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

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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 yr) 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.

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., 2015). Global warming, accompanied by more frequent droughts projected for Mediterranean regions, will probably 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; Barros et al., 2014; Doblas-Miranda et al., 2015). 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; García et al., 2014). In addition, climatic factors are often confounded, making it very difficult to make accurate predictions of biodiversity shifts independently for temperature and precipitation change (Beaumont et al., 2011; Liu et al., 2017). Some studies have reported that increasing temperature and decreasing precipitation could impose similar and additive selection pressures on plant species performance within communities, because both forces decrease soil moisture, while increasing evapotranspiration rates and nutrient mineralization (Myers et al., 2000; Sardans et al., 2008; Williams et al., 2012). However, the combined effects of temperature and precipitation are highly context-dependent. For example, both warming and decreased precipitation may increase the aridity of an already dry and warm habitat, thereby limiting plant growth. However, in cooler habitats not limited by water, warming may have positive...
effects on the vegetation (e.g. extending the growing season and promoting growth and reproduction) and decreasing precipitation may have little effect on plant growth (Garcia et al., 2014; Andresen et al., 2016). Therefore, approaches are needed that are able to detect the influences of several key climatic factors on the structure and function of ecological communities that are widely applicable and able to disentangle ‘climate change’ into the separate drivers.

Currently, one of the most mechanistic ways to study plant community responses to climate change is through long-term climate manipulation experiments (Elmendorf et al., 2015; Kräel-Dulay et al., 2015; Andresen et al., 2016; Zhu et al., 2016; Liu et al., 2017). Such studies impose a continuously altered climatic factor onto a local community, providing a known and controlled-for climate change impact, capturing the results of local interactions. This method therefore overcomes some of the confounding effects of long-term observational data (Gottfried et al., 2012), it follows impacts over a continuous time-scale (unlike time-for-time-based approaches; Estiarte et al., 2016; Metz & Tielbörger, 2016), and importantly incorporates the local levels of plasticity and evolutionary adaptations found within a community (unlike gradient space-for-time approaches; Tielbörger et al., 2014). However, for total community parameters (e.g. above-ground net primary production, biomass, species richness) climate manipulation experiments often reveal little to no-net change or difficult to explain altering responses over time (Grime et al., 2008; Barbeta et al., 2013; Tielbörger et al., 2014; Andresen et al., 2016; Mueller et al., 2016). Interestingly, often single species and multiple species are shown to change in abundance within these experiments (Harte & Shaw, 1995; Lloret et al., 2009; Fridley et al., 2011; Bilton et al., 2016). But with many species increasing and decreasing in the community, the task is to have a simple, general and perhaps more informative way to interpret these patterns. It seems logical to hypothesize that, by somehow ranking the species based on a factor related to climate, climate change response predictions may be drawn and tested.

One technique for ranking species in relation to climate is given by their climatic niche distribution, for example species within the same community that more commonly occur in wetter or drier habitats. In theory, the climatic niche of a species could act as the primary predictor of species sensitivity to climate change (Thuiller et al., 2005; Hijmans & Graham, 2006; De Frenne et al., 2013). The climatic niche principle has commonly been used in distribution models (Thomas et al., 2004; Thuiller et al., 2005; McMahon et al., 2011; Araújo & Peterson, 2012), but has also shown promise in a process named ‘thermophilization’ for identifying directional changes in whole community composition in observational data under climate warming (Gottfried et al., 2012); for example, the average temperature niche of elevated mountain communities has increased over time due to natural warming. More recently, the thermophilization principle has also proved capable of revealing community shifts in tundra communities under experimentally manipulated warming (Elmendorf et al., 2015). More so, when divided into species groups (climatic niche groups, CNGs) the climatic niche principle has most recently identified more precise details (i.e. identifying which components of the community increase or decrease) about the compositional shifts and community dynamics for annual species under experimentally manipulated rainfall over time (Bilton et al., 2016).

Therefore, defining species by their climatic niche, and monitoring their responses within climate experiments, may be an informative and hypothesis-driven method for examining compositional change within communities. When using the climatic niche principle alongside experiments, the response of species can be displayed along the niche axis and some general conclusions about species increasing or decreasing can be drawn. Furthermore, by categorizing the species into groups of similar climatic niche distribution (CNGs), the method assumes a level of species equivalence, thereby overcoming some natural species absences/presences in time and space, as well as being less reliant on precise niche definition. Certainly, a main strength of grouping is its ability to allow for the simple monitoring of changing responses over time for different components of the community. Finally, CNGs may group together many different traits/adaptations that plants may possess to survive in particular climates, thereby strengthening both the power of the test and the interpretation of the result (Lavorel et al., 1997). Indeed, if aspects of species-specific adaptations to climatic variables can be partly captured by this approach, it would provide further information about the community dynamics and ecology. While promise has been shown, the climatic niche principle has not yet been applied to separate climatic factors in manipulative field experiments, in order to tease apart the possible responses of species and community composition to the impacts of future temperature and precipitation regimes.

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

Study site

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

The study site was established on a hill with south-facing aspect (slope = 13%). The area had been cultivated but was abandoned more than 100 yr ago and thereafter colonized by a coniferous forest. This forest experienced two wildfires in summer 1982 and spring 1994, after which succession began. The current vegetation is dominated by the shrubs Erica multisella and Globularia alypum, which coexist with small evergreen plants, such as Dorycnium pentaphyllum, Rosmarinus officinalis and Ulex parviflorus (Supporting Information Table S1 for a full list of species).

Experimental design

We carried out moderate nocturnal-warming and drought treatments during the period 1999–2014, with 1998 acting as a pre-treatment year. Triplicate 20 m² (5 × 4 m) plots were randomly established for each treatment (warming, drought and control; nine plots in total). All samples were collected from the central 12 m² (4 × 3 m) to avoid edge effects.

The warming treatment was achieved by covering the plots at night with reflective curtains to reduce infrared radiation to the atmosphere, simulating global warming by increasing the minimum temperature at night (Beier et al., 2004; Peñuelas et al., 2007; Prieto et al., 2009). A light scaffolding (1.2 m above the ground) was built to support the reflective curtains. The curtains reflected 97% of the direct and 96% of the diffuse radiation while allowing the transfer of water vapor. The covering was operated automatically by the light level (<200 lux), rainfall (<0.3 mm) and wind (<10 m s⁻¹) throughout the study. The warming treatment increased soil temperatures at 5 cm depth by an average of 0.6°C, depending on the season and meteorological conditions (Fig. S1a).

The drought treatment was applied in the spring and autumn (main and secondary growing seasons respectively) by covering each plot with a transparent waterproof sheet of plastic (Beier et al., 2004; Peñuelas et al., 2007; Prieto et al., 2009). The facilities were similar in the drought and warming plots except the material of the curtains. The rain sensors during the treatment period activated the waterproof sheet to cover the vegetation during rainfall > 1 mm and were removed after the rain had stopped. The water collected by the sheet was drained outside the plots. The curtains were folded automatically if the wind speed exceeded a threshold (>10 m s⁻¹) to avoid damage. The drought plots were treated in the same as the control plots during the rest of the year. The drought treatment excluded c. 40% of the precipitation and decreased soil moisture by c. 20% throughout the study period (Fig. S1b).

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

Vegetation sampling

Five fixed and parallel transects 3 m long were permanently established in all nine plots at equal distances of 0.8 m. A point-intercept method was applied to record the species composition and abundance at points distributed at 5 cm intervals along the five transects (305 points in each plot). A thin steel pin (3 mm diameter) was vertically dropped at each point, and the parameters (species identity and contacts per pin) were recorded (Prieto et al., 2009). The data were collected annually in the dry season (July and August) from 1998 (pretreatment) to 2014 (16 yr of manipulation). Our experimental plots contained a total of 31 species (Table S1). Species contacts in each plot were summed to estimate the abundance. Species abundances per plot were log transformed (log+1) to adjust for the large positive skew in distribution, and summed to form groups or total community measures.

Grouping of plant species

To determine community compositional change with respect to the different treatments, we classified the species in the community into CNGs using temperature and precipitation variables. We initially tested a number of climate niche parameters (maximum temperature in hottest month, average and seasonal temperature, and annual and seasonal precipitation) to rank the species to form CNGs (Tables 1, S1–S4). However, we continued the analysis with the most consistent descriptors of community composition response – and those which were assumed to be most valid a priori – which were: summer temperature (mean temperature from June to August), as this period was most likely to be important for selecting for summer survival of species; and spring precipitation (accumulated precipitation from December to May), as this had most effect on early season growth at the site. We created three CNGs for each climatic variable: T1, T2 and T3 (warm to cold) for summer temperature and P1, P2 and P3 (dry to wet) for spring precipitation.

To create these groups, we first obtained the species’ geographical distributions in mainland Spain, France and Portugal (southwestern Europe) from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/), one of the most extensive open-access biodiversity databases available. Distribution
Research models were derived from log-transformed species level contact For the main statistical analyses, the response variables in our Statistical analyses of abundances that vary in terms of their extreme temperature or precipitation or warm-dry groups (Table 1). However, there are several species that there is a large correlation of the species present in wet-cold c group was among groups, so that the sum of the (log) species contacts per systemically apportioning plant community abundance from a climatic GIS layer separately for each species for each occurrence. We tested multiple ways of calculating each species niche value from these climate distribution values to test the impact of niche edges on the group response: the median (med) climatic value associated with all observations per species; the 25\textsuperscript{th} percentile of the climatic values (25\%); or the 75\textsuperscript{th} percentile of climatic values (75\%) (see Table S1 for multiple niche values associated with each species). For the remainder of the main article, we display results only from niche values calculated using the 25\textsuperscript{th} percentile of summer temperature values and median spring precipitation values, because the results for the various approaches were essentially the same. Information for the summer temperatures and spring precipitation was extracted from the WorldClim database (30 arc-seconds, c. 1 km) (http://www.worldclim.org/), which contains climatic data for 1950–2000. Species were allocated to three CNGs per climatic variable by systematically apportioning plant community abundance among groups, so that the sum of the (log) species contacts per group was c. 33\% of the total sum of (log) species contacts recorded during the experiment (regardless of year or treatment) (Tables S2, S3). Note that these are not true community percentage values, but are calculated from summing log-transformed species abundances. In effect, our method assigns relatively more weight to rare species in a group. We think this method is well suited to normal community percentages may only contain one or two species. In addition, to create our arbitrary groups, species at a boundary with very similar/same niche values were kept together in the same group. These rules for species allocation ensured that each group contained at least six species and that the climatic ranges defined by a group exceeded a certain value (precipitation > 20 mm, temperature > 1\textdegree C) (Tables 1, S3). Note that there is a large correlation of the species present in wet-cold or warm-dry groups (Table 1). However, there are several species that vary in terms of their extreme temperature or precipitation group allocation (Tables 1, S2).

Statistical analyses of abundances

For the main statistical analyses, the response variables in our models were derived from log-transformed species level contact hits per plot from 1999 to 2014 (Eqn 1). Four main response variables were analyzed: total community sum-log-abundance (sum of log contact hits of all the species) (Eqn 1), temperature CNG sum-log-abundance (sum of log contact hits belonging to species for each temperature CNG group) (Eqn 1), precipitation CNG sum-log-abundance (sum of log contact hits belonging to species for each precipitation CNG group) (Eqn 1) and species log-abundance (log contact hits belonging to a single species).

\[ \sum_{i=1}^{n} \log(\text{hits sp}_i). \]  

Eqn 1

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

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

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

A full range of environmental factors (spring, summer and annual temperature and precipitation) of the study site were tested, but the variance (based on the lowest Akaike information criterion (AIC) values) was explained best for all analyses by the environmental recordings for spring temperature (ST), spring precipitation (SP) and their interaction. The initial values for sum-log-abundances in the preliminary year (1998) were

| Table 1 Cross-correlation table of species allocation to the main climatic niche groups (CNGs) shown throughout the article  |
|---|
| Precipitation CNGs | P1 (drier) | P2 (intermediate) | P3 (wetter) | Temperature CNGs total |
| Temperature CNGs | T1 (warmer) | 5 | 0 | 2 | 7 |
| | T2 (intermediate) | 2 | 5 | 1 | 8 |
| | T3 (cooler) | 0 | 4 | 12 | 16 |
| Precipitation CNGs total | 7 | 9 | 15 | 31 |

CNGs were allocated in order of aridity: niche values of summer temperature (25\%) CNGs from warm to cold (T1 > T2 > T3), and niche values of spring precipitation (median) CNGs from dry to wet (P1 < P2 < P3).
included as an underlying covariate (‘Pre-treat’). Finally, the continuous variable ‘Year’ (16 yr: 1999–2014) and the two-level categorical variable ‘Treatment’ (drought vs control, or warming vs control) were included. For the analysis of CNG sum-log-abundances, the models also included the three-level explanatory categorical variable ‘CNG’ (either T1, T2, T3 or P1, P2, P3), with the main interaction of interest between Treatment × Year × CNG. The full models for our analyses were therefore:

Total community sum-log-abundance
\[ ST \ SP + \text{Pre-treat} + \text{Year} \times \text{Treatment}, \quad \text{Eqn 2} \]

CNG sum-log-abundance
\[ ST \times SP + \text{Pre-treat} + \text{Year} \times \text{Treatment} \times \text{CNG identity}, \quad \text{Eqn 3} \]

Species log-abundance
\[ ST \times SP + \text{Pre-treat} + \text{Year} \times \text{Treatment}. \quad \text{Eqn 4} \]

Plot was included as a random effect term in all models. All analyses were performed in R v.3.2.2 using package LME4 (v.1.1-7; Bates et al., 2015). Post-hoc analyses of the differences in CNG slopes/responses over time were tested by least-squares means using the lstrend command of the R package LSMMEANS (Lenth, 2016).

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

Effect size (Year) = (μ_treatment Year − μ_treatment 1998) − (μ_control Year − μ_control 1998),

\[ \text{Eqn 5} \]

where μ_treatment and μ_control are the average (sum) log-abundances in the treatment (warming or drought) and control plots (\( n = 3 \)), respectively, in a given year. Effect sizes were adjusted for (sum) log-abundance differences in the pretreatment year (1998) as representative of the LMEMs. Raw sum-log-abundance plots are shown in Fig. 2, and raw data can be viewed in Notes S1.

**Group robustness analysis**

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

**Single species response plotted against niche**

As a further test of the climatic niche approach, single species responses to the manipulation treatments were plotted against their corresponding climatic niche value. This was formally tested and displayed using generalized additive models (GAMs) using the R-package ‘mgcv’ (Wood, 2011). The response variables in the GAMs were the \( t \)-values of the LMEMs performed on each species (Eqn 4; Table S5) describing the difference in model estimate for the response slope over time between control and
treatment (Year × Treatment interaction term). The explanatory variables were the climatic niche values associated with each species (Table S1). GAMs were run for the climate niche values presented in the main article (25% summer temperature; median spring precipitation), and for multiple other climate niche values to check the robustness of different niche axes (Fig. S3). A simple smoothing parameter was fitted to each GAM set at a value of 0.15 throughout. Each species was also weighted by its corresponding log-community percentage value (Table S2). Raw data can be viewed in Notes S1.

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 yr 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 \((SP, P<0.0001; ST, P<0.001)\) and their interaction term \((P<0.0001)\).

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 \((P<0.05, \text{Table 2})\). The

### Table 2: Total community sum-log-abundance responses to 16 yr of climatic manipulation

| Fixed effect                  | df | 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   |

ANOVA type I table for linear mixed-effects models analyzing the changes in abundances in response to either the warming or the drought treatment compared to the control. Start value indicates the sum-log-abundance in the initial year of the experiment (1998 before manipulation). \(P\)-values in bold are statistically significant to an alpha value of 0.05. num df, numerator degrees of freedom; den df, denominator degrees of freedom. 

P-value: ns, not significant \((>0.05)\); *, \(P≤0.05\); ***, \(P≤0.001\); ****, \(P≤0.0001\).
Namely, the difference between sum-log-abundance in drought vs control treatments increased for the first 9 yr 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 SP and the interaction term between SP and 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). By 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. 2d; 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 3 yr 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 drier origins) increased steadily in the drought compared to the control (estimated difference in slopes = 0.24, P<0.01, Table S4), particularly after 2007 when they were higher in relative abundance in the drought treatment than in the control. Taken together, the responses of the three groups explain the U-shaped response found in the total community data. Similar to the temperature CNGs, the three-way interaction was not significant (P=0.188, Table 3) when applying the classification of precipitation CNGs to analyze the sum-log-abundance changes in the warming treatment (Fig. 2c). However, uncorrected post-hoc tests did reveal a significant difference in slope between control and warming for P3 (decrease as predicted for wettest species: slope difference = −0.18, P<0.05, Table S4).

**Robustness analysis**

Multiple CNG analyses were performed in the same manner as the main results presented above, using different niche values to rank species and create groups. Results were generally consistent with the presented findings, and some results of this can be seen in Table S4. In general, most methods highlighted a statistically significant decrease of cool or wet species under warming and that temperature CNGs regularly failed to explain changes in community composition under drought. Annual precipitation CNGs sometimes managed to capture community composition change under both manipulation treatments (drought and warming), whereas spring precipitation CNGs were generally stronger

| Table 3 | Climatic niche group (CNG) sum-log-abundance responses to 16 yr of climatic manipulation |
| Fixed effect | df | num | den | Temperature CNGs | Precipitation CNGs | Drought CNGs |
| | | | | df | num | den | df | num | den | df | num | den |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 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 |
| Year (Yr) | 1 | 268 | 247.49 | **** | 471.95 | **** | 427.57 | **** | 132.76 | **** |
| 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 | * |
| Yr × Trt × CNG | 2 | 268 | 6.57 | ** | 1.68 | ns | 6.58 | ** | 2.14 | ns |

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 the 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.

num df, numerator df; den df, denominator df.

P-value: ns, not significant (>0.05); *, P≤0.05; **, P≤0.01; ***, P≤0.001; ****, P≤0.0001.
for drought response but did not significantly describe changes under warming, despite revealing hierarchical responses among CNGs as predicted (i.e. the drier CNG1 responded less negatively to warming than the wetter CNG3).

A full display of results and discussion of the cumulative group analysis can also be found in Figs S4–S6 and Notes S2. In general, it was clear that groups more often than not overcame variance in the single species responses to describe community change as predicted. Under warming, for groups containing a few species, high temperature CNGs increased (although not significantly) and low temperature CNGs significantly decreased relative to control (Fig S4). Similarly, but more pronounced, under drought, dry precipitation CNGs increased and wet precipitation CNGs decreased (Fig S6). These results were most consistent when using summer temperature (25th percentile) CNGs to describe warming, and spring precipitation (median) CNGs to describe drought (Figs S4, S5, respectively). In addition, when testing CNG responses in opposing climate manipulations, patterns were generally less clear and more variable (Fig S6). In combination, this confirmed that group boundaries had little qualitative effect on the main results presented.

**Single species responses plotted along niche axis**

Single species LMEM analyses revealed that under warming, of the 24 species tested, two increased over time and four decreased over time relative to control (alpha $P$-value of 0.05 with no multiple test correction, Table S5). For the 23 species tested under drought, three increased over time and four decreased over time relative to control (Table S5). Some care must be taken in interpreting these findings, as due to the large volume of analyses, linearity was rarely confirmed nor unconfirmed.

When single species responses ($t$-values of the difference between control and treatment over time) were plotted against the climatic niche axes, while there is some variation in patterns, as revealed by the CNG analyses, it was generally the cooler species which decreased under warming (Fig. 3a). Likewise, also confirming the findings from the CNG analyses, it was generally the drier species that increased under drought, and the wetter species that decreased under drought, relative to control (Fig. 3b). Plotting single species warming responses by their precipitation niche, and drought responses by their temperature niche, sometimes produced similar patterns but these were never as strong or consistent as when using the associated climate niche parameter (Figs 3c,d, S3). This remained consistent with the CNG findings.

**Discussion**

Our overall findings from the 16 yr 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°C) gradually accumulated. However, previous studies at the same experimental site did not find significant abundance changes after 7 yr 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 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 et al., 2015). These patterns thus suggest that under the future higher temperatures and associated extreme heat waves predicted for the Mediterranean regions (Dai, 2013; Barros et al., 2014), the abundance of species from relatively cold origins is likely to decrease.

The CNG analysis was even more enlightening for the drought treatment. Here again, the species hypothesized to possess less adaptations to reduced water levels responded visibly: in general the species associated with wetter climates (P3) immediately decreased in abundance in the drought treatment. The abundances of these species also abruptly shifted between the third and fourth year, which could be due to the additive impact of the experimental drought and an extreme natural drought in 2001. In addition, the CNG analysis revealed that species from dry climates (P1) showed a general increase in abundances in the drought treatment after a delay of 9 yr, and were more present in the drought plots than the control ones after this point. Therefore, for the predicted future scenario of reduced rainfall, the potential losses of species from the system may be partly offset by a gain in drought-adapted species (Sala et al., 2000; Barros et al., 2014; Andresen et al., 2016).

In general, while both temperature and precipitation manipulations had a negative impact on the community, the overall effect of the drought treatment in terms of immediate change and community shift was greater. This was probably due to the different severity of warming and drought treatments or differential sensitivity of the community to the two climatic factors (Beaumont et al., 2011; Garcia et al., 2014). In our already warm and dry system, elevated temperature can act as a climatic limitation for species establishment and growth, because the associated increased vapor pressure deficit increases the likelihood of high autotrophic respiration, transpiration from plants and evaporation from the soil (Beier et al., 2004; Williams et al., 2012; Peñuelas et al., 2013). Higher temperatures may therefore accelerate water outputs, greatly increasing the water stress for plants (Beier et al., 2004; Williams et al., 2012; Anderegg et al., 2013). Greater immediate impacts of the drought manipulation in our study were apparent in the responses of total community abundance after the first year. Such strong plant responses to reduced precipitation levels are supported by the growing number of studies reporting that water availability is a crucial determinant of species distribution and persistence across global ecosystems (Myers et al., 2000; Peñuelas et al., 2007; Beaumont et al., 2011; Doblas-Miranda et al., 2015; Harrison et al., 2015). Taking together evidence from our study and that from previous findings suggests that reduced precipitation may be a stronger and more immediate selective agent for determining structure and community composition in natural ecosystems, whereas warming could be a progressive and accumulative process (Beier et al., 2004; Prieto et al., 2009; Wu et al., 2011; Liu et al., 2017).

Notably, we show evidence that the impacts exerted by temperature and drought alone selected for some different species, with responses determined by their climatic niche distributions. The temperature CNGs only explained the response of the composition to the warming treatment, regularly failing to explain results under drought. For precipitation CNGs, while there was some correlation in species responses under both treatments, precipitation CNGs generally explained the response to drought treatment far better than to the warming treatment. This suggests that despite the fact that both climate stressors decrease water availability to plants, they can also select independently for specific adaptations (Mittler, 2006; Beaumont et al., 2011; Garcia et al., 2014). Some care must be taken in fully extracting evidence for independent selection under the different climatic variables, because many of the species in this study were correlated and were indeed either cool-wet distributed (e.g. *Rubia peregrina*, which responded negatively under both treatments) or warm-dry distributed species (e.g. *G. alypum*, which increased under drought and had no response under warming – the general CNG response). However, the few species to express opposing niches also performed as hypothesized by their niche distribution. For example, *U. parviflorus* (a warm-wet distributed species) had no response under warming, and decreased in abundance under drought. This contrasting response under opposing manipulation treatments, not solely in the direction expected by a reduction in water under warming, suggests that it is likely that in some cases the balance between traits related to cooling, capturing water and preventing water loss (e.g. stomatal closure, rooting depth, leaf thickness) could be uniquely tailored to the specific needs in response to climatic stress (Mittler, 2006; De Frenne et al., 2013). In our study system, this appears to be reflected by their distribution ranges across climates. Clues for the precise adaptations/mechanisms defining the groups and underlying these changes are revealed by results at the same study site, which reported: demographic changes in seedling numbers of a subset of species (Lloret et al., 2009); rapid genetic shifts in the dry (P1) and warm (T1) species *Fumana thymifolia* (Jump et al., 2008), which we showed to increase under both manipulations; and potential physiological acclimation – in terms of water-use efficiency, shoot water potential and net photosynthetic rate – of a dry distributed species *E. multiflora* under the drought treatment.
(Liu et al., 2016). Indeed, a valuable next step could be a trait screening exercise of species from the distinct niches to confirm precisely which adaptations are similar and different for determining plant responses under the opposing climate drivers. Ultimately, while higher temperatures and lower precipitation are both likely to increase the aridity of the Mediterranean Basin by increasing evapotranspiration (Mittler, 2006; García et al., 2014), some species will not suffer equally from the future temperature and precipitation regimes.

In many climate manipulation studies, including our own, often whole community variables (total density, species richness, community productivity) show either limited to no-net effects (Grime et al., 2008; Tielbörger et al., 2014; Estiarte et al., 2016) or dampening over time (Leuzinger et al., 2011; Barbeta et al., 2013; Liu et al., 2015; Andresen et al., 2016). Under the drought manipulation in our study, we also showed a clear polynomial response pattern for total community abundance relative to control, which is often interpreted as a dampening of the treatment/climate effect over time (Andresen et al., 2016). One of our most interesting findings was that this polynomial pattern could be explained by clear contrasting shifts among the different precipitation CNGs. This is intriguing, because dampening effects have often been interpreted as an ‘adaptation’ of the system back to its original state, due to acclimation (Leuzinger et al., 2011; Barbeta et al., 2013; Liu et al., 2015; Andresen et al., 2016). Without our in-depth community-level analyses we would have probably come to the same erroneous conclusion, and possibly community composition changes may help to explain contrasting response patterns over time in other long-term manipulation studies (Andresen et al., 2016). Importantly, our findings enabled us to identify that the impact of the drought treatment is not dampening, but remains strong, and the effect seen for total community was the result of a decrease in abundance of wet-distributed species and a delayed increase in the abundance of dry-distributed species. It seems likely that the reduction in competition exerted from the wet-distributed species may have been responsible for this switch in dominance hierarchy, and that particularly in shrubland systems such as ours, these switches may require long periods of time to emerge (Smith et al., 2009; De Boeck et al., 2015; Andresen et al., 2016; Liu et al., 2017).

The use of CNGs to observe, follow and predict community dynamics under climate manipulation experiments/climate change scenarios has proved to be a simple and robust technique to extract general and interpretable trends in community dynamics. The use of many different climate parameters often showed similar qualitative results to the main climate parameters presented here (summer temperature and spring precipitation). In addition, the cumulative group analyses revealed that the conclusions rarely altered due to where the group boundaries were set. Also, by plotting single species responses along a niche axis we revealed very similar conclusions about which species – in terms of niche distribution – would increase or decrease in abundance in response to the manipulations. A more detailed discussion on some of the different niche parameters used can be viewed in Notes S3. However, in general we conclude that while niche range would be extremely valuable to consider across large areas, within a community it would seem that an average value (median or mean) captures well both potential increasers and decreasers under manipulations (Elmendorf et al., 2015; Bilton et al., 2016). A valid next step could be to test simple or more complex species distribution model predictions of species responses under manipulations to give a different view on the use of the climatic niche principle.

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

However, the decline in the abundance of some climate-sensitive species may be balanced by an increase in resistant species distributed in warmer or drier niches. This was seen in our study with the delayed increase in species associated with dry climates in our drought treatment (e.g. G. alypum). Indeed, growing observational (Gottfried et al., 2012; Duque et al., 2015) and experimental (Harte & Shaw, 1995; Elmendorf et al., 2015) evidence suggests that communities are shifting towards a higher proportion of species associated with warmer climates in response to global warming. Crucially, our findings suggest that similar and, more importantly, independent conclusions can also be drawn for species responses to drought. Therefore, evidence provided here from the CNG approach suggests that it may be possible to depict, on a global scale, how the magnitude of changes to either temperature and/or precipitation may affect those climate-sensitive species. Encouragingly, databases are becoming more readily available for species distributions (Global Biodiversity Information Facility, GBIF) and are sufficiently precise to define the sensitivity of species by their climatic niche and to group the species in an index of similar niches (Bilton et al., 2016), allowing for the application of the CNG principle to a wide array of habitats for comparison. We therefore advocate the combined use of both manipulation experiments and the climatic niche principle to improve assessments of community responses to future climate change scenarios.

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Author contributions

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

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Fig. S1** Treatment effects on soil temperature between control and warming and 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 25th 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.

**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 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 climatic niche groups 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 yr of climatic manipulation

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 vs climatic niche analysis’ (Fig. 3).

Notes S2 Cumulative group analyses: CNG robustness testing.

Notes S3 Discussion of niche parameter estimation for forming CNGs.

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