

1 **Warming reduces the cover, richness and evenness of lichen-dominated biocrusts but**
 2 **promotes moss growth: Insights from an eight-year experiment**

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4 Heading: Warming reduces lichen-dominated biocrust cover but promotes moss growth

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23 **Summary**

- 24 • Despite the important role that biocrust communities play in maintaining ecosystem
25 structure and functioning in drylands worldwide, few studies have evaluated how climate
26 change will affect them.
- 27 • Using data from an eight-yr old manipulative field experiment located in Central
28 Spain, we evaluated how warming, rainfall exclusion and their combination affected the
29 dynamics of biocrust communities in areas that initially had low (<20%, LIBC plots) and
30 high (>50%, HIBC plots) biocrust cover.
- 31 • Warming reduced the richness (35±6%), diversity (25±8%) and cover (82±5%) of
32 biocrusts in HIBC plots. The presence and abundance of mosses increased with warming
33 through time in these plots, although their growth rate was much lower than the rate of
34 lichen death, resulting in a net loss of biocrust cover. On average, warming caused a
35 decrease in the abundance (64±7%) and presence (38±24%) of species in the HIBC plots.
36 Over time, lichens and mosses colonized the LIBC plots, but this process was hampered by
37 warming in the case of lichens.
- 38 • The observed reductions in the cover and diversity of lichen-dominated biocrusts
39 with warming will lessen the capacity of drylands such as that studied here to sequester
40 atmospheric CO₂ and to provide other key ecosystem services associated to these
41 communities.

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43 **Key words:** biocrust cover, biological soil crust, climate change, drylands, evenness,
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54 **Introduction**

55 Understanding how drylands (comprised of hyperarid, arid, semiarid and dry subhumid
56 ecosystems) are responding to ongoing climate change is critical for establishing effective
57 sustainability policies. Drylands currently cover ~45% of the Earth's land surface
58 (Právělie, 2016), and forecasted increases in aridity will expand them by up to 23%
59 globally by the end of this century (Huang *et al.*, 2016). Biocrusts, communities living in
60 the uppermost few millimeters of the soil and composed of autotrophic (e.g., lichens,
61 mosses, liverworts, cyanobacteria and green algae) and heterotrophic (e.g., bacteria, fungi
62 and microfauna) organisms, are prevalent in drylands worldwide (Weber *et al.* 2016a).
63 These communities grow intimately linked to soils from hyperarid to subhumid
64 ecosystems. In the most extreme climate regions, biocrusts are only composed by the
65 microscopic constituents, but as aridity decreases, macroscopic lichens, mosses and
66 liverworts become more prevalent (Bowker *et al.*, 2016). They are involved in many
67 important ecosystem processes, including carbon (C) and nitrogen (N) cycling (Evans &
68 Lange, 2003; Hu *et al.*, 2015; Barger *et al.*, 2016; Sancho *et al.*, 2016), surface energy
69 balance (Rodríguez-Caballero *et al.*, 2015; Couradeau *et al.*, 2016; Rutherford *et al.*,
70 2017), erosion (Zhao & Xu, 2013; Cantón *et al.*, 2014; Chamizo *et al.*, 2017) and water
71 redistribution (Bowker *et al.*, 2013a; Kidron & Büdel, 2014; Chamizo *et al.*, 2016), just to
72 name a few. Biocrusts have also been found to modulate the magnitude of responses of C
73 and N cycling to climate change in experimental studies (Delgado-Baquerizo *et al.*, 2014;
74 Maestre *et al.*, 2013; Hu *et al.*, 2014). Recent surveys have also found that their relative
75 importance as a provider of functions related to nutrient cycling increases along aridity
76 gradients (Delgado-Baquerizo *et al.*, 2016). Therefore, biocrusts will be critical for
77 maintaining the multiplicity of functions and services provided by drylands in a warmer
78 and more arid Earth. Nevertheless, it is not clear how the abundance and composition of
79 these communities will respond to climate change. This limits our ability to understand and
80 predict its impacts on ecosystem functioning in ecosystems where biocrusts are a prevalent
81 biotic community.

82 Expected decreases in the cover of vascular plants under increased aridity scenarios
83 (Delgado-Baquerizo *et al.*, 2013) could provide biocrusts new available surface for
84 colonization. However, short- and long-term experiments conducted in cold (e.g., Wertin *et*

85 *al.*, 2012; Zelikova *et al.*, 2012; Ferrenberg *et al.*, 2015) and hot (Escolar *et al.*, 2012;
86 Maestre *et al.*, 2013, 2015) drylands have shown detrimental effects of climate change
87 treatments on biocrust cover and development, as well as important shifts in their
88 composition. For example, in the Colorado Plateau (USA), a single season of increased
89 summer rainfall frequency caused a drastic mortality of mosses and an increase in the
90 abundance of cyanobacteria (Zelikova *et al.*, 2012), whereas the implementation of nearly
91 six years of experimental warming was necessary to record negative effects on mosses and
92 lichens (Ferrenberg *et al.*, 2015). In Central and SE Spain, important declines (up to 40%)
93 in the cover of biocrust-forming lichens appear after two/three years of warming (Escolar
94 *et al.* 2012, Maestre *et al.*, 2015). These results highlight the importance of evaluating
95 multiple biocrust constituents in long-term experiments conducted under different
96 environmental settings when assessing climate change impacts on biocrust communities.

97 In this study, we describe how simulated climate change (2–3°C warming, ~35%
98 rainfall reduction and the combination of both) and the degree of biocrust development
99 affect the cover, richness, diversity, evenness and composition of mosses and lichens in a
100 semiarid ecosystem from Central Spain during the first eight years after the setup of the
101 experiment in 2008. This experiment, still ongoing, is the only of its kind being carried out
102 in an European dryland and, together with that of Ferrenberg *et al.* (2015), is one of the
103 very few experiments that have evaluated climate change impacts on biocrusts for more
104 than six years. Our goal is to expand the previous findings reported by Escolar *et al.* (2012)
105 with new data and statistical approaches aiming to assess how simulated climate change is
106 affecting biocrust community attributes at the short (2008–2011) and medium (2011–2016)
107 term. We also aim to determine the species-specific responses of lichens, the dominant
108 biocrust constituent in our study area, and mosses to simulated climate change.

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110 **Materials and Methods**

111 *Study area and experimental design*

112 The study was conducted at the Aranjuez Experimental Station, located in central Spain
113 (40°02'N–3°32'W; 590 m a.s.l.). The climate is Mediterranean semi-arid, with mean
114 annual temperature and rainfall values of 15°C and ~350 mm, respectively. The soil is
115 classified as Gypsic Leptosol (IUSS Working Group WRB, 2006). Perennial plant

116 coverage is lower than 40%, and is dominated by the perennial herbaceous species
117 *Macrochloa tenacissima*. To a lesser extent, there are also isolated individuals of shrubs
118 such as *Helianthemum squamatum*, *Gypsophila struthium* and *Retama sphaerocarpa*. Open
119 areas between plants contain a well-developed biocrust community dominated by lichens
120 such as *Diploschistes diacapsis*, *Squamarina lentigera*, *Fulgensia subbracteata* and
121 *Buellia zoharyi*. Moss-dominated crust with species such as *Pleurochaete squarrosa* and
122 *Didymodon acutus* are also present (mostly under the canopy of *M. tenacissima*), as well as
123 cyanobacteria of the genera *Microcoleus*, *Schizothrix*, *Tolypothrix*, *Scytonema* and *Nostoc*
124 (Cano-Díaz *et al.*, 2018). See Maestre *et al.* (2013) for a complete species checklist of
125 visible biocrust constituents at our study site.

126 In 2008, we established a full factorial experiment with three factors, each with two
127 levels: initial biocrust cover (IBC; <20% vs. >50%), warming (WARM; control vs.
128 temperature increase), and rainfall exclusion (RE; control vs. rainfall reduction). Ten
129 replicates per combination of treatments were randomly established in the study area,
130 resulting in 80 experimental plots in total. A minimum separation distance of 1 m between
131 plots was kept to minimize the risk of lack of independence between treatments. The
132 applied warming by 2–3°C is in line with several Atmosphere-Ocean General Circulation
133 Models for the second half of this century in Spain (De Castro *et al.*, 2005; Collins *et al.*,
134 2013). Although precipitation predictions are subject to a higher level of uncertainty in the
135 Mediterranean Basin, projected changes point to an intensification of water scarcity in this
136 region (Christensen *et al.*, 2007, 2013; Giorgi & Lionello, 2008). To achieve a temperature
137 increase within the forecasted range, we used open top chambers (OTCs) with hexagonal
138 design and sloping sides of 40 × 50 × 32 cm. These chambers were built with methacrylate
139 sheets, a material which ensures high transmittance in the visible spectrum (92%,
140 according to the manufacturer; Decorplax S.L., Humanes, Spain) and a very low emission
141 in the infrared wavelength. They are suspended 3–5 cm over the ground by a metal frame
142 to allow free air circulation at the soil surface level to avoid an excessive overheating and
143 to minimize obstacles for propagule dispersion. Passive rainfall shelters (RS) based on the
144 design of Yahdjian & Sala (2002) were used to achieve a reduction of rainfall amount of
145 ~35% without changing the frequency of rainfall events. Each RS has an area of 1.44 m²
146 (1.2 × 1.2 m) and a roof composed by three gutters of methacrylate with an inclination of

147 20° and a mean height of 1 m, which cover ~37% of this area. For logistic reasons, OTCs
148 and RS were set up in July and November of 2008, respectively. More details of these
149 infrastructures and their microclimatic effects are available in Escolar *et al.* (2012) and
150 Maestre *et al.* (2013).

151 *Quantification of water inputs*

152 The duration, nature and timing of water inputs are key determinants of the physiological
153 status of biocrust constituents such as lichens and mosses (Pintado *et al.*, 2010; Green *et*
154 *al.*, 2011; Ladrón de Guevara *et al.*, 2014). As such, the interaction of our treatments with
155 features of water inputs could be essential for interpreting their effects on biocrust
156 communities. We recorded rainfall events using an on-site meteorological station (Onset
157 Corp., MA, USA). Periods with data gaps due to technical problems of this station were
158 filled with records from of another station near to this area provided by the Spanish
159 Agency of Meteorology (AEMET; Aranjuez station, located 4 km from our experiment).
160 To consider non-rainfall water inputs (NRWIs), potential fog events —likely the main
161 NRWI in this area— were estimated with relative air humidity sensors (Hobo U23 Pro v.2
162 Temp/RH, Onset Corp., MA, USA; and DS1923 iButton Temp/RH Logger, Dallas
163 Semiconductor, TX, USA) and consecutive filter criteria programmed in R (version. 3.2.4;
164 R Foundation for Statistical Computing, Vienna, Austria) for their differentiation from
165 rainfall inputs (see more details in Supporting Information Fig. S1).

166 *Monitoring changes in biocrust assemblages through time*

167 During the setup of the experiment, we inserted a PVC collar of 20 cm diameter in each
168 plot to monitor changes in the cover, richness, diversity, evenness and composition of
169 biocrust communities through time. We recorded the presence and frequency of all visible
170 biocrust constituents (mosses and lichens) at the beginning of the experiment (June 2008)
171 and later in May 2011 and 2016 using the point-sampling method. A wire mesh of 12 cm
172 each side with 1 × 1 cm grid (144 sampling points) was placed over the collars, and the
173 species located under each of the sampling points was recorded. Although four different
174 species of bryophytes have been identified in this site (Maestre *et al.*, 2013), they were
175 clustered in a single category (mosses) due to the difficulty of identifying them with
176 confidence in the field. For the same reason, some lichen species of the same genus present
177 in the area were clustered in this last taxonomic level (i.e., *Fulgensia* spp., *Collema* spp.,

178 *Endocarpon* spp.). Using data from these surveys, we calculated species richness, diversity
179 (using the exponential Shannon index with the natural logarithm in the formula; Shannon,
180 1948) evenness (using Pielou's index; Pielou, 1966) and composition (measured using both
181 the relative abundance and presence/absence of each species). In each collar, annual
182 changes in the total cover of the whole biocrust community were also estimated throughout
183 the experiment using repeated photographs and the software GIMP (<http://www.gimp.org>),
184 as explained in Maestre *et al.* (2013). Cover estimates obtained by this method correlate
185 well with the values obtained from the point-sampling method (Supporting Information
186 Fig. S2).

187 *Statistical analyses*

188 We used general linear mixed models (LMMs) to analyze the temporal effects of the
189 climate change treatments on the cover, richness, diversity and evenness of the biocrust
190 community. WARM, RE, IBC and year of survey (Year), as well as their interactions, were
191 included in the models as fixed factors. The influence of the variability between replicates
192 was also tested by including them in the model as a random factor and by supervising the
193 effect of this inclusion on the Akaike's Information Criterion (AIC, Akaike, 1973) of the
194 model. Validation of the assumptions of the models were performed by checking the
195 autocorrelation function plot, the Pearson standardized residuals vs. fitted values plot and
196 the distribution of these residual by a QQ-plot. After running the best fitted model
197 (considering AIC values) and checking the compliance of the model assumptions, the
198 number of interactions in the fixed part was reduced to gain degrees of freedom, and thus
199 to increase the power of the model. The exclusion started from the interaction with more
200 terms up to the most complex interaction with a significant (< 0.05) P value. The final
201 models were run using a restricted maximum likelihood (REML) procedure, and when
202 significant differences were detected in interactions or in the factor Year (the only one with
203 more than two levels), Fisher's least significant difference (LSD) test was applied.

204 Changes in the relative abundance and presence/absence of species through time
205 caused by the treatments were analyzed using permutational multivariate analysis of
206 variance (PERMANOVA). These analyses were performed on Bray-Curtis similarity
207 matrices of fourth-root transformed species abundances and dichotomous species
208 presence/absence data, respectively. Very rare species not detected in any of the three

209 point-sampling surveys were not retained in the analyses. Since our dataset contained
210 samples with very few species records, thus significantly increasing the variability of the
211 data, a dummy variable (weight 1; i.e., a fictitious species with value = 1 in all plots) was
212 added to the matrix (Clarke & Gorley, 2006). For balanced designs such as ours,
213 PERMANOVA is a robust method to the heterogeneity of multivariate dispersions
214 (Anderson & Walsh, 2013). As in the LMM analyses, the four factors and all their
215 interactions were introduced in a first step, and a reduction of interactions was applied in a
216 second step following the criterion explained above. *P*-values were calculated using 999
217 permutations of the residuals under a reduced model, which is the method with the best
218 power and the most accurate Type I error for complex designs (Anderson, 2005). Post-hoc
219 pair-wise comparisons were done with all significant interactions and the factor Year.

220 The magnitude of the temporal effects of each treatment on the relative abundance
221 (fourth-root transformed) and presence/absence of species were also modeled and
222 visualized using Principal Response Curves (PRC, Van den Brink & Ter Braak, 1998,
223 1999). This method evaluates the differences between the values of the variables in the
224 treatments and those in the control (standardized to zero-value) in each survey. In addition
225 to scores for each treatment through time, PRC also offers scores for each species, which
226 allow assessing their weight on the overall response (i.e., changes in the relative abundance
227 and presence) of the whole community to the climatic treatments evaluated. In addition, we
228 conducted SIMPER analyses to disentangle the contribution of each species to the overall
229 compositional shifts caused by the factors with significant interactions detected in the
230 PERMANOVA analyses. SIMPER analyses show the percentage of contribution of each
231 species to the average Bray-Curtis dissimilarity or Euclidean squared distance between the
232 levels of the factors evaluated (Clarke & Warwick, 1994).

233 LMMs, LSD tests and the plots for the validation of the assumptions were performed
234 using the software InfoStat Version 2014 (Di Rienzo *et al.*, 2014). PERMANOVA and
235 SIMPER analyses were carried out with the PERMANOVA+ 1.0.1 for the PRIMER 6.1.11
236 statistical package (PRIMER-E Ltd, Plymouth Marine Laboratory, UK). PRC analyses
237 using the package ‘vegan’ (Oksanen *et al.*, 2016) in the R statistical environment. The data
238 used in our analyses are available from figshare (Ladrón de Guevara *et al.*, 2017).

239

240 **Results**

241 *Responses of biocrust cover to climatic treatments*

242 The analysis of cover data revealed two significant interactions among the experimental
243 factors (IBC \times Year and WARM \times Year, Table S1). As only two-term interactions were
244 significant in the saturated models, in a second step of the analyses the more complex
245 interactions were eliminated. This analysis did not detect any statistically significant effect
246 of rainfall exclusion on cover, neither as a main effect nor as a term in the interactions
247 (Table S1). Plots with low IBC (LIBC) and without warming experienced a significant
248 increase of their cover between 2008–2011 (from $5\pm 0.9\%$ to $15\pm 2.2\%$ on average), had a
249 static period between 2011–2015 and started to increase their cover again in 2016 (Fig. 1a).
250 The cover of these plots also increased by 2011 under warming, but at a significantly lower
251 rate than without this treatment, and after this year, decreased to values similar to those
252 observed in 2008. Changes in cover through time in plots with high IBC (HIBC) followed
253 a distinct pattern (Fig. 1b). From 2008 to 2013, the cover of plots without warming
254 decreased by $41\pm 3.9\%$. This tendency was reversed after 2013, but without reaching the
255 initial cover values ($\sim 80\%$ on average). The decrease observed in WARM plots was more
256 abrupt and did not stop in 2013. As a result, the loss of cover in these plots was large over
257 the course of the experiment, with an $82\pm 5\%$ of reduction over the course of the
258 experiment and with final cover values lower than those found in the plots with low IBC
259 and without warming. Significant differences in cover with warming were detected three
260 years after the setup of the experiment in both LIBC and HIBC plots (Fig. 1).

261 *Treatment effects on biocrust community attributes through time*

262 As found with cover, only two-term interactions were statistically significant when
263 analyzing the richness, diversity and evenness of biocrust assemblages (Table S2). The
264 IBC \times Year interaction reflected natural trends on their richness and diversity, although
265 they are intermixed with the effects of the climate change treatments. Biocrust richness and
266 diversity decreased during the period 2008–2011, but recovered thereafter in the controls
267 with HIBC (Fig. 2) and in all HIBC plots (Fig. 3). Such a decrease did not occur in the
268 LIBC plots; the significant rise of richness and diversity observed after 2011 was the result
269 of the intensification of the natural colonization of these plots by biocrusts. The WARM \times
270 Year interaction observed in the LMM analyses also indicated that biocrust colonization

271 did not happen in WARM plots. Warming promoted a fast and significant decline in
272 biocrust richness and diversity throughout the duration of the experiment (Fig. 3). Rainfall
273 exclusion negatively affected biocrust diversity only in the HIBC plots, as noted by the
274 statistically significant IBC \times RE interaction (Table S2), but the magnitude of this effect
275 was lower than that promoted by WARM (Fig. 2). Changes in evenness were driven by
276 IBC \times WARM and WARM \times RE interactions. In the first case, species evenness only
277 decreased in the LIBC plots subjected to warming, and in the second such a reduction was
278 only observed in WARM + RE plots (Fig. 3).

279 Warming was the primary treatment promoting differences on species composition
280 when compared to control plots, an effect that increased through time (Fig. 4).
281 PERMANOVA analyses indicated that the effects of warming became significant during
282 the first experimental period (2008–2011). The magnitude of this effect was similar in
283 LIBC and HIBC plots, but was greater when analyzing presence/absence than relative
284 abundance data (46% and 53% greater in LIBC and HIBC plots, respectively). However,
285 the main driver of community shifts differed between LIBC and HIBC plots. As found
286 when evaluating changes in cover, an increase of the values of the species composition
287 attributes without warming took place in the LIBC plots during the period 2008–2016 (Fig.
288 4a,c). This process did not occur under warming. This treatment negatively affected the
289 growth of biocrusts, and therefore the values of species composition attributes were similar
290 throughout the course of the experiment in LIBC plots (Fig. 4a,c). The major shifts in
291 species composition took place in plots without warming, as also indicated by the positive
292 values of the parameter taxon weights observed in the PRC analysis. In the LIBC plots,
293 most species increased their presence and relative abundance, but such an increase was
294 particularly noticeable for *Fulgensia* spp., *D. diacapsis*, *S. lentigera* and *Toninia sedifolia*.
295 Only *Squamarina cartilaginea* had a negative score in the PRC analyses (Fig. 4a,c). On the
296 other hand, warming was a main driver of changes in the composition of high HIBC plots,
297 especially when evaluating changes in the relative abundance of species. The abundance of
298 species in plots without warming was stable over the monitoring time, while the number of
299 species present in these plots increased (Fig. 4b,d). Warming decreased the relative
300 abundance and presence of most of the studied species. The opposite trends in the presence
301 of species promoted the greater differences between the control and warming treatments

302 detected in the PRC analysis. Across all treatments, we found a clear decline in the relative
303 abundance of *D. diacapsis*, in the presence of *T. sedifolia* and in both the relative
304 abundance and presence of *Fulgensia* spp. and *Psora decipiens* (Fig. 4b,d). However, we
305 found an increase in both the relative abundance and presence of mosses through time.

306 PERMANOVA analyses revealed a significant IBC \times Year interaction when analyzing
307 both relative abundance and species presence data (Table S3). The Bray-Curtis similarity
308 index showed an increase in the homogeneity of the compositional attributes between
309 LIBC and HIBC plots throughout the 2008–2016 period (Table S4). SIMPER analyses
310 showed temporal changes of main species leading the compositional variations at both IBC
311 levels (Table S5). This last analysis highlighted *D. diacapsis* as the most dynamic species
312 throughout the experiment, as it showed the highest colonizing capacity on LIBC plots,
313 and was the third species with the largest losses in both the presence and relative
314 abundance in the HIBC plots (Table S5). As a result, in 2016 the average relative
315 abundance of this species was slightly higher in the LIBC than in the HIBC plots.
316 *Fulgensia* spp. largely contributed to the observed changes in species relative abundance
317 throughout the experiment, whereas *T. sedifolia* had a relevant role in the changes of
318 presence/absence observed during the same period (Table S5). Reductions in the relative
319 abundance of *Fulgensia* spp. in the HIBC plots were much more important than increases
320 on its relative abundance in the LIBC plots. The contribution of this species to
321 presence/absence changes was only relevant in the 2011–2016 period, with important
322 declines in their presence at both LIBC and HIBC plots. The dynamics of the presence of
323 *T. sedifolia* changed during the experiment. It suffered a large decline during the 2008–
324 2011 period in the HIBC plots, and did not increase in the LIBC plots. However, its
325 presence increased in the 2011–2016 period at both LIBC and HIBC plots, particularly in
326 the former. SIMPER analyses also suggested that the decline in richness and diversity in
327 the 2008–2011 period was mainly driven by reductions in both the relative abundance and
328 presence of *Acarospora nodulosa*, *D. diacapsis*, *Fulgensia* spp. and *T. sedifolia* (Table S5),
329 and their recovery in the 2011–2016 period was led by mosses and *T. sedifolia*. Mosses
330 and lichens such as *B. zoharyi*, *D. diacapsis* and *T. sedifolia* were main actors in the
331 colonization process observed in the LIBC plots through time.

332 The Bray-Curtis index showed a low degree of similarity in the compositional
333 attributes within WARM plots and between the 2008–2016 period (Table S4). Overall,
334 both the PERMANOVA and SIMPER results revealed that, over the course of the
335 experiment, *D. diacapsis*, *Fulgensia* spp. and *T. sedifolia* were the species most affected by
336 warming (Table S5). *Fulgensia* spp. showed the largest reductions in presence and relative
337 abundance, although this response was particularly evident in the 2011–2016 period. *T.*
338 *sedifolia* and *D. diacapsis* had a greater contribution to changes in species
339 presences/absences and relative abundance, respectively. Unlike *Fulgensia* spp., these
340 species had a faster response to warming. The WARM \times Year interaction also elucidated
341 in part the changing dynamics explained above for *T. sedifolia*; in the 2011–2016 period, a
342 greater expansion of this species took place in the non-WARM plots along with its neutral
343 response to warming, likely because during 2008–2011 this species disappeared from most
344 WARM plots. The observed WARM \times RE interaction revealed that the negative effect of
345 warming observed in *D. diacapsis* was enhanced under rainfall exclusion. Warming caused
346 greater declines of both the relative abundance and presence of *Fulgensia* spp. in plots
347 without rainfall exclusion, as well as in the presence of *P. decipiens*. PERMANOVA
348 analyses revealed that the significant IBC \times RE interaction detected when analyzing
349 species diversity was largely driven by reductions in both the relative abundance and
350 presence of *P. decipiens* in the high IBC plots subjected to rainfall exclusion.

351

352 Discussion

353 *Warming drastically reduced the cover of lichen-dominated biocrusts but promoted moss*
354 *growth*

355 In contrast with the widespread perception over the past several decades that biocrust
356 constituents, especially crustose lichens, conform a fairly static community due to their
357 slow growth and resistance to extreme environments (Garvie *et al.*, 2008; Armstrong &
358 Bradwell, 2010; Meeßen *et al.*, 2013), our findings highlight the dynamism of biocrust
359 cover and its fast response to environmental changes. Similar results have been found with
360 biocrust-forming lichens in drylands from other parts of the world (e.g., Belnap *et al.*,
361 2006, 2007; Jimenez Aguilar *et al.*, 2009; Read *et al.*, 2011; Maestre *et al.*, 2015). Cover or
362 biomass of these communities can stay static or decline substantially during drought events

363 or other stressful conditions. But terricolous lichens can have pulses of fast growth during
364 wet periods (Belnap *et al.*, 2006; Weber *et al.*, 2016a). In addition, another feature of some
365 terricolous lichen species is the possession of certain capacity of mobility by dispersion of
366 thallus fragments (Heinken, 1999), such as *D. diacapsis*, the most dynamic species
367 detected in this study. This species can have different degrees of attachment in the soil,
368 sometimes being it able to detach easily (Ballesteros *et al.*, 2017). Thus, the fast losses of
369 cover of this species detected in the warming treatment are likely due to a detachment of
370 fragments from the soil and their dispersion through wind to other places. Similarly, we
371 have also detected new, but well established, large thallus of *D. diacapsis* from one year to
372 another in the other treatments, which likely have an external origin (i.e. they come from
373 outside the plots). Therefore, the semi-erratic behaviour of this species, together with its
374 growth capacity when conditions are optimal (Lázaro *et al.*, 2008), are presumably the two
375 features that allow the dynamic response to the climate change treatments evaluated. The
376 fast response of these communities to environmental conditions caused a contrasted cover
377 dynamic in the two IBC levels of the control plots. During the experimental period, there
378 were two consecutive wet seasons (2010–2011 and 2011–2012) where soil moisture was
379 below the usual average values (~15%) for this season in this area (Fig. S1). This decrease
380 in water availability could be not too strong to limit lichen colonization in areas with low
381 competition for this resource (LIBC), but enough to trigger a decline of lichens in HIBC,
382 where competition interactions were very likely stronger. In addition, we estimated a very
383 low number of fog events in the wet season 2012–2013, a period that coincided with the
384 greatest cover decline in HIBC.

385 The great loss of biocrust cover observed (Fig. 1) was clearly driven by warming,
386 probably due to its indirect negative effect on soil surface moisture. Although we did not
387 directly measure this effect due to the lack of appropriate sensors to accurately measure
388 soil moisture in the first mm of soil depth, which have been developed very recently
389 (Weber *et al.*, 2016b), our continuous monitoring of soil subsurface moisture (0–5 cm
390 depth) showed a highly significant negative effect of warming on soil water gains after
391 rainfall events (Lafuente *et al.*, 2017). Other studies have also reported negative effects of
392 passive warming by OTCs on soil moisture (e.g., Klein *et al.*, 2005; Bokhorst *et al.*, 2016).
393 In addition, we have already observed that reductions in soil surface moisture negatively

394 affect the C fixation rate of biocrust-dominated areas during the first years of our
395 experiment (Maestre *et al.*, 2013; Ladrón de Guevara *et al.*, 2014). We cannot rule out a
396 possible direct effect of warming on lichen physiology because the increase of dark
397 respiration with temperature is well documented in these organisms (e.g., Lange *et al.*,
398 1998; Lange & Green, 2004; Ouyan & Hu, 2017). Nevertheless, we think that it was not
399 the main physiological impact since mosses had a positive response to warming, and
400 increases in their respiration with warming can be similar or even greater than those
401 observed in lichens (Weber *et al.*, 2012; Ouyang & Hu, 2017). During late autumn and
402 winter, the periods when biocrust-forming lichens are most active in Mediterranean
403 drylands (Pintado *et al.*, 2010; Raggio *et al.*, 2014), net photosynthesis also increases with
404 temperature because the optimal temperature values for the photosynthetic activity of these
405 organisms are not surpassed. However, in an annual basis, the periods of C losses are in
406 general greater than those of C gains (Evans & Lange, 2003), and the combination of both
407 processes (increment of C losses and reductions in C gains directly and indirectly caused
408 by warming, respectively) can produce C starvation in biocrust-forming lichens.
409 Reductions in the production of photoprotective pigments are another documented effect of
410 a lower availability of C for metabolic functions (Belnap *et al.*, 2004). Although we did not
411 measure pigment concentrations, fluorescence values (F_v/F_m) recorded in this experiment
412 and in another site in southern Spain indicated that radiation did not damage the
413 photosynthetic system of biocrust constituents (Escolar *et al.*, 2012; Ladrón de Guevara *et al.*,
414 2014). Therefore, we discard declines in pigment production as a main cause of the
415 biocrust mortality observed in our experiment.

416 The observed declines in cover are in line with those recorded after ten years of
417 warming and rainfall manipulations in a cold desert of North America (Ferrenberg *et al.*,
418 2015), although with differences in the main biocrust constituents affected, the drivers of
419 the responses observed and the timing when significant effects were detected. In the study
420 of Ferrenberg *et al.* (2015), an increase of small rainfall events during summer caused a
421 fast response of the biocrust community driven by the high mortality of mosses during the
422 first year of climatic manipulations. Warming and rainfall manipulation separately had
423 variable effects on the cover of lichens throughout the experiment, but their interaction
424 caused a significant decrease in their cover nearly five years after the beginning of the

425 experiment, with no signs of recovery after that period. Conversely, warming was the main
426 driver of lichen cover losses in both our study and in another similar experiment conducted
427 in SE Spain (Maestre *et al.*, 2015). In both cases, warming promoted a significant decline
428 in the cover of lichens compared to control plots (~35–45%) just after three years of the
429 treatment implementation, while the cover of mosses was not negatively impacted by
430 warming. Even in our study, a clear increase of moss growth was promoted by this
431 treatment (Fig. 4 and Table S5). Thus, the main drivers of changes in cover differed in
432 these studies —warming in our study and the increment of small rainfall events during
433 summer in Ferrenberg *et al.* (2015)— primarily due to differences in the dominant biocrust
434 constituents and in the climatic treatments applied. In addition, it is possible that the
435 different warming methods used in both studies (OTCs in this study *vs.* infrared lamps in
436 Ferrenberg *et al.* 2015) have significantly influenced in the timing of the lichen cover
437 responses, since OTCs could have a larger impact on air and soil moisture than infrared
438 lamps (Reed *et al.*, 2016; Young *et al.*, 2017).

439 Effects of OTCs on other microclimatic variables (e.g., reduction in PAR and greater
440 diurnal variability in air temperature) have also been reported (e.g., Klein *et al.*, 2005;
441 Bokhorst *et al.*, 2013). However, we believe that such effects are having minor impacts on
442 our results given the transparency of the plastic material used and the lack of significant
443 effects of OTCs on the variability of air temperature registered in our experiment (Maestre
444 *et al.*, 2013). We also consider that other possible disturbances unrelated to the treatments
445 evaluated, such as those created by ourselves during the surveys had a minimal impact in
446 the results due to the precautions adopted (something that was also indicated by the
447 increases in cover observed in the LIBC control plots). However, we must acknowledge
448 that the imposed rate of warming in our experiment is faster than that occurring naturally.
449 The fact that we simulate in years a process that will happen in decades is likely causing a
450 higher loss of maladapted species than that expected under the more gradual warming.
451 Therefore, it is probably that in the abrupt biocrust decline detected in this study will be
452 ameliorated, at least in part, by changes in increases in the cover of mosses, which we have
453 found to respond positively to warming, and cyanobacteria, which have already been found
454 to increase their abundance in response to climate change simulations in Ferrenberg *et al.*
455 experiment.

456 *Climate change treatments altered biocrust community attributes*

457 Understanding the effects of climate drivers on the assemblage of biotic communities is
458 essential to predict how climate change will impact ecosystem dynamics and functioning
459 (Jing *et al.*, 2015; Maestre *et al.*, 2016; Pecl *et al.*, 2017). In our experiment, warming was
460 involved four times in three different interactions that caused significant responses in the
461 richness, diversity and/or evenness of biocrusts. However, rainfall exclusion had only two
462 significant effects as a term of two different interactions, and did not significantly affect
463 species richness. Warming reduced all community attributes (Figs. 1–4). These warming-
464 induced changes were evident as early as three years since the setup of the experiment, a
465 similar time span as that observed by Maestre *et al.* (2015) but faster than the changes
466 detected by Ferrenberg *et al.* (2015), as noted above. In addition, the divergent results
467 regarding the response of mosses between this last study and ours were likely because our
468 warming treatment decreased the frequency of very short wetting events, which in mosses
469 promote C losses. Observed responses in both experiments are in agreement with the
470 different strategies used by lichens and mosses to cope with desiccation/rehydration cycles
471 (reviewed by Green *et al.*, 2011), and therefore, changes in biocrust drying–wetting cycles
472 was the main modulator in the responses of the community assemblage in both studies.
473 Succinctly, lichens are less tolerant to long desiccation periods, but have higher ability to
474 fix C under suboptimal water content conditions. Both characteristics make frequent
475 NRWIs critical for their C economy. On the other hand, mosses have a higher maximal
476 water content, which enables them to continue photosynthesis for longer periods when the
477 soil surface is saturated after rainfall events. However, they also have higher respiration
478 rates than lichens during dehydration processes. Furthermore, mosses have a reduced
479 ability to exploit water resources below their optimum water content, and, therefore,
480 reducing the frequency of very small wetting events decreases the number of metabolic
481 activation processes that could result in a negative C balance.

482 Rainfall exclusion did not have any negative effect on species richness, but reduced
483 the diversity of the high HIBC plots and the evenness of both LIBC and HIBC plots when
484 interacted with warming (Fig. 3). These effects were not detected during the first years of
485 the experiment (Escobar *et al.*, 2012), highlighting the importance of conducting long-term
486 experiments when assessing the responses of biocrusts to climate change. It is plausible to

487 speculate that rainfall exclusion, which has a much lower negative impact on biocrusts than
488 warming (Fig. 4), will also affect species richness in the future. Our findings show that the
489 frequency of species (incorporated in diversity and evenness attributes) has a faster
490 response to rainfall exclusion than richness because the former varies instantaneously with
491 the dynamics of the most sensitive species, whereas changes in richness require the total
492 mortality of these species. Although warming was the main factor driving changes in
493 surface soil moisture in our experiment, the most critical water source for biocrusts, our
494 rainfall exclusion probably had an effect on the infiltration depth of the large rainfall
495 events. This treatment presumably reduced this infiltration depth, decreasing also the water
496 stored in the soil after these rainfall events. This could have negative effects on the activity
497 periods of biocrust, as this water is available for these organisms when it rises by
498 capillarity to the surface due to evaporative forces (Colesie *et al.*, 2016). This effect was
499 observed previously in our experiment (Ladrón de Guevara *et al.*, 2014), as rainfall
500 exclusion reduced the duration of photosynthetic events in a day with antecedent rainfalls,
501 whereas this treatment did not affect such duration in days without antecedent water inputs.

502 Although warming reduced the relative abundance and presence of all lichen species
503 (Fig. 4), this effect was clearly less negative in *Fulgensia* spp, and to a lesser extent in *P.*
504 *decipiens*, when rainfall exclusion was also present (Table S5). Within the biocrust
505 community studied, the presence of the organic compound anthraquinone is an exclusive
506 chemical trait of these two species (Concostrina-Zubiri *et al.*, 2014). Anthraquinones are
507 metabolites that can act as UV-protectors (Nguyen *et al.*, 2013) and thus these pigments
508 could have a different photoprotective effectiveness than those presented in the other
509 species under the combination of warming and rainfall exclusion. However, this possible
510 advantage of anthraquinones against other photoprotective pigments has not been studied
511 as far as we know, and therefore we can only speculate that this is the mechanism
512 underlying the responses observed. They could also be related to the depression of net
513 photosynthesis observed at high thallus water contents. Species from the same habitat can
514 show a gradient in the intensity of this depression (Lange *et al.*, 1993), ranging for example
515 from 0% in *Cladonia convoluta* to 100% in *Fulgensia fulgens* (Lange *et al.*, 1995; Lange
516 & Green, 2003). Intraspecific differences in the magnitude of this depression can also take
517 place between habitats due to the important role that the attachment to substratum plays in

518 the distribution of water within lichen thalli (Souza-Egipsy *et al.*, 2002; Lange & Green,
519 2004). Thus, a reduction of the events that could cause a water saturation of the thallus
520 with our rainfall exclusion treatment might have favored species that, in this study area,
521 suffer a total net photosynthesis depression under water suprasaturation. We also found
522 temporal species-specific responses to warming. The presence and/or relative abundance of
523 *Collema* spp., *D. diacapsis*, *P. decipiens*, *S. lentigera* and *T. sedifolia* showed important
524 reductions during the 2008–2011 period (Table S5), while these responses were especially
525 relevant in the 2011–2016 period for *B. zoharyi* and *Fulgensia* spp. This suggests that these
526 two species have a combination of specific functional traits that provided them short-term
527 resistance to warming, although when the temporal threshold of three years was crossed
528 the negative effects of this treatment on their abundance were dramatic.

529 *Concluding remarks*

530 Our results indicate that climate change, and warming in particular, will trigger a fast loss
531 of late successional biocrust constituents and will reduce the richness, diversity and
532 evenness of lichen-dominated biocrust communities. The impacts of biocrusts on
533 ecosystem functioning, and especially on nutrient cycling, are largely driven by these
534 community attributes (Maestre *et al.*, 2012; Bowker *et al.*, 2013b). In addition, biocrust-
535 forming species have unique contributions to individual ecosystem functions (Bowker *et al.*,
536 2011; Gotelli *et al.*, 2011; Liu *et al.*, 2017), suggesting that changes in the composition
537 of biocrusts can have large impacts on ecosystem functioning (Maestre *et al.*, 2012). As
538 such, the changes in the community attributes of biocrusts observed in this study will
539 lessen the capacity of drylands such as the studied one here to perform key ecosystem
540 functions associated to these communities in a warmer, and more arid, world.

541

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551

552 **Author contributions**

553 F.T.M. planned and designed the research, M.L.G., B.G., J.R. and M.P. conducted
554 fieldwork, M.L.G., B.G., J.R. and A.L. processed and analysed data, M.L.G. and F.T.M.
555 wrote the manuscript and all authors contributed in the final review.

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845

846 **Brief legends of figures and tables available in Supporting Information**

847 **Fig. S1** Characterization of water input events throughout the experiment and average soil
848 subsurface moisture in control plots during lichens growth season.

849 **Fig. S2** Relationship between the cover estimates obtained with the two methods used.

850 **Table S1** Results of a general linear mixed model showing the effects of the treatments on
851 biocrust cover.

852 **Table S2** Results of general linear mixed models showing the effects of the treatments on
853 biocrust attributes (richness, diversity and evenness).

854 **Table S3** Results of PERMANOVA models showing the effects of the treatments on
855 biocrust composition.

856 **Table S4** Results of PERMANOVA models showing the average values between/within
857 groups of the Bray-Curtis similarity index.

858 **Table S5** Results from SIMPER analysis showing the contribution of lichen species and
859 mosses to the Euclidean squared distance in species relative abundance and presence.

860

861 **Figure legends in the main text**

862 **Fig. 1** Temporal changes in total biocrust cover (including mosses and lichens) as response
863 to climate treatments in plots with low (a) and high (b) initial biocrust cover (IBC). Data
864 are means \pm SE ($n = 10$). Asterisks indicate the first year where significant differences in
865 total biocrust cover between the plots with and without warming are detected in each level
866 of IBC according to the post-hoc test Fisher's least significant difference (LSD). WARM =
867 Warming and RE = Rainfall exclusion.

868 **Fig. 2** Temporal changes in richness, diversity and evenness in all the treatments. Data are
869 means \pm SE ($n = 10$). WARM = Warming, RE = Rainfall exclusion and IBC = Initial
870 biocrust cover.

871 **Fig. 3** Results of the Fisher's LSD post-hoc test conducted after significant ($P < 0.05$) two-
872 term interactions observed when analyzing species richness, diversity and evenness. Data
873 are means \pm SE (n varies with the interaction of factors). Panels with white background
874 indicate that the significant interactions resulted from the linear mixed model analyses (see
875 Table S2). In each panel, factor levels without letters in common show significant
876 differences among them ($P < 0.05$). WARM = Warming, RE = Rainfall exclusion and IBC
877 = Initial biocrust cover (LIBC = Low IBC and HIBC = High IBC).

878 **Fig. 4** Principal Response Curves showing the regression coefficients and weights obtained
879 for particular taxa. These coefficients indicate the magnitude of the treatment effects on
880 species composition (i.e., the spatial distance of the treatments regarding the control with
881 constant 0 values in the y-axis). Asterisks indicate significant P values in the Year \times
882 Warming (WARM) interaction, as revealed by PERMANOVA analyses ($* = P < 0.01$; $** =$
883 $P < 0.001$). Numbers in blue represent the mean of the sum of all relative abundance (Σ RA)

884 and presence (ΣP) values per plot at each time for the control treatment. The same symbols
885 in red are showing these values for the warming treatment. Taxon weights show the relative
886 contribution of each taxon to community changes, and can be interpreted as the weight of
887 each taxon in the response to the treatments. Positive values indicate an increase in their
888 relative abundance (a, b) or presence (c, d). Negative values indicate a reduction in these
889 community attributes. For example, in panel a *Fulgensia* spp. was the species with the
890 highest increment in relative abundance considering the whole study period and all
891 observed responses to the treatments, suggesting that its colonization of control plots was a
892 process with greater effects on its abundance than those promoted by the other treatments.
893 RE = Rainfall exclusion and IBC = Initial biocrust cover.

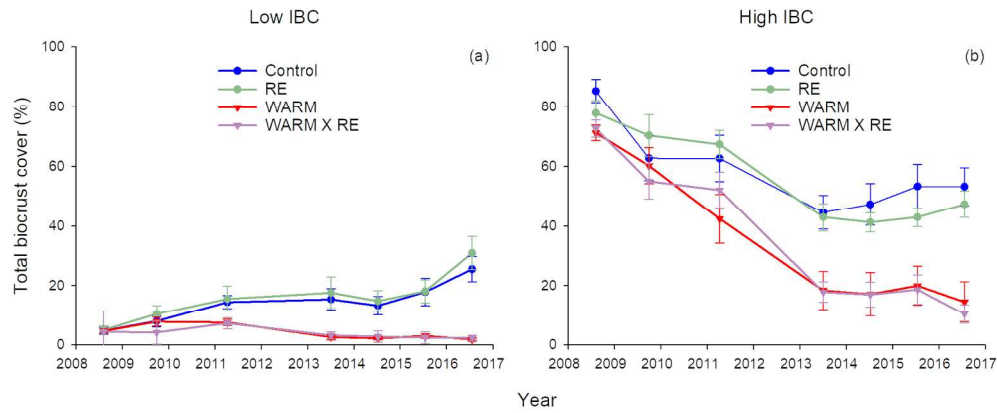


Fig. 1 Temporal changes in total biocrust cover (including mosses and lichens) as response to climate treatments in plots with low (a) and high (b) initial biocrust cover (IBC). Data are means \pm SE ($n = 10$). Asterisks indicate the first year where significant differences in total biocrust cover between the plots with and without warming are detected in each level of IBC according to the post-hoc test Fisher's least significant difference (LSD). WARM = Warming and RE = Rainfall exclusion.

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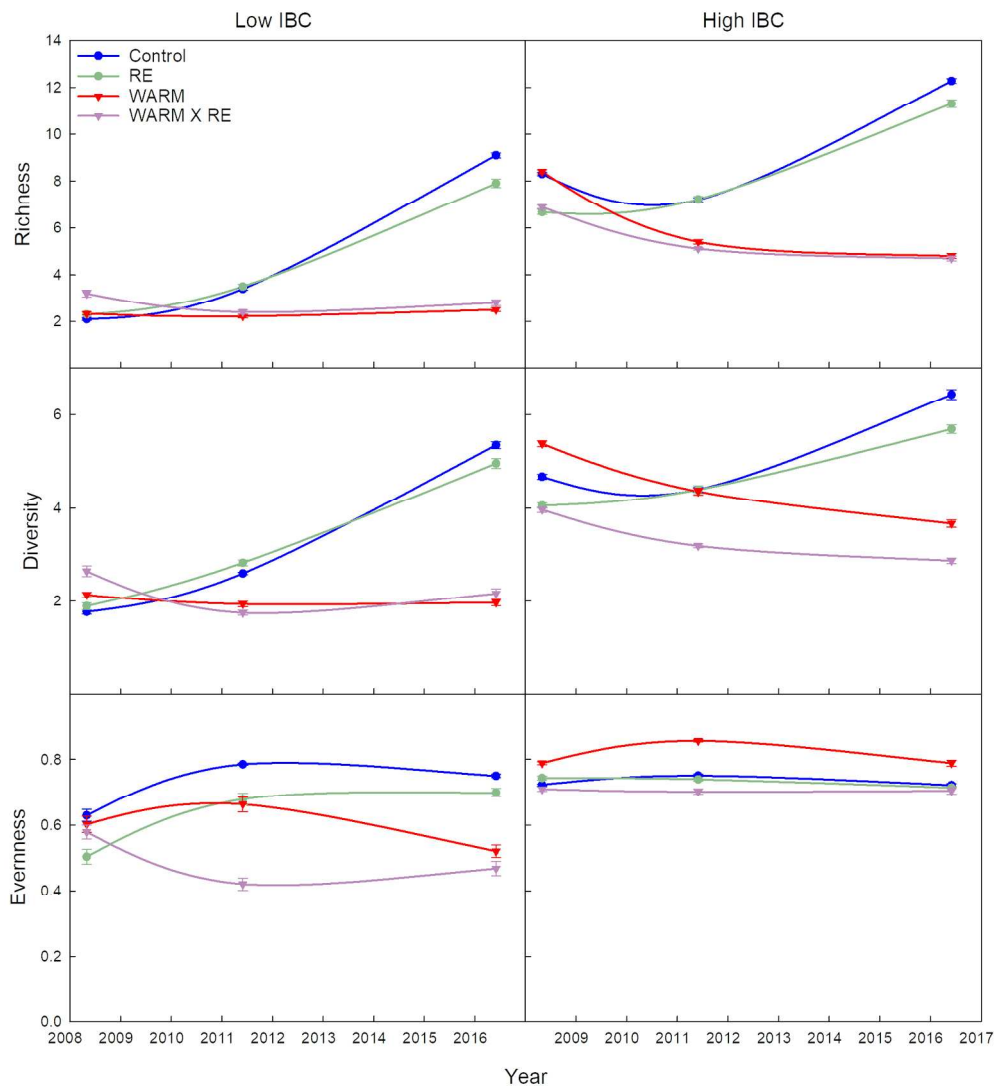


Fig. 2 Temporal changes in richness, diversity and evenness in all the treatments. Data are means \pm SE (n = 10). WARM = Warming, RE = Rainfall exclusion and IBC = Initial biocrust cover.

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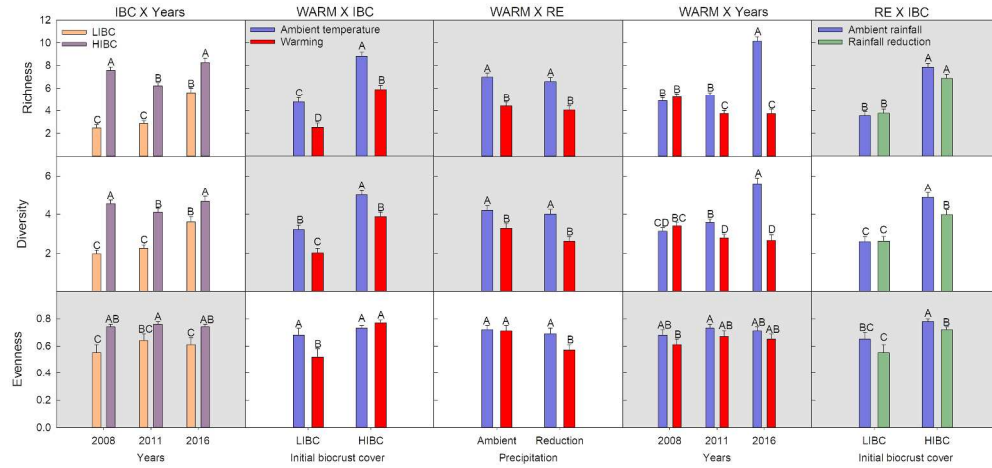


Fig. 3 Results of the Fisher’s LSD post-hoc test conducted after significant ($P < 0.05$) two-term interactions observed when analyzing species richness, diversity and evenness data. Panels with white background indicate that the significant interactions resulted from the linear mixed model analyses (see Table S2). In each panel, factor levels without letters in common show significant differences among them ($P < 0.05$). IBC = Initial biocrust cover, WARM = Warming and RE = Rainfall exclusion.

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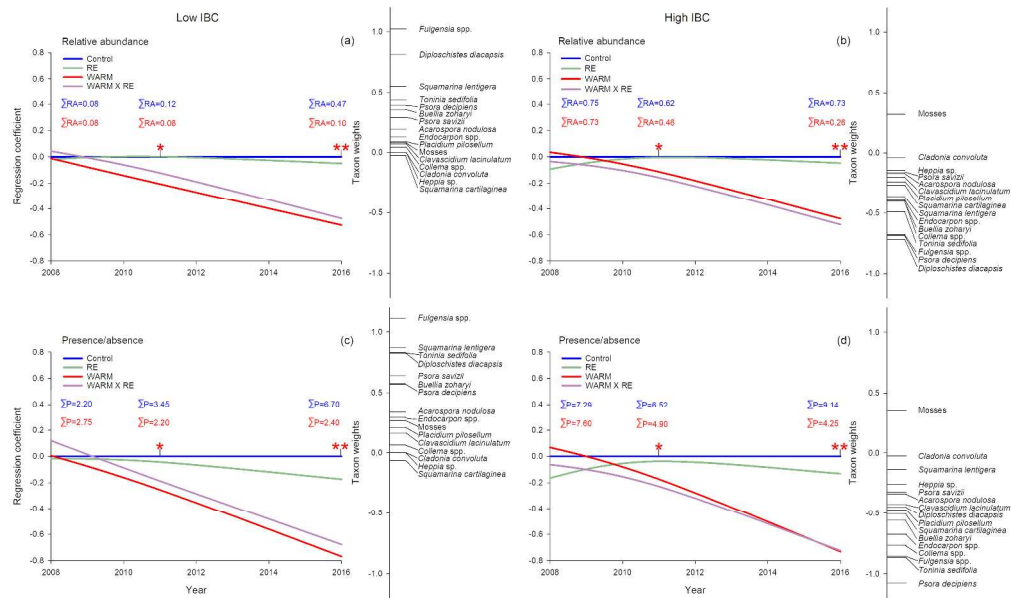


Fig. 4 Principal Response Curves showing the regression coefficients and weights obtained for particular taxa. These coefficients indicate the magnitude of the treatment effects on species composition (i.e., the spatial distance of the treatments regarding the control with constant 0 values in the y-axis). Asterisks indicate significant P values in the Year × Warming (WARM) interaction, as revealed by PERMANOVA analyses (* = P < 0.01; ** = P < 0.001). Numbers in blue represent the mean of the sum of all relative abundance (ΣRA) and presence (ΣP) values per plot at each time for the control treatment. The same symbols in red are showing these values for the warming treatment. Taxon weights show the relative contribution of each taxon to community changes, and can be interpreted as the weight of each taxon in the response to the treatments. Positive values indicate an increase in their relative abundance (a, b) or presence (c, d). Negative values indicate a reduction in these community attributes. For example, in panel a Fulgensia spp. was the species with the highest increment in relative abundance considering the whole study period and all observed responses to the treatments, suggesting that its colonization of control plots was a process with greater effects on its abundance than those promoted by the other treatments. RE = Rainfall exclusion and IBC = Initial biocrust cover.

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