S. lentigera* (Fig. 1b), and a very strong positive correlation with *Cladonia convoluta* (Table A2-2).

SINGLE-SITE DATA SET

In the single-site data set, none of the lichen species were well correlated with phosphatase activity (Table A2-3). This was in sharp contrast to β -glucosidase, which was variously affected by 11 of the 17 species found (Table A2-3). The most important effects included very strong positive effects of *D. diacapsis*, and very strong negative effects of *S. lentigera*, *Fulgensia subbracteata*, *Collema crispum*, *Psora decipiens*, and *Acarospora reagens* (Fig. 2). Urease activity was similarly correlated at least moderately with 13 different species, most of which exerted positive effects (Table A2-3). Most importantly, *D. diacapsis* was very strongly negatively correlated with urease activity, and the following species were very

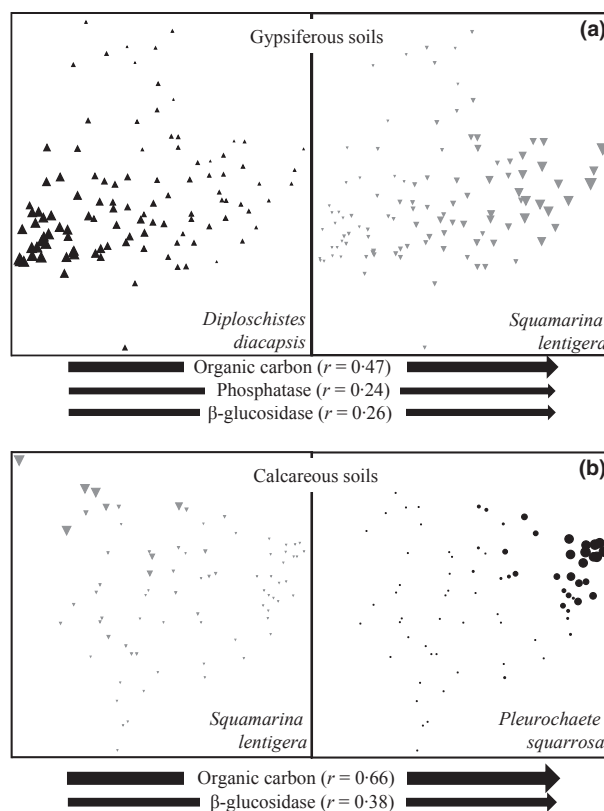


Fig. 1. Non-metric multidimensional scaling ordinations of samples in the multi-site study in community space, illustrating selected correlations between biological soil crust species and particular functions. Side by side panels show an identical ordination with symbols resized to be proportional with the indicated species. (a) In gypsiferous soils, the ordination is rotated so that the correlation with organic carbon is maximized on the horizontal axis. Coincidentally, the correlation with β -glucosidase is also maximized, and with phosphatase nearly maximized. (b) In calcareous soils the ordination is also rotated so that the correlation with organic carbon is maximized on the horizontal axis. Coincidentally, the axis is also correlated with β -glucosidase.

strongly positively correlated: *C. convoluta*, *P. decipiens*, *C. crispum*, *F. subbracteata*, and *Squamarina* spp. (Fig. 2). Total N pools were less affected by soil crust community structure, exhibiting a moderate negative correlation with *A. reagens*, and a strong positive correlation with *C. convoluta* (Table A2-3).

FUNCTIONAL PROFILES

When the results of the two present studies were compiled with those of two published studies conducted at small scales in single sites from central Spain, a large degree of functional singularity and lack of redundancy is apparent. Over half of the 23 most common species considered (>0.5% of total abundance or frequency) had functional profiles that were completely unique (Table 1). Some notable functional profiles included the three most abundant species: (i) *P. squarosum* was positively associated with β -glucosidase, organic C and infiltration; (ii) *D. diacapsis* was negatively associated

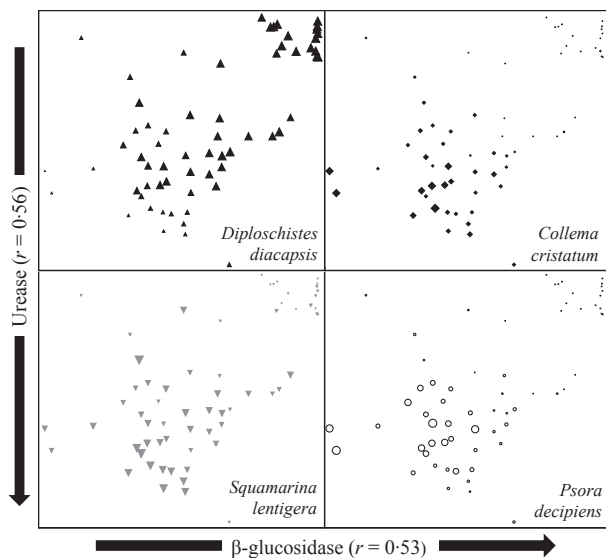


Fig. 2. Non-metric multidimensional scaling ordinations of samples in the single-site study in community space, illustrating selected correlations between soil crust species and particular functions. All panels show an identical ordination with symbols resized to be proportional with the indicated species. The ordination is rotated so that the correlation with β -glucosidase is maximized on the horizontal axis. Coincidentally, the correlation between the vertical axis and urease is nearly maximized.

with most functions but could have either positive or negative effects on β -glucosidase and some bacteria; (iii) *S. lentigera* was positively associated with phosphatase, urease, and total N, was negatively associated with infiltration, and could have either negative or positive associations with β -glucosidase and organic C. These examples highlight functional singularity of the dominant species present in the studied BSC communities.

Discussion

FUNCTIONAL PROFILING AT A COMMUNITY LEVEL: ADVANTAGES AND LIMITATIONS

In this study we applied a correlative approach to determine associations between BSC-forming bryophytes and lichens and various ecosystem functions, and compiled them with similar information from recent studies to create functional profiles. Our approach has strengths and weaknesses. In a community context, it may be difficult to know which species is influencing which ecosystem function. A species may be correlated with a particular function, for the sole reason that it co-occurs with another species which exerts an actual effect on a function. By intentionally, non-randomly selecting samples with strongly contrasting dominance and community composition, we can reduce this problem. Drawing inference about rarer or always less abundant species is, however, difficult using this strategy.

On the other hand, the community approach allows us to simultaneously evaluate the effects of multiple species on the

environment, and allows us to view the total effects of an organism on its environment whether they be direct or indirect. It might be argued that the results are biased because the effect of a given species on the environment might be enhanced or suppressed by associated species. We counter that the functionality of these species occurs in a community context, thus, to isolate them biases the estimate of their contribution to ecosystem function. Since BSC species exist in tightly-knit communities rather than in isolation, the true functional profile of a species, in our opinion, includes indirect effects that are mediated by synergistic or antagonistic species interactions.

TRANSFORMATIVE AND TRANSMISSIVE FUNCTIONS

Given the above cautionary points, when the data from multiple studies are pooled, we can infer much about the functional diversity in BSC communities. BSC are an example of an ecological boundary between atmosphere and soil (Belnap, Hawkes & Firestone 2003). Boundaries tend to take on emergent properties that neither bordering region possess, and will tend to modulate transfer of materials and energy from one side to the other (Strayer *et al.* 2003). Many of the functions we examined are related to movement of materials across the soil-atmosphere boundary. From our functional profiles (Table 1), it appears important whether or not a particular functional outcome requires a transmissive or transformative behaviour in the boundary created by the soil crust. Transmissive boundary behaviours allow the passage of some portion of a material to pass unaltered from one patch type to another (Strayer *et al.* 2003). Transformative boundary behaviours change a material from one form into another as it passes from one side of the boundary to the other (Strayer *et al.* 2003). Infiltration is an example of the transmittance of water into the soil, and appears largely to be an outcome of physical morphology. The larger statured and more loosely tufted mosses *P. squarrosa* and *Syntrichia ruralis* are most strongly positively correlated with infiltration, whereas the common lichen species are negatively correlated with it. This could have been predicted well by morphological groups (Eldridge & Rosentreter 2000), and we suspect that this may be true of other transmissive functions of the crust, such as dust trapping. Such morphometric functional traits are well reported in the taxonomic treatments (Brodo, Sharnoff & Sharnoff 2001).

The transformative boundary functions, such those related to soil C and N cycling, are more difficult to predict, as evidenced by very different functional profiles of the most common lichen species, regardless of their morphological group. This is also true of other transformative functions that do not involve boundaries, such as soil phosphatase activity. Likely, this is because a species' contribution to these functions depends upon its physiological characteristics and its chemical composition, which are only sparsely reported in the literature (but see Lange 2003). Another complicating feature is that a lichen or moss may induce a functional response *via* more than one pathway. Some of the chemical effects of

Table 1. Functional profiles of the most common (>0.5% of total abundance or frequency) biological soil crust species encountered (mosses and lichens)

| | Phosphatase activity | β -glucosidase activity | Organic C pool | Respiration | Effects on bacteria | Urease activity | Total N pool | Infiltration |
|--------------------------------|----------------------|-------------------------------|----------------|-------------|---------------------|-----------------|--------------|--------------|
| <i>Leproloma</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | nd |
| <i>Cladonia rangiformis</i> | 0 | 0 | 0 | 0 | nd | 0 | 0 | nd |
| <i>Tortula revolvens</i> | 0 | 0 | 0 | 0 | nd | 0 | 0 | 0 |
| <i>Didymodon</i> sp. | 0 | 0 | 0 | 0 | nd | 0 | 0 | 0 |
| <i>Catapyrenium piloselum</i> | 0 | 0 | nd | 0 | 0 | 0 | 0 | nd |
| <i>Syntrichia ruralis</i> | 0 | 0 | 0 | 0 | nd | 0 | 0 | + |
| <i>Psora albicum</i> | 0 | 0 | nd | 0 | - | 0 | 0 | nd |
| <i>Endocarpon</i> | 0 | 0 | 0 | 0 | - | + | 0 | nd |
| <i>Toninia sedifolia</i> | 0 | 0 | 0 | 0 | - | + | 0 | nd |
| <i>Fulgensia fulgens</i> | 0 | 0 | - | 0 | nd | 0 | 0 | nd |
| <i>Buellia zoharii</i> | 0 | 0 | -/+ | 0 | 0 | 0 | 0 | 0 |
| <i>Cladonia convoluta</i> | 0 | 0 | + | 0 | 0 | + | 0 | - |
| <i>Weissia</i> sp. | 0 | - | - | 0 | nd | 0 | 0 | 0 |
| <i>Placidium squamulosum</i> | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Psora saviczii</i> | 0 | + | 0 | 0 | 0 | + | 0 | nd |
| <i>Acarospora reagens</i> | 0 | + | 0 | 0 | 0 | + | 0 | 0 |
| <i>Collema cristatum</i> | 0 | + | 0 | 0 | - | + | 0 | 0 |
| <i>Squamarina cartilaginea</i> | 0 | + | 0 | 0 | - | + | 0 | - |
| <i>Fulgensia subbracteata</i> | 0 | + | 0 | - | - | + | 0 | - |
| <i>Psora decipiens</i> | 0 | + | - | -* | 0 | + | 0 | - |
| <i>Pleurochaete squarrosa</i> | 0 | + | + | 0 | nd | 0 | 0 | + |
| <i>Diploschistes diacapsis</i> | - | -/+ | - | -* | -/+ | - | - | - |
| <i>Squamarina lentigera</i> | + | -/+ | -/+ | 0 | 0 | + | + | - |

We tabulated effects of at least moderate strength from multiple sources considering the following cases: (1) Multi-site study calcareous soils, (2) multi-site study gypsiferous soils, (3) single-site study, (4) previous studies conducted in a single site (Castillo-Monroy *et al.* 2010; Eldridge *et al.* 2010; Martínez *et al.* 2006). A positive record (+) indicates that the species has been shown to exhibit a positive effect of at least moderate strength ($P < 0.10$) in at least one case, with no studies exhibiting a negative effect. A negative record (-) indicates that, regardless of soil type, the species has been shown to exhibit a negative effect of at least moderate strength in at least one case, with no studies exhibiting a positive effect. A null record (0) indicates that at least one case contained an available measurement, but no effects of moderate or greater strength were detected. A mixed record (-/+) indicates that at least one positive and at least one negative moderate or stronger effect were observed in multiple cases. All data on effects on bacteria are from Castillo-Monroy *et al.* (2010). All data on infiltration are from Eldridge *et al.* (2010).

*Data from Martínez *et al.* (2006).

nd, no data available. See Appendix S2 for more details including exact P -values from the present studies.

species might be rather straightforward; for example, it would be reasonable to think that the lichen *S. lentigera* may exhibit high phosphatase activity. On the other hand, because of their secondary metabolites, a given lichen species could induce such a response even if it is incapable of producing phosphatases. This is because it may produce chelators that alter the nutrient environment, numerous acids which can lower the pH, or antibacterial agents (Tay *et al.* 2004; Hauck *et al.* 2009), all of which could alter the microbial community and its net phosphatase activity.

There are hundreds of chemical compounds that are known only from lichens (Fahsel 1994). The mosses may also hide an impressive diversity of secondary chemicals (Mues 2000). Given the diversity of secondary metabolites, and the multiple pathways of influencing transformative functions, it is clear that before we can ascribe chemical traits to particular functions, we need: (i) a better idea of what chemicals are involved in certain functions; (ii) a better mechanistic understanding of the ways in which they work; and (iii) a more complete accounting of the chemical composition of moss and lichen species.

A ROLE FOR COMPETITION IN DETERMINATION OF BSC FUNCTION

The functional outcomes of the great variety in chemical attributes in BSC-forming mosses and lichens led to some stark contrasts. Two of the most dominant lichens of gypsum soils contrast sharply in the ways that they interact with their environment, and both contrast sharply with the dominant moss. *D. diacapsis* and *S. lentigera* were negatively and positively correlated with both urease and phosphatase activity, respectively. Regarding variables related to C cycling, both species tended to exert strong effects, although the effects shifted from positive to negative depending on the data set. Even in these cases, where species-level effects on a function tend to be inconsistent, these two species were consistently opposite to one another. The main way in which they are similar is in retarding infiltration, which contrasts them sharply with *P. squarrosa*. *Pleurochaete* was also a very strong promoter of soil C-cycling, more so than either lichen in calcareous soils. Most gypsiferous sites are dominated by one of these species, which compete intensely and reciprocally (Bowker, Soliveres

& Maestre 2010b). It appears in this case that the outcome of this key competition battle would go a long way towards explaining the net functional attributes of the community.

Yachi & Loreau (2007) modelled a situation where niche complementarity of a three dimensional plant community and competitive imbalance interacted to determine whether biodiversity enhanced an ecosystem function (productivity). In this model, complementarity in canopy height could offset light competition, but this alone was not enough to result in the positive biodiversity–productivity relationship, suggesting that there must also be competitive imbalance. Mulder, Uliassi & Doak (2001) used experimental moss communities to demonstrate that under high abiotic stress facilitative interactions led to a greater dependency of productivity on diversity. In the case of BSC communities studied here, the first model may not apply because there is a relative lack of niche complementarity, and the second may not apply because competition, rather than facilitation, is the dominant type of interaction (Bowker, Soliveres & Maestre 2010b). Recently, using both BSC and vascular plant study systems, Maestre *et al.* (2010) concluded that compared to other community attributes, indicators of community-wide competition intensity in biological crusts were very poor predictors of various ecosystem functions. Perhaps the reason why this is so is that ecosystem functioning depends primarily on the identity of the winner of the competition and its functional profile (Hooper *et al.* 2005), rather than the intensity of community-wide competition.

FUNCTIONAL SINGULARITY OF CRUST MOSSES AND LICHENS

When the effects of BSC species on multiple ecosystem functions are tabulated, it becomes apparent that there are few pairings of the common species with identical combinations of functional attributes, in effect there is a low degree of redundancy (Naeem 1998). Of the twenty-three most common species, thirteen do not match the functional profile of any other species. This group includes the species that are by far most likely to dominate BSC communities. Another three species form a perfect match with only one other species. There are five species which appear to be neutral regarding their effects on the functions examined, however this may arise simply because none of them are particularly abundant nor do they ever dominate, thus it is difficult to determine their functional profile without isolating them. A more focused look at these species might determine that they mask functional diversity.

These observations are perhaps consistent with other recent findings. In four data sets, species richness of BSCs outperformed functional group richness in predicting various ecosystem function indicators (Bowker, Maestre & Escolar 2010a). This may have arisen because functional groups identified for a specific set of ecosystem properties may not be relevant to other properties (Hooper *et al.* 2005). This failure of functional groups to explain ecosystem function may reveal that, to a large degree, BSC species are functionally singular.

This implies that each species is effectively a unique functional group, a conclusion which is supported by our functional profiles. Even in a well-studied vascular plant ecosystem, it was found that functional diversity based upon richness of commonly-applied *a priori* groups explained productivity no better than randomly derived groups (Wright *et al.* 2006). Efforts are currently underway to establish databases of functional traits of vascular plants (e.g. TraitNET; Naeem & Bunker 2009), and similar groundwork has been laid for cryptogams (Cornelissen *et al.* 2007; Bowker, Maestre & Escolar 2010a). We believe that enabling and applying a functional trait-based index of diversity for BSC organisms would be very valuable in elucidating the effects of biodiversity and community structure on ecosystem functions.

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References

- Bates, S.T. & Garcia-Pichel, F. (2009) A culture-independent study of free-living fungi in biological soil crusts of the Colorado Plateau: their diversity and relative contribution to microbial biomass. *Environmental Microbiology*, **11**, 56–67.
- Belnap, J. (2002) Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biology and Fertility of Soils*, **35**, 128–135.
- Belnap, J., Hawkes, C.V. & Firestone, M.K. (2003) Boundaries in miniature: two examples from soil. *BioScience*, **53**, 739–749.
- Belnap, J. & Lange, O.L., eds (2003) *Biological Soil Crusts: Structure Function and Management*. Springer-Verlag, Berlin.
- Bowker, M.A., Maestre, F.T. & Escolar, C. (2010a) Biodiversity of biological crusts influences ecosystem function: a review and reanalysis. *Soil Biology and Biochemistry*, **42**, 405–417.
- Bowker, M.A., Soliveres, S. & Maestre, F.T. (2010b) Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *Journal of Ecology*, **98**, 551–560.
- Bowker, M.A., Miller, M.E., Belnap, J., Sisk, T.D. & Johnson, N.C. (2008) Prioritizing conservation effort through the use of biological soil crusts as ecosystem function indicators in an arid region. *Conservation Biology*, **22**, 1533–1543.
- Brodo, I.M., Sharnoff, S.D. & Sharnoff, S. (2001) *Lichens of North America*. Yale University Press, New Haven, Connecticut.
- Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, **4**, e5695.
- Castillo-Monroy, A.P., Maestre, F.T., Delgado-Baquerizo, M. & Gallardo, A. (2010) Biological soil crust modulate nitrogen availability in semi-arid ecosystem: insights from a Mediterranean grassland. *Plant and Soil*, **333**, 21–34.
- Castillo-Monroy, A.P., Bowker, M.A., Maestre, F.T., Rodríguez-Echeverría, S., Martínez, I., Barraza-Zepeda, C.E. & Escolar, C. (2011) The relative importance of biological soil crust and soil bacterial diversity and abundance as drivers of ecosystem functioning in a semi-arid environment. *Journal of Vegetation Science*, **22**, 165–174.
- Chaudhary, V.B., Bowker, M.A., O'Dell, T.E., Grace, J.B., Redman, A.E., Rillig, M.C. & Johnson, N.C. (2009) Untangling the biological contributions to soil stability in semiarid shrublands. *Ecological Applications*, **19**, 110–122.
- Cornelissen, J.H.C., Lang, S.J., Soudzilovskaia, N.A. & During, H.J. (2007) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, **99**, 987–1001.

- Eldridge, D.J. & Rosentreter, R.R. (2000) Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. *Journal of Arid Environments*, **42**, 11–25.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Alonso, P., Mau, R.L., Papadopoulos, J. & Escudero, A. (2010) Interactive effects of three ecosystem engineers on infiltration in a semi-arid grassland. *Ecosystems*, **13**, 499–510.
- Fahsel, D. (1994) Secondary biochemistry of lichens. *Symbiosis*, **16**, 117–165.
- Froment, A. (1972) Soil respiration in a mixed oak forest. *Oikos*, **23**, 273–277.
- Green, L.E., Porras-Alfaro, A. & Sinsabaugh, R.L. (2008) Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland. *Journal of Ecology*, **96**, 1076–1085.
- Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.
- Hauck, M., Jürgens, S.R., Willenbruch, K., Huneck, S. & Leuschner, C. (2009) Dissociation and metal-binding characteristics of yellow lichen substances suggest a relationship with site preferences of lichens. *Annals of Botany*, **103**, 13–22.
- Hbirkou, C., Martius, C., Khamzina, A., Lamers, J.P.A., Welp, G. & Amelung, W. (2011) Reducing topsoil salinity and raising carbon stocks through afforestation in Khorezm, Uzbekistan. *Journal of Arid Environments*, **75**, 146–155.
- Hector, A. & Bagchi, R. (2007) Biodiversity and ecosystem multifunctionality. *Nature*, **448**, 188–190.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Jin, Z., Dong, Y.S., Qi, Y.C. & An, Z.S. (2010) Soil respiration and net primary productivity in perennial grass and desert shrub ecosystems at the Ordos Plateau of Inner Mongolia, China. *Journal of Arid Environments*, **74**, 1248–1256.
- Kéfi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., Papanastasis, V.P., El Aich, A. & de Ruiter, P. (2007) Spatial vegetation patterns and imminent desertification in Mediterranean arid. *Nature*, **449**, 213–217.
- Kuzyakov, Y. (2006) Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry*, **38**, 425–448.
- Lange, O.L. (2003) Photosynthesis of soil-crust biota as dependent on environmental factors. Biological soil crusts: structure, function, and management (eds J. Benlap & O.L. Lange), pp. 263–280. Springer-Verlag, Berlin.
- Lange, O.L., Kidron, G., Büdel, B., Meyer, A., Kilian, E. & Abeliovich, A. (1992) Taxonomic composition and photosynthetic characteristics of the “biological soil crusts” covering sand dunes in the western Negev Desert. *Functional Ecology*, **6**, 519–527.
- Maestre, F.T., Escobar, C., Martínez, I. & Escudero, A. (2008) Are soil lichen communities structured by biotic interactions? A null model analysis. *Journal of Vegetation Science*, **19**, 261–266.
- Maestre, F.T., Bowker, M.A., Puche, M.D., Escobar, C., Soliveres, S., Mouro, S., García-Palacios, P., Castillo-Monroy, A.P., Martínez, I. & Escudero, A. (2010) Do biotic interactions modulate ecosystem functioning along abiotic stress gradients? Insights from semi-arid plant and biological soil crust communities. *Philosophical Transactions of the Royal Society B*, **365**, 2057–2070.
- 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.
- McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities*. MJM Software Design, Gleneden Beach, Oregon, USA.
- Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I., Valiente-Banuet, A. & Callaway, R.M. (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, **9**, 767–773.
- Mues, R. (2000) Chemical constituents and biochemistry. *Bryophyte Biology* (eds A. J. Shaw & B. Goffinet), pp. 150–181. Cambridge University Press, UK.
- Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001) Physical stress and diversity-productivity relationships: the role of positive interactions. *Proceedings of the National Academy of Sciences*, **98**, 6704–6708.
- Naeem, S. (1998) Species redundancy and ecosystem reliability. *Conservation Biology*, **12**, 39–45.
- Naeem, S. & Bunker, D.E. (2009) TraitNet: furthering biodiversity research through the curation, discovery, and sharing of species trait data. *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective* (eds S. Naeem, D. E. Bunker, A. Hector, M. Loreau & C. Perrings), pp. 281–289. Oxford University Press, Oxford.
- Naeem, S., Loreau, M. & Inchausti, P. (2002) Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. *Biodiversity and Ecosystem Functioning* (eds M. Loreau, S. Naeem & P. Inchausti), pp. 3–11. Oxford University Press, New York.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can affect the functioning of ecosystems. *Nature*, **368**, 734–737.
- Nannipieri, P., Ceccanti, B., Cervelli, S. & Matarese, E. (1980) Extraction of phosphatase, urease, protease, organic carbon and nitrogen from soil. *Agronomy Journal*, **44**, 1011–1016.
- Neher, D.A., Lewins, S.A., Weicht, T.R. & Darby, B.J. (2009) Microarthropod communities associated with biological soil crusts in the Colorado Plateau and Chihuahuan deserts. *Journal of Arid Environment*, **73**, 672–677.
- Ninyerola, M., Pons, X. & Roure, J.M. (2005) *Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica*. ISBN 932860-8-7. Universidad Autónoma de Barcelona, Bellaterra.
- Reynolds, R., Belnap, J., Reheis, M., Lamothe, P. & Luiszer, F. (2001) Aeolian dust in Colorado Plateau soils: nutrient inputs and recent change in source. *Proceedings of the National Academy of Sciences*, **98**, 7123–7127.
- Scanlon, T.M., Caylor, K.K., Levin, S.A. & Rodriguez-Iturbe, I. (2007) Positive feedbacks promote power-law clustering of Kalahari vegetation. *Nature*, **449**, 209–212.
- Strayer, D.L., Power, M.E., Fagan, W.F., Pickett, S.T.A. & Belnap, J. (2003) A classification of ecological boundaries. *BioScience*, **53**, 723–729.
- Tabatabai, M.A. (1982) Soil enzymes. *Methods of Soil Analyses Part 2, Chemical and Microbiological Properties* (eds A. L. Miller, R. H. Miller & D. R. Keeney), pp. 903–947. American Society of Agronomy, Madison, WI.
- Tabatabai, M.A. & Bremner, J.M. (1969) Use of p-nitrophenylphosphate for assay of soil phosphatase activity. *Soil Biology and Biochemistry*, **1**, 301–307.
- Tay, T., Türk, A.Ö., Yilmaz, M., Türk, H. & Kivanc, M. (2004) Evaluation of the antimicrobial activity of the acetone extract of the lichen *Ramalina farinacea* and its (+)-usnic acid, norstictic acid, and protocetraric acid constituents. *Zeitschrift für Naturforschung*, **59**, 384–388.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.
- Wright, J.P., Naeem, S., Hector, A., Lehman, C., Reich, P.B., Schmid, B. & Tilman, D. (2006) Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters*, **9**, 111–120.
- Yachi, S. & Loreau, M. (2007) Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecology Letters*, **10**, 54–62.
- Yeomans, J. & Bremner, J.M. (1989) A rapid and precise method for routine determination of organic carbon in soil. *Communications in Soil Science and Plant Analysis*, **19**, 1467–1476.
- Zavaleta, E.S., Pasari, J.R., Hulvey, K.B. & Tilman, G.D. (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences*, **107**, 1443–1446.
- Zedda, L., Gröngroft, A., Schultz, M., Petersen, A., Mills, A. & Rambold, G. (2011) Distribution patterns of soil lichens across the principal biomes of southern Africa. *Journal of Arid Environments*, **75**, 215–220.
- Zornoza, R., Guerrero, C., Mataix-Solera, J., Arcenegui, V., García-Orenes, F. & Mataix-Beneyto, J. (2006) Assessing air-drying and rewetting pre-treatment effect on some soil enzyme activities under Mediterranean conditions. *Soil Biology and Biochemistry*, **38**, 2125–2134.
- Zornoza, R., Mataix-Solera, J., Guerrero, C., Arcenegui, V. & Mataix-Beneyto, J. (2009) Storage effects on biochemical properties of air-dried soil samples from southeastern Spain. *Arid Land Research and Management*, **23**, 213–222.

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Supporting Information

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

Appendix S1. Study Sites.

Table A1-1. Locations and key abiotic characteristics of study sites.

Appendix S2. Complete correlations of biological soil crust species, with rotated NMDS ordinations.

Table A2-1. Correlations of biological soil crust species with NMDS ordinations in gypsiferous soils of the multi-site study.

Table A2-2. Correlations of biological soil crust species with NMDS ordinations in calcareous soils of the multi-site study.

Table A2-3. Correlations of biological soil crust species with NMDS ordinations in the single-site study.

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