



**HAL**  
open science

## Shrub species richness decreases negative impacts of drought in a Mediterranean ecosystem

Natalia Rodriguez-Ramirez, Mathieu Santonja, Virginie Baldy, Christine Ballini, Nicolas Montès

► **To cite this version:**

Natalia Rodriguez-Ramirez, Mathieu Santonja, Virginie Baldy, Christine Ballini, Nicolas Montès. Shrub species richness decreases negative impacts of drought in a Mediterranean ecosystem. *Journal of Vegetation Science*, 2017, 28 (5), pp.985-996. 10.1111/jvs.12558 . hal-01617556

**HAL Id: hal-01617556**

**<https://univ-rennes.hal.science/hal-01617556v1>**

Submitted on 4 May 2018

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 **AUTHOR NAMES:** Natalia Rodriguez-Ramirez, Mathieu Santonja, Virginie Baldy, Christine  
5 Ballini & Nicolas Montès

6

7 **ADDRESSES AND EMAIL ADDRESSES**

8 Rodriguez-Ramirez, N. (Corresponding author, natalia.rodriguez@imbe.fr)<sup>1\*</sup>

9 Santonja, M. (mathieu.santonja@gmail.com)<sup>1,2\*</sup>

10 Baldy, V. (virginie.baldy@imbe.fr)<sup>1</sup>

11 Ballini, C. (christine.ballini@imbe.fr)<sup>1</sup>

12 Montès, N. (nicolas.montes@imbe.fr)<sup>1</sup>

13

14 <sup>1</sup>Aix Marseille Univ, Univ Avignon, CNRS, IRD, IMBE, Marseille, France

15 <sup>2</sup>Université Rennes 1 - UMR CNRS 6553 ECOBIO, Campus de Beaulieu, Rennes, France

16

17 \* = Natalia Rodriguez-Ramirez and Mathieu Santonja have equal contribution to the work.

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<sup>-1</sup>  
122 <sup>1</sup>; [www.infoclimat.fr](http://www.infoclimat.fr)). The last fire occurred in 1997 (35 km<sup>2</sup> burnt from a total of 100 km<sup>2</sup>  
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<sup>-1</sup> (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 m<sup>2</sup>  
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 m<sup>2</sup> 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 m<sup>2</sup>) 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<sup>-2</sup>.

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  $8.4 \pm 0.5$  dry shoot.m<sup>-2</sup> 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 m<sup>2</sup> 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 16m<sup>2</sup> 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

#### 419 **ACKNOWLEDGMENTS**

420 We thank our colleagues from CEFE UMR5175 (Montpellier) and from IMBE UMR  
421 7263 (Marseille) for their contribution to the set-up of the experiment and the field work.  
422 Special thanks go to Sylvie Dupouyet for her tireless assistance during the field work and the  
423 laboratory analyses. This study was funded by the Agence Nationale pour la Recherche  
424 (ANR) through the project CLIMED (ANR-09-CEP-007). N. Rodriguez-Ramirez received a  
425 PhD grant from the Colombian Institute for the Development of Science and Technology-  
426 COLCIENCIAS and M. Santonja received a PhD grant from Europe and the PACA region  
427 of France.

428

#### 429 **REFERENCES**

430 Alegre, J., Alonso-Blázquez, N., De Andrés, E.F., Tenorio, J.L. & Ayerbe, L. 2004.  
431 Revegetation and reclamation of soils using wild leguminous shrubs in cold semiarid  
432 Mediterranean conditions: litterfall and carbon and nitrogen returns under two aridity  
433 regimes. *Plant and Soil* 263: 203-212.

434 Baeza, M.J., Santana, V.M., Pausa, J.G. & Vallejo, V.R. 2011. Successional trends in  
435 standing dead biomass in Mediterranean basin species. *Journal of Vegetation Science* 22:  
436 467-474.

437 Baquenado, F.J. & Castillo, F.J. 2007. Drought tolerance in the Mediterranean species  
438 *Quercus coccifera*, *Quercus ilex*, *Pinus halepensis*, and *Juniperus phoenicea*.  
439 *Photosynthetica* 45: 229-238.

440 Barbeta, A., Mejia-Chang, M., Ogaya, R., Voltas, J., Dawson, T.E. & Peñuelas, J. 2015. The  
441 combined effects of a long-term experimental drought and an extreme drought on the use  
442 of plant-water sources in a Mediterranean forest. *Global Change Biology* 21: 1213-1225.

443 Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Peñuelas, J., Emmett, B., Korner, C., de  
444 Boeck, H, Christensen, JH, Leuzinger, S, Janssens, IA & Hansen, K 2012. Precipitation  
445 manipulation experiments - challenges and recommendations for the future. *Ecology*  
446 *Letters* 15: 899-911.

447 Bulleri, F., Bruno, J.F., Silliman, B.R. & Stachowicz, J.J. 2016. Facilitation and the niche:  
448 implications for coexistence, range shifts and ecosystem functioning. *Functional*  
449 *Ecology* 30: 70-78.

450 Canellas, I. & San Miguel, A. 1998. Litter fall and nutrient turnover in Kermes oak (*Quercus*  
451 *coccifera* L.) shrublands in Valencia (eastern Spain). *Annales des Sciences Forestières* 55:  
452 589-597.

453 Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G. & Peñuelas, J. 2011. Widespread  
454 crown condition decline, food web disruption, and amplified tree mortality with increased  
455 climate change-type drought. *Proceedings of the National Academy of Sciences of the*  
456 *United States of America* 108: 1474-1478.

457 Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L.,  
458 Balvanera, P., O' Connor, M.I. & Gonzalez, A. 2011. The functional role of producer  
459 diversity in ecosystems. *American Journal of Botany* 98: 572-592.

460 Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich,  
461 P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H.  
462 2003. A handbook of protocols for standardized and easy measurement of plant functional  
463 traits worldwide. *Australian Journal of Botany* 51: 335-380.

464 Dai, A. 2012. Increasing drought under global warming in observations and models. *Nature*  
465 *Climate Change* 3: 52-58.

466 de Dato, G.D., Pellizzaro, G., Cesaraccio, C., Sirca, C., De Angelis, P., Duce, P., Spano, D.,  
467 Scarascia Mugnozza, G. 2008. Effects of warmer and drier climate conditions on plant  
468 composition and biomass production in a Mediterranean shrubland community. *iForest* 1:  
469 39-48.

470 Del Cacho, M. & Lloret, F. 2010. Resilience of Mediterranean shrubland to a severe drought  
471 episode: the role of seed bank and seedling emergence. *Plant Biology* 14: 458-466.

472 De Luis, M., Raventós, J., Wiegand, T., & Carlos González-Hidalgo, J. 2008. Temporal and  
473 spatial differentiation in seedling emergence may promote species coexistence in  
474 Mediterranean fire-prone ecosystems. *Ecography* 31: 620-629.

475 Dias, B., Diaz, S., McGlone, M., Hector, A., Wardle, D.A., Ruark, G., Gitay, H., Toivonen,  
476 H., Thompson, I., Mulongoy, K.J., Guariguata, M.R., Straka, P. & Burianek, V. 2003.  
477 Biodiversity and linkages to climate change. In: *Interlinkages between Biological*  
478 *Diversity and Climate Change - Advice on the Integration of Biodiversity Considerations*  
479 *into the Implementation of the United Nations Framework Convention on Climate Change*  
480 *and Its Kyoto Protocol*. CBD Technical Series 10.

481 Doblas-Miranda, E., Martínez-Vilalta, J., Lloret, F., Alvarez, A., Avila, A., Bonet, F.J.,  
482 Brotons, L., Castro, J., Curiel Yuste, J., Diaz, M., Ferrandis, P., Garcia-Hurtado, E.,  
483 Iriondo, J.M., Keenan, T.F., Latron, J., Llusia, J., Loepfe, L., Mayol, M., More, G., Moya,

484 D., Peñuelas, J., Pons, X., Poyatos, R., Sardans, J., Sus, O., Vallejo, V.R., Vayreda, J. &  
485 Retana, J. 2015. Reassessing global change research priorities in Mediterranean terrestrial  
486 ecosystems: how far have we come and where do we go from here? *Global Ecology and*  
487 *Biogeography* 24: 25-43.

488 FAO, F. 1988. FAO/UNESCO Soil Map of the World, Revised Legend, with corrections and  
489 updates. World Resources Report 60, FAO, Rome, Italy.

490 Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley, C., Rounsevell,  
491 M.D.A., Dube, O.P., Tarazona, J. & Velichko, A.A. 2007. Ecosystems, their properties,  
492 goods and services. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., Hanson, C.E. & van  
493 der Linden, P.J. (eds.) *Climate Change 2007: impacts, adaptation and vulnerability.*  
494 *Contribution of working group II to the fourth assessment report of the intergovernmental*  
495 *panel on climate change*, pp 211-272. Cambridge University Press, Cambridge, US.

496 Flexas, J., Bota, J., Cifre, J., Escalona, J., Galmés, J., Gulías, J., Lefi E.K., Martínez-Cañellas,  
497 S.F., Moreno, M.T., Ribas-Carbó, M., Riera, D., Sampol, B. & Medrano, H. 2004.  
498 Understanding down-regulation of photosynthesis under water stress: future prospects and  
499 searching for physiological tools for irrigation management. *Annals of Applied Biology*  
500 144: 273-283.

501 Floret, C., Galan, M.J., Le Floc'h, E., Leprince, F. & Romane, F. 1989. Description of plant  
502 annual cycles (France). In: Orshan, G. (eds.) *Plant Pheno-morphological Studies in*  
503 *Mediterranean Type Ecosystems*, pp 9-97. Kluwer Academic Publishers, Dordrecht,  
504 Netherlands.

505 Garcia-Palacios, P., Querejeta, J.I., Maestre, F.T., Escudero, A. & Valladares, F. 2012.  
506 Impact of simulated changes in rainfall regime and nutrient deposition on the relative

507 dominance and isotopic composition of ruderal plants in anthropogenic grasslands. *Plant*  
508 *and Soil* 352: 303-319.

509 Gibelin, A.L. & Deque, M. 2003. Anthropogenic climate change over the Mediterranean  
510 region simulated by a global variable resolution model. *Climate Dynamics* 20: 327-339.

511 Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its  
512 relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169-1194.

513 Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek,  
514 S., Carter, T.R., Cramer, W., Kuhn, I. & Sykes, M.T. 2012. Projecting the future  
515 distribution of European potential natural vegetation zones with a generalized, tree  
516 species-based dynamic vegetation model. *Global Ecology and Biogeography* 21: 50-63.

517 Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H.,  
518 Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer,  
519 J. & Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of  
520 current knowledge. *Ecological Monographs* 75: 3-35.

521 Konstantinidis, P., Tsiourlis, G. & Galatsidas, S. 2005. Effects of wildfire season on the  
522 resprouting of kermes oak (*Quercus coccifera* L.). *Forest Ecology and Management* 208:  
523 15-27.

524 Kröel-Dulay, J., Ransijn, J., Kappel Schmidt, I., Beier, C., De Angelis, P., de Dato, G.,  
525 Dukes, J.S., Emmett, B., Estiarte, M., Garadnai, J., Kongstad, J., Kovacs-Lang, E.,  
526 Steenberg Larsen, K., Liberati, D., Ogaya, R., Riis-Nielsen, T., Smith, A.R., Sowerby, A.,  
527 Tietema, A. & Peñuelas, J. 2015. Increased sensitivity to climate change in disturbed  
528 ecosystems. *Nature Communications* 6: 6682.

529 Ksontini, M., Louguet, P., La Ray, D. & Nejib Rejeb, M. 1998. Comparaison des effets de la  
530 contrainte hydrique sur la croissance, la conductance stomatique et la photosynthèse de



531 jeunes plants de chênes méditerranéennes (*Quercus suber*, *Q. faginea*, *Q. coccifera*) en  
532 Tunisie. *Annales des Sciences Forestières* 55: 477-495.

533 Leemans, R. & Halpin, P.N. 1992. Global change and biodiversity. In: Groombridge, B.  
534 (eds.) *Biodiversity 1992: Status of the Earth's Living Resources*, pp 254-255. Chapman  
535 Hall, London, UK.

536 Leibold, M.A. 1995. The Niche Concept Revisited - Mechanistic Models and Community  
537 Context. *Ecology* 76: 1371-1382.

538 Limousin, J.M., Rambal, S., Ourcival, J.M., Rocheteau, A., Joffre, R. & Rodriguez-Cortina,  
539 R. 2009. Long-term transpiration change with rainfall decline in a Mediterranean *Quercus*  
540 *ilex* forest. *Global Change Biology* 15: 2163-2175.

541 Lloret, F., Peñuelas, J. & Estiarte, M. 2004. Experimental evidence of reduced diversity of  
542 seedlings due to climate modification in a Mediterranean-type community. *Global*  
543 *Change Biology* 10: 248-258.

544 Liu, D., Ogaya, R., Barbeta, A., Yang, X. & Peñuelas, J. 2015. Contrasting impacts of  
545 continuous moderate drought and episodic severe droughts on the aboveground-biomass  
546 increment and litterfall of three coexisting Mediterranean woody species. *Global Change*  
547 *Biology* 21: 4196-4209.

548 MacCann, K. 2000. The diversity-stability debate. *Nature* 405: 228-233.

549 Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. 2009. Refining the stress-  
550 gradient hypothesis for competition and facilitation in plant communities. *Journal of*  
551 *Ecology* 97: 199-205.

552 Mediavilla, S. & Escudero, A. 2003. Photosynthetic capacity, integrated over the lifetime of  
553 a leaf, is predicted to be independent of leaf longevity in some tree species. *New*  
554 *Phytologist* 159: 203-211.

555 Milla, R., Castro-Díez, P., Maestro-Martínez, M. & Montserrat-Martí G. 2005. Does the  
556 Gradualness of Leaf Shedding Govern Nutrient Resorption from Senescing Leaves in  
557 Mediterranean Woody Plants? *Plant and Soil* 278: 303-313.

558 Montès, N., Maestre, F.T., Ballini, C., Baldy, V., Gauquelin, T., Planquette, M., Greff, S.,  
559 Dupouyet, S. & Perret, J.B. 2008. On the relative importance of the effects of selection  
560 and complementarity as drivers of diversity productivity relationships in Mediterranean  
561 shrublands. *Oikos* 117: 1345-1350.

562 Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. 2000.  
563 Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

564 Paula, S. & Pausas, J.G. 2011. Root traits explain different foraging strategies between  
565 resprouting life histories. *Oecologia* 165: 321-331.

566 Pausas, J.G., Alessio, G.A., Moreira, B. & Corcobado, G. 2012. Fires enhance flammability  
567 in *Ulex parviflorus*. *New Phytologist* 193: 18-23.

568 Pavón, N.P., Briones, O. & Flores-Rivas, J. 2005. Litterfall production and nitrogen content  
569 in an intertropical semi-arid Mexican scrub. *Journal of Arid Environments* 60: 1-13.

570 Peñuelas, J., Gordon, C., Llorens, L., Nielsen, T., Tietema, A., Beier, C., Bruna, P., Emmett,  
571 B., Estiarte, M. & Gorissen, A. 2004. Nonintrusive field experiments show different plant  
572 responses to warming and drought among sites, seasons, and species in a north-south  
573 European gradient. *Ecosystems* 7: 598-612.

574 Polade, S.D., Pierce, D.W., Cayan, D.R., Gershunov, A. & Dettinger, M.D. 2014. The key  
575 role of dry days in changing regional climate and precipitation regimes. *Scientific Reports*  
576 4: 4364.

577 Prieto, P., Peñuelas, J., Llusà, J., Asensio, D. & Estiarte, M. 2009. Effects of experimental  
578 warming and drought on biomass accumulation in a Mediterranean shrubland. *Plant*  
579 *Ecology* 205: 179-191.

580 Rapp, M., Bachelier, G. 1971. Cycle de la matière organique et des éléments minéraux dans  
581 quelques écosystèmes méditerranéens. Centre National de la Recherche Scientifique (ed.),  
582 Paris, FR.

583 Raventós, J., Wiegand, T. & de Luis, M. 2010. Evidence for the spatial segregation  
584 hypothesis: a test with nine-year survivorship data in a Mediterranean shrubland. *Ecology*  
585 91: 2110-2120.

586 Roth-Nebelsick, A. Fernandez, V., Peguero-Pina, J.J. Sancho-Knapik, D. & Gil-Peegrín, E.  
587 2013. Roth-Nebelsick, A. 2013. Stomatal encryption by epicuticular waxes as a plastic  
588 trait modifying gas exchange in a Mediterranean evergreen species (*Quercus coccifera*  
589 L.). *Plant, Cell and Environment* 36: 579-589.

590 Rotondi, A., Rossi, F., Asunis, C., & Cesaraccio, C. 2003. Leaf xeromorphic adaptations of  
591 some plants of a coastal Mediterranean macchia ecosystem. *Journal of Mediterranean*  
592 *Ecology* 4: 25-35.

593 Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E.,  
594 Cornelissen, J.H.C. & Gurevitch, J. 2001. A meta-analysis of the response of soil  
595 respiration, net nitrogen mineralization, and aboveground plant growth to experimental  
596 ecosystem warming. *Oecologia* 126: 543-562.

597 Santonja, M., Baldy, V., Fernandez, C., Balesdent, J. & Gauquelin, T. 2015. Potential shift  
598 in plant communities with climate change in a Mediterranean Oak forest: consequence on

599 nutrients and secondary metabolites release during litter decomposition. *Ecosystems* 18:  
600 1253-1268.

601 Santonja, M., Rancon, A., Fromin, N., Baldy, V., Hättenschwiler, S., Fernandez, C., Montès  
602 N. & Mirleau, P. 2017. Plant litter diversity increases microbial diversity and carbon and  
603 nitrogen cycling in a Mediterranean shrubland. *Soil Biology and Biochemistry* 111: 124-  
604 134.

605 Sardans, J. & Peñuelas, J. 2013. Plant-soil interactions in Mediterranean forest and  
606 shrublands: impacts of climatic change. *Plant and Soil* 365: 1-33.

607 Shihan, A., Hättenschwiler, S., Milcu, A., Joly, F.X., Santonja, M. & Fromin, N. 2017.  
608 Changes in soil microbial substrate utilization in response to altered litter diversity and  
609 precipitation in a Mediterranean shrubland. *Biology and Fertility of Soils* 53: 171-185.

610 Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution* 19: 605-  
611 611.

612 Stevens, M.H.H. & Carson, W.P. 2001. Phenological complementarity, species diversity, and  
613 ecosystem function. *Oikos* 92:291-296.

614 Tilman, D., Lehman, C.L. & Thomson, K.T. 1997. Plant diversity and ecosystem  
615 productivity: Theoretical considerations. *Proceedings of the National Academy of  
616 Sciences of the United States of America* 94: 1857-1861.

617 Turnbull, L.A., Levine, J.M., Loreau, M. & Hector, A. 2013. Coexistence, niches and  
618 biodiversity effects on ecosystem functioning. *Ecology Letters* 16: 116-127.

619 Vautard, R., Gobiet, A., Sobolowski, S., Kjellstrom, E., Stegehuis, A., Watkiss, P., Mendik,  
620 T., Landgen, O., Nikulin, G., Teichmann, C. & Jacob, D. 2014. The European climate  
621 under 2 C global warming. *Environmental Research Letters* 9: 034006.

622 Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J. & Hungate, B.A. 2011. Responses of terrestrial  
623 ecosystems to temperature and precipitation change: a meta-analysis of experimental  
624 manipulation. *Global Change Biology* 17: 927-942.  
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 mm<sup>2</sup>, 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

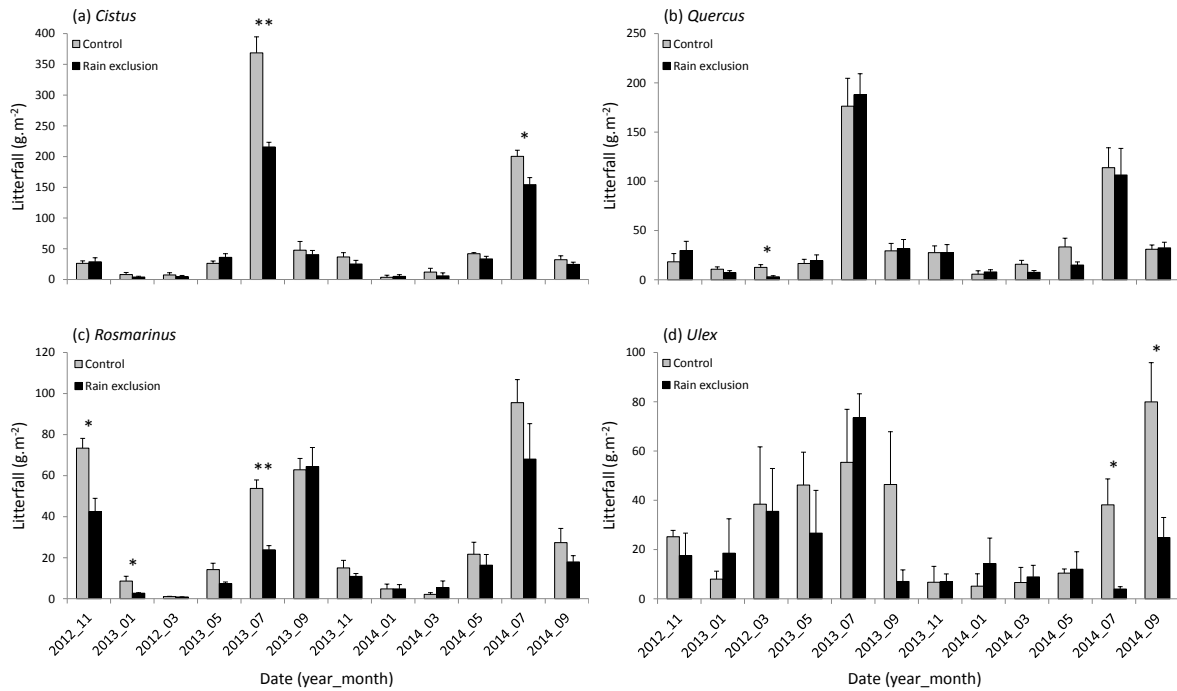
	Strategy after disturbance	Clonality	Succesional stage	Life span	Root system	Leaf type	Leaf cover	Leaf Area	Stomata protection
<i>Cistus albidus</i>	obligate seeder	no	early	short (10-15 years)	shallow	mallacophyllous	indumentum	257 $\pm$ 5	encrypted stomata
<i>Quercus coccifera</i>	resprouter	yes	late	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

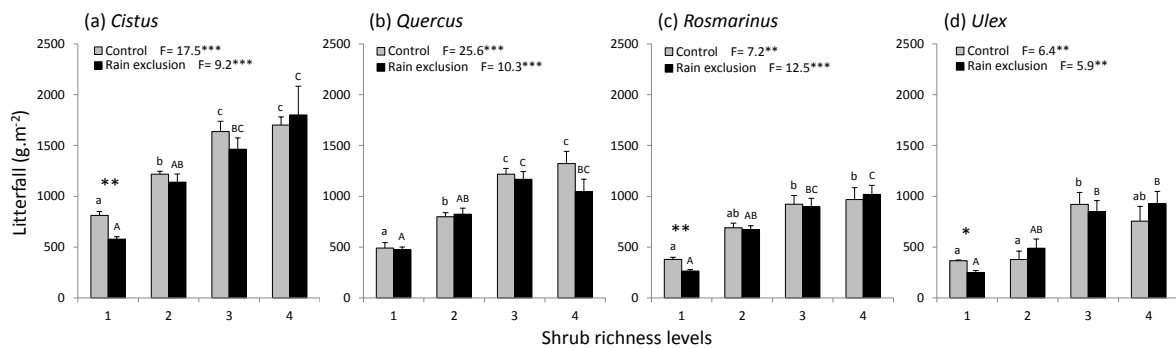


638

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



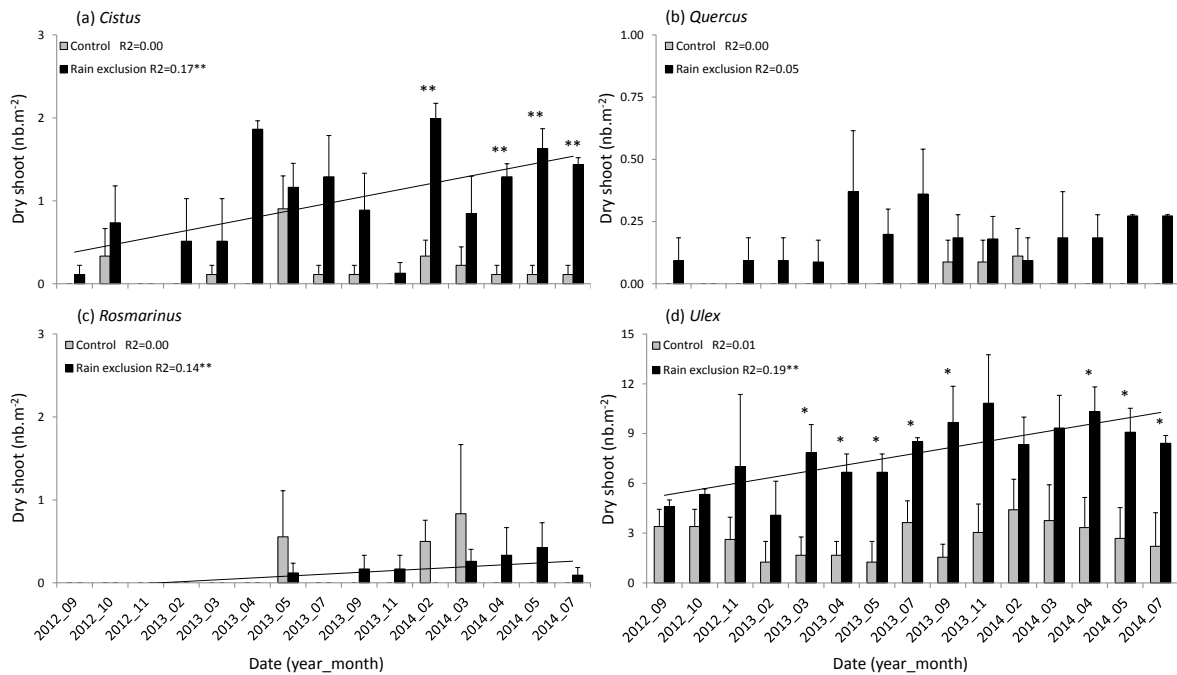
652

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

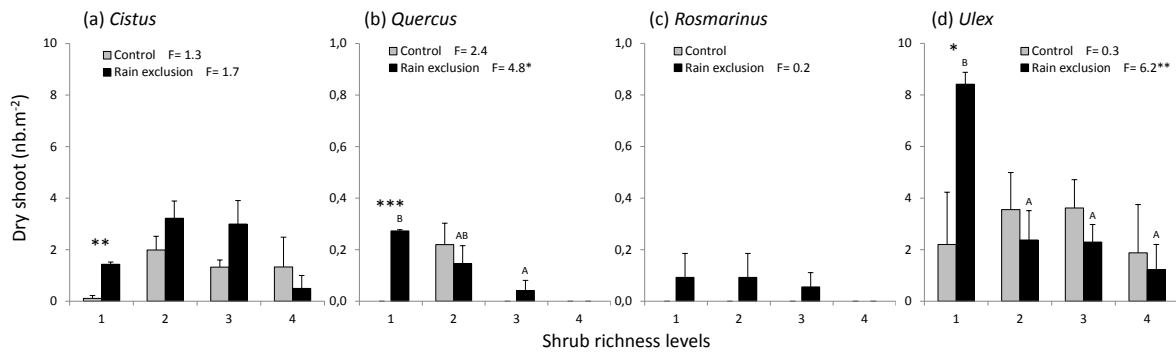


660

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  $0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ .

673

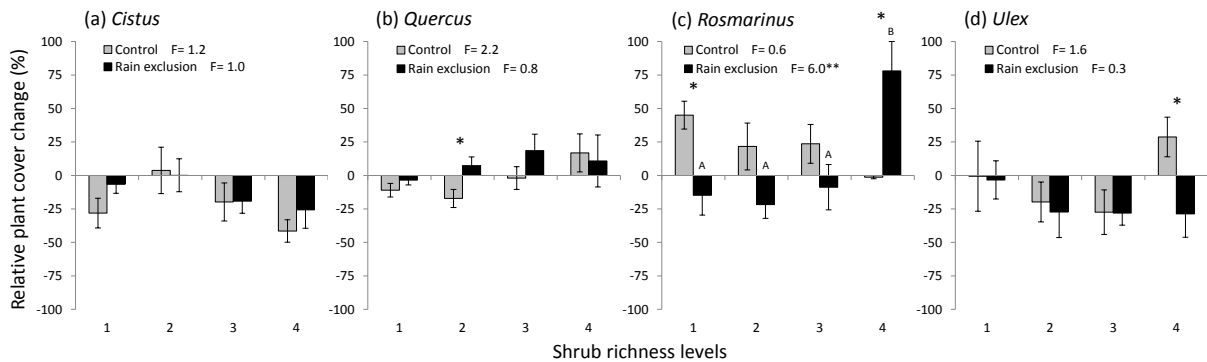


674

675

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  $P < 0.01$ .

686



687

688