Relict deciduous oaks show high resilience to drought despite the effect of land-use legacies

AJ Perez-Luque; G. Gea-Izquierdo; …

# 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 estimates of growth and MODIS satellite images as proxies of secondary and primary growth respectively.
* The studied relict populations showed expressions of management, likely reflecting the origin of the current forest structure. 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), despite the ‘a priori’ vulnerability that we were expecting them to express in respone climate change on relict stands resulting from intensive land-use in history at their current rear-edge. Furthermore, the coldest stands show a positive growth trend since the end of the 1970s matching the simultaneous increase in temperature observed.
* Resilience indices showed ecological coherence along a gradient of drought severity in time. In addition, oak 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, they showed high resilience in response to drought. Yet, the high sensitivity to water availability expressed and positive growth trends only in the coldest and more humid stands suggest divergent response to a changing climate along very short climatic gradients and suggest that dynamics (i.e. not only adult performance but also regeneration) of those stands located at the lowest elevations, hence the altitudinal rear-edge, need to be monitored under future expected drier and warmer climatic scenarios and, particularly, if high management pressure remains.

# Introduction

Drought is a natural phenomenon occurring when water availability is significantly below-normal levels (Dai 2011). It is one of the most frequent and widespread climatic extremes affecting ecological systems across every climatic zone worldwide (Mishra and Singh 2010, Dai 2011, Ummenhofer and Meehl 2017). Summer drought is a characteristic feature of the Mediterranean climate (Lionello 2012), but an increase in the frequency and severity of drought events have been recorded for the Mediterranean region (Hoerling et al. 2012), particularly for southern Europe (Vicente-Serrano et al. 2014b, Spinoni et al. 2015, Stagge et al. 2017) where a trend towards drier summers has been reported for at least the last three decades (Spinoni et al. 2017a). Climate change projections suggest that extreme events, like droughts, will become more frequent and severe (IPCC 2013, Trenberth et al. 2014), specially in the Mediterranean area (Spinoni et al. 2017b).

Drought causes significant changes in ecosystem productivity and water dynamics that can severely affect forests through changes in plant physiology, phenology and carbon allocation (Allen et al. 2010, Ummenhofer and Meehl 2017). In the last decades the assessment of the drought impacts on ecosystems has gained attention (Allen et al. 2010, Clark et al. 2016), especially considering some studies that suggest an increase in severity, geographic extent and frequency of droughts as a result of climate change (Dai 2011, Trenberth et al. 2014). The functional response of vegetation to drought has been analyzed at different scales, from global (*e.g*. Allen et al. 2010, Vicente-Serrano et al. 2013, Norman et al. 2016) to local scales (see Martínez-Vilalta and Lloret 2016 for a revision).

Vegetation responses to drought are influenced by other drivers of environmental change (Fischer et al. 2006, Oliver and Morecroft 2014, Franklin et al. 2016, Peñuelas et al. 2017), and some authors states that the impacts of drought on ecosystem must be evaluated in a context of global change considering the interactions with other drivers of environmental change (Archaux and Wolters 2006, Clavero 2011), such us land-use change (Doblas-Miranda et al. 2017). This is especially relevant for areas with a long history of landscape modification such as the Mediterranean region where land-use change is a key driver of the global change (Navarro-González et al. 2013, Ameztegui et al. 2016). REVIEW For instance, Doblas-Miranda et al. (2017) in a recent review, found that land use changes and more especially drought, are crucial factors in the interactions among the drivers of global change for Mediterranean forests.

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 likey 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. 2010).

Several studies analyzed the drought effects on Mediterranean tree species representing the southermost limit of their distribution REVIEW(Camarero et al. 2011, Pasho et al. 2011, Sánchez-Salguero et al. 2012, 2017, Linares et al. 2014, Dorado-Liñán et al. 2017b, Caminero et al. 2018), some focused on the resilience to drought of rear-edge populations (*e.g.* Sánchez-Salguero et al. 2013, Herrero 2014). Resilience is the capacity of an ecosystem, community or individual to recover pre-disturbance structure and function after a disturbance (Holling 1973, Lloret et al. 2011, Hodgson et al. 2015). The assessment of forest resilience to climatic disturbances, such as extreme droughts, provides critical information about the capacity of 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.

Here we assessed the resilience to drought of rear-edge populations of a tree Mediterranean species combining several approaches: remote sensing and dendroecologial estimates of growth. Remote sensing can be used for studying droughts impacts on ecosystems (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 (Vicente-Serrano et al. 2013, Assal et al. 2016) and for Mediterranean area there were studies covering all region (Gouveia et al. 2017) and others focused on local scales (Lloret et al. 2007, Vicente-Serrano 2007, Zribi et al. 2016).

Dendroecological estimates of growth (*i.e.* tree-ring width) are a widely used proxy to study tree vitality (Fritts 1976, Dobbertin 2005, Bhuyan et al. 2017a) 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). Several studies combined the use of satellite information with dendroecological data to assess the effect of droughts on vegetation (Dorman et al. 2013, Vicente-Serrano et al. 2013, Sangüesa-Barreda et al. 2014, Coulthard et al. 2017); and recently, Gazol et al. (2018) evaluated the resilience of several forests in Spain combining information derived from remote sensing and tree-ring data.

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.) located in Sierra Nevada, which is considered a rear-edge of species distribution and species performance is considered to be threatened. We are also interested in assessing resilience of these forests both to several extreme drought episodes and to climate change in the long-term in the last decades. We hypothesized that, relict populations driven by historical land-use at their climatic (either altitudinal or latitudinal) rear-edge are particularly vulnerable to climate change, and hence they will show low-values of resilience after several extreme droughts. Specifically, the aims of this work 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 successive extreme drought events, both in recent times and in the long-term 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. In addition, within the region of study we were interested to assess 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 (Vilches de la Serna 2014) 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, García and Jiménez 2009), with summer rainfall being a key factor in the distribution of the species, which can hence be considered to have low drought tolerance compared to genuine evergreen Mediterranean taxa (Gavilan et al. 2007, Río et al. 2007).

The forests of this species reaches their REVIEW 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 is considered a glacial refugia for deciduous *Quercus* species (Brewer et al. 2002, Olalde et al. 2002, Rodríguez-Sánchez et al. 2010) and these populations are considered as a rear edge of the habitat distribution, which is important in determining habitat responses to expected climate change (Hampe and Petit 2005). For this reason, the populations of Pyrenean oak forests at Sierra Nevada are considered relict forests (Melendo and Valle 2000, Vivero et al. 2000), having these forests undergone intensive anthropic use in history (Camacho-Olmedo et al. 2002, Valbuena-Carabaña et al. 2010, 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 Mediterranean evergreen oak and pine species (Gea-Izquierdo et al. 2013).REVIEW CITA

## 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 and Trigo 2014, Gouveia et al. 2015, 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 those 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. 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. (2015) (see Table S3).

## Greenness data

Vegetation indices derived from remote sensing information have been widely used to derive descriptors of ecosystem functioning (*e.g* Alcaraz-Segura et al. 2009) because they are linked with primary productivity (Ruimy et al. n.d.). 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 maximun 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. 2010, 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

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 warm site located at southern aspect (Figure 1; Table 1). For the southern site two elevations were sampled: CA-Low and CA-High, which constitutes the current altitudinal tree-line 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 dominant trees 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 using a girth tape and a Vertex IV ultrasonic hypsometer (Haglöf, Sweden) respectively. 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 (Dunn 1964) with Bonferroni adjustment to correct significance values. These analysis were performed uisng the PMCMR package in R (Pohlert 2014).

### Dendroecological analyses

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 the dplR (Bunn 2008, 2010) package. 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>) (Cofiño et al. 2018, 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. 2017).

Relationships between residual site chronologies and climatic variables were assessed ussing bootstrapped Pearson’s correlations estimated using the treeclim package (Zang and Biondi 2015). The bootstrapped confidence intervals were used to estimate significance (p < 0.05) of the correlation coefficients.

### 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, Fraver and White 2005).

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, MOP 1943, 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.* Bonet et al. 2014a); 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. 2014b, Jiménez-Olivencia et al. 2015, Moreno-LLorca et al. 2016).

## Resilience

To evaluate the effects of drougth events on greeennes and tree growth (BAI) 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 drougth event respectively. A period of three years was chosen because we found similar results comparing periods of two, three and four years (Appendix 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 1900 and compared them with drought severity (Figure S5).

## 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) using several packages (see Supplementary REVIEW S?)

# 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. During the 2005 the lowest values of EVI standardized anomalies were recorded, particularly for northern populations (Figure 2). In fact, a “browning” episode () was observed for *Q. pyrenaica* forests during this drought event, yet no changes in greenness were observed in response to the 2012 drought (Figure 3).

## Radial growth trends and growth disturbances

The trees of the southern population were older than northern ones, particularly for the high elevation site (CA-High) which had bigger and taller trees than the other sites (Tables 1, 2). REVIEW meter en Discussion This can be likely explained as a consequence of their different management origin (*i.e.* land-use legacy), as shown by the release event in SJ suggesting their coppice origin and (references). END REVIEW Competition was similar among sites but plot basal area was greatest in CA-High (Table 1), which however also exhibited the highest individual BAI growth (Figure 4). REVIEW In addition, trees from this location showed a positive growth trend since the late 1970s (Figure 4), which was not found for any of the other two locations. END REVIEW For southern population differences in growth were observed. CA-Low growth was lower than that of CA-High but similar to growth of the northern population (SJ) (Figures 4 and S6).

For 2005 and 2012 we found a greater reduction of RWI for northern site (SJ) but weaker for southern sites (CA-High and CA-Low). Yet, the lowest pointer year (*i.e.* the lowest growth) since 1950 was 1995 in all chronologies (Figure S3).

The analysis of growth changes revealed differences in forest history between sites (Figures 5 and S4). Northern site (SJ) showed two release events (GC > 50 %) detected at stand-wise scale (occurring in more than 50 % of sampled trees): the first during the 1940 decade and the second in the period 1994-2001. These periods alternate with periods of supression. Southern sites (CA-High and CA-Low) showed no release event except one for CA-High at the beginning of the REVIEW1840s? and no suppression event in the last 50 years.

## Resilience of greenness and radial tree-growth to drought events

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 REVIEW(1900 - 2017), revealed a positive relation between resilience (*Rs*) and drought severity ( = 0.336) (Figure 6). A similar pattern was found for recovery (*Rc*; = 0.438) but negative for resistance (*Rt*, = 0.155). Resilience values of tree-growth for 2005 was the lowest of the drought events analyzed (Figure 6) even not being the most severe drought events. REVIEW (CONEXION con el siguiente parrafo)

*Q. pyrenaica* forest showed significantly lower resistance values (*Rt*) to the 2005 drought event than to that in 2012 for greenness and for radial growth (Table 3; Figure 7). The 2005 drought reduced greenees and growth more than that of 2012 (Tables S1 and S2). Resistance values to drought for greenness and tree-growth varied between sites (Table 3). Southern populations showed significantly higher values of resistance than northern ones (Tables S1 and S2). It was particularly important for the 2005 drought event where the growth was reduced to 44.5 % respect to that of the preceding period (Figure 7).

Recovery (*Rc*) of greenness and growth were significantly different bewteen drought events and sites (Table 3). In the 3-year period after the 2005 drought, greenness was 112 % (Rc = 1.12) and after 2012 was 105.7 % (Rc = 1.057) (Table S1). An opposite pattern was found for tree-growth, with significantly lower values of recovery after the 2005 drought, staying at levels of *Rc* < 1 (Figure 7, Table S2). Northern populations showed significantly higher values of recovery than southern sites for greenness and tree-growth (Table S2). For southern populations, no significant differences were found for recovery of greenness after the 2005 and 2012 drought event (p = 0.2453; Figure 7; Table S1). Recovery values for tree-growth of southern populations were below or close to 1 (Figure 7, Table S2).

Significantly higher values of resilience (*Rs*) were observed for the 2012 drought event than for the 2005 in both variables (greenness and tree-growth) (Tables S1-S2; Figure 7). Resilience values varied significantly between sites for greenness, but not for tree-growth (Table 3). Southern populations showed higher resilience values (*Rs*) than the northern ones (Tables S1-S2). For greenness, the differences of resilience between sites were not significant for the 2005 drought event (p = 0.036; Figure 7). For tree-growth, opposites resilience values were found for the interaction between sites and drought event: higher values of resilience for northern populations than southern ones (CA-High and CA-Low) during the 2012 drought event but opposite pattern during the 2005 (Table S2).

The exploration of resilience metrics of tree-growth for all severe droughts in our climatic data (period 1900-2017?),

## Climate and tree-growth

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), specially for the northern population (r > 0.6). 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 maximum temperatures of the previous August were the only negative significant for the northern one (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

## Impacts of severe droughts on rear-edge populations

Our findings show that recent severe drought events, such as 2005 and 2012, provoked a reduction in greenness and especially in the growth of *Q. pyrenaica*. During the 2005 drought, one of the worst drought events recorded in the Iberian Peninsula (García-Herrera et al. 2007), we found a browning of the *Q. pyrenaica* forests, but no changes in EVI standardized anomalies were recorded for 2012, which can be explained because 2012 drought event was a winter-drought (Trigo et al. 2013). Tree-growth was also affected by drought as evidenced by the reduction in detrended tree-rings (RWI) during the most severe drought events (Figure S3). The decline in growth observed in our study sites is consistent with several works reporting tree-growth reductions for Mediterranean tree species during severe droughts, particularly for 2005 (*e.g.* Sánchez-Salguero et al. 2013, Camarero et al. 2018, Gazol et al. 2018).

## Oaks show high resilience in response to recent drought events

Although 2005 and 2012 were two severe droughts recorded for the south of the Iberian Peninsula (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 the forests of *Q. pyrenaica* located in their rear edge. Our results agree with those obtained by previous works using other remote-sensing vegetation indices (Pérez-Luque et al. 2015b, Alcaraz-Segura et al. 2016), which suggests an increase in primary productivity during the last years for rear-edge populations of this species.

For tree-growth, a similar positive trend was observed in the last decades, particularly for the southern high-elevation site (CA-High, Figure 4). This result differs from those previous reported for *Q. pyrenaica* along their distribution range (Gea-Izquierdo et al. 2013, Gea-Izquierdo and Cañellas 2014). Gea-Izquierdo and Cañellas (2014) found a general decline in the growth of this species since the 1970s, particularly sharp for populations located in their dry-edge. This decline trend in growth have also been oberved for other tree species located in their rear-edges (*e.g.* Sánchez-Salguero et al. 2012, 2017, Dorado-Liñán et al. 2017a). Furthermore, growth projections have forecasted a decrease in productivity for *Q. pyrenaica* that would increase vulnerability of this species to climate warming at the dry edges locations (Gea-Izquierdo et al. 2013). However, our results for similar locations have revealed a recovery in tree-growth for the last years (Figure 4). In addition, a similar positive trend in BAI for the last years, has been reported for another *Q. pyrenaica* population of the Sierra Nevada (Rubio-Cuadrado et al. 2018).

Aunque los valores de resiliencia (*Rs*) para el greenness y el tree-growth fueron inferiores o muy cercanos a 1, observamos en ambas variables, una mayor resiliencia tras la sequía de 2012 (Figure 7). La sequía de 2012, que fue mas severa e intensa que la registrada en 2005 (Table S3), ocurrió durante el invierno de 2012 (Trigo et al. 2013), lo cual puede explicar un menor efecto, sobre todo en el greenness de *Q. pyrenaica*. Por otro lado, al analizar la resiliencia del tree-growth para otros eventos de sequía (long-term perspective), observamos como estas poblaciones presentan altos valores de resiliencia. Como muestran nuestros resultados, los mayores valores de resiliencia fueron registrados para dos de los eventos mas severos de sequía (1995 y 1999), con valores de resiliencia por encima de 1.2 en ambos eventos (Figure 6).

Desde una perspectiva a largo plazo, es destacable el hecho de que las poblaciones de *Q. pyrenaica* en Sierra Nevada, aún habiendo sufrido varios eventos de sequía severa, presentan altos valores de Recovery y de Resiliencia, tal y como indican nuestros resultados (Figure 6). Las poblaciones situadas en su rear edge viven en estrechos márgenes ambientales y pequeños variaciones en las condiciones ambientales pueden provocar que las restricciones ambientales sean mas severas (Hampe and Petit 2005). Así, frecuentemente se asume una alta vulnerabilidad a la sequía de las poblaciones situadas en su dry rear-edge (Martínez-Vilalta 2018), tal y como se ha visto para *Q.pyrenaica* (Gea-Izquierdo and Cañellas 2014) y para otras especies (citas). Sin embargo, algunos estudios están demostrando que esto no es siempre así (ver por ejemplo Cavin and Jump 2017, Granda et al. 2018), tal y como sugieren nuestros resultados, con altos valores de resiliencia para poblaciones de *Q. pyrenaica* situadas en su rear-edge.

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. Esto último se ve reforzado por el hecho de que Sierra Nevada is considered a glacial refugia for deciduous *Quercus* species (Brewer et al. 2002, Olalde et al. 2002, Rodríguez-Sánchez et al. 2010); además las poblaciones de *Q. pyrenaica* en Sierra Nevada presentan una alta resiliencia genética (Valbuena-Carabaña and Gil 2013, 2017).

## Site environment shapes differential sensitivity to climate and drought of rear-edge oak populations

Our results showed differences for greenness and tree-growth between northern and southern oak populations (Table 3). Las poblaciones del norte, que presentan condiciones mas secas (Table 1), se vieron mas afectadas por los eventos de sequía. 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 (Roig et al. 2009, Gea-Izquierdo and Cañellas 2014, Gea-Izquierdo et al. 2014, González-González et al. 2014, Leal et al. 2015, Camisón et al. 2016, 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 results are consistent with previous findings that pointed out 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. 2017).

When we explored the chracteristics of the southern sites, we firstly observed a difference in elevation. Bhuyan et al. (2017a), 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). In fact, the differences in available water of soils could explain our results. Cobo-Díaz et al. (2017), in a work analyzing the variation of the microbiota along an elevational gradient within this location, found higher values of available water of the forest soils located on high elevation compared with those located at low elevations. 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 is a system 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). The network of traditional ditches present in one of our sampling site (Cáñar) was recentlty described, 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.

## Land-use legacy effects shape distribution and sensitivity to climate change of read-edge oak populations

Although our sampled sited showed similar tree competence levels (Table 1), the review of historical documents showed that la historia de manejo humano ha sido diferente para cada sitio. Different values of tree-growth were observed between populations and for different elevations within southern location (Figure 4). Low-elevation sites showed lower BAI values than higher-elevation site. A reason that could explain these results is the different degree of anthropic impact related to elevation. Los bosques situados a mas elevación presentan menor presión antrópica que los localizados a menor altitud, por el simple hecho de que estos últimos están mas accesibles. During the last decades, the rural abandonment has lead an decrease of anthropic pressures on the high-elevations zones of Mediterranean mountains (INLCUIR CITA).

comentario –> Aqui pretendo incluir la idea que hablamos en su momento. Quizá están creciendo donde les están dejando crecer (menor impacto antrópico en las zonas mas altas, al menos en los últimos años -abandono de zonas rurales?-) He ralizado una revisión de trabajos que utilicen dendro de Q. pyrenaica para ver si existe una relación entre la edad de las cronos con la elevación.

* Son bosques relativamente jóvenes comentaio –> Aquí me falta desarrollar este apartado algo más incluyendo cosas de los documentos históricos (la minería, etc, etc) Los tres sitios mostraron una reducción en los valores de BAI durante las sequías de 1995 y 2005, y menos evidente para el año 2012 (Figure 5). La población del norte (SJ) mostró una gran liberación en torno a 1945 fruto quizá de cortas asociadas a la actividad minera de la zona. Asimismo, esta población mostró un marcado descenso en BAI durante el periodo 1986 - 1999.

Climatic drivers are key factors determining the growth of tree species, especially at the rear edge of their distribution. Para *Q. pyrenaica* se ha visto que moisture availability es el factor limitante que determina el crecimiento en las poblaciones situadas en su rear edge (Gea-Izquierdo and Cañellas 2014), pero para otras especies (*i.e.* *Pinus nigra*, *P. sylvestris*) la temperatura tiene mas peso que la disponibilidad de agua (Herrero et al. 2013, Matías et al. n.d.). Pero es importante considerar además la historia de manejo que han tenido esos bosques a la hora de la forest management (Doblas-Miranda et al. 2017, Peñuelas et al. 2017), ya que, como observamos en nuestros resultados puede condicionar el crecimiento y la resiliencia de las especies.

En este sentido, sabemos que estos robledales han estado sometido a muchos ciclos de coppiccing, lo que podrían haber reducido su diversidad genética, y por tanto su resiliencia. Pero varios trabajos (Valbuena-Carabaña and Gil 2013, 2017) han encontrado que esta especie en su límite de distribución sur, muestra unos altos niveles de resiliencia (en este caso genética).

Methodological approach

comentario: tengo que rematar este apartado.

Vegetation reflects the environmental conditions, and the effects of drought on vegetation can be observed using information from several methodological approaches (see Norman et al. 2016 for a review). Several works revealed the utility of remote-sensing (*e.g*. Zhang et al. 2013, AghaKouchak et al. 2015) and of the dendrochronology (*e.g.* Eilmann and Rigling 2012, Bhuyan et al. 2017a) to quantify the drought impacts on vegetation at different spatial and temporal scales, but to our knowledge the combination of both approaches is scarce (Vicente-Serrano et al. 2013, 2016, Bhuyan et al. 2017b, Wu et al. 2018). Estos trabajos han observado que existe de forma general a positive relationship between vegetation indices derived from remote sensing and annual tree growth (Vicente-Serrano et al. 2016, Bhuyan et al. 2017b, Gazol et al. 2018).

Aunque existen algunos trabajos que han utilizado RWI y remote sensing nuestra aproximación (creo) es interesante, sobre todo porque la aplicamos al estudio de poblaciones que están en su límite de distribución (rear-edge) (Jump et al. 2010). Los estudios sobre poblaciones localizadas en el rear-edge de su distribución requieren de aproximaciones multidisciplinares que analicen la respuesta de las poblaciones al cambio climático y su resiliencia utilizando diferentes aproximaciones metodológicas, por ejemplo combinando dendro y remote sensing (Jump et al. 2010).

* Nosotros aqui utilizamos la combinación de técnicas de remote sensing con dendro para analizar la vulnerabilidad de poblaciones de Q. pyrenaica situadas en su reaar edge frente a los eventos de sequía.
* Hemos encontrado diferencias en cuanto a la resiliencia utilizando RS y RWI. Diferente sensibilidad de satélite frente a los datos de campo. Esto también se ha observado en Gazol et al. (2018), que analizaron la resiliencia a la sequia de 1986, 1994-1995, 1999 y 2005, usando RS y TR. Encontraron que los datos de TR son mas sensibles para la resiliencia del bosque a la sequía que los datos de RS
* De hecho, Jump et al. (2010) recomienda el uso de una aprox combinda de dendro, remote sensing y ground-based assessment para analizar los efectos del cambio global en las poblaciones situadas en el rear edge.
* La utilización de datos de tree-ring nos permite contextualizar los resultados obtenidos con remote sensing, ya que los datos de tree-ring reflejan anomalías en el crecimiento de los árboles (inducidas por clima o por disturbances) durante décadas o siglos (**???**) (… Combined analyses may also allow climate-induced variability in forest growth to be disentangled from that driven by community-level ecological processes. )
* Nota from Jump et al. (2010): Whilst lower resolution data, whether from remote sensing or ground-based monitoring, can inform on widespread regional changes in forest condition, these data are often not adequate for monitoring changes occurring at equatorial range margins owing to their complex distribution and/or topographical variability. In such regions, targeted collection of high-resolution data is necessary in order to identify currently occurring changes and predict the magnitude and spatial distribution of future decline. (Jump et al. 2010)

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