

## RESEARCH ARTICLE

# Rainy years counteract negative effects of drought on taxonomic, functional and phylogenetic diversity: Resilience in annual plant communities

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## Abstract

1. Climate models forecast changes in the amount and distribution of rain, which may affect ecosystems worldwide, especially in drylands where water is already the limiting factor for plant life. Annual plant communities are common in drylands where they can complete their entire life cycle during the rainy period while avoiding the dry season. Moreover, seed dormancy allows them to disperse over time by remaining in the seed bank for long periods. However, the extent to which these communities will be able to tolerate increasing drought is uncertain.
2. We performed a 5-year rainfall reduction treatment under field conditions and determined its effects on annual plant communities in a Mediterranean gypsum ecosystem. We assessed the taxonomic, functional and phylogenetic diversity of these communities each year for 5 years.
3. The taxonomic and functional diversity decreased under the rainfall reduction treatment, whereas the phylogenetic diversity increased. Moreover, the relative importance of species with drought-resistant functional designs increased in the community assemblages. However, after a rainy season with above average rainfall, all of the diversity values recovered completely even under the rainfall reduction treatment.
4. Our results provide important insights into the responses of these plant communities under a climate change scenario, where they indicate high losses of diversity during drought events but rapid recovery in milder years.
5. *Synthesis.* Our findings highlight the great resilience of annual plant communities in drylands, which may allow them to tolerate increased drought under the present climate change scenario.

## KEYWORDS

annual communities, drought, functional traits, gypsum soils, Mediterranean drylands, phylogenetic diversity, rain shelters

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## 1 | INTRODUCTION

Changes in the rainfall regime are among the major consequences of climate change (Christensen & Christensen, 2007; The Core Writing Team IPCC, 2015). These changes are particularly critical in drylands, which currently comprise 45% of the Earth's terrestrial surface (Prävälje, 2016), because models predict less and more extreme rainfall events concentrated in shorter time periods (Dore, 2005). Severe droughts are expected in southern Europe (Spinoni et al., 2018; Vicente-Serrano et al., 2014), which will limit the availability of water (Milly et al., 2005) and possibly compromise the development of plants in drylands that often already live at the limit of their ecological tolerance (Hoover et al., 2015, 2017; Maestre et al., 2016). Evidence for the effects of drought on drylands includes increases in plant mortality (Batllori et al., 2020; Breshears et al., 2005), reproductive failure (Lloret et al., 2004), negative population dynamics (McCluney et al., 2012), changes in plant-plant and plant-herbivore interactions (McCluney et al., 2012), shifts in community compositions and diversity losses (Harrison et al., 2015; Lloret et al., 2009) and alterations in ecosystem functions such as carbon fixation (Winkler et al., 2019). However, despite the evidence for these negative effects, it is unclear how droughts might threaten diversity in plant communities and whether these communities might possess mechanisms to counteract them (Berdugo et al., 2017).

Annual plant communities are common in drylands where their 'escape' strategy allows them to take advantage of the rainy period and to avoid dry periods (Mulroy & Rundel, 1977). Therefore, annual plants are highly dependent on the timing of rainfall events because they must germinate and complete their entire life cycle within each favourable season (Levine et al., 2011). In Mediterranean-type climates with unpredictable inter-annual rainfall patterns, the annual habit is combined with diverse germination behaviours (Donohue et al., 2010; Estrelles et al., 2015; Sánchez et al., 2014) and the ability to persist in the soil seed bank (Levine et al., 2011; Mulroy & Rundel, 1977; Willis et al., 2014). Therefore, a new assemblage generated from the soil seed bank every year is mainly a function of the rainfall amount and timing (Levine et al., 2011; Werner et al., 2020). Consequently, the presence and abundance of species each year can be modulated depending on whether the environmental conditions are favourable or adverse according to a bet hedging strategy (Venable, 2007). Even when adverse conditions occur over a longer period of time, annual plants may persist in the soil seed bank as part of the so-called dark diversity (Pärtel et al., 2011).

Environmental conditions can become even more restrictive for annual plants when the constraints imposed by the climate co-occur with restrictive substrates such as gypsum, serpentine or saline soils (Rajakaruna, 2018). In particular, gypsum soils have a low capacity for retaining water and nutrients (Escudero et al., 2015). Furthermore, a biocrust community formed by autotrophic and heterotrophic organisms often covers the soil surface that acts as a physical barrier that reduces germination and limits the incorporation of seeds into

the soil seed bank (Li et al., 2005; Martínez et al., 2006). In addition, it has also been found that when biocrust is well preserved, it can contribute to the maintenance of soil moisture by reducing evapotranspiration (Berdugo et al., 2014) and facilitating water infiltration (Chamizo et al., 2012). Despite their biological value, there is still no consensus regarding how annual gypsum communities might be affected by climate change (Corlett & Tomlinson, 2020; Damschen et al., 2012; Rajakaruna, 2018). It has been hypothesized that the reduced availability of water and already severe restrictions will lead to losses of the diversity present in annual gypsum communities at the taxonomic, functional and phylogenetic levels, as observed on other special substrates (Li et al., 2019). However, these communities might be resilient and able to tolerate the negative effects of severe drought due to the pre-existing adaptations of specialized flora for withstanding high levels of stress (Copeland et al., 2016; Tielbörger et al., 2014). These stress-tolerant traits and the ability to germinate under highly unpredictable climatic conditions (Rajakaruna, 2018) together with the different strategies of seed dormancy and bet-hedging in permanent seed banks (Venable, 2007) may allow these specialists to locally persist under future climate conditions (Corlett & Tomlinson, 2020).

Evidence from previous observational (Luzuriaga et al., 2012) and experimental studies (Peralta et al., 2016, 2019) suggests that dramatic declines occur in all aspects of plant diversity during dry years in these annual communities, with concurrent losses of species, functional designs and clades. However, the number of observational studies is limited and their results do not imply a cause-effect relationship, and the dynamics of the community (e.g. soil seed bank) are disrupted in the case of experimental monoliths.

Here, we conduct an experimental drought simulation under field conditions for 5 years in a Mediterranean gypsum ecosystem. This approach allowed us to observe the dynamics of these annual communities, where the soil seed bank was allowed to operate and respond naturally, and we could determine how a reduction in the amount of rainfall for 5 years affected the taxonomic, functional and phylogenetic diversity. We hypothesized that under the most stressful conditions, the resulting communities would be poorer in terms of (i) species richness; (ii) functional designs, with increased importance for stress-resistant species (smaller plants with tough leaves and heavier seeds) and (iii) phylogenetic clades if more adapted designs are not evenly distributed across the phylogeny in the community. However, we did not expect a linear decrease in community diversity due to the succession of climatically contrasting conditions occurring throughout the study period. We are more cautious regarding the effect of biocrust cover on annual plant communities, and although we hypothesized that biocrust would mostly produce a physical barrier effect by filtering out seeds that, these can also play a key role in maintaining soil moisture when conditions are too dry. Our approach allowed us to observe the effects of a global change scenario (Knapp et al., 2015), including the inter-annual variability in rainfall patterns (Luzuriaga et al., 2012; Peralta et al., 2019), and test whether these communities could thrive under sustained drought conditions.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

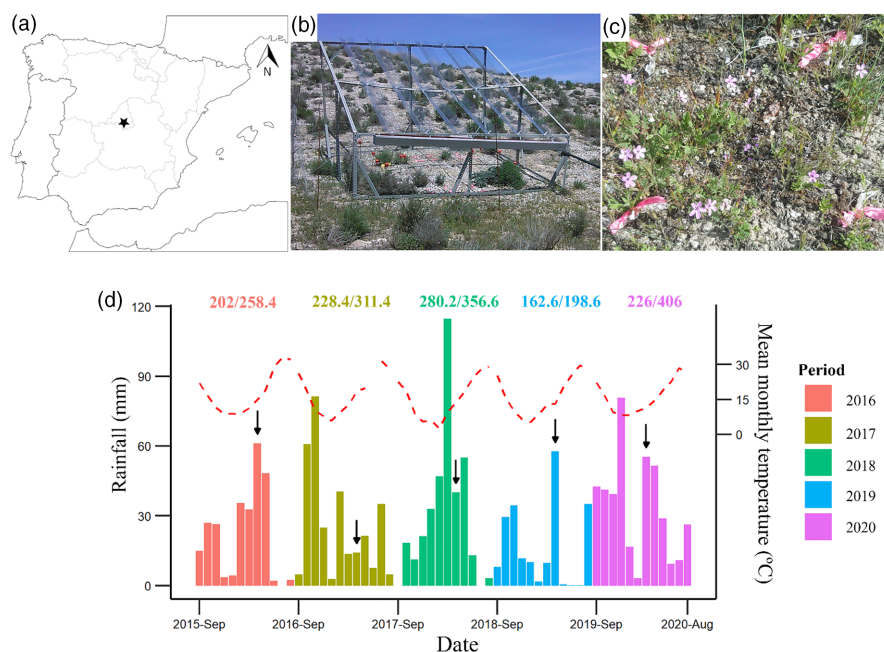
Our experiment was conducted on a gypsum steppe at El Espartal experimental station located in central Spain (40°11'11.5''N, 3°37'47.0''W; elevation 570 m a.s.l.), which is located in the protected area of the Sureste Regional Park (Madrid Autonomous Community permit reference 10/058764.9/15). The annual mean temperature is 15°C and the annual mean precipitation is 365 mm/year (Getafe AEMET Weather Station; 40°17'58''N, 3°43'20''W; elevation 620 m a.s.l.; period 1981–2010). Rain is distributed over two main rainy periods during the autumn and spring, although marked variability is observed between years. The vegetation is dominated by gypsum specialist shrubs such as *Helianthemum squamatum* (L.) Dum. Cours. and *Lepidium subulatum* L., which cover around 20% of the soil surface. Areas among shrubs are permanently covered by a biocrust, which is mainly dominated by crustose lichens, and seasonally covered by a very rich annual plant community. The annual community is dominated by tiny plants, which comprise a high proportion of the plant diversity in these Mediterranean gypsum drylands (up to 38 plant species/0.25 m<sup>2</sup>; Luzuriaga et al., 2012). Some of these plant species are gypsum specialists such as *Chaenorhinum reyesii* (C. Vicioso and Pau) Benedí, *Campanula fastigiata* Dufour ex DC, and *Reseda stricta* Pers. However, the most abundant species occur facultatively on gypsum (e.g. *Bromus rubens* L., DC, *Campanula erinus* L. and *Erodium cicutarium* (L.) L'Her. ex Ait.).

### 2.2 | Drought simulation

We conducted a rainfall reduction field experiment to simulate drought in September 2015. The experimental setting comprised

seven passive rainfall collector shelters, which are located and aligned perpendicular to a south–southeast oriented slope. The shelters comprised a metal frame (maximum height = 190 cm, minimum height = 80 cm, length × width of roof = 3 × 3 m; see Figure 1b), which supported six V-shaped methacrylate gutters that covered ~44% of the surface, following the Drought-Net protocol (<https://drought-net.colostate.edu/>). The methacrylate gutters had an inclination of 20° and the collected rainwater was directed through a system of pipes into a water tank. The water was emptied after each rainfall event to estimate the percentage of water collected by the gutters on the shelters, which is about 45% of the rainfall (see Gherardi & Sala, 2013; Yahdjian & Sala, 2002). Under the shelter, an effective area of 2 × 2 m was demarcated with a 50 cm buffer area at the shelter borders.

A control area of the same size (2 × 2 m) was established 3 m away from each shelter and in the same position along the slope. We considered each pair of rainfall reduction shelter and control area as one plot. Each plot was completely surrounded by a metal mesh to avoid grazers, mainly rabbits (*Oryctolagus cuniculus* L.). Eight 25 × 25 cm subplots were prepared in each plot (Figure 1c), with four in the control area and four under the shelter, thereby making a total of 56 subplots in the seven plots. The subplots were located inside the 2 × 2 m area but near the perimeter, away from the influence of any shrubs and at sites where the well-preserved biocrust indicated a lack of perturbation. The positioning of the subplots in the outermost part of the perimeter area of the plots allowed us to easily observe them and the effect of trampling was minimized. According to previous studies (Peralta et al., 2016, 2019), a surface of 20 × 20 cm is considered representative of the heterogeneous variability in these communities. Each year, we identified all species (annuals, non-woody perennials and shrub seedlings) present in each subplot and estimated their coverage. In total, 69 species from 16 different families were identified over the five study years (Appendices Table S1).



**FIGURE 1** (a) Location of the study area in Central Spain. (b) Rainfall reduction structure used in the experiment. (c) Close-up view of the community in a 25 × 25 cm subplot. (d) Monthly rainfall (colour bars) and mean monthly temperature (red dashed line) during the 5 years of the experiment ordered as hydrological years (September–August in the following year). Above each year is the amount of rainfall up to the moment of the sampling/total amount of water (mm). Arrows show when the annual sampling was conducted each year

We also assessed the total coverage of the biocrust in each subplot (Figure S1). These observations were conducted during the flowering peak to ensure the maximum development of the annual community. Seedlings of perennial species were clipped out after taking measures to prevent their establishment in the subplots, thereby avoid dynamic changes due to the appearance of shrubs.

The air temperature and relative humidity were monitored using automated sensors (Ibuttons DS1923, Maxim) placed in the central plot. The soil moisture was constantly monitored at two depths of 5 and 10 cm (Data logger Em5b; EC-5 and 10HS soil moisture probes, Decagon Devices Inc.; see Figure S2). Soil measurements were acquired in the control areas and under the shelter in two of the plots. Precipitation was also assessed using a tipping bucket rain gauge that counted each pulse of 0.2 mm (Rain Collector II). The station was placed at 6 m from the central plot, thereby avoiding any interference from the rainfall reduction structures.

Due to the seasonal rainfall distribution in the local Mediterranean type of climate, we will refer to the hydrological year. So, year 2016 corresponds to the autumn–winter of 2015 and the spring and summer of 2016 (see Figure 1d).

### 2.3 | Plant functional traits

Nine functional traits that can be considered good indicators of drought resistance were measured (Nunes et al., 2017). In particular, we assessed the root length (mm), plant size (measured as the maximum width (mm) and maximum height (mm)), and root:shoot ratio (calculated as the below-ground/above-ground dry mass). We also included functional traits related to leaf economics comprising the specific leaf area (SLA) and leaf dry matter content (LDMC). To consider investment in reproduction, we measured the seed mass ( $\mu\text{g}$ ) and the relative ratio of the dry biomass allocated to the reproductive and vegetative parts (reproductive ratio). In addition, we categorized the species in three groups based on their substrate affinity: indifferent for species that occur on both acidic and basic soils; basic affinity for species with an affinity for gypsum and calcareous soil; and strict gypsophytes for species that occur only on gypsum soils. The functional traits were calculated for the species based on at least 10 individuals per species, which were all randomly collected near to the study area but outside of the plots. All traits were measured according to the guidelines given by Cornelissen et al. (2003). Some functional traits were taken from previous studies (for additional information, see Table S1).

### 2.4 | Diversity estimates

Each taxonomic, functional and phylogenetic diversity parameter was calculated at the subplot level ( $25 \times 25$  cm) each year. Taxonomic diversity was calculated based on the richness, inverse Simpson index and Simpson evenness with the R package *VEGAN* (Oksanen et al., 2016). Functional structure and diversity were calculated as

the community-weighted mean (CWM) and Rao index, respectively. The CWM measures the mean value of a trait based on the abundances of species in a given assemblage. Therefore, directional shifts in CWMs under our rainfall reduction treatment would indicate changes in the distribution of functional traits. The Rao index was used to represent the variability of each functional trait in the community and whether functional filtering (functional convergence) occurred as a consequence of the rainfall reduction treatment, where it is invariant with richness. We also calculated a multi-trait Rao index with a distance matrix by including all the traits of each species (functional diversity). Functional indexes were computed with the R package *FD* (Laliberté & Legendre, 2010). Not all traits were available for all species (see Table S1 for more details), so each index was calculated with a different number of species, resulting a 5-year average of 87.96% for the total coverage and 78.29% for the total richness (see Table S2 in appendices for more details).

Phylogenetic diversity was quantified by constructing a phylogenetic tree based on the 69 species that appeared over the 5 years. We used the mega-tree in the R package *V.PHYLOMAKER* by introducing the species identified by genus into the phylogeny. We used the Scenario 1 to bind the species to the tree (for more details, see Jin & Qian, 2019). Two phylogenetic indexes comprising the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) were calculated using the R package *PICANTE* (Kembel et al., 2010). MPD is the average of all pairwise phylogenetic distances between species in a community. MNTD is the mean pairwise distance of the shortest distances between species and it indicates differences in terminal branching (Tucker et al., 2017; Webb et al., 2002). Therefore, both indexes could indicate whether the communities obtained under the rainfall reduction treatment were more closely related at different depths in the phylogenetic tree.

### 2.5 | Statistical analyses

We conducted repeated measures linear mixed model analyses to examine the effects of the rainfall reduction treatment, year and biocrust cover on the community diversity indexes (taxonomic diversity, phylogenetic diversity and functional diversity). Treatment, year and biocrust cover were used as fixed factors and plot as a random factor. We also included the interactions between the rainfall reduction treatment with year and biocrust cover. All model analyses were performed with the R package *LME4* (Bates et al., 2015). We calculated  $R^2_m$  and  $R^2_c$  as indicators of the variability explained by all of the fixed factors and by the whole model, respectively (see Table S3), with the R package *MuMIn* (Bartoń, 2019). All statistical analyses were performed using R 3.6.2 (Core R Team, 2019).

## 3 | RESULTS

During the 5 years of the study, we found high variability in the rainfall regime in terms of the total amount, but also its seasonality and

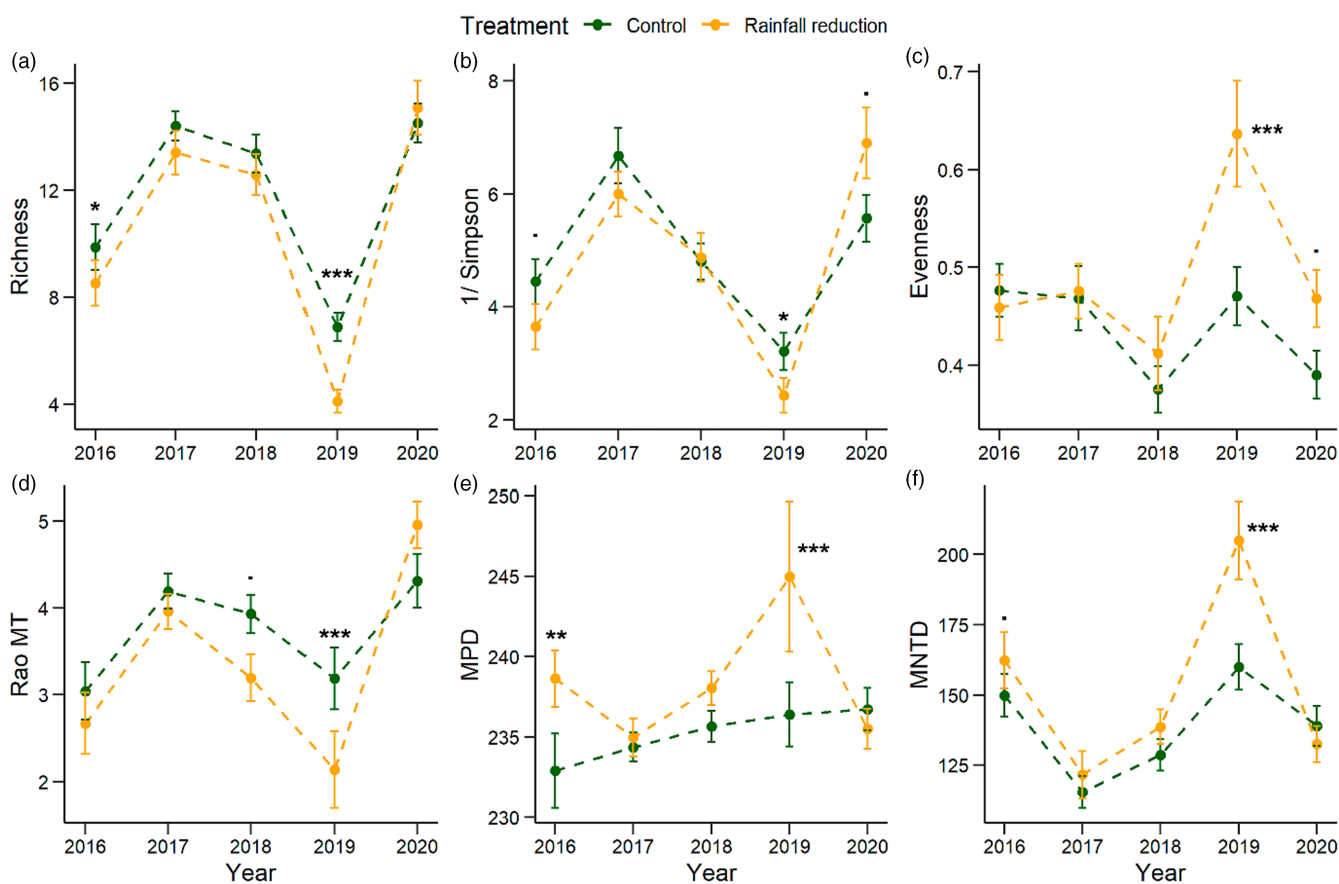
frequency (Figure 1d). The wettest year was 2020 (406 mm) with a wet autumn and continuous rainfall during the growing season, and 2019 (199 mm) was characterized by an extremely dry spring. The other years had average rainfall, where 2016 (258 mm) was the second driest year with a fairly dry autumn but a wet winter–spring period, whereas the opposite occurred in 2017 (311 mm) with a wet autumn and a slightly drier winter–spring period. Finally, 2018 (357 mm) had a dry autumn and a very wet spring but with late rainfall.

All three taxonomic indexes (i.e. richness, inverse Simpson and evenness) were modulated by the interaction between rainfall reduction and year, with richness and evenness being reduced by the rainfall reduction treatment (Figures 2a,b,c and 3). The richness and the inverse Simpson index were higher in wet years (2017 and 2020) than dry years (2019). Just the opposite happened with the evenness, which was higher under the rainfall reduction treatment and in specially the drier years than in control and wet years. The richness model explained 72% of the total variability, inverse Simpson model accounted for 43% and evenness explained 38% where most of the variability was due to fixed factors (49.13%, 31.19% and 22%, respectively; Table S3).

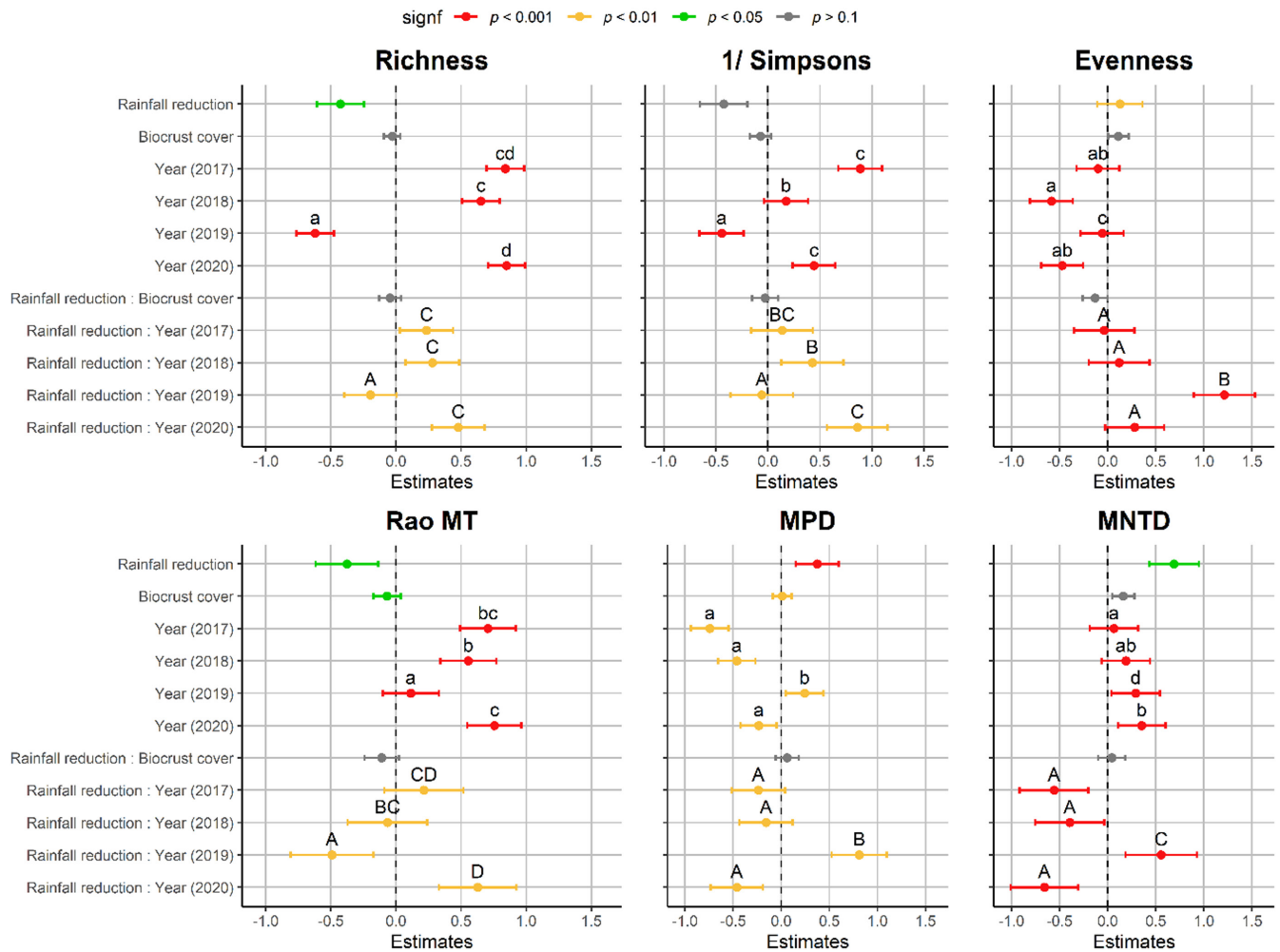
The multi-trait functional diversity (Rao MT) decreased under the rainfall reduction treatment and in dry years (2016 and 2019),

and thus the species that appeared in the communities were more functionally similar under drier conditions (Figures 2d and 3). Under the rainfall reduction treatment, the communities contained species with longer roots and lower SLA values, that is, smaller and thicker leaves (Figures 4 and 6). Rao values indicate less variability in the SLA, LDMC and reproductive ratio under the rainfall reduction treatment (Figures 5 and 6). In addition, there was a strong evidence of effect of the interaction between the rainfall reduction treatment and year with the root length, and with the substrate affinity. The rainfall reduction treatment reduced the variability of both, the root length and the substrate affinity trait, only in dry years (2016 and 2019; Figures 5 and 6). We also detected a moderate evidence of effect of the same interaction with SLA and LDMC, and a weak evidence of the effect of the interaction with plant size (plant width and plant height). In all these cases, there was a reduction of variability of the traits in dry years under rainfall reduction treatment.

Mean pairwise distance remained fairly stable in the control plots, whereas it was much more variable under the rainfall reduction treatment. Both phylogenetic diversity indexes (MPD and MNTD) increased under the rainfall reduction treatment (Figure 3) and in drier years (2016 and 2019; Figure 2e,f). The models fitted to both indexes explained 20% and 54% of the total variability in MPD



**FIGURE 2** Trends in taxonomic diversity (a) richness, (b) inverse Simpson index and (c) Simpson evenness, (d) functional diversity (multi-trait Rao index), and phylogenetic diversity (e) MPD and (f) MNTD under control environmental conditions and rainfall reduction treatment throughout the 5 years of the field experiment. Data are expressed as the mean value  $\pm$  standard error. Significant differences found in each year between control and rainfall reduction treatment are indicated as:  $\cdot$ ,  $p < 0.1$ ; \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$



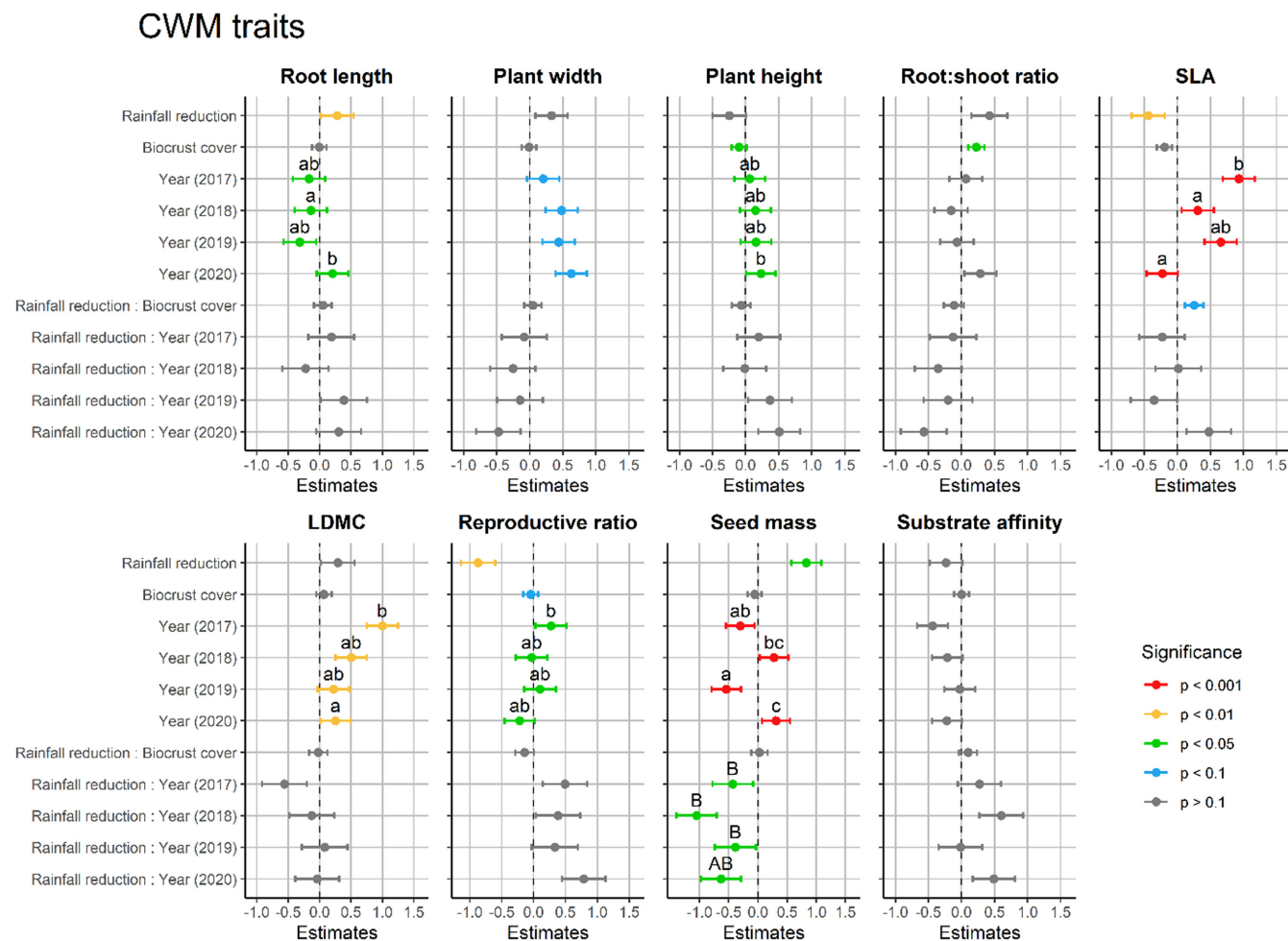
**FIGURE 3** Summary of repeated measures linear mixed models fitted to link taxonomic, functional and phylogenetic diversity with rainfall reduction treatment, biocrust cover and each year. Richness represents the number of species, 1/Simpsons is the inverse Simpson diversity index, evenness represents the Simpson evenness, Rao MT is the multi-trait Rao index, MPD is the mean pairwise distance within the shortest paths connecting pairs of nodes in the phylogenetic tree, and MNTD is the mean nearest taxon distance, which indicates differences in terminal branching. Fixed factors were the rainfall reduction treatment, biocrust cover and year (repeated measures factor), and the random factor was plot. Significance values are from ANOVA type II and the letters represent the differences detected with post-hoc analysis compared of the year factor (lowercase letters) and the interaction with the treatment (capital letters)

and MNTD, respectively, and 15% and 28% of the total variability in the fixed factors (Table S3).

Biocrust cover was affected by the reduction of rainfall showing less cover under rainfall reduction treatment. Furthermore, the coverage of biocrusts was drastically reduced in the driest year but did not show a recovery in 2020 as was the case for the annual plant community (Figure S1). However, the results indicated that the biocrust cover affected the community assembly as well as the rainfall reduction treatment and year. The communities had higher phylogenetic diversity when the biocrust cover was higher, with an increase in MPD and lower functional diversity (Figure 3). The plants that occurred in areas with high biocrust cover were shorter with an increase in the root:shoot ratio (Figure 4). These plants also exhibited lower variability in the SLA and reproductive ratio (Figure 5). There was no interaction between biocrust cover and the rainfall reduction treatment.

## 4 | DISCUSSION

Our results demonstrated that diversity losses occurred under the rainfall reduction treatment, where the taxonomic, functional and phylogenetic diversity components were affected in the annual plant communities throughout the 5 years of this study. The effects of the rainfall reduction treatment were greater in dry years, but it was remarkable that the communities in wet years were able to withstand the cumulative negative effect of the experimental drought. Indeed, our results demonstrated the resilience of these communities against simulated drought because the decreased diversity found under the rainfall reduction treatment recovered rapidly in rainy years (Luzuriaga et al., 2012; Olano et al., 2012). As we hypothesized, severe rainfall reduction led to a greatly reduced number of species and functionally poorer communities (Peralta et al., 2019). The CWM patterns showed that the species present under drought

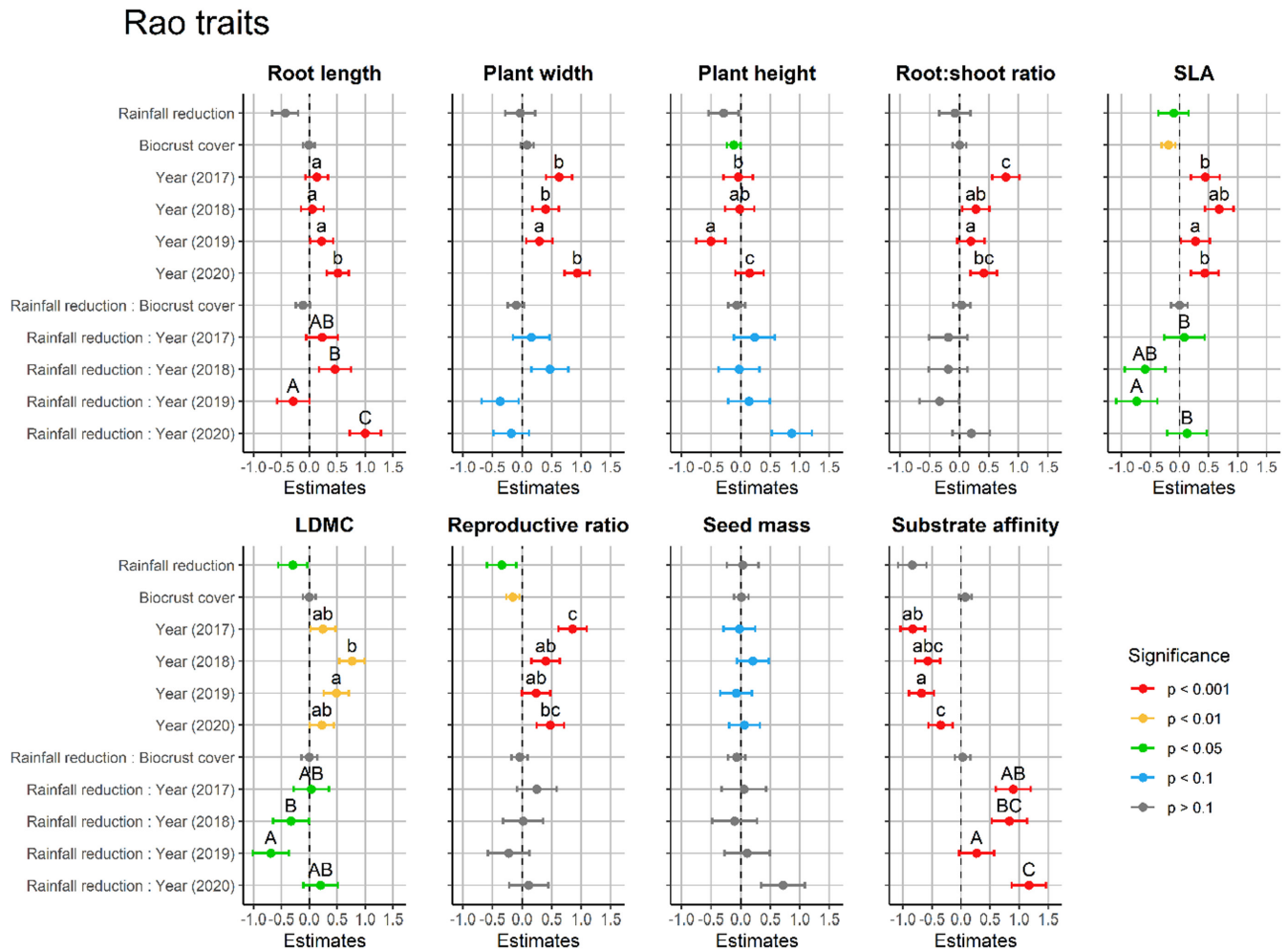


**FIGURE 4** Summary of repeated measures linear mixed models to link the CWM values based on the nine traits measured with rainfall reduction treatment, biocrust cover and each year. SLA is the specific leaf area, LDMC is the leaf dry matter content and substrate affinity is a categorical value denoting the proxy substrate affinity (indifferent, basic affinity or strict gypsophyte). Fixed factors were the rainfall reduction treatment, biocrust cover, and year for repeated measures, and the random factor was plot. Significance values are from ANOVA type II and the letters represent the differences detected with post-hoc analysis of the year factor (lowercase letters) and the interaction with the treatment (capital letters). See appendices Table S4 (CWM) for the summary of the  $R^2$  of the models

conditions had a more drought-resistant functional design, with smaller heights, longer roots and lower SLA values. By contrast, the phylogenetic diversity was greater in communities under the rainfall reduction treatment, thereby indicating that species were less related to each other. We found no evidence that the community was affected by the simulated drought in terms of affinity for the substrate. Thus, we did not observe a shift towards assemblies with a higher proportion of strict gypsophytes, as hypothesized by Rajakaruna (2018). Our results also demonstrated the barrier effect of the biocrust acting like a functional filter, which increased the phylogenetic diversity and reduced the functional diversity.

We observed a negative effect of rainfall reduction on taxonomic diversity, which is consistent with previous studies (Carmona et al., 2012; Harrison et al., 2015; Luzuriaga et al., 2012; Miranda et al., 2011). Due to water shortages, annual plants tend to reduce their germination and the seeds remain in the permanent soil seed bank (Claus & Venable, 2000). In addition, reduced availability of

water can lead to the increased mortality of plants that are unable to withstand the increased stress. Furthermore, as we hypothesized, rainfall reduction treatment reduced the functional diversity in terms of several traits (root:shoot ratio, SLA, LDMC and reproductive ratio) and the multi-trait diversity index, which may reflect the effect of functional filtering promoting a drought-resistant design in the realized assemblage (Peralta et al., 2019). This design comprised plants with small heights and long roots to obtain better access to water (Harrison & LaForgia, 2019; Lloret et al., 1999), and resistant leaves (lower SLA) to avoid drying out (Wellstein et al., 2017; Wright et al., 2004). These species also had a lower reproductive ratio and heavier seeds. Larger seeds can reduce seedling mortality to facilitate the establishment of seedlings under harsh conditions (Metz et al., 2010). Furthermore, this filtering effect was not influenced by whether species were strict gypsophytes or generalists, thereby indicating that the drought-resistant design was independent of the substrate affinity. However, the number of strict gypsophytes was



**FIGURE 5** Summary of repeated measures linear mixed models to link the Rao values based on the nine traits measured with rainfall reduction treatment, biocrust cover and each year (see Figure 4 for details on the abbreviations). Significance values are from ANOVA type II and the letters represent the differences detected with post-hoc analysis of the year factor (lowercase letters) and the interaction with the treatment (capital letters). See appendices Table S4 (Rao) for the summary of the  $R^2$  of the models

low in our community (8/69 species) and this result might differ in communities with a higher number of soil specialists.

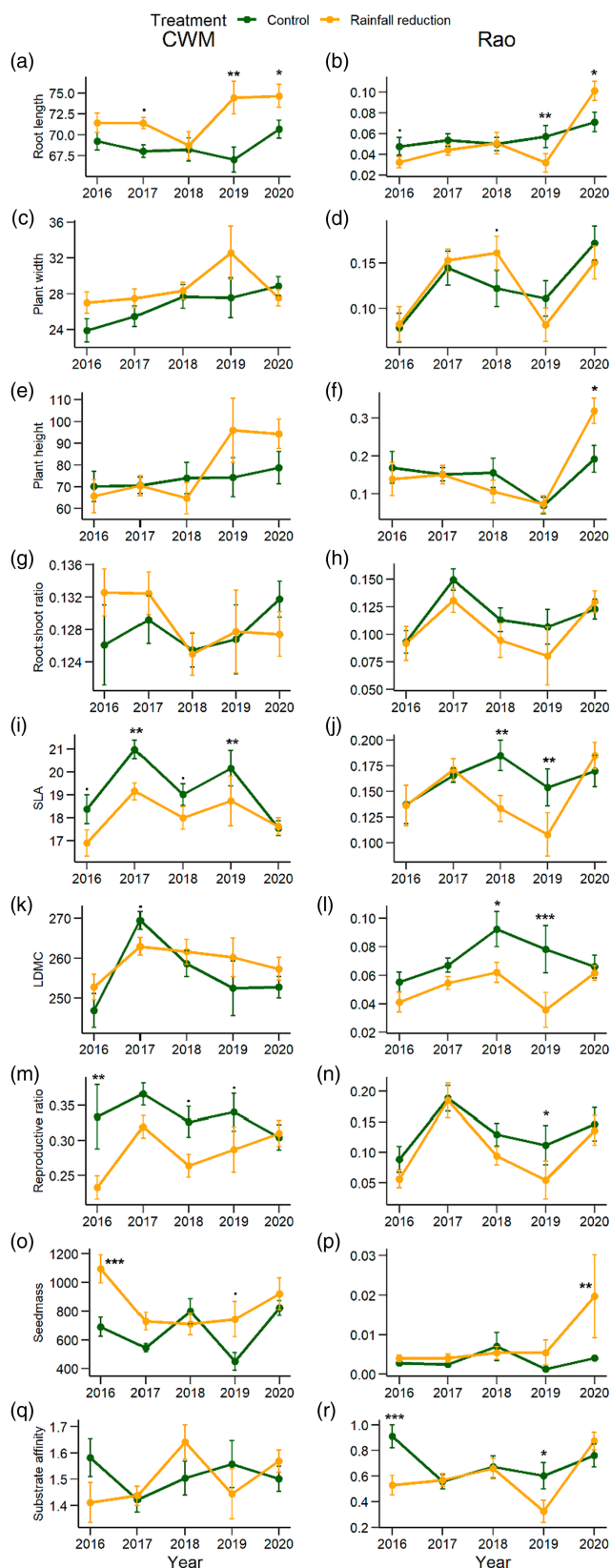
In contrast to previous studies (Harrison, 2020; Li et al., 2019), the phylogenetic diversity was higher under the rainfall reduction treatment in our experiment, which may imply that the drought-resistant design was not confined to certain plant families and that it could have evolved independently in different lineages (García-Camacho et al., 2017). This increase in the phylogenetic diversity as well as the reductions in both taxonomic and functional diversity suggests that strong functional convergence occurred towards the drought-resistant design in multiple lineages (Webb et al., 2002) under the harsh conditions in our experimental system. Furthermore, previous studies have detected very weak phylogenetic signals for most of these functional traits (García-Camacho et al., 2017; Sánchez et al., 2022).

Our 5-year study was sufficiently long to observe high inter-annual variability in the rainfall patterns in terms of both the amount and timing. Moreover, this inter-annual variability was the main factor that affected the community assemblage and it had a larger effect

than the rainfall reduction treatment itself. Previous studies have shown that inter-annual variability in rainfall has a great influence on assemblage of these ephemeral communities (Luzuriaga et al., 2012; Peralta et al., 2016, 2019) and other Mediterranean grassland communities (Carmona et al., 2012; Tielbörger et al., 2014). Indeed, this inter-annual variability in the rainfall pattern is commonly found in Mediterranean drylands and is responsible for maintaining the high diversity of species in these communities (Carmona et al., 2012). These changing conditions allow the entry of different species into assemblages, thereby resulting in high inter-annual variability in the community composition (Luzuriaga et al., 2012).

The effect of the rainfall reduction treatment was much more severe in the realized assemblage during the dry years because the effects of climate and the rainfall reduction treatment were additive, thereby leading to severe drought. Indeed, it has been observed that these communities begin to exhibit drastic losses in taxonomic and functional diversity only under severe water shortage conditions (Peralta et al., 2019). However, severe drought does not have an irreversible effect because the diversity levels of the community





**FIGURE 6** Trends in CWM values (left column) and Rao values (right column) based on the nine traits measured. Root length (mm) (a and b), plant width (mm) (c and d), plant height (mm) (e and f), root:shoot ratio (g and h), SLA is the specific leaf area (i and j), LDMC is the leaf dry matter content (k and l), reproductive (m and n), seed mass ( $\mu\text{g}$ ) (o and p) and substrate affinity is a categorical value denoting the proxy substrate affinity (indifferent = 0; basic affinity = 1; strict gypsophyte = 2) (q and r) under control environmental conditions and the simulated rainfall reduction treatment throughout the 5 years of the field experiment. Data are expressed as the mean value  $\pm$  standard error. Significant differences found in each year between control and rainfall reduction treatment are indicated as: ·,  $p < 0.1$ ; \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$

et al., 2012; Peralta et al., 2016). This seed reservoir is the result of a variable rate of seed dormancy as a generalized bet hedging strategy in annual species (Caballero et al., 2008; Venable, 2007). Thus, a percentage of the seeds will not germinate due to dormancy even if the necessary conditions are met, so they can remain in the soil to compensate for bad years and reduce mortality (DeMalach et al., 2021), thereby enhancing community resilience.

The inter-annual variability in the rainfall patterns was evident in terms of the total amount of rainfall but also its timing. During 2016, 2017 and 2018, the changes observed in all three types of diversity were due to the seasonality of rainfall, whereas the heavy losses in 2019 and the fast recovery in 2020 were mainly attributable to the amount of rainfall. In particular, we found that years with rainy autumns (2017 and 2020) had greater diversity (taxonomic and functional) than years with wet springs but low autumn precipitation (Figure 1d), which suggests that the rainy period in the autumn-winter is most critical for the assemblage of these communities (Peralta et al., 2019). This period mainly affects the germination and growth of seedlings, which are demographic bottlenecks for these ephemeral species (Donohue et al., 2010; Levine et al., 2008). Our results highlight the strong influence of the inter-annual variability in the rainfall patterns on community assembly. First, the periodicity of wet and dry years conditions the regeneration of the seed bank, and thus the regeneration of the community. Second, the period when rainfall occurs is one of the main environmental cues perceived by species and it determines the time of germination and establishment of species (Levine et al., 2008). These factors contributed to the great variability in the community composition between years in our study and they resulted in a high number of species occurring at the same time.

In addition to the rainfall pattern, the biocrust cover modulated the annual community by reducing the functional diversity and increasing the phylogenetic diversity. Species that occurred in areas with higher biocrust coverage were generally shorter in height with smaller leaves, possibly because the biocrust acted as a strong physical barrier that prevented the germination and establishment of species (Peralta et al., 2016, 2019). However, it has also been shown that a well-preserved biocrust can facilitate the survival of plants in periods of water scarcity, especially annual plants. Biocrusts can contribute to the maintenance of soil moisture by reducing evapotranspiration (Berdugo et al., 2014) and facilitating water infiltration

recover after a single rainy season. In our study, the diversity losses recovered in 2020 after the extremely dry year of 2019, even after the previous 4 years of rainfall reduction treatment. The recovery of lost diversity is probably reliant on the community seed bank (Olano

(Chamizo et al., 2012). These effects might not have occurred in our rainfall reduction treatment plots as biocrust cover was affected by the treatment. Biocrust cover was drastically reduced (Figure S1); thus, it is possible that the physical barrier effect could have been stronger than that on retaining soil moisture as the biocrust coverage was much lower and discontinuous.

The high resilience and regeneration under changing environmental conditions in our study community is consistent with that found in other plant communities with soil specialists (gypsum (Luzuriaga et al., 2012; Olano et al., 2012) and serpentine (Eskelinen & Harrison, 2015)) and other annual plant communities (Miranda et al., 2011; Salguero-Gómez et al., 2012). Since our results showed a drought-resistant design independent of the substrate affinity, it is possible that species resilience is linked to the annual life form more than substrate affinity. Therefore, these species may have developed special features such as stress-tolerant functional designs or seed bank strategies (Webb et al., 2002), which may favour their survival in the event of changes in conditions (Corlett & Tomlinson, 2020; Damschen et al., 2012). However, our results in terms of community resilience should be treated cautiously as 5 years is not a very long period. Therefore, to really see the resilience of these communities, it would be necessary to have a longer time series of data. Furthermore, we also hypothesize that the observed capacity for resilience would only be possible if the recurrence of benign years does not exceed the time of species residence in the soil seed bank (Caballero et al., 2008). This mechanism was shown to be effective during the 5 years of drought in our study but possibly not if extreme droughts become more frequent (Spinoni et al., 2018). Therefore, this mechanism combined with the low dispersal capacity of these species (Venable et al., 2008) and the island-like distribution of gypsum outcrops (Escudero et al., 2015; Matesanz et al., 2018) may mean that local extinctions are still feasible under future climate change.

## 5 | CONCLUSIONS

Our results provide important insights into the potential fate of gypsum annual plant communities under a drought scenario. In dry years, the communities are taxonomically and functionally poorer but they can recover the lost diversity in wet years. Our experimental approach proved the resilience of these annual communities because of their ability to tolerate changing rainfall patterns under the Mediterranean climate. We conclude that diversity levels will be maintained provided that dry years are interspersed with benign years. However, longer term studies would be necessary to confirm the evidence of resilience in the gypsum annual plant communities detected in our study. Long-term studies could also identify which combinations of drought intensity and frequency of rainy years are needed to avoid soil seed bank depletion and consequent diversity losses.

### AUTHORS' CONTRIBUTIONS

A.M.S. and A.E. designed the experimental study and statistical analyses; A.M.S. and R.L.-R. conducted the community surveys and

traits measurements; R.L.-R. and D.S.P. performed the statistical analyses; R.L.-R. wrote the first draft and all authors contributed to subsequent versions.

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### CONFLICT OF INTEREST

The authors declare no conflict of interest.

### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13948>.

### DATA AVAILABILITY STATEMENT

All data necessary to reproduce the analyses are deposited at Zenodo: <https://doi.org/10.5281/zenodo.6584981> (López-Rubio et al., 2022).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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