

Research

Warming reduces the growth and diversity of biological soil crusts in a semi-arid environment: implications for ecosystem structure and functioning

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Biological soil crusts (BSCs) are key biotic components of dryland ecosystems worldwide that control many functional processes, including carbon and nitrogen cycling, soil stabilization and infiltration. Regardless of their ecological importance and prevalence in drylands, very few studies have explicitly evaluated how climate change will affect the structure and composition of BSCs, and the functioning of their constituents. Using a manipulative experiment conducted over 3 years in a semi-arid site from central Spain, we evaluated how the composition, structure and performance of lichen-dominated BSCs respond to a 2.4°C increase in temperature, and to an approximately 30 per cent reduction of total annual rainfall. In areas with well-developed BSCs, warming promoted a significant decrease in the richness and diversity of the whole BSC community. This was accompanied by important compositional changes, as the cover of lichens suffered a substantial decrease with warming (from 70 to 40% on average), while that of mosses increased slightly (from 0.3 to 7% on average). The physiological performance of the BSC community, evaluated using chlorophyll fluorescence, increased with warming during the first year of the experiment, but did not respond to rainfall reduction. Our results indicate that ongoing climate change will strongly affect the diversity and composition of BSC communities, as well as their recovery after disturbances. The expected changes in richness and composition under warming could reduce or even reverse the positive effects of BSCs on important soil processes. Thus, these changes are likely to promote an overall reduction in ecosystem processes that sustain and control nutrient cycling, soil stabilization and water dynamics.

Keywords: climate change; lichens; mosses; biological soil crusts; Mediterranean; semi-arid

1. INTRODUCTION

There is ample scientific consensus that ongoing global environmental change (hereafter global change), which is promoted by multiple drivers (e.g. increases in atmospheric carbon dioxide concentration [CO₂], changes in climate and nutrient deposition and in land use), will profoundly impact the structure, dynamics and functioning of terrestrial ecosystems, affecting a broad range of organisms (reviewed in [1–5]). The worldwide increase in temperature constitutes one of the clearest signals of climate change, and is

one of the global change drivers most heavily studied to date (see [4–6] for reviews). Overall, the rate of warming during the last 100 years (1906–2005) has been approximately 0.74°C, with most years from 1995 ranking among the warmest years since the establishment of meteorological records [3]. As a consequence, important changes in the phenology and distribution of organisms, and in the composition and dynamics of communities are being documented in terrestrial ecosystems worldwide [7–10]. In addition, climate change will promote important modifications in rainfall patterns, such as the overall reduction in rainfall amounts and the increase in its intensity in many regions worldwide [3,11–13]. These rainfall changes can modulate the ability of plants and microbes to respond to warming [2,14,15]. Thus, the analysis of how organisms will respond to climate change must consider changes in both temperature and rainfall, particularly in ecosystems where rainfall is already

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scarce and unpredictable, such as in drylands [2]. These environments are of paramount importance at the global scale, as they occupy over 41 per cent of the terrestrial surface, are the home of 38 per cent of the global human population and provide ecosystem services that are critical for the maintenance of life on Earth [2,16].

One particularly important component of drylands, biological soil crusts (BSCs) are under-studied in terms of their response to global change. BSCs are a complex and highly specialized community composed of cyanobacteria, algae, mosses, liverworts, fungi, bacteria and lichens that live in the uppermost millimetres of the soil surface [17–19]. They are particularly prevalent in dry and/or extremely cold environments, where they may compose up to 70 per cent of the total living cover [20]. They play critical functional roles, as they contribute to atmospheric carbon and nitrogen fixation [21–23], control nitrogen mineralization and availability [24,25], stabilize the soil against erosion [26] and modulate infiltration and runoff processes [27,28]. In addition, they affect the abundance, diversity and performance of microbial [29,30], arthropod [31] and plant [32,33] communities.

Because BSC organisms are poikilohydric, their metabolism and physiological functions are highly dependent on ambient moisture and temperature [34–36]. Thus, changes in rainfall and temperature expected with climate change are likely to affect the functioning and dynamics of BSCs, as has been shown in a handful of experimental studies [37–40]. In dryland areas receiving a considerable portion of their rainfall during summer, such as some deserts of the southwestern USA, experimental field studies have shown that increased summer rainfall frequency negatively affects the functioning of moss- and lichen-dominated BSCs, leading to a reduction in their cover and to a replacement of these communities by cyanobacteria [37,39,40]. Interestingly, experimental increases of temperature up to 2°C in this region had negligible impacts on the development and physiology of these communities [39,40], although temperature can modulate negative effects of UV augmentation on their photosynthetic activity [38]. Rain frequency and duration of dry periods have been also found to be key factors controlling the development and composition of BSCs along a 2000 km natural transect in southwestern Africa [41]. While these studies point to the importance of changes in rainfall, results can be substantially different in ecosystems that do not receive summer rainfall, and in areas where dew is a key moisture source for BSC constituents [42,43]. For example, Pintado *et al.* [36] found that the BSC-forming lichen *Diploschistes diacapsis* (Ach.) Lumbsch, common across a semi-arid site from southeast Spain, was active only during the 20 per cent of the year that experienced dewfall [44], an activity that mainly occurred during conditions of relatively low temperature and photosynthetically active radiation. Increases in temperature can reduce the inputs of water through dew, and can also modify the number of days where BSC-forming lichens are active. Castillo-Monroy *et al.* [45] found that, over a 3.5 year period, soil CO₂ efflux rates in lichen-dominated BSCs were

significantly higher than those found in bare ground areas devoid of BSCs in a semi-arid site from central Spain, and that the rate of increase in soil respiration in response to increased temperature (Q_{10}) was augmented with the degree of cover and development of BSCs. Similar results have been observed by Maestre *et al.* [46], who reported a significant increase in soil respiration in BSC-dominated microsites, but not in bare ground areas, in response to a 2.4°C experimental increase in temperature. Although these authors did not measure changes in the BSC constituents themselves, their results suggest that ongoing increases in temperature will affect their physiological activity.

Recent research has shown that the richness of BSC communities is positively linked to ecosystem functioning and multifunctionality, i.e. the ability of ecosystems to maintain multiple functions, such as carbon storage, productivity and the build-up of nutrient pools [47,48]. Other studies have found that the functional redundancy of BSC-forming species is very low [49,50]. Overall, these results indicate that maintaining species-rich BSC communities is crucial to maintain the overall functionality of ecosystems dominated by these organisms. Therefore, evaluating how the composition and diversity of BSCs will be affected by future changes in temperature and rainfall is crucial to fully understand how ongoing climate change will impact the structure and functioning of drylands. Observational studies carried out over large spatial scales have not reported consistent results to date. For example, Rogers [51] found that the number of lichens decreased with reductions in annual rainfall in drylands from Australia. Studies carried out along a Namibian–South African transect have found that the richness and cover of lichen species are positively related to lower temperature, higher altitude and increased water availability ([52], but see [41,53] for contrasting results along the same transect). Results from these studies may not, however, be directly applicable to smaller spatial scales because other abiotic factors that are important determinants of BSC distribution, such as soil type and texture [20,41], often covary with rainfall and temperature.

While drylands are known to be among the most sensitive biomes to global change [54,55], there are many uncertainties surrounding the ecological consequences of such change on these ecosystems [2]. This is particularly evident when considering climate change impacts on BSCs, as only a handful of experimental studies have explicitly evaluated how future climatic conditions affect the performance, dynamics and functioning of their constituents [38–40,46,56,57]. Furthermore, none of these have evaluated how simultaneous changes in temperature and rainfall jointly affect the composition, richness, diversity and physiological performance of BSC communities as a whole. We aimed to evaluate how different climate change drivers could affect BSCs by carrying out an experiment in central Spain. In this experiment, we evaluated responses of the BSC community and its main constituents to a 2.4°C increase in temperature, and to an approximately 30 per cent reduction of total annual rainfall, climatic conditions

that mimic those forecasted for the last half of the twenty-first century in our study area [58]. Specifically, we tested the hypothesis that the transition to a more arid climate will reduce the physiological performance of BSCs, as warmer temperatures and lower rainfall will promote a more frequent and rapid desiccation of BSC constituents, which may impair their ability to function within a positive carbon balance [37,56,58,59]. As a result, we expected their growth to be reduced and important shifts in the composition of BSC communities to occur.

2. MATERIAL AND METHODS

(a) *Study area*

This study was conducted in the Aranjuez Experimental Station, located in the centre of the Iberian Peninsula (40°02' N–3°32' W; 590 (m)a.s.l.). The climate is Mediterranean semi-arid, with a mean annual temperature and rainfall of 15°C and 349 mm, respectively (Aranjuez Meteorological Station, 40°02' N–3°32' W; 540 (m)a.s.l.; average data from the 1983–1988 and 1997–2011 periods). The soil is derived from gypsum, and is classified as Xeric Haplogypsid [60]. Perennial plant cover is below 40 per cent, and is dominated by the tussock grass *Stipa tenacissima* L. and the shrubs *Helianthemum squamatum* (L.) Dum. Cours and *Retama sphaerocarpa* (L.) Boiss. The open areas between perennial plants are colonized by well-developed BSCs dominated by lichens such as *D. diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (Weber) Poelt and *Fulgensia subbracteata*, and mosses such as *Pleurochaete squarrosa* (Brid.) Lindb. and *Didymodon acutus* (Brid.) K. Saito (see the electronic supplementary material, appendix S1 for a species checklist).

(b) *Experimental design*

We established a factorial experimental design with three factors, each with two levels: BSC cover (poorly developed BSC communities with cover less than 25% versus well-developed communities with cover greater than 75%), warming (control versus a 2.4°C annual temperature increase) and rainfall exclusion (control versus an approx. 30% rainfall reduction in total annual rainfall). The working plots (1.2 × 1.2 m) were randomly placed on either bare ground (8.6 ± 0.8% of BSC cover; mean ± s.e., $n = 40$; hereafter Bare plots) or BSC-dominated (73.8 ± 1.7% of BSC cover; mean ± s.e., $n = 40$; hereafter Crust plots) microsites. A minimum separation distance between plots of 1 m was ensured to minimize the risk of sampling non-independent areas. The different combinations of treatments were randomly assigned to Bare and Crust plots. Ten replicates per combination of treatments were established, resulting in a total of 80 plots.

The warming treatment aimed to simulate the average of predictions derived from six atmosphere–ocean general circulation models for the second half of the twenty-first century (2040–2070) in central Spain [58]. These models predict an increment of annual temperature ranging from 2.6°C (B2 IPCC scenario) to 2.8°C (A2 IPCC scenario). This increment ranges between 2.1–2.3°C during winter months (B2 and

A2 scenarios, respectively) and 3.2–3.5°C during summer months (B2 and A2 scenarios, respectively). To achieve a temperature increase within this range, we used open-top chambers (OTCs) similar to those employed in warming experiments carried out in arctic [61] and dryland [57] areas. OTCs were built with methacrylate plates, which have a high transmittance in the visible spectrum and a very low emission of the infrared wavelength, using a hexagonal design with sloping sides of 40 × 50 × 32 cm. The chambers are open on the top to allow rainfall and air to enter. The bottom edge of all chambers was situated 5 cm above the surface, to allow air flow and avoid excessive temperatures (see the electronic supplementary material, appendix S2). OTCs were installed in the field in July 2008.

Forecasted changes in rainfall for our study area are subject to a high degree of uncertainty, but all models predict a significant reduction of rainfall, mostly during existing wet months (spring and fall; the number of days with rainfall higher than 1 mm is predicted to be reduced between 10 and 50% during these seasons [58]). To achieve a rainfall reduction similar to that forecasted, we set up passive rainfall shelters (RSs) based upon the design described by Yahdjian & Sala [62]. Each RS has an area of 1.44 m² (1.2 × 1.2 m), and a mean height of 1 m. Each roof has an inclination of 20° and is composed of three gutters of methacrylate that cover approximately 37 per cent of the surface, connected to containers that collect the excluded water (see the electronic supplementary material, appendix S2). The RS did not modify the frequency of rainfall events, which has been shown to be an important component of climate change in other regions and to strongly affect BSC functioning and dynamics [37–40], but effectively reduced the size of individual rain events and the total amount of rainfall reaching the soil surface (see the electronic supplementary material, appendix S3). The RSs were set up during November 2008.

The effects of the OTCs and RSs on air temperature and humidity, and on soil temperature, were monitored using automated sensors (HOBO Pro v.2 Temp/RH and H8 Data Loggers, Onset corporation, Bourne, MA, USA).

(c) *Biological soil crust measurements*

In each plot, and prior to the setup of the OTCs, we placed a permanent circular plot (20 cm diameter) to monitor changes in the cover, diversity, composition and physiological performance of BSCs. In each plot, we estimated the composition of the main visible components of the BSC community (mosses and lichens) in June 2008 and May 2011 using the point-sampling method (1 × 1 cm grid; 120 sampling points per plot). With these data, we calculated the total cover of the BSC community, species richness, diversity (using the exponential Shannon diversity index [63]) and evenness (using Pielou's index [64]). To assess the changes in these variables through time, we estimated a difference index (Dif) as $R_{\text{final}} - R_{\text{initial}}$, where R is the value of the variable of interest in May 2011 (final) and June 2008 (initial).

We preferred using this index over other relative indices commonly employed, such as Relative Interaction Index [65] or Relative Neighbour Effect [66], to avoid the extreme values in the relative difference created by the presence of zeros in some of the variables measured at the beginning of the experiment. We obtained Dif values for the cover, diversity, richness and evenness of the whole BSC communities and lichens, as well as for the cover of the dominant lichen species (*S. lentigera* and *D. diacapsis*; electronic supplementary material, appendix S1) and mosses.

The physiological performance of BSCs was evaluated in the Crust plots by measuring the maximum photochemical efficiency of photosystem II (F_v/F_m) as an overall indicator of the status of this photosystem, and as a measure of the efficiency of the photosynthetic process [21,39,43,57,67]. Measurements were taken seasonally at midday from November 2008 until November 2011 on sunny days by using an FMS 2 Pulse Modulated Chlorophyll Fluorometer (Hansatech Instruments Ltd, King's Lynn, UK). Measurements taken at this moment of the day are commonly used when evaluating the physiological performance of BSC-forming organisms [21,68]. We found these measurements to be representative of those obtained in other moments of the day such as during early morning (see the electronic supplementary material, appendix S4), when BSC-forming lichens are physiologically most active in environments such as those studied [36]. F_v/F_m was calculated as the ratio between the variable (F_v) and the maximum (F_m) fluorescence signal. Lichens were dark adapted for 30 min prior to measurements by using dark cloth. Fluorometer measurements were made in six replicated plots per combination of treatments for the whole community, and for *S. lentigera* and *D. diacapsis*. Six measurements per plot were taken in all cases, which were averaged for further analyses.

(d) *Statistical analyses*

Changes in cover and diversity metrics (richness, diversity and evenness) between 2008 and 2011, as measured with Dif, did not follow a normal distribution, nor did they show homogeneity of variances, in most cases. Thus, we evaluated the effects of the warming (WA) and rainfall exclusion (RE) treatments (fixed factors), and their interaction, on these data using permutational multivariate analysis of variance (PERMANOVA [69]). This method is based on the use of permutation tests to obtain p -values, does not rely on the normality assumption of ANOVA and can handle experimental designs such as those used here. For these analyses, the Euclidean distance and 10 000 permutations (permutation of raw data [70]) were used to analyse our data. To investigate higher-order interactions, data were divided into subsets based on one of the factors of the interaction, and then were subject to PERMANOVA. In addition to PERMANOVA analyses, we evaluated whether median Dif values obtained for each treatment and variable were different from zero using the non-parametric Wilcoxon signed-rank test.

To evaluate how the treatments affected community composition during the study period, we conducted a

PERMANOVA analysis with warming (WA), rainfall exclusion (RE) and year (2008 or 2011) as fixed factors. Prior to these analyses, which were carried out using the Bray–Curtis distance, we square-root transformed the data. As an additional interpretive tool, we determined individual species contributions to average Bray–Curtis dissimilarity from the beginning to the end of the experiment in each treatment using the SIMPER approach [71]. This method allows consideration of which species along the treatments are primarily responsible for any observed difference in abundance between the 2 years.

Seasonal F_v/F_m data were analysed by a three-way (WA, RE and time) ANOVA with repeated measures of one of the factors (time). Analyses were carried out separately for the whole BSC community, *S. lentigera* and *D. diacapsis*. Community and *S. lentigera* data did not follow the sphericity assumption (Mauchly's test < 0.010 , $p < 0.011$), and thus we used the Greenhouse–Geisser estimate to evaluate the significance of within-subjects tests in both cases [72].

PERMANOVA analyses were carried out with the PERMANOVA+ for the PRIMER statistical package (PRIMER-E Ltd, Plymouth Marine Laboratory, UK). SIMPER and repeated-measures ANOVA analyses were carried out using PRIMER and SPSS v. 15 (SPSS Inc, Chicago, IL, USA), respectively. As suggested by Gotelli & Ellison [73], the experiment-wide error rate was not adjusted, and all the interpretations of the effects of the different treatments were performed by evaluating the exact p -values. The data used in this article and not included in the appendices are deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.c2pd5>.

3. RESULTS

Throughout the experimental period, our warming treatment promoted an average increase of 2.4°C and 2.7°C per year in air and soil temperatures, respectively (see the electronic supplementary material, appendix S5). Such an increase was particularly evident during summer, with increases in daily averages in OTC plots relative to control plots higher than $3 \pm 0.44^\circ\text{C}$ and $4 \pm 0.87^\circ\text{C}$ (means \pm s.e.) in air and soil temperatures, respectively. During winter months, such increases were of $1.5 \pm 0.18^\circ\text{C}$ and $1.7 \pm 0.16^\circ\text{C}$ (means \pm s.e.) for air and soil temperatures, respectively. RSs did not substantially modify air and soil temperatures, as differences in annual temperature between control and RS plots were below 0.4°C on average. These shelters were effective in reducing the amount of rainfall reaching the soil, as they excluded between 7 and 50 per cent of the incoming rainfall depending on the event (approx. 30% on average; electronic supplementary material, appendix S3).

(a) *Changes in biological soil crust cover and composition*

Changes in total BSC cover during the first 3 years of our experiment varied with the initial BSC cover ($p = 0.022$, figure 1a; electronic supplementary material, appendix S6). Averaged across all treatments, there was a 5 per cent increase and 14 per cent decrease in

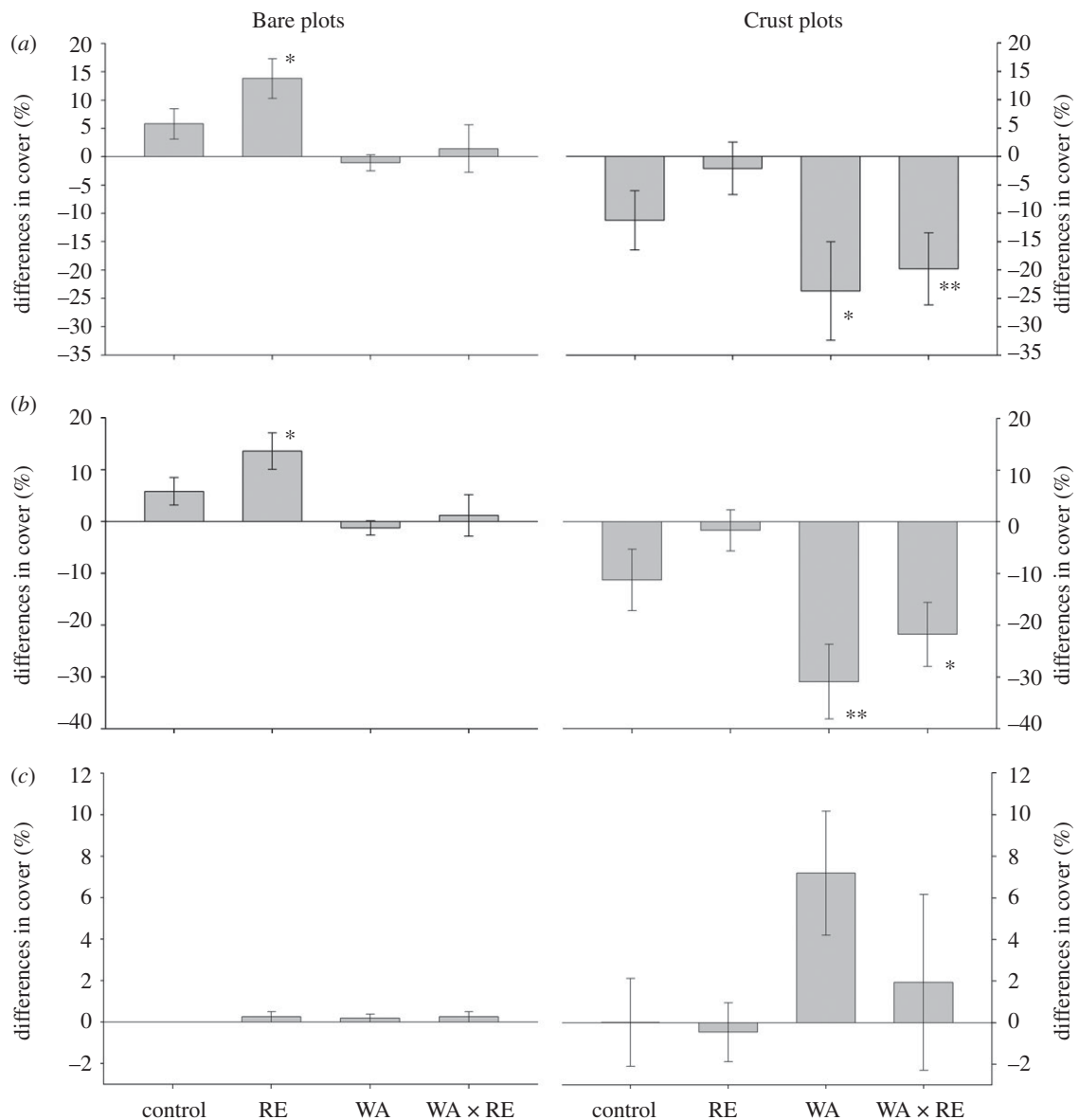


Figure 1. Differences in the total cover of the whole BSC community (including lichens and mosses) (a), lichens (b) and bryophytes (c) in areas without (Bare plots) and with well-developed biological soil crusts (Crust plots) between June 2008 and May 2011. Data represent means \pm s.e. ($n = 9-10$). RE, rainfall exclusion; WA, warming; and WA \times RE, warming and rainfall exclusion. Asterisks indicate p -values from the Wilcoxon test: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. See the electronic supplementary material, appendices S13–15 for raw data.

BSC cover in Bare and Crust plots, respectively. The magnitude of the effect of the warming treatment differed between Bare and Crust plots, as indicated by a significant WA \times BSC interaction ($p = 0.018$, electronic supplementary material, appendix S6). In Bare plots, total BSC cover increased by 5 per cent in the control, while it decreased by 1 per cent in plots subjected to warming (figure 1a, PERMANOVA, $F_{WA} = 9.29$, $p = 0.004$). In Crust plots, total cover decreased in both the control and WA treatment, but this reduction was substantially higher in the latter (figure 1a, PERMANOVA, $F_{WA} = 5.29$, $p = 0.029$). Overall, we found no significant effects of RE, although a marginally significant RE \times BSC interaction ($p = 0.076$, electronic supplementary material, appendix S6) was found when analysing variations in total cover. However, some responses to RE must be noted, as we found a significant increase in total

cover in the Bare plots when rainfall was excluded (figure 1a).

The analysis of variations in cover for lichens (figure 1b) yielded similar results to those described for the whole BSC community, but without any significant effects of either WA or RE treatments when all the data were analysed together (see the electronic supplementary material, appendix S7). However, the increase in cover observed in the Bare plots in the RE treatment was significant, as well as the reductions in this variable observed in the WA and WA \times RE treatments in the Crust plots (figure 1b). Significant increases in the cover of *S. lentigera* were observed in the Bare plots (control and RE treatment, figure 2a), albeit we did not find significant effects of WA or RE (see the electronic supplementary material, appendix S8). Overall, the cover of *D. diacapsis* decreased under warming (figure 2b, $p = 0.001$, electronic

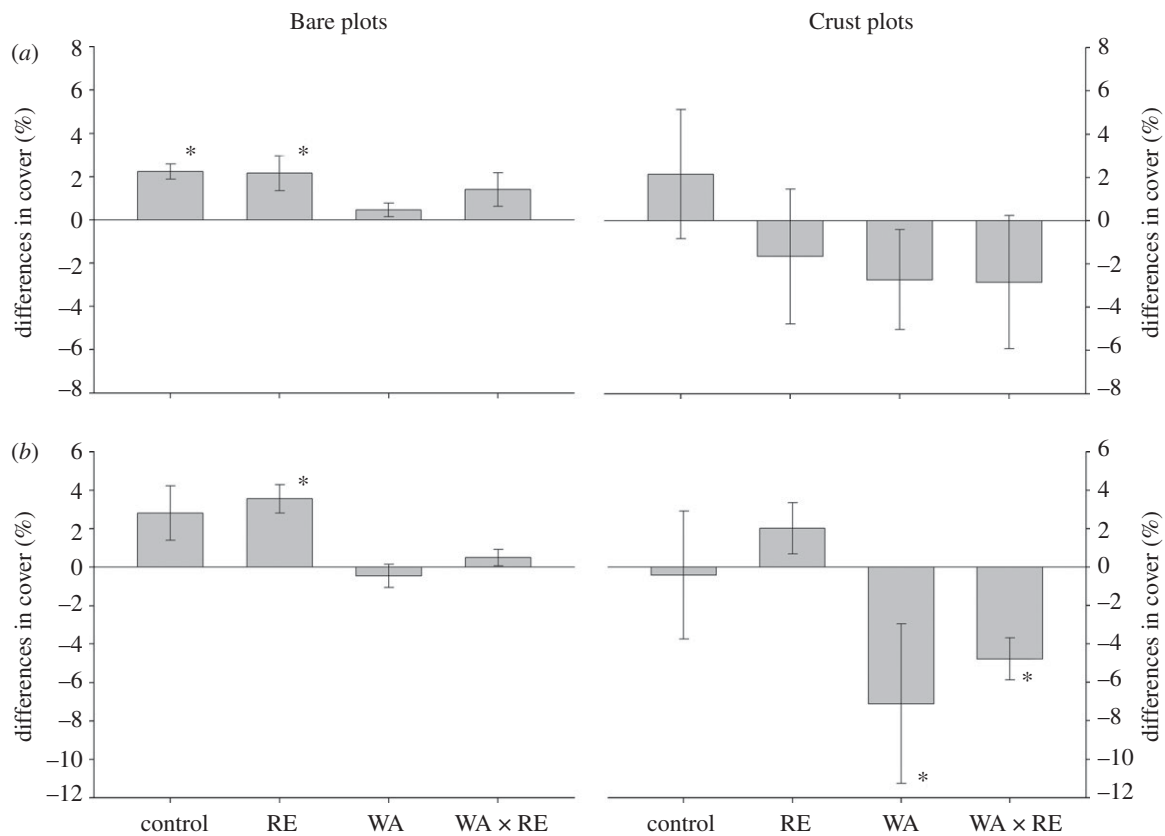


Figure 2. Differences in total cover of *S. lentigera* (a) and *D. diacapsis* (b) in areas without (Bare plots) and with well-developed biological soil crusts (Crust plots) from June 2008 until May 2011. Data represent means \pm s.e. ($n = 9-10$). See the electronic supplementary material, appendix S15 for raw data. Rest of legend as in figure 1.

supplementary material, appendix S8), but increased when rainfall was excluded (figure 2b, $p = 0.001$; electronic supplementary material, appendix S8). A significant increase in the cover of bryophytes was observed in the WA treatment (figure 1c, $p < 0.001$; electronic supplementary material, appendix S8), albeit this effect was largely observed in the Crust plots ($F_{\text{WA} \times \text{BSC}} = 4.19$, $p = 0.037$).

At the beginning of the experiment, the BSC community was clearly dominated by lichens, which constituted over 96 per cent and almost 100 per cent of the total BSC cover in Crust and Bare plots, respectively (see the electronic supplementary material, appendix S1). During the first 3 years of the experiment, we found important changes in the composition of the BSC community ($p = 0.011$, electronic supplementary material, appendices S1 and S9), which also varied between Crust and Bare plots ($p < 0.001$, electronic supplementary material, appendix S9). Significant RE \times BSC ($p = 0.017$) and RE \times WA ($p = 0.011$) interactions were also found when analysing composition data (see the electronic supplementary material, appendix S9). Overall, and after the 3 years of our experiment, the main species of lichens that contributed to the observed changes in community composition in Bare plots were *D. diacapsis*, *S. lentigera*, *F. subbracteata* and *Psora decipiens* (Hedw.) Hoffm. (see the electronic supplementary material, appendix S10). Together with *Buellia zoharyi* Galun., they were the most important species driving the changes in community composition in the Crust

plots observed (see the electronic supplementary material, appendix S10). The contribution of the different species to these changes, however, varied depending on the treatment considered. For example, in Crust plots subjected to warming, a strong decrease in the abundance of *Toninia sedifolia* (Scop.) Timdal. largely determined changes in community composition, while increases in the abundance of *Collema crispum* (Huds.) F. H. Wigg. in the RE treatment were the main driver of such changes in this treatment (see the electronic supplementary material, appendix S10). In the case of bryophytes, *D. acutus* (Brid.) K. Saito is the only moss species contributing to increase the dissimilarity between years in all the Crust plots, increasing its abundance in all of them (see the electronic supplementary material, appendix S10).

(b) Changes in biological soil crust diversity

At the beginning of the experiment, a total of 21 species of lichens and mosses were identified (see the electronic supplementary material, appendix S1). Three years later, species richness of the whole BSC community increased and decreased in the control treatment at Bare and Crust plots, respectively (figure 3a). Warming significantly reduced species richness at both plot types (PERMANOVA, $F_{\text{Bare}} = 11.10$, $p = 0.002$; $F_{\text{Crust}} = 18.20$, $p < 0.001$), although it was particularly evident in the Crust plots, where differences in richness were significantly lower than zero (figure 3a). A significant RE \times BSC interaction ($p = 0.013$, electronic

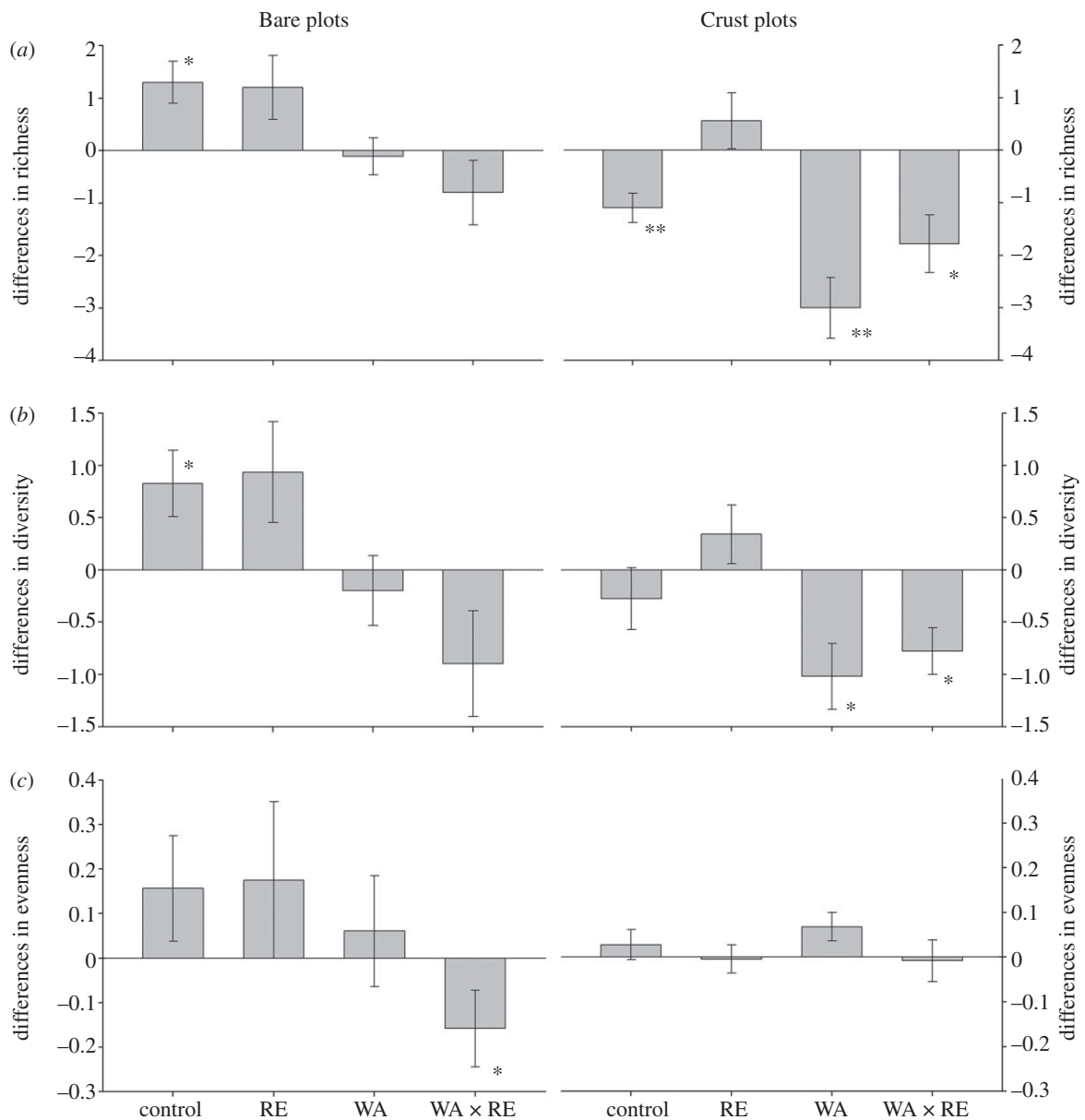


Figure 3. Total differences in richness (a), diversity (b) and evenness (c) of the whole BSC community in areas without (Bare plots) and with well-developed biological soil crusts (Crust plots) from June 2008 until May 2011. Data represent means \pm s.e. ($n = 9-10$). See the electronic supplementary material, appendix S13 for raw data. Rest of legend as in figure 1.

supplementary material, appendix S6) was also found when analysing richness data. Separate analyses for Bare and Crust plots revealed that, overall, richness was reduced in the RE treatment in the later plots (PERMANOVA, $F = 8.48$, $p = 0.006$). When evaluating changes in richness for lichens only, results mimicked those obtained for the whole BSC community (see the electronic supplementary material, appendices S7 and S11).

Community diversity, like richness, was negatively affected by warming, albeit differences were only significantly lower than zero in Crust plots (figure 3b). When all the data were analysed together, no significant effects were found for the treatments evaluated (electronic supplementary material, appendix S6). Results obtained for lichens were very similar (see the electronic supplementary material, appendix S11), but a significant BSC \times RE interaction was found ($p < 0.05$, electronic supplementary material,

appendix S7). Species evenness decreased in response to warming (figure 3c, $p < 0.001$; electronic supplementary material, appendices S6 and S7). It is interesting to note how differences in species evenness were significantly lower than zero in Bare plots subjected to both RE and WA treatments (figure 3c).

(c) Changes in biological soil crust performance

During the course of the experiment, F_v/F_m of both the BSC community and the dominant lichens was significantly higher under warming (figure 4a-c, $p < 0.001$; electronic supplementary material, appendix S12). However, this response was not consistent throughout the study period, as indicated by significant time \times WA interactions (repeated-measures ANOVA, community, $F_{5.2,108.7} = 4.59$, $p = 0.001$; *D. diacapsis*, $F_{10,210}$, $p < 0.001$; *S. lentigera*, $F_{5.7,119.0} = 5.61$, $p < 0.001$).

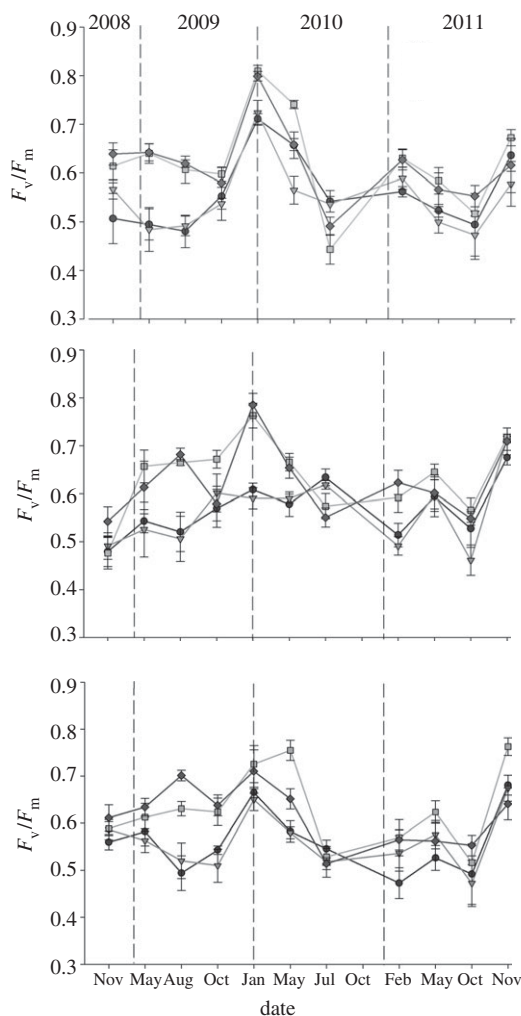


Figure 4. Maximum photochemical efficiency of PSII (F_v/F_m) of the whole BSC community (a), *S. lentigera* (b), and *D. diacapsis* (c) between November 2008 and November 2011. Data represent means \pm s.e. ($n = 6$). Brown lines, control; orange lines, rainfall exclusion; light green lines, warming; dark green lines, warming and rainfall exclusion.

4. DISCUSSION

We found important changes in the composition, structure, dynamics and functioning of the studied BSC community in response to changes in climate, and to warming in particular. Overall, and after 3 years, warming had negative effects on the cover, richness and diversity of lichens in well-developed BSC communities, and reduced notably the degree of colonization of bare ground areas by lichens, which was observed in control plots. We also found evidence of significant increases in the cover of mosses in those places where lichens were declining (e.g. Crust plots under warming). The effects of warming were largely independent of those of rainfall, which were also negligible on many of the variables evaluated. The strong and negative effects of warming, and the lack of important effects of rainfall reduction, on BSC composition and structure have not been previously reported, and contrast with climate change studies conducted in other regions [39,40]. These contrasting results highlight the need to conduct studies at multiple locations before BSC responses to climate change can be generalized.

(a) Responses of biological soil crust communities to simulated climate change

Warming promoted a dramatic decrease in the cover of lichens in Crust plots during the first 3 years of our experiment, a response that was not modulated by changes in the total rainfall amount. At the same time, this treatment promoted an increase in the cover of mosses in these plots. These findings contrast with the general impression that lichens are long-lived and extremely stress-tolerant organisms that have a limited ability to respond quickly to changes in environmental conditions because of their slow growth rate [74]. However, despite that BSC-forming lichens are long-lived organisms, they can be quite dynamic, and can quickly respond to changes in environmental conditions and disturbances of the soil surface. Lázaro *et al.* [75] and Dojani *et al.* [76] have reported significant increments in the cover of BSC-forming lichens in the semi-arid areas from Spain and South Africa, respectively, in a few years, with increments in the cover of a particular species (e.g. *S. lentigera*) above 20 per cent in a year [75]. Belnap *et al.* [77] found decreases in the cover of some lichen species in the Colorado Plateau in response to an increase in monthly maximum temperatures over 8 years. Grote *et al.* [56] used a physiological argument to suggest that in cyanobacteria-dominated BSCs, warming is likely to reduce carbon uptake and growth because it will increase respiration rates without a comparable increase in photosynthetic rates. An interesting exception is that BSCs dominated by mosses were relatively unaffected by experimental warming [39], suggesting a lower sensitivity than lichens or cyanobacteria to increases in temperature. Warming-induced decreases in lichen abundance are not restricted to drylands, as similar results have also been detected in arctic ecosystems [78]. However, the primary stress factor in these ecosystems is cold temperatures, rather than low water availability. Studies conducted in these areas have attributed decreases in lichens or mosses to an increase in vascular vegetation with warming [79,80]. However, this is an unlikely explanation for our study because BSC plots were located in areas where vascular vegetation was excluded and plant litter was nearly non-existent. Furthermore, annual plants were carefully clipped from the plots surveyed every spring.

The large declines in lichen cover observed under warming could be promoted by higher respiration rates in this treatment [56], which would lead to increases in mortality and decreases in cover if the photosynthetic rate cannot compensate these carbon losses [40]. In this direction, soil respiration in BSC-dominated areas is clearly enhanced by experimental warming in our experiment [46], albeit we cannot separate the fraction of this respiration corresponding to the BSCs themselves. At first glance, our F_v/F_m data would not fully support this potential mechanism underlying declines in lichen cover; F_v/F_m was significantly higher in plots subjected to warming, suggesting higher efficiency of the photosynthetic process (figure 4). We must highlight, however, that the decrease in cover observed with warming was mainly attributable to species such as *B. zoharyi*, *T. sedifolia*

and *F. subbracteata* (see the electronic supplementary material, appendix S10), while the species where F_v/F_m was specifically measured either decreased slightly in cover (*D. diacapsis*) or increased it (*S. lentigera*) in response to this treatment (see the electronic supplementary material, appendix S10). As these species were the most abundant at our study site in the crust plots subjected to warming (see the electronic supplementary material, appendices S1 and S10), and the community measurements of F_v/F_m consisted of random measurements over each sampling plot, the later measurements reflected mostly the behaviour of the dominant species (figure 4), and thus did not capture properly the physiological status of the species that were mostly affected by warming. Indeed, significant reductions in the F_v/F_m of BSC-forming lichens with a 2.1–3.8°C warming and an approximately 30 per cent reduction in dew and fog inputs have been found in South Africa [57].

Why do mosses respond differently to warming than lichens? Possibly, this is because an early break of dormancy and reactivation with warming promoted initiation of new stems, mosses being more adapted for the new conditions than lichens [81,82]. Such a response would probably occur during the favourable seasons in terms of humidity and soil moisture, such as during autumn and the early part of the winter, where bryophytes in the warming plots could encounter a rare convergence of warm temperatures and adequate moisture. In this regard, mosses may be more phenotypically plastic than lichens in their ability to change their seasonal activity in order to increase their cover [83]. This could also reduce competition for living space with lichens, which is likely to be very intense in the studied communities [84], increasing the abundance and cover of mosses at the expense of lichens.

Another potential mechanism that could explain our results is mediation by pigments such as zeaxanthin, which is formed to protect chlorophyll during the desiccation process (normally in darkness) and to promote faster acclimation when conditions return to the optimal situation [85]. In this context, recent studies [85,86] suggest that if desiccation occurs faster than in normal conditions, photoprotective mechanisms do not work properly, and, as a consequence, structural damages are likely to occur. This mechanism has already been demonstrated in the lichen *Lobaria pulmonaria* (L.) Hoffm. [86], and could explain declines in lichen cover with warming, as desiccation should occur much faster because of the temperature increase in this treatment (see the electronic supplementary material, appendix S5). Mosses usually show more structural complexity than lichens [83,87], and this may allow mosses to have quicker responses to desiccation [88]. Very few data on desiccation tolerance of BSC constituents are available, and most of the studies on the topic have been carried out on bryophytes [83]. This work suggests that mosses could be more tolerant to desiccation than lichens [89], but there is not enough evidence to affirm this with confidence. Because of the known structural limitation of the lichen thallus, if bryophytes desiccate more slowly than lichens at our study site,

mosses could have the opportunity to activate protective mechanisms against warming, and thus to be well prepared to compete against lichens and increase their abundance and cover under warming. This mechanism, however, cannot be proved by our results, and further studies are needed to evaluate its role in the changes in the cover of lichens and mosses observed in our experiment.

Given the proven importance of rainfall to lichens and mosses, it was surprising to find that, unlike warming, rainfall reduction did not have negative effects on the cover and performance of BSCs, although some negative effects on species richness were found. Our results could be due to the fact that their apparent sensitivity to changes in rainfall is more conditioned by the size, duration and timing of rainfall events than on average rainfall [37,39]. We expect that more so than with warming, the response of BSCs will be strongly dependent on the timing and characteristics of rainfall pulses in a given locality, and thus may vary widely from place to place. Carbon balance in BSC-forming mosses of the Mojave Desert (a winter-rainfall desert) seems to largely depend on the size of individual events (and thus the length of the hydration period), in addition to the length of desiccation periods in between them and seasonality of the event [90]. Our manipulation did not influence seasonality, but influenced event size, and in consequence indirectly affected length of desiccation period because smaller events hydrate BSCs for less time. In our study region, autumn and spring rainfall events can be both large and frequent compared with the much more arid Mojave Desert. Thus, we can only hypothesize that an approximately 30 per cent reduction in the natural event size is insufficient to induce change in only a few years, though we cannot rule out longer term changes.

The different treatments (warming and rainfall exclusion) promoted important differences in the dynamics of the BSC community studied during the first 3 years of our experiment. We found increases in the abundance of species such as *D. diacapsis*, *S. lentigera*, *F. subbracteata* and *P. decipiens* in all treatments in the Bare plots. This suggests that these species may be some of the first colonizing species after disturbance situations or in natural conditions [75,91]. Overall, BSC richness and diversity, but not evenness, decreased with warming. In the Crust plots, reductions in rainfall also promoted a reduction in species richness, albeit it was mainly evident under warming. Similar decreases in the richness and diversity of BSC components have been reported in arctic ecosystems subjected to warming [78].

(b) Consequences of biological soil crust decline in semi-arid Mediterranean regions

The observed changes in the diversity, richness and cover of BSCs, and in the abundance of particular lichen and moss species could have profound consequences on ecosystem functioning. Previous studies carried out in BSC-dominated ecosystems have found positive effects of species richness and other components of biodiversity in maintaining processes

important for ecosystem structure and functioning, such as soil stability [47,92], dust trapping [47] and N cycling [46]. Bowker *et al.* [49] suggest that there may be a high degree of functional singularity among different BSC mosses and lichens in Spanish drylands, indicating that a species loss is not likely to be compensated for by another species.

Changes in the composition of BSC species with warming could also have important implications on the water balance and the maintenance of plant patches in semi-arid areas. Studies carried out in our study site have found overall positive and negative effects of mosses and lichens, respectively, on infiltration [27]. Thus, decreases in the cover of lichens and increases in that of mosses suggested by our results would increase the infiltration in BSC-dominated areas, reducing the amount of runoff that would normally be redistributed and captured by the plants [93]. Given the dependence of plants such as *S. tenacissima* on water inputs coming from runoff [94], promoted by the concentration of the roots of this species under its canopy, such an effect would further exacerbate the negative effects on the performance and growth of semi-arid Mediterranean vegetation expected with ongoing climate change [95].

Recent research has found that BSC-dominated microsites are the main contributor to soil CO₂ efflux in our study site [45]. In areas with well-developed BSCs, increases in such flux in response to increases in temperature during spring and autumn are higher than in areas without or with low BSC cover [45]. In the Kalahari Desert, the same pattern was found, whereby soil respiration was enhanced with increases in air temperature, which could represent a net loss of carbon storages and a potential process of soil deterioration [22,96]. Ongoing measurements of soil CO₂ efflux at our site indicate that this flux was higher in warmed plots throughout most of the study period, and that this effect is particularly evident in Crust plots (C. Escolar & F. T. Maestre 2012, unpublished data). Overall, these results suggest that warming would promote C losses in BSC-dominated areas. Given that these areas are also losing lichen cover, and that the BSC communities are becoming less diverse, this response would be exacerbated in the future because of reduced photosynthetic capacity of BSCs.

(c) *Concluding remarks*

According to our results, increases in air temperature such as those expected by the middle of the twenty-first century will have profound negative impacts on the cover, composition and diversity of BSCs in Mediterranean regions. Contrary to the common vision about these organisms, BSCs respond quickly (in terms of years) to the environmental changes created, and seem to be less tolerant to drought than they are usually considered to be. These results add to existing studies, which in most cases suggest that BSCs are most likely to be negatively affected by projected warming. We are much farther from a generalization about the response of BSCs to reduced rainfall. Our results suggest that BSCs of the Mediterranean may be slow to change based on rainfall reduction alone,

but there is evidence from various localities around the world that suggest that timing, frequency and individual event size may exert very rapid effects [39,40].

Our findings indicate that the expected changes in total cover, richness and composition under warming would reduce or even negate the positive effects of BSCs on important functional variables, promoting an overall reduction in ecosystem functioning in terms of carbon fixation, nutrient pools, water infiltration and soil stabilization. These changes could also exacerbate direct effects of climate change on processes such as soil CO₂ efflux, and could also propagate beyond BSC communities to affect plant patches, and thus the overall structure of drylands. Future studies aiming to evaluate climate change effects on these regions must explicitly consider the importance of biological soil crusts, as this is crucial for a full understanding of the role of these organisms and their attributes as drivers of ecosystem functioning in drylands, and of their responses to ongoing climate change.

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