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REGULAR ARTICLE

Laboratory-based techniques for assessing the functional traits of biocrusts

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Abstract

Background and aims Functional traits are increasingly being used to assess the degree to which ecosystems maintain key processes. The functional traits of vascular plants are well-documented but those of non-vascular plants are poorly known. We describe a comprehensive methodology to measure the functional traits of soil-borne lichens, mosses and liverworts making up biocrust (biological soil crust) communities.

Methods We collected 40 biocrust taxa from across 10,000 km^2 of eastern Australia, and measured eight functional traits using a combination of mensurative studies and laboratory-based experiments. These traits were sediment capture, absorptivity, root (or rhizine) length, height, and the activity of four enzymes involved in key nutrient cycles; β-glucosidase, β-D-cellobiosidase, N-acetyl-β-glucosaminidase and phosphatase.

Results Taxa were distributed across a broad range of trait values. Sediment capture values ranged from 2 % in the crustose lichen *Diploschistes thunbergianus* to 83 % in the tall moss *Triquetrella papillata*. The highest absorptivity value was observed in the moss *Bartramia hampeana* ssp. *hampei*, which was able to absorb 12.9 times its dry mass in water, while the lowest value, 0.3, was observed in *Diploschistes thunbergianus*. Multivariate analyses revealed that biocrust morphological groups differed significantly in their functional profiles.

Conclusions Our results indicate that biocrust taxa vary greatly in their functional traits and that morphological groups explain, in part, the ability of biocrusts to sequester resources (sediment, moisture) and to undertake key processes associated with the cycling of carbon, nitrogen and phosphorus. This methodology will enhance our understanding of ecosystem functioning in drylands where biocrusts make up a large component of the surface cover and provide a range of ecosystem goods and services.

Keywords Biocrust · Functional traits · Ecosystem function · Drylands · Morphogroups

Introduction

The widespread adoption of trait-based approaches over the past decade has revolutionised the way we view ecosystems, their processes and their biota (Díaz and Cabido 2001; Naeem and Wright 2003; Westoby and Wright 2006; Kunstler et al. 2016). Functional traits are considered useful indicators of the effects of organisms on ecosystem functioning (effect traits) and of the responses of organisms to environmental filtering

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(response traits) (Díaz and Cabido 2001). For example, hairiness in vascular plants is a typical response trait associated with herbivory (McIntyre et al. 1999). Functional traits can respond to environmental filtering and also have an effect on ecosystem functioning (Lavorel and Garnier 2002).

A broad range of approaches has been devised to assess functional diversity, richness and evenness using functional traits (e.g. Petchey and Gaston 2002; Botta-Dukát 2005; Cornwell et al. 2006; Villéger et al. 2008; Laliberté and Legendre 2010). Alpha diversity, the number of species within a defined area weighted by species abundance, is the conventional measure of biodiversity, but this has been shown to be a poor surrogate for functional diversity. For example, Ernst et al. (2006) reported a difference in functional diversity of amphibians among different logging regimes but were unable to detect a difference in species diversity. In a few studies, species diversity and functional diversity exhibit opposite associations with the same environmental variables (Biswas and Mallik 2010; Villéger et al. 2010; Concostrina-Zubiri et al. 2014). This discrepancy between diversity indices is mostly due to the effect of functionally redundant taxa (Cadotte et al. 2011), but in some studies may be due to the use of an index that violates the assumption that functional diversity should not decrease with the addition of new species ('set monotonicity'; Solow et al. 1993). Unlike taxonomic diversity, functional diversity is closely related to the provision of ecosystem goods and services and can therefore be used as a tool for managing ecological communities and their environments (Díaz et al. 2007; de Bello et al. 2010; Lavorel 2013).

To date, vascular plants are grossly overrepresented in the functional ecology literature. Standardised protocols for measuring the traits of vascular plants are readily available (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013) but those for non-vascular plants are in their infancy. Morphological groups (morphogroups) have been proposed as indicators of ecosystem function in biocrusts (biological soil crusts), on the basis that taxa within a given morphological group possess similar functional traits (Eldridge and Rosentreter 1999; Read et al. 2014). Indeed, Read et al. (2014) provided compelling evidence that morphogroup abundance was a good predictor of surface disturbance, with different morphogroups varying in their response to disturbance. Biocrusts are assemblages of cyanobacteria, lichens, mosses, liverworts, algae, fungi, bacteria and archaea that are found in close association with surface soils (Eldridge and Greene 1994; Soule et al. 2009). Biocrusts affect numerous ecosystem processes including hydrology (Belnap 2006), erosion (Bailey et al. 1973; Belnap and Gillette 1998; Eldridge and Leys 2003) and nutrient cycling (Reynolds et al. 2001; Barger et al. 2006; Bowker et al. 2013), and interact with a wide range of taxa as competitors, facilitators, habitat formers and providers of sustenance (Chown and Scholtz 1989; Su et al. 2009; Maier et al. 2014; Mendoza-Aguilar et al. 2014; Bokhorst et al. 2015). The functioning of biocrusts warrants further investigation for several reasons: they are ubiquitous (Belnap et al. 2003), easily manipulated for experimentation (Castillo et al. 2008), provide a range of ecosystem goods and services (Belnap 2003a), and are useful as indicators of ecosystem condition, air pollution and climate change (Daly 1970; Eldridge and Koen 1998; Sancho et al. 2007; Read et al. 2014). Biocrusts are the dominant ground cover in drylands (Belnap et al. 2003), which comprise 40 % of Earth's land surface (White and Nackoney 2003). For these reasons, biocrusts have been proposed as a model system for examining biodiversity-function relationships (Bowker et al. 2010). Unfortunately, the majority of functional traits used in the study of vascular plants cannot be measured in biocrust organisms because crust organisms are markedly smaller and vary in structure and their effects on ecosystem processes (Cornelissen et al. 2007).

This paper describes a comprehensive, laboratory-based methodology to assess the functional traits of specific taxa that comprise the major macroscopic components of biocrust communities (lichens, mosses and liverworts). To our knowledge, four previous studies have measured functional traits in individual biocrust taxa (Gavazov et al. 2010; Bowker et al. 2011; Michel et al. 2013; Concostrina-Zubiri et al. 2014). Quantitative functional traits are measured in only two of these studies: Gavazov et al. (2010) measured rates of nitrogen fixation in 15 subarctic biocrust species and their associated microbial communities, and Michel et al. (2013) measured absorptivity and other water-related traits in five species of mosses. In addition, several studies have measured photobiont type, reproductive strategy and growth form in epiphytic lichen species (Pinho et al. 2011, 2012; Giordani et al. 2012, 2013; Llop et al. 2012; Matos et al. 2015).

Given the paucity of quantitative biocrust functional trait data, we measured eight quantitative functional traits for a range of relatively common taxa that are major components of biocrust communities in eastern Australia (Eldridge and Tozer 1996), most of which have a global distribution (Rogers and Lange 1972). The activities of four enzymes (β-glucosidase, β-D-cellobiosidase, N-acetyl-β-glucosaminidase and phosphatase) were selected as these enzymes are associated with key nutrient cycles. Sediment capture and root (or rhizine, in lichens) length were considered functional traits as they directly influence the capacity of taxa to aggregate soil particles and therefore control erosion. Absorptivity, the capacity of taxa to trap and store moisture, was considered functional as this is a substantial hydrological effect of biocrusts (Belnap 2006). Finally, taxon height was considered functional, as taller taxa provide more three-dimensional space for invertebrates, and are more likely to trap resources and to ameliorate environmental conditions at the surface (e.g. Danin and Ganor 1991). We used a combination of mensurative studies and laboratory-based experiments to derive the values of these functional traits for taxa that were collected from across a large area (~10,000 km^2) of eastern Australia.

Methods

Collection sites

Biocrust specimens were collected from reserves across a large area of semi-arid drylands in eastern Australia (33°40′-34°32’S, 146°3′-148°9’E; elevation range 98–415 m). The reserves included Jindalee State Forest, Ingalba Nature Reserve, Ardlethan State Forest, Binya State Forest, Cocoparra National Park, Jimberoo State Forest and Nombinnie Nature Reserve (Table 1). Soils at the collection sites were predominantly loams and sandy loams, and occurred on landscapes ranging from sandplains to level plains, and ranges and rocky hills. Contrasting environments were sampled in order to obtain a full range of different morphological types. For example, the thallose liverwort *Asterella drummondii* was found in moist environments beneath rocky ledges, where it receives additional run on (e.g. Cocoparra National Park; Binya State Forest). Similarly, we sampled highly calcareous loamy soils at the drier end of the gradient (Nombinnie Nature Reserve) in order to collect specimens of the crustose lichen *Diploschistes*, the squamulose *Psora decipiens* and *P. crystallifera* and foliose *Xanthoparmenia* spp. (Eldridge 1996, Eldridge and Koen 1998). A full list of taxa by site is presented in Table 2. Collection sites spanned an annual rainfall gradient from 685 mm in the east to 396 mm in the west (Bureau of Meteorology 2015). Mean annual minimum daily temperatures range from 7.6 °C to 10.2 °C from east to west across the study area, while mean annual maximum daily temperatures range from 22.3 °C to 24.0 °C along the same gradient.

Species and morphogroup classification

Taxa were identified to species level using available keys in Filson and Rogers (1979); McCarthy (1991);

Table 1 Description of the geomorphology, soils and vegetation communities where biocrust samples were collected

Location	Geomorphology, soils and rainfall	Vegetation community
Jindalee State Forest	Plains and low hills of stony calcareous earths; 350 mm	Open woodland with of *Eucalyptus populnea*, *Callitris glaucophylla*, *Eucalyptus dwyeri* and *Callitris endlicheri*
Ingalba State Forest	Plain and low rises of shallow, loamy lithosols; 580 mm	Open woodland to dense forest of *Eucalyptus sideroxylon*, *Eucalyptus macrocarpa* and *Callitris glaucophylla*
Ardlethan State Forest	Gently undulating plains of deep calcareous red earths; 490 mm	Open to dense forest of *Callitris glaucophylla*
Binya State Forest	Level plains of deep calcareous red earths; 455 mm	Open to dense forest of *Callitris glaucophylla* and *Eucalyptus populnea*
Cocoparra National Park	Hills and ranges with sandy to loamy lithosols; 378 mm	Open woodland dominated by *Callitris glaucophylla*, *Eucalyptus dwyeri*, *Eucalyptus melliodora* and *Brachychiton populnea*
Jimbaroo National Park	Plains and low hills of stony calcareous earths; 385 mm	Open to dense woodlands of *Eucalyptus populnea*, *Callitris glaucophylla and Eucalyptus dwyeri*
Nombinnie Nature Reserve	Sandplains and low dunes of sandy red loams and clay loams; 340 mm	Dense shrubland and woodland of *Eucalyptus* spp. (mallee), *Eucalyptus populnea* and *Callitris glaucophylla*

Table 2 Species name, code, taxon type and locations in which biocrust specimens were collected

Species name	Code	Type	Ard	Bin	Coc	Ing	Jim	Jin	Nom
Asterella drummondii	Asdr	Liverwort	P	P	P	P	-	P	-
Barbula calycina	Baca	Moss	P	P	P	P	P	P	P
Bartramia hampeana ssp. *Hampei*	Baha	Moss	-	-	-	-	-	-	-
Bryum argenteum	Brar	Moss	-	-	-	-	-	-	P
Campylopus introflexus	Cain	Moss	-	-	-	-	-	-	-
Cladia aggregata	Clag	Lichen	-	-	-	-	-	-	-
Cladia beaugleholei	Clbe	Lichen	P	-	-	-	-	P	-
Cladia corallaizon	Clco	Lichen	-	P	P	-	-	-	-
Cladia muelleri	Clmu	Lichen	-	-	P	P	-	-	-
Cladonia spp.	Clzz	Lichen	P	P	-	P	-	P	P
Collema coccophorum	Coco	Lichen	P	P	P	-	P	P	P
Diploschistes thunbergianus	Dith	Lichen	P	P	-	P	-	P	P
Didymodon torquatus	Dito	Moss	P	-	-	-	-	P	P
Eccremidium spp.	Eczz	Moss	P	-	P	P	-	P	P
Entosthodon muehlenbergii	Enmu	Moss	-	-	-	P	-	P	-
Endocarpon spp.	Enzz	Lichen	P	-	-	P	-	P	P
Fissidens megalotis	Fime	Moss	-	P	-	-	-	-	-
Fissidens taylorii	Fita	Moss	P	P	P	-	-	-	-
Fossombronia spp.	Fozz	Liverwort	P	P	P	-	-	P	P
Gemmabryum pachytheca	Gepa	Moss	-	P	P	-	-	P	P
Gigaspermum repens	Gire	Moss	-	-	P	-	-	-	P
Goniomitrium acuminatum ssp. *enerve*	Goen	Moss	-	-	-	-	P	-	P
Lecidea spp.	Lezz	Lichen	P	-	P	P	-	P	P
Pseudocrossidium crinitum	Pccr	Moss	-	P	P	-	-	-	-
Pseudocrossidium hornschuchianum	Pcho	Moss	-	-	-	P	P	P	-
Peltula spp.	Pezz	Lichen	P	P	P	-	-	P	P
Pleuridium nervosum	Plne	SM	-	-	-	P	-	P	-
Psora crystallifera	Pscr	Lichen	-	P	-	-	P	-	P
Psora decipiens	Psde	Lichen	P	P	-	-	-	-	-
Riccia limbata	Rili	Liverwort	-	-	-	-	P	-	P
Riccia nigrella	Rini	Liverwort	P	-	P	P	P	P	-
Riccia spongiosula	Risp	Liverwort	-	-	P	-	-	P	-
Rosulabryum billardieri	Robi	Moss	-	-	-	P	-	-	-
Rosulabryum campylothecium	Roca	Moss	P	-	P	P	-	P	-
Tortula atrovirens	Toat	Moss	-	-	-	-	-	P	P
Trichostomum brachydontium	Trbr	Moss	-	-	-	-	-	-	P
Trapelia coarctata	Trco	Lichen	-	-	-	P	-	-	-
Triquetrella papillata	Trpa	Moss	-	P	P	P	-	P	-
Xanthoparmelia semiviridis	Xase	Lichen	-	P	-	-	-	P	-
Xanthoparmelia spp.	Xazz	Lichen	-	P	P	-	-	P	P

P = present, − not found, Ard = Ardlethan State Forest, Bin = Binya National Park, Coc = Cocoparra National Park, Ing = Ingalba Nature Reserve, Jim = Jimbaroo National Park, Jin = Jindalee State Forest, Nom = Nombinnie Nature Reserve

Catcheside (1980); 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. Voucher specimens have been lodged with The John T Waterhouse Herbarium at the University of New South Wales. Taxa were assigned to morphogroups according to Eldridge and Rosentreter (1999), though mosses were further partitioned into tall and short mosses, consistent with Read et al. (2014) (Table 3).

Sediment capture

Sediment capture experiments involved covering biocrust samples with a standard amount of soil and measuring the mass of soil retained after one minute of exposure to a simulated wind event. Attached and unattached (vagant) taxa were prepared differently. Taxa attached to the soil were collected at their highest observed density as monospecific aggregates of approximately 10 cm^2. The soil portion of the aggregate was soaked for one minute in 1:1 water:glue (Selleys Aquadhere glue) to ensure that measurements of soil mass after wind exposure were not influenced by detachment of soil originating from the base of the sample. After drying, the soil aggregates were glued to 10 × 10 cm squares of cardboard. A soil aggregate without attached biocrust organisms and prepared in the same manner served as a procedural control. For unattached taxa such as *Xanthoparmelia semiviridis*, the specimens were glued directly onto cardboard squares. *Xanthoparmelia semiviridis* firmly attaches to leaf litter and traps resources in a similar manner to attached taxa, requiring wind speeds in excess of 46 km h^{-1} to initiate the movement of its thallus (Eldridge and Leys 1999).

The area of each aggregate was calculated using ImageJ (Abràmoff et al. 2004). We passed a sample of sandy loam soil from the study area through a 2 mm sieve and placed an area-standardized mass of sieved soil (0.2 g per cm^2) in the centre of each aggregate. Using a wide range of particle sizes allowed us to test the ability of biocrust taxa to capture particles moving by creep, saltation and suspension. A smaller particle size fraction was tested (<0.02 mm), but we were unable to detect differences between taxa at the lower end of the sediment capture spectrum. The aggregate, sediment and cardboard were weighed before being placed in a portable wind tunnel. The wind tunnel was a 100 × 100 × 695 mm long square tube made from 18 mm medium-density fibreboard (MDF) with a Soler and Palau TD-250/100 in-line mixed flow duct fan situated at one end. Samples were taped onto an 18 mm high square block of MDF to place them directly into the oncoming wind path, 150 mm from the fan. Each sample was exposed to a wind speed of 19 km h^{-1} for 30 s, then rotated 180° for a further 30 s of wind exposure in order to simulate natural wind conditions, which are known to switch directions across the study area. The sample was then detached from the block and reweighed. Sediment capture was measured as the proportion of sediment retained after exposure to the wind event, i.e., sediment retained divided by total sediment applied. Five independent replicates were performed for each of 27 biocrust taxa as well as the experimental control. For all traits, with the exception of relatively rare taxa, we used replicates from different locations across the study area in order to maximise the capture of variation within taxa.

Absorptivity

Absorptivity, defined as the capacity of organisms to trap and retain moisture on their surfaces and in their tissues, was measured by calculating the difference in

Table 3 Classification of morphogroups based on Eldridge and Rosentreter (1999) and Read et al. (2014)

Morphogroup	Code	Description
Thallose liverwort	TL	strap-like, flattened thallus
Leafy liverwort	LL	prostrate, green, leafy, with a mid-vein
Fruticose lichen	RL	shrub-like, branched thallus
Foliose lichen	OL	leaf-like, flattened thallus
Squamulose lichen	SL	scale-like thallus
Crustose lichen	CL	crust-like growth, tightly attached to substrate
Small moss	SM	mean height < 15 mm
Tall moss	TM	mean height > 15 mm
Gelatinous lichen	GL	unlayered thallus, jelly-like when wet, cyanobacterial photobiont

mass between wet and dried samples of biocrust taxa. Biocrust organisms were first separated from the soil. For each replicate sample, a known mass of each taxon (approximately 0.1 g) was saturated with water; 5 ml water per 0.1 g was sufficient to saturate the samples. We kept the mass of each sample constant across replicates. Samples were kept in a water treatment undisturbed for 5 min, then removed, weighed and reweighed after oven drying at 80 °C for 1 h. Absorptivity was measured as the mass of water absorbed per gram of biocrust sample. Five replicates were performed for each of 24 taxa.

Height and root length

The height above ground and the length of the longest root (mosses and liverworts) or rhizine (lichens) were measured in 20 replicate organisms per taxa with Vernier calipers, to an accuracy of ±0.1 mm. Stem height (excluding leaves) was used as the measure of height for mosses, consistent with existing protocols for mosses (Catcheside 1980). For crustose and squamulose lichens, the height was equal to the thallus thickness (with the exception of *Cladonia* spp., which have fruiting bodies (podetia) that extend above the thallus). All taxa were measured in their dormant, desiccated state. Measurements of roots and rhizines were taken after carefully removing soil from around these structures.

Enzyme activity

The activity of four enzymes was measured in 16 biocrust taxa according to Bell et al. (2013). The enzymes are predominantly produced by microorganisms on the surface of macroscopic biocrust organisms, and are involved in carbon, nitrogen and phosphorus cycles (Table 4). Because the protocol was designed for soil analyses, minor changes were made to allow the measurement of enzymes in biocrust organisms.

Once taxa were separated from the soil, 0.1 g samples were placed directly into deep-well plates, allowing four replicate wells per enzyme per taxon (16 wells total for each taxon). After 1200 μl of sodium acetate buffer was pipetted into each well, the plates were shaken at 150 rpm for 30 min using an orbital shaker rather than being centrifuged. After shaking, fluorescently-labelled substrates were added to the appropriate wells, according to Bell et al. (2013). Plates were then covered, and samples incubated at 35 °C for 90 min. For all other steps, the protocol of Bell et al. (2013) was followed.

Data analysis

In total, we measured eight functional traits across 40 taxa, though due to the scarcity or minute size of several taxa, only a subset could be measured for some traits (Table 3, Supplementary data). Spearman's rank correlation coefficient (ρ) was used to examine correlations among traits because numerous associations were nonlinear.

To illustrate the functional similarities and differences among taxa, we performed a non-metric multidimensional scaling (NMDS) ordination in multi-trait space. Ability to fix nitrogen, a binary functional trait possessed exclusively by the cyanolichens *Collema coccophorum* and *Peltula* spp., was included in the ordination in addition to the eight quantitative traits described above. The NMDS distance matrix was calculated using Gower distance because it tolerates missing values and different types of data (Gower 1971).

Permutational Multivariate Analysis of Variance (PERMANOVA) was used to assess functional differences among morphogroups and taxonomic divisions (i.e. lichen, moss and liverwort). The leafy liverwort morphogroup was removed prior to analysis because it comprised only one taxon. The PERMDISP approach of Anderson (2006) was used to test the homogeneity of multivariate dispersions within groups, because data with heterogeneous dispersions can produce misleading results, particularly when groups are unbalanced (Warton et al. 2012; Anderson and Walsh 2013). When homogeneity was not satisfied, Tukey pairwise comparisons were conducted to identify the groups with significantly different dispersions.

All statistical analyses were performed in R, version 3.2.2. (R Core Team 2015). The *cluster* package was used to generate a distance matrix based on Gower distance (Maechler et al. 2015), while NMDS, PERMANOVA and PERMDISP were computed using the *vegan* package (Oksanen et al. 2015). Barplots were produced in SigmaPlot Version 11.0, while all other figures were generated using the *ggplot2* package (Wickham 2009).

Results

Our biocrust taxa were distributed broadly across the range of each trait. In general, mosses captured the most sediment and absorbed the most water (Fig. 1). Most notable of these was *Triquetrella papilla*, *Barbula calycina* and *Bartramia hampeana* ssp. *hampei*.

Table 4 Summary of enzymes measured and their functional roles

Enzyme	Nutrient cycle	Function	Produced by
β-glucosidase	Carbon	Sugar degradation	Microorganisms
β-D-cellobiosidase	Carbon	Cellulose degradation	Microorganisms
N-acetyl-β-glucosaminidase	Nitrogen	Chitin degradation	Microorganisms and lichens
Phosphatase	Phosphorus	Phosphorus mineralization	All biocrust organisms

Conversely, lichens (and their associated microorganisms) generally showed the highest enzyme activities (Fig. 2). These lichens were a mixture of crustose (*Diploschistes*, high phosphatase and NAG) and squamulose (greater NAG and glucosidase) forms. Several traits were correlated. For example, sediment capture was highly correlated with height (Spearman's $\rho = 0.77$; Fig. S1) and absorptivity ($\rho = 0.76$). There were also strong positive correlations between enzyme traits ($\rho = 0.51–0.84$). There was no significant correlation between height and root length across all taxa ($\rho = -0.05$; Fig. 3), but correlations were stronger when data were partitioned into taxonomic divisions ($\rho = 0.45$ for mosses, −0.45 for lichens and 0.10 for liverworts). A summary of all trait data is presented in Table S1.

Taxon dispersion varied significantly among morphogroups (PERMDISP: $F_{7,31} = 2.86$, $P = 0.02$) and taxonomic divisions (PERMDISP: $F_{2,37} = 11.91$ $P = 0.0001$). While there were too few divisions to adjust for group heterogeneity by removing some members, morphogroups had similar dispersion after squamulose and fruticose lichen morphogroups were removed (PERMDISP: $F_{5,27} = 2.24$, $P = 0.08$) because these groups accounted for most of the variation in dispersion (Tukey's test: $P < 0.05$). We were therefore unable to undertake a PERMANOVA on the complete dataset without potentially confounding dispersion and location effects (Warton et al. 2012). However, removing squamulose and fruticose lichens from analyses revealed strong evidence for functional differences between the remaining morphogroups (PERMANOVA: Pseudo-$F_{5,27} = 10.38$, $P = 0.001$). Although this result should be interpreted with caution, due to the removal of two morphogroups, it is consistent with the ordination results (NMDS), which showed that morphogroups loosely clustered together in multi-trait space (Fig. 4). When we performed NMDS ordination using the Bray-Curtis dissimilarity measure, on a reduced dataset with no missing values, a similar arrangement of morphogroups resulted (Fig. S2).

Discussion

In this study, we developed a novel protocol to assess the functional traits of biocrust taxa. Our study showed that: 1) lichens and bryophytes were not distributed evenly throughout the range of each functional trait; and 2) there was some evidence that morphogroups are functionally different.

Tall mosses and large, strongly three-dimensional lichens such as *Cladia* spp. trapped more sediment than shorter mosses, liverworts and more compressed, largely two-dimensional lichens. These sediment capture values are consistent with the notion that taller taxa provide a more effective barrier to trap soil particles (Eldridge and Rosentreter 1999) than shorter taxa. Moss density and thallus continuity in lichens may have also had an effect on resource capture (Eldridge and Rosentreter 1999). The scattered arrangement of most samples of *Gigaspermum repens*, for example, likely contributed to the low sediment capture values of this species. Furthermore, reproductive structures, such as sporophytes in bryophytes and podetia in lichens, enhance sediment capture by providing additional height. The threshold velocity required to entrain particles increases with increasing height of taxa (Leys and Eldridge 1998). The procedural control effectively quantified sediment capture by surface roughness; the mean value was not zero because some sediment was retained in micro-depressions.

Sediment capture affects related ecosystem processes such as nutrient cycling and hydrology through its effects on erosion. Eroded soils are relatively rich in nutrients because finer soil fractions, such as fine organic particles, are mobilised during the initial phases of a wind erosion event (Pimentel et al. 1995; Larney et al. 1998). The trapping of windborne particles thus reduces nutrient losses from a system. By trapping windborne silt and clay, biocrust organisms also affect hydrology through increasing the water-holding capacity of surrounding soil (Danin and Ganor 1991). Deposition of

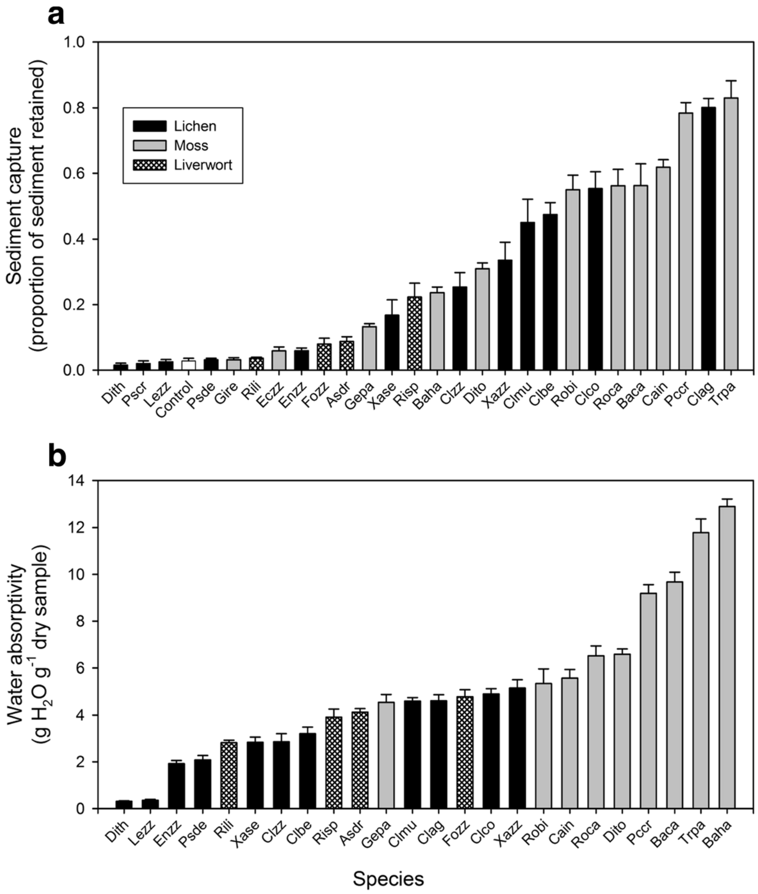


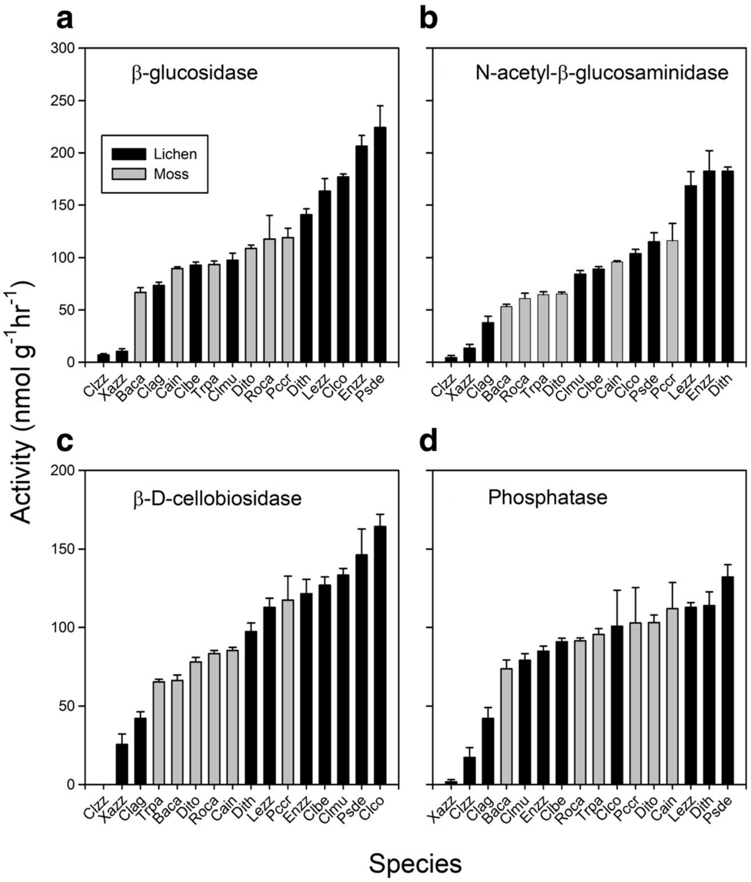
Fig. 1 **a** Sediment capture (mean ± SE, *n* = 5); and **b** water absorptivity (mean ± SE, *n* = 5) of biocrust taxa. Species codes are given in Table 2

soil on biocrust organisms would reduce their ability to photosynthesise; thus strong sediment capture abilities may appear to be a deleterious trait for individual biocrust organisms. However, previous studies have shown that mosses inhabiting areas with high levels of wind erosion are surprisingly resilient when covered with sediment (Moore and Scott 1979; Danin and Ganor 1991). For example, Moore and Scott (1979) reported that some individuals of the moss species *Didymodon torquatus* were able to survive being buried under 4 cm of sand for three months. Because many of these species have leaves that twist around their stems (Family Pottiaceae), they have the ability to shake off sediment as the plants become hydrated (Danin and Ganor 1991), effectively ‘swimming’ through the soil. Their capacity to grow through layers of sediment is obvious when one looks at photomicrographs of soil taken from moss-covered soils (Eldridge 1998).

Mosses, unlike lichens, have specialised terminal structures (e.g. hair points) and structures on the leaves, such as papillae and lamellae, which trap and store water, respectively (Catcheside 1980). Their ability to trap as well as directly absorb water may partly explain the observation that mosses, in general, were able to absorb more water than lichens and liverworts. It is possible that we underestimated absorptivity values in liverworts because they usually take longer than five minutes to return to their active hydrated condition and probably had the potential to imbibe more water (Campbell 1904).

Given the well-established relationship between root and shoot systems in vascular plants (Mokany et al. 2006), the finding that height and root length were unrelated in biocrust taxa was unexpected. These results may reflect the structural diversity of biocrust taxa, including unattached species of lichen with no rhizines, compressed squamulose lichens with dense rhizines and minute mosses with long roots and abundant protonemata. Most height measurements for mosses were near or beyond the lower limits of the range provided by Catcheside (1980). For example, *Didymodon torquatus*

Fig. 2 **a** β-glucosidase activity (mean ± SE, *n* = 4); **b** β-D-cellobiosidase activity (mean ± SE, *n* = 4), **c** N-acetyl-β-glucosaminidase activity (mean ± SE, *n* = 4); and **d** phosphatase activity (mean ± SE, *n* = 4) of biocrust taxa. Enzyme activity was measured in nmol g^{-1} h^{-1}. Species codes are given in Table 2



stems are described as 5–20 mm in length in the literature (Catcheside 1980), a range that lies above our mean value of 3.4 mm. The inconsistency between values for moss height between field-based measures and published literature indicates that generalised trait data from published works may not adequately reflect the true value of these traits and may underestimate or overestimate their values for certain ecosystem functions. In addition, Catcheside (1980) may have

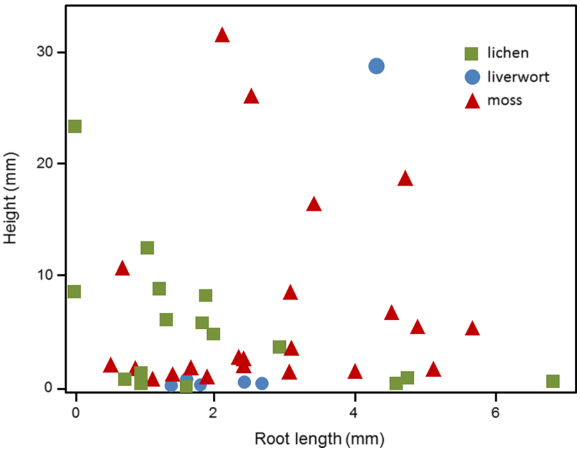


Fig. 3 Correlation between root (or rhizine) length and height of lichens (Spearman's ρ = −0.45), liverworts (ρ = 0.10) and mosses (ρ = 0.45). When all groups were combined, ρ = −0.05

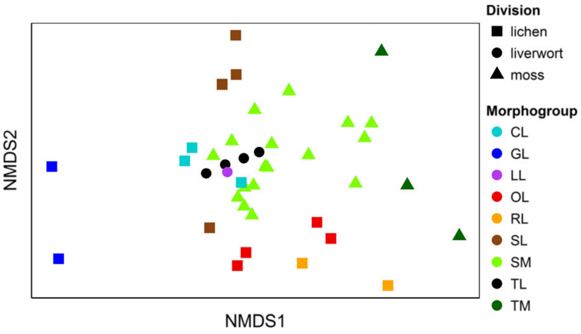


Fig. 4 NMDS ordination of 40 biocrust taxa in multi-trait space (stress =0.18). CL = crustose lichen, GL = gelatinous lichen, LL = leafy liverwort, OL = foliose lichen, RL = fruticose lichen, SL = squamulose lichen, SM = short moss, TL = thallose liverwort, TM = tall moss. Square symbols = lichens, circles = liverworts, triangles = mosses

measured the mosses in their taller, hydrated state, rather than their dormant, desiccated state, which is their predominant condition in our study area.

Macroscopic biocrust organisms and microbial communities are tightly interlinked (Belnap 2003b; Castillo-Monroy et al. 2015). The four enzymes we assessed all provide a measure of the functional role of macroscopic biocrust organisms in decomposition processes. For example, phosphatase is produced by macroscopic and microscopic components of the biocrust in response to low levels of phosphorus. Phosphatase mineralises organically-bound phosphorus, making it available for vascular plants and other organisms (Malcolm 1983). Inorganic phosphorus is a critical component of nucleic acids, adenosine triphosphate (ATP) and other biomolecules (Duff et al. 1994; Schachtman et al. 1998). One observation from the measurement of enzyme activities was that lichens and their associated microbial communities generally had higher N-acetyl-β-glucosaminidase activity than mosses. Chitin is a major component of the cell walls of the lichen mycobiont (Galun et al. 1976), but is not found in the plant kingdom (Muzzarelli 2011). Bacteria, fungi and archaea produce chitinases, such as N-acetyl-β-glucosaminidase, in order to decompose and consume chitin, or in the case of some fungi, to regulate their own structure during morphogenesis (Adams 2004; Bhattacharya et al. 2007). It comes as no surprise, therefore, that most lichens had a higher N-acetyl-β-glucosaminidase activity than mosses, as mosses do not produce chitin.

Biocrusts have substantial effects on soil microbial activity by moderating soil temperatures, altering hydrology and secreting anti-microbial metabolites (Huneck 1999; Escolar et al. 2015). Lichens, particularly squamulose and crustose morphological types, have a close affinity with soil microbial activity as they cover a large continuous area at the soil surface interface. Biocrust-forming lichens have even been shown to have species-specific effects on their underlying soil microbial communities (Delgado-Baquerizo et al. 2015). One possible explanation for the difference in β-glucosidase and β-D-cellobiosidase activities across taxa is that some soil microbes and their products would have been retained on lichen thalli or on rhizines, despite our attempts to remove all traces of soil. Mosses and foliose lichens, which were clipped at the base of the stem or thallus, would not have had this additional input of microbial products.

There was some evidence that biocrust taxa within morphogroups are functionally similar, supporting the notion that morphological structure is a reasonable proxy of an organism's effect on ecological function (Eldridge and Rosentreter 1999; Read et al. 2014). For example, the smooth thallus of crustose lichens does not permit high levels of sediment capture, whereas the prominent tall mosses have a morphology that is more effective at performing this function. However, there was some overlap in our ordination resulting from continuous variation within morphogroups. For example, the thalli of some squamulose lichen taxa such as *Cladonia* spp. can be vertical or raised at the edges, enhancing their capacity to trap resources over and above other squamulose lichens lacking such structures. The finding that morphogroups are functionally distinct reinforces their utility in rapid, low-cost assessments of ecosystem condition (Eldridge and Rosentreter 1999; Read et al. 2014).

Our study detailed eight methods of measuring functional traits in macroscopic biocrust taxa. Although our data are from eastern Australia, they represent taxa with a broad global distribution (Rogers and Lange 1972). Our results and methods are relevant therefore for areas of drylands globally. However, for this research to be applied in future studies, further work is required to establish trait data for a larger suite of biocrust taxa. A test of the reliability of our methodology using variance partitioning is highly recommended. It would also be useful to compare the traits of distant populations of taxa, to determine whether mean values for various traits can be applied globally with sufficient accuracy. Notwithstanding these limitations, our protocol has the potential to improve the way we view ecosystem functioning in the context of biocrust communities, which are important providers of essential ecosystem goods and services.

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