

Biocrust-forming mosses mitigate the negative impacts of increasing aridity on ecosystem multifunctionality in drylands

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Summary

- The increase in aridity predicted with climate change will have a negative impact on the multiple functions and services (multifunctionality) provided by dryland ecosystems worldwide. In these ecosystems, soil communities dominated by mosses, lichens and cyanobacteria (biocrusts) play a key role in supporting multifunctionality. However, whether biocrusts can buffer the negative impacts of aridity on important biogeochemical processes controlling carbon (C), nitrogen (N), and phosphorus (P) pools and fluxes remains largely unknown.
- Here, we conducted an empirical study, using samples from three continents (North America, Europe and Australia), to evaluate how the increase in aridity predicted by climate change will alter the capacity of biocrust-forming mosses to modulate multiple ecosystem processes related to C, N and P cycles.
- Compared with soil surfaces lacking biocrusts, biocrust-forming mosses enhanced multiple functions related to C, N and P cycling and storage in semiarid and arid, but not in humid and dry-subhumid, environments. Most importantly, we found that the relative positive effects of biocrust-forming mosses on multifunctionality compared with bare soil increased with increasing aridity. These results were mediated by plant cover and the positive effects exerted by biocrust-forming mosses on the abundance of soil bacteria and fungi.
- Our findings provide strong evidence that the maintenance of biocrusts is crucial to buffer negative effects of climate change on multifunctionality in global drylands.

Introduction

Drylands are extremely important for achieving global sustainability, as they constitute *c.* 41% of Earth's land surface (Reynolds *et al.*, 2007), an area that will probably expand by the end of this century as a result of expected increases in aridity with climate change (Dai, 2013; Feng & Fu, 2013). Such changes in aridity can further exacerbate soil erosion, land degradation and desertification in global drylands (Reynolds *et al.*, 2007; Dai, 2013; Feng & Fu, 2013), which already threaten the livelihood of over 250 million people, mostly living in developing countries (Reynolds *et al.*, 2007). Soil communities dominated by mosses, lichens and cyanobacteria (biocrusts hereafter) are common biotic components of boreal, arctic, temperate and dryland ecosystems worldwide (Eldridge & Greene, 1994; Belnap, 2006; Lindo & Gonzalez, 2010; Elbert *et al.*, 2012). These communities support a wide range of ecosystem functions, including soil stability, carbon (C) and nitrogen (N) fixation, CO₂ flux, and N

mineralization (Eldridge & Greene, 1994; Belnap, 2006; Bowker *et al.*, 2011; Maestre *et al.*, 2012a). Biocrusts can also modulate the response of C and N cycling to climate change in these areas (Reed *et al.*, 2012; Maestre *et al.*, 2013; Delgado-Baquerizo *et al.*, 2014). Given the global distribution of biocrusts (Belnap, 2006; Lindo & Gonzalez, 2010; Elbert *et al.*, 2012) and their key functional roles in the ecosystems where they are prevalent (Belnap, 2006; Bowker *et al.*, 2011; Maestre *et al.*, 2011, 2012a), understanding how climate change will affect the capacity of these organisms to maintain multiple ecosystem functions simultaneously (*i.e.* multifunctionality; Maestre *et al.*, 2012b; Bradford *et al.*, 2014; Byrnes *et al.*, 2014) is critical in formulating sustainable natural resource management and conservation policies in drylands worldwide.

The influence of biocrusts on multifunctionality also extends below the soil surface through their interactions with soil microbes. Soil microbial communities carry out almost every planetary function and ecosystem service, including

decomposition, nutrient cycling and climate regulation (Bodelier, 2011; Bardgett & van der Putten, 2014). Biocrusts can influence the abundance (Bates *et al.*, 2010; Delgado-Baquerizo *et al.*, 2014) and activity (Miralles *et al.*, 2012; Castillo-Monroy *et al.*, 2015) of the soil microbial communities existing below them, and recent studies suggest that these microbial communities are highly sensitive to climate change (Garcia-Pichel *et al.*, 2013; Delgado-Baquerizo *et al.*, 2014). Thus, complex interactions between the above- (e.g. mosses, lichens) and below-ground (microbes) biocrust communities may mediate the effects of climate change on ecosystem functioning. However, the impacts of climate change on multifunctionality, mediated by interactions between microorganisms (e.g. fungi and bacteria) and biocrust constituents, are yet to be evaluated in natural environments.

Climatic controls on multifunctionality are particularly important in drylands because their biological activity is mainly driven by water availability (Whitford, 2002). Recent studies suggest that the predicted increase in aridity for the late 21st century in global drylands (Dai, 2013; Feng & Fu, 2013) will negatively affect the cover and richness of their vascular vegetation (Maestre *et al.*, 2012b; Delgado-Baquerizo *et al.*, 2013a). Interestingly, the decline in plant cover observed with increases in aridity (Delgado-Baquerizo *et al.*, 2013a) could expand the cover of biocrusts by increasing the surface available for colonization and growth of their constituent organisms (Belnap *et al.*, 2001; Thomas *et al.*, 2011; but see Escolar *et al.*, 2012). It has recently been suggested that biocrusts can promote the resistance of some ecosystem functions to simulated climate change (Delgado-Baquerizo *et al.*, 2014). Therefore, the expected increases in aridity might lead to an increased ecosystem dependency on biocrusts to maintain dryland multifunctionality. However, little is known about how climate change will affect the capacity of biocrusts to maintain multifunctionality under increasingly arid conditions, as there is a lack of evidence from large-scale field studies on this topic.

Herein, we hypothesize that: biocrust-forming mosses promote multiple functions related to C, N and phosphorus (P) cycle in terrestrial ecosystems (i.e. extracellular enzyme activities (β -glucosidase and phosphatase), total N, total organic C and available P; see the rationale on the selected functions in the Materials and Methods section); the positive effects of biocrust-forming mosses on multifunctionality compared with bare soil will increase with increasing aridity; and the positive effects of biocrust-forming mosses on multifunctionality are driven via concurrent positive effects exerted by biocrusts on the abundance of soil bacteria and fungi. To test these hypotheses, we conducted an empirical study using soil samples collected from three continents (North America, Europe and Australia) to evaluate how increasing aridity, a common expression of climate change in drylands worldwide (Dai, 2013; Feng & Fu, 2013), affects the capacity of biocrust-forming mosses to alter multifunctionality. We used moss-dominated biocrusts as our model system because they make up a significant proportion of biocrusts globally (Lindo & Gonzalez, 2010; Elbert *et al.*, 2012), are commonly found across wide environmental gradients (e.g. from humid to arid systems; Lindo & Gonzalez, 2010; Elbert *et al.*, 2012), and contribute substantially to key ecosystem functions, including primary production, soil C

fixation and N transformations in soils, infiltration and soil erosion (Eldridge *et al.*, 2010; Lindo & Gonzalez, 2010). In addition, we evaluated the role of soil microbial communities living under biocrusts in maintaining multifunctionality along aridity gradients.

Materials and Methods

Study sites and data collection

Field data were collected from 40 sites located in the USA, Spain and Australia (Fig. 1; Supporting Information Table S1). Locations for this study were chosen to represent a wide aridity gradient; we included arid ($n=6$ sites), semiarid ($n=25$), dry-subhumid ($n=4$) and humid ($n=5$) ecosystems, which are threatened by predicted increases in aridity (Dai, 2013). The sites surveyed encompass a wide variety of vegetation types, including grasslands, shrublands, savannas, dry seasonal forests and open woodlands dominated by trees. Mean annual precipitation and temperature and soil pH of the study sites ranged from 140 to 1167 mm, from 8.1 to 19.5°C, and from 4.6 to 8.4, respectively.

Data collection was carried out between July 2012 and March 2014 according to a standardized sampling protocol (Maestre *et al.*, 2012b). At each site, we established a 30 m \times 30 m plot representative of the dominant vegetation. The cover of vascular plants and plant richness at each site were measured using four 30 m transects and the line-intercept method, as described in Maestre *et al.* (2012b). The coordinates of each plot were recorded *in situ* with a portable global positioning system, and were standardized to the WGS84 ellipsoid for visualization and analyses. Aridity was determined as $1 - \text{aridity index (AI)}$, where $\text{AI} = \text{precipitation/potential evapotranspiration}$ (United Nations Environment Programme, 1992; Delgado-Baquerizo *et al.*, 2013a). Data of the AI were obtained from the global aridity map of the Food and Agriculture Organization of the UN (FAO; <http://data.fao.org/map?entryId=221072ae-2090-48a1-be6f-5a88f061431a>).

At each site, three soil cores (0–5 cm depth) were collected under the most common biocrust-forming mosses, and in naturally occurring open areas devoid of perennial vegetation and without visible biocrust constituents. The most common mosses in this study were *Syntrichia caninervis*, *Syntrichia ruralis* and *Bryum* spp. (USA), *Pleurochaete squarrosa*, *Tortula revolvens*, *Weissia* sp. and *Bryum* spp. (Spain) and *Desmatodon convolutus*, *Barbula calycina*, *Didymodon torquatus* and *Bryum* spp. (Australia). A total of 240 soil samples were collected and analyzed. Soil sampling was always conducted during the dry season (July 2012 (before the monsoon season began) in the USA, July 2013 in Spain and March 2014 in Australia) to reduce bias among study sites resulting from seasonal changes in the soil variables studied. A minimum separation distance between samples, and between these and plant patches, of 1 m was maintained to remove potential sources of nonindependence between samples (Delgado-Baquerizo *et al.*, 2013b). After field sampling, the mosses and plant roots were carefully separated from the soil, which was sieved (2 mm mesh) and separated into two fractions.

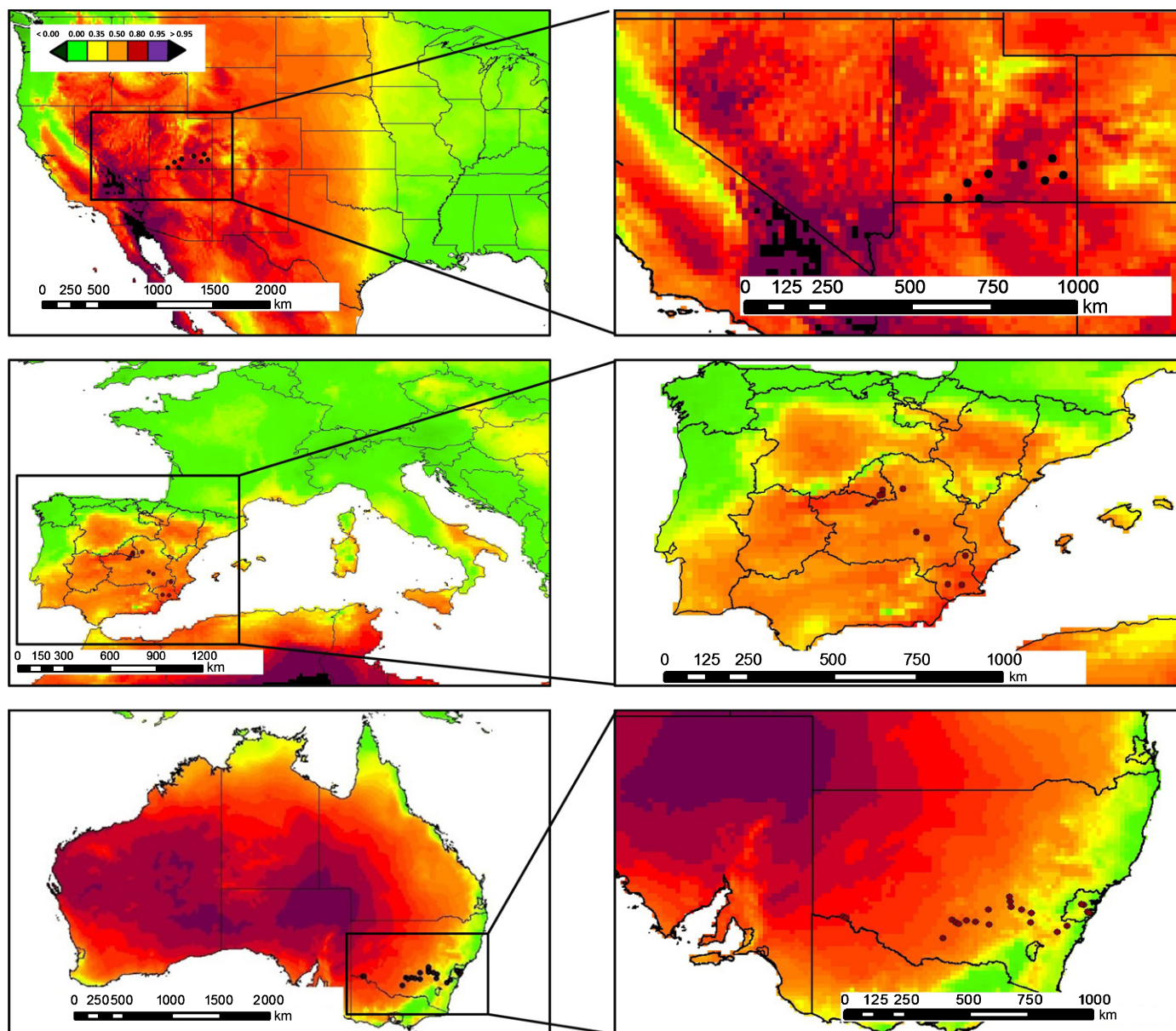


Fig. 1 Locations of the study sites in the USA ($n = 8$), Spain ($n = 10$) and Australia ($n = 22$). Color patterns indicate aridity (1 – aridity index) gradients. Aridity increases from green to purple in the graphs.

One soil fraction was immediately frozen at -20°C for quantifying the abundance of bacteria and fungi in our samples (which was assessed in a composite sample per plot in both biocrusts and bare ground microsites). The other fraction was air-dried and stored for 1 month before C, N and P analyses. Previous studies have found that air drying and further storage of dryland soils do not appreciably alter variables such as those we studied (Zornoza *et al.*, 2006, 2009). It is also important to note that the soil was also dry (gravimetric soil moisture at $0\text{--}5\text{ cm} < 1\%$) when we conducted our sampling. Thus, the potential bias induced by our drying treatment is expected to be minimal. In addition, this storage approach is also commonly used when analyzing soil variables such as those evaluated here in large-scale surveys (e.g. Maestre *et al.*, 2012b; Tedersoo *et al.*, 2014).

Measurement of individual ecosystem functions

In all soil samples, we measured five variables that are linked to the stocks and cycling of C, N and P: organic C, β -glucosidase, total N, activity of phosphatase and Olsen inorganic P. Overall, these variables (hereafter functions) constitute a good proxy of nutrient cycling, biological productivity, and build-up of nutrient pools (Schade & Hobbie, 2005; Perroni-Ventura *et al.*, 2009; Reiss *et al.*, 2009; Jax, 2010; Maestre *et al.*, 2012a,b; Bell *et al.*, 2014). In particular, organic C is considered a good proxy of decomposition and C storage in soil (Walker & Syers, 1976; McGill & Cole, 1981; Perroni-Ventura *et al.*, 2009; Jax, 2010). Extracellular enzymes activities such as phosphatase and β -glucosidase are produced by soil bacteria, fungi, and archaea, and are

involved in the processing, stabilization and destabilization of soil organic matter and nutrient cycling in terrestrial ecosystems (Bell *et al.*, 2014). They are also considered a good indicator of nutrient demand by plants and soil microorganisms (Bell *et al.*, 2014). In particular, phosphatase is related to the release of inorganic P from organic matter, and β -glucosidase supports sugar degradation (Bell *et al.*, 2014). N and P are the nutrients that most frequently limit primary production in terrestrial ecosystems, particularly in drylands (Vitousek *et al.*, 2002; Delgado-Baquerizo *et al.*, 2013a). While total N has a biological origin (e.g. atmospheric N fixation and litter decomposition), inorganic P is the main P source for plants and microorganisms, and its availability is linked to the desorption and dissolution of P from soil minerals, and, to a lesser extent, the decomposition of organic matter (Walker & Syers, 1976; McGill & Cole, 1981; Schlesinger & Bernhardt, 2013).

The concentration of soil total organic C was determined by colorimetry after oxidation with a mixture of potassium dichromate and sulfuric acid as described in Anderson & Ingram (1993). Soil total N was measured with a CN analyzer (Leco CHN628 Series; Leco Corporation, St Joseph, MI, USA). Phosphatase activity was measured by determination of the amount of p-nitrophenol (PNF) released from 0.5 g soil after incubation at 37°C for 1 h with the substrate p-nitrophenyl phosphate in MUB buffer (Tabatabai & Bremner, 1969). The activity of β -glucosidase was assayed following the procedure for phosphatase, but using p-nitrophenyl- β -D-glucopyranoside as substrate and Tris-hydroxymethyl aminomethane instead of NaOH when preparing the buffer (Tabatabai, 1982). The concentration of Olsen inorganic P was measured from NaHCO₃ 0.5 M soil extracts, as described in Tiessen & Moir (1993). In brief, soil extracts in a ratio of 1 : 5 were shaken in a reciprocal shaker at 200 rpm for 2 h. An aliquot of the centrifuged extract was used for the colorimetric determination of available inorganic P (PO₄³⁻), based on the reaction with ammonium molybdate and development of the 'Molybdenum Blue' color (Bray & Kurtz, 1945).

Assessing multifunctionality

Here, we used three different approaches to assess ecosystem multifunctionality: individual functions assessed separately (organic C, total N, activity of β -glucosidase and phosphatase and Olsen P); the average approach (Maestre *et al.*, 2012b); and the multiple-threshold method (Maestre *et al.*, 2012b; Bradford *et al.*, 2014; Wagg *et al.*, 2014; Lundholm, 2015). Average multifunctionality calculates the average of the previously standardized multiple functions measured (Maestre *et al.*, 2012b). This approach is increasingly being used (Maestre *et al.*, 2012b; Bradford *et al.*, 2014; Wagg *et al.*, 2014; Lundholm, 2015), and provides a straightforward and easily interpretable measure of multifunctionality (Byrnes *et al.*, 2014). To obtain our average multifunctionality index (hereafter, multifunctionality) for each microsite (biocrust and bare ground) and site, we first standardized each of our five variables to a 0–1 scale by dividing each value by the maximum value for that particular variable. Raw data were log₁₀-transformed as needed to improve normality

before these calculations. Following this, the standardized variables were averaged to obtain our multifunctionality index. This index was strongly related to the same index calculated with other popular standardization approaches such as the z-standardization (Fig. S1). For simplicity and practicality (i.e. averaging multifunctionality index allows further numerical analyses), we used this multifunctionality index in our manuscript. However, the averaging approach cannot distinguish between: two functions having similar values; and one function having high values compensating for a second function with low values (Byrnes *et al.*, 2014). To account for this issue, we also estimated multifunctionality using the multiple-threshold method of Byrnes *et al.* (2014), which evaluates the number of functions that simultaneously exceed multiple critical thresholds. The multiple-threshold approach of multifunctionality, which was originally developed by Byrnes *et al.* (2014), captures the number of functions that perform the best. In brief, this approach calculates the maximum value of each measured function and counts the number of functions that exceed a pre-established threshold. For our analyses, we used thresholds from 5 to 100% (Bradford *et al.*, 2014). This method provides information about the threshold in which our variable maximizes the effect on the number of functions beyond that threshold. If this threshold is low, it means that the effect of our variable is constrained or is more important for low functional ecosystems, whereas if it peaks in high thresholds, the effect of our variable is more important for high functional ecosystems. These analyses were conducted using MATLAB v.7.0 (MathWorks Inc., Natick, MA, USA).

Assessment of microbial abundance

We measured the abundance of total fungi and bacteria for biocrusts and bare ground using quantitative PCR (qPCR). Soil DNA was extracted from 0.5 g of defrosted soil samples using the Powersoil DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, CA, USA) according to the instructions provided by the manufacturer. We quantified the total amount of bacteria and fungi using qPCR; each sample was run in triplicate using 96-well plates on a CFX96 Touch Real-Time PCR Detection System (Foster City, CA, USA). Total bacterial *16S* and fungal *ITS* genes were amplified with the *Eub* 338-*Eub* 518 (Lane, 1991) and *ITS1*-5.8S (Vilgalys & Hester, 1990) primer sets, respectively, as described in Delgado-Baquerizo *et al.* (2014). Efficiencies for all quantification reactions were > 90%, with *R*²-values ranging from 0.90 to 0.99. The abundances of fungi and bacteria were expressed as the number of DNA copies g⁻¹ of dry soil. To obtain these units, we first calculated the number of DNA copies ng⁻¹ of DNA in our PCR reaction. Then, we obtained the number of DNA copies in our whole DNA extraction (100 μ l). Finally, we obtained the number of DNA copies g⁻¹ of dry soil.

Evaluating the effects of biocrusts on individual functions, multifunctionality and microbial abundance

To evaluate how the effects of biocrusts on multifunctionality change with aridity, we first calculated the RII index for each

microsite and site as $(M_{\text{bio}} - M_{\text{bg}})/(M_{\text{bio}} + M_{\text{bg}})$, where M_{bio} and M_{bg} are the average values of multifunctionality under the biocrusts and in bare ground for a given site, respectively (Armas *et al.*, 2004). The RII index has previously been used to explore biocrust effects on soil fertility (e.g. Concostrina-Zubiri *et al.*, 2013; Delgado-Baquerizo *et al.*, 2015). Here, we changed the concept of fertility for one of multifunctionality and applied this approach to our dataset. Values of this index ranged from -1 to $+1$, with positive values indicating increases in multifunctionality under the canopy of biocrusts compared with bare ground, and negative values the opposite. Similarly, we calculated the RII index for each of the soil functions used in the multifunctionality index and for both bacterial and fungal abundance.

Statistical analyses

We examined the effects of biocrusts on multifunctionality and on each individual function evaluated by conducting a nested ANOVA, with microsite (biocrust-forming mosses and bare ground) as a fixed factor and site as a random factor nested within microsite (Quinn & Keough, 2002). These analyses were conducted independently for the arid, semiarid, dry-subhumid and humid sites sampled. Because we only measured microbial abundance in a composite sample per site, we evaluated differences in microsite on bacterial and fungal abundances by conducting a one-way ANOVA, with microsite as a fixed factor. Before these analyses, total organic C, total N, Olsen P, activity of β -glucosidase and phosphatase, and total fungi and bacteria were log-transformed to improve normality.

To assess how the effects of biocrusts on multifunctionality change along aridity gradients, we fit linear regressions between aridity ($1 - \text{AI}$) and the RII values obtained with multifunctionality data. Similar regressions were carried out for the RII values of bacterial and fungal abundance, and for those soil variables used to calculate the multifunctionality index. In addition, it could be argued that our data may suffer from spatial influence (samples collected within three continents). To address this issue, we conducted partial correlations between aridity and RII multifunctionality, controlling for latitude and longitude.

Finally, we used structural equation modelling (SEM) to identify the mechanisms that control for the effects of biocrusts on multifunctionality (RII multifunctionality) across our aridity gradient; these are the indirect impacts from aridity on RII multifunctionality via soil pH, plant features (cover and richness) and the effects of biocrusts on the abundance of fungi and bacteria (RII bacterial and fungal abundance, respectively). SEM is particularly useful in large-scale correlative studies (Grace, 2006) because it allows us to partition causal influences among multiple variables, and to separate the direct and indirect effects of the predictors included in the model. We established an *a priori* model based on our current knowledge (Fig. S2). Some data manipulation was required before modeling. We examined the distributions of all our endogenous variables, and tested their normality. Aridity was x^2 -transformed to improve normality. In addition, to reduce the number of variables, and because RII bacterial and fungal abundance were highly correlated (Pearson's

$r = 0.63$; $P < 0.001$), we reduced these two variables to a single variable using a principal component analysis (PCA) based on a correlation matrix. We then introduced the first component of this PCA as a new variable into the model (RII microbial abundance). RII microbial abundance was highly correlated to both RII bacterial and RII fungal abundance (Pearson's $r = 0.91$; $P < 0.001$ in both cases). After these transformations, all the variables were normally distributed. With a good model fit (see below in this paragraph), we were free to interpret the path coefficients of the model and their associated P -values. A path coefficient is analogous to the partial correlation coefficient, and describes the strength and sign of the relationships between two variables (Grace, 2006). We then parameterized our model using our dataset and tested its overall goodness of fit. There is no single universally accepted test of overall goodness of fit for SEM, applicable in all situations regardless of sample size or data distribution. Here we used the chi-squared test (χ^2 ; the model has a good fit when χ^2 is low ($c. \leq 2$) and P is high (traditionally > 0.05); Schermelleh-Engel *et al.*, 2003) and the root-mean-square error of approximation (RMSEA; the model has a good fit when RMSEA is low ($c. \leq 0.05$) and P is high (traditionally > 0.05); Schermelleh-Engel *et al.*, 2003). All the SEM analyses were conducted using AMOS 20.0 (IBM, SPSS, New York, USA).

Results

Plant cover and species richness declined with increasing aridity (Fig. S3; $P < 0.05$). In addition, for the Australian sites, the cover of biocrust-forming mosses was positively related to aridity (Fig. S3; $P < 0.001$). Our results indicate that soils beneath biocrust-forming mosses had higher soil multifunctionality than those found in bare soil in arid and semiarid ecosystems, but not in dry-subhumid and humid ecosystems (Fig. 2a,b). These results were robust to the choice of approaches used to estimate multifunctionality (Figs S4, S5). Thus, we report in the text, and use in further analyses (described later), only results from the averaging method.

Our results further indicate that the positive relative effects of biocrusts on multifunctionality, as measured with the RII index, increased with aridity (Fig. 2c; $P < 0.001$). The partial correlation results indicated that the positive relationship between aridity and RII multifunctionality is maintained when the effects of spatial influence (latitude and longitude) were controlled for (Pearson's $r = 0.370$; $P = 0.011$). In addition, we found that the effect of biocrusts on multifunctionality was positively related to the cover of biocrust-forming mosses at the Australian sites, which account for the full range of aridity conditions evaluated (Fig. S6).

Similarly, soils under biocrust-forming mosses promoted higher soil organic C, β -glucosidase and phosphatase activities than those located in bare ground in the most arid places (Fig. 3). This was particularly evident for organic C and enzyme activities compared with P availability (Fig. 3). As with RII multifunctionality, our results indicate that the positive relative effects of biocrusts on soil organic C, total N, β -glucosidase and phosphatase activities and Olsen P were augmented with aridity

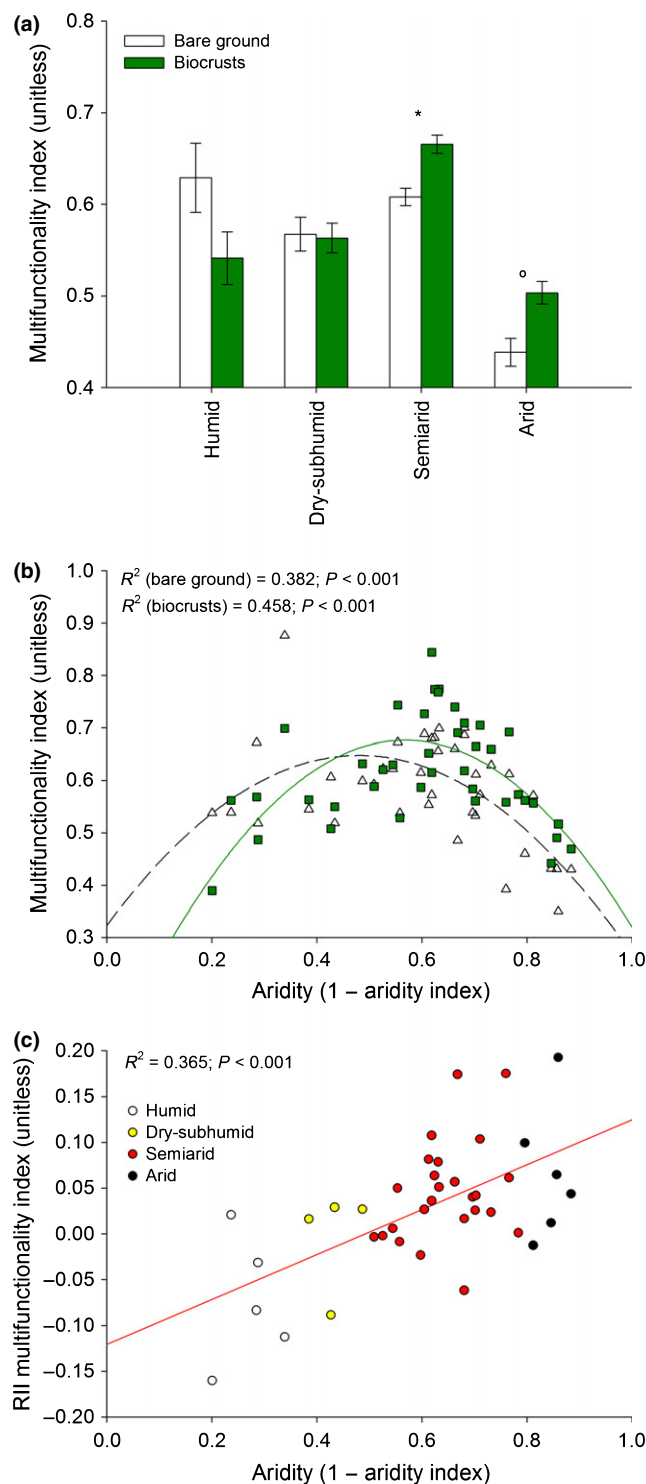


Fig. 2 (a) Multifunctionality values (means \pm SE) for the different biomes and microsites included in this study: humid ($n=5$), dry-subhumid ($n=4$), semiarid ($n=25$) and arid ($n=6$). Differences between biocrust and bare ground for each biome are as follows: °, $P=0.09$; *, $P=0.01$. (b) Relationship between aridity and the multifunctionality index used in this study for the soils under biocrusts and bare ground areas. The solid and dashed lines represent the fitted quadratic regressions for biocrusts and bare ground samples, respectively. Open triangles, bare ground; green squares, biocrusts. (c) Relationship between aridity and RII multifunctionality (i.e. relativized difference between biocrust and bare ground). The solid line represents the fitted linear regression.

(Fig. 4; $P \leq 0.05$). This effect was especially important for extra-cellular enzyme activities (Fig. 4; $R^2 > 0.40$; $P \leq 0.001$).

Soils under biocrust-forming mosses showed a higher microbial abundance (Fig. 5a,b) than those from bare ground, especially in the most arid places (Fig. 5c,d; $P \leq 0.001$). Further, the positive relative effects of biocrusts on microbial abundance (RII fungal and bacterial abundance as measured with qPCR) were positively related to those on multifunctionality (Fig. 5e,f; $P < 0.001$). Biocrust-forming mosses showed the highest positive effect on fungal compared with bacterial abundance (Fig. 5), but both RII bacterial and fungal abundance showed similar positive effects on RII multifunctionality (Fig. 5e,f).

Finally, our SEM explained 50% of the variance found in the RII multifunctionality (Fig. 6a). Our *a priori* SEM model was satisfactorily fitted to our data, as suggested by the χ^2 test ($\chi^2 = 0.00$; $P = 0.99$; $df = 1$) and RMSEA (RMSEA = 0.00; $P = 0.99$) values. Our SEM model revealed indirect positive effects of aridity on RII multifunctionality via plant cover (–), plant richness (–), soil pH (+) and RII microbial abundance (+), but we did not find any significant direct effect of aridity on RII multifunctionality (Fig. 6a). Plant cover and soil pH had a positive direct effect on RII microbial abundance. Altogether, aridity showed the highest total standardized effect (sum of all indirect and/or direct effects) on RII multifunctionality followed by RII microbial abundance and plant cover (Fig. 6b).

Discussion

Our results provide strong evidence that biocrust-forming mosses promote multifunctionality compared with bare ground areas in arid and semiarid ecosystems, but not in dry-subhumid and humid areas. Most importantly, the positive relative effects of biocrusts on multifunctionality, as measured with the RII index, increased with aridity. We also found that the positive effect of biocrusts on multifunctionality increased with the cover of mosses at the Australian sites, which spanned the full range of aridity conditions evaluated. These observations are supported by previous reports of positive effects on biocrusts on selected soil variables (Bowker *et al.*, 2011; Maestre *et al.*, 2012a; Concostrina-Zubiri *et al.*, 2013; Delgado-Baquerizo *et al.*, 2014, 2015). In addition, these results are consistent with a large body of the literature suggesting that biotic components (e.g. plant cover) often promote fertility islands in dryland ecosystems (Tongway *et al.*, 1989; Bolling & Walker, 2002; Schade & Hobbie, 2005; Perroni-Ventura *et al.*, 2009).

Our results further indicate that the positive relative effects of biocrusts on multifunctionality strengthen with increases in both aridity and biocrust cover. A major implication of our study is that biocrusts can be critical for maintaining multifunctionality under predicted increases in aridity in drylands worldwide. Consequently, any loss of biocrust cover resulting from changes in land use (e.g. soil disturbance from grazing; Eldridge *et al.*, 2010) may result in losses of soil C and nutrient availability (e.g. via erosion) affecting important ecosystem

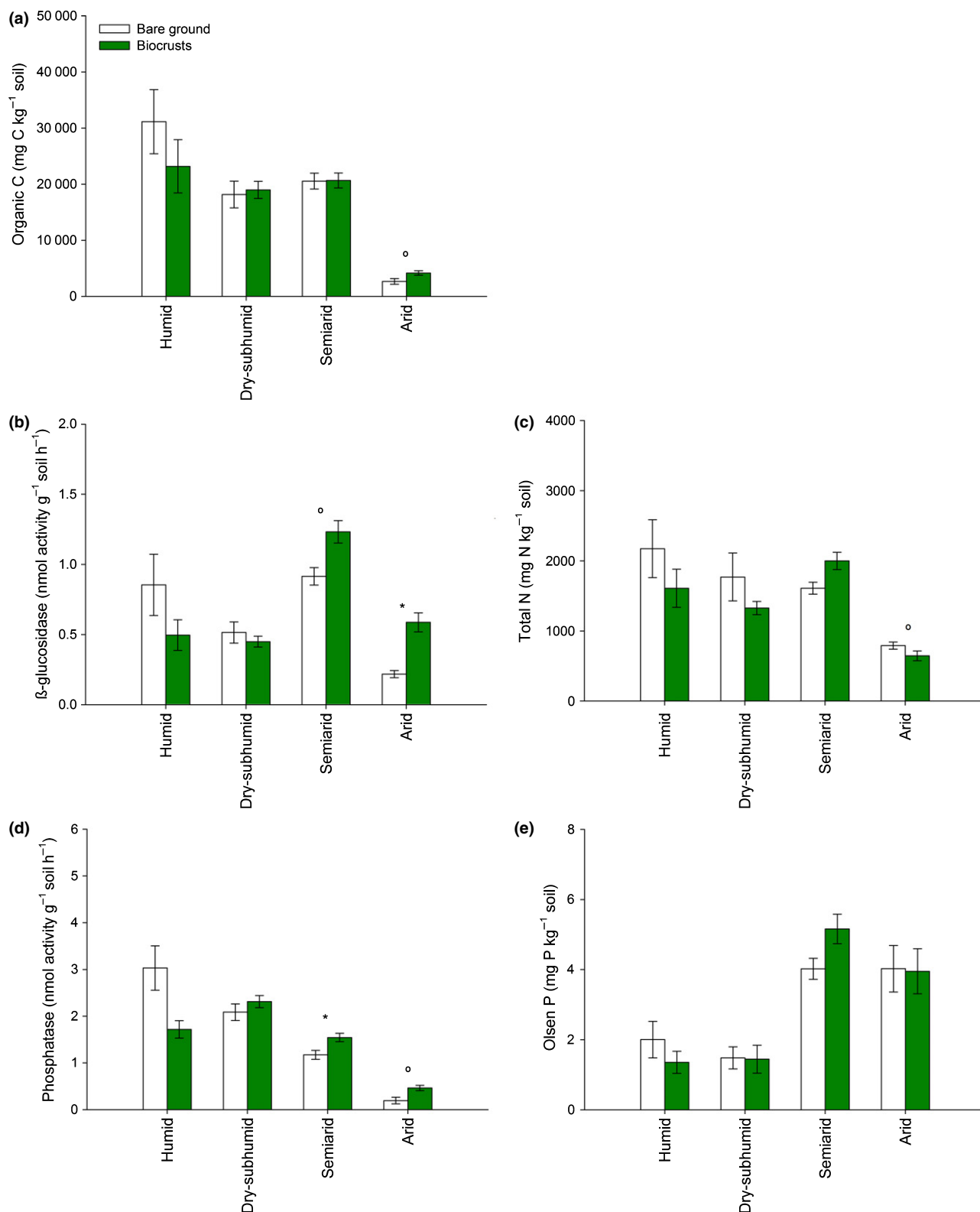


Fig. 3 Values of the different functions measured in the different biomes and microsites studied: (a) organic carbon (C); (b) activity of β -glucosidase; (c) total nitrogen (N); (d) activity of phosphatase; and (e) Olsen phosphorus (P). Data are means \pm SE; n is as follows: humid ($n=5$), dry-subhumid ($n=4$), semiarid ($n=25$) and arid ($n=6$). Differences between biocrust and bare ground for each biome are as follows: $^{\circ}$, $P \leq 0.10$; * , $P < 0.05$.

services such as C storage, climate regulation and plant productivity at the global scale (Lal, 2004). The effects of biocrusts will be particularly important in the most arid

environments as a result of their naturally low microbial activity and nutrient availability (Maestre *et al.*, 2012b; Delgado-Baquerizo *et al.*, 2013a,b).

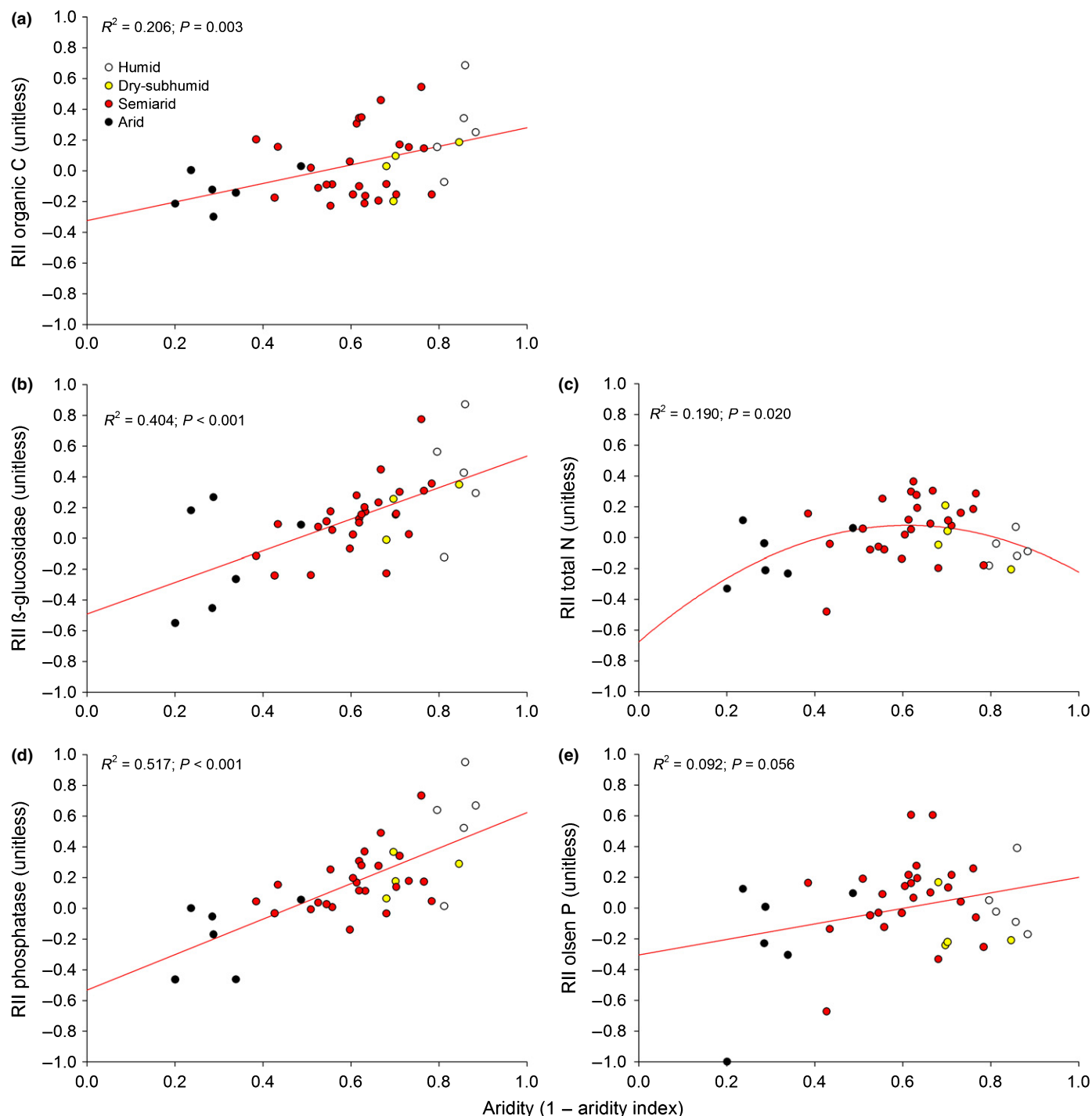


Fig. 4 Relationship between aridity and the effect of biocrust-forming mosses (RII index, i.e. relativized difference between biocrust and bare ground) on the different soil variables used in this study. The solid lines represent the fitted linear or quadratic regressions.

Although the effects of biocrust-forming mosses showed similar positive trends for each of the single functions studied (Figs 3, 4), of special interest was the fact that these organisms had the least influence on the availability of soil P compared with other variables related to soil organic matter such as organic C, total N (i.e. RII total N) and enzyme activities. This interesting result may be linked to the different degrees in which organic matter and P are related to biological and

geochemical processes in drylands (Walker & Syers, 1976; McGill & Cole, 1981; Cross & Schlesinger, 2001; Delgado-Baquerizo *et al.*, 2013a). It is well known that the availability of organic matter (i.e. C and N) is primarily linked to biological processes (e.g. photosynthesis, mineralization and atmospheric N fixation), and thus can be largely influenced by biocrusts (Evans & Ehleringer, 1993; Belnap, 2003; Castillo-Monroy *et al.*, 2010). For example, Castillo-Monroy *et al.*

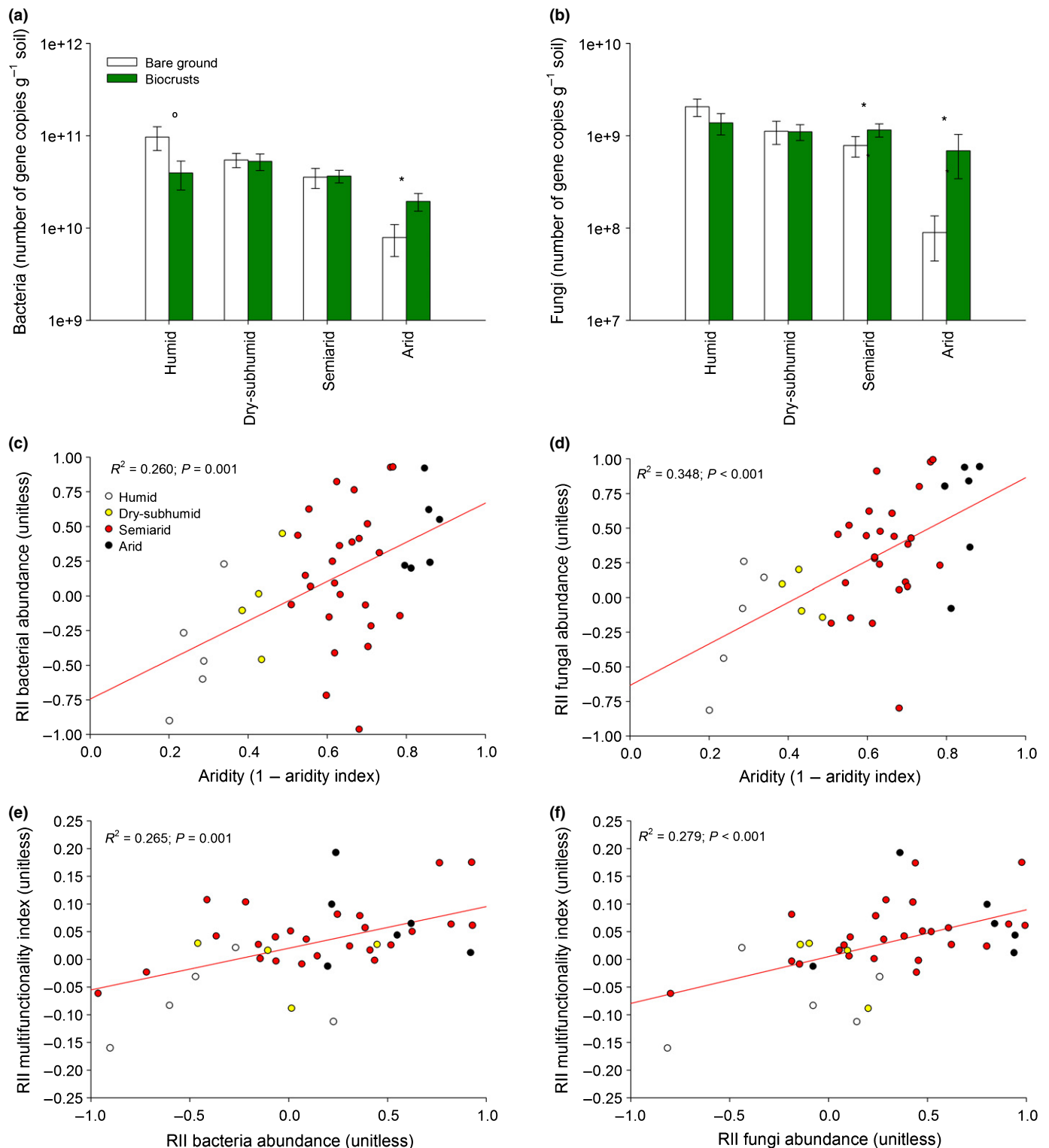


Fig. 5 Abundance of bacteria (a) and fungi (b) in the different biomes and microsites studied. Data are means \pm SE; n is as follows: humid ($n = 5$), dry-subhumid ($n = 4$), semiarid ($n = 25$) and arid ($n = 6$). Differences between biocrust and bare ground for each biome are as follows: $^{\circ}$, $P < 0.10$; *, $P < 0.05$. (c, d) The relationship between aridity and the effect of biocrust-forming mosses on the abundance of bacteria (c) and fungi (RII bacteria/fungi abundance) (d). (e, f) The relationship between RII bacteria/fungi abundance and the effects of biocrusts on multifunctionality (RII multifunctionality). The solid lines represent the fitted linear regressions.

(2010) and Evans & Ehleringer (1993) reported that biocrusts are an important source of C and N in drylands. However, the availability of P in drylands is linked to the dissolution of

P from soil minerals and, to a lesser extent, to organic matter decomposition (Walker & Syers, 1976; McGill & Cole, 1981; Delgado-Baquerizo *et al.*, 2013a). The lower extent to which P

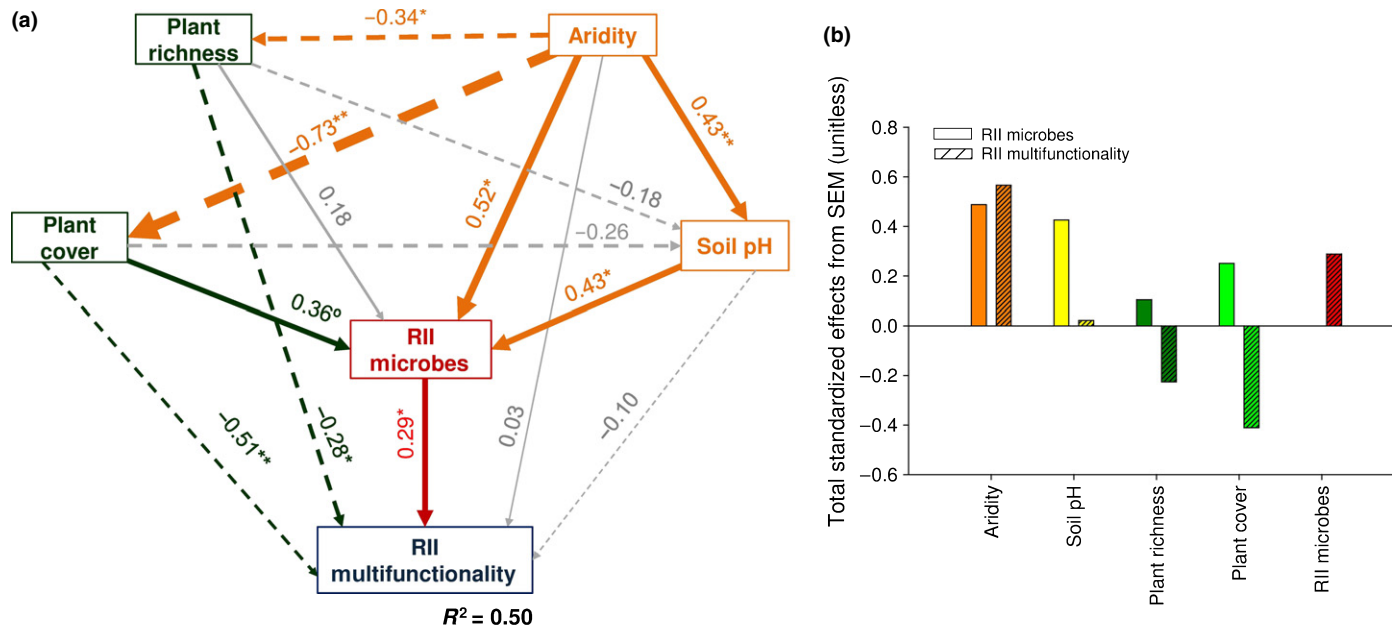


Fig. 6 (a) Structural equation model assessing the indirect and direct effects of multiple drivers of the effect of biocrusts on soil microbes and multifunctionality (RII microbes and RII multifunctionality), respectively. Numbers adjacent to arrows are indicative of the effect size of the relationship. Continuous and dashed arrows indicate positive and negative relationships, respectively. Significance levels are as follows: °, $P < 0.10$; *, $P < 0.05$; **, $P < 0.01$. (b) Total effects of the different drivers of RII multifunctionality and RII microbes.

is linked to biological process in drylands may explain why biocrusts exert the weakest observed influence on this particular variable. However, although biocrusts had less influence on available P than on those variables related to organic matter, we still found a positive effect of biocrust-forming mosses on RII P availability. This result suggests that biocrust-forming mosses can still have some control on the P availability of drylands, which is probably derived from their positive effects on extracellular enzymes related to the P cycle observed here (e.g. phosphatase; $\rho_{\text{RII P availability}} = 0.44$; $P = 0.004$) and by others (Bowker *et al.*, 2011; Maestre *et al.*, 2012b).

Soils under biocrust-forming mosses had greater microbial abundance (Fig. 5a,b) than those from bare soils, particularly in the most arid places (Figs 4, 5c). Positive effects of biocrusts on the abundance of soil fungi and bacteria have been observed previously (Bates *et al.*, 2010; Delgado-Baquerizo *et al.*, 2014). Our results suggest that the effect of biocrusts on microbial abundance increases with aridity (Figs 5c,d, 6a), a response that has not been reported before. We found a positive relationship between the RII values for multifunctionality and for microbial abundance (Fig. 5e,f). Thus, biocrust-induced changes in the abundance of fungi and bacteria may trigger the observed effects of biocrusts on multifunctionality along aridity gradients (Figs 5e,f, 6). Biocrusts probably provide better habitats for microbial communities than bare ground areas, particularly in the most arid environments where they are likely to buffer extremes of temperature and water availability (Bates *et al.*, 2010; Delgado-Baquerizo *et al.*, 2014). Compared with these areas, biocrusts therefore support the highest relative multifunctionality in these environments (Bodelier, 2011; Bardgett & van der Putten, 2014).

Although we found that aridity and RII microbial abundance were highly related to RII multifunctionality, these results are correlative in nature, and hence potentially noncausal. To address this issue, we conducted SEM analyses to identify the relative importance and indirect effects of aridity on RII multifunctionality via soil pH, plant features (cover and richness) and RII microbial abundance (first axis of a PCA with RII bacterial and fungal abundance). Our model indicates that aridity is driving RII multifunctionality via plant cover, plant richness, soil pH and RII microbial abundance, confirming the important role of microbial abundance on ecosystem multifunctionality discussed earlier (Fig. 6b). These results are not surprising, as factors such as plant influence and soil pH are largely known to be positively related to the soil microbial community (Prober *et al.*, 2015). Indeed, we identified plant cover as the largest driver of the effects of biocrusts on multifunctionality in response to increasing aridity. As aridity increases, plant cover is reduced, thereby diminishing its influence on ecosystem multifunctionality in the surrounding bare areas (Maestre *et al.*, 2003, Maestre *et al.*, 2012b; Eldridge *et al.*, 2010; Delgado-Baquerizo *et al.*, 2013a). Furthermore, as observed here and by others (Belnap *et al.*, 2001; Buis *et al.*, 2009; Thomas *et al.*, 2011), increasing aridity (Fig. S3) and decreasing plant cover promote the coverage of biocrust-forming mosses (for Australia, $\rho_{\text{plant cover} - \text{biocrust cover}} = -0.90$; $P < 0.001$). Discrete plant patches influence the nutrient content of surrounding open areas in drylands (Maestre *et al.*, 2009), the cover of plants is reduced with aridity, and the relative importance of biocrusts to ecosystem multifunctionality increases compared with bare ground areas, reducing the negative impacts of aridity on multifunctionality in the most arid places. Thus, by controlling both

the biocrust cover and the soil functionality of surrounding areas, plant cover can drive the relative effects of biocrusts on multifunctionality (RII multifunctionality).

Consistent with our results for plant cover, plant richness was negatively related to the effect of biocrusts on multifunctionality (Fig. 6b). Plant richness has been reported to promote positive effects on ecosystem multifunctionality in global drylands (Maestre *et al.*, 2012b). In this respect, landscapes with high plant richness are expected to promote multifunctionality of surrounding open areas between plant canopies (Maestre *et al.*, 2012b), masking the positive effects of biocrusts on multifunctionality. Plant richness is often reported to decline with aridity in drylands (e.g. this study; Maestre *et al.*, 2012b). In this respect, the biocrust effects on ecosystem multifunctionality will be particularly important in the most arid environments where the positive effects on multifunctionality of other biotic attributes, such as the cover and richness of vascular plants, will probably be reduced with climate change (Fig. S3b,c; Maestre *et al.*, 2012b; Delgado-Baquerizo *et al.*, 2013a).

Conclusions

Our study provides novel, empirical evidence that the effects of moss-dominated biocrusts on multifunctionality become more positive with increases in aridity, such as those expected with climate change in drylands worldwide. This was particularly evident for organic C and enzyme activities compared with P availability. We also found that the positive effects of biocrust-forming mosses on multifunctionality are mediated by the positive effects exerted by these organisms on the abundance of soil bacteria and fungi. Our findings identify the need to maintain and preserve biocrusts to mitigate the negative impacts of climate change on multifunctionality in drylands worldwide.

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Author contributions

M.D.-B. designed this study in consultation with F.T.M., D.J.E. and B.K.S. Field data were collected by M.D.-B., M.A.B., D.J.E. and J.V. Laboratory analyses were done by M.D.-B., V.O. and B.G. Data analyses were done by M.D.-B. and M.B., with the assistance of F.T.M. and B.K.S. The first draft of this paper was written by M.D.-B. and all co-authors significantly contributed to improve it.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Relationship between multifunctionality index used in this study and the same index calculated using *z*-score standardization.

Fig. S2 *A priori* generic structural equation model (SEM) used in this study.

Fig. S3 Relationships between aridity and cover of biocrust-forming mosses, plant species richness and plant cover.

Fig. S4 Relationships between the presence of biocrusts and the number of functions at or above a threshold of the maximum observed function for the different biomes studied.

Fig. S5 The slope of the relationship between the presence of biocrusts and the number of functions at or above a threshold of the maximum observed function for the different biomes studied.

Fig. S6 Relationship between the cover of biocrust-forming mosses and ecosystem multifunctionality under biocrusts, and between this cover and RII multifunctionality.

Table S1 Location, aridity index and biome of the study sites in USA, Spain and Australia

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