

Biocrust functional traits reinforce runoff-runoff patchiness in drylands

David J. Eldridge^a, Max Mallen-Cooper^{a,b}, Jingyi Ding^{a,*}

^a Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia

^b Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia

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ABSTRACT

Spatial patchiness in resources is a pervasive feature of drylands worldwide. This patchiness manifests itself as two distinct geomorphic zones that are characterised by the loss (runoff) or gain (runon) of resources such as water, seed and organic matter. Most studies have examined how vascular plants vary across these two distinct zones, but there are few studies of the non-vascular components of these patterned landscapes. We examined the distribution of soil crust lichens and bryophytes (moss, liverworts) in relation to three geomorphic positions within a patterned *Acacia aneura* woodland grazed by sheep and kangaroos. We found that the distribution of biocrust taxa was strongly related to geomorphic position, with lichens dominating the runoff zones and liverworts restricted to the runon areas (groves). The runon zones were characterised by a greater cover of litter, and greater species richness, cover, and functional richness of biocrusts, while biocrusts in the runoff zones had greater functional diversity and dispersion. Importantly, biocrusts growing in the runon areas were taller, had shorter rhizines, and a greater capacity to trap sediment and absorb water. There were no effects of grazing intensity nor herbivore type (sheep *cf.* kangaroo) on any diversity or functional measures of biocrusts. Overall, our study indicates that the functional attributes of biocrusts align with those reported for vascular plants (e.g., perennial grasses), by affecting hydrological processes and sediment capture, albeit at smaller spatial scales. Biocrusts may be important, therefore, for sequestering small falls of water emanating from resource-shedding zones, thereby reinforcing landscape patchiness, particularly as hotter and drier climates reduce the cover of vascular plants in drylands.

1. Introduction

Empirical data and theoretical predictions indicate that global drylands are strongly patterned, at different spatial scales ranging from that of individual plants to entire landscapes (Thiery et al., 1995). At landscape scales, this patterning resembles stripes, bands and stipples, which represent patches of perennial vegetation that function as resource sinks. These systems are maintained by the redistribution of resources such as water, sediment, organic matter and nutrients (White, 1969; Montaña, 1992). These resource accumulating zones (runon zones or resource sink zones) occur at lower landscape positions, and are separated by extensive, gentle slopes that shed resources (runoff zones or resource source zones). This strong vegetation patterning is driven mainly by differences in geomorphology, particularly slope, and water movement through processes of runoff and runon, with runoff and sediment removal from upslope areas captured by the vegetated patches downslope (Thiery et al., 1995). Feedbacks between soil and vegetation

lead to strong controls on landscape function and therefore ecosystem diversity and productivity (Ludwig et al., 1997; Hiernaux and Gérard, 1999; López-Portillo and Montaña, 1999).

Vegetation type and density vary markedly between the two geomorphic zones, with runon zones supporting dense patches or groves of woody vegetation, and runoff zones characterised mainly by open savannah, with a variable cover of perennial grasses. Such environments include dense stands of *Combretum* trees in West Africa (Thiery et al., 1995), mulga (*Acacia aneura*) savanna (Tongway and Ludwig, 1990) and chenopod (*Atriplex*, *Maireana*) shrublands in eastern Australia (Dunkerley and Brown, 1995), and various shrub-grassland systems dominated by *Prosopis*, *Flourensia* and *Larrea* species in North America (Schlesinger et al., 1990; López-Portillo and Montaña, 1999; Montaña et al., 2001).

Despite the well-known roles of vascular plant communities in drylands, the more diminutive and often overlooked components of patterned landscapes are biocrusts. These communities comprise a rich

* Corresponding author.

E-mail address: jingyi.ding@student.unsw.edu.au (J. Ding).

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assemblage of lichens, mosses, liverworts and minute organisms such as fungi and bacteria growing on the near surface soil layers (Weber et al., 2016). Biocrusts have a wide global distribution and are known to occupy the soils across a range of geomorphic zones (Bowker et al., 2016). For example, patterned landscapes are known to support a rich assortment of cyanobacteria, bacteria and fungi (Malam Issa et al., 1999), and mosses and lichens differ markedly across different geomorphic zones (Eldridge, 1999; Eldridge et al., 2001), or beneath perennial plants and in the interspaces (Soliveres and Eldridge, 2020).

The spatial distribution and composition of biocrusts communities might also be modulated by grazing (Mallen-Cooper et al., 2018). Grazing is a significant landuse in drylands and is known to have direct and indirect impacts on soils, plants, and a range of ecosystem functions (Mallen-Cooper et al. 2018). Overgrazing has been shown to reduce the size and connectivity of perennial patches, particularly grass tussocks (Tongway and Ludwig 1994). This leads to a breakdown in source-sink relationships such that landscapes become 'leaky' (Ludwig et al. 2000) and unable to retain critical resources such as water, nutrients and organic matter within the system (Ludwig et al. 2000). Although biocrusts are key components of soil surfaces characterising patterned landscapes (Eldridge et al. 2001), we still have a relatively poor understanding of potential compositional shifts between different geomorphic zones under different grazing intensities. This is unsurprising, given their small size, the difficulties associated with their identification, and little information on their functional attributes.

As with vascular plants, the functional traits of biocrusts also play an important role in ecological processes (Mallen-Cooper et al., 2020). For example, larger biocrusts might have a greater capacity to trap water and sediments, and biocrusts with long rhizoids can increase the erosion resistance of the soil, thereby providing a stable habitat for microbes (Williams et al., 2012; Gao et al., 2017). However, little is known about how the morphological and functional traits of biocrusts might vary among zones, and therefore, the potential roles of biocrusts in creating or maintaining landscape heterogeneity. This information is important because it will increase our understanding of the potential effects that this important group of organisms might have on the formation and maintenance of patterned landscapes. This is particularly important under future drier climates where biocrusts are predicted to dominate some landscapes and play crucial roles in maintaining dryland ecosystem functions (Bowker et al., 2013; Ding and Eldridge, 2020).

Here we report on a study of the distribution of biocrust organisms in relation to geomorphic position within a patterned mulga (*Acacia aneura*) woodland under different intensities of grazing by sheep and kangaroos. Based on our current understanding of biocrusts, we predicted that richness and cover would be greater in the runoff zones dominated by sparse trees and shrubs, where groundstorey plant and litter cover are sparse. Furthermore, we applied a functional diversity approach, using a suite of biocrust functional attributes (Mallen-Cooper and Eldridge, 2016) to examine differences in floristic and functional diversity among zones of geomorphic position and in relation to grazing intensity. We anticipated that the effects of grazing intensity on floristic and functional diversity would be subordinate to that of the effects of geomorphic position, given the relatively small difference in grazing intensity and the fact that geomorphic position is a strong driver of environmental conditions (soil moisture, shading) that are known to have marked effects on biocrusts (Weber et al., 2016).

2. Methods

2.1. Study site

The study was conducted at Lake Mere (−30.4°, 144.7°), approximately 100 km west of Bourke in north-western New South Wales, Australia. The climate is semi-arid with a low and highly variable rainfall averaging about 310 mm annually. Rainfall is evenly distributed throughout the year, and average diurnal temperatures range from a

maximum of 35 °C in summer to 3 °C in winter. Annual evaporation at Cobar (180 km south-east of the study site) is approximately 2575 mm.

The geomorphology is predominantly low undulating stony ridges of sedimentary rock interspersed with weakly defined dendritic drainage lines on low slopes (Walker, 1991). The soils are predominantly fine sandy clay loams grading gradually to light clays, sometimes with calcareous nodules or powdered calcium carbonate in the profile (Tongway and Ludwig, 1990).

The study was located within a 200-ha site in near pristine condition, that is, resembled a typical pre-European patterned landscape (Ludwig et al., 1997). The study site displayed a clear sequence of three geomorphic zones. On the upper slopes are the runoff zones dominated by a sparse cover of perennial grasses within an open savannah-like matrix supporting sparse cover of *Eucalypt populnea*, *Grevillea striata* and assorted shrub species. This zone has a variable cover of biocrusts, often has stony soils with low levels of infiltration and nutrient cycling. Lower-lying landscape positions are the runon zones occupied by resource accumulating woodlands dominated by an overstorey of *Acacia aneura* and a groundstorey of dense perennial grasses including *Eragrostis eriopoda*, *Aristida contorta* and *Thyridolepis mitchelliana*. At the margins of the two zones is a narrow interception zone covered by a band of perennial grasses. This band forms a transitional zone between the resource shedding runoff zone and the resource accumulating *Acacia aneura* grove. Soils in the groves have higher levels of electrical conductivity, and organic carbon and nitrogen, and lower pH and available phosphorus (Tongway and Ludwig, 1990).

In functional uneroded systems, there is a tight cycling of resources (water, nutrients, organic matter) within the groves (runon zones), which have high infiltration rates and biological activity. Runoff zones tend to occupy about 60% of the landscape and the groves about 30%, with a thin interception zone (~10%) where nutrient cycling is moderately well-controlled (Ludwig et al. 1997). This sequence of runoff-interception-grove is repeated at regular intervals down the slope, presenting the appearance of a banded landscape. This banded landscape has been described widely in other arid and semiarid ecosystems (d'Herbès et al., 2001). Overgrazing and disturbance disrupt the natural patterning in these landscapes, leading to reductions in the available nitrogen and phosphorus, organic carbon, infiltration rates and plant productivity (Tongway and Ludwig, 1994).

2.2. Field measurements

The study site had been the site of a large grazing study in the 1990s undertaken by the Division of Wildlife and Ecology, Commonwealth Scientific and Industrial Research Organisation (CSIRO; Ludwig et al. 1997). The study site was divided into a number of paddocks, of variable size (range 7.5 to 30 ha) to examine the impacts of different stocking intensities of sheep, with and without kangaroos, on plant and soil function (Ludwig et al., 1997). We used 12 of these paddocks for our study. There were two paddocks at each of the following long-term grazing intensities: 0.3, 0.4, 0.5, 0.6, 0.7 and 0.8 dry sheep equivalents (DSE) per hectare. One DSE represents a grazing intensity that is equivalent to one non-lactating ewe over a 12-month period. One paddock of each grazing intensity was stocked with sheep only, and the other with sheep and kangaroos, with animal numbers in each paddock adjusted to establish the appropriate grazing intensity.

Within each of the 12 paddocks, we positioned a 50 m transect perpendicular to the slope in one each of a typical runoff zone, interception zone, and runon zone (grove). At the time of the survey (May 1998), the area had received approximately 15 mm of rainfall, so that the three zones could be easily distinguished by water ponding on the surface and the presence of vascular plants. Along this transect we placed ten 0.5 m² quadrats (0.72 × 0.72 m) within which we measured the cover of all vascular plants, litter and biocrusts. We also assessed the morphology of the soil in terms of four surface features using methods contained within the Soil Surface Condition module of Landscape

Function Analysis (LFA; Tongway and Hindley, 2004). (1) Surface integrity is a measure of the absence of erosion in the quadrat and defined as 100 minus the cover of all erosion in the quadrat including sheet and rill erosion, surface pedestalling, and evidence of gravel and sand movement. (2) Surface roughness is a measure of the micro-topography of the surface assessed by estimating the average difference between the highest and lowest points in a quadrat and categorized in five categories; 1 = < 3 mm difference from lowest to highest point, 2 = 3–8 mm, 3 = 8–25 mm, 4 = large depressions with base, 5 = very large depressions > 100 mm. Roughness provides a measure of the extent to which the surface can retain water or sediment. (3) Sheet erosion indicates evidence of the movement of sediment by overland flow. It was assessed because it is the primary form of erosion on the runoff slopes. (4) Soil cracking is a measure of the brokenness of the soil crust. Broken crusts are more susceptible to erosion, but cracks are indicative of potential microsites for seeds to settle. It was assessed on a quantitative scale of 1 = extensively broken, 2 = moderately broken, 3 = slightly broken, 4 = intact crust.

Samples of every visible biocrust species were collected from each of the 10 quadrats, in each of the three geomorphic zones in each of the 12 paddocks. All bryophytes and lichens were identified, mostly to species level, using keys in Filson (1988, 1992), Filson and Rogers (1979), McCarthy (1991), Scott (1985) and Scott and Stone (1976), as well as more recent generic revisions. Nomenclature followed Buck and Vitt (2006) for mosses, McCarthy (2006) for liverworts, McCarthy (2015) for lichens, and where appropriate, more recent taxonomic revisions, as well as more recent generic revisions. Lichen nomenclature conforms with McCarthy (1991) or more recent monographs. Voucher specimens were lodged with the National Herbarium of New South Wales (NSW).

2.3. Assessing functional diversity metrics

We used data on biocrust taxon morphology and function sourced from Mallen-Cooper and Eldridge (2016). We assigned functional values to each of our biocrust taxa based on five functional traits: rooting (bryophyte rhizoids, lichen rhizines) depth, taxon height, ability to capture sediment (sediment capture) and absorb water (absorptivity), and dry biomass per unit area. Rooting depth is the vertical distance from the soil surface to the lowest point reached by a rhizine or rhizoid. The biomass trait is a new addition to the database and was measured, with four replicates per taxon, by 1) carefully removing soil and below-ground biomass from a sample, 2) drying the sample in an oven for 7 days at 60 °C, 3) weighing the sample in a mass balance, and 4) calculating the precise area of the sample using ImageJ software (Abramoff et al., 2004). These functional traits reflect the responses of individual taxa to environmental changes and the effects of different taxa on critical ecosystem services and functions such as nutrient cycling, water infiltration and resistance to erosion (Bowker et al., 2010; Mallen-Cooper and Eldridge, 2016; Soliveres and Eldridge, 2020).

Using these data, we calculate three measures of functional diversity (functional richness, divergence and evenness; Villéger et al., 2008) and a measure of functional dispersion (Laliberté and Legendre, 2010) using the “FD” package in R (Laliberté et al., 2014; R Core Team, 2020). The three measures of functional diversity reflect the amount of trait space occupied by species in the community (functional richness), how evenly they occupy this trait space (functional evenness) and the extent to which they maximise divergence in functional characters within the community (functional divergence; Mason et al. 2005). We also calculated Rao’s Q (Botta-Dukát, 2005) but removed it in further analyses due to its strong correlations with functional dispersion. We also calculated a community-weighted mean for each trait in each replicate patch, which represents the mean trait value weighted by the abundance of taxa within the patch.

Prior to calculating these indices, we removed five species (*Acarospora nodulosa*, *Buellia subcoronata*, *Crossidium davidai*, *Peltula* sp., *Riccia sorocarpa*) due to insufficient trait data, and data were averaged at

the genus level for *Endocarpon* (four taxa) and *Caloplaca* spp. (three taxa). Functional trait information was available for 21 of the resulting 25 taxa, representing 98% of the total abundance within all sites.

2.4. Statistical analyses

We used permutation multi-variate analysis of variance with the PERMANOVA + for PRIMER (V6) statistical package (Anderson et al. 2008), and using the Bray-Curtis similarity matrix, to examine potential differences in the complement of biocrust taxa in relation to grazing intensity, geomorphic position, and their interaction. Our model structure comprised two strata. The first stratum considered the effects of the six grazing intensities. The second stratum (geomorphic position) was nested within grazing intensity, allowing us to examine effects of geomorphic position and its interaction with grazing intensity. Compositional data were calculated as the percentage of quadrats, out of 10, in which a given taxon was found for a given transect. We used linear models to examine the effects of geomorphic zone on our dependent variables (various measures of functional and structural diversity, plant and litter cover, biocrust functions). The data structure was the same as that used in the PERMANOVA analyses. Differences in relation to geomorphic position or grazing intensity were examined using least significant difference (LSD) tests after checking for homogeneity of variance (Levene’s Test) in the R statistical software.

The degree of association of different biocrust taxa with the three geomorphic zones was assessed using Indicator-Species Analysis (Dufréne and Legendre, 1997) in the “indicspecies” package in R (Cáceres and Legendre, 2009). Indicator values combine information on relative abundance and frequency of species. The maximum indicator value (IV = 100) is obtained when all individuals of a given species are restricted to a particular geomorphic zone or all samples from the particular geomorphic zone contain an occurrence of that species. Species data were randomized, and a Monte Carlo randomization procedure performed with 1000 iterations in order to determine the statistical significance of the indicator values.

3. Results

We detected a significant difference in the complement of biocrust species among the three geomorphic zones (PERMANOVA: Pseudo $F_{2,12} = 9.47$, P (perm) = 0.001), with a significantly different species assemblage in all zones (Fig. 1a). The relative abundance of lichens was greatest in the runoff and least in the groves (runoff zones), and this corresponded to an increase in the relative abundance of liverworts from runoff zones to groves (Fig. 1b). Two squamulose lichens (*Psora decipiens*, *Buellia subcoronata*) and a crustose lichen (*Lecidea ochroleuca*) were strongly indicative of runoff zones (Table 1). The perennial and biennial thallose liverworts (*Riccia* spp., i.e., *R. crinita*, *R. lamellosa* and *R. limbata*) were strongly indicative of groves, and the interception zones comprised a mixture of both liverwort and lichen taxa.

Biocrust richness ($F_{2,12} = 14.1$, $P = 0.001$; Fig. 1c) and cover ($F_{2,12} = 6.22$, $P = 0.014$), and vascular plant ($F_{2,12} = 41.4$, $P < 0.001$) and litter ($F_{2,12} = 80.4$, $P < 0.001$) cover were significantly greater in the groves. We also found a number of differences in functional measures of biocrusts among the three geomorphic zones. For example, functional richness (Fig. 2a) increased substantially from runoff zones to groves ($P < 0.001$), and both functional diversity (Fig. 2c, $P = 0.036$) and functional dispersion (Fig. 2d, $P = 0.005$) were significantly greater in the runoff zones than in the groves. There was no evidence of differences in functional evenness among zones (Fig. 2b, $P = 0.38$). Differences in weighted mean values of morphological attributes were also apparent among geomorphic zones. Average rhizine/rhizoid length was greater (Fig. 2f, $P = 0.019$), and taxa were significantly taller (Fig. 2g, $P < 0.001$) but had lower biomass (Fig. 2h, $P < 0.001$) in the groves. There was also substantially greater sediment trapping capability (Fig. 2i) and water absorptivity (Fig. 2j) in the groves than either runoff or

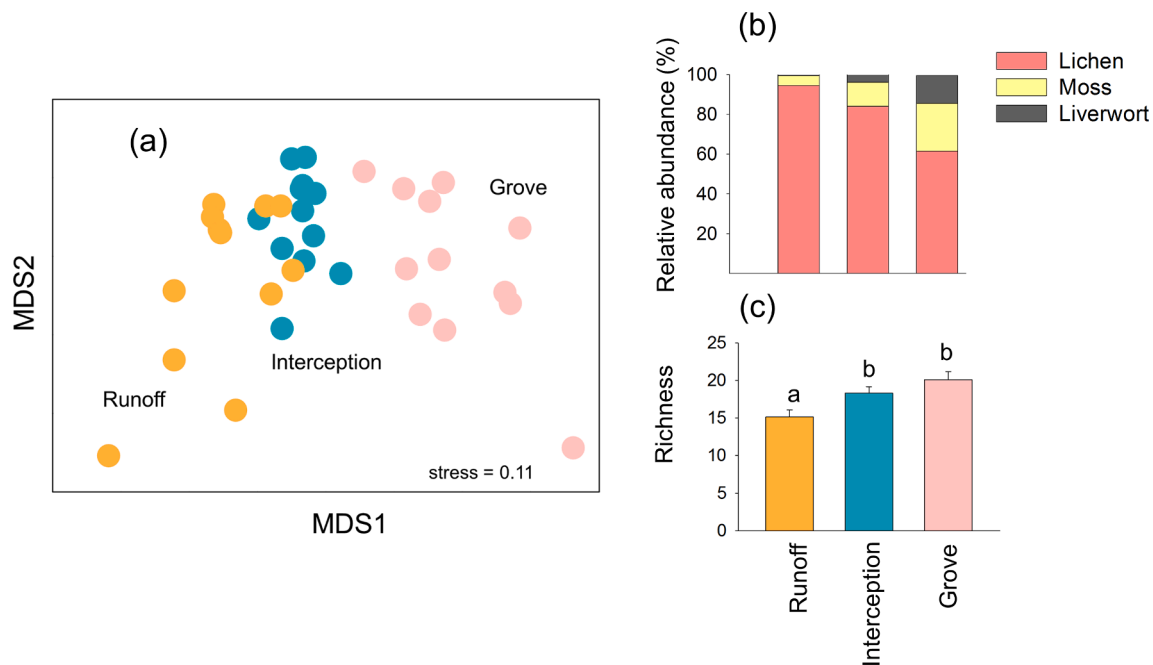


Fig. 1. (a) Non-metric MDS biplot of species based on relative abundance for three geomorphic zones, (b) Relative abundance of lichens, mosses and liverworts in runoff, interception and grove zones, and (c) mean (\pm SE) biocrust richness (total number of species) in the three zones. Different superscripts represent significant differences ($P < 0.05$) in richness among zones.

Table 1

Indicator Species Analysis for runoff and interception zones, and timbered runoff groves. Only significant ($P < 0.05$) indicators are shown.

Geomorphic zone	Taxon type	Taxon	Indicator value (%)	P-value
Runoff	Lichen	<i>Psora decipiens</i>	71.5	0.003
Runoff	Lichen	<i>Buellia subcoronata</i>	68.5	0.020
Runoff	Lichen	<i>Lecidea ochroleuca</i>	67.9	0.003
Interception	Lichen	<i>Heppia despreauxii</i>	70.4	0.008
Interception	Lichen	<i>Endocarpon simplicatum</i> ssp. <i>bisporum</i>	66.0	0.002
Interception	Lichen	<i>Collema coccophorum</i>	64.1	0.010
Interception	Liverwort	<i>Riccia sorocarpa</i>	60.9	0.033
Interception	Liverwort	<i>Fossombronia</i> spp.	59.8	0.040
Grove	Lichen	<i>Didymodon torquatus</i>	83.1	0.001
Grove	Lichen	<i>Cladonia</i> spp.	64.0	0.012
Grove	Moss	<i>Gemmabryum pachytheicum</i>	85.1	0.001
Grove	Liverwort	<i>Riccia crinita</i>	83.8	0.001
Grove	Liverwort	<i>Riccia lamellosa</i>	76.2	0.001
Grove	Liverwort	<i>Riccia limbata</i>	75.1	0.003

interception zones ($P < 0.001$).

We also detected some important correlations among functional attributes of biocrust taxa and morphology of the surface soils (Fig. 3). First, there were twice as many negative as positive correlations between soil surfaces and functional attributes of biocrusts. Second, greater litter cover and plant cover were positively correlated with taller plants that a greater ability to absorb water or trap sediment (Fig. 3), but correlations with functional measures of richness were either non-significant or negative. Third, soil surface roughness and surface cracking were uncorrelated with functional attributes.

Differences in grazing intensity had no significant effect on biocrust cover or richness (data not shown), nor on any measures of functional diversity (Fig. S1), plant attributes, or our two measures of ecosystem function, sediment capture (Fig. S2d) and water absorptivity (Fig. S2e). Similarly, there were no effects of different grazing assemblages (sheep cf. sheep plus kangaroos) on measures of functional diversity (Fig S3) or attributes (Fig. S4).

4. Discussion

Our study showed evidence of substantial differences in moss, lichen and liverwort taxa, and their functional attributes, among the three geomorphic zones, but no significant effects of either grazing intensity or herbivore assemblage on biocrust communities. Geomorphic effects were greatest in the timbered runoff zones and least in the erosional runoff zones. Our results also suggest that differences in biocrust taxa among the zones correspond to different functional mechanisms associated with water and sediment capture, consistent with our understanding of the importance of biocrusts in hydrological and depositional processes, and comparable to the functional effects of vascular plants across geomorphic zones. Furthermore, our study highlights the fact that biocrusts function similarly to vascular plants by maintaining or reinforcing patterning in drylands by affecting runoff/runon processes. Our study provides empirical evidence that biocrusts might partly compensate for the maintenance of hydrological function in drylands where vascular plants are sparse or have been removed. Mosses, in particular, have the capacity to absorb small amounts of runoff water even in the absence of vascular plants.

There was clear evidence of different biocrust life forms among the three geomorphic zones, with runoff zones characterised by lichens, whereas liverworts were restricted mainly to the runoff zones. The interception zones supported a mixture of biocrust life forms, which is not unexpected, given their combination of resource accumulating and shedding surfaces. That lichens dominated most zones, particularly the runoff zones, is consistent with our understanding of the physiology of lichen taxa in arid areas. Lichens are highly tolerant of high temperatures and solar exposure (Kranner et al., 2008), which are the characteristic environmental conditions in the runoff zones (Yair, 1983). Lichens have the capacity to remain in a dormant state (Green et al., 2011, Pintado et al., 2010), and resume photosynthesis once relative humidity increases (Baldauf et al., 2020), which in drylands, is often initiated by dew deposits (Lange et al., 1990). However, sustained higher temperatures can reduce water availability and intensify drought stress in biocrusts (Baldauf et al., 2020). Unlike lichens, liverworts require free water to reproduce (Sperry, 2003), so prefer microhabitats

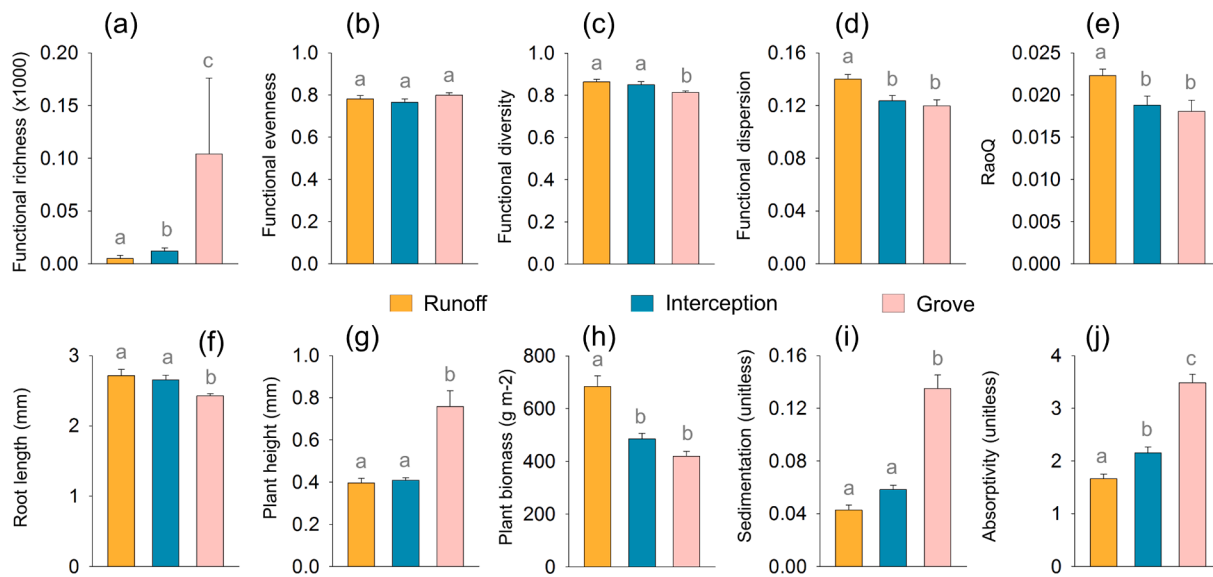


Fig. 2. Mean (\pm SE) values of biocrust functional indices (a-e) and community-weighted means (f-j) in the three geomorphic zones. Different subscripts indicate differences in mean values at $P < 0.05$.

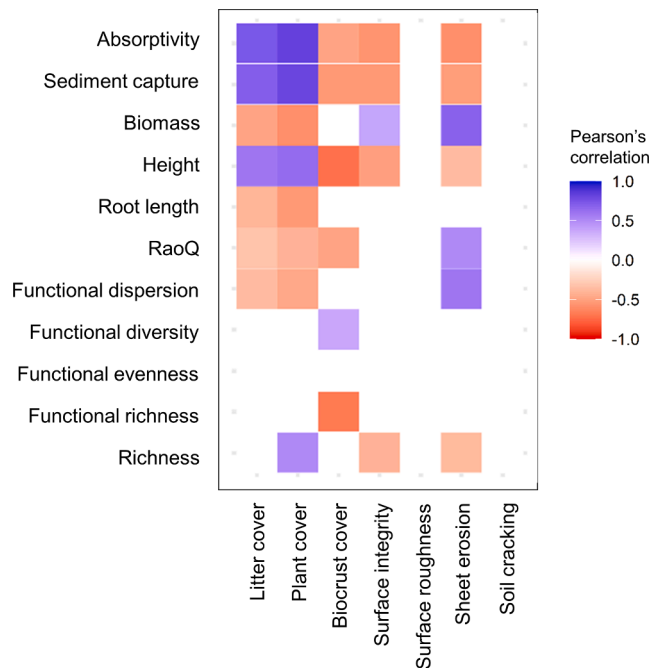


Fig. 3. Heat map based on the correlations (Pearson's r) between functional indices of biocrust taxa and soil environmental conditions. Only significant ($P < 0.05$) correlations are shown.

such as the timbered groves that act as moist refugia in hot deserts (Rogers, 1994), or locations close to snowmelt in cold deserts (Kennedy, 1995). This likely accounts for the greatest relative abundance of liverworts in the groves (runon zones) found in our study, consistent with studies from western Queensland showing a prevalence of liverworts in non-arid microsites along shaded drainage lines (Rogers, 1994).

Our results showed that, at the landscape scale, biocrust communities in the runoff zones have lower functional richness, yet greater functional diversity and dispersion, than the runon zones. Functional richness *sensu* Villéger et al. (2008) computes the convex hull volume of a community in multidimensional trait space, which can be quite sensitive to outliers (Laliberté & Legendre 2010). It seems likely that a few

biocrust taxa, such as *Eremastrella crystallifera* and *Cladia beaugleholei*, which have extreme trait values and are found exclusively in the runoff groves, enhanced the functional richness of these communities. There may also be a selection effect operating in the groved runon areas whereby the greater number of taxa increases the probability of including those with distinct sets of traits (Loreau & Hector, 2001; Mallen-Cooper et al., 2018). Functional diversity and dispersion (*sensu* Villéger et al. 2008) are generally considered to be more robust predictors of ecosystem functioning than functional richness (Cadotte et al. 2011), and greater values of these indices in the runoff zones suggest that biocrust taxa inhabiting these zones are particularly distinct in their functional traits. A possible implication of this finding is that biocrusts in the runoff zones have the potential to amplify their rate or output of an ecosystem function through complementarity (Loreau & Hector 2001). For example, a community with diverse biocrust species would expect to have a wide range of rhizine lengths, which could stabilise multiple layers of topsoil, resulting in greater erosion resistance than a community whose rhizines were concentrated at a particular depth. It might be assumed that patches with greater surface roughness would support a more functionally diverse biocrust community, as microtopography can induce microclimates that favour different taxa (Davidson et al., 2002), but our results found no relationship, which most likely reflects the coarseness of the ordinal roughness index. The lack of difference in functional evenness among geomorphic zones suggests that all the studied biocrust communities have similar abundance structures, and effectively means there are no hyper-abundant species with highly distinct traits in any particular zone.

We also found some evidence of trait-based relationships among different biocrust taxa and specific geomorphic zones. For example, biocrust taxa in the runoff zones were taller, but had shorter roots (rhizoids/rhizines) and less biomass, than those in the runoff zones. Bryophyte growth is known to be suppressed by deep litter, which has the potential to reduce light levels (Van Cleve et al., 1983). Thus, greater stature could be a response to greater litter cover in the groves, releasing biocrusts from the potential negative effects of overshadowing, exposure to plant-based chemicals, and the effects of invertebrate herbivory under decomposing vascular plant leaves (Natalia et al., 2008). Lower biocrust biomass in the runon zones might seem at odds with taller taxa, but is likely due to idiosyncratic differences in thallus structure and mass of different taxa across the geomorphic zones. Taxa, mainly lichens such as *Psora decipiens* and *Lecidea ochroleuca* that are indicative of the runoff

zones, have denser thalli and therefore greater biomass per plant than liverworts (*Riccia* spp.) and mosses (*Gemmabryum pachythecum*) that dominate the runoff zones. Biocrusts from the runoff zones were also characterised by short stature and longer rhizines. Rhizoids assist in anchoring germinating bryophyte spores and mature taxa to the substrate (Ligrone et al. 2012), but also play a role in maintaining the plant integrity during periods of water stress (Ligrone et al., 2000), which is characteristic of the runoff zones (Tongway and Ludwig, 1990). Being squat and having slightly longer rhizoids would advantage biocrusts growing on unstable substrates that experience frequent water and sediment movement (Gao et al., 2017). For example, the cosmopolitan moss *Bryum argenteum* is known to grow prolifically in areas of active erosion (Eldridge, 1999) and in disturbed microsites such as roadside verges and recovering soils (Proctor et al., 2007). We have previously shown that overland flow is an important vector for dispersal of moss and lichen fragments during overland flow events (Eldridge, 1996a). Rainfall simulation studies indicate that mosses tend to be more resistant to removal by splash erosion than squamulose lichens such as *Endocarpon* spp., with moss detaching only during the latter stages of rainfall application (Eldridge, 1996b). In these laboratory-based rainfall simulation experiments, species whose vegetative material readily dispersed by splash erosion were short, ephemeral types with short rhizines; an advantage in a hostile environment where water is rapidly shed from the surface. Our smallest moss, *Stonea oleaginosa*, is <0.1 mm tall, has extremely short rhizoids, and therefore lives amongst a matrix of eroded and depositional crust with coarse sand grains that are typical of the runoff environments.

Morphology is known to control sediment capture (Danin and Ganor, 1991; Eldridge and Rosentreter, 1999; Williams et al., 2012), with organism size controlling the size of trapped particles (Williams et al., 2012). Our trait-based approach also revealed that biocrust taxa in the groves had substantially greater capacity for sediment capture and water absorption than those in the runoff or interception zones. The capture of water and sediments in the groves, and the maintenance of a tightly coupled system with minimal resource leakage is critical for the maintenance of patterned, two-phase systems (Tongway and Ludwig, 1994; Thiery et al., 1995). For example, biocrust patches dominated by mosses with high absorptivity and sediment capture in the runoff zones can act as sinks that capture small trickle flows generated from upslope open areas where the soil surface is covered by lichens and short mosses (Yair, 1983). This then leads to more resource accumulation and clumped biocrusts and vascular plants on the runoff zones, enhancing the heterogeneity in soils (Tongway and Ludwig, 1994), plant cover (Caballero et al., 2008), biocrust species (Eldridge and Greene, 1994) and litter (Carrera and Bertiller, 2013), thereby reinforcing the patterned landscape in drylands (Valentin et al., 2001). Thus, the growth and persistence of biocrust taxa in the groves has the capacity to augment this critical geomorphic function, albeit on a micro scale dependent on the scaling effect of smaller patches (Ludwig et al., 2000), and could present a potential role for biocrusts in the restoration of hydrological function following overgrazing in the groves or removal of the permanent grass cover.

Despite the array of trait-based effects, we failed to find effect of changes in grazing intensity or herbivore composition on biocrust species, or any of the functional traits. It is difficult to know exactly why this is, but it likely results from the fact that the small paddocks used in this grazing experiment had very low numbers of animals, despite big differences in stocking densities. Further, the Lake Mere paddocks had been conservatively managed prior to the experiment and represented some of the most functional and intact examples of groved mulga woodlands in eastern Australia. Had these paddocks not been so well vegetated, or supported large numbers of animals in the experiments, then we might have expected strong effects of grazing on our biocrust community, similar to results from other published studies (e.g., Concostrina-Zubiri et al., 2014; Tabeni et al., 2014).

Overall, our study provides empirical evidence that biocrusts

composition is markedly different among geomorphic zones, reinforcing the notion that resources are highly heterogeneous across patterned landscapes in drylands, from vegetation and soils at broad scales, to biocrust communities at micro scales. Here we show that, despite their small size, the non-vascular components of biocrusts are effective at capturing water and reducing sediment accretion in the runoff zones. Our work highlights the fact that biocrusts undertake a similar function to vascular plants by influencing hydrological processes and resource distribution in drylands. Our study moves beyond a simple discussion of biocrusts at small scales to consider their roles at larger scales that are driven by landscape-level processes of resource loss and accumulation. Our results therefore are relevant to the many systems globally where vegetation is organised into discrete patterns of runoff and runoff (d'Herbès et al., 2001). Our work suggests that biocrust communities could have a role in the reinforcement or restoration of resource capture in landscapes where vascular plants are eliminated (e.g., overgrazing, plant removal, mining), as even small increases in cover are sufficient to capture resources and trigger recovery in patterned environments (Berghuis et al., 2020). Furthermore, predicted hotter and drier climates would result in a sparser vascular plant cover, but a greater dominance of biocrusts (Ding and Eldridge, 2020), which would play an important role in redistributing resources and maintaining the functions of patterned landscapes in drylands.

Ethical approval

The authors declare that this paper does not contain any study with human participants or animals.

Authorship contribution statement

David Eldridge designed the study, collected the data and wrote the first draft. Max Mallen-Cooper and Jingyi Ding analysed the data, and contributed to the first draft and subsequent editing.

Data accessibility

The data are available on the figshare data repository <https://doi.org/10.6084/m9.figshare.14442794>.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2021.115152>.

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