



Biotic and abiotic effects on biocrust cover vary with microsite along an extensive aridity gradient

Jingyi Ding · David J. Eldridge

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Abstract

Aims Biocrusts are globally distributed and important for sustaining critical ecosystem functions. Little is known about their continental drivers and how smaller-scale microsite differences might affect biocrusts along aridity gradients. This limits our ability to manage biocrusts effectively under drier climates.

Methods We collected data on biocrust cover, biotic (plants, litter, grazing intensity) and abiotic (soil texture, soil stability and integrity) attributes from four microsites (trees, shrubs, grasses, open) at 150 sites along an extensive aridity gradient in eastern Australia.

Results At the sub-continental scale, average biocrust cover increased with declining litter cover, and crust cover became more variable with increasing aridity. Biocrust cover was greatest in open microsites and least under trees, and differences were related to the effects of soil texture, vegetation and grazing intensity, which either increased or declined with increasing aridity.

Conclusions Our study reveals that biotic and abiotic effects on biocrust cover vary at different spatial scales along an aridity gradient. Predicted increases in aridity in eastern Australia will likely enhance biocrust cover whereas microsite-level effects are likely to be driven by land management actions such as vegetation removal and overgrazing.

Keywords Biological soil crust · Climatic gradient · Soil surface condition · Grazing · Vascular plants · Spatial scale

Introduction

Soil surfaces, stabilized by vascular plants and biocrusts, are extremely important for supporting terrestrial productivity and for global sustainability, but are threatened by climate change, resulting in soil erosion, land degradation and desertification under increasing aridity (Dai 2013; Garcia-Pichel et al. 2013). Biocrusts dominated by lichens, bryophytes, and minute organisms such as cyanobacteria, bacteria and fungi are common biotic component that are found on the surface of the soil across terrestrial biomes (Belnap 2003; Delgado-Baquerizo et al. 2016; Eldridge and Greene 1994). In drylands, they account for almost 70% of the biotic cover (Rutherford et al. 2017; Ferrenberg et al. 2017). Biocrust communities support numerous ecosystem functions, mitigate the impact of increasing dryness on ecosystem processes, and protect soils from degradation (Concostrina-Zubiri et al. 2017; Delgado-Baquerizo

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J. Ding (✉) · D. J. Eldridge
Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia
e-mail: jingyi.ding@student.unsw.edu.au

D. J. Eldridge
e-mail: d.eldridge@unsw.edu.au

et al. 2016). Over the past decade, biocrust research has tended to focus on their effects on ecosystem functions, the impacts of land use intensification such as grazing and vegetation removal, and their roles in soil restoration (Daryanto et al. 2013; Delgado-Baquerizo et al. 2016; Zaady et al. 2013). While a great deal is known about the global distribution of biocrust cover (Rodríguez-Caballero et al. 2018), we know less about the continental drivers of biocrust cover, and how smaller-scale microsite effects (e.g. different microclimate caused by vegetation type, microtopography; Bowker et al. 2006) might vary across larger gradients. This knowledge is important, because land use changes that involve soil disturbance and vegetation removal have the capacity to reduce suitable biocrust habitat, with potential impacts on soil functions such as hydrology, nitrogen fixation, surface integrity and the provision of habitat for microbes (Darby and Neher 2016; Eldridge and Greene 1994; Ferrenberg et al. 2006).

Studies of the biogeography of biocrusts suggest that continental shifts in temperature, and the amount and seasonality of precipitation, influence biocrust cover and composition, but most studies have been restricted to regional environmental gradients (Eldridge and Delgado-Baquerizo 2019; Garcia-Pichel et al. 2013; Reed et al. 2012). These relationships are thought to be due to physiological mechanisms or functional traits of the component organisms. For example, rainfall seasonality and the length of dry periods are known to limit the distribution of the soil lichen *Chondropsis semiviridis* in south-eastern Australia by restricting its photosynthetic capacity (Rogers 1971). Aridity can also affect biocrust cover, growth form and reproduction traits, and change the photobiont associated with lichens in the crust (Matos et al. 2015). Climate could also indirectly affect biocrusts across large environmental gradients, by changing how they interact with vascular plants. Thus, as environments become more arid, reduced resource competition from vascular plants, higher light availability, and lower levels of litter cover would favor biocrusts (Garcia-Pichel et al. 2013; Muñoz-Martín et al. 2019; O'Bryan et al. 2009). Differences in soil properties such as substrate type, clay content or soil moisture can also drive large-scale changes in biocrust cover (Büdel et al. 2009; Concostrina-Zubiri et al. 2014; Grishkan et al. 2006). Many of these studies, however, have focused on relatively short gradients in biotic and abiotic factors (e.g. soil properties,

disturbance level, vascular plants), so it remains unclear how changes along continental or extensive sub-continental gradients might affect biocrust cover.

Vascular plant cover is known to decline in response to continental shifts in climate (e.g. aridity), so that the distribution of biocrusts is likely complicated by smaller-scale microsite effects driven by changes in vascular plant cover (Bowker et al. 2016). Plants are known to suppress the development of biocrusts in more mesic areas, but an increasing body of evidence suggests that they may have strong facilitatory effects on biocrusts in drier environments (Concostrina-Zubiri et al. 2014; Maestre et al. 2009). Perennial plants can buffer environment stresses by reducing fluctuations in temperature and soil moisture, capturing resources, such as aeolian dust, or preventing the ingress of herbivores that trample biocrusts (Eldridge et al. 2006; Maestre 2003; Ochoa-Hueso et al. 2018; Soliveres and Eldridge 2020). Any effects of vegetation might be expected to vary with microsites, but there is little information on such effects. Exploring how small-scale effects of different microsites might change along extensive environmental gradients would help us to improve our prediction of how the distribution of biocrusts might change under predicted drier climates, and identify those microsites that might act as biocrust refugia under warmer or drier climates.

Here we describe a study where we explored the continental drivers and changes in biocrust cover in four markedly different microsites (beneath trees, shrubs and grasses, and in open interspaces) along an aridity gradient in eastern Australia that extended from mesic coastal forests to arid open woodlands. We used a combination of regression analyses and structural equation modelling to address two predictions. First, we expected that biocrust cover would increase with increasing aridity across the sub-continental gradient, corresponding to declines in vascular plant cover and therefore reductions in resource competition, and with increasing cover of bare soil that provides suitable habitat for biocrusts (Delgado-Baquerizo et al. 2013; Maestre et al. 2010). Second, we predicted that the magnitude of biocrust cover would differ among the four microsites due to marked differences in biotic (litter cover, plant cover) and abiotic (soil texture, soil stability, disturbance intensity) conditions among microsites (Bowker et al. 2016; Vandendorj et al. 2017).

Methods

Study area

Our study was conducted along an extensive aridity gradient in eastern Australia, extending 1500 km from the east coast to the dry interior (29.0°S – 35.1°S, 140.7°E – 151.4°E; Fig. 1). The gradient covered humid, dry sub-humid, semiarid and arid zones. Average annual rainfall varied from 1299 mm on the coast to 184 mm in the interior. Rainfall seasonality varied from summer dominant in the north-east, to uniform in the centre, predominantly winter dominant in the south-west, and low rainfall in the north-west (Bureau of

Meteorology 2019). The average annual temperature varied from 13 °C – 21 °C, with diurnal temperatures typically hot in summer (>30 °C) and mild in winter (>10 °C) (Bureau of Meteorology 2019). Soils across the survey area ranged from heavy clays to clayey sands, with soil pH generally increasing, but total soil carbon and nitrogen declining, with increasing aridity. Vegetation communities across the gradient were highly variable, ranging from coastal forest to semiarid woodlands to arid shrublands dominated by *Eucalyptus* spp., *Callitris* spp., *Acacia aneura*, accompanied by grasses (e.g., *Lomandra* spp., *Aristida* spp., *Austrostipa* spp., *Enteropogon* spp.) and shrubs (e.g. *Persoonia* spp., *Leptospermum* spp., *Acacia* spp., *Dodonaea* spp.,

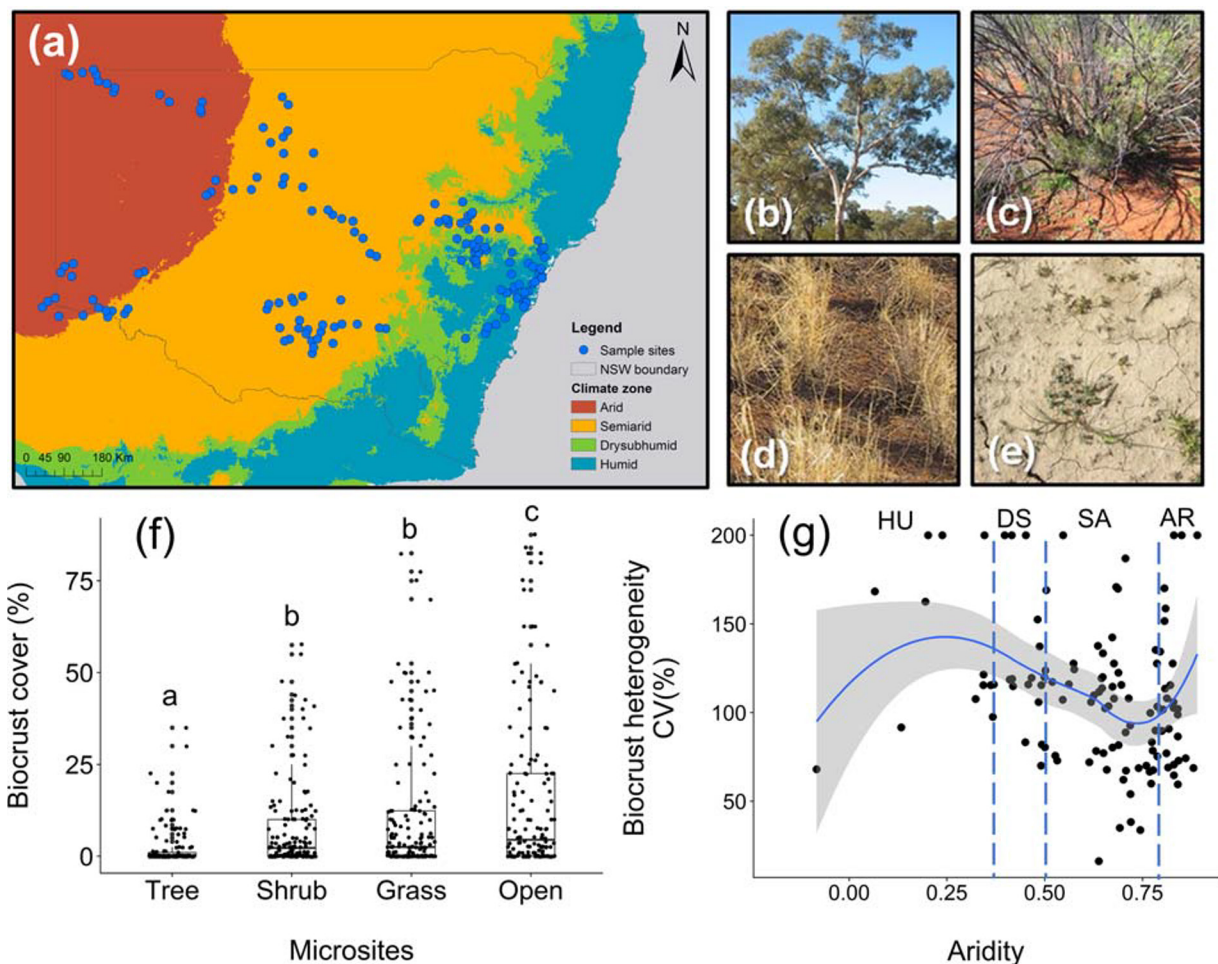


Fig. 1 (a) Location of the 150 sample sites in relation to aridity, and images of (b) tree, (c) shrub, (d) grass, (e) open microsite; (f) box plots and scatter points for biocrust cover in the four microsites; the inside horizontal line represents the median value and the vertical line outside the box indicates the variability outside the upper and lower quartiles (box edges); different letters

indicate a significant difference at $P < 0.05$; (g) heterogeneity of biocrust cover along the aridity gradient. NSW, New South Wales, Australia; CV%, coefficient of variation; blue solid line is loess regression fit curve and the blue vertical broken lines are the boundaries of climatic zones (HU - humid zone; DS - dry subhumid zone; SA - semiarid zone; AR - arid zone)

Eremophila spp.) with vascular plant density and richness declined with increasing aridity (Table S1 in Appendix S1). Biocrusts ranged from moss-dominated mats (e.g. *Campylopus* spp., *Funaria* spp.) in mesic areas, to lichen-dominated biocrusts in dry subhumid and semi-arid environments (*Diploschistes thunbergianus*, *Placidium* spp., *Endocarpum* spp., *Psora decipiens*, *Xanthoparmelia* spp.). In arid areas, biocrusts were dominated by a sparse cover of cyanolichens (*Peltula* spp., *Collema* spp.) and cyanobacteria (Eldridge and Tozer 1997).

Field survey

We sampled across the four aridity zones (Aridity ranges from -0.2 to 0.9), with generally more sites sampled in the semiarid area due to its larger spatial proportion (Fig. 1). Aridity was determined as $1 - \text{Aridity Index (AI)}$, where $\text{AI} = \text{precipitation/potential evapotranspiration}$ (United Nations Environment Programme 1992). Data on the AI were obtained from Consortium for Spatial Information (CGIAR-CSI) for the 1950–2000 period (Zomer et al. 2008) (<http://www.cgiar-csi.org/data/global-aridity-and-pet-database>). Along the aridity gradient, 150 sites were totally sampled in the humid ($n = 30$ sites), dry sub-humid ($n = 30$ sites), semi-arid ($n = 60$ sites), and arid ($n = 30$ sites) areas. To control for the confounding effects of climate variability (i.e., rainfall variability, temperature variability) and overgrazing along the aridity gradient, we sampled sites in areas with a low rainfall and temperature variability (coefficient variation, $\text{CV} < 30\%$), and focused our site selection on conservation areas (i.e., national parks, state forests, traveling stock reserves) where the vegetation communities are subjected to low levels of grazing intensity. To avoid the effect of other disturbances (e.g., wildfires, vehicle tracks) on biocrust cover, we surveyed in natural areas that naturally had been unburned in the past 30 years and were away from major tracks.

Data were collected between February 2018 and August 2019. At each site, geography information was recorded using a Garmin Montana 680 T (Garmin Corp.,

Olathe, KS, USA), and the condition of the soil surface assessed beneath trees, shrubs, grasses and in the open using small circular quadrat (64 cm diameter). Quadrats were placed under the dominant plant species found at each site. For trees, eucalypts were chosen across the whole gradient, but shrub species varied from *Acacia* and *Banksia* species in mesic areas, to

Eremophila and *Dodonaea* in arid environments. Because there was no single grass species that spanned the entire gradient, we sampled under different species across the gradient. Soil surface condition was assessed by recording the status of soil surface attributes (Tongway 1994). This procedure has been used extensively across a range of environments to identify how well surface soils function in terms of nutrient cycling (Eldridge et al. 2019), water flow and soil stability (Eldridge et al. 2017). In each quadrat, we assessed nine attributes: (1) the total cover of biocrusts, including cyanobacteria, fungi, lichens, and mosses, (2) soil stability (the stability of surface soil aggregates assessed using the Slake Test, Emerson 1967; 0 = not applicable, 1 = very unstable, 2 = unstable, 3 = moderately stable, 4 = very stable), (3) soil integrity (the cover of eroded soil surface; 1 = $> 50\%$, 2 = 20–50%, 3 = 10–25%, 4 = $< 10\%$), (4) plant cover (projected foliage cover of groundstorey perennial and annual plants in the quadrat; 0–100%), (5) plant richness (total number of vascular plants), (6) litter cover (0–100%), (7) litter depth (mm), (8) soil sand content based on categorical values of soil texture, with higher value indicating greater sand content (1 = silty to heavy clay, 2 = sandy clay loam to sandy clay, 3 = sandy to silty loam, 4 = sand to clayey sand). We also counted the dung of all herbivores within the quadrats to obtain a measure of (9) recent grazing intensity. We removed litter from the soil surface to assess groundstorey plants and biocrusts after measuring litter attributes. To estimate the grazing intensity, we used the relationship between dung counts and the dry mass of dung of each herbivore (Eldridge et al. 2017) to calculate the dry mass of herbivores per hectare, and classified it into three categories: (1) ungrazed (no dung), (2) low grazing (dung dry mass $< 15 \text{ kg ha}^{-1}$), (3) moderate grazing (dung dry mass $> 15 \text{ kg ha}^{-1}$). Kangaroos (74%) and to a lesser extent, feral goats (18%) were the two main herbivores at our sites. Kangaroos exert a lower pressure on the soil surface than livestock (Bennett 1999). We sampled two replicates of each microsite and averaged the values of each attribute.

Statistical analysis

We used statistical tests and regression analyses to explore the variability of biocrust cover at the site scale and along environmental gradient. First, we used linear models to test for potential differences among the four microsites (tree, shrub, grass and open) then used the

post-hoc Fisher's Least Significant Difference (LSD) test to examine where differences occurred and where a significant microsite effect was detected. We then calculated the variability in biocrust cover (% coefficient variation, CV) among the four microsites at each site and used a loess regression to detect the pattern of variability along the aridity gradient. We used piecewise linear regression to explore the magnitude of change in biocrust cover along continuous gradients in aridity, plant cover and litter cover. Quantile regression (95th and 5th percentile) was used to fit the boundaries of biocrust cover along these continuous gradients. Both piecewise regression and quantile regression are widely used in ecology to illustrate changes in linear relationships and quantify the boundaries of scatter points against environment gradients (Scharf et al. 1998). Linear regression models were then used to explore changes in biocrust cover with categorical levels of soil sand content. Analyses were performed using 'quantreg', 'tidyr' and 'ggplot2' packages in R 3.4.1 version (R Core Team 2018).

We used Structural Equation Modelling (SEM; Grace 2006) to explore the direct and indirect effects of biotic (i.e. litter cover and depth, plant cover and plant richness) and abiotic attributes (i.e. aridity, soil sand content, soil stability, soil integrity and grazing intensity) on biocrust cover in tree, shrub, grass and open microsites. We developed an *a priori* model of how we expected these biotic and abiotic factors to influence biocrust cover (Fig. S1 in Appendix S2). Among factors included in the model, aridity was used to represent the impact of climate, and soil sand content (sand) used to indicate the impact of soil texture. We used litter cover, litter depth, soil stability and soil integrity as measures of soil surface condition. Plant cover and plant richness were used to illustrate the effect of vascular plants and we used grazing intensity to explore the impact of recent grazing on biocrust cover. In this *a priori* model, we predicted that aridity would have a direct effect on biocrust cover, as well as indirect effects mediated by soil sand content, grazing intensity, plants or soil surface conditions. We expected that grazing and soil sand content would either directly affect biocrust cover or indirectly affect biocrusts by influencing soil surface condition and the development of vascular plants. Plant cover and richness have been shown to reduce biocrusts directly due to resource competition (Havrilla et al. 2019) and we also expected an indirect effect of vascular plants by affecting soil surface condition (e.g., soil

stability). Overall goodness-of-fit probability tests were performed to determine the absolute fit of the best models, using the χ^2 statistic. The goodness of fit test is used to estimate the likelihood of the observed data given an *a priori* model structure. Thus, high probability values indicate that these models have highly plausible causal structures underlying the observed correlation. Models with low χ^2 and Root Mean Error of Approximation (RMSEA < 0.05) and high Goodness of Fit Index (GFI) and R^2 were selected as the best fit model for our data. In addition, we calculated the standardized total effects of each explanatory variables to show the total effect of each variable. Analyses were performed using AMOS 22 (IBM, Chicago, IL, USA) software.

Results

Biocrust cover varies with environment factors

Biocrust cover was greatest in the open ($15.3 \pm 1.8\%$; mean \pm SE), least beneath trees ($2.2 \pm 0.4\%$), and intermediate in grass and shrub microsites (Fig. 1f). Heterogeneity (CV%) in biocrust cover among the four microsites declined from dry subhumid ($123.2 \pm 6.8\%$) to semiarid areas ($100.5 \pm 4.8\%$), but increased in arid areas ($111.6 \pm 8.1\%$) (Fig. 1g).

Biocrust cover increased with increasing aridity, particularly where aridity exceeded 0.25 (i.e. dry subhumid to arid areas; Fig. 2a), with the rate of increase greater in open areas than under shrubs and trees (Table S2, S3 in Appendix S3). Biocrust cover also declined in open, grass and shrub microsites, but not beneath trees, as soils became increasingly sandier (Fig. 2b). Biocrust cover declined with increasing litter cover and plant cover across all microsites, particularly under condition of low litter (< 30%; Fig. 2c) and plant (< 38%; Fig. 2d) cover.

Drivers of biocrust cover across microsites

Aridity and litter cover were the factors that were consistently associated with biocrust cover across all microsites, whereas the effects of soil sand content, grazing intensity and plants differed among microsites. Aridity was indirectly associated with greater biocrusts in two ways. First, increases in aridity suppressed the negative effect of litter cover on biocrust cover in all microsites, or suppressed the negative effect of plant richness in the open only (Fig. 3d). Second, increasing

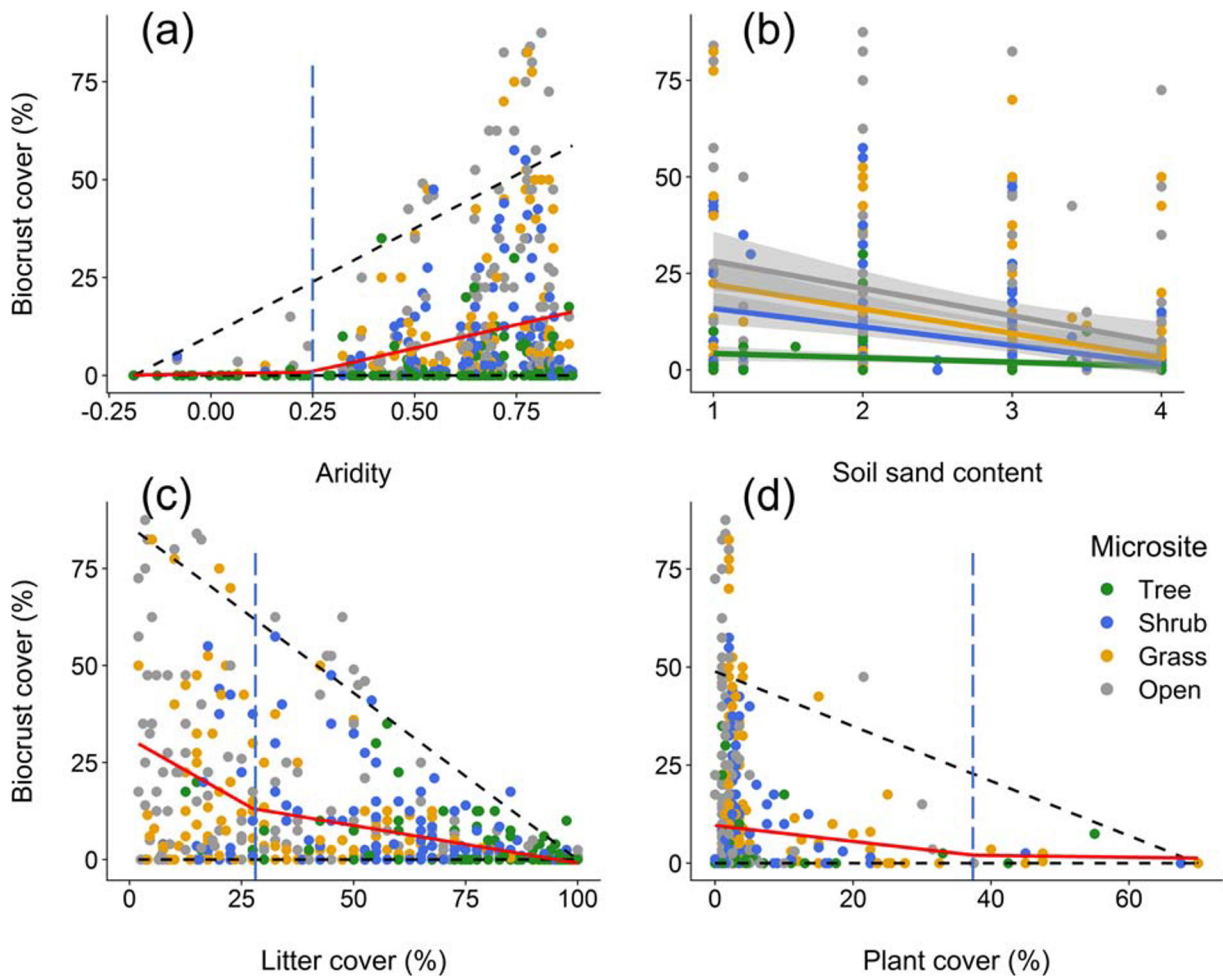


Fig. 2 Biocrust cover changes with (a) increasing aridity, (b) soil sand content, (c) litter cover and (d) plant cover. The red line in Figs. 2a–d represent the curve derived from the piecewise regression and the blue vertical broken line represents the point of

inflection. The black broken lines represent the 95% and 5% percentiles. For Fig. 2b, lines were fitted with linear regression for each microsite

aridity had a positive effect on biocrust cover by enhancing the positive effect of soil stability beneath trees, shrubs and grasses (Figs. 3a–c). These positive effects were mediated by some negative effects of aridity. For example, increasing aridity suppressed the positive effect of soil integrity beneath shrubs and in the open (Fig. 3b, d), while it exacerbated the negative effect of grazing in shrub and grass microsites (Fig. 3b, c).

Among attributes of soil surface condition, litter cover had the strongest effects on biocrusts (standardized total effects [STE] = -0.26 to -0.45 ; Fig. 4), with increasing litter cover associated with strong reductions in biocrust cover across all microsites. However, the effects of soil stability and surface integrity differed among microsites. Increasing biocrust cover was

associated with greater soil stability in grass, shrub and tree microsites (Figs. 3a–c), and greater surface integrity under shrubs and in open microsites (Fig. 3b, d).

Soil sand was negatively associated with biocrust cover directly in shrub and grass microsites (Figs. 3b, c; path coefficients = -0.23 and -0.14 , respectively) and indirectly in tree, shrub and grass microsites through its association with lower soil stability (Fig. 3a–c and 4a–c; STE = -0.10 to -0.32). Similarly, increasing grazing intensity was negatively associated with biocrust cover in shrub and grass microsites (Figs. 3b, 3c; path coefficient = -0.13 and -0.17 , respectively), but reinforced the negative effect of increasing plant richness on biocrust cover in the open (Figs. 3d and 4d; STE = -0.13). Plant cover and richness were generally

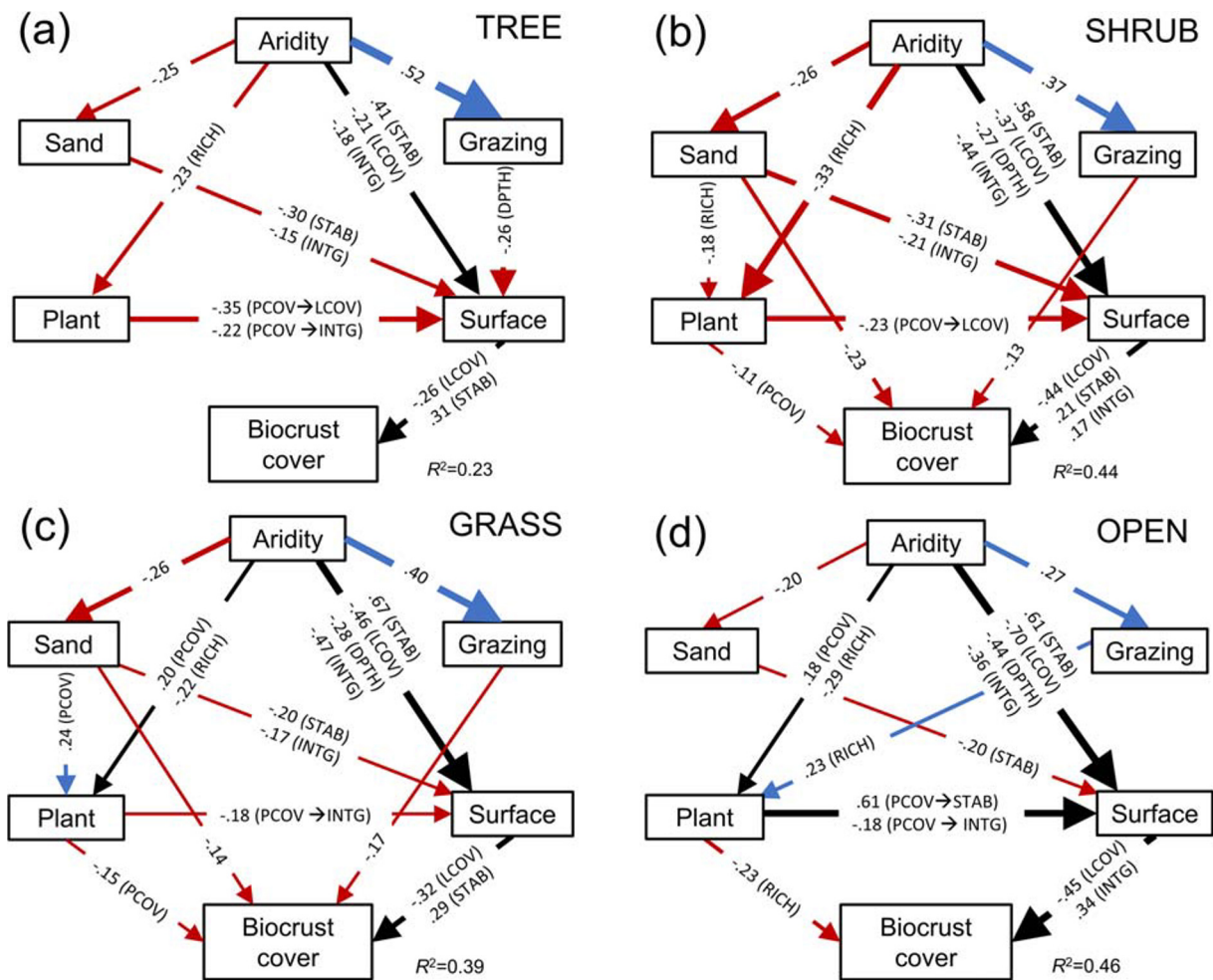


Fig. 3 Structural equation model assessing the indirect and direct effects of aridity, soil sand content (sand), grazing, plant and soil surface condition (surface) on biocrust cover in tree (a), shrub (b), grass (c) and open (d) microsite. ‘Plant’ is represented by plant cover (PCOV) and plant richness (RICH); ‘Surface’, attributes described the soil surface condition, comprises litter cover (LCOV), litter depth (DPTH), soil stability (STAB), soil integrity (INTG). Standardized path coefficients, adjacent to the arrows, are analogous to partial correlation coefficients, and indicative of the effect size of the relationship. The width of arrows reflects the

magnitude of the coefficient. Pathways are significant negative (red unbroken line), significant positive (blue unbroken line) or mixed significant negative and significant positive (black unbroken lines). Non-significant pathways were not shown. Model fit: Tree: $\chi^2 = 8.81$, $df = 4$, $P = 0.07$, $R^2 = 0.23$, RMSEA = 0.09, Bollen-Stine = 0.07. Shrub: $\chi^2 = 3.04$, $df = 4$, $P = 0.55$, $R^2 = 0.44$, RMSEA = 0, Bollen-Stine = 0.53. Grass: $\chi^2 = 8.54$, $df = 4$, $P = 0.07$, $R^2 = 0.39$, RMSEA = 0.09, Bollen-Stine = 0.05. Open: $\chi^2 = 6.00$, $df = 4$, $P = 0.20$, $R^2 = 0.46$, RMSEA = 0.06, Bollen-Stine = 0.24

associated with reduced biocrust cover in shrub, grass and open microsites, either directly, or indirectly, by effect on reduced soil integrity (Fig. 3b-d, Fig. 4b-d).

Discussion

Our study provides strong empirical evidence that biotic and abiotic drivers of biocrust cover vary along an extensive aridity gradient at different spatial scales. At

the sub-continental scale, biocrust cover increased with declining litter cover as aridity increased from humid coastal areas to the dry interior. Variability in biocrust cover declined from dry subhumid to semiarid areas and was regulated by the interactions between vascular plants and biocrusts. At the site level, biocrust cover differed among microsites, consistent with expectation, with the greatest cover in open areas and the least under trees. Our results indicate that variability in biocrust cover among microsites results from the effects of

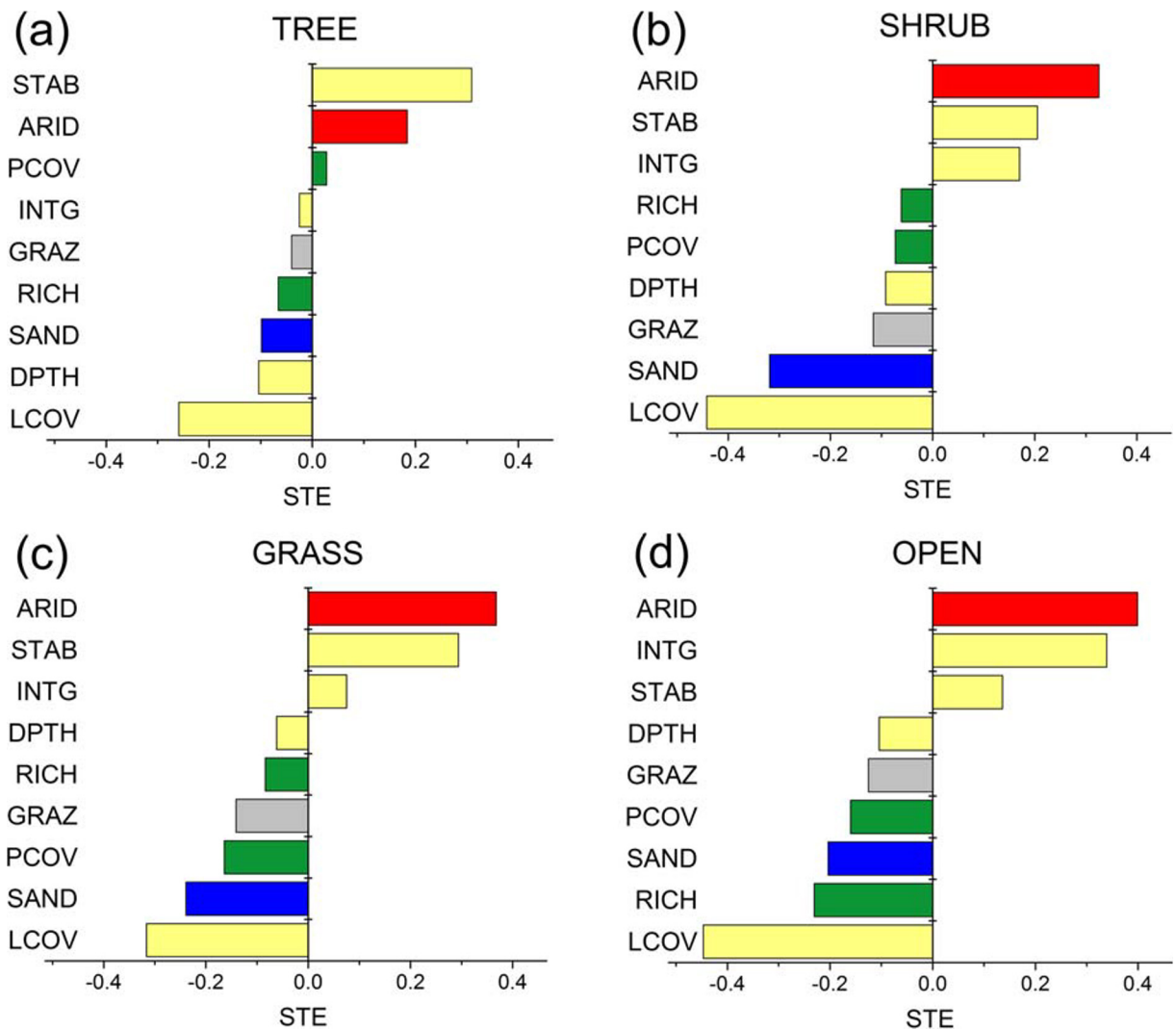


Fig. 4 Histograms illustrate the standardized total effects (STE: sum of direct plus indirect effects) derived from the structural equation modelling in tree (a), shrub (b), grass (c), and open (d) microsite. ARID, aridity; STAB, soil stability; INTG, soil

integrity; GRAZ, grazing intensity; PCOV, plant cover; RICH, plant richness; SAND, soil sand content; LCOV, litter cover; DPTH, litter depth. Different colors represent different group of driving factors (i.e. aridity, sand, grazing, surface, plant)

different drivers; soil texture, vegetation and grazing intensity, with effects either mitigated or enhanced by increasing aridity. For example, soil sand, plant cover and grazing intensity were directly associated with reduced biocrust cover in grass and shrub microsites, and indirectly associated with reduced biocrust cover under trees and in open areas. Our results provide insights into the mechanisms driving biocrust cover at both the microsites and the sub-continental scales along an extensive aridity gradient, improving our understanding of how small- and large-scale variability in biocrust cover may change under future climate change scenarios.

Biotic attributes affect biocrust cover at different spatial scales

Biotic attributes (i.e. litter cover, plant cover and richness) affected biocrust cover at both small (microsite) and large (sub-continental) scales, with increasing litter cover reducing biocrust cover consistently across all microsites. Litter cover is likely to have an effect on the microenvironment (e.g. light, moisture, temperature) of biocrusts, with small amounts of litter promoting biocrust growth by buffering environmental stresses (e.g., heat and drought stress) (Belnap et al. 2016;

Serpe et al. 2013). But this effect diminishes with increasing litter quantity (Xiong and Nilsson 1999). For example, burial beneath litter can restrict the growth of biocrust organisms by reducing light exposure and inhibiting its metabolisms (e.g. photosynthesis, respiration), which eventually kills biocrusts through light deprivation (Briggs and Morgan 2008). Litter might also be associated with increased disturbance, such as increased invertebrate activity (e.g. termites, litter-borne arthropods) or create conditions for the spread of wild-fire (Boeken and Orenstein 2001; Serpe et al. 2013; Whitford et al. 1992).

Our results demonstrated that an increase in litter cover would reduce biocrust cover, particularly over 30% of litter cover (Fig. 2c). Despite the positive association between the overstorey plant community and litterfall, litter cover is more likely related to site-level ecosystem productivity (Catovsky et al. 2002), which is regulated by large-scale environmental factors such as rainfall and temperature. For example, we found that the suppressive effect of litter cover was mediated as sites become more arid. As aridity increases, litter supply declines with reductions in plant cover, allowing greater penetration of light to the soil surface and increasing surface niches for biocrust colonization (Belnap 2003; Delgado-Baquerizo et al. 2013). However, the increase in biocrust cover with aridity may be accompanied by reductions in biocrust diversity as the response of biocrusts is highly species specific (Maestre et al. 2015; Mallen-Cooper et al. 2018). For example, a European study found that crustose and fruticose lichens were restricted to more mesic areas than foliose species (Matos et al. 2015), and a global study showed that aridity was negatively related to fungal, but not moss, richness (Delgado-Baquerizo et al. 2018).

Vascular plants coexist with biocrusts at local scales by creating mosaics of vegetation interspersed with biocrust-covered microsites (Maestre et al. 2010; Zhang et al. 2016) as the result of competition and facilitation (Havrilla et al. 2019). In our study, we found that biocrust cover was correlated with declining vascular plant cover in shrub and grass microsites. Small patches of vascular plants could benefit biocrusts by reducing evaporation and increasing water availability (Martínez et al. 2006). However, these facilitatory effects would become negative when increasing plant cover intensifies resource competition, reduces light availability and niches for biocrust establishment (Dettweiler-Robinson et al. 2018; Durham et al. 2018),

particularly when plant cover exceeded about 40% (Fig. 2d). Conversely, biocrust cover in open microsites declined with increasing plant richness, which could intensify resource competition (e.g. water, nutrition) between vascular plants and biocrusts under conditions of scarce resources (e.g., low moisture, low soil nutrition). These negative effects were mitigated as conditions became drier, providing support for the notion that the interaction between vascular plants and biocrusts promotes their coexistence under conditions of increasing dryness (Miller and Damschen 2017; Zhang et al. 2016).

Interactions among vascular plants and biocrusts also regulate the variability in biocrust cover among microsites along the aridity gradient. In humid areas, vascular plants dominate the community, with enclosed canopies, deep contiguous litter, and low light availability, which restrict biocrusts to small open patches (Belnap et al. 2016; Jia et al. 2019), resulting in high variability among microsites. In arid areas, biocrusts have a competitive advantage over vascular plants due to their high tolerance to desiccation, extremes of temperature, and light, allowing them to occupy microsites that would not support vascular plants (Belnap 2006). By comparison, facilitatory and competitive effects of vascular plants on biocrusts are more likely to be neutral in dry subhumid and semiarid regions. An extensive cover of biocrusts can benefit vascular plants by increasing the availability of runoff water and by reducing evaporation (Chamizo et al. 2016), but these facilitatory effects will decline with increases in vascular plants as patches of bare soil, and therefore runoff, decline. This feedback process enables biocrusts to coexist with vascular plants, reducing the variability in biocrust cover among microsites (Belnap 2003; Delgado-Baquerizo et al. 2013).

Abiotic attributes regulate biocrusts differences among microsites

Soil texture plays an important role in determining the fine-scale distribution of biocrusts (Belnap et al. 2016) as it affects soil surface stability and the capacity to retain moisture (e.g., infiltration, water-holding capacity; Noy-Meir 1973). In our study, sand content reduced biocrust cover either directly, in shrub and grass microsites, or indirectly, by reducing soil stability and integrity in tree, shrub and grass microsites. The addition of fine particles to the soil can increase biocrust development and soil stability (Felde et al. 2018),

whereas sandy soils, often colonized by cyanobacteria, are more susceptible to disturbance in drier environments (Chung et al. 2019). We found that the negative effects of increasing sand content were mediated by increasing aridity. In drier environments, overstorey canopies buffer the variability in environmental stressors (e.g., high evaporation, light damage, extreme temperatures; Li et al. 2010), minimise soil disturbances (e.g., wind and water erosion; Maestre 2003) and capture limited resources (e.g., fine soil particles, water, nutrients; Ochoa-Hueso et al. 2018), further stabilizing the soil surface and providing suitable conditions for biocrust development (Belnap et al. 2016). We did not detect any significant effect of soil texture on biocrust cover in the open, with sand content only weakly affecting soil stability. This might be explained by the fact that open microsites are more often disturbed by livestock trampling or more susceptible to wind and water erosion than biocrusts beneath the protective cover of plants. Thus, the potential impact of disturbance and erosion on soil stability may outweigh the influence of soil texture in open microsites (Belnap and Gillette 1998), resulting in the weak effect of sand on biocrust cover that we found.

Negative effects of grazing on biocrusts under grasses and shrubs

Grazing intensity affects the fine-scale distribution of biocrust cover by trampling and surface disturbance, which varies among microsites. We found that grazing generally reduced biocrust cover in grass and shrub microsites, consistent with abundant literatures on the effects of grazing-induced disturbance on biocrusts (Concostrina-Zubiri et al. 2017; Daryanto and Eldridge 2010; Eldridge et al. 2017; Velasco Ayuso et al. 2019). Such a negative effect on biocrusts was exacerbated as grazing intensity increased with aridity, resulting in greater herbivory and trampling on shrub and grass microsites in drier areas. Increasing grazing was also indirectly associated with reduced biocrust cover in the open, via an increase in the suppressive effect of plant richness, which would intensify resource competition (i.e. water, nutrition) and restrict the growth of biocrusts (Belnap 2003; Reisner et al. 2013). We failed to find any significant effects of grazing on biocrust cover beneath trees, potentially due to the weak effect of herbivory and trampling beneath trees or the fact that sites beneath trees are rarely preferred habitats for biocrusts.

Compared with shrub and grass microsites, trees had sparse groundstorey plant cover, fewer palatable species and therefore, a lower level of herbivory. Further, high levels of litter cover (80% on average; Fig. S2 in Appendix S4) would mitigate any negative effect of trampling or resting by herbivores on the soil surface (Li et al. 2014), thereby resulting in a weak effect of grazing on biocrust cover.

Concluding remarks

Our study indicates that different biotic and abiotic attributes are associated with biocrust cover at microsite and sub-continental scales along an aridity gradient, suggesting that environmental changes resulting from an increase in aridity could produce very different outcomes at the two spatial scales. Based on our results, it is likely that projected increases in dryness under current climate change scenarios will increase biocrust cover across the continent, possibly with a more homogeneous biocrust composition and therefore reduced function, as suggested by continental research (Delgado-Baquerizo et al. 2018). Changes in biocrust cover among microsites are more likely related to uncertain changes in grazing intensity under climate change. Although increasing dryness is predicted to reduce the amount of land available to support livestock grazing (Mysterud et al. 2001), increasing pressure on a smaller land base will likely intensify any negative effects of grazing (Cobon et al. 2009). The combination of increasing dryness and more intensive livestock grazing is likely to reduce biocrust cover, composition and function (Mallen-Cooper et al. 2018), particularly in grass and shrub microsites, leading to increased soil degradation in drylands (Concostrina-Zubiri et al. 2017) and potentially, lower inputs of soil nitrogen (N) from N-fixing biocrusts (Eldridge et al. 2017; Delgado-Baquerizo et al. 2016). Future land management decisions should consider the effects of grazing intensity on biocrusts, which are critically important for maintaining a range of essential ecosystem services and functions in drylands.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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