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RESEARCH ARTICLE

Climate change legacies contrastingly affect the resistance and resilience of soil microbial communities and multifunctionality to extreme drought

Marina Dacal[1,2] | Pablo García-Palacios[2,3] | Sergio Asensio[1] | Juntao Wang[4,5] | Brajesh K. Singh[4,5] | Fernando T. Maestre[1,6]

[1]Instituto Multidisciplinar para el Estudio del Medio 'Ramon Margalef', Universidad de Alicante, San Vicente del Raspeig, Spain; [2]Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Spain; [3]Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, Madrid, Spain; [4]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia; [5]Global Centre for Land-Based Innovation, Western Sydney University, Penrith South DC, NSW, Australia and [6]Departamento de Ecología, Universidad de Alicante, San Vicente del Raspeig, Spain

Correspondence
Marina Dacal
Email: marina.dacal@ua.es

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Abstract

1. Soil microbial communities largely determine the ability of soils to provide multiple functions simultaneously (i.e. soil multifunctionality; multifunctionality hereafter). However, a major research challenge is understanding how soil microbial communities and associated multifunctionality resist and recover from extreme climate events such as droughts, and how the legacy of past climatic conditions may constrain such responses.
2. Here, we used soils subjected to 7 years of reduced rainfall (~35% reduction), warming (3°C temperature increase) and their combination to assess climate change legacies on the resistance and resilience of both soil fungal and bacterial communities and multifunctionality to a subsequent extreme drought event (2 weeks at 3% water-holding capacity). At the end of the extreme drought, and 1, 15 and 60 days after rewetting, we assessed bacterial and fungal community composition, richness and abundance, as well as a multifunctionality index based on eight functions related with soil carbon (C), nitrogen (N) and phosphorous (P) cycling.
3. Climate change legacies influenced the resistance and resilience of bacterial and fungal abundance to extreme drought, but not those of community composition, richness and multifunctionality. The resistance of bacterial and fungal abundance showed opposite responses to warming and reduced rainfall. Specifically, climate change legacies increased the resistance of fungal abundance, whereas they reduced that of bacterial abundance. The resistance and resilience of multifunctionality to extreme drought were not related to the resistance or resilience

of bacterial and fungal communities. Yet, the resistance of multifunctionality was related to that of *Chytridiomycota*, whereas its resilience was related to that of *Proteobacteria*.

4. Overall, our results indicate that climate change legacies affected the resistance and resilience of soil bacterial and fungal abundance to a subsequent extreme drought event, but not those of their community composition, richness and multifunctionality. Our results provide new insights on how climate change legacies contrastingly influence the resistance and resilience of soil microbial communities and multifunctionality. Furthermore, our findings highlight the role that specific microbial taxa play in maintaining soil multifunctionality and recovering from extreme drought events predicted under anthropogenic climate change.

KEYWORDS
Bacteria, drought, fungi, multifunctionality, reduced rainfall, resilience, resistance, warming

1 | INTRODUCTION

Soil microbes are the most abundant and diverse organisms on Earth (Fierer & Jackson, 2006; Locey & Lennon, 2016), and are intricately linked to soil functioning, as they play a key role in organic matter decomposition, carbon (C) storage and nutrient cycling (Bardgett & Van Der Putten, 2014; Delgado-Baquerizo et al., 2016). Soil microbial communities are sensitive to both warming and changes in precipitation patterns associated with anthropogenic climate change (De Vries & Shade, 2013; Kaisermann et al., 2017; Rousk et al., 2013). For instance, reductions in both bacterial and fungal biomass, and shifts in microbial community composition with warming have been observed in multiple ecosystem types (Frey et al., 2008; Rinnan et al., 2007; Yergeau & Kowalchuk, 2008). Similarly, reduced rainfall has been reported to decrease soil bacterial abundance, leading to changes in soil microbial community composition, growth rates and activity (Gordon et al., 2008; Ochoa-Hueso et al., 2018; Schimel et al., 2007).

Beyond increases in mean temperatures and changes in rainfall patterns, climate change is expected to increase the frequency of extreme climate events, such as short-term but intense droughts, particularly in drylands (Gibelin & Déqué, 2003; Huntington, 2006; Seneviratne et al., 2012). Despite the fact that climate change components (i.e. mean change and extreme events) occur simultaneously (Meehl et al., 2007; Walter et al., 2013), few studies have addressed their interactive effects on soil biodiversity and functioning. Existing evidence also suggests that past climatic conditions determine soil microbial communities and functioning (Delgado-Baquerizo, Bissett, et al., 2017; Ye et al., 2019), and their responses to current changes in soil moisture (Hawkes & Keitt, 2015; Hawkes et al., 2017). Furthermore, soil microbial communities can acclimate and shift from sensitive bacterial-dominated communities to more drought-tolerant fungal-dominated communities after long-term exposure to rainfall reduction (Bouskill et al., 2013; Evans & Wallenstein, 2012; Curiel Yuste et al., 2011), altering the ability of soil functioning to cope with extreme drought events as a result of the different response of fungal and bacterial communities (De Vries, Liiri, Bjørnlund, Bowker, et al., 2012). Specifically, soil fungi have been demonstrated to be generally more resistant—but less resilient—than bacteria given their thicker cell walls, sporulation activity, and the capacity of fungal hyphae to break through air-filed pores to access water and nutrients in dry soils (Barnard et al., 2013; De Vries, Liiri, Bjørnlund, Bowker, et al., 2012; Gordon et al., 2008).

Previous research on below-ground communities has evaluated the response of soil microbial communities and functioning to extreme drought using two key components that determine ecosystem stability: resistance and resilience during and after the drought event, respectively (De Vries, Liiri, Bjørnlund, Setälä, et al., 2012; Hawkes et al., 2017, 2020; Waring & Hawkes, 2015). However, this research has evaluated the responses of soil microbial communities and soil functions separately (Bouskill et al., 2013; De Vries, Liiri, Bjørnlund, Setälä, et al., 2012; Preece et al., 2019), or addressed only individual functions such as soil respiration (Hawkes et al., 2017, 2020). To gain a broader understanding that is crucial for management and conservation, we need to assess whether the responses of soil microbial communities to climate change alter overall ecosystem functioning (Delgado-Baquerizo, Eldridge, et al., 2017). In this line, the ability of soil microbes to perform multiple functions simultaneously (i.e. soil multifunctionality; multifunctionality hereafter) has been proposed as a meaningful metric (Manning et al., 2018) Furthermore, most previous studies have only evaluated the effect of being previously subjected (i.e. legacies, hereafter) to a reduction in rainfall (Bouskill et al., 2013; De Vries, Liiri, Bjørnlund, Setälä, et al., 2012), neglecting the effect of other components of climate change components such as global warming. Consequently, the legacies of different climate change scenarios that simulate mean temperatures and rainfall changes on the resistance and resilience of both soil microbial communities and multifunctionality to extreme drought events, and the

link between the stability of soil microbial communities and that of multifunctionality, remain largely unexplored.

Here, we evaluated the effect of climate change legacies on the resistance and resilience of soil bacterial and fungal communities (community composition, richness and abundance) and multifunctionality (estimated using eight functions related to soil C, N and P cycling) to a subsequent extreme drought event. Moreover, we assessed whether the resistance and resilience of soil microbial communities to extreme drought were related to those of multifunctionality. We collected soils subjected to four climate change scenarios in a manipulative experiment (i.e. control, reduced rainfall, warming and their combination; Valencia et al., 2018) for 7 years and exposed them to extreme drought in the laboratory (i.e. 3% water-holding capacity [WHC] for 2 weeks) to assess the resistance of soil microbial communities and multifunctionality. Then, we rewetted the soils at 60% WHC and assessed the resilience of soil microbial communities and multifunctionality 1, 15 and 60 days after rewetting. We hypothesized that (i) soil fungal communities subjected to reduced rainfall will be more resistant but less resilient to a subsequent extreme drought than bacterial communities (De Vries, Liiri, Bjørnlund, Bowker, et al., 2012); (ii) the resistance and resilience of fungal and bacterial communities to extreme drought will be lower in warmed than in control soils than in the control ones, as already disturbed soil communities may be less stable to a different subsequent disturbance (Griffiths & Philippot, 2013); (iii) the resistance and resilience of multifunctionality will be lower in warmed and higher in reduced rainfall soils compared to control ones encompassing the expected responses of soil microbial communities described in our two first hypotheses given that soil microbial communities mediate multifunctionality (Delgado-Baquerizo, Eldridge, et al., 2017; Delgado-Baquerizo et al., 2016); and (iv) the resistance and resilience of soil microbial communities and multifunctionality to an extreme drought event will be related, as microbes play a key role in driving multifunctionality (De Vries & Shade, 2013; Orwin et al., 2006).

2 | MATERIALS AND METHODS

2.1 | Climate change experiment simulating mean changes in air temperature and rainfall

We used soil from a climate change experiment conducted in the Outdoor Climate Change Laboratory of Rey Juan Carlos University (URJC, Móstoles, Spain: 40°20′37″N, 3°52′00″W; Figure S1a; Valencia et al., 2018), to establish an independent laboratory experiment. To conduct this fieldwork, no license or permission was required. The climate of the site is Mediterranean semi-arid, with mean annual temperature and precipitation values of 16.6°C and 362 mm, respectively. In April 2011, we established a full factorial experiment at this site with two climate change treatments (see Valencia et al., 2018 for details): warming (control vs. +3°C temperature increase) and reduced rainfall (control vs. ~35% reduction in total annual rainfall; Figure 1 and Figure S1b–d). The climate change treatments and their main effects on air and soil moisture are detailed in Supporting Materials and Methods. For this climate change experiment, we used plastic pots (depth 38 cm, internal diameter 28 cm, volume 0.023 m^3) filled with a silty loam soil (sand content 73.5%, silt content 18.5%, clay content 8.0%, pH 7.6, electrical conductivity 1,128 μS/cm and organic carbon content 0.52%.). The pots were filled with soil and subjected to the different climate change scenarios for 7 years, until February 2018, when they were collected for our laboratory experiment.

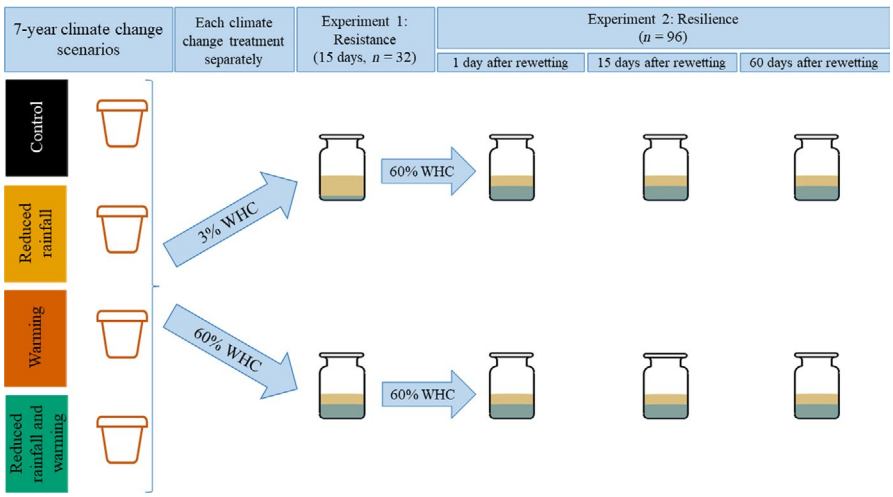

FIGURE 1 Laboratory experimental setup. Soils were subjected to 7 years of climate change scenarios (i.e. reduced rainfall, warming, their combination and control) in a common garden experiment. We used a composite soil sample of each climate change scenario to conduct two separated experiments. For the resistance experiment (Experiment 1), the soils were incubated at two soil moisture levels (control 60% WHC vs. drought 3% WHC). At the end of the extreme drought disturbance, the soils were destructively sampled. After that harvesting, the remaining microcosms were rewetted to 60% WHC for the resilience experiment (Experiment 2). The soils were destructively sampled 1, 15 and 60 days after rewetting. We used four replicates per combination of treatments, resulting in a total of 128 microcosms: 32 for the resistance experiment and 96 for the resilience experiment

Soils from the four climate change scenarios (control, reduced rainfall, warming and the combination of reduced rainfall and warming; four replicates per treatment) were sieved at 2 mm mesh, bulked and homogenized to get one composite sample per climatic treatment. We used a composite soil sample instead of individual soils because assessing the effects of spatial variability of climatic conditions was not the main objective of our study (Gundale et al., 2017). Instead, we aimed to evaluate the climate change legacies on the resistance and resilience of soil microbial communities and functions. The approach followed has been widely used when evaluating previous climate legacies on the resistance and resilience of soils to drought (De Vries, Liiri, Bjørnlund, Bowker, et al., 2012; De Vries, Liiri, Bjørnlund, Setälä, et al., 2012; Meisner et al., 2018).

2.2 | Extreme drought experiment

Soils from the four climate change scenarios were transferred to a total of 128 microcosms (0.25 L microcosms; 100 g of dry soil per microcosm) to conduct two separate laboratory experiments (Figure 1). First, to assess the resistance of soil microbial communities and multifunctionality to an extreme drought event, microcosms were incubated at two levels of soil moisture (extreme drought, 3% WHC and control, 60% WHC) for 2 weeks at 25°C in a growth chamber with dark and moisture control to avoid water loss. At the end of the drought event, a fraction of the microcosms was destructively harvested (four replicates per combination of climate change and drought treatments, 32 microcosms in total). The second experiment aimed to assess the resilience of soil microbial communities and multifunctionality to an extreme drought event. For that purpose, the remaining microcosms were rewetted to 60% WHC and incubated for almost 9 weeks. The resilience of the soil microbial community and multifunctionality was measured 1, 15 and 60 days after rewetting. At the end of each sampling date, 32 microcosms were destructively harvested (four replicates per combination of climate change and drought treatments). At each sampling date, soil respiration was measured in each microcosm during the incubation and prior to harvesting using non-destructive techniques. Then, a fraction of each of the sampled soils was immediately frozen at −20°C for microbial analyses, and the remaining soil was air-dried for a month for biogeochemical analyses. Storage of air-dried soils for biogeochemical analyses is a normal procedure in dryland environments, where soils are usually dry under field conditions for a prolonged period, until they are rewetted with seasonal rain pulses (Cantón et al., 2004; Makhalanyane et al., 2015; Rey et al., 2011). Furthermore, previous studies have found that the storage of air-dried soils from drylands have small or negligible effects on soil biogeochemical variables such as soil organic C contents and enzymatic activities (Zornoza et al., 2006, 2009). Consequently, this storage approach is generally used both in local-scale studies (Maestre et al., 2013; Mancinelli et al., 2013) and large-scale surveys (e.g. Bahram et al., 2018; Delgado-Baquerizo, Eldridge, et al., 2017; Maestre et al., 2012).

2.3 | Soil individual functions and multifunctionality

We selected the following variables that constitute good proxies of the processes driving soil C, nitrogen (N) and phosphorus (P) cycling and the build-up of nutrient pools (Delgado-Baquerizo, Eldridge, et al., 2017; Maestre et al., 2012): soil organic C (SOC), total available *N* (TAN), labile inorganic P (Olsen P), soil respiration, potential net N mineralization, α- and β-glucosidase (starch degradation), N-acetyl-glucosaminidase (chitin degradation), cellobiohydrolase (cellulose degradation), xylanase (hemicellulose degradation), phosphatase (organic P mineralization) and leucine aminopeptidase (peptide breakdown). The concentration of SOC was determined by colorimetry (Anderson & Ingram, 1993). To measure TAN and dissolved inorganic N (DIN), a fraction of each soil sample was incubated in a growth chamber at 30°C for 14 days at 80% WHC (Allen et al., 1986). Then, both N forms concentrations were measured in both incubated and non-incubated subsamples by colorimetry using the indophenol blue method (Sims et al., 1995). Potential net N mineralization rate was then estimated as the difference in DIN before and after the incubation (Delgado-Baquerizo & Gallardo, 2011). To determine Olsen P, soil samples were extracted with 0.5 M Na_2HCO_3 in a 1:5 ratio by orbital shaking at 180 rpm for 2 hours (Olsen et al., 1954). Soil basal respiration was measured in all microcosms at the experiment setup and before each harvest using the modification of the MicroResp™ protocol (Campbell et al., 2003) described in García-palacios et al. (2013). Finally, we measured the soil enzymatic activities using a fluorescence method (Bell et al., 2013), and derived the cumulative C (α- and β-glucosidase, cellobiohydrolase and xylanase), N (N-acetyl-glucosaminidase and leucine aminopeptidase) and P (phosphatase) enzymes (Fanin & Bertrand, 2016; Piton et al., 2020).

Soil multifunctionality was calculated based on the eight single functions described above, which were weakly correlated ($\rho < 0.6$) with each other (Table S1). First, we standardized separately such functions (*F*) using the *Z*-score transformation:

$$Z\text{-score}_{ij} = F_{ij} - \text{Mean } F_i / SD\ F_i, \quad (1)$$

where F_{ij} is the value of function *i* in the mesocosm *j*, Mean and $SD\ F_i$ are the mean and the standard deviation of the function F_i calculated for the 128 mesocosms studied, respectively. Then, multifunctionality was obtained for each mesocosm as the average of the Z-scores of the eight functions considered. This multifunctionality index has good statistical properties and is a straightforward and easily interpretable measure of multifunctionality (Byrnes et al., 2014; Maestre et al., 2012).

2.4 | Soil microbial analyses

Soil DNA extractions were performed using the DNeasy Powersoil Kit (Qiagen). We assessed the abundance of both soil bacteria and fungi using qPCR on an ABI 7300 Real-Time PCR (Applied

Biosystems). The bacterial 16S-rRNA gene was amplified with the Eub 338-Eub 518 primer set, while for fungal ITS amplification the ITS 1-5.8S primer set was used (Evans & Wallenstein, 2012). We describe more deeply the method used to determine the total abundance of soil bacteria and fungi using qPCR in Supporting Materials and Methods. We conducted amplicon sequencing using the Illumina MiSeq platform at the Next Generation Genome Sequencing Facility of Western Sydney University. The primer sets used were the 341F/805R for bacteria and FITS7/ITS4 for fungi (Herlemann et al., 2011; Ihrmark et al., 2012). The bioinformatic analyses conducted on the data resulting from amplicon sequencing are described in Supporting Materials and Methods. We determined the dominant bacterial and fungal phyla as those with a mean relative abundance greater than 2% and 1.5%, respectively (Preece et al., 2019).

2.5 | Resistance and resilience of soil microbial communities and multifunctionality to extreme drought

We used two different types of resistance and resilience indices: one for microbial community composition and the other for the rest of the variables considered in this study. First, we used resistance and resilience indices based on Bray–Curtis similarity for the bacterial and fungal community composition (De Vries et al., 2018; Shade et al., 2011; see Supporting Materials and Methods for more details). Second, we used the Orwin and Wardle (2004) indices to evaluate the resistance and resilience of the rest of the variables considered in our study (i.e. soil bacterial and fungal richness, abundance, and dominant phyla, and the eight single functions) to an extreme drought. Given the multivariate nature of soil community composition data, we had to use a different index for community composition (Piton et al., 2020; Shade et al., 2011). However, both types of indices are consistent (Piton et al., 2020). Specifically, either of the resistance indices measured the changes caused by an extreme drought, with higher values (i.e. values close to 1) indicating greater resistance and values close to 0 indicating no resistance. Similarly, both types of resilience indices indicate the proportion of changes caused during the extreme drought event that was recovered between the end of such disturbance and each of the sampling times during the recovery (i.e. 1, 15 or 60 days after rewetting; Piton et al., 2020). For both resilience indices, values close to 1 indicate complete resilience, values close to 0 indicate no recovery at all and negative values indicate a greater difference between control and disturbed soil at the end of the recovery period (i.e. 1, 15 or 60 days after rewetting) than at the end of the disturbance (Piton et al., 2020).

The resistance and resilience indices of the eight single functions considered in our study were used to calculate the resistance and resilience of multifunctionality, following the same approach of Delgado-Baquerizo, Eldridge, et al. (2017). Specifically, we first calculated the resistance and resilience of the eight single functions considered in our study, which were not strongly correlated ($\rho < 0.6$) with each other (Table S2). The resistance and resilience of multifunctionality were thus obtained for each microcosm as the average of resistance or resilience of the eight functions (Delgado-Baquerizo, Eldridge, et al., 2017).

2.6 | Statistical analyses

To evaluate the legacy effect of climate change treatments on the resistance and resilience of soil bacterial and fungal community composition, richness, abundance, dominant phyla, multifunctionality and the different functions considered in our study to an extreme drought event using linear models (LMs). Resistance LMs included reduced rainfall, warming and their interaction as fixed factors (hypotheses i, ii and iii). Resilience LMs also included time after rewetting (i.e. 1, 15 and 60 days), and all two-way and three-way interactions as fixed factors (hypotheses i, ii and iii).

Similarly, we assessed the effects of climate change legacies on soil bacterial and fungal community composition after and during the recovery from a simulated drought event (hypotheses i and ii) using the VEGAN R package (Oksanen et al., 2019). Specifically, the effects of warming, reduced rainfall, drought, and all two-way and three-way interactions were evaluated after the extreme drought with a permutational multivariate analysis of variance (PERMANOVA) using the *adonis2* function with 9,999 permutations. All factors and interactions were considered as fixed in this analysis. The time after rewetting (i.e. 1, 15 and 60 days) and its interaction with climate change and the simulated drought event were also included as fixed factors when addressing their effects during the recovery from the simulated drought event.

Moreover, we evaluated the effect of climate change legacies on the absolute response of multifunctionality after and during the recovery from a simulated drought event (hypothesis iii) using LMs. Specifically, we built a LM that include warming, reduced rainfall, drought, and all two-way and three-way interactions as fixed factors to evaluate the effects of climate change legacies and an extreme drought event after such disturbance. The LMs used to evaluate the effect of these treatments during the recovery from the simulated drought event also include time after rewetting (i.e. 1, 15 and 60 days).

To help elucidating which individual functions drive the resistance and resilience of multifunctionality to an extreme drought event, we correlated the resistance or resilience of multifunctionality and the resistance or resilience of individual soil functions using Spearman correlations. We then evaluated whether the resistance and resilience of particular soil microbial attributes (e.g. community composition, richness, abundance and dominant microbial phyla) to an extreme drought event were related to those of multifunctionality (hypothesis iv). To do so, we correlated the resistance or resilience of soil microbial attributes and that of multifunctionality using Spearman correlations. Similarly, we correlated the resistance or resilience of soil microbial attributes and that of soil individual functions using Spearman correlations. All statistical analyses were conducted using the R 3.3.2 statistical software (R Core Team, 2015).

3 | RESULTS

3.1 | Resistance and resilience of soil microbial communities to extreme drought

We did not find a significant effect of climate change legacies on the resistance or resilience of bacterial and fungal community composition to extreme drought ($p > 0.1$; Table S3 and Figure 2). The resistance of fungal community composition was higher than that of bacterial community composition across all climate change scenarios (Figure 2A,B), whereas the opposite results were observed for the resilience to an extreme drought (Figure 2C,D). Similarly, climate change legacies did not affect the resistance or resilience of the bacterial or fungal richness ($p > 0.05$; Table S4 and Figure 3A,B for resistance, while c and d for resilience). We also observed that both bacterial and fungal richness were highly resistant to an extreme drought event (i.e. resistance values over 0.6; Figure 3A,B). Additionally, we also observed that the differences within treatments were greater in the resistance of fungal community composition and richness compared to the resistance of these attributes of bacterial communities (Figure 2A,B for microbial community composition, and Figure 3A,B for microbial richness). Accordingly, we observed that the simulated extreme drought event had a significant effect on bacterial ($p < 0.05$; Table S5 and Figure S2) but not on fungal ($p > 0.1$; Table S5 and Figure S2) community composition, both at the end of the drought and during the recovery stage. However, we found that climate change legacies do not modulate the outcome of the extreme drought, either at the end of the event or during the recovery ($p > 0.1$ for the two-way interactions between warming or reduced rainfall and simulated drought, and the three-way interaction; Table S5; Figure S2).

When evaluating the resistance and resilience of microbial abundance to extreme drought, we found that the resistance of bacterial abundance in soils previously subjected to reduced rainfall, warming and its combination was lower than in control soils ($p = 0.002$ for both climate change treatments; Table S6, Figure 4A), whereas this resistance was higher when evaluating fungal abundance ($p = 0.004$; Table S6; Figure 4B). Although the resilience of bacterial abundance to an extreme drought event was greater in soils subjected to reduced rainfall compared to control soils ($p = 0.015$; Table S6; Figure 4C), climate change legacies did not influence the resilience of fungal abundance ($p > 0.1$; Table S6; Figure 4D).

Different microbial phyla dominated the soil bacterial and fungal communities (Figure S3). We did not find any climate change legacies on the resistance of the dominant bacterial and fungal phyla to extreme drought ($p > 0.05$, Tables S7 and S8 for the dominant bacterial and fungal phyla, respectively). However, we observed contrasting climate change legacies on the resilience of specific dominant bacterial phyla ($p < 0.05$; Table S7), but not on that of dominant fungal phyla ($p < 0.05$; Table S8). For example, the resilience of *Actinobacteria* was greater in soils exposed to reduced rainfall compared to control soils ($p = 0.019$; Table S7).

3.2 | Resistance and resilience of multifunctionality to extreme drought

Neither the resistance nor the resilience of multifunctionality to drought were affected by climate change legacies or the extreme drought event ($p > 0.1$; Table S9; Figure 5). Similarly, climate change legacies did not influence the absolute response of multifunctionality to a simulated extreme drought either at the

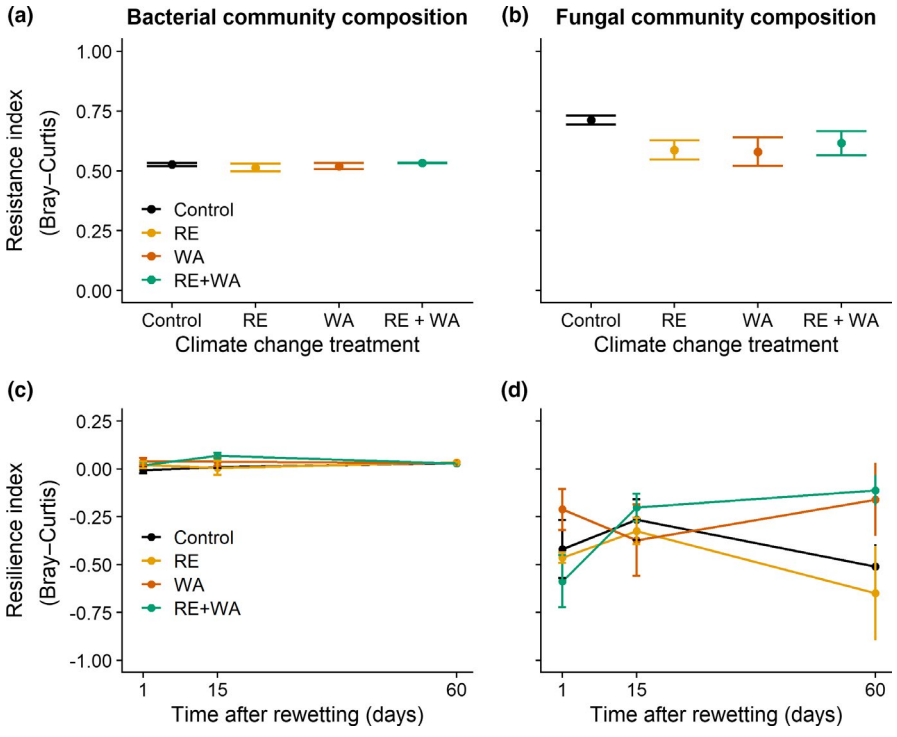

FIGURE 2 Climate change legacies on the resistance and resilience of bacterial (A and C, respectively) and fungal (B and D, respectively) community composition (i.e. Bray–Curtis similarity) to extreme drought. Although the legend shows four treatment levels, statistical analyses were conducted as the interaction of two climate change treatments (i.e. reduced rainfall and warming; see Section 2). RE, reduced rainfall, WA, warming; RE + WA, combination of reduced rainfall and warming. Both the resistance and resilience plots show means ± *SE* ($n = 4$)

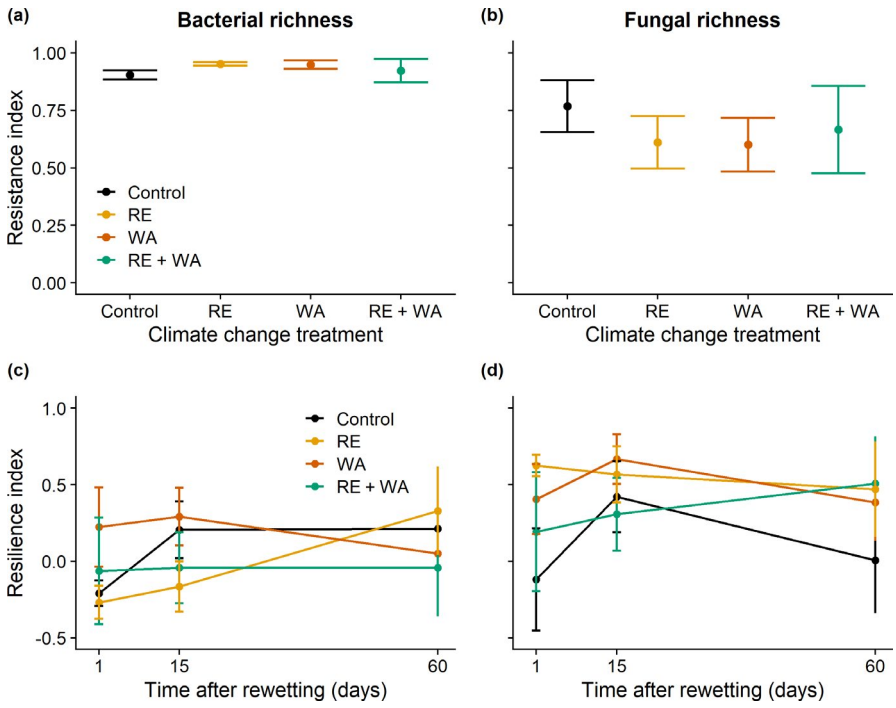

FIGURE 3 Climate change legacies on the resistance and resilience of the bacterial (A and C, respectively) and fungal (B and D, respectively) richness to extreme drought. Rest of the legend as in Figure 2

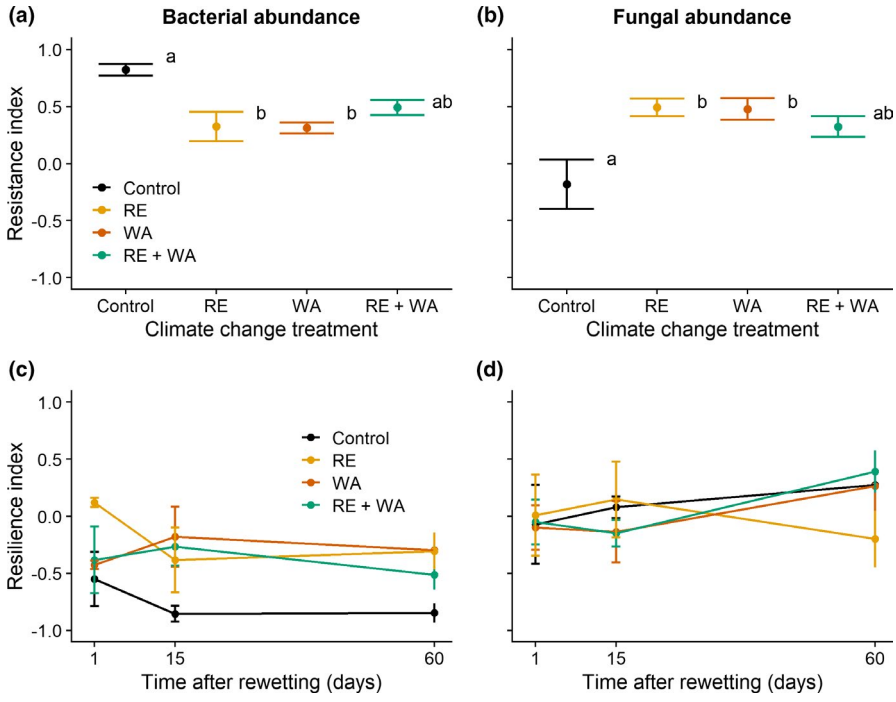

FIGURE 4 Climate change legacies on the resistance and resilience of bacterial (A and C, respectively) and fungal (B and D, respectively) abundance to extreme drought. Letters denote significant differences at $p < 0.05$. Rest of the legend as in Figure 2

end of this disturbance or during the recovery ($p > 0.05$ for the two-way interactions between prolonged warming or prolonged reduced rainfall and laboratory drought and the three-way interaction; Figure S4; Table S10). The resistance and resilience of individual soil functions followed patterns similar to those observed for multifunctionality (Table S11). Therefore, no significant climate change legacies were observed in the resistance and resilience of the eight single soil functions evaluated ($p > 0.05$; Table S12; Figures S5–S7).

3.3 | Coordination between the responses of soil microbial communities and multifunctionality to an extreme drought event

The resistance and resilience of multifunctionality were not correlated with those of soil bacterial and fungal attributes (i.e. community composition, richness and abundance; $p > 0.1$; Table S13). However, the resistance and resilience of multifunctionality were correlated with those of specific dominant phyla. Specifically, the

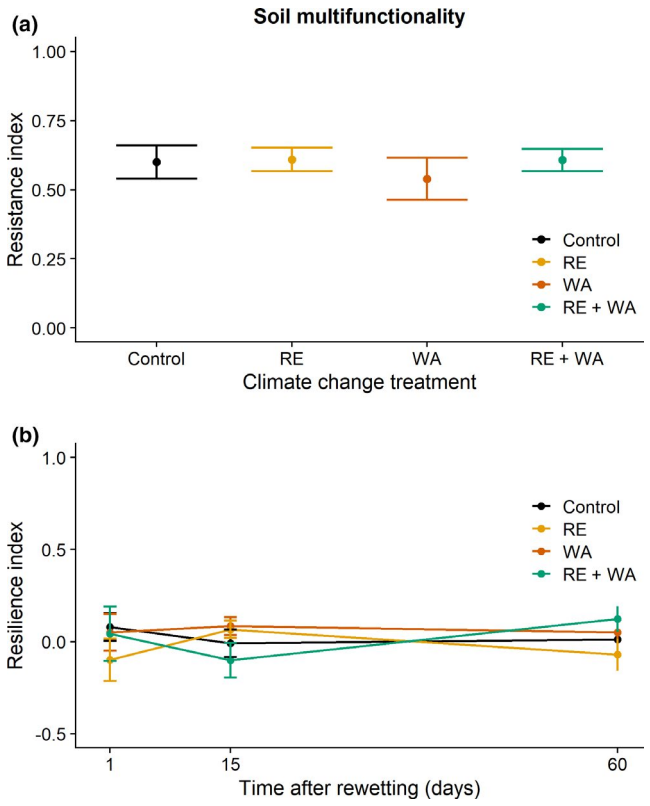

FIGURE 5 Climate change legacies on the resistance (a) and resilience (b) of multifunctionality to extreme drought. Rest of the legend as in Figure 2

resistance of multifunctionality was positively and negatively correlated with that of *Chytridiomycota* and *Proteobacteria*, respectively ($p < 0.05$; Table S13). We found similar results when we correlated the resistance or resilience of soil individual functions and those of soil microbial attributes (Tables S14–S16). The resistance and resilience of most individual functions were not correlated to those of bacterial and fungal community composition, richness and abundance (Tables S14–S16). However, the resistance and resilience of soil individual functions were linked to those of certain bacterial and fungal dominant phyla (Tables S14–S16).

4 | DISCUSSION

The legacy effect of warming and reduced rainfall did not alter the resistance and resilience of soil bacterial and fungal community composition and richness to extreme drought. Accordingly, climate change legacies did not affect the absolute response of bacterial and fungal community composition to an extreme drought at the end of the event and during the recovery. Such findings contrast with our first and second hypotheses, and with previous studies showing important legacy effects of previous climatic conditions on the responses of soil microbial communities to a subsequent drought event (Bouskill et al., 2013; De Vries, Liiri, Bjørnlund, Setälä, et al., 2012; Hawkes & Keitt, 2015; Kaisermann et al., 2017). We hypothesize two mechanisms to explain the absence of climate change legacies. First, the influence of adaptive physiological responses (to 7 years of different climate change scenarios) typically tended to be less pronounced than the responses of soil microbial communities and certain functions that they mediate, such as soil respiration, to current ambient climatic regimes (i.e. the extreme drought that we used in the laboratory experiment; Bradford et al., 2010; Hochachka & Somero, 2002). Therefore, these microbial adaptations to previous climatic conditions could be quickly overcome if the subsequent drought event is large enough to reduce the fitness of existing microbial taxa (Hawkes & Keitt, 2015). More precisely, most previous studies showing significant legacy effects used mild droughts such as 20%–30% of soil WHC (Bouskill et al., 2013; De Vries, Liiri, Bjørnlund, Setälä, et al., 2012; Meisner et al., 2018), while we dried soils up to 3% of their WHC. Consequently, a very intense drought such as that imposed in our study may overcome the legacy effects of 7 years of warming and reduced rainfall. Second, soils in dryland ecosystems, such as our study area, are naturally subjected to dry conditions for prolonged periods of time (Castillo-Monroy et al., 2011; Makhalanyane et al., 2015; Rey et al., 2011). Therefore, the microbial communities from dryland soils, independently of the climate change scenario they are subject to, are already adapted to dry conditions (Curiel Yuste et al., 2014; Dacal et al., 2020; García-Palacios et al., 2018). Consequently, the magnitude of climate change legacies may be less pronounced in drylands compared to more humid areas such as temperate (De Vries, Liiri, Bjørnlund, Bowker, et al., 2012; Kaisermann et al., 2017; Meisner et al., 2018) or tropical (Bouskill et al., 2013) ecosystems.

We found a high heterogeneity in the resistance of fungal community composition and richness to an extreme drought within each of the climate change scenarios, which may cancel their effect. This result may explain the absence of climate change legacies on the resistance of fungal community composition and richness observed. Most importantly, fungal community composition was more resistant, but less resilient than bacterial community composition to drought regardless of climate change legacies. Accordingly, bacterial community composition was significantly affected by extreme drought, both at the end of this disturbance and during the recovery, whereas these effects were not observed for the fungal communities. These results agree with previous evidence showing that fungi are more resistant than bacteria to drought, likely because of their thicker cell walls and their ability to survive in spore forms, whereas bacteria are more resilient due to their ability to rapidly grow after rewetting (Barnard et al., 2013; De Vries & Shade, 2013; Fierer et al., 2003; Schimel et al., 2007). Moreover, the high resistance of both bacterial and fungal richness (i.e. resistance index over 0.6) to drought observed in our experiment is consistent with previous studies (Acosta-Martínez et al., 2014; Bachar et al., 2010; Naylor & Coleman-Derr, 2018).

Despite the absence of climate change legacies on microbial community diversity (composition and richness), such legacies altered the resistance and resilience of bacterial and fungal abundance to extreme drought. In support of our first hypothesis, fungal

abundance was more resistant in soils previously subjected to reduced rainfall compared to control soils, whereas no climate change legacies were found on the resilience of fungal abundance. Similarly, we found a positive legacy effect of warming on the resistance of fungal abundance, which contrasts with our expectation that fungal abundance will be less resistant in soils previously exposed to warming (i.e. hypothesis ii). The increased resistance of fungal abundance to drought may be explained by the selection of drought-tolerant fungi under warming and reduced rainfall (Castro et al., 2010; Fierer et al., 2003; Schimel et al., 2007). Therefore, our findings suggest that the microbial traits responsible of drought and heat tolerance are strongly related (De Vries & Shade, 2013). When addressing bacterial abundance, the resistance to extreme drought was lower in warming and reduced rainfall soils, in agreement with our first and second hypotheses. Prolonged changes in mean climatic conditions may reduce the ability of soil microbes to cope with a subsequent extreme drought event (Griffiths & Philippot, 2013). Conversely, bacterial abundance was more resilient in soils subjected to reduced rainfall compared to control soils, suggesting an increased capacity to regrow using the labile C sources that are typically released after rewetting (De Vries, Liiri, Bjørnlund, Bowker, et al., 2012; Fierer et al., 2003). Consequently, our findings showing that either ongoing warming or prolonged drought influences the resistance and resilience of soil microbial abundance to extreme drought suggest that the effects of different climate change drivers (sustained warming and rainfall reduction, and short extreme events) interact, conditioning the abundance of soil microbial communities.

Our findings also indicate that, contrary to our third hypothesis, climate change does not affect the resistance or the resilience of multifunctionality. Recent evidence suggested that climate change legacies primarily occur via altered soil microbial communities (Canarini et al., 2021). Therefore, our results may be due to the absence of climate change legacies on soil microbial community composition and richness observed. This finding supports the results of a previous study showing no legacy effects of 4.5 years of altered precipitation on the response of soil respiration to a subsequent drought (Hawkes et al., 2020). Furthermore, our results agree with a recent study showing that the multifunctionality of plots subjected to 10 years of recurrent drought events did not differ from that of control plots (Canarini et al., 2021). We observed that multifunctionality neither strongly resists nor recovers from an extreme drought, as we found low resistance and resilience values (i.e. between 0 and 0.5) regardless of climate change legacies. Such result may be caused by the observed reduction in microbial activity under drought conditions due to: (a) limited substrate diffusion at low levels of soil moisture and (b) microbial strategies to avoid dehydration and death, such as switching to dormant states and accumulating compatible solutes inside their cells to equilibrate their internal water potential (Borken & Matzner, 2009; Fierer & Schimel, 2003; Schimel et al., 2007). Furthermore, the low resistance and resilience of multifunctionality found in our study could be explained by the small amount of SOC observed in our soils (i.e. SOC < 1% in all soils). It has been found that soils with low SOC contents have lower resistance and resilience of soil functions (e.g. soil respiration, N leaching and N_2O emission) to disturbances than soils with high SOC contents (De Vries, Liiri, Bjørnlund, Bowker, et al., 2012; De Vries, Liiri, Bjørnlund, Setälä, et al., 2012; Orwin et al., 2006). Low SOC content is typical of drylands mainly due to climate. Drylands are characterized by low precipitation which limits plant production and organic matter inputs into the soil, whereas they have high temperatures which promote decomposition (Lal, 2004; Plaza et al., 2018). This nutrient scarcity usually found in drylands (Cookson et al., 2006; Schlesinger et al., 1990) could lead to low values of multifunctionality, because some of these nutrients (e.g. SOC or N) are induvial functions used to calculate multifunctionality indices. Such low multifunctionality values in dryland soils may explain the small differences in the resistance and resilience observed between climate change scenarios. Moreover, our results suggest that there were no climate change legacies on the resistance and resilience of none of any of the eight single functions evaluated. Consequently, our results indicate that under an extreme drought such as that imposed in our experiment, soil microbes from C-poor dryland soils are not fully able to sustain and recover multiple soil functions simultaneously. These findings suggest that SOC content might predict the resistance and resilience of multifunctionality at a broader scale. Moreover, our results provide new insights about the ecosystem-level implications of the interactive effects of different climate change components (i.e. mean change and extreme events, which may inspire future studies at a mechanistic-individual soil function level.

Previous findings have demonstrated that soil microbial diversity and abundance determine multifunctionality (Delgado-Baquerizo et al., 2016; Wagg et al., 2014), and that the resistance of certain soil functions, such as soil respiration, to drought is controlled by soil microbial abundance and the fungal:bacteria ratio (De Vries, Liiri, Bjørnlund, Bowker, et al., 2012; De Vries & Shade, 2013). However, much less is known about the relationship between the resistance and resilience of multifunctionality and those of the soil microbial community. Our results provide empirical evidence that neither the resistance nor the resilience of multifunctionality were significantly related to those of bacterial and fungal community composition, richness and abundance. These findings, which are in contrast with our fourth hypothesis, agree with a previous study showing that the resistance of multifunctionality was not related to soil microbial diversity (Delgado-Baquerizo, Eldridge, et al., 2017). However, our results indicate that the resistance and resilience of multifunctionality were linked to those of specific bacterial and fungal dominant phyla. This could be explained by our findings showing that prolonged climate change affects specific soil microbial taxa, but not microbial community composition or richness, as it was also observed in previous studies (Acosta-Martínez et al., 2014; Ochoa-Hueso et al., 2018; Preece et al., 2019). Interestingly, we found that the resistance of multifunctionality was correlated with that of *Chytridiomycota* and that the resilience of multifunctionality is linked to that of *Proteobacteria*. These results are consistent with previous evidence suggesting that observed links between the resistance of multifunctionality and microbial community composition occur through key microbial taxa that

control the resistance of soil functioning to climate change (De Vries & Shade, 2013; Delgado-Baquerizo, Eldridge, et al., 2017). Given that *Chytridiomycota* degrade a wide array of substrates including chitin and cellulose (Longcore & Simmons, 2020; Powell, 1993) and *Proteobacteria* are involved in different processes of the N cycle such as nitrification (Miller & Smith, 2009; Teske et al., 1994), both phyla play a key role in soil functioning, especially in nutrient cycling. The ability of *Chytridiomycota* to resist drought (Gleason et al., 2004, 2006) and that of *Proteobacteria* to rapidly recover from this disturbance after rewetting (Placella et al., 2012; Singh et al., 2010) may explain their importance in driving the resistance and resilience of multifunctionality to extreme drought, respectively.

In conclusion, our results indicate that the anthropogenic climate change legacies (warming and reduced rainfall) on soil microbial communities can substantially alter the ability of overall bacterial and fungal community abundance and specific microbial taxa to cope with an extreme drought event. Interestingly, the magnitude and direction of the legacy effect were similar for both warming and reduced rainfall, indicating that microbial traits related to the response to both climate change scenarios are intricately linked. However, multifunctionality and bacterial and fungal community composition and richness did not show any climate change legacies. These findings suggest that extreme events may be more important drivers of multifunctionality than sustained climate change conditions such as warming and reduced rainfall. Most importantly, the observed links between the resistance and resilience of multifunctionality to extreme drought and those of specific microbial taxa highlight the importance of preserving and improving soil microbial communities with special attention to the conservation of key microbial taxa that are essential to maintain multifunctionality under forecasted climate change scenarios. Our findings provide new insights that advance our understanding of the interacting effects between multiple climate change components that occur simultaneously and their implications for soil biodiversity and functioning.

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AUTHORS' CONTRIBUTIONS

F.T.M. designed the experiment; F.T.M., M.D. and P.G.-P. developed the original idea of the analyses presented in the manuscript; M.D. and S.A. conducted the laboratory work; B.K.S. and J.W. provided the amplicon sequencing data and bioinformatics analyses; M.D. performed the statistical analyses with inputs from F.T.M. and P.G.-P. All authors contributed to data interpretation. M.D. wrote the first version of the manuscript, which was revised by all co-authors.

COMPETING INTERESTS

Pablo García-Palacios is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this article.

DATA AVAILABILITY STATEMENT

Data in support of these findings and the R code for the statistical models are available on Figshare at https://doi.org/10.6084/m9.figshare.15052344

ORCID

Marina Dacal https://orcid.org/0000-0002-1321-9373
Pablo García-Palacios https://orcid.org/0000-0002-6367-4761
Sergio Asensio https://orcid.org/0000-0003-4376-2964
Juntao Wang https://orcid.org/0000-0002-1822-2176
Brajesh K. Singh https://orcid.org/0000-0003-4413-4185
Fernando T. Maestre https://orcid.org/0000-0002-7434-4856

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