

Functional Ecology

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Dual community assembly processes in dryland biocrusts communities

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Abstract

1. Biocrusts are critical components of drylands where they regulate a wide range of ecosystem functions, however, their response to the worldwide phenomenon of shrub encroachment and to livestock grazing, the most extensive land use in drylands, are not well studied. Grazing by livestock and increases in shrub cover could influence biocrust communities directly via trampling or shading, or indirectly, by altering biotic interactions amongst biocrust taxa. The extent of these changes in biocrust cover, diversity and composition are poorly known.
2. We used linear models and structural equation modelling to examine the direct effects of grazing and shrubs on biocrust community composition and the indirect effects mediated by changes in species interactions.
3. Biocrust richness and cover increased with increasing shrub cover at the site level. This pattern occurred despite the negative response we found (lower cover and richness) under shrub patches vs open areas, which was consistent irrespective of grazing level. Functional diversity and evenness were similar between shrubs and open at low grazing intensity, but at high grazing functional diversity was greater in the open. Competition between biocrust species was an important driver of their community assembly irrespective of shrub cover, grazing intensity or patch type. Structural equation models showed that the effects of grazing and shrub cover on functional evenness, functional diversity and richness were controlled by biotic interactions within the shrub microsites. In the open, however, these effects were either direct or mediated by changes in cover.
4. Biocrust cover, species richness and functional diversity increase with shrub cover at the site scale, despite the negative effects at the microsite level. We demonstrate here that drivers of community assembly differ markedly at small spatial scales. Though biocrust communities were directly driven by environmental filtering in the open, biotic interactions played a fundamental role in their assembly when growing beneath shrubs.

Keywords: Competition, soil crust, intransitivity, functional diversity, shrub encroachment, lichens, bryophytes

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Introduction

Biological soil crusts (biocrusts) are communities of mosses, lichens, cyanobacteria and fungi associated with the surface of dryland soils and influence their functioning (Belnap & Lange, 2003; Maestre et al. 2016). Cover, composition and species richness of biocrust communities are strongly affected by environmental conditions such as livestock grazing, aridity, or the presence of vascular plants. Since biocrust composition drive processes such as N fixation, hydrological properties, soil respiration and soil erosion (Eldridge & Greene 1994; Bowker et al. 2013; Concostrina-Zubiri et al. 2013), understanding how these environmental factors drive changes in biocrust communities can, therefore, help predicting changes in dryland functioning under contrasting environmental and land use scenarios. Although the response of biocrust communities to increasing aridity is relatively well-known (Escolar et al. 2012; Reed et al. 2012; Concostrina-Zubiri et al. 2014a), their responses to other environmental factors are less well understood.

In addition to water availability, most dryland ecosystems are characterised by being two-phase mosaics dominated by vegetation patches and areas of bare ground. Patches of perennial vegetation have generally positive, facilitatory effects on understorey species (Gómez-Aparicio, 2009; Soliveres & Maestre, 2014), including the diversity and cover of biocrust communities (e.g., Maestre et al. 2002; 2009; Concostrina-Zubiri et al., 2014b). However, these facilitatory effects at the patch-scale may become negative when the density of plants increases and when their canopies reduce light levels, increase the build-up of dense litter layers, or compete for nutrients (Facelli & Temby, 2002; Baez & Collins, 2008; Riginos et al., 2009; Soliveres et al., 2014). While effects of increasing plant densities of woody species ('shrub or woody encroachment') on understorey plant communities and soil properties in drylands are known, the response of biocrust communities to this encroachment has received far less attention (Maestre et al., 2009; Eldridge et al., 2011). Together with the widespread phenomenon of shrub encroachment, livestock grazing is the most common land use in drylands worldwide. As with increasing aridity or shrub influence, livestock grazing affects the composition and functioning of biocrust communities (Warren & Eldridge, 2001; Concostrina-Zubiri et al., 2017; Mallen-Cooper et al., 2018). Grazing can dramatically alter the composition and functioning of biocrust communities in contrasting directions. Intensive livestock grazing can foster local extinctions of functional groups such as fruticose lichens, which enhance soil water retention and reduce soil surface temperature (Concostrina-Zubiri

et al., 2017), but are sensitive to trampling. Conversely, overgrazing can also create gaps necessary for pioneering taxa such as cyanobacteria and cyanolichens (Eldridge et al., 2010a; Bowker et al., 2013; Concostrina-Zubiri et al., 2014b).

A number of studies over the past two decades have addressed the individual effects of these two major environmental changes (livestock grazing and, to a lesser extent, woody encroachment) on biocrust communities. However, these effects may not be independent, and their interactive effects have not been studied. For example, species growing in open microsites or in areas with sparse shrub cover may be more negatively impacted by grazing because they are accessible to livestock whereas those under the canopy of shrubs, or growing beneath dense shrub stands may be protected from herbivores (Ibañez & Schupp, 2001; Smit et al., 2007; Riginos & Grace, 2008). Therefore, grazing effects on biocrust communities may vary among different patch types and levels of encroachment, as has been observed in vascular plants (Riginos et al., 2009; Sitters et al., 2013; Soliveres & Eldridge, 2015).

As with vascular plants, grazing and shrub encroachment (at both the patch- and the landscape scales) can affect the composition of biocrusts both directly and indirectly, by altering how different biocrust species interact. Grazing and shrub patches can alter directly biocrust composition via trampling, shading or resource competition, and also by changing the species pool available to colonize a given site (i.e., by environmental filtering). However, both grazing and shrub encroachment can also indirectly alter biocrust composition by affecting resources for which biocrusts compete, or by altering how different species interact with each other (see Soliveres et al., 2011; McIntire & Fajardo, 2013). The latter can occur either by shifting the sign of the interactions (e.g., from competition to facilitation under contrasting environments; Maestre et al., 2008; Bowker et al., 2010a) or by changing the way these species compete. These indirect effects may be particularly important for biocrust species, as their composition is more susceptible to biotic interactions (e.g., Concostrina-Zubiri et al., 2014a), which can shift from hierarchical to non-hierarchical competition when environmental stress declines (Bowker et al., 2010a). The lack of absolute competitor winners (non-hierarchical competition, or competition intransitivity) allows a greater number of species to coexist because no species is consistently a weak competitor (Gilpin, 1975; Laird & Schamp, 2006). In addition to enhance species richness, competition intransitivity may also affect other facets of diversity such as the variety of functional traits (Maynard et

al., 2017; Ulrich et al., 2018) and therefore could affect the functioning of biocrust communities. Both grazing and shrub encroachment could alter competition networks of biocrust species through changes in environmental heterogeneity (Allesina & Levine, 2011; Soliveres et al., 2015) or productivity (Bowker et al., 2010a; Soliveres et al., 2018). However, the extent to which changes in biocrust cover, diversity and composition are driven by these indirect effects mediated by biotic interactions have been seldom quantified.

To address these research gaps, we report on the response of biocrust cover, species richness, and their species and functional composition, to the interactive effects of shrub encroachment and livestock grazing. We use structural equation modelling to separate the direct effects of grazing and shrubs on the species richness and functional diversity of biocrusts, from the indirect effects via changes in how these species compete. We predict that grazing and shrubs will interact in driving biocrust communities, with stronger effects in their cover and composition than in their species richness. Second, we predict that part of the effect of grazing and shrubs will be mediated by changes in how biocrust species interact with each other.

Materials and methods

Site description

Our study was carried out in semi-arid woodlands near Buronga (34°06'S, 142°06'E) in south-western New South Wales (NSW), Australia. Rainfall at the site is low and variable (mean annual rainfall: 220 to 280 mm), with high evapotranspiration (~1500 mm annum⁻¹), dry hot summers (daily mean temperature: 30°C, 15% less rain than in winter) and cool moist winters (daily mean: ≤ 17°C). The soils are dominated by fine-textured loams and clay loams (Calcarosols; pH ranging between 7-9), and support a rich biocrust community dominated by mosses, lichens and liverworts (Appendix S2).

Thirty-two sites (0.25 ha = 50 m × 50 m each) varying in shrub cover and grazing levels, but with otherwise similar soils and vegetation type, were selected (Fig. S1). Shrub cover (ranging from 0-50%) was measured on each of these plots with three, 50-m long transects aligned through the ends and centre of the plot (see details in Eldridge et al., 2013). The sites

are typical of encroached woodlands in semi-arid eastern Australia where open patches between trees have become encroached by shrubs of a range of species (*Eremophila sturtii* R. Br., *Senna artemisioides* Randell, *Dodonaea viscosa* Jacq.), dominated by cohorts of a single size (age) class.

These 32 sites were divided into two grazing categories. Sixteen sites were located in Mallee Cliffs National Park, which has been ungrazed by livestock since 1977 but is lightly grazed by kangaroos and rabbits (Supporting Information Appendix S3). The Park covers about 580 km² and has had very low levels of grazing since the 1990s due to a combination of removal of ground water supplies and control of feral grazing populations. The other 16 sites were established in adjoining pastoral properties that are relatively heavily grazed by cattle or sheep, and also have higher densities of goats, kangaroos and rabbits than our low grazing sites (Appendix S3). Overall, these 32 sites allowed us to examine differences in grazing intensity (light vs heavy) and shrub cover (0 to ~ 50% cover), which are within the range of values reported for shrub encroached sites (Soliveres & Eldridge 2015). We considered the 32 sites to be independent because they were separated by distances of 1 to 12 km. All sites were selected within a single land unit (flats and depressions) to avoid confounding influence of landform on-site attributes.

Cover, species richness and composition of biocrusts

At each site, five shrub and five open (interspace) patches (hereafter ‘microsites’) were randomly selected, and within each of these microsites, a 5 cm-diameter circular subplot was sampled under the canopy or in the open ($N = 320$ in total). This plot size is enough to fit several individuals and colonies of biocrust species (Appendix S2). In March 2014 (late summer), each subplot was carefully removed from the ground using plastic Petri dishes and slightly wetting the soil to avoid any damage, placed in a paper bag, and stored in a cool place until the cover by species of lichens, mosses and liverworts was measured. Once in the laboratory, each taxon was identified to species level using keys in Filson & Rogers (1979), McCarthy (1991), Catcheside (1980), Scott (1985) and Scott & Stone (1976) and more recent generic revisions. Nomenclature followed Buck & Vitt (2006) for mosses, McCarthy (2006) for liverworts, McCarthy (2015) for lichens, and where appropriate, more recent taxonomic revisions. From these data, species richness and cover were directly obtained. Changes in species composition were assessed using non-metric multidimensional scaling ordination

(nMDS) and the Bray-Curtis distance measure on log-transformed abundance data (to reduce the influence of the most abundant species in the results) with the PRIMER/PERMANOVA statistical package (PRIMER-E Ltd., Plymouth Marine Laboratory, UK).

Functional attributes were assigned to each of our biocrust taxa based on eight functional traits: root (rhizine) length, taxon height, sediment capture, absorptivity, and the activity of four enzymes associated with carbon (β -glucosidase, β -D-cellobiosidase), nitrogen (N-acetyl- β -glucosaminidase) and phosphorus (phosphatase) cycling. These functional traits are linked to competitive ability and response to the environment in biocrust taxa, but also to their effects on important ecosystem functions such as nutrient cycling, water infiltration and resistance to erosion (see Bowker et al., 2010b; Mallen-Cooper & Eldridge, 2016). From this information, we calculated two complementary metrics of functional diversity: i) RaoQ (sum of pairwise distances in multidimensional trait space), and ii) functional evenness (a measure of the extent to which different trait strategies are evenly distributed in the community; see Pakeman, 2014 for a review). Functional metrics were calculated using the FD package in R (Laliberté et al., 2014). Functional dispersion and functional richness were also considered, but removed in further analyses due to their strong correlations with RaoQ ($\rho = 0.97$ [functional dispersion]) and species richness ($\rho = 0.75$ [functional richness]). Functional trait information was available for 23 of the 53 species we found, and these represented $56.1 \pm 3.08\%$ (mean \pm SE) of the total cover within the 320 subplots. All functional diversity metrics were weighted by the relative cover of each species.

Changes in biocrusts interactions

To calculate the degree of competition intransitivity, the inverse Markov-chain approach of Ulrich et al. (2014) was used as implemented in the free software *Transitivity*. This approach provides a metric for intransitivity (I), which ranges between 0 (total competition hierarchy) and 1 (total competition intransitivity). The metric is based upon the number of competition reversals, i.e., how many times the competitor dominant(s) loses over time (see Laird & Schamp, 2006; Ulrich et al., 2014 for details). With this approach the number of species to analyse cannot exceed one less than the number of sites, therefore in our case, four species. Thus, we analysed the degree of intransitivity on the four dominant species at each plot \times microsite combination (as we had five replicates of each microsite \times site combination).

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Together with the levels of intransitivity, the software calculates a measure (*Match*) of how well the simulated Markov chains fit the observed abundances. This *Match* metric is an indicator of the importance of competition for the assembly of the studied species (values close to one indicate that simulated and observed abundances are strongly related, and since simulations are only based on species replacements, this mean that competition is strongly driving the observed patterns). The *Match* metric also indicates how reliably the level of intransitivity has been estimated and in our case was independent of whether the biocrusts were moss- or lichen-dominated. Only in three out of the 64 microsite \times site combinations was this metric below 0.6 (60% of the observed abundances explained by the simulated Markov chains). Therefore, it can be assumed that competition was a dominant interaction among the studied species and that the level of intransitivity was reliably estimated (see Ulrich et al., 2014; Soliveres et al., 2015 for further details on the methods).

To account for changes in composition, we applied this approach to two different datasets: one including the four dominant species across all sites (therefore removing changes in composition), and one including the four dominant species at each site (therefore accounting for effects of changes in composition + environment). The intransitivity metrics obtained using the overall dominant species or those most dominant at each site rendered similar results ($\rho = 0.41$; $P = 0.017$; $N = 33$), although in the former case, this metric could only be calculated in half of the 64 microsite \times site combinations because these species were not present in all subplots. Thus, we only report results from the metrics calculated for the four dominant species at each site.

Overall, we analysed changes in biocrust communities by examining total cover, species richness and composition, functional composition, the importance of competition for community assembly, and the degree of competition intransitivity. For the taxonomic and cover measures, we used our full database. For the functional diversity metrics, we used a reduced database of the 23 taxa for which we had functional trait data. Finally, to assess the interactions among different biocrust species, we used the four dominant species.

Statistical analyses

Changes in biocrust cover, species richness, functional diversity (functional evenness and diversity [RaoQ]) and the level of intransitivity among the four dominant species in each

microsite \times site combination) were analysed by using linear models with shrub cover (0-50%), microsite (shrub *vs* open) and grazing level (low *vs* high), and their interactions as fixed factors using the 'lme4' package (Bates et al., 2015) within R statistical software (Version 3.4.4, R core Team 2018).

To further interpret compositional changes, the degree of association of biocrust species in relation to patch type and grazing was measured with Indicator Species Analysis in R (De Caceres, 2013) using a data matrix of 56 species and 64 combinations of microsite \times site. Indicator values combine information on the relative cover of each species and their frequency. Indicator values are maximal (IV=100%) when all individuals of a given species are restricted to a particular microsite (e.g. shrub), and all samples from that particular microsite contain an occurrence of that species. Data were randomized among the factors with a Monte Carlo procedure and 1000 iterations in order to determine their statistical significance.

Finally, we used Structural Equation Modelling (SEM) to examine the direct and indirect effects (i.e. mediated by total biocrust cover and the way species interact) of increasing grazing intensity and shrub cover, on biocrust richness, functional diversity, and composition. In order to evaluate possible interactions among the importance of each driver and their direct and indirect effects for a given microsite, we fitted separate models for open and shrub patches. Structural equation modelling tests the plausibility of a causal model, based on *a priori* information (Appendix S4), in explaining the relationships among different variables. In our model we predicted that grazing would have direct effects on individual crust attributes (e.g. functional composition, richness; Eldridge et al. 2013; Bowker et al. 2013; Concostrina-Zubiri et al., 2017) but also indirect effects *via* changes in intransitivity (Bowker et al., 2010a; Soliveres et al., 2015) and biocrust cover (as larger patches are more likely to support more species which are likely more competitive, therefore modulating biotic interactions). Similarly, the changes in heterogeneity and productivity induced by shrub patches and increasing density at the plot scale should directly affect the composition of biocrust communities (Maestre et al., 2002), but also their cover and how they interact. Overall goodness of fit probability tests (χ^2 and Bollen-Stine) were performed to determine how well our *a priori* model structure fit the data, with high probability values indicating that the model is a plausible causal structure underlying the observed correlations. All SEM analyses were conducted using AMOS Software Version 20.

Results

Direct effects of grazing and shrub encroachment on biocrust communities

We recorded 57 species of mosses, lichens and liverworts in the study. Biocrust cover was significantly greater in the open ($4.8 \pm 0.28\%$; mean \pm SE) than under the shrubs ($3.3 \pm 0.40\%$; $F_{1,28} = 9.73$, $P < 0.001$; Fig. 1). Similarly, open microsites had almost twice the richness (14.3 species) as shrub microsites (8.0 species; $F_{1,28} = 117.0$; $P < 0.001$; Fig. 2), and this did not differ between light and heavy grazing (grazing \times microsite interaction: $P = 0.46$; Table 1). Despite the lower cover and richness of biocrusts under shrubs at the patch-scale, both biocrust attributes increased linearly with shrub cover at the plot scale ($F_{1,28} > 5.00$; $P < 0.05$ in both cases; Figs. 1 and 2; Table 1). Indeed, the suppressive effect of shrub microsites on richness diminished when shrub densities at the plot scale were high (significant cover \times microsite interaction; Table 1).

Biocrust composition, as measured by the first dimension of the nMDS biplot, differed significantly between microsites and with increasing shrub cover. Fifteen species (nine mosses and six lichens) were significant indicators of open microsites (Table 2). Thus, increased shrub cover was associated with reductions in the cover of these taxa, particularly, the mosses *Didymodon torquatus* (Spearman's $\rho = -0.55$), *Tortula atrovirens* ($\rho = -0.44$) and *Gemmabryum pachythea* ($\rho = -0.38$), and the lichen *Psora decipiens* ($\rho = -0.38$). The second dimension of the nMDS biplot was associated with weak increases in the lichens *Psora decipiens* ($\rho = 0.34$) and *Psora crystallifera* ($\rho = 0.31$; Appendix S2). Values of RaoQ and functional evenness differed with grazing and microsite. Under low levels of grazing, values were similar under shrubs and in the open, but under high grazing, functional diversity was greater in the open microsites (Fig. 1; Table 1). Despite the negative effects of shrub microsites on RaoQ, the latter increased with shrub cover at the plot scale, similar to results found for species richness.

Effects mediated by biotic interactions between biocrust species

Competition was an important driver of the assembly of the studied biocrust communities, as shown by the high Match levels between the simulated and observed species covers (Fig. 2). Match levels ranged between 0.5 and 0.9 in most cases, suggesting that competition explained between 50% and 90% of variation in the observed relative covers of the four dominant species. The importance of inter-specific interactions was not affected by microsite, grazing or shrub cover at the plot scale (Table 1). However, when considering shrub microsites only, the level of competition intransitivity increased with shrub cover and decreased with grazing (Fig. 2). Competition was also more intransitive in open than in shrub microsites (0.42 ± 0.03 cf. 0.29 ± 0.02 ; Table 1) and had an overall positive effect on biocrust richness.

Shrub cover, grazing, biocrust cover and the degree of intransitivity explained between 67% (composition under the shrubs; nMDS1) and 9% (functional diversity [RaoQ] in the open; Fig. 3) of the variance in our SEM models. For biocrust richness, the shrub models explained twice the amount of variance as the models for open microsites. For the rest of compositional measures (nMDS, functional evenness and RaoQ), open models explained more than, or similar amounts of variance than, shrub models. In general, the effects of grazing and shrub cover on biocrust composition were either direct or mediated by cover in the open (i.e. controlled by environmental filters), but indirect under the shrub (i.e. mediated by intransitivity; Fig. 3). For shrub microsites, the total effects of shrub cover, and grazing were substantially greater than any direct effects, due to indirect effects mediated by crust cover and intransitivity (Table 3 vs path coefficients reported in Fig. 3). Thus, the effects of grazing and shrub cover seem to be controlled by biotic interactions within the shrub microsites (no direct paths from these predictors to biocrusts' attributes) whereas these effects are direct or mediated by cover in the open microsites, this was the case of biocrust richness, RaoQ and functional evenness (Figures 3 and 4).

Discussion

Direct effects of grazing and shrub encroachment on biocrust communities

In partial contrast to our predictions, overall effects of increasing shrub cover and grazing intensity were stronger drivers for biocrust richness and composition than for cover, although

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this depended on the environmental driver considered. Thus, we found equally strong effects of increasing shrub cover on biocrust cover, richness and composition, but grazing had a stronger effect on composition than on cover. We found little evidence for a response of biocrust richness and cover to grazing, despite the previously strong effects found for these contrasting levels of grazing on soils and vascular plants (Eldridge et al., 2013; Soliveres & Eldridge, 2014). These weak responses are consistent with previous literature showing species-specific responses in Argentina (Gómez et al., 2012), Mexico (Concostrina-Zubiri et al., 2014b), the Namibia Desert (Lalley & Viles, 2008) or Australia (Hodgins & Rogers, 1997), to name a few (reviewed in Warren & Eldridge, 2001). The interplay of “winner” and “loser” taxa could, therefore, obscure any overall response at the community level. Importantly, we show that these weak effects are microsite dependent, as shown by the significant microsite \times grazing interactions for composition, RaoQ and functional evenness (Table 1), and even persist when not including changes in cyanobacteria (which are winner taxa under grazing; Concostrina-Zubiri et al., 2014b).

Grazing had a strong negative effect on biocrust species richness in the open, with effect sizes similar to those reported for declining rainfall in the Colorado Plateau (Bowker et al., 2010b) or those observed under differential grazing levels elsewhere (Concostrina-Zubiri et al., 2014b). The more pronounced effect in the open, together with the species-specific responses often found for biocrust species under grazing, translated into a positive effect on functional evenness and a reduction in pairwise functional differences (RaoQ; Fig. 3). These effects on functional diversity also accord with previous reports from semiarid environments in Portugal and Mexico (Concostrina-Zubiri et al., 2014a,b) and should be considered when accounting for the effects of grazing on dryland functioning. The mechanism underlying these effects could relate to reductions in functionally redundant taxa through grazing, permitting an increase in a small number of functionally different species. An example of this could be the cyanolichens *Collema coccophorum* and *Peltula patellata*, which are pioneering species typically found in degraded or recovering surfaces (Rogers & Lange, 1971; Rogers, 1972; Eldridge, 1998) or sites that have had a long history of overgrazing.

In contrast, the direct effects of grazing on the composition of biocrust communities were negligible under shrubs, perhaps due to their protective effect from trampling, or due to the already depauperate (less cover and species richness) communities found beneath shrubs. These results show that grazing, or any other effect of the environment on biocrust

communities, should be studied together with small scale variations in microsite availability, as these may be as important, or even more, than large scale environmental gradients (Maestre et al. 2009; Concostrina-Zubiri et al. 2014a). The availability of microsites is strongly influenced by landscape-scale shrub cover. Despite the negative effects of shrub patches, the overall effect of shrub cover at the plot scale was clearly positive for biocrust cover and richness, and functional diversity. Shrub canopies affect temperature, shade and relative humidity, have deeper and more extensive litter layers, and exhibit a different soil surface morphology than open areas. These environmental changes have been shown to be strong drivers of species segregation in biological soil crust communities (Eldridge & Tozer, 1977; Bowker et al., 2010) and could explain the negative effects at the patch scale but the positive overall effects at the landscape scale, as the niches provided by shrubs are different to those in open environments. To the best of our knowledge, this is the first study addressing these positive effects of shrub encroachment, as a continuous gradient, on biocrust communities (but see Maestre et al., 2009; Eldridge et al. 2011 for comparisons between encroached and unencroached sites). Interestingly, the differences between shrub microsite and landscape effects are in sharp contrast to the responses found for vascular plants (either less or equally positive effects of shrub patches with encroachment; Riginos et al., 2009; Soliveres & Eldridge, 2015). We speculate, therefore, that the contrasting responses could be driven by competition between biocrust and vascular plant communities, in addition to the direct effects of shading, litter and soil morphology of shrub microsites on biocrust species.

Direct and indirect effects are mediated by biocrust interactions

Despite the importance of competition for the assembly of biocrust communities, as previously observed elsewhere (Maestre et al., 2008; Bowker et al., 2010a; Concostrina-Zubiri et al., 2014a), we found that this influence is modulated by the microsite in which biocrusts inhabit. In other words, we found two different community assembly mechanisms driving biocrust community composition. In open microsites, biocrust communities were driven mainly by direct (or cover-mediated) environmental changes caused by shrub encroachment and grazing, with little influence of the way species compete. Conversely, under shrub canopies, direct environmental effects were less common, and biotic interactions (specifically intransitive competition) played a major role as a driver of biocrust diversity and composition.

The levels of intransitivity we found are similar to those reported in experimental and observational studies on moss (Soliveres et al., 2018) and biocrust (Bowker & Maestre, 2012) communities. Competition intransitivity declined under grazing pressure (under shrub canopies), contrary to that observed in vascular plants (Soliveres et al., 2015) and increased with shrub encroachment. This type of competition may increase when productivity and heterogeneity are high (Gilpin, 1975; Allesina & Levine, 2011; but see Soliveres et al., 2018), and these conditions were met under shrub encroachment (more biocrust cover, light and water heterogeneity; Breshears, 2006), but not necessarily with grazing. Interestingly, high levels of intransitive competition enhanced species richness, as previously observed in vascular plants (Soliveres et al., 2015; Ulrich et al. 2018), but this only occurred under shrub canopies. In open microsites, intransitivity levels were almost as high as those found under shrubs, yet this type of competition was not associated with increases in species richness. This can be explained by two causes: i) we only analysed here competition intransitivity for the four dominant species, and this could differ from a situation where we analysed rarer species as well (Soliveres et al., 2015, 2018). Thus, if the other species compete more hierarchically, one could expect this to dampen the positive intransitivity-richness relationship, and ii) for intransitive competition to effectively enhance species richness, a certain degree of niche differentiation is necessary (e.g., Godoy et al., 2017), and this is more easily achievable when environments are heterogeneous, such as those beneath the canopy of shrubs in comparison with open areas (see full rationale in Soliveres et al., 2011).

Conclusions

Our study shows that biocrust cover, species richness and functional diversity (measured with RaoQ) increase with shrub cover at the site scale, despite the negative effects at the patch level. Further, we show inconsistent and idiosyncratic effects of grazing on biocrust communities, likely due to species-specific responses to this major environmental change. Overall, biocrust cover was less responsive to environmental changes than species richness or composition. By comprehensively analysing the response of biocrust communities, we were able to demonstrate that the drivers of community assembly differ markedly at very small spatial scales (shrub vs open microsites). Although biocrust communities were directly driven by environmental filtering in the open, biotic interactions played a fundamental role in their assembly when growing beneath shrubs.

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Data Accessibility

Data from this study is accessible in dryad, dataset "Dual community assembly processes in dryland biocrusts communities" (doi:10.5061/dryad.kh1893228).

Authors' contributions statement

Both authors contributed equally to this work. SS and DJE conceived the idea, conducted the field work, analysed the data and wrote the paper

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Table 1. General linear model results (*F*-statistics) for the effects of increasing shrub cover, grazing intensity (low, high) and microsite (shrub, open), and their two-way interactions, on a range of biocrust attributes. There were no significant grazing by shrub cover effects or significant three-way interactions. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Biocrust attributes	Shrub cover	Grazing	Microsite	Cover x Microsite	Grazing x Microsite
Biocrust richness	6.73*	0.49	97.21***	4.62*	4.15*
RaoQ	6.80*	3.25	0.01	2.04	4.15*
Functional evenness	2.63	0.11	0.27	1.23	6.00*
Biocrust cover	6.64*	0.19	9.94**	3.51	0.38
Importance of competition	0.12	1.65	0.56	1.51	1.24
Competition intransitivity	11.20**	0.97	22.80**	6.90*	1.16
Composition (MDS1)	5.97*	0.32	64.30***	3.53	2.23

Table 2. Biocrust taxa that are significantly associated with open microsites using Indicator Species Analysis Species Analysis. IV = Indicator Value. No species were significant indicators of shrub patches.

Species	Type	IV	P
<i>Gigaspermum repens</i>	Moss	0.89	0.001
<i>Didymodon torquatus</i>	Moss	0.87	0.001
<i>Heppia despreauxii</i>	Lichen	0.82	0.001
<i>Stonea oleaginosa</i>	Moss	0.80	0.002
<i>Collema coccophorum</i>	Lichen	0.79	0.003
<i>Gemmabryum pachytheca</i>	Moss	0.79	0.018
<i>Tortula atrovirens</i>	Moss	0.77	0.006
<i>Psora crystallifera</i>	Lichen	0.71	0.010
<i>Crossidium gehepii</i>	Moss	0.64	0.005
<i>Gonomitrium acuminatum</i> subsp. <i>enerve</i>	Moss	0.62	0.004
<i>Psora decipiens</i>	Lichen	0.59	0.032
<i>Placidium squamulosum</i>	Lichen	0.58	0.032
<i>Endocarpon simplicatum</i> var <i>bisporum</i>	Lichen	0.55	0.046
<i>Phascum robustum</i>	Moss	0.52	0.042
<i>Crossidium davidaii</i>	Moss	0.46	0.027

Table 3. Standardized total effects (sum of direct and indirect effects) of grazing and shrub cover on measures of biocrust diversity and composition, for shrub and open microsites, separately. Underlining indicates that trends for 1) functional evenness for grazed sites, and 2) functional diversity (RaoQ) for shrub cover, differ markedly between shrub and open.

Biocrust attributes	Shrub microsites		Open microsites	
	Grazing	Shrub cover	Grazing	Shrub cover
Richness	-0.22	0.51	-0.27	0.31
Functional evenness	0.03	-0.21	0.35	-0.23
RaoQ	0.25	0.28	0.27	-0.23
MDS1	0.01	0.36	0.04	0.33

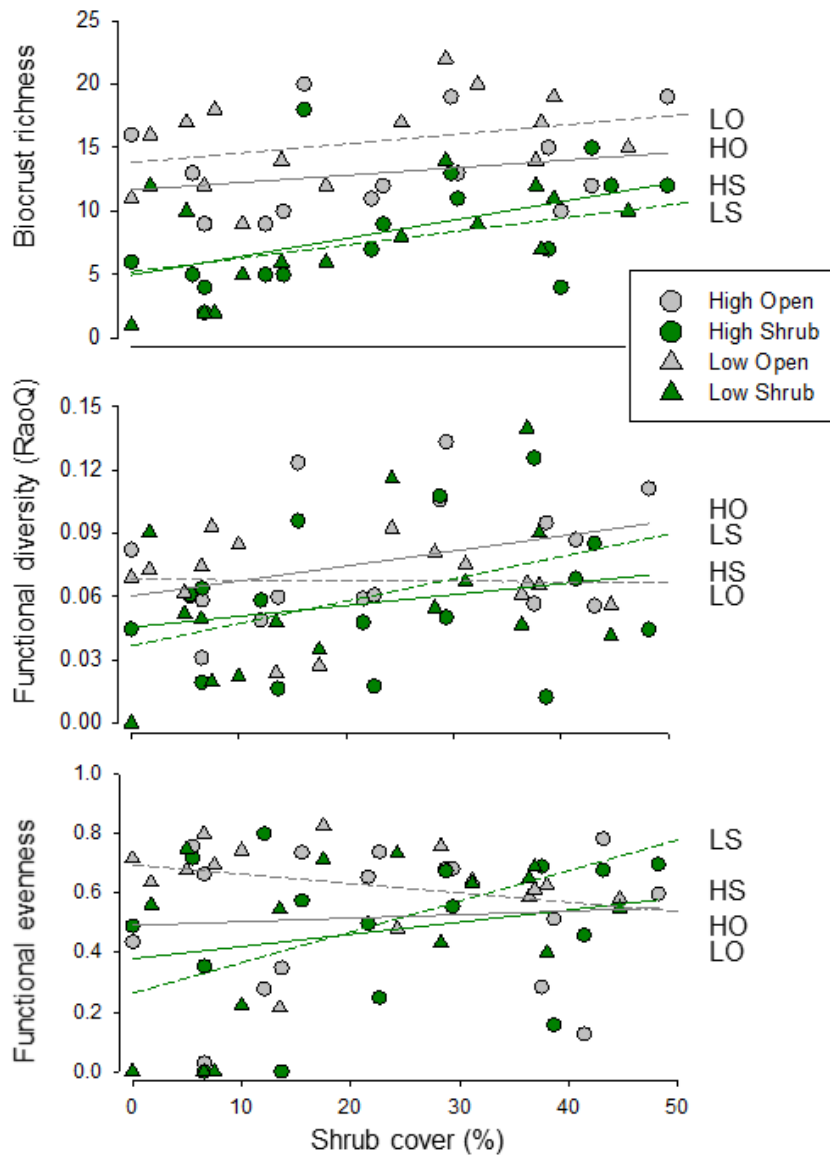


Figure 1. Biocrust diversity attributes (species richness, functional diversity and evenness) in relation to increasing shrub cover for open and shrub microsites under low and high grazing.

HS = high grazing shrub, LS = low grazing shrub, HO = high grazing open, LO = low grazing open. Statistical results associated to these graphs can be found in Table 1.

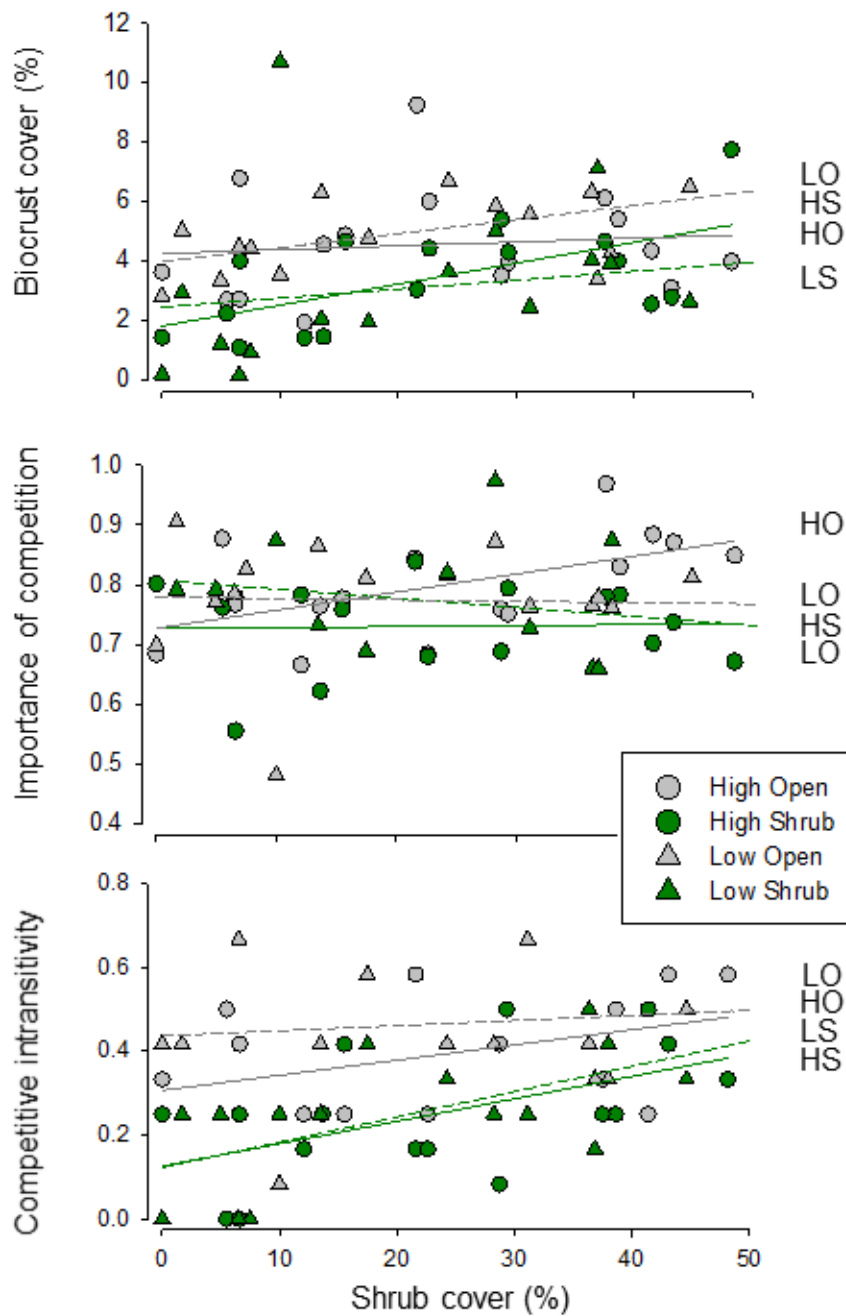


Figure 2. Biocrust community attributes (cover, importance of competition, and degree of intransitivity) in relation to increasing shrub cover for open and shrub microsites under low and high grazing. HS = high grazing shrub, LS = low grazing shrub, HO = high grazing open, LO = low grazing open. Statistical results associated to these graphs can be found in Table 1.

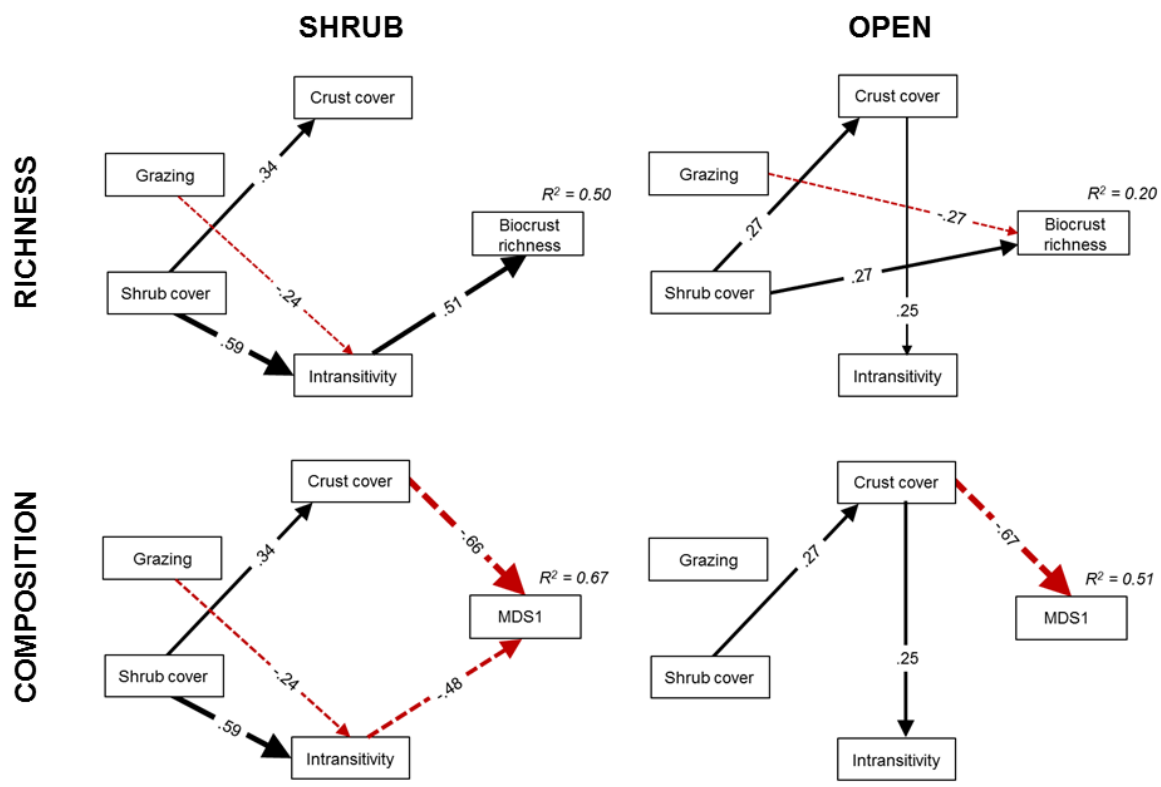


Figure 3. Structural equation models depicting the effects of grazing, shrub cover, crust cover and intransitivity on biocrust richness, composition (first nMDS axis), functional diversity (RaoQ) and evenness. Data are divided in shrub and open microsites. The width of arrows is proportional to the path coefficient, with continuous (positive) and dashed (negative) lines indicating the sign of the relationships. The strength of the path coefficient is superimposed upon each pathway. Non-significant pathways have been omitted for clarity. The R^2 value indicates the amount of variance in functional diversity or crust richness explained by the particular model. Goodness-of-fit metrics were well above $P > 0.05$ in all cases ($P [\chi^2] > 0.2$, P [Bollen-Stine] > 0.10 in the four models shown).

EVENNESS

RAOQ

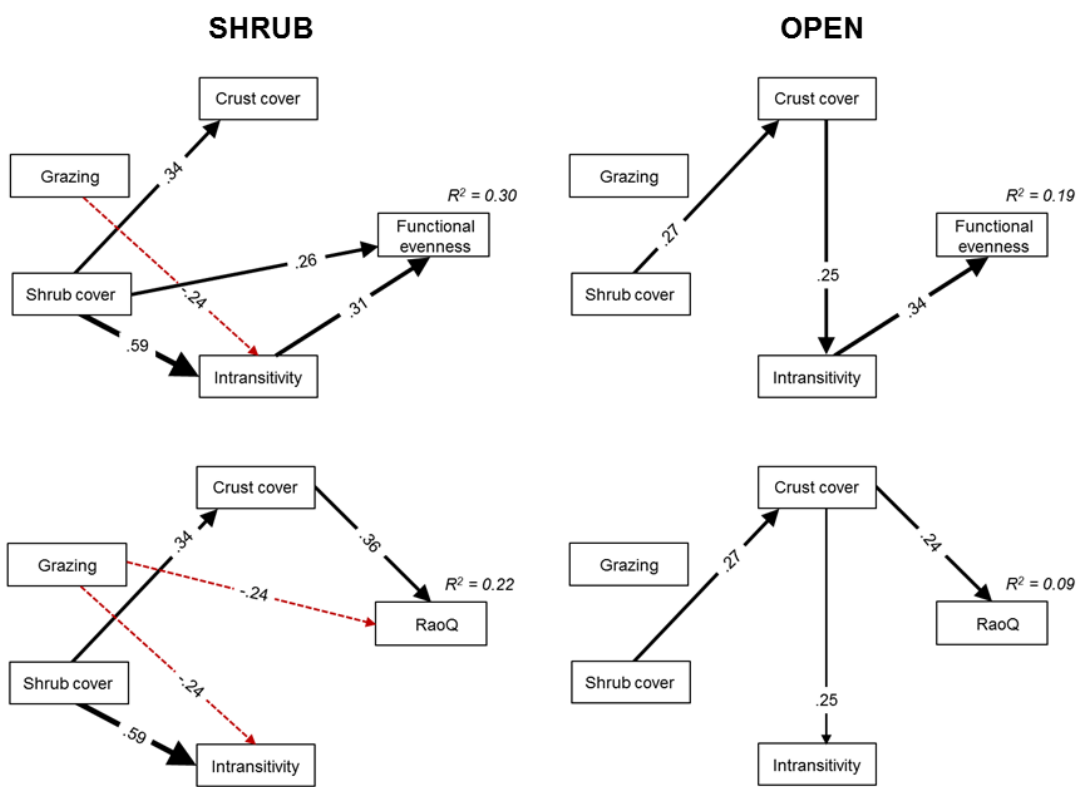


Figure 4. Structural equation models depicting the effects of grazing, shrub cover, crust cover and intransitivity on biocrust richness, composition (first nMDS axis), functional diversity (RaoQ) and evenness. Data are divided in shrub and open microsites. The width of arrows is proportional to the path coefficient, with continuous (positive) and dashed (negative) lines indicating the sign of the relationships. The strength of the path coefficient is superimposed upon each pathway. Non-significant pathways have been omitted for clarity. The R^2 value indicates the amount of variance in functional diversity or crust richness explained by the particular model. Goodness-of-fit metrics were well above $P > 0.05$ in all cases ($P [\chi^2] > 0.2$, P [Bollen-Stine] > 0.10 in the four models shown).