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

Daijun Liu[1,2*], Marc Estiarte[1,2], Romà Ogaya[1,2], Xiaohong Yang[3], Josep Peñuelas[1,2*]

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

[2] CREAF, Cerdanyola del Vallès (Catalonia) E-08193, Spain,

[3]Key Laboratory of Horticulture Science for Southern Mountainous Regions, Ministry of Education, Southwest University, Chongqing 400716, China

*Corresponding author: Daijun Liu, Josep Peñuelas

Telephone: +34935814850, fax: +34 935814151

E-mail: d.liu@creaf.uab.es

Key words: Global warming; Frequent droughts; Mediterranean ecosystems; Long-term climatic experiments; Species richness; Community diversity; Functional groups; Composition shifts

Paper type: Primary Research Articles

Abstract

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

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

Introduction

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

Strong evidence for the direction and magnitude of the impacts of climate change on plant community structure and composition, however, remains unclear. Ecological modelling (e.g. bioclimatic envelope and dynamic vegetation models) has been commonly used in recent decades for predicting the response of biodiversity to future climate change, such as extinction and shifts in species ranges and abundance (Leuzinger *et al.*, 2011; Araújo & & Peterson, 2012; Bellard *et al.*, 2012). Most of the models, however, have grossly underestimated the importance of species plasticity (e.g. physiological, phenological and morphological plasticity) and biotic interactions (e.g. competition, facilitation and mutualism) (Tylianakis *et al.*, 2008; Leuzinger *et al.*, 2011; Bellard *et al.*, 2012; Tilman *et al.*, 2014). Indeed, many studies have reported physiological (photosynthetic activities) (Llorens *et al.*, 2003; Prieto *et al.*, 2009b; Liu *et al.*, 2016), phenological (earlier or delayed) and morphological (leaf size, number and longevity) (Peñuelas *et al.*, 2004, 2009; Bernal *et al.*, 2011; Scheffers *et al.*, 2016; Thackeray *et al.*, 2016) adjustments associated with climate change as well as evolutionary adaptions (Jump & Peñuelas, 2005; Jump *et al.*, 2008; Hoffmann & Sgrò, 2011; Scheffers *et al.*, 2016) to rapid warming and drought. Species loss or changes in abundance predicted by models do not therefore satisfactorily represent changes in community structure and composition in terrestrial ecosystems under future climatic scenarios. Some models have incorporated species plasticity, acclimation and biotic interactions, but most typically analyze data parameterized on short timescales (Luo *et al.*, 2011; Beier *et al.*, 2012; Estiarte *et al.*, 2016). The responses of community structure and composition to climate change, however, will be driven by slow processes over decadal or even longer timescales (Smith *et al.*, 2009; Luo *et al.*, 2011; Peñuelas *et al.*, 2013; Estiarte *et al.*, 2016). Accurately assessing the changes in community structure and composition caused by long-term processes is thus essential for validating the models and providing realistic supporting information for future climate change.

Long-term experiments of climatic manipulation are among the best methods for studying the responses of species interactions and community dynamics under predicted climatic regimes (Luo *et al.*, 2011; Wu *et al.*, 2011; Beier *et al.*, 2012; Estiarte *et al.*, 2016). A few long-term (>10 years) climatic-manipulation experiments have been established in natural ecosystems in the last three decades (Leuzinger *et al.*, 2011; Luo *et al.*, 2011; Estiarte *et al.*, 2016). These experiments have demonstrated increasing (Walker *et al.*, 2006; Smith *et al.*, 2009; Elmendorf *et al.*, 2015), decreasing (dampening) (Leuzinger *et al.*, 2011; Barbeta *et al.*, 2013; Liu *et al.*, 2015) and unchanged (Grime *et al.*, 2008; Tielbörger *et al.*, 2014; Estiarte *et al.*, 2016) impacts of manipulation on community dynamics. Community responses to manipulative experiments have been reported for tundra (Walker *et al.*, 2006; Elmendorf *et al.*, 2015) and temperate grassland (Yang *et al.*, 2011) ecosystems, whereas no net (or chronic) changes have been reported for semiarid Mediterranean ecosystems (Tielbörger *et al.*, 2014; Estiarte *et al.*, 2016). Large shifts in community structure and composition, as proposed by the hierarchical-response framework, will likely come because of continuous and cumulative climatic disturbances (Smith *et al.*, 2009). Contrasting community responses to long-term climatic-manipulation experiments can be due to differential effects in functional groups or dominant species, indicating alterations in dominance hierarchies and relative abundances (Smith *et al.*, 2009; Luo *et al.*, 2011; Yang *et al.*, 2011; Peñuelas *et al.*, 2013). The shortage of long-term field manipulations has greatly limited our understanding of the alterations in plant community structure and composition and in functional groups and dominance shifts. The cumulative effects of long-term climate change, however, may also be abrupt or non-linear when thresholds (tipping points) are exceeded, exacerbated by climatic extremes (Ciais *et al.*, 2005; Peñuelas *et al.*, 2007; Jentsch *et al.*, 2011; Reichstein *et al.*, 2013; Doblas-Miranda *et al.*, 2014). Long-term manipulative field experiments are thus likely to record transformative changes and to identify the mechanisms of community dynamics in response to the overlapping effects of climatic variability and extremes (Smith *et al.*, 2009; Luo *et al.*, 2011; Jentsch *et al*., 2011; Kreyling *et al*., 2011; Estiarte *et al.*, 2016).

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

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

2. Materials and method

2.1 Study site

The study site was in a Mediterranean shrubland on a south-facing slope (13%) in the Garraf Natural Park, near Barcelona (northeastern Spain) (41º18´N, 1º49´E; 210 m a.s.l.). The climate is typically Mediterranean, with hot and dry summers (June to August, average temperature of 22.8 °C) and wet springs (March to May, average rainfall of 147.8 mm) and autumns (September to November, average rainfall of 204.8 mm). The mean annual temperature and mean annual precipitation at the study site are 15.2 °C and 571 mm, respectively. The soil is calcareous, and the substrate is composed of marls and limestone, with rocky outcrops. This shrubland appeared after two severe wildfires in 1982 and 1994 in a *Pinus halepensis* forest. The vegetation is composed mainly of short perennial shrubs (<1.5 m) that dominated the regrowth after the two fires. The dominant species of the shrubland are *Globularia alypum* and *Erica multiflora* (total proportion more than 50%), which are accompanied by other Mediterranean shrub species, such as *Ulex parviflorus*, *Dorycnium pentaphyllum* and *Rosmarinus officinalis*. The undergrowth consists mainly of annual herbaceous plants (mostly Poaceae species) (Species information as described in Table S1).

2.2 Manipulation experiments

We conducted a nocturnal-warming experiment from 1999 to 2014 and a drought experiment from 1999 to 2015 on three replicate blocks selected along a south-facing slope (Llorens *et al.*, 2003; Peñuelas *et al.*, 2007; Prieto *et al.*, 2009a, 2009b; Liu *et al.*, 2016). Each block contained three randomly distributed replicate warming, drought and control plots (4×5 m) (Peñuelas et al., 2004), for a total of nine plots for all treatment. The warming experiment was established by passive nocturnal warming by covering the vegetation with reflective aluminum curtains (ILS ALU, AB Ludvig Svensson, Kinna, Sweden) at night that reduced outgoing infrared radiation. The curtains were activated automatically by preset light conditions (<200 lux). The drought experiment was conducted by excluding precipitation with transparent waterproof plastic covers during the wettest seasons (spring and autumn) to prolong the summer drought. A rain sensor activated the covers to intercept precipitation and retracted them when the rain stopped. The coverings for the warming and drought experiments were removed at wind speeds >10 m s^{-1} to prevent damage. Scaffolding (1.2 m height) was installed in each plot to support the covering systems. Scaffolding was also installed in the control plots, but no curtains or covers were used. The soil temperature at a depth of 5 cm was 0.6 °C higher in the warming treatment than the control, and soil moisture in the 0-15 cm layer was 16.7 % lower annually in the drought treatment than the control, throughout the 17-year experiment.

2.3 Measurements of vegetation and environmental parameters

Vegetation was assessed by pin-pointing once a year at the end of July or beginning of August (after the main growing season) from 1998 (the pre-treatment year) to 2015. The pin-point method describes the vegetation profile, including plant frequencies, that allows the estimation of community structure and composition. Only the central 3×4 m area of each plot was measured to avoid edge effects. Five parallel 3-m transects 0.8 m apart were permanently marked across this central area at the start of the study. Each transect had a sampling point every 5 cm (totaling 61 points per transect and 305 points per plot). We lowered a long steel pin (3 mm diameter) through the vegetation at each sampling point for recording the height, species, organ (leaf, reproductive structure or stem) and state (alive or dead) of all plants the pin touched.

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

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

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

2.4 Statistical analysis

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

Biodiversity parameters = SPEI + Treatment   (1)

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

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

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

Community compositions= Treatment + SPEI (2)

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

3. Results

3.1 Site conditions and abiotic variables of the experimental treatments

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

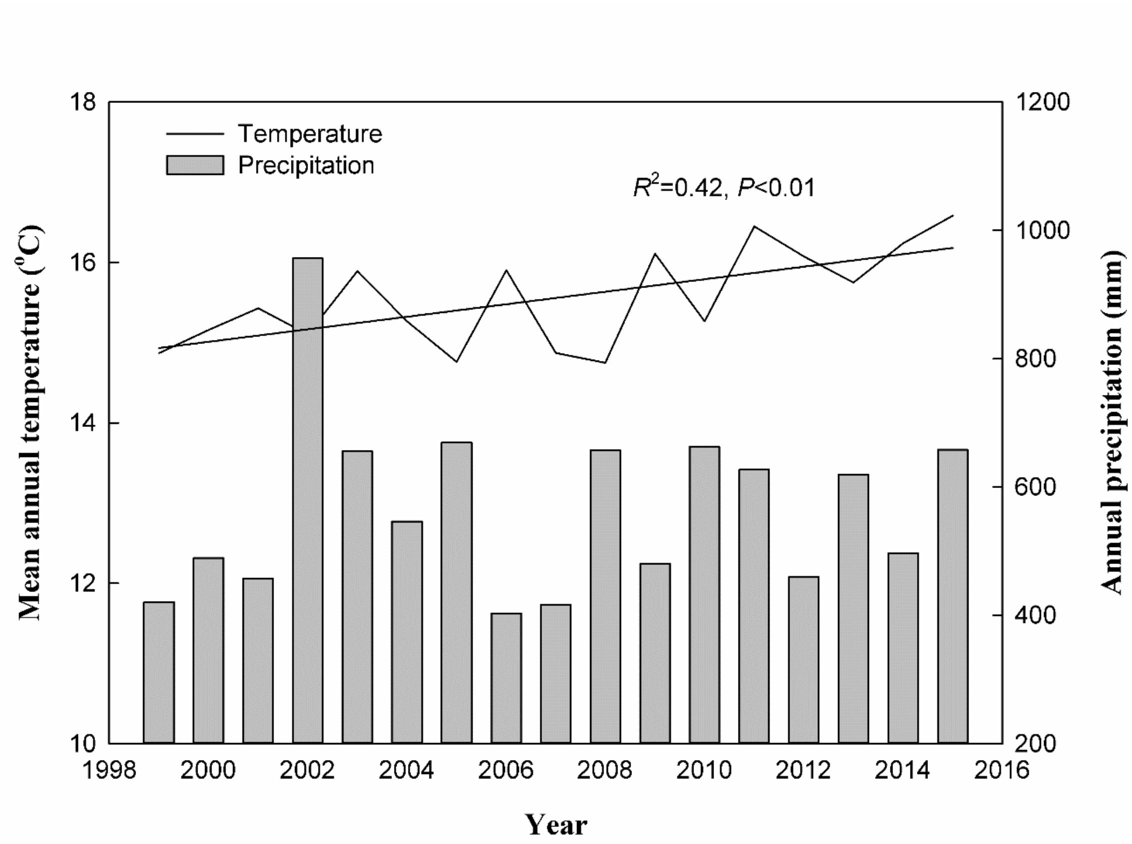

Fig. 1 Mean annual temperature and annual precipitation during the study period 1999-2015.

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

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

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

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

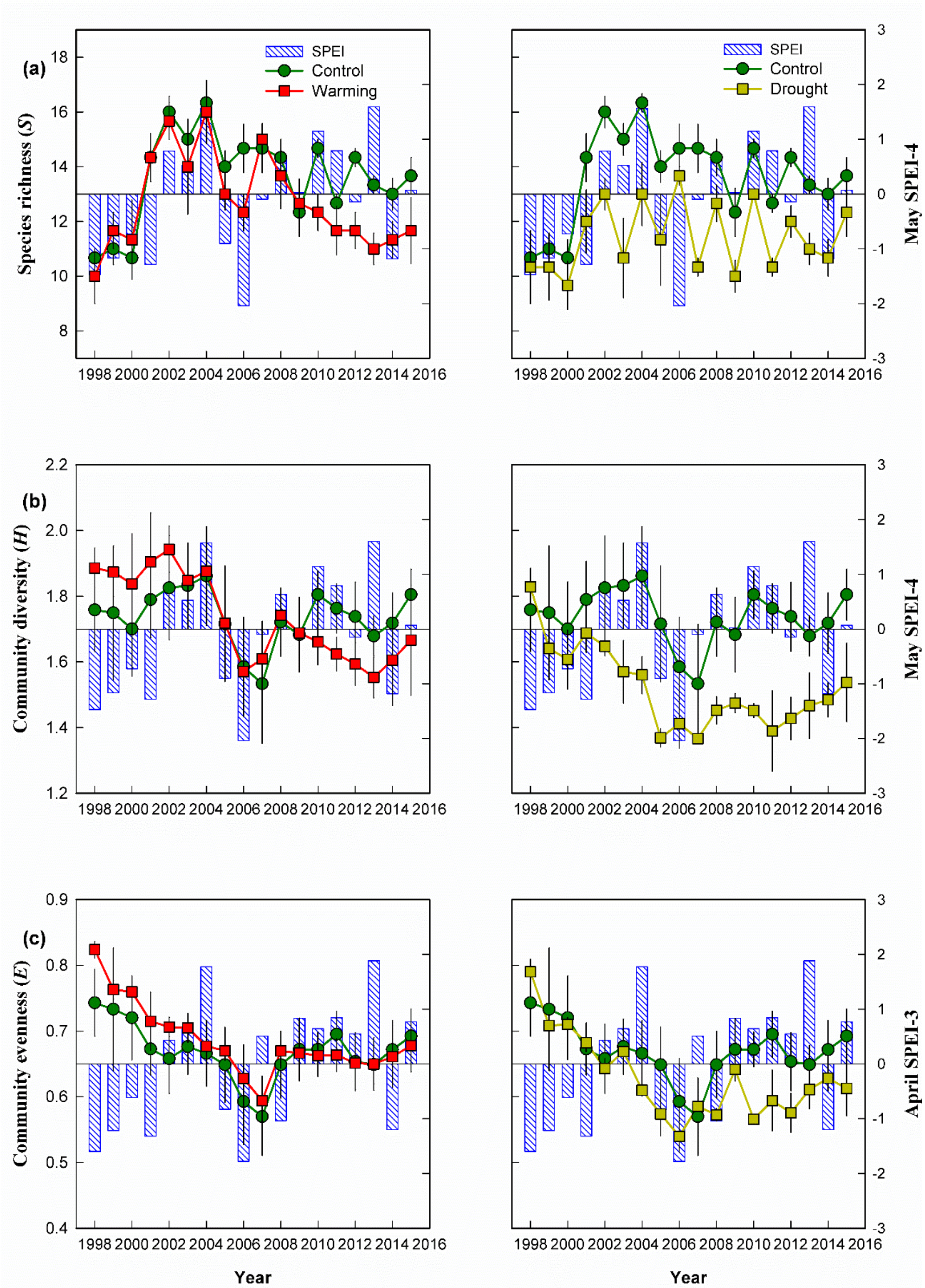

Fig. 2 Changes in (a) species richness (*S*), (b) community diversity (*H*) and (c) community evenness (*E*) in the warming, drought and control treatments during the study period 1998-2015. May SPEI-4 was the covariate factor for the changes in *S* and *H*, and April SPEI-3 was the covariate factor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

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

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

3.3 The responses of *S* for the functional groups

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

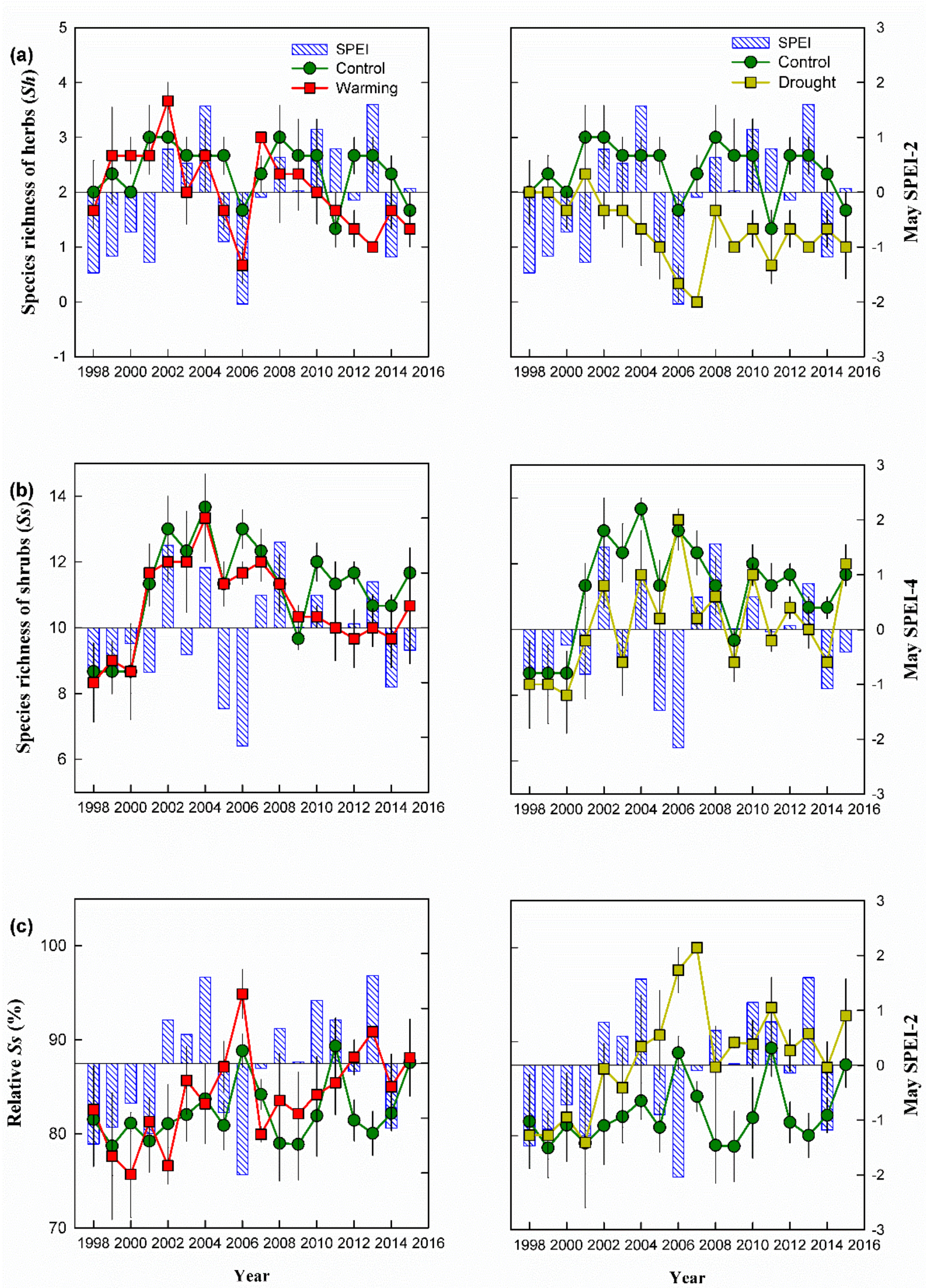

Fig. 3 Changes in the species richness of (a) herbs (Sh), and (b) shrubs (Ss) and (c) in Relative *Ss* in the warming, drought and control treatments during the study period 1998-2015. May SPEI-2 was the covariate factor for the changes in *Sh*, and May SPEI-4 was the covariate factor for the changes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

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

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

	Sh		*Ss*		Relative *Ss*	
	Difference	*P*	Difference	*P*	Difference	*P*
Warming-control						
SPEI	**0.3**	*****	**0.49**	****	**0.02**	***
Warming	**-0.35**	***	-0.52	ns	0.02	ns
Drought-control						
SPEI	**0.13**	**(*)**	**0.43**	****	0.002	ns
Drought	**-1.11**	*****	**-1.04**	****	**0.08**	*****

3.4 The response of abundance for the functional groups

Ah and *As* fluctuated differently, with a gradual decreasing trend for *Ah* in the first half of the experimental period (1999-2006) and an increasing trend in the second half (2007-

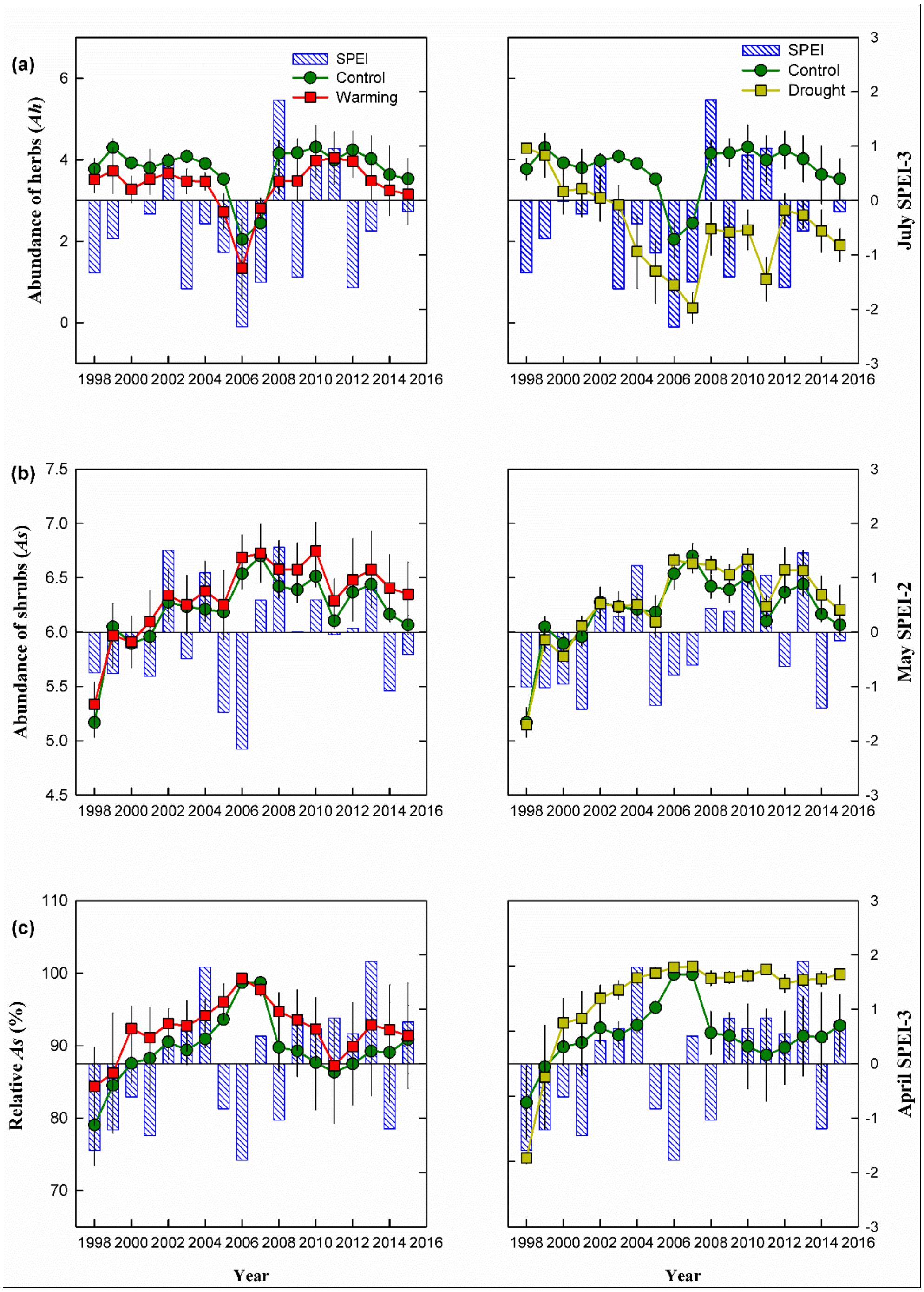

Fig. 4 Changes in the abundance of (a) herbs (*Ah*) and (b) shrubs and in (c) Relative *As* in the warming, drought and control treatments during the study period 1998-2015. July SPEI-3, May SPEI-2 and April SPEI-3 were the covariate factors for the changes in *Ah*, *As* and Relative *As*, respectively.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

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

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

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

drought (difference=0.06, P<0.01). *Ah*, *As* and Relative *As* were associated with SPEIs (Table 3). *Ah* was positively correlated with July SPEI-3 in warming-control (difference=0.28, P<0.001) and drought-control (difference=0.17, P<0. 1) comparisons, *As* was positively correlated with May SPEI-2 in warming-control (difference=0.1,

P<0.01) and drought-control (difference=0.11, P<0.01) comparisons and Relative *As*was negatively correlated with April SPEI-3 in the drought-control comparison (difference=-0.02, P<0.01).

3.5 Shifts in community composition in the treatments

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

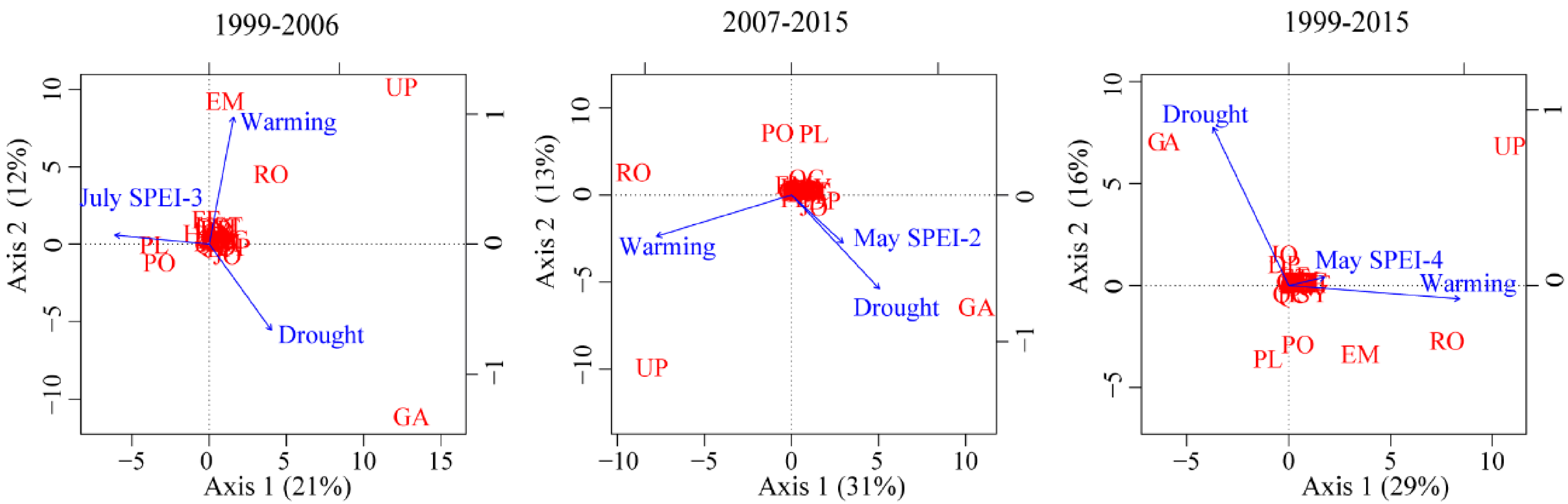

Fig. 5 Shifts of community composition in the first half of the experimental period (1999-2006), the second half (2007-2015) and the entire period (1999-2015). July SPEI-3, May SPEI-2 and May SPEI-4 were the covariate factors for the first half, second half and the entire study period, respectively.

4. Discussion

Community biodiversity

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

The drought treatment had early and strong influences on *S*, *H* and *E*, probably due to the intensity of the treatment (decreases in soil-water content of ca. 16.7%). Water is the most limiting factor for plant growth and reproduction in Mediterranean ecosystems, and significant changes in the structure and composition of plant communities at early successional stages have been reported under water deficits (Peñuelas *et al.*, 2007; Prieto *et al.*, 2009a). Manipulative reductions in precipitation have decreased plant growth (biomass accumulation and aboveground net primary productivity (ANPP)) (Peñuelas *et al.*, 2007; Prieto *et al.*, 2009c; Liu *et al.*, 2015), reproductive outputs (Del Cacho *et al.*, 2013) and seedling establishment (Lloret *et al.*, 2004, 2009). These effects will likely influence the dynamics of *S* and the patterns of plant community structure on long timescales. Moreover, large decreases in community biodiversity (*S*, *H* and *E*) under drought may strongly influence species dominance, trophic relationships and ecosystemic functioning (Peñuelas *et al.*, 2007, 2013; Estiarte *et al.*, 2016). Indeed, manipulative droughts (alterations in amounts, patterns and timing of precipitation) around the globe have had stronger impacts on community structure and ecosystemic functioning than other climatic drivers such as warming, because plant growth and reproduction are more sensitive to water stress (Peñuelas *et al.*, 2004, 2013; Wu *et al.*, 2011; Beier *et al.*, 2012). Drier conditions (from both climatic warming and lower precipitation) are likely to emerge in Mediterranean ecosystems in the coming decades, likely leading to loss of biodiversity and decreases in ecosystemic functioning and services (Dai, 2013; Peñuelas *et al.*, 2013).

S and abundance of the functional groups

Experimental warming significantly decreased *Sh* but not *Ss* or Relative *Ss*. The more conspicuous effects of warming on *Sh* than *Ss* are likely due to their different root systems. Deeper root systems may give shrubs an advantage for accessing larger pools of water and nitrogen under moderate warming (Peñuelas *et al.*, 2013). The reductions in *Sh* with experimental warming largely accounted for the decreases in *S* at the community level. Changes in *Ah* and *As*, however, differed under experimental warming, with decreases in *Ah* but increases in *As* that led to an increase in Relative *As*. Previous studies at our experimental site have indicated that moderate warming increased the photosynthetic rates of the shrubs *E. multiflora* and *G. alypum* in cold seasons, in agreement with the increase in growth for shrub species (Prieto *et al.*, 2009b; Liu *et al.*, 2016). Species reorganizations and shifts in community composition are therefore likely at the current magnitude and rate of warming because of severe declines or losses of herbs, whereas shrubs may have a competitive advantage (growth and reproduction), shifting composition toward the establishment of shrub species.

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

Shifts in community composition

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

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

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

Biodiversity parameters and meteorological droughts (SPEI)

The significant correlations between winter-spring SPEIs and the community parameters (*S*, *H* and *E*), species richness (*Sh, Ss* and Relative *Ss*) and abundance (*Ah*, *As* and Relative *As*) of the functional groups, the abundance of the typical species and the shifts in community composition indicated the importance of water balance to changes in structure and composition in this early-successional shrubland ecosystem. These changes in biodiversity were also closely correlated with short-timescale SPEIs (1-4 months), indicating drought sensitivity to water deficits (Vicente-Serrano *et al.*, 2010). In addition, most of these changes in biodiversity were positively correlated with winter-spring (May SPEI-4, May SPEI-2 and April SPEI-3) and summer (July SPEI-3) water balances. As described above, the herb functional group was extremely sensitive to water deficits in summer drought. For example, *Sh* was higher after the wet winter-springs of 2002 and 2004 and lower in the 2005-2007 dry period (Fig. 3a). *Ah* was lowest (mostly for Poaceae at our study site) in the 2005-2007 dry period (Fig. S4c; Table S2), reinforcing the premise of sensitivity to extreme drought. Extreme droughts in spring and summer, however, severely affected *H*. The extreme heat and drought in 2003 that reduced ecosystemic productivity throughout Europe (Ciais *et al.*, 2005) also significantly decreased *S*, plant growth and ANPP at our study site (Peñuelas *et al.*, 2007). We also detected low water availabilities in winter-spring and summer during 2003-2006 that probably caused the severe reductions in *S*, *H*, *E*, *Sh* and *Ah* for that period and in 2007. Natural severe droughts, however, increased Relative *Ss* and *As*, favoring shrubs, especially in the drought treatment (Figs. 3c, 4c). Indeed, the growth and ANPPs of Mediterranean forests have been correlated with the winter-spring water balance, and mortality rates and branch litterfall have been correlated with summer water balance (Barbeta *et al.*, 2013; Liu *et al.*, 2015). The structure and composition of Mediterranean shrubland ecosystems would therefore be substantially degraded if future climate change continues to decrease water reserves in winter-spring and summer.

Sensitivity of successional recovery from climate change

The developmental stage of an ecosystem may affect the responses of the vegetation to climatic disturbances (Peñuelas *et al.*, 2007; Prieto *et al.*, 2009a; Kröel-Dulay *et al.*, 2015; Brose & Hillebrand, 2016). Community structure and composition responded strongly to the climatic treatments, especially the drought treatment, in our early-successional shrubland ecosystem. The effects of climatic treatments, however, are not apparent in some ecosystems, even long-term treatments (Grime *et al.*, 2008; Tielbörger *et al.*, 2014; Estiarte *et al.*, 2016). These climatic treatments may be conducted in moderately mature or stable ecosystems, so the structure of plant communities is not influenced by slow climate change due to the well-developed structure and trophic complexity of the ecosystems (Smith *et al.*, 2009; Tielbörger *et al.*, 2014). Terrestrial ecosystems, however, are likely to experience anthropogenic and/or natural climatic disturbances that could push ecosystems into unstable or earlier successional stages (Chapin *et al.*, 2000; Peñuelas *et al.*, 2013; Seddon *et al.*, 2016). These unstable ecosystems would be strongly influenced by future climate change, leading to large changes in biodiversity and ecosystemic functioning (Kröel-Dulay *et al.*, 2015; Brose & Hillebrand, 2016). For example, Mediterranean ecosystems have historically suffered intense anthropogenic disturbances and are highly vulnerable to the ongoing climate change, because they are near critical ecosystemic tipping points (or thresholds) (Myers *et al.*, 2000; Peñuelas *et al.*, 2007, 2013; Scheffer *et al.*, 2009; Doblas-Miranda *et al.*, 2014). Global warming and drought represent selection pressures on plant species in local communities, which are leading to large losses of species diversity and decreases in ecosystemic functioning (Lloret *et al.*, 2004, 2009; Prieto *et al.*, 2009a; Kröel-Dulay *et al.*, 2015; Scheffers *et al.*, 2016). Future extreme climatic regimes (heat waves and droughts) would especially influence the functioning and services of ecosystems if critical thresholds are surpassed (Ciais *et al.*, 2005; Smith *et al.*, 2009; Jentsch *et al.*, 2011; Kreyling *et al.*, 2011; Reichstein *et al.*, 2013). Changes in community structure and composition could be persistent and even more abrupt as climate change projected by models progresses into the future (Dai, 2013; Doblas-Miranda *et al.*, 2014; Tilman *et al.*, 2014). Long-term climatic manipulations in ecosystems at different successional stages are thus critically necessary for projecting losses of ecosystemic biodiversity, functioning and services in response to future climate.

Acknowledgements

This research was financially supported by the European Research Council Synergy grant ERC-2013-SyG-610028 IMBALANCE-P, the Spanish government project CGL 2013-48074-P and the Catalan government project SGR2014-274. We thank all the people who conducted the field experiment and collected the data during the study period. We are also grateful for the financial support of the China Scholarship Council.

References

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.

Beier C, Beierkuhnlein C, Wohlgemuth T et al. (2012) Precipitation manipulation experiments - challenges and recommendations for the future. *Ecology Letters*, **15**, 899–911.

Bellard C, Bertelsmeier C, Leadley P et al (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Bernal M, Estiarte M, Peñuelas J (2011) Drought advances spring growth phenology of the Mediterranean shrub Erica multiflora. *Plant Biology*, **13**, 252–257.

Brose U, Hillebrand H (2016) Biodiversity and ecosystem functioning in dynamic landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **371**, 20150267.

Del Cacho M, Saura-Mas S, Estiarte M et al (2012) Effect of experimentally induced climate change on the seed bank of a Mediterranean shrubland. *Journal of Vegetation Science*, **23**, 280–291.

Del Cacho M, Peñuelasa J, Lloret F (2013) Perspectives in plant ecology, evolution and systematics reproductive output in Mediterranean shrubs under climate change experimentally induced by drought and warming. *Perspectives in Plant Ecology, Evolution and Systematics*, **15**, 319–327.

Chapin FS, Zavaleta ES, Eviner VT et al. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234–42.

Ciais P, Reichstein M, Viovy N et al. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Dai AG (2013) Increasing drought under global warming in observations and models. *Nature Climate Change*, **3**, 52–58.

Dieleman CM, Branfireun BA, Mclaughlin JW, Lindo Z (2015) Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology*, **21**, 388–395.

Doblas-Miranda E, Martínez-Vilalta J, Lloret F et al. (2015) Reassessing global change research priorities in mediterranean terrestrial ecosystems: How far have we come and where do we go from here? *Global Ecology and Biogeography*, **24**, 25–43.

Elmendorf SC, Henry GHR, Hollister RD et al. (2015) Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proceedings of the National Academy of Sciences*, **112**, 448–452.

Estiarte M, Vicca S, Peñuelas J et al. (2016) Few multi-year precipitation-reduction experiments find a shift in the productivity-precipitation relationship. *Global Change Biology*, n/a-n/a.

Gottfried M, Pauli H, Futschik A et al. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, **2**, 111–115.

Grime JP, Fridley JD, Askew AP et al (2008) Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 10028–10032.

Harte J, Shaw R (1995) Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science,* **267**, 876–880.

Hoffmann A, Sgrò C (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

Jentsch A, Kreyling J, Elmer M, et al. (2011) Climate extremes initiate ecosystem-regulating functions while maintaining productivity. *Journal of ecology*, **99**, 689–702.

Jump AS, Peñuelas J (2005) Running to stand still: A daptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.

Jump AS, Peñuelas J, Rico L et al (2008) Simulated climate change provokes rapid genetic change in the Mediterranean shrub *Fumana thymifolia*. *Global Change Biology*, **14**, 637–643.

Kreyling J, Jentsch A, Beierkuhnlein C. (2011) Stochastic trajectories of succession initiated by extreme climatic events. *Ecology letters*, **14**,758–764.

Kröel-Dulay G, Ransijn J, Schmidt IK et al. (2015) Increased sensitivity to climate change in disturbed ecosystems. *Nature communications*, **6**, 6682.

Leuzinger S, Luo Y, Beier C et al. (2011) Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends in Ecology & Evolution*, **26**, 236–241.

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**, 53–61.

Llorens L, Peñuelas J, Filella I (2003) Diurnal and seasonal variations in the photosynthetic performance and water relations of two co-occurring Mediterranean shrubs, Erica multiflora and Globularia alypum. *Physiologia plantarum*, **118**, 84–95.

Lloret F, Penuelas J, Estiarte M (2004) Experimental evidence of reduced diversity of seedlings due to climate modification in a Mediterranean-type community. *Global Change Biology*, **10**, 248–258.

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.

Luo Y, Melillo J, Niu S et al. (2011) Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology*, **17**, 843–854.

Myers N, Mittermeier RA, Mittermeier CG, da Fronseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Peñuelas J, Filella I, Zhang X et al. (2004) Complex spatiotemporal phenological shifts as a response to rainfall Changes. *New Phytologist*, **161**, 837–846.

Peñuelas J, Prieto P, Beier C et al. (2007) Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: Reductions in primary productivity in the heat and drought year of 2003. *Global Change Biology*, **13**, 2563–2581.

Peñuelas J, Rutishauser T, Iolanda F (2009) Phenology feedbacks on climate change.

Science, **324**, 887–888.

Peñuelas J, Sardans J, Estiarte M et al. (2013) Evidence of current impact of climate change on life: A walk from genes to the biosphere. *Global Change Biology*, **19**, 2303–2338.

Prieto P, Peñuelas J, Lloret F, Llorens L, Estiarte M (2009a) Experimental drought and warming decrease diversity and slow down post-fire succession in a Mediterranean shrubland. *Ecography*, **32**, 623–636.

Prieto P, Peñuelas J, Llusià J, Asensio D, Estiarte M (2009b) Effects of long-term experimental night-time warming and drought on photosynthesis, Fv/Fm and stomatal conductance in the dominant species of a Mediterranean shrubland. *Acta Physiologiae Plantarum*, **31**, 729–739.

Prieto P, Peñuelas J, Llusià J, Asensio D, Estiarte M (2009c) Effects of experimental warming and drought on biomass accumulation in a Mediterranean shrubland. *Plant Ecology*, **205**, 179–191.

Reichstein M, Bahn M, Ciais P et al. (2013) Climate extremes and the carbon cycle. *Nature*, **500**, 287–295.

Scheffer M, Bascompte J, Brock WA et al. (2009) Early-warning signals for critical transitions. *Nature*, **461**, 53–59.

Scheffers BR, DeMeester L, Bridge TCL et al. (2016) The broad footprint of climate change from genes to biomes to people. *Science*, **354**, 7671.

Schröter D, Cramer W, Leemans R et al (2005) Ecosystem Service Supply and Vulnerability to Global Change in Europe. *Science*, **310**, 1333–1337.

Seddon AWR, Macias-Fauria M, Long PR, Benz D, Willis KJ (2016) Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, **531**, 1–15.

Smith MD, Knapp AK, Collins SL (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, **79**, 3–24.

Thackeray SJ, Henrys PA, Hemming D et al. (2016) Phenological sensitivity to climate across taxa and trophic levels. *Nature*, **535**, 241–245.

Tielbörger K, Bilton MC, Metz J et al. (2014) Middle-Eastern plant communities tolerate 9 years of drought in a multi-site climate manipulation experiment. *Nature communications*, **5**, 5102.

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 471–493.

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. *Journal of Climate*, **23**, 1696–1718.

Walker M, Wahren C, Hollister R et al. (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 1342–1346.

Walther G, Post E, Convey P et al. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Global Change Biology*, **17**, 927–942.

Yang H, Wu M, Liu W, Zhang Z, Zhang N, Wan S (2011) Community structure and composition in response to climate change in a temperate steppe. *Global Change Biology*, **17**, 452–465.