

1 **Livestock grazing and aridity reduce the functional diversity of biocrusts**

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21 **Running header:** Functional diversity of biocrusts

22

23 **Abstract**

24

25 *Background and aims* Livestock grazing and climate change are two of the most important
26 global change drivers affecting ecosystem functioning in drylands. Grazing and climate are
27 known to influence the cover and composition of biocrusts, which are substantial components
28 of dryland soils globally. Much less is known, however, about how these global change
29 drivers affect the functional diversity of biocrust communities in these ecosystems.

30

31 *Methods* Here, we evaluate the role of increasing aridity and grazing intensity in driving the
32 functional diversity of biocrusts. We collected data on multiple biocrust functional traits and
33 community composition, recent and historic grazing intensity, and vascular plants at 151 sites
34 from drylands in eastern Australia. We then used structural equation modelling and a fourth
35 corner analysis to examine the combined effects of aridity and grazing on biocrust functional
36 diversity and individual functional traits.

37

38 *Results* Aridity had a significant direct suppressive effect on biocrust functional diversity.
39 Effects of grazing by livestock, kangaroos and rabbits on functional diversity were
40 predominantly indirect and suppressive, mediated by a reduction in biocrust cover. Grazing
41 did, however, promote functional diversity *via* an increase in vascular plant richness, with a
42 concomitant increase in biocrust richness. The overall effect of grazing on biocrust functional
43 diversity however was negative. Fourth corner analyses revealed that livestock grazing had a
44 significant negative effect on the ability of biocrusts to stabilise the soil. Aridity had strong
45 negative effects on biocrust height and their ability to absorb water and capture sediment.
46 Few significant relationships were detected between enzyme-related traits and environmental
47 variables.

48

49 *Conclusions* Our findings provide novel evidence that the combination of increasing aridity
50 and intensified livestock grazing will reduce the functional diversity and capabilities of
51 biocrust communities, with resultant declines in ecosystem functioning.

52

53

54 **Keywords:** Trait; Biological soil crust; soil crusts; ecosystem function; functional diversity;
55 livestock; Drylands

56

57 **Introduction**

58

59 Biocrusts inhabit most terrestrial ecosystems but are particularly abundant in drylands as a
60 consequence of their high tolerance to temperature and moisture extremes (Weber et al.
61 2016). In these ecosystems, biocrusts play important roles in moderating key ecosystem
62 functions such as water infiltration and nutrient cycling (Bowker et al. 2013; Delgado-
63 Baquerizo et al. 2013). Biocrust attributes such as cover and taxonomic richness have been
64 reported to be highly vulnerable to climate change and land use intensification (Ferrenberg et
65 al. 2015; Concostrina-Zubiri et al. 2016). Much less is known, however, about how the
66 functional diversity of biocrusts will respond to the combined effects of aridity and land use
67 intensification.

68

69 The way in which biodiversity, commonly quantified as taxonomic diversity (e.g. number of
70 species), interacts with ecosystem functioning has been long studied. In these studies,
71 however, taxonomic diversity is a surrogate for functional diversity, relying on a correlation
72 that is frequently, but not consistently, positive (Diaz and Cabido 2001). For example, studies
73 that measure both functional and taxonomic diversity often show that both respond
74 differently to the same environmental drivers (de Bello et al. 2006; Ernst et al. 2006; Villéger
75 et al. 2010). Since functional effect traits directly measure the mean effects of taxa or
76 functional types on ecosystem functioning, conclusions drawn from the link between
77 functional diversity indices and ecosystem functioning are theoretically more valid than those
78 drawn from simple taxonomic diversity.

79

80 Livestock grazing and climate change are two of the most important drivers of ecosystem
81 function in drylands (Maestre et al. 2016). Overgrazing by livestock alters ecosystem
82 functions, particularly in drier environments (Eldridge et al. 2016b), and pressures from
83 grazing are predicted to intensify by up to 70% by 2050 (FAO 2017). Livestock grazing
84 reduces crust cover directly by trampling (Eldridge 1998) and indirectly, via its effects on
85 vascular plant cover (Tabeni et al. 2014). Climate is also likely to have substantial effects on
86 biocrusts by altering composition (Maestre et al. 2013; Ochoa-Hueso et al. 2016) and the
87 ability of crusts to produce radiation-resistant pigments (Belnap et al. 2004; Reed et al. 2012;
88 Ferrenberg et al. 2015). Improving our understanding of how grazing and climate affect
89 biocrust function is critically important if we are to manage drylands sustainably.

90

91 Despite the mounting literature on the effects of livestock disturbance and climate change on
92 biocrust attributes, there are three major knowledge gaps. First, most studies have focused on
93 biocrust cover and taxonomic richness, but little is known of the combined effects of climate
94 change and disturbance in driving functional diversity of biocrusts. Second, most studies
95 provide evidence of the vulnerability of biocrusts to disturbances at the local scale, but much
96 less is known about how climate and grazing affect biocrust functional diversity at regional
97 scales, which are aligned with the scales at which aridity and grazing operate (Maestre et al.
98 2016). Finally, we lack studies exploring the role of long-term climate changes (e.g. aridity)
99 and land use intensification across environmental gradients (“real world” situations), as most
100 information comes from laboratory-based studies simulating short-term climate changes (e.g.
101 drought or sudden increases in temperature).

102

103 A recent study showed a positive relationship between rainfall and the functional diversity of
104 biocrusts on the Iberian Peninsula (Concostrina-Zubiri et al. 2014). Others have provided
105 evidence of multiple interactions among biocrust traits and environmental variables (Bowker
106 et al. 2011; Michel et al. 2013), or similarities in traits among functional groups of biocrusts
107 (Gavazov et al. 2010; Kidron and Tal 2012; Mallen-Cooper and Eldridge 2016). Here, we
108 aim to build a system-level understanding of the direct roles of aridity and grazing in driving
109 biocrust function, and indirectly, *via* multiple environmental drivers and biocrust attributes.
110 To do this we used two different modelling approaches; a structural equation model, to
111 examine the combined effects of aridity and grazing on biocrust functional diversity, and a
112 fourth corner model, to investigate the effects of these drivers on specific traits of species
113 (Brown et al. 2014).

114

115 With limited previous research on biocrust function, it is difficult to make a comprehensive
116 set of *a priori* predictions about environment-trait interactions derived from the fourth corner
117 model. Nevertheless, Concostrina-Zubiri et al. (2014) showed that drier regions support
118 biocrust taxa with thicker attachment structures. Consequently, we expected that our drylands
119 would support taxa with longer roots (or rhizines in lichens). We also expected grazing to
120 hinder the establishment of taller taxa, as they are more susceptible to trampling, but that
121 aridity would promote communities with taller taxa, as they are better able to withstand the
122 high levels of erosion and regular depositional events associated with more arid regions
123 (Read et al. 2014).

124

125 **Methods**

126

127 *Study area*

128

129 Our study area covered an area of about 0.4 M ha in eastern Australia (31.5°S - 36°S, 145°E
130 – 148.3°E; Figure 1). The climate in this region is mostly semi-arid and dry-subhumid
131 (Aridity Index = 0.19 to 0.63; FAO 2013), and rain falls uniformly throughout the year, with
132 slightly more rainfall in winter in the southernmost sites. Average annual rainfall varied along
133 a northwesterly gradient from 850 mm in the southeast to 320 mm in the northwest. Average
134 annual temperatures (~18°C) varied little across the area (BOM 2017). The 151 sites were
135 non-contiguous fragments of woodland dominated by the tree species White cypress pine
136 (*Callitris glaucophylla*). These communities have been used extensively for livestock grazing
137 and forestry over the past ~200 years (Thompson and Eldridge 2005). The soils are relatively
138 deep sands to clay loams that support a moderate cover of biocrusts (Figure 1).

139

140 *Data collection*

141

142 In order to capture a range of grazing intensities, we selected sites from a range of tenures
143 including roadside reserves used for moving livestock (Travelling Stock Reserves),
144 conservation reserves, exclosures and private land. We also used Arc GIS to stratify sites to
145 capture a range of distances from permanent water, which is regarded as a useful surrogate of
146 grazing intensity (Andrew 1988).

147

148 At each site we established a 200 m transect that ran perpendicular to the nearest livestock
149 watering point. Along this transect we placed five 25 m² (5 m x 5 m) quadrats (henceforth
150 ‘large quadrat’) 50 m apart (i.e. at the 0 m, 50 m, 100 m, 150 m and 200 m points). Within
151 each large quadrat, we selected a uniform area of biocrust for placement of a smaller 0.25 m²
152 quadrat (‘small quadrat’). Within each small quadrat we estimated total crust cover. At the 50
153 m position at all sites we also counted the number of individuals of each biocrust
154 morphospecies within the small quadrat using a 20x hand lens, and collected representative
155 samples of all taxa present. These were placed into a paper bag and transported back to the
156 laboratory, where they were identified using dissecting and compound microscopes and
157 standard taxonomic keys described in Mallen-Cooper and Eldridge (2016). To assess
158 abundance, we counted the number of individuals in a sample. However, we recognise that

159 the assessment of biocrust abundance can be problematic because counting the discrete crust
160 entities (the method we used) equates a near-microscopic moss with a crustose lichen the size
161 of a small dinner plate. This could potentially skew the functional dispersion centroid towards
162 small mosses and away from large lichens with continuous thalli. Biomass would be more
163 representative than counts in this case, particularly as most traits were measured per gram.

164

165 We identified and estimated the cover of groundstorey plants and shrubs in the five large
166 quadrats at each site (Eldridge et al. 2016a). To estimate recent grazing intensity, we first
167 identified and counted the faecal pellets of all mammalian herbivores (cattle, sheep/goat,
168 kangaroo, rabbit) in the large quadrat at each site. We were unable to differentiate between
169 sheep and goat dung, or between European rabbit (*Oryctolagus cuniculus*) and European hare
170 (*Lepus europaeus*) dung. Samples of dung were also collected at 20 sites, dried and weighed
171 in order to calculate the relationship between dung counts and dry mass for each herbivore.
172 We used this relationship to calculate the dry mass of dung at each site as a measure of recent
173 grazing intensity (see Eldridge et al. 2016a). For each site we recorded the width and depth of
174 all livestock tracks crossing the 200 m transect, calculated the cross-sectional area of tracks,
175 and used this as a measure of historic grazing history. We extracted values of the Aridity
176 Index (AI), which measures the relationship between precipitation and potential
177 evapotranspiration, from the CGIAR-CSI Global-Aridity and Global-PET Database
178 (<http://www.cgiar-csi.org>, Zomer et al. 2008). We then used this index to calculate aridity, as
179 $1 - AI$, so that increasing values of aridity corresponded with increasing dryness.

180

181 *Biocrust trait data*

182

183 Biocrust organisms have highly diverse morphologies, yet biocrust traits must be applicable
184 to all constituent organisms, or at the very least, the macroscopic organisms. In a previous
185 study we devised and measured eight functional effect traits in individual macroscopic
186 biocrust species (Mallen-Cooper and Eldridge 2016): (1) absorptivity, (2) sediment capture,
187 (3) height and (4) root (or rhizine) length relate to erosional and hydrological functions
188 (Table 1; Bowker et al. 2010); (5) phosphatase (PHOS) and (6) N-acetyl- β -glucosaminidase
189 (NAG) activity provide a measure of the degree to which each biocrust species contributes to
190 phosphorus and nitrogen cycles respectively; (7) β -D-cellobiosidase (CB) and (8) β -

191 glucosidase (BG) activity are surrogates of species' contributions to the carbon cycle through
192 decomposition (Delgado-Baquerizo et al. 2015; Mallen-Cooper and Eldridge 2016).

193

194 The biocrusts of south eastern Australia are known to contain many rare species (Eldridge et
195 al. 2006). Unfortunately, measuring traits across large environmental gradients is only
196 feasible in the more abundant species. Rare species, however, are unlikely to contribute
197 greatly to ecosystem functioning, according to the mass ratio hypothesis (Grime 1998).

198

199 *Data analysis*

200

201 We used two complementary approaches to analyse the data: a structural equation model
202 (SEM; Shipley 2000) and a fourth corner model (Brown et al. 2014). To date, there are no
203 standardised methods of measuring functional diversity (Pavoine and Bonsall 2011). The
204 Laliberté and Legendre (2010) measure of functional diversity (Functional dispersion –
205 FDis), however, has garnered considerable support in recent field and simulation studies due
206 to several desirable properties (Paquette and Messier 2011; Mason et al. 2013; Gagic et al.
207 2015). First, the index can be weighted by species abundances, which has been shown to
208 improve explanatory power (Gagic et al. 2015). Second, it varies independently of taxonomic
209 richness and evenness, a necessary condition identified by Mason et al. (2005). Third, it
210 tolerates any number and type of traits. Functional dispersion, however, does not allow for
211 intraspecific variation, which accounts for a sizeable fraction of the total trait variation in real
212 world situations (Siefert et al. 2015).

213

214 For each site, the functional diversity index (FDis) used here calculates the mean distance of
215 species in multivariate trait space to a centroid that is weighted by species' abundances. To
216 compute functional diversity, we firstly generated a Gower dissimilarity matrix between
217 species for which we had sufficient trait data (Supplementary Material S1). Gower
218 dissimilarity was used because it tolerates missing values. Principle coordinates analysis
219 (PCoA) was performed on this matrix in the *FD* package version 1.0-12 in R (Laliberté et al.
220 2014), which derived a value of functional diversity for each of the 129 sites that contained
221 biocrust samples. A site where only one species is present is allocated a value of zero for
222 functional diversity. The 22 sites where no species were recorded were excluded from these
223 analyses because the aim of this study was to determine how the traits of biocrusts vary,
224 rather than the environmental conditions controlling the presence or absence of biocrusts.

225

226 We then used structural equation modelling to build a systems understanding of the direct and
227 indirect effects of grazing and aridity on functional diversity. In our *a priori* model both
228 aridity and grazing had direct effects on functional diversity and indirect effects, mediated by
229 changes in perennial plant cover, plant richness, biocrust cover and biocrust richness. We
230 used perennial plant cover rather than total cover because perennial plants are persistent and
231 provide substantial ecosystem stability, and would be expected to support communities with
232 an extensive crust cover. The effects of recent and historic grazing were combined in our
233 models into a single composite variable ('grazing'), which increased with increasing grazing
234 intensity. The SEM allowed us to partition direct and indirect effects of one variable upon
235 another and to estimate the strengths of these multiple effects. To improve normality, the six
236 predictor values were standardized (z-transformed) prior to analyses. Overall goodness of fit
237 probability tests were performed to determine the absolute fit of the best models. The
238 goodness of fit test estimates the long-term probability of the observed data given the *a priori*
239 model structure. Thus high probability values indicate that these models are highly plausible
240 causal structures underlying the observed correlations. All SEM analysis was conducted
241 using AMOS Software Version 20. The stability of these models was evaluated as described
242 in Reisner et al. (2013).

243

244 Fourth corner analysis is being used increasingly in ecological studies. Unlike other methods,
245 which are more indirect (such as community-weighted means), fourth corner analysis
246 combines traits, environmental variables and species abundances into the same predictive
247 model (Brown et al. 2014). It also provides a detailed insight into the effects of drivers like
248 aridity and grazing on specific ecosystem functions. Fourth corner analysis describes the
249 process of using three matrices – sites by environmental variables, sites by species'
250 abundances, and species by functional traits – to derive a 'fourth' matrix of functional traits
251 by environmental variables (Legendre et al. 1997). We followed the method of Brown et al.
252 (2014), whereby a predictive species distribution model is fitted with environmental
253 variables, species traits and their interaction as explanatory variables. The environment-trait
254 interaction produces the fourth corner coefficients, which represent the pairwise relationships
255 between each functional trait and environmental variable. To calculate the fourth corner
256 coefficients, we used the *mvabund* package version 3.11.9 in R (Wang et al. 2012). The same
257 predictors used in the structural equation model were used in this model, excepting biocrust
258 cover and richness. Only species for which we had complete trait data were included in the

259 fourth corner analyses because the calculations do not allow for missing values. Using the
260 enzyme traits we had data for 104 sites and 16 species, and for physical traits 115 sites and 24
261 species. We therefore analysed enzyme and physical trait data sets separately in order not to
262 compromise the power of the four physical traits. Both models were fitted with a binomial
263 distribution. A least absolute shrinkage and selection operator (LASSO) was used to
264 determine which environment-trait interactions lowered the Bayesian Information Criterion
265 (BIC) of the model. Interactions that did not lower the BIC were set to zero and were deemed
266 non-significant. Livestock tracks and all dung variables were log-transformed in order to
267 satisfy statistical assumptions. Graphical outputs were produced in the R packages *ggplot2*
268 version 2.2.0 (Wickham 2009) and *lattice* version 0.20-34 (Sarkar 2008). For the functional
269 diversity index used in the SEMs, abundance was measured on a log (10) scale. For the fourth
270 corner analysis, abundance was binary transformed (i.e. presence or absence) in order to
271 improve model fit.

272

273 **Results**

274

275 We identified a total of 59 biocrust species across 151 sites. However, due to a shortage of
276 trait data, only 40 of these species from 129 sites could be included in the structural equation
277 model (Supplementary Material S1). Functional diversity was unrelated to biocrust species
278 richness (Spearman's $\rho = 0.006$; $P < 0.01$) after removal of a cluster of zeroes; Figure 3).

279

280 *Grazing and aridity effects on functional diversity*

281

282 Our structural equation model explained 32% of the variance in biocrust functional diversity
283 ($\chi^2 = 0.074$, $df = 1$, $P = 0.79$; Figure 2). We detected no direct effects of grazing on
284 functional diversity, but indirect effects on biocrust richness mediated by changes in biocrust
285 cover and plant richness. Perennial plant cover had a weak positive effect on biocrust
286 functional diversity and aridity a direct suppressive effect (Figure 2). Overall, the
287 standardized total effects were strongly negative for aridity (-0.22) and strongly positive for
288 biocrust richness (0.58) and cover (0.22), and to a lesser extent, plant richness and cover
289 (0.12; Figure 2).

290

291 *Grazing and aridity interactions with species traits*

292

293 There were a number of significant interactions among biocrust traits and environmental
294 variables (Figure 4, Supplementary Material S2). Aridity was negatively correlated with
295 sediment capture, height and absorptivity of water. Thus, as aridity increased, biocrust
296 communities not only became functionally less complex, but also shorter, less able to capture
297 sediment and less able to absorb water. Grazing herbivores had predominantly negative
298 associations with traits, with the exception of rabbits, which enhanced the height of biocrust
299 communities and their ability to capture sediment. Few significant interactions were detected
300 between enzyme traits and environmental variables, which may be a consequence of
301 relatively low statistical power.

302

303 **Discussion**

304

305 Our study provides evidence that the functional diversity of biocrusts is highly vulnerable to
306 increases in aridity and grazing. All effects from grazing on functional diversity were
307 indirectly driven *via* changes in other biocrust attributes such as cover and taxonomic
308 richness. Our results support the general notion that livestock grazing has overall negative
309 impacts on ecosystem functions, though grazing by livestock, rabbits and native herbivores
310 (kangaroos) showed a positive indirect effect *via* vascular plant richness, which did not
311 counteract other indirect negative effects from grazing on biocrust functional diversity. The
312 increase in plant richness is likely to be skewed towards exotic species, which tend to be
313 enhanced by introduced grazers (Oduor et al. 2010). Aridity, however, showed strong and
314 significant negative direct effects on the functional diversity of biocrusts, likely because of
315 the reduced number of functional groups able to survive very arid conditions. Aridity also
316 had negative effects on traits associated with erosion resistance, invertebrate habitat and
317 hydrology. Our results imply that the combination of increasing aridity with intensified
318 livestock grazing could have detrimental consequences for the functional composition of
319 biocrust communities; with implications for the adequate functioning of drylands, the largest
320 biome on Earth.

321

322 *Indirect effect of grazing on functional diversity*

323

324 Interestingly, we did not observe a direct effect of grazing animals on biocrust functional
325 diversity. Rather, any effect from grazing on functional diversity was indirectly driven *via*

326 biocrust cover and richness. Livestock are well-known to directly reduce cover by trampling
327 (e.g. Eldridge 1998), though other indirect mechanisms, which were not measured in the
328 present study, are possible and would contribute to the direct effect in our simplified model.
329 Our study suggests that grazing does not directly affect the suite of functional traits in a given
330 biocrust community, but rather reduces the overall cover of these organisms, indirectly
331 reducing the ranges of functional traits. In drylands, cover, or any measure of abundance, and
332 species richness are almost always positively correlated, although a theoretical consensus
333 explaining this relationship has yet to be reached (Bock et al. 2007). The accompanying
334 increase in functional diversity that follows an increase in species richness is likely due to the
335 ‘niche complementarity effect’, whereby a species-rich community is more likely to contain a
336 greater range of functional traits, and thus use resources more efficiently, than a relatively
337 species-poor community (Loreau 1998). Another more controversial explanation is the
338 ‘selection effect’ (Díaz and Cabido 2001).

339

340 We found a weak relationship between livestock tracks and ‘root’ length. These results are
341 consistent with results from Liu et al. (2009) who found that heavy grazing reduced the
342 ability of biocrusts to stabilise the soil. Increasing grazing by sheep reduced the capacity of
343 biocrusts to capture sediments but had no effect on biocrust height, which is one property that
344 influences sediment capture (Eldridge and Rosentreter 1999). This finding suggests that
345 sheep are affecting a different property of biocrusts that influences their ability to capture
346 sediment, perhaps by favouring species that grow in a dispersed, scattered arrangement rather
347 than those that grow in dense clumps (e.g. Eldridge 1998). Unlike Read et al. (2014), who
348 found that shorter biocrust taxa were indicators of heavily grazed sites while taller taxa were
349 indicators of protected sites, we found no relationships between the intensity of livestock
350 grazing and biocrust height. Interestingly, we found no relationship between absorptivity and
351 grazing. This result contrasts with Concostrina-Zubiri et al. (2016), who found grazed plots
352 had a lower abundance of fruticose lichens, which had particularly high water absorptivity
353 and retention values.

354

355 *Strong suppressive effects of aridity on functional diversity*

356

357 Aridity had a strong negative effect on the functional diversity of biocrusts and reduced the
358 prevalence of biocrust taxa with extreme values of some traits. The extremes of temperature
359 and moisture which characterise arid regions are important environmental filters, as not all

360 biocrust functional groups are able to establish and survive in such harsh conditions (Coe et
361 al. 2014). This process of habitat filtering constrains the range of various traits, resulting in
362 lower values of functional diversity (Cornwell and Ackerly 2009). Increases in aridity have
363 been reported to increase the cover of biocrusts (Delgado-Baquerizo et al. 2016), but our
364 results suggest that the likely increase in functional diversity linked to increases in cover with
365 aridity will not offset the strong reduction in functional diversity related to aridity *per se*. This
366 interesting result suggests that increases in aridity from climate change may promote the
367 cover of biocrust communities with strongly reduced functional diversity. Ecosystem
368 functioning in drylands is dependent to a large extent on biocrusts because as aridity
369 increases and biocrust communities are less able to stabilise soils and cycle nutrients, dryland
370 landscapes may become severely degraded.

371

372 We also found that increasing aridity strongly reduced sediment capture ability and generally
373 reduced biocrust height. The lack of relationship between root length and aridity contravenes
374 our hypothesis, revealing differential effects of aridity on the length and thickness of biocrust
375 attachment structures. Although there are occasional resource pulses, arid regions generally
376 have sparser vegetation, drier soils and stronger desiccating winds than more humid regions,
377 leading to high rates of erosion (Maestre et al. 2016). Biocrust communities in arid regions
378 are thus likely to be assembled from taxa with a poor ability to capture sediment because
379 those taxa which more readily capture sediments in their leaves and thalli are more likely to
380 be buried. The negative relationship between aridity and height goes against our hypothesis.
381 Read et al. (2014) found that short biocrust taxa were more likely to be found in areas
382 protected from high winds, and attributed this to the high likelihood of burial by wind-borne
383 sediment, thus preventing the establishment and persistence of these taxa in more exposed
384 areas. Despite taller taxa being better equipped to deal with high rates of aeolian erosion, it is
385 possible that there is a limitation on growth in arid conditions (e.g. productivity, soil
386 nutrients, or desiccation). Since there is a reasonably strong positive correlation between
387 height and sediment capture (Mallen-Cooper and Eldridge 2016), another possibility is that
388 being tall increases a biocrust organism's likelihood of surviving burial but also increases the
389 likelihood of being buried.

390

391 *Concluding remarks*

392

393 It is likely that the projected increase in aridity with climate change will be accompanied by a
394 reduction in the functional diversity of biocrusts and in specific biocrust functional traits,
395 irrespective of the reported increase in biocrust cover with aridity. Given that trait-based
396 functional diversity is fundamentally linked to the provision of ecosystem goods and services
397 (Díaz et al. 2007), a number of ecosystem services provided by biocrusts, such as soil
398 stabilisation and nitrogen fixation, may be threatened under current climate change scenarios.
399 It may be possible to artificially improve the resilience of biocrusts to climate change through
400 ‘assisted migration’ (Young et al. 2016). This might necessitate introducing taxa adapted to
401 very arid areas into areas that are expected to develop similar climatic profiles in time.
402 However, such promising developments are still in their infancy.

403

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405

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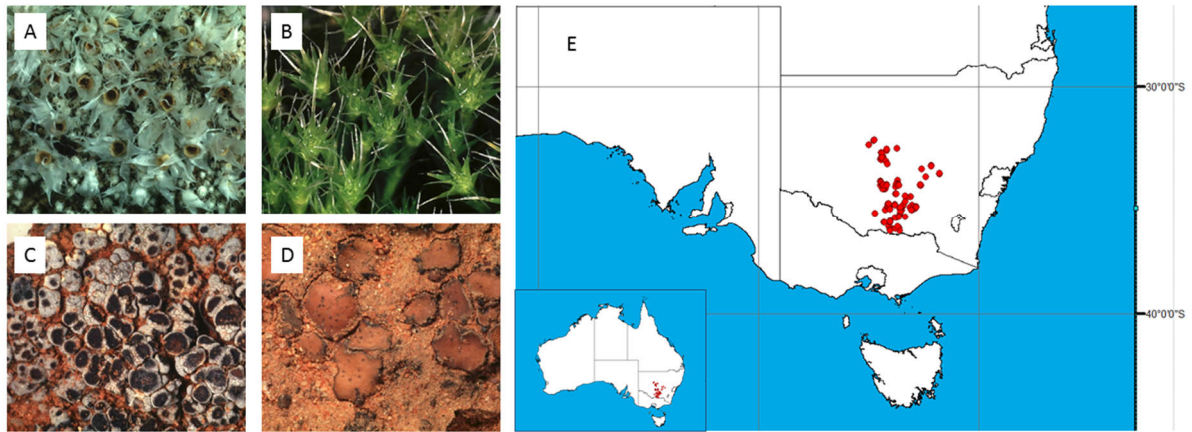
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629 Table 1. Summary of biocrust traits. The number of species measured and the number of
 630 replicates per taxa differed for each trait. The functional roles of each of these traits are also
 631 briefly described. PHOS = phosphatase activity, NAG = N-acetyl- β -glucosaminidase
 632 activity, CB = β -D-cellobiosidase activity and BG = β -glucosidase activity. ‘Root’ includes
 633 moss roots and lichen rhizines.
 634

Trait	# Species	Replicates	Functional role
Absorptivity	24	5	Infiltration, runoff
Sediment capture	27	5	Erosion resistance, resource trapping, soil texture
Height	46	20	Habitat for invertebrates, resource trapping, surface roughness
Root length	40	20	Soil aggregation, erosion resistance
PHOS	16	4	Phosphorus cycle (phosphorus mineralisation)
NAG	16	4	Nitrogen cycle (chitin degradation)
CB	16	4	Carbon cycle (cellulose degradation)
BG	16	4	Carbon cycle (sugar degradation)

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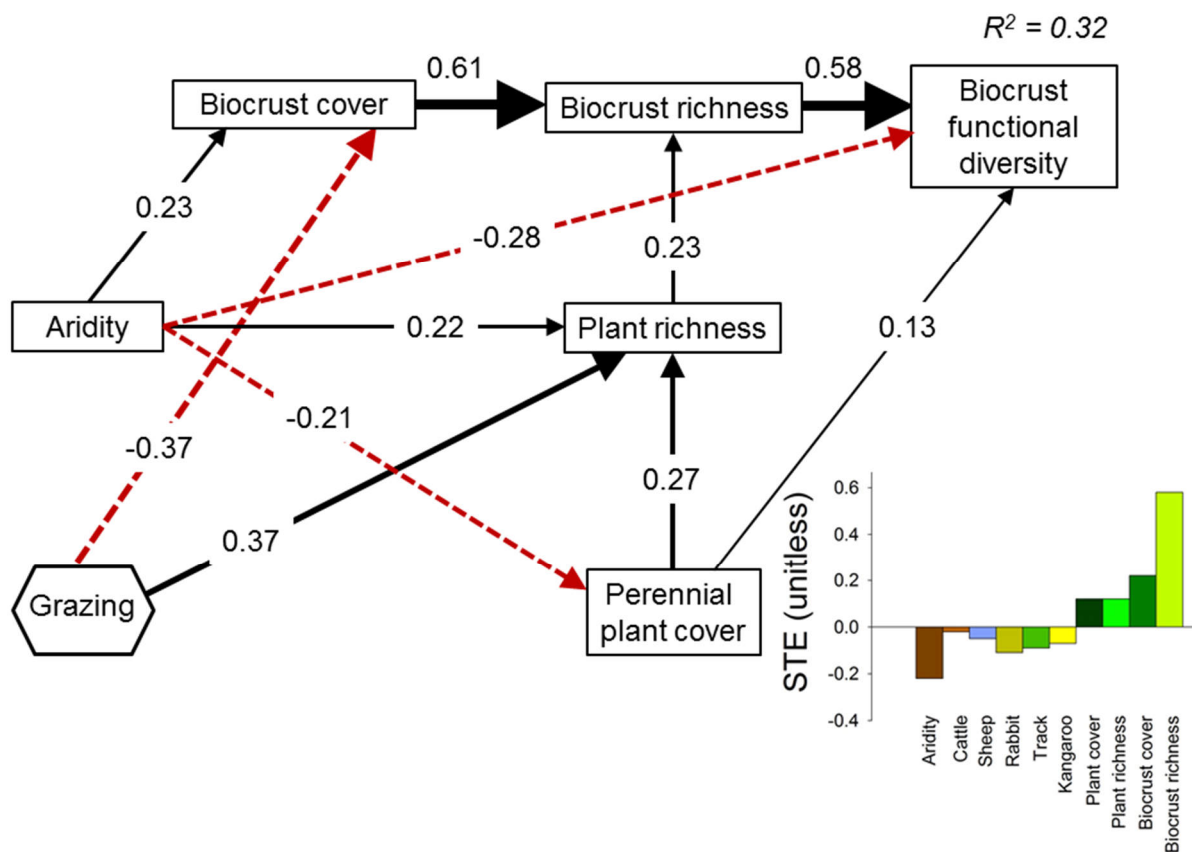
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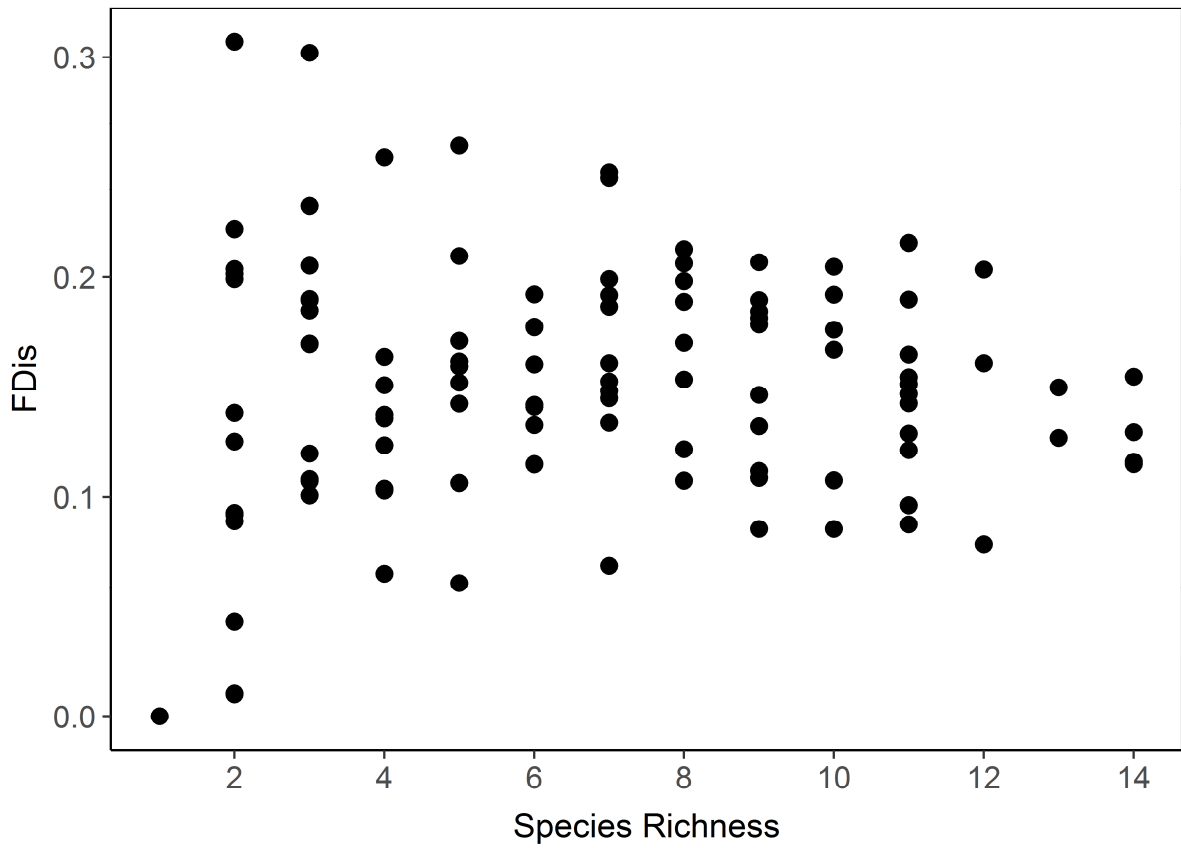
Figure 1. Images of short (A) and tall (B) mosses, and crustose (C) and squamulose (D) lichens from semi-arid Australia, and site map (E) showing the location of the study sites in eastern Australia. Photographs: Heino Lepp.



642

643 Figure 2. Final structural equation model illustrating direct and indirect effects of aridity and
 644 grazing on the functional diversity of biocrusts. The hexagon represents a composite variable,
 645 comprising livestock tracks and dung counts from cattle, sheep, rabbits and kangaroos. Line
 646 thickness represents strength of relationship.

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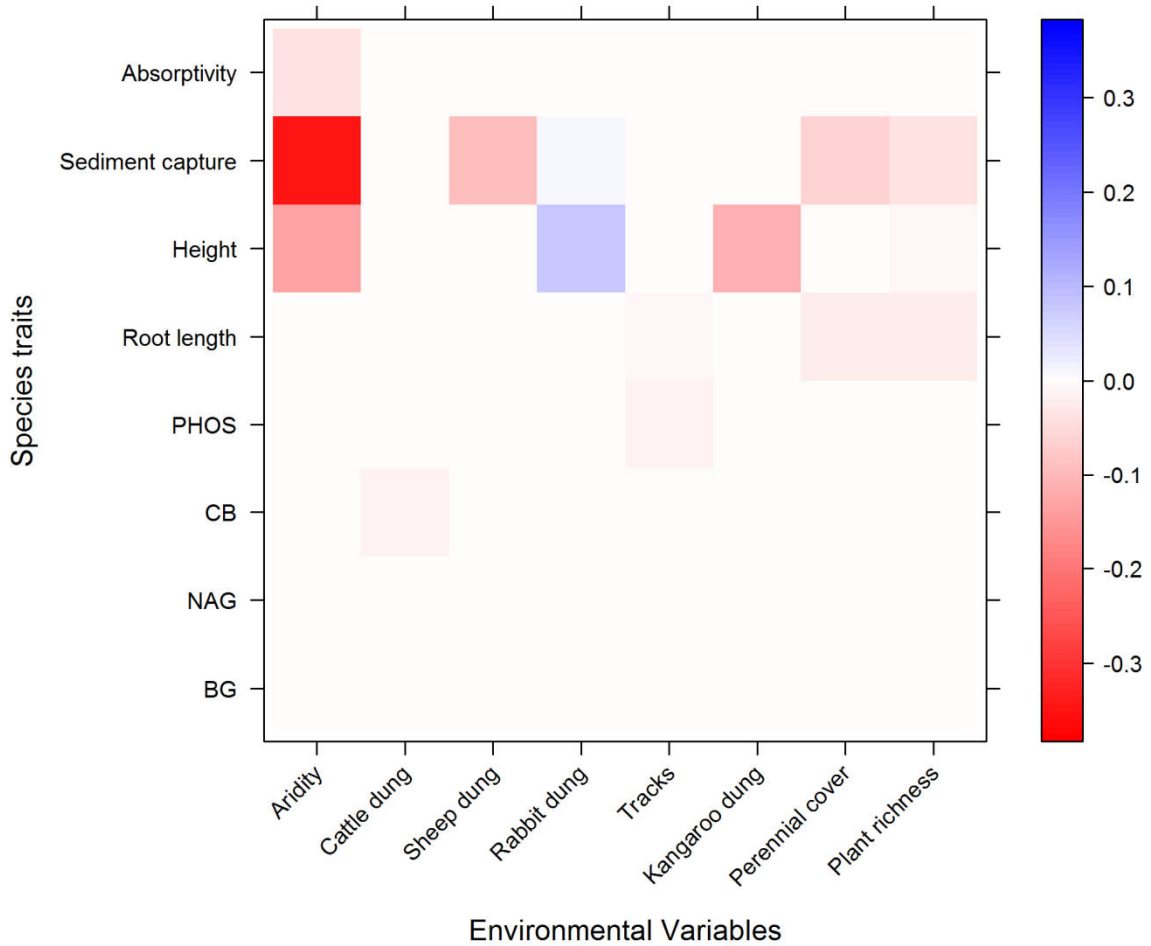
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650 Figure 3. Relationship between the functional diversity (FDIs) and species richness of
 651 biocrusts ($n_{\text{sites}} = 129$, $n_{\text{traits}} = 8$, $n_{\text{species}} = 40$). The point at (1,0) represents 21 sites which
 652 contained 1 species and were therefore assigned a value of 0 functional diversity. When these
 653 zeroes are removed, Spearman's $\rho = 0.00635$.

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655



656

657 Figure 4. Fourth corner interaction coefficients between biocrust traits and environmental
 658 predictors. Significant positive and negative associations, shown respectively in blue and red,
 659 were selected using a LASSO penalty. For the physical traits, $n_{\text{sites}} = 115$ and $n_{\text{species}} = 24$.
 660 Enzyme traits phosphatase (PHOS), β -D-cellobiosidase (CB), N-acetyl- β -glucosaminidase
 661 (NAG) and β -glucosidase (BG) activity had sample size $n_{\text{sites}} = 104$ and $n_{\text{species}} = 16$.