

1 **Shift in community structure mainly by the losses of herbs in long-term warming**  
2 **and drought experiments and natural extreme droughts in an early-successional**  
3 **Mediterranean shrubland**

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23 **Abstract**

24 Global warming and recurring drought are expected to accelerate water limitation for  
25 plant communities in semiarid Mediterranean ecosystems and produce directional shifts  
26 in structure and composition that are not easily detected, and supporting evidence is  
27 scarce. We conducted a long-term (17 years) nocturnal-warming (+0.6 °C) and drought  
28 (-40% rainfall) experiment in an early-successional Mediterranean shrubland to study the  
29 changes in community structure and composition, contrasting functional groups and  
30 dominant species, and the superimposed effects of natural extreme drought. Species  
31 richness decreased in both the warming and drought treatments. Responses to the  
32 moderate warming were associated with decreases in herb abundance, and responses to  
33 the drought were associated with decreases in both herb and shrub abundance. The  
34 drought also significantly decreased community diversity and evenness. Changes in  
35 abundance differed between herbs (decreases) and shrubs (increases or no changes). Both  
36 warming and drought, especially drought, increased the relative species richness and  
37 abundance of shrubs, favoring the establishment of shrubs. Both warming and drought  
38 produced significant shifts in plant community composition. Experimental warming  
39 shifted the community composition from *Erica multiflora* toward *Rosmarinus officinalis*,  
40 and drought consistently shifted the composition toward *Globularia alypum*. The  
41 responses in biodiversity (e.g. community biodiversity, changes of functional groups and  
42 compositional shifts) were strongly correlated with atmospheric drought (SPEI) in winter-  
43 spring and/or summer, indicating sensitivity to water limitation in this early-successional

44 Mediterranean ecosystem, especially during continuous natural severe droughts. Our  
45 results suggest that long-term nocturnal warming and drought, combined with natural  
46 severe droughts, will accelerate shifts in species assembles and community diversity and  
47 composition in early-successional Mediterranean shrublands, highlighting the necessity  
48 for assessing the impacts on ecosystemic functioning and services and developing  
49 effective measures for conserving biodiversity.

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67 **Introduction**

68 The ecological consequences of the losses of biodiversity and ecosystemic functioning  
69 and services have been strongly associated with global climate change (Chapin *et al.*,  
70 2000; Walther *et al.*, 2002; Bellard *et al.*, 2012; Peñuelas *et al.*, 2013; Tilman *et al.*, 2014;  
71 Scheffers *et al.*, 2016). Ecosystems in the Mediterranean Basin, one of Earth's foci of the  
72 effects of climate change on biodiversity, will likely be affected by rapid warming and  
73 drought (Myers *et al.*, 2000; Peñuelas *et al.*, 2007, 2013; Dai, 2013). Climate-induced  
74 changes in plant community structure and composition in Mediterranean ecosystems have  
75 been documented, such as the losses of endemic species (Myers *et al.*, 2000; Schröter *et*  
76 *al.*, 2005; Peñuelas *et al.*, 2007; Gottfried *et al.*, 2012), changes in patterns of diversity  
77 (Chapin *et al.*, 2000; Walther *et al.*, 2002; Prieto *et al.*, 2009a; Kröel-Dulay *et al.*, 2015)  
78 and declines in community stability and resilience (Chapin *et al.*, 2000; Prieto *et al.*,  
79 2009a; Doblas-Miranda *et al.*, 2014; Brose & Hillebrand, 2016). The trends in  
80 meteorological records and the projections of climatic models suggest future climatic  
81 scenarios that would continue to trigger large and irreversible structural and  
82 compositional changes in Mediterranean plant communities, which would affect multiple  
83 ecosystemic functions and climatic feedback (Myers *et al.*, 2000; Peñuelas *et al.*, 2013;  
84 Doblas-Miranda *et al.*, 2014; Tilman *et al.*, 2014).

85 Strong evidence for the direction and magnitude of the impacts of climate change on  
86 plant community structure and composition, however, remains unclear. Ecological  
87 modelling (e.g. bioclimatic envelope and dynamic vegetation models) has been  
88 commonly used in recent decades for predicting the response of biodiversity to future

89 climate change, such as extinction and shifts in species ranges and abundance (Leuzinger  
90 *et al.*, 2011; Araújo & Peterson, 2012; Bellard *et al.*, 2012). Most of the models,  
91 however, have grossly underestimated the importance of species plasticity (e.g.  
92 physiological, phenological and morphological plasticity) and biotic interactions (e.g.  
93 competition, facilitation and mutualism) (Tylianakis *et al.*, 2008; Leuzinger *et al.*, 2011;  
94 Bellard *et al.*, 2012; Tilman *et al.*, 2014). Indeed, many studies have reported  
95 physiological (photosynthetic activities) (Llorens *et al.*, 2003; Prieto *et al.*, 2009b; Liu *et*  
96 *al.*, 2016), phenological (earlier or delayed) and morphological (leaf size, number and  
97 longevity) (Peñuelas *et al.*, 2004, 2009; Bernal *et al.*, 2011; Scheffers *et al.*, 2016;  
98 Thackeray *et al.*, 2016) adjustments associated with climate change as well as  
99 evolutionary adaptations (Jump & Peñuelas, 2005; Jump *et al.*, 2008; Hoffmann & Sgrò,  
100 2011; Scheffers *et al.*, 2016) to rapid warming and drought. Species loss or changes in  
101 abundance predicted by models do not therefore satisfactorily represent changes in  
102 community structure and composition in terrestrial ecosystems under future climatic  
103 scenarios. Some models have incorporated species plasticity, acclimation and biotic  
104 interactions, but most typically analyze data parameterized on short timescales (Luo *et*  
105 *al.*, 2011; Beier *et al.*, 2012; Estiarte *et al.*, 2016). The responses of community structure  
106 and composition to climate change, however, will be driven by slow processes over  
107 decadal or even longer timescales (Smith *et al.*, 2009; Luo *et al.*, 2011; Peñuelas *et al.*,  
108 2013; Estiarte *et al.*, 2016). Accurately assessing the changes in community structure and  
109 composition caused by long-term processes is thus essential for validating the models and  
110 providing realistic supporting information for future climate change.

111 Long-term experiments of climatic manipulation are among the best methods for  
112 studying the responses of species interactions and community dynamics under predicted  
113 climatic regimes (Luo *et al.*, 2011; Wu *et al.*, 2011; Beier *et al.*, 2012; Estiarte *et al.*,

114 2016). A few long-term (>10 years) climatic-manipulation experiments have been  
115 established in natural ecosystems in the last three decades (Leuzinger *et al.*, 2011; Luo *et*  
116 *al.*, 2011; Estiarte *et al.*, 2016). These experiments have demonstrated increasing (Walker  
117 *et al.*, 2006; Smith *et al.*, 2009; Elmendorf *et al.*, 2015), decreasing (dampening)  
118 (Leuzinger *et al.*, 2011; Barbeta *et al.*, 2013; Liu *et al.*, 2015) and unchanged (Grime *et*  
119 *al.*, 2008; Tielbörger *et al.*, 2014; Estiarte *et al.*, 2016) impacts of manipulation on  
120 community dynamics. Community responses to manipulative experiments have been  
121 reported for tundra (Walker *et al.*, 2006; Elmendorf *et al.*, 2015) and temperate grassland  
122 (Yang *et al.*, 2011) ecosystems, whereas no net (or chronic) changes have been reported  
123 for semiarid Mediterranean ecosystems (Tielbörger *et al.*, 2014; Estiarte *et al.*, 2016).  
124 Large shifts in community structure and composition, as proposed by the hierarchical-  
125 response framework, will likely come because of continuous and cumulative climatic  
126 disturbances (Smith *et al.*, 2009). Contrasting community responses to long-term  
127 climatic-manipulation experiments can be due to differential effects in functional groups  
128 or dominant species, indicating alterations in dominance hierarchies and relative  
129 abundances (Smith *et al.*, 2009; Luo *et al.*, 2011; Yang *et al.*, 2011; Peñuelas *et al.*, 2013).  
130 The shortage of long-term field manipulations has greatly limited our understanding of  
131 the alterations in plant community structure and composition and in functional groups  
132 and dominance shifts. The cumulative effects of long-term climate change, however, may  
133 also be abrupt or non-linear when thresholds (tipping points) are exceeded, exacerbated  
134 by climatic extremes (Ciais *et al.*, 2005; Peñuelas *et al.*, 2007; Jentsch *et al.*, 2011;  
135 Reichstein *et al.*, 2013; Doblas-Miranda *et al.*, 2014). Long-term manipulative field  
136 experiments are thus likely to record transformative changes and to identify the  
137 mechanisms of community dynamics in response to the overlapping effects of climatic

138 variability and extremes (Smith *et al.*, 2009; Luo *et al.*, 2011; Jentsch *et al.*, 2011;  
139 Kreyling *et al.*, 2011; Estiarte *et al.*, 2016).

140 Most natural terrestrial ecosystems around the globe are disturbed either by  
141 anthropogenic activities or natural climatic events and are either not in equilibrium or are  
142 recovering (Scheffer *et al.*, 2009; Seddon *et al.*, 2016). The successional status of an  
143 ecosystem is an influential factor that must be considered for accurately forecasting  
144 community dynamics under climate change (Prieto *et al.*, 2009a; Kröel-Dulay *et al.*, 2015;  
145 Brose & Hillebrand, 2016; Estiarte *et al.*, 2016). The reestablishment of species or  
146 structural reordering in these dynamic ecosystems at early successional stages, however,  
147 may be strongly affected under the predicted scenarios of climate change (Jump *et al.*,  
148 2008; Prieto *et al.*, 2009a; Peñuelas *et al.*, 2013; Kröel-Dulay *et al.*, 2015). Field  
149 experiments have demonstrated that continuous warming and drought manipulations have  
150 influenced reproductive outputs and seedling compensation, which could potentially lead  
151 to substantial shifts in plant community structure and composition in early-successional  
152 shrubland ecosystems (Lloret *et al.*, 2004, 2009; Del Cacho *et al.*, 2012). Some reports,  
153 however, have indicated that experimental climatic treatments in early-successional  
154 ecosystems have increased physiological adjustments (photosynthetic activities, stomatal  
155 conductance and water-use efficiency) (Llorens *et al.*, 2003; Prieto *et al.*, 2009b; Liu *et*  
156 *al.*, 2016), altered phenological activities (Peñuelas *et al.*, 2004; Bernal *et al.*, 2011) and  
157 invoked rapid genetic changes toward seedling phenotypes to adapt warming and drought  
158 (Jump & Peñuelas, 2005; Jump *et al.*, 2008). Whether physiological, phenological and  
159 genetic modifications can increase the occurrence and relative abundance of more  
160 resistant species and can compensate for species loss or decreases in the abundance of  
161 sensitive species on long-term temporal scales remains unclear. Our understanding of  
162 species competition, community dynamics and their mechanisms also remains poor,

163 especially for early-successional ecosystems (Kröel-Dulay *et al.*, 2015; Estiarte *et al.*,  
164 2016). Long-term manipulative experiments in early-successional or recovering  
165 ecosystems and monitoring the responses of community structure, functional groups or  
166 species dominance to global climate change are therefore urgently needed.

167 Long-term nocturnal-warming (0.6 °C average temperature increase) and drought (40%  
168 decrease in precipitation) experiments have been conducted in an early-successional  
169 Mediterranean shrubland since 1999. We hypothesized that long-term manipulations of  
170 both nocturnal warming and drought would decrease biodiversity at the community level  
171 (species richness (*S*), community diversity (*H*) and evenness (*E*)) and trigger different  
172 performances (species richness and abundance) between functional groups, ultimately  
173 leading to the decline or loss of sensitive groups (or species) and shifts in community  
174 composition to more resistant groups (or species). The specific objectives of this study  
175 were to determine: 1) if both warming and drought would significantly decrease  
176 community biodiversity (*S*, *H* and *E*) throughout the study period, 2) if contrasting  
177 responses of functional groups would decrease *S* and *H*, 3) if long-term experimental  
178 warming and drought would shift community composition by altering species dominance  
179 and 4) if changes in biodiversity were associated with the impacts of severe droughts  
180 (different timescales of the Standardized Precipitation Evapotranspiration Index (SPEI))  
181 The results of this study could provide experimental evidence to help the management  
182 and regulation of future biodiversity conservation.

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## 190 **2. Materials and method**

### 191 2.1 Study site

192 The study site was in a Mediterranean shrubland on a south-facing slope (13%) in the  
193 Garraf Natural Park, near Barcelona (northeastern Spain) (41°18'N, 1°49'E; 210 m a.s.l.).

194 The climate is typically Mediterranean, with hot and dry summers (June to August,  
195 average temperature of 22.8 °C) and wet springs (March to May, average rainfall of 147.8

196 mm) and autumns (September to November, average rainfall of 204.8 mm). The mean  
197 annual temperature and mean annual precipitation at the study site are 15.2 °C and 571

198 mm, respectively. The soil is calcareous, and the substrate is composed of marls and  
199 limestone, with rocky outcrops. This shrubland appeared after two severe wildfires in

200 1982 and 1994 in a *Pinus halepensis* forest. The vegetation is composed mainly of short  
201 perennial shrubs (<1.5 m) that dominated the regrowth after the two fires. The dominant

202 species of the shrubland are *Globularia alypum* and *Erica multiflora* (total proportion  
203 more than 50%), which are accompanied by other Mediterranean shrub species, such as

204 *Ulex parviflorus*, *Dorycnium pentaphyllum* and *Rosmarinus officinalis*. The undergrowth  
205 consists mainly of annual herbaceous plants (mostly Poaceae species) (Species

206 information as described in Table S1).

### 207 2.2 Manipulation experiments

208 We conducted a nocturnal-warming experiment from 1999 to 2014 and a drought  
209 experiment from 1999 to 2015 on three replicate blocks selected along a south-facing

210 slope (Llorens *et al.*, 2003; Peñuelas *et al.*, 2007; Prieto *et al.*, 2009a, 2009b; Liu *et al.*,  
211 2016). Each block contained three randomly distributed replicate warming, drought and  
212 control plots (4×5 m) (Peñuelas *et al.*, 2004), for a total of nine plots for all treatment.  
213 The warming experiment was established by passive nocturnal warming by covering the  
214 vegetation with reflective aluminum curtains (ILS ALU, AB Ludvig Svensson, Kinna,  
215 Sweden) at night that reduced outgoing infrared radiation. The curtains were activated  
216 automatically by preset light conditions (<200 lux). The drought experiment was  
217 conducted by excluding precipitation with transparent waterproof plastic covers during  
218 the wettest seasons (spring and autumn) to prolong the summer drought. A rain sensor  
219 activated the covers to intercept precipitation and retracted them when the rain stopped.  
220 The coverings for the warming and drought experiments were removed at wind  
221 speeds >10 m s<sup>-1</sup> to prevent damage. Scaffolding (1.2 m height) was installed in each plot  
222 to support the covering systems. Scaffolding was also installed in the control plots, but  
223 no curtains or covers were used. The soil temperature at a depth of 5 cm was 0.6 °C higher  
224 in the warming treatment than the control, and soil moisture in the 0-15 cm layer was  
225 16.7 % lower annually in the drought treatment than the control, throughout the 17-year  
226 experiment.

### 227 2.3 Measurements of vegetation and environmental parameters

228 Vegetation was assessed by pin-pointing once a year at the end of July or beginning of  
229 August (after the main growing season) from 1998 (the pre-treatment year) to 2015. The  
230 pin-point method describes the vegetation profile, including plant frequencies, that allows  
231 the estimation of community structure and composition. Only the central 3×4 m area of  
232 each plot was measured to avoid edge effects. Five parallel 3-m transects 0.8 m apart were  
233 permanently marked across this central area at the start of the study. Each transect had a  
234 sampling point every 5 cm (totaling 61 points per transect and 305 points per plot). We

235 lowered a long steel pin (3 mm diameter) through the vegetation at each sampling point  
236 for recording the height, species, organ (leaf, reproductive structure or stem) and state  
237 (alive or dead) of all plants the pin touched.

238  $S$  was obtained for each plot and year as the total number of species recorded. Species  
239 were classified by their life forms into two functional groups, herbs ( $h$ ) and shrubs ( $s$ ),  
240 and the richness of shrubs relative to the total number of species (*Relative Ss*) was  
241 calculated. Community diversity was estimated by the Shannon-Wiener index ( $H$ ) for  
242 each plot and year as:  $H = -\sum P_i \ln P_i$ , where  $P_i$  is the number of pin-point contacts for  
243 species  $i$  divided by the total number of contacts.  $E$  was estimated by the Pielou index for  
244 each plot and year as:  $E = (-\sum P_i \ln P_i) / \ln S$ , where  $S$  is the number of species. The  
245 abundance of each species within a plot and year was obtained as the total number of pin-  
246 point contacts. The abundances of the two functional groups were calculated using the  
247 abundances of species of each life form and were then log-transformed for estimating the  
248 abundance of herbs ( $Ah$ ) and shrubs ( $As$ ) and the abundance of shrubs relative to the total  
249 abundance of all species (*Relative As*). The abundances of typical species, *G. alypum*,  
250 Poaceae species (PO) and *R. officinalis*, were also log-transformed for calculating the  
251 changes in abundance due to warming and drought.

252 Daily air temperature and precipitation were recorded by a meteorological station at  
253 the study site. Temperature means were calculated for various periods (annual, AT;  
254 winter-spring, WST, from December to May and summer, ST, from June to August), and  
255 accumulated precipitation was calculated for the same periods (AP, WSP and SP,  
256 respectively). Soil moisture in the plots was measured (bi)weekly by three time-domain  
257 reflectometric probes permanently installed in each plot to a depth of 15 cm. Soil  
258 temperature in the plots at a depth of 5 cm was measured by temperature RTD Pt100 1/3  
259 DIN probes (Desin Company, Barcelona, Spain) permanently installed in the soil from

260 2000 to 2015. We used the data from a nearby meteorological station to determine the  
261 historical climatic trends for 1951-2015 (Fig. S1). We calculated the SPEI drought index  
262 (Vicente-Serrano *et al.*, 2010) using the historical data for 1951-2015 and our data at the  
263 site. SPEI incorporates the influences of precipitation and potential evapotranspiration  
264 (caused by warming temperatures) and provides information of the water balance at  
265 different timescales. We selected the winter-spring (May SPEI-4, from February to May)  
266 and summer (August SPEI-3, from June to August) water balances to identify the water  
267 deficits during the historical period 1951-2015 (Fig. S2), whereas several timescales were  
268 used for modelling the changes in biodiversity.

#### 269 2.4 Statistical analysis

270 The effects of the treatments on the parameters of community biodiversity ( $S$ ,  $H$  and  $E$ ),  
271 species richness of functional groups ( $Sh$ ,  $Ss$  and Relative  $Ss$ ), abundance of functional  
272 groups ( $Ah$ ,  $As$  and Relative  $As$ ) and abundance of the typical species were analyzed, and  
273 each parameter was analyzed separately (warming vs control and drought vs control) by  
274 linear mixed-effects models. We tested various models, including combinations of the  
275 covariates of temperature (AT, WST and ST), precipitation (AP, WSP and SP), SPEIs at  
276 different timescales and treatment as fixed variables. We selected a random structure  
277 among the random factors block, plot and plot nested within block (block/plot). The best  
278 models with the lowest Akaike information criteria included block as a random factor and  
279 the covariates:

$$280 \text{ Biodiversity parameters} = \text{SPEI} + \text{Treatment} \quad (1)$$

281 The SPEI timescales of the best model differed among the biodiversity parameters. May  
282 SPEI-4 was applied to analyze the changes in  $S$ ,  $H$ ,  $Ss$ , Relative  $Ss$  and the abundance of  
283 *G. alypum*; May SPEI-2 was applied to analyze the changes in  $Sh$ ,  $As$  and Relative  $Ss$ ;

284 April SPEI-3 was applied to analyze the changes in *E*, Relative *As* and the abundance of  
285 *R. officinalis* and July SPEI-3 was applied to analyze the changes in *Ah* and the abundance  
286 of Poaceae. All models used the lme4 package in R version 3.2.5.

287 The shifts in community composition were analyzed by a redundancy analysis (RDA)  
288 of species abundance, with treatment (control and separately warming or drought) and  
289 environmental factors as explanatory variables. Environmental factors included  
290 temperature (AT, WST and ST), precipitation (AP, WSP and SP) and SPEIs at different  
291 timescales. RDAs were performed separately for various periods to identify the temporal  
292 treatment effects on community composition: the first half of the experimental period  
293 (1999-2006), the second half (2007-2015) and the entire period (1999-2015). Treatments  
294 and SPEIs were selected for each period for analyzing the changes in community  
295 composition as:

296 Community compositions= Treatment + SPEI (2)

297 Various SPEI timescales (July SPEI-3, May SPEI-2 and May SPEI-4) were selected for  
298 analyzing compositional changes during the 1999-2006, 2007-2015 and 1999-2015  
299 periods. We also tested the significance of the changes in community composition for all  
300 variables (treatments and SPEIs) by analysis of variance (ANOVA) or each variable  
301 (treatments or SPEIs) using a Monte Carlo permutation test. The RDAs were conducted  
302 with the vegan package in R version 3.2.5.

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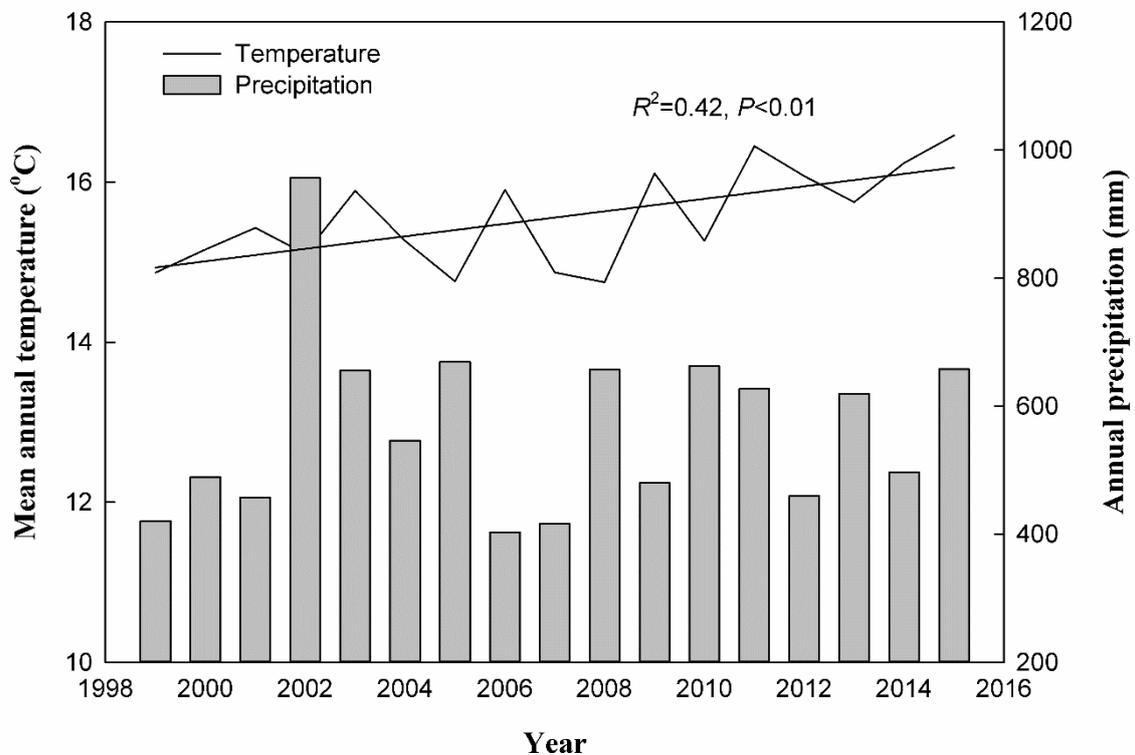
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### 310 3. Results

#### 311 3.1 Site conditions and abiotic variables of the experimental treatments

312 The historical climatic series (1951-2015) from the nearby meteorological station  
313 exhibited a warming trend of annual temperature (AT) ( $R^2=0.38$ ,  $P<0.001$ ) and a  
314 moderately stable annual precipitation (AP) (Fig. S1a). The warm and dry summers  
315 characteristic of the Mediterranean climate were exacerbated by a trend of increasing ST  
316 ( $R^2=0.24$ ,  $P<0.001$ ) and decreasing SP ( $R^2= 0.11$ ,  $P<0.01$ ) during this period (Fig. S1b).



317

318 Fig. 1 Mean annual temperature and annual precipitation during the study period 1999-

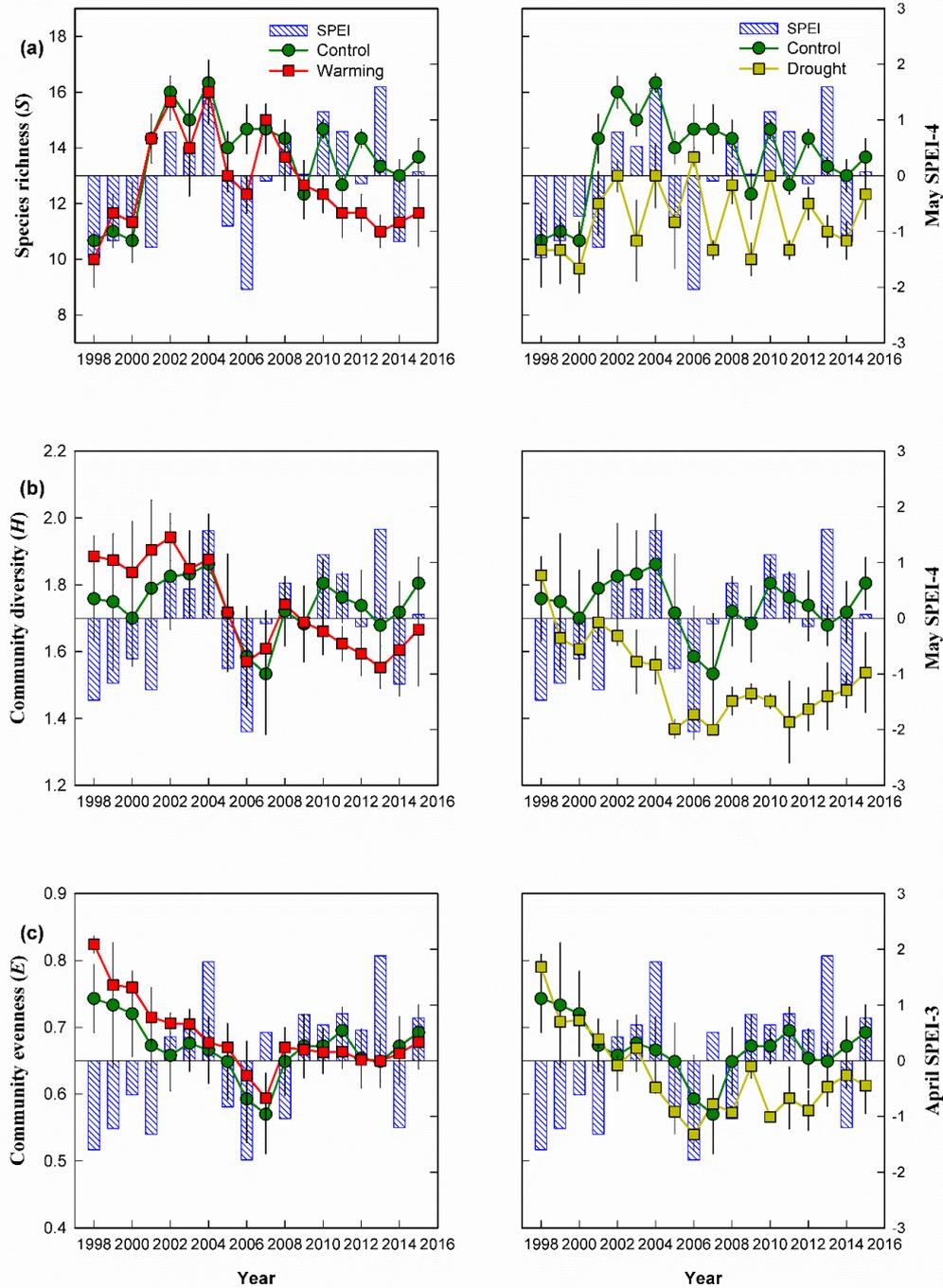
319 2015.

320 The trend in August-SPEI (for June, July and August) accordingly indicated a trend of  
321 increasing water deficits ( $R^2=0.13$ ,  $P<0.01$ ) (Fig. S2b). Average AT increased linearly  
322 during 1999-2015 ( $R^2=0.42$ ,  $P<0.01$ ) (Fig. 1), but AP fluctuated greatly, from 403.1 mm  
323 in 2006 to 956.2 mm in 2002. The study site experienced three extreme spring water  
324 deficits in 1999-2001, 2005-2006 and 2014 and four extreme summer water deficits in  
325 1999-2001, 2003-2006, 2009 and 2012-2013 (Fig. S2a, b).

326 Soil temperature at a depth of 5 cm varied greatly inter-annually during the study period  
327 but averaged 0.6 °C (anova,  $P<0.001$ ) higher in the nocturnal-warming treatment than  
328 the control (Fig. S3b). Soil moisture (SM) in the 0-15 cm layer also varied greatly during  
329 the study period (Fig. S3a) but decreased significantly by 16.7% in the drought treatment  
330 relative to the control (anova,  $P<0.001$ ). SM was similar in the control and drought  
331 treatments in 2006 and 2010 due to damage to the covering systems. SM was not  
332 significantly affected in the warming treatment throughout the study period.

### 333 3.2 *S*, *H* and *E* at the community level

334 *S*, *H* and *E* varied greatly throughout the study period (Fig. 2; Table 1). *S* was lower in  
335 both the warming (difference=-0.91,  $P<0.05$ ) and drought (difference=-2.19,  $P<0.001$ )  
336 treatments relative to the control. *H* and *E* were not affected by the experimental warming  
337 but both were significantly lower in the drought treatment than the control (difference=-  
338 0.22,  $P<0.001$ ; difference=-0.04,  $P<0.01$ ). The changes in *S*, *H* and *E* were associated  
339 with winter-spring SPEIs in the models. *S* was positively correlated with May SPEI-4 for  
340 warming-control (difference=0.62,  $P<0.001$ ) and drought-control (difference=0.45,  
341  $P<0.01$ ) comparisons. *H*, however, was poorly correlated with May SPEI-4 for warming-  
342 control and drought-control comparisons, and *E* was negatively correlated with April  
343 SPEI-3 for the warming (difference=-0.12,  $P<0.05$ ) and drought (difference=-0.11,  
344  $P<0.05$ ) models.



345

346 Fig. 2 Changes in (a) species richness ( $S$ ), (b) community diversity ( $H$ ) and (c) community  
 347 evenness ( $E$ ) in the warming, drought and control treatments during the study period  
 348 1998-2015. May SPEI-4 was the covariate factor for the changes in  $S$  and  $H$ , and April  
 349 SPEI-3 was the covariate factor for the changes in  $E$  in the models. Vertical bars indicate  
 350 the standard errors of the means (n=3 plots).

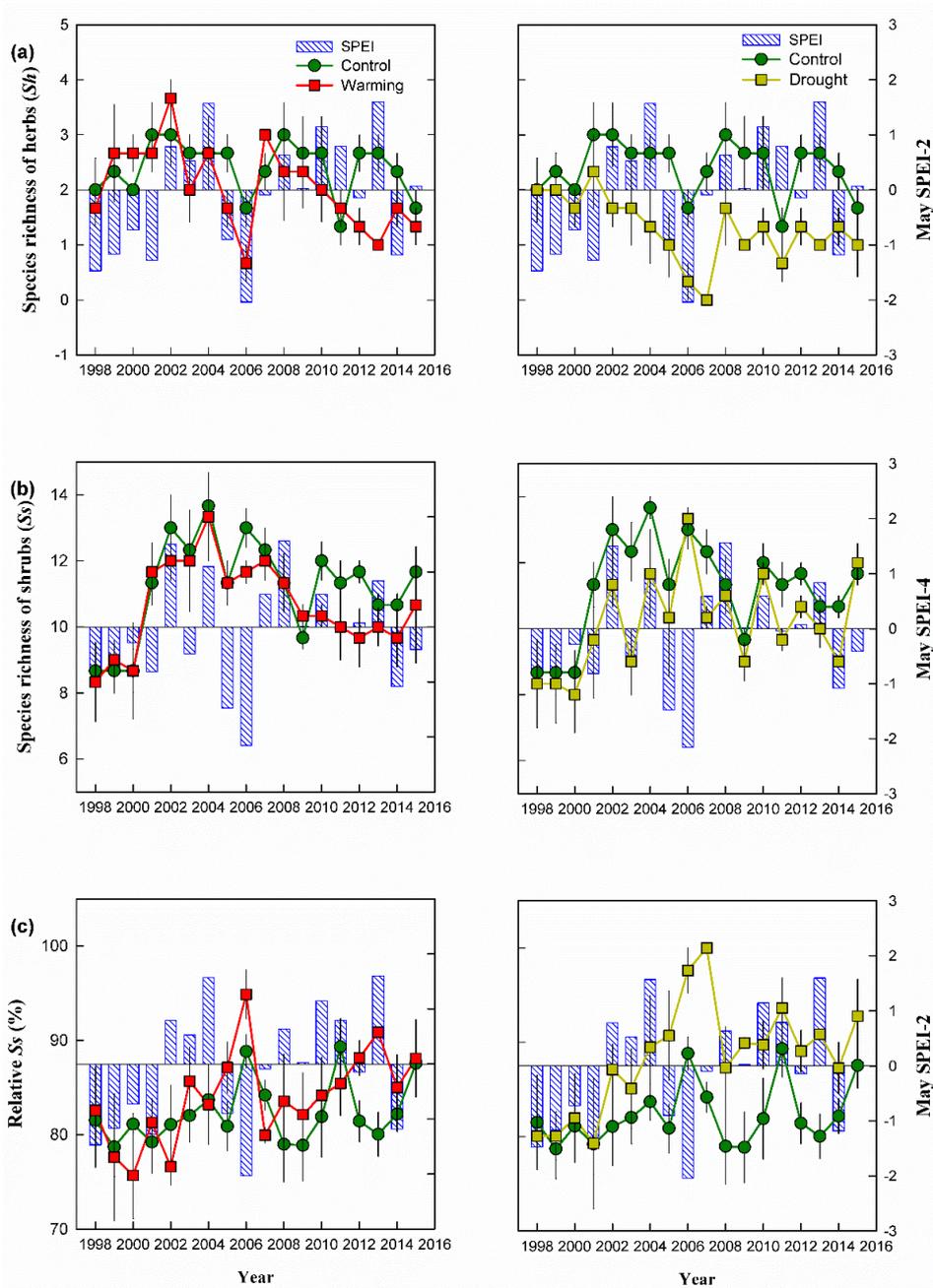
Table 1 Results from the best models for the responses of species richness (*S*), community diversity (*H*) and evenness (*E*) of the plant community to experimental warming and drought throughout the study period 1998-2015. The changes in *S* and *H* were associated with May SPEI-4 and the changes in *E* were associated with April SPEI-3 in the models. Warming-control and drought-control differences were analyzed. Significant differences are labeled with asterisks: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ . Significant effects are highlighted in bold type.

	<i>S</i>		<i>H</i>		<i>E</i>	
	Difference	<i>P</i>	Difference	<i>P</i>	Difference	<i>P</i>
Warming-control						
SPEI	<b>0.62</b>	***	0.01	ns	<b>-0.12</b>	*
Warming	<b>-0.91</b>	*	-0.004	ns	0.01	ns
Drought-control						
SPEI	<b>0.45</b>	**	0.001	ns	<b>-0.11</b>	*
Drought	<b>-2.19</b>	***	<b>-0.22</b>	***	<b>-0.04</b>	**

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### 352 3.3 The responses of *S* for the functional groups

353 *S* fluctuated differently for the herbs and shrubs during the study period (Fig. 3; Table 2),  
354 with *Sh* more stable. In contrast, *Ss* increased gradually, peaked ( $13.7 \pm 0.33$ ) in 2004 and  
355 then gradually decreased. *Sh* decreased under both warming (difference = -0.35,  $P < 0.05$ )  
356 and drought (difference = -1.11,  $P < 0.001$ ) relative to the control. *Ss*, however, did not  
357 change under warming but decreased under drought (difference = -1.04,  $P < 0.01$ ). Relative  
358 *Ss* therefore increased substantially under drought (difference = 0.08,  $P < 0.001$ ). The  
359 changes in *Sh*, *Ss* and Relative *Ss*, however, were associated with the water balance at  
360 different SPEI timescales (Table 2). *Sh* was positively correlated with May SPEI-2 in



361

362 Fig. 3 Changes in the species richness of (a) herbs ( $Sh$ ), and (b) shrubs ( $Ss$ ) and (c) in  
 363 Relative  $Ss$  in the warming, drought and control treatments during the study period 1998-  
 364 2015. May SPEI-2 was the covariate factor for the changes in  $Sh$ , and May SPEI-4 was  
 365 the covariate factor for the changes in  $Sh$  and Relative  $Ss$  in the models. Vertical bars  
 366 indicate the standard errors of the means ( $n=3$  plots).

367 warming-control (difference=0.30,  $P<0.001$ ) and drought-control (difference=0.13,  
 368  $P<0.1$ ) comparisons, and  $S_s$  was positively correlated with May SPEI-4 in warming-  
 369 control (difference=0.49,  $P<0.01$ ) and drought-control (difference=0.43,  $P<0.01$ )  
 370 comparisons. Relative  $S_s$ , however, was negatively correlated with May SPEI-2 only in  
 371 the warming-control comparison (difference=0.02,  $P<0.05$ ).

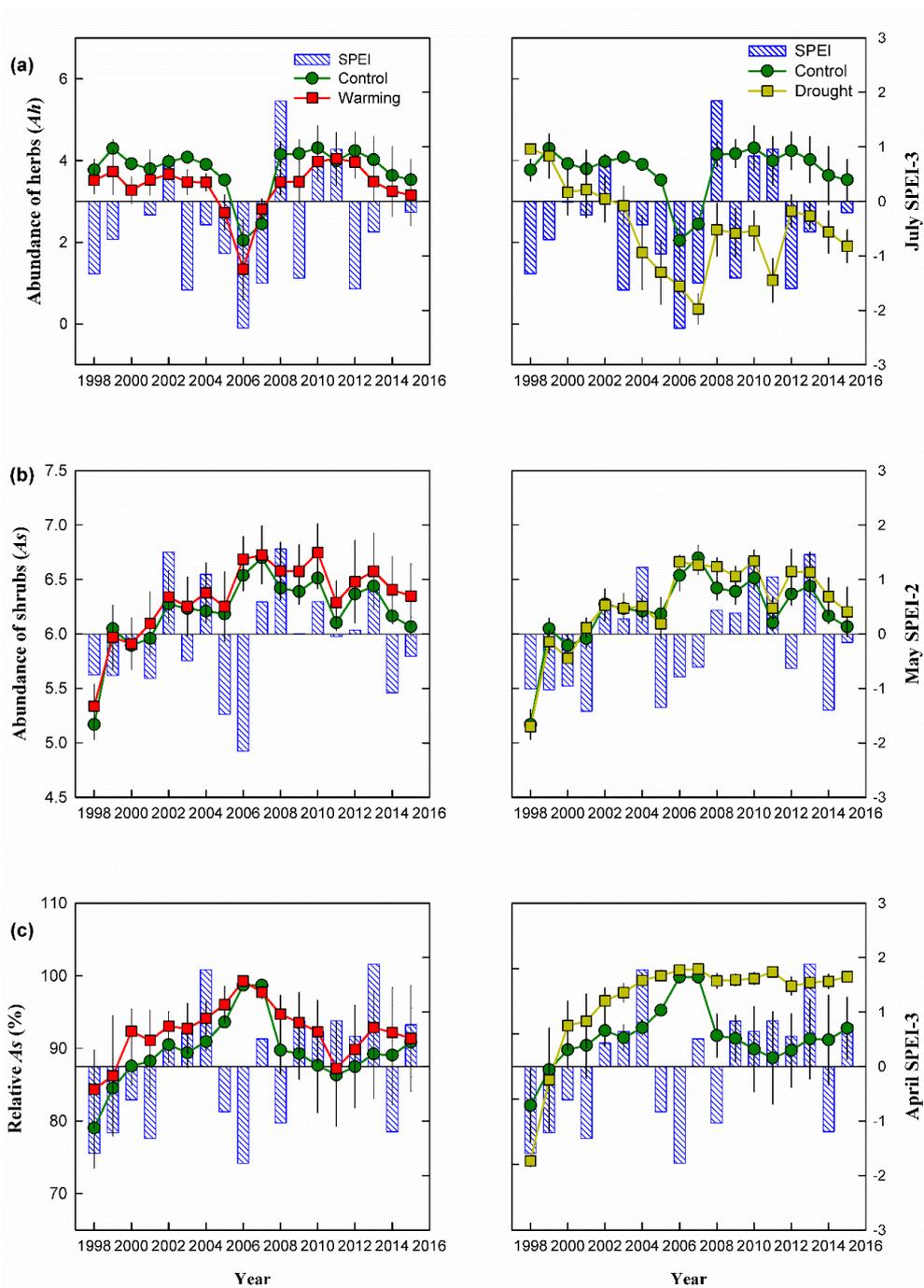
Table 2 Results from the best models for the responses of the species richness of herbs ( $Sh$ ) and shrubs ( $S_s$ ) and of Relative  $S_s$  to experimental warming and drought throughout the study period 1998-2015. The changes in  $Sh$  were associated with May SPEI-2 and the changes in  $Sh$  and Relative  $S_s$  were associated with May SPEI-4 in the models. Drought-control and warming-control differences were analyzed. Significant differences are labeled with asterisks: (\*)  $P<0.1$ , \*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$ . Significant effects are highlighted in bold type.

	$Sh$		$S_s$		Relative $S_s$	
	Difference	$P$	Difference	$P$	Difference	$P$
Warming-control						
SPEI	<b>0.3</b>	***	<b>0.49</b>	**	<b>0.02</b>	*
Warming	<b>-0.35</b>	*	-0.52	ns	0.02	ns
Drought-control						
SPEI	<b>0.13</b>	(*)	<b>0.43</b>	**	0.002	ns
Drought	<b>-1.11</b>	***	<b>-1.04</b>	**	<b>0.08</b>	***

372

### 373 3.4 The response of abundance for the functional groups

374  $A_h$  and  $A_s$  fluctuated differently, with a gradual decreasing trend for  $A_h$  in the first half  
 375 of the experimental period (1999-2006) and an increasing trend in the second half (2007-



376

377 Fig. 4 Changes in the abundance of (a) herbs (*Ah*) and (b) shrubs and in (c) Relative *As*  
 378 in the warming, drought and control treatments during the study period 1998-2015. July  
 379 SPEI-3, May SPEI-2 and April SPEI-3 were the covariate factors for the changes in *Ah*,  
 380 *As* and Relative *As*, respectively. Vertical bars indicate the standard errors of the means  
 381 (n=3 plots).

2015) and with a gradual increasing trend for *As* during the entire 1999-2015 period (Fig. 4; Table 3). *Ah* decreased both under warming (difference=-0.41,  $P<0.01$ ) and drought (difference=-1.4,  $P<0.001$ ) throughout the experiment relative to the control, but *As* marginally increased with warming (difference=0.13,  $P<0.1$ ) and was not affected by drought. Relative *As* increased under both warming (difference=0.03,  $P<0.05$ ) and

Table 3 Results from the best models for the responses of the abundance of herbs (*Ah*) and shrubs (*As*) and of Relative *As* to experimental warming and drought throughout the study period 1998-2015. The changes in *Ah*, *As* and Relative *As* were associated with July SPEI-3, May SPEI-2 and April SPEI-3 respectively in the models. Drought-control and warming-control differences were analyzed. Significant differences are labeled with asterisks: (\*)  $P<0.1$ , \*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$ . Significant effects are highlighted in bold type.

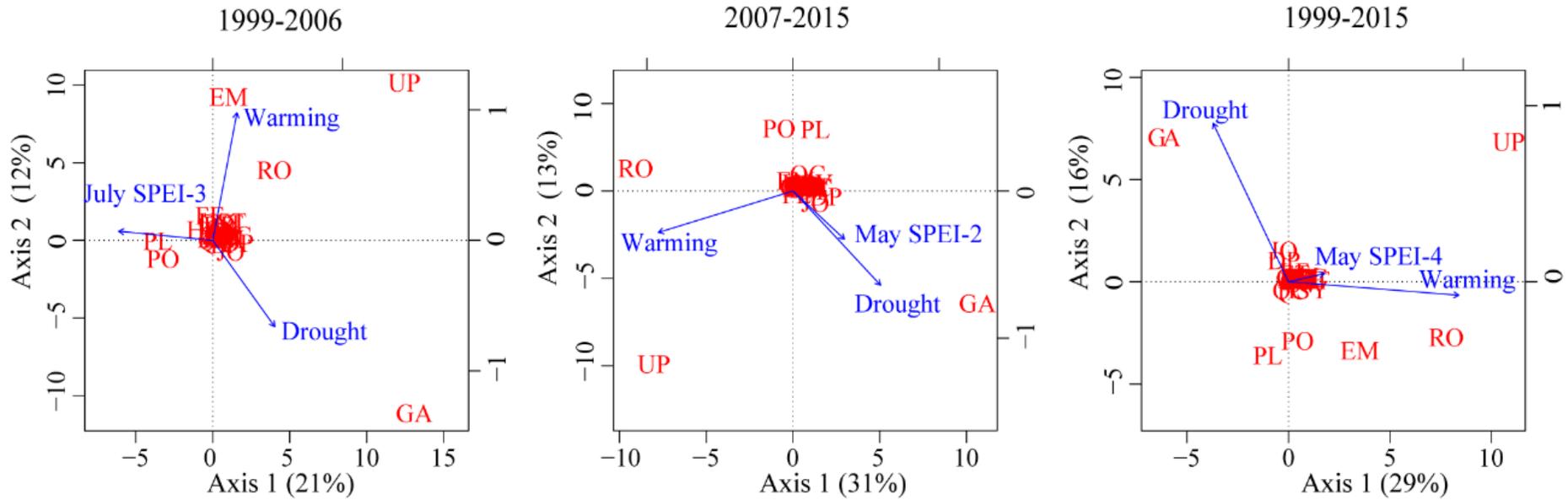
	<i>Ah</i>		<i>As</i>		Relative <i>As</i>	
	Difference	<i>P</i>	Difference	<i>P</i>	Difference	<i>P</i>
Warming-control						
SPEI	<b>0.28</b>	***	<b>0.1</b>	**	-0.006	ns
Warming	<b>-0.41</b>	**	<b>0.13</b>	(*)	<b>0.03</b>	*
Drought-control						
SPEI	<b>0.17</b>	(*)	<b>0.11</b>	**	<b>-0.02</b>	**
Drought	<b>-1.4</b>	***	0.06	ns	<b>0.06</b>	**

drought (difference=0.06,  $P<0.01$ ). *Ah*, *As* and Relative *As* were associated with SPEIs (Table 3). *Ah* was positively correlated with July SPEI-3 in warming-control (difference=0.28,  $P<0.001$ ) and drought-control (difference=0.17,  $P<0.1$ ) comparisons, *As* was positively correlated with May SPEI-2 in warming-control (difference=0.1,

392  $P < 0.01$ ) and drought-control (difference=0.11,  $P < 0.01$ ) comparisons and Relative  $A_s$  was  
393 negatively correlated with April SPEI-3 in the drought-control comparison (difference=-  
394 0.02,  $P < 0.01$ ).

### 395 3.5 Shifts in community composition in the treatments

396 Community composition changed significantly in the warming and drought treatments  
397 over the first half of the experimental period (1999-2006) ( $P < 0.001$ ), the second half  
398 (2007-2015) ( $P < 0.001$ ) and the entire period (1999-2015) ( $P < 0.001$ ) (Fig. 5). The RDA  
399 indicated that the climatic treatments and the covariates explained 33% (21 and 12% for  
400 axes 1 and 2, respectively), 44% (31 and 13% for axes 1 and 2, respectively) and 45%  
401 (29 and 16% for axes 1 and 2, respectively) of the total variability in species composition.  
402 The RDA indicated that experimental warming shifted the community composition  
403 toward *R. officinalis*, *E. multiflora* and *U. parviflorus* during 1999-2006 but favored *R.*  
404 *officinalis* when including 2007-2015 and the entire experimental period in the analysis.  
405 The drought treatment consistently shifted the community composition, favoring the  
406 expansion of *G. alypum* for the first and second half and the entire study period. The RDA  
407 also indicated that the changes in community composition were associated with July  
408 SPEI-3 during 1999-2006 ( $P < 0.01$ ) and May SPEI-2 during 2007-2015 ( $P < 0.05$ ). The  
409 analysis of species abundance by the statistical models (Table S2) indicated that warming  
410 would drive the shifts in composition toward *R. officinalis*, which increased significantly  
411 in abundance under experimental warming (difference=0.98,  $P < 0.001$ ) but did not  
412 change under drought Fig. S4a. Drought consistently drove shifts in community  
413 composition toward the dominant species, *G. alypum*, which increased significantly in  
414 abundance in the long-term drought treatment (difference=0.29,  $P < 0.001$ ) but decreased  
415 in the warming treatment (Fig. S4b).



416

417 Fig. 5 Shifts of community composition in the first half of the experimental period (1999-2006), the second half (2007-2015) and the entire period  
 418 (1999-2015). July SPEI-3, May SPEI-2 and May SPEI-4 were the covariate factors for the first half, second half and the entire study period,  
 419 respectively.

#### 420 **4. Discussion**

##### 421 *Community biodiversity*

422 *S* decreased under long-term experimental warming in the early-successional  
423 Mediterranean shrubland. *S* did not decrease at an earlier stage of the same experiment  
424 (Peñuelas *et al.*, 2007; Prieto *et al.*, 2009a), indicating a delayed or cumulative effect with  
425 long-term warming. The delay may also be due to continuous influences on seedling  
426 recruitment and diversity (Lloret *et al.*, 2004, 2009) or to seed-bank density (Del Cacho  
427 *et al.*, 2012) under long-term experimental warming. The reductions in *S* with long-term  
428 (17 years) experimental warming were in accordance with the decreases in *S* of  
429 temperature-sensitive species with natural warming, which have decreased biodiversity  
430 in most Mediterranean montane ecosystems (Gottfried *et al.*, 2012). The experimental  
431 warming, however, did not affect *H* or *E*, possibly due to the moderate warming in the  
432 treatment (0.6 °C average increase). Previous studies reported that experimental warming  
433 increased plant growth in spring and autumn and also increased summer physiological  
434 adjustments (stomatal conductance and water-use efficiency) (Prieto *et al.*, 2009b; Liu *et*  
435 *al.*, 2016). *S* and plant community structure, however, may likely shift substantially in  
436 Mediterranean ecosystems under future warming, because climatic effects are cumulative  
437 or even nonlinear, especially if combined with extreme heatwaves and droughts (Smith  
438 *et al.*, 2009; Peñuelas *et al.*, 2013).

439 The drought treatment had early and strong influences on *S*, *H* and *E*, probably due to  
440 the intensity of the treatment (decreases in soil-water content of ca. 16.7%). Water is the  
441 most limiting factor for plant growth and reproduction in Mediterranean ecosystems, and  
442 significant changes in the structure and composition of plant communities at early  
443 successional stages have been reported under water deficits (Peñuelas *et al.*, 2007; Prieto  
444 *et al.*, 2009a). Manipulative reductions in precipitation have decreased plant growth

445 (biomass accumulation and aboveground net primary productivity (ANPP)) (Peñuelas *et*  
446 *al.*, 2007; Prieto *et al.*, 2009c; Liu *et al.*, 2015), reproductive outputs (Del Cacho *et al.*,  
447 2013) and seedling establishment (Lloret *et al.*, 2004, 2009). These effects will likely  
448 influence the dynamics of *S* and the patterns of plant community structure on long  
449 timescales. Moreover, large decreases in community biodiversity (*S*, *H* and *E*) under  
450 drought may strongly influence species dominance, trophic relationships and ecosystemic  
451 functioning (Peñuelas *et al.*, 2007, 2013; Estiarte *et al.*, 2016). Indeed, manipulative  
452 droughts (alterations in amounts, patterns and timing of precipitation) around the globe  
453 have had stronger impacts on community structure and ecosystemic functioning than  
454 other climatic drivers such as warming, because plant growth and reproduction are more  
455 sensitive to water stress (Peñuelas *et al.*, 2004, 2013; Wu *et al.*, 2011; Beier *et al.*, 2012).  
456 Drier conditions (from both climatic warming and lower precipitation) are likely to  
457 emerge in Mediterranean ecosystems in the coming decades, likely leading to loss of  
458 biodiversity and decreases in ecosystemic functioning and services (Dai, 2013; Peñuelas  
459 *et al.*, 2013).

#### 460 *S and abundance of the functional groups*

461 Experimental warming significantly decreased *Sh* but not *Ss* or Relative *Ss*. The more  
462 conspicuous effects of warming on *Sh* than *Ss* are likely due to their different root systems.  
463 Deeper root systems may give shrubs an advantage for accessing larger pools of water  
464 and nitrogen under moderate warming (Peñuelas *et al.*, 2013). The reductions in *Sh* with  
465 experimental warming largely accounted for the decreases in *S* at the community level.  
466 Changes in *Ah* and *As*, however, differed under experimental warming, with decreases in  
467 *Ah* but increases in *As* that led to an increase in Relative *As*. Previous studies at our  
468 experimental site have indicated that moderate warming increased the photosynthetic  
469 rates of the shrubs *E. multiflora* and *G. alypum* in cold seasons, in agreement with the

470 increase in growth for shrub species (Prieto *et al.*, 2009b; Liu *et al.*, 2016). Species  
471 reorganizations and shifts in community composition are therefore likely at the current  
472 magnitude and rate of warming because of severe declines or losses of herbs, whereas  
473 shrubs may have a competitive advantage (growth and reproduction), shifting  
474 composition toward the establishment of shrub species.

475 The drought treatment reduced both *Sh* and *Ss*, which could account for the substantial  
476 decreases in *S* at the community level. The experimental drought also decreased *Ah* but  
477 did not affect *As*. Both Relative *Ss* and *As* consequently increased under the drought  
478 treatment, perhaps due to the higher drought resistance of shrubs than herbs. For example,  
479 *G. alypum* (the dominant shrub at our site) can persist under dry conditions and can  
480 increase by regulating its physiological activities (e.g. stomatal conductance and water-  
481 use efficiency) (Llorens *et al.*, 2003; Prieto *et al.*, 2009a; Liu *et al.*, 2016) and altering its  
482 phenological periods (Peñuelas *et al.*, 2004). The decline or loss of herbs may indicate a  
483 selective sweep in a future drier climate, similar to the effects of warming, especially for  
484 lower precipitation during the growing season, which could decrease the presence and  
485 abundance of herbs. In contrast, shrubs were more resistant to both the warming and  
486 drought treatments, so they may persist with future rapid climate change. Whether the  
487 increases in the relative abundance (density) of shrubs in arid Mediterranean ecosystems  
488 would increase above- and/or belowground carbon accumulations, which may also  
489 influence shrubland productivity and ecosystemic carbon feedback, however, remains  
490 unclear.

#### 491 *Shifts in community composition*

492 Experimental warming in our shrubland community led to significant shifts in community  
493 composition, consistent with the effects of warming treatments on communities in a  
494 montane meadow (Harte & Shaw, 1995), temperate steppe (Yang *et al.*, 2011) and

495 peatland (Dieleman *et al.*, 2015). Shifts in community composition are ascribed to  
496 alterations in competitive hierarchies and the relative abundance of dominances or sub-  
497 dominances under warming (Harte & Shaw, 1995; Smith *et al.*, 2009; Yang *et al.*, 2011;  
498 Dieleman *et al.*, 2015). In our study, experimental warming shifted the community  
499 composition toward *R. officinalis*, *E. multiflora* and *U. parviflorus* in the first half of the  
500 experimental period (1999-2006) but favoring *R. officinalis* when including the second  
501 half (2007-2015) and consequently the entire period (1999-2015) in the analysis. Previous  
502 studies have reported that the growth of *E. multiflora* was more limited by summer  
503 drought, despite the enhanced growth in cold seasons via higher photosynthetic activities  
504 due to experimental warming (Llorens *et al.*, 2003; Prieto *et al.*, 2009a, 2009b; Liu *et al.*,  
505 2016). *R. officinalis* thus tended to increase significantly in abundance in response to  
506 warming (Fig. S4a; Table S2), indicating an interspecific competitive advantage over  
507 coexisting species under warming. Shifts in dominance under warming in semiarid  
508 Mediterranean ecosystems, however, may be slow, so short-term studies would not detect  
509 these shifts in community composition. Long-term warming experiments are thus  
510 essential for tracking the changes in community composition in response to future climate  
511 change.

512 Community composition also shifted significantly under drought in our early-  
513 successional Mediterranean shrubland. Similar changes in response to increased drought  
514 have been observed in shorter-term studies at the same site (Prieto *et al.*, 2009a; Kröel-  
515 Dulay *et al.*, 2015). Moreover, drought consistently increased the expansion of the  
516 dominant species, *G. alypum*, when including all periods in the analysis. Other studies at  
517 the same experimental site also indicated that *G. alypum* adjusted physiologically (e.g.  
518 photosynthesis and stomatal conductance) (Llorens *et al.*, 2003; Prieto *et al.*, 2009b) and  
519 phenologically (e.g. delay in flowering time) (Peñuelas *et al.*, 2004) to the dry conditions.

520 The abundance (assessed as number of contacts) of *G. alypum* was also higher in the  
521 drought than the control treatment (Fig. S4b; Table S2). *G. alypum* may therefore  
522 maintain its dominant position in response to drought in this early-successional shrubland.  
523 Future climate change may shift the community composition, favoring *R. officinalis*  
524 under warming and *G. alypum* under drought, implying that shrubland ecosystems may  
525 become unstable or transitional.

#### 526 *Biodiversity parameters and meteorological droughts (SPEI)*

527 The significant correlations between winter-spring SPEIs and the community parameters  
528 (*S*, *H* and *E*), species richness (*Sh*, *Ss* and Relative *Ss*) and abundance (*Ah*, *As* and Relative  
529 *As*) of the functional groups, the abundance of the typical species and the shifts in  
530 community composition indicated the importance of water balance to changes in structure  
531 and composition in this early-successional shrubland ecosystem. These changes in  
532 biodiversity were also closely correlated with short-timescale SPEIs (1-4 months),  
533 indicating drought sensitivity to water deficits (Vicente-Serrano *et al.*, 2010). In addition,  
534 most of these changes in biodiversity were positively correlated with winter-spring (May  
535 SPEI-4, May SPEI-2 and April SPEI-3) and summer (July SPEI-3) water balances. As  
536 described above, the herb functional group was extremely sensitive to water deficits in  
537 summer drought. For example, *Sh* was higher after the wet winter-springs of 2002 and  
538 2004 and lower in the 2005-2007 dry period (Fig. 3a). *Ah* was lowest (mostly for Poaceae  
539 at our study site) in the 2005-2007 dry period (Fig. S4c; Table S2), reinforcing the premise  
540 of sensitivity to extreme drought. Extreme droughts in spring and summer, however,  
541 severely affected *H*. The extreme heat and drought in 2003 that reduced ecosystemic  
542 productivity throughout Europe (Ciais *et al.*, 2005) also significantly decreased *S*, plant  
543 growth and ANPP at our study site (Peñuelas *et al.*, 2007). We also detected low water  
544 availabilities in winter-spring and summer during 2003-2006 that probably caused the

545 severe reductions in *S*, *H*, *E*, *Sh* and *Ah* for that period and in 2007. Natural severe  
546 droughts, however, increased Relative *Ss* and *As*, favoring shrubs, especially in the  
547 drought treatment (Figs. 3c, 4c). Indeed, the growth and ANPPs of Mediterranean forests  
548 have been correlated with the winter-spring water balance, and mortality rates and branch  
549 litterfall have been correlated with summer water balance (Barbeta *et al.*, 2013; Liu *et al.*,  
550 2015). The structure and composition of Mediterranean shrubland ecosystems would  
551 therefore be substantially degraded if future climate change continues to decrease water  
552 reserves in winter-spring and summer.

### 553 *Sensitivity of successional recovery from climate change*

554 The developmental stage of an ecosystem may affect the responses of the vegetation to  
555 climatic disturbances (Peñuelas *et al.*, 2007; Prieto *et al.*, 2009a; Kröel-Dulay *et al.*, 2015;  
556 Brose & Hillebrand, 2016). Community structure and composition responded strongly to  
557 the climatic treatments, especially the drought treatment, in our early-successional  
558 shrubland ecosystem. The effects of climatic treatments, however, are not apparent in  
559 some ecosystems, even long-term treatments (Grime *et al.*, 2008; Tielbörger *et al.*, 2014;  
560 Estiarte *et al.*, 2016). These climatic treatments may be conducted in moderately mature  
561 or stable ecosystems, so the structure of plant communities is not influenced by slow  
562 climate change due to the well-developed structure and trophic complexity of the  
563 ecosystems (Smith *et al.*, 2009; Tielbörger *et al.*, 2014). Terrestrial ecosystems, however,  
564 are likely to experience anthropogenic and/or natural climatic disturbances that could  
565 push ecosystems into unstable or earlier successional stages (Chapin *et al.*, 2000;  
566 Peñuelas *et al.*, 2013; Seddon *et al.*, 2016). These unstable ecosystems would be strongly  
567 influenced by future climate change, leading to large changes in biodiversity and  
568 ecosystemic functioning (Kröel-Dulay *et al.*, 2015; Brose & Hillebrand, 2016). For  
569 example, Mediterranean ecosystems have historically suffered intense anthropogenic

570 disturbances and are highly vulnerable to the ongoing climate change, because they are  
571 near critical ecosystemic tipping points (or thresholds) (Myers *et al.*, 2000; Peñuelas *et*  
572 *al.*, 2007, 2013; Scheffer *et al.*, 2009; Doblas-Miranda *et al.*, 2014). Global warming and  
573 drought represent selection pressures on plant species in local communities, which are  
574 leading to large losses of species diversity and decreases in ecosystemic functioning  
575 (Lloret *et al.*, 2004, 2009; Prieto *et al.*, 2009a; Kröel-Dulay *et al.*, 2015; Scheffers *et al.*,  
576 2016). Future extreme climatic regimes (heat waves and droughts) would especially  
577 influence the functioning and services of ecosystems if critical thresholds are surpassed  
578 (Ciais *et al.*, 2005; Smith *et al.*, 2009; Jentsch *et al.*, 2011; Kreyling *et al.*, 2011;  
579 Reichstein *et al.*, 2013). Changes in community structure and composition could be  
580 persistent and even more abrupt as climate change projected by models progresses into  
581 the future (Dai, 2013; Doblas-Miranda *et al.*, 2014; Tilman *et al.*, 2014). Long-term  
582 climatic manipulations in ecosystems at different successional stages are thus critically  
583 necessary for projecting losses of ecosystemic biodiversity, functioning and services in  
584 response to future climate.

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