1

2   DR. DAVID JOHN ELDRIDGE (Orcid ID : 0000-0002-2191-486X)

3   DR. MANUEL DELGADO-BAQUERIZO (Orcid ID : 0000-0002-6499-576X)

4

5

7

8

9

10   Corresponding author mail id: d.eldridge@unsw.edu.au

11

12   **The influence of climatic legacies on the distribution of dryland biocrust communities**

13

14

15   David J. Eldridge[1] and Manuel Delgado-Baquerizo[2,3]

16

17

18   1.   Office of Environment and Heritage, c/- Centre for Ecosystem Science, School of

19   Biological, Earth and Environmental Sciences, University of New South Wales,

20   Sydney, New South Wales 2052, Australia

21

22   2.   Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior

23   de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Calle Tulipán

24   Sin Número, Móstoles 28933, Spain.

25

26   3.   Cooperative Institute for Research in Environmental Sciences, University of Colorado,

27   Boulder, CO 80309.

28

29   *Abstract*

30

31 Predicting the distribution of biocrust species, mosses, lichens and liverworts associated with

32 surface soils is difficult, but climatic legacies (changes in climate over the last 20ky) can

33 improve our prediction of the distribution of biocrust species. To provide empirical support

34 for this hypothesis, we used a combination of network analyses and structural equation

35 modelling to identify the role of climatic legacies in predicting the distribution of ecological

36 clusters formed by species of mosses, lichens and liverworts using data from 282 large sites

37 distributed across 0.6 million km^2 of eastern Australia. Two ecological clusters contained

38 87% of the 120 moss, lichen and liverwort species. Both clusters contained lichen, moss and

39 liverwort species, but were dominated by different families. Sites where the air temperature

40 increased the most over 20k years (positive temperature legacies) were associated with

41 reductions in the relative abundance of species from the lichen (Peltulaceae, Teloschistaceae)

42 and moss (Bryaceae) families (Cluster A species), greater groundstorey plant cover and lower

43 soil pH. Sites where precipitation has increased over the past 20k years (positive precipitation

44 legacy) were associated with increases in the relative abundance of lichen (Cladoniaceae,

45 Lecideaceae, Thelotremataceae) and moss (Pottiaceae) families (Cluster B species) and lower

46 levels of soil pH. Sites where temperatures have increased the most in the past 20k years

47 suppressed the negative effects of plant cover on Cluster B by reducing plant cover. Increased

48 intensity of grazing suppressed the negative effect of soil pH, and the positive effect of soil

49 carbon, on the relative abundance of Cluster B taxa. Finally, increasing temperature and

50 precipitation legacies reduced the negative effect of soil pH on Cluster B. Understanding of

51 the importance of climatic legacies improves our ability to predict how biocrust assemblies

52 might respond to on-going global environmental change associated with increasing land use

53 intensification, increasing temperature and reduced rainfall.

54

55 **Keywords:** soil crust, bryophyte, lichen, liverwort, drylands, ecological clusters

56

57 **Running header:** Biocrust distribution and climatic legacies

58

59 **Introduction**

60

61 Biocrusts are complex assemblages of lichens, bryophytes (mosses and liverworts),

62 cyanobacteria, fungi and microscopic organisms such as archae and bacteria that occupy the

63 top few centimetres of soil across a myriad of arctic, arid and temperate ecosystems (Weber

64 et al. 2016). Because of their intimate connection with surface soils, biocrusts play critical

65 roles in soil nutrient cycling and sequestration, soil hydrology, seedling establishment,

66 surface temperature regulation and provide habitat for soil micro-organisms (Delgado-

67 Baquerizo et al. 2016; Weber et al. 2016). Globally, biocrusts play substantial roles in the

68 carbon and nitrogen cycles (Weber et al. 2015). However, despite their huge importance in

69 drylands, where they are often the dominant form of land cover, there have been few fruitful

70 attempts to predict their distribution across large spatial scales (but see a recent global

71 modelling study by Rodriguez-Caballero et al. 2018). Rather, most studies have tended to

72 focus on specific study areas at the local scale (e.g. Eldridge 1996, Weber et al. 2008;

73 Rodriguez-Caballero et al. 2014; Chamizo et al. 2012; Garcia-Pichel et al. 2013).

74

75 Predicting the distribution of biocrusts is not an easy task. Although the current distribution

76 of these organisms is thought to be related to climatic, edaphic, topographic and biotic factors

77 (Bowker et al. 2016), many areas that would be expected to support particular crust species

78 are often devoid of crusts, and *vice versa*. Overall, therefore, we know relatively little about

79 what determines the distribution of soil crusts at broad regional scales (Steven et al. 2013).

80 Part of the reason could be that large areas of biocrust worldwide have been heavily modified

81 by land use practices such as overgrazing (Chiquoine et al. 2016) and these effects may

82 persist for many years. Surfaces disturbed during nuclear testing in arid Australia in the late-

83 1950s had still not recovered their full complement of species, particularly foliose lichens,

84 after more than 40 years (Eldridge and Ferris 1999). Similar scenarios exist for other areas

85 where biocrusts have been disturbed (Kuske et al. 2012), reinforcing the notion that it is

86 extremely difficult to accurately predict the current distribution of biocrusts. Given that

87 biocrust community composition is strongly driven by climate (e.g. Rogers 1971; Reed et al.

88 2012; Kuske et al. 2012; Lafuente et al. 2017) and that biocrusts are often considered slow

89 growing communities (decades to centuries), climatic legacies (changes in precipitation and

90 temperature over the last 20k years) might have also played a key role in shaping their current

91 distribution. Recent studies across a range of environments have shown that paleo-legacies

92 are important for predicting the effects of climate on microbial and plant communities

93 (Delgado-Baquerizo et al. 2017; Pärtel et al. 2017). Similarly, Lopez-Merino et al. (2017)

94 showed that paleo-climatic erosion events caused by flooding have had substantial effects on

95 the current growth of aquatic communities of *Posodonia*. However, an integrated approach

96 considering past climatic legacies for predicting the contemporary distribution of biocrust

97 communities is lacking, and requires knowledge of both current and past climatic condition

98 as well as multiple environmental attributes. An understanding of how biocrusts and their

99 associated taxa are distributed in drylands is a critically important research question that can

100 help us to manage potential change resulting from human-induced land use and climate-

101 related changes. Particularly lacking is an understanding of what historical conditions drive

102 the distribution of biocrust communities; specifically those from previous climates.

103 Information on climatic legacies could therefore, provide a useful way to improve our

104 capacity to predict the distribution of ecological assemblies of biocrusts across southern

105 Australia, but potentially somewhere else.

106

107 The contemporary distribution of bryophytes and lichens in soil crusts indicates that they are

108 closely tied to climate, particularly rainfall and temperature. For example, in eastern

109 Australia, the distribution of lichens is strongly driven by temperature and summer rainfall,

110 with biocrust lichens and bryophytes largely restricted to areas of winter rainfall (Eldridge

111 1996; Eldridge and Tozer 1996). Therefore, changes in precipitation and temperature over the

112 last 20k years might help explain the current distribution of mosses and lichen species today.

113 While we have a relatively good knowledge of the current status of biocrusts over many areas

114 (Weber et al. 2016), we still lack a clear understanding of how they might have changed in

115 response to altered climatic conditions over the past 20k years and whether these changes

116 have imposed a legacy effect on the distribution of crusts that we see today. A knowledge of

117 how climatic legacies might have affected, and continue to affect, biocrust distribution is

118 critical if we are to be able to separate changes resulting from human-induced impacts from

119 those that represent a legacy effect of former climates. By climate legacy we mean the

120 difference between climatic conditions 20k years ago and current conditions. For example, a

121 location would have a 'positive temperature legacy' if the temperature at that site is currently

122 greater than it was 20 k years ago. A knowledge of climate legacies could help to explain

123 why two locations with a similar current climate do not always support the same community

124 assembly. Predicting how the distribution of biocrusts might have changed and the likelihood

125 of recovery under current climates is critically important to allow us to allocate scarce

126 financial and intellectual resources to those areas most at risk of degradation and to prioritise

127 restoration efforts with limited finances. This could include activities such as inoculation,

128 which is designed to promote biocrust establishment and associated ecosystem services.

129

130 Here we used network analyses and a regional survey including data on the distribution of

131 biocrust lichen and bryophyte species across 0.6 million km^2 of eastern Australia to test the

132   hypothesis that climatic legacies (changes in temperature and rainfall conditions experienced

133   about 20k years ago), can help explain the current distribution ecological clusters formed by

134   biocrust species strongly co-occurring, and which might share environmental preferences. For

135   instance, certain species of mosses (e.g., *Fissidens* spp.) and lichens (e.g. *Xanthoparmelia*

136   spp.) are known to prefer more mesic conditions. Our focus here was on biocrust taxa, though

137   vascular plant clusters are also likely respond to climatic legacies.

138

139   **Materials and Methods**

140

141   *The study area*

142

143   The survey was conducted over an area of about 0.6 million km^2 in New South Wales, Australia and

144   bounded by the Queensland Border in the north (-29.00°), the South Australian border in the west

145   (141.00°), in the south by the Murray River, and in the east by longitude 147.50°. Annual rainfall

146   across the survey area ranged from ~400 mm in the north-east to ~ 150 mm in the north-west (Fig.

147   1), and is spatially and temporally variable. Seasonal distribution of rainfall was mainly summer-

148   dominant in the north-east to predominantly winter dominant (~30% more rainfall during the winter

149   months) in the south-west. Diurnal temperatures are typically hot in summer (> 40°C) and mild in

150   winter (>10°C), and evaporation increases from south to north and from east to west (Bureau of

151   Meteorology 2015).

152

153   Most of the survey area lies within the Murray-Darling Basin, a depositional landscape overlain by a

154   mosaic of Quaternary aeolian sediments, most of which is characterised by high pH soils. These

155   depositional landscapes ranged from level to slightly undulating plains of Quaternary aeolian

156   sediments and colluvial materials (Pickard and Norris 1994), to footslopes and ranges. Linear and

157   sub-parabolic dunes are superimposed upon broad sand sheets across the plains. Plains of Quaternary

158   alluvium are found on the Riverine Plain in the south-east, and along the floodplains of the major

159   rivers, particularly the Darling, Murrumbidgee and Murray Rivers which drain extensive areas of the

160   survey area. Soils across the survey area range from calcareous to neutral earths on the plains, to

161   shallow siliceous sands on the ranges to deep sands on the dunes. A more detailed description of the

162   soils and landscapes is given in Keith (2017).

163

164   Vegetation across the survey area was highly variable but could broadly be described as semi-arid

165   woodlands dominated by eucalypts (e.g. *Eucalyptus populnea, Eucalyptus intertexta*), white cypress

166   pine (*Callitris glaucophylla*) or mulga (*Acacia aneura*), with a grassy (*Austrostipa* spp.,

167   *Austrodanthonia* spp.) or shrubby (*Dodonaea*, *Eremophila* and *Senna* spp.) understorey. Plains of

168   quaternary alluvium are dominated by shrubs of the family Chenopodiaceae (*Atriplex, Maireana*,

169   Eldridge et al. 2017), and sandplains and dunefields by assorted eucalypts (Keith 2017). The

170   predominant land use over much of the area is livestock grazing on native pastures, with smaller

171   areas used for conservation (national parks) and forestry. With small areas of opportunistic cropping

172   along the eastern margins and in the south-west.

173

174   *Field methods*

175

176   We traversed the survey area using roads and major tracks to form a regular grid of sites, at distances

177   of 10-30 km, in order to provide a comprehensive survey of the area. We sampled a total of 282 sites,

178   chosen randomly based on maps of the study area (Fig. 1). Areas of particular interest (e.g. long-term

179   grazing exclosures, railway corridors, regeneration sites, national parks) were also included. At each

180   site we used a random process to select an area of 100 m by 30 m along which we centrally located a

181   100 m transect. The transect was placed at least 100 m from the track in order to avoid possible

182   disturbances. If a randomly chosen site was too disturbed (e.g. a dump site), we selected the next site

183   along the road at a predetermined distance from the original site. Along each transect we placed ten,

184   evenly spaced 0.5 m^2 quadrats, which were used to collect data on biocrust composition,

185   groundstorey plant cover and soils.

186

187   Within each quadrat we assessed the total cover (%) of biocrusts and the relative contribution of

188   three main types; lichens, bryophytes and cyanobacteria (Fig. 1). Only cyanobacteria that were

189   visible on the surface were assessed. We then collected samples of all different visible types of soil

190   crusts from each quadrat to obtain ten bags of composite crust samples. Sufficient samples were

191   collected to provide voucher specimens for lodgement in herbaria. The community composition of

192   biocrust species was identified using keys in Filson (1988, 1992), Filson and Rogers (1979),

193   McCarthy (1991), Scott (1985) and Scott and Stone (1976), as well as more recent generic revisions.

194   Nomenclature followed Buck and Vitt (2006) for mosses, McCarthy (2006) for liverworts, McCarthy

195   (2015) for lichens, and where appropriate, more recent taxonomic revisions, as well as more recent

196   generic revisions. Some taxa, particularly crustose lichens, were infertile and therefore could not be

197   identified (e.g. sterile *Lecidea* spp., *Cladonia* spp.). Two morphological type of *Collema*

198   *coccophorum* were identified, based on thallus shape, habit, and morphology or lobes and isidia

199   (Eldridge 1996). Lichen nomenclature conforms with McCarthy (1991) or more recent monographs.

200   Voucher specimens were lodged with the National Herbarium of New South Wales (NSW). Within

201   the same 10 quadrats we estimated the total above-ground vegetation cover, and took a sample of the

202   top 2 cm of the surface from every second quadrat. These soils were bulked, air-dried, sieved to > 0.2

203   mm for an assessment of soil organic C using the Walkely-Black oxidation method, and soil pH on a

204   1:5 soil water extract.

205

206   *Statistical analyses*

207

208   We used correlation network ('co-occurrence networks') analysis to identify ecological

209   clusters ('modules') of strongly associated biocrust taxa according to Delgado-Baquerizo et

210   al. (2018). In brief, we calculated all pairwise Spearman's (ρ) rank correlations between all

211   taxa (% of cover), focussing exclusively on positive correlations because they provide

212   information on species that may respond similarly to different soil, plant, climatic, and

213   grazing conditions (Barberan et al. 2012). We considered a co-occurrence to be robust if the

214   Spearman's correlation coefficient was > 0.25 and $P < 0.01$ (see Barberan et al. 2012 for a

215   similar approach). This cut-off has a biological meaning, because we only focus on taxa that

216   are significantly strongly co-occurring, which are therefore more likely to interact with each

217   other within a given plant community. The network was visualized with the interactive

218   platform Gephi (Bastian et al. 2009). We then used default parameters (network resolution =

219   2.0 in all cases) from the interactive platform Gephi to identify ecological clusters of the most

220   strongly interacting biocrust taxa. We then computed the relative abundance of each

221   ecological cluster by averaging the standardized relative abundances (z-scores) of the taxa

222   from each ecological cluster. Standardizing the data allowed us to exclude any effect of

223   merging data from different biocrust groups e.g. lichen *vs* moss.

224

225   We then used Structural Equation Modelling (SEM) to build a system-level understanding of

226   the effects of paleoclimatic legacies on the composition of the two species-rich ecological

227   clusters. We developed an *a priori* model of how we expected our biocrust system to behave

228   with changes in paleoclimatic legacies over the past 20k years (Supporting Information

229   Appendix S1). In this *a priori* model we predicted that paleoclimatic legacies (changes in

230   temperature and rainfall over the past 20k years), grazing (by cattle), differences in soils (pH

231   and total carbon), groundstorey plant cover, and location (latitude, longitude) would have

232   direct effects on both biocrust ecological clusters, separately, and that there would be a

233   number of indirect effects, mediated by soils, plants and grazing (Electronic Appendix S1).

234 Grazing has been shown to have indirect effects on soil crust composition by altering plant

235 cover (Eldridge and Koen 1998) but affecting soil surface stability and therefore soil carbon

236 levels (Eldridge et al. 2017). We also included current climate in our models to account for

237 variation in any response due to current climatic conditions. Current and paleoclimatic data

238 were obtained from the WorldClim database. Paleoclimatic data from the Last Glacial

239 Maximum (about 20 k years ago) were downscaled from simulations using Global Climate

240 Models (CCSM4), and calibrated (bias corrected) using WorldClim 1.4 as the baseline

241 'current' climate.' WorldClim provides information on 19 climatic variables, but we only

242 used a subset of three of these (1) for simplicity (we kept the most comprehensive climatic

243 variables, which are largely used in the literature) and more importantly, (2) to avoid strong

244 multicollinearity issues in our models as most of the 19 variables are highly correlated.

245

246 Hypothesized pathways in our *a priori* model were compared with the variance-covariance

247 matrix of our data in order to calculate an overall goodness-of-fit using the χ^2 statistic. The

248 goodness of fit test estimates the likelihood of the observed data given the *a priori* model

249 structure. Thus, high probability values indicate that models are highly plausible causal

250 structures underlying the observed correlations. Before fitting empirical data to our *a priori*

251 models, we examined the univariate correlations among all variables and standardized (z-

252 transformed) the data. The stability of the resultant models was evaluated as described in

253 Reisner et al. (2013). Analyses were performed using the AMOS 22 (IBM, Chicago, IL,

254 USA) software. After fitting our empirical data to the *a priori* model (Fig. S1), we interpreted

255 a good model fit as one with a low χ^2, high Goodness of Fit Index [GFI] and high Normal Fit

256 Index [NFI]).

257

258 For our dataset we found some gaps (~ 2%) in our soil pH and C data due to loss of

259 laboratory samples. To overcome this, we obtained soil pH data from Hengl et al. (2017),

260 who present global maps of multiple soil properties at a resolution of 250m. Missing soil C

261 data were obtained similarly. We found a strong positive and significant correlation between

262 the observed and predicted pH ($\rho = 0.46$; $P < 0.0001$) and soil C ($\rho = 0.55$; $P < 0.0001$). For

263 each of our sites we estimated the density of cattle using data from Robinson et al. (2014) that

264 are based on 1 km resolution global maps. A demonstration of the validity of predicted cattle

265 density, soil C and pH for the NSW region and Australia is presented in Delgado-Baquerizo

266 et al. (2018).

267

268 **Results**

269

270 We recorded 120 lichen, moss and liverwort taxa across the study area. Mosses accounted for

271 46% of all taxa, and crustose (18%) and squamulose (15%) forms were the most common

272 lichens. Our network analysis discriminated six ecological clusters, two of which had 87% of

273 all taxa. These two main ecological clusters included 41 (Cluster A) and 52 (Cluster B) taxa.

274 The additional four small clusters comprising between 2 and 13 taxa (Fig. 2a). Clusters A and

275 B had a similar richness of mosses, lichens and liverworts (Electronic Appendix S2). Some

276 biocrust taxa were strongly indicative of the two major clusters. For example, taxa from the

277 lichen families Peltulaceae and Teloschistaceae were restricted to Cluster A, while

278 Cladoniaceae, Lecideaceae and Thelotremataceae were restricted to Cluster B. For the

279 mosses, Bryaceae were dominant in Cluster A and there was slightly greater abundance of

280 Pottiaceae in Cluster B (Fig. 2b).

281

282 Our SEM provided a system-level understanding on the role of multiple ecological attributes

283 in predicting the distribution of biocrust communities. Interestingly, we found that climatic

284 legacies have an important influence on the relative abundance of the two major ecological

285 clusters but had no significant effects on the remaining clusters. Specifically, sites with the

286 greatest increases in temperature over the last 20k years (positive temperature legacies) were

287 associated with reductions in the relative abundance of Cluster A taxa (Fig. 3), while sites

288 where precipitation has increased over the past 20k years (positive precipitation legacy) were

289 associated with increases in the relative abundance of Cluster B (Fig. 4). Climatic legacies

290 also influenced other ecological attributes. For example, sites where the temperature has

291 declined over the past 20k years (negative temperature legacy) had less groundstorey plant

292 cover, but higher levels of soil pH, and sites where precipitation has increased (positive

293 precipitation legacy) compared with current levels also had lower levels of soil pH. We also

294 found some indirect effects of climatic legacies on the relative abundance of Cluster B. Sites

295 exhibiting the greatest increases in temperatures in the past 20k years suppressed the negative

296 effects of plant cover on the relative abundance of Cluster B by reducing plant cover.

297 Similarly, increased intensity of grazing suppressed the negative effect of pH, and the

298 positive effect of soil carbon, on the relative abundance of Cluster B. Finally, increasing

299 temperature and precipitation legacies reduced the negative effect of soil pH on Cluster B

300 (Fig. 4).

301

302   Of course, other environmental variables were also important predictors of the relative

303   abundance of ecological clusters of biocrusts (Fig. 4). For example, sites with greater current

304   precipitation had a greater relative abundance of both Clusters A and B, and sites with greater

305   radiation were associated with increases in Cluster B. Conversely, locations of greater

306   contemporary temperature was associated with declines in Cluster B (Fig. 4). Increases in the

307   relative abundance of ecological Cluster B were associated with lower levels of soil carbon,

308   but less plant cover and lower soil pH. Unlike Cluster B, however, we found no direct effects

309   of soils or plants on the relative abundance of Cluster A.

310

311   **Discussion**

312

313   Our study provides empirical evidence that climatic legacies can influence the current

314   distribution of major ecological clusters of biocrust species. Climatic legacies had different

315   effects on the relative abundance of different ecological assemblies of biocrust organisms,

316   with significant effects on two of the six ecological clusters that together comprised 78% of

317   all lichen and bryophyte taxa found across ~ 0.6 million km^2 of eastern Australia. Thus,

318   precipitation and temperature legacies were associated with the relative abundance of

319   ecological clusters A and B, respectively. Our results could help to explain why biocrusts are

320   absent from particular locations where they would be expected to thrive. Alternatively, our

321   results could also shed light on why some species occur in areas where they are not predicted

322   to occur under current climates, such as the case for foliose lichens in areas of summer

323   rainfall in central Australia (Eldridge 1996). Our work is important for two reasons. First, it

324   provides insights into why species are absent from the areas that have not been impacted by

325   human-induced disturbance or *vice versa*. Second, a understanding that climate legacies can

326   explain part of the current distribution of biocrusts safeguards us against unreasonable

327   expectations that species can be predicted from distribution models based on the current

328   known distributions. Third, our research improves our understanding of the effects of long-

329   term changes in climate on organisms that have been little studied but are believed to be

330   relatively resilient to changes in climate. Overall, a knowledge of the importance of climate

331   legacies helps us to moderate our decisions about investing in landscape restoration based on

332   a lack of knowledge of the true drivers.

333

334   Our structural equation models provide evidence of the negative correlation between

335   increasing temperature legacies and the relative abundance of taxa in Cluster A. In other

336   words, taxa in ecological Cluster A were associated with the smallest increase in temperature

337   over the past 20k years. This cluster was dominated largely by mosses from the family

338   Bryaceae (e.g. *Rosulabryum* spp.; Fig. 2B). Dominant biocrust traits for the species within

339   this cluster could help explain this result. For example, ecological cluster A moss species

340   such as *Goniomitrium acuminatum* and *Acaulon integrifolium* have 'annual shuttle'

341   strategies, maintaining a high reproductive effort by maintaining a short life span and

342   producing a few relatively large spores (Kürschner and Frey 2012). Although they can

343   withstand high temperatures, their photosynthetic optimum is between 10° and 28°C (Lange

344   et al. 1999), and higher temperatures for prolonged periods may compromise their ability to

345   regenerate (Stark and McLetchie, 2006). This could account for the fact that sites with the

346   lowest increase in temperature over the past 20k years are closer to the photosynthetic optima

347   for Cluster A mosses. Lichen taxa in Ecological Cluster A included *Xanthoparmelia*

348   *semiviridis* (syn. *Chondropsis semiviridis*), which is known to be strongly influenced by

349   changes in diurnal summer temperatures (Rogers 1972). Photosynthesis of some lichens can

350   be suppressed when high summer temperatures, particularly when the thallus is hydration

351   (Lange et al. 2001). *Xanthoparmelia semiviridis* is a sessile lichen that cannot maintain gas

352   exchange after exposure to temperatures of only 55°C for 30 mins (Rogers 1972). Thus,

353   locations with the largest increases in temperature over the last 20 k years would likely have

354   resulted in a lower relative abundance of this species.

355

356   Increasing precipitation legacy was positively related to the relative abundance of Ecological

357   Cluster B taxa. Again, functional traits associated to the species within this cluster might help

358   explain this result. For example, cluster B contained the thallose liverworts *Asterella*

359   *drumondii, Riccia lamellosa, R. limbata* and *R. nigrella*, all of which require free water to

360   reproduce and maintain their osmotic balance (Sperry 2003). Studies in arid northern

361   Australia have shown that *Riccia* spp. tend to occur in areas where water accumulates after

362   rainfall (Rogers 1994). Highly variable or erratic rainfall will limit the distribution of

363   liverworts (Scott 1985), and in water-limited environments such as hot deserts, or cold

364   deserts such as Antarctica, their distribution is likely to be restricted to areas receiving

365   supplementary water in the form of snow melt (Kennedy 1995) or runoff water (Eldridge and

366   Tozer 1996, Eldridge 1998). Ecological Cluster B also contained the foliose and fruticose

367   lichens (*Xanthoparmelia* spp., *Cladia* spp., *Cladonia* spp., *Heterodea* spp.), consistent with

368   our models that indicate a significant positive relationship between this cluster and the

369   contemporary distribution of rainfall (Fig. 4). Our previous research has shown that

370   *Heterodea* spp. are more common in zones that intercept runoff (Eldridge 1998). This extra

371   water may be necessary to support the larger thallus structure of these taxa. Therefore,

372   locations with the largest increases in precipitation over the last 20 k years might have

373   resulted in a larger relative abundance for this cluster.

374

375   We also found evidence for multiple indirect effects of climatic legacies on ecological cluster

376   B *via* changes in plant cover and soil pH (Fig. 4). For example, sites where temperature has

377   increased the most over the past 20 k years will likely be associated with a lower plant cover,

378   which was associated with an increase in the relative abundance of ecological cluster B (Fig.

379   4) but no significant effect on ecological cluster A (Fig. 3). Increasing plant cover is known

380   to suppress the cover of certain mosses and lichens species such as Cladonia spp. in cluster B

381   (Allen 1929; Pharo and Beattie 1997) by occupying suitable bare soil niches (Pharo and

382   Beattie 1997; Vanderpoorten and Engel 2003; Vanderpoorten *et al.* 2005; Martínez *et al.*

383   2006). Grazing had an overall suppressive effect on Cluster B taxa (standardised total effects

384   [STE] = -0.17), and one potential mechanism was *via* the suppression of the positive effect of

385   carbon on Ecological Cluster B taxa. Carbon is a proxy for organic matter (Schmidt et al.

386   2011), so taxa from Ecological Cluster A would be expected to prefer high fertility conditions

387   or sites of low soil pH. Support for this comes from a study of the micro-scale distribution of

388   biocrust taxa across three microhabitats within a *Callitris* woodland. The interception zone,

389   an area where a change in slope produces a series of alternating depressions, was dominated

390   by taxa from Ecological Cluster B such as *Asterella drummondii, Fossombronia* spp., and the

391   thallose liverworts *Riccia* spp.; Eldridge 1998). The tendency of these species to occur in

392   areas of water and organic matter accumulation may be related to their preference for sites

393   with high levels of organic carbon.

394

395   Another interesting outcome from this study is that the dominant ecological clusters in our

396   region included a similar number of moss and lichen species. A priori, we might have

397   expected that one cluster would be dominated by mosses and the other by lichens, based on

398   the notion that mosses (and liverworts) would dominate areas where precipitation has

399   increased over the past 20k years while lichens would show the opposite response. This is

400   based on the perception that mosses prefer more mesic, and lichens more arid, environments.

401   However, this was not the case. Rather, both mosses and lichens species were well

402   represented in each cluster, indicating that no dichotomy between the two clusters and

403   suggesting that multiple mosses and lichen species can potentially share environmental

404   preferences. Notwithstanding the effects of current climate and climate legacy, soil

405   chemistry, plant cover and grazing, the low explanatory power of our models (0.06 to 0.38)

406   indicates that other unmeasured factors could influence the different clusters. Nonetheless,

407   the aim of this study was to examine whether we could identify an association between

408   climatic legacies and contemporary distribution of biocrust taxa after accounting for well-

409   known ecological predictors of biocrust. Future modelling could include other potential

410   drivers flooding or fire, which were not modelled, to improve predictability. Biocrusts are

411   known to be killed by frequent fires (Eldridge and Bradstock 1994), the return interval for

412   fire in western NSW is relatively long (Leigh and Noble 1981).

413

414   Although climatic legacies and climate change are not directly comparable, mainly because

415   of their different temporal scales (centuries vs. thousands of years), we believe that our

416   results can still provide some potential insights to help understanding the future distribution

417   of biocrusts species across large regions. For example, temperatures are predicted to rise by

418   1-5°C across Australia's drylands over the next 50 years, depending on location and

419   modelling scenario (Stokes et al. 2008). Climatic projections for much of our study area

420   include an increase of up to 3°C in temperature, with the greatest increases in the north, an

421   increase of 10-20% in summer rainfall, but substantial reductions (20-50%) in winter

422   precipitation (Eldridge and Beecham 2017). This could mean a contraction of taxa in

423   Ecological Cluster A to areas experiencing lower rates of temperature increase, such as areas

424   in the south of the study area, and a potential expansion of Ecological Cluster B species

425   northward into areas of increased rainfall. The management and ecological implications of

426   these changes have not been adequately addressed. However, there are likely to be changes in

427   ecosystem functions associated with these changes. For example, the cyanolichens *Collema*

428   *coccophorum* and *Peltula* spp. (Ecological Cluster A), which have cyanobacteria as their

429   phytobionts, may retract to the south, altering the inputs of N into the soil (Belnap 2002). The

430   extent to which these potential changes lead to ecosystem-wide changes in soil N pools is,

431   however, unknown.

432

433   Our work indicates that climatic legacies influence the current distribution of biocrusts

434   ecological clusters of species across large spatial scale. Information on climatic legacies

435   could therefore, provide a useful way to improve our capacity to predict the distribution of

436   ecological assemblies of biocrusts across southern Australia, but potentially somewhere else.

437   Given that biocrusts have such as broad global distribution, we encourage others to use

438   regional biocrust species databases to test whether clusters of similar species from other

439   drylands exhibit similar responses to those in our study. This knowledge can help us to

440   improve our predictions of how biocrust assemblies might respond to on-going global

441   environmental change associated with increasing land use intensification, increasing

442   temperature and reduced rainfall, with important implications for future sustainable

443   management and conservation policies. It might also help us to prioritise activities such as

444   inoculation that is designed to promote the establishment of biocrusts and their associated

445   ecosystem services.

446

447   **References**

448

449   Barberán, A., Fernández-Guerra, A., Bohannan, B.J. & Casamayor, E.O. (2012) Exploration

450   of community traits as ecological markers in microbial metagenomes. *Molecular Ecology,* **21**,

451   1909-1917.

452

453   Bastian, M., Heymann, S. & Jacomy, M. (2009) Gephi: An Open Source Software for

454   Exploring and Manipulating Networks. In International AAAI conference on weblogs and

455   social media: San Jose, California.

456

457   Belnap. J. (2002) Nitrogen fixation in biological soil crusts from southeast Utah, USA.

458   *Biology and Fertility of Soils*, **35**, 128–135.

459

460   Bowker, M.A., Belnap, J., Büdel, B., Sannier, C., Pietrasiak, N., Eldridge, D.J. & Rivera-

461   Aguilar, V. (2016) Controls on distribution patterns of biological soil crusts at micro-to

462   global scales. *Biological Soil Crusts: An Organizing Principle in Drylands*. Ecological

463   Studies 226, (eds B Weber, B. Büdel & J. Belnap), pp. 173-197. Springer, New York.

464

465   Buck, W.R. & Vitt, D.H. (2006) Key to the Genera of Australian Mosses. *Flora of Australia*

466   *Volume 51*, Australian Biological Resources Study, Canberra.

467

468   Bureau of Meteorology (2015) Bureau of Meteorology, Australian Government.

469   http://www.bom.gov.au/. Accessed 8 February 2018.

470

471   Chamizo, S., Stevens, A., Cantón, Y., Miralles, I., Domingo, F. & Van Wesemael, B. (2012)

472   Discriminating soil crust type, development stage and degree of disturbance in semiarid

473   environments from their spectral characteristics. *European Journal of Soil Science,* **63**, 42-53.

474

475   Chiquoine, L.P., Abella, S.R. & Bowker, M.A. (2016) Rapidly restoring biological soil crusts

476   and ecosystem functions in a severely disturbed desert ecosystem. *Ecological Applications*,

477   **26**, 1260-1272.

478

479   Delgado-Baquerizo, M., Maestre, F.T., Eldridge, D.J., Bowker, M.A., Ochoa, V., Gozalo,

480   B….., Singh, B.K. (2016) Biocrust-forming mosses mitigate the negative impacts of

481   increasing aridity on ecosystem functionality in drylands. *New Phytologist*, **209**, 1540-1552.

482

483   Delgado-Baquerizo, M., Bissett, A., Eldridge, D.J., Maestre, F.T., He, J-Z., Wang, J.T. ….

484   Fierer, N. (2017) Palaeoclimate explains a unique proportion of the global variation in soil

485   bacterial communities. *Nature Ecology & Evolution*, **1**, 1339-1347.

486

487   Delgado-Baquerizo, M., Eldridge, D.J., Travers, S.K., Val, J., Oliver, I. & Bissett, A. (2018)

488   Effects of climate legacies on above- and below-ground community assembly. *Global*

489   *Change Biology* https://doi.org/10.1111/gcb.14306

490

491   Eldridge, D.J. & Koen, T.B. (1998) Cover and floristics of microphytic soil crusts in relation

492   to indices of landscape health. *Plant Ecology,* **137**, 101-114.

493

494   Eldridge, D.J. (1998) Dynamics of moss- and lichen-dominated soil crusts in a patterned

495   *Callitris glaucophylla* woodland in eastern Australia. *Acta-Oecologica,* **20**, 159-170.

496

497   Eldridge, D.J. & Tozer, M.E. (1996) Distribution and floristics of bryophytes in soil crusts in

498   semi-arid and arid eastern Australia. *Australian Journal of Botany,* **44**, 223-247.

499

500   Eldridge, D.J. (1996) Distribution and floristics of terricolous lichens in soil crusts in arid and

501   semi-arid New South Wales, Australia. *Australian Journal of Botany,* **44**, 581-599.

502

503   Eldridge, D.J. & Beecham, G. (2017) The impact of climate variability on land use and

504   livelihoods in Australia's rangelands. *Climate Variability, Land-Use and Impact on*

505   *Livelihoods in the Arid Lands,* (ed M.K. Gaur & V.R. Squires), pp. 293-315. Springer, New

506   York.

507

508   Eldridge, D.J. & Bradstock, R.A. (1994). The effect of time since fire on the cover and

509   composition of cryptogamic soil crusts on a eucalypt shrubland soil. *Cunninghamia* **3**, 521-

510   527.

511

512   Eldridge, D.J. & Ferris, J.M. (1999) Recovery of populations of the soil lichen *Psora crenata*

513   after disturbance in arid South Australia. *The Rangeland Journal*, **21**, 194-198.

514

515   Eldridge, D.J., Travers, S.K., Facelli, A.F., Facelli, J.M. & Keith, D.A. (2017) The Chenopod

516   Shrublands. *Australian Vegetation*, 3rd Edition, (ed. D.A. Keith), pp. 599-625. Cambridge

517   University Press, Cambridge.

518

519   Filson, R.B. (1988) The lichen genera *Heppia* and *Peltula* in Australia. *Muelleria*, **6**,495-517.

520

521   Filson, R.B. (1992) Heterodeaceae. *Flora of Australia. Vol. 54* (ed A.S. George.), pp. 198-

522   200. Australian Government Publishing Service, Canberra.

523

524   Filson, R.B. & Rogers, R.W. (1979) Lichens of South Australia. Government Printer, South

525   Australia.

526

527   Garcia-Pichel, F., Loza, V., Marusenko, Y., Mateo, P. & Potrafka, R.M. (2013) Temperature

528   drives the continental-scale distribution of key microbes in topsoil communities. *Science*,

529   **340**, 1574–1577.

530

531   Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M.,

532   Blagotić, A., …. Kempen, B. (2017) SoilGrids250m: Global gridded soil information based

533   on machine learning. *PLoS 1* doi.org/10.1371/journal.pone.0169748

534

535   Keith, D.A. (2017) *Australian Vegetation*, 3rd edn. Cambridge University Press, Cambridge.

536

537 Kennedy, A.D. (1995) Antarctic terrestrial ecosystem response to global environmental

538 change. *Annual Review of Ecology & Systematics*, **26**, 683–704.

539

540 Kürschner, H. & Frey, W. (2012) Life strategies in bryophytes - a prime example for the

541 evolution of functional types. *Nova Hedwigia,* **96**, 83-116.

542

543 Kuske, C.R., Yeager, C.M., Johnson, S., Ticknor, L.O. & Belnap, J. (2012) Response and

544 resilience of soil biocrust bacterial communities to chronic physical disturbance in arid

545 shrublands. *The ISME Journal*, **6**, 886-897.

546

547 Lafuente, A., Berdugo, M., Ladrón de Guevara, M., Gozalo, B. & Maestre, F.T. (2017)

548 Simulated climate change affects how biocrusts modulate water gains and desiccation

549 dynamics after rainfall events. *Ecohydrology* doi.org/10.1002/eco.1935

550

551 Lange, O.L., Green, T.G.A. & Reichenberger, H. (1999) The response of lichen

552 photosynthesis to external CO_2 concentration and its interaction with thallus water-status.

553 *Journal of Plant Physiology*, **154**, 157-166.

554

555 Lange, O.L., Green, T.G.A. & Heber, U. (2001) Hydration-dependent photosynthetic

556 production of lichens: what do laboratory studies tell us about field performance? *Journal of*

557 *Experimental Botany*, **52**, 2033-2042.

558

559 Leigh, J.H. & Noble, J.C. (1981). The role of fire in the management of rangelands in

560 Australia. *Fire and the Australian Biota,* (ed A.M. McGill, R.H. Groves & I.R. Noble), pp.

561 471-495. Australian Academy of Sciences, Canberra.

562

563 López-Merino, L., Colás-Ruiz, N.R., Adame, M.F., Serrano, O., Martínez Cortizas, A. &

564 Mateo, M.A. (2017) A six thousand-year record of climate and land-use change from

565 Mediterranean seagrass mats. *Journal of Ecology*, **105**, 1267-1278.

566

567 Martínez, I., Escudero, A., Maestre, F.T., de la Cruz, A., Guerrero, C. & Rubio, A. (2006)

568 Small-scale patterns of abundance of mosses and lichens forming biological soil crusts in two

569 semi-arid gypsum environments. *Australian Journal of Botany*, **54**, 339-348.

570

McCarthy, P.M. (1991) The lichen genus *Endocarpon* Hedwig in Australia. *Lichenologist*,
23, 27-52.

573

McCarthy, P.M. (2006) Checklist of Australian Liverworts and Hornworts. Australian
Biological Resources Study, Canberra. Viewed 06 March 2016.
http://www.anbg.gov.au/abrs/liverwortlist/liverworts_intro.html

577

McCarthy, P.M. (2015) Checklist of Australian Lichenicolous Fungi. Australian Biological
Resources Study, Canberra. Version 10 December 2015.
http://www.anbg.gov.au/abrs/lichenlist/Lichenicolous_Fungi.html

581

Pärtel, M., Chiarucci, A., Chytrý, M. and Pillar, V.D. (2017). Mapping plant community
ecology. *Journal of Vegetation Science*, **26**, 1-3

584

Pharo, E.J. & Beattie, A.J. (1997) Bryophyte and lichen diversity: A comparative study.
Australian Journal of Ecology, **22**, 151-162.

587

Pickard, J. & Norris, E.H. (1994) The natural vegetation of north-western New South Wales: notes to
accompany the 1:1 000 000 vegetation map sheet. *Cunninghamia*, **3**,423-464.

590

Reed, S.C., Koe, K., Sparks, J.P., Housman, D., Zelikova, T.J. & Belnap, J. (2012) Changes
to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nature Climate
Change*, **2**, 752-755.

594

Reisner, M.D., Grace, J.B., Pyke, D.A. & Doescher, P.S. (2013) Conditions favouring
Bromus tectorum dominance of endangered sagebrush steppe ecosystems. *Journal of Applied
Ecology*, **50**, 1039-1049.

598

Robinson, T.P., Wint, J.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., …
Gilbert, M. (2014) Mapping the global distribution of livestock. *PLoS One*
doi.org/10.1371/journal.pone.0096084.

602

603 Rodriguez-Caballero, E., Belnap, J., Büdel, B., Crutzen, P.J., Andreae, M.O., Pöschl, U. &
604 Weber, B. (2018) Dryland photoautotrophic soil surface communities endangered by global
605 change. *Nature Geoscience*, **11**, 185-189.

607 Rodriguez-Caballero, E., Escribano, P. & Canton, Y. (2014) Advanced image processing
608 methods as a tool to map and quantify different types of biological soil crust. *International*
609 *Journal of Photogrammetry and Remote Sensing*, **90**, 59-67.

611 Rogers, R.W. (1972) Soil surface lichens in arid and semi-arid south-eastern Australia. III.
612 The relationship between distribution and environment. *Australian Journal of Botany*, **20**,
613 301-316.

615 Rogers, R.W. (1994) Zonation of the liverwort *Riccia* in a temporary watercourse in
616 subtropical, semi-arid Australia. *Australian Journal of Botany*, **42**, 657-662.

618 Rogers, R.W. (1971) Distribution of the lichen *Chondropsis semiviridis* in relation to its heat
619 and drought resistance. *New Phytologist*, **70**, 1069-1077

621 Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A.,
622 Kleber, M. ….Trumbore, S.E. (2011) Persistence of soil organic matter as an ecosystem
623 property. *Nature*, **478**, 49-56.

625 Scott, G.A.M. (1985) Southern Australian Liverworts. Australian Government Publishing
626 Service, Canberra.

628 Sperry, J.S. (2003) Evolution of water transport and xylem structure. *International Journal of*
629 *Plant Science*, **164**, 115-127.

631 Stark, L.R. & McLetchie, F.N. (2006) Gender-specific heat-shock tolerance of hydrated
632 leaves in the desert moss *Syntrichia caninervis. Physiologia plantarum*, **126**, 187-195.

634 Steven, B., Gallegos-Graves, L.V., Belnap, J. & Kuske, C.R. (2013) Dryland soil microbial
635 communities display spatial biogeographic patterns associated with soil depth and soil parent
636 material. *FEMS Microbial Ecology*, **86**, 1-13.

Stokes, C.J., Ash, A. & Howden, S.M. (2008) Climate change impacts on Australian Rangelands. *Rangelands*, **30**, 40-45.

Vanderpoorten, A., Sotiaux, A. & Engels, P. (2005) A GIS-based survey for the conservation of bryophytes at the landscape scale. *Biological Conservation*, **121**, 189-194.

Vanderpoorten, A. & Engels, P. (2003) Patterns of bryophyte diversity and rarity at a regional scale. *Biodiversity & Conservation*, **12**, 545–553.

Weber, B., Büdel, B. & Belnap, J. (2016) *Biological Soil Crusts: An Organizing Principle in Drylands*. Ecological Studies 226, Springer, Amsterdam.

Weber, B., Wu, D., Tamm, A., Ruckteschler, N., Rodríguez-Caballero, E., Steinkamp, J., … Pöschl, U. (2015). Biological soil crusts accelerate the nitrogen cycle through large NO and HONO emissions in drylands. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 15384–15389.

Weber, B., Olehowskid, C., Knerr, T., Hill, J., Deutschewitz, K., Wessels, C.J…. Büdel, B. (2008) A new approach for mapping of biological soil crusts in semidesert areas with hyperspectral imagery. *Remote Sensing of the Environment*, **112**, 2187-2201.

Captions for figures

Fig. 1. Distribution of the 282 sampling sites in eastern Australia (inset Australia) and some typical soil crust taxa. (a) *Xanthoparmelia semiviridis* (foliose lichen, Cluster A), (b) scanning electron microscopy image of cyanobacterial filaments (cyanobacterium, Cluster E), (c) *Didymodon torquatus* (moss, Cluster B), (d) *Asterella drummondii* (thallose liverwort, Cluster B). Photographs: D.J. Eldridge

Fig. 2. Network diagram showing the location of the six clusters (A-F) and histograms showing the abundance of different moss and lichen families in Clusters A (red) and B (yellow). Histograms on the left-hand side show that there is a greater abundance of mosses
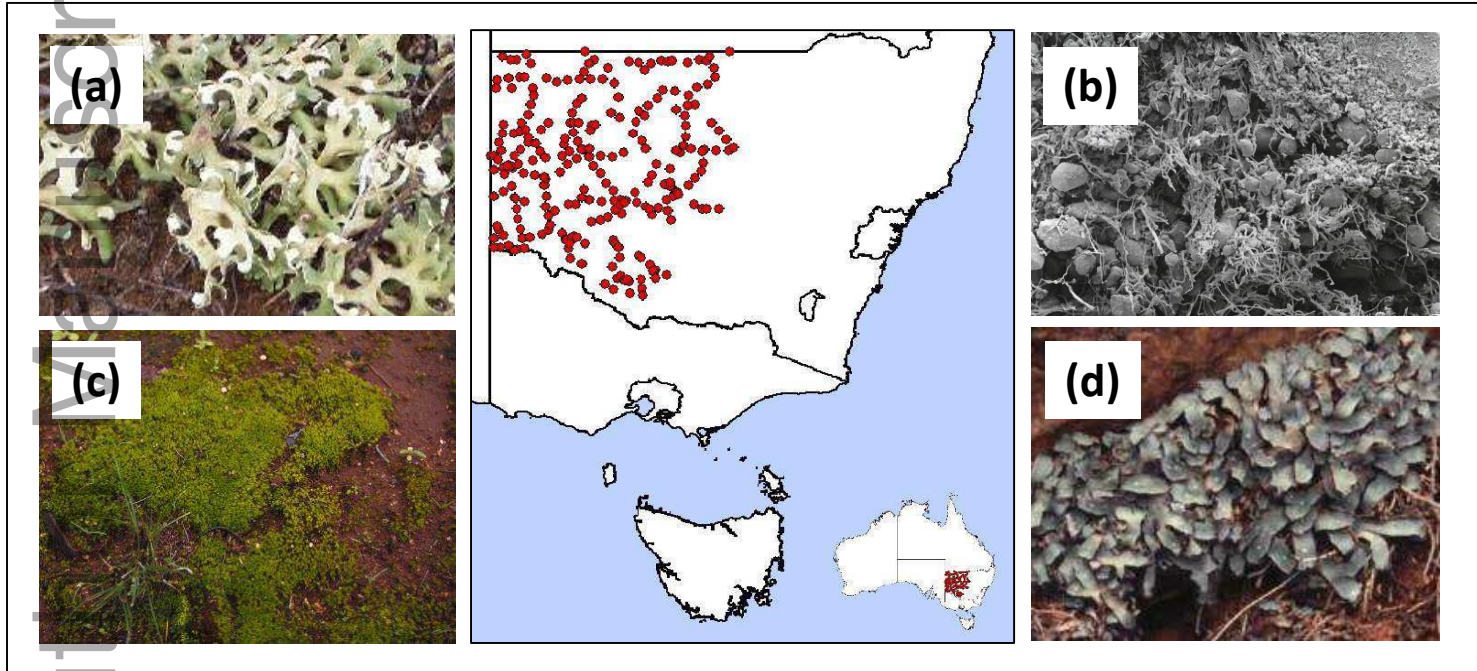
670   from the family Pottiacea in Cluster B, and liverworts, lichens (Family Verrucariaceae) and

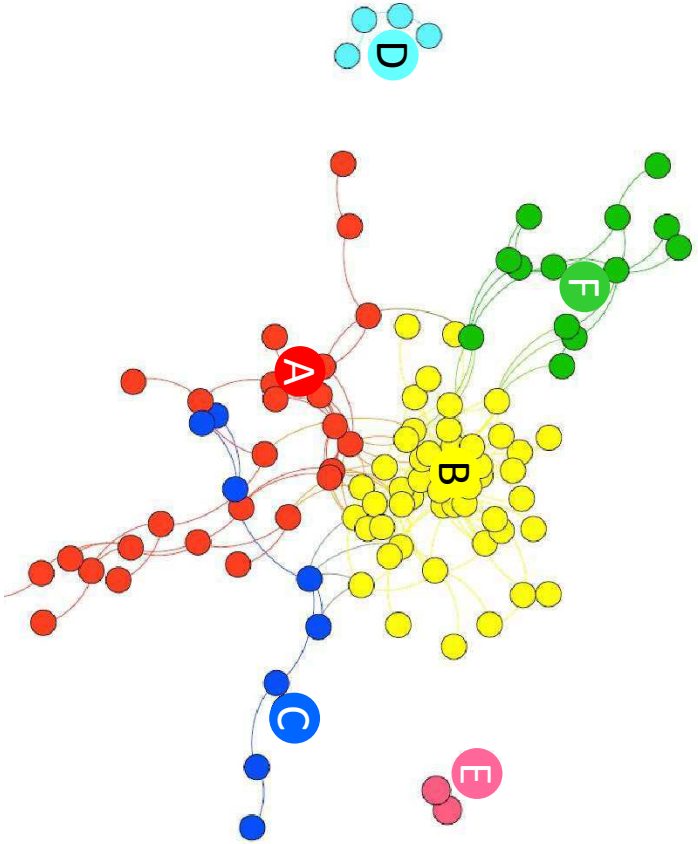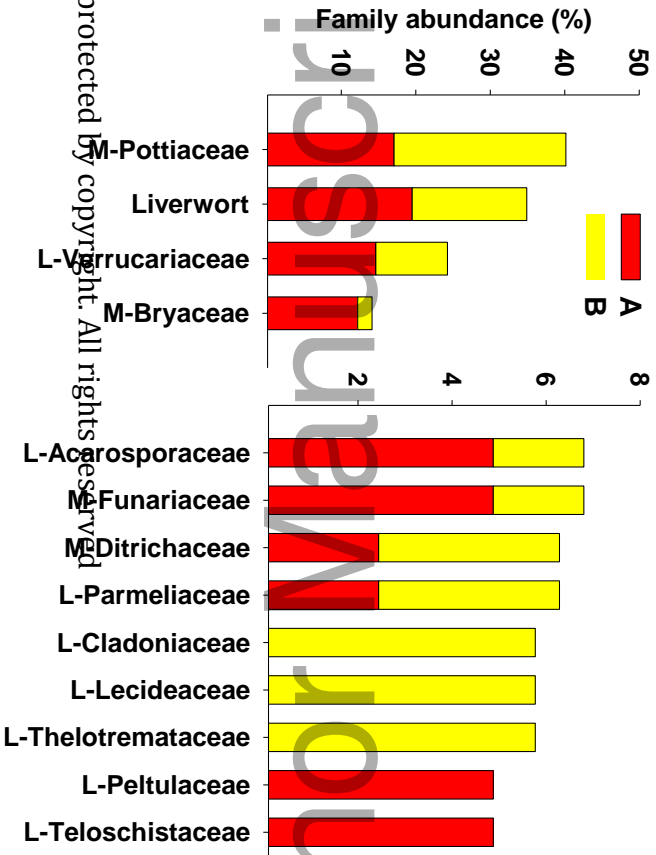671   mosses (Bryaceae) in Cluster A.

672

673   Fig. 3. Structural equation modeling of the direct and indirect effects of current and paleo

674   climatic legacies (both including mean annual temperature [MAT_C & MAT_L], mean annual

675   precipitation [MAP_C & MAP_L], and radiation RAD), grazing (cattle grazing), soils (organic

676   carbon [C] and pH), and groundstorey plants (cover) on Cluster A. All variables were

677   included as independent observable variables. Multiple path coefficients are presented on the

678   same arrow in order to reduce the number of boxes and the number of arrows, resulting in

679   considerable simplification of the model structure. Correlations among different groups of

680   variables e.g. pH and C, or legacy MAT and legacy MAP, were allowed to covary.

681   Standardized path coefficients, superimposed on the arrows, are analogous to partial

682   correlation coefficients, and indicative of the effect size of the relationship. $\chi^2 = 5.57$, df = 3,

683     $P = 0.134$, GFI = 0.996, RMSEA = 0.056, Bollen-Stine = 0.90. Only significant path

684   coefficients are shown. The proportion of variance explained (R^2) appears below the three

685   soil health response variables in the models. For pathway A in both models: $MAT_C \rightarrow$ pH (-

686   0.68), $MAP_C \rightarrow$ pH (-0.81), RAD$\rightarrow$ C (-0.60).

687

688   Fig. 4. Structural equation modeling of the direct and indirect effects of current and paleo

689   climatic legacies (both including mean annual temperature [MAT_C & MAT_L], mean annual

690   precipitation [MAP_C & MAP_L], and radiation RAD), grazing (cattle grazing), soils (organic

691   carbon [C] and pH), and groundstorey plants (cover) on Cluster B. Multiple path coefficients

692   are presented on the same arrow in order to reduce the number of boxes and the number of

693   arrows, resulting in considerable simplification of the model structure. Correlations among

694   different groups of variables e.g. pH and C, or legacy MAT and legacy MAP, were allowed

695   to covary. Standardized path coefficients, superimposed on the arrows, are analogous to

696   partial correlation coefficients, and indicative of the effect size of the relationship. $\chi^2 = 5.57$,

697   df = 3, $P = 0.134$, GFI = 0.996, RMSEA = 0.056, Bollen-Stine = 0.90. Only significant path

698   coefficients are shown. The proportion of variance explained (R^2) appears below the three

699   soil health response variables in the models. For pathway A in both models: $MAT_C \rightarrow$ pH (-

700   0.68), $MAP_C \rightarrow$ pH (-0.81), RAD$\rightarrow$ C (-0.60).

Grazing

Current climate

Climate legacy

Soils

Plants

Cluster A

$R^2 = 0.06$

-.57 (RAD)

.28 (MAP_C)

-.17 (C)

-.38 (MAT_L)

-.31 (MAT_L)

.43 (MAT_C)
-.53 (MAP_C)
-.72 (RAD)

.42 ($MAT_L \rightarrow$ pH)
-.28 ($MAP_L \rightarrow$ pH)

A

-.15 (pH)