1 **Species selection under long-term experimental warming and drought explained**

2 **by climatic distributions**

3 Daijun Liu[1,2,†], Josep Peñuelas[1,2], Romà Ogaya[1,2], Marc Estiarte[1,2], Katja Tielbörger[3],

4 Fabian Slowik[3], Xiaohong Yang[4], Mark C. Bilton[3,†]

5 [1] CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra (Catalonia) E-08193, Spain;

6 [2] CREAF, Cerdanyola del Vallès (Catalonia) E-08193, Spain; [3] University of Tübingen,

7 Plant Ecology Group, Institute of Evolution and Ecology, Auf der Morgenstelle 5, D-

8 72076 Tübingen, Germany; [4] Key Laboratory of Horticulture Science for Southern

9 Mountainous Regions, Ministry of Education, Southwest University, Chongqing 400716,

10 China

11 [†] Corresponding authors: Daijun Liu *(Tel: +34 667094190; E-mail: d.liu@creaf.uab.es);*

12 Mark Bilton *(Tel: +49 (0)7071 29 73235; mark.bilton@uni-tuebingen.de)*

13 Brief title: Climatic Niche Group responses under long-term warming and drought

14 manipulations (Twitter: Daijun Liu)

Total word count (excluding summary, references and legends):	6828	Acknowledgements:	69
Summary:	199	No. of figures:	3(All in colour)
Introduction:	1330	No. of Tables:	3
Materials and Methods:	2271	No of Supporting Information files:	13 (Table S1-S5; Fig. S1-S6; Notes S1-S3)
Results:	1126		
Discussion:	2101		

Summary

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

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

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

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

37

Key words: global warming; frequent drought; Mediterranean ecosystems; long-term

manipulation experiments; climatic niche groups; composition shifts; biodiversity loss

40

41

42

43

44

45

46

47

48

49

50

Introduction

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

The forecasting of climate change impacts on species diversity and composition may be impeded by the interrelationships among many simultaneously changing climatic factors, and directional shifts in species composition to these changes cannot be easily detected (McMahon *et al.*, 2011; Bellard *et al.*, 2012; Garcia *et al.*, 2014). In addition, climatic factors are often confounded, making it very difficult to make accurate predictions for biodiversity shifts independently for temperature and precipitation change (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.

8

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   calcixerept 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^2 (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^2 (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^{-1})

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^{-1}) 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 $$\sum_{i=1}^{i=n} \log(hits\ sp\ i)$$

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

14

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:

Total Community sum-log-Abundance	$= ST*SP + Pre\text{-}treat + Year*Treatment$	(Eq. 2)
CNG sum-log-Abundance	$= ST*SP + Pre\text{-}treat + Year*Treatment*CNG$ identity	(Eq. 3)
Species log-Abundance	$= ST*SP + Pre\text{-}treat + Year*Treatment$	(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   Effect size (Year) = $(\mu_{treatmentYear} - \mu_{treatment1998}) - (\mu_{controlYear} - \mu_{control1998})$ (Eq. 5)

314   where $\mu_{treatment}$ and $\mu_{control}$ 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

Results

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

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

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

treatment (Fig. 2a, Table 3). The LMEM demonstrated a significant three-way CNG ×

Treatment × Year interaction for the sum-log-abundance changes of temperature CNGs

($p<0.01$). Among these temperature CNGs, the sum-log-abundances of T1 and T2 (from

relatively warmer origins) remained fairly constant in the warming treatment when

compared to the control, whereas the sum-log-abundance of T3 (from colder origins)

decreased gradually and linearly throughout the study period (estimated difference in

slopes = -0.37, p<0.0001) (Fig. 2a, Table S4). In contrast, the three-way interaction was

not significant ($p=0.12$, Table 3) when applying the classification of temperature CNGs

to analyze sum-log-abundance changes under the drought manipulations (Fig. 2c). Here,

while response slopes comparing drought log-compositions over time to control were

ranked in hierarchical order (T1>T2>T3) no temperature-CNG slope differences were

significant (Fig. 2c, Table S4).

As hypothesized, precipitation CNGs also accounted for the contrasting changes in

species abundances in the drought treatment (Fig. 2b, Table 3). The LMEM demonstrated

a significant three-way CNG × Treatment × Year interaction for the sum-log-abundance

changes of precipitation CNGs ($p<0.01$, Table 3). The response patterns differed greatly

among the three CNG-groups. P3 (from wetter origins) initially decreased in sum-log-

abundance compared to the control (estimated difference in slopes = -0.22, p<0.01, Table

S4), with an abrupt shift after three years of the drought manipulation (after 2001) and

fairly constant sum-log-abundances for the remaining years of the study. P2 sum-log-

abundances (from moderately dry origins) were similar in the control and drought

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

Discussion

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

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

607   **Acknowledgements**

615

616

617

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.

624

625

626

627

628

References

Anderegg WRL, Kane JM, Anderegg LDL. **2013**. Consequences of widespread tree

mortality triggered by drought and temperature stress. *Nature Climate Change* **3**: 30–36.

Andresen LC, Müller C, de Dato G, Dukes JS, Emmett BA, Estiarte M, Jentsch A,

Kröel-Dulay G, Lüscher A, Niu S, *et al*. **2016.** Shifting impacts of climate change: long-

term patterns of plant response to elevated CO2, drought and warming across ecosystems.

Advances in Ecological Research **55**: 437-473

Araújo MB, Peterson AT. 2012. Uses and misuses of bioclimatic envelope modeling.

Ecology **93**: 1527–1539.

Barbeta A, Ogaya R, Peñuelas J. **2013**. Dampening effects of long-term experimental

drought on growth and mortality rates of a Holm oak forest. *Global Change Biology* **19**:

3133–3144.

Barros V, Field CB, Dokke DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee M,

Ebi K. L, Estrada YO, Genova RC. 2014. *Climate change 2014: Impacts, Adaptation,*

and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the

Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge,

UK & New York, NY, USA: Cambridge University Press.

Bates D, Sarkar D, Bates MD, Matrix L. 2007. The lme4 package. R package version

2: 74.

Beaumont LJ, Pitman A, Perkins S, Zimmermann NE, Yoccoz NG, Thuiller W. **2011**.

Impacts of climate change on the world 's most exceptional ecoregions. *Proceedings of*

the National Academy of Sciences of the United States of America **108**: 2306–2311.

651   **Beier C, Emmett B, Gundersen P, Tietema A, Peñuelas J, Estiarte M, Gordon C,**

652   **Gorissen A, Llorens L, Roda F** *et al*. **2004**. Novel approaches to study climate change

653   effects on terrestrial ecosystems in the field : drought and passive nighttime warming.

654   *Ecosystems* **7**: 583–597.

655   **Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F**. **2012**. Impacts of

656   climate change on the future of biodiversity. *Ecology Letters* **15**: 365–377.

657   **Bilton MC, Metz J, Tielbörger K**. **2016**. Climatic niche groups: A novel application of

658   a common assumption predicting plant community response to climate change.

659   *Perspectives in Plant Ecology, Evolution and Systematics* **19**: 61–69.

660   **Brose U, Hillebrand H**. **2016**. Biodiversity and ecosystem functioning in dynamic

661   landscapes. *Phil. Trans. R. Soc. B* **371**: 20150267.

662   **Dai AG**. **2013**. Increasing drought under global warming in observations and models.

663   *Nature Climate Change* **3**: 52–58.

664   **De Boeck HJ, Vicca S, Roy J, Nijs I, Milcu A, Kreyling J, Jentsch A, Chabbi A,**

665   **Campioli M, Callaghan T,** *et al*. **2015**. Global change experiments : challenges and

666   opportunities. *Biosciences* **65**: 922–931.

667   **De Frenne P, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend**

668   **M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J,** *et al.* **2013**.

669   Microclimate moderates plant responses to macroclimate warming. *Proceedings of the*

670   *National Academy of Sciences of the United States of America* **110**: 18561–5.

671   **Diamond SE, Nichols LM, McCoy N, Hirsch C, Pelini SL, Sanders NJ, Ellison AM,**

672   **Gotelli NJ, Dunn RR**. **2012**. A physiological trait-based approach to predicting the

673 responses of species to experimental climate warming. *Ecology* **93**: 2305–2312.

674 **Doblas-Miranda E, Martínez-Vilalta J, Lloret F, Álvarez A, Ávila A, Bonet FJ,**

675 **Brotons L, Castro J, Curiel Yuste J, Díaz M *et al*. 2015**. Reassessing global change

676 research priorities in mediterranean terrestrial ecosystems: How far have we come and

677 where do we go from here? *Global Ecology and Biogeography* **24**: 25–43.

678 **Dormann CF, 2007.** Promising the future? Global change projections of species

679 distributions. *Basic and Applied Ecology* **8**: 387-397.

680 **Duque A, Stevenson PR, Feeley KJ. 2015**. Thermophilization of adult and juvenile tree

681 communities in the northern tropical Andes. *Proceedings of the National Academy of*

682 *Sciences of the United States of America* **112**: 10744–9.

683 **Elmendorf SC, Henry GHR, Hollister RD, Fosaa AM, Gould WA, Hermanutz L,**

684 **Hofgaard A, Jónsdóttir IS, Jorgenson JC, Lévesque E, *et al.* 2015**. Experiment,

685 monitoring, and gradient methods used to infer climate change effects on plant

686 communities yield consistent patterns. *Proceedings of the National Academy of Sciences*

687 **112**: 448–452.

688 **Estiarte M, Vicca S, Peñuelas J, Bahn M, Beier C, Emmett BA, Fay PA, Hanson PJ,**

689 **Hasibeder R, Kigel J, *et al.* 2016**. Few multi-year precipitation-reduction experiments

690 find a shift in the productivity-precipitation relationship. *Global Change Biology* **22**:

691 2570–2581.

692 **Fridley JD, Grime JP, Askew AP, Moser B, Stevens CJ. 2011.** Soil heterogeneity

693 buffers community response to climate change in species-rich grassland. *Global Change*

694 *Biology* **17**: 2002-2011.

695 **Garcia RA, Cabeza M, Rahbek C, Araújo MB**. **2014**. Multiple Dimensions of Climate

696 Change and Their Implications for Biodiversity. *Science* **344**: 1247579.

697 **Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barančok P, Benito Alonso JL,**

698 **Coldea G, Dick J, Erschbamer B, Fernández Calzado MR, *et al.* 2012**. Continent-

699 wide response of mountain vegetation to climate change. *Nature Climate Change* **2**: 111–

700 115.

701 **Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR**. **2008**.

702 Long-term resistance to simulated climate change in an infertile grassland. *Proceedings*

703 *of the National Academy of Sciences of the United States of America* **105**: 10028–10032.

704 **Harrison SP, Gornish ES, Copeland S**. **2015**. Climate-driven diversity loss in a

705 grassland community. *Proceedings of the National Academy of Science USA* **112**: 8672–

706 8678.

707 **Harte J, Shaw R**. **1995**. Shifting dominance within a montane vegetation community:

708 results of a climate-warming experiment. *Science* **267**: 876–880.

709 **Hijmans RJ, Graham CH**. **2006**. The ability of climate envelope models to predict the

710 effect of climate change on species distributions. *Global Change Biology* **12**: 2272–2281.

711 **Jump AS, Peñuelas J, Rico L, Ramallo E, Estiarte M, Martinez-Izquierdo JA, Lloret**

712 **F. 2008.** Simulated climate change provokes rapid genetic change in the Mediterranean

713 shrub *Fumana thymifolia*. *Global Change Biology* **14**: 637-643.

714 **Kröel-Dulay G, Ransijn J, Schmidt IK, Beier C, De Angelis P, de Dato G, Dukes JS,**

715 **Emmett B, Estiarte M, Garadnai J, *et al.* 2015**. Increased sensitivity to climate change

716 in disturbed ecosystems. *Nature communications* **6**: 6682.

Lavorel S, McIntyre S, Landsberg J, Forbes TDA. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution* **5347**: 474–478.

Leuzinger S, Luo Y, Beier C, Dieleman W, Vicca S, Körner C . 2011. Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends in Ecology & Evolution* **26**: 236–241.

Lenth RV. 2016. Least-squares means: the R Package lsmeans. *Journal of Statistical Software* **69**: 1-33.

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

Liu D, Llusia J, Ogaya R, Estiarte M, Llorens L, Yang X, Peñuelas J. **2016**. Physiological adjustments of a Mediterranean shrub to long-term experimental warming and drought treatments. *Plant Science* **252**: 63-61.

Liu D, Estiarte M, Ogaya R, Yang X, Peñuelas J. **2017**. Shift in community structure in an early-successional Mediterranean shrubland driven by long-term experimental warming and drought and natural extreme droughts. *Global Change Biology* **23**: 4267–4279.

Lloret F, Peñuelas J, Prieto P, Llorens L, Estiarte M. **2009**. Plant community changes induced by experimental climate change: Seedling and adult species composition. *Perspectives in Plant Ecology, Evolution and Systematics* **11**: 53–63.

739 **McMahon SM, Harrison SP, Armbruster WS, Bartlein PJ, Beale CM, Edwards ME,**

740 **Kattge J, Midgley G, Morin X, Prentice IC**. **2011**. Improving assessment and modelling

741 of climate change impacts on global terrestrial biodiversity. *Trends in Ecology &*

742 *Evolution* **26**: 249–259.

743 **Metz J, Tielbörger K. 2016.** Spatial and temporal aridity gradients provide poor proxies

744 for plant-plant interactions under climate change: a large-scale experiment. *Functional*

745 *Ecology* **30**: 20-29.

746 **Mittler R**. **2006**. Abiotic stress, the field environment and stress combination. *Trends in*

747 *Plant Science* **11**: 15–19.

748 **Mueller KE, Blumenthal DM, Pendall E, Carrillo Y, Dijkstra FA, Williams DG,**

749 **Follett RF, Morgan JA. 2016.** Impacts of warming and elevated CO2 on a semi‐arid

750 grassland are non-additive, shift with precipitation, and reverse over time. *Ecology Letters*

751 **19**: 956-966.

752 **Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000**.

753 Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

754 **Parmesan C, Yohe G**. **2003**. A globally coherent fingerprint of climate change impacts

755 across natural systems. *Nature* **421**: 37–42.

756 **Peñuelas J, Prieto P, Beier C, Cesaraccio C, de Angelis P, de Dato G, Emmett BA,**

757 **Estiarte M, Garadnai J, Gorissen A,** *et al.* **2007**. Response of plant species richness and

758 primary productivity in shrublands along a north-south gradient in Europe to seven years

759 of experimental warming and drought: Reductions in primary productivity in the heat and

760 drought year of 2003. *Global Change Biology* **13**: 2563–2581.

761 **Peñuelas J, Sardans J, Estiarte M, Ogaya R, Carnicer J, Coll M, Barbeta A, Rivas-**

762 **Ubach A, Llusià J, Garbulsky M, *et al.* 2013**. Evidence of current impact of climate

763 change on life: a walk from genes to the biosphere. *Global change biology* **19**: 2303–38.

764 **Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH,**

765 **Roberts CM, Sexton JO**. **2014**. The biodiversity of species and their rates of extinction,

766 distribution, and protection. *Science* **344**: 1246752.

767 **Prieto P, Peñuelas J, Lloret F, Llorens L, Estiarte M**. **2009**. Experimental drought and

768 warming decrease diversity and slow down post-fire succession in a Mediterranean

769 shrubland. *Ecography* **32**: 623–636.

770 **Reichstein M, Bahn M, Ciais P, Frank D, Mahecha MD, Seneviratne SI, Zscheischler**

771 **J, Beer C, Buchmann N, Frank DC *et al.* 2013**. Climate extremes and the carbon cycle.

772 *Nature* **500**: 287–295.

773 **Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald**

774 **E, Huenneke LF, Jackson RB, *et al.* 2000**. Global Biodiversity Scenarios for the Year

775 2100. *science* **1770**: 1770–1775.

776 **Sardans J, Peñuuelas J, Estiarte M, Prieto P**. **2008**. Warming and drought alter C and

777 N concentration, allocation and accumulation in a Mediterranean shrubland. *Global*

778 *Change Biology* **14**: 2304–2316.

779 **Seddon AWR, Macias-Fauria M, Long PR, Benz D, Willis KJ**. **2016**. Sensitivity of

780 global terrestrial ecosystems to climate variability. *Nature* **531**: 1–15.

781 **Šmilauer P, Lepš J.** 2014. Multivariate Analysis of Ecological Data using CANOCO 5.

782 Cambridge University Press, Cambridge, UK.

783 **Smith MD, Knapp AK, Collins SL**. **2009**. A framework for assessing ecosystem

784 dynamics in response to chronic resource alterations induced by global change. *Ecology*

785 **79**: 3–24.

786 **Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC,**

787 **Erasmus BFN, de Siqueira MF, Grainger A, Hannah L** *et al*. **2004**. Extinction risk

788 from climate change. *Nature* **427**: 145–148.

789 **Thuiller W, Lavorel S, Araújo MB**. **2005**. Niche properties and geographical extent as

790 predictors of species sensitivity to climate change. *Global Ecology and Biogeography* **14**:

791 347–357.

792 **Tielbörger K, Bilton MC, Metz J, Kigel J, Holzapfel C, Lebrija-Trejos E, Konsens I,**

793 **Parag HA, Sternberg M**. **2014**. Middle-Eastern plant communities tolerate 9 years of

794 drought in a multi-site climate manipulation experiment. *Nature communications* **5**: 5102.

795 **Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J,**

796 **Hoegh-Guldberg O, Bairlein F**. **2002**. Ecological responses to recent climate change.

797 *Nature* **416**: 389–395.

798 **Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM,**

799 **Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD,** *et al.* **2012**. Temperature

800 as a potent driver of regional forest drought stress and tree mortality. *Nature Climate*

801 *Change* **3**: 292–297.

802 **Wood SN.** 2011. Fast stable restricted maximum likelihood and marginal likelihood

803 estimation of semiparametric generalized linear models. *Journal of the Royal Statistical*

804 *Society (B)* **73**: 3-36.

805 **Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate B. 2011**. Responses of terrestrial

806 ecosystems to temperature and precipitation change: a meta-analysis of experimental

807 manipulation. *Global Change Biology* **17**: 927–942.

808 **Zhu K, Chiariello NR, Tobeck T, Fukami T, Field CB. 2016.** Nonlinear, interacting

809 responses to climate limit grassland production under global change. *Proceedings of the*

810 *National Academy of Science USA* **113**: 10589–10594.

Table legend

811

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 | | | |
		P1 (drier)	P2 (intermediate)	P3 (wetter)	Temp. CNGs Total
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

834

835

836

837

838

839

840

841

842

843

844

845 Table 2 Total community sum-log-abundance responses to 16 years of climatic

846 manipulation. ANOVA type I table for Linear Mixed-Effects Models analyzing the

847 changes in abundances in response to either the warming or drought Treatment compared

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

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

852

853

854
855
856
857
858
859
860

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

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

44

numDF, numerator degrees of freedom; denDF, denominator degrees of freedom

P-value: ns = not significant (>0.05); * ≤0.05; ** ≤0.01; *** ≤0.001; **** ≤0.0001

861

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.

880

881

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.

894

895

896

897

898

899

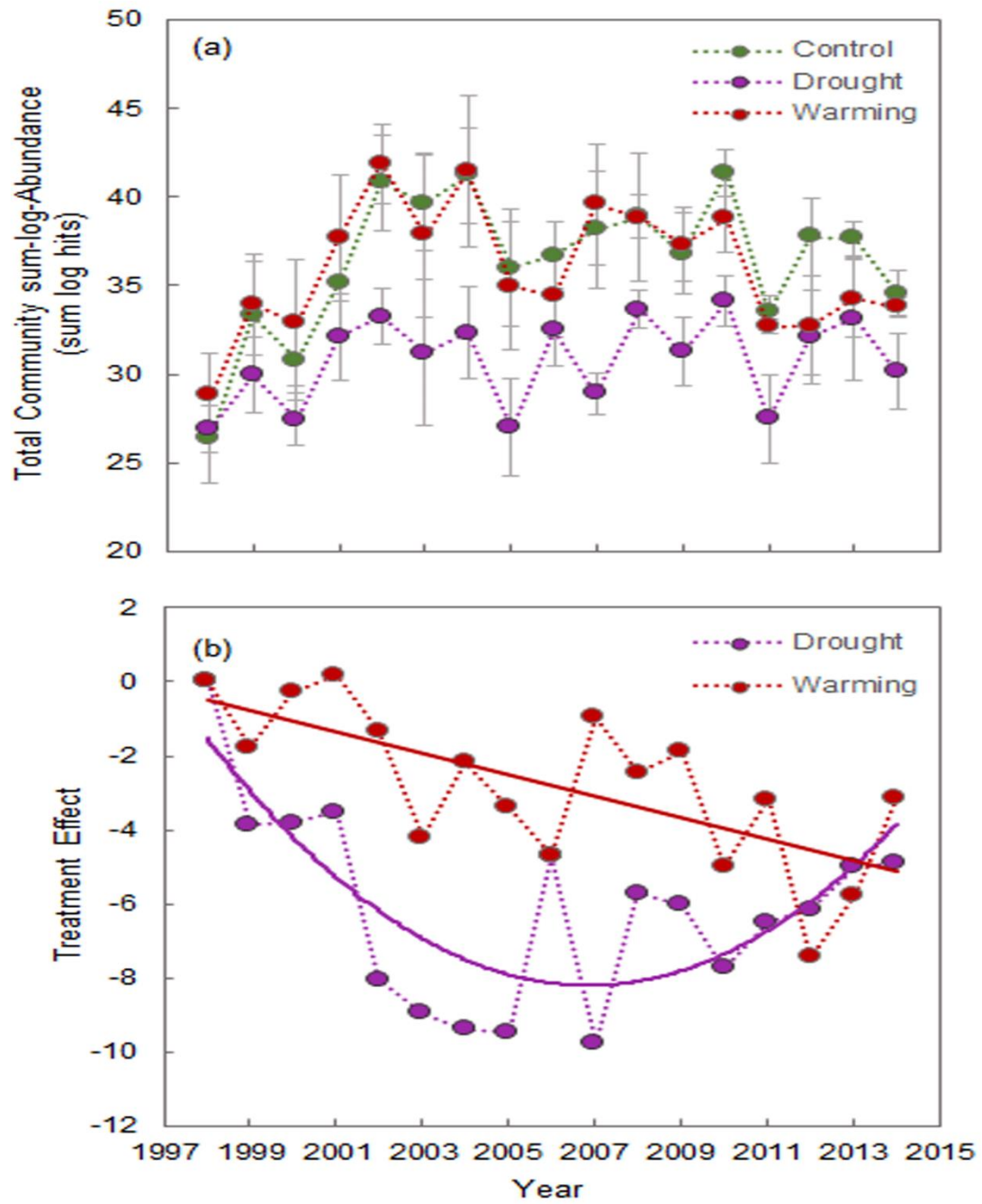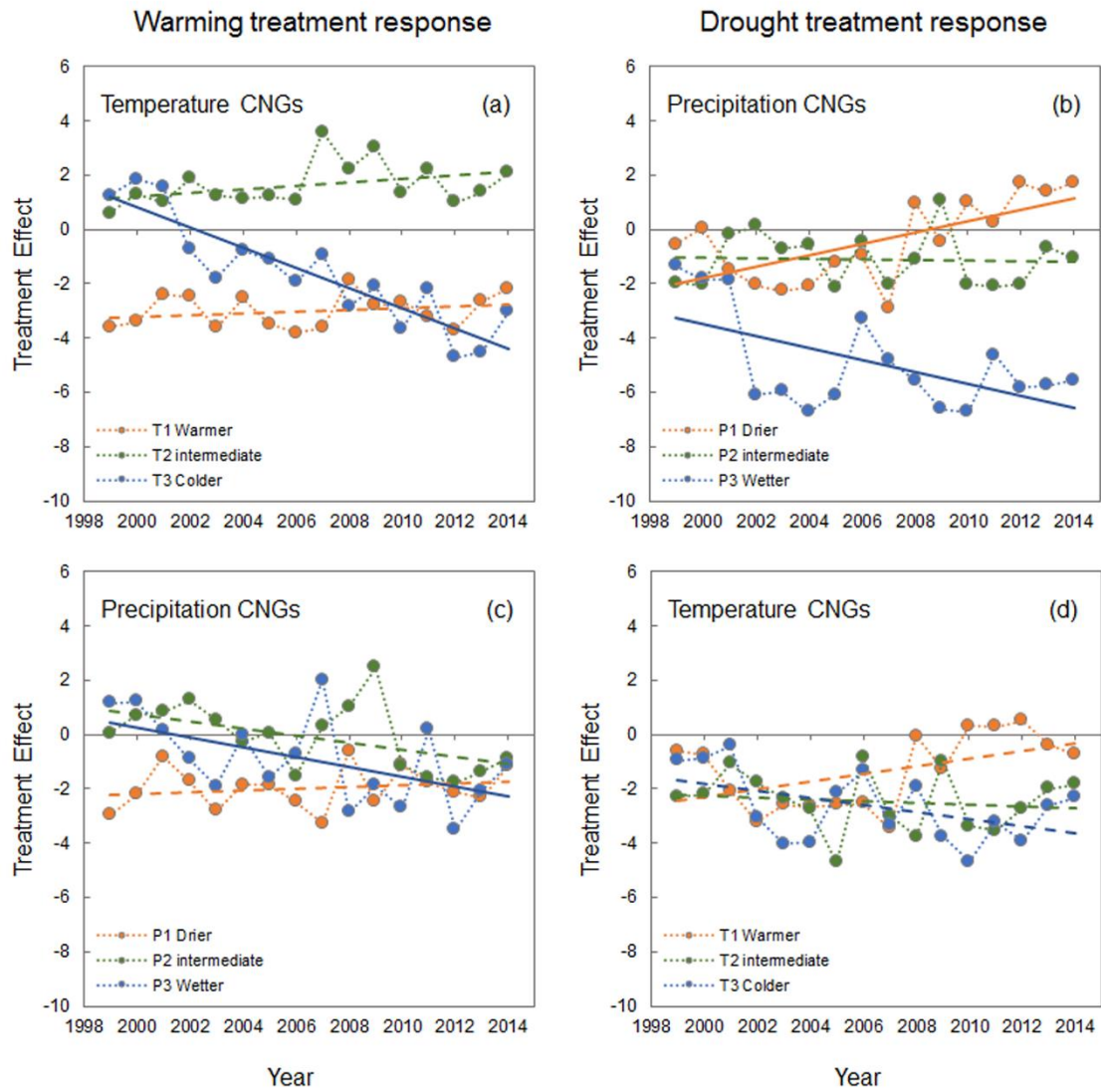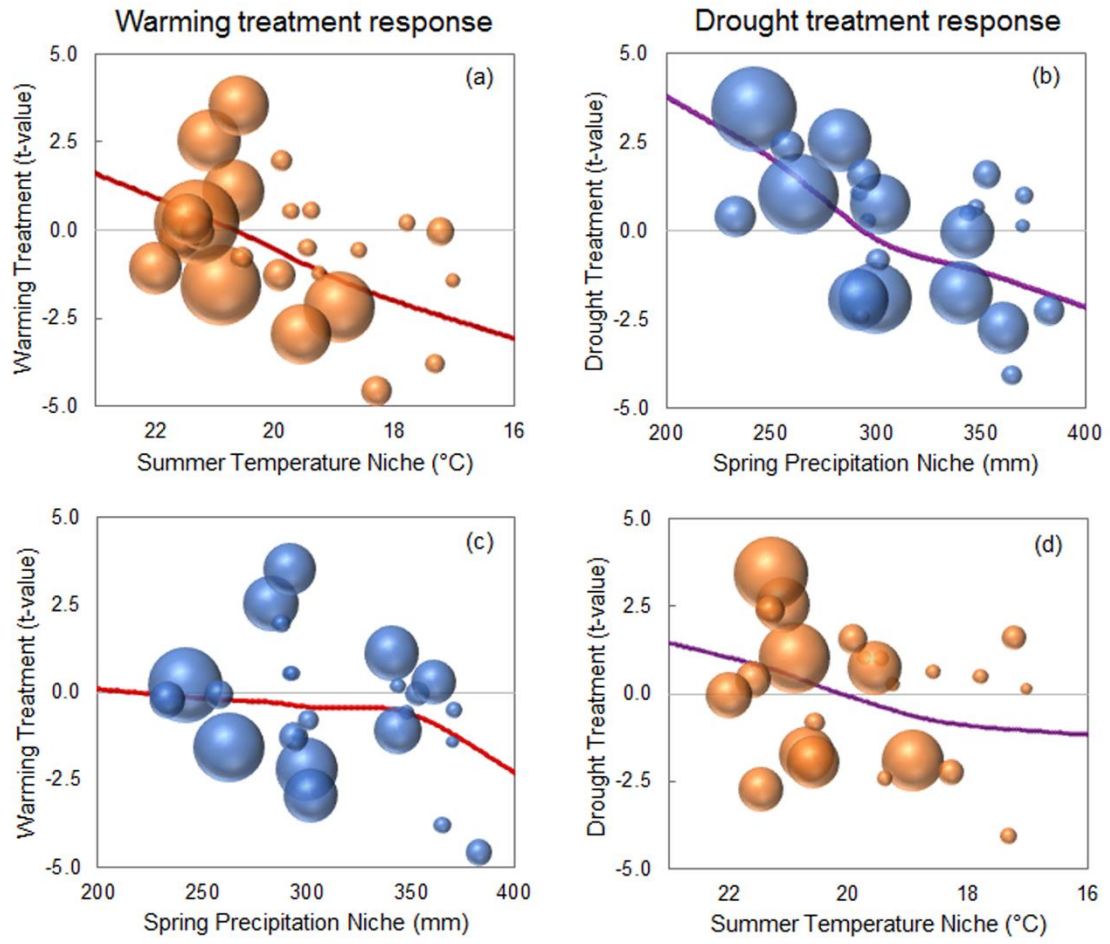900

901

902

903

904   Fig 1

905

906

907

908

909

Fig. 2

912

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.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

914