New Phytologist

Research

Biocrust-forming mosses mitigate the impact of aridity on soil microbial communities in drylands: observational evidence from three continents

Manuel Delgado-Baquerizo[1,2], Fernando T. Maestre[3], David J. Eldridge[4], Matthew A. Bowker[5], Thomas C. Jeffries[2] and Brajesh K. Singh[2,6]

[1]Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80309, USA; [2]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia; [3]Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, c/Tulipán s/n, 28933 Móstoles, Spain; [4]Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia; [5]School of Forestry, Northern Arizona University, 200 S. Pine Knoll Drive, Box 15018, Flagstaff, AZ 86011, USA; [6]Global Centre for Land-Based Innovation, Western Sydney University, Penrith, NSW 2751, Australia

Author for correspondence:
Manuel Delgado-Baquerizo
Tel: +1 303 735 5185
Email: M.DelgadoBaquerizo@gmail.com

Received: *11 January 2018*
Accepted: *16 February 2018*

New Phytologist (2018)
doi: 10.1111/nph.15120

Key words: aridity, bacteria, biodiversity, drylands, fungi, microbial composition.

Summary

- Recent research indicates that increased aridity linked to climate change will reduce the diversity of soil microbial communities and shift their community composition in drylands, Earth's largest biome. However, we lack both a theoretical framework and solid empirical evidence of how important biotic components from drylands, such as biocrust-forming mosses, will regulate the responses of microbial communities to expected increases in aridity with climate change.
- Here we report results from a cross-continental (North America, Europe and Australia) survey of 39 locations from arid to humid ecosystems, where we evaluated how biocrust-forming mosses regulate the relationship between aridity and the community composition and diversity of soil bacteria and fungi in dryland ecosystems.
- Increasing aridity was negatively related to the richness of fungi, and either positively or negatively related to the relative abundance of selected microbial phyla, when biocrust-forming mosses were absent. Conversely, we found an overall lack of relationship between aridity and the relative abundance and richness of microbial communities under biocrust-forming mosses.
- Our results suggest that biocrust-forming mosses mitigate the impact of aridity on the community composition of globally distributed microbial taxa, and the diversity of fungi. They emphasize the importance of maintaining biocrusts as a sanctuary for soil microbes in drylands.

Introduction

The diversity and composition of soil microbial communities are implicated in the regulation of almost every terrestrial ecosystem function and service, including nutrient cycling, climate regulation, organic matter decomposition and plant production (Jing *et al.*, 2015; Delgado-Baquerizo *et al.*, 2016b, 2017). A growing body of experimental and observational results indicate that global environmental drivers such as land use change, nitrogen (N) enrichment and climate change are impacting upon both microbial diversity and community composition in terrestrial ecosystems (Gans *et al.*, 2005; Garcia-Pichel *et al.*, 2013; Maestre *et al.*, 2015). For example, a recent global assessment of microbial communities demonstrated that increases in aridity will reduce the diversity of fungi and bacteria and drive shifts in their community structure in global drylands (Maestre *et al.*, 2015). Thus, any impacts of increasing aridity on soil microbial communities can potentially have important consequences for the provision of ecosystem services in terrestrial environments (Delgado-Baquerizo *et al.*, 2016b). Drylands are crucial to achieve global sustainability, as they cover *c.* 45% of Earth's land surface (Prăvălie, 2016), support over 38% of the global human population (Reynolds *et al.*, 2007), harbour a very rich and unique biodiversity (Maestre *et al.*, 2012), and play critical roles in the global carbon (C) cycle (Poulter *et al.*, 2014). The global significance of drylands is going to increase due to climate change, as forecasted increases in aridity worldwide will expand the global extent of drylands by up to 23% by the end of this century (Huang *et al.*, 2016). Therefore, understanding how increasing aridity affects soil microbial communities, and how different

ecosystem features may modulate such impacts, is essential to develop new mitigation and adaptation strategies to climate change.

Drylands are highly heterogeneous ecosystems that are typically formed by a matrix of discrete vegetation patches embedded in a matrix of open areas devoid of perennial vegetation (Valentin *et al.*, 1999). These open areas are commonly occupied by soil surface communities dominated by cyanobacteria, mosses and lichens (biocrusts hereafter), which are one of the most widespread and important biotic components in drylands worldwide (Belnap, 2006; Lindo & Gonzalez, 2010). Biocrust-forming mosses, like plants (e.g. Prober *et al.*, 2015; Liu *et al.*, 2016, 2017), provide habitat for soil organisms, including bacteria and fungi that thrive in the soil beneath them (Kuske *et al.*, 2012; Steven *et al.*, 2013), and largely influence their abundance and activity (Bates *et al.*, 2010; Miralles *et al.*, 2012; Delgado-Baquerizo *et al.*, 2016a). A growing number of experiments are providing evidence that microbial communities associated with biocrusts (e.g. cyanobacteria) are highly vulnerable to climate change from local to regional scales (Reed *et al.*, 2012; Garcia-Pichel *et al.*, 2013; Ferrenberg *et al.*, 2015). Previous studies also have highlighted the role of biocrusts in promoting the resistance and resilience of soil functioning (e.g. nutrient cycling) to climate change (Reed *et al.*, 2012; Delgado-Baquerizo *et al.*, 2014, 2016a; Liu *et al.*, 2016). However, despite the acknowledged importance of biocrust-forming mosses for ecosystem functioning (Delgado-Baquerizo *et al.*, 2016a), we know little about how they impact the composition and diversity of microbial communities across environmental gradients. Indeed, and to the best of our knowledge, no study to date has explicitly addressed the role of biocrust-forming mosses in regulating the response of microbial communities to increasing aridity at a continental scale.

Herein we present a conceptual model of microbial responses to changes in aridity under two different microsites: biocrusts and bare ground (Fig. 1). In our model, shifts in community composition (i.e. relative abundance of microbial taxa) and diversity (i.e. richness: number of phylotypes) in response to increases in aridity are relatively small in biocrust-forming mosses compared to bare ground microsites (Fig. 1). Therefore, our conceptual model predicts that, compared with open areas without visible biocrust constituents (i.e. bare ground), biocrust-forming mosses should reduce any fluctuations in the richness and composition of microbial communities caused by increasing aridity (Fig. 1). The rationale underpinning our model is that biocrust-forming mosses provide habitat that is more conducive to microbial growth and survival than bare ground (Baran *et al.*, 2015). For example, well-developed biocrust-forming mosses often have roughened surfaces that, in some ecosystems, trap water, allowing them to maintain humid conditions for longer and buffering extreme environmental conditions typical of drylands (Eldridge *et al.*, 2010; Berdugo *et al.*, 2014; Chamizo *et al.*, 2016). Further, biocrust-forming mosses provide a reliable and consistent supply of resources such as C and N for microbial communities, which may promote their resistance to increasing aridity. Finally, we clarify that our approach explicitly assumes that naturally occurring patches of bare ground and biocrusts are the drivers of microsite amelioration rather than reflecting pre-existing conditions. Such an assumption is supported by previous experimental studies providing evidence that biocrusts modulate the response of soil microbes and microbially driven functions to global change drivers (Reed *et al.*, 2012; Delgado-Baquerizo *et al.*, 2013b; Liu *et al.*, 2016, 2017).

In order to test our conceptual model, we conducted a field survey covering two microsites (bare ground and biocrust-forming mosses) in 39 locations from three continents (North America, Europe and Australia) across a wide aridity gradient (from arid to humid ecosystems), and characterized bacterial and fungal communities in the soil surface using the Illumina Miseq profiling of ribosomal genes and internal transcribed spacer markers, respectively. In addition, we used four surrogates of ecosystem functions linked to C, N and phosphorus (P) cycling (total N, activity of β-glucosidase, activity of phosphatase and available P) to evaluate the relationships between microbial

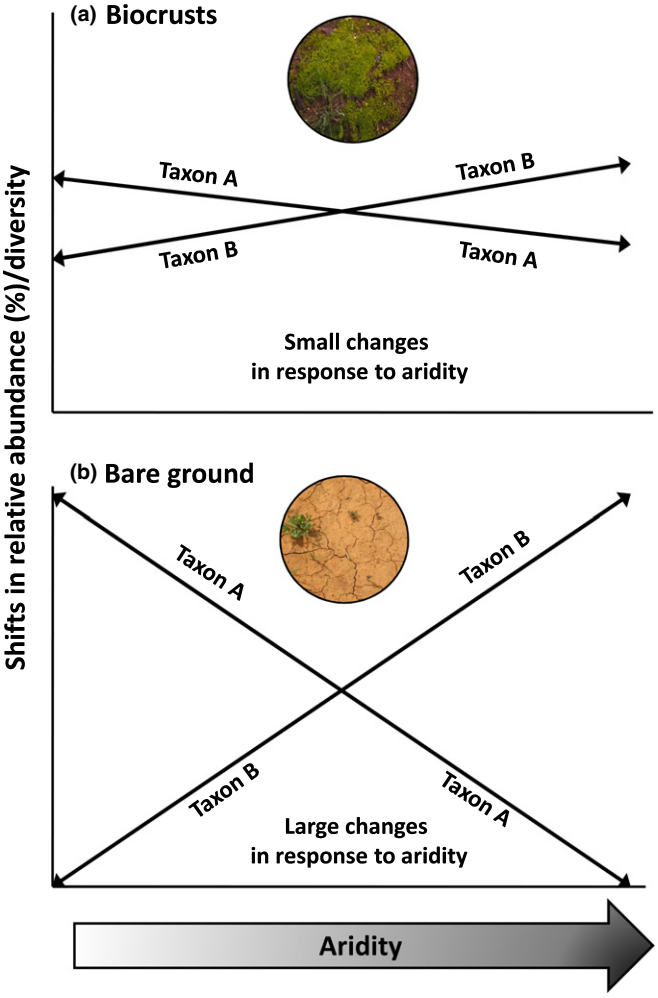

Fig. 1 *A priori* conceptual framework exploring how biocrust-forming mosses modulate the effects of aridity on soil microbes. (a) Biocrust-forming mosses (vs (b) bare ground) promote microbial resistance in response to climate change by buffering reductions in soil humidity and resource availability derived from increasing aridity. Thus, we expect lower shifts in main microbial taxa and diversity across different aridity conditions in biocrust-forming mosses compared to bare ground microsites.

composition/richness and ecosystem functioning along aridity gradients.

Materials and Methods

Study sites and data collection

We collected field data from 39 sites located in USA, Spain and Australia (Supporting Information Fig. S1; Table S1). Locations for this study were chosen to represent a wide aridity gradient; we included arid (aridity index = 0.05–0.20; $n = 6$ sites), semiarid (aridity index = 0.20–0.50; $n = 24$ sites), dry-subhumid (aridity index = 0.50–0.65; $n = 4$ sites) and humid (aridity index > 0.65; $n = 5$ sites) ecosystems. To improve interpretation, aridity was presented as 1–Aridity Index (AI), where AI = precipitation/potential evapotranspiration (Delgado-Baquerizo *et al.*, 2013a). This alters the aridity scale such that sites with higher aridity values are more arid. Aridity index data were obtained from the global aridity map of the FAO (http://www.fao.org/geonetwork/srv/en/main.home?uuid=221072ae-2090-48a1-be6f-5a88f061431a). The selected sites included 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 pH 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.*, 2012). At each site, we established a 30 × 30 m plot representative of the dominant vegetation. All soils were collected during the dry season (July 2012 in the USA, July 2013 in Spain, March 2014 in Australia) to reduce bias among study sites due to seasonal changes in the soil variables studied. To the best of our knowledge, the sampled areas did not undergo dramatic climatic changes within this timeframe. At each site, a composite sample (from three 0–5 cm deep cores) was collected under the most common biocrust-forming mosses, and in bare ground; this is naturally occurring (i.e. nondisturbed) open areas devoid of perennial vegetation and without visible biocrust constituents. We maintained a minimum separation distance of 1 m between samples or away from perennial plant patches to remove potential sources of dependence among samples (Delgado-Baquerizo *et al.*, 2016a). A total of 78 soil samples were analyzed for this study. After field sampling, biocrust-forming mosses and plant roots were carefully separated from the soil, which was sieved (2-mm mesh) and separated into two fractions. One soil fraction was immediately frozen at −20°C for quantifying the diversity and community composition of bacteria and fungi in our samples. The other fraction was air-dried and stored for 1 month before biogeochemical analyses.

We focused on biocrust-forming mosses because they are globally distributed (in boreal, arctic, temperate and dryland ecosystems) and are commonly found across wide environmental gradients worldwide (e.g. from humid to arid systems; Lindo & Gonzalez, 2010), and because they contribute directly or indirectly (i.e. through cyanobacterial associates) to critical ecosystem functions, including nutrient cycling, soil stability, infiltration and gas exchange (Eldridge *et al.*, 2010; Lindo & Gonzalez, 2010). The most common biocrust-forming mosses in our study sites 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 *Rosulabryum* spp. (Australia). In the Australian plots, where these data were available, the cover of biocrust-forming mosses naturally increased with aridity as open spaces become more available and plant cover decreased (Fig. S2).

Assessing microbial diversity and composition

In the present study, we worked with microbial diversity (number of phylotypes) at the operational taxonomic units (OTU) level and community composition at a higher level of taxonomic classification (i.e. phyla). The main reasons to work with community composition of bacteria and fungi at the phylum level are: the main phyla are globally distributed and common across samples, allowing us to directly compare our soil samples across continents (e.g. Ramirez *et al.*, 2012); the use of a high level of taxonomic classification is suggested as an appropriate method of predicting broad patterns in ecosystem functioning (Philippot *et al.*, 2010); and functional information has become increasingly available at the phylum level (Fierer *et al.*, 2007; Trivedi *et al.*, 2013). For example, the richness and relative abundance of major microbial phyla representatives (e.g. Actinobacteria, Proteobacteria, Bacteroidetes and Firmicutes) have been recently reported to strongly regulate soil multifunctionality in microcosm experiments (Delgado-Baquerizo *et al.*, 2017).

Molecular analyses were separately conducted on composite samples of each microsite (bare ground and biocrust-forming mosses) pooled within a site (two samples per site). 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. The extracted DNA samples were frozen and shipped to the Next Generation Genome Sequencing Facility of the Western Sydney University (Australia), where they were defrosted and sequenced using the Illumina MiSeq platform (Caporaso *et al.*, 2012) and the 341F/805R (bacteria; Herlemann *et al.*, 2011) and FITS7/ITS4 (fungi, Ihrmark *et al.*, 2012) primer sets (See Methods S1 for bioinformatic analyses). We kept main bacterial and fungal taxa (i.e. bacterial and fungal phyla accounting for > 95% of relative abundance; Fig. S3) and richness (number of OTUs at a 97% similarity threshold) for further analyses.

Surrogates of soil functions

We used four variables related to carbon (C), nitrogen (N) and phosphorus (P) cycling and storage as surrogates of ecosystem functioning (functions, hereafter): available P, total N, activity of β-glucosidase and phosphatase. Overall, these variables constitute good proxies of processes driving nutrient cycling, biological productivity and the build-up of nutrient pools (Maestre *et al.*, 2012). Soil total N was measured with a CN analyzer (Leco

CHN628 Series; Leco Corp., St Joseph, MI, USA). Phosphatase and β-glucosidase activities were measured as described in Maestre *et al.* (2012). The concentration of Olsen inorganic P was measured from $NaHCO_3$ 0.5 M soil extracts, as described in Delgado-Baquerizo *et al.* (2016a).

Statistical analyses

We first explored the 'effects' of biocrust-forming mosses on microbial community composition and richness (number of OTUs at a 97% sequence similarity). To do this, we calculated the relative interaction index (RII) for each site and microsite as $(Micr_{bio} - Micr_{bg})/(Micr_{bio} + Micr_{bg})$, where $Micr_{bio}$ and $Micr_{bg}$ are values of microbial richness and relative abundance of main microbial phyla under the biocrust-forming mosses and in bare ground areas for a given site, respectively (Armas *et al.*, 2004). This index provides the relativized difference between biocrust-forming mosses and bare ground microsites. We then compared the average (across sites) values of RII of each of the evaluated microbial variables between these microsites. Values of this index ranged from −1 to +1, with positive values indicating increases in microbial diversity/relative abundance of main taxa under the canopy of biocrust-forming mosses compared to bare ground, and negative values the opposite.

We then used a nonmetric multidimensional ordination (NMDS) to explore the overall effects of microsite (biocrust-forming mosses and bare ground) and aridity conditions on bacterial and fungal community composition (i.e. relative abundance of all bacterial and fungal phyla), respectively. The 2D NMDS solution, using Euclidean distance, provided a suitable representation of both the bacterial and fungal community NMDS data. Before these analyses, data were log-transformed to reduce the influence of extreme values. We conducted NMDS analyses with the PRIMER v.6 statistical package for Windows (Primer-E Ltd; Plymouth Marine Laboratory, Plymouth, UK) using the Euclidean distance.

Our conceptual model assumes that microsite modulates the effects of aridity on bacterial and fungal community composition (Fig. 1). This implies an interaction between aridity class (arid, semiarid, dry-subhumid and humid) and microsite (biocrust-forming mosses vs bare ground), which requires statistical validation before analyses. Therefore, we explicitly tested for this interaction using a two-way MANOVA, with aridity class and microsite as fixed factors. In these analyses we focused on phyla that represent > 95% of the relative abundance of fungal and bacterial communities, respectively. We found a strongly significant aridity class × microsite interaction for the composition of both bacteria ($F = 1.67$, $P < 0.001$; Fig. S3) and fungi ($F = 1.88$, $P = 0.003$; Fig. S4). Once we had provided evidence of microsite-dependency in the response of microbial community to climate change, we explored the impacts of different aridity classes (i.e. arid, semiarid, dry-subhumid and humid) on microbial composition, independently, for each microsite. To do this, we conducted a one-way ANOVA with aridity class as a fixed factor for the relative abundance of each microbial phyla studied and for the diversity of both bacteria and fungi. Moreover, we repeated these analyses using a more conservative approach. We examined the effects of aridity classes on microbial variables by conducting a nested ANOVA, with aridity classes as a fixed factor and country (Australia, Spain and USA) as a random factor nested within aridity classes, respectively (Quinn & Keough, 2002). These analyses were conducted independently for each microsite. This approach aims to control for any effect of the geographical location (country) in our analyses.

In addition, we used linear regressions to determine the relationship between aridity (1 – Aridity Index) and both microbial composition (NMDS axes 1 and 2 and the relative abundance of main phyla) and richness. Separate analyses were conducted for bare ground and biocrust-forming mosses microsites. We further repeated these analyses, but evaluating the linear regressions between aridity (1-aridity index) and the residuals of the different microbial variables (NMDS axes, relative abundance of main phyla and microbial richness) for bare ground (bare) and biocrust-forming mosses microsites. Residuals for microbial variables were obtained from a one-way ANOVA with country (Spain, Australia and USA) as a fixed factor. These analyses are carried out separately for bare ground (bare) and biocrust-forming mosses microsites. The main goal of these analyses was to reduce the influence of any unexplained variation that might arise from the fact that samples were collected in different countries. The resulting residuals from these ANOVAs were therefore not influenced by country selection (see Delgado-Baquerizo *et al.*, 2016c for a similar approach).

Moreover, to statistically evaluate whether the relationship between aridity and the main bacterial and fungal phyla followed a similar trend in both the biocrust-forming mosses and bare ground, we explored the interaction between microsite and aridity class using a linear model for each of the analyzed microbial variables. If, as hypothesized, biocrust-forming mosses regulate the response of microbial taxa to increasing aridity, we would expect to find either no relationship or a lower slope in the relationship between aridity and each microbial variable in biocrust-forming mosses compared with areas of bare ground. To further explore differences in the response of microbial composition and diversity in biocrust-forming mosses and bare ground, we calculated the coefficient of variation across sites for microbial diversity and the relative abundance of each of the evaluated phyla (Tilman *et al.*, 2014).

Finally, to evaluate how possible shifts in microbial composition could affect ecosystem functioning, we calculated the correlations (Spearman's rank) among microbial community composition/richness and the surrogates of soil functions evaluated (available P, total N and activity of β-glucosidase and phosphatase). Correlations and ANOVA analyses were performed using SPSS 15.0 software (SPSS Inc., Chicago, IL, USA).

Data accessibility

Data associated with this paper have been deposited in figshare: https://figshare.com/s/e459fe6097cf9fa9c845 (10.6084/m9.figshare.5782263).

Results

Soils from this study were dominated by the bacterial phyla *Actinobacteria* and *Proteobacteria*, and by the fungal phylum *Ascomycota* (Fig. S3). Biocrust-forming mosses had an overall positive effect, as measured with the RII, on the relative abundance of *Armatimonadetes*, *Bacteroidetes*, *Cyanobacteria*, *Planctomycetes*, *Proteobacteria*, *Verrucomicrobia* and on fungal diversity, and a negative effect on the relative abundance of *Actinobacteria* (Fig. 2). This was particularly evident in the most arid locations (Fig. S4). Conversely, biocrust-forming mosses had no overall effect on either bacterial diversity or the relative abundance of main fungal taxa (Fig. 2). In general, biocrust-forming mosses and bare ground areas had similar fungal composition but, on average, biocrust-forming mosses had a slightly higher relative abundance of undetermined taxa, an outcome that was particularly evident in the most arid locations (Fig. S5). Biocrust-forming mosses also had a much lower and higher relative abundance of *Basidiomycota* than bare ground in the most humid and arid locations, respectively (Fig. S5).

The first axis of the NMDS conducted with bacterial phyla (Fig. 3a) was strongly positively related to the relative abundance of *Proteobacteria* (Spearman $\rho = 0.67$; $P < 0.001$) and *Acidobacteria* (Spearman $\rho = 0.47$; $P < 0.001$), but negatively related to the relative abundance of *Actinobacteria* (Spearman $\rho = -0.71$; $P < 0.001$) and *Chloroflexi* (Spearman $\rho = -0.68$; $P < 0.001$), whereas the second NMDS axis (Fig. 3a) was positively related to *Planctomycetes* (Spearman $\rho = 0.60$; $P < 0.001$). Likewise, the first axis of the NMDS conducted with fungal phyla (Fig. 3b) was strongly negatively related to the relative abundance of *Ascomycota* (Spearman $\rho = -0.90$; $P < 0.001$) and positively related to *Basidiomycota* (Spearman $\rho = 0.83$; $P < 0.001$), whereas the second NMDS axis (Fig. 3b) was positively related to Unidentified phyla (Spearman $\rho = 0.91$; $P < 0.001$) and negatively related to the relative abundance of *Zygomycetous* fungi (Spearman $\rho = -0.52$; $P < 0.001$).

We found significant relationships between aridity and the first axis of the bacterial and fungal NMDS ordinations (−), fungal richness (−) and the relative abundance of *Actinobacteria* (+), *Proteobacteria* (−), *Planctomycetes* (−), *Acidobacteria* (−), *Chloroflexi* (+), *Gemmatimonadetes* (+), *Verrucomicrobia* (−), *Ascomycota* (+), *Zygomycota* (–) in the bare ground microsite (Table 1; Figs 3c,d, S6–S8). However, these relationships disappeared when analyzing data collected under biocrust-forming mosses. The slopes of the relationships between aridity and all microbial composition and diversity variables were steeper for bare ground than for biocrust-forming mosses (see aridity × microsite interaction in Table 1; Figs 3, S5, S6). This was particularly notable for the relative abundance of *Actinobacteria*, *Proteobacteria*, *Chloroflexi*, *Verrucomicrobia* and *Ascomycota* (Table 1; $P < 0.05$). In support of this, the coefficient of variation of the first NMDS axis of bacterial and fungal phyla, and that of the relative abundance of *Actinobacteria*, *Proteobacteria*, *Planctomycetes*, *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Verrucomicrobia*, *Ascomycota* and fungal richness along the aridity gradient was always lower under biocrust-forming mosses than in

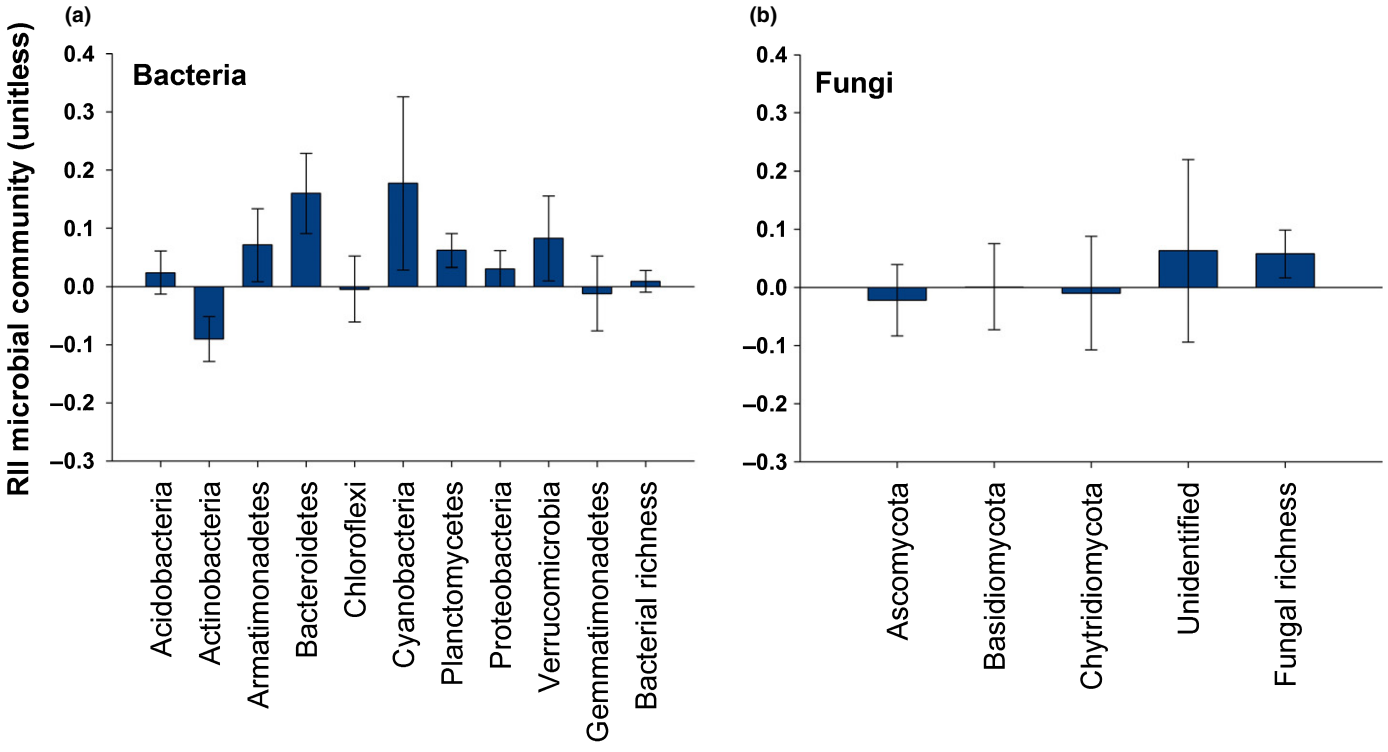

Fig. 2 Effects of biocrust-forming mosses, as measured with the relative interaction index (RII), on (a) bacterial and (b) fungal composition (relative abundance of main phyla) and diversity (operational taxonomic unit (OTU) richness). Values represent means ± 90% bootstrap confidence intervals ($n = 39$). Relative abundance data for biocrust and bare ground microsites are available in Supporting Information Figs S2–S4.

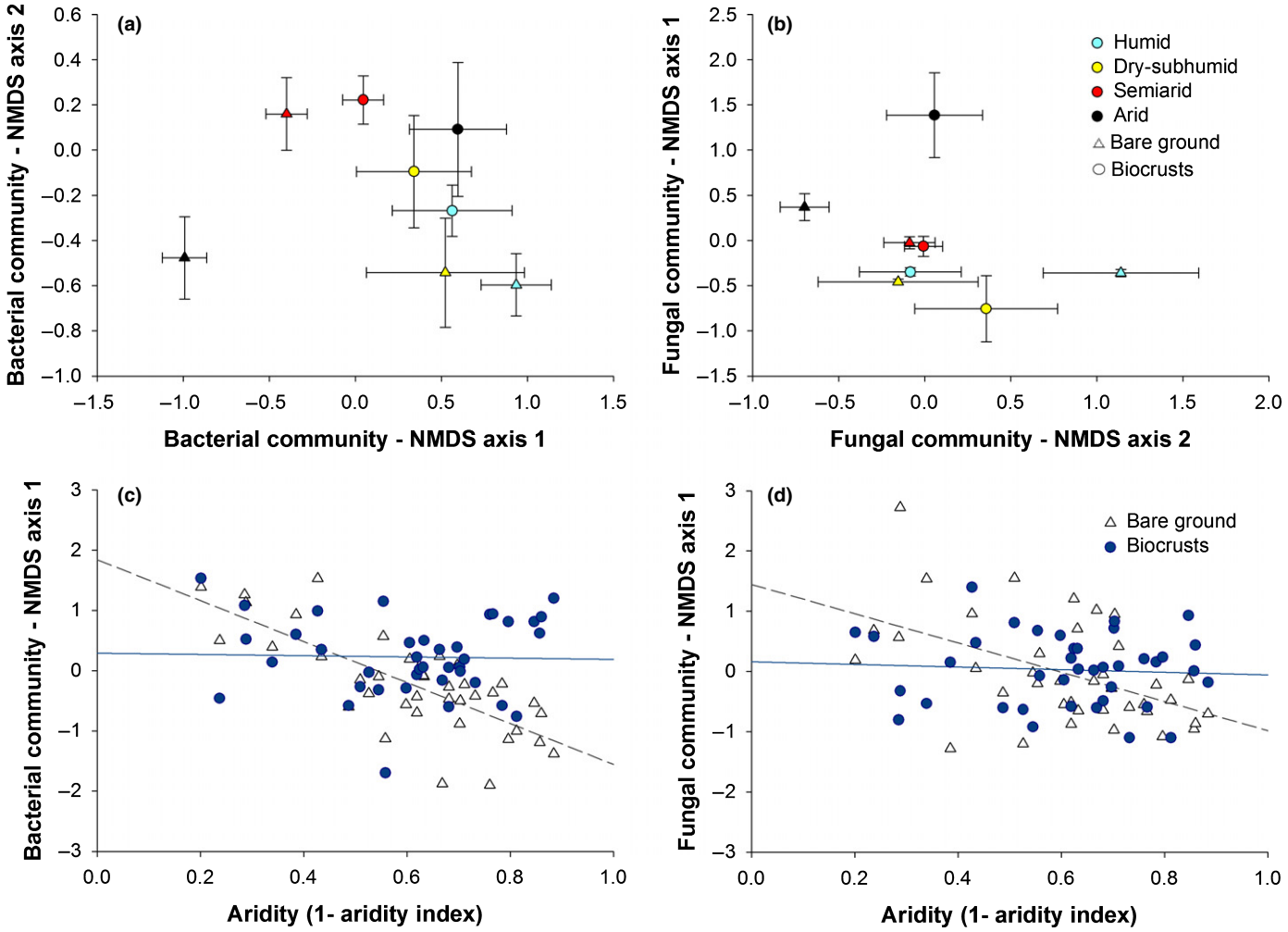

Fig. 3 Nonmetric multidimensional scaling (NMDS) plots showing the relative differences in community composition of soil (a) bacteria and (b) fungi for biocrust-forming mosses (circles) and bare ground (triangles) microsites along the aridity gradient studied. Lower panels show the relationship between aridity and the first axis from the NMDS of soil (c) bacteria and (d) fungi in biocrust-forming mosses and bare ground microsites, respectively. Solid and dashed lines represent linear regressions fitted to biocrust-forming mosses and bare ground microsites, respectively. Slope, R^2 and *P*-values for these regressions are available in Table 1. Data in (a) and (b) are mean values ± SE ($n = 39$).

bare ground (Table 1). In general, we found similar results when we explored the relationships between aridity and the residuals of microbial variables – controlled by country (Table S2) – that is, we found that the slopes of the relationships between aridity and all microbial composition and diversity variables were steeper for bare ground than for biocrust-forming mosses (Table S2).

Likewise, we only found significant differences among aridity conditions for the relative abundance of *Proteobacteria*, *Planctomycetes*, *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Verrucomicrobia*, *Ascomycota* and *Basidiomycota* for bare ground, but not for biocrust-dominated, microsites (Fig 4; Table S2). Interestingly, the largest shifts in the relative abundance of the microbial communities studied occurred from dry-subhumid to semiarid, and from semiarid to arid ecosystems (Fig 4; Table S3). Aridity had similar effects on the second NMDS axis conducted with fungal phyla and on the relative abundance of *Bacteroidetes* (+), *Armatimonadetes* (+), *Cyanobacteria* (+), *Basidiomycota* (−) and Unidentified fungal phyla (+) in both bare ground and biocrust-dominated microsites (Table 1; Figs S6, S7, S9). However, the relationship between aridity and the relative abundance of *Armatimonadetes*, *Basidiomycota* and Unidentified fungal phyla still had a lower slope and coefficient of variation in the biocrust-forming mosses than the bare ground microsites. We also found similar results when using the nested ANOVA to evaluate the effects of aridity classes on the relative abundance of major taxa in the two microsites evaluated (Table S3 vs S4). Again, we found an overall larger effect of aridity classes on the microbial variables in bare ground areas than under biocrust-forming mosses microsites (Table S4).

We found that the diversity and relative abundance of several microbial phyla were positively related to surrogates of soil functions. The relative abundance of these taxa were negatively correlated with aridity on bare ground areas, but not under biocrust-forming mosses. For example, the diversity of fungi, and the relative abundance of *Acidobacteria, Planctomycetes*, *Basidiomycota* and *Gemmatimonadetes* were positively correlated

Table 1 Summary results of linear regressions between aridity (1–Aridity Index) and different microbial variables (nonmetric multidimensional scaling (NMDS) axes, relative abundance of main phyla and microbial richness) for bare ground (bare) and biocrust microsites

	Bare				Biocrust				Interaction
Microbial variable	R^2	Slope	*P*	CV(%)	R^2	Slope	*P*	CV(%)	*P*
Bacterial NMDS 1	0.564	−3.399	**< 0.001**	48.46	0.001	−0.103	0.863	30.643	**< 0.001**
Bacterial NMDS 2	0.009	0.412	0.546	28.382	0.027	0.492	0.322	19.143	0.925
Fungal NMDS 1	0.246	−2.425	**0.001**	70.208	0.004	−0.220	0.691	45.684	**0.003**
Fungal NMDS 2	0.359	1.269	**< 0.001**	21.684	0.224	2.324	**0.002**	46.502	0.170
Bacterial richness	0.006	255.3	0.636	17.874	0.004	220.600	0.717	19.648	0.966
Fungal richness	0.098	−322.1	**0.052**	29.122	0.053	−234.200	0.158	25.996	0.702
Actinobacteria	0.134	13.122	**0.022**	25.659	0.029	−4.924	0.298	24.808	**0.015**
Proteobacteria	0.411	−21.538	**< 0.001**	30.061	0.037	−4.830	0.238	21.445	**0.006**
Planctomycetes	0.171	−10.069	**0.009**	29.574	0.025	−3.030	0.340	21.291	0.147
Acidobacteria	0.175	−8.939	**0.008**	30.166	0.048	−4.617	0.180	28.704	0.355
Chloroflexi	0.358	19.673	**< 0.001**	51.678	0.064	6.086	0.121	41.166	**0.022**
Gemmatimonadetes	0.197	4.815	**0.005**	47.291	0.045	1.974	0.193	42.831	0.197
Bacteroidetes	0.138	3.166	**0.019**	63.33	0.267	7.624	**< 0.001**	71.133	0.072
Verrucomicrobia	0.387	−5.379	**< 0.001**	53.052	0.022	−0.731	0.366	27.552	**0.001**
Armatimonadetes	0.365	2.096	**< 0.001**	59.615	0.280	1.347	**< 0.001**	40.656	0.198
Cyanobacteria	0.199	3.317	**0.004**	96.63	0.199	6.583	**0.004**	115.354	0.184
Ascomycota	0.113	29.236	**0.036**	27.641	0.064	−20.175	0.120	26.752	**0.009**
Basidiomycota	0.350	−47.218	**< 0.001**	56.297	0.121	−23.28	**0.030**	48.164	0.109
Unidentified fungi	0.395	23.666	**< 0.001**	79.51	0.318	46.366	**< 0.001**	125.351	0.066
Zygomycota	0.307	−20.369	**< 0.001**	142.194	0.039	−10.432	0.227	178.821	0.318

Interaction between aridity and microsite was calculated using a two-way MANOVA; $P \leq 0.05$ in bold.

with total N and the activity of β-glucosidase (Table 2). We note that, in the Australian sites, where these data were available, the concentration of total N was highly positively correlated with dissolved inorganic N, total available N (dissolved inorganic and organic N), microbial biomass N and N-acetyl-β-glucosaminidase (an enzyme related to N cycle; Fig. S10). Fungal richness and the relative abundance of *Verrucomicrobia*, *Basidiomycota* and *Zygomycota* were positively related to the activity of phosphatase. Finally, the relative abundance of *Gemmatimonadetes* and fungal unidentified phyla, which peaked in the most arid locations and under biocrust-forming mosses microsites, was positively correlated to the availability of P in soil (Table 2).

Discussion

Our results, from an observational cross-continental survey, suggest that biocrust-forming mosses have the potential to mitigate the impact of aridity on the composition of soil bacterial and fungal communities, and on the diversity of fungi, in drylands. In particular, increasing aridity altered the relative abundance of the majority of microbial communities (*c.* 90% and *c.* 60% for bacteria and fungi, respectively) including *Actinobacteria*, *Proteobacteria*, *Planctomycetes*, *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Verrucomicrobia*, *Ascomycota*, *Zygomycota* and fungal richness on areas of bare ground. However, increasing aridity had a much lower influence on the community composition and diversity of soil microbes under biocrust-forming mosses. Most importantly, the slopes of the relationships between aridity and all the microbial composition and diversity variables evaluated were steeper for bare ground than for biocrust-forming mosses, suggesting the presence of greater stability in these microbial features across the aridity gradient under biocrust-forming mosses. Together, our results suggest that biocrust-forming mosses have the potential to buffer the negative effects of aridity on the relative abundance of the main bacterial and fungal phyla.

Several mechanisms could explain the observed lack of relationship between aridity and the richness and/or community composition of soil bacteria and fungi along the aridity gradient for biocrust-forming mosses compared with bare ground microsites. For example, biocrusts are known to modify microclimate, infiltration and soil water availability dynamics compared with adjacent crust-free surfaces (Almog & Yair, 2007; Eldridge *et al.*, 2010; Berdugo *et al.*, 2014; Chamizo *et al.*, 2016; but see Bowker *et al.*, 2013). Increasing aridity is a major threat to microbial community composition (i.e. relative abundance of main taxa) and diversity in drylands (Maestre *et al.*, 2015). Therefore, biocrust-forming mosses could potentially buffer some of the negative effects of aridity on microbial composition by maintaining higher water availability for longer after rainfall events, and by providing a refuge for bacterial and fungal communities in drylands. Interestingly, the only reported overall negative effect of biocrust-forming mosses on the relative abundance of microbial taxa was found on *Actinobacteria* (Fig. 2), which are highly resistant to desiccation (Battistuzzi & Hedges, 2009), as evidenced by its dominance in bare ground areas under the most arid conditions. Thus, dominant *Actinobacteria* taxa might prefer drier environments (Maestre *et al.*, 2015) and be suppressed by other microbial communities as soil moisture increases under biocrust-forming mosses. Another mechanism explaining our results is related to the capacity of biocrust-forming mosses to

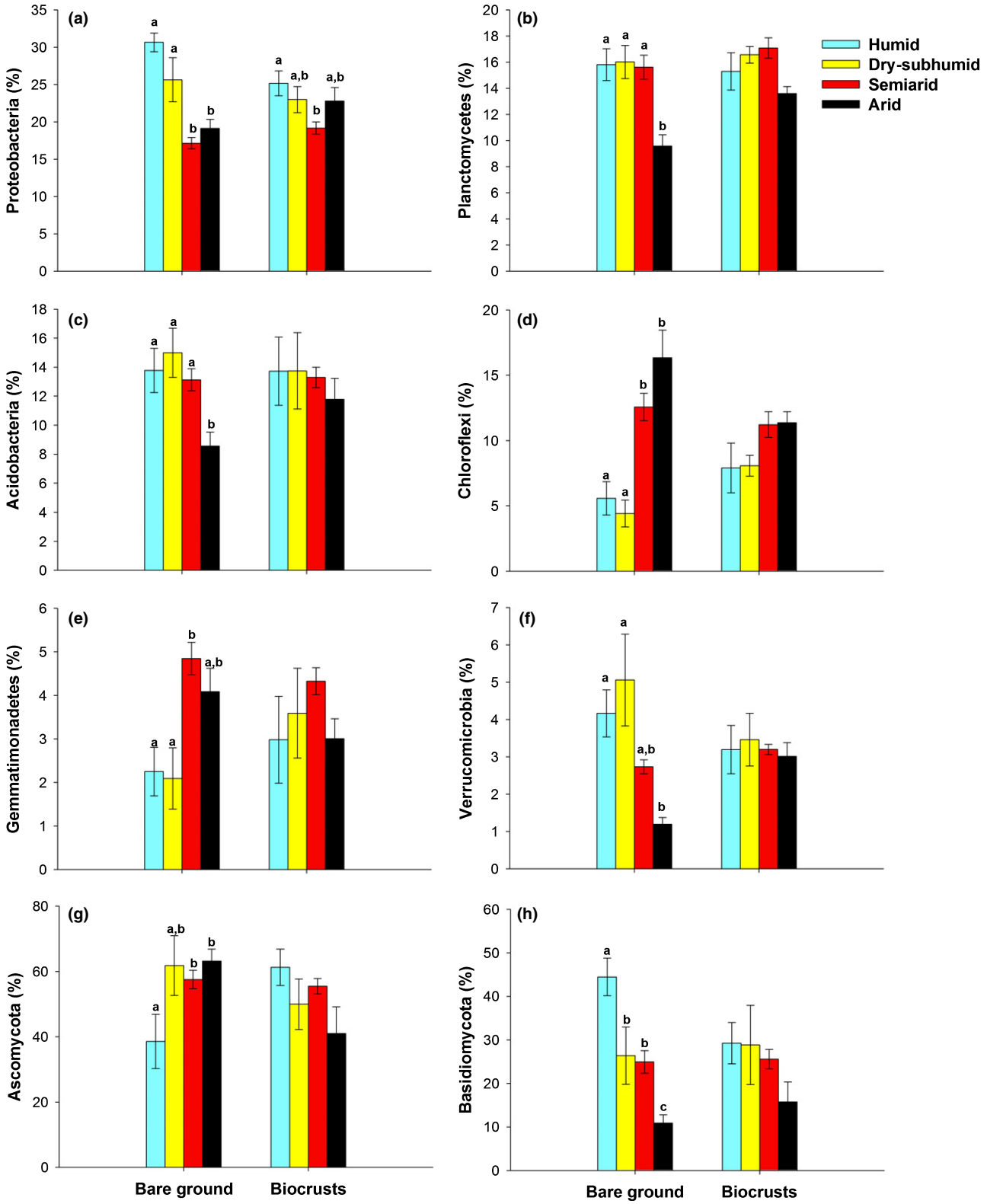

Fig. 4 Relative abundance of main (a–f) bacterial and (g, h) fungal phyla in biocrust-forming mosses and bare ground microsites across different aridity conditions. Data represent means ± SE, *n* as follows: humid ($n = 5$), dry-subhumid ($n = 4$), semiarid ($n = 24$) and arid ($n = 6$). Different letters indicate significant differences between aridity conditions ($P < 0.05$; *post-hoc* tests after one-way ANOVA). Analyses were done independently for bare ground and biocrusts microsites (see Supporting Information Table S3 for full ANOVA results).

Table 2 Spearman correlation coefficient (ρ) between microbial attributes (bacterial and fungal composition and diversity) and four surrogates of ecosystem functions (total nitrogen (N), phosphatase, glucosidase and available phosphorus (P); $n = 78$)

Taxa	Parameters	Glucosidase	Total N	Phosphatase	Olsen P
Acidobacteria	ρ	0.354	0.285	0.107	−0.082
	P-value	0.001	0.011	0.350	0.477
Actinobacteria	ρ	−0.337	−0.120	0.089	0.049
	P-value	0.003	0.296	0.439	0.669
Bacteroidetes	ρ	0.355	−0.076	−0.308	0.425
	P-value	0.001	0.509	0.006	< 0.001
Chloroflexi	ρ	−0.111	−0.204	−0.309	0.152
	P-value	0.332	0.073	0.006	0.183
Cyanobacteria	ρ	0.109	−0.162	−0.328	0.343
	P-value	0.340	0.157	0.003	0.002
Planctomycetes	ρ	0.528	0.660	0.107	0.088
	P-value	< 0.001	< 0.001	0.351	0.445
Proteobacteria	ρ	−0.249	−0.219	0.183	−0.347
	P-value	0.028	0.054	0.109	0.002
Verrucomicrobia	ρ	0.211	0.186	0.430	−0.252
	P-value	0.064	0.103	< 0.001	0.026
Gemmatimonadetes	ρ	0.414	0.244	−0.034	0.508
	P-value	< 0.001	0.032	0.764	< 0.001
Armatimonadetes	ρ	−0.048	−0.331	−0.229	0.249
	P-value	0.678	0.003	0.044	0.028
Bacterial richness	ρ	0.533	0.447	0.163	0.361
	P-value	< 0.001	< 0.001	0.154	0.001
Ascomycota	ρ	−0.128	0.060	0.140	0.067
	P-value	0.264	0.600	0.221	0.558
Basidiomycota	ρ	0.037	0.269	0.379	−0.285
	P-value	0.745	0.017	0.001	0.012
Unidentified fungi	ρ	0.196	−0.194	−0.671	0.503
	P-value	0.085	0.088	< 0.001	< 0.001
Zygomycota	ρ	−0.045	0.157	0.374	−0.286
	P-value	0.698	0.171	0.001	0.011
Fungal richness	ρ	0.311	0.392	0.458	−0.006
	P-value	0.006	< 0.001	< 0.001	0.957

promote 'fertility islands' in drylands, enhancing atmospheric carbon (C) and nitrogen (N) fixation and phosphorus (P) desorption from bedrock compared to adjacent bare ground areas (Concostrina-Zubiri *et al.*, 2013; Delgado-Baquerizo *et al.*, 2016a). Thus, by providing a constant source of resources (carbon inputs, e.g. via photosynthetic processes and moss decomposition) and holding soil moisture for longer after rainfall events, biocrust-forming mosses may promote the stability of soil microbial communities to conditions of increasing aridity.

Our results suggest that biocrust-forming mosses might buffer the negative impacts of aridity on key functional microbial groups such as *Acidobacteria*, *Planctomycetes*, *Verrucomicrobia* and *Basidiomycota*, and on the diversity of fungi (Fierer *et al.*, 2007; Trivedi *et al.*, 2013; Wagg *et al.*, 2014; Jing *et al.*, 2015; Maestre *et al.*, 2015). These microorganisms were highly positively associated with multiple surrogates of ecosystem functions, including soil enzyme activities (linked to decomposition), total N and available P (Table 2). They also may play a critical role in the decomposition of litter originating from the mosses themselves (Hagemanna & Moronic, 2015). Bacterial and fungal phyla such as *Acidobacteria*, *Planctomycetes*, *Verrucomicrobia* and *Basidiomycota* have a large capacity to degrade a range of organic C compounds (Fierer *et al.*, 2007; Trivedi *et al.*, 2013). Likewise, fungal richness may also play an important role in breaking down litter from biocrust-forming mosses. This is supported by a growing number of studies highlighting the role of microbial diversity in supporting soil processes such as nutrient cycling and organic matter decomposition (Wagg *et al.*, 2014; Jing *et al.*, 2015; Delgado-Baquerizo *et al.*, 2016b).

Given the overall lack of change of microbial community composition and diversity to increasing aridity under reported biocrust-forming mosses, our results suggest that compared with bare ground, biocrust-forming mosses may buffer reductions in soil fertility that are likely to result from a drying climate (Delgado-Baquerizo *et al.*, 2013a). The area occupied by biocrust-forming mosses is often higher in semiarid and arid areas due to reductions in competition from a dwindling vascular plant cover (Fig. S2) and therefore to the greater potential area for colonization and growth resulting from reduced plant cover (e.g. Belnap *et al.*, 2001; Thomas *et al.*, 2011; Delgado-Baquerizo *et al.*, 2016a). Recent experimental studies also have found that the area occupied by mosses may expand with warming (Ladrón de Guevara *et al.*, 2018). However, biocrusts are highly sensitive to physical disturbance associated with grazing (Eldridge *et al.*, 2010; Kuske *et al.*, 2012), and to other human activities such as agriculture (Zaady *et al.*, 2016). In this respect, any negative impacts of

physical disturbance on biocrust-forming mosses may result in a reduction in microbial resistance, and thus on the resultant goods and services that they provide (e.g. soil fertility). It is imperative, therefore, that any disturbance to biocrusts is minimized, particularly in the most arid areas.

Finally, it is important to note that our results only consider the role of biocrust-forming mosses in regulating the response of microbial community composition and richness to increases in aridity. Our choice of biocrust type was due to their ubiquity in drylands (biocrust-forming mosses are globally distributed and present across multiple biomes; Lindo & Gonzalez, 2010; Elbert *et al.*, 2012), practicality and influence on ecosystem functioning (Eldridge *et al.*, 2010; Lindo & Gonzalez, 2010). The sign (positive) of the effects of mosses on microbial stability reported here might be shared across other biocrust types such as lichens, have been previously reported to promote both soil microbial activity and functioning previously (Liu *et al.*, 2017). However, it is also probable that the magnitude of the positive effects from biocrusts on soil microbial stability are dependent upon the identity of biocrusts, as recent studies point to species-specific effects on soil functions and microbial abundance in biocrust communities (Delgado-Baquerizo *et al.*, 2016a; Liu *et al.*, 2016).

Together, our results provide observational evidence that aboveground biotic communities have the potential to regulate the responses of soil microbial community composition and diversity to increases in aridity. In particular, we found an overall lack of relationship between aridity and the relative abundance and richness of main microbial taxa in biocrust-forming mosses compared to bare ground microsites. our results may be explained, in part, by the often reported positive effect of biocrust-forming mosses on moisture and resource availability. Microbial taxa beneath biocrust-forming mosses that are relatively unresponsive to aridity include key functional microbial phyla such as *Acidobacteria*, *Planctomycetes*, *Verrucomicrobia* and *Basidiomycota*. Effects also were greatest on the diversity of fungi, which are known to play important roles in providing a highly functional environment below biocrust-forming mosses. Together our results emphasize that it is critically important to establish effective policies and management practices to protect these organisms. This will not only reduce the risk of soil erosion and therefore land degradation and subsequent desertification, but will ensure that dryland microbial communities are able to function effectively and support key ecosystem services in a warmer, and more arid, world.

Acknowledgements

We thank Santiago Soliveres, Miguel García-Gómez and Enrique Valencia for their assistance during fieldwork. We also thank Victoria Ochoa and Beatriz Gozalo for their help with lab analyses. M.D-B. also acknowledge support from the Marie Sklodowska-Curie Actions of the Horizon 2020 Framework Programme H2020-MSCA-IF-2016 under REA grant agreement no. 702057. M.D-B. is also supported by the British Ecological Society (BES grant agreement no. LRB17\1019 (MUSGONET)). F.T.M. was supported by the European Research Council (ERC Grant agreement nos. 242658 (BIOCOM) and 647038 (BIODESERT)) and by the Spanish Ministry of Economy and Competitiveness (BIOMOD project, CGL2013-44661-R). B.K.S. was supported by the Australian Research Council (project D170104634).

Author contributions

M.D-B. designed this study; field samplings were conducted by M.D-B., D.J.E., M.A.B. and F.T.M.; laboratory analyses were done by F.T.M. and M.D-B.; sequencing analyses were provided by B.K.S.; bioinformatic analyses were done by T.C.J.; statistical modeling was done by M.D-B.; the manuscript was written by M.D-B. with contributions from all co-authors.

ORCID

Manuel Delgado-Baquerizo http://orcid.org/0000-0002-6499-576X

References

Almog R, Yair A. 2007. Negative and positive effects of topsoil biological crusts on water availability along a rainfall gradient in a sandy arid area. *Catena* **70**: 437–442.

Armas C, Ordiales R, Pugnaire FI. 2004. Measuring plant interactions: a new comparative index. *Ecology* **85**: 2682–2686.

Baran R, Brodie EL, Mayberry-Lewis J, Hummel E, Da Rocha UN, Chakraborty R, Bowen BP, Karaoz U, Cadillo-Quiroz H, Garcia-Pichel F *et al.* 2015. Exometabolite niche partitioning among sympatric soil bacteria. *Nature Communications* **6**: 8289.

Bates ST, Nash TH, Sweat KG, Garcia-Pichel F. 2010. Fungal communities of lichen-dominated biological soil crusts: diversity, relative microbial biomass, and their relationship to disturbance and crust cover. *Journal of Arid Environments* **74**: 1192–1199.

Belnap J. 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrological Processes* **3178**: 3159–3178.

Belnap J, Kaltenecker JH, Rosentreter R, Williams J, Leonard S, Eldridge D. 2001. *Biological soil crusts: ecology and management. Technical reference no 1730–2.* Denver, CO, USA: US Geological Survey.

Berdugo M, Soliveres S, Maestre FT. 2014. Vascular plants and biocrusts modulate how abiotic factors affect wetting and drying events in drylands. *Ecosystems* **17**: 1242–1256.

Battistuzzi FU, Hedges SB. 2009. A major clade of prokaryotes with ancient adaptations to life on land. *Molecular Biology and Evolution* **26**: 335–343.

Bowker MA, Eldridge DJ, Val J, Soliveres S. 2013. Hydrology in a patterned landscape is co-engineered by soil-disturbing animals and biological crusts. *Soil Biology and Biochemistry* **61**: 14–22.

Caporaso JG, Lauber CL, Walters WA, Berg-Lyons D, Huntley J, Fierer N, Betley J, Fraser L, Bauer M, Gormley N *et al.* 2012. Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. *The ISME Journal* **6**: 1621–1624.

Chamizo S, Cantón Y, Rodríguez-Caballero E, Domingo F. 2016. Biocrusts positively affect the soil water balance in semiarid ecosystems. *Ecohydrology* **9**: 1208–1221.

Concostrina-Zubiri L, Huber-Sannwald E, Martínez I, Flores JL, Escudero A. 2013. Biological soil crusts greatly contribute to small-scale soil heterogeneity along a grazing gradient. *Soil Biology and Biochemistry* **64**: 28–36.

Delgado-Baquerizo M, Maestre FT, Eldridge DJ, Bowker MA, Ochoa V, Gozalo B, Berdugo M, Val J, Singh BK. 2016a. Biocrust-forming mosses mitigate the negative impacts of increasing aridity on ecosystem multifunctionality in drylands. *New Phytologist* **209**: 1540–1552.

Delgado-Baquerizo M, Maestre FT, Escolar C, Gallardo A, Ochoa V, Gozalo B, Prado-Comesaña A. 2014. Direct and indirect impacts of climate change on microbial and biocrust communities alter the resistance of the N cycle in a semiarid grassland. *Journal of Ecology* **102**: 1592–1605.

Delgado-Baquerizo M, Maestre FT, Gallardo A, Bowker MA, Wallenstein MD, Quero JL, Ochoa V, Gozalo B, García-Gómez M, Soliveres S *et al.* 2013a. Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature* **504**: 667–672.

Delgado-Baquerizo M, Maestre F, Reich P, Jeffries T, Gaitan J, Encinar D, Berdugo M, Campbell C, Singh BK. 2016b. Microbial diversity drives multifunctionality in terrestrial ecosystems'. *Nature Communications* **7**: 10541.

Delgado-Baquerizo M, Maestre FT, Reich PB, Trivedi P, Osanai Y, Liu Y, Hamonts K, Jeffries TC, Singh BK. 2016c. Carbon content and climate variability drive global soil bacterial diversity patterns. *Ecological Monographs* **86**: 373–390.

Delgado-Baquerizo M, Morillas L, Maestre FT, Gallardo A. 2013b. Biocrusts control the nitrogen dynamics and microbial functional diversity of semi-arid soils in response to nutrient additions. *Plant and Soil* **372**: 643–654.

Delgado-Baquerizo M, Trivedi P, Trivedi C, Eldridge DJ, Reich PB, Jeffries TC, Singh BK. 2017. Microbial richness and composition independently drive soil multifunctionality. *Functional Ecology* **31**: 2330–2343.

Elbert W, Weber B, Burrow S, Steinkamp J, Büdel B, Andreae MO, Pösch U. 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience* **5**: 459–462.

Eldridge D, Bowker MA, Maestre FT, Alonso P, Mau RL, Papadopoulos J, Escudero A. 2010. Interactive effects of three ecosystem engineers on infiltration in a semi–arid Mediterranean grassland. *Ecosystems* **13**: 499–510.

Ferrenberg S, Reed SC, Belnap J. 2015. Climate change and physical disturbance cause similar community shifts in biological soil crusts. *Proceedings of the National Academy of Sciences, USA* **112**: 12116–12121.

Fierer N, Morse J, Berthrong S, Bernhardt ES, Jackson RB. 2007. Environmental controls on the landscape-scale biogeography of stream bacterial communities. *Ecology* **88**: 2162–2173.

Gans J, Wolinsky M, Dunbar J. 2005. Computational improvements reveal great bacterial diversity and high metal toxicity in soil. *Science* **309**: 1387–1390.

Garcia-Pichel F, Loza V, Marusenko Y, Mateo P, Potrafka RM. 2013. Temperature drives the continental-scale distribution of key microbes in topsoil communities. *Science* **340**: 1574–1577.

Hagemanna U, Moronic MT. 2015. Moss and lichen decomposition in old-growth and harvested high-boreal forests estimated using the litterbag and minicontainer methods. *Soil Biology and Biochemistry* **87**: 10–24.

Herlemann DP, Labrenz M, Jürgens K, Bertilsson S, Waniek JJ, Andersson AF. 2011. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *The ISME Journal* **5**: 1571–1579.

Huang J, Yu H, Guan X, Wang G, Guo R. 2016. Accelerated dryland expansion under climate change. *Nature Climate Change* **6**: 166–171.

Ihrmark K, Bodeker ITM, Cruz-Martinez K, Friberg H, Kubartova A, Schenck J, Strid Y, Stenlid J, Brandstrom-Durling M, Clemmensen KE *et al.* 2012. New primers to amplify the fungal ITS2 region–evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology* **82**: 666–677.

Jing X, Sanders NJ, Shi Y, Chu H, Classen AT, Zhao K, Chen L, Shi Y, Jiang Y, He JS. 2015. The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. *Nature Communications* **6**: 8159.

Kuske CR, Yeager CM, Johnson S, Ticknor LO, Belnap J. 2012. Response and resilience of soil biocrust bacterial communities to chronic physical disturbance in arid shrublands. *The ISME Journal* **6**: 886–897.

Ladrón de Guevara M, Gozalo B, Raggio J, Lafuente A, Prieto M, Maestre FT. 2018. Warming reduces the cover, richness and evenness of lichen-dominated biocrusts but promotes moss growth: insights from an 8 yr experiment. *New Phytologist*. doi: 10.1111/nph.15000.

Lindo Z, Gonzalez A. 2010. The bryosphere: an integral and influential component of the Earth's biosphere. *Ecosystems* **13**: 612–627.

Liu YR, Delgado-Baquerizo M, Trivedi P, He J-Z, Singh BK. 2016. Species identity of biocrust-forming lichens drives the response of soil nitrogen cycle to altered precipitation frequency and nitrogen amendment. *Soil Biology and Biochemistry* **96**: 128–136.

Liu YR, Delgado-Baquerizo M, Trivedi P, He J-Z, Wang JT, Singh BK. 2017. Identity of biocrust species and microbial communities drive the response of soil multifunctionality to simulated global change. *Soil Biology and Biochemistry* **107**: 208–217.

Maestre FT, Delgado-Baquerizo M, Jeffries TC, Eldridge DJ, Ochoa V, Gozalo B, Quero JL, García-Gómez M, Gallardo A, Ulrich W *et al.* 2015. Increasing aridity reduces soil microbial diversity and abundance in global drylands. *Proceedings of the National Academy of Sciences, USA* **112**: 15684–15689.

Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, García-Gómez M, Bowker MA, Soliveres S, Escolar C *et al.* 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* **335**: 214–218.

Miralles I, Domingo F, García-Campos E, Trasar-Cepeda C, Carmen Leirós M, Gil-Sotres F. 2012. Biological and microbial activity in biological soil crusts from the Tabernas desert, a sub-arid zone in SE Spain. *Soil Biology and Biochemistry* **55**: 113–121.

Philippot L, Andersson SGE, Battin TJ, Prosser JI, Schimel JP, Whitman WB, Hallin S. 2010. The ecological coherence of higher bacterial taxonomic ranks. *Nature Reviews Microbiology* **8**: 523–52910.

Poulter B, Frank D, Ciais P, Myneni RB, Andela N, Bi J, Broquet G, Canadell JG, Chevallier F, Liu YY *et al.* 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* **29**: 600–603.

Prăvălie R. 2016. Drylands extent and environmental issues: a global approach. *Earth Science Reviews* **161**: 259.

Prober SM, Leff JW, Bates ST, Borer ET, Firn J, Harpole WS, Lind EM, Seabloom EW, Adler PB, Bakker JD *et al.* 2015. Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. *Ecology Letters* **1**: 85–95.

Quinn G, Keough K. 2002. *Experimental design and data analysis for biologists.* New York, NY, USA: Cambridge University Press.

Ramirez KS, Craine JM, Fierer N. 2012. Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes. *Global Change Biology* **6**: 1918–1927.

Reed SL, Coe K, Sparks JP, Housman DC, Zelikova TJ, Belnap J. 2012. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nature Climate Change* **2**: 752–755.

Reynolds JF, Smith MS, Lambin EF, Turner BL, Mortimore M, Batterbury SPL, Downing TE, Dowlatabadi H, Fernández RJ, Herrick JE *et al.* 2007. Global desertification, building a science for dryland development. *Science* **316**: 847–851.

Steven B, Lionard M, Kuske CR, Vincent WF. 2013. High bacterial diversity of biological soil crusts in water tracks over permafrost in the High Arctic Polar Desert. *PLoS ONE* **8**: e71489.

Thomas AD, Hoon SR, Dougill AJ. 2011. Soil respiration at five sites along the Kalahari Transect: effects of temperature, precipitation pulses and biological soil crust cover. *Geoderma* **167–168**: 284–294.

Tilman D, Isbell F, Cowles JM. 2014. biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* **45**: 471–493.

Trivedi P, Anderson IC, Singh BK. 2013. Microbial modulators of soil carbon storage: integrating genomic and metabolic knowledge for global prediction. *Trends in Microbiology* **21**: 641–665.

Valentin C, d'Herbès JM, Poesen J. 1999. Soil and water components of banded vegetation patterns. *Catena* **37**: 1–24.

Wagg C, Bender FS, Widmer F, van der Heijden MGA. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences, USA* **111**: 5266–5270.

Zaady E, Eldridge DJ, Bowker MA. 2016. *Effects of local scale disturbance on biocrust. Biological soil crusts: an organizing principle in drylands.* Ecological Studies Series, Berlin, Germany: Springer.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Locations of the study sites in USA ($n = 8$), Spain ($n = 10$) and Australia ($n = 21$).

Fig. S2 Relationships between aridity and the cover of biocrusts and plants in the 21 locations from Australia.

Fig. S3 Relative abundance of major bacterial and fungal phyla in bare ground and biocrust microsites.

Fig. S4 Relative abundance of major bacterial phyla in bare ground and biocrust microsites across different aridity conditions.

Fig. S5 Relative abundance of major fungal phyla in bare ground and biocrust microsites across different aridity conditions.

Fig. S6 Relationships between aridity and the relative abundance of main bacterial taxa in bare ground and biocrust microsites.

Fig. S7 Relationships between aridity and the relative abundance of four main fungal taxa in bare ground and biocrust microsites.

Fig. S8 Relationships between aridity and the richness of bacteria and fungi in bare ground and biocrust microsites.

Fig. S9 Relationships between aridity and the second axis of the nonmetric multidimensional scaling (NMDS) ordination conducted with soil bacteria and fungi.

Fig. S10 Relationship between total N and dissolved inorganic N (DIN), total available N (dissolved inorganic and organic N), microbial biomass N and N-acetyl-β-glucosaminidase in the 21 plots from Australia.

Table S1 Location, aridity index and aridity class of the study sites

Table S2 Summary results of linear regressions between aridity and the residuals of the different microbial variables for bare ground and biocrust microsites

Table S3 Results of one-way ANOVAs testing the effects of aridity class on microbial composition and diversity in bare ground and biocrust microsites

Table S4 Results of one-way nested ANOVAs testing the effects of aridity class on microbial composition and diversity in bare ground and biocrust microsites

Methods S1 Bioinformatic analyses.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.