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Effects of decadal experimental drought and climate extremes on vegetation growth in Mediterranean forests and shrublands

Short running title: Vegetation growth to decadal drought

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Abstract

Increased drought combined with extreme episodes of heatwaves, are triggering severe impacts on vegetation growth, particularly for plant communities in arid and semiarid ecosystems. Although there is an abundance of short-term field drought experiments in natural ecosystems, remaining knowledge gaps limit the understanding and prediction of vegetation growth to ongoing and future climate scenarios. Here, we assessed the impacts of long-term (1999-2016) experimental drought (ca. -30% rainfall) on the vegetation growth of a Mediterranean high (H-) and low (L-) canopy forests and an early successional shrubland, as indicated by aboveground biomass increment (ABI) and standing density, respectively. We found habitat context (historical climate change impact, soil depth and successional status) of the study sites significantly affected the magnitude of climate impacts; there were synergistic effects of experimental drought and meteorological drought (Standardised Precipitation-Evapotranspiration Index, SPEI) as well as extreme dry years on vegetation growth. Long-term experimental drought decreased the ABI for the two forest canopy types and the standing density for the shrubland. Water availabilities in winter-spring (SPEIs) were positively correlated with the ABI and standing density. Moreover, the experimental drought decreased the vegetation growth in extreme dry years for the shrubland. We propose that future work not only study the vegetation dynamics with physiological, phenological and demographical changes at long-term process and across climate gradients, but also should explore the changes of simultaneous multiple functions (e.g. multifunctionality) under long-term process and extremes. This type of analysis of long-term data is essential to understand and predict biodiversity loss, composition shifts, declines in ecosystem function and carbon budgets at temporal and spatial scales, to enable policymakers to design and implement strategies for the maintenance of sustainable ecosystem function under future climate change scenarios.

Key words: Mediterranean ecosystems; decadal drought experiment; vegetation growth; aboveground biomass increment (ABI); standing density; habitat context;

Introduction

Drought, largely due to rapid warming and shifts in precipitation have increased water stress across the terrestrial ecosystems, resulting in ecological consequences for the dynamics of plant community structure and ecosystem functions (Walther et al. 2002; Bellard et al. 2012; Peñuelas et al. 2013; Seddon et al. 2016). Mediterranean ecosystems are particularly susceptible to declines in soil water availability and the more frequent combination of climate extremes such as heatwaves and drought events during the summer (Myers et al. 2000; Peñuelas et al. 2017; 2018; Cramer et al. 2018). Indeed, unprecedented impacts of water deficit on vegetation have been widely documented, such as episodes of tree mortality and forest die-off (Peñuelas et al. 2001; Lloret, Siscart, et al. 2004; Carnicer et al. 2011; Saura-Mas et al. 2015), shifts in community composition (Peñuelas & Boada, 2003; Peñuelas et al. 2007; Ruiz-Benito et al. 2017) and declines in ecosystem carbon uptake and storage (Ciais et al. 2005; Vicente-Serrano et al. 2013; Papadopoulos et al. 2017). By the end of this century, water deficits in the Mediterranean Basin are expected to increase in severity and frequency under the projected scenarios of 2-4 °C increases in temperature and the concurrent decreases of up to 30% in precipitation (Cramer et al. 2018; Lionello & Scarascia, 2018). These increases in frequency and intensity of climate extremes will further trigger forest degradation and land desertification, especially within the overarching context of land-use change, habitat fragmentation and biotic invasions (Doblas-Miranda et al. 2017; Peñuelas et al. 2017; 2018; Cramer et al. 2018). Therefore, understanding and predicting vegetation dynamics to future climate change is essential, especially if the impacts are to be effectively mitigated through the design and implementation of ecosystem restoration in future.

The effective method to measure the vegetation response to climate regime is still limited. Manipulating drought experiments (i.e. reduced rainfall) in natural ecosystems are considered as one of the useful methods to track the climate-caused vegetation responses, such as physiological changes, plant growth, community composition and ecosystem functioning (Luo et al. 2011; Beier et al. 2012; Liu et al. 2015; 2017). These studies provide an essential opportunity to explore the response of a local community to climatic change. However, the result of plant responses and other ecological processes by drought regime is based on short-term studies (less than 5 years). It is still unclear whether the direction and magnitude of the effects of drought on vegetation will continue over time. Short-term experiments have shown immediate and transient vegetation responses to simulated climate change, and the effects could be accumulative and lag behind at long-term processes (Smith et al., 2009; Peñuelas et al. 2013; 2018). A recent study has reported that drought effect on aboveground net primary productivity (ANPP) of Mediterranean forest is increasing over 15 years under 27% rainfall exclusion (Gavinet et al. 2019), which is not detected in the short-term. It is also likely that plants rely on their plasticity to tolerate the shifts in climate regimes at short-term climate regimes. It has been reported no net change in standing biomass and species diversity for the shrublands across 9 years of reduced rainfall in Israel (Tielbörger et al. 2014; Metz & Tielbörger, 2016). Moreover, the impacts of climate on plant growth can be decreased or dampened over time (Leuzinger et al., 2011; Barbeta et al., 2013). A number of studies have reported that plants can adapt to drought through physiological, phenological and morphological adjustments, community recruitment (i.e. regrowth and new seedling) and biotic interactions (i.e. increased mycorrhizae-plant associations) (Bellard et al. 2012; Peñuelas et al. 2013; 2018; Liu, et al. 2017). Thus, gaining knowledge on longer temporal scale of vegetation responses to climate change is urgently required.

Long-term (decadal) drought experiment is a promising method to evaluate vegetation growth over time that can capture the results of plant adjustments and ecological interactions (Luo et al., 2011; Liu et al., 2017, Liu, Ogaya, et al. 2018). The magnitude of long-term drought effects could be especially responsive in such already water-deficit ecosystems. Strong responses in plant species diversity and composition have been found in decadal drought experiments for the shrublands in the Mediterranean ecosystems, whereas nearly no responses have been observed in the shrublands of wet sites in UK (Clocaenog) and Denmark (Brandbjerg) (Kröel-Dulay et al. 2015; Estiarte et al. 2016; Reinsch et al. 2017). Moreover, unprecedent and severe climate extremes may increase the drought intensity for the experimental plot, leading to severe negative impacts on carbon assimilation, water transport and growth limitation beyond the bounds of plasticity and endurance of the Mediterranean plants (Limousin et al., 2012; Liu, et al. 2016; 2017). Some studies have reported that experimental drought and combined extreme droughts significantly affect flower and fruit development, which may decrease the new recruitment (Peñuelas et al. 2004; Misson et al., 2011). In recent extreme dry years, higher stem mortality and crown defoliation (i.e. leaf and branch litterfall) in a holm oak forests were reported in experimental drought plots than in control plots (Barbeta et al. 2015; Liu et al., 2015; Liu, Ogaya, et al. 2018). Interestingly, the effect of long-term drought may also relate to the climate, soil depth and vegetation composition of the study site (Martin-Stpaul et al., 2013; Liu, Ogaya, et al. 2018). These issues have not been addressed by long-term drought experiments, hindering an accurate prediction of vegetation dynamics to climatic regime.

The aim of this study is to analyze plant biomass dynamics from two long-term (1999-2016) drought experiments in the Mediterranean region, one in a holm oak forest (with a high and low canopy, details in Method and Materials) and the other in an early successional shrubland. These two experiments have provided evidence for the impacts of short-term drought on plant physiological (carbon assimilation) processes, especially during summer (Llorens et al. 2003; Prieto et al. 2009; Liu et al. 2016: Zhang et al., 2017), phenology (advanced and delayed leaf and flower opening) (Peñuelas et al. 2004; Ogaya & Peñuelas, 2007a; Bernal et al. 2011) and genetic responses (increased genetic differentiation) (Jump et al. 2008; Rico et al. 2014). We hypothesize that long-term experimental drought combined with meteorological drought (Standardized Precipitation-Evapotranspiration Index, SPEI) will significantly decrease the plant biomass accumulation for the Mediterranean forest (especially in low canopy) and shrubland. The primary objective of our study is to analyze the vegetation growth (aboveground biomass increment, ABI in the forest and standing density in the shrubland) in response to the 18 years of experimental drought and explore the responses with the effects of meteorological drought (SPEIs) and extreme drought episodes. This study aims, thus to improve the understanding of the responses of plant growth to ongoing and future climate change, and inform the design of effective strategies to maintain ecosystem carbon sink capacity.

Method and Materials

Long-term drought experiments

1) *Mediterranean forest*

The forest site is located at a south-facing slope (ca. 25º) in Prades mountains in southern Catalonia, northeastern Iberian Peninsula (41°21´N, 1°2´E; 930 m above sea level; Fig. 1C). This forest is a typical Mediterranean holm oak forest, dominated by the evergreen tree *Quercus ilex*, and usually accompanied with the shrubs *Phillyrea latifolia* and *Arbutus unedo*. The forest has not been disturbed by anthropogenic thinning and copping since 1940s. The vegetation structure and height are naturally variable due to the heterogeneity of nutrient availability, soil depth and bedrock type (Liu, Ogaya, et al. 2018). The vegetation at deep soil sites is usually composed by tall and big stands and dominated by *Q. ilex* individual 8-10 m tall (High, indicated as H-canopy hereafter), whereas at the shallow soil sites *Q. ilex* is mixed with several shrubs including *P. latifolia* reaching 4-6 m in height (Low, indicated as L-canopy hereafter) (detailed feature for the two canopy types in Table 1) (Liu, Ogaya, et al. 2018). We simulated a drier climate by excluding 30% of annual precipitation (similar to the predicted scenarios of precipitation reduction in coming decades) with a nonintrusive system based on the installation of transparent plastic long strips (0.5-0.8 m wide) within drought plots (Fig. 1A, B). Four plots (10 x 15 m per plot) were respectively established in both H- and L-canopy, and half of them (two replicates per each type) were randomly selected for drought treatment whereas the other two were assigned as control treatment. At the upper edges of the drought plots, we built ditches (0.8-1 m deep) to intercept the water runoff into the plots. Throughout the study period of 1999-2016, annual soil moisture in the H-canopy and L-canopy was decreased by ca. 15% (see details in Table S1).

In 1998, all living trees (Diameter > 2 cm) were labelled at a height of 50 cm (D50) and since then their diameter was measured in winter, a growth-less season. Aboveground biomass (AB) at plot level was estimated from stem diameters by allometric relationships (Ogaya & Peñuelas, 2007b; Liu et al. 2015). The aboveground biomass increment (ABI) was calculated annually using the differences in AB between years for the two canopy types. This growth metric is a good proxy for exploring the forest growth dynamic in response to experimental drought and natural droughts.

A meteorological station installed at the study site automatically recorded daily temperature and precipitation since the pre-treatment in 1998. Soil moisture at 0-15 cm depth was measured seasonally throughout the experimental period by Time Domain Reflectometry (TDR, Tektronix 1502C, Tektronix, Beaverton, OR, USA) using probes permanently installed in the soil at four randomly selected locations in each plot. Monthly temperature and precipitation for 1975-2001 were obtained from the nearby meteorological station of Poblet Monastery (5.6 km away from the study plots and at 510 m a.s.l.) (linear regression for 1998-2001: $R^2=0.97$ for temperature and $R^2=0.75$ for precipitation). Based on the data collected at the site and at the nearby meteorological station, we calculated the Standardized Precipitation-Evapotranspiration Index (SPEI), a drought index that takes into account both precipitation and temperature fluctuations, and identifies the drought severity according to the intensity and duration (Vicente-Serrano et al. 2013). Thus, a database of monthly difference between precipitation and the potential evapotranspiration by temperature changes (D values) was constructed from 1975-2016, and then applied to calculated the SPEI with different timescales (1-36 months) by SPEI package (version 1.6). The SPEI index is widely used to explore the relationships between plant responses and water deficits at different temporal scales. The range of this drought index is from -3 to 3, lower values represent more drought stress. SPEI with different timescales stand for the levels of drought-sensitivity, higher drought-sensitivity usually at shorter temporal scale while more drought-resistance at longer temporal scale (a detailed calculation was described in Barbeta et al. (2013) and Liu et al. (2015, 2017)). We used SPEI to evaluate the drought severity from 1975 to 2016. At the forest site, mean annual SPEIs and August SPEI-3 decreased ($R^2 = 0.09$, $p < 0.1$ and $R^2 = 0.26$, $p < 0.001$; respectively) during the period of 1975-2016 (Fig. 2A, C). Moreover, we defined the extreme dry years based on the lowest 10 percentile mean annual precipitation (MAP) (Knapp et al. 2015) during the period of 1975-2016 and we identified 2001, 2005-06 and 2015 as extreme dry years during the study period 1999-2016.

2) *Mediterranean shrubland*

The shrubland site is located at a south-facing slope (ca. 13°) hill of Garraf Natural Park in central coastal Catalonia (northeastern Iberian Peninsula) (41°18′N, 1°49′E; 210 m above sea level; Fig. 1C). The soil in the study site is typically calcareous, and the substrate is mainly composed of marls and limestone with rocky outcrops. The dominant vegetation changed to short perennial shrubs after the two wild fires in 1982 and 1994 eliminated coniferous forest. The main plant species are the shrubs *Globularia alypum* and *Erica multiflora* whose composition is higher than 50% of the total community and are accompanied by other Mediterranean shrubs such as *Rosmarinus officinalis*, *Dorycnium pentaphyllum* and *Ulex parviflorus* and herbs such as *Euphorbia serrata* (see details in Liu et al. 2017). To simulate future drought regimes, we excluded precipitation with a nonintrusive system that automatically extends a transparent waterproof cover to intercept precipitation during spring and autumn growing season (May-September) during 1999-2015 (Peñuelas et al. 2007; Liu et al. 2016; 2017) and transparent V-type plastic to intercept the rainfall since the damage of automatic system after 2015. Six plots (4 x 5 m) were built along the same slope, three plots randomly selected as drought treatment while the rest were used as control (Fig. 1D, E; Table 1). Throughout the study period of 1999-2016, the drought treatment reduced annually the precipitation around 30%, and the soil moisture at 0-15 cm depth around a 15% compared to control.

From the pre-treatment in 1998 to 2016, the vegetation growth in the shrubland was measured once per year in end July, when growth is stopped, using the point-intercept method. Vegetation measurements were conducted at the central area (3 x 4 m) of each plot using five parallel 3-m long transects permanently fixed at the beginning of the study. Along each transect 61 points were evenly distributed totaling 305 points per plot. We lowered a long steel pin (3 mm diameter) through each sampling point and every time the pin hit a plant we recorded plant species, organs (e.g. leaf, reproductive structure or stem) and state (live or dead). The growth metric is calculated as the stand biomass (or density) for this study site.

Daily air temperature and precipitation during the study period were recorded by a meteorological station at the study site. Since the start of this experiment in 1998, soil moisture at of 0-15 cm depth was measured biweekly using Time Domain Reflectometry (TDR) by probes permanently inserted at three points per plot. Historical climate data since 1975 was collected from a nearby meteorological station (10 km away from the study plots and at 200 m a.s.l.) to get the background climate regimes for the study site (Liu et al. 2017). The SPEI drought index was calculated based on the site climate data from 1998-2016 and historical climate (linear regression with our station for 1998-2010: R^2=0.99 for temperature and R^2=0.83 for precipitation). The calculation of SPEI in the shrubland site is similar with the forest site described above. No trends in mean annual SPEIs was detected in the shrubland, but August SPEI-3 decreased significantly ($R^2 = 0.09$, $p < 0.\ 05$) across the period of 1975-2016 (Fig. 2B, D). As described for the forest site, in the shrubland we identified 2001, 2005-06 and 2016 as extreme dry years based on the lowest 10 percentile MAP (Knapp et al. 2015) during the period 1975-2016.

Statistical analysis

To analyze the vegetation responses to drought throughout the period from the pre-treatment year 1998 to 2016, vegetation growth of ABI for the forest and the standing density for the shrubland were tested respectively. In the forest we analyzed separately the two canopy types. In the shrubland, first we log-transformed the abundance or frequency for each species, and then the values of all the species were summed and given equal weight for all species at community level. This method reduces the overrepresentation of highly dominating species such as *G. alypum* and *E. multiflora* (Šmilauer & Lepš, 2014; Liu, Peñuelas, et al. 2018). The vegetation growth for forests and shrubland were taken as the responsive variables to the drought treatment combined with natural droughts (SPEIs). The SPEIs were calculated for different timescales ranging from 3 to 12 months, and the growing season was considered during the rainfall accumulative period from December to June in Mediterranean region (Barbeta et al. 2013; Liu et al. 2015; 2017). Then we applied these different SPEIs to test the correlations with plant growth for forest and shrubland. The best-fitted SPEIs with the vegetation growth for forest (separately for high and low canopies) and shrubland were selected based on the stronger correlations (the details were described in the Appendix). We used a linear mixed model for growth responses (Growth=Drought*SPEI) at both forest and shrubland sites according to the lowest Akaike information criterion (AIC). The plot nested with year (plot+year) was selected as random factor, to explain the spatial and temporal autocorrelation. Moreover, significant differences for the slopes between control and drought for the vegetation growth were statistically tested by least-Squares Means (lsmeans package). The vegetation responses of control and drought at extreme dry years were assessed by repeated measures ANOVA. All the analyses were performed with the R program (R version 3.5.0).

Results

Vegetation responses to experimental drought

Long-term experimental drought decreased either aboveground biomass increment (ABI) in both the Mediterranean forests or standing density in the shrubland. Experimental drought decreased the ABI values for both H-canopy and L-canopy (t-value = -3.52, $p < 0.001$ and t-value = -2.41, $p < 0.05$; respectively) (Fig. 3A, B). The effects of experimental drought on ABI were stronger for the first 5 years (1999-2004), especially for L-canopy. Experimental drought decreased the standing density for the whole 1999 to 2016 period in the early-successional shrubland (t-value = -7.71, $p < 0.001$), but the effect tended to be more stable after the year 2002 (Fig. 3C).

The changes of vegetation growth to natural drought (SPEIs)

The values of vegetation growth were also correlated positively with the natural meteorological droughts (SPEI) during spring-winter season (Fig. 4 and Table 2). In the forest, ABIs increased with May SPEI-7 for the H-canopy (t-value = 2.77, $p < 0.05$) and with May SPEI-5 in the L-canopy (t-value = 2.41, $p < 0.05$) (Fig. 4A, B). Interestingly, we found there was a significant interaction between May SPEI-5 and experimental drought treatment for the ABI in the L-canopy according to the best fitted model (t-value = 2.07, $p < 0.05$) (Fig. 4B). In the H-canopy, the slope of the ABI versus May SPEI-7 correlation did not differ among control and drought plots (common slope = 1.20, ns) (Fig. 4A). In the L-canopy, ABI correlation with May SPEI-5 was stronger in drought ($R^2 = 0.51$, $p < 0.001$) than control plots ($R^2=0.32$, $p < 0.01$), and the slopes were marginally steeper for drought than control plots (common slope = 1.69, $p < 0.1$) (Fig. 4B).

In the shrubland, the standing density was positively correlated with May SPEI-4 during the study period (t-value = 3.53, $p < 0.001$). The positive correlation was stronger in control ($R^2= 0.34$, $p < 0.01$) rather than in drought plots ($R^2=0.15$, $p<0.1$). The slopes of the density versus May SPEI-4 correlation differed among control and drought (common slope = 2.29, $p < 0.05$) (Fig. 4C).

The severe effect of extreme dry episodes

Vegetation growth to extreme dry years were strong and apparent both in the forest and the shrubland. In the forest, the ABI decreased more in drought than in control plots in extreme dry episodes in both H- and L-canopy types (Fig. 5A, B). In the shrubland, there was significant lower biomass accumulation for the drought at extreme dry years (Fig. 5C, ANOVA, F = 11.02, $p < 0.01$).

Discussion

Decreases in vegetation growth in response to the long-term drought experiments and the progressive meteorological drought

The declines in vegetation growth were accelerated by natural extreme droughts. ABI decreased in response to the experimental drought in the two canopy types (Fig. 3A, B) as reported already in previous studies (Barbeta et al. 2015; Liu et al. 2015; Liu, Ogaya, et al. 2018). However, the decrease in ABI appeared earlier and stronger in L-canopy due to shallowest soil site. Indeed, soil depth is a determinant of soil water holding capacity and is likely a modulator of the intensity of plant responses to climate change. Continuous drought reduces the ground water levels limiting the uptake of ground water that is vital for the maintenance of water balance in the hot and dry Mediterranean summer, which leads to hydraulic failure (Barbeta et al. 2015; Liu et al. 2015; Liu, Ogaya, et al. 2018). For this reason, tree mortality and forest die-back have been observed in disturbed Mediterranean forests with shallow soils (Lloret, Siscart, et al. 2004; Carnicer et al. 2011; Saura-Mas et al. 2015). In the early-successional shrubland, we also found negative effects of experimental drought on standing density over time (Fig. 3C). Nowadays, the anthropogenic changes in land-use changes such as habitat fragmentation have affected most vegetation ecosystems which may increase ecosystem instability and push back to early-successional status (Seddon et al. 2016; Peñuelas et al. 2013; 2018). Rapid climate regimes could also trigger sharp and strong effects on species diversity and composition shifts (Peñuelas et al. 2007; Kröel-Dulay et al. 2015; Liu et al. 2017). Thus, habitat context may be a key driver of vegetation responses to climate change, so we recommend that future climate experiments account for the factors, such as soil depth and successional status, to improve the understanding and prediction of vegetation dynamic under continuous climate change.

Plant growth was closely correlated with SPEIs at growing season. Generally, ABI of forest and standing density of shrubland were positively related with water availability in the winter-spring seasons (Table 2), which is consistent with the findings that rainfall in winter-spring is the most essential for plant growth and establishment in Mediterranean ecosystems

(Barbeta et al. 2013; 2015; Liu et al. 2017; Gavinet et al. 2019). The SPEI timescales for forests varied differentially, with longer timescales in H-canopy (Fig. 3, 4). The result indicates higher stem water storage in H-canopy forest than L-canopy in response to water limitation (Vicente-Serrano et al. 2013; Barbeta et al. 2013; Liu et al. 2015; Liu, Ogaya, et al. 2018). In addition, H-canopy can successfully access deep soil water and groundwater with longer root depth, allowing it to buffer shorter drought events than L-canopy (Barbeta et al. 2015; Liu, Ogaya, et al. 2018). On the contrary, L-canopy with shallow soil likely have shallow roots and shrubland stores less water in stems, may suffer more severe and negative impacts by meteorological droughts in future. Indeed, the mean annual SPEIs and summer SPEIs of August SPEI-3 also suggest that water deficit is becoming more severe and stronger over the latest four decades (Fig. 2), which may increase soil water deficit and cause episodes of tree mortality and forest canopy die-off (Carnicer et al., 2011; Saura-Mas et al. 2015). Furthermore, the trend of summer water deficit is continuing, which will potentially decrease the ecosystem carbon sink and drought recovery in the most immediate future.

The correlations with the SPEIs varied greatly between drought treatment and control. For L-canopy, the sensitivity was higher in the drought plot, i.e. the slope of the ABI and SPEI was steeper in drought than that of control, which could be related with the limitation on stem growth and higher mortality rate in the experimental drought (Barbeta et al. 2015; Liu et al. 2015; Liu, Ogaya, et al. 2018). For shrubland, there was a strong (steeper slope) and significant relationship between SPEI and standing biomass in control than that of drought plots, indicating the plants in control was more responsive to meteorological drought. However, we observed that the correlations to meteorological drought were similar between control and drought plots for H-canopy, suggesting a consistent sensitivity to natural drought (Fig 3A). Therefore, a new climate status simulated by experimental drought (30% rainfall exclusion) had negative impacts on L-canopy and shrubland, which may also result in different species assembles and composition compared to control plots.

Strong decreases in vegetation growth were found in drought plots at extreme dry years. Throughout the extreme dry years, the average ABI in forests and standing biomass of shrubland were more reduced in the drought treatments than in the control. The results might be related to the limitations on leaf carbon sequestration, stem/branch hydraulic failure and higher mortality rates in drought plots than in control plots for the holm oak forests (Barbeta et al. 2015; Liu et al. 2015; Liu, Ogaya, et al. 2018). These frequent and intense extreme episodes might significantly change forest productivity over time due to the decreases in plant growth, higher stem mortality and composition shifts (Allen et al. 2015; Martinez-

Vilalta et al. 2017). Indeed, a continental-scale reduction in net primary productivity across a large area of Europe was caused by extreme water deficit in summer 2003 (Ciais et al. 2005). Significant differences in standing density between control and drought plots were also found in the extreme dry years in the shrubland (Fig. 5C). Therefore, such plant community in the arid and semi-arid ecosystems may be more sensitive to extreme droughts than more mesic ecosystems in the near future, thus presenting more changes in plant density, community diversity and evenness.

Contrasting results in other long-term drought experiments in Mediterranean ecosystems

Plant responses to long-term drought varied among experiments cited in the literature. The high risk for limitation of carbon uptake could come from lower photosynthetic activities and/or increase higher respiration rates (Wu et al. 2011; Beier et al. 2012; Reinsch et al. 2017). However, it has been shown that decadal drought did not affect species richness and aboveground biomass in Mediterranean shrublands in Israel, possibly as a result of ecosystem resistance with stable species diversity and composition (Tielbörger et al. 2014; Metz & Tielbörger 2016). An experimental drought that started in 2004 in another Mediterranean holm oak forest (Puébachon State Forest, South France) had no effect on stem growth (Martin-Stpaul et al. 2013), but strongly decreased stem sap flow, leaf and acorn production (Limousin et al. 2009; 2012; Gavinet et al. 2019). Recently, it was reported that long-term (15 years) drought have decreased 10% ANPP possibly owing to the lower leaf and acorn production over time (Gavinet et al. 2019). The varying drought effect on stem growth was possibly related to the site differences between Prades and Puébachon, such as in climate of (650 mm vs 936 mm), stem number (stem ha^{-1}:13273 in H-canopy and 19005 in L-canopy vs 5933) and basal area (m^2 ha^{-1}: 47.1 in H-canopy and 35.2 in L-canopy vs 24.9). From the above, we can infer our study sites could be more sensitive to drought due to more severe water limitation and stronger competition. However, longer experimental drought (15 years) significantly decreased forest ANPP possibly owing to the lower stem sap flow, leaf and acorn production (Limousin et al. 2009; Martin-Stpaul et al. 2013; Gavinet et al. 2019). Thus, the contrasting responses of drought effect on vegetation across study sites are probably linked to site-specific climate, vegetation structure and composition. Therefore, future studies should focus not only on the physiological, phenological and morphological responses to long-term process, but also on the different context of the study sites in comparison.

Implication for the future experiments

Our results have shown that long-term drought (30% rainfall reduction for 18 years), combined with meteorological drought and extreme dry years are decreasing vegetation growth in the water-limited Mediterranean forest and shrubland ecosystems. Such experiments provide an opportunity to estimate ecosystem function dynamic under future climate change and also a validation of the predictions by dynamic global vegetation modelling (DGVM). However, knowledge gaps still remain that hinder our understanding of future carbon storage in natural ecosystems in a changing climate. Firstly, the magnitude of plant responses to drought differs for temporal processes (short-term vs long-term), and are strongly associated with extremes. Secondly, the response of vegetation growth to climate change may vary greatly with study sites depending on soil depth, water availability and community composition as well as successional status. Since most of previous studies rarely tested these responses, understanding of the dynamics at regional and continental scales remains limited. Thirdly, plant growth to climate change is correlated with multiple physiological, phenological and demographical adjustments that should also be taken into consideration. Fourthly, the responses of vegetation dynamics are complex and multidimensional. For example, drought regimes may decrease plant aboveground biomass and productivity, but increase biomass allocation to belowground plant organs (e.g. root mass), increase fungal and/or bacterial activities. Future studies should also probe the multiple ecological functions (e.g. multifunctionality), such as vegetation growth, seed production, nutrient use and decomposition by the combination of long-term process and/or extremes. Conducting long-term field experiments in contrasting natural ecosystems under different climate regimes and exploring multivariate data analysis of interactions and trade-offs is thus necessary.

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Author contributions

D.L and C.Z analysed the data and wrote the paper and J.P conceived the idea and provided in-depth suggestions for the manuscript. J.P, M.E and R.O designed the experiment, performed the research and revised the manuscript.

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Tables

Table 1. Characteristics of forests (H- and L- canopies) and shrubland sites. Soil depth and mean tree height represent the range of minimum and maximum and the others show the mean and standard error values. Aboveground biomass for forest and shrubland were measured at the pre-treatment year of 1998 (n=4 and n=6; respectively).

Characteristic	High canopy	Low canopy	Shrubland
Soil depth (cm)	30-50	10-30	5-30
Mean height (m)	8-10	4-6	0.5-1.5
Mean stems at pre-treatment (stem ha$^{-1)}$	13273±17.5	19005±29.8	-
Mean basal area and aboveground biomass (m^2/Ha and g/m^2, respectively)	47.1±3.1	35.5±7.9	36.6±2.4
Soil moisture in control plots for 1999-2016 (%)	17.19±0.58	16.32±0.6	19.02±0.8
Soil moisture in drought plots for 1999-2016 (%)	14.79±0.6	13.96±0.6	15.88±0.8

Table 2. The community responses of above ground biomass increment ABI and density to long-term drought and natural droughts for the forest and shrubland sites. The responses were statistically analysed by linear mixed models based on the lowest AIC values. The variables of experimental drought, SPEI (May SPEI-7 and May SPEI-5) and interaction of experimental drought and SPEI were applied into the models for the two canopy types. And the variables of experimental drought and May SPEI-4 were applied into the model for shrubland. The significance and non-significance were listed.

Plant communities	Variables	t-value	p-value
H-canopy	Experimental drought	-3.52	$p < 0.001$
	May SPEI-7	2.77	$p < 0.05$
	Experimental drought x May SPEI-7	1.01	ns
L-canopy	Experimental drought	-2.41	$p < 0.05$
	May SPEI-5	2.42	$p < 0.05$
	Experimental drought x May SPEI-5	2.07	$p < 0.05$
Shrubland	Experimental drought	-7.71	$p < 0.001$
	May SPEI-4	3.53	$p < 0.001$

Figures with legends

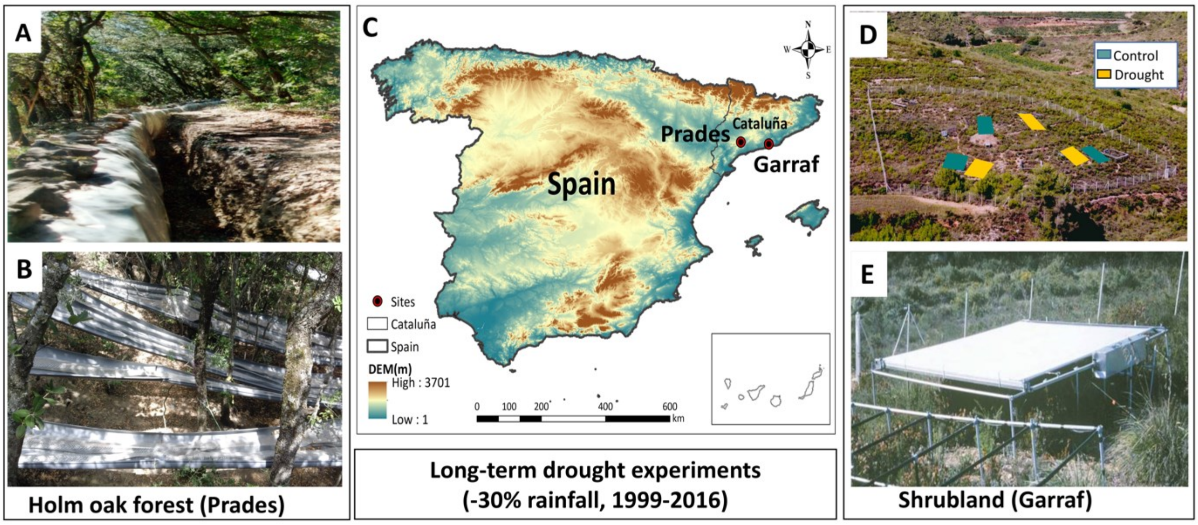
Fig. 1 Two long-term drought experiments in a Mediterranean forest and shrubland. Plastic cover system used to rainfall runoff (A) and exclusion (B) from the forest plots; (C) The location of the two long-term drought experiments; (D, E) And plastic cover system used to exclude rainfall from the shrubland study site

Fig. 2 Meteorological drought at summer and spring for the forest (A, C) and shrubland (B, D) sites. The SPEI (Standardized Precipitation Evapotranspiration Index) for summer (August SPEI-3) and growing season (May SPEI-5 and May SPEI-4) are presented. And the trends were tested by linear regression, and the significance ($p < 0.05$) were highlighted with lines.

Fig. 3 Vegetation responses of aboveground biomass increment (ABI) for two canopy types of forest and standing density (sum ln) for the shrubland. The bars are the best-correlated SPEI (Standardized Precipitation Evapotranspiration Index) for H- and L-canopy forests (May SPEI-7 and May SPEI-5; respectively) the shrubland (May SPEI-4). The vertical bars stand for the standard error (se) of the mean for forests and shrubland (n=2 and n=3, respectively).

Fig. 4 The comparations for the slopes between control and drought experiments of aboveground biomass increment (ABI) for two canopy forests and standing density of the shrubland. The differences between control and drought are analyzed by smatr test.

Fig. 5 Effects of experimental drought on vegetation responses of forest aboveground biomass increment (ABI) and shrubland standing density in extreme dry years. The years 2001, 2005-2006 and 2015 were extreme dry years for the forest and 2001, 2005-2006, 2016 were extreme dry years for shrubland based on the definition of mean annual precipitation (MAP) <10th percentile during the period 1975-2016. There were no significant differences between control and experimental drought during extreme years for the two forest canopies. But we observed the significant differences for the shrubland site ($F = 11.02$, $p < 0.01$).

A
B
C
D
E
Holm oak forest (Prades)
Shrubland (Garraf)
Long-term drought experiments
(-30% rainfall, 1999-2016)
Spain
Prades
Cataluña
Garraf
N
W
E
S
Sites
Cataluña
Spain
DEM(m)
High : 3701
Low : 1
0
100
200
400
600
km
Control
Drought

708

709 Fig. 1

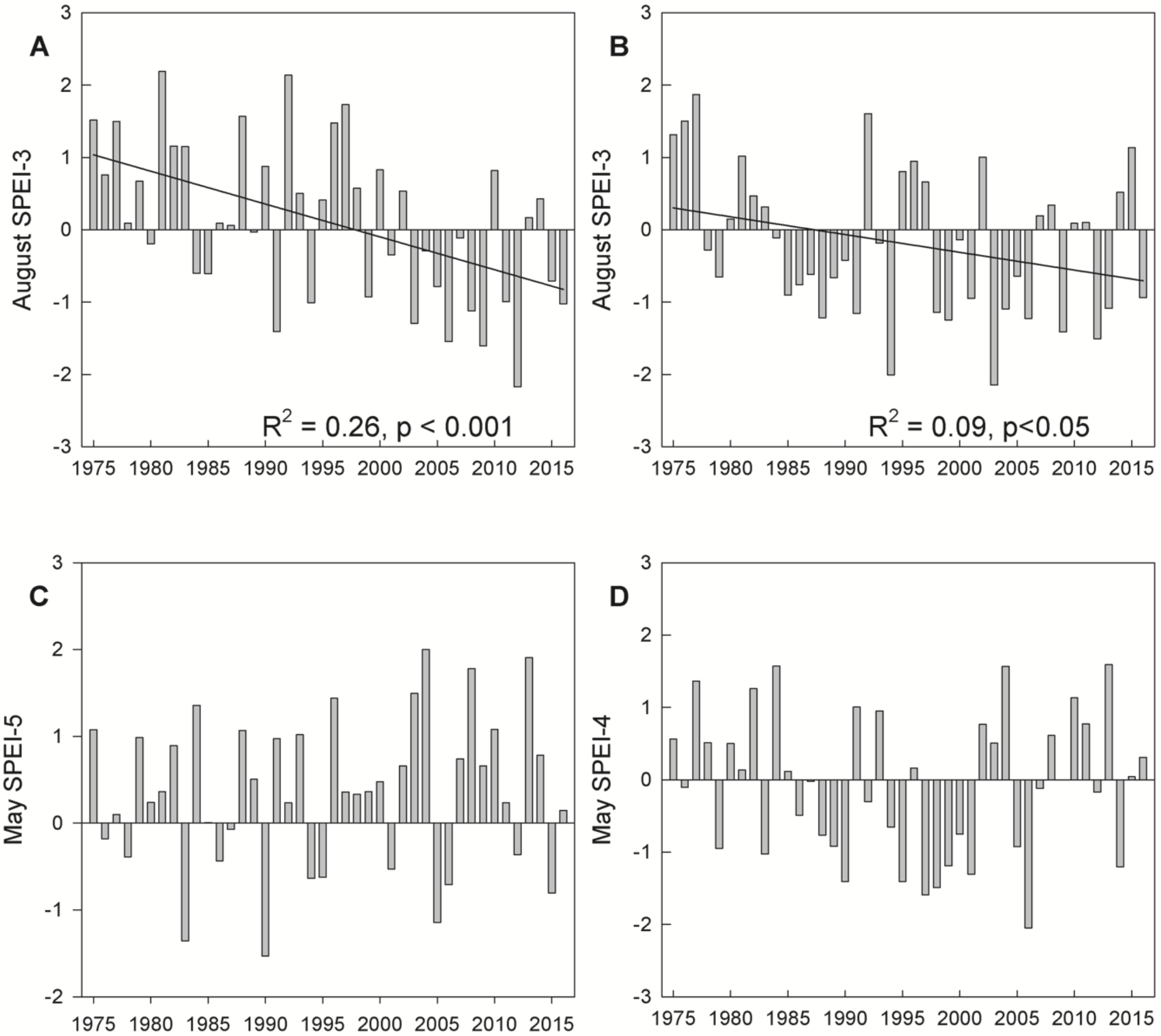

A
August SPEI-3
$R^2 = 0.26, p < 0.001$
B
August SPEI-3
$R^2 = 0.09, p<0.05$
C
May SPEI-5
D
May SPEI-4
3
2
1
0
-1
-2
-3
1975
1980
1985
1990
1995
2000
2005
2010
2015

Fig. 2

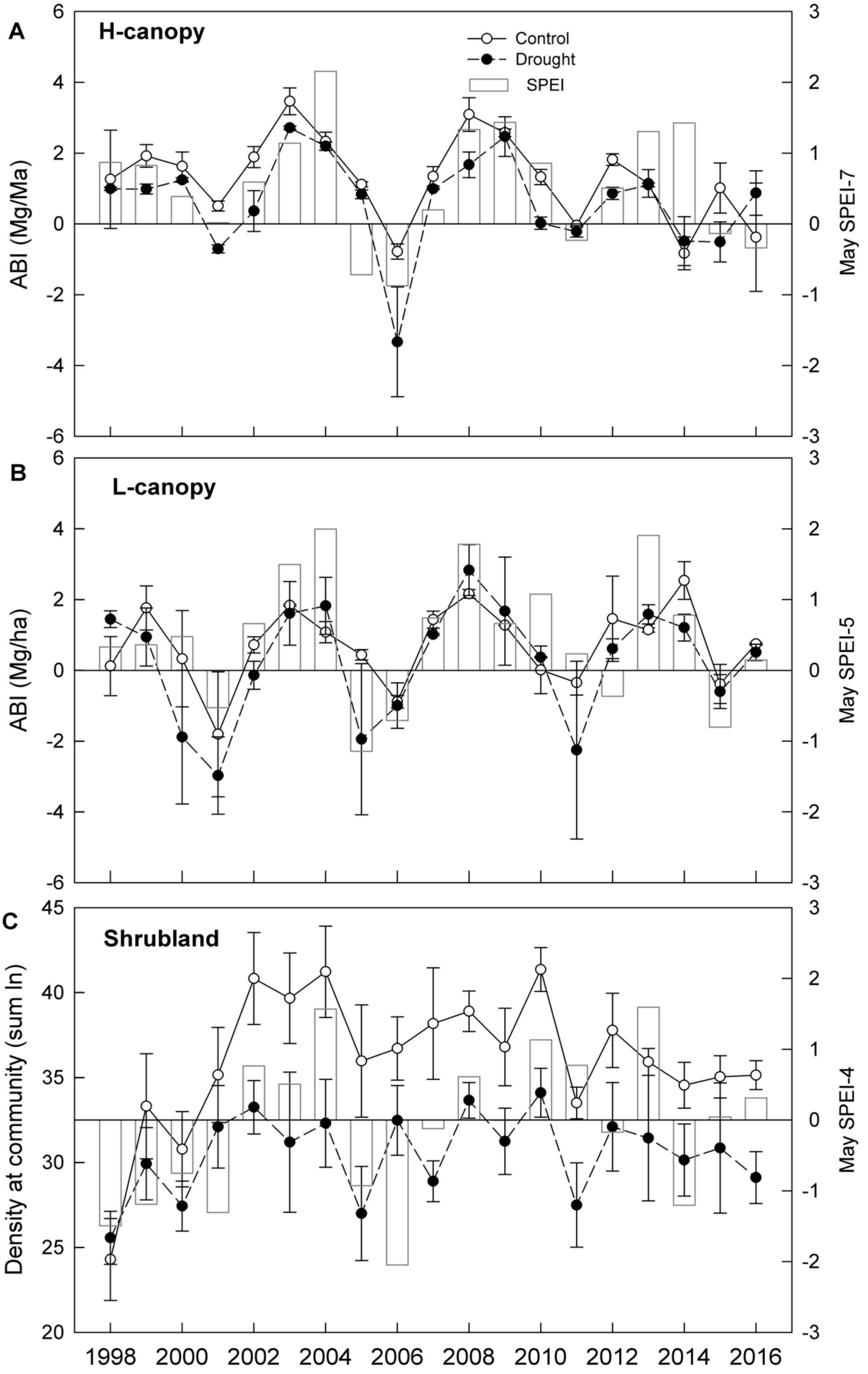

A
H-canopy
Control
Drought
SPEI
ABI (Mg/Ma)
May SPEI-7
B
L-canopy
ABI (Mg/ha)
May SPEI-5
C
Shrubland
Density at community (sum ln)
May SPEI-4
6
4
2
0
-2
-4
-6
3
2
1
0
-1
-2
-3
45
40
35
30
25
20
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016

Fig. 3

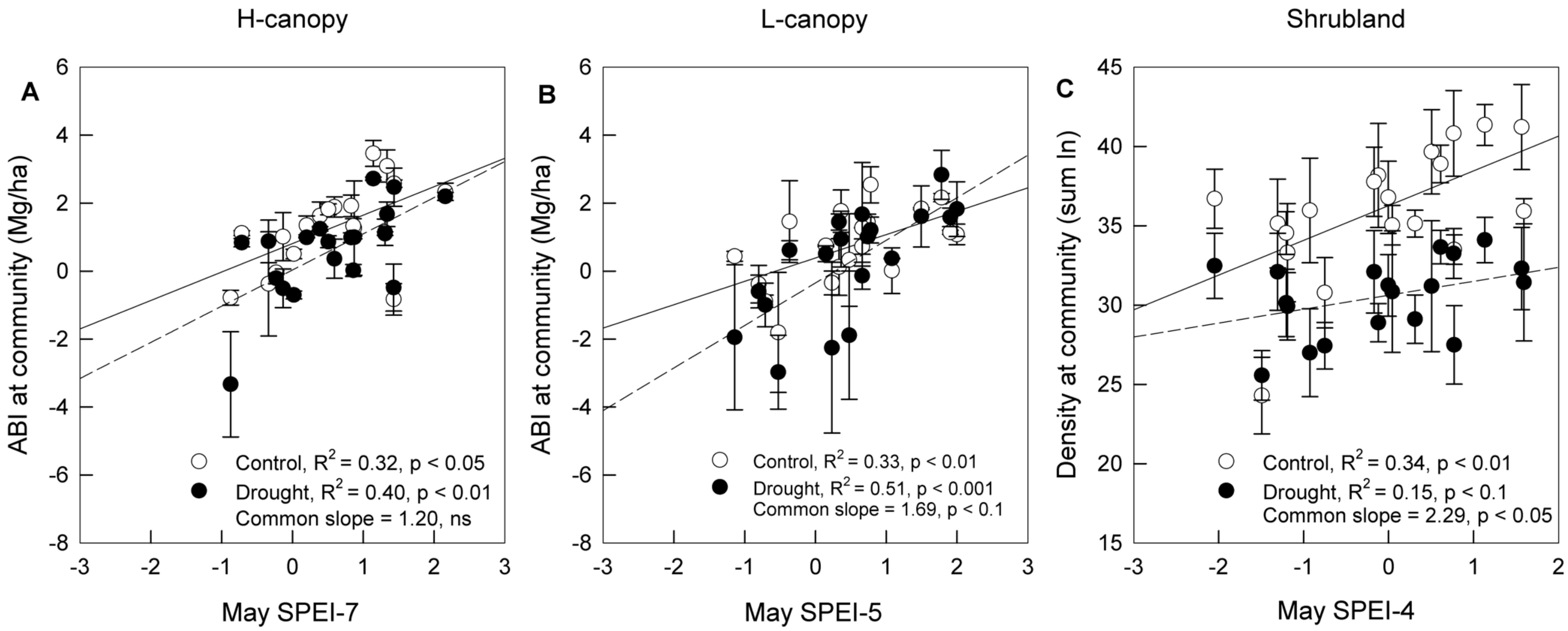

H-canopy
L-canopy
Shrubland
A
B
C
ABI at community (Mg/ha)
ABI at community (Mg/ha)
Density at community (sum ln)
6
4
2
0
-2
-4
-6
-8
45
40
35
30
25
20
15
-3
-2
-1
0
1
2
3
May SPEI-7
May SPEI-5
May SPEI-4
Control, R^2 = 0.32, p < 0.05
Drought, R^2 = 0.40, p < 0.01
Common slope = 1.20, ns
Control, R^2 = 0.33, p < 0.01
Drought, R^2 = 0.51, p < 0.001
Common slope = 1.69, p < 0.1
Control, R^2 = 0.34, p < 0.01
Drought, R^2 = 0.15, p < 0.1
Common slope = 2.29, p < 0.05

Fig. 4

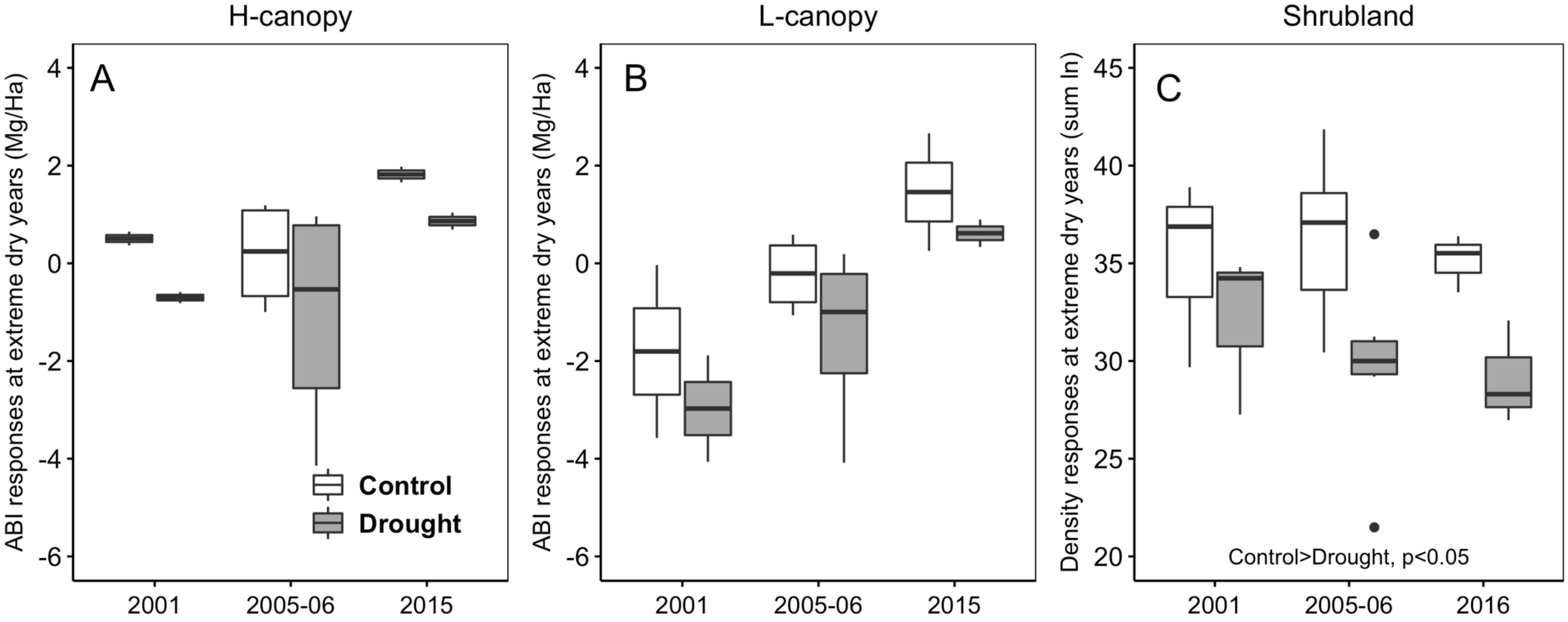

H-canopy
L-canopy
Shrubland
A
B
C
ABI responses at extreme dry years (Mg/Ha)
Density responses at extreme dry years (sum ln)
4
2
0
-2
-4
-6
45
40
35
30
25
20
2001
2005-06
2015
2016
Control
Drought
Control>Drought, p<0.05

Fig. 5