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

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15
16 **Summary**

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

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

29 **3.** We found that autumn droughts acted as abiotic filters by favouring the germination and
30 establishment of species with greater investment in the root biomass. Under severe droughts
31 (66% water reduction), the experimental assemblies were dominated by species with
32 functional traits adapted to water shortage conditions: high leaf dry matter content, low
33 specific leaf area, small individual size, low reproductive ratio, and high root:shoot ratio. We
34 identified two roles of BSCs in annual plant species assemblies: 1) as a biotic filter that limited
35 the establishment of species based on seed size, and 2) as a buffer against water stress
36 conditions by reducing soil evapotranspiration.

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

45
46 **Key words:** annual plant, biological soil crust, biotic and abiotic filters, coexistence,
47 community assembly, drought, functional diversity, gypsum soil, Mediterranean grassland,
48 precipitation seasonality.

49 **Resumen**

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

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

85

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

88 **Introduction**

89 Understanding the mechanisms that underlie species assembly has been a crucial topic in ecology for
90 many years. Plant assemblies are a consequence of deterministic and stochastic processes acting
91 together (Lortie *et al.* 2004; Vellend 2010, Weiher *et al.* 2011; Escudero & Valladares 2016), which
92 leave detectable signals in the properties of a community (McIntire & Fajardo 2009; Pavoine *et al.*
93 2011). Among the deterministic processes, which are usually called assembly rules (Diamond 1975;
94 Götzenberger *et al.* 2012), ecological filters are widespread probabilistic ‘sieves’ that allow some
95 species with certain functional features to emerge and become part of the standing assembly (Shipley
96 2010). Filters are temporally and spatially variable abiotic or biotic factors. Biotic filters are related
97 to the complex network of interactions that each individual plant establishes throughout its ontogeny
98 with other plants or organisms (Lortie *et al.* 2004; Escudero *et al.* 2007; Rajaniemi *et al.* 2009;
99 Luzuriaga *et al.* 2012).

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

113 and for testing hypotheses based on the species assemblies found in observational studies
114 (Götzenberger *et al.* 2012, HilleRisLambers *et al.* 2012).

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

125 Annual plant communities are an excellent model system for conducting experiments based on
126 community monoliths for the following four reasons (Huxman *et al.* 2013). (1) Annual plant
127 communities have a very rich regional species pool and high species densities in reduced areas due
128 to their small size (Luzuriaga *et al.* 2012, 2015). (2) According to soil seed bank studies conducted
129 in similar communities (Caballero *et al.* 2008; Olano *et al.* 2012; Peralta *et al.* 2016), the soil seed
130 banks were very similar in terms of the species composition in all of the study systems, probably
131 because species dispersal is not limited (Luzuriaga *et al.* 2018). (3) Annuals have short life spans, so
132 their complete life cycle can be observed in a few months. (4) Mediterranean annual plants are able
133 to germinate in different conditions but they are highly synchronized throughout their short life cycle,
134 which results in the clear prevalence of different processes during the growing season (Sánchez *et al.*
135 2014). Moreover, annual plant communities are amenable to simple experimental manipulation
136 because they can be entirely translocated by taking pieces of intact soil from the field during the
137 community dormancy period immediately before germination. These community monoliths

138 containing intact soil seed banks and intact BSC structures can be subjected to experimental
139 treatments, and new assemblies will develop within a short period (6 or 7 months).

140 The main aim of this study was to test the simultaneous effects of probable abiotic and biotic filters
141 on the assembly of annual plant communities. Given that plant communities can be structured
142 according to multiple factors and their interactions (de Bello *et al.* 2013; López-Angulo *et al.* 2018),
143 we studied their simultaneous effects on the plant composition and richness, as well as on the
144 functional trait diversity in different life stages for the community, ranging from germination and
145 seedling establishment to the reproductive phenological peak. We selected functional traits related to
146 the leaf economics spectrum (specific leaf area (SLA) and leaf dry matter content (LDMC)),
147 reproduction trade-offs (seed mass and reproductive ratio), establishment of size hierarchies (plant
148 height), and resource uptake (root:shoot dry mass ratio) (Cornelissen *et al.* 2003; Wright *et al.* 2004;
149 Hirose *et al.* 2005; Craine 2009). We extracted soil monoliths from the field with the intact annual
150 plant community in the soil seed bank. Although this method has rarely been used (but see Insausti
151 *et al.* 1999; Weltzin *et al.* 2000, Harmens *et al.* 2004; Debouk *et al.* 2015), this technique allows the
152 experimental manipulation of the whole natural community, without the need for creating artificial
153 communities. We manipulated previously established critical assembly factors in these communities
154 comprising the rainfall amount (i.e., drought intensity) and timing (Experiment 1: abiotic filters), as
155 well as the rainfall amount and physical structure of the BSC (intact or highly perturbed; Experiment
156 2: abiotic and biotic filters).

157 We hypothesized that both the abiotic and biotic factors as well as their interactions would determine
158 the community assemblies at fine spatial scales in the experimentally manipulated annual plant
159 communities. These factors may filter species based on specific functional traits and eventually
160 determine the final species composition in the community (Götzenberger *et al.* 2012). Thus, we
161 considered the following hypotheses. (i) Experimental variations in the biotic and abiotic conditions
162 would cause changes in the species composition (see our conceptual model in Fig. 2). (ii) Directional

163 shifts in the community-weighted means (CWMs) would probably be associated with the species
164 sorting process among contrasting scenarios. For example, we expected that the CWMs of traits
165 related to water-resource economy would tend to be more conservative under reduced water
166 availability conditions (i.e., low SLA values, high LDMC values, and high root:shoot ratios). (iii) The
167 Rao index estimates the functional divergence of a community, so the Rao values should converge
168 when abiotic/biotic conditions become harsher, which may imply the existence of a probabilistic sieve
169 for certain functional traits. By focusing on traits measured at maturity, we assumed that changes in
170 the functional traits were determined only by changes in the species composition (Leps *et al.* 2011),
171 which is a conservative expectation considering the potential amplifying effect of intraspecific trait
172 variability.

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

183 **Materials and methods**

184 STUDY SITE

185 We collected soil monoliths containing the entire annual plant community in the soil seed bank
186 from a semiarid gypsum steppe. In this system, plants experience limiting environmental
187 conditions, such as the nutrient poor soil derived from gypsum outcrops containing large amounts
188 of calcium sulphate, which can interfere with nutrient uptake (Bosccaiu *et al.* 2011). In addition, the
189 high rate of evapotranspiration develops physical soil crusts on the soil surface, which may hinder
190 seedling establishment (Escudero *et al.* 2015). The collection area was located in Ciempozuelos (40
191 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
192 rainfall of 365 mm m⁻². The habitat comprises a gypsum steppe where specialist shrubs
193 (*Helianthemum squamatum* (L.) Dum. Cours., *Lepidium subulatum* L., *Centaurea hyssopifolia*
194 Vahl, and *Gypsophila struthium* L. in Loefl.) are scattered in a matrix of BSCs dominated by
195 lichens (e.g., *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (G.H. Weber) Poelt,
196 *Fulgensia subbracteata* (Nyl.) Poelt, and *Psora decipiens* (Hedw.) Hoffm) and seasonally covered
197 by a very rich annual plant community (ca. 38 plant species/0.25 m², Luzuriaga *et al.*, 2012), which
198 develops mainly on bare ground areas. Annuals mainly germinate during the autumn months and
199 the plants remain as seedlings until early spring when they grow and reproduce to complete their
200 life cycle before May. This annual community comprises tiny plants (mean height = 10 cm) and
201 some are strict gypsophytes (Luzuriaga *et al.* 2015). The most abundant annual species in the
202 community are *Campanula erinus* L., *Neatostema apulum* (L.) I.M. Johnst, *Micropyrum tenellum*
203 (L.) Link, and *Plantago afra* L., as well as *Chaenorrhinum reyesii* (C. Vicioso and Pau) Benedí and
204 *Campanula fastigiata* Dufour ex DC among the strict gypsophytes.

205 We collected community monoliths from open areas, which were at least 50 cm away from the
206 perennial vegetation patches, and they had well-developed and non-perturbed BSCs (>50% cover)
207 (see details in Fig. 1). The first 3 cm of the soil layer containing the soil seed bank (Russi *et al.*, 1992)

208 was extracted with a square coring device measuring 10×10 cm. Before extracting the community
209 monoliths, the soil surface was watered in order to facilitate BSC conservation and to avoid the loss
210 of the soil's vertical structure. The extracted samples were placed on plastic trays and transported to
211 the experimental station at Rey Juan Carlos University (Móstoles, Madrid, Spain: $40^{\circ}18'48''\text{N}$,
212 $3^{\circ}52'57''\text{W}$) located 40 km west of the field site, but with a similar elevation and climate. Community
213 monoliths were collected in September during 2013 and 2014 (384 community monoliths were taken
214 each year from a surface area of ca. 0.02 ha) before the autumn germination commenced. Thus, the
215 samples contained the complete soil seed bank, i.e., seeds from the persistent seed bank and seeds
216 dispersed in the previous spring. The meteorological conditions were average in the previous year.

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

233 EXPERIMENTAL DESIGN

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

238 *Experiment 1 (abiotic filters)*

239 In 2013, the rainfall timing (three levels) and rainfall amount (two levels) were manipulated according
240 to an orthogonal design to generate six experimental rainfall scenarios. The three rainfall timing
241 treatments simulated in this study were: typical distribution of rainfall (typical timing), dry autumn
242 with a wet spring (dry autumn), and wet autumn with a dry spring (dry spring). In addition, two
243 rainfall amount levels were considered: mean rainfall amount (270 mm/growing period, from October
244 to April) and slight drought treatment (25% rainfall reduction) (Appendix S1). All of the treatments
245 were based on rainfall data recorded at the nearest weather station in Getafe, which is located ca. 30
246 km away from the study site and at a similar altitude (www.aemet.es). The typical rainfall timing
247 throughout the growing season (October–April) in our study area comprised wetter autumns than
248 springs (40% and 25% of the annual precipitation, respectively). The remaining precipitation
249 occurred outside the growing season, mainly in May and September. The rainfall amounts imposed
250 in the dry autumn and dry spring treatments in our experiment were highly realistic because they
251 occurred naturally in 16% and 20% of the last 30 years, respectively. The typical distribution
252 treatment was considered as the mean rainfall in the last 30 years (1981–2010). We performed
253 separate calculations of the rainfall during autumn (October, November, and December), winter
254 (January), and spring (February, March, and April). The rainfall was distributed equally among the
255 three months of each season in every scenario. In order to set the rainfall timing for the dry autumn
256 and dry spring treatments, we considered the mean rainfall in the five wettest springs and five wettest
257 autumns during the last 30 years, respectively. We divided this quantity equally among the three

258 spring/autumn months. We also maintained a constant rainfall amount (30 L m^{-2}) for January in all
259 of the treatments. Finally, the remaining rainfall up to the average of 270 L m^{-2} recorded for the whole
260 period was divided equally among the three autumn/spring months. In the slight drought scenario, we
261 reduced the amount of water during each month by 25% in each timing scenario, thereby yielding six
262 experimental treatments.

263 *Experiment 2 (abiotic x biotic filters)*

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

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

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

281 *Sampling of the experimental communities*

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

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

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

304 STATISTICAL ANALYSES

305 We conducted repeated measures generalized linear mixed model analyses to model CWM and Rao
306 for each trait across all sampling times. Sequential observations of the same pot throughout the

307 growing season were considered to be repeated measures. The rainfall timing, rainfall amount, life
308 stage, and the interactions between them were used as fixed predictors in the first experiment. In the
309 second experiment, the explanatory variables were the rainfall amount, BSC perturbation, life stage,
310 and the interactions between them. We used the *glmer* function from the *lme4* package in R (Bates et
311 al., 2014) to fit the repeated measures models, and we considered pot as a repeated measures random
312 factor. We assumed Gaussian distributions and identity link functions for all CWM and Rao indices.
313 To ensure that the data conformed with the assumption of normality, we log-transformed seed
314 mass_{CWM} and height_{CWM} in the analyses of the first experiment, and seed mass_{CWM} in the analyses of
315 the second experiment. Poisson and negative binomial distributions were assumed for species
316 richness and plant abundance (total number of individuals per pot), respectively, in Experiment 1 and
317 negative binomial for both in Experiment 2. We used Type III sum of squares. Post hoc Tukey tests
318 were performed with the *lsmeans* package (Russell 2015).

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

332 treatments in Experiment 2. PERMANOVA and NMDS analyses were performed in R ('vegan'
333 package, Oksanen *et al.* 2015).

334 **Results**

335 EXPERIMENT 1

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

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

351 With the typical rainfall timing, the CWMs were similar throughout the whole growing season (except
352 LDMC_{CWM} increased significantly in the final reproductive stage) (Fig. 4). However, the dry autumn
353 or dry spring rainfall timing affected the functional traits of the experimental communities throughout
354 the growing season. The dry spring treatment resulted in similar height_{CWM} values to those with the
355 typical timing, but the dry autumn treatment led to significant increases in height_{CWM} from the

356 seedling to the vegetative life stages. The reproductive ratio_{CWM} values differed greatly between the
357 timing treatments, where they were fairly constant under the typical rainfall timing conditions,
358 whereas they decreased in the dry spring and increased in the dry autumn from the seedling stage to
359 reproductive adults. The opposite pattern was determined for the root:shoot ratio_{CWM} where the values
360 decreased with the dry autumn timing and increased with the dry spring timing throughout the
361 community life stages. A reduction of 25% in the mean rainfall amount had no significant effects on
362 most of the trait CWMs (except for the interaction with timing for the root:shoot CWM; Table 3).
363 The Rao functional diversity index tended to be maximized under the typical rainfall timing for all of
364 the plant traits considered in this study (Fig. 4). The reproductive ratio_{Rao} was significantly different
365 at each rainfall timing and it remained higher in the typical treatment.

366 *EXPERIMENT 2*

367 We registered 6559 individuals from 61 species (Appendix S2), where 54.2% of the individuals
368 belonged to five species: *Asterolinon linum-stellatum*, *Campanula erinus*, *Sedum gypsicola* Boiss.
369 and Reuter, *Micropyrum tenellum*, and *Erodium cicutarium* (L.) L'Hér. ex Aiton. The rainfall amount
370 was critical for the species compositions from the seedling to the reproductive stages (Table 1, Fig.
371 3). At the seedling stage, all three treatments differed (pairwise PERMANOVA, $p = 0.036$ between
372 100% and 33% rainfall reduction; $p < 0.003$ between 66% rainfall reduction and the other two
373 treatments). At the reproductive stage, significant differences in the species composition were only
374 observed between 66% rainfall reduction and the other two treatments ($p < 0.003$). No effects of BSC
375 perturbation or its interaction with rainfall amount were detected on the species composition (Table
376 1).

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

381 The increase in the drought severity compared with Experiment 1 allowed us to determine the effects
382 of drought on the annual plant assemblies. Moderate drought (33% rainfall reduction) only decreased
383 the taxonomic diversity slightly, but severe drought (66% rainfall reduction) reduced it dramatically
384 and shifted the mean community values for most of the functional traits. The effects of severe drought
385 on the CWMs were indicated by the higher seed mass_{CWM}, LDMC_{CWM}, and root:shoot ratio_{CWM}, and
386 lower values for the SLA_{CWM} and reproductive ratio_{CWM} (Table 4, Fig. 5). BSC perturbation changed
387 the functional patterns of the experimental assemblies by leading to a generally lower height_{CWM} and
388 reproductive ratio_{CWM}, but an increase in LDMC_{CWM} during the reproductive community life stage.

389 The severe drought treatment significantly reduced the Rao functional diversity indices, except for
390 seed mass_{Rao} (Table 4, Fig. 6). In addition, BSC perturbation increased SLA_{Rao} throughout the
391 growing season under moderate drought conditions (–33%) but decreased it under severe drought (–
392 66%) conditions. BSC perturbation also increased seed mass_{Rao} but decreased height_{Rao}, especially
393 with severe drought. Finally, BSC perturbation also reduced LDMC_{Rao}, reproductive ratio_{Rao}, and
394 root:shoot ratio_{Rao} only in the interaction with the reproductive life stage, especially under severe
395 drought conditions (Table 4, Fig. 6).

396 **Discussion**

397 Our results provide experimental evidence for the effects of abiotic and biotic filters throughout the
398 community assembly process. Moreover, these filters operate via functionally driven mechanisms
399 (assembly rules *sensu* Götzenberger *et al.* 2012) to determine the community functional diversity.
400 Both the rainfall pattern and BSC structure favoured the entry of species with certain functional traits
401 in the final assembly (Shipley 2010), thereby inducing shifts in the CWMs (Chacón-Labela *et al.*
402 2016) and reducing the functional diversity associated with these traits in some cases, and thus they
403 operated as ecological filters (Bernard-Verdier *et al.* 2012).

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

421 recognizable ecological assembly rules. Furthermore, these functional shifts were related to
422 detectable changes in the species compositions of the communities.

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

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

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

457 These findings suggest that evolution operates on the entire plant rather than on isolated plant traits
458 (Reich *et al.* 2003b), which is in agreement with other studies that found evidence of multi-trait
459 syndromes across plant organs at the species level (Wright & Westoby 1999; Liu *et al.* 2010; Reich
460 2014). Overall, our results suggest that traits are phenotypically integrated as an adaptation to multiple
461 ecological dimensions of the Mediterranean climate (Tielbörger *et al.* 2014; Laughlin & Messier
462 2015). In fact, under severe droughts, the constant CWM and Rao values indicate that the germinated
463 species were already equipped with this set of traits. Thus, germination and seedling establishment
464 appeared to control the community functional diversity throughout the whole growing season
465 (Donohue *et al.* 2010; Jiménez-Alfaro *et al.* 2016).

466 The importance of BSCs for annual plant community attributes (Luzuriaga *et al.* 2012; Peralta *et al.*
467 2016) as well as for germination and seedling establishment (Escudero *et al.* 2007; Langhans *et al.*
468 2009) are widely recognized, but their effects on community assemblies have not been assessed in
469 previous experimental studies. Our results support the ecological importance of BSCs in semi-arid

470 ecosystems (Chamizo *et al.* 2012; Luzuriaga *et al.* 2012, 2015; Maestre *et al.* 2013; Berdugo *et al.*
471 2014; Peralta *et al.* 2016). When the BSCs were mechanically perturbed, the traits related to plant
472 economics (i.e. height, LDMC, SLA, root:shoot, and reproductive ratio) converged, especially under
473 severe drought conditions. The values of the CWMs for the assemblies formed under perturbed BSCs
474 were similar to those when the availability of water was scarce (i.e., shorter species with higher
475 LDMC values, lower reproductive ratios, lower SLA values, and larger root:shoot values). The most
476 likely explanation for these effects is that the BSCs alleviated the scarcity of water by reducing soil
477 evapotranspiration. Lichens are known to retain water inside their thallus or to seal the soil surface
478 (crustose thallus), thereby creating wetter and more benign conditions at the fine scale at which annual
479 plants are established (Berdugo *et al.* 2014). Thus, BSCs can buffer the effects of drought, which may
480 be critical in future conditions under global warming. These findings support the BSC–annual plant
481 interaction suggested by Luzuriaga *et al.* (2012) who found no relationship between BSC and annuals
482 in wet years and positive associations in dry years. In addition, when the BSCs were perturbed, the
483 species in the communities had more diverse seed sizes, whereas the species had more homogeneous
484 seed sizes in the well-conserved BSCs, thereby suggesting that the BSCs acted as a filter during
485 germination and seedling establishment via the seed mass (Escudero *et al.* 2007; Hernández &
486 Sandquist 2011).

487 **Conclusions**

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

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

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

508 **Authors' contributions**

509 A.M.S., A.L.L., and A.E. designed the experimental study and statistical analyses. A.L.P. prepared
510 the community monoliths and conducted the community surveys and traits measurements. A.L.P. and
511 F.B. performed the statistical analyses. A.L.P. wrote the first draft and all authors contributed to
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522 **Data Accessibility**

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

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775

Experiment	Seedlings						Vegetative						Reproductive					
	df	SS	MS	F	R2	<i>p</i> -value	Df	SS	MS	F	R2	<i>p</i> -value	Df	SS	MS	F	R2	<i>p</i> -value
Experiment 1																		
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			
	Df	Spp Richness	Plant abundance	Chisq	Df	Spp Richness	Plant abundance	Chisq
(Intercept)	1	336.22 ***	436.80 ***		(Intercept)	1	1455.60 ***	1408.14 ***
Life Stage	2	30.98 ***	4.62 .		Life stage	1	2.79 .	38.73 ***
Rain Timing	2	4.95 .	3.02		Rain amount	2	56.85 ***	54.37 ***
Rain Amount	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: ***, $p < 0.001$; **, $0.001 < p < 0.01$; *, $0.01 < p < 0.05$.

CWM	Df	Seed mass		Height		SLA		LDMC		Reproductive ratio		Root:shoot	
		Chisq	***	Chisq	***	Chisq	***	Chisq	***	Chisq	*	Chisq	***
(Intercept)	1	8136.62	***	18761.54	***	6070.62	***	23341.83	***	810.39	***	5149.65	***
Life Stage	2	17.98	***	4.68	.	26.35	***	32.32	***	8.67	*	5.41	.
Rain Timing	2	1.02		2.00		4.38		3.19		7.60	*	1.35	
Rain Amount	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 Stage	2	0.16		5.61	.	1.12		17.87	***	5.48	.	5.25	.
Rain Timing	2	0.93		3.26		1.51		2.82		9.41	**	4.02	
Rain Amount	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: ***, $p < 0.001$; **, $0.001 < p < 0.01$; *, $0.01 < p < 0.05$; ‘.’, $0.05 < p < 0.1$.

CWM	Df	Seed mass		Height		SLA		LDMC		Reproductive ratio		Root:shoot	
		Chisq		Chisq		Chisq		Chisq		Chisq		Chisq	
(Intercept)	1	7360.79	***	470.23	***	8638.49	***	17781.82	***	2214.52	***	4343.27	***
Life Stage	1	6.69	**	0.52		4.35	*	9.42	**	0.04		0.68	
Rain Amount	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 Stage	1	0.00		0.24		0.15		2.27		1.14		2.41	
Rain Amount	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

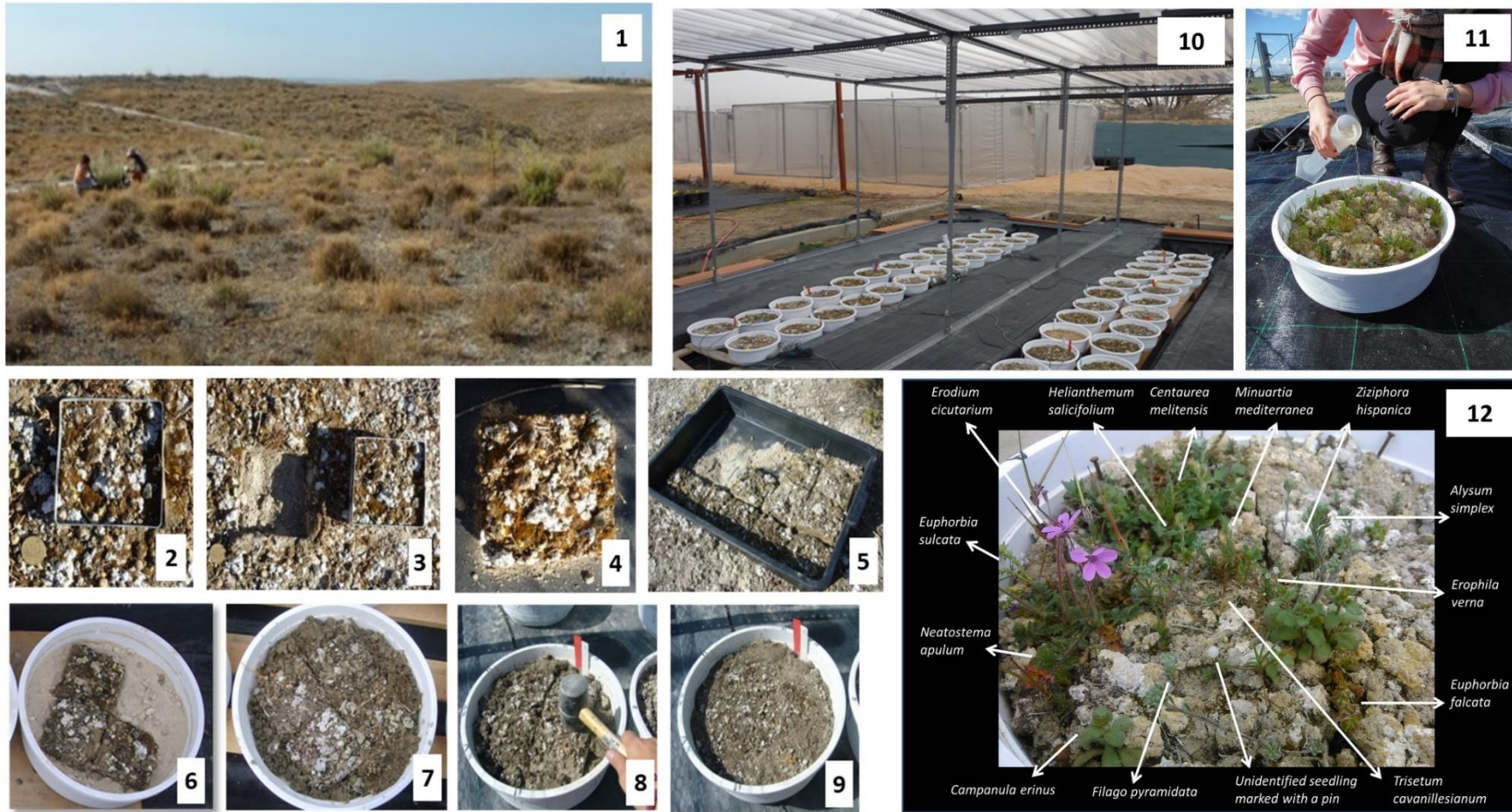


Figure 2

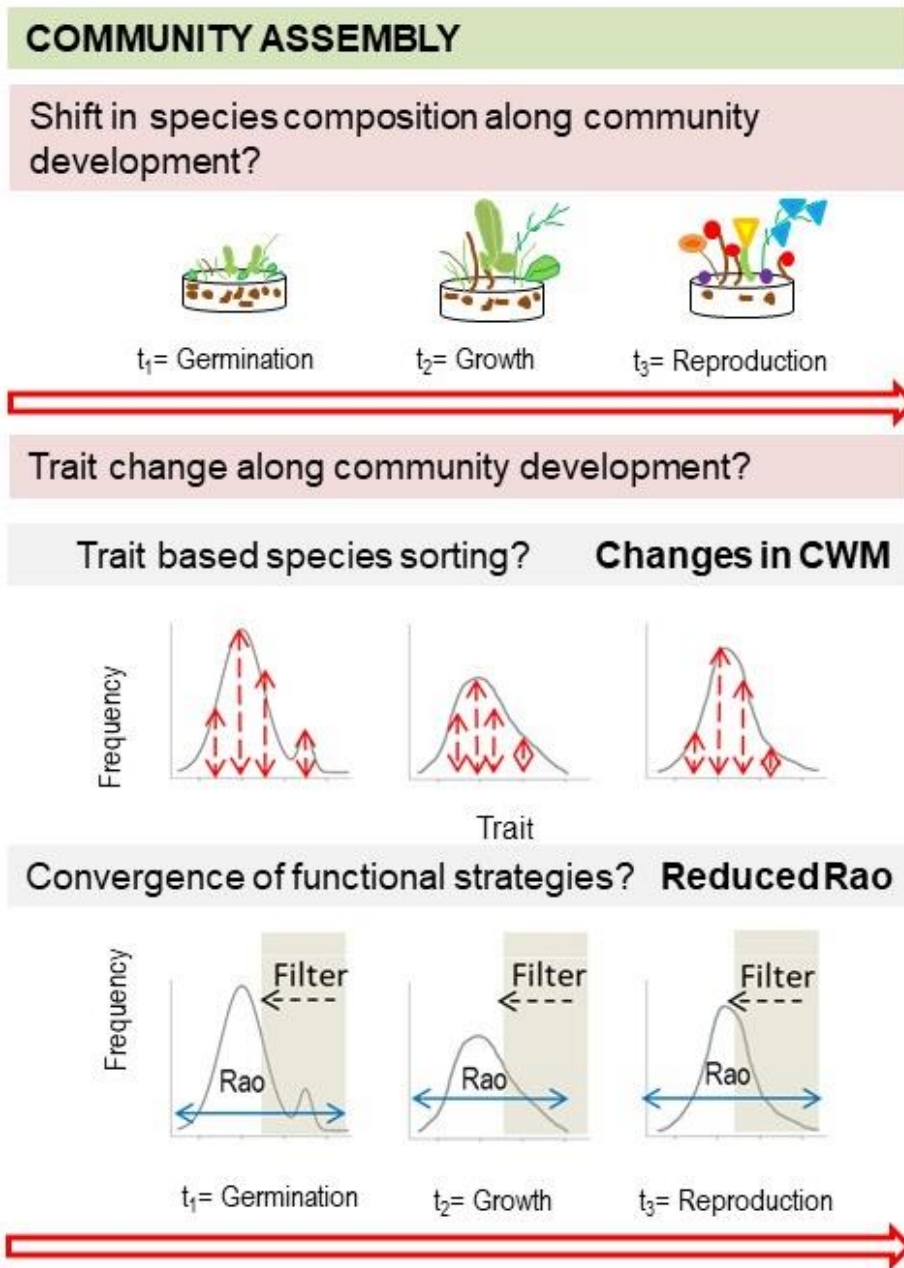


Figure 3

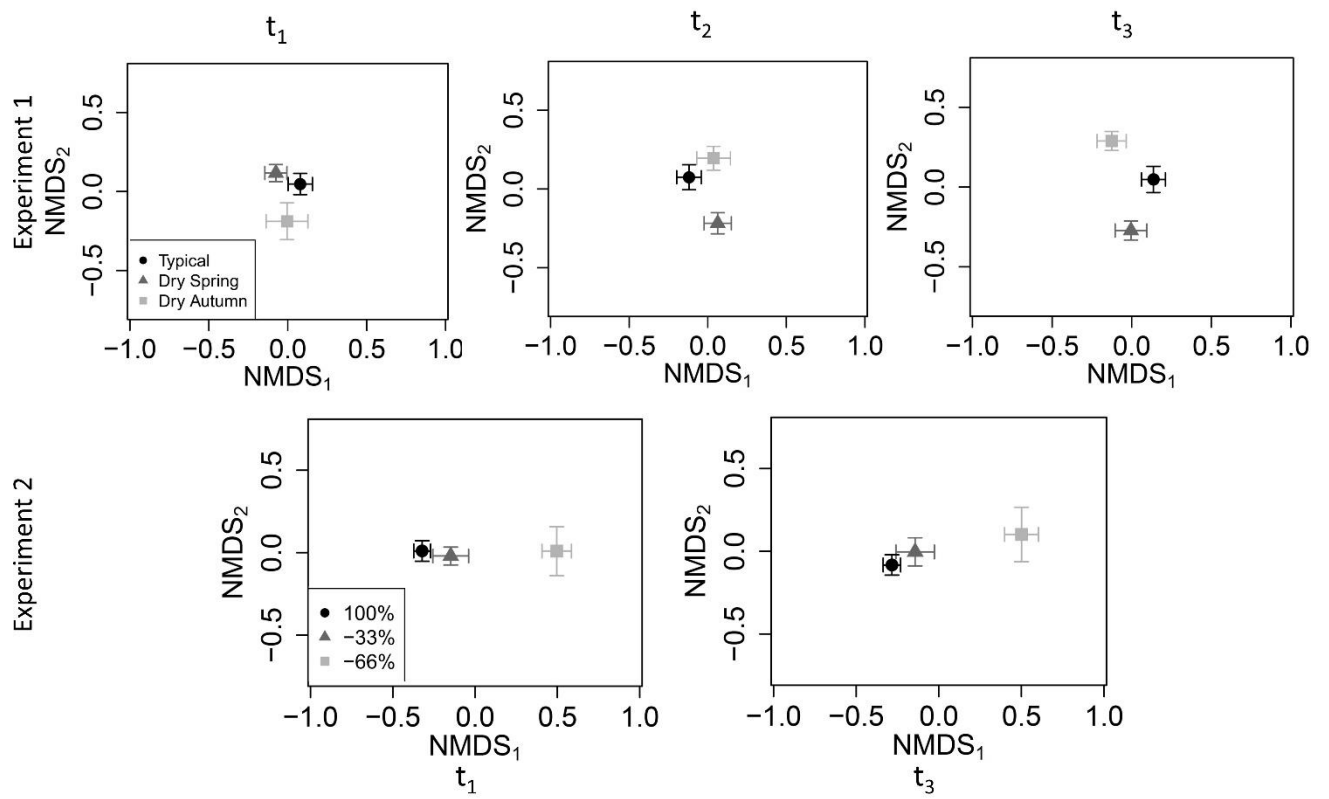


Figure 4

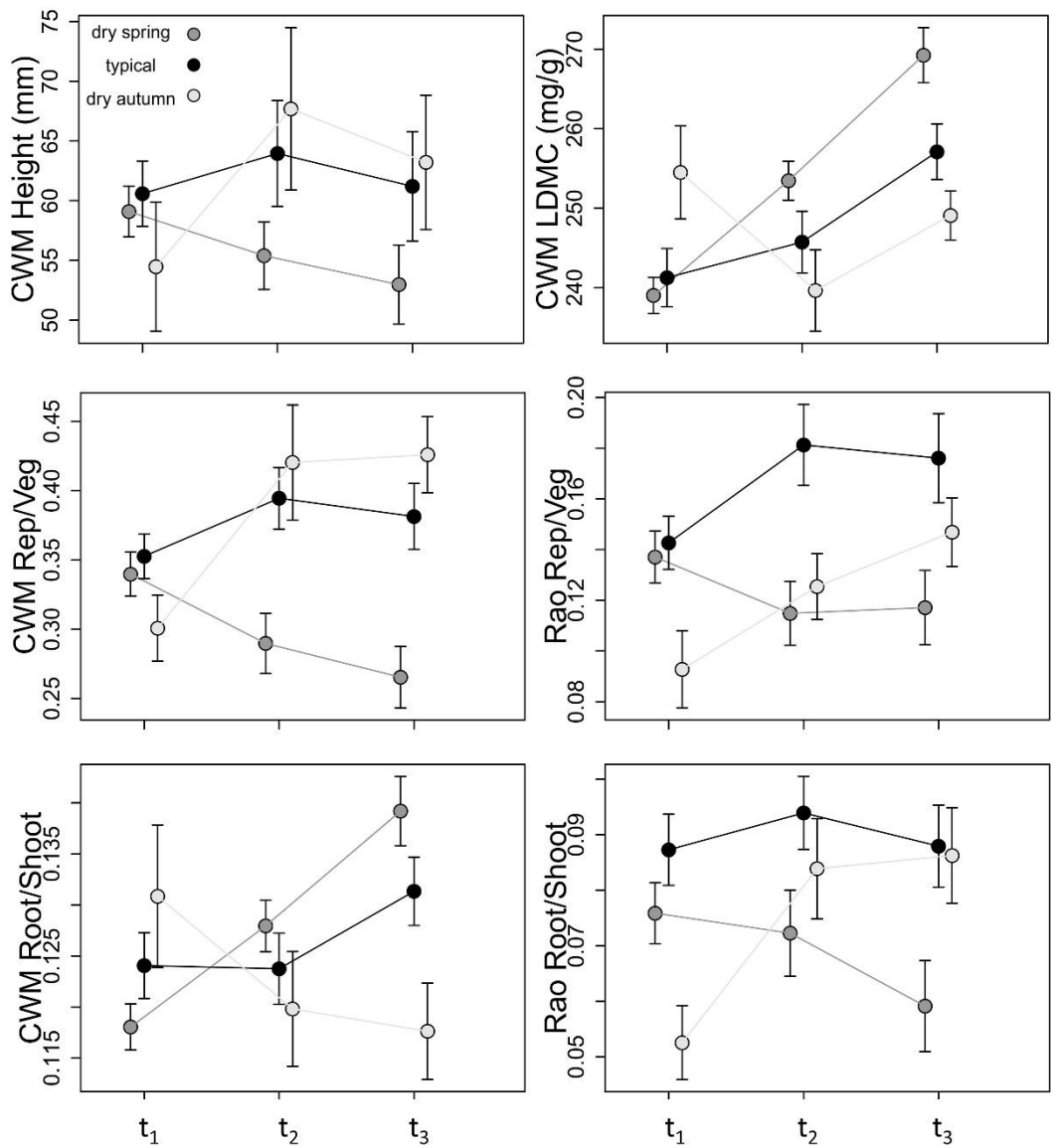


Figure 5

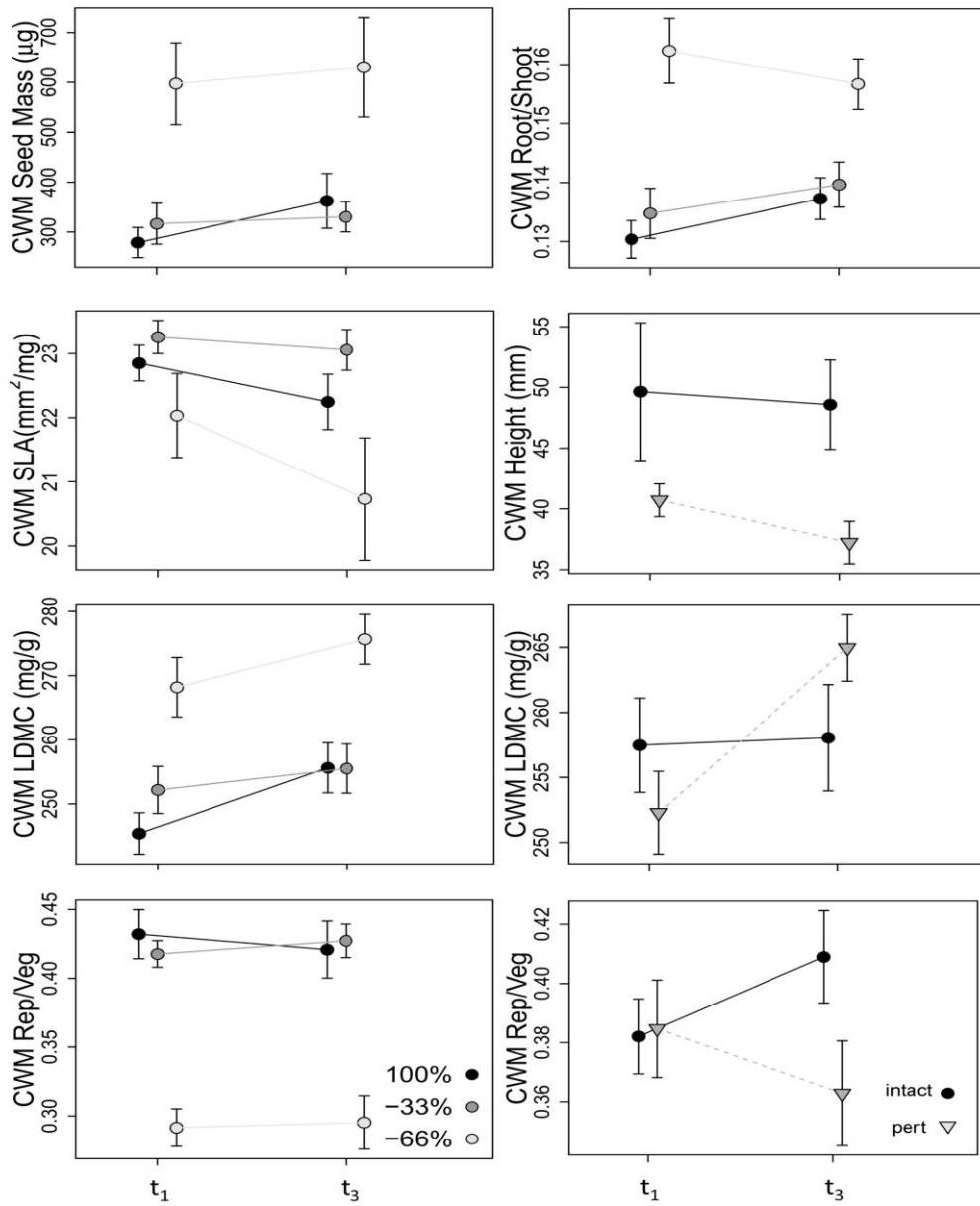


Figure 6

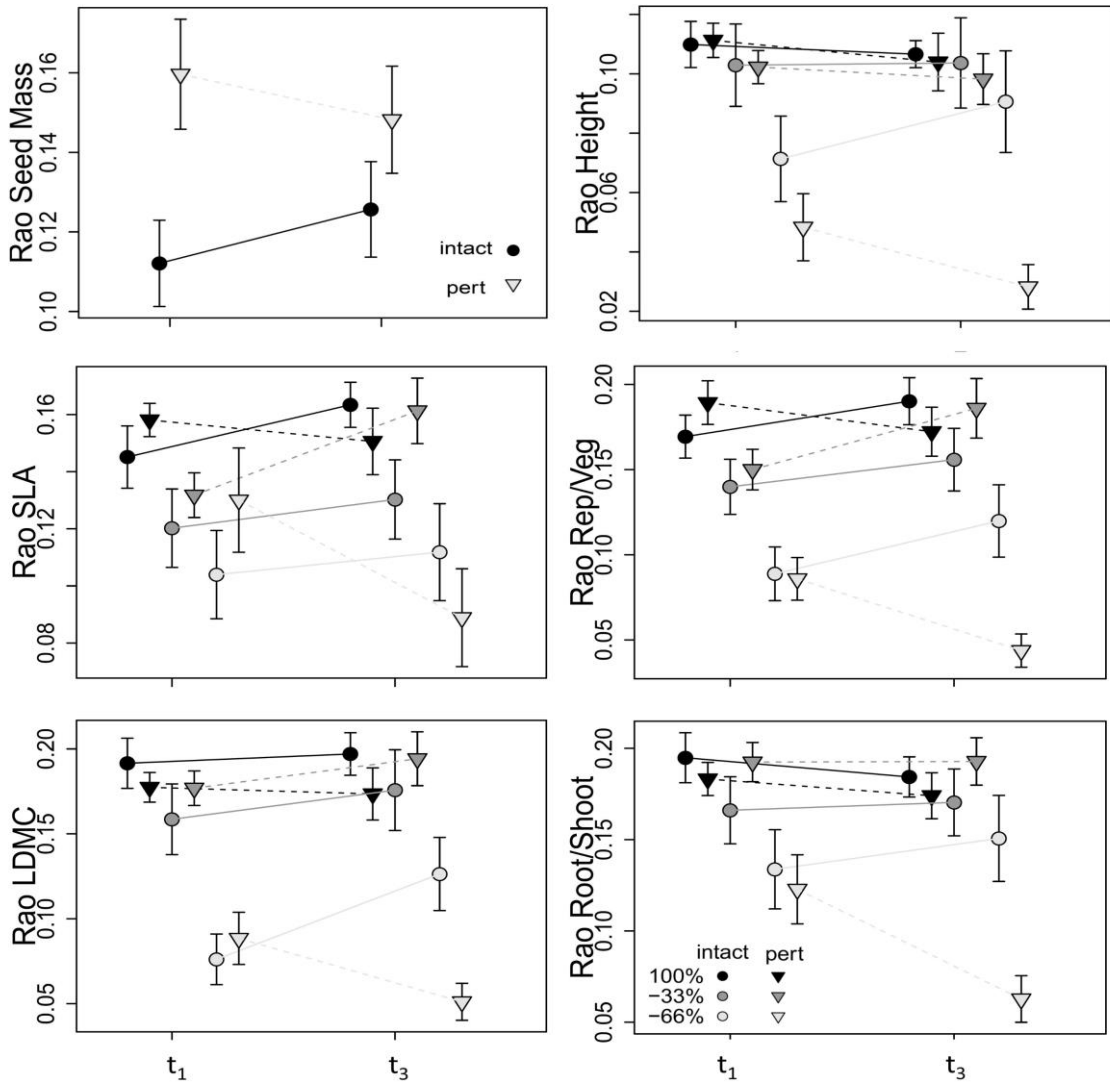


Fig. 1. Study site where the community samples were collected (1). Detailed illustration of the extraction process for the community monoliths (2–5). Arrangement of the community monoliths in plastic pots filled with gypsum (6–7). Biological soil crust perturbation treatment (8–9). Placement of pots 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.