

1 **Species selection under long-term experimental warming and drought explained**  
 2 **by climatic distributions**

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16 **Summary**

17 Global warming and reduced precipitation may trigger large-scale species losses and  
18 vegetation shifts in ecosystems around the world. However, currently lacking are practical  
19 ways to quantify the sensitivity of species and community composition to these often-  
20 confounded climatic forces.

21 Here we conducted long-term (16 years) nocturnal-warming (+0.6°C) and reduced  
22 precipitation (-20% soil moisture) experiments in a Mediterranean shrubland. Climatic  
23 Niche Groups (CNGs) – species ranked or classified by similar temperature or  
24 precipitation distributions – informatively described community responses under  
25 experimental manipulations.

26 Under warming, CNGs revealed that only those species distributed in cooler regions  
27 decreased. Correspondingly, under reduced precipitation, a u-shaped treatment effect  
28 observed in the total community, was the result of an abrupt decrease in wet-distributed  
29 species, followed by a delayed increase in dry-distributed species. Notably, while partially  
30 correlated, CNG explanations of community response were stronger for their respective  
31 climate parameter, suggesting some species possess specific adaptations to either  
32 warming or drought that may lead to independent selection to the two climatic variables.

33 Our findings indicate that when climatic distributions are combined with  
34 experiments, the resulting incorporation of local plant evolutionary strategies and their  
35 changing dynamics over time, leads to predictable and informative shifts in community  
36 structure under independent climate change scenarios.

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38 **Key words:** global warming; frequent drought; Mediterranean ecosystems; long-term  
39 manipulation experiments; climatic niche groups; composition shifts; biodiversity loss

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51 **Introduction**

52 Climate change has already markedly altered community composition and structure,  
53 which has accelerated the loss of biodiversity and degradation of ecosystem functioning  
54 in many habitats around the world (Walther *et al.*, 2002; Parmesan & Yohe, 2003;  
55 Peñuelas *et al.*, 2013; Pimm *et al.*, 2014; Brose & Hillebrand, 2016). Biodiversity  
56 hotspots, such as Mediterranean ecosystems, have experienced drastic losses of  
57 biodiversity over the past several decades, attributable in large part to corresponding rapid  
58 climate change (Myers *et al.*, 2000; Sala *et al.*, 2000; Peñuelas *et al.*, 2013; Doblas-  
59 Miranda *et al.*, 2014). Global warming, accompanied with more frequent droughts  
60 projected for Mediterranean regions, will likely add to the vulnerability of these  
61 ecosystems and possibly intensify the species and ecosystem function losses in the  
62 coming decades (Sala *et al.*, 2000; Walther *et al.*, 2002; Doblas-Miranda *et al.*, 2014;  
63 Barros *et al.*, 2014). However, we still lack the mechanistic knowledge that would enable  
64 us to predict, and thus attempt to manage, the impacts of climate change on natural  
65 ecosystems.

66 The forecasting of climate change impacts on species diversity and composition may  
67 be impeded by the interrelationships among many simultaneously changing climatic  
68 factors, and directional shifts in species composition to these changes cannot be easily  
69 detected (McMahon *et al.*, 2011; Bellard *et al.*, 2012; Garcia *et al.*, 2014). In addition,  
70 climatic factors are often confounded, making it very difficult to make accurate  
71 predictions for biodiversity shifts independently for temperature and precipitation change  
72 (Beaumont *et al.*, 2011; Liu *et al.*, 2017). Some studies have reported that increasing

73 temperature and decreasing precipitation could impose similar and additive selection  
74 pressures on plant species performance within communities, because both forces decrease  
75 soil moisture, while increasing evapotranspiration rates and nutrient mineralization  
76 (Myers *et al.*, 2000; Sardans *et al.*, 2008; Williams *et al.*, 2012). However, the combined  
77 effects of temperature and precipitation are highly context dependent. For example, both  
78 warming and decreased precipitation may increase the aridity of an already dry and warm  
79 habitat, thereby limiting plant growth. However, in cooler habitats not limited by water,  
80 warming may have positive effects on the vegetation (e.g. extending the growing season  
81 and promoting growth and reproduction) and decreasing precipitation may have little  
82 effect on plant growth (Garcia *et al.*, 2014; Andresen *et al.* 2016). Therefore, approaches  
83 are needed that are able to detect the influences of several key climatic factors on the  
84 structure and function of ecological communities that are widely applicable and able to  
85 disentangle ‘climate change’ into the separate drivers.

86       Currently, one of the most mechanistic ways to study plant community responses to  
87 climate change is through long-term climate manipulation experiments (Elmendorf *et al.*,  
88 2015; Kröel-Dulay *et al.*, 2015; Andresen *et al.*, 2016; Zhu *et al.*, 2016; Liu *et al.*, 2017).  
89 Such studies impose a continuously altered climatic factor onto a local community,  
90 providing a known and controlled-for climate change impact, capturing the results of local  
91 interactions. This method therefore overcomes some of the confounding effects of long-  
92 term observational data (Gottfried *et al.*, 2012), it follows impacts over a continuous time-  
93 scale (unlike time-for-time based approaches (Metz & Tielbörger, 2016; Estiarte *et al.*,  
94 2016)), and importantly incorporates the local levels of plasticity and evolutionary

95 adaptations found within a community (unlike gradient space-for-time approaches  
96 (Tielbörger *et al.*, 2014)). However, for total community parameters (e.g. ANPP, biomass,  
97 species richness) climate manipulation experiments often reveal little to no-net change or  
98 difficult to explain altering responses over time (Grime *et al.*, 2008; Barbeta *et al.*, 2013;  
99 Tielbörger *et al.*, 2014; Andresen *et al.*, 2016; Mueller *et al.*, 2016). Interestingly, often  
100 single species and multiple species are shown to change in abundances within these  
101 experiments (Harte & Shaw 1995; Lloret *et al.*, 2009; Fridley *et al.*, 2011; Bilton *et al.*,  
102 2016). But with many species increasing and decreasing in the community, the task is to  
103 have a simple, general, and perhaps more informative way to interpret these patterns. It  
104 seems logical to hypothesise that, by somehow ranking the species based on a factor  
105 related to climate, climate change response predictions may be drawn and tested.

106       One technique for ranking species in relation to climate is given by their climatic  
107 niche distribution e.g. species within the same community that more commonly occur in  
108 wetter or drier habitats. In theory, the climatic niche of a species could act as the primary  
109 [predictors](#) of species sensitivity to climate change (Thuiller *et al.*, 2005; [Hijmans &](#)  
110 [Graham, 2006](#); De Frenne *et al.*, 2013). The climatic niche principle has commonly been  
111 used in distribution models (Thomas *et al.*, 2004; Thuiller *et al.*, 2005; McMahon *et al.*,  
112 2011; Araújo & Peterson, 2012), but has also shown promise in a process named  
113 “thermophilization” for identifying directional changes in whole community composition  
114 in observational data under climate warming (Gottfried *et al.*, 2012) e.g. the average  
115 temperature niche of elevated mountain communities has increased over time due to  
116 natural warming. More recently, the thermophilization principle has also proved capable

117 of revealing community shifts in tundra communities under experimentally manipulated  
118 warming (Elmendorf *et al.*, 2015). More so, when divided into species groups (Climatic  
119 Niche Groups CNGs) the climatic niche principle has most recently identified more  
120 precise details (i.e. identifying which components of the community increase or decrease)  
121 about the compositional shifts and community dynamics for annual species under  
122 experimentally manipulated rainfall over time (Bilton *et al.*, 2016).

123 Therefore, defining species by their climatic niche, and monitoring their responses  
124 within climate experiments, may be an informative and hypothesis-driven method for  
125 examining compositional change within communities. When using the climatic niche  
126 principle alongside experiments, response of species can be displayed along the niche  
127 axis and some general conclusions about species increasing or decreasing can be drawn.  
128 Furthermore, by categorizing the species into groups of similar climatic niche distribution  
129 (CNGs), the method assumes a level of species equivalence, thereby overcoming some  
130 natural species absences/presences in time and space, as well as being less reliant on  
131 precise niche definition. Certainly a main strength of grouping is its ability to allow for  
132 the simple monitoring of changing responses over time for different components of the  
133 community. Finally, CNGs may group together many different traits/adaptations that  
134 plants may possess to survive in particular climates, thereby strengthening both the power  
135 of the test and the interpretation of the result (Lavorel *et al.*, 2016). Indeed, if aspects of  
136 species-specific adaptations to climatic variables can be partly captured by this approach,  
137 it would provide further information about the community dynamics and ecology. While  
138 promise has been shown, to date, the climatic niche principle has not been applied to

139 separate climatic factors in manipulative field experiments, in order to tease apart the  
140 possible responses of species and community composition to the impacts of future  
141 temperature and precipitation regimes.

142 Here, we applied the climatic niche theory into a unique long-term (16 years)  
143 experiment to test, for the first time, whether two climatic variables may independently  
144 explain species-specific responses to climate change. We conducted nocturnal-warming  
145 (+0.6 °C) and sustained-drought (-20% soil moisture) treatments in a Mediterranean  
146 early-successional shrubland (1999-2015). Importantly, we ranked the coexisting species  
147 by the similarity of their climatic niches, and additionally classified them into climatic  
148 niche groups (CNGs). We defined CNGs for the coexisting species based on two climatic  
149 variables: temperature and precipitation (Methods for full details). In doing so, firstly we  
150 hypothesized, for this already warm and dry region of southern Europe, that changes in  
151 community composition in response to either manipulated warming or drought could be  
152 explained by species association with climatic niches. Specifically, those species in the  
153 community with core distributions in colder or wetter regions would disproportionately  
154 decrease under warming or drought; or even that species distributed in warmer or drier  
155 regions may increase under warming or drought, relative to control. Secondly, by  
156 incorporating two climate manipulation treatments and two climate niche parameters for  
157 our CNGs, due to specific adaptations species possess for temperature and precipitation  
158 regimes, we hypothesized that the separate climate change drivers may select for different  
159 species within the community which would be related to their climate niche distribution.

160 **Materials and methods**

161 *Study site*

162 We conducted the study in a semi-arid Mediterranean shrubland in Garraf Natural Park  
163 near Barcelona (southwestern Europe) (41°18'N, 1°49'E; 210 m a.s.l.). The site has a  
164 Mediterranean climate with hot and dry summers and precipitation mainly in the spring  
165 and autumn. The mean annual temperature during the study period (1998-2014) was  
166 15.5 °C, fluctuating from 14.7 °C to 16.2 °C. The highest temperature often occurs in  
167 summer (June, July and August), averaging 23.4 °C throughout the study period. The  
168 mean annual precipitation was 560.9 mm during the study period of 1998-2014, ranging  
169 from 403.1 mm in 2006 to 956.2 mm in 2002. The thin (10-40 cm) soil is a petrocalcic  
170 calcixercept and has a loamy texture and abundant calcareous nodules.

171 The study site was established on a hill with south-facing aspect (Slope=13%). The  
172 area had been cultivated but was abandoned more than a hundred years ago and thereafter  
173 colonized by a coniferous forest. This forest experienced two wildfires in summer 1982  
174 and spring 1994, after which succession began. The current vegetation is dominated by  
175 the shrubs *Erica multiflora* and *Globularia alypum*, which coexist with small evergreen  
176 plants, such as *Dorycnium pentaphyllum*, *Rosmarinus officinalis* and *Ulex parviflorus*  
177 (Table S1 for a full list of species).

178 *Experimental design*

179 We carried out moderate nocturnal-warming and drought treatments during the period of  
180 1999 to 2014, with 1998 acting as a pre-treatment year. Triplicate 20 m<sup>2</sup> (5 × 4 m) plots  
181 were randomly established for each treatment (warming, drought and control; nine plots

182 in total). All samples were collected from the central 12 m<sup>2</sup> (4 × 3 m) to avoid edge effects.

183 The warming treatment was achieved by covering the plots at night with reflective  
184 curtains to reduce the infrared radiation to the atmosphere, simulating global warming by  
185 increasing the minimum temperature at night (Beier *et al.*, 2004; Peñuelas *et al.*, 2007;  
186 Prieto *et al.*, 2009). A light scaffolding (1.2 m above the ground) was built to support the  
187 reflective curtains. The curtains reflected 97% of the direct and 96% of the diffuse  
188 radiation while allowing the transfer of water vapor. The covering was operated  
189 automatically by the light level (<200 lux), rainfall (<0.3 mm) and wind (<10 m s<sup>-1</sup>)  
190 throughout the study. The warming treatment increased soil temperatures at -5 cm depth  
191 by the average of ca. 0.6 °C, depending on the season and meteorological conditions (Fig.  
192 S1 (a)).

193 The drought treatment was applied in the spring and autumn (main and secondary  
194 growing seasons respectively) by covering each plot with a transparent waterproof sheet  
195 of plastic (Beier *et al.*, 2004; Peñuelas *et al.*, 2007; Prieto *et al.*, 2009). The facilities were  
196 similar in the drought and warming plots except the material of the curtains. The rain  
197 sensors during the treatment period activated the waterproof sheet to cover the vegetation  
198 during rainfall >1 mm and were removed after the rain had stopped. The water collected  
199 by the sheet was drained outside the plots. The curtains were folded automatically if the  
200 wind speed exceeded a threshold (>10 m s<sup>-1</sup>) to avoid damage. The drought plots were  
201 treated the same as the control plots during the rest of the year. The drought treatment  
202 excluded about 40% of the precipitation and decreased soil moisture by ca. 20%  
203 throughout the study period (Fig. S1 (b)).

204 A control treatment without manipulations was run in parallel to the warming and  
205 drought treatments. All of the control plots also had similar scaffolding but without  
206 curtains. Meteorological data was collected at the experimental site at half-hourly  
207 intervals since 1999.

#### 208 *Vegetation sampling*

209 Five fixed and parallel transects 3 m long were permanently established in all nine plots  
210 at equal distances of 0.8 m. A point-intercept method was applied to record the species  
211 composition and abundance at points distributed at 5 cm intervals along the five transects  
212 (305 points in each plot). A thin steel pin (3 mm diameter) was vertically dropped at each  
213 point, and the parameters (species identity and contacts per pin) were recorded (Prieto *et*  
214 *al.*, 2009). The data were collected annually in the dry season (July and August) from  
215 1998 (pre-treatment) to 2014 (16 years of manipulation). Our experimental plots  
216 contained a total of thirty-one species (Table S1). Species contacts in each plot were  
217 summed to estimate the abundance. Species abundances per plot were log transformed  
218 (log+1) to adjust for the large positive skew in distribution, and summed to form groups  
219 or total community measures.

#### 220 *Grouping of plant species*

221 To determine community compositional change with respect to the different treatments,  
222 we classified the species in the community into climatic niche groups (CNGs) using  
223 temperature and precipitation variables. We initially tested a number of climate niche  
224 parameters (maximum temperature in hottest month, average and seasonal temperature,  
225 and annual and seasonal precipitation) to rank the species to form CNGs (Tables 1, S1,

226 S2, S3, S4). However, we continued the analysis with the most consistent descriptors of  
227 community composition response – and those which were assumed to be most valid *a*  
228 *priori* – which were: i) summer temperature (mean temperature from June to August),  
229 since this period was most likely to be important for selecting for summer survival of  
230 species; and ii) spring precipitation, (the accumulated precipitation from December to  
231 May), as this had most effect on early season growth at the site. We created three CNGs  
232 for each climatic variable: T1, T2 and T3 (warm to cold) for summer temperature and P1,  
233 P2 and P3 (dry to wet) for spring precipitation.

234 To create these groups, we first obtained the species' geographical distributions in  
235 mainland Spain, France and Portugal (southwestern Europe) from the Global Biodiversity  
236 Information Facility (GBIF, <http://www.gbif.org/>), one of the most extensive open-access  
237 biodiversity databases available. Distribution observations were filtered to exclude  
238 islands, and reduced to one value per 30 arc cell (~1 km). We then extracted a climatic  
239 value from a climatic GIS layer separately for each species for each occurrence. We tested  
240 multiple ways of calculating each species niche value from these climate distribution  
241 values to test the impact of niche edges on group response: the median (med) climatic  
242 value associated to all observations per species; the 25 percentile of the climatic values  
243 (25%); or the 75 percentile of climatic values (75%) (Table S1 for multiple niche values  
244 associated with each species). For the remainder of the main article, we display results  
245 only from niche values calculated using the 25 percentile of summer temperature values  
246 and median spring precipitation values, because the results for the various approaches  
247 were essentially the same. Information for the summer temperatures and spring

248 precipitation was extracted from the WorldClim database (30 arc-seconds (~1 km))  
249 (<http://www.worldclim.org/>), which contains climatic data for 1950-2000). Species were  
250 allocated to three CNGs per climatic variable by systemically apportioning plant  
251 community abundance among groups, so that the sum of the (log) species contacts per  
252 group was approximately 33% of the total sum of (log) species contacts recorded during  
253 the experiment (regardless of year or treatment) (Tables S2 and S3). Note that these are  
254 not true community percentage values, but ones which are calculated from summing log  
255 transformed species abundances. In effect, our method assigns relatively more weight to  
256 rare species in a group. We think this method is well justified because, due to the  
257 dominance of some species and also the point quadrat method of revealing abundance,  
258 groups created from normal community percentages may only contain one or two species.  
259 In addition, to create our arbitrary groups, species at a boundary with very similar/same  
260 niche values were kept together in the same group. These rules for species allocation  
261 ensured that each group contained at least six species and that the climatic ranges defined  
262 by a group exceeded a certain value (precipitation >20 mm, temperature >1 °C) (Tables  
263 1, S3). Note that there is a large correlation of the species present in wet-cold or warm-  
264 dry groups (Table 1). However, there are a number of species which vary in terms of their  
265 extreme temperature or precipitation group allocation (Tables 1, S2).

#### 266 *Statistical analyses of abundances*

267 For the main statistical analyses, the response variables in our models were derived from  
268 log-transformed species level contact hits per plot from 1999-2014 (Eq. 1). Four main  
269 response variables were analyzed: total community sum-log-abundance (sum of log

270 contact hits of all the species) (Eq. 1), temperature CNG sum-log-abundance (sum of log  
271 contact hits belonging to species for each temperature CNG group) (Eq. 1), precipitation  
272 CNG sum-log-abundance (sum of log contact hits belonging to species for each  
273 precipitation CNG group) (Eq. 1) and species log-abundance (log contact hits belonging  
274 to a single species).

$$275 \quad \sum_{i=1}^{i=n} \log(\text{hits } sp \ i)$$

276 (Eq. 1)

277 For total community sum-log-abundance  $i=1$  to total number of sp (species) within the  
278 community; For CNGs,  $i=1$  to number of sp (species) within the group.

279 Note here, that the abundances of species (in a given plot and time point) were logged  
280 prior to summing to form groups/total (equivalent to a geometric mean). To our  
281 knowledge, this appears to be a novel response variable and although testing was carried  
282 out, the full properties are partly unknown. However, logging at the species level first is  
283 synonymous with log transformations that are commonly applied to reveal community  
284 composition change (e.g. in Redundancy Analysis Šmilauer & Lepš, 2014). Similarly, the  
285 properties of the sum-log-abundance response variable conclude that a doubling or  
286 halving of any species within the group/community is given equal weight, which when  
287 analysed over time reveal general increases or decreases of multiple species in the  
288 group/community rather than absolute changes highly weighted by a single dominant  
289 species. This is a more general reflection of composition shifts over time, which may be  
290 important for identifying shifts in relation to climate change/manipulations, particularly

291 in a shrub dominated community such as ours.

292 The effects of the climatic manipulation treatments on (sum) log-abundances were  
293 analyzed using linear mixed-effects models (LMEM). Different models were created to  
294 analyze either the effect of warming treatment versus the control or the effect of drought  
295 treatment versus the control.

296 A full range of environmental factors (spring, summer and annual temperature and  
297 precipitation) of the study site were tested, but the variance (based on the lowest AIC  
298 values) was explained best for all analyses by the environmental recordings for spring  
299 temperature (ST), spring precipitation (SP) and their interaction. The initial values for  
300 sum-log-abundances in the preliminary year (1998) were included as an underlying  
301 covariate ('Pre-treat'). Finally, the continuous variable 'Year' (16 years: 1999-2014) and  
302 the two-level categorical variable 'Treatment' (drought vs. control, or warming vs. control)  
303 were included. For the analysis of CNG sum-log-abundances, the models also included  
304 the three-level explanatory categorical variable 'CNG' (either T1, T2, T3 or P1, P2, P3),  
305 with the main interaction of interest between Treatment  $\times$  Year  $\times$  CNG. The full models  
306 for our analyses were therefore:

$$\text{Total Community sum-log-Abundance} = \text{ST*SP} + \text{Pre-treat} + \text{Year*Treatment} \quad (\text{Eq. 2})$$

$$\text{CNG sum-log-Abundance} = \text{ST*SP} + \text{Pre-treat} + \text{Year*Treatment*CNG identity} \quad (\text{Eq. 3})$$

$$\text{Species log-Abundance} = \text{ST*SP} + \text{Pre-treat} + \text{Year*Treatment} \quad (\text{Eq. 4})$$

307 Plot was included as a random effect term in all models. All analyses were performed  
308 in R version 3.2.2 using package lme4 (version 1.1-7 (Bates *et al.*, 2007)). Post-hoc

309 analyses of the differences in CNG slopes/responses over time were tested by least-  
310 squares means using the `lstrend` command of R package `lsmeans` (Lenth, 2016).

311 For visual representations of the statistical models (Figs. 1 & 2), treatment effect size  
312 was calculated as:

$$313 \quad \text{Effect size (Year)} = (\mu_{\text{treatmentYear}} - \mu_{\text{treatment1998}}) - (\mu_{\text{controlYear}} - \mu_{\text{control1998}}) \text{ (Eq. 5)}$$

314 where  $\mu_{\text{treatment}}$  and  $\mu_{\text{control}}$  are the average (sum) log-abundances in the treatment  
315 (warming or drought) and control plots (n=3), respectively in a given year. Effect sizes  
316 were adjusted for (sum) log-abundance differences in the pre-treatment year (1998) as  
317 representative of the LMEMs. Raw sum-log-abundance plots are shown in [Fig. S2](#), and  
318 [raw data can be viewed in Notes S1](#).

### 319 *Group Robustness analysis*

320 In addition to testing CNGs created from multiple species niche values (Table S4), we  
321 also performed a formal test of robustness to ensure any emerging patterns from the CNG  
322 analyses were not an artefact of the boundaries chosen. To do this we followed the  
323 protocol set out in Bilton et al. (2016) and performed Cumulative Group Analyses. This  
324 methodology adds one species at a time in niche value rank order to form a group. In  
325 effect, this analysis was testing treatment responses over time for all possible group  
326 boundaries for CNG1 (accumulating most arid species up to total community), and  
327 separately for all possible group boundaries for CNG3 (accumulating most humid species  
328 up to total community). For further details on the methodology and the interpretation refer  
329 to [Notes S2](#).

### 330 *Single species response plotted against niche*

331 As a further test of the climatic niche approach, single species responses to the  
332 manipulation treatments were plotted against their corresponding climatic niche value.  
333 This was formally tested and displayed using Generalized Additive Models (GAMs)  
334 using R-package “mgcv” (Wood, 2011). The response variable in the GAMs were the t-  
335 values of the LMEMs performed on each species (Eq. 4; Table S5) describing the  
336 difference in model estimate for the response slope over time between control and  
337 treatment (Year x Treatment interaction term). The explanatory variables were the  
338 climatic niche values associated with each species (Table S1). GAMs were run for the  
339 climate niche values presented in the main article (25% summer temperature; median  
340 spring precipitation), and for multiple other climate niche values to check robustness of  
341 different niche axes (Fig. S3). A simple smoothing parameter was fitted to each GAM set  
342 at a value of 0.15 throughout. Each species was also weighted by their corresponding log-  
343 community percentage value (Table S2). [Raw data can be viewed in Notes S1.](#)  
344

345 **Results**

346 The total community sum-log-abundance was affected by the moderate warming (0.6 °C)  
347 as shown by a significant Year × Treatment interaction ( $p < 0.05$ , Table 2). Namely, across  
348 the 16 years of the experiment, the general log-species' abundances decreased  
349 progressively and linearly under the warming treatment relative to the control (Fig. 1b).  
350 The LMEM also indicated that both natural yearly temperature and precipitation  
351 accounted for the variance in abundances among years, with significant main effects of  
352 both natural variables (SP,  $p < 0.0001$ ; ST,  $p < 0.01$ ) and their interaction term ( $p < 0.05$ ).

353 More visibly, the drought treatment had an immediate impact on total community  
354 sum-log-abundance, decreasing it compared to the control (Fig. 1a) which was reflected  
355 by a significant main effect of the drought treatment ( $p < 0.05$ , Table 2). The Year ×  
356 Treatment interaction was not significant for drought, with no linear decrease (or increase)  
357 in sum-log-abundance in the drought treatment compared to the control over the course  
358 of the experiment. However, the effect size of the drought treatment followed a distinct  
359 polynomial shape over time (Fig. 1b). Namely, the difference between sum-log-  
360 abundance in drought vs. control treatments increased for the first nine years of the  
361 drought manipulation (until 2007) and then gradually decreased until the end of the study  
362 period reminiscent of a dampening effect in a whole-community parameter. The statistical  
363 model also indicated that natural yearly spring precipitation (SP) and the interaction term  
364 between SP and spring temperature (ST) significantly affected total community sum-log-  
365 abundances ( $p < 0.0001$  for both respectively).

366 Temperature CNGs accounted for the changes in species abundances in the warming

367 treatment (Fig. 2a, Table 3). The LMEM demonstrated a significant three-way CNG ×  
368 Treatment × Year interaction for the sum-log-abundance changes of **temperature** CNGs  
369 ( $p < 0.01$ ). Among these temperature CNGs, the sum-log-abundances of T1 and T2 (from  
370 relatively warmer origins) remained fairly constant in the warming treatment when  
371 compared to the control, whereas the sum-log-abundance of T3 (from colder origins)  
372 decreased gradually and linearly throughout the study period (estimated difference in  
373 slopes =  $-0.37$ ,  $p < 0.0001$ ) (Fig. 2a, Table S4). In contrast, the three-way interaction was  
374 not significant ( $p = 0.12$ , Table 3) when applying the classification of temperature CNGs  
375 to analyze sum-log-abundance changes under the drought manipulations (Fig. 2c). Here,  
376 while response slopes comparing drought log-compositions over time to control were  
377 ranked in hierarchical order (T1 > T2 > T3) no temperature-CNG slope differences were  
378 significant (Fig. 2c, Table S4).

379 As hypothesized, precipitation CNGs also accounted for the contrasting changes in  
380 species abundances in the drought treatment (Fig. 2b, Table 3). The LMEM demonstrated  
381 a significant three-way CNG × Treatment × Year interaction for the sum-log-abundance  
382 changes of **precipitation** CNGs ( $p < 0.01$ , Table 3). The response patterns differed greatly  
383 among the three CNG-groups. P3 (from wetter origins) initially decreased in sum-log-  
384 abundance compared to the control (estimated difference in slopes =  $-0.22$ ,  $p < 0.01$ , Table  
385 S4), with an abrupt shift after three years of the drought manipulation (after 2001) and  
386 fairly constant sum-log-abundances for the remaining years of the study. P2 sum-log-  
387 abundances (from moderately dry origins) were similar in the control and drought  
388 treatment throughout the study period. However, the sum-log-abundances of P1 (from

389 drier origins) steadily increased in the drought compared to the control (estimated  
390 difference in slopes = 0.24,  $p < 0.01$ , Table S4), particularly after 2007 when they were  
391 higher in relative abundance in the drought treatment than the control. Taken together, the  
392 responses of the three groups explain the u-shaped response found in the total community  
393 data. Similar to the temperature CNGs, the three-way interaction was not significant  
394 ( $p = 0.188$ , Table 3) when applying the classification of **precipitation** CNGs to analyze the  
395 sum-log-abundance changes in warming treatment (Fig. 2d). However, uncorrected post-  
396 hoc tests did reveal a significant difference in slope between control and warming for P3  
397 (decrease as predicted for wettest species: slope difference = -0.18,  $p < 0.05$ , Table S4).

#### 398 *Robustness analysis*

399 Multiple CNG analyses were performed in the same manner as the main results presented  
400 above, using different niche values to rank species and create groups. Results were  
401 generally consistent with the presented findings, and some results of this can be seen in  
402 Table S4. In general, most methods highlighted a statistically significant decrease of cool  
403 or wet species under warming and that temperature CNGs regularly failed to explain  
404 changes in community composition under drought. Annual **precipitation** CNGs  
405 sometimes managed to capture community composition change under both manipulation  
406 treatments (drought and warming), whereas **spring precipitation** CNGs were generally  
407 stronger for drought response but did not significantly describe changes under warming,  
408 despite revealing hierarchical responses among CNGs as predicted (i.e. drier CNG1  
409 responded less negatively to warming than the wetter CNG3).

410 A full display of results and discussion of the Cumulative Group Analysis can also

411 be found in [Figs. S4, S5 and S6](#) and [Notes S2](#). In general, it was clear that groups more  
412 often than not overcame variance in the single species responses to describe community  
413 change as predicted. Under warming, for groups containing a few species, warm  
414 temperature CNGs increased (although not significantly), and cool temperature CNGs  
415 significantly decreased, relative to control ([Fig. S4](#)). Similarly, but more pronounced,  
416 under drought, dry precipitation CNGs increased, and wet precipitation CNGs decreased  
417 ([Fig. S6](#)). These results were most consistent when using [summer temperature](#) (25  
418 percentile) CNGs to describe warming, and [spring precipitation](#) (median) CNGs to  
419 describe drought ([Figs. S4 and S5 respectively](#)). In addition, when testing CNG responses  
420 in opposing climate manipulations, patterns were generally less clear and more variable  
421 ([Fig. S6](#)). In combination, this confirmed that group boundaries had little qualitative effect  
422 on the main results presented.

#### 423 *Single species responses plotted along niche axis*

424 Single species LMEM analyses revealed that under warming, out of the 24 species tested,  
425 two species increased over time, and four decreased over time relative to control (Alpha  
426 p-value of 0.05 with no multiple test correction, [Table S5](#)). For the 23 species tested under  
427 drought, three species increased over time, and four decreased over time relative to  
428 control ([Table S5](#)). Some care must be taken in interpreting these findings, as due to the  
429 large volume of analyses, linearity was rarely confirmed nor unconfirmed.

430 When single species responses (t-values of difference between control and treatment  
431 over time) were plotted against the climatic niche axes, while there is some variation in  
432 patterns, as revealed by the CNG analyses, it was generally the cooler species which

433 decreased under warming (Fig. 3a). Likewise, also confirming the findings from the CNG  
434 analyses, it was generally the drier species which increased under drought, and the wetter  
435 species which decreased under drought, relative to control (Fig. 3b). Plotting single  
436 species warming responses by their precipitation niche, and drought responses by their  
437 temperature niche, sometimes produced similar patterns but were never as strong or  
438 consistent as when using the associated climate niche parameter (Fig. 3c, d & Fig. S3).  
439 This remained consistent with the CNG findings.  
440

441 **Discussion**

442 Our overall findings from the 16-year experiment showed a strikingly clear differentiation  
443 between plant community response to increasing temperatures and to drought. By  
444 classifying species into CNGs we revealed that community changes were highly  
445 predictable and based on the species' distribution with respect to climate. In addition, our  
446 CNG analyses revealed some interesting explanations for a dampening effect in  
447 community-level parameters that without our approach, would have gone unnoticed. In  
448 the following, we discuss the effects of the two treatments on the community dynamics  
449 within our experiment, when species were defined along two climate niche axes.

450 The impacts of the warming treatment increased over time, probably because the  
451 effects of slightly higher temperatures (+ 0.6 °C) gradually accumulated. However,  
452 previous studies at the same experimental site did not find significant abundance changes  
453 after 7-years exposed to the warming treatment (Prieto *et al.*, 2009). The clear but slow  
454 effect of warming on community composition in our study, highlights the need for long-  
455 term experiments in climate change studies (Smith *et al.*, 2009; Leuzinger *et al.*, 2011;  
456 De Boeck *et al.*, 2015). More interestingly, the CNG analyses revealed that the gradual  
457 decreases in the total community abundance to experimental warming was limited to  
458 decreases only in those species associated with cooler (and sometimes wetter) climates,  
459 and therefore presumably those species not well adapted to exposure to higher  
460 temperatures. Conversely, species with distribution ranges centered in intermediate and  
461 warmer/drier climates were remarkably unaffected by warming, possibly due to inherent  
462 adaptations to higher temperatures (Gottfried *et al.*, 2012; Duque *et al.*, 2015; Elmendorf

463 *et al.*, 2015). These patterns thus suggest that under the future warmer temperatures and  
464 associated extreme heat waves predicted for the Mediterranean regions (Dai, 2013; Barros  
465 *et al.*, 2014), abundance of the species from relatively cold origins is likely to decrease.

466 The CNG analysis was even more enlightening for the drought treatment. Here again,  
467 the species hypothesized to possess less adaptations to reduced water levels responded  
468 visibly, i.e. in general the species associated with wetter climates (P3) immediately  
469 decreased in abundance in the drought treatment. The abundances of these species also  
470 abruptly shifted between the third and fourth year, which could be due to the additive  
471 impact of the experimental drought and an extreme natural drought in 2001. In addition,  
472 the CNG analysis revealed that species from dry climates (P1) showed a general increase  
473 in abundances in the drought treatment after a delay of nine years, and were more present  
474 in the drought plots than the control ones after this point. Therefore, for the predicted  
475 future scenario of reduced rainfall, the potential losses of species from the system may be  
476 partly offset by a gain in drought-adapted species (Sala *et al.*, 2000; Barros *et al.*, 2014,  
477 Andresen *et al.* 2016).

478 In general, while both temperature and precipitation manipulations had a negative  
479 impact on the community, the overall effect of the drought treatment in terms of  
480 immediate change and community shift was greater. This was likely due to the different  
481 severity of warming and drought treatments or differential sensitivity of the community  
482 to the two climatic factors (Beaumont *et al.*, 2011; Garcia *et al.*, 2014). In our already  
483 warm and dry system, elevated temperature can act as a climatic limitation for species  
484 establishment and growth, because the associated increased vapor pressure deficit

485 increases the likelihood of high autotrophic respiration, transpiration from plants, and  
486 evaporation from the soil (Beier *et al.*, 2004; Williams *et al.*, 2012; Peñuelas *et al.*, 2013).  
487 Higher temperatures may therefore accelerate water outputs, greatly increasing the water  
488 stress for plants (Beier *et al.*, 2004; Williams *et al.*, 2012; Anderegg *et al.*, 2013). Greater  
489 immediate impacts of the drought manipulation in our study were apparent in the  
490 responses of total community abundance after the first year. Such strong plant responses  
491 to reduced precipitation levels are supported by the growing number of studies reporting  
492 that water availability is a crucial determinant of species distribution and persistence  
493 across global ecosystems (Myers *et al.*, 2000; Peñuelas *et al.*, 2007; Beaumont *et al.*, 2011;  
494 Doblas-Miranda *et al.*, 2015; Harrison *et al.*, 2015). Taking together evidence from our  
495 study and that from previous findings suggests that reduced precipitation may be a  
496 stronger and more immediate selective agent for determining structure and community  
497 composition in natural ecosystems, whereas warming could be a progressive and  
498 accumulative process (Beier *et al.*, 2004; Prieto *et al.*, 2009; Wu *et al.*, 2011; Liu *et al.*,  
499 [2017](#)).

500 Notably, we show evidence that the impacts exerted by temperature and drought  
501 alone selected for some different species, with responses determined by their climatic  
502 niche distributions. The temperature CNGs only explained the response of the  
503 composition to the warming treatment, regularly failing to explain results under drought.  
504 For precipitation CNGs, while there was some correlation in species responses under both  
505 treatments, precipitation CNGs generally explained the response to drought treatment far  
506 better than to the warming treatment. This suggests, that despite the fact that both climate

507 stressors decrease water availability to plants, they can also select independently for  
508 specific adaptations (Mittler, 2006; Beaumont *et al.*, 2011; Garcia *et al.*, 2014). Some care  
509 must be taken in fully extracting evidence for independent selection under the different  
510 climatic variables, because many of the species in this study were correlated and were  
511 indeed either cool-wet distributed (e.g. *Rubia peregrina* which responded negatively  
512 under both treatments), or warm-dry distributed species (e.g. *Globularia alypum* which  
513 increased under drought and had no response under warming - the general CNG response).  
514 However, the few species to express opposing niches, also performed as hypothesized by  
515 their niche distribution. For example, *Ulex parviflorus* (a warm-wet distributed species)  
516 had no response under warming, and decreased in abundance under drought. This  
517 contrasting response under opposing manipulation treatments, not solely in the direction  
518 expected by a reduction in water under warming, suggests that it is likely that in some  
519 cases the balance between traits related to cooling, capturing water, and preventing water  
520 loss (e.g. stomatal closure, rooting depth, leaf thickness), could be uniquely tailored to  
521 the specific needs in response to climatic stress (Mittler, 2006; De Frenne *et al.*, 2013).  
522 In our study system, this appears to be reflected by their distribution ranges across  
523 climates. Clues for the precise adaptations/mechanisms defining the groups and  
524 underlying these changes are revealed by results at the same study site which reported:  
525 demographic changes in seedling numbers of a subset of species (Lloret *et al.*, 2009);  
526 rapid genetic shifts in the dry (P1) and warm (T1) species *Fumana thymifolia* (Jump *et*  
527 *al.*, 2008) which we showed to increase under both manipulations; and potential  
528 physiological acclimation – in terms of water-use efficiency, shoot water potential and

529 net-photosynthetic rate - of a dry distributed species *Erica multiflora* under the drought  
530 treatment (Liu *et al.*, 2016). Indeed, a valuable next step could be a trait screening exercise  
531 of species from the distinct niches to confirm precisely which adaptations are similar and  
532 different for determining plant responses under the opposing climate drivers. Ultimately,  
533 while higher temperatures and lower precipitation are both likely to increase the aridity  
534 of the Mediterranean Basin by increasing evapotranspiration (Mittler, 2006; Garcia *et al.*,  
535 2014), some species will not suffer equally from the future temperature and precipitation  
536 regimes.

537         In many climate manipulation studies, including our own, often whole community  
538 variables (total density, species richness, community productivity) either show limited to  
539 no-net effects (Grime *et al.*, 2008; Tielbörger *et al.*, 2014; Estiarte *et al.*, 2016) or  
540 dampening over time (Leuzinger *et al.*, 2011; Barbeta *et al.*, 2013; Liu *et al.*, 2015;  
541 Andresen *et al.*, 2016). Under the drought manipulation in our study, we also showed a  
542 clear polynomial response pattern for total community abundance relative to control,  
543 which is often interpreted as a dampening of the treatment/climate effect over time  
544 (Andresen *et al.*, 2016). One of our most interesting findings was that this polynomial  
545 pattern could be explained by clear contrasting shifts among the different precipitation  
546 CNGs. This is intriguing, because dampening effects have often been interpreted as an  
547 ‘adaptation’ of the system back to its original state, due to acclimation (Leuzinger *et al.*,  
548 2011; Barbeta *et al.*, 2013; Liu *et al.*, 2015; Andresen *et al.*, 2016). Without our in-depth  
549 community-level analyses we would have probably come to the same erroneous  
550 conclusion, and possibly community composition changes may help explain contrasting

551 response patterns over time in other long-term manipulation studies (Andersen *et al.*,  
552 2016). Importantly, our findings enabled us to identify that the impact of the drought  
553 treatment is not dampening, but remains strong, and the effect seen for total community  
554 was the result of a decrease in abundance of wet-distributed species and a delayed  
555 increase in the abundance of dry-distributed species. It seems likely that the reduction in  
556 competition exerted from the wet-distributed species may have been responsible for this  
557 switch in dominance hierarchy, and that particularly in shrubland systems such as ours,  
558 these switches may require long periods of time to emerge (Smith *et al.*, 2009; De Boeck  
559 *et al.*, 2015; Andresen *et al.*, 2016; Liu *et al.*, 2017).

560       The use of CNGs to observe, follow, and predict community dynamics under climate  
561 manipulation experiments/ climate change scenarios has proved to be a simple and robust  
562 technique to extract general and interpretable trends in community dynamics. The use of  
563 many different climate parameters often showed similar qualitative results to the main  
564 climate parameters presented here ([summer temperature and spring precipitation](#)). In  
565 addition, the Cumulative Group Analyses revealed that the conclusions rarely altered due  
566 to where the group boundaries were set. Also, by plotting single species responses along  
567 a niche axis we revealed very similar conclusions about which species – in terms of niche  
568 distribution - would increase or decrease in abundance in response to the manipulations.  
569 A more detailed discussion on some of the different niche parameters used can be viewed  
570 in [Notes S3](#). However, in general we conclude that while niche range would be extremely  
571 valuable to consider across large areas, within a community it would seem that an average  
572 value (median or mean) captures well both potential increasers and decreasers under

573 manipulations (Elmendorf *et al.*, 2015; Bilton *et al.*, 2016). A valid next step could be to  
574 test simple or more complex Species Distribution Model predictions of species responses  
575 under manipulations to give a different view on the use of the climatic niche principle.

576       The highly consistent and predictable species responses to the treatments may have  
577 an interesting conservation aspect. Namely, our results suggest that with the advent of  
578 predicted increases in temperature, decreases in precipitation, along with increases in  
579 extreme events in the future (Dai, 2013; Reichstein *et al.*, 2013; Barros *et al.*, 2014), there  
580 would be an associated decline in species with a lower capability to persist under either  
581 warming or drought or both. By applying a CNG approach to manipulation experiments,  
582 we show valuable evidence that climatic niche distributions may be able to identify which  
583 species may be most vulnerable to shifts in these climate change factors either  
584 independently or in conjunction. Therefore, by exploring in more detail the within  
585 community dynamics, CNGs may aid in providing predictions for rates of species loss,  
586 which at the global scale remains continuing or even sharply increasing (Bellard *et al.*,  
587 2012; Kröel-Dulay *et al.*, 2015; Seddon *et al.*, 2016).

588       However, the decline in the abundance of some climate-sensitive species, may be  
589 balanced by an increase in resistant species distributed in warmer or drier niches. This  
590 was seen in our study with the delayed increase in species associated with dry climates in  
591 our drought treatment (e.g. *G. alypum*). Indeed, growing observational (Gottfried *et al.*,  
592 2012; Duque *et al.*, 2015) and experimental (Harte & Shaw, 1995; Elmendorf *et al.*, 2015)  
593 evidence suggests that communities are shifting towards a higher proportion of species  
594 associated with warmer climates in response to global warming. Crucially, our findings

595 suggest that similar, and more importantly, independent conclusions can also be drawn  
596 for species response to drought. Therefore, our evidence provided here from the CNG  
597 approach suggests that it may be possible to depict, on a global scale, how the magnitude  
598 of changes of either temperature and/or precipitation may affect those climate-sensitive  
599 species. Encouragingly, data bases are becoming more readily available for species  
600 distributions (Global Biodiversity Information Facility, GBIF) and are sufficiently precise  
601 to define the sensitivity of species by their climatic niche and to group the species in an  
602 index of similar niches (Bilton *et al.*, 2016), allowing for the application of the CNG  
603 principle to a wide array of habitats for comparison. We therefore advocate the combined  
604 use of both manipulation experiments and the climatic niche principle to improve  
605 assessments of community responses to future climate change scenarios.

606

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618 **Author contribution**

619 D.L analyzed the data and wrote the paper and M.B. conceived the idea, helped in data  
620 analysis and provided in-depth editing of the manuscript. J.P. designed the experiment,  
621 performed the research and revised the manuscript. R.O. and M.E. performed the research  
622 and provided the experimental data. K.T. provided extensive editing and conceptual  
623 advice. F.S. helped with data analysis. X.Y. helped in manuscript revision.

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811 **Table legend**

812 Table 1 Cross-correlation table of species allocation to the main Climatic Niche Groups  
813 (CNGs) shown throughout the article. CNGs were allocated in order of aridity: niche  
814 values of summer temperature (25%) CNGs from warm to cold ( $T1 > T2 > T3$ ), and niche  
815 values of spring precipitation (median) CNGs from dry to wet ( $P1 < P2 < P3$ ).

816 Table 2 Total community sum-log-abundance responses to 16 years of climatic  
817 manipulation. ANOVA type I table for Linear Mixed-Effects Models analyzing the  
818 changes in abundances in response to either the warming or drought Treatment compared  
819 to the control. Start value indicates the sum-log-abundance in the initial year of the  
820 experiment (1998 before manipulation). P-values in bold are statistically significant to an  
821 alpha value of 0.05.

822 Table 3 Climatic Niche Group (CNG) sum-log-abundance responses to 16 years of  
823 climatic manipulation. ANOVA type I table for Linear Mixed-Effects Models. Shown  
824 separately are results for the temperature CNG and precipitation CNG responses to both  
825 the warming and drought treatments. Underlined is the interaction of most interest to the  
826 study. Start value indicates the sum-log-abundances in the initial year of the experiment  
827 (1998 before manipulation). P-values in bold are statistically significant to an alpha value  
828 of 0.05.

829

830 Table 1 Cross-correlation table of species allocation to the main Climatic Niche Groups  
 831 (CNGs) shown throughout the study. CNGs were allocated in order of aridity: niche  
 832 values of 25% summer temperature (25%) CNGs from warm to cold (T1>T2>T3), and  
 833 niche values of spring precipitation (median) CNGs from dry to wet (P1<P2<P3).

		Precipitation CNGs			Temp. CNGs Total
		P1 (drier)	P2 (intermediate)	P3 (wetter)	
Temperature CNGs	T1 (warmer)	5	0	2	7
	T2 (intermediate)	2	5	1	8
	T3 (cooler)	0	4	12	16
Prec. CNGs Total		7	9	15	31

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845 Table 2 Total community sum-log-abundance responses to 16 years of climatic  
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 848 to the control. Start value indicates the sum-log-abundance in the initial year of the  
 849 experiment (1998 before manipulation). P-values in bold are statistically significant to an  
 850 alpha value of 0.05.

851

Fixed effect	DF		Warming Treatment		Drought Treatment	
	num	den	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Spring precipitation (SP)	1	85	<b>38.15</b>	<b>****</b>	<b>29.62</b>	<b>****</b>
Spring temperature (ST)	1	85	<b>7.04</b>	<b>***</b>	2.24	ns
Start value	1	85	8.68	ns	4.50	ns
Year	1	85	0.23	ns	<b>5.34</b>	*
Treatment	1	3	1.91	ns	<b>12.38</b>	*
SP × ST	2	85	<b>16.62</b>	<b>****</b>	<b>17.02</b>	<b>****</b>
Year × Treatment	2	85	<b>4.60</b>	*	0.03	ns

numDF, numerator degrees of freedom; denDF, denominator degrees of freedom  
 P-value: ns = not significant (>0.05); \* ≤0.05; \*\*\* ≤0.001; \*\*\*\* ≤0.0001

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853

854 Table 3 Climatic Niche Group (CNG) sum-log-abundance responses to 16 years of  
855 climatic manipulation. ANOVA type I table for Linear Mixed-Effects Models. Shown  
856 separately are results for the **temperature** CNG and **precipitation** CNG responses to both  
857 the warming and drought treatments. Underlined is the interaction of most interest to the  
858 study. Start value indicates the sum-log-abundances in the initial year of the experiment  
859 (1998 before manipulation). P-values in bold are statistically significant to an alpha value  
860 of 0.05.

Fixed Effect	DF	Warming Treatment Response		Drought Treatment Response	
		<b>Temperature</b>		<b>Precipitation</b>	
		<b>CNGs</b>	Precipitation CNGs	<b>CNGs</b>	Temperature CNGs
	num den	<i>F</i> <i>p</i>	<i>F</i> <i>p</i>	<i>F</i> <i>p</i>	<i>F</i> <i>p</i>
Spring (SP) precipitation	1 268	<b>24.21</b> *** *	<b>29.02</b> *****	<b>20.30</b> *****	<b>16.08</b> *****
Spring (ST) temperature	1 268	<b>4.47</b> *	<b>5.36</b> *	1.53 ns	1.21 ns
Start value	1 268	<b>247.49</b> *** *	<b>471.95</b> *****	<b>427.57</b> *****	<b>132.76</b> *****
Year (Yr)	1 268	0.15 ns	0.18 ns	3.66 ns	2.90 ns
Treatment (Trt)	1 4	2.41 ns	2.04 ns	<b>15.56</b> *	<b>11.52</b> *
CNG	2 268	<b>93.74</b> *** *	<b>16.12</b> *****	<b>83.72</b> *****	<b>74.49</b> *****
SP × ST	1 268	<b>10.55</b> *** *	<b>12.64</b> ***	<b>11.66</b> ***	<b>9.24</b> **
Yr × Trt	1 268	2.92 ns	3.50 ns	0.02 ns	0.02 ns
Yr × CNG	2 268	<b>23.75</b> *** *	<b>3.49</b> *	0.41 ns	<b>10.21</b> *****
Trt × CNG	2 268	<b>16.62</b> *** *	<b>6.54</b> **	<b>36.27</b> *****	<b>3.05</b> *
<u>Yr × Trt × CNG</u>	2 268	<u><b>6.57</b></u> **	1.68 ns	<u><b>6.58</b></u> **	2.14 ns

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numDF, numerator degrees of freedom; denDF, denominator degrees of freedom  
P-value: ns = not significant ( $>0.05$ ); \*  $\leq 0.05$ ; \*\*  $\leq 0.01$ ; \*\*\*  $\leq 0.001$ ; \*\*\*\*  $\leq 0.0001$

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## 862 **Figure Legends**

863 Fig. 1 (a) Total community sum-log-abundance (sum of all log transformed species  
864 contact hits) within plots under control (no manipulation), nocturnal-warming and  
865 drought treatments throughout the study period 1999-2014. Warming and drought were  
866 not manipulated in 1998. Points represent means and the error bars represent their  
867 associated standard errors (n=3 plots). (b) The effect sizes (treatments minus control) for  
868 total community sum-log-abundance under warming and drought throughout the study  
869 period. Effect sizes are corrected for initial pre-treatment difference in 1998 (Eq. 5).

870

871 Fig. 2 Responses of summer temperature (25 percentile) CNGs to warming (a) and spring  
872 precipitation (median) CNGs response to drought (b) throughout the study period 1999  
873 to 2014. Also shown are the opposing less-well-fitted responses of temperature CNGs to  
874 drought (d) and precipitation CNGs to warming (c). Points indicate mean effect sizes  
875 (treatments minus control) in a given year corrected for initial pre-treatment difference in  
876 1998 (Eq. 5). CNGs are listed in order of aridity: niche values of temperature CNGs from  
877 warm to cold ( $T1>T2>T3$ ), and niche values of precipitation CNGs from dry to wet  
878 ( $P1<P2<P3$ ). Solid lines indicate significant differences between slopes under treatment  
879 and control, and dotted lines indicate no significant differences.

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882 Fig. 3 Single species responses to the warming (a & c) and drought (b & d) treatments  
883 when plotted along their climatic niche axis: Species niche values defined by (a & d).  
884 Summer temperature (in reverse order) for 25 percentile values of distribution range  
885 observations; (b & c) [spring](#) precipitation for median values of distribution range. N.B.  
886 generally better fit for temperature niche with warming (a), and precipitation niche with  
887 drought (b). Y-axis are the t-values of single species Linear Mixed Model (LMEM) tests  
888 comparing slope response over time under control to treatments (positive values indicate  
889 increase in abundances under treatment, negative values indicate decrease under  
890 treatment over time relative to control) . Bubbles are displayed in relative size to the log-  
891 community percentage each species occurred throughout the experiment. Fit lines were  
892 derived from Generalized Additive Models (GAMs) weighted by species log-community  
893 percentage.

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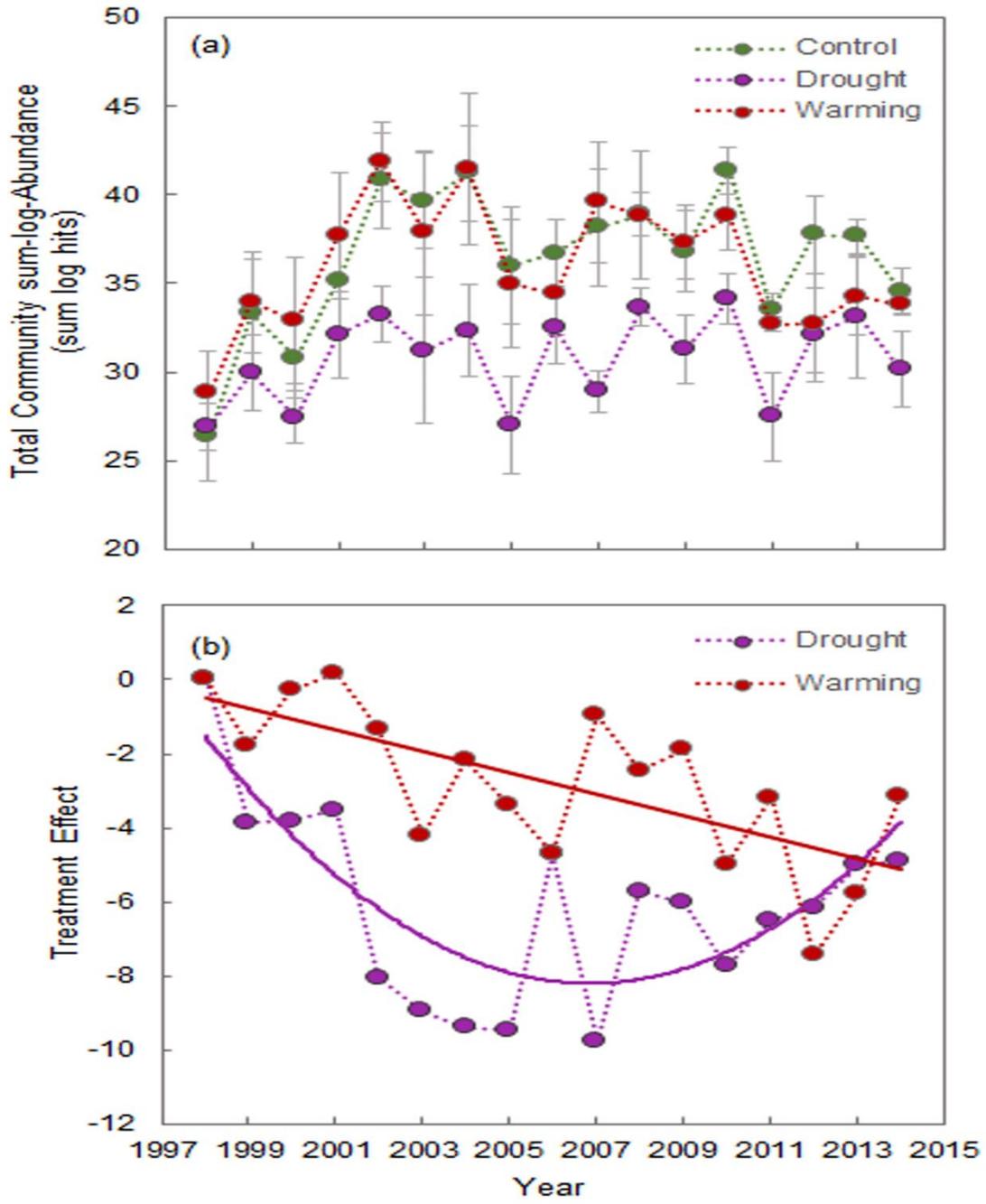
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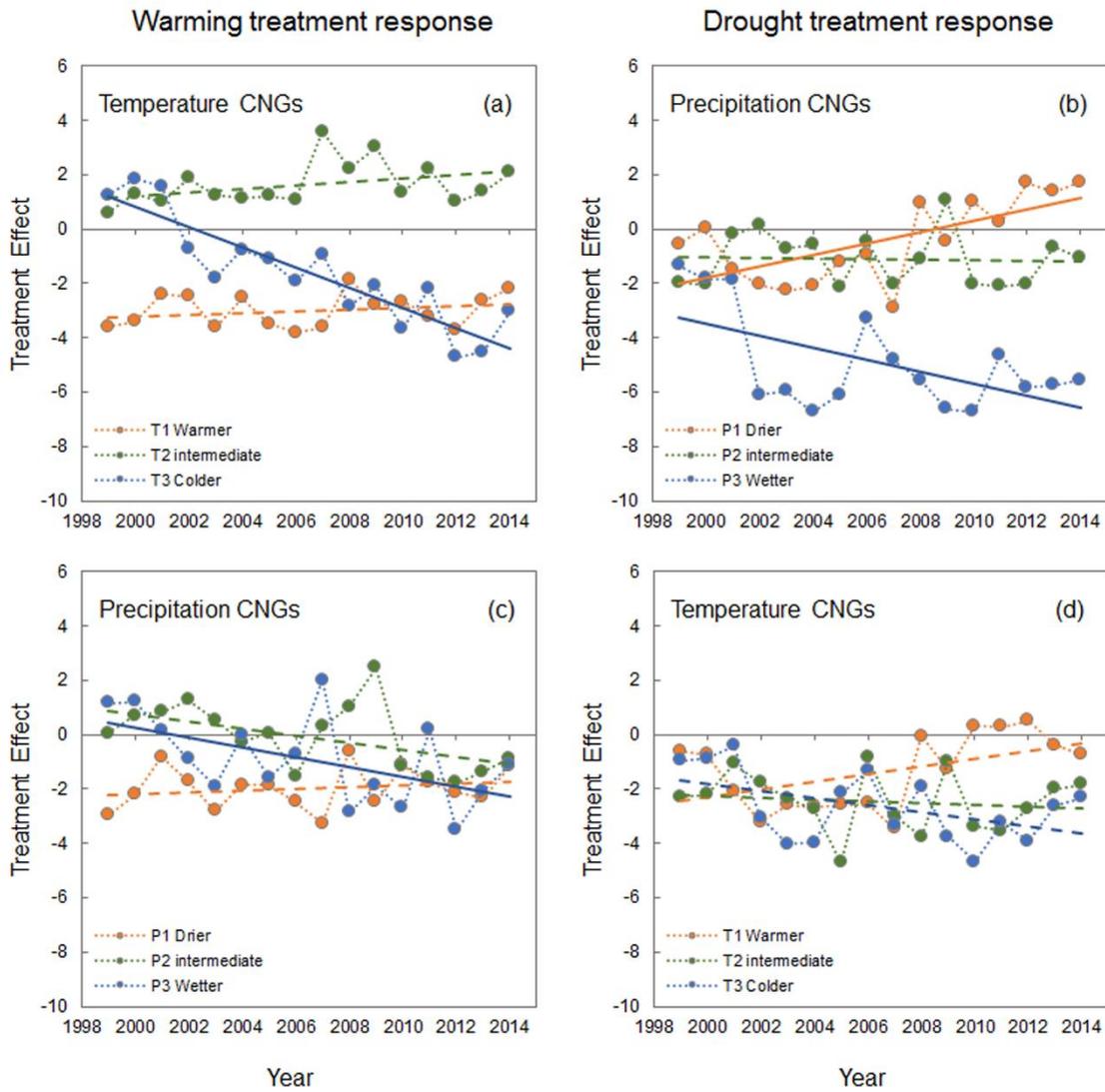
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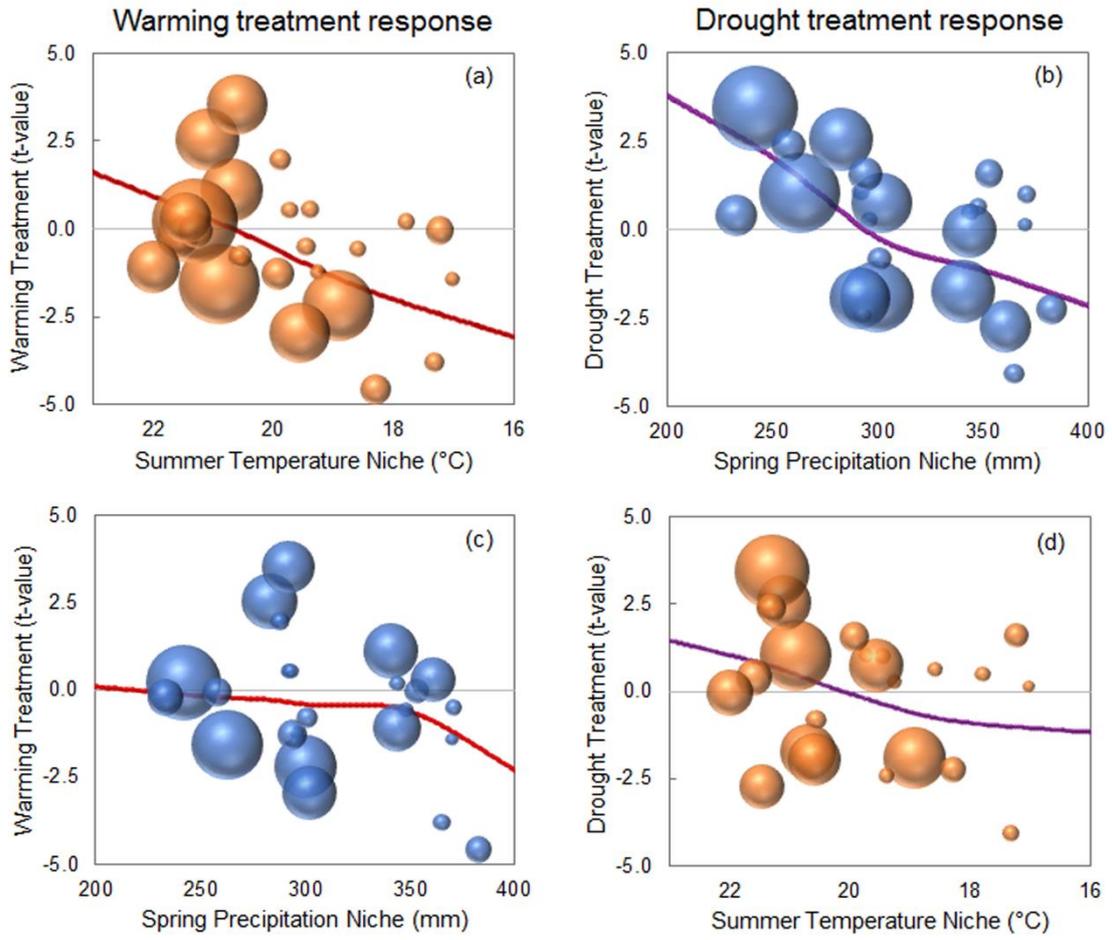
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911 Fig. 2



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913 Fig. 3

## Supporting Information

Additional supporting information may be found in the online version of this article.

**Table S1** Species list of all recorded individuals collected in the studied plots and their associated climatic niche values.

**Table S2** Species list and their associated Climatic Niche Groups (CNGs) and community percentage.

**Table S3** MetaData for the Climatic Niche Groups, describing the number of species per group, community percentage per group, and group niche boundaries.

**Table S4** Statistical test results for the multiple CNGs tested, displaying the coefficient values and p-values of the interaction term testing the hypothesis.

**Table S5** Statistical test results for single species responses to 16 years of climatic manipulation.

**Fig. S1** Treatment effects on (a) soil temperature between control and warming and (b) soil moisture between control and drought during the study period of 1999-2014.

**Fig. S2** Warming Cumulative Group Analyses for species groups defined by summer temperature niches in response to manipulated warming.

**Fig. S3** Drought Cumulative Group Analyses for species groups defined by spring precipitation niches in response to manipulated drought.

**Fig. S4** Opposing Cumulative Group Analyses for species groups defined by median spring precipitation niches in response to manipulated warming, and species groups defined by 25 percentile summer temperature niches in response to manipulated drought.

**Fig. S5** Single species responses to the warming and drought manipulation treatments when plotted along multiple climatic niche axes.

**Fig. S6** Climatic Niche Group (CNG) raw abundance (sum of log contact hits) within plots under control (no manipulation), nocturnal-warming and drought treatments

throughout the study period.

**Notes S1** Raw data for the statistical analyses carried out in the main article: “Total community analysis” (Fig. 1); “CNG analysis” (Fig. 2); and the “Single species versus climatic niche analysis” (Fig. 3). (Separate excel file).

**Notes S2** Cumulative Group Analyses: CNG robustness testing. A methodology, results and discussion of the robustness testing.

**Notes S3** Discussion of niche parameter estimation for forming CNGs.

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