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RESEARCH ARTICLE

Microhabitat-specific differences on the composition and function of biological soil crust communities

Maximiliano J. Bustos · **Irene A. Garibotti** ·
Norma Cech · **M. Cecilia Navarro** ·
Marina Gonzalez Polo · **Patricia Satti**

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Abstract

Aims Biological soil crusts (BSC) are key drivers of ecosystem functioning in drylands. Yet understanding their composition/function relationship is still limited due to the poor knowledge about their variability, particularly in terms of small-scale microhabitat differences.

Methods We investigated how changes in BSC community composition (species identity and cover) affect surrogates of soil functions, such as soil erosion resistance, water dynamics and nutrient cycling, in vegetated mound and intermound microhabitats on a semi-arid shrubland of Argentina. We used a correlative approach to evaluate the composition/function relationship, and we compiled information available in the literature about species functional traits to explain the observed patterns.

Results Most BSC species were present in both vegetated mounds and intermounds, and variations in community composition between microhabitat were mainly related to differences in the relative cover of each species. BSC cover improved soil surface stability in both microhabitat, irrespective of the community composition. However, soil functions related to nutrient cycling and water dynamics were correlated to changes in BSC composition, varying in dependence of the cover of species of lichens and mosses characterized by different morphological, anatomical and physiological traits. Most community composition/function relationships did not differ between microhabitat.

Conclusion Our results provide novel evidence that changes in BSC species and functional groups create soil heterogeneity in key soil properties and processes, and those effects are no context-dependent in terms of microhabitat. We identified some functional attributes of the species that may deserve greater attention for improving BSC functional-trait analyses in diverse natural communities.

Keywords Biocrusts · Soil aggregate stability · Soil infiltration · Soil nutrients · Functional heterogeneity · Spatial heterogeneity

Abbreviations

BSC	Biological soil crust

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M. J. Bustos · I. A. Garibotti (✉) · M. Gonzalez Polo · P. Satti
Instituto de Investigaciones en Biodiversidad y Medioambiente, Universidad Nacional del Comahue, CONICET, Bariloche, Argentina
e-mail: ireneg@comahue-conicet.gob.ar

N. Cech · M. C. Navarro
Facultad de Ciencias del Ambiente y la Salud, Universidad Nacional del Comahue, Neuquén, Argentina

Introduction

Biological soil crusts (BSCs) are soil surface communities of intermixed cyanobacteria, algae, lichen and mosses, which cover ~12% of the global terrestrial soil surface forming an ecological boundary between atmosphere and soil that is critical to life on Earth (Belnap et al. 2003; Rodriguez-Caballero et al. 2018). BSCs modulate the inputs and outputs across the soil surface, and affect resource storage and distribution in the soil (e.g. nutrient and water), influencing the functioning of ecological systems (Bowker et al. 2018). BSCs communities are inherently compositionally heterogeneous at different spatial scales, from global to microscale, which can result in differences in many characteristics and functions of the atmosphere-soil boundary (Belnap et al. 2003). Therefore, characterizing the relationship of composition and function is a central challenge in BSC ecology, as it could greatly improve our understanding of how BSCs contribute to ecological systems work, and also contributes to predict potential consequences of climate change on soil ecosystem function and helps develop robust strategies for restoring soil functioning in disturbed areas.

BSC ecology research has been dominated by the consideration of BSCs as a unique entity or by the rough analysis of community characteristics. Some studies have discriminated BSCs according to readily discernible features such as external morphology, level of development and color (Belnap et al. 2012; e.g. Eldridge and Rosentreter 1999). Another commonly used approach has been the study of BSCs that are defined by the component present with the highest proportion of cover, and assumed to dominate BSC function, i.e. cyanobacteria-, lichen- and moss- dominated communities. These communities are generally considered to represent sequential stages of succession, which gradually improve soil nutrient content, water retention and surface stability (Weber et al. 2016).

However, a growing body of research indicates that the lack of a more detailed characterization of BSC composition can result in information loss. Some studies have shown species-specific functional differences (Büdel et al. 2013; Castillo-Monroy et al. 2011; Concostrina-Zubiri et al. 2013; Delgado-Baquerizo et al. 2015), and a trait-based BSC ecology has emerged during the last years (Concostrina-Zubiri et al. 2021; Mallen-Cooper et al. 2019). Studies at the community level show that the identity and abundance of species influences the function of BSCs, and that even species present in relatively low cover in the communities can exert important functions regulating ecological processes (Bowker et al. 2011; Castillo-Monroy et al. 2011; Eldridge et al. 2021; Garibotti et al. 2018; Ochoa-Hueso et al. 2011). For example, production of secondary metabolites by some low-abundant lichen species can be responsible of soil biochemical functions by exerting negative effects on some soil bacterial species (Castillo-Monroy et al. 2011). In addition, it has become evident that the function of the different component species cannot be simply predicted from monospecific cultures, but requires their consideration at the BSC community level, as interactions among individual organisms result in emergent properties that may vary depending on the community species composition and arrangement (Castillo-Monroy et al. 2011; Elumeeva et al. 2011; Michel et al. 2012). Going deep into the composition of BSC, considering both species identity and species-specific traits in natural diverse communities, is hence a further step to advance in the understanding of how BSC community composition determines multiple types of ecosystem functions (Cornelissen et al. 2007; Deane-Coe and Stanton 2017).

It is well established that habitat configuration and complexity have pervasive effects on community composition, and that the association between habitat characteristics and species richness operate to affect the functioning of ecosystems at different spatial scales, from global to microscale. In particular, semiarid ecosystems display spatially heterogeneous vegetation patterns, which are frequently associated to the formation of raised mounds, influencing the small-scale distribution of BSCs (Bowker et al. 2006; Concostrina-Zubiri et al. 2013). Dominant BSC species and functional groups shift between microhabitats, with shrub mounds usually favoring the dominance of moss-BSCs, and intermounds the dominance of cyanobacteria and lichens (Ochoa-Hueso et al. 2011; Soliveres and Eldridge 2019). Despite these broad differences in the composition of BSCs, the number of studies dealing with BSCs in vegetated patches is enormously small as compared to the studies that have analyzed BSCs in interspaces between perennial plants, this research bias limiting our possibility of scaling up local-scale results to the ecosystem scale. Therefore, additional research is needed to understand how BSCs affect ecosystem functioning in different microsites.

The objective of this study was to assess the composition and function of BSC communities in different microhabitats. We evaluate (1) whether BSC communities exhibit spatial structure at the scale of microhabitat, if so, (2) whether these differences in community composition are associated to variations in soil functions related to erosion resistance, water regulation and nutrient dynamics, (3) and which traits of the dominant BSC components and species are associated to the variations in the ecological processes. With this purpose we analyzed the composition of BSC communities and measured multiple indicators of soil functioning in vegetated mounds and intermounds. In this study we considered two primary components of the community composition: species identity and species relative cover. We focused on the composition of the BSC community at the species level, in order to evaluate potential species-specific effects on soil functioning. We thoroughly analyzed our results in the context of available information about morphological, anatomical and physiological traits of lichen and moss species, and evaluated how these traits may drive ecosystem processes. With this study we aim to contribute towards resolving the role of species traits and identity on different ecological processes, in line with current efforts to develop a trait-based BSC ecology.

Materials and methods

Study area and field sampling

The study was conducted in the northwest of the Patagonia Region, Argentina (38 ° 55’S, 68 ° 14’W). The climate is temperate semi-arid with mean annual precipitation of 212 mm, concentrated in fall and winter. Air humidity remains around 60% during fall and winter (may to august), and is below 25% during the summer months. Mean annual temperature is 15.6 °C, being January the warmest month with a mean temperature of 25 °C and July the coolest with a mean temperature of 7 °C and ~ 13 freezing days (Appendix 1). The geomorphology corresponds to old alluvial plains with a gentle slope of 2%. Soil is classified as Typic Petrocalcid, Typic Petroargid and Typic Torripsament with coarse textures. The vegetation corresponds to the Monte biogeographical region, being characterized by a medium to high shrub steppe dominated by *Larrea cuneifolia* and *Atriplex lampa,* which dominantly occur on raised mounds. BSCs develop in both shrub undercanopy and interspace microsites (Fig. 1).

Sampling was performed in late winter-early spring 2019 in an area of approximately 1.5 km^2 that is homogeneous in soils and vegetation type, with no or slight signs of human disturbance; there is no livestock. To quantify the percentage of vegetation and BSCs in shrub mounds and intermounds we used the point quadrat method, making records every 20 cm along five 25 m length transect lines separated about 500 m. Then, to estimate the composition and function of BSCs we selected 20 plots in shrub mounds dominated by *Larrea divaricata* and 20 plots in intermounds. We attempted to minimize variability within sampling units in order to increase our ability to closely match estimations of BSC composition and function. For this purpose, sample plots were relatively small in size (20 × 20 cm), and were selected to have a homogeneous soil surface appearance by visual inspection of both physical and biological characteristics. Sample plots included the whole cover gradient of BSCs (from 100% cover to apparent bare soil). At each plot, we extracted a surface soil sample by inserting a 9 cm-diameter Petri dish

Fig. 1 General landscape view of the study area in the Monte phytogeographical region in Argentina showing well-developed BSCs underneath the canopy of shrubs and in the interspaces. Shrub species in the photo are *Atriplex lampa* (white leaves) and *Larrea cuneifolia* (green leaves)

for the analysis of BSC community composition, and two soil samples (0-10 cm depth) for soil chemical analysis. In addition, in the same plots we performed soil surface stability and infiltration measurements, as explained below. We chose to sample the upper 10 cm soil layer, as it may be critical to better elucidate the influence of BSCs on ecosystem processes, by taking into account both the direct influence of the BSC forming components on the chemical processes and their indirect influence by affecting other BSC-associated soil microbes and microfaunal communities.

CBS community characterization

To characterize the BSC communities collected in the Petri dishes we identified the species present and estimated their percent cover. We performed the analysis by using a manual image-classification method in a 225-point grid overlaid on high-resolution vertical image of each sample (Booth et al. 2006). We checked the samples under the microscope to identify the organisms below each sample point. We identified lichens and mosses to the species level using standard morphological, anatomical, and chemical methods. Cyanobacteria and green algae identification was not attempted, but the filamentous morphology of the cyanobacteria most frequently registered was closely similar to *Microcoleus vaginatus*. Counts of the species in the 225 points were converted to percentage cover in each sample.

Soil properties and functions

We characterized shrub mounds and intermounds microsites using soil variables related to soil fertility, water dynamics and soil erosion resistance. As for surrogates of nutrient cycling we measured five soil chemical properties. Total C and N were measured by dry combustion (Thermo Electron, FlashEA 1112). Inorganic N (NO_3^--N and NH_4^+-N) was extracted with KCl (2 M), NO_3^--N was determined by copperized Cd reduction and NH_4^+-N by the indophenol-blue method (Keeney and Nelson 1982). Olsen-P extracted with $NaHCO_3$ (0.5 M) was determined by the ascorbic acid-molybdate method (Kuo 1996).

We measured aggregate soil stability as a surrogate of soil erosion resistance by immersing a soil surface fragment (8 mm diameter) in distilled water, and determined soil stability classes according to the time required for the fragment to collapse or the proportion of the fragment that remains intact after one minute (Herrick et al. 2001). Infiltration was measured as a surrogate of water dynamics using a double ring infiltrometer (5 cm diameter inner ring) and the infiltration rate was calculated using Kostiakov's infiltration model (Kostiakov 1932).

Statistical analyses

The BSC community attributes analyzed were total cover, cover of each BSC component, species richness, the Shannon-Wiener diversity and evenness indexes. To test for differences between microsites we used the univariate Kruskal-Wallis test on BSC community attributes, with microsites (shrub mounds and intermounds) as a fixed factor. We chose a non-parametric analysis due to data heteroscedasticity and deviations from normality. In addition, we estimated the Berger-Parker index to construct rank abundance distribution plots for species in mounds and intermounds. Then, to assess differences in overall BSC species composition and cover between microsites we used a multivariate generalized linear model (mGLM) with negative binomial error distribution given the proportion nature of data (manyglm(), R package mvabund, Wang et al. 2012). We checked model assumptions by examining the residuals against the fitted model. To visualize the level of BSC composition similarity between samples we used a generalized linear latent model with negative binomial error distribution (lvsplot, R package Boral, Hui 2016). We conducted multivariate analyses with species occurring in at least four study quadrats.

We used regression analyses to examine BSC community attributes and species cover in relation to the soil properties that were measured as surrogates of ecosystem functioning. First, we evaluated the homogeneity of slopes between microsites in the BSC community/function relationship using an F-test. This was done to offset any possible error caused by differences between microsites not attributable to changes in BSC composition. If H_0 was not rejected, we could more efficiently estimate the common effect of BSC composition on functions by pooling sample data from both microsites. If H_0 was rejected, then we concluded that there were differences between microsites in the slope of the composition/function relationship, hence we were interested in evaluating what these differences are by performing separate regressions for each microsite. We assessed the residual plots to check the model assumptions. The strength and direction of the linear relationship was estimated using the Pearson's correlation coefficient. In the case of soil surface stability, as it is an ordinal categorical variable, we used an ordinal multinomial regression, and then estimated the Spearman's rank-order correlation coefficient.

Statistical analyses were performed using PAST 3.11 (Hammer et al. 2001), Statistica 10.0 (StatSoft, Inc. 2011, Tulsa, USA) and R statistical software version 3.6.1 (R Core Team 2019, Vienna, Austria). Graphs were constructed using SigmaPlot 12.0 (Systat Software, Inc. 2012, Bangalore, India).

Results

Mounds represented 66.7 ± 4.5% of the total surface in the study area with an average size of 10.2 m^2. The flora on mounds was dominated by the shrubs *Larrea divaricata*, *L. cuneifolia* and *Atriplex lampa*, covering around 45.9 ± 4.2% of the total area (Appendix 2). In average, shrubs were 1.3 m height. Well-developed BSCs cover 39.6 ± 1.2% and 37.5 ± 6.7% of the soil surfaces in mounds and intermounds, respectively.

BSCs in both microsites were composed of intermixed mosses, lichens, cyanobacteria and green algae (Fig. 2a). Mosses were present in high cover in both mounds and intermounds, but cover of lichens was higher (not significant) in the intermounds than in the mounds. Cyanobacteria and green algae represented a small proportion of the BSC community cover in both microsites. We found a total of 15 lichens and 4 moss species (Table 1). Most species were found in both microsites, with 6 species per community sample on average (Fig. 2b). Species diversity and evenness were significantly higher in the intermounds than in mounds (Fig. 2c). In average across all samples, *Tortula inmermis* and *Syntrichia ruralis* were the two more abundant species in mounds contributing with 72% of the total cover, and *Encalypta vulgaris* and *Tortula inermis* were the more abundant in intermounds, contributing with 47% of the total cover. There was a more even distribution of cover among the non-dominant species in the intermounds than in the mounds (Fig. 2d).

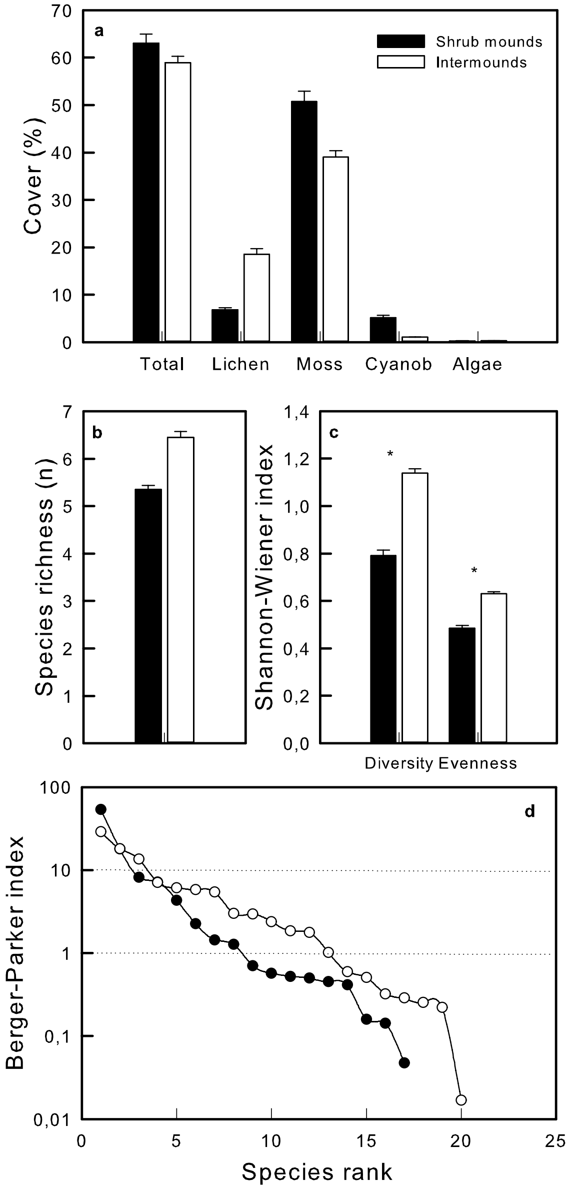

Fig. 2 Community attributes of BSCs in shrub mounds and intermounds. (**a**) Cover of the BSC components, (**b**) Species richness, (**c**) Species diversity and evenness estimated using the Shannon-Wiener indexes, and (**d**) Rank abundance plots estimated using the Berger-Parker dominance index. Data are means (SE). Asterisks indicate significant differences between mounds and intermounds ($p < 0.05$)

Ordination analysis of BSC community composition indicated a clear separation among samples related to changes in total cover, mainly mosses, as represented along the first axis. The second ordination axis suggests some separation between samples

Table 1 Percent mean cover (SE) and frequency (% of plots) of BSC species in shrub mounds and intermounds

	Abbreviated name	Mounds		Intermounds	
		Cover	Frequency	Cover	Frequency
Cyanobacteria					
Microcoleus vaginatus (Vaucher) Gomont.	Mvag	5.2 (0.5)	45	1.0 (0.1)	50
Green algae					
Coccoid unicellular	Galgae	0.3 (0.0)	35	0.3 (0.0)	45
Lichens					
Acarospora terricola H. Magn.	Aterric	0.4 (0.0)	25	1.7 (0.2)	20
Aspicilia praecrenata (Nyl.) Hue.	Aprae	0.0 (0.0)	0	0.2 (0.0)	5
Candelariella citrina B. de Lesd.	Ccitr	0.0 (0.0)	10	0.1 (0.0)	15
Enchylium tenax (Sw.) Ach.	Eten	0.4 (0.1)	10	3.2 (0.2)	55
Endocarpon pusillum Hedw.	Epusi	0.1 (0.0)	10	0.4 (0.1)	5
Lempholemma chalazanum (Ach.) B. de Lesd.	Lchal	0.3 (0.1)	10	3.6 (0.6)	15
Lichinella sp.	Lsp	0.3 (0.0)	15	0.2 (0.0)	10
Peccania subnigra (B. de Lesd.) Wetmore	Psubn	2.7 (03)	70	4.2 (0.5)	55
Peltula obscurans (Nyl.) Gyeln.	Pobs	0.3 (0.1)	5	1.4 (0.2)	25
Phaeorrhiza nimbosa (Fr.) H. Mayrh. & Poelt	Pnimb	0.1 (0.0)	10	0.0 (0.0)	0
Placidium squamulosum (Ach.) Breuss	Psqua	0.8 (0.1)	40	1.8 (0.2)	40
Psora sp.	Psp	1.4 (0.2)	20	0.2 (0.0)	20
Psora decipiens (Hedw.) Hoffm.	Pdeci	0.0 (0.0)	0	1.1 (0.2)	15
Squamulose green lichen	Sqg	0.0 (0.0)	0	0.6 (0.1)	5
Squamulose yellow lichen	Sqy	0.0 (0.0)	0	0.0 (0.0)	5
Mosses					
Bryum argenteum Hedw.	Barg	0.9 (0.1)	75	3.4 (0.2)	95
Encalypta vulgaris Hedw.	Evulg	4.5 (0.3)	60	17.0 (1.0)	100
Syntrichia ruralis (Hedw.) F. Weber & D. Mohr.	Srur	11.3 (1.2)	50	8.0 (0.9)	30
Tortula inermis (Brid.) Mont.	Tine	34.0 (2.0)	45	10.7 (0.9)	35

mostly given by differences in the BSC composition, depending on species richness and lichen cover (Fig. 3, Table 2). Despite ordination did not evidence a clear distinction in the assemblage composition between microsites, a multivariate test of significance showed significant differences in BSC composition between microsites (mGLM: Pr(>Dev) = 0.003, Dev = 49.06). In the intermounds, BSCs had a higher frequency and cover of the mosses *E. vulgaris* and *Bryum argenteum,* and the lichens *Acarospora terricola, Enchylium tenax, Lempholemma chalazanum, Peccania subnigra, Peltula obscurans* and *Placidium squamulosum*, in comparison to BSCs in shrub mounds. The cover of the cyanobacteria *Microcoleous vaginatus* and an unidentified lichen species of the genus *Psora* was higher in the mounds than in the intermounds (Table 1).

Evaluation of soil variables showed high variability within microsites, which could be related to differences in either BSC total cover and/or species identity (Figs. 4 and 5, Table 3). For most community attributes versus soil functions regressions, comparison of slopes tests were not significant (Appendix 3), justifying fitting a common slope for both microsites, and suggesting a similar trend between BSC attributes and soil functions in vegetated and interspace microsites.

Soil surface aggregate stability was positively related to BSC total cover, with stable soils being characterized by a BSC total cover higher than 50% of the soil surface (Fig. 4a). In mounds, soil stability was significantly correlated with the cover of mosses, and in intermounds stable soils had either high cover of mosses, lichens, or a mix of both (Fig. 5a). Shifts in the species identity of the BSC communities also influenced soil surface stability (Table 3). For

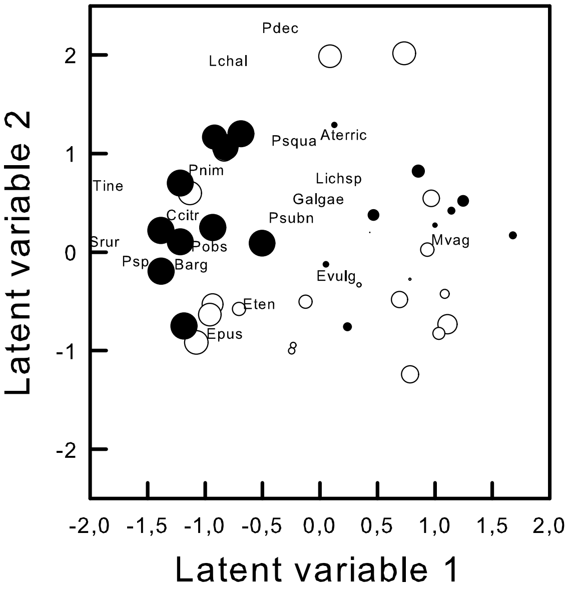

Fig. 3 Ordination of BSC communities in shrub mounds (black dots) and intermounds (white dots) using a generalized linear latent model. Symbol size is proportional to the total cover of BSCs in each sample. The position of the species in the ordination portrays indicator species characterizing the samples. The first and second axes explained 62.2% and 29.7% of the total variance, respectively

Table 2 Pearson correlation estimates between BSC community attributes and the compositional-structure of the BSC communities estimated as the axes of a generalized linear latent variable ordination based on the species covers. Statistical significant values are in bold ($P < 0.05$)

	Axis 1	Axis 2
Total cover	**−0.67**	0.25
Lichen cover	0.14	**0.48**
Moss cover	**−0.76**	−0.03
Species richness	0.13	**0.43**
Diversity	0.09	0.14
Evenness	0.07	−0.08

example, stable soils tended to present high cover of the mosses *T. inermis* and *S. ruralis* in both mounds and intermounds, but sites dominated by the moss *E. vulgaris* in the intermounds were unstable or very unstable despite having among 45 and 75% of BSC total cover. In addition, the squamulose lichen species *L. chalazanum,* which was present with relatively high cover in intermounds, was positively correlated to soil stability.

Soil infiltration rate was not related to BSC total cover, but it was negatively related to lichen cover (Figs. 4b and 5b). Indeed, very low values of soil infiltration rates were measured in some samples taken from the intermounds, which had a high lichen cover dominated by *L. chalazanum, P. subnigra, P. squamulosum* and *P. decipiens.* The cover of the moss *B. argenteum* was also negatively correlated to soil infiltration rate (Table 3).

Soil total N and C increased and P decreased with the cover of BSCs (Fig. 4c-e). Mosses positively contributed to N but negatively to P (Fig. 5c,e), being both nutrients closely related with changes in the cover of the species *E. vulgaris*, *S. ruralis* and *T. inermis* (Table 3). Instead, soil total C was significantly related to the cover and composition of lichens in the intermounds (Fig. 5d), being positively correlated with the cover of the lichen species *A. terricola, L. chalazanum, P. squamulosum* and *P. decipiens* (Table 3).

In mounds, the concentration of inorganic N decreased with the cover of BSCs, mainly related to changes in the cover of mosses (Figs. 4f,g and 5f,g). Concentration of inorganic N was very low in the intermounds, and was not related to BSC cover and composition. Most lichen and moss species were negatively (not significant) correlated with the concentration of inorganic N (Table 3).

Discussion

There is an ever-increasing interest in evaluating the species composition/ecosystem functioning relationship in BSC communities, but advances in this research topic are still limited. Some major limitations arise from difficulties in surveying BSCs, as components are difficult to identify to the species level. In addition, BSC communities are often diverse yet there is no clear approach for evaluating the relative importance of the individual species in the community on different ecological processes. High spatial variability in community composition also adds complexity in this topic. We overcome some of these methodological limitations by carefully sampling BSCs which appear visually homogeneous, and returning samples to the laboratory in order to confidently identify and quantify the lichen and moss species in the community. We approached the BSC

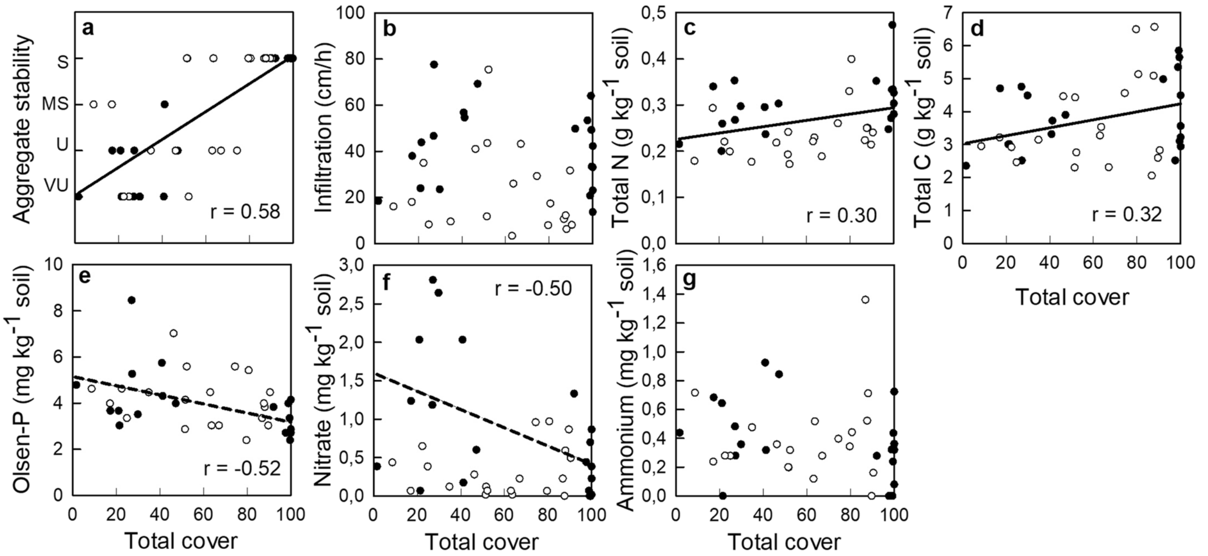

Fig. 4 Relationship between BSC total cover and soil properties measured as surrogates of ecosystem functioning in shrub mounds (black dots) and intermounds (white dots). Only significant regressions are shown ($p < 0.05$). Categories for aggregated stability are: stable (S), moderately stable (MS), unstable (U) and very unstable (VU). Solid lines represent a common regression slope for both microsites justified by a comparison of slope test, and dashed lines are regression estimates for the shrub mounds

spatial variability at the microscale by comparing BSCs beneath plant canopies and in the interspaces. To address the BSC species composition/functioning relationship we used a correlative approach, which has been successfully applied in previous studies (Bowker et al. 2011; Castillo-Monroy et al. 2011; Eldridge et al. 2010). We acknowledge that the latter is a critical point in the study, as it is difficult to know about the relevance of individual species in diverse communities. Commonly-used ecological approaches based on the relative abundance of the species in the community may not apply in the study of the BSC composition/function relationship, as even low-abundant species seem to exert significant effects on some particular soil function (e.g. Castillo-Monroy et al. 2011). Despite this, we considered that the study of the function of individual species in mixed communities, interacting with other species and in a natural context, is a valuable alternative and complementary approach to results of species functions in monocultures. As such, in our study, we support the interpretation of the results by means of a careful revision of the literature available in relation to the functional traits of cryptogam species, providing new data that contribute to improve our understanding about differences in the BSC species composition and the effects on an ecosystem functioning at the scale of microenvironments. In addition, we develop hypothesis about species functional traits that may regulate the composition/function relationship, this hypothesis contributing to current efforts to develop a trait-based BSC ecology.

We found that the species identity and richness of the BSC communities were similar in vegetated and open microhabitats, with the majority of the species being ubiquitous in the study area, but species covers varied widely between microhabitats determining distinct community configurations (Fig. 2, Table 1). The significant differences we observed in the distribution of cover among species between microhabitat types likely reflect divergent niche-based community assembly patterns (Garibotti and Gonzalez Polo 2021). The dominance of few moss species in the vegetated mounds could have been due to the prevalence of competition between BSC species given ameliorated conditions under the shrub canopy (Soliveres and Eldridge 2019). The more even distribution of cover among moss and lichen species on open intermounds may reflect the coexistence of competing species where environmental conditions are probably

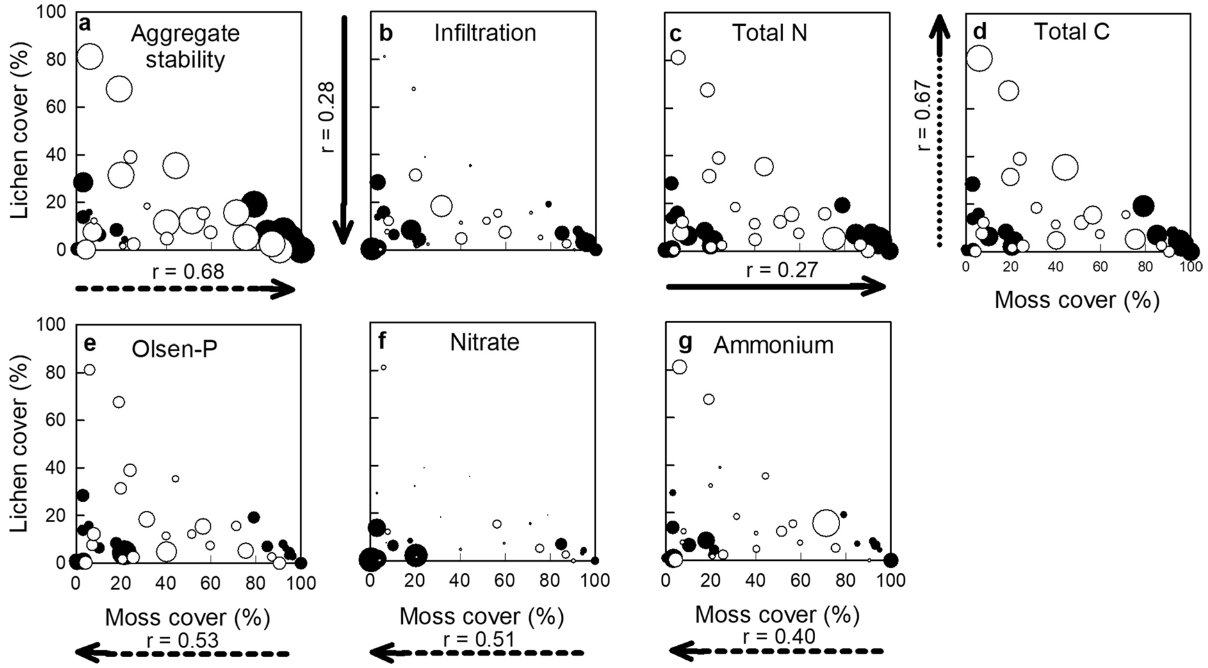

Fig. 5 Relationship between BSC community composition and soil functioning. Percent cover of mosses and lichens in the studied BSC communities is shown in the x-axis and y-axis, respectively. Each plot panel shows one soil property measured as surrogates of ecosystem functioning, with symbol size representing the relative value of that function in each studied sample. Arrows represent simple regressions between the axes and the soil functions; only significant regressions are shown ($p < 0.05$). Solid arrows represent a common regression slope for both microsites justified by a comparison of slope test, black dots and dashed lines are regression estimates for the shrub mounds, and white dots and dotted lines are regression estimates for the intermounds

Table 3 Correlation coefficients between BSC species cover and soil variables measured as surrogates of ecosystem functioning. Results are shown for the most frequent species with a relatively high cover. Statistical significant values are in bold ($P < 0.05$)

	Aggregate stability	Infiltration rate	Total N	Total C	Olsen-P	Nitrate	Ammonium
Acarospora terrícola	0.15	−0.09	−0.05	**0.34**	0.02	**−0.13**	0.31
Enchylium tenax	−0.08	−0.01	−0.10	0.03	0.09	−0.21	−0.17
Lempholemma chalazanum	**0.30**	−0.19	0.10	**0.48**	−0.21	−0.01	0.00
Peccania subnigra	−0.06	−0.20	−0.10	0.06	−0.16	−0.20	−0.09
Peltula obscurans	0.16	−0.05	−0.15	−0.04	−0.13	−0.25	0.11
Placidium squamulosum	0.17	−0.21	0.02	**0.44**	−0.07	0.07	0.17
Psora sp.	0.22	−0.06	0.21	0.19	−0.14	−0.18	−0.12
Psora decipiens	0.21	−0.26	−0.05	**0.38**	−0.03	−0.12	0.17
Bryum argenteum	0.23	**−0.39**	−0.22	−0.11	−0.25	−0.21	−0.07
Encalypta vulgaris	**−0.47**	−0.03	**−0.39**	0.00	**0.42**	−0.09	0.10
Syntrichia ruralis	**0.73**	−0.14	**0.46**	0.18	**−0.43**	−0.20	−0.14
Tortula inermis	**0.58**	−0.09	**0.29**	0.18	**−0.30**	−0.07	−0.13

highly variable both in time and space, determining niche partitioning and the occurrence of windows of favorable conditions that fit the requirements of different species (Chesson and Warner 1981).

In the present study we had successfully documented changes in surrogates of different types of independent ecosystem functions, which were associated with the observed shifts in the BSC community cover and species identity at the microhabitat scale. We observed that a BSC total cover higher than 50% was enough for stabilizing soil surface in both microhabitat types (Fig. 4a), which is in-between the cover thresholds of 37 and 67% for soil erosion resistance reported by Gao et al. (2020) and Silva et al. (2019), respectively. Soil surface aggregate stability was given by mosses in vegetated mounds, and both lichens and mosses contribute to soil stability in open intermounds (Fig. 5a). Moss rhizoids and lichen tufts of rhizohyphae penetrate deep into the substrate probably contributing to keep together soil particles (Eldridge et al. 2021). The only exception we found is the moss species *E. vulgaris*, which correlated negatively to soil surface stability despite being present at covers between 40 to 60% in some intermound samples (Table 3). This is probably because of its short, loose tuft morphology that determines the species low ability to stabilize the soil (Mallen-Cooper et al. 2019), in comparison to the dense tuft and cushion morphology of the other species present in the study area. Therefore, our results suggest that most BSC components positively contributed to soil surface stability both in vegetated and open microhabitat, in agreement with the general acceptance that BSCs are the functionally active components that contribute the most to soil surface stability in drylands (Chaudhary et al. 2009).

Closely related to soil surface stability are soil processes that regulate water dynamics (i.e. infiltration and runoff rates), since water is an important agent of soil erosion in drylands. The role of BSCs in this function is still a matter of major debate. Some previous studies have found that soil surface roughness produced by the development of BSCs increases infiltration rate and decreases erosion (Rodríguez-Caballero et al. 2012). However, infiltration varies significantly between and within BSC types (Chamizo et al. 2012; Eldridge et al. 2021). Our results are in agreement with this later point of view, as soil infiltration was non-significantly related to BSC total cover (Fig. 4b) but depended on community composition (Fig. 5b, Table 3). Lichens had a negative effect on infiltration rates (Fig. 4b), probably because most of the species in our study area were minute squamulose and foliose, which are known to have hydrophobic properties and to clog soil pores (Bowker et al. 2011; Souza-Egipsy et al. 2002). Microlichens of the same genus found in our study area have been reported to be characteristic of runoff areas (Eldridge et al. 2021). Interestingly, the moss *B. argenteum,* which was ubiquitous in both studied microsites, was also negatively correlated to soil infiltration (Table 3). This species forms short and high-density colonies that grow closely attached to the substrate, and have waxy materials on the surface that increases the resistance to water penetration (Jia et al. 2020). Shoots of this species are distinct in that leaves are small, they are arranged in a dense overlapping spiral around each stem, and they lack awns or other projections which in other moss species serve as retention structures of the water that is conducted to the underlying soil (Coe et al. 2019). This suite of shoot and leaf traits, which are known to reduce desiccation and prevent water logging of the moss thalli, could have likely contributed to reduce water infiltration in biocrusts with the presence of *B. argenteum*. This was unexpected, since the majority of the previous studies that evaluated the hydrological behavior of moss species in mixed BSC communities have reported positive effects on soil infiltration, as a function of morphological traits of the colonies that increase water capture, disregarding results showing negative and neutral effects of other moss species (Bowker et al. 2013, 2011; Eldridge et al. 2010). However, understanding negative effects of moss species on infiltration is also of relevance to evaluate how BSC structure generates hydrophilic and hydrophobic spots that contribute to small-scale patterning in the soil hydrological function. According to our results for *B. argenteum*, functional traits of the shoots and the leaves, such as leaf size, shape, and arrangement, can contribute to effectively predict the effects of different mosses on soil infiltration, either positive or negative, improving dryland BSC-moss trait ecology that so far has been most frequently oversimplified to stand-level structural characteristics, such as thalli stature (short versus tall) and density. Overall, our results evidence a clear link between BSC community composition and the soil infiltration function suggesting that the spatial heterogeneity in the distribution of microlichens (crustose, squamulose and foliose) and *B. argenteum* probably promoted hydrophobic soil spots in both studied microsites.

Perhaps one of the most difficult to understand role of BSCs is their effect on soil biogeochemical processes, because it depends upon poorly known physiological characteristics of the species (Bowker et al. 2011). Some previous advances have been done in the study of BSC-lichens, showing species-specific effects related to chemical and morphological traits of the species (Castillo-Monroy et al. 2011; Concostrina-Zubiri et al. 2013; Concostrina-Zubiri et al. 2021; Delgado-Baquerizo et al. 2015; Miralles et al. 2012). We found particularly important positive effects of BSC cover on soil total C and N but negative on soil P availability (Fig. 4c-e), with the differential importance of certain BSC components and species in the different microsites (Fig. 5c-e, Table 3), evidencing a close connection between composition and biochemical function in the studied mixed natural BSC communities.

The significant relationship we found between moss cover and soil total N (Fig. 5c) suggests that mosses play an important role in soil N availability in the studied system, representing mantles of fertility (Garcia-Pichel et al. 2003). According to our results *S. ruralis* and *T. inermis* have positive and *E. vulgaris* negative influences on soil total N. A possible explanation is related to the soil-surface aggregate stability provided by *S. ruralis* and *T. inermis*, as discussed above, which probably protects from N loss by runoff and wind- and waterborne sediment export (Barger et al. 2016; Belnap et al. 2003). At the same time, their tall structure may favor the capture of N-rich dust (Mallen-Cooper et al. 2019). Yet we cannot discard species-specific differences in the input of N to the soil by the leaching from moss-associated epiphytic cyanobacteria, a process that has received little attention in dryland BSCs. Dryland mosses are relatively small (few centimeters in height), so the possibility of species-specific limitations in cyanobacteria colonization given by slow hydration rates, as occurs in larger thalli from mesic areas (Liu and Rousk 2021) seems unlikely. Most possible, *S. ruralis* and *T. inermis* have some advantage to be colonized by epiphytic cyanobacteria due to their leaf strategies retarding desiccation rates, such as the presence of awns (in *S. ruralis*), surface papillae, and concave leaves or recurving leaf margins (Glime 2017). In addition, the species dense packing of shoots and leaves forming tufts or cushion, and the accumulation of dead biomass beneath the green parts of the thalli, are morphological traits that may favor epiphytic cyanobacteria growth in moist leaf axils and within the lumen of dead cells, protected from environmental stress (Solheim et al. 2004). Overall, our results suggest that the effect of mosses on soil total N is species-specific, and that it can be partially attributed to water-related shoot- and leaf-level characteristics of the species, which control the cyanobacteria-moss association and chemical processes.

Mosses were also the main BSC component related to P availability, with a negative relationship in the vegetated mounds (Fig. 5e, Table 3). This is particularly relevant as it is generally conceived that BSCs positively contribute to soil P by releasing extracellular phosphatases into the soil environment, but it has been reported an important positive effect of BSC-lichens but weak of BSC-mosses (Delgado-Baquerizo et al. 2015, 2016). The fact that we actually found the contrary pattern to what it was expected according to the literature (but Bowker et al. 2006), suggests that other processes may be of relevance regulating the influence of mosses on soil P in our area. Indeed, the differential negative effect of *S. ruralis* and *T. inermis* on soil P in our area could conceivably be explained by the accumulation of nutrient-rich, dead recalcitrant biomass beneath the living part of the thalli, where P may remain immobilized in the long term. In addition, although little is known about species-specific variations in the decomposability of xerophilous moss, the brown dead tissues of *S. ruralis* have relatively low water retention capacity (Voortman et al. 2014), a characteristic that may inhibit or lower decomposition rates. Therefore, besides the classical approach that evaluated the influence of BSCs on soil P by the measurement of phosphatase concentration, we suggest that the ratio between green and brown moss tissues, which Voortman et al. (2014) has used as a water-related functional trait of mosses, might be further investigated as a possible trait related to the effect of mosses on soil P. Overall, it seems that BSC-mosses are main drivers of P availability in our area, probably because their strategies of nutrient accumulation and conservation make only a small proportion of the P to enter the cycling pool.

On the contrary, we found that soil C was closely related to lichen cover in intermounds (Figs. 4d and

5d and Table 3). Lichens can significantly contribute to soil annual carbon by the release of labile C forms (Concostrina-Zubiri et al. 2021; Miralles et al. 2012) or via decomposition of lichen litter that can be as fast as that from vascular plants (Berdugo et al. 2021). In our results, most of the species that correlated positively with soil C were chlorolichens, such as *A. terricola*, *P. squamulosum* and *P. decipiens*, and the cyanolichen species *L. chalazanum* (Table 3). It has been shown that chlorolichens have some photosynthetic advantage in habitats that regularly experience high air humidity over cyanolichens that rely on liquid water (Büdel et al. 2013; Matos et al. 2015). This is a plausible explanation for our results, as in our area precipitation as liquid water is very low throughout the year, but air humidity remains around 60% during the winter months. In coincidence with our results, Delgado-Baquerizo et al. (2015) has reported high soil C content under *P. decipiens,* linked to high C content in their tissues due to photosynthesis. From our results it also becomes apparent important differences between cyanolichen species in their contribution to soil C, since *E. tenax*, *P. subnigra* and *L. chalazanum* were present with similar cover in our study area, but only the latter species correlated positively with soil C (Tables 1 and 3). Despite all, these are gelatinous lichen species that can accumulate considerable quantities of water, differences in morphological features are very important determining thallus water relations, which are strongly linked to their photosynthetic capacity (Gauslaa 2014). Crustose lichens, such as *L. chalazanum*, retain water at the lichen-soil interface, benefiting the thallus hydric status and photosynthetic performance (Souza-Egipsy et al. 2002), but reducing the net photosynthesis depression at high degrees of hydration that occurs in foliose lichens such as *E. tenax* (Lange et al. 1998). On the other hand, the dwarf-fruticose morphology of *P. subnigra* may result in rapid drying, and consequently poor photosynthetic capacity. Therefore, species-specific differences among BSC-lichens in their ecological role on soil C could be at least partially explained by the combined and interactive effects of photobiont type and thallus morphological traits, which integrates physiological differences in relation to their water-use strategy.

Implications for BSC trait-based ecology

In this study we provide empirical evidence on the contribution of mixed natural BSC communities to different types of independent ecosystem functions in different microhabitat contexts. We found that soil surface stability was closely related to BSC total cover, irrespectively of community composition, suggesting that most BSC components contribute to this soil function both in vegetated and interspace microsites. However, surrogates for soil water and nutrient dynamics were closely related to shifts in BSC composition, with some microhabitat context-dependent differences in the composition/functioning relationship related to the dominant species in the community.

Although our approach based on correlation does not allow to confidently establish causality relationships between variations in BSC community composition and functioning, we combined our field data with bibliographic information to identify ecologically relevant community and species traits that likely influenced these particular soil functions. Based on these results, we suggest that future studies on BSC trait-based ecology could be greatly benefited by the consideration of many readily applied qualitative traits that have been thoroughly used in lichenology and bryology, but still poorly considered in BSC ecology. This is especially true for shoot and leaf traits of BSC-mosses, as well as the greenness trait related with the accumulation of dead parts, which may contribute to predict the effect of different moss species on water-holding and water-retention capacities, and in turn processes related to the availability of soil nutrients. For BSC-lichens, besides using photobiont type as a trait related to the species N-fixation capacity, we suggest that the combination of photobiont type and growth form traits can contribute to predict their influence on C availability, as it is related to the species photosynthetic performance.

We conclude that our approach analyzing BSC composition/functioning linkages in natural communities substantially complements current efforts aiming to establish a quantitative trait database for BSCs using laboratory-based techniques (Mallen-Cooper et al. 2019), as it contributes to uncover simpler to measure relevant functional traits and it extends our knowledge about species functional traits in mixed assemblages and under microhabitat heterogeneity.

Authors' contributions M.J.B. and I.A.G. designed the study; field data and samples were collected by M.J.B., N.C. and M.C.N.; microscopic analyses were done by M.J.B.; chemical laboratory analyses were done by I.A.G., M.G.P. and P.S.; M.J.B., N.C. and I.A.G. analyzed the data; I.A.G. wrote the first draft of this manuscript, and all co-authors contributed to improve it.

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Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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