

Diversity and Patch-Size Distributions of Biological Soil Crusts Regulate Dryland Ecosystem Multifunctionality

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ABSTRACT

Recent studies report that multifunctionality—the simultaneous provision of multiple ecosystem functions—in drylands depends on biodiversity. Others report that specific size distributions of vegetation patches indicate overall ecosystem health and function. Using a biocrust (micro-vegetation of mosses, lichens, and cyanobacteria) model system, and multivariate modeling, we determined the *relative* importance of biodiversity, patch-size distribution, and total abundance to nutrient cycling and multifunctionality. In most cases we explained at least 20%, and up to 65%, of the variation in ecosystem functions, and 42% of the variation in multifunctionality. Species richness was the most important determinant of C cycling, constituting an uncommonly clear link between diversity and function in a non-experimental field setting. Regarding C cycling in gypsiferous soils, we found that patch size distributions with a greater frequency of small to medium patches, as opposed to very small patches, were more

highly functional. Nitrogen cycling was largely a function of biocrust cover in two soil types, whereas in gypsiferous soils, more central-tending patch size distributions were less functional with regards to N cycling. All three community properties were about equally important to multifunctionality. Our results highlight the functional role of biotic attributes other than biodiversity, and indicate that high cover and diversity, together with a particular patch-size distribution, must be attained simultaneously to maximize multifunctionality. The results also agree with trends observed with other terrestrial and aquatic communities that more biodiversity is needed to sustain multifunctionality compared to single functions considered independently.

Key words: biodiversity; drylands; enzyme activities; lichens; mosses; patch-size distribution; ecosystem multifunctionality; mediterranean ecosystems; structural equation modeling.

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INTRODUCTION

The well-being of human societies depends on ecosystem goods and services which may be direct outcomes of ecosystem function (Mooney and others 2004). Ecosystem function encompasses the interactive ability of ecological communities and

their environments to cycle, emit, and store materials and energy. For decades, determining which properties of biological communities determine ecosystem function has been a major topic in ecology (Grace and others 2007; Kinzig and others 2002; Naeem and others 2002; Shulze and Mooney 1993). Efforts at determining what controls ecosystem function have typically either focused on only one ecosystem function at a time, or have considered multiple functions but not integrated them (for example, Van der Heijden and others 1998; Worm and others 2006). In contrast, the emerging view is that societies depend upon ecosystem multifunctionality: the simultaneous maintenance of multiple ecosystem functions (Cardinale and others 2012; Gamfeldt and others 2008; Hector and Bagchi 2007; Zavaleta and others 2010).

Since the 1990s, a great deal of research has established that, often, greater biodiversity leads to greater function (hereafter biodiversity–function; Cardinale and others 2012). There has been considerable debate surrounding experimental studies of biodiversity–function (Naeem and Wright 2003; Wardle 1999), but generally there is a monotonic positive relationship between diversity and ecosystem functions which may or may not saturate at some level of biodiversity (Cardinale and others 2012; Naeem and others 2002). Although most studies have focused on experimental systems, biodiversity–function relationships have been harder to demonstrate in natural ecosystems (Grace and others 2007). Early work primarily focused on primary production, but many ecosystem functions are actually processes that occur in litter and soil. Past research on biodiversity–function initially focused on terrestrial plant communities (mostly grasslands), and has moved on to model microbial systems, and aquatic communities (Cardinale and others 2011; Giller and others 2004; Hooper and others 2005), but a strong focus on the processes occurring in soils is still emerging. Even though this topic has attracted the attention of soil ecologists during the last decade (for example, Cragg and Bardgett 2001; Deacon and others 2006; Griffiths and others 2001), very few studies so far have evaluated how biodiversity of producers or heterotrophs affects multifunctionality in soils (He and others 2009; Maestre and others 2012a). As a consequence, our understanding of biodiversity–function relationships is lagging behind that achieved aboveground or in aquatic environments (Bardgett 2005; Fitter and others 2005; Hooper and others 2005).

The patch-size distribution of vegetation has been proposed to be linked to ecosystem function

in drylands (Kéfi and others 2007; Scanlon and others 2007). Vegetation patches in these environments may follow a power law distribution—characterized by a hyper-abundance of small patches but also a small number of large patches—and deviations from the power law distribution may indicate decreased function and the advancement of desertification due to the loss of large patch size classes (Kéfi and others 2007; but see Maestre and Escudero 2009). Changes in the patch-size distributions have also been associated with ecosystem degradation in marine diatoms (Weerman and others 2012). However, the applicability of these findings to other communities is unknown.

Although the effects of biodiversity, patch-size distributions and other community properties on ecosystem function have been studied in isolation, it is rare for more than one of them to be considered in the same study (but see Bowker and others 2010a; Maestre and others 2005) and rarer still for such a study to focus on multifunctionality, particularly with communities other than vascular plants (Maestre and others 2012a). To fill this gap, we undertook an extensive field study to determine the relative importance of climate and three key community properties (total cover, diversity, and patch-size distribution) on several ecosystem functions related to phosphorus (P), carbon (C), and nitrogen (N) cycling and on a composite measurement of ecosystem multifunctionality. We used biological soil crusts (biocrusts) as our study system. These are a soil surface community composed of mosses, lichens and cyanobacteria that are common in the drylands of the world (Figure A1.1 in Supporting Information). They exhibit multiple characteristics that suit them for our study: (1) they can be diverse in a small area (Maestre and others 2008), (2) they are inherently patchy (Bowker and Maestre 2012), and (3) the biocrust community as a whole is active in a especially wide array of functions: C- and N-fixation, decomposition and major nutrient transformations, reduction of erosion, modification of water redistribution to hydrology (Bowker and others 2010a; Eldridge and others 2010; Maestre and others 2011). Our objective was to determine the relative importance of multiple properties of the biocrust community which have been proposed to be drivers of ecosystem functioning. Our study attempts to move beyond simply affirming biodiversity–multifunctionality relationships, and address the outstanding question of whether such effects are comparable to other known and hypothesized regulators of ecosystem function (Cardinale and others 2012).

METHODS

Study System

This study was conducted at 20 sites dispersed across an area of about 112,400 km² over central, southern, and eastern Spain (Table A1.1). This area represents the range of environmental conditions under which biocrusts are a prevalent type of ground cover in Spain (Maestre and others 2011). Among the sites, average annual precipitation and average annual temperatures ranged from 334 to 632 mm and from 13 to 18°C, respectively (Table A1.2). Although it is impossible to know the very long land-use history in Spain, we selected uncropped and relatively undisturbed remnants of native vegetation to conduct our sampling where biocrusts would likely be found in great enough abundance to sample. The specific vegetation community was not part of our selection strategy, although in most cases vegetation was dominated by grass steppes of *Stipa tenacissima* L., whereas in three sites it was composed of open woodlands which contained an overstory of *Pinus halapensis* Miller with an herbaceous or shrubby understory. These are typical remnant vegetation communities in semi-arid Spain, and soil crust communities tend to be similar among them if soils are similar. Eight sites were located on soils derived from limestone or calcareous marl, whereas the remaining 12 sites were located on gypsum-rich soils. All selected sites exhibited continuous or, more commonly, patchy biological crust cover in interspaces between plants (Figure S1) with sharp differences in community structure between the limestone-derived and gypsumiferous soils.

Field Sampling

In each site, 7–10 1.5-m line intercept transects were sampled for the assessment of community properties (one site is represented by 7 transects). Transects were non-randomly placed across multi-specific biocrusts to intentionally capture a wide variety in biocrust richness, cover, and dominance within each site. This sampling strategy has the advantage of ensuring no pseudoreplication, because although multiple transects are sampled within a site, each one is intentionally distinct in its biocrust properties. Transect placement was greater than 30 cm from the nearest perennial plant. In a few cases, small interspace size necessitated two parallel 75-cm transects spaced about 30 cm apart. Along the length of each transect, the beginning and end of every interception of a biocrust moss, lichen, or unoccupied patch was recorded to a

1-mm resolution. Whenever possible, mosses and lichens were identified to a species-level in the field.

Estimation of Community Attributes

Abundance was characterized by the summed intersection length of all moss and lichen species in each transect. The number of species observed per transect was used to estimate species richness. This measure of richness was selected over functional group richness, because our past work suggests that species richness is better correlated to function (Bowker and others 2010a); also taxonomic richness can be a good indicator of trait-based biodiversity concepts (Mouillot and others 2011). We quantified species evenness using the Pielou J statistic (Pielou 1969).

Based upon prior related work, we created two measurements describing the patch-size distribution of biocrust communities. Bowker and Maestre (2012) found that, unlike vascular plant vegetation (Kéfi and others 2007; Scanlon and others 2007), biocrust patches tend to follow a log-normal distribution. This is a patch-size distribution that we believe may arise either in the absence of species interactions or in systems where the patch sizes are partially determined by competitive species interactions rather than facilitation. We previously demonstrated that using an Akaike Information Criterion (AIC)-based model selection approach (Burnham and Anderson 2002) the log-normal distribution was a superior model to a power law distribution in about 60% of cases (Bowker and Maestre 2012). Thus, here we use the second-order AIC (AICc) value of the log-normal distribution subtracted from the AICc value of the power law distribution for each transect as an index of the distribution type (referred to hereafter as ΔAIC). When this index is negative, the log-normal distribution is a better model of the distribution, and when the index is positive, the power law distribution is a better model of the distribution (Bowker and Maestre 2012; Burnham and Anderson 2002). The log-normal distribution has two parameters, μ and σ . We adopted μ as a measure of the degree of central tendency in the patch-size distribution. As μ decreases to very small values, a log-normal distribution more closely resembles a power law distribution; therefore, μ and ΔAIC are correlated. We note that even in cases where the power law distribution is a better model of the data than a log-normal distribution, μ is closely related to the exponent of the power law distribution, and thus it is a reasonable descriptor of the shape of power law

distributions as well (Maestre and Escudero 2009). Community properties are summarized for each site in Table A1.3.

Measuring Ecosystem Functioning

The following soil variables were measured as surrogates of ecosystem functioning in all transects: respiration, organic C, total N, and activity of three enzymes related to the P (phosphatase), C (β -glucosidase), and N (urease) cycles. These variables either measure “true” ecosystem functions (sensu Reiss and others 2009, for example, soil respiration) or are key properties/processes (sensu Jax 2010, for example, organic C, total N, and soil enzymes) that together constitute a good proxy of nutrient cycling, a main determinant of ecosystem functioning in drylands (Maestre and others 2012b). Soil sampling and analysis methodology is summarized in Appendix 1 in Supplementary Material.

We integrated data on multiple ecosystem functions into a novel multifunctionality index. Briefly, its application involves rescaling data based on a theoretical or observed maximum, cross-multiplying n functional indicators, and then rescaling the index by taking the n th root (see Appendix 1 in Supplementary Material). Central to our index is its multiplicative nature: if any single function is measured and found to be zero or below detection limits, multifunctionality must also be zero (Table A1.2). In addition, high functionality in any function cannot completely compensate for very low values in another. Maximal multifunctionality can only be obtained when all functions are maximized.

Statistical Analyses

We developed an a priori model and tested it using structural equation modeling (SEM, Figure S2; Appendix 1 in Supplementary Material). The variables in our a priori model included the following: (1) “Climate” is conceived as the additive effects of annual precipitation and annual average temperature at the study site, and modeled as a composite variable (see Appendix 1 in Supplementary Material for detailed explanation of composite variables). In the case of calcareous soils, these variables are negatively correlated, thus the sign of the composite effect is not interpretable and is presented as an absolute value; (2) “Biodiversity” is also conceived as a composite variable which represents the additive effects of richness and evenness of ecosystem functions; (3) “Patch-size distribution” is modeled as a composite variable which represents the additive effects of parameter μ

of the log-normal distribution and the relative fit based upon the differences in Δ AIC values of the log-normal and power law distributions; (4) Total cover is represented simply as a measured variable; and (5) Ecosystem functions are split into three groups of related variables. Because P cycling has only one indicator, it was modeled using the measured phosphatase activity. “Carbon cycling” is conceived as a latent variable with three correlated measured variable indicators: Soil respiration, β -glucosidase activity, and the organic C pool. Likewise, “Nitrogen cycling” is conceived as a latent variable with two correlated measured variable indicators: Urease activity and total N pool. Separate models were created for each of these three groups. Whenever possible, we used a multigroup fitting approach to determine the degree to which parameter estimates differed among gypsiferous and calcareous soils. The advantage of this approach is that we can determine which parameters (for example, sign or magnitude of path coefficients) differ among groups, and obtain a separate parameter estimate for each group. If, on the other hand, a given parameter is approximately the same in both groups, it is estimated using the pooled data of both groups. We used the Bollen-Stine bootstrap test as our primary test because some data were not normally distributed, but also conducted the maximum likelihood χ^2 test and the RMSEA (root mean square error of approximation) test. Appendix 1 in Supplementary Material contains a detailed description of the SEM conducted, the development of our a priori model, and our model building process.

RESULTS

Phosphorous Cycling Model

We found several substantive differences among calcareous and gypsiferous soils in the P cycling model (Figure 1; Table A1.4). In addition to the general set of differences among soil types (Appendix 1 in Supplementary Material), the relationship between Δ AIC and phosphatase was allowed to differ among soil types. In gypsiferous soils, only about 20% of the variance was explained in phosphatase activity. This was due primarily to strong effects of the abiotic environment and moderate effects of patch size. In the calcareous soils our model explained 39% of the variance in phosphatase activity, which was largely a function of the abiotic environment. Among the community properties, patch size and diversity were of moderate importance. There were several

additional differences among soil types common to this and all models, summarized in Appendix 1 (Supplementary Material). In both soil types, environmental effects were primarily due to precipitation, diversity effects to J, and patch-size distribution effects to μ (indicating greater central-tendency), all of which were positive correlations (Table A1.4).

Carbon Cycling Models

In the case of C cycling, the multigroup modeling approach was not successful because models followed different structures in the two soil types (a latent variable “carbon cycling” functioned well in gypsiferous but not calcareous soils). Thus, it was

simplest to construct separate models for calcareous and gypsiferous soils, which means that differences among the groups can only be described qualitatively (Figure 2).

In gypsiferous soils, our model variant performed exceptionally well, explaining 65% of the variance in the C-cycling latent variable and 39% in soil respiration (Figure 2). In the case of the “C cycling” latent variable, diversity was the strongest influence, an effect primarily accounted for by richness (Figure 2; Table A1.4). Patch-size distribution also contributed a moderate effect, whereas cover and site-level climate had minor effects. In the case of respiration, all predictors had at least minor effects: patch-size distribution, cover, site-level climate, and diversity. Log-normal distributions were more functional than power-law distributions.

The model performed well in calcareous soils, and was able to explain 56% of the variance in organic C, 58% in β -glucosidase, and 40% in soil respiration (Figure 2). Climate and diversity were both strong predictors of organic C and soil respiration. β -Glucosidase was most strongly predicted by diversity and moderately by climate and patch size distribution.

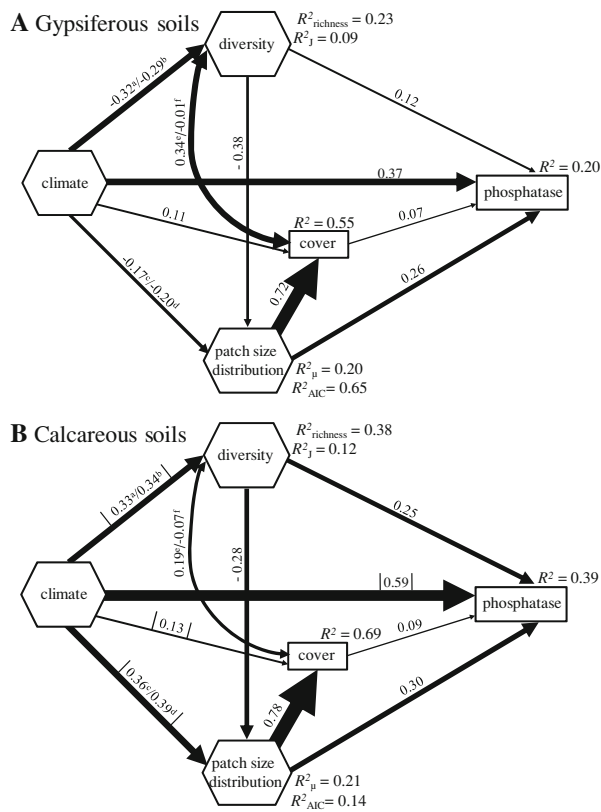


Figure 1. Final fitted structural equation models depicting relative effects of biological crust community attributes and abiotic climate variables on phosphatase activity in **A** gypsiferous and **B** calcareous soils. Boxes represent measured variables. Hexagons represent composite variables composed of the additive effects of multiple measured variables (in calcareous soils, the sign of the climate composite is not interpretable, thus absolute values are presented). a = climate → richness, b = climate → J, c = climate → μ , d = climate → Δ AIC, e = rich ↔ cover, f = J → cover. The overall fit of the model was satisfactory (Bollen-Stine bootstrap $P = 0.164$, RMSEA = 0.047, $P = 0.517$, $\chi^2 = 27.9$, $P = 0.113$).

Nitrogen Cycling Model

Due to a weaker than expected correlation ($r < 0.7$) between total N and urease activity, these variables were not used together in a latent variable; rather they were modeled as two separate variables. We found several substantive differences among calcareous and gypsiferous soils in the N cycling model (Figure 3). Paths differing among groups included: richness → total N, richness → urease, μ → total N, Δ AIC → total N, Δ AIC → urease activity.

In gypsiferous soils, our model explained 21 and 11% of the variance in total N and urease activity, respectively (Figure 3). Total N was best predicted by cover, diversity, and patch size distribution. The best predictor of urease was diversity. In contrast, richness accounted for positive effects of diversity, and μ accounted for a negative patch size effects (Table A1.4).

In calcareous soils, our model explained 30 and 26% of the variance in total N and urease activity, respectively (Figure 3). In the case of total N, cover was the strongest predictor, followed by site-level climate, and patch-size distribution. Diversity had essentially no effect. In the case of urease activity, the patch-size distribution was the best predictor, followed by site-level climate. The effects of the latter variable were primarily attributable to a

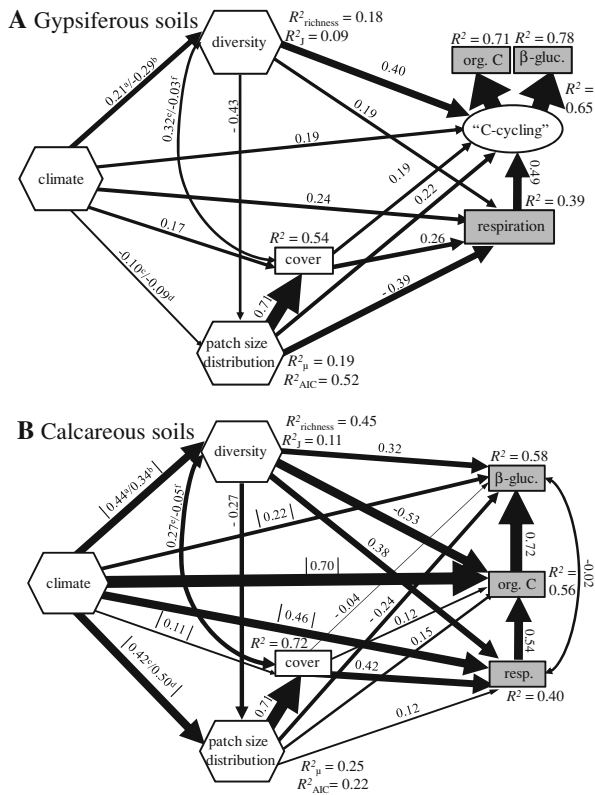


Figure 2. Final fitted structural equation models depicting relative effects of biological crust community attributes and abiotic climate variables on carbon cycling in **A** gypsiferous and **B** calcareous soils. Boxes represent measured variables. Hexagons represent composite variables (in calcareous soils, the sign of the climate composite is not interpretable, thus absolute values are presented). a = climate → richness, b = climate → J, c = climate → μ, d = climate → ΔAIC, e = rich ↔ cover, f = J → cover. The fit of the model was satisfactory in calcareous (Bollen-Stine bootstrap $P = 0.155$, RMSEA = 0.112, $P = 0.182$, $\chi^2 = 5.74$, $P = 0.125$) and gypsiferous (Bollen-Stine bootstrap $P = 0.384$, RMSEA = 0.024, $P = 0.607$, $\chi^2 = 11.7$, $P = 0.389$) soils.

negative effect of temperature, whereas those of patch size were due to a positive effect of μ (Table A1.4).

Multifunctionality Model

Aside from the general suite of differences between the two soil types, calcareous soils also differed from gypsiferous soils in the effects of both patch size variables on multifunctionality (Figure 4). In gypsiferous soils, our model explained 43% of the variance in multifunctionality (Figure 4). All predictors exerted at least moderate effects on multifunctionality in the following order: diversity, site

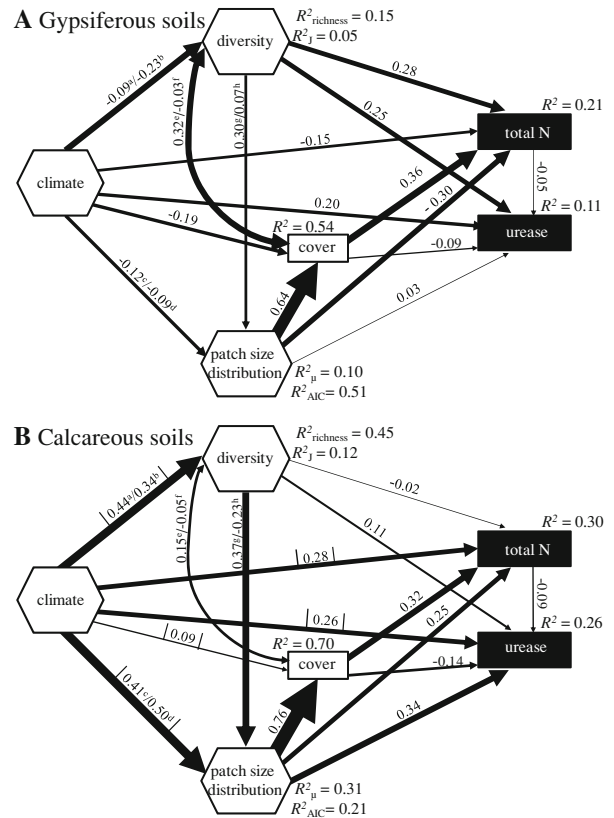


Figure 3. Final fitted structural equation models depicting relative effects of biological crust community attributes and abiotic climate variables on nitrogen cycling in **A** gypsiferous and **B** calcareous soils. Boxes represent measured variables. Hexagons represent composite variables (in calcareous soils, the sign of the climate composite is not interpretable, thus absolute values are presented). a = climate → richness, b = climate → J, c = climate → μ, d = climate → ΔAIC, e = rich ↔ cover, f = J → cover, g = J → μ, h = rich ↔ μ. The overall fit of the model was satisfactory (Bollen-Stine bootstrap $P = 0.174$, RMSEA = 0.041, $P = 0.606$, $\chi^2 = 30.1$, $P = 0.145$).

level climate, total cover, and patch-size distribution. In calcareous soils, our model explained 42% of the variance in multifunctionality. The site-level climate and total cover were strong predictors, whereas the patch-size distribution and diversity made moderate contributions.

In both soil types (Figure 4), positive diversity effects were mostly accounted for by richness (Figure 5) and site-level climate effects were mostly accounted for by a negative effect of temperature and a positive effect of precipitation (Table A1.4). Patch-size distribution effects were about equally attributable to ΔAIC and μ, although distributions that were more power law-like were more highly

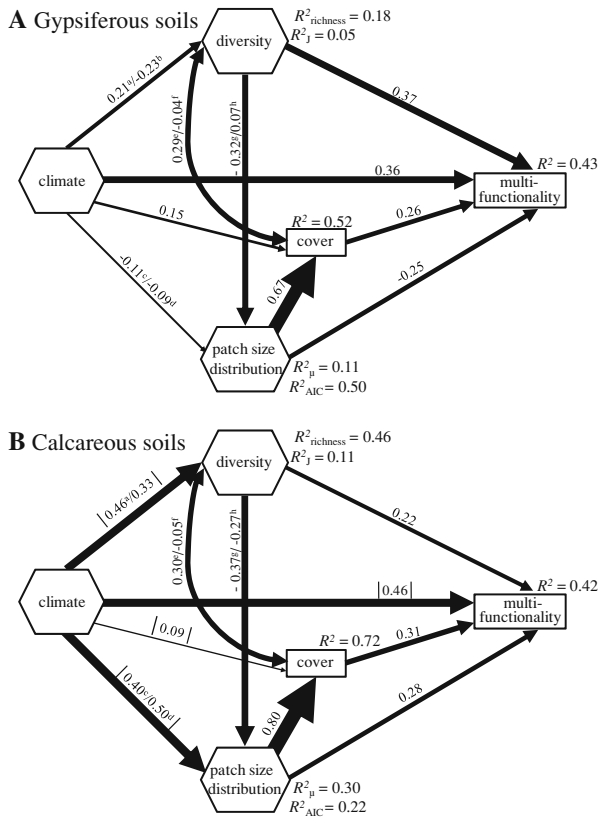


Figure 4. Final fitted structural equation models depicting relative effects of biological crust community attributes and abiotic climate variables on multifunctionality in **A** gypsiferous and **B** calcareous soils. Boxes represent measured variables. Hexagons represent composite variables composed of the additive effects of multiple measured variables (in calcareous soils, the sign of the climate composite is not interpretable, thus absolute values are presented). a = climate → richness, b = climate → J, c = climate → μ, d = climate → ΔAIC, e = rich ↔ cover, f = J → cover, g = J → μ, h = rich ↔ μ. The overall fit of the model was satisfactory in calcareous and gypsum soils (Bollen-Stine bootstrap $P = 0.62$, RMSEA = 0.000, $P = 0.89$, $\chi^2 = 17.5$, $P = 0.55$).

functional in calcareous soils and those that were more log-normal-like were more highly functional in gypsiferous soils (Appendix 1 in Supplementary Material).

DISCUSSION

Non-saturating Effects of Biodiversity on Ecosystem Function and Multifunctionality

There is an emerging consensus that biodiversity, specifically species richness, is often linked to greater function in the biocrust study system and

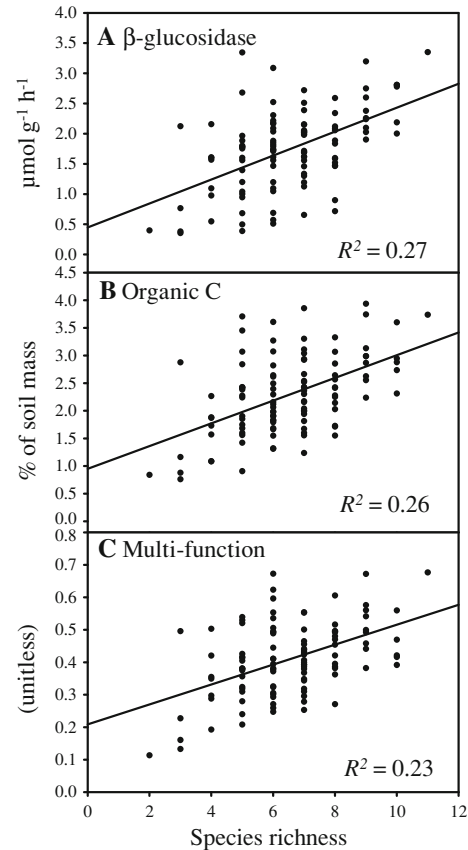


Figure 5. Bivariate relationships in gypsiferous soils between species richness and β -glucosidase (**A**), organic C (**B**), and multifunctionality (**C**).

most of these relationships are positive. This assertion is supported in field data spanning orders of magnitude differences in spatial scale on two continents (Bowker and others 2010a), and in experimentally constructed biocrusts (Maestre and others 2012a). Especially in gypsiferous soils, species richness was strongly positively related to various aspects of C-cycling. Richness also influenced C-cycling in calcareous soils and N-cycling in gypsiferous soils. Of all the community attributes that affected function, richness was among the most ubiquitous and in some cases the strongest. Similar relationships have been observed previously in four datasets obtained in naturally occurring biocrust communities from Spain and the USA, encompassing a variety of different ecosystem functions (Bowker and others 2010a). Most notable is that relationships between these ecosystem function surrogates and species richness are approximately linear (Figure 5, Bowker and others 2010a), suggesting that they do not saturate at low levels of diversity like other soil communities [for example, saprophytic fungi (Setälä and MacLean

2004), microarthropods (Liiri and others 2002), and mesofaunal species (Laakso and Setälä 1999)]. We interpret these linear richness-function relationships as further evidence that biocrust-forming mosses and lichens are closer to functionally singular than to functionally redundant; if the richness-function relationship saturates, it generally does so at uncommonly observed levels of richness. Early biodiversity-function experiments were criticized because it is difficult to distinguish complementarity from a sampling effect whereby the number of randomly drawn species added increases the probability of encountering a highly functional species (Wardle 1999). Because sampling effects are unlikely to play a role in these field data (compositions are not random draws), complementarity in functional attributes is the most likely explanation for the results observed. Regarding C-cycling, such complementarity could take the form of species-specific C fluxes, temporal dynamics or metabolic requirements (Lange and others 1997), anti- or pro-biotic activity (Castillo-Monroy and others 2011), complementary enzyme production (Sedia and Ehrenfeld 2006), or differential effects on infiltration and thus soil moisture (Eldridge and others 2010). For N cycling, complementarity may also arise by the ability of some lichen species to fix atmospheric N (for example, *Collema*, Belnap 2002) and by the effects of particular moss and lichen species on other biocrust constituents that are able to fix N, such as free-living bacteria and cyanobacteria.

Recent research in plant (Hector and Bagchi 2007; Maestre and others 2012b; Zavaleta and others 2010) and soil bacterial (He and others 2009) communities suggests that greater biodiversity appears to be required to sustain multiple ecosystem functions simultaneously. Experimental research supports that this may be true in biocrusts as well (Maestre and others 2012a). Here, we see an approximately linear relationship between the multifunctionality index and species richness in gypsiferous soils (Figure 5). This indicates that, according to the estimated slope of this regression (Figure 5), it would require nearly 26 species to maximize P, N, and C cycling simultaneously. In contrast, about 15 species are needed to maximize organic C and β -glucosidase (Figure 5), and 17 are needed to maximize total N (data not shown). These numbers are based on extrapolations beyond the range of the data shown in Figure 5, but it is clear that when considering one function at a time, a greater proportion of maximal function can be obtained with fewer species compared to multiple simultaneous functions. It may also be true that it is

not possible to attain high values of all functions simultaneously, regardless of diversity, and that distinct communities are required to maximize different functions (Zavaleta and others 2010).

Patch-Size Distributions Have a Functional Significance Independent of Cover

Our data lend some credence in a general sense to the ideas of Kéfi and others (2007), who proposed that changes in the patch-size distribution can be used to detect functional changes in ecosystems. Their study suggested that deviation from a power law such that the infrequent but important largest patches are lost, might signify a threshold change, leading to desertification and potentially system collapse; the loss of these patches leads to a truncated form of the distribution. Maestre and Escudero (2009) extended this idea and tested whether the rate at which very large, rare patches are lost might be related to empirically measured ecosystem functions. They reasoned that the exponent of a power law distribution describes this loss rate. They found that apparent effects of the loss rate of large patches on ecosystem function could be explained by the correlation of this parameter with total cover, a much more straightforward community property (Maestre and Escudero 2009). This suggests that patch-size distributions are less influential to ecosystem function than the total cover of all patches. Kéfi and others (2010) suggested that the meaning of the exponent of a truncated power law is too poorly known to be considered an indicator of the loss rate of large patches, and the relationship of ecosystem function to power law distributional parameters may obey a non-linear behavior that would not have been detected in the Maestre and Escudero (2009) study.

Here we demonstrate a situation that is distinct from either previous study. The first difference is that, in our data, patch-size distributions of biocrust-forming mosses and lichens may or may not follow a power law, and fitting the truncated form of the function was problematic (Bowker and Maestre 2012). In cases where there is deviation from a power law distribution (~60% of cases), the data are generally well-described by a log-normal distribution. These distributions are similar in that they are positively skewed, but dissimilar in that the smallest patches are also the most frequent in a power law distribution whereas log-normal distributions are relatively more central-tending. Deviation from a power law is caused more by an increasing prevalence of small to medium-sized

patches at the expense of the very smallest patches, rather than by a loss of the largest patches as in previous studies. Log-normal distribution of patches was associated with positive effects on some ecosystem functions in gypsiferous soils, especially respiration (Figure 6), and total N to a lesser degree. The converse was true in calcareous soils, where more power law-like distributions led to higher urease activity. The second key difference is that the effects of the patch-size distribution were independent of the effects of cover, contrary to Maestre and Escudero (2009). Cover is determined by both the number of patches and the shape of the patch-size distribution encountered in a sample of finite length or area. Because we included cover in our models, any observed direct effects of the patch-size distribution are independent of cover. In fact, it was just as common to observe effects of patch-size distribution variables as those due to cover. Thus, patch-size distributions of the biocrust community may contain information about ecosystem function and, by extension, desertification processes. The difference is that a different distribution predominates (the log-normal) and exerts a mixture of positive and negative effects in different ecological settings.

What do the effects of patch-size distribution on ecosystem function mean ecologically? Unlike in vascular plant communities (Kéfi and others 2007; Maestre and Escudero 2009; Scanlon and others

2007), our biocrust communities do not appear to be structured by local facilitation, rather, due to a large degree of niche overlap, competition for living space can be crucial (Bowker and others 2010b). In previous work, we suggested that increasing competition intensity could shift a log-normal distribution of patch to a more power-law-like distribution (Bowker and Maestre 2012). Shifting toward a more power law-like distribution here appears to suppress multifunctionality and soil respiration in gypsiferous soils. Therefore, the effects observed in gypsiferous soils could represent a unique mechanism by which the competition-facilitation continuum can affect ecosystem function—competition among species suppresses their function because they are unable to attain optimal productivity. An alternate explanation is that it is best to strike a balance between the number and size of patches, rather than having a majority of patches that are trivially small and having all function confined to a few large patches. In vascular plant communities, it appears that large patches drive function (Kéfi and others 2007; but see Maestre and Escudero 2009), whereas in gypsiferous biocrust communities it may be the small to medium sized patches that are functionally more relevant (Figure 6).

Is There a Recipe for Multifunctionality?

In the comparison of biotic and abiotic contributions to ecosystem function, it is important to account for environment, as generally function responds more strongly to abiotic cues in calcareous soils and community properties in gypsiferous soils. This may not be surprising given that, in general, biocrusts attained greater cover in gypsiferous soils and accounted for a greater proportion of the total activity in these ecosystems. The ability of climate to explain variance in our dataset is limited because it does not vary at the transect level; it varies only at the site level. Had microclimatic data existed, or been possible to collect for all transects, we probably would have seen much greater abiotic effects.

Nevertheless, the strong effects of the various community attributes suggest there is a large degree of biotic control over ecosystem function. This assertion leads to the question of whether there is an ideal suite of community attributes which constitutes high multifunctionality. Perhaps the most general conclusion we can draw is that no single community property is responsible for maintaining function in biocrust-dominated ecosystems. It is more appropriate to say that total biomass, biodiversity, and community patch-size distribution codetermine ecosystem functions, and

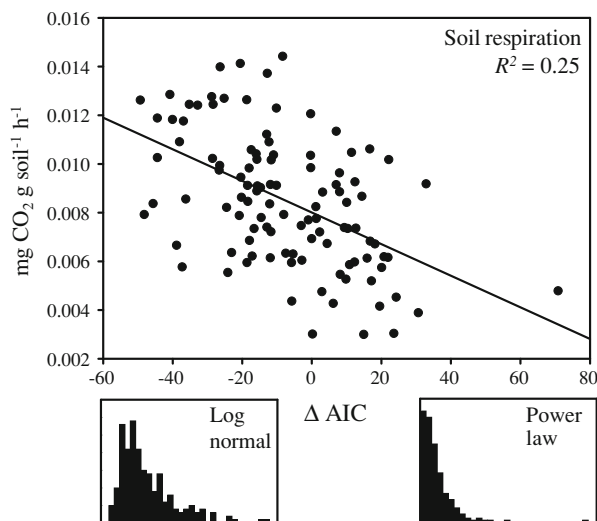


Figure 6. Bivariate relationships in gypsiferous soils between the second-order AIC (AICc) value of the log-normal distribution subtracted from the AICc value of the power law distribution (Δ AIC) and a selected ecosystem function (respiration). As Δ AIC becomes larger, the patch size distribution resembles a power law distribution more.

their relative importance changes depending on the abiotic environment and particular ecosystem function being investigated. Support for this statement can also be found in Maestre and others (2012a), where richness, species composition, and to a lesser degree spatial aggregation codetermined ecosystem function. Further, there are idiosyncrasies unique to particular habitats. For example, the ideal patch-size distribution seems to resemble a more central-tending one in calcareous soils, and a more skewed one in gypsiferous soils. This is especially true when we consider multifunctionality rather than the maximization of one function at a time. In models of multifunctionality, the different community properties were remarkably evenly important in calcareous soils, whereas in gypsiferous soils diversity was somewhat more important but total cover and patch-size distribution also made key contributions. Thus high cover, or high diversity, or particular patch-size distributions alone are not enough to result in high multifunction; all three must be attained simultaneously.

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