Relict deciduous oaks show high resilience to drought despite the effect of land-use legacies along a climatic gradient in the rear-edge

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# Abstract

* Global change challenges forest ecosystems particularly in species-specific dry locations where land-use legacies have modified species composition and the forest structure as a result of intensive human pressure in the past. We analyzed forest resilience of adult trees to drought and climate change of relict Mediterranean *Quercus pyrenaica* Willd. populations in the Southern Iberian Peninsula. Forest resilience was analyzed using both dendroecological growth estimates and MODIS satellite images as proxies for secondary and primary growth respectively.
* Intense land-use in history in the studied populations were likely expressed by disturbance chronologies, hence partly reflecting the origin of the current forest structure and land-use legacies. Trees expressed a high sensitivity to drought. Both resilience indices of primary and secondary growth expressed that trees showed high resilience both to recent drought events and also to long-term climatic changes (*i.e.* warming). This would contradict the the ‘*a priori*’ vulnerability that we expected in respone to climate change of the studied relict stands at the species current rear-edge. Yet, there was variation in the response to climate and resilience following a water-stress gradient along our three studied forests. We found a positive growth trend that was strongest in the high elevation stand and non-significant in the most xeric site (or the most transformed????) since the end of the 1970s matching the simultaneous increase in temperature observed.
* Resilience to drought followed a dryness gradient among the three populations studied: Northern populations thriving under a drier climate were less resilient to drought both in primary and secondary growth than Southern populations where lower altitudes were also less resilient than those at high-altitudes.
* Despite being considered relict stands at the dry rear-edge for the species, the trees showed high resilience in response to drought. Yet, there was a divergent response to a changing climate along very short climatic gradients. The oaks were more sensitive to sensitive to water availability expressed at the most xeric sites whereas they exhibited positive growth trends only in the coldest and more humid stands. These results suggest that stand dynamics (i.e. not only adult performance but also regeneration) particularly at the lowest elevations (i.e. the altitudinal rear-edge) need to be monitored under future expected drier and warmer climatic scenarios bearing in mind that management legacies likely play a key role in current stand dynamics.

# Introduction

Intense drought is one of the most frequent and widespread climatic extremes affecting ecological systems worldwideis considered a key feature of the Mediterranean climate ((Dai 2011, Lionello 2012). There has been an increase in the frequency and severity of drought events in the last decades, along with a trend towards drier summers particularly for southern Europe (Vicente-Serrano et al. 2014b, Stagge et al. 2017). This is especially critical, since the climate change projections for the Mediterranean area forecast that climate extreme events, like droughts, will become more frequent and severe (IPCC 2013, Spinoni et al. 2017).

Drought causes significant changes in ecosystem productivity and water dynamics that can severely affect forests through changes in plant physiology, phenology and carbon allocation. The assessment of the drought impacts on ecosystems has gained attention in the last decades (Allen et al. 2010, Clark et al. 2016), and the functional response of vegetation to drought has been analyzed at global (*e.g.*, Vicente-Serrano et al. 2013, Norman et al. 2016) and at local scales (see Martínez-Vilalta and Lloret 2016 for a revision).

Ecosystem responses to drought are influenced by other drivers of environmental changes (Oliver and Morecroft 2014, Peñuelas et al. 2017) In a global-change context, the impacts of drought on vegetation need to be evaluated considering the interactions with other drivers of change (Doblas-Miranda et al. 2017). This is especially relevant for areas with a long history of landscape modification, such us the Mediterranean region, where land-use change play a significant role in current ecosystem ecology (Navarro-González et al. 2013), considering also that the interactions of these two factors, namely drought and land-use change, are crucial for Mediterranean forests (Doblas-Miranda et al. 2017).

The impacts of drought are also especially relevant for populations located in the rear edge (either latitudinal or altitudinal along climatic gradients) of their distribution, where climatic conditions often corresponds to the species-limits and the populations are likely to be more sensitive to small variations on climate (Hampe and Petit 2005). The response of rear-edge populations to variations on climate could be useful to estimate the adaptation of the species to predicted climatic changes (Jump et al. 2010). It becomes even more important for relict populations driven by historical land-uses, which can harbour high levels of intraspecific genetic diversity (Valbuena-Carabaña et al. 2010a).

Many studies have analyzed the effects of drought effects on Mediterranean tree species representing the southernmost limit of their distribution (*e.g.*, Sánchez-Salguero et al. 2012, Dorado-Liñán et al. 2017b, Caminero et al. 2018). Some of these studies focused on the resilience to drought of rear-edge populations (*e.g.*, Herrero and Zamora 2014). Resilience is the capacity of an ecosystem, community or individual to recover pre-disturbance structure and function after a disturbance (Holling 1973). The assessment of resilience to climate disturbances like droughts provides critical information about the capacity of the forests to maintain their structure and to continue providing valuable ecosystem services. This is particularly relevant for populations located in the rear-edge of their current distribution, especially when they are located in Mediterranean mountains.

The resilience to drought of species is better assessed when several approaches like remote sensing and dendroecology are combined simultaneously. Dendroecological estimates of growth (*i.e.* tree-ring width) are a widely used proxy to study tree vitality and the analysis of annual-tree ring widths can be used to study changes in growth as response to drought at the individiual tree-scale (Fritts 1976, Dobbertin 2005). The combination of both approaches (remote sensing and dendroecology) has been used to assess the effects of droughts on vegetation along ecological or elevational gradients (*e.g.*, Dorman et al. 2013, Vicente-Serrano et al. 2013, Coulthard et al. 2017), and also for the analysis of growth resilience to drought on several tree species (Gazol et al. 2018)- Remote sensing can be used for studying droughts impacts on ecosystems (*e.g.*, Michel Deshayes et al. 2006, Zhang et al. 2013, AghaKouchak et al. 2015, McDowell et al. 2015, Norman et al. 2016). Vegetation indices obtained from satellite, such us EVI (Enhanced Vegetation Index) are used as a proxy for assessing vegetation functioning and aboveground net primary production (Huete et al. 2002), and changes in the patterns of these indices are considered as an indicator of the forest response to external environmental factors, such us droughts (*e.g.* Vicente-Serrano et al. 2013, Vicca et al. 2016). Drought impacts on vegetation using remote sensing have been analyzed at different scales. For instance, a global-scale study showed a stronger influence of drought for drier biomes (Vicente-Serrano et al. 2013) whereas for Mediterranean area, studies at regional and local scales found a large spatial and seasonal variability of the effects of drought on vegetation (Vicente-Serrano 2007, Gouveia et al. 2017).

In this work we used remote sensing information and dendroecological methods to evaluate the drought impacts in both canopy greenness (as a proxy to primary growth) and tree-radial growth of a Mediterranean tree species (*Quercus pyrenaica* Willd.) on Southern relict forests at tge rear-edge of the species distribution and where species performance is considered to be threatened by climate change. We also assessed the resilience of these forests both to several extreme drought episodes and to climate change in the long-term in the last decades. Our main hypothesis is that these relict populations driven by historical land-use at their present climatic (either altitudinal or latitudinal) rear-edge are particularly vulnerable to climate change, and hence they will show lower-values of resilience after several extreme droughts only at the dry edge of climatic gradients. To address this hypothesis our specifics aims were: (*i*) To quantify how two recent extreme drought events influenced primary and secondary growth of *Q. pyrenaica* forests in their rear edge; (*ii*) to analyze the long-term resilience of these forests to extreme drought events using time-series of radial growth; (*iii*) and to explore differences in the resilience metrics between populations located in contrasting ecological conditions within the rear edge of the distribution of this species to detect vulnerability to climate change along climatic gradients. To achieve goal (iii) within the region of study we assessed whether the effect of aspect and microclimatic conditions expressed in northern and southern populations of Pyrenean oak forests differ in their resistance, resilience and recovery to extreme drought events.

# Materials and methods

## Tree species and study site

Pyrenean oak (*Quercus pyrenaica* Willd.) forests extend through south-western France and the Iberian Peninsula reaching its southern limit in mountains areas of northern Morocco (Franco 1990). In the Iberian Peninsula these forests live on siliceous soils, or soils poor in basic ions under meso-supramediterranean and mesotemperate areas and subhumid, humid and hyperhumid ombroclimate (Rivas-Martínez et al. 2002). *Q. pyrenaica* requires over 650 mm of annual precipitation and a summer minimal precipitation between 100 and 200 mm (Martínez-Parras and Molero-Mesa 1982). Summer rainfall is a key factor for the species, which is considered to have low drought tolerance compared to genuine evergreen Mediterranean taxa (Gavilán et al. 2007, Río et al. 2007).

The forests of this species reaches one of their southernmost European limit in Sierra Nevada, a high-mountain range located in southern Spain (37°N, 3°W) with elevations between 860 m and 3482 m *a.s.l.*. The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought (July-August). There are eight Pyrenean oak patches (2400 Has) identified in this mountain range (Figure 1), ranging between 1100 and 2000 m *a.s.l.* and often associated to major river valleys. Sierra Nevada mountain is considered a glacial refugia for deciduous *Quercus* species (Brewer et al. 2002, Olalde et al. 2002, Rodríguez-Sánchez et al. 2010). In this mountain region, *Q.* *pyrenaica* woodlands represent a rear edge of their habitat distribution, which is important for determining habitat responses to expected climate change (Hampe and Petit 2005). They are considered relictic forests (Melendo and Valle 2000, Vivero et al. 2000), and the richest vascular-plant forest formation of Sierra Nevada (Pérez-Luque et al. 2014), sheltering several endemic and endangered plant species (Blanca et al. 1998, Lorite et al. 2008). These forests have undergone very intensive anthropic use in history (Camacho-Olmedo et al. 2002, Valbuena-Carabaña et al. 2010a, Valbuena-Carabaña and Gil 2017). Furthermore, conservation status of this species for southern Spain is considered “Vulnerable” (Vivero et al. 2000) and they are expected to suffer the impact of climate change, reducting its suitable habitats in the rear-edge due to their greater hydric requirements compared to other more drought-tolerant genuine Mediterranean evergreen oak and pine species (Gea-Izquierdo et al. 2013).

## Drought episodes

During the second half of the twentieth century the Iberian Peninsula suffered several extreme drought episodes (*e.g*. 1994-1995, 1999, 2005, 2012) (Vicente-Serrano et al. 2014b, Guerreiro et al. 2017).The 2005 and 2012 drought events have been documented among the worst droughts in the last decades for the southern Iberian Peninsula (García-Herrera et al. 2007, Trigo et al. 2013, Gouveia et al. 2017, Guerreiro et al. 2017, Páscoa et al. 2017) and they were characterized as extreme drought in our climatic data (Figures S1-S2; Table S3). We focused on these two drought events because they were included in the period where there is availability of high-spatial resolution remote sensing information (MODIS started on 2000; see below). Nevertheless, for radial growth-time series, a greater number of older drought events were also analyzed to contextualize results obtained in 2005 and 2012 drought events and analyze forest resilience to drought in a longer term (see Table S3). The identification of a drought event were done using the Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010) following similar procedure as proposed by Spinoni et al. (2017b). We used SPEI-12 months scale for all 0.5º grid cells covering Sierra Nevada obtained from Global SPEI Database (<http://spei.csic.es/database.html>). A severe drought event starts in the month when SPEI falls below the threshold of -1.28 (Páscoa et al. 2017, Spinoni et al. 2017b). A drought event is considered only when SPEI values are below the threshold for at least two consecutive months (*e.g.* Spinoni et al. 2017b). Several indicators were computed for each drought event: ***duration*** as the number of consecutive months with the SPEI lower than a certain threshold; ***severity*** of a drought event is the sum of the SPEI values (absolute values) during the duration of the drought event; the ***intensity*** and the ***Lowest SPEI*** refer to the mean and lowest value of SPEI respectively during the drought event duration.

## Greenness data

Vegetation indices derived from remote sensing information have been widely used to derive descriptors of ecosystem functioning because they are linked with primary productivity (*e.g* Alcaraz-Segura et al. 2009) .Here, vegetation greenness of *Q. pyrenaica* was characterized by means of the *Enhanced Vegetation Index* (EVI), derived from MOD13Q1 product of the *Moderate Resolution Imaging Spectroradiometer* (MODIS) sensor (Didan 2015). MODIS EVI Data (Collection 6) were obtanied using Google Earth Engine platform for the period 2000 - 2016. EVI data consits of 16-day maximum value composite images (23 per year) of the EVI value with a spatial resolution of 250 m x 250 m. We selected the pixels covering the distribution of *Q. pyrenaica* forests in Sierra Nevada (*n* = 928 pixels). Then, a data filtering was applied to select EVI valid values. For this purpose, complementary information accompanying the EVI data was used (VI Usefulness Indices and quality flags). Values affected by high content of aerosols, clouds, snow and shadows, were filtered out following recommendations for mountain regions (Reyes-Díez et al. 2015).

As a surrogate of mean annual primary production, annual mean EVI () value was computed for each pixel for the period 2000 - 2016. To explore the effect of drought on greenness, the EVI standardized anomaly () was computed pixel-by-pixel, since it minimizes biases in the evaluation of anomalies, providing more information about the magnitude of the anomalies (Samanta et al. 2012, Gao et al. 2016). For each pixel, an annual EVI value was obtained by averaging EVI valid values. Then, the standardized anomaly was computed as:

where is the EVI standardized anomaly for year ; the annual mean value of EVI for year ; the average of the annual EVI values for the period of reference 2000-2016 (all except year); and the standard deviation for the reference period. Each pixel was categorized according the EVI standardized anomalies as “greening” (EVI standardized anomalies greater than + 1), “browning” (EVI standardized anomalies less than - 1) or “no changes” (EVI standardized anomalies between − 1 and + 1) (Samanta et al. 2012).

Rather than other vegetation indices like the NDVI, was chosen since it is highly stable under the use of any filter (Reyes-Díez et al. 2015) and because it showed high significant correlations with annual ( = 0.81) and seasonal EVI values ( = 0.76 and = 0.88). For exploratory purposes, temporal trends of were explored at a pixel scale. The nonparametric Mann–Kendall test (Kendall, 1975; Mann, 1945) was applied using the trend package in R (Pohlert 2017). The alpha level for the test was set to 0.05.

## Field sampling and dendrochronological methods

Tree sampling was carried out during autumn 2016. Trees were sampled at two locations in contrasting N-S slopes of Sierra Nevada: San Juan (SJ), a xeric site located at northern aspect; and Cáñar (CA), a humid but warmer site located at the southern aspect (Figure 1; Table 1). For the southern site two elevations were sampled: CA-Low and CA-High, which constitutes the current altitudinal rear-edge (CA-low) and tree-line (CA-High), respectivley in the sampled slope. All the sites were oak monospecific and representatives of the population clusters identified for the species in this mountain range (Pérez-Luque et al. 2015a). In each site between 15 and 20 trees from either the single dominant-codominant layer (CA) or the open canopy (SJ) were randomly selected. Two cores of 5 mm of diameter were taken from each tree at breast heigth (1.3 m) using an increment borer. Diameter at breast height (DBH) and total height were measured from each tree. In addition stand competition of target trees was assessed by recording distance, azimuth, DBH, species and total height of all neighboring living trees with DBH > 7.5 cm within a circular plot of 10 m radius. Several competition indices were calculated: the distance independent indices *density* (), and *basal area* (BA, ); and the distance dependent index size ratio proportional to distance (*srd*) as . Then, non-parametric Kruskal-Wallis rank sum tests (Sokal and Rohlf 1995) were used to analyse differences between sites for height, DBH and competition indices. When significant differences were observed, we run multiple comparisons using the Dunn’s-test with Bonferroni adjustment to correct significance values using the PMCMR package in R (Pohlert 2014).

Tree cores were air dried, glued onto wooden mounts and sanded. Annual radial growth (ring width, RW) was measured with a LINTAB measuring device (Rinntech, Heidelberg, Germany) coupled to a stereomicroscope, with an accuracy of 0.001 mm. Individual ring series were first visually and statistically cross-dated with TSAP software (Rinntech, Heidelberg, Germany), using the statistics Gleichläufigkeit (GLK), t-value and the crossdating index (CDI). Cross-dating validation was finally done using COFECHA software (Holmes 1983).

The growth trends were analyzed at different time scales. To study the response of growth to the inter-annual variability of climate (short-term response), pre-whitened residual chronologies (RWI) were used. They were calculated from ratios between raw growth measurements and individual cubic splines with a 50 % frequency cutoff at 30 years (Fritts 1976). Tree-ring width series were standardized and detrended using dplR (Bunn 2010). Mean residual site chronologies were obtained computing the biweight robust mean of all prewhitened growth indices for the trees of the same site (Cook and Kairukstis 1990). The statistical quality of each chronology was checked via the expressed population signal. A threshold value of EPS > 0.85 was used to determine the cutoff year of the time span that could be considered reliable (Wigley et al. 1984).

The long-term growth response was analyzed using basal area increment (hereafter BAI, ). Theoretically, BAI represents a more accurate indicator of growth than ring-width, since it removes variation in growth attributable to increasing stem circumference after 30-40 years of juvenile increasing growth (Biondi and Qeadan 2008). Raw ring-widths and measured DBH were used to compute BAI by subtracting twice the annual ring width from the annual diameter, starting from the measured diameter outside the bark (Piovesan et al. 2008). We used the following equation:

where is the radius of the tree and is the year of tree-ring formation. For each individual tree, a mean BAI serie was calculated. Then, mean site BAI chronologies were obtained by averaging individual tree BAI time series.

Both RWI and BAI chronologies were compared to different climatic indices to analyse the low and the high-frequency response to climate of trees. Statistical descriptive parameters, including the mean, standard deviation, first-order autocorrelation of raw series, the mean sensitivity (a measure of the year-to-year variability) and the mean correlation between individual series of residual ring-width indices, were also calculated for each site chronology (Fritts 1976).

### Climate and growth

Climate data were obtained from the European Daily High-Resolution Observational Gridded Dataset (E-OBS v16) (Haylock et al. 2008). Monthly precipitation and minimum and maximum temperatures were obtained at a 0.25 x 0.25 º resolution for the 1950-2016 period. We selected grid cells covering each sampled sites. Data were downloaded and preprocessed using the climate4R bundle (<http://www.meteo.unican.es/en/climate4R>) (Frías et al. 2018). The Standardized Precipitation-Evapotranspiration Index (SPEI), a multiscalar drought index that incorporates both precipitation and temperature (Vicente-Serrano et al. 2010, Beguería et al. 2014), was also used to characterize the drought conditions for the period 1961-2014. SPEI values with a temporal scale of 6 months and a spatial resolution of 1.1 km, were obtanied from the Drought indices dataset (<http://monitordesequia.csic.es/>), a high resolution database of drought indices for Spain (Vicente-Serrano et al. 2017b).

Relationships between residual site chronologies and climatic variables were assessed ussing bootstrapped Pearson’s correlations estimated using the treeclim package (Zang and Biondi 2015) with a significance of p < 0.05.

### Disturbance analyses

Disturbance chronologies were built using tree-ring width to identify abrupt and sustained increases (release events from competition) or decreases (supressions) in radial growth (Nowacki and Abrams 1997) as indirect estimates of possible disturbance events (e.g. logging, neighbor mortality) in the past. By using a temporal window of reasonable length this method is intended to filter out the response to short-term changes in temperature and precipitation and minimizes the long-term growth trends (Nowacki and Abrams 1997). Growth changes (GC) were calculated for the individual tree-ring series using a 10-year running window as either positive (PGC) or negative (NGC) growth changes:

where is preceding 10-year median and is subsequent 10-year median. Medians were used since they are more robust estimator of central tendency than means (Rubino and McCarthy 2004, Camarero et al. 2011). Site disturbance chronologies were constructed by averaging the individual disturbances series annually. To separate growth peaks produced by disturbance events and expressing stand-wise disturbances from those by climate, we considered a threshold of 50 % of GC and more than 50% of the individual trees displaying the same growth changes was considered a stand-wise disturbance.

In addition, the forest history of San Juan and Cáñar sites was inferred from a detailed analysis of historical land-use changes. For this purpose, an exhaustive review of historical documents was done to compile information about socio-economical activities affecting forest: land-uses, forest managment actions, mining, wildfires, etc. Several documentary sources were reviewed: historical documents and maps (*e.g.* Catastro 1752, Titos 1990); detailed mining reports (*e.g.* Maestre 1858); official information about recent wildfires events (Regional Ministry for the Environment of the Government of Andalusia) and forest management practices (Bonet et al. 2016); livestock farming (*e.g.* Moreno-Llorca et al. 2014); traditional irrigation ditches (Martín-Montañés et al. 2015, Ruiz-Ruiz 2017) and other studies reviewing the socioeconomic dynamics of forest of Sierra Nevada at different scales (Bonet et al. 2014, Jiménez-Olivencia et al. 2015, Moreno-LLorca et al. 2016).

## Assessing ecosystem and tree individual resilience to drought

To evaluate the effects of drougth events on ecosystem resilience (using greeennes data) and tree individual resilience (using BAI growth data) we used resilience indices proposed by Lloret et al. (2011): resilience (*Rs*), resistance (*Rt*), and recovery (*Rc*). The resistance index (*Rt*) quantifies the severity of the impact of the disturbance in the year it occurred. It is estimated as the ratio between the performance during and before the disturbance (drought) event: Resistance (*Rt*) = Drought / Predrought. The Recovery index (*Rc*) is the ability to recover from disturbance relative to its severity, and it is estimated as the ratio between performance after and during disturbance:Recovery (*Rc*) = Postdrought / Drought. The Resilience index (*Rs*) is the capacity to reach pre-disturbance performance levels, and it is estimated as the ratio between the performance after and before disturbance: Resilience (*Rs*) = Postdrought / Predrought.

The values of these indices were computed for tree growth (BAI) and greenness (EVI mean) during each drought event. 2005 and 2012 were considered as single drought events. The predrought and postdrought values of each target variable (*i.e.* BAI or EVI) were computed as the mean value during a period of three years before and after the drought event respectively. A period of three years was chosen because we found similar results comparing periods of two, three and four years (Figure S6) and this length was used in other studies (*e.g.* Gazol et al. 2017). To put in context in a longer-term the resilience observed for 2005 and 2012 drought events, as well as to test whether the resilience indices were ecologically meaningful, resilience metrics for BAI data were additionally computed for the most severe drought events since 1950 and compared them with drought severity (Figure 6, Table S3).

## Statistical analysis

For each of the three resilience indices studied, robust two-way ANOVAs were used to test for differences between drought events (2005 and 2012) and the two studied oak populations (northern and southern aspects). These tests were used because original and log-transformed data did not follow the assumptions of normality and homogeneity of variance (Wilcox 2012). Robust measures of central tendency (M-estimator based on Huber’s Psi) were used since they were close to the mean value in all cases (Wilcox 2012). When running the robust ANOVA test, data were boostrapped 3000 times and trimmed automatically to control the potential influence of outliers (Field et al. 2012, Wilcox 2012). Post-hoc differences were assessed pairwise using a similar boostrap test. All the robust ANOVA and post-hoc tests were carried out using the WRS2 (Mair et al. 2017) and rcompanion (Mangiafico 2017) R packages. The level of significance was set to 0.05 and adjusted for multiple comparisons. All analyses were carried out in R software (R Core Team 2017).

# Results

## Time trends in vegetation greenness

The analysis of greenness time trends showed that EVI in 78.9 % of the pixels of *Quercus pyrenaica* forests experienced a positive trend for the 2000-2016 period. The lowest values of EVI standardized anomalies for the studied period were recorded during the 2005 drought,, and the minimum EVI values were expressed in northern (dry) populations (Figure 2). In fact, a “browning” episode () was observed for *Q. pyrenaica* forests during this drought event, whereas no changes in greenness were observed in response to the 2012 drought (Figure 3).

## Analysis of radial growth trends and disturbances

The trees of the southern population were older than those from the northern one. In addition trees from the Southern population at high altitude were taller and their growth was significantly faster than that of trees from the other two sites (Tables 1, Figure 4). Both growth and height of trees from the northern and the low-elevation southern population were similar (Figures 4 and S6). Competition was similar among all sites. Yet plot basal area was greatest in CA-High (Table 1) despite the highest individual BAI growth at that site (Figure 4). Only trees from the southern sites showed significant positive growth trends since the late 1970s (Figure 4), being more pronunced for the highest site (CA-High).,

Drought events produced reduction of RWI for all sites (Figure S3), being particularly evident the negative effect of the 1995 drought, when the greatest reduction of tree-growth were recorded for all chronologies. Southern sites (CA-High and CA-Low) showed weaker reductions than the northern site (SJ), especially for 2005 and 2012 (Figure S3). Trees from northern site also suffered a great reduction during the 1945-1946 drought event (Figure….).

The analysis of growth changes revealed differences between sites (Figures 5 and S4). The Northern site (SJ) showed two major release events (GC > 50 % occurring in more than 50 % of sampled trees): the first during the 1940 decade (the most evident) and the second in the period 1995-2000. These periods alternate with periods of suppression for over 40 years. The two Southern sites showed no release events except for CA-High at the beginning of the 1830s and no suppression events in the last 50 years.

## Resilience to drought events at the stand and individual tree levels

The strength of the response of the resilience indices was related to drought severity. The exploration of resilience metrics of tree-growth for all severe droughts in our climatic data (1900 - 2017) (Table S3), revealed a positive relation between resilience (*Rs*) and drought severity ( = 0.336, p = 0.048) (Figure 6). A similar pattern was found for recovery (*Rc*; = 0.438, p = 0.019) but negative for resistance (*Rt*, = 0.155, p = 0.205). Trees showed the highest value of tree-growth resilience for the worst drought event in our study area (1995, see Table S3).

During the last two drought events, resilience metrics for greenness and tree-growth were significantly different bewteen drought events (Table 3). The 2005 drought event reduced greennes and growth more than that of 2012 (Tables S1 and S2) but the two metrics of resilience generally covaried in the same direction???. We obtained significantly higher Resilience (*Rs*) and Resistance (*Rt*) values for the 2012, the most severe event, than for 2005 in both variables (Tables S1-S2; Figure 7). Recovery (*Rc*) showed contrasting pattern for EVI and tree-growth. Recovery values for greenness was higher for 2005 than for 2012 drought event (Table S1, Figure 7).

Resilience metrics significantly varied between sites, except for Resilience (*Rs*) of tree-growth (p = 0.534; Table 3). The two Southern populations showed lower values for Recovery (*Rc*) than the northern site both for greenness and tree-growth (Tables S1 and S2). In contrast, Resistance and Resilience values were significantly higher for southern sites than for northern ones (Tables S1 and S2).

## Tree-growth response to climate

Tree-growth exhibited a significant greater response to water availability than to temperatures, as it can be expected for a Mediterranean site and a species located closer to its xeric/dry distribution limit (rear-edge). Cumulative precipitation of the hydrological year was the climatic variable with the highest relationship with growth and influenced similarly and positively the tree-growth for both northern and southern populations (Figure 8a). Precipitation of previous december was also positively correlated with tree growth in the northern population and in the highest location of the southern population. Hydrological, Spring and Summer SPEI showed a strong positive correlation with tree-growth (Figure 8a), being this relationship higher in the northern population (r > 0.6 vs. r<0.45??). Relationships with temperatures were lower than those with moisture variables. Yet there were differences between northern and southern populations: spring maximum temperature was the most significant limitation for the tree-growth of the southern population at both elevations while no significant limitations were recorded for northen site regarding the temperatures (Figure 8b and 8c). Remarkably minimum and maximum temperatures of current September positively influenced the tree-growth only in the northern population. No positive relationship with temperature was found for southern trees.

# Discussion

## Rear-edge oaks show high resilience in response both to recent drought events and long-term climatic variability.

Severe drought events negatively affected to primary and secondary growth of *Q. pyrenaica* forests in the rear edge of their distribution. Our findings show that 2005 and 2012 drought events, provoked reductions in greenness and tree-growth of these forests. These results are consistent with previous studies that reported significant reductions of tree-growth for this oak species during extreme drought events (Corcuera et al. 2006, Gea-Izquierdo and Cañellas 2014). In fact, when we explore the effects of drought at a longer-term scale, we observed the greatest reduction of tree-growth during the 1995 drought, a characteristic pointer-year that caused severe and extensive damage to the Mediterranean vegetation across the Iberian Peninsula (Peñuelas et al. 2001, Gazol et al. 2018).

Although the south of Iberian Peninsula suffered severe drought events in the last decades (*e.g* 2005 and 2012 were considered two of the worst recorded drought; García-Herrera et al. 2007, Trigo et al. 2013, Vicente-Serrano et al. 2014b) (Table S3), we found a positive trend for vegetation greenness of *Q. pyrenaica* (78.9 % of the pixels showed a positive trend during the 2000 to 2016 period). This confirms previous findings that pointed out an increase in primary productivity for these forests (Pérez-Luque et al. 2015b), being the most productive ecosystems in this mountain region during that period (Alcaraz-Segura et al. 2016). For tree-growth, we also observed positive trends in the last decades, particularly for the southern high-elevation site (CA-High, Figure 4). Similar long-term trends were described for this species along its distribution range (Gea-Izquierdo and Cañellas 2014) and could be related to the rising of the temperatures in the last decades (Gea-Izquierdo and Cañellas 2014) particularly after 1970 (Vicente-Serrano et al. 2017a). Howewer, the observed pattern for our sites (a rear-edge) differs from the decline trends observed for several Mediterranean and temperate tree-species located in their rear-edges (*e.g.*, *Pinus nigra*; *P. sylvestris*; Sánchez-Salguero et al. 2012, Camarero et al. 2015b, *Fagus sylvatica*; Dorado-Liñán et al. 2017a).

Resilience (*Rs*) values observed in our study sites for the latest drought events in both tree-growth and greenness were close to 1, except for the tree-growth during 2005 event (Tables S1 and S2). Despite the 2012 drought event was more severe and intense than 2005, according with our analysis with SPEI data (Table S3), resilience values for greenness and tree-growth were greater for 2012 than for 2005. These results could be explained by the different timing of the two droughts, *i.e.* the 2012 drought was a winter drought (Trigo et al. 2013) that occurred earlier than the 2005 drought. The latter lasted less than 2012 drought, but matched the period of maximum growth for *Q. pyrenaica* forests (Pérez-de-Lis et al. 2017) (Figure S7). Our results are in line with recently studies that indicate the timing of the drought as a key factor determining tree recovery after drought (Huang et al. 2018), that also has been observed for other Mediterranean oak species (*e.g.* Holm oak; Camarero et al. 2015a).

As we mentioned previously, we found strong declines of tree-growth during the most severe drought events occurred (1995 and 1999) (Table S3; Figure S3), matching similar declining patterns observed for other species in their rear edge (Sánchez-Salguero et al. 2012, Camarero et al. 2015b). But, interestingly, we obtained the highest values of resilience for tree-growth for these two drought events (Figure 6). In addition, the analysis from a long-term perspective of the severe droughts suggests a positive relation between the tree-growth resilience and drought severity (Figures 6). Surprisingly this result seems contradict our initial hypothesis in which we predict low resilience values for this oak species in their rear-edge after extreme drought events.

Rear-edge populations live in environmental narrow margins, and small variations in environmental conditions can increase the vulnerability of the species (Hampe and Petit 2005). A high vulnerability to drought is often assumed for populatios located at their rear-edge (Martínez-Vilalta 2018). However we obtained positive trends in greenness and tree-growth for the rear-edge of *Q. pyrenaica* and high values of resilience to severe droughts were also reported. Our findings are in agreenment with those studies that have shown that the assumed higher vulnerability of dry edges does not necesarily hold (Cavin and Jump 2017). Martínez-Vilalta (2018) pointed out the importance of the local adaptation and plasticity, and also of the local environmental factors on the vulnerability showed by rear-edge populations. The high values of resilience to drought reported here together with previously works showing high values of genetic resilience for those forests at Sierra Nevada, seem to be indicative of high local adaptation of this oak to this mountain range. In addition the local environmental conditions of the sites where this species inhabit at Sierra Nevada would explain the low vulnerability to drought showed by this oak. Algunos autores han apuntando que cuando se estudian poblaciones del rear-edge, hay que poner atención a la forma en la que se define la marginalidad, esto es, si se define atendiendo a criterios geográficos, climáticos, o según otros factores ecológicos (Martínez-Vilalta 2018). En este sentido, los altos valores de resiliencia a los eventos de sequía que hemos observado, podrían sugerir que las poblaciones de *Q. pyrenaica* en Sierra Nevada están situados en un rear-edge geográfico, pero no climático.

A remarkably result is the higher values of resilience for tree-growth obtained during the worst and more severe drought events in our study area (1995 and 1999) (Table S3; Figure 6). A plausible explanation could be the water availability previously and after the drought event. For instance, cumulative precipitation of the 1992-1994 years (pre-1995 drought) had precipitation values below the mean of the whole period (Figure S1), while 1996-1998 years (post-1995 drought) showed a wet opposite pattern. In fact, the first months of 1996 recorded the highest cumulative rainfall of the past century for our southern site (Cáñar) (Mesa-Torres 2009). This could explain the higher values of recovery found for 1995 (Figure 6).

Greenness and tree-growth of *Q. pyrenaica* showed different sensitivity to severe droughts. During the last drought events EVI was reduced to 90.25 % (Table 1), whereas BAI was reduced to 70.83 % (Table S2), suggesting a lower sensitivity of the greenness than tree-growth to drought, particularly for sites under drier climate. For our driest site (SJ, the northern one), BAI were reduced to 44.5 % respect to that of the preceding period during 2005 drought event, whereas the EVI was reduced to 81.9 % (Tables S1 and S2). These findings are in accordance with previously works which showed that tree-growth are more sensitive metrics of forest resilience than net primary productivty (*e.g.* Babst et al. 2013, Coulthard et al. 2017, Gazol et al. 2018). Besides the different scales of both approaches, *i.e.* tree-based *versus* pixel-based; the growth reduction seems to be more mediated by sink that by source limitations (Gazol et al. 2018). Response of greenness to drought not only reflects response of tree, because remote sensing indices (EVI) captures signals from all vegetation covered by the pixel (not only tree but also understory vegetation) (see Dionisio et al. 2012). On the other hand, tree-ring width data provide an accurate measure of growth responses to droughts (Bhuyan et al. 2017, Gazol et al. 2018).

## Microenvironment shapes differential sensitivity to climate and drought of rear-edge oaks

Our results showed differences for greenness and tree-growth between northern and southern oak populations (Table 3). The former, which have drier conditions (Table 1), were more impacted by the drought events than the latter. For instance, the northern site showed more negative EVI standardized anomalies (higher browning intensity) than the southern sites during the 2005 drought event (Figure 2). In addition, the stronger correlations of tree-growth with SPEI (Hydrological and summer) observed for northern site (Figure 8), can be interpreted as higher sensitivity to drought of a drier site (Gea-Izquierdo and Cañellas 2014).

Moisture availability has been reported as the most limiting factor driving radial growth of *Q. pyrenaica* along their distribution range in Iberian Peninsula (Gea-Izquierdo and Cañellas 2014). We found a singnificant positive relation between precipitacion (hydrological year and previous December) and tree-growth (Figure 8a). Our results are consistent with previous studies highlighting the influence of precipitation on tree-ring growth in oaks (e.g. Gea-Izquierdo and Cañellas 2014, González-González et al. 2014, García-González and Souto-Herrero 2017)

A striking result is the difference for tree growth between sites (Figure 4). The trees of CA-High site, which are located around 1900 m. *a.s.l.* and representing the upper limit of the treeline of the species in this southernmost location (Pérez-Luque 2011), showed higher BAI than those located at low-elevations sites (CA-Low and SJ) (Figure 4). This is especially interesting for southern sites, which are very close to each other. Our findings are in line with previous works that pointed out that tree growth and tree responses to drought are site-dependent (e.g. soil features, tree competence, etc.) (e.g. Babst et al. 2013, Vicente-Serrano et al. 2014a), particularly for rear-edge populations (Cavin and Jump 2017, Dorado-Liñán et al. 2017b).

When we explored the chracteristics of the southern sites, we firstly observed a difference in elevation. Bhuyan et al. (2017), in a recent work across the European continent, found a clearly effect of elevation on the resistance to drought of several tree-species, where stands located at higher elevations were less drought sensitive. The higher values of tree growth that we observed in CA-High site could be related with lower water stress at high-elevation sites, since moisture availability is a key factor limiting tree growth for *Q. pyrenaica* (Gea-Izquierdo and Cañellas 2014). Soil analyses along an elevational gradient in this location revealed higher content of available water for forest soils located on high elevation (Cobo-Díaz et al. 2017). In this sense, a remarkable observation is the presence of traditional irrigation ditches which could provide an additional water supply. In most of the high-mountain watersheds of Sierra Nevada, there are systems of historical irrigation channels, know as *acequias de careo*, that was used since Middle Age to cultivated these valleys (Martín-Civantos 2014, Martín-Civantos and Bonet-García 2016). These ditches run through the hillsides of valleys releasing water through several points that filtrate the water to recharge the aquifer and then irrigates the foot of the slopes (Martín-Civantos 2014, Jódar et al. 2017). Several works have recently described the network of traditional ditches for our southern sites (Cáñar), with detailed information about water use (Ruiz-Ruiz 2017) and its hydrological functioning (Martín-Montañés et al. 2015). There is a ditch (*Acequia de la Era Alta*) located uphill the CA-High site, which functions from March to June (Ruiz-Ruiz 2017). It brings water from snowmelt and from a nearby stream, soaking the *Q. pyrenaica* forests. This traditional system could supply an extra of water that could be used by the trees located downstream of these channels. This extra of water is particularly important for trees of this dry-rear edge and could explain the higher values of BAI for trees located in CA-High site.

In addition to the lower water stress, it is likely that the sites at higher elevation had a lower anthropic impact and the abandonment of traditional uses was earlier, due to their farthest location from human settlements and therefore less access to forest resources.

## Land-use legacies shape distribution and sensitivity to climate change at the read-edge

The Mediterranean mountains, even at high elevations, have suffered strongly transformation of the landscapes driven by human activities throughout history (Regato and Salman 2008). Multiple evidence from palaeoecological studies indicated an intense human impact on vegetation of Sierra Nevada since 3000 cal year BP (Anderson et al. 2011, Jiménez-Moreno et al. 2013, García-Alix et al. 2017, Mesa-Fernández et al. 2018). From that moment onwards, increases on fire occurrence and both grazing and mining activities, were recorded for this mountain region, with an sharp intensification of the human activities in the last 150 years (García-Alix et al. 2017, Mesa-Fernández et al. 2018). Mining, forest clearings, fuelwood and charcoal exploitations, pastoralism and also wars, have strongly impacted on the forest resources in Sierra Nevada. As a consequence of all those activities a loss of about 90% of broadleaf *Quercus* species cover from medium and low elevation occurred in this mountain region (Jiménez Olivencia 2015).

Our study sites have been subjected to an intense exploitation of forest resources in history and landscape transformation. Although the estimated age for our sampled trees was not more than 180 years (Tables 1, 2), several documents reported the presence of oaks before that date. For instance, the inventories of trees made by the Spanish Navy during the second half of 18th century for Cáñar site more than two million trees were reported, most of them juveniles, suggesting recent wood fellings and similar features for SJ (Cruz 1991). These numbers are a reflect of the intense exploitation of the forest resources occurring up to the end of nineteenth century (Valbuena-Carabaña et al. 2010b, Calatrava and Sayadi 2019) and also concur with the regeneration peaks observed for many Iberian oak woodlands (e.g. Gea-Izquierdo and Cañellas 2014, Gea-Izquierdo et al. 2015, Dorado-Liñán et al. 2017a).

We found similar tree competence levels in our sampled sites (Table 1), but differences in tree size and age suggest different management origin (*i.e.* land-use legacy). The review of historical documents revealed that our study sites had different land-use trajectories driven mainly by the differential pattern of the natural resource use (Martín-Civantos 2014, Jiménez-Olivencia et al. 2015). On the one hand, the northern sites (*e.g.* San Juan), show a sequentially distribution of the land uses along the elevational gradient (Zoido and Jiménez Olivencia 2015): grasslands and shrublands for cattle farming are located at high elevations; then forests formation with some croplands; and at lowlands, irrigated terraces with tree crops. Other activities (*e.g.* mining) could also determine the use of natural resources, and therefore the forest structure. For instance, the SJ oak woodland is located in an area with a high concentration of mines and quarries that have been exploited intermittently throughout history (Navarro et al. 2014). Historical documents indicated two periods of intense mining activity: the second half of the 19th century after the publication of detailed mineralogical reports by (Maestre 1858); and during the first decades of the twentieth century until 1960, which is the last year in which there is evidence of the existence of mining activity (Martín Martín et al. 2009). On the other hand, woodland areas of the southern slopes (Cáñar) are mixed with a greater percentage of croplands, even reached high elevation (mainly barley, rye and potatoes) (Calatrava and Sayadi 2019). Forest resources, like firewood, charcoal and acorns, have been continuously exploited in southern sites through history (Jiménez-Serrano and Serrano-Gutiérrez 2004, Valbuena-Carabaña and Gil 2013). In Cáñar site, there were an arraigated tradition of charcoal extraction since fifteenth century (Jiménez-Serrano and Serrano-Gutiérrez 2004) up to middle of the 20th century. From this moment to the present, there were a sharp decrease of the wood extraction, mainly due to rural abandonment (Mesa-Torres 2009, Bonet et al. 2014). Acorn resources have been tradiotionally exploited in this location up to 1950s (Mesa-Torres 2009, Bonet et al. 2014).

Those different patterns of resource uses can help to understand the tree-growth changes recorded in our chronologies (Figure 5). We observed a tree-growth release event at 1940s in the SJ oak woodland (Figures 5, S4) which concurs with one period of maximum mining activity for this area. Several documentary sources indicate an apogee of the mining activity during 1925 to 1957 period, supported by both the improvement of the paths to transport the mineral and by the creation of new railway connections (Titos 1990). During this period there were an increase on the use of timbers for the tunnels of the mines and several furnaces that required great quantities of fuelwood to melt the mineral were active in this area (Titos 1990). This heavily exploitation of the forest resources could affect to a major part of this oak woodland, since percentage of trees affected by GC > 50 % reaches values above 50 % (Figure S4). Our results also coincide with a concurrent but less intense tree-growth release event reported for a closed oak woodland (Gea-Izquierdo and Cañellas 2014). In addition, paleoecological studies carried out in nearby alpine bogs have recorded increases in the heavy metals concentration since the end of 18th century until mid-20th, which coincides with the maximum activity of the mining in this area (García-Alix et al. 2017).

The other release event observed for SJ site during 1995-2000 was lower than the occurred at 1940, but affecting more trees (Figures 5, S4). We revised the forest practices carried out in this area in the last 30 years (Bonet et al. 2016), but we did not find any clearing or cutting event during 1995 - 2000 period. Two non-mutually exclusive ways could explain the tree-growth release observed. Firstly it could be related with a natural drought-induced mortality event after 1995, as was reported for Mediterranean tree species (*e.g.* Peñuelas et al. 2000, Lloret et al. 2004). On the other hand, we obtained strong positive correlations of SPEI with tree-growth for this site (Figure 8), which suggests a high sensitivity to water availability of this slightly more xeric site (Table 1) (Gea-Izquierdo and Cañellas 2014). Previous works reported a sharp decline (or non-production) in latewood production during extreme drought events (Corcuera et al. 2006). Since latewood are less vulnerable to embolism than earlywood vessels (Corcuera et al. 2006), the reduction or even the non-production of former could negatively affect to tree-growth and also enhanced the mortality, particularly for drier sites (Corcuera et al. 2006, Gea-Izquierdo and Cañellas 2014).

The only positive release events showed for CA-High site could be related with conversion from closed forest to an open silvopastoral system, a common management applied in the past (Cañellas et al. 2004, Gea-Izquierdo and Cañellas 2014) documented in this site (Valbuena-Carabaña and Gil 2013, Vila-Traver 2015).

Climatic drivers are key factors determining the growth of tree species, especially at the rear edge of their distribution but in Mediterranean forests we must also considered the management history, *i.e* *land-use legacies* (Navarro-González et al. 2013, Doblas-Miranda et al. 2017, Peñuelas et al. 2017) since, as we inferred from our results, the land-use legacy can conditioned tree-growth and resilience of tree species. Although the abandonment of the traditional activities have provoked a stagnation for this species (Cañellas et al. 2004), we have observed an increase in the growth, especially in the high elevation sites, where the water is less-limiting resource. This pattern concurs with a forest expansion into marginal abandonded croplands and an increase in the tree-cover (Camacho-Olmedo et al. 2002).

# Conclusions

Severe drought events have provoked important reductions in primary and secondary growth of *Q. pyrenaica* forests. However, despite the expected vulnerability for those relict stands, the positive trends for both primary (*i.e.* greenness) and secondary growth (BAI) observed ar our study site and the high resilience values to drought showed at long term scale we observed positive trends in primary growth (since 2000) and secondary growth (since 1970) of *Q. pyrenaica* in Sierra Nevada mountain range but particularly at the most humid site along the climatic gradient analyzed. Surprisingly we observed high values of resilience to drought, particularly at long-term scales. These results are consistent with research showing high genetic resilience values, and overall suggests that this mountain region still acts as a safe refuge for deciduous *Quercus* . The differences observed in tree-growth and resilience to drought between very close sites show that responses to drought were site-dependent. This is particularly relevant for rear-edge populations where topographic and biophysical variablity facilitates the existence of microrefugia, as reflected along the climatic gradient analysed. (Vilà-Cabrera et al. 2019). The analysis of tree-growth dynamics revealed suppression and release events that are consistent with legacies left by land-use in local forest dynamics, as inferred from an exhaustive review of historical documents. In this sense our results highligth the importance of landuse legacies for highly transformed Mediterranean systems.This is relevant for tree species with higher sensitivity to climate change, such us *Q. pyrenaica*, not only for conservation per se of this species, but for all ecosystem services that these singular forests offer at Mediterranean mountain.IFollowing our study it is necessary to disentanble how ecosystem services and stand dynamics are affected by the combination of climate change and land-use legacies in highly transformed landscapes like the one studied here.

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