

RESEARCH ARTICLE

Linking biological soil crust attributes to the multifunctionality of vegetated patches and interspaces in a semiarid shrubland

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Abstract

1. Understanding the importance of biotic community structure on ecosystem functioning, and whether communities inhabiting different microhabitats in highly heterogeneous areas provide different ecological functions is a challenge in ecological research in the face of biodiversity and habitat loss. Biological soil crusts (BSCs) have been largely treated as unique entities, and have been mostly examined in interspaces between perennial plants, limiting current understanding of their role as drivers of ecosystem functioning and their relative contribution in comparison to vascular plants.
2. We assessed the role of BSCs on ecosystem functioning in vegetated patches and interspaces, and how individual soil functions and ecosystem multifunctionality are related to changes in BSC species- and community-level attributes. We contemplated nine ecosystem functions associated with soil water dynamics, nutrient cycling and erosion potential.
3. We found that vegetated patches improve infiltration rates, soil stability and net potential nitrogen (N) mineralization compared to interspaces, and thus dominate multifunctionality. However, well-developed BSCs improve soil moisture and N pool in both microsites, and are multifunctional stabilizing soils and regulating soil moisture and infiltration in the interspaces. BSC surface microstructure, including changes in total cover, species richness, morphological functional groups and surface discontinuities, has significant effects on soil moisture. Differences in soil N and phosphorous are mostly related to the presence of BSC-lichens. The effect of BSCs on multifunctionality varies in dependence of the particular set of functions that are sought to simultaneously maximize.
4. Our results suggest that vascular plants and BSCs have idiosyncratic effects on different key ecosystem functions and multifunction, and BSCs substitute vascular plants in stabilizing soils and regulating water dynamics in the interspaces. BSCs greatly contribute to small-scale heterogeneity in the functioning of vegetated patches and interspaces, hence consideration of BSCs in different microsites is essential for enhancing our understanding of their functional relevance at a regional scale. In addition, quantification of BSC microstructure is crucial, owing to the contrasting effects of BSC species- and community-level attributes on different functions and multifunction.

KEYWORDS

BSC floristic composition, BSC functional structure, soil aggregate stability, soil moisture, soil nutrients, spatial distribution

1 | INTRODUCTION

Arid and semiarid ecosystems, commonly referred to as drylands due to their potential water deficit, present a two-phase mosaic structure of vegetated patches and interspaces with sparse vegetation (Schlesinger, Raikes, Hartley, & Cross, 1996). The soil surfaces both in the vegetated patches and the interspaces are often colonized by biological soil crusts (BSCs), which are communities mainly composed of cyanobacteria, lichens and mosses. It is considered that the functioning of drylands, defined as the utilization, cycling and flux of resources (e.g. carbon, water, nutrients), is largely determined by the BSCs due to their roles in critical ecological processes, such as soil stability (Chaudhary et al., 2009), infiltration and runoff (Eldridge et al., 2010) and nutrient cycles (Castillo-Monroy, Maestre, Delgado-Baquerizo, & Gallardo, 2010; Hu et al., 2015). In addition, BSCs are considered multifunctional communities due to their simultaneous effect on various ecological processes (Bowker, Maestre, & Mau, 2013). The concept of ecosystem multifunctionality has emerged during the recent years to depict that ecological processes are interrelated in the ecosystems (Zavaleta, Pasari, Hulvey, & Tilman, 2010).

Although during the last decades there has been an increasing interest in assessing the contribution of BSCs to ecosystem functioning, contradictory or ambiguous results have been obtained probably due to differences in the spatial and taxonomical approximations of studies. Some researches considered BSCs as unique entities and did not take into account the characteristics of the studied communities (e.g. Berdugo, Soliveres, & Maestre, 2014; Chaudhary et al., 2009). Broad types of BSCs (i.e. cyanobacteria-, lichen- or moss-dominated communities) have been also extensively studied (e.g. Bowker, Eldridge, Val, & Soliveres, 2013; Bu, Wu, Han, Yang, & Meng, 2015; Chamizo, Canton, Rodriguez-Caballero, & Domingo, 2016). However, it has become evident that these approaches constitute a serious limitation to understand the relevance of BSCs upon particular functions, given that community structure can be an important determinant of BSC ecological role (Concostrina-Zubiri, Huber-Sannwald, Martínez, Flores Flores, & Escudero Alcántara, 2013; Eldridge et al., 2010). Following earlier studies on vascular plant functional traits, within the past few years some studies on BSCs invested efforts to elucidate the functionality of individual species (Bowker, Mau, Maestre, Escolar, & Castillo-Monroy, 2011; Delgado-Baquerizo et al., 2015; Mallen-Cooper & Eldridge, 2016; Michel, Payton, Lee, & During, 2013), and others considered a community approach that represents the interaction between intimately associated species (Castillo-Monroy, Bowker, García-Palacios, & Maestre, 2015; Eldridge et al., 2010; Maestre, Castillo-Monroy, Bowker, & Ochoa-Hueso, 2012). These studies have greatly contributed to the biodiversity-function theory and to better understand the ecological function of BSCs, but linking community structure to function still remains a central challenge in BSC ecological research.

Probably due to the assumed preponderant role of vascular plants regulating the dynamics of vegetated patches, most studies on BSC functioning have been performed in open spaces between vegetation patches, and little is known about the relative importance of BSCs growing underneath the canopies of perennial plants (but see Bu et al.,

2015; Eldridge et al., 2010; Kidron, 2016; Maestre, Huesca, Zaady, Bautista, & Cortina, 2002; Xiao & Hu, 2017; Yang, Bu, Mu, Shao, & Zhang, 2014; Zhao & Xu, 2013). This is a major knowledge gap, since BSCs have complementary functions to those of plants, and might largely contribute to modulate different ecosystem processes in the vegetated patches. Indeed, a major challenge of ecological research in drylands is the study of the relative contributions and the combined effects of different biological components of the system (Berdugo et al., 2014; Bu et al., 2015; Chaudhary et al., 2009; Eldridge et al., 2010). For example, Wang et al. (2012) have identified the need of research efforts focusing on the hydrological function of BSCs growing under the canopy of perennial plants in order to better understand the consequences of shrub encroachment in arid and semiarid systems. Some recent studies suggest that under-canopy BSCs decrease soil moisture and increase runoff (e.g. Kidron, 2016; Xiao & Hu, 2017), but knowledge is still limited making necessary further research. Overall, spatially explicit data of soil ecosystem functions and biotic communities is an emerging need to evaluate ecosystem dynamics and services in heterogeneous landscapes (Zavaleta et al., 2010).

In this study, we aim to advance into elucidating the contribution of BSCs to ecosystem functioning and the links between the structure and functionality of the BSC communities in a heterogeneous semiarid ecosystem. Our specific objectives were: (1) to assess the importance of BSCs in vegetated patches and interspaces in relation to three ecosystem functions that are of major relevance to maintaining the integrity of arid ecosystems, i.e. soil erosion potential, water dynamics and nutrient cycling; (2) to evaluate the relationship between the taxonomic and functional-trait structure of BSCs and ecosystem functionality; and (3) to evaluate the two previous objectives in relation to ecosystem multifunctionality. The study was performed in an area within the Arid Diagonal that crosses South America from southern Perú to the tip of the continent in the southeast of Argentina, for which knowledge about BSCs is very limited and demands further research.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was performed in the Sierra de Las Quijadas National Park, in west-central Argentina (32° 40'S, 67° 7'W). The climate is continental, with mean monthly temperatures of 31.0°C in summer and 3.1°C in winter. Mean annual rainfall is 300 mm, mainly concentrated in spring and summer, with a long dry period from May to September (APN, 2006). The landscape is characterized by a gentle uniform slope of 1%–2% in the East–West direction. Soils are about 1 m depth and are classified as Typic Torriorthent, with a sandy-loam texture uniform throughout the profile (50% sand, 42% silt and 8% clay) and c. 50% of gravel (Peña Zubiarte & d'Hriart, 2006).

The area is a shrubland characterized by vegetated patches that are usually formed by a single individual of the species *Larrea cuneifolia* Cav. (Figure 1). This species is a multi-stemmed, evergreen shrub, with a relatively open, inverted shape cone canopy, and has a profuse root system (Morello, 1955). Plants are c. 1 m high and c. 0.75 m² in cross

FIGURE 1 General landscape view of the studied *Larrea cuneifolia* shrubland and representative photographs of bare soil (unC) and soil covered by well-developed BSCs (C) underneath the canopy of *L. cuneifolia* (V) and in the interspaces (I)



section. The BSC exhibits a patchy distribution, i.e. patches of soil with a well-developed BSC cover and directly adjacent patches that seems bare with the naked eye (Figure 1).

2.2 | Surveys and experimental design

Surveys were performed over an area of c. 1,000 m² in order to assure homogeneous climatic, soil and vegetation conditions. Sampling was performed at the beginning of the period of maximum precipitation in early spring, when we expect that measurements of the biotic attributes and functional response variables would be representative of the period of BSC maximum activity. We quantified the proportion of vegetated patches and interspaces occupied by BSCs using the point quadrat method (Kent & Coker, 1992), recording the presence/absence of aerial vegetation and BSCs every 10 cm along four 10 m length transect lines. To estimate the structure and function of BSC communities, we used an experimental approach based in intact soil-core microcosms. We choose this approach because BSC composition and other attributes can be accurately analyzed in the laboratory, and microcosms can be successfully used to measure different ecological processes, such as infiltration and nutrient dynamics (e.g. Castillo-Monroy et al., 2015; Thiet, Boerner, Nagy, & Jardine, 2005). We randomly selected 20 plots (0.25 cm²) beneath the mid-canopy zone of *L. cuneifolia* and 20 in open interspaces (hereafter vegetated patches and interspaces, respectively). Plots have a homogeneous surface appearance. We took advantage of the naturally occurring spatial heterogeneity in the distribution of the BSCs to select half of the plots with well-developed BSCs and the others in apparently bare soil (hereafter biocrusted and uncrusted soils, respectively). This procedure has been recommended to measure the effect of BSCs on ecosystem processes (Belnap, 2006). Within each plot, an intact soil-core was extracted by inserting a 10 cm-diameter aluminium pipe into the ground to a depth of 6 cm. In addition, a surface soil sample (0–0.5 cm depth) was collected to estimate chlorophyll *a* concentration and the sub-BSC soils (0.5–5 cm depth) for analyses of soil chemical properties, potential net N mineralization and soil moisture.

2.3 | Characterization of BSC communities

The BSC communities in the microcosms were characterized based on their floristic and functional-trait composition, total cover, chlorophyll

a concentration and surface spatial continuity. Lichens were identified to the species level and were classified in functional groups according to their growth form, color, type of photobiont and type of anchoring organs. Information from the literature suggests that these traits play a key role on different ecosystem processes (Tables S1 and S2). Mosses were infertile so they were identified to the genus level, and were differentiated in functional groups according to their growth form; moss growth form is related to their function on soil moisture and stability (Elumeeva, Soudzilovskaia, During, & Cornelissen, 2011; Mallen-Cooper & Eldridge, 2016; Michel et al., 2013). Identification of cyanobacteria was not attempted because it requires molecular-based methodologies, but the species most often observed under the microscope has a filamentous morphology closely resembling *Microcoleus vaginatus* (Vaucher) Gomont. Cyanobacteria are considered a unique functional group due to their contribution to soil fertility by fixing carbon and nitrogen (Belnap, 2002), and their filamentous structure and the production of exometabolites that bind soil particles affecting soil hydrology and erosion resistance (Belnap, 2006; Chaudhary et al., 2009).

High-resolution vertical images of the microcosm were obtained using a digital camera, and the percent cover of each species was estimated using a manual image-classification method in a grid of 225 sample points (Booth, Cox, & Berryman, 2006). We checked the microcosms under the stereoscopic microscope in order to confirm the identity of the species present in each sample point. In addition, the frequency of discontinuities of different sizes on the BSC surface (e.g. fissures or spaces between squamules, individuals or colonies) was estimated from the images as a measure of the BSC spatial continuity.

To estimate chlorophyll *a* from BSCs we follow the method of Castle, Morrison, and Barger (2011) that is suitable for communities formed by cyanobacteria, lichens and mosses. BSC samples were air dried and ground to a fine powder with mortar; chlorophyll *a* was extracted with ethanol.

2.4 | Measurement of ecosystem functions and estimation of multifunctionality

Six chemical soil properties or processes were measured as surrogates of nutrient cycling. Inorganic Olsen-P was extracted with NaHCO₃ and determined by the molybdate ascorbic acid method (Kuo, 1996). Total nitrogen (N) and organic carbon (C) were determined by dry

combustion (Thermo Electron, FlashEA 1112). Inorganic N was extracted with KCl, determining ammonium by the indophenols-blue method and nitrate by copperized Cd reduction (Keeney & Nelson, 1982). To estimate potential net N mineralization, soil samples were incubated aerobically at 25°C and field capacity for 16 weeks.

We measured the slaking of the soil as a surrogate of the water erosion potential (Tongway & Hindley, 2004). We used the soil stability test proposed by Tongway and Hindley (2004) that estimates the cohesion of soil fragments (1 cm³) that are immersed in distilled water. Four classes are defined according to the time required for a fragment to collapse, or according to the proportion of the fragment that remains intact over a period of a minute. We used air-dry soil fragments from each microcosm surface.

We measured infiltration and soil moisture content as variables related to the soil water dynamics. Infiltration rates were measured under ponded conditions because BSCs enhance soil surface roughness and increase the tendency for water to pond on the surface (Rodríguez-Caballero, Aguilar, Canton, Chamizo, & Aguilar, 2015). Hence, their effect on soil infiltration is more apparent under ponding than under tension, being representative of what may happen in the field under natural rain events (Bowker, Eldridge, et al., 2013; Eldridge et al., 2010). Microcosms were mounted on a funnel fitted into the opening of a beaker that collected the infiltrated water. We used a constant water head of 5 cm and the volume of water exiting the microcosm was recorded until reaching a steady-state infiltration rate. The steady-state saturated hydraulic conductivity (K_s) was estimated, using Darcy's equation (Hillel, 1998). In addition, field soil moisture content at the time of sampling was determined gravimetrically using 20 g of soil sample oven-dried at 105°C during 48 hr.

Data on ecosystem functions were integrated to calculate BSC multifunctionality. Three different multifunctionality indices were constructed for: (1) all functions together, (2) soil variables related to the nutrient cycling function, and (3) soil slaking, infiltration and moisture content related to the functioning of the BSCs on soil erosion and water dynamics. Multifunctionality was estimated as the mean of the ecosystem functions in each microcosm, after normalizing the value of each function to the maximum value measured across all microcosms (Maestre et al., 2012).

2.5 | Statistical analyses

To evaluate the variability in the BSC structure in the study area, we used a combination of ANOVA and pairwise multiple comparisons considering the presence/absence of well-developed BSCs (biocrusted/uncrusted soils) and microsities (vegetated/interspaces) as fixed factors. To examine chlorophyll *a* concentration, species richness and species diversity (Shannon–Wiener index, H') we used two-way ANOVAs, followed by Tukey's pairwise comparisons for all factor level combinations when the interaction term was significant. Due to heteroscedasticity or deviations from normality, total cover data and the frequency and size of discontinuities on the BSC surface were analysed using two-way distance-based PERMANOVAs on Euclidean distances, followed by Bonferroni corrected pairwise comparisons. We

used PERMANOVA on the Bray–Curtis distance measure and pairwise comparisons corrected using Bonferroni to examine in more detail the overall differences in the taxonomic and functional-trait of lichens, which are the more diverse BSC group in our study area. PERMANOVA is a semiparametric method that can be applied to do multivariate and univariate ANOVA in base of any distance measure, using permutations of the observations for significance testing (Anderson, 2005).

Second, we used ANOVA to test whether microsite and the presence/absence of well-developed BSCs have a significant effect on the variables measured as surrogates of soil ecosystem functions and multifunctionality. Data on nutrient concentrations, soil moisture content and steady-state infiltration rate did not meet normality and homoscedasticity assumptions even after attempt transformations, so they were analysed using PERMANOVA based on Euclidean distances. To determine significant effects of the fixed factors on each dependent variable, we used univariate PERMANOVAs and performed pairwise comparisons of the factor levels corrected using Bonferroni correction. The effect of microsite and BSC on the level of soil aggregate stability was analysed using ordered multinomial logistic regression (logit link function), and the effects on soil potential N mineralization rates and on the three multifunctionality indices were tested using two-way ANOVAs and Tukey's pairwise comparisons. Data of multifunctionality related to nutrient cycling were log transformed to meet ANOVA assumptions.

We assessed the relationship between BSC structure and functioning by using linear and nonlinear regression models, to relate all aspects of the taxonomic and functional structure of the BSCs to the variables measured as surrogates of ecosystem functioning and the multifunctionality indices. The community-level attributes considered as independent variables were: total cover of the BSC, cover of cyanobacteria, lichens and mosses, chlorophyll *a* concentration, surface spatial continuity, species richness and diversity. Species-level trait data of lichens were also considered as independent variables to evaluate the effects of functional groups, but this analysis could not be performed for mosses because the moss species encountered in the microcosms correspond to only one functional group. Models for multifunctionality indices included as predictor variables the cover, species richness and diversity of BSCs, which are community attributes that have been shown to affect ecosystem multifunctionality in other biotic communities. We expected nonlinear relationships, thus we first applied a generalized additive model (GAM) that depicts the form of the relationship between the response and predictor variables by smoothing-fitting the data. We also fitted the data using linear models and we used Akaike's information criterion (AIC) to evaluate whether the added complexity of GAMs improves the goodness-of-fit over the linear model. The residuals and the determination coefficient were examined to evaluate the fit of the model. The data were log-transformed when necessary to meet assumptions related to the distribution of the dependent variable. In the case of continuous dependent variables, we selected a normal distribution function and an identity link function. In the case of soil stability, we selected an ordinal multinomial distribution function and a logit link function, and then estimated a "pseudo" determination coefficient.

Statistical analyses were performed, using PAST 3.11 (Hammer, Harper, & Ryan, 2001) and STATISTICA 10.0 (StatSoft, Inc., 2011).

3 | RESULTS

3.1 | Vegetation and BSC community characteristics

Vegetation covers about 50% of the total area in the study site, with the other half of the area corresponding to interspaces. Well-developed BSC communities cover $41.2 \pm 4.0\%$ and $40.2 \pm 4.1\%$ of the area under shrub canopies and the interspaces, respectively (Table 1). A measurable quantity of photoautotrophic organisms, predominantly cyanobacteria and some lichen species, is also present in uncrusted soils in both microsites (Figure 2, Table 2). Well-developed BSCs in vegetated patches and interspaces are similar in their total cover, chlorophyll *a* concentration, species richness, diversity and surface continuity (Figure 2, Tables S3 and S4). However, short-statured mosses and cyanobacteria dominate biocrusted soils in vegetated patches, and cyanobacteria and lichens in the interspaces (Figure 2b, Table 2). Lichen assemblages of well-developed BSCs in vegetated patches and interspaces are floristically different, but similar in their functional trait composition (Tables 2, Tables S2 and S5).

3.2 | Effect of microsite and the presence of BSC on ecosystem function and multifunction

The presence of well-developed BSCs on the soil surface (biocrusted vs. uncrusted soils) has a significant multivariate main effect on overall soil properties or processes measured as surrogates of nutrient cycling and water dynamics (Table S6). There is also a significant microsite (vegetated vs. interspaces) effect, although smaller than the effect of BSCs (compare the mean squares in Table S6). Well-developed BSCs significantly increase soil moisture and total N concentration at both microsites, but reduce the availability of ammonium in the interspaces (Figure 3a,e,f and Table S7). Steady-state infiltration, soil aggregate stability and N mineralization rates are significantly higher in vegetated patches than in interspaces (Figure 3b,c,i and Tables S7, S8 and S9).

Aggregation of all individual functions into a multifunctionality index shows slightly higher values in vegetated patches than in interspaces (Figure 4a and Table S10). However, microsites and BSCs have no significant effect when multifunctionality solely considered the functions related to nutrient cycling (Figure 4b). Significant effects of

TABLE 1 Landscape structure measured as the percentage of the area occupied by vascular plants and interspaces, and average biological soil crust (BSC) cover underneath each vascular plant growth form and in the interspaces. Data are mean percentages (SE) of the total area surveyed, $n = 10$

	Shrubs	Grasses	Cacti and other succulent plants	Interspaces
Area (%)	39.2 (5.1)	10.4 (4.7)	0.5 (0.3)	49.9 (7.0)
BSC cover as percentage of the total area	16.1 (2.3)	0	0	20.1 (2.9)

microsite and BSCs were detected for the multifunctionality that aggregates functions related to soil erosion and water dynamics, with soils with a well-developed BSC in the interspaces reaching values that do not differ significantly from those found in vegetated microsites, and uncrusted soils in the interspaces exhibiting a significantly lower multifunctionality (Figure 4c).

3.3 | Relationship between BSC structure and ecosystem functioning

Our results indicate a positive effect of BSC total cover and chlorophyll *a* biomass on soil moisture. Moreover, soil moisture is higher under species-rich, lichen- and cyanobacteria-dominated BSC communities that have a relatively discontinuous surface (Table 3), particularly increasing with the cover of squamulose and crustose lichens that have umbiculus or rhizohyphae as anchoring organs (Table 4). Soil infiltration is also closely related to species-rich BSCs and intermediate cover of lichens (Table 3). Particularly, foliose lichens that anchor to the substrate through hapters have a positive effect upon infiltration rates, and umbiculate lichens have a negative effect (Table 4).

We found a relatively weak effect of chlorophyll *a*, total moss cover and BSC diversity on soil aggregate stability (Table 3). Increasing cover of foliose lichens and lichens with rhizines and hapters as anchoring organs also increases the probability of finding stable soils (Table 4).

Inorganic N concentrations are mostly negatively influenced by cyanobacteria and lichen cover in the BSCs (Table 3). Moreover, soil ammonium concentration is negatively affected by BSC species richness, diversity and chlorophyll *a* concentration (Table 3). On the contrary, soil total C and N are positively affected by the concentration of chlorophyll *a* in the BSCs (Table 3), with a particularly strong positive effect of both cyano- and chlorolichens upon the concentration of N (Table 4). Lichen cover also promotes a higher concentration of extractable P in the soils (Table 3).

Models for multifunctionality indices show that BSC community attributes have different effects on particular ecosystem multifunctions. BSC cover, species richness and diversity have positive effects on the total multifunctionality index (Figure 5a–c). The multifunctionality related to soil erosion and water dynamics also shows a significant positive trend as the cover, species richness and diversity of the BSC increases, saturating at the higher levels of species richness (Figure 5g–i). On the contrary, the multifunctionality related to nutrient cycling is not significantly related to BSC cover, is negatively related to changes in species richness, and is positively affected by diversity (Figure 5d–f). Relatively high values of the multifunctionality indices are also found in some vegetated microsites with poorly developed BSC communities.

4 | DISCUSSION

4.1 | Effects of vascular plants and BSCs on soil water dynamics

Infiltration and soil moisture retention are both very valuable ecosystem functions that regulate the availability of soil water. In our area,

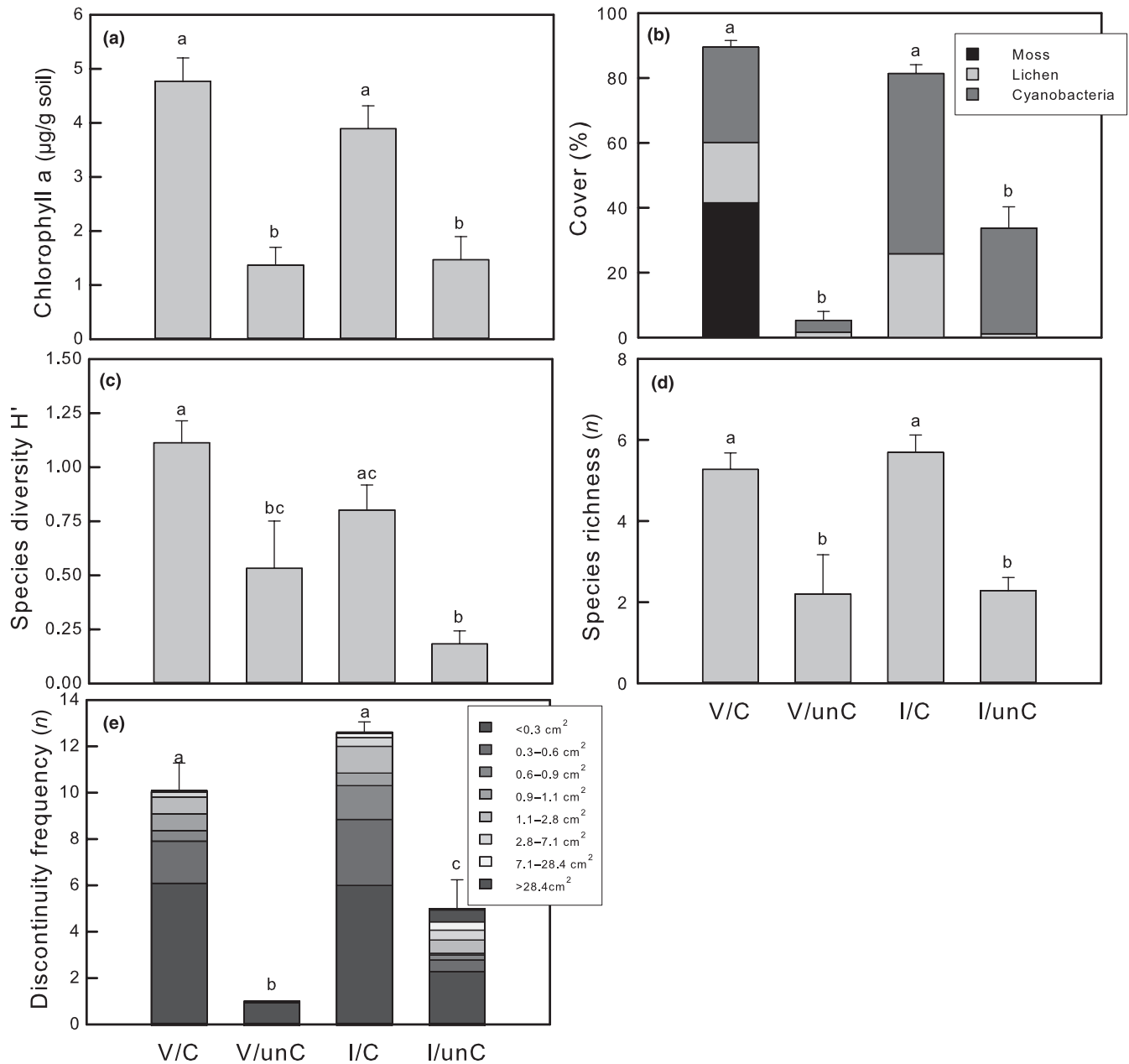


FIGURE 2 Biological characteristics for uncrusted (unC) and biological soil crust (C) covered soils in vegetated patches (V) and interspaces (I): (a) chlorophyll *a* concentration, (b) cover of the BSC components, (c) diversity, (d) species richness, and (e) surface spatial continuity. Uncrusted soils seem bare with the naked eye, while BSC covered soils have a conspicuous community of lichens, mosses and cyanobacteria growing on the soil surface. Data are means (SE), $n = 10$. Different letters indicate significant differences ($p \leq .05$)

the hydrological function of *L. cuneifolia* is evident in the process of soil infiltration (Figure 3b), probably related to its profuse root system, and consistent with the dominant role of plants improving soil porosity in drylands (Wang et al., 2012). However, it does not affect surface soil moisture availability (Figure 3a), probably due to unimportant effects increasing soil water-holding capacity or modulating evaporative losses due to its relatively open canopy structure (Figure 1), as also occurs with *Larrea divaricata* (Kropfl, Cecchi, Villasuso, & Distel, 2002). At the microscale of our study, soil moisture is related to the presence of closely distributed crusted/uncrusted soils (Figure 3a). Previous studies have shown that the small-scale heterogeneity on BSC distribution is mostly

consequence of subtle differences in surface microtopography or micronutrient concentrations (Bowker, Belnap, Davidson, & Goldstein, 2006). Following their establishment, BSCs modify soil physico-chemical properties (Concostrina-Zubiri et al., 2013), in turn affecting the water content of the underlying soil (Kidron & Benenson, 2014). Hence, we interpret that BSCs have a dominant role controlling subsurface soil moisture in the studied ecosystem, as has been reported in other drylands (Xiao & Hu, 2017), and we conclude that complementarity between vascular plants and BSCs is essential to regulate water balance.

The effect of BSCs on soil moisture is largely related to the community structure, although there is less certainty on the BSC attributes that

TABLE 2 Percent mean cover (SE) of lichens, mosses and cyanobacteria for uncrusted (unC) and biological soil crust (C) covered soils in vegetated patches (V) and interspaces (I). Uncrusted soils seem bare with the naked eye, while biological soil crust (BSC) covered soils have a conspicuous community of lichens, mosses and cyanobacteria growing on the soil surface

	V/C	V/unC	I/C	I/unC
Lichens				
<i>Collema tenax</i> (Sw.) Ach.	1.5 (0.4)	0	0.2 (0.1)	0.1 (0.1)
<i>Enchylium coccophorum</i> (Tuck.) Otálora, P.M. Jørg. & Wedin	0.2 (0.1)	0.1 (0.1)	0.2 (0.1)	0.3 (0.1)
<i>Endocarpon pusillum</i> Hedw.	7.9 (1.3)	0.7 (0.3)	3.2 (0.6)	0.2 (0.1)
<i>Gloeoheppia turgida</i> (Ach.) Gyeln.	0.7 (0.5)	0.1 (0.1)	4.1 (0.9)	0.1 (0.0)
<i>Peccania aff. subnigra</i> (B. de Lesd.) Wetmore	2.1 (2.1)	0	1.4 (1.10)	0
<i>Peltula euploca</i> (Ach.) Poelt	0	0	0.4 (0.2)	0
<i>Peltula obscurans</i> (Nyl.) Gyeln.	0.7 (0.3)	0	0.2 (0.1)	0
<i>Peltula placodizans</i> (Zahlbr.) Wetmore	0	0	0.1 (0.1)	0
<i>Phaeorrhiza aff. nimbose</i> (Fr.) H. Mayrh. & Poelt	0.1 (0.1)	0	0	0
<i>Placynthiella ulginosa</i> (Schrad.) Coppins & P. James	5.4 (2.6)	0.8 (0.6)	16.0 (4.1)	0.6 (0.2)
Mosses				
<i>Tortula</i> sp.	27.7 (1.0)	0	0	0
<i>Aloina</i> sp.	13.8 (0.5)	0	0	0
Cyanobacteria				
Unidentified	29.4 (1.2)	3.6 (0.9)	55.6 (1.5)	32.5 (1.7)

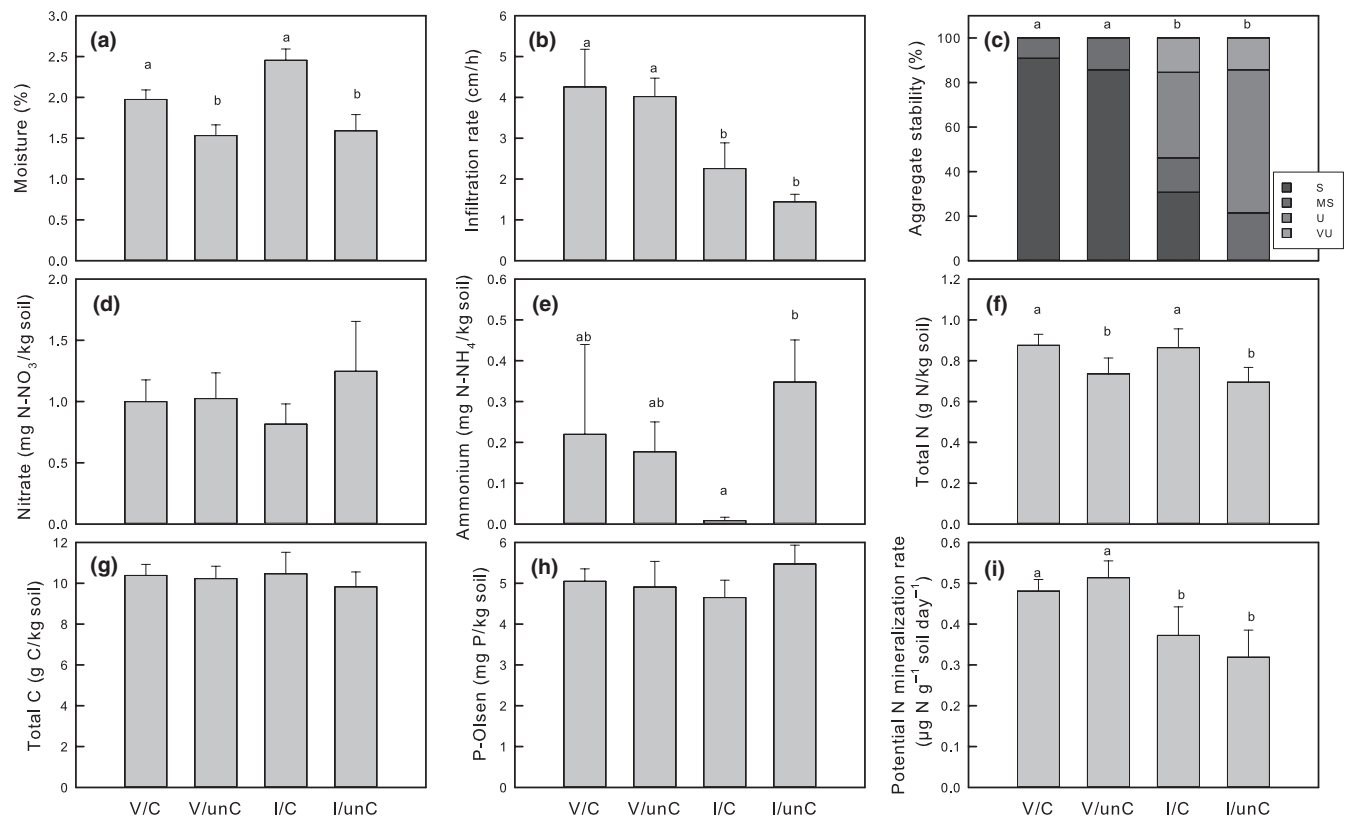


FIGURE 3 Soil properties for uncrusted (unC) and biological soil crust (C) covered soils in vegetated patches (V) and interspaces (I): (a) moisture, (b) steady-state infiltration rate, (c) aggregate stability, (d) nitrate concentration, (e) ammonium concentration, (f) total N concentration, (g) total C concentration, (h) P-Olsen concentration, and (i) potential N mineralization rate. Data are means (SE), $n = 10$, but aggregate stability data that correspond to the percent of samples classified as stable (S), moderately stable (MS), unstable (U) and very unstable (VU). Different letters indicate significant differences ($p \leq .05$)

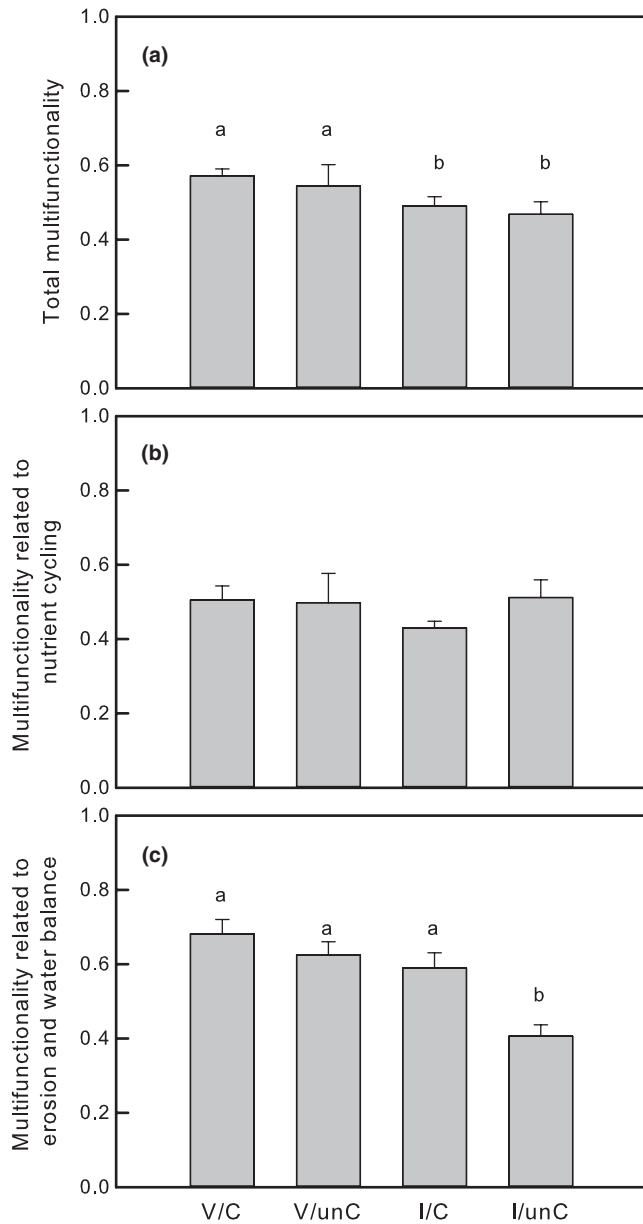


FIGURE 4 Multifunctionality indices for uncrusted (unC) and biological soil crust (C) covered soils in vegetated patches (V) and interspaces (I): (a) total multifunctionality, (b) multifunctionality related to nutrient cycling, and (c) multifunctionality related to soil erosion potential and water balance processes. Data are means (SE), $n = 10$. Different letters indicate significant differences ($p \leq .05$)

actually influences soil water (Belnap, 2006; Bowker, Eldridge, et al., 2013). We found that BSC cover and species richness contributes to soil moisture (Table 3), suggesting that BSC development improves soil water balance. However, the cover of BSC organisms is seldom continuous, but presents small (mm to cm) bare spaces between squamules, individual thalli or colonies. We found that these surface discontinuities improve soil moisture status (Table 3), probably by constituting channels through which water can filter into the soil (Souza-Egipsy, Ascaso, & Sancho, 2002) and by producing surface roughness that enhances soil infiltration capacity and the quantity of water infiltrated in each rainy event (Rodríguez-Caballero et al., 2015). BSC heterogeneity can

TABLE 3 Results from regression models evaluating the dependence of ecological functions on biological soil crust (BSC) community attributes. Direction of the relationship is positive linear (✓), positive nonlinear (∩, ∪), negative (∩, ∪), increasing (∩), decreasing (∪) at intermediate values of the predictor variable. Blank cells correspond to non-significant results ($p > .05$)

	Moisture (%)	Infiltration rate (cm/h)	Aggregate stability	Nitrate (mg N-NO ₃ /kg)	Ammonium (mg N-NH ₄ /kg)	Total N (g/kg)	Total C (g/kg)	P-Olsen (mg/kg)
Chlorophyll a	$R = .37, p = .03$ (✓)		$R_{MCF} = .25, p = .03$ (✓)		$R = .37, p = .03$ (∩)	$R = .55, p = .04$ (∩)	$R = .50, p = .05$ (∩)	
Total cover	$R = .49, p < .01$ (✓)					$R = .53, p = .03$ (∩)		
Lichen cover	$R = .46, p < .01$ (✓)	$R = .50, p = .05$ (∩)			$R = .35, p = .04$ (∩)	$R = .36, p = .03$ (∩)	$R = .57, p < .01$ (∩)	
Moss cover			$R_{MCF} = .38, p = .02$ (✓)					
Cyanobacteria cover	$R = .39, p = .02$ (✓)			$R = .48, p < .01$ (∩)				
Species richness	$R = .49, p < .01$ (✓)	$R = .61, p < .01$ (∩)		$R = .53, p < .01$ (∩)			$R = .59, p < .01$ (∩)	
Diversity (H')		$R = .62, p = .02$ (∩)	$R_{MCF} = .22, p = .05$ (✓)	$R = .55, p < .01$ (∩)			$R = .59, p < .01$ (∩)	
Discontinuities on BSC surface	$R = .50, p < .01$ (✓)							

TABLE 4 Results from regression models evaluating the dependence of ecological functions on lichen functional groups defined according to species growth form, color, type of photobiont and type of anchoring organs. Direction of the regression is positive linear (✓), positive nonlinear (∩) and negative (∪). Blank cells correspond to non significant results ($p > .05$). Note that only one light-colored species with relatively low cover was present in our samples, so models were not fitted for this color category

	Moisture (%)	Infiltration rate (cm/h)	Aggregate stability
Growth form			
Squamulose	$R = .41, p = .02$ (✓)		
Foliose		$R = .36, p = .05$ (✓)	$R_{MCF} = .34, p < .01$ (✓)
Crustose	$R = .41, p = .02$ (✓)		
Fruticose			
Color			
Dark	$R = .41, p = .02$ (✓)		
Intermediate	$R = .41, p = .02$ (✓)		
Anchoring organs			
Rhizine			$R_{MCF} = .25, p = .05$ (✓)
Hapter		$R = .42, p = .02$ (✓)	$R_{MCF} = .27, p = .04$ (✓)
Umbiculus	$R = .50, p < .01$ (✓)	$R = .37, p = .04$ (∪)	
Rhizohyphae	$R = .39, p = .03$ (✓)		
	Total N (g/kg)	Total C (g/kg)	P-Olsen (mg/kg)
Photobiont type			
Green algae	$R = .35, p = .05$ (✓)		$R = .57, p = .04$ (∩)
Cyanobacteria	$R = .64, p < .01$ (✓)	$R = .38, p = .04$ (∩)	$R = .58, p < .01$ (✓)

also increase the capture of fine materials that affects soil infiltration and water holding capacity (Bowker, Eldridge, et al., 2013).

Conflicting views exist on the effects of the different BSC components on soil hydrology. It is particularly interesting that lichens and cyanobacteria played a more relevant role than mosses explaining soil moisture heterogeneity in our study area (Table 3). There is general consensus that BSC-mosses have high water retention capacity, despite discrepancies persist in whether this characteristic positively or negatively influences soil infiltration and humidity (e.g. Kidron, 2016; Xiao & Hu, 2017). Short-statured mosses, as those present in our study area (Table 2), have relatively low water storage capacity and fast evaporation (Michel et al., 2013), and thus we could have expected a negative effect on subsurface soil moisture. However, we found neutral effects of mosses on soil moisture (Table 3), similar to results reported by Bowker, Eldridge et al. (2013) in Australia. This result may be explained by the fact that the hydrological function of BSC-mosses is largely the result of their tight growth forming continuous homogeneous carpets (Elumeeva et al., 2011), but it may not persist in scattered patches or in diverse communities (Michel, Lee, During, & Cornelissen, 2012). Our samples have also a large proportion of cyanobacteria and lichens that contributes to the significant effects of BSCs on soil moisture (Table 3). Cyanobacteria have a positive effect upon water retention due to the production of polysaccharide exudates determining hydrophilic soil properties (Belnap, 2006). Heterogeneous effects have been reported for lichen-dominated BSCs (Belnap, 2006; Chamizo et al., 2016). We found that soil moisture is mainly related to the presence of crustose and squamulose lichens with an umbiculus or rhizohyphae as anchoring organs (Tables 3 and 4), in clear contraposition to the conception that lichens with these morphologies seal soil pores (Belnap, 2006; Chamizo et al., 2016; Rodríguez-Caballero et al., 2015). Structural studies of some crustose and squamulose species

have found that water can filter between the squamules or microfissures and that rhizohyphae in the lower side of the thallus intercept water from run-offs; then water is effectively retained at the lichen-soil interface reducing losses by evaporation (Kappen & Valladares, 2007; Souza-Egipsy et al., 2002). Other water-related attributes, such as the wettability and imperviousness of the tissues or the absorptivity of the thallus, can further contribute in explaining the BSC hydrological function (Mallen-Cooper & Eldridge, 2016).

Overall, the present study is in line with Eldridge et al. (2010) and Bowker et al. (2011) who emphasized that the effect of BSCs on soil water dynamics depends on the intimate association between the different components that form hydrophobic and hydrophilic patches. We add that the frequency of surface discontinuities (i.e. micro-gaps of bare soil) is also a valuable community attribute to explain the BSC hydrological function.

4.2 | Influence of vascular plants and BSCs on nutrient availability

The general view of drylands as been characterized by vegetated patches that act as fertility islands (Schlesinger et al., 1996) greatly depends on the characteristics of the dominant vascular plants (Mudrak, Schafer, Fuentes-Ramirez, Holzapfel, & Moloney, 2014). In our area, fertility islands are poorly developed beneath *L. cuneifolia* plants (Figure 3f,g), in accordance to previous studies in the region (Mazzarino, Oliva, Abril, & Acosta, 1991). This is probably due to the open, inverted cone shape canopy that may be unable to trap and retain materials (Figure 1), as has been registered for the congeneric *Larrea tridentata* in some Northern Hemisphere drylands (Mudrak et al., 2014). In addition, *L. cuneifolia* is a non-N-fixing and evergreen species, with tough, N poor leaves that may retard decomposition

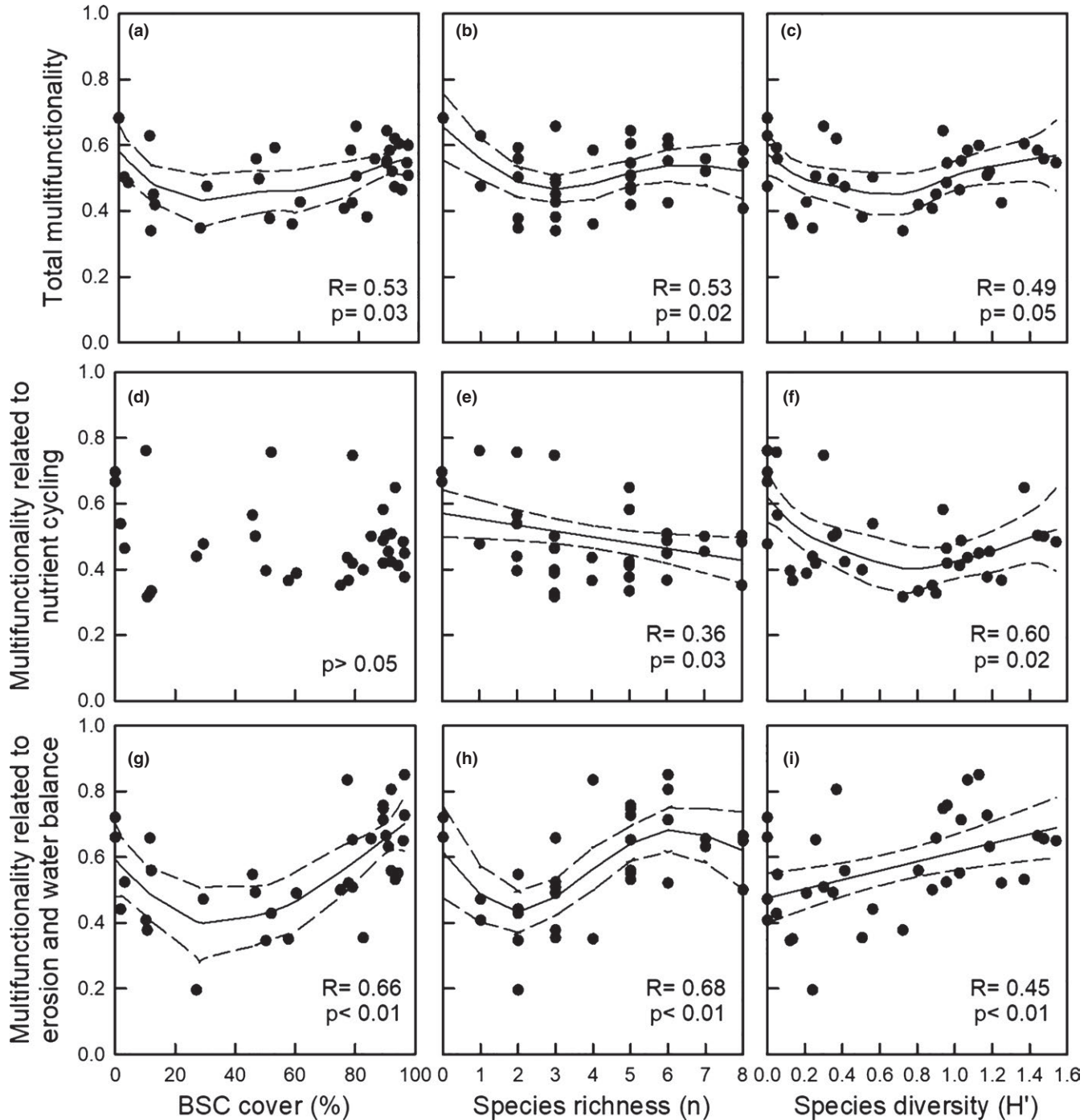


FIGURE 5 Relationship between multifunctionality and BSC community attributes: (a–c) total multifunctionality, (d–f) multifunctionality related to nutrient cycling, and (g–i) multifunctionality related to soil erosion potential and water balance processes. Dots correspond to the data points, and curves represent the significant ($p < .05$, $n = 40$) fitted generalized linear and additive models (continuous line) and 95% confidence bands (dashed lines)

(Mazzarino et al., 1991). Instead, BSCs contribute significantly to soil N enrichment (Figure 3f). Accumulation of soil N is a highly valuable ecosystem function in drylands, and despite the role of BSCs on N dynamics has not been assessed in our study area, it has been found in other drylands that BSCs stimulate N storage during the non-growing season and N cycling during the growing season (Hu et al., 2015). Thus, we conclude that BSCs promote N-rich fertility mantles (sensu

Garcia-Pichel, Johnson, Youngkin, & Belnap, 2003), which are likely fundamental for the functioning of the studied ecosystem.

We found that variation in total N concentration is mostly influenced by the cover of lichens (Tables 3 and 4), which are known to input to the soil large amounts of N that is fixed by the photobiont in cyanolichens (Barger, Weber, Garcia-Pichel, Zaady, & Belnap, 2016; Belnap, 2002) or by non-photobiont lichen-associated N fixing bacteria

in chlorolichens (Sigurbjornsdottir, Andresson, & Vilhelmsson, 2016). Additionally, lichens can trap N-rich dust particles and reduce N losses by soil erosion (Mallen-Cooper & Eldridge, 2016). We did not find a relationship between cyanobacteria cover and total N pool (Table 3), despite N fixation by BSC-cyanobacteria could be also an important soil N input pathway (Belnap, 2002; Garcia-Pichel et al., 2003). This may be due to the efficiency of lichens retaining N in their biomass, but most of the N fixed by cyanobacteria is released to the soil and rapidly up-taken by other organisms or lost from the system (Barger et al., 2016). Facultative cyanobacteria associated to mosses make an unimportant contribution to N inputs in drylands (Barger et al., 2016; Cornelissen, Lang, Soudzilovskaia, & During, 2007), explaining the non-significant moss cover to total N relationship in our samples.

Besides their relevance in nitrogen fixation, BSCs are dominant drivers of other N pathways. Lichens can inhibit the mineralization processes due to the production of highly recalcitrant organic material and by producing allelopathic substances that affect soil microbes (Castillo-Monroy et al., 2010; Miralles, Trasar-Cepeda, Leirós, & Gil-Sotres, 2013), which could explain their positive effects on total N but negative effects on the concentration of ammonium (Table 3). Similarly, the negative relationship between cyanobacteria cover and nitrate concentration in the soils (Table 3) can be explained by their effect inhibiting nitrifying microbes (e.g. Castillo-Monroy et al., 2010; Hu et al., 2015; Thiet et al., 2005). Decreases in both ammonium and nitrate concentrations may also be caused by the preferential uptake of these N forms by lichens and cyanobacteria (Barger et al., 2016). Interestingly, we found that lichens have a preponderant role on the availability of P in the soil (Table 3), concurring with previous studies (Delgado-Baquerizo et al., 2015). Soil P is predominately of mineral origin in drylands, and secondary metabolites produced by lichens and lichen-associated bacteria promote the chemical weathering of this mineral. Lichens also produce phosphatases that release inorganic P from organic matter (Cornelissen et al., 2007). Overall, our results suggest that differences in the proportion of lichens and cyanobacteria in the BSCs modulate the availability of soil N and P at the initiation of the wet period.

4.3 | Influence of vascular plants and BSCs on multifunctionality

The fact that vascular plants are primordial regulating the functioning of drylands is also evident in our study area where vegetated patches enhance total multifunctionality (Figure 4a). One previous study has also found a positive effect of vascular plants and an insignificant effect of BSCs on a multifunctionality index that combines functions related to soil water dynamics and nutrient cycling (Zhang, Eldridge, & Delgado-Baquerizo, 2016). This result is counterintuitive to our previous analysis of individual functions that showed that vascular plants do not satisfy many individual functions that are highly relevant to drylands. Indeed, our results show that BSCs are multifunctional stabilizing soils against erosion and regulating soil moisture and infiltration in the interspaces (Figure 4c), suggesting that BSCs have the potential of functionally substitute vascular plants in areas with reduced plant cover in drylands. Moreover, the non-significant effect of BSCs on

multifunctionality related to nutrient cycling (Figure 4b) could have been consequence of a tradeoff between the role of BSCs on the storage and cycling of N in the system, as it is suggested by the positive effect on soil total N but negative on the concentration of inorganic N especially in the interspaces (Figure 3). Functional traits associated with nutrient release, uptake and conservation can simultaneously enhance one of the processes underlying the cycling of nutrients and weakens others (Cornelissen et al., 2007). For example, some N-fixing lichens have strategies of internal nutrient recycling and conservation analogous to those of vascular plants (Ellis, Crittenden, Scrimgeour, & Ashcroft, 2005), that potentially reduce decomposability and the input of the fixed N to the ecosystem. As far as we know, tradeoffs between functions have not been assessed in BSCs, despite it is well known that their characterization is essential to better understand the ability of biotic communities to provide multifunctionality (Zavaleta et al., 2010). We conclude that the assessment of separate functions recognizes that BSCs are multifunctional and, at the same time, contributes to advance the understanding about their role on multiple ecosystem functions that may be obscured when the analysis is exclusively based in the calculation of aggregated multifunctionality indices (Bradford et al., 2014).

A relevant topic of current ecological research is to identify the main attributes of biotic communities that can predict ecosystem multifunctionality. In a study using BSCs as model system, Bowker, Maestre, et al. (2013) have asked whether there is a recipe to multifunctionality, concluding that, yes, multifunctionality is maximized in communities with high cover, species richness and evenness. In our dataset, the answer is probably no, because the magnitude and direction of the relationship between community attributes and ecosystem multifunctionality depend on the particular functions considered to estimate the aggregate multifunctionality indices (Figure 5). For instance, our results suggest some redundancy among species as agents stabilizing soils against erosion and regulating soil moisture (saturating effect of species richness, Figure 5h), for example among species with similar morphology, and at the same time some complementarity (positive effect of diversity, Figure 5i) that could have been gained by differential effects of morphogroups, such as short mosses and foliose lichens increasing infiltration and crustose and squamulose lichens intercepting water from surface run-offs and retaining water for long periods due to their substrate-hydrophilic behaviour (Kappen & Valladares, 2007; Souza-Egipsy et al., 2002). On the contrary, multifunctionality related to nutrient cycling is improved by an even cover distribution of a reduced number of species (Figure 5e,f), probably because BSCs with intermediate number of species and maximal evenness have higher diversity and biomass of soil microbial communities with potential relevance to nutrient cycling (Castillo-Monroy et al., 2015).

Overall, owing to the contrasting effects of different BSC species- and community-level attributes on different functions, it is not surprising to find that effects on multifunctionality depend on the individual functions considered to estimate the aggregate multifunctionality index. Biogeochemical processes dominate the literature on ecosystem multifunctioning, and to our knowledge, our study is the second (after Zhang et al., 2016) to consider the multifunctionality of vascular

plants and BSCs in relation to other functions that are highly relevant to the sustaining of ecosystem integrity, such as water dynamics and soil stability. Further studies should systematically examine the value of individual ecological functions and possible tradeoffs to improve current understanding of the BSC effects on multifunctionality.

5 | CONCLUSIONS

Our findings show that BSCs and vascular plants have idiosyncratic effects on ecosystem functionality and multifunctionality, and provides evidences that well-developed BSC communities generate small-scale heterogeneity in terms of soil function and multifunction in both vegetated patches and interspaces. This reinforces the notion that BSCs are main structural and functional components in drylands, and highlights that it is critical their assessment in different microhabitat if we aim to better understand their role as drivers of ecosystem functioning in highly heterogeneous ecosystems such as drylands. Owing to the contrasting effects of BSC species- and community-level attributes on different functions and multifunction, quantification of BSC microstructure is necessary to improve current knowledge that is mostly based in the study of broad BSC types dominated by cyanobacteria, lichens or mosses.

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AUTHORS' CONTRIBUTIONS

I.A.G. designed the study in contribution with S.T. and M.G.P.; field data, soil cores and soil samples were collected by I.A.G. and S.T.; laboratory analyses were done by M.G.P. and I.A.G.; I. A. G. analysed the data and wrote the first draft of this manuscript, and all co-authors contributed to improve it.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.sv4md> (Garibotti, Gonzalez Polo, & Tabeni, 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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