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1 **TITLE:** Shrub species richness decreases negative impacts of drought in a Mediterranean
2 ecosystem.

3

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18

19 **KEYWORDS:** climate change; Mediterranean ecosystem; plant performances; shrubland;
20 species richness

21

22 **RUNNING HEAD:** Impact of increased drought and plant richness on shrub performances

23

24 **ABSTRACT**

25 **Questions:** Global change projections predict biodiversity changes and increased drought
26 intensity in the Mediterranean Basin in the decades to come. This will presumably affect
27 plant performances, plant community composition, and ecosystem functioning. Shrublands
28 are widespread in the Mediterranean area, yet we have no clear understanding of shrubland
29 responses to the combined effects of increased drought and changes in plant diversity.

30 **Location:** Natural Mediterranean shrubland, Marseille, South of France (43°22' N; 5°25' E).

31 **Methods:** A rainfall manipulation experiment was conducted in a Mediterranean shrubland
32 in southern France to examine the performances of four dominant shrub species in response
33 to increased drought. The study assemblages spanned a gradient of 4 shrub richness levels
34 (mono-, bi-, tri-, and tetraspecific plant mixtures) and 15 different shrub combinations.
35 Throughout the two years of non-destructive experiment (2012-2014), we measured plant
36 litterfall, stand necromass and plant cover of the 4 dominant plant species: *Cistus albidus*,
37 *Quercus coccifera*, *Rosmarinus officinalis* and *Ulex parviflorus*.

38 **Results:** Increasing shrub richness levels in the plant community led to higher litter
39 production by all 4 species and a decrease of dry shoots for *Quercus* and *Ulex*. Shrub species
40 responses were affected by the rain exclusion treatment, but the effects were mainly
41 dependent on shrub richness level. In monospecific plots, aggravated drought conditions led
42 to a decrease of litterfall of *Cistus*, *Rosmarinus* and *Ulex* and an increase of necromass of all
43 4 species. In general, these negative drought effects disappeared as number of shrub species
44 in the plant community increased. Under rain exclusion treatment, *Rosmarinus* cover
45 decreased in monospecific plots whereas *Quercus* cover increased in bispecific plots and
46 *Rosmarinus* cover increased in tetraspecific plots. We observed two drought tolerance

47 patterns, with *Quercus* and *Rosmarinus* being more tolerant species and *Ulex* and *Cistus* less
48 tolerant.

49 **Conclusions:** The magnitude of drought effects on shrub performance is species-specific,
50 and plant species combination-dependent. High shrub richness levels could modulate the
51 negative impacts of aggravated drought conditions. Our results pointed to a probable shift of
52 interspecific relationships in response to water resource shortage. As drought impacts are not
53 mediated in low-diversity communities, species-specific responses to drier conditions could
54 lead to shifts in plant community composition favoring the most drought-resistant species,
55 i.e. *Quercus* and *Rosmarinus* here. Maintaining a high diversity level appears critical to
56 mediate drought effect for less resistant species (*Cistus* and *Ulex* in our study).

57 INTRODUCTION

58 Biodiversity and ecosystem functioning in the Mediterranean Basin are already heavily
59 threatened, a trend that is expected to continue and increase with ongoing climate change
60 (Myers et al. 2000). Since Mediterranean ecosystems are expected to be among those most
61 affected in Europe in the coming decades (Hickler et al. 2012; Vautard et al. 2014), we need
62 to improve our knowledge on their responses to the future environmental conditions (Sardans
63 & Peñuelas 2013). In Mediterranean ecosystems, water availability is a crucial factor
64 determining plant growth, plant distribution and diversity (Lloret et al. 2004; Carnicer et al.
65 2011; Wu et al. 2011). Regional climate models predict an increase in temperature and a
66 decrease in precipitation in the Mediterranean region by the end of this century (Gibelin &
67 Deque 2003; Polade et al. 2014). These changes are expected to result in increased frequency,
68 intensity and duration of drought, especially during the warm season (Dai 2012; Polade et al.
69 2014). In the past few decades, field precipitation manipulation experiments have been
70 implemented around the world in order to study the effects of altered precipitation regimes
71 on plant performances and ecosystem functioning (Wu et al. 2011; Beier et al. 2012; Liu et
72 al. 2015). However, responses of plant performances, plant productivity and other ecosystem
73 processes to climate change appear to show strong variability, as studies have reported
74 increases, decreases, or no change (Rustad et al. 2001; Peñuelas et al. 2004; Doblas-Miranda
75 et al. 2015).

76 Interestingly, the magnitude of the effects also depends on plant species composition and
77 richness (Lloret et al. 2004; Doblas-Miranda et al. 2015; Santonja et al. 2015), in line with
78 the general consensus that biodiversity and ecosystem functioning are positively related
79 (Hooper et al. 2005; Montès et al. 2008; Cardinale et al. 2011). As a rule, higher diversity in
80 plant communities leads to higher resource use due to niche differentiation while in less

81 diverse communities, individuals of the same species compete for resources in the same way
82 (Leibold 1995; Tilman et al. 1997). Biodiversity could also help to buffer community changes
83 through the positive diversity-stability relationship (MacCann 2000). However, depending
84 on functional diversity, losses but also shifts of the dominant plant species are likely to alter
85 performances of associated species across trophic levels and thus alter ecosystem functioning
86 (Leemans & Halpin 1992; Fischlin et al. 2007; Santonja et al. 2017). Consequently, the effect
87 of drier conditions on plant performance could depend on plant-specific attributes (i.e.
88 species traits) but also on plant community properties (i.e. richness and composition) (Hooper
89 et al. 2005; Kröel-Dulay et al. 2015; Liu et al. 2015).

90 There has been intensive research into the responses of forest and grassland ecosystems
91 to climate change (Beier et al. 2012) but few experiments have been performed in natural
92 shrubland ecosystems (Peñuelas et al. 2004; Beier et al. 2012; Kröel-Dulay et al. 2015). In
93 particular, to our knowledge, no field precipitation manipulation experiment has ever been
94 performed in shrublands dominated by *Quercus coccifera*, one of the most important shrub
95 species in the Mediterranean area (Konstantinidis et al. 2005; Montès et al. 2008).

96 To address this gap, we assessed the effects of increased drought conditions (decreased
97 precipitation) in different levels of species richness and composition on performances
98 (litterfall, stand necromass and aboveground biomass) of the 4 dominant shrub species
99 (*Quercus coccifera*, *Cistus albidus*, *Rosmarinus officinalis* and *Ulex parviflorus*) of a
100 Mediterranean shrubland (Marseille, South of France).

101 According to long-term studies in dry ecosystems, a decrease in water availability
102 generally leads to an increase in litterfall and standing necromass and a decrease in
103 aboveground biomass (Prieto et al. 2009; Liu et al. 2015). Here we hypothesized an increase
104 in litterfall and stand necromass and a decrease in aboveground biomass in response to drier

105 conditions. As more diverse plant communities are likely to better resist change in
106 environmental conditions (Dias et al. 2003; Hooper et al. 2005), we hypothesized that the
107 negative impact of drier conditions on plant performances would diminish with higher plant
108 species richness, due to niche differentiation.

109

110 **MATERIAL AND METHODS**

111

112 *Study site*

113 The study was carried out in the “Chaîne de l’Etoile” massif located at the northern end
114 of Marseille city (43°22’ N; 5°25’ E, South of France). The site is 275 m a.s.l., with a mean
115 annual temperature of 14.6 °C and mean annual precipitation of 552 mm (mean values over
116 the 2002-2012 period averaged across two meteorological stations in Marignane (43°26’N,
117 5°12’E) and Marseille (43°15’N, 5°22’E) closest to our experimental site). Total annual
118 precipitation during the years of the experiment was 441.3 mm, 542.0 mm and 661.06 mm
119 for 2012, 2013 and 2014, respectively (data from Marignane station). Mean slope is less than
120 1°. Climate is Mediterranean and characterized by hot and dry summers, and wind throughout
121 the year (on average over 30 years, a hundred days with a minimum wind-speed of 57 km.h⁻¹
122 ¹; www.infoclimat.fr). The last fire occurred in 1997 (35 km² burnt from a total of 100 km²
123 covered by garrigue in the “Chaîne de l’Etoile” area) and included the whole study area. Soil
124 is classified as shallow rendzina on limestone (FAO 1988), with mean depth less than 20 cm,
125 high percentage of stones (66% in the top 50 cm), mean pH of 7.9, mean C:N ratio of 18:1
126 and mean CEC of 36.8 cmol.kg⁻¹ (means from 92 different soil samples taken in the study
127 plots; see Shihan et al. (2017) for details).

128 The vegetation is a woody shrub-dominated “garrigue”, with shrub heights ranging
129 between 0.2 and 1.4 m (Montès et al. 2008) and total plant cover ranging from 25% to 95%.
130 Of 27 plant species encountered at the study site, 5 dominate the community and account for
131 97% of total vegetation cover. These include the perennial grass *Brachypodium retusum* P.
132 Beauv. (Poaceae) and the 4 woody shrubs *Cistus albidus* L. (Cistaceae), *Quercus coccifera*
133 L. (Fagaceae), *Rosmarinus officinalis* L. (Lamiaceae) and *Ulex parviflorus* Pourr. (Fabaceae)
134 (Table 1), accounting for 22%, 19%, 36%, 12% and 8% of relative vegetation cover,
135 respectively (Appendix S1). Regarding leaf life span, *Quercus* and *Rosmarinus* are typical
136 evergreen species, *Cistus* is a summer-deciduous, and *Ulex* exhibits a particular morphology
137 with tiny leaves on photosynthetic stems which entirely senesce.

138

139 ***Experimental setup***

140 The study site is characterized by a natural small-scale mosaic of assemblages of distinct
141 compositions of the 4 dominant woody shrub species, (i.e. *C. albidus*, *Q. coccifera*, *R.*
142 *officinalis* and *U. parviflorus*, named *Cistus*, *Quercus*, *Rosmarinus* and *Ulex* hereafter),
143 allowing to determine a series of plots varying in species richness of these 4 shrub species.
144 In spring 2011, we selected plots including all 15 possible combinations of mono-, bi-, tri-,
145 and tetraspecific shrub mixtures with a replication of 6 plots per species combination, and 8
146 replicates for tetraspecific mixtures, resulting in a total of 92 plots. Each plot covers 16 m²
147 (4 m × 4 m) across a total area of 2.5 ha, all fenced off to prevent the passage of the hikers
148 and wild boars. Because these patches of varying species composition established naturally,
149 the relative contribution of each species was not exactly equal along the species richness
150 gradient. Half of the plots within each species richness level were randomly assigned to a
151 control treatment, and the other half to a rain exclusion treatment. All plots were equipped

152 with a 4 m × 4 m solid aluminum frame, held 2 m above the ground by aluminum posts at
153 the outer circumference of the 16 m² plot area and fixed to the ground with reinforcing bars.
154 Stainless steel gutters were mounted on top of the aluminum frame. Contrary to the rain
155 exclusion plots, the gutters in the control plots were mounted upside down in order to let the
156 precipitation fall on the vegetation. A supplementary PVC gutter and a pipe mounted at the
157 border of the frame allowed to evacuate the rainwater away from the plots. The experimental
158 rain exclusion treatment was set up in October 2011. Compared to control plots, the rain
159 exclusion plots received on average $12 \pm 2\%$ less rainfall. This exclusion resulted in an annual
160 average lower soil moisture of -6.5% (that could reach between -13% and -24% during rain
161 events) at 10 cm soil depth between control and rain exclusion plots (Appendix S2; see
162 Santonja et al. (2017) for details).

163

164 *Litterfall, necromass and shrub cover measurements*

165 *Litterfall*

166 To quantify the litter production corresponding to shrub composition of each plot, three
167 plastic litter traps (0.041 m²) were installed under the shrub canopy of the dominant plant
168 species. The litter traps were installed in September 2012 and litterfall was harvested every
169 two months from October 2012 to September 2014, i.e. 12 sampling dates. The litter pool
170 collected in the three litter traps per plot was put in plastic bags before being transferred to
171 the laboratory, separated into species, oven-dried at 60°C for 72 h, and weighed to obtain
172 litter dry mass data for each species per plot. Litterfall was expressed as g.m⁻².

173

174 *Necromass*

175 We monitored number of completely dry shoots (i.e. with all their aboveground biomass
176 - stems, branches, leaves, thorns - totally dry from the base of the shoot) per dominant shrub
177 species per plot, in order to estimate plant necromass as a complement to the litterfall
178 monitoring. Indeed, *Cistus* and *Ulex* keep large amounts of standing dead biomass for a long
179 time (Baeza et al. 2011; Pausas et al. 2012), while clonal growth form of *Quercus*, due to its
180 resprouting capacity after severe drought and fire (Baeza et al. 2011), makes it impossible to
181 affirm that an individual is dead, so monitoring the number of dry shoots allowed us to
182 estimate the impact of drought over the species through senescence and to observe their
183 ability to recover after a severe drought event (Cornelissen et al. 2003). Dry shoots were
184 quantified per species and per plot from September 2012 to July 2014, monthly in spring and
185 summer and every two months in autumn and winter. For each species, number of dry shoots
186 per plot was weighted by its initial cover.

187

188 *Shrub cover*

189 In June and July 2012, corresponding to the dormant season for Mediterranean shrubland
190 (Prieto et al. 2009), we performed an exhaustive flora survey in each of the 92 plots. The
191 survey was done after the growing season in order to let the vegetation recover from any
192 mechanical damage due to the installation of the rain exclusion devices (from September to
193 December 2011). We measured plant cover, which is a good proxy of biomass (Stevens &
194 Carson 2001; Garcia-Palacios et al. 2012), for the 4 shrub species of each plot in 2012 and
195 2014. Relative cover change was then calculated for each dominant shrub species over these
196 two years, weighted by the initial cover per plot:

$$197 \quad \text{Relative cover change} = \frac{\%Cover Sp_{ij} 2014 - \%Cover Sp_{ij} 2012}{\%Cover Sp_{ij} 2012}$$

198 where i = one of the 4 shrub species and j = a study plot from 1 to 92. A positive relative
199 change in percentage of cover was read as an increase of aboveground biomass. Conversely,
200 a negative relative change was read as to a decrease of aboveground biomass.

201

202 *Statistical analysis*

203 All statistical analyses were performed with R software (version 3.3.1, The R Foundation
204 for Statistical Computing, Vienna, Austria). Values for litterfall and dry shoot number of the
205 4 plant species per plot were weighted by initial cover in order to examine relative increase
206 or decrease according to plant species richness or composition.

207 We used analysis of variance (ANOVA), followed by Tukey tests for post hoc pairwise
208 comparisons, on litterfall over the 2 years, number of dry shoots at the end of monitoring in
209 July 2014, and change in plant cover between 2012 and 2014 of the 4 shrub species (*Cistus*,
210 *Quercus*, *Rosmarinus* and *Ulex*). ANOVA were performed to test the effects of the factors
211 plant species richness (i.e. mono, bi-, tri- and tetraspecific plots), plant species composition
212 (i.e. 8 possible combinations for each species), and precipitation conditions (i.e. control or
213 rain exclusion). Due to the existing significant interactions between factors, we performed
214 one-way ANOVAs to test the effects of plant species richness and composition in control or
215 in rain exclusion conditions for each of the 4 shrub species. Student's t -tests were used to test
216 whether litterfall, number of dry shoots and change in plant cover were altered by the rain
217 exclusion treatment at both the 4 levels of plant species richness per plot and the 8 plant
218 species combinations for each of the 4 shrub species.

219 We explored the dynamics of the necromass in monospecific communities over the
220 experiment period by performing a linear regression between the weighted dry shoot number
221 and the number of months since the beginning of the survey.

222

223 **RESULTS**

224

225 *Litterfall patterns*

226 Litterfall of the 4 species showed strong seasonality, with a peak at the summer period
227 (June to September 2013 and 2014; Fig. 1) and the lowest values from January to March.

228 From October 2012 to September 2014, litterfall differed strongly among the 4 plant
229 species along the gradient *Ulex* ($646.5 \pm 50.9 \text{ g.m}^{-2}$) < *Rosmarinus* ($770.4 \pm 38.8 \text{ g.m}^{-2}$) <
230 *Quercus* ($968.8 \pm 43.8 \text{ g.m}^{-2}$) < *Cistus* ($1346.3 \pm 59.2 \text{ g.m}^{-2}$) ($F = 41.9, P < 0.0001$). Litterfall
231 for each plant species was strongly influenced by shrub species richness (Fig. 2), with a
232 general increase of litterfall as the number of dominant shrub species increased (Appendix
233 S3). *Cistus*, *Rosmarinus* and *Ulex* litterfalls were affected by the rain exclusion treatment,
234 but this effect was dependent on number of shrub species in the plant community (Fig. 2).
235 Precipitation reduction had a negative effect on litterfall in monospecific stands with -28.7%
236 ($t = 5.1, P = 0.0068$; Fig. 2a), -30.1% ($t = 4.7, P = 0.0090$; Fig. 2c) and -31.8% ($t = 3.1, P =$
237 0.0359 ; Fig. 2d) litterfall for *Cistus*, *Rosmarinus* and *Ulex*, respectively. In addition, lower
238 litterfall in rain-excluded plots was also observed in bispecific plots for *Cistus* in *Cistus/Ulex*
239 mixture (-17.5%; $t = 3.4, P = 0.0274$; Appendix S4a) and for *Rosmarinus* in
240 *Cistus/Rosmarinus* mixture (-15.3%; $t = 3.6, P = 0.0237$; Appendix S4c). Precipitation
241 reduction had no effect on litterfall of *Quercus* nor litterfall of shrubs in mixture with
242 *Quercus*, regardless of plant species richness (Fig. 3) or composition (Appendix S4).

243

244 *Dry shoot response to plant diversity and increased drought*

245 Contrary to litterfall, dry shoot quantity showed no seasonality during the survey period
246 (Fig. 3). Number of dry shoots of *Cistus*, *Rosmarinus* and *Ulex* in monospecific plots only
247 increased under rain exclusion during the survey period (Fig. 3).

248 In July 2014, after 2.5 years of rain exclusion, the number of dry shoots differed among
249 the 4 plant species, with fewer dry shoots for *Quercus* and *Rosmarinus* than for *Cistus* and
250 *Ulex* ($F = 27.2$, $P < 0.0001$). We observed no dry shoots for *Quercus* and *Rosmarinus* in
251 several plots and up to 8.4 ± 0.5 dry shoot.m⁻² for *Ulex* in monospecific plots under rain
252 exclusion conditions (Fig. 4). We observed a decrease of dry shoot number according to plant
253 species richness only for *Quercus* (Fig. 4b) and *Ulex* (Fig. 4d) under rain exclusion
254 conditions. Rain exclusion treatment increased the number of dry shoots of *Cistus*, *Quercus*
255 and *Ulex* only in low-species-richness communities (Fig. 4). Indeed, dry shoot numbers
256 significantly increased for *Cistus* ($t = 8.2$, $P = 0.0039$; Fig. 4a), *Quercus* ($t = 41.0$, $P < 0.0001$;
257 Fig. 4b) and *Ulex* ($t = 3.0$, $P = 0.0404$; Fig. 4d) in monospecific plots under rain exclusion
258 conditions. For all 4 shrubs, necromass was not different between plots with different
259 compositions belonging to the same richness level whatever the rainfall conditions
260 (Appendix S5).

261

262 ***Cover change response to plant diversity and drought***

263 Plant cover changes from early summer 2012 to early summer 2014 differed among the
264 4 plant species from $-28.7\% \pm 17.4$ (*Ulex* in tetraspecific plots in rain exclusion conditions)
265 to $+78.1\% \pm 21.9$ (*Rosmarinus* in tetraspecific plots in rain exclusion conditions; Fig. 5).
266 Rain exclusion treatment affected cover change of *Quercus*, *Rosmarinus* and *Ulex*, but this
267 effect differed according to shrub richness level (Fig. 5). *Quercus* plant cover increased in
268 bispecific plots ($+24.6\%$; $t = 2.6$, $P = 0.0182$; Fig. 5b) and *Rosmarinus* plant cover increased

269 in tetraspecific plots (+79.4%; $t = 3.1$, $P = 0.0283$; Fig. 5c) whereas *Rosmarinus* plant cover
270 decreased in monospecific plots (-59.8%; $t = 3.3$, $P = 0.0298$; Fig. 5c), and *Ulex* plant cover
271 decreased in tetraspecific plots (-57.4%; $t = 2.5$, $P = 0.0456$; Fig. 5d).

272

273 **DISCUSSION**

274 The litterfall of all 4 species showed strong seasonality with a peak occurring in late
275 spring to early summer (i.e. June and July). This was not surprising for *Cistus* as summer leaf
276 abscission is a typical drought-avoiding strategy (De Dato et al. 2008). We expected a change
277 in the timing of leaf fall in rain exclusion plots, as a result of a shift in the onset of leaf
278 senescence due to drier conditions. However, there was an apparent synchrony between
279 treatments, which could be due to the coarse temporal resolution of the samplings. This
280 synchrony also appeared between species. Some older studies in Mediterranean shrublands
281 have documented litterfall peak occurring in April-May (in Spain: Canellas & San Miguel
282 1998; Milla et al. 2005; in France: Rapp & Bachelier 1971; Floret et al. 1989). Leading on
283 from these earlier studies, the phenological shift towards a later litterfall peak in late spring-
284 early summer could be a consequence of progressive global climate warming and drying over
285 the past decade. This effect could outmatch the exclusion effect on the phenological cycle of
286 the evergreen species. Maximum leaf abscission was found to occur at the time of new
287 growth (Mediavilla & Escudero 2003), and here litterfall was observed to increase in April-
288 May but remained low compared to the peak litterfall of June-July.

289 There was a general increase of litterfall with increasing number of dominant shrub
290 species, suggesting higher litter production in more diverse shrub communities, in line with
291 previous results suggesting higher productivity in more diverse plant communities (Hooper
292 et al. 2005; Montès et al. 2008; Cardinale et al. 2011). After two years of rain exclusion,

293 litterfalls of *Cistus*, *Rosmarinus* and *Ulex* decreased in monospecific plots whereas *Quercus*
294 litterfall was not altered. These results suggest species-specific responses to the rain
295 exclusion treatment, which is consistent with previous studies conducted in temperate and
296 Mediterranean shrublands (Peñuelas et al. 2004) and in Mediterranean forests (Liu et al.
297 2015). The absence of effect on *Quercus* could suggest a higher tolerance to drier conditions.
298 The decrease in litterfall for *Cistus*, *Rosmarinus* and *Ulex* was contrary to what we first
299 hypothesized and to what some long-term studies have found (Prieto et al. 2009; Liu et al.
300 2015). Our results suggested a reduction of growth and leaf production in these species as a
301 short-term response to drier conditions, leading to a subsequent decrease in litterfall. Growth
302 reduction would thus be a drought-resistance strategy allowing nutrient and water saving.
303 Our results are more consistent with some short time-scaled studies showing that lower
304 precipitation induces lower litter production, whether in a natural ecosystem (Pavón et al.
305 2005) or under controlled hydric conditions (Alegre et al. 2004). The reduction of leaf
306 production or leaf area could be interpreted as a conservative strategy to reduce transpiration
307 and maintain hydraulic conductance under water depletion (Limousin et al. 2009; Barbeta et
308 al. 2015). The lack of effect of increased drought on litterfall in plurispecific plots highlights
309 the role of plant diversity in the mitigation of environmental changes.

310 The principal causes of necromass increase (as a proxy of mortality) in Mediterranean
311 ecosystems are drought and herbivory (Raventós et al 2010). Here, the number of dry shoots
312 was greater for *Cistus* and *Ulex* than for *Quercus* and *Rosmarinus*, in accordance with Baeza
313 et al. (2011) who found that early successional species (i.e. *Cistus* and *Ulex*) exhibit higher
314 quantities of standing dead biomass than later successional species (i.e. *Quercus* and
315 *Rosmarinus*) after 15 to 20 years since the last fire. *Cistus* and *Ulex* are shorter-lived than
316 *Quercus* and *Rosmarinus* and exhibit faster biomass turnover (De Luis et al. 2008; Baeza et

317 al. 2011). Since the shrubland here was 15 years old, we could reasonably expect higher
318 necromass from the oldest individuals. Nevertheless, this possible bias occurred in both
319 control and exclusion plots. *Ulex* also has some phenological and architectural traits resulting
320 in long-standing necromass before dropping. The contrasting results between species could
321 be explained by their successional status and life span (Baeza et al. 2011), but also by their
322 functional traits.

323 As for litterfall, the effect of drier conditions on necromass was also species-specific as
324 reported for plant mortality in Mediterranean ecosystems after severe droughts or fires (del
325 Cacho & Lloret 2010; Raventós et al. 2010). Necromass production was low in *Quercus* and
326 *Rosmarinus*: in monospecific stands, *Quercus* and *Rosmarinus* showed 0.25 and 0.09 dry
327 shoots per m² under rain exclusion, respectively. These responses could point to a high
328 resistance to drought. Indeed, *Rosmarinus* has leaf traits characteristics of xerophytic species
329 that could help to physiologically resist to water deficit, high summer temperatures and
330 radiation (Rotondi et al. 2003). *Quercus* has deep vertical roots allowing it to reach water
331 stored at depth (Ksontini et al. 1998; Baquedano & Castillo 2007). The deepest soil layers
332 were probably not affected by the rain exclusion treatment. We also cannot rule out the
333 possibility that the roots of *Quercus* may have escaped from the 16m² plots, which means the
334 necromass data warrant careful interpretation. *Quercus* also has leaf traits with physiological
335 benefits for water conservation such as sclerophyllous leaves (Ksontini et al. 1998) or
336 individually encrypted stomata by epicuticular waxes to minimize transpiration (Rotondi et
337 al. 2003; Roth-Nebelsick et al. 2013). Consequently, it can maintain its leaf water potential
338 and at most avoid a hydraulic failure (Roth-Nebelsick et al. 2013). Conversely, *Cistus* and
339 *Ulex* produced significantly more necromass under rain exclusion in monospecific plots.
340 *Cistus* is the only species with malacophyllous leaves and larger lamina (Table 1) that could

341 mean higher transpiration. Interestingly, even though *Ulex* had thorny photosynthetic stems
342 with extreme leaf reduction, considered an evolutionary characteristic of resistance to
343 drought (Cornelissen et al. 2003), its necromass was significantly higher under rain exclusion
344 in monospecific plots. This could be due to an intraspecific competition, as previously found
345 by Raventós et al. (2010). In plurispecific communities, species diversity appeared to
346 mitigate the negative effects of rainfall exclusion on *Ulex*. *Quercus* also showed a decrease
347 of dry shoots in rain exclusion plots according to species richness levels. Both responses
348 suggest lower necromass in more diverse shrub communities. Dominant plant diversity
349 highlights a niche differentiation (Turnbull et al. 2013): there may be less competition for
350 water resource in plurispecific plots due to the diversity of water acquisition traits
351 (Silvertown 2004). Note that *Cistus*, *Rosmarinus* and *Ulex* significantly increased necromass
352 under drier conditions during the monitoring period. Besides the fact that *Cistus* and *Ulex*
353 exhibit a long-standing necromass (Baeza et al. 2011; Pausas et al. 2012), this may indicate
354 an accentuation of the negative effect on plant performance and the hydric deficit over time.
355 Indeed, it has been found that plant capacity to recover after hydric stress can diminish with
356 number of drying cycles, even in drought-adapted species (Flexas et al. 2004).

357 The direction and magnitude of change in plant cover were also species-specific, as
358 reported in other studies (Lloret et al. 2004; Liu et al. 2015). The near overall decrease of
359 *Cistus* and *Ulex* cover (except for *Ulex* in tetraspecific plots) regardless of hydric conditions
360 could be partly due to the increase of necromass, lower biomass allocation to vegetative
361 growth, and/or changes in recruitment (Prieto et al. 2009). Del Cacho & Lloret (2010)
362 reported a decrease in Mediterranean woody seedling emergence when mortality increased
363 and a negative effect of drought on seedling establishment. Here, *Ulex* cover increased in
364 tetraspecific plots under control condition, suggesting a positive effect of shrub diversity on

365 *Ulex* performance (Montès et al. 2008; Cardinale et al. 2011). Nevertheless, under drier
366 conditions the positive effect on *Ulex* disappeared, probably by a shift of interspecific
367 relationships in response to the water resource shortage (Maestre et al. 2009). Contrary to
368 what frequently is reported as legume-facilitating effects, we did not observe a positive effect
369 of *Ulex* on the cover of the other species. This result is consistent with a previous study on a
370 near-identical shrubland close to the experimental site (Montès et al. 2008) and suggests that
371 the main limiting factor is not nitrogen soil level but probably soil water availability. Only
372 *Quercus* and *Rosmarinus* cover increased in drier conditions. We can posit that they could
373 take advantage of higher mortality of *Cistus* and *Ulex*, through life traits (Table 1) that confer
374 a high resistance to drought. This idea is further strengthened by the low mortality of
375 *Rosmarinus* and, to a lesser extent, of *Quercus*, suggesting a higher competitive ability to
376 reach water resources or an ability to maintain efficient photosynthesis under drier conditions
377 (Ksontini et al. 1998; Rotondi et al. 2003; Roth-Nebelsick et al. 2013). *Quercus* and
378 *Rosmarinus* responses revealed that biodiversity could modulate the negative effects of drier
379 conditions on biomass production, but the threshold for evident positive effects is species
380 dependent.

381

382 **CONCLUSION**

383 Shrub species responses were affected by the rain exclusion treatment, but these effects
384 were species-specific and mainly dependent on shrub richness level. Increasing shrub
385 richness in the plant community led to a higher litter production for all 4 species in both
386 control and exclusion plots. This was not induced by a higher necromass and may be related
387 to higher biomass production, and it suggests that species richness could reduce the negative
388 impact of increased drought on shrub communities (Lloret et al. 2004; Doblas-Miranda et al.

389 2015). The positive effect of shrub diversity, that attenuated the increased impacts of drought,
390 was also noticeable on necromass production for some species. Necromass of *Cistus*,
391 *Quercus* and *Ulex* was significantly higher under rain exclusion only in monospecific stands.
392 Necromass of *Quercus* and *Rosmarinus* was almost negligible in control plots and low in rain
393 exclusion plots.

394 All the species studied are stress-tolerant sensu Grime (i.e. all stresses which contribute
395 to a decrease of the productivity; Grime 1977). In the present study, we observed a drought
396 tolerance gradient from *Quercus* (the most tolerant) to *Rosmarinus* (intermediate tolerant)
397 and finally *Ulex* and *Cistus* (less tolerant). We observed that positive interactions seemed
398 dominant in drought conditions (i.e. high abiotic stress) but only occurred in plots with the
399 highest shrub species richness (i.e. tri- and tetra-specific plots). We can hypothesize that
400 intraspecific competition in Mediterranean shrublands with low shrub richness could emerge
401 (*Ulex*) or be exacerbated (*Cistus*) by the decrease of water resources, and lead to an increase
402 of necromass. Based on the dominant species' functional and life traits, it seems that these
403 species probably do not use water resources in the same temporal or spatial pattern. Our
404 results support the idea that in more diverse Mediterranean shrubland communities, niche
405 differentiation (complementarity) drives the positive diversity effect on plant growth and
406 survival under drier conditions, in relation to plant functional diversity (Bulleri et al. 2016).
407 In the context of future climate change in the Mediterranean region, maintaining a high
408 diversity level appears critical to mitigate drought effects on less-resistant species (*Cistus*
409 and *Ulex*). Nevertheless, our results shows that future conditions may favor highly drought-
410 resistant species (*Quercus* and *Rosmarinus*), leading to shifts in plant community
411 composition (del Cacho & Lloret 2010), a possible loss of diversity, and/or changes in
412 ecosystem functioning. One of the challenges to contend with future changes in ecosystem

413 functioning under increasing drought is to identify the most sensitive plant species in
414 competition for a scarce resource and the effect of diversity on their survival. Research in
415 this direction could clarify what type of species interactions would dominate under new
416 environmental conditions. This would paint a quite realistic picture of the composition,
417 functioning and thus environmental services of ecosystems under predicted global changes.

418

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428

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625

626 **Table 1.** Characteristics of the four shrub species (Ksontini et al 1998; Rotondi et al. 2003;
 627 Baquedano and Castillo 2007; Baeza et al. 2011; Paula and Pausas 2011; Roth-Nebelsick
 628 2013). Leaf area (expressed as mm², mean \pm SE, n =140 to 340) was measured in control
 629 plots of the present study. Dash symbol indicates an absence of data.

630

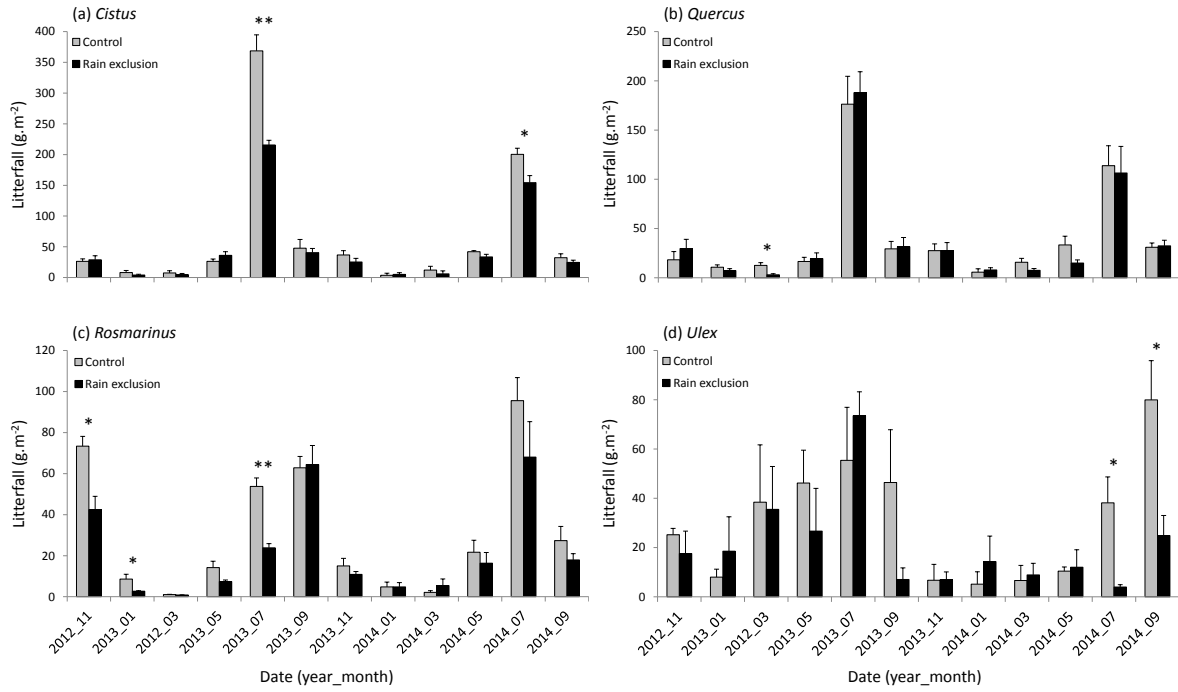
	Strategy after disturbance	Clonality	Succesional stage	Life span	Root system	Leaf type	Leaf cover	Leaf Area	Stomata protection
<i>Cistus albidus</i>	obligate seeder	no	early	short (10-15 years)	shallow	mallacophyllous	indumentum	257 \pm 5	encrypted stomata
<i>Quercus coccifera</i>	resprouter	yes	late	long (4-50 years)	deep vertical	coriaceous	waxes	170 \pm 3	encrypted stomata
<i>Rosmarinus officinalis</i>	obligate seeder	no	late	medium (30-40 years)	shallow	coriaceous	indumentum	42 \pm 3	revolute margins
<i>Ulex parviflorus</i>	obligate seeder	no	early	short (10-15 years)	shallow	-	-	-	-

631

632

633 **Fig. 1.** Dynamics of litter fall of (a) *Cistus*, (b) *Quercus*, (c) *Rosmarinus* and (d) *Ulex*
 634 according to the two environmental conditions (control and rain exclusion) in mono-specific
 635 plots. Values are mean \pm SE; n = 3. Significant differences between control and rain exclusion
 636 plots are indicated: * $P < 0.05$, ** $P < 0.01$.

637

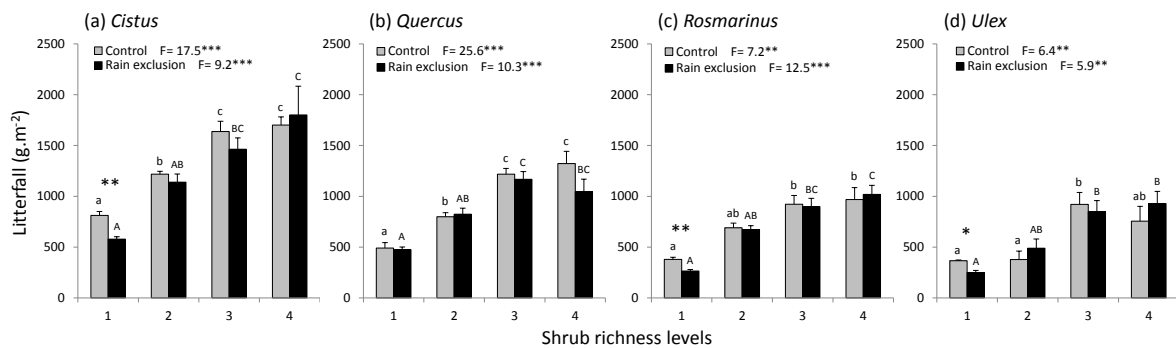


638

639

640 **Fig. 2.** Accumulated litter production from Oct 2012 to Sept 2014 of the four shrub species
 641 according to the two environmental conditions (control and rain exclusion) and the four shrub
 642 richness levels (mono-, bi-, tri- and tetra-specific plots). Values are mean \pm SE; $n = 6$ for
 643 mono-specific plot, $n = 18$ for bi-specific plot, $n = 18$ for tri-specific plot and $n = 8$ for tetra-
 644 specific plot. One-way ANOVA were performed to test for effects of plant species richness
 645 on litter fall on both control and rain exclusion conditions (F -values and associated P -values
 646 reported). Different letters denote significant differences between species richness level with
 647 $a < b < c$. Lowercase letters indicate significant differences between richness levels in control
 648 plots. Uppercase letters indicate significant differences between richness levels in rain
 649 exclusion plots. Significant differences between control and rain exclusion plots are
 650 indicated: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

651

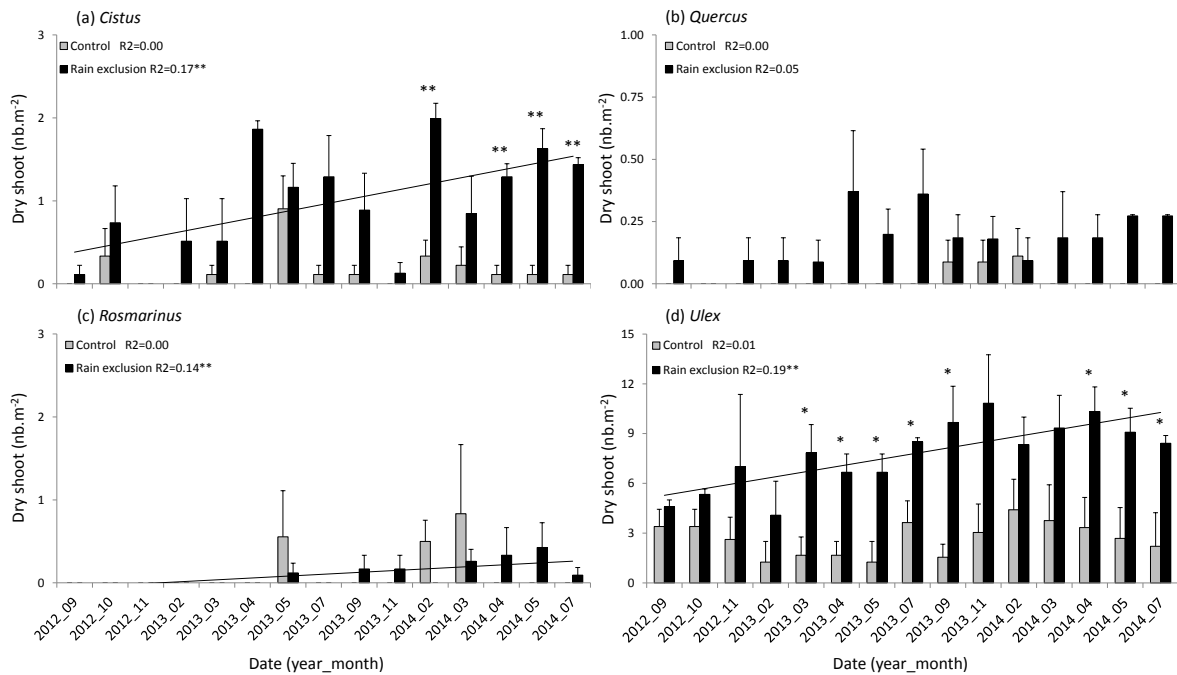


652

653

654 **Fig. 3.** Dynamics of dry shoot number of (a) *Cistus*, (b) *Quercus*, (c) *Rosmarinus* and (d)
 655 *Ulex* according to the two environmental conditions (control and rain exclusion) in
 656 monospecific plots. Values are mean \pm SE, n = 3. Significant differences between control
 657 and rain exclusion plots are indicated: * $P < 0.05$, ** $P < 0.01$. Significant linear relationships
 658 in rain exclusion plots are indicated: ** $P < 0.01$.

659

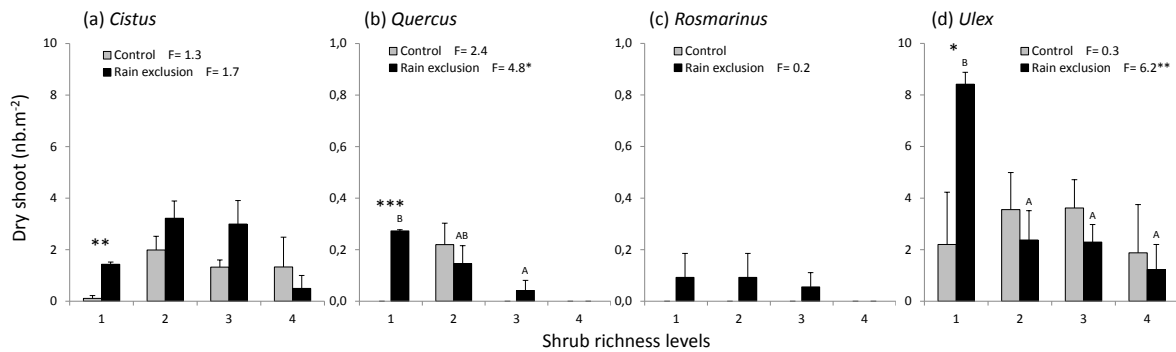


660

661

662 **Fig. 4.** Number of dry shoots of the four shrub species at end of monitoring period according
 663 to the two environmental conditions (control and rain exclusion) and to the four shrub
 664 richness levels (mono-, bi-, tri- and tetra-specific plots). Values are mean \pm SE, n = 6 for
 665 mono-specific plot, n = 18 for bispecific plot, n = 18 for tri-specific plot and n = 8 for tetra-
 666 specific plot. One-way ANOVA (or Kruskal-Wallis test when normality and
 667 homoscedasticity conditions were not met) were performed to test for effects of plant species
 668 richness on dry shoot number in both control and rain exclusion conditions (*F*-values and
 669 associated *P*-values reported). Different letters denote significant differences between
 670 species richness level with a < b. Significance between richness levels is designated as in
 671 Fig. 2. Significant differences between control and rain exclusion plots are indicated: **P* <
 672 0.05, ***P* < 0.01, ****P* < 0.001.

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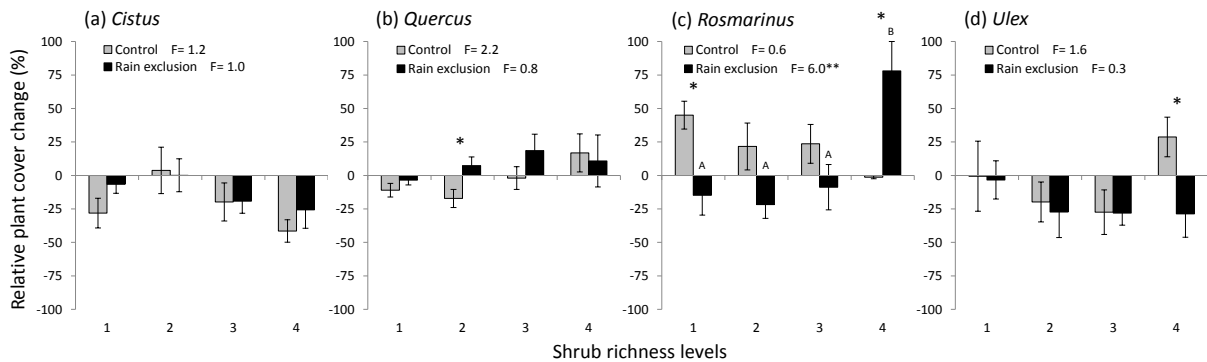


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676 **Fig. 5.** Relative change in plant cover from June 2012 to June 2014 of the four shrub species
 677 according to the two environmental conditions (control and rain exclusion) and to the four
 678 shrub richness levels (mono-, bi-, tri- and tetraspecific plots). Values are mean \pm SE; n= 6
 679 for monospecific plot, n= 18 for bispecific plot, n= 18 for trispecific plot and n= 8 for
 680 tetraspecific plot. One-way ANOVA were performed to test for the effects of plant species
 681 richness on plant change cover on both control and rain exclusion conditions (F -value and
 682 associated P -values are reported). Different letters denote significant differences between
 683 species richness levels with $a < b$. Significance between richness levels is designated as in Fig.
 684 2. Significant differences between control and rain exclusion plots are indicated with the
 685 respective symbols * for $P < 0.05$ and ** for $P < 0.01$.

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