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# Evidence of functional species sorting by rainfall and biotic interactions: A community monolith experimental approach

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## Summary

1. Understanding the mechanisms that underlie species assembly is a central concern in community ecology. Abiotic and biotic filters are probabilistic ‘sieves’ that allow species with certain functional traits to become part of the community, or not. We manipulated natural plant assemblies in order to identify variations in the timings of biotic and abiotic filters that determine community trait assemblies.
2. We extracted soil portions when the investigated annual plant community was in its seed phase (‘community monolith’), thereby maintaining the structure and similar soil

characteristics to the field conditions. Community monoliths were subjected to experimental manipulation in terms of the rainfall timing and amount, and perturbations of the biological soil crust (BSC; intact vs. perturbed). We surveyed the experimental community assembly over time based on the functional diversity by considering important functional traits in different life stages.

**3.** We found that autumn droughts acted as abiotic filters by favouring the germination and establishment of species with greater investment in the root biomass. Under severe droughts (66% water reduction), the experimental assemblies were dominated by species with functional traits adapted to water shortage conditions: high leaf dry matter content, low specific leaf area, small individual size, low reproductive ratio, and high root:shoot ratio. We identified two roles of BSCs in annual plant species assemblies: 1) as a biotic filter that limited the establishment of species based on seed size, and 2) as a buffer against water stress conditions by reducing soil evapotranspiration.

**4.** *Synthesis*. We demonstrated the importance of the timing and amount of rainfall for shaping annual plant communities, and identified germination filters as the main process that determined community assemblies. Our results suggest that the phenotypic integration of functional traits facilitates resistance to drought during the life cycle. The BSC–annual plant relationship shifted from negative, by acting as a germination filter, to positive, by acting as a buffer in later stages. Climatic fluctuations and fine scale biotic determinants of spatial heterogeneity emerged as sources of changes in the community assembly in time and space to possibly promote species coexistence and trait differences among the communities studied.

**Key words:** annual plant, biological soil crust, biotic and abiotic filters, coexistence, community assembly, drought, functional diversity, gypsum soil, Mediterranean grassland, precipitation seasonality.

## Resumen

1. **1.** Entender los mecanismos que intervienen en el ensamblaje de las especies ha sido una cuestión central en ecología de comunidades. En este contexto, los filtros abióticos y bióticos juegan un importante papel ya que pueden determinar la probabilidad de que las especies se incorporen a la comunidad en función de sus atributos funcionales. En este estudio se manipularon experimentalmente comunidades naturales de plantas de ciclo anual para identificar la importancia y el momento en el que distintos filtros ambientales determinan la estructura funcional de la comunidad.
2. **2.** Para ello se extrajeron porciones de suelo durante el periodo en el que la comunidad se encuentra en fase de semilla, conservando su estructura vertical y la composición natural de la comunidad. Estos "community monoliths" fueron sometidos a distintos tratamientos de cantidad y estacionalidad de precipitación, así como a distintos estados de la costra biológica del suelo (costra intacta *vs*. perturbada). La composición de las comunidades experimentales resultantes fue observada en distintos momentos a lo largo de su desarrollo y su estructura funcional se estableció a partir de datos propios para una serie de caracteres funcionales relevantes.
3. **3.** La sequía otoñal actuó como un filtro abiótico favoreciendo la germinación y establecimiento de las especies con una mayor inversión en biomasa radicular. Bajo sequía severa (66% de reducción de la precipitación), el ensamble experimental estuvo dominado por especies con caracteres funcionales adaptativos en escenarios de escasez de agua: LDMC elevado, SLA bajo, individuos de pequeño tamaño, ratio entre inversión en peso seco reproductivo y vegetativo bajo y ratio entre peso seco radicular y aéreo alto. Se identificaron dos roles de la costra biológica del suelo: 1) actuó como un filtro biótico dificultando el establecimiento de las especies con semillas grandes y 2) moderó el efecto de la sequía reduciendo la evapotranspiración.

4. *Síntesis*. Este estudio constata experimentalmente la importancia de la estacionalidad y la cantidad de precipitación en la configuración de las comunidades de anuales. Además, los datos obtenidos apuntan a la germinación como el proceso más determinante del ensamble de las especies en comunidades. Al mismo tiempo, los resultados parecen sugerir la existencia de integración fenotípica de los caracteres implicados en la resistencia a la sequía a lo largo del ciclo vital. La interacción entre la costra biológica y las plantas anuales pasa de restrictiva durante la germinación a positiva durante las fases siguientes. Podemos concluir que las fluctuaciones climáticas y la estructura espacial que la costra biológica presenta a pequeña escala, suponen una fuente de heterogeneidad tanto espacial como temporal que determina el ensamble de las comunidades y promueve la coexistencia de especies.

Palabras clave: costra biológica del suelo, diversidad funcional, ensamble de la comunidad, estacionalidad de la precipitación, gypsisoles, pastizales mediterráneos, plantas anuales, sequía.

## Introduction

Understanding the mechanisms that underlie species assembly has been a crucial topic in ecology for many years. Plant assemblies are a consequence of deterministic and stochastic processes acting together (Lortie *et al.* 2004; Vellend 2010, Weiher *et al.* 2011; Escudero & Valladares 2016), which leave detectable signals in the properties of a community (McIntire & Fajardo 2009; Pavoine *et al.* 2011). Among the deterministic processes, which are usually called assembly rules (Diamond 1975; Götzenberger *et al.* 2012), ecological filters are widespread probabilistic 'sieves' that allow some species with certain functional features to emerge and become part of the standing assembly (Shipley 2010). Filters are temporally and spatially variable abiotic or biotic factors. Biotic filters are related to the complex network of interactions that each individual plant establishes throughout its ontogeny with other plants or organisms (Lortie *et al.* 2004; Escudero *et al.* 2007; Rajaniemi *et al.* 2009; Luzuriaga *et al.* 2012).

Exploring plant assemblies from a functional viewpoint can allow us to identify the causal rules associated with community assembly (Lavorel & Garnier 2002; Grime 2006; McGill *et al.* 2006). This functional perspective relies on the prevalence of niche specialization and functional differences among species (MacArthur 1970; Weiher & Keddy 1999; Kraft *et al.* 2015) as well as the corresponding relationships between them, which are mainly competitive but also facilitative (Bertness & Callaway 1994). Functional traits can indicate the different features of each species niche related to critical life stages, such as germination (Donohue *et al.* 2010; Peco *et al.* 2009), nutrient uptake (Carmona *et al.* 2014), pollinator attraction (Sargent & Ackerly 2008), and other processes that determine species interactions and overall performance. Plant trait-based ecology is providing new insights into old questions related to community ecology (Escudero & Valladares 2016; Shipley *et al.* 2016). In particular, instead of common garden community designs that consider a selection of species for testing a particular hypothesis, experimental manipulations of monolith communities are essential for merging the experimental approach with a realistic picture of the overall community, and for testing hypotheses based on the species assemblies found in observational studies (Götzenberger *et al.* 2012, HilleRisLambers *et al.* 2012).

Rainfall, specifically its amount and timing, is the most critical abiotic determinant of annual plant communities in drylands (Levine *et al.* 2011; Huxman *et al.* 2013). For instance, in the Mediterranean gypsum soil steppes, climate variability among years (Luzuriaga *et al.* 2012; 2015) and the species-specific germination response to water availability (Sánchez *et al.* 2014) can yield different annual plant community compositions and structures each year. Biological soil crusts (BSCs) increase water infiltration and reduce evaporation (Chamizo *et al.* 2012; Berdugo *et al.* 2014), and thus the interaction between BSCs and rainfall may be critical for annual plant assemblies. The importance of BSCs has been demonstrated during soil seed bank formation (Peralta *et al.* 2016), seed germination and seedling establishment (Escudero *et al.* 2007), and for the mature-plant communities during the community phenological peak (Luzuriaga *et al.* 2012, 2015).

Annual plant communities are an excellent model system for conducting experiments based on community monoliths for the following four reasons (Huxman *et al.* 2013). (1) Annual plant communities have a very rich regional species pool and high species densities in reduced areas due to their small size (Luzuriaga *et al*. 2012, 2015). (2) According to soil seed bank studies conducted in similar communities (Caballero *et al*. 2008; Olano *et al*. 2012; Peralta *et al*. 2016), the soil seed banks were very similar in terms of the species composition in all of the study systems, probably because species dispersal is not limited (Luzuriaga *et al*. 2018). (3) Annuals have short life spans, so their complete life cycle can be observed in a few months. (4) Mediterranean annual plants are able to germinate in different conditions but they are highly synchronized throughout their short life cycle, which results in the clear prevalence of different processes during the growing season (Sánchez *et al.* 2014). Moreover, annual plant communities are amenable to simple experimental manipulation because they can be entirely translocated by taking pieces of intact soil from the field during the community dormancy period immediately before germination. These community monoliths containing intact soil seed banks and intact BSC structures can be subjected to experimental treatments, and new assemblies will develop within a short period (6 or 7 months).

The main aim of this study was to test the simultaneous effects of probable abiotic and biotic filters on the assembly of annual plant communities. Given that plant communities can be structured according to multiple factors and their interactions (de Bello *et al.* 2013; López-Angulo *et al.* 2018), we studied their simultaneous effects on the plant composition and richness, as well as on the functional trait diversity in different life stages for the community, ranging from germination and seedling establishment to the reproductive phenological peak. We selected functional traits related to the leaf economics spectrum (specific leaf area (SLA) and leaf dry matter content (LDMC)), reproduction trade-offs (seed mass and reproductive ratio), establishment of size hierarchies (plant height), and resource uptake (root:shoot dry mass ratio) (Cornelissen *et al.* 2003; Wright *et al.* 2004; Hirose *et al.* 2005; Craine 2009). We extracted soil monoliths from the field with the intact annual plant community in the soil seed bank. Although this method has rarely been used (but see Insausti *et al*. 1999; Weltzin *et al*. 2000, Harmens *et al*. 2004; Debouk *et al*. 2015), this technique allows the experimental manipulation of the whole natural community, without the need for creating artificial communities. We manipulated previously established critical assembly factors in these communities comprising the rainfall amount (i.e., drought intensity) and timing (Experiment 1: abiotic filters), as well as the rainfall amount and physical structure of the BSC (intact or highly perturbed; Experiment 2: abiotic and biotic filters).

We hypothesized that both the abiotic and biotic factors as well as their interactions would determine the community assemblies at fine spatial scales in the experimentally manipulated annual plant communities. These factors may filter species based on specific functional traits and eventually determine the final species composition in the community (Götzenberger *et al.* 2012). Thus, we considered the following hypotheses. (i) Experimental variations in the biotic and abiotic conditions would cause changes in the species composition (see our conceptual model in Fig. 2). (ii) Directional shifts in the community-weighted means (CWMs) would probably be associated with the species sorting process among contrasting scenarios. For example, we expected that the CWMs of traits related to water-resource economy would tend to be more conservative under reduced water availability conditions (i.e., low SLA values, high LDMC values, and high root:shoot ratios). (iii) The Rao index estimates the functional divergence of a community, so the Rao values should converge when abiotic/biotic conditions become harsher, which may imply the existence of a probabilistic sieve for certain functional traits. By focusing on traits measured at maturity, we assumed that changes in the functional traits were determined only by changes in the species composition (Leps *et al.* 2011), which is a conservative expectation considering the potential amplifying effect of intraspecific trait variability.

The expected effects of abiotic or biotic filters should appear throughout the ontogeny of the community, although they may differ in terms of their intensities in each stage. In particular, deviations from the typical rainfall amounts and timings should reduce the functional diversity of traits related to water and resource economy (i.e., SLA, LDMC, root:shoot ratio, height, and reproductive ratio). Physical perturbation of the BSC could also lead to effects that are more complex. Thus, we expected an increase in the functional diversity of traits related to germination and seedling establishment (i.e., seed mass and root:shoot ratio) in the perturbed BSC treatments due to the absence of physical restrictions on seedling establishment. In addition, we expected a reduction in the functional diversity of traits related to water stress tolerance (SLA and LDMC) due to the reduced capacity of the perturbed BSC to retain water.

## Materials and methods

### STUDY SITE

We collected soil monoliths containing the entire annual plant community in the soil seed bank from a semiarid gypsum steppe. In this system, plants experience limiting environmental conditions, such as the nutrient poor soil derived from gypsum outcrops containing large amounts of calcium sulphate, which can interfere with nutrient uptake (Bosccaiu *et al*. 2011). In addition, the high rate of evapotranspiration develops physical soil crusts on the soil surface, which may hinder seedling establishment (Escudero *et al*. 2015). The collection area was located in Ciempozuelos (40 km south of Madrid, Central Spain, 40°08′36.9′′N 3°36′60.0′′W) at 568 m.a.s.l. with annual mean rainfall of 365 mm $m^{-2}$. The habitat comprises a gypsum steppe where specialist shrubs (*Helianthemum squamatum* (L.) Dum. Cours., *Lepidium subulatum* L., *Centaurea hyssopifolia* Vahl, and *Gypsophila struthium* L. *in* Loefl.) are scattered in a matrix of BSCs dominated by lichens (e.g., *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (G.H. Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt, and *Psora decipiens* (Hedw.) Hoffm) and seasonally covered by a very rich annual plant community (ca. 38 plant species/0.25 $m^2$, Luzuriaga *et al.*, 2012), which develops mainly on bare ground areas. Annuals mainly germinate during the autumn months and the plants remain as seedlings until early spring when they grow and reproduce to complete their life cycle before May. This annual community comprises tiny plants (mean height = 10 cm) and some are strict gypsophytes (Luzuriaga *et al.* 2015). The most abundant annual species in the community are *Campanula erinus* L., *Neatostema apulum* (L.) I.M. Johnst, *Micropyrum tenellum* (L.) Link, and *Plantago afra* L., as well as *Chaenorrhinum reyesii* (C. Vicioso and Pau) Benedí and *Campanula fastigiata* Dufour *ex* DC among the strict gypsophytes.

We collected community monoliths from open areas, which were at least 50 cm away from the perennial vegetation patches, and they had well-developed and non-perturbed BSCs (>50% cover) (see details in Fig. 1). The first 3 cm of the soil layer containing the soil seed bank (Russi *et al.*, 1992) was extracted with a square coring device measuring 10 × 10 cm. Before extracting the community monoliths, the soil surface was watered in order to facilitate BSC conservation and to avoid the loss of the soil's vertical structure. The extracted samples were placed on plastic trays and transported to the experimental station at Rey Juan Carlos University (Móstoles, Madrid, Spain: 40°18′48′′N, 3°52′57′′W) located 40 km west of the field site, but with a similar elevation and climate. Community monoliths were collected in September during 2013 and 2014 (384 community monoliths were taken each year from a surface area of ca. 0.02 ha) before the autumn germination commenced. Thus, the samples contained the complete soil seed bank, i.e., seeds from the persistent seed bank and seeds dispersed in the previous spring. The meteorological conditions were average in the previous year.

The day after collection, the community monoliths were carefully placed in plastic pots with a diameter of 30 cm and depth of 10 cm, which had previously been filled with 5 kg of seed free gypsum soil. Broken or damaged samples were discarded. We randomly placed four community monoliths measuring 10 × 10 cm in each pot to give a total surface of 20 × 20 cm, which constituted a replicate of the community and our experimental unit. A surface of 20 × 20 cm was sufficiently representative of the soil seed bank and the micro-heterogeneous variability in this community (data from Peralta *et al.*, 2016). The gypsum soil used to fill the pots was collected near the field site from a deep soil layer in order to ensure that no seeds were present. However, five pots containing only gypsum soil were also included to control for seed contamination. The pots containing the experimental communities were placed under two rainout shelters, where the principal structure measured 6 m long × 5 m wide with slotted angle steel bars and a sloping methacrylate roof. The height varied from 2.4 m to 2 m to allow water evacuation. The soil under the shelters was covered with geotextile in order to prevent the growth of external plants, thereby avoiding shadows or seed contamination. The pots containing the experimental communities were placed in two rows inside the shelters and at least 1 m away from the edges to avoid rain. Each year, 96 pots were monitored (16 replicates × six experimental scenarios). Each pot was a sampling unit.

## EXPERIMENTAL DESIGN

In order to test our specific hypotheses, we set up two complementary experiments. The first experiment evaluated the effects of two critical abiotic factors on the communities (rainfall amount and timing). In the second experiment, the abiotic factor was exacerbated (rainfall amount) and combined factorially with a biotic factor (perturbation of BSC).

### *Experiment 1 (abiotic filters)*

In 2013, the rainfall timing (three levels) and rainfall amount (two levels) were manipulated according to an orthogonal design to generate six experimental rainfall scenarios. The three rainfall timing treatments simulated in this study were: typical distribution of rainfall (typical timing), dry autumn with a wet spring (dry autumn), and wet autumn with a dry spring (dry spring). In addition, two rainfall amount levels were considered: mean rainfall amount (270 mm/growing period, from October to April) and slight drought treatment (25% rainfall reduction) (Appendix S1). All of the treatments were based on rainfall data recorded at the nearest weather station in Getafe, which is located ca. 30 km away from the study site and at a similar altitude (www.aemet.es). The typical rainfall timing throughout the growing season (October–April) in our study area comprised wetter autumns than springs (40% and 25% of the annual precipitation, respectively). The remaining precipitation occurred outside the growing season, mainly in May and September. The rainfall amounts imposed in the dry autumn and dry spring treatments in our experiment were highly realistic because they occurred naturally in 16% and 20% of the last 30 years, respectively. The typical distribution treatment was considered as the mean rainfall in the last 30 years (1981–2010). We performed separate calculations of the rainfall during autumn (October, November, and December), winter (January), and spring (February, March, and April). The rainfall was distributed equally among the three months of each season in every scenario. In order to set the rainfall timing for the dry autumn and dry spring treatments, we considered the mean rainfall in the five wettest springs and five wettest autumns during the last 30 years, respectively. We divided this quantity equally among the three spring/autumn months. We also maintained a constant rainfall amount (30 L m$^{-2}$) for January in all of the treatments. Finally, the remaining rainfall up to the average of 270 L m$^{-2}$ recorded for the whole period was divided equally among the three autumn/spring months. In the slight drought scenario, we reduced the amount of water during each month by 25% in each timing scenario, thereby yielding six experimental treatments.

### *Experiment 2 (abiotic x biotic filters)*

In 2014, we performed an additional experiment to simultaneously evaluate the effect of a biotic (BSC) and abiotic (rainfall amount) factor on the community assembly process. We set three rainfall levels and two BSC treatments in a factorial design, thereby testing six scenarios. We used the same temporal rainfall distribution employed in the typical rainfall timing treatment in experiment 1 and we only manipulated the amount of rainfall (not the timing).

We established three rainfall treatments: mean rainfall with no drought = 100% of the mean rainfall recorded in every month during the last 30 years; moderate drought = 33% reduction of the mean rainfall during every month; and severe drought = 66% reduction of the mean during every month. Two BSC perturbation levels were tested: intact and perturbed. In the perturbed replicates, the BSC structure was mechanically destroyed with a mace (Fig. 1).

In both experiments, irrigation was provided each week with the corresponding quantities of water for each month and scenario (S1). The effects of the treatments on the soil moisture levels were recorded in two pots per treatment with Hobo data loggers and a time domain reflectometer. We also placed three Hobo data loggers inside and outside the rainout shelters to control for potential warming due to a greenhouse effect and the size effect throughout the area covered by the shelter. The rainout shelters increased the mean temperature by 0.7°C and we did not detect any fine scale effects within the shelter.

### *Sampling of the experimental communities*

Community sampling was conducted at three different times in experiment 1 (December, February, and April) in order to observe different life stages throughout community development, i.e., the emergence and seedling stage, vegetative stage, and reproductive peak. In Experiment 2, only seedlings and reproductive plants were recorded. For each experimental community and sample date, we registered each individual of every species and we then calculated the species richness and plant abundances as the total number of individuals in each pot.

### *Measurement of species functional traits and community functional estimates*

Species functional traits were estimated based on at least 10 individuals per species, all of which were randomly collected from the study area where the community monoliths were sampled (not from the pots). We obtained functional trait data for about 90% of the species found in our experimental communities. We selected non-correlated functional traits related to different functions and processes associated with plant development and community assembly: (1) seed mass; (2) maximum plant height (omitting inflorescences); (3) SLA; (4) LDMC; (5) reproductive ratio (reproductive:vegetative dry mass ratio); and (6) root:shoot ratio (belowground:aboveground dry mass ratio). All of the traits were measured according to the protocols described by Cornelissen *et al.* (2003). The period from the first to the last sampling was three months, so it was highly probable that the seedling and adult trait values would be highly correlated (see Grzesiak *et al*. 2012; Dodig *et al*. 2015 for studies on maize). In addition, we were mostly interested in assessing the main functional strategies in coexisting species, and thus we focused on trait differences at comparable life stages (Cornelissen *et al*. 2003). We calculated CWMs and Rao indices for each trait with the *melodic* function in R, where these functional indices indicated the mean value and functional diversity of each trait at the community level, respectively.

## STATISTICAL ANALYSES

We conducted repeated measures generalized linear mixed model analyses to model CWM and Rao for each trait across all sampling times. Sequential observations of the same pot throughout the growing season were considered to be repeated measures. The rainfall timing, rainfall amount, life stage, and the interactions between them were used as fixed predictors in the first experiment. In the second experiment, the explanatory variables were the rainfall amount, BSC perturbation, life stage, and the interactions between them. We used the *glmer* function from the *lme4* package in R (Bates et al., 2014) to fit the repeated measures models, and we considered pot as a repeated measures random factor. We assumed Gaussian distributions and identity link functions for all CWM and Rao indices. To ensure that the data conformed with the assumption of normality, we log-transformed seed $\text{mass}_{\text{CWM}}$ and $\text{height}_{\text{CWM}}$ in the analyses of the first experiment, and seed $\text{mass}_{\text{CWM}}$ in the analyses of the second experiment. Poisson and negative binomial distributions were assumed for species richness and plant abundance (total number of individuals per pot), respectively, in Experiment 1 and negative binomial for both in Experiment 2. We used Type III sum of squares. Post hoc Tukey tests were performed with the lsmeans package (Russell 2015).

PERMANOVA models were constructed to evaluate changes in species compositions between the rainfall timing treatments and rainfall amount treatments in experiment 1, as well as between the rainfall amount treatments and BSC perturbation treatments in experiment 2. The community data were square root-transformed to reduce the weightings of the dominant species. We used dissimilarity matrices based on the Bray–Curtis distance (Legendre and Legendre, 1998) and type III sums of squares. The significance of each model was tested using a Monte-Carlo test based on 9999 permutations. In addition, we manually conducted three pairwise PERMANOVA analyses to evaluate differences in the species composition between the three rainfall timing treatments in Experiment 1 and the three drought treatments in Experiment 2. Differences were only considered significant when the *p*-values were smaller than 0.0166 (0.05 divided by the number of analyses). Finally, we performed non-metric multidimensional scaling (NMDS) for each life stage (seedlings, vegetative, and reproductive community) to visualize the differences in the species compositions between the three rainfall timing treatments in Experiment 1, and between the drought treatments and BSC treatments in Experiment 2. PERMANOVA and NMDS analyses were performed in R ('vegan' package, Oksanen *et al.* 2015).

## Results

### EXPERIMENT 1

In the first experiment, we registered 2663 individuals from 70 species (Appendix S2), where 53.4% of the individuals belonged to five species: *Campanula erinus* L., *Micropyrum tenellum* (L.) Link, *Plantago afra* L., *Asterolinon linum-stellatum* (L.) Duby in DC, and *Sherardia arvensis* L. The timing of rainfall determined the species composition from the beginning (seedling stage) and subsequently during community development (Table 1, Fig. 3). The rainfall timing treatments did not affect the species richness or plant abundances (Table 2), but they led to significant differences in the species composition. Thus, the communities that developed in dry autumn conditions and dry spring conditions had similar plant abundances or species richness in the adult stage, but they differed in terms of their species composition (pairwise PERMANOVA, $p < 0.003$). Slight drought (–25%) or its interaction with rainfall timing had no effect on species composition (Table 1).

Life stage explained the highest proportion of the variation in the plant functional trait CWMs, both directly and through the interaction with rainfall timing (Table 3). Seed mass$_{CWM}$ and LDMC$_{CWM}$ (except for the initial high LDMC$_{CWM}$ for the seedlings in the dry autumn) increased and SLA$_{CWM}$ decreased consistently throughout the life stages in all treatments, whereas the other plant traits exhibited different temporal patterns of variation in the different rainfall timing scenarios.

With the typical rainfall timing, the CWMs were similar throughout the whole growing season (except LDMC$_{CWM}$ increased significantly in the final reproductive stage) (Fig. 4). However, the dry autumn or dry spring rainfall timing affected the functional traits of the experimental communities throughout the growing season. The dry spring treatment resulted in similar height$_{CWM}$ values to those with the typical timing, but the dry autumn treatment led to significant increases in height$_{CWM}$ from the seedling to the vegetative life stages. The reproductive ratio$_{\mathrm{CWM}}$ values differed greatly between the timing treatments, where they were fairly constant under the typical rainfall timing conditions, whereas they decreased in the dry spring and increased in the dry autumn from the seedling stage to reproductive adults. The opposite pattern was determined for the root:shoot ratio$_{\mathrm{CWM}}$ where the values decreased with the dry autumn timing and increased with the dry spring timing throughout the community life stages. A reduction of 25% in the mean rainfall amount had no significant effects on most of the trait CWMs (except for the interaction with timing for the root:shoot CWM; Table 3). The Rao functional diversity index tended to be maximized under the typical rainfall timing for all of the plant traits considered in this study (Fig. 4). The reproductive ratio$_{\mathrm{Rao}}$ was significantly different at each rainfall timing and it remained higher in the typical treatment.

### *EXPERIMENT 2*

We registered 6559 individuals from 61 species (Appendix S2), where 54.2% of the individuals belonged to five species: *Asterolinon linum-stellatum, Campanula erinus, Sedum gypsicola* Boiss. and Reuter, *Micropyrum tenellum*, and *Erodium cicutarium* (L.) L'Hér. *ex* Aiton. The rainfall amount was critical for the species compositions from the seedling to the reproductive stages (Table 1, Fig. 3). At the seedling stage, all three treatments differed (pairwise PERMANOVA, $p = 0.036$ between 100% and 33% rainfall reduction; $p < 0.003$ between 66% rainfall reduction and the other two treatments). At the reproductive stage, significant differences in the species composition were only observed between 66% rainfall reduction and the other two treatments ($p < 0.003$). No effects of BSC perturbation or its interaction with rainfall amount were detected on the species composition (Table 1).

The species richness and abundance decreased according to the drought severity (Table 2, Appendix S3). The plant abundance also decreased throughout the community life stages. BSC perturbation led to an initial increase in richness, followed by a decrease to values similar to those observed under the intact BSC.

The increase in the drought severity compared with Experiment 1 allowed us to determine the effects of drought on the annual plant assemblies. Moderate drought (33% rainfall reduction) only decreased the taxonomic diversity slightly, but severe drought (66% rainfall reduction) reduced it dramatically and shifted the mean community values for most of the functional traits. The effects of severe drought on the CWMs were indicated by the higher seed $\text{mass}_{\text{CWM}}$, $\text{LDMC}_{\text{CWM}}$, and root:shoot $\text{ratio}_{\text{CWM}}$, and lower values for the $\text{SLA}_{\text{CWM}}$ and reproductive $\text{ratio}_{\text{CWM}}$ (Table 4, Fig. 5). BSC perturbation changed the functional patterns of the experimental assemblies by leading to a generally lower $\text{height}_{\text{CWM}}$ and reproductive $\text{ratio}_{\text{CWM}}$, but an increase in $\text{LDMC}_{\text{CWM}}$ during the reproductive community life stage.

The severe drought treatment significantly reduced the Rao functional diversity indices, except for seed $\text{mass}_{\text{Rao}}$ (Table 4, Fig. 6). In addition, BSC perturbation increased $\text{SLA}_{\text{Rao}}$ throughout the growing season under moderate drought conditions (–33%) but decreased it under severe drought (–66%) conditions. BSC perturbation also increased seed $\text{mass}_{\text{Rao}}$ but decreased $\text{height}_{\text{Rao}}$, especially with severe drought. Finally, BSC perturbation also reduced $\text{LDMC}_{\text{Rao}}$, reproductive $\text{ratio}_{\text{Rao}}$, and root:shoot $\text{ratio}_{\text{Rao}}$ only in the interaction with the reproductive life stage, especially under severe drought conditions (Table 4, Fig. 6).

## Discussion

Our results provide experimental evidence for the effects of abiotic and biotic filters throughout the community assembly process. Moreover, these filters operate via functionally driven mechanisms (assembly rules *sensu* Götzenberger *et al*. 2012) to determine the community functional diversity. Both the rainfall pattern and BSC structure favoured the entry of species with certain functional traits in the final assembly (Shipley 2010), thereby inducing shifts in the CWMs (Chacón-Labella *et al*. 2016) and reducing the functional diversity associated with these traits in some cases, and thus they operated as ecological filters (Bernard-Verdier *et al*. 2012).

The rainfall treatments that replicated the average conditions (typical timing and average rainfall amount) produced the maximum niche width and diversification throughout the whole growing season in terms of the measured species richness and functional diversity. The population dynamics are highly synchronous in these communities, so we could more clearly identify the filters that operated in the early life stages during the assembly process. The effects of these filters during germination and seedling emergence involved most of the plant functional traits, and they determined the overall plant functional diversity in the phenological peak. Overall, our findings demonstrate that germination was the key process for the assembly of these communities (Donohue *et al*. 2010), where they suggested the phenotypic integration of multiple characters in annual plant species (Freschet *et al*. 2015). Our analyses highlight the importance of evaluating the effects of environmental factors on community assemblies throughout community development (Schiffers & Tielbörger 2006) and of considering the interactions among factors (López-Angulo *et al*. 2018) because processes that lead to opposite effects can hinder their detection and interpretation (Conti *et al*. 2017). The effect of manipulating the BSCs illustrated the influence of environmental factors because BSCs acted as a germination filter for seed size and as a buffer to attenuate drought severity during the following life stages. This complex network of effects sometimes occurred in opposed directions and it was difficult to unravel, but the functional signals determined based on the species assembly were compatible with recognizable ecological assembly rules. Furthermore, these functional shifts were related to detectable changes in the species compositions of the communities.

Water availability (rainfall timing and amount) is a well-known abiotic filter for semi-arid annual plant communities (Chesson *et al*. 2004; Miranda *et al*. 2011; Espigares & Peco 1995; Carmona *et al*. 2012). In particular, the rainfall timing explained the taxonomic and functional changes in the observed assemblies better than slight and moderate changes in the rainfall amount. Timing shifts are known to be specific cues for germination pulses (Sánchez *et al*. 2014) and they are also associated with differential species mortality in drier seasons (Espigares & Peco 1995). In addition, autumn droughts were more critical for the species assemblies than spring droughts. The dry autumn timing decreased the species richness and restricted the range of root:shoot ratio values in the community, which is consistent with the selection of long-rooted species under water restriction scenarios in another study (Craine 2009). Unexpectedly, we found that the Rao values for reproductive:vegetative and root:shoot traits increased throughout the life cycle of the annual plant communities in the dry autumn treatment. Dry autumn conditions limited germination, whereas subsequent irrigation to simulate wet spring triggered the germination of a few new species to increase Rao in the community’s final stages.

In terms of the rainfall amount, only extreme droughts acted as a filter by changing the species composition and leading to the convergence of functional traits. Drought events are relatively frequent in this environment (one in five years), which suggests that a long-term adaptive scenario has shaped the regional species pool by favouring species that can cope with the average semiarid conditions but also with their stochastic variability (Tielbörger *et al*. 2014). Thus, annual species can experience a wide range of conditions and they must be highly resilient to drought events. However, we found that when drought surpassed a certain threshold of severity, water shortage acted as a strong abiotic filter to yield a simplified community in terms of species richness and functional diversity.

Under severe drought, species with functional traits that facilitated coping with water scarcity dominated the communities. In particular, larger seeded species were favoured under water shortage conditions (Metz *et al*. 2010; Leishman *et al*. 2000) as well as short species and species with low reproductive ratios, which indicated their more efficient water use (Karlsson & Méndez 2005; Huxman *et al*. 2013; Eskelien & Harrison 2015). Similarly, species with high root:shoot ratios that could acquire water more efficiently during drought events (Lloret *et al*., 1999; Craine 2009; Zeppel *et al*. 2014) were also favoured in severe drought scenarios. By contrast, plant traits that indicated high growth rates, such as a high SLA and low LDMC (Reich *et al*. 1997; Freschet *et al*. 2010; Wright *et al*. 2004; Gibert *et al*. 2016), were rare in the assemblies under water shortage scenarios. Therefore, we found that species had a higher probability of occurring in the assemblies under drought conditions when they had a higher seed mass, LDMC, and root:shoot ratios, but a lower SLA, reproductive ratio, and height.

These findings suggest that evolution operates on the entire plant rather than on isolated plant traits (Reich *et al*. 2003b), which is in agreement with other studies that found evidence of multi-trait syndromes across plant organs at the species level (Wright & Westoby 1999; Liu *et al*. 2010; Reich 2014). Overall, our results suggest that traits are phenotypically integrated as an adaptation to multiple ecological dimensions of the Mediterranean climate (Tielbörger *et al*. 2014; Laughlin & Messier 2015). In fact, under severe droughts, the constant CWM and Rao values indicate that the germinated species were already equipped with this set of traits. Thus, germination and seedling establishment appeared to control the community functional diversity throughout the whole growing season (Donohue *et al*. 2010; Jiménez-Alfaro *et al*. 2016).

The importance of BSCs for annual plant community attributes (Luzuriaga *et al*. 2012; Peralta *et al*. 2016) as well as for germination and seedling establishment (Escudero *et al*. 2007; Langhans *et al*. 2009) are widely recognized, but their effects on community assemblies have not been assessed in previous experimental studies. Our results support the ecological importance of BSCs in semi-arid ecosystems (Chamizo *et al*. 2012; Luzuriaga *et al*. 2012, 2015; Maestre *et al*. 2013; Berdugo *et al*. 2014; Peralta *et al*. 2016). When the BSCs were mechanically perturbed, the traits related to plant economics (i.e. height, LDMC, SLA, root:shoot, and reproductive ratio) converged, especially under severe drought conditions. The values of the CWMs for the assemblies formed under perturbed BSCs were similar to those when the availability of water was scarce (i.e., shorter species with higher LDMC values, lower reproductive ratios, lower SLA values, and larger root:shoot values). The most likely explanation for these effects is that the BSCs alleviated the scarcity of water by reducing soil evapotranspiration. Lichens are known to retain water inside their thallus or to seal the soil surface (crustose thallus), thereby creating wetter and more benign conditions at the fine scale at which annual plants are established (Berdugo *et al*. 2014). Thus, BSCs can buffer the effects of drought, which may be critical in future conditions under global warming. These findings support the BSC–annual plant interaction suggested by Luzuriaga *et al*. (2012) who found no relationship between BSC and annuals in wet years and positive associations in dry years. In addition, when the BSCs were perturbed, the species in the communities had more diverse seed sizes, whereas the species had more homogeneous seed sizes in the well-conserved BSCs, thereby suggesting that the BSCs acted as a filter during germination and seedling establishment via the seed mass (Escudero *et al*. 2007; Hernández & Sandquist 2011).

## Conclusions

The results obtained in this study demonstrate the important effects of abiotic factors that lead to interannual environmental variability (Carmona *et al*. 2014; Stark *et al*. 2017) as well as biotic factors that operate at fine spatial scales (Conti *et al*. 2017) on the functional diversity of annual plant communities. We measured functional traits for adult plants but we still detected the meaningful sorting of species related to environmental filters in our study. Thus, the functional traits measured in the adult stages of annual plants are useful for understanding species assembly in other life stages based on the high correlations between seedling and adult traits in annual plants (Grzesiak *et al*. 2012;

Dodig *et al*. 2015). Furthermore, our results strongly suggest that many plant functional traits are highly correlated.

We found that rainfall, specifically autumn droughts, acted as a critical filter by favouring species with better characteristics in terms of stress resistance (high LDMC and low SLA) and resource economy (short species with low reproductive ratio and higher root:shoot ratios). In addition, we identified two roles for BSCs acting: i) as a biotic filter that prevented the germination and establishment of species with larger seeds; and ii) as a buffer against abiotic stressful conditions by reducing soil evapotranspiration. Thus, climatic fluctuations and fine scale biotic determinants of spatial heterogeneity emerged as sources of niche differentiation in time and space, thereby promoting species coexistence and leading to the high diversity levels found in these communities. However, extreme droughts can reduce the community diversity, especially when they are combined with BSC perturbations. These extreme conditions may yield a simplified (filtered) community with fewer species and lower functional diversity.

## Authors' contributions

A.M.S., A.L.L., and A.E. designed the experimental study and statistical analyses. A.L.P. prepared the community monoliths and conducted the community surveys and traits measurements. A.L.P. and F.B. performed the statistical analyses. A.L.P. wrote the first draft and all authors contributed to subsequent versions.

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## Data Accessibility

Data deposited in the Dryad repository: https://doi.org/10.5061/dryad.tf7s2s5

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|  | Seedlings |  |  |  |  |  |  | Vegetative |  |  |  |  |  |  | Reproductive |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Experiment 1** | df | SS | MS | F | R2 | *p*-value |  | Df | SS | MS | F | R2 | *p*-value |  | Df | SS | MS | F | R2 | *p*-value |  |
| Rain **Timing** | 2 | 2.31 | 1.15 | 4.40 | 0.09 | <0.001 | *** | 2 | 1.33 | 0.66 | 2.29 | 0.05 | <0.001 | ** | 2 | 2.26 | 1.13 | 3.85 | 0.09 | <0.001 | *** |
| Rain **Amount** | 1 | 0.22 | 0.22 | 0.86 | 0.01 | 0.59 |  | 1 | 0.14 | 0.14 | 0.48 | 0.01 | 0.93 |  | 1 | 0.22 | 0.22 | 0.75 | 0.01 | 0.68 |  |
| T × A | 2 | 0.63 | 0.32 | 1.21 | 0.03 | 0.22 |  | 2 | 0.32 | 0.16 | 0.55 | 0.01 | 0.96 |  | 2 | 0.37 | 0.18 | 0.63 | 0.01 | 0.91 |  |
| Residuals | 83 | 21.77 | 0.26 |  | 0.87 |  |  | 78 | 22.55 | 0.29 |  | 0.93 |  |  | 77 | 22.61 | 0.29 |  | 0.89 |  |  |
| Total | 88 | 24.92 |  |  | 1.00 |  |  | 83 | 24.36 |  |  | 1.00 |  |  | 82 | 25.49 |  |  | 1.00 |  |  |
| **Experiment 2** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Rain Amount | 2 | 4.26 | 2.13 | 10.21 | 0.19 | <0.001 | *** |  |  |  |  |  |  |  | 2 | 3.33 | 1.67 | 7.57 | 0.15 | <0.001 | *** |
| BSC | 1 | 0.21 | 0.21 | 1.01 | 0.01 | 0.40 |  |  |  |  |  |  |  |  | 1 | 0.38 | 0.38 | 1.71 | 0.02 | 0.06 | . |
| A × BSC | 2 | 0.33 | 0.16 | 0.79 | 0.01 | 0.73 |  |  |  |  |  |  |  |  | 2 | 0.55 | 0.28 | 1.26 | 0.02 | 0.18 |  |
| Residuals | 87 | 18.15 | 0.21 | 0.79 |  |  |  |  |  |  |  |  |  |  | 84 | 18.48 | 0.22 | 0.81 |  |  |  |
| Total | 92 | 22.95 | 1.00 |  |  |  |  |  |  |  |  |  |  |  | 89 | 22.74 | 1.00 |  |  |  |  |

**Table 1.** PERMANOVA analyses of the species composition in Experiment 1 with respect to the rainfall timing (T) and amount (A) treatments in the seedling, vegetative, and reproductive life stages (n = 89, n = 84, n = 83, respectively). Only the dry autumn pots differed from the dry spring and typical timing in the germination (pairwise PERMANOVA $p$ < 0.003 for both) and vegetative stages ($p$ = 0.027 and $p$ = 0.009,

respectively). In the reproductive stage, significant differences in species composition were observed among the three rainfall timing treatments ($p < 0.003$ between all treatments). In Experiment 2, PERMANOVA analyses were conducted based on the species composition relative to the rainfall amount and biological soil crust (BSC) perturbation treatments in the seedling and reproductive life stages (n = 93, n = 90, respectively). In the seedling stage, all three treatments differed (pairwise PERMANOVA $p = 0.036$ between 100% and 33% rain reduction; $p < 0.003$ between 66% rain reduction and the other two treatments). In the reproductive stage, significant differences in species composition were observed between 66% rain reduction and the other two treatments ($p < 0.003$).

| | | **Experiment 1** | | | | | | **Experiment 2** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Spp Richness | | Plant abundance | | | | Spp Richness | | Plant abundance | |
| | Df | Chisq | | Chisq | | | Df | Chisq | | Chisq | |
| (Intercept) | 1 | 336.22 | *** | 436.80 | *** | (Intercept) | 1 | 1455.60 | *** | 1408.14 | *** |
| Life **S**tage | 2 | **30.98** | ******* | 4.62 | . | Life stage | 1 | 2.79 | . | **38.73** | ******* |
| Rain **T**iming | 2 | 4.95 | . | 3.02 | | Rain amount | 2 | **56.85** | ******* | **54.37** | ******* |
| Rain **A**mount | 1 | 0.79 | | 0.34 | | BSC | 1 | 0.13 | | 0.37 | |
| S × T | 4 | **95.23** | ******* | **36.34** | ******* | S × A | 2 | 0.91 | | 0.12 | |
| S × A | 2 | 3.71 | | 0.56 | | S × BSC | 1 | **5.48** | ***** | 3.11 | . |
| T × A | 2 | 2.44 | | 2.77 | | A × BSC | 2 | 3.87 | | 2.16 | |
| S × T × A | 4 | 2.28 | | 7.00 | | S × A × BSC | 2 | 1.97 | | 2.40 | |

**Table 2.** Generalized linear mixed models (GLMM) employed to explain the variations in plant abundance and species richness. In Experiment 1, rainfall timing (T), rainfall amount (A), and life stage (S), as well as their interactions, were included in the models as fixed effects. In Experiment 2, rainfall amount (A), biological soil crust perturbation (BSC), and community life stage (S), as well as their interactions, were included in the models as fixed effects. Pot was also included in the models as a repeated measures random factor. Significant results are shown in bold and indicated with asterisks: ***, $p < 0.001$; **, $0.001 < p < 0.01$; *, $0.01 < p < 0.05$.

|  |  | **Seed mass** |  | **Height** |  | **SLA** |  | **LDMC** |  | **Reproductive ratio** |  | **Root:shoot** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **CWM** | Df | Chisq |  | Chisq |  | Chisq |  | Chisq |  | Chisq |  | Chisq |  |
| (Intercept) | 1 | 8136.62 | *** | 18761.54 | *** | 6070.62 | *** | 23341.83 | *** | 810.39 | *** | 5149.65 | *** |
| Life **S**tage | 2 | **17.98** | *** | 4.68 | . | **26.35** | *** | **32.32** | *** | **8.67** | * | 5.41 | . |
| Rain **T**iming | 2 | 1.02 |  | 2.00 |  | 4.38 |  | 3.19 |  | **7.60** | * | 1.35 |  |
| Rain **A**mount | 1 | 0.88 |  | 0.04 |  | 0.20 |  | 1.17 |  | 0.08 |  | 1.02 |  |
| S × T | 4 | 7.61 |  | **21.34** | *** | 7.75 |  | **37.62** | *** | **52.23** | *** | **27.57** | *** |
| S × A | 2 | 1.40 |  | 0.78 |  | 3.17 |  | 0.84 |  | 4.10 |  | 0.66 |  |
| T × A | 2 | 1.77 |  | 3.89 |  | 0.59 |  | 1.30 |  | 2.30 |  | **8.33** | * |
| S × T × A | 4 | 2.52 |  | **10.26** | * | 1.63 |  | 1.69 |  | 4.56 |  | 1.11 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Rao** |  |  |  |  |  |  |  |  |  |  |  |  |  |
| (Intercept) | 1 | 177.08 | *** | 288.71 | *** | 581.61 | *** | 343.82 | *** | 489.76 | *** | 448.28 | *** |
| Life **S**tage | 2 | 0.16 |  | 5.61 | . | 1.12 |  | **17.87** | *** | 5.48 | . | 5.25 | . |
| Rain **T**iming | 2 | 0.93 |  | 3.26 |  | 1.51 |  | 2.82 |  | **9.41** | ** | 4.02 |  |
| Rain **A**mount | 1 | 0.25 |  | 0.09 |  | 2.06 |  | 1.56 |  | **4.52** | * | 0.60 |  |
| S × T | 4 | 3.32 |  | 7.27 |  | 2.23 |  | 8.97 | . | **17.00** | ** | **27.84** | *** |
| S × A | 2 | 2.39 |  | 1.09 |  | 0.10 |  | 0.75 |  | 0.55 |  | 1.04 |  |
| T × A | 2 | 0.44 |  | 0.23 |  | 2.72 |  | 1.29 |  | 1.61 |  | 2.29 |  |
| **S** × T × A | 4 | 2.00 |  | 2.33 |  | 0.69 |  | 0.51 |  | 1.14 |  | 1.59 |  |

**Table 3.** Generalized linear mixed models employed to explain the variations in the CWMs and Rao values for each trait in Experiment 1. Rainfall timing (T), rainfall amount (A), and life stage (S), as well as their interactions, were included in the models as fixed effects. Pot was also included in the models as a repeated measures random factor. Significant results are shown in bold and indicated with asterisks: ***, $p < 0.001$; **, $0.001 < p < 0.01$; *, $0.01 < p < 0.05$; '.', $0.05 < p < 0.1$.

|  |  | **Seed mass** |  | **Height** |  | **SLA** |  | **LDMC** |  | **Reproductive ratio** |  | **Root:shoot** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **CWM** | Df | Chisq |  | Chisq |  | Chisq |  | Chisq |  | Chisq |  | Chisq |  |
| (Intercept) | 1 | 7360.79 | *** | 470.23 | *** | 8638.49 | *** | 17781.82 | *** | 2214.52 | *** | 4343.27 | *** |
| Life **S**tage | 1 | **6.69** | ** | 0.52 |  | 4.35 | * | **9.42** | ** | 0.04 |  | 0.68 |  |
| Rain **A**mount | 2 | **17.94** | *** | 2.58 |  | **9.20** | ***** | **22.40** | *** | **58.67** | *** | **26.89** | *** |
| BSC | 1 | 3.46 | . | **6.57** | ***** | 0.58 |  | 0.05 |  | 2.65 |  | 3.08 | . |
| S × A | 2 | 5.35 | . | 5.09 | . | 1.69 |  | 2.70 |  | 1.94 |  | **8.69** | ***** |
| S × BSC | 1 | 0.78 |  | 0.26 |  | 0.05 |  | **5.02** | ***** | **5.24** | ***** | 0.54 |  |
| A × BSC | 2 | 1.83 |  | 0.78 |  | 0.87 |  | 4.22 |  | 2.76 |  | 0.30 |  |
| S × A × BSC | 2 | 0.62 |  | 3.49 |  | 0.55 |  | 0.28 |  | 1.74 |  | 2.68 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Rao** |  |  |  |  |  |  |  |  |  |  |  |  |  |
| (Intercept) | 1 | 329.92 | *** | 740.21 | *** | 1215.69 | *** | 746.56 | *** | 833.43 | *** | 1137.11 | *** |
| Life **S**tage | 1 | 0.00 |  | 0.24 |  | 0.15 |  | 2.27 |  | 1.14 |  | 2.41 |  |
| Rain **A**mount | 2 | 0.05 |  | **40.83** | ******* | **24.43** | ******* | **63.65** | ******* | **67.72** | ******* | **39.21** | ******* |
| BSC | 1 | **5.53** | ***** | **5.55** | ***** | 0.80 |  | 0.72 |  | 0.56 |  | 1.63 |  |
| S × A | 2 | 4.66 | . | 0.13 |  | **7.07** | ***** | 0.99 |  | 4.43 |  | 1.94 |  |
| S × BSC | 1 | 3.10 | . | 2.32 |  | 3.04 | . | **7.69** | ****** | **6.05** | ***** | **4.65** | ***** |
| A × BSC | 2 | 4.95 | . | **8.19** | ***** | 1.68 |  | 2.94 |  | 5.87 | . | **9.20** | ***** |
| S × A × BSC | 2 | 1.67 |  | 2.21 |  | **6.55** | ***** | **8.42** | ***** | **8.92** | ***** | **6.52** | ***** |

**Table 4.** Generalized linear mixed models employed to explain the variations in CWMs and Rao values for each trait observed in Experiment 2. Rainfall amount (A), biological soil crust perturbation (BSC), and life stage (S), as well as their interactions, were included in the models as fixed effects. Pot was also included in the models as a repeated measures random factor. Significant results are shown in bold and indicated with asterisks: ***, $p < 0.001$; **, $0.001 < p < 0.01$; *, $0.01 < p < 0.05$; '.', $0.05 < p < 0.1$.

**Figure 1**

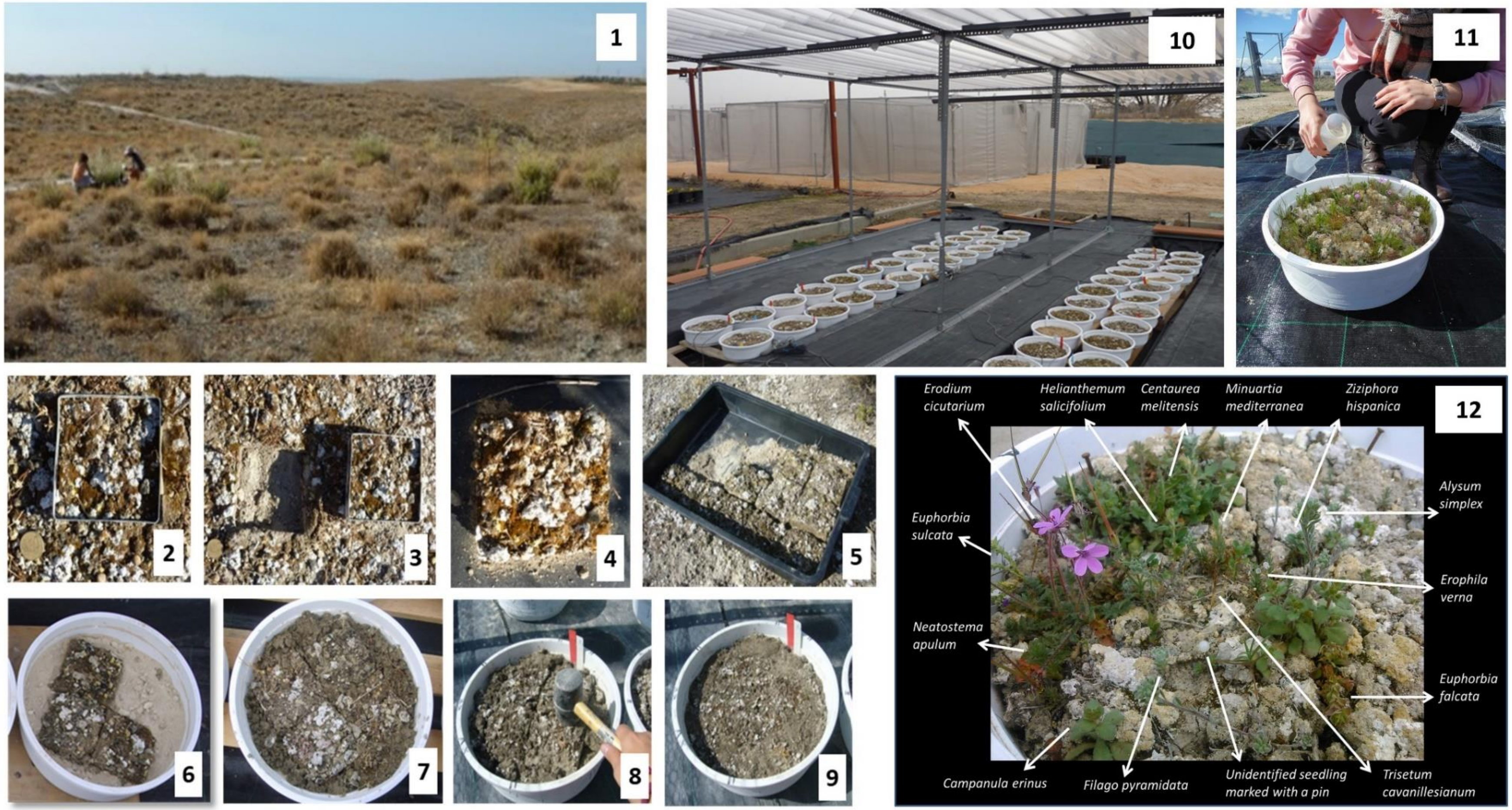
1
10
11
2
3
4
5
6
7
8
9
12
Erodium cicutarium
Helianthemum salicifolium
Centaurea melitensis
Minuartia mediterranea
Ziziphora hispanica
Alysum simplex
Euphorbia sulcata
Erophila verna
Neatostema apulum
Euphorbia falcata
Campanula erinus
Filago pyramidata
Unidentified seedling marked with a pin
Trisetum cavanillesianum

**Figure 2**

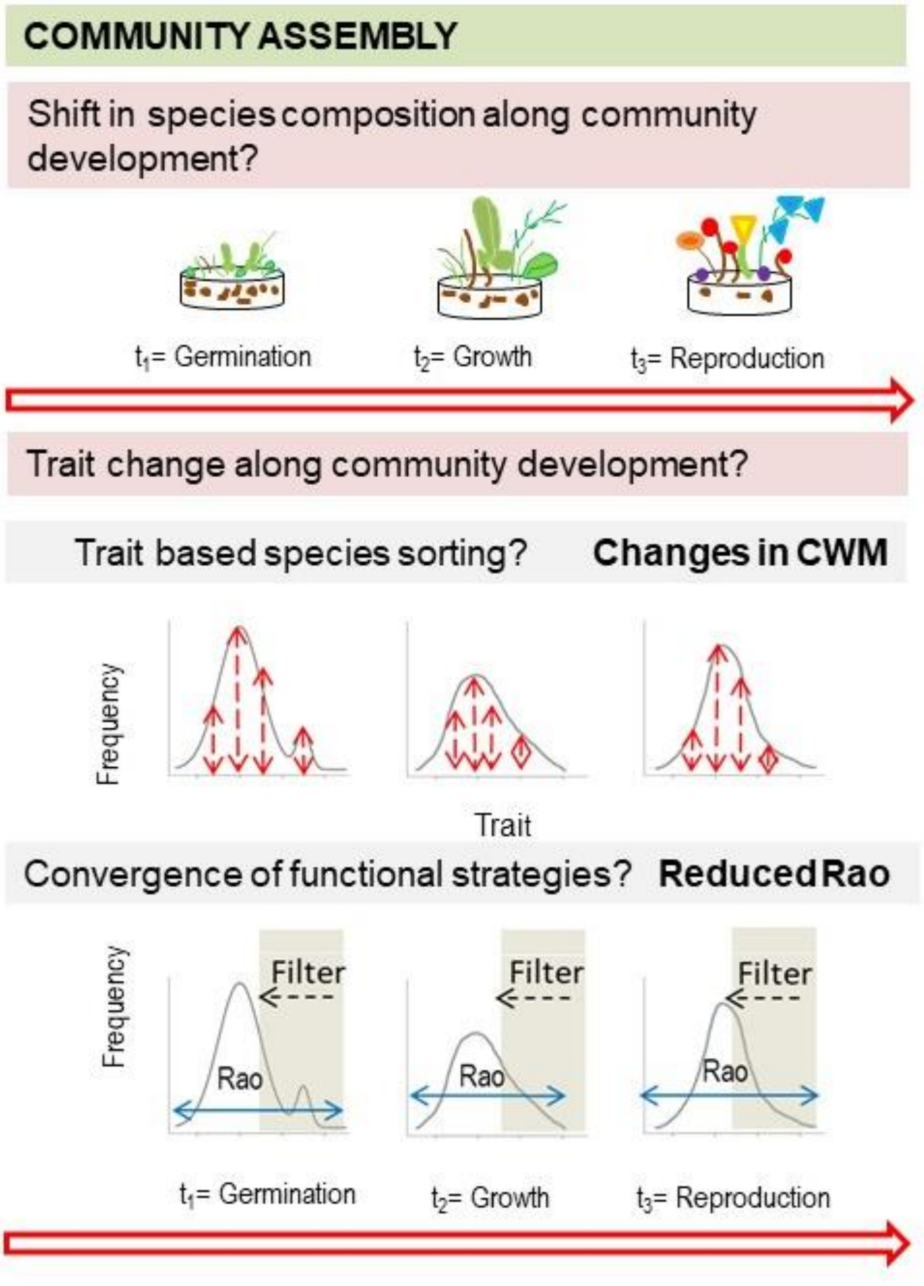
COMMUNITY ASSEMBLY
Shift in species composition along community development?
$t_1$= Germination
$t_2$= Growth
$t_3$= Reproduction
Trait change along community development?
Trait based species sorting?
Changes in CWM
Frequency
Trait
Convergence of functional strategies?
Reduced Rao
Frequency
Filter
Rao
Filter
Rao
Filter
Rao
$t_1$= Germination
$t_2$= Growth
$t_3$= Reproduction

**Figure 3**

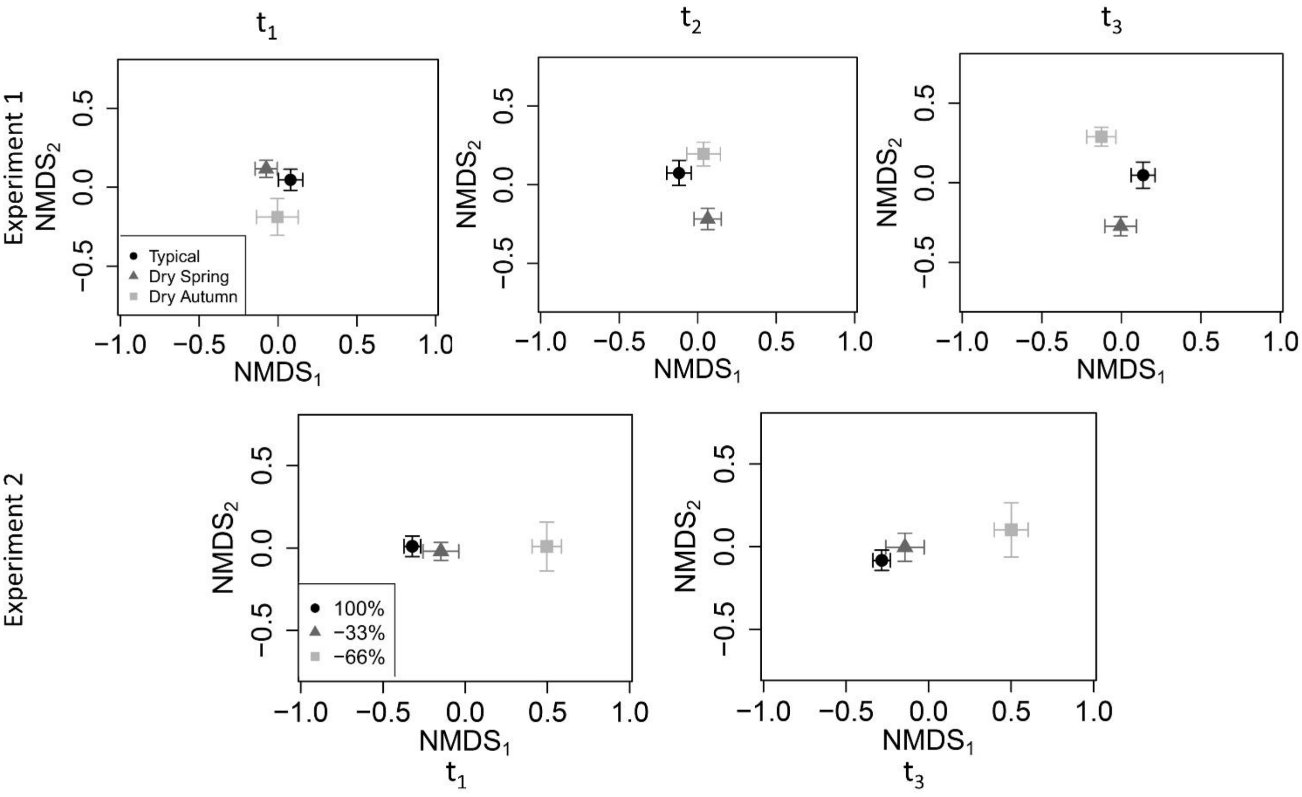
$t_1$
$t_2$
$t_3$
Experiment 1
Experiment 2
NMDS$_2$
NMDS$_1$
0.5
0.0
−0.5
−1.0
−0.5
0.0
0.5
1.0
Typical
Dry Spring
Dry Autumn
100%
−33%
−66%
$t_1$
$t_3$

**Figure 4**

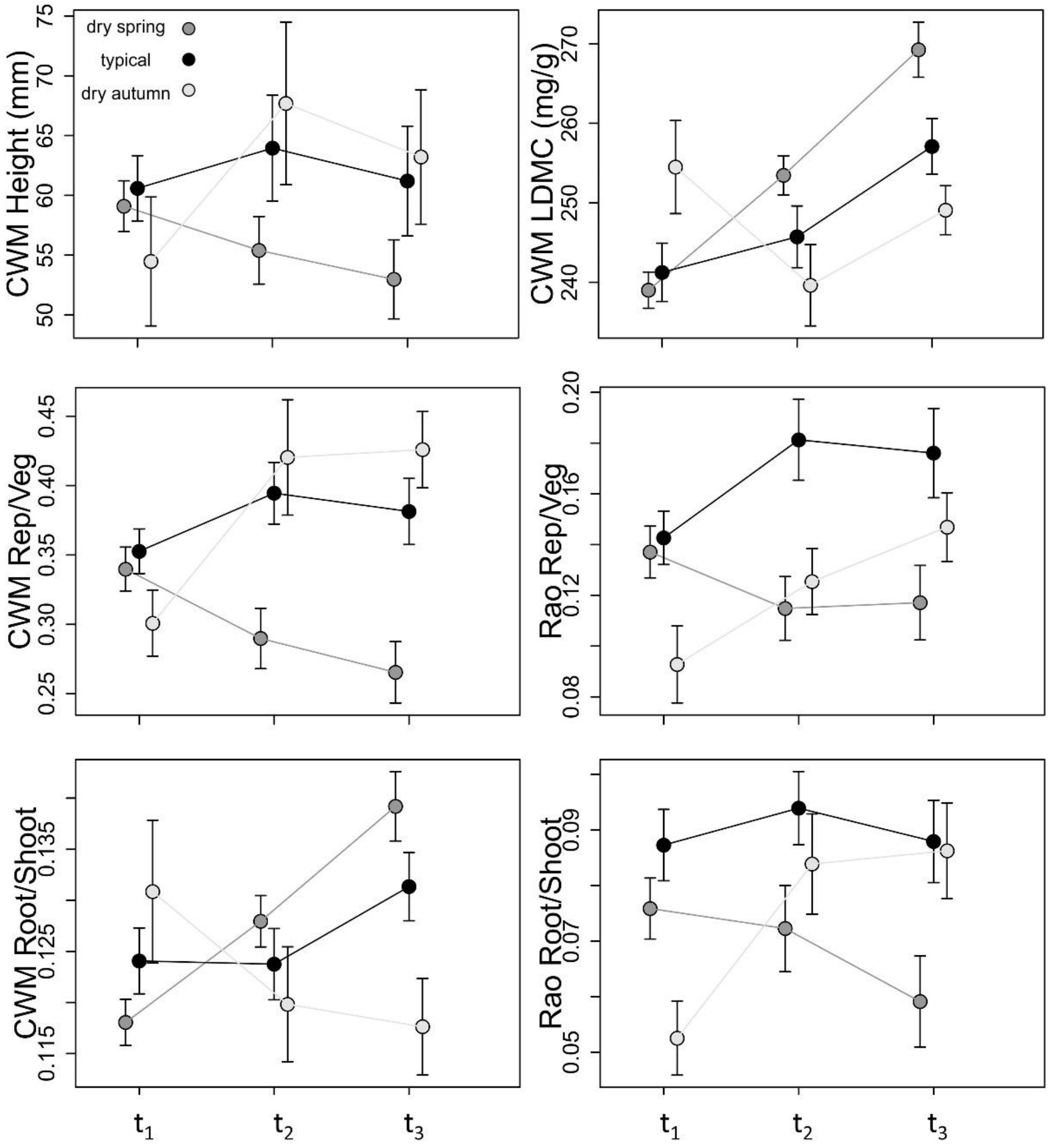
dry spring ●
typical ●
dry autumn ○
CWM Height (mm)
50
55
60
65
70
75
CWM LDMC (mg/g)
240
250
260
270
CWM Rep/Veg
0.25
0.30
0.35
0.40
0.45
Rao Rep/Veg
0.08
0.12
0.16
0.20
CWM Root/Shoot
0.115
0.125
0.135
Rao Root/Shoot
0.05
0.07
0.09
$t_1$
$t_2$
$t_3$
$t_1$
$t_2$
$t_3$

**Figure 5**

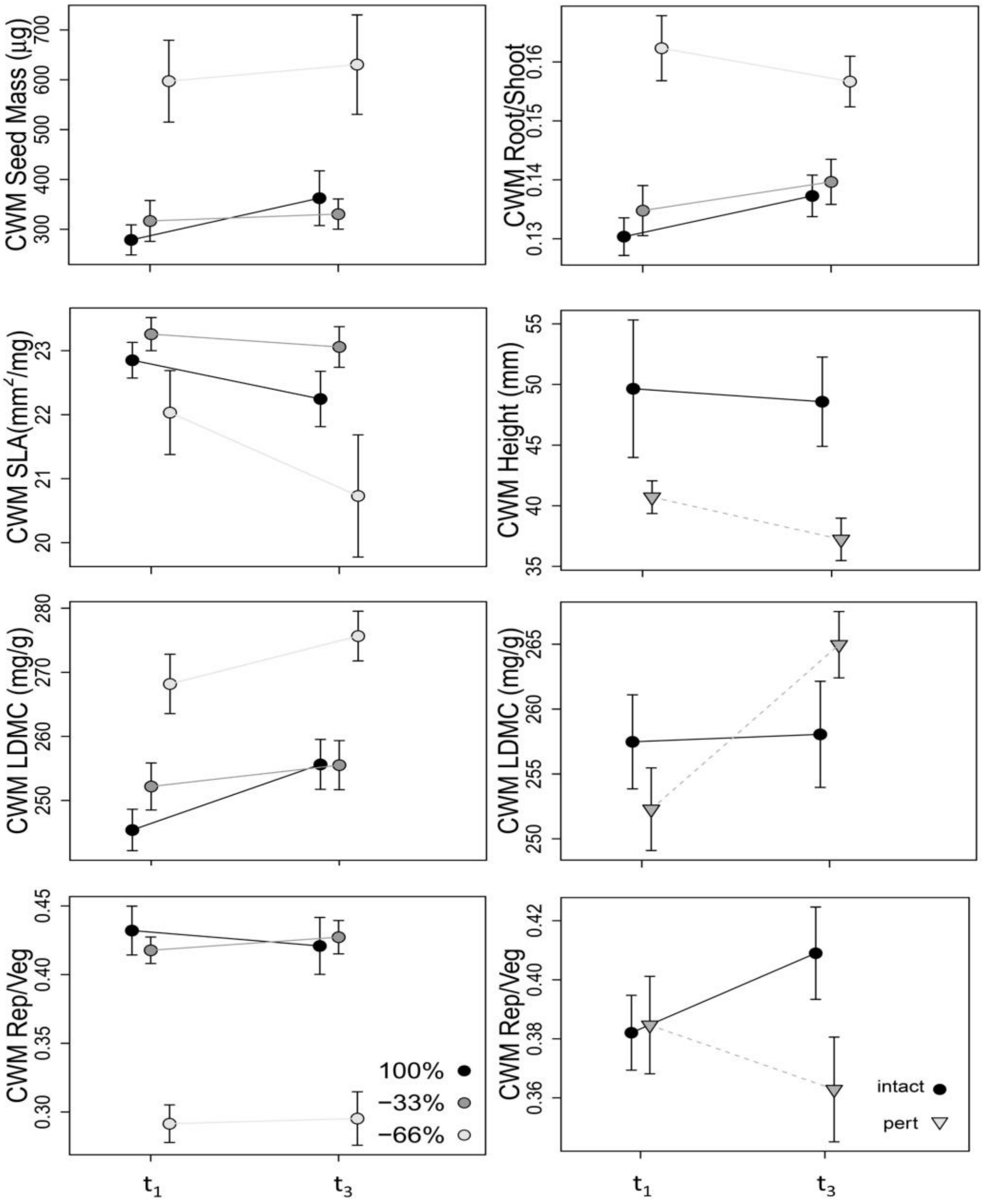
CWM Seed Mass (µg)
300
400
500
600
700
CWM Root/Shoot
0.13
0.14
0.15
0.16
CWM SLA(mm²/mg)
20
21
22
23
CWM Height (mm)
35
40
45
50
55
CWM LDMC (mg/g)
250
260
270
280
CWM LDMC (mg/g)
250
255
260
265
CWM Rep/Veg
0.30
0.35
0.40
0.45
100% ●
−33% ●
−66% ○
CWM Rep/Veg
0.36
0.38
0.40
0.42
intact ●
pert ▽
t₁
t₃
t₁
t₃

**Figure 6**

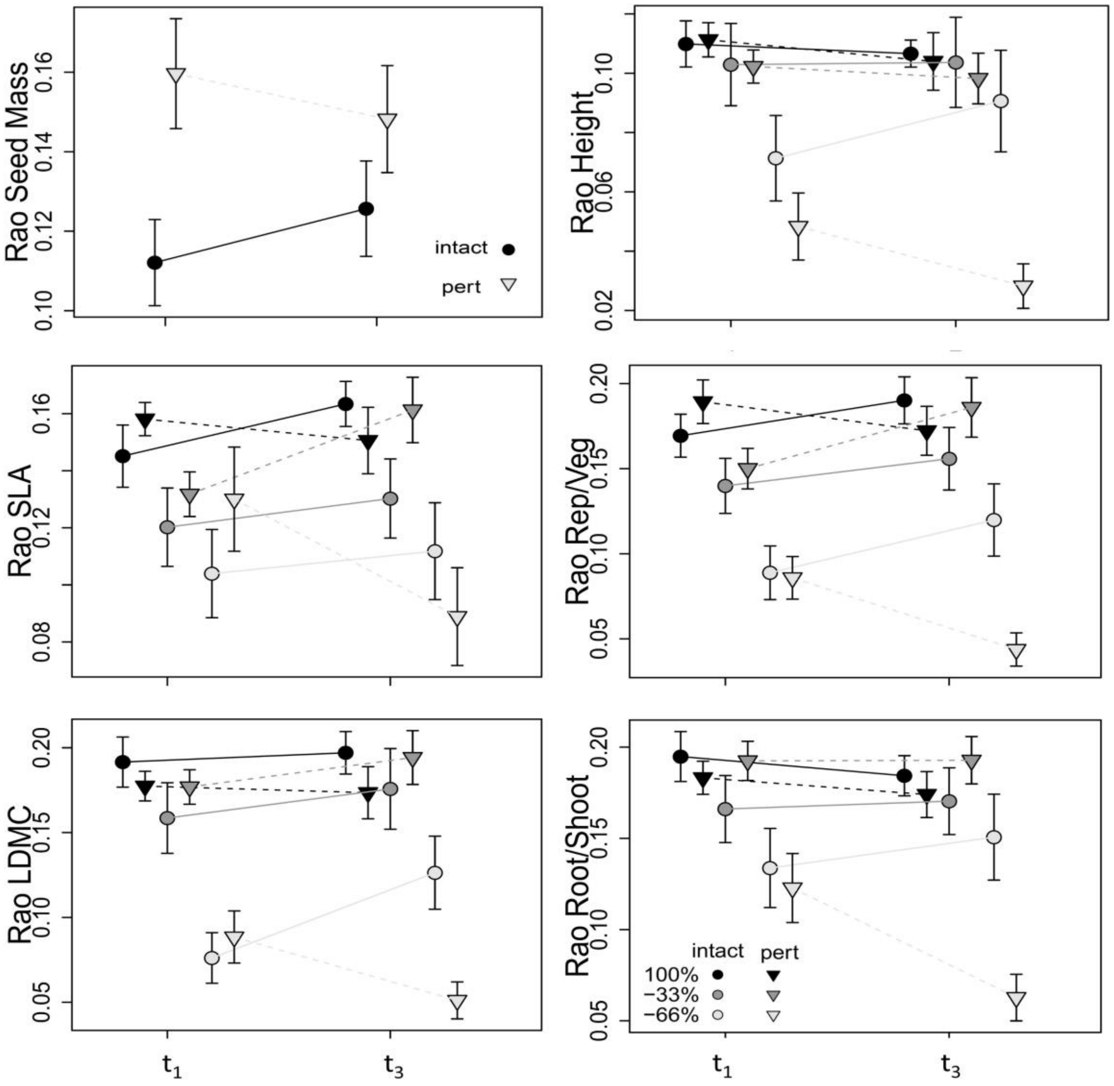
Rao Seed Mass
0.10
0.12
0.14
0.16
intact ●
pert ▽
Rao Height
0.02
0.06
0.10
Rao SLA
0.08
0.12
0.16
Rao Rep/Veg
0.05
0.10
0.15
0.20
Rao LDMC
0.05
0.10
0.15
0.20
Rao Root/Shoot
0.05
0.10
0.15
0.20
intact pert
100% ● ▼
−33% ● ▼
−66% ○ ▽
$t_1$
$t_3$
$t_1$
$t_3$

**Fig. 1.** Study site where the community samples were collected (1). Detailed illustration of the extraction process for the community monoliths (2–5). Arrangement of the community monoliths in plastic pots filled with gypsum (6–7). Biological soil crust perturbation treatment (8–9). Placement of pots under the rainout shelters (10) and irrigation (11). Community developed in a plastic pot after five months (12).

**Fig. 2.** Conceptual model illustrating the expected effects of abiotic (rainfall) and biotic (biological soil crust) factors on community assembly and functional diversity. Our experimental approach allowed us to observe the assembly processes for annual plant communities after manipulating the rainfall amount and timing scenarios, as well as contrasting with the biological soil crust status (mechanically perturbed *vs*. intact). We evaluated the effects related to the experimental manipulation of abiotic and biotic factors throughout the community ontogeny (represented by the red arrows) from the seedling stage immediately after germination until the adult stage when the plants flowered. We expected that the manipulated factors would determine the species that might enter the community from the species pool, thereby leading to changes in the species composition (top panel) and functional trait values (middle panel) among the contrasting scenarios and along the community ontogeny. Moreover, they might modify the community functional diversity by promoting trait-based species sorting and/or the convergence of functional strategies, i.e., functional filtering (bottom panel).

**Fig. 3.** Non-metric multidimensional scaling (NMDS) ordination based on the species compositions in pots. Centroids and error bars for the rainfall timing treatments are shown. Seedling ($t_1$), vegetative ($t_2$), and reproductive ($t_3$) life stages in experiment 1 are represented in the three upper panels (black circles = typical rainfall timing treatment, dark grey triangles = dry spring timing, and light grey squares = dry autumn timing). Seedling ($t_1$), and reproductive ($t_3$) life stages in experiment 2 are represented in the three lower panels (black circles = 100% mean rainfall treatment, dark grey

triangles = 33% reduction, and light grey squares = 66% reduction of mean rainfall). Stress values for all the ordinations were always below 0.22.

**Fig. 4.** Experiment 1: Mean values for community weighted means (CWM) and functional diversity indices (Rao) for the significant terms shown in Table 3 for the seedling ($t_1$), vegetative ($t_2$), and reproductive ($t_3$) life stages. The three rainfall timing treatments are shown (black circles = typical rainfall timing, dark grey triangles = dry spring timing, and light grey squares = dry autumn timing). Vertical bars represent standard errors. See appendices S4 (CWM) and S6 (Rao) for the post hoc Tukey's test differences in the least square mean differences among treatments.

**Fig. 5.** Experiment 2: Mean values of the community weighted Means (CWM) for the significant terms shown in Table 4 for the seedling ($t_1$) and reproductive ($t_3$) life stages. Three rainfall treatments (black circles = 100% rainfall amount, dark grey triangles = 33% reduction of the average rainfall values, and light grey squares = 66% reduction of the average rainfall values) and biological soil crust (BSC) perturbation treatments (circles = intact BSC and triangles = perturbed BSC) are shown. Vertical bars represent standard errors. See appendix S5 for the post hoc Tukey's test differences in the least square mean differences among treatments.

**Fig. 6.** Experiment 2: Mean values of the functional diversity indices (Rao) for the significant terms shown in Table 4 for the seedling ($t_1$) and reproductive ($t_3$) life stages. Three rainfall treatments (black circles = 100% rainfall amount, dark grey triangles = 33% reduction of the average rainfall values, and light grey squares = 66% reduction of the average rainfall values) and biological soil crust (BSC) perturbation treatments (circles = intact BSC and triangles = perturbed BSC) are shown. Vertical bars represent standard errors. See appendix S7 for the post hoc Tukey's test differences in the least square mean differences among treatments.