RESEARCH ARTICLE

Biocrusts increase the resistance to warming-induced increases in topsoil P pools

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Abstract

1. Ongoing global warming and alterations in rainfall patterns driven by climate change are known to have large impacts on biogeochemical cycles, particularly on drylands. In addition, the global increase in atmospheric nitrogen (N) deposition can destabilize primary productivity in terrestrial ecosystems, and phosphorus (P) may become the most limiting nutrient in many terrestrial ecosystems. However, the impacts of climate change on soil P pools in drylands remain poorly understood. Furthermore, it is unknown whether biocrusts, a major biotic component of drylands worldwide, modulate such impacts.

2. Here we used two long-term (8–10 years) experiments conducted in Central (Aranjuez) and SE (Sorbas) Spain to test how a ~2.5°C warming, a ~30% rainfall reduction and biocrust cover affected topsoil (0–1 cm) P pools (non-occluded P, organic P, calcium bound P, occluded P and total P).

3. Warming significantly increased most P pools—except occluded P—in Aranjuez, whereas only augmented non-occluded P in Sorbas. The rainfall reduction treatment had no effect on the soil P pools at any experimental site. Biocrusts increased most soil P pools and conferred resistance to simulated warming for major P pools at both sites, and to rainfall reduction for non-occluded and occluded P in Aranjuez.

4. *Synthesis*. Our findings provide novel insights on the responses of soil P pools to warming and rainfall reduction, and highlight the importance of biocrusts as modulators of these responses in dryland ecosystems. Our results suggest that the observed negative impacts of warming on dryland biocrust communities will decrease their capacity to buffer changes in topsoil P driven by climate change.

KEYWORDS
Biological soil crusts, climate change, dryland ecosystems, phosphorus deposition, phosphorus fractions

1 | INTRODUCTION

Water and nitrogen (N) availability have been traditionally considered the main limiting resources for life in dryland ecosystems (Delgado-Baquerizo et al., 2013b; Robertson and Groffman, 2015; Sardans et al., 2008; Schlesinger et al., 1995), which cover 41% of terrestrial surface (Cherlet et al., 2018). Thus, it is not surprising to find that most research conducted so far on the impacts of ongoing climate change on dryland biogeochemistry have focused on the responses of C and N (Delgado-Baquerizo et al., 2013a; Jiao et al., 2016; Nielsen and Ball, 2015). In recent years, however, there is a growing interest in understanding the role of P in drylands, particularly after studies suggesting that increases in aridity, a hallmark of climate change in drylands worldwide (Huang et al., 2015), imbalance the proportion of N and P in the soil (Delgado-Baquerizo et al., 2013a; Jiao et al., 2016). Despite so, the impacts of climate change drivers such as warming and altered rainfall patterns on the complex diversity of P forms in dryland soils remain largely unexplored (García-Velázquez et al., 2020) and have not, to the best of our knowledge, been assessed experimentally yet. This lack of knowledge limits our ability to incorporate changes in the availability of P and its impacts on processes such as productivity into models aiming to forecast ecosystem responses to climate change.

The inputs of P into the soils come mainly from parent rock weathering (Lajtha and Schlesinger, 1988; Walker and Syers, 1976) and, to a lesser extent, from deposition of the P present in atmospheric dust (Okin et al., 2004). The latter is quite insoluble in the soil solution (Chen et al., 2006; Shafqat et al., 2016), but it could be an essential source of P in ecosystems limited by this macronutrient (Chadwick et al., 1999; Okin et al., 2004). Over 95% of soil total P is associated with primary or secondary minerals, constituted in organic forms or occluded by soil minerals and immediately unavailable for plants (Condron and Newman, 2011; Shen et al., 2011). Organic P has a key role in plant nutrition since it is transformed to inorganic P fractions through mineralization mediated by the release of phosphatase enzymes from microbes and plant roots (Condron et al., 2005; Turner and Engelbrecht, 2011). Both biological (i.e. mineralization/immobilization) and geochemical (i.e. precipitation/dissolution and sorption/desorption) processes contribute to P availability (Cross and Schlesinger, 2001; Hou et al., 2018a; Vitousek et al., 2010), and are strongly dependent on precipitation and temperature (Belnap, 2011; Feng et al., 2016; Hou et al., 2018a). Increases in temperature have been shown to favour P sorption on secondary minerals and increase the occluded P (Hou et al., 2018a), and to reduce P availability due to the loss of soil moisture (Sardans et al., 2006; Sardans and Peñuelas, 2004). Moreover, low precipitation blocks microbial activity, ion diffusion and nutrient uptake by plants (Belnap, 2011; Sardans and Peñuelas, 2004). Drier conditions thus promote a slowdown in P release due to decreased litter decomposition rate and enzymatic activity, contributing to increases in soil humic compounds that keep P in less available forms (Sardans and Peñuelas, 2004). Finally, the synergistic effects of temperature

and precipitation control the rates of solubilization and release of labile P bound to carbonates into the soil solution (Belnap, 2011). Thus, high temperatures and drier conditions, such as those expected for drylands under climate change (Greve et al., 2014; Huang et al., 2015), would deter both the increases in concentrations of soil carbonic acid and the decrease in soil pH, reducing the dissolution rate of carbonates and the transition of P to soil solution phase (Devau et al., 2010). However, we have no experimental evidence of temperature and precipitation effects on P availability in dryland soils.

The low moisture content of dryland soils favours that P inputs (from rock weathering, dry deposition and decomposition of litter and organic matter) are not washed to deeper horizons, and thus concentrate in the topsoil (Verrecchia et al., 1995; White et al., 2004). This makes soil P fractions sensitive to the activity of organisms living on the soil surface, such as biocrusts (communities composed by lichens, mosses, bacteria, cyanobacteria, fungi, algae and liverworts that are a major biotic feature of drylands worldwide; Weber et al., 2016). Biocrusts are known to influence soil P availability through secretion of organic acids, chelating agents and the excretion of H+ during respiration, which solubilize mineral bound P increasing available P (Baumann et al., 2017, 2019; Belnap, 2011). Furthermore, the microtopography created by biocrust constituents like lichens could facilitate the capture of silt and clay particles from dust (Fick et al., 2020), increasing soil water and nutrient contents (Delgado-Baquerizo et al., 2015; Eldridge et al., 2020), promoting higher rates of microbial activity (Delgado-Baquerizo et al., 2015) and avoiding P losses via lixiviation (Belnap, 2011; Belnap et al., 2004). Different experiments have shown how warming and altered rainfall regimes such as those forecasted under climate change can dramatically decline the cover and abundance of lichen- and moss-dominated biocrusts (Ferrenberg et al., 2015; Ladrón de Guevara et al., 2018; Maestre et al., 2015), with cascading effects on the C and N cycles driven by this decline (Delgado-Baquerizo et al., 2014; Liu et al., 2016, 2017; Maestre et al., 2013; Reed et al., 2012). However, there is no experimental evidence about whether dryland biocrusts can modulate all P soil fractions, which will determine its availability for plants at short, medium and long terms, in the topsoil under climate change.

Understanding how the interactions between biocrusts and climate change affect soil P fractions in drylands is essential to better comprehend its impacts on these ecosystems and their capacity to provide essential ecosystem services in a warmer world. However, few studies so far have evaluated how simulated climate change affect soil P fractions in drylands, and these have been focused on a few P fractions (e.g. Olsen-P, NaOH-EDTA), have evaluated the effects of warming in isolation from other climate change drivers and have been conducted on dry-subhumid shrublands and forests (e.g. Sardans et al., 2006, 2008; Sardans and Peñuelas, 2004; Zhang et al., 2014). Here we aimed to evaluate how warming (~2.5°C increase), rainfall reduction (~30% reduction) and biocrust cover (<20% vs. >50%) affect soil P pools (non-occluded P, organic P, calcium bound P, occluded P and total P) on the top 1 cm of the soil and

their resistance to climate change in two semi-arid grasslands from central and southeastern Spain. We focus on the effects of warming and precipitation on soil depths which biocrust have the potential to alter. Still, we are aware that deeper depths have also the potential to be altered by these climatic variables. We tested the general hypothesis that climate change and biocrusts will directly or indirectly affect to all major organic and mineral P pools because they are interconnected by microbial processes (García-Velázquez et al., 2020). More specifically, we hypothesized that (a) soils under biocrusts will have higher concentration of both labile and stable P pools (Baumann et al., 2017, 2019); (b) warming and, to a lesser extent, rainfall reduction will positively affect both more labile (i.e. non-occluded P, organic P) and stable (i.e. calcium bound P and occluded P) P pools of surface soil layer influenced by biocrusts (Hou et al., 2018a; Sardans and Peñuelas, 2004); and (c) well-developed biocrusts will increase the resistance (according the Orwin and Wardle index; Orwin and Wardle, 2004) of all P pools to warming and, to a lesser extent, to rainfall reduction (Belnap, 2011; Delgado-Baquerizo et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Study area

This research was conducted in two sites located in central (Aranjuez, 40°02′N 3°32′W; 590 m a.s.l.) and southeast (Sorbas, 37°05′N 2°04′W; 397 m a.s.l.) Spain (Figure S1). Both sites have a Mediterranean semiarid climate, with an average annual temperature and rainfall of 15°C and 349 mm for Aranjuez and 17°C and 274 mm for Sorbas, respectively, with precipitation falling mainly in autumn/winter and spring (Maestre et al., 2013). They have soils derived from gypsum, classified as Gypsiric Leptosols (IUSS Working Group WRB, 2006), which have pH mean values of 7.0 and 7.5 in Aranjuez and Sorbas, respectively. Perennial plant cover is sparse (<40% at both sites) and dominated by the grass *Stipa tenacissima* L. and the shrubs *Retama sphaerocarpa* L. Boiss, *Gypsophila struthium* L. and *Helianthemum squamatum* (L) Dum Cours. In both places, open areas between plants patches are composed of well-developed BSCs dominated by lichens such as *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (Weber) Poelt and *Fulgensia subbracteata* (Nyl.) Poelt (see Maestre et al., 2013 for a species checklist).

2.2 | Experimental design and soil sampling

At each site, we established a factorial experimental design with three factors, each with two levels: biocrust cover (incipient biocrust communities with cover <20% vs. well-developed communities with cover >50%; Figure S2), warming (control vs. 1.98°C and 1.39°C mean annual temperature increase for each study period in Aranjuez and Sorbas, respectively) and rainfall reduction (control vs. a ~30% rainfall reduction; Figure S3). Ten and eight replicated plots (1.25 × 1.25 and 1.2 × 1.2 m size in Aranjuez and Sorbas, respectively)

per combination of treatments were established in Aranjuez and Sorbas, respectively. These plots were randomly placed either on incipient biocrust cover (<20% of biocrust cover; hereafter low cover plots) or biocrust-dominated (>50% of biocrust cover; hereafter high cover plots) microsites resulting in a total of 80 and 64 plots in Aranjuez and Sorbas, respectively. The plots were carefully chosen to be comparable, with no *a priori* reason to attribute the observed differences in visible biocrust cover.

We simulated the average of predictions derived from six Atmosphere-Ocean General Circulation Models for the second half of the 21st century (2040–2070) in central and south-eastern Spain (De Castro et al., 2005). To achieve such degree of warming, we used open top chambers (OTCs) of hexagonal design with sloping sides of 40 cm × 50 cm × 32 cm. Both the design and installation of the open top chambers were carried out in such a way that reduced undesirable experimental artefacts (Hollister and Webber, 2000). Some studies have reported the impact of the warming methodology on soil moisture (see Bokhorst et al., 2016; Klein et al., 2005; Reed et al., 2016). However, the values of soil moisture registered during the experiment (Moisture$_{RR}$ = 0.09 ± 0.06 m^3 m^{-3} soil; 0.08 ± 0.05 m^3 m^{-3} soil and Moisture$_{WA+RR}$ = 0.09 ± 0.06 m^3 m^{-3} soil; 0.08 ± 0.05 m^3 m^{-3} soil in Aranjuez and Sorbas, respectively) reflect that OTCs had minor effects on our study.

Although future rainfall forecasts for our study areas are uncertain, most models estimate significant reductions in the total amount of rainfall, particularly during spring and autumn (between 10% and 50%; De Castro et al., 2005; Giorgi and Lionello, 2008; IPCC, 2021). Rainfall reduction was achieved using passive rainfall shelters (RS), which allowed to reduce ~33% and ~36% of rainfall in Aranjuez and Sorbas, respectively (Maestre et al., 2013). We continuously monitored the effects of treatments on soil temperature (0–2 cm depth) and soil moisture (0–5 cm depth) using automated sensors (HOBO Pro v2 Temp/RH and H8 Data Loggers, Onset Corporation, Bourne, USA and ECH2O humidity sensors, Decagon Devices Inc.). Additional details of the experimental design can be found in Escolar et al. (2015) and Maestre et al. (2013).

The experimental plots kept a minimum separation of 1 m to ensure sampling independent areas. The full experiments have been running continuously since November 2008 and May 2010 in Aranjuez and Sorbas, respectively. Since the beginning of the experiment, we carried out six samplings in Aranjuez (sampling years: 2009, 2011, 2012, 2013, 2015 and 2017), and four samplings in Sorbas (sampling years: 2011, 2013, 2015 and 2017). At each sampling, composite soil samples (0–1 cm depth) were obtained in five selected plots per combination of treatments. We chose this depth because it the first top cm of topsoil is considered as a 'critical zone' in drylands (see Pointing and Belnap, 2012), where most exchanges of matter and energy between the atmosphere and the soil take place, and because it is a depth largely affected by biocrust activity (Belnap et al., 2003; Maestre et al., 2013; Weber et al., 2016). These five sampled plots were randomly selected in the first sampling years. However, and to minimize the disturbance impact of sampling on the same plots, alternated samples were selected in subsequent

sampling years. Visible biocrusts were carefully removed from the soil before sieved (2-mm mesh). After sieving, soil samples were air dried for 1 month and kept in polyethylene bags until laboratory analyses.

2.3 | Assessing soil P fractions

We quantified both labile and more stable P pools using the modified sequential extraction method of Tiessen and Moir (1993), which is based on the Hedley fractionation technique (Hedley et al., 1982). This extraction estimates different P fractions of decreasing bioavailability. Inorganic P (P_i), extracted with ion exchange resins (Resin P_i), represents the most bioavailable P fraction, which is absorbed on surfaces of soil crystalline compounds. Bicarbonate-extractable P is weakly absorbed by soil colloids and it is still available for plant uptake. Both P_i and organic P (P_o) extracted with NaOH are strongly chemisorbed by soil Fe-Al components, and are not considered immediately plant-available P. Finally, the procedure ends with the extraction of the most stable forms of P, HCl-extractable P_i, which is typically associated to Ca in soils, and residual P, which represents the P pool from the primary mineral such as apatite (Hedley et al., 1982; Tiessen et al., 1984).

In short, 0.5 g of soil samples were placed in 50 ml polyethylene centrifuge tubes together with 30 ml of demineralized water and two 4 × 2 cm anion-exchange membranes (AMI-7001S, Membranes International Inc., New Jersey). After tubes were shaken, resins were removed and placed in a clean 50 ml tubes adding 0.7 M NaCl to extract PO_4^{3-} (Guppy et al., 2000). Then, soil samples were sequentially extracted with 30 ml aliquots of 0.5 M $NaHCO_3$ (adjusted to pH 8.5), 0.1 M NaOH, 1 M HCl and 0.5 M H_2SO_4 after a 550°C soil combustion for 1 h. For each extraction, tubes were shaken for 16 h and then centrifuged at 900 g for 30 min (Guppy et al., 2000). The concentration of $PO_4^{3-} - P$ in the supernatant was used to estimate P_i associated with each P fraction. P_o fractions were estimated by subtracting P_i from the total P obtained after digesting the P_o into P_i in the 0.5 M $NaHCO_3$, and 0.1 M NaOH extracts. We used an alkaline digestion with 0.148 M $K_2S_2O_8$ and 3 M NaOH for the $NaHCO_3$ extract ($NaHCO_3$-P_t), and an acid digestion with $(NH_4)_2S_2O_8$ and 0.9 M H_2SO_4 for the NaOH extract (NaOH-P_t). Both digestions were made in the autoclave at 121°C for 1 h and 1 h 30 min, respectively (Tiessen and Moir, 2006). For the determination of residual P, soil samples were heated in a furnace at 550°C for 1h. Then, the burned soil residue was extracted with 5 ml of 0.5 M H_2SO_4, shaken for 1h, filtered and the PO_4^{3-} concentration measured in this extract (Chen et al., 2015). We used the Malachite Green Method (Fernández et al., 1985; modified from Hess and Derr, 1975) to estimate $PO_4^{3-} - P$ concentration in the extracts. Malachite green was found to be the most sensitive basic dye for phosphate determination (Itaya and Ui, 1966). The pH of the extracts was adjusted to neutral pH to reach a correct colour development of samples as necessary. The absorbance of samples was measured at 655 nm wavelength by triplicate in a microplate reader (Jupiter, Asys Hitech GmbH).

The different P fractions were grouped according to the Walker and Syers's (1976) model. We defined calcium P (Ca-P) as the inorganic P extracted with HCl (1M), and occluded P as the residual P fraction derived from primary minerals such as apatite. We estimated non-occluded P (bioavailable P) as the sum of resin-P_i, $NaHCO_3$-P_i and NaOH-P_i, whereas organic P (P_o) was the sum of $NaHCO_3$-P_o and NaOH-P_o (Feng et al., 2016; Walker and Syers, 1976). We will refer to these grouped functional fractions as 'P pools' (Cross and Schlesinger, 1995; Hou et al., 2018b) to differentiate them from the 'P fractions' originated by the original fractionation procedure.

2.4 | Estimating the resistance of soil P pools to simulated climate change

Resistance is defined as the degree to which a variable is changed due to a disturbance (Pimm, 1984). To assess whether biocrusts increase the resistance of soil P pools (non-occluded P, organic P, Ca-P, occluded P and total P) to simulated climate change, we calculated the Resistance Index (RI) of Orwin and Wardle (2004):

$$RI(t_0) = 1 - \frac{2|D_0|}{(C_0 + |D_0|)},$$

where D_0 is the difference of concentrations in a given P pool with respect to the control (C_0) before starting the experimental treatments (i.e. warming and rainfall reduction) and at the end of the applied period of each treatment for each soil sample. To calculate the resistance index, we selected the samples of the warming and rainfall reduction treatments, both before (2008 and 2010 in Aranjuez and Sorbas, respectively) and at the end (2017 in both Aranjuez and Sorbas) of the treatment. Values for RI are in the range of −1 and +1, which indicate minimal and maximal resistance to disturbance of each treatment, respectively.

2.5 | Statistical analyses

To test the effect of biocrust cover, warming (WA), rainfall reduction (RR) and their interactions on the soil concentrations of the different P pools (hypotheses i and ii), we first checked for normality and homogeneity of variances in our data, and used the log transformation (and the Tukey's Ladder of Powers transformation when the log transformation failed) to normalize them. Giving the singularity of the sampling protocol chosen to minimize plot disturbance, we applied repeated measurements ANOVA only in those plots sampled at least three times. The time variable corresponded to the first, second and third time a single plot was sampled. For repeated measurements ANOVA, we tested the sphericity assumption using the Mauchly sphericity test. When the sphericity assumption was rejected (i.e. Mauchly's test, $p < 0.05$), we applied the Greenhouse–Geisser sphericity correction. The degree to which all soil P pools changed due to a WA and RR treatments (resistance index) of biocrusts (hypothesis

iii) were tested through permutational multivariate analysis of variances (PERMANOVA, replicate permutations = 999; function Adonis from the VEGAN package (Oksanen et al., 2012). This method does not rely on the normality assumption of ANOVA and can handle experimental designs such as those used here. All analyses were conducted in R version 4.1.1 (R Core Team, 2020).

3 | RESULTS

3.1 | Simulated climate change effects

We found a high temporal variability for all P pools at both study sites, independent of climate change treatments and biocrust development (Figure 1). Soil concentrations of non-occluded P, P_o, Ca-P, occluded P and total P were significantly higher in high biocrust cover plots at both study sites (Figure 1; see Table S1 for F- and p-values; Tables S3 and S4 for means and standard errors of the different P pools/fractions concentrations, respectively).

Warming significantly increased the concentration of non-occluded P, P_o, Ca-P and total P (Table S1; Figure 1a), the later through their effects on both $NaHCO_3$ P_i and NaOH P_o in Aranjuez (see Table S4 for F- and p-values and Table S5 for means and standard errors of the different P fractions concentrations). Occluded P was not significantly related to warming at this site. In contrast to Aranjuez, we only detected a significant warming effect on non-occluded P at Sorbas (Table S1, Figure 1b), which was driven by the increase in $NaHCO_3$ extracted P_i in warmed plots (Table S4 for F- and p-values; Table S5 for means and standard errors of the different P fractions concentrations). Overall, rainfall reduction did not have any significant effect on soil P pools, neither Aranjuez nor in Sorbas (Table S1 for F- and p-values; Table S3 for means and standard errors of the different P pools concentrations).

3.2 | Resistance of P pools to climate change

The resistance of all major P pools (i.e. non-occluded P, Ca-P, occluded P and total P) to warming was lower in low than in high biocrust cover plots in Aranjuez, whereas in Sorbas this response was only found for Ca-P and Total P (Table S2 for Pseudo F- and p-values, Figure 2). The differences between low and high biocrust cover plots in non-occluded and total P pools were driven by changes in the $NaHCO_3$-P_i, $NaHCO_3$-P_t fractions in Aranjuez, and in NaOH-P_o and NaOH-P_t fractions in Sorbas (see Table S6 for Pseudo F- and p-values). We found a significantly higher resistance to rainfall reduction in soils under well-developed biocrusts for non-occluded and occluded P in Aranjuez (Table S2 for Pseudo F- and p-values, Figure 2). In Sorbas, we did not find any significant effect of biocrust cover on resistance to rainfall reduction for the major P pools. However, we found higher resistance in soils under well-developed biocrusts for the NaOH-P_o fraction at this site (Table S6 for Pseudo F- and p-values).

4 | DISCUSSION

Our climate change treatments affected all soil P pools, including organic, inorganic and recalcitrant pools. Well-developed biocrusts are known to confer resistance to the effects of climate change on biotic and abiotic soil attributes (i.e. N and C cycle, soil respiration, abundance and activity of microbial communities, etc.) in drylands (Delgado-Baquerizo et al., 2016; Escolar et al., 2015), and play major roles in the transformation of inorganic to organic P pools in Central European forests (Baumann et al., 2017). Our results expand findings from previous studies and provide novel evidence showing the key role biocrusts play regulating responses of soil P pools to climate change in drylands.

4.1 | Biocrust impacts on soil P pools and their responses to simulated climate change

The degree of biocrust development had a significant effect on soil P pools independently of simulated climate change treatments, supporting our first hypothesis (i.e. soils under biocrusts will have higher concentration of both labile and stable P pools). Former studies have reported the enrichment in total organic P under biocrusts compared with bare soil (Baumann et al., 2017, 2019; Belnap et al., 2003; Pointing and Belnap, 2012; Reynolds et al., 2001). Our findings expand these findings to include all P fractions. Biocrusts can contribute extra amounts of P to the soil through the addition of biocrust metabolites (e.g. phosphatidyglycerol, inositol phosphate, phosphatidylserine; Dembitsky et al., 1991) and dead biomass, and by favouring organic matter decomposition and microbial activity and consequently, all types of P-releasing processes (Belnap, 2011; Cross and Schlesinger, 2001; Shen et al., 2011). Even so, possible differences on the substrate properties, not apparently visible, that may affect the development of the biocrust cover could also contribute to the differences found.

Our results partially support our third hypothesis (i.e. that well-developed biocrusts increase the resistance of P pools to warming), as biocrusts increased the resistance of some P pools to warming. Biocrusts did not confer more resistance to warming for organic P, something probably related with the reductions in biocrust cover and photosynthetic activity induced by this treatment (Ladrón de Guevara et al., 2014, 2018; Figure S5). One would expect that the largest microbial abundance typically observed under biocrusts (Castillo-Monroy et al., 2011; Delgado-Baquerizo et al., 2013b) could promote higher immobilization rates and consequently higher resistance of the organic P in these soils. However, the warming-induced reductions in biocrust cover observed in our experiments (Figure S5) may have reduced this effect. Biocrusts also conferred resistance to rainfall reduction in the mineral P pools in Aranjuez. Both microbial solubilization through organic acids and chemical weathering of primary minerals could be favoured due to the retention of water inlets under a well-developed biocrust compared with an incipient biocrust. In contrast, the frequent dew events at Sorbas favour less
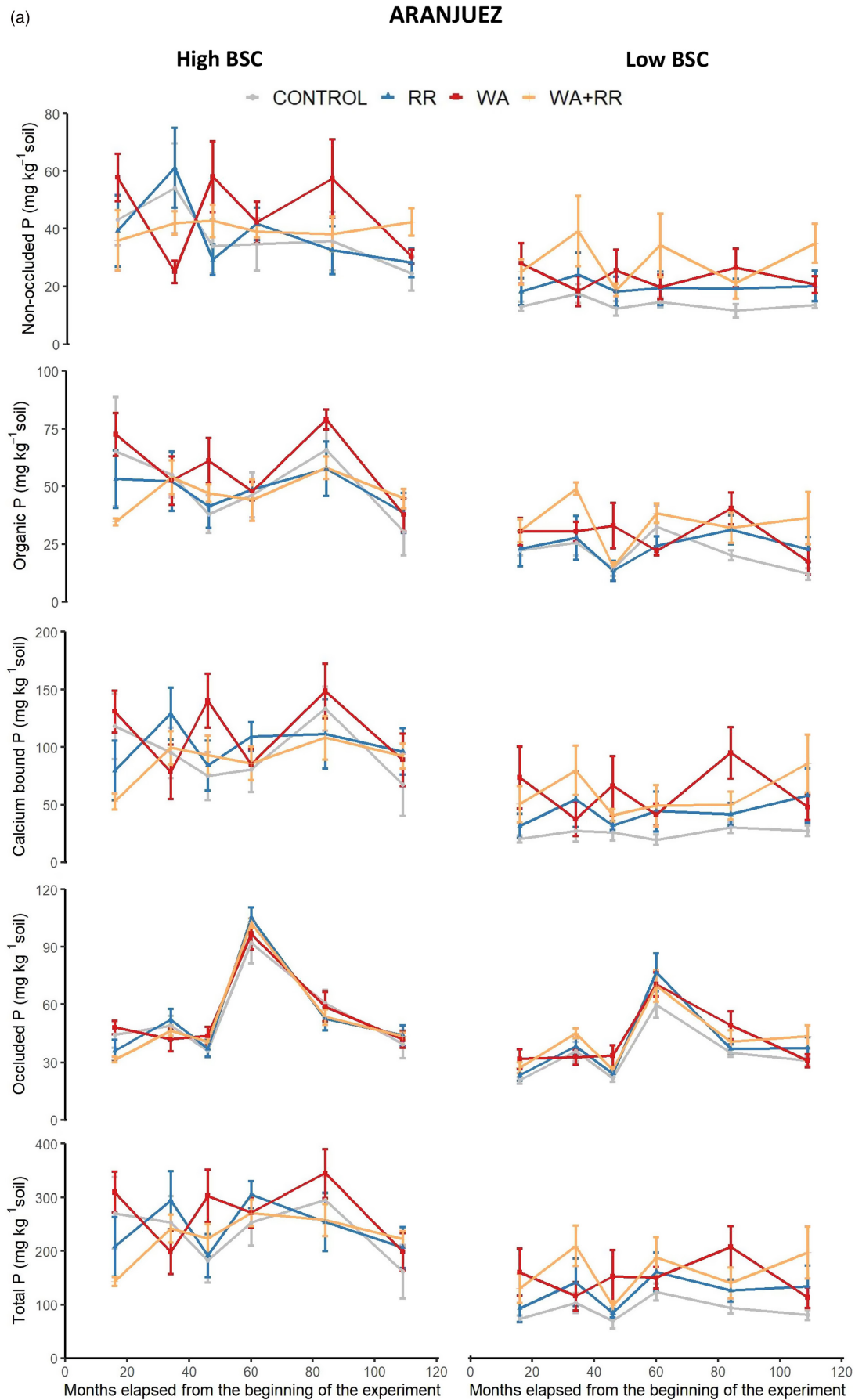
FIGURE 1 Concentrations (mean + standard error) of non-occluded P, organic P, calcium bound P, occluded P and total P for control and simulated climate change treatments: warming (WA), rainfall reduction (RR) and its interaction (WA+RR) in low (right column) and high (left column) biocrust cover plots in Aranjuez (a) and Sorbas (b), respectively.
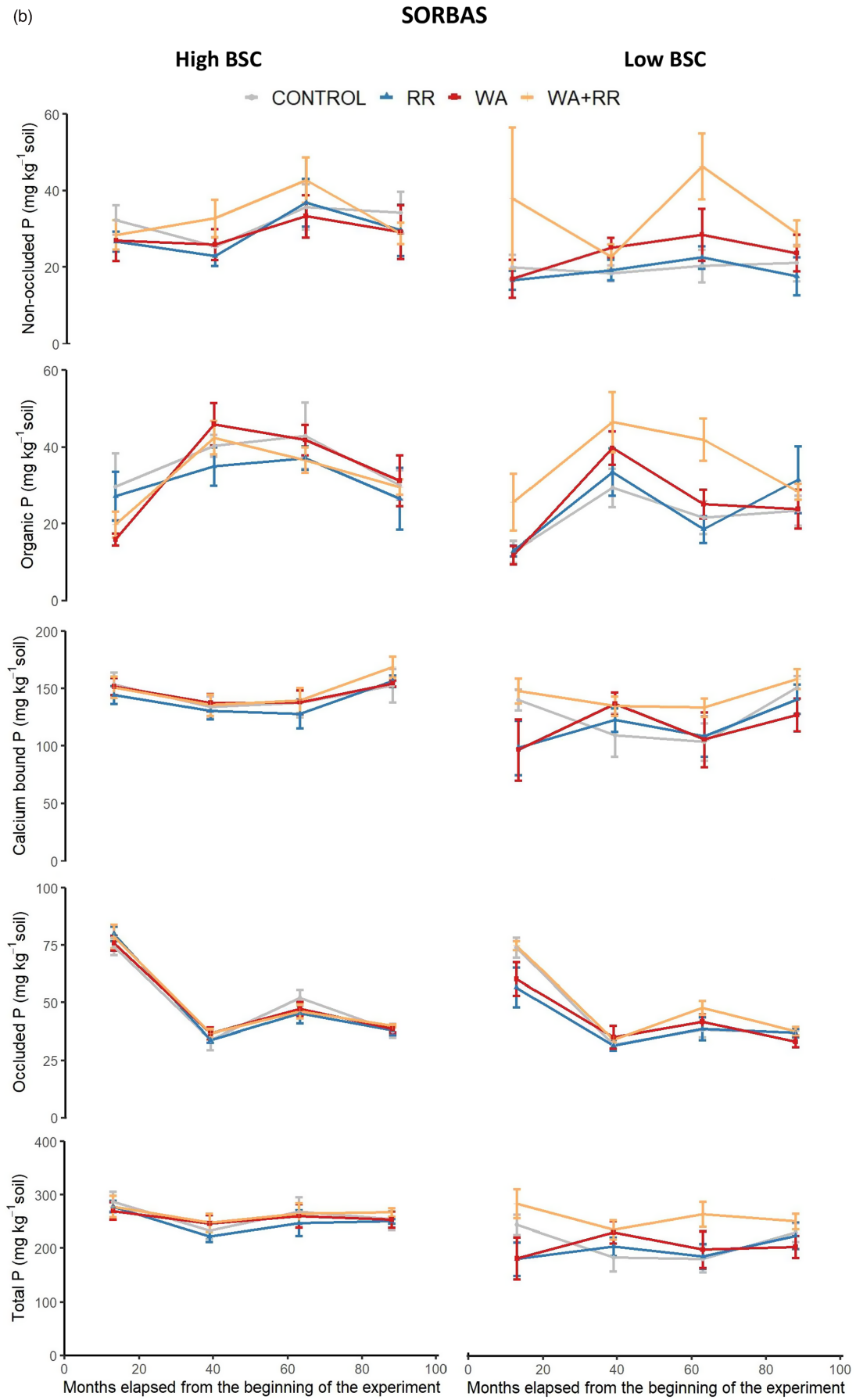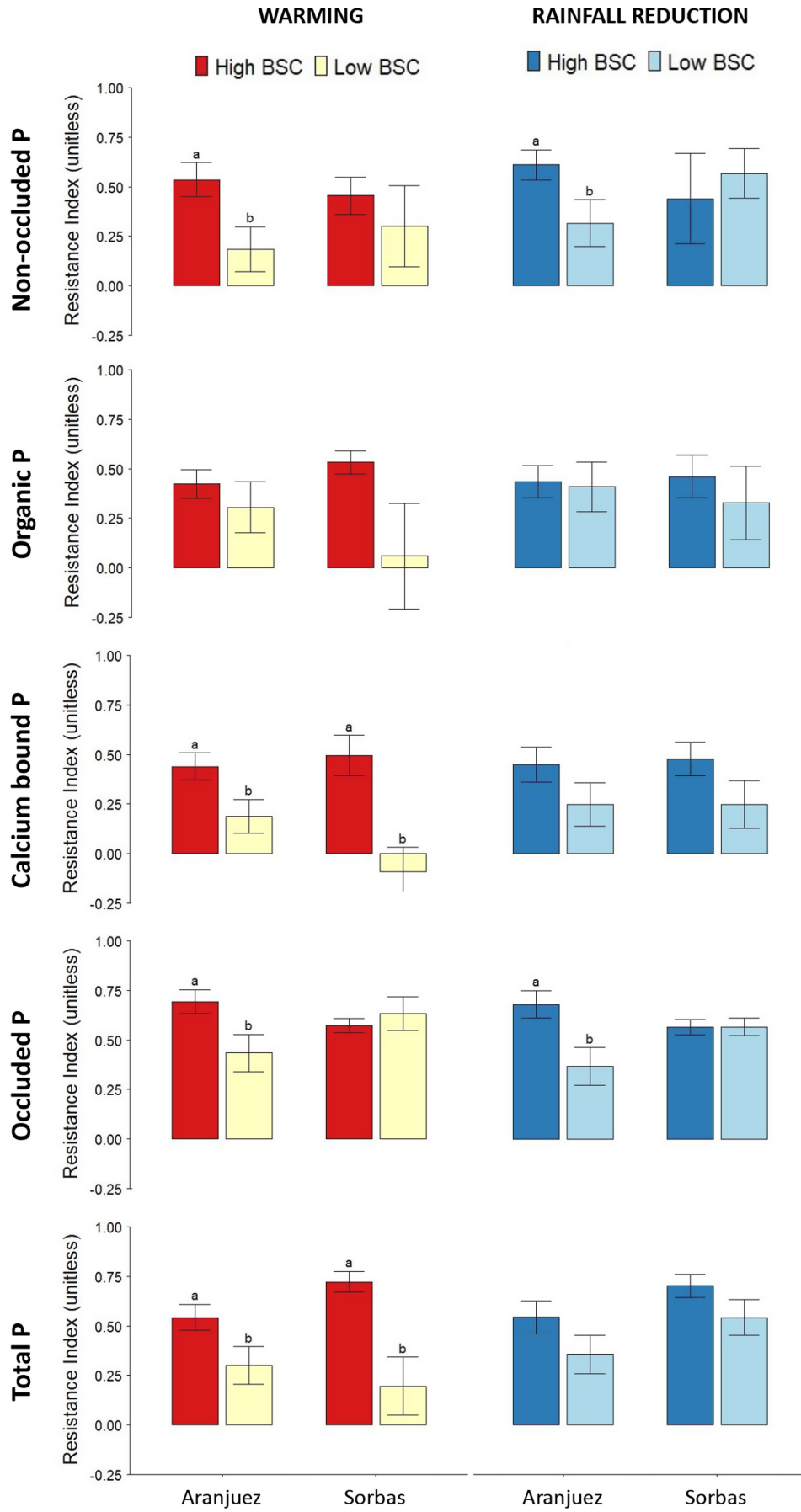
SORBAS

FIGURE 1 (Continued)

FIGURE 2 Differences between high and low biocrust cover plots in the resistance to warming and rainfall reduction of different P pools in Aranjuez and Sorbas. To calculate the resistance index (RI), we selected the warming and rainfall reduction samples, both before (2008 and 2010 in Aranjuez and Sorbas, respectively) and at the end (2017 in both Aranjuez and Sorbas) of the climate change treatments. Values for RI are in the range of −1 and +1, indicating minimal and maximal resistance to disturbance of each treatment, respectively. Differences between biocrust covers ($p < 0.05$, after PERMANOVA test) are indicated by different lowercase letters.

stressful conditions for biocrust constituents, which may minimize the impact of the simulated precipitation reduction treatment at this experimental site (Ladrón de Guevara et al., 2014; Uclés et al., 2015).

4.2 | Warming affects soil P pools

Our study provides experimental evidence that soil warming may increase topsoil P pools concentrations in semi-arid grasslands (hypothesis ii, i.e. warming and to a lesser extent, rainfall reduction will positively affect to both more labile and stable P pools). Although the mechanism explaining the observed changes in soil P pools is still poorly understood, the increase in soil total-P with warming observed may be related to the large decline in biocrust cover observed with warming in the high biocrust cover plots in Aranjuez (>80% reduction over the first 8 years of the experiment; Ladrón de Guevara et al., 2018). Thus, P from dead lichen tissues is likely transferred to the topsoil and incorporated to occluded and non-occluded forms through biological and chemical transformations (García-Velázquez et al., 2020). Strong evidence of rapid lichen litter decomposition increased by warming in the same area of our study has been recently found (Berdugo et al., 2021). Taken together, these results suggest that the microbial community could transfer mid-term available P coming from lichen tissues to more labile ones through microbial P solubilization from occluded P contributing to the increase in P available for plants. Additionally, soil warming could increase the mineral weathering rate of apatite by microorganisms (White et al., 1999; White and Blum, 1995), accelerating the kinetics of soil chemical reactions and contributing to new P inputs to the soil (Dixon et al., 2016).

Previous experiments conducted in drylands have reported that simulated warming has been found to reduce microbial diversity and biomass (DeAngelis et al., 2015; Delgado-Baquerizo et al., 2014; Maestre et al., 2015), the cover of biocrust-forming lichens (Ladrón de Guevara et al., 2018) and higher UV degradation of plant and lichen litter (Almagro et al., 2015; Belnap, 2011; Berdugo et al., 2021; Castenholz and Garcia-Pichel, 2012). The death of biocrust-forming lichens (including the release of immobilized P by the microbes) and the subsequent decomposition of their tissues mediated by warming (Berdugo et al., 2021; Ladrón de Guevara et al., 2018) may explain the increase in labile P and organic P in the topsoil in our experiment. The parallel increase in mineral recalcitrant pools, such as Ca-P and occluded P with warming, is less obvious, but P solubilizing bacteria and fungi, which are responsible of the transfer of P from mineral to organic pools, may be less favoured with the increase in available inorganic and organic P observed under warming (García-Velázquez et al., 2020).

Rainfall reduction had no significant effects on P pools, in partial agreement with the low impacts of this treatment found by Sardans et al. (2006). Turner et al. (2003) suggested that microbes can transfer substantial amounts of P to the soil due to lysis of bacterial cells after rapid rewetting of dry soils promoted by the intermittent water inputs in drylands. We thought that our rainfall reduction treatment might reflect this microbial effect. However, our data did not support this mechanism, and the expected transfer of microbial immobilized P to non-occluded P triggered by reduced soil moisture (Luo et al., 2020) did not show up in our experiment. Instead, our data support that soil micro-organisms are highly resistant to drought in drylands (Delgado-Baquerizo et al., 2014; Yuste et al., 2014).

Interestingly, our warming treatment had minor effects in Sorbas. This remarkable difference respect to Aranjuez could be explained by the large influence that local atmospheric dust deposition, dew inputs and soil erosion have on the chemical composition of topsoil in dryland and biocrust-dominated ecosystems (Reynolds et al., 2001; Wang et al., 2017). First, Mediterranean areas are significantly affected by the Saharan dust deposition (Okin et al., 2004; Rodriguez-Navarro et al., 2018). Particularly, the Southeast of Spain, where Sorbas is located, is the area of the Iberian Peninsula most affected by Saharan dust intrusions (Israelevich et al., 2012; Morales-Baquero and Pérez-Martínez, 2016; Pey et al., 2013; Rodríguez et al., 2010; Russo et al., 2020). Morales-Baquero and Pérez-Martínez (2016) estimated that large amounts of dust particles (75 kg ha^{-1} year^{-1}) and P (0.07 kg ha^{-1} year^{-1}) from the Sahara Desert are deposited on Southeast Spain. In support of this, we found that our 0–1 cm soils fit well with the typical gypsiferous soil profile in Aranjuez, but not so well in Sorbas, where the mineral composition was dominated by calcite and silicates, including illite, kaolinite and palygorskite which are the dominant mineral components of Saharan dust (Ehrmann et al., 2017; Formenti et al., 2014; Gelado-Caballero, 2015; Marsden et al., 2019; Figure S4). The higher frequency of atmospheric dust deposition events on Sorbas than in Aranjuez could thus reduce and/or nullify the effects of the experimental treatments of warming and rainfall reduction. Biocrusts also capture of atmospheric dust containing P and clay particles (Belnap, 2011; Reynolds et al., 2001), contributing to the thickening of soil P reservoirs and subsequently to the fertility of this ecosystem (Belnap, 2011). Second, the water inlets via dewfall in Sorbas, which are a major water source for biocrust-forming organisms such as lichens (Chamizo et al., 2021; Ladrón de Guevara et al., 2014), are much more numerous in Sorbas than in Aranjuez due to its proximity to the sea (Ladrón de Guevara et al., 2014). Uclés et al. (2013) showed that dewfall condensation was observed 78% of the nights in a study site near Sorbas. Thus, the impact of the warming treatment could be lower, and the conditions less stressful for biocrusts in Sorbas than in Aranjuez, where

microbes may keep the P mineral solubilizing activity during longer periods of time. Additionally, heavy rainfall events produced by extreme atmospheric phenomena are more frequent in coastland areas of southern and eastern Mediterranean than in inland areas of the Iberian Peninsula (Millán et al., 1995; Pastor et al., 2000; Riesco Martín et al., 2013). This may have eroded the soil surface in Sorbas, inducing higher variability in the different P pools evaluated between years.

5 | CONCLUSIONS

Our study is the first to experimentally assess the joint effects of major climate change drivers and biocrusts on major soil P pools in drylands. Our results highlight the important role of biocrusts in regulating major P pools in dryland soils, and in increasing the resistance of the P cycle to the impacts of simulated climate change. We also found large impacts of warming on the P fractions evaluated, with significant increases in major pools (such as non-occluded P, organic P, Ca-P and total P, which may be related both the decomposition of BSC tissues; Berdugo et al., 2021; Ladrón de Guevara et al., 2018) and the decrease in the activity of P solubilizing bacteria and fungi responsible for the transfer of mineral to organic P pools (García-Velázquez et al., 2020). Given the observed negative impacts of warming and altered rainfall regimes on the diversity, abundance and composition of dryland biocrust communities (Ferrenberg et al., 2015; Guan et al., 2017; Ladrón de Guevara et al., 2018), their capacity to buffer changes in topsoil P pools driven by climate change will likely be significantly diminished in a warmer and more arid world.

AUTHORS' CONTRIBUTIONS

F.T.M. designed the experiment; A.G. and F.T.M. conceived the study and designed the methodology; B.G., V.O. and R.L. collected the data; L.G.-V., B.G. and V.O. analysed the data; L.G.-V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data used in the primary analyses are publicly available from figshare (https://doi.org/10.6084/m9.figshare.16768933.v3; García-Velázquez et al., 2022).

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