

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

Short Title

Relict oaks resilience at their rear-edge (max. 45 characters)

Authors¹

A.J. Perez-Luque^{1,2,a}; G. Gea-Izquierdo^{3,b} and Zamora, R.^{1,2,c}

¹ Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía (CEAMA), Universidad de Granada. Avda. del Mediterráneo s/n, E-18006 Granada, Spain

² Grupo de Ecología Terrestre, Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, Avda. Fuentenueva s/n, E-18071 Granada, Spain

³ INIA-CIFOR. Ctra. La Coruña km 7.5. E-28040 Madrid, Spain

^a ajperez@ugr.es

^b gea.guillermo@inia.es

^c zamora@ugr.es

Manuscript highlights

- Quercus pyrenaica* rear-edge forests showed high resilience at tree and stand-levels
- The responses to climate and resilience followed a water-stress gradient
- Trees and stand expressed high sensitivity to drought and land-use legacies

1 Author Contributions. AJPL, GGI and RZ conceived the study, conducted field work and collected the data. AJPL and GGI conducted lab work and led article preparation. AJPL analyzed data and led the writing of the paper. GGI and RZ contributed in the writing process. All authors contributed to the drafts and gave final approval for publication.

Comentado [GG1]: 'and artible preparation abajo igual lo puedes quitar. No sé por qué no me deja insertar ahí el comentario.'

19 Abstract

- 20 • Global change challenges ecosystems in dry locations transformed by intensive human use. We
21 analyzed resilience to drought of relict Mediterranean *Quercus pyrenaica* Willd. populations in the
22 Southern Iberian Peninsula. Forest resilience to drought was analyzed in relation to historical
23 records of land-use using dendroecological growth and greenness (EVI) as proxies for secondary
24 and primary growth.
- 25 • The growth trends reflected a strong influence of land-use legacies (e.g. firewood extraction) in the
26 current forest structure. Trees were highly sensitivity to drought and both primary and secondary
27 growth expressed high resilience to drought events in the short- and the long-term. The response to
28 climate and resilience followed a water-stress gradient. Primary and secondary growth of more xeric
29 populations (i.e. Northern aspect and low elevations) was less resilient to drought than that at more
30 mesic sites. In addition, a positive growth trend matching the warming climate since the late 1970s
31 was particularly evident in mesic high-elevation stands, but absent in the most xeric site.
- 32 • The species showed high resilience to drought despite being relict and at its rear-edge. Yet, the
33 trees exhibited a variable response to the changing climate along a very short climatic gradient. The
34 trees were more sensitive to water availability at most xeric sites whereas only the coldest and more
35 humid stands exhibited a recent positive growth trend. Stand dynamics at the most xeric locations
36 (i.e. the altitudinal rear-edge) needs to be monitored under future expected climatic scenarios
37 bearing in mind that land-use legacies play a key role in stand dynamics.

38 Keywords

39 extreme drought, resilience, rear-edge, *Quercus pyrenaica*, tree-growth, dendrocronology, remote-
40 sensing

41 Introduction

42 Intense drought is one of the most frequent and widespread climatic extremes affecting ecological
43 systems worldwide and is considered a key feature of the Mediterranean climate (Dai 2011). There has
44 been an increase in the frequency and severity of drought events in the last decades, along with a trend
45 towards drier summers particularly for southern Europe (Vicente-Serrano and others 2014b; Stagge and
46 others 2017). This is especially critical, since climate change projections for the Mediterranean area
47 forecast that climate extreme events will become more frequent and severe (Spinoni and others 2017).

48 Drought causes significant changes in ecosystem productivity and dynamics that can severely affect
49 forests through changes in plant physiology, phenology and carbon allocation. Thus, assessment of

Comentado [GG2]: 250 palabras.

Eliminado: that trees showed

Eliminado: both

Eliminado: recent

Eliminado: and to

Eliminado: climatic changes

Eliminado: R

Eliminado: following

Eliminado: We found a positive growth trend since the end of the 1970s, that was strongest in the high-elevation stand and non-significant in the most xeric site.

Eliminado: Northern

Eliminado: were

Comentado [GG3]: ¿Es esto verdad? Figs 6 y 7: Rt menor en SJ pero Rs y Rc son (no siempre) mayores. Sería al revés entonces? Más estrés, más resiliencia (en BAL) pero menos resistencia? Revisalo para ... [2]

Eliminado: both in primary and secondary grov ... [1]

Eliminado: D

Eliminado: being considered

Eliminado: stands

Eliminado: the

Eliminado: dry

Eliminado: for the species

Eliminado: , the trees showed high resilience if ... [3]

Eliminado: re

Eliminado: were

Eliminado: divergent

Eliminado: a

Eliminado: s

Eliminado: oaks

Eliminado: expressed

Eliminado: the

Eliminado: they

Eliminado: s only in the coldest and more hum ... [4]

Eliminado: These results suggest that s

Eliminado: , particularly

Eliminado: lowest elevations

Eliminado: ,

Eliminado: drier and warmer

Eliminado: management

Eliminado: likely

Eliminado: current

96 drought impacts on ecosystems has gained much attention in last decades (Allen and others 2010; Clark
97 and others 2016), and the functional response of vegetation to drought has been analyzed at global and
98 local scales (e.g., Vicente-Serrano and others 2013; see Martínez-Vilalta and Lloret 2016 for a revision).

99 Ecosystem responses to drought are influenced by other drivers of environmental changes. In a global-
100 change context, the impacts of drought on vegetation need to be evaluated considering the interactions
101 with other drivers of change (Doblas-Miranda and others 2017). This is especially relevant for areas with
102 a long history of landscape modification, such as the Mediterranean region, where land-use change plays
103 a significant role in current ecosystem ecology (Navarro-González and others 2013), considering also that
104 the interactions of these two factors, namely drought and land-use change, are crucial for Mediterranean
105 forests (Doblas-Miranda and others 2017).

106 The impacts of drought are also especially relevant for populations located in the rear edge (either
107 latitudinal or altitudinal along climatic gradients) of their distribution, where climatic conditions often
108 corresponds to the species-limits and the populations are likely to be more sensitive to small variations on
109 climate and the microtopography (Hampe and Petit 2005). The response of rear-edge populations to
110 variations on climate could be useful to estimate the adaptation of the species to predicted climatic
111 changes (Jump and others 2010). This becomes even more important for relict populations driven by
112 historical land-use if they harbour high levels of intraspecific genetic diversity (Valbuena-Carabaña and
113 Gil 2013).

114 Many studies have analyzed the effects of drought on Mediterranean tree species representing the
115 southernmost limit of their distribution (e.g., Sánchez-Salguero and others 2012; Dorado-Liñán and others
116 2017b), and some focused on the resilience to drought of rear-edge populations (e.g., Herrero and
117 Zamora 2014). Resilience is the capacity of an ecosystem, community or individual to recover its pre-
118 disturbance structure and function after a disturbance (Holling 1973). The assessment of resilience to
119 climate disturbances like droughts provides critical information about the capacity of forests to maintain
120 their structure and to continue providing valuable ecosystem services.

121 Vegetation responses to drought requires of integrative and multidisciplinary strategies for assessing the
122 impacts of disturbances on forest at several scales (Hartmann and others 2018). The resilience to
123 drought of species is better assessed when several approaches like remote sensing and dendrochronology
124 are combined simultaneously. Dendroecological estimates of growth (*i.e.* tree-ring width) are a widely
125 used proxy to study tree vitality (Fritts 1976; Bhuyan and others 2017) and the analysis of annual-tree ring
126 widths can be used to study changes in growth as response to drought at the individual tree-scale (Fritts
127 1976). The combination of both approaches (remote sensing and dendroecology), has been used to
128 assess the effects of droughts on vegetation along ecological or elevational gradients (e.g. Vicente-
129 Serrano and others 2013; Coulthard and others 2017), and also for the analysis of growth resilience to
130 drought on several tree species (Gazol and others 2018). Remote sensing can be used for studying

Comentado [GG4]: Es la primera vez que cita 2017a, debería ser a y no el b

131 droughts impacts on ecosystems, hence the stand level (e.g. Zhang and others 2013). Vegetation indices
132 obtained from satellite are used as a proxy for assessing vegetation functioning and aboveground net
133 primary production (Alcaraz-Segura and others 2009), and changes in the patterns of these indices are
134 considered as an indicator of the forest response to external environmental factors, such as drought (e.g.
135 Vicente-Serrano and others 2013). Drought impacts on vegetation using remote sensing have been
136 analyzed at different scales. For instance, a global-scale study showed a stronger influence of drought for
137 drier biomes (Vicente-Serrano and others 2013) whereas for Mediterranean area, studies at regional and
138 local scales found a large spatial and seasonal variability of the effects of drought on vegetation (Gouveia
139 and others 2017). Several works assessed vegetation responses in term of resistance and resilience to
140 drought events highlighting a stronger response of tree-ring (tree-level) to drought variability compared to
141 the greenness (ecosystem-level) (e.g. Peña-Gallardo and others 2018; Gazol and others 2018).
142 Nonetheless, it is crucial to know if the responses at the tree level differ from responses at the ecosystem
143 level, particularly in rear edge populations.

144 In this work we used remote sensing information and dendroecological methods to evaluate the drought
145 impact in both canopy greenness (as a proxy to primary growth) and tree-radial growth (as a proxy to
146 secondary growth) of a Mediterranean tree species (*Quercus pyrenaica* Willd.) on southern relict forests
147 at the rear-edge of the species distribution and where species performance is considered to be
148 threatened by climate change. We also assessed the resilience of these forests both to several extreme
149 drought episodes and to climate change (i.e. warming) in the long-term in the last decades. Our main
150 hypothesis is that these relict populations driven by historical land-use are particularly vulnerable to
151 climate change at their present climatic (either altitudinal or latitudinal) rear-edge, and will show low
152 resilience after extreme drought particularly at the dry edge along climatic gradients at the small scale
153 within the rear-edge. To address this hypothesis our specific aims were: (i) To quantify how recent
154 extreme drought events influenced primary and secondary growth of *Q. pyrenaica* forests in their rear
155 edge; (ii) to analyze the long-term resilience of these forests to extreme drought events using time-series
156 of radial growth; (iii) and to explore differences in the resilience metrics between populations located in
157 contrasting ecological conditions within the rear edge of this species to detect vulnerability to climate
158 change along climatic gradients. To achieve goal (iii) we assessed within the region of study whether the
159 effect of aspect and microclimatic conditions expressed in northern and southern populations of Pyrenean
160 oak forests differ in their resistance, resilience and recovery to extreme drought events.

161 **Materials and methods**

162 **Tree species and study site**

163 Pyrenean oak (*Quercus pyrenaica* Willd.) forests extend through south-western France and the Iberian
164 Peninsula reaching its southern limit in mountains areas of northern Morocco (Franco 1990). In the
165 Iberian Peninsula these forests live on siliceous soils under meso-supramediterranean and
166 mesotemperate areas and subhumid, humid and hyperhumid ombroclimate. *Q. pyrenaica* requires over
167 650 mm of annual precipitation and a summer minimal precipitation between 100 and 200 mm. Summer
168 rainfall is a key factor for the species, which is considered to have low drought tolerance compared to
169 genuine evergreen Mediterranean taxa (Río and others 2007).

170 The forests of this species reach their southernmost European limit in mountains from Southern
171 Andalusia like Sierra Nevada (37°N, 3°W), a high-mountain range with elevations between 860 m and
172 3482 m a.s.l.. The climate is Mediterranean, characterized by cold winters and hot summers, with
173 pronounced summer drought (July-August). There are eight Pyrenean oak patches (2400 Has) identified
174 in this mountain range (Figure 1), ranging between 1100 and 2000 m a.s.l. and often associated to major
175 river valleys. Sierra Nevada is considered a glacial refugia for deciduous *Quercus* species (Olalde and
176 others 2002). Today, *Q. pyrenaica* woodlands in this mountain region represent a rear edge of their
177 habitat distribution, which is important for determining habitat responses to expected climate change
178 (Hampe and Petit 2005). They are the richest vascular-plant forest formation of Sierra Nevada, sheltering
179 several endemic and endangered plant species (Lorite and others 2008). These relict forests undergone
180 intensive anthropic use in history (Camacho-Olmedo and others 2002; Valbuena-Carabaña and Gil
181 2017). Furthermore, conservation status of this species for southern Spain is considered "Vulnerable" and
182 it is expected to suffer the impact of climate change, reducing its suitable habitats in the rear-edge (Gea-
183 Izquierdo and others 2013).

184 **Drought episodes**

185 The Iberian Peninsula suffered several extreme drought episodes in the last decades of the twentieth
186 century (e.g. 1994-1995, 1999, 2005, 2012) (Vicente-Serrano and others 2014b). The 2005 and 2012
187 drought events have been documented among the worst droughts in the last decades for the southern
188 Iberian Peninsula (García-Herrera and others 2007; Páscoa and others 2017) and they were
189 characterized as extreme drought in our climatic data (Figures S1-S2; Table S3). We focused on these
190 two drought events because they were included in the period where there is availability of high-spatial
191 resolution remote sensing information (MODIS started on 2000; see below). Nevertheless, for radial
192 growth-time series, a greater number of older drought events were also analyzed to contextualize results
193 obtained in 2005 and 2012 drought events and analyze forest resilience to drought in a longer term (see

Comentado [GG5]: Mucho parece esto, no? un 30% del total?

Table S3). The identification of a drought event were done using the Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano and others 2010) following similar procedure as proposed by Spinoni and others (2015). We used SPEI-12 months scale for all 0.5° 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 and others 2017; Spinoni and others 2017). A drought event is considered only when SPEI values are below the threshold for at least two consecutive months. 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.

Greenness data to assess ecosystem resilience

Vegetation greenness of *Q. pyrenaica* was characterized by means of the *Enhanced Vegetation Index* (EVI), derived from MOD13Q1 product of the MODIS (*Moderate Resolution Imaging Spectroradiometer*) sensor. MODIS EVI Data (Collection 6) were obtained for the period 2000 - 2016. EVI data consists 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). Values affected by high content of aerosols, clouds, snow and shadows, were filtered out following recommendations for mountain regions (Reyes-Díez and others 2015).

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

$$EVI_{sa,i} = \frac{EVI_{mean,i} - EVI_{mean,ref}}{\sigma_{ref}}$$

where $EVI_{sa,i}$ is the EVI standardized anomaly for year i ; $EVI_{mean,i}$ the annual mean value of EVI for year i ; $EVI_{mean,ref}$ the average of the annual EVI values for the period of reference 2000-2016 (all except i year); and σ_{ref} the standard deviation for the reference period. Each pixel was categorized according the EVI standardized anomalies as “greening” ($EVI_{sa} > 1$), “browning” ($EVI_{sa} < -1$) or “no changes” ($-1 > EVI_{sa} > 1$)(Samanta and others 2012).

Rather than other vegetation indices like the NDVI, EVI_{mean} was chosen since it is highly stable under the use of any filter (Reyes-Díez and others 2015) and because it showed high significant correlations with

annual ($r = 0.81$) and seasonal EVI values ($r_{spring} = 0.76$ and $r_{summer} = 0.88$). For exploratory purposes, temporal trends of EVI_{mean} were explored at a pixel scale, using Mann–Kendall nonparametric test.

Field sampling and dendrochronological methods to assess individual resilience

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 the northern aspect; and Cáñar (CA), a more 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 constitute the current altitudinal rear-edge (CA-Low) and tree-line (CA-High), respectively in the sampled slope. Sampling sites follow a moisture gradient: $SJ < CA-Low < CA-High$ (Table 1). All the sites were oak monospecific and representatives of the population clusters identified for the species in this mountain range (Pérez-Luque and others 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 height (1.3 m) using an increment borer. Diameter at breast height (DBH) and total height were measured for 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* (trees · ha⁻¹), and *basal area* (BA, m² · ha⁻¹); and the distance dependent index size ratio proportional to distance (*srd*) as $srd = \sum_{i=1}^n (dbh_j/dbh_i) \cdot [1/(dist_{ij} + 1)]$. Differences between sites for height, DBH and competition indices were analysed using non-parametric Kruskal-Wallis rank sum tests. When significant differences were observed, we run multiple comparisons using the Dunn's-test with Bonferroni adjustment to correct significance values.

Tree cores were air dried, glued onto wooden mounts and sanded. Annual radial growth (ring width, RW) was measured with a measuring device 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 verified using COFECHA (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 dp1R (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 (Fritts 1976). 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.

260 The long-term growth response was analyzed using basal area increment (hereafter BAI, $\text{cm}^2 \cdot \text{year}^{-1}$).
 261 Theoretically, BAI represents a more accurate indicator of growth than ring-width, since it removes
 262 variation in growth attributable to increasing stem circumference after 30-40 years of juvenile increasing
 263 growth (Biondi and Qeadan 2008). Raw ring-widths and measured DBH were used to compute BAI by
 264 subtracting twice the annual ring width from the annual diameter, starting from the measured diameter
 265 outside the bark (Piovesan and others 2008). We used the following equation:

$$266 \quad \text{BAI} = \pi(r_t^2 - r_{t-1}^2)$$

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

270 Both RWI and BAI chronologies were compared to different climatic indices to analyse the low and the
 271 high-frequency response to climate of trees.

272 **Climate and growth**

273 Climate data were obtained from the European Daily High-Resolution Observational Gridded Dataset (E-
 274 OBS v16) (Haylock and others 2008). Monthly precipitation and minimum and maximum temperatures
 275 were obtained at a $0.25 \times 0.25^\circ$ resolution for the 1950-2016 period. We selected grid cells covering each
 276 sampled sites. The Standardized Precipitation-Evapotranspiration Index (SPEI) with a temporal scale of 6
 277 months was used to characterize the drought conditions for the period 1961-2014.

278 Relationships between residual site chronologies and climatic variables were assessed using
 279 bootstrapped Pearson's correlations estimated using `treeclim` (Zang and Biondi 2015).

280 **Disturbance analyses**

281 Disturbance chronologies were built using tree-ring width to identify abrupt and sustained increases
 282 (release events from competition) or decreases (suppressions) in radial growth (Nowacki and Abrams
 283 1997) as indirect estimates of possible disturbance events (e.g. logging, drought induced neighbor
 284 mortality) in the past. Growth changes (GC) were calculated for the individual tree-ring series using a 10-
 285 year running window as either positive (PGC) or negative (NGC) growth changes:

$$286 \quad \%GC = \left[\frac{(M1 - M2)}{M2} \right] \times 100$$

287 where $M1$ is the preceding 10-year median and $M2$ is the subsequent 10-year median. Medians were
 288 used since they are a more robust estimator of central tendency than means (Rubino and McCarthy
 289 2004). Site disturbance chronologies were constructed by averaging the individual disturbances series

Comentado [GG6]: No presentas desde 1950 en algunos casos?

290 annually. To separate growth peaks produced by disturbance events and expressing stand-wise
291 disturbances from those by climate, we considered a threshold of 50 % of GC and more than 50% of the
292 individual trees displaying the same growth changes was considered a stand-wise disturbance (e.g. Gea-
293 Izquierdo and Cañellas 2014).

294 In addition, the forest and management history of our sampling sites was inferred from a detailed analysis
295 of historical land-use changes. For this purpose, an exhaustive review of existing abundant historical
296 documents was done to compile information about socio-economical activities affecting the studied
297 forests (Table S4).

298 **Assessing ecosystem and tree individual resilience to drought**

299 To evaluate the effects of drought events on ecosystem resilience (using greenness data) and tree
300 individual resilience (using BAI data) we used resilience indices proposed by Lloret and others (2011):
301 resilience (R_s), resistance (R_t), and recovery (R_c). The Resistance index, estimated as the ratio between
302 performance during and before the disturbance ($R_t = Drought/PreDrought$), quantifies the severity of
303 the impact of the disturbance in the year it occurred. The Recovery index, computes as the ratio between
304 performance after and during disturbance ($R_c = PostDrought/Drought$), represents the ability to recover
305 from disturbance relative to its severity. Finally, the Resilience index ($R_s = PostDrought/PreDrought$) is
306 the capacity to reach pre-disturbance performance levels. The values of these indices were computed for
307 tree growth (BAI) and greenness (EVI mean) during each drought event. The predrought and postdrought
308 values of each target variable (*i.e.* BAI or EVI) were computed as the mean value during a period of three
309 years before and after the drought event respectively. A period of three years was chosen because we
310 found similar results comparing periods of two, three and four years (Figure S6) and this length was used
311 in other studies (*e.g.* Gazol and others 2018). To put in context in a longer-term the resilience observed
312 for 2005 and 2012 drought events, as well as to test whether the resilience indices were ecologically
313 meaningful, resilience metrics for BAI data were additionally computed for the most severe drought
314 events since 1950 and compared them with drought severity (Figure 6, Table S3).

315 **Statistical analysis**

316 For each of the three resilience indices studied, robust two-way ANOVAs were used to test for differences
317 between drought events (2005 and 2012) and the studied oak populations (northern and southern
318 aspects). These tests were used because original and log-transformed data did not follow the
319 assumptions of normality and homogeneity of variance (Wilcox 2012). Robust measures of central
320 tendency (M-estimator based on Huber's Psi) were used since they were close to the mean value in all
321 cases (Wilcox 2012). When running the robust ANOVA test, data were bootstrapped 3000 times and
322 trimmed automatically to control the potential influence of outliers. Post-hoc differences were assessed

pairwise using a similar bootstrap test. All the robust ANOVA and post-hoc tests were carried out using the WRS2 package. The level of significance was set to 0.05 and adjusted for multiple comparisons.

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). A "browning" episode ($EVI_{sa} < -1$) was observed for 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 (Table 1, Figure 4), despite competition measured as plot basal area was greatest in CA-High (Table 1). Growth and height of trees from the northern and the low-elevation southern population were similar (Figures 4 and S6). Only trees from the southern sites showed significant positive growth trends since the late 1970s (Figure 4), being much more pronounced for the highest, hence more humid, site (CA-High).

Drought events produced reduction in RWI for all sites (Figure S3), being particularly evident the negative effect of the 1995 drought (the worst drought spell in our climatic record, Table S3), when the greatest growth reduction was recorded for all chronologies. The southern sites (CA-High and CA-Low) showed weaker reductions of tree-growth than the northern site (SJ), especially for 2005 and 2012 (Figure S3). Tree-growth reduction followed a moisture-gradient, being weaker for the wetter wettest site (CA-High, Figure 5).

The northern site (SJ) showed two major release events ($GC > 50$ % occurring in more than 50 % of sampled trees): the first during the 1940s (the most evident) and the second in 1995-2000. These periods alternated with periods of suppression. In contrast, 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.

351 Resilience to drought events at the ecosystem and individual tree levels

352 Resilience metrics of tree-growth for drought events since 1950 (*i.e.* shared period among the three
353 chronologies excluding the juvenile years, Table S3) revealed a positive relationship between drought
354 severity and Recovery (R_c), significant for all oak populations (Figure 6). A similar pattern was obtained
355 for Resilience (R_s) but only significant for SJ site (Figure 6). Importantly, non-significant patterns were
356 obtained if we excluded 1995 from the analysis, except for R_c in SJ (Figure S8). Trees showed the
357 highest value of tree-growth resilience for 1995, the worst drought event in our study area (Table S3), and
358 particularly SJ, where our results suggest a major release event after 1995 (Figure 5).

359 During the last two drought events, resilience metrics for greenness and tree-growth were significantly
360 different between drought events (Table 3). The 2005 drought event reduced greenness and growth more
361 than that of 2012 (Tables S1 and S2) but the two metrics of resilience generally covaried in the same
362 direction. We obtained significantly higher Resilience (R_s) and Resistance (R_t) values for the 2012, the
363 most severe event, than for 2005 in both variables (Tables S1-S2; Figure 7). Recovery (R_c) showed
364 contrasting pattern for EVI and tree-growth. Recovery values for greenness were higher for 2005 than for
365 2012 drought event (Table S1, Figure 7).

366 Overall, resilience metrics significantly varied between sites, except for Resilience (R_s) of tree-growth ($p =$
367 0.534; Table 3), which was similar among the three sites. The two southern populations showed lower
368 values for Recovery (R_c) than the northern site both for greenness and tree-growth (Tables S1 and S2).
369 In contrast, Resistance and Resilience values were significantly higher for southern sites than for northern
370 ones (Tables S1 and S2).

371 Tree-growth response to climate

372 The response of tree-growth to water availability was greater than that to temperatures, as it can be
373 expected for a Mediterranean site and particularly a species located closer to its xeric/dry distribution limit
374 (rear-edge). Cumulative precipitation of the hydrological year and seasonal SPEI values (*i.e.* for the
375 Hydrological year, Spring and Summer) were the climatic variables exhibiting the highest (positive)
376 relationship with growth for all populations (Figure 8a). Yet there were some differences between northern
377 and southern populations: the positive relationship with SPEI was highest in the northern population ($r >$
378 0.6 vs. $r < 0.5$; Figure 8a). In addition, spring maximum temperature was the most significant limitation for
379 tree-growth only for the southern populations (Figure 8b and 8c). Minimum and maximum temperatures of
380 current September positively influenced tree-growth only in the northern population.

Comentado [GG7]: Ves lo que digo en el abstract: en realidad los mayores valores de resiliencia están en SJ. Cuidado con esto.

Comentado [GG8]: Cuidado al discutir esto: se recupera mejor de la mayor sequía en 2012... pero porque le afecta mucho menos (Fig 2).

Comentado [GG9]: Cuidado que esto sea coherente con Figuras 6 y 7... donde se muestra esa información también.

Comentado [GG10]: Te borro cosas:
1) para abreviar
2) porque no se ven claras y luego no van a aportar (diría) a la discusión.

Es bueno ser conciso aquí y solo comentar lo que luego se discute en el siguiente apartado.

381 Discussion

382 Relict oaks show high resilience to recent drought events and long-term climatic variability

383 Severe drought negatively affects both primary and secondary growth of *Q. pyrenaica* forests. This was
384 expressed by the observed reduction in greenness and tree-growth in response to the 2005 and 2012
385 drought events, and the consistent radial growth suppression for this oak species during extreme drought
386 events (Corcuera and others 2006; Gea-Izquierdo and Cañellas 2014). Furthermore, the greatest
387 reduction of tree-growth was observed during the 1995 drought, a characteristic pointer-year that caused
388 severe and extensive damage to the Mediterranean vegetation across the Iberian Peninsula (Peñuelas
389 and others 2001; Gazol and others 2018). Although the south of Iberian Peninsula suffered severe
390 drought events in the last decades (e.g. 2005 and 2012 were considered two of the worst recorded
391 drought; García-Herrera and others 2007; Trigo and others 2013; Vicente-Serrano and others 2014b)
392 (Table S3), we found a positive trend for vegetation greenness of *Q. pyrenaica* for the last 16 years (78.9
393 % of the pixels showed a positive trend during the 2000 to 2016 period). This confirms previous findings
394 that pointed out a recent short-term increase in primary productivity for these forests coinciding with a
395 rather humid decade in the 2000s after a dry decade in the 1990s (Pérez-Luque and others 2015b), being
396 the most productive ecosystems in this mountain region during that period (Alcaraz-Segura and others
397 2016). For tree-growth, we also observed positive trends in the last decade, particularly for the southern
398 high-elevation site (CA-High, Figure 4). Similar long-term trends were described for this species along its
399 distribution range only a high elevation sites (Gea-Izquierdo and Cañellas 2014), which could be related
400 to a non-linear positive effect of warming at species-wise cold limited high elevation sites (Salzer et al.
401 2009; Gea-Izquierdo and Cañellas 2014). However, the observed pattern for our sites (a rear-edge)
402 differs from the decline trends observed for several Mediterranean and temperate tree-species located in
403 their rear-edges (e.g., *Pinus nigra*; *P. sylvestris*; Sánchez-Salguero and others 2012; Camarero and
404 others 2015b; *Fagus sylvatica*; Dorado-Liñán and others 2017a).

405 Despite the 2012 drought event was more severe and intense than 2005 (Table S3), resilience values for
406 greenness and tree-growth were greater for 2012. This could be explained by the different timing of the
407 two droughts, i.e. the 2012 drought was a winter drought (Trigo and others 2013) occurring earlier than
408 the 2005 drought. The latter lasted less than 2012 drought, but matched the period of maximum growth
409 for *Q. pyrenaica* forests (Figure S7). Thus, this highlights the importance of the timing of drought as a key
410 factor determining tree recovery (Huang and others 2018), as also observed for other Mediterranean oak
411 species (e.g. Holm oak; Camarero and others 2015a). In addition, we found strong declines of tree-
412 growth during the most severe drought events occurred (1995 and 1999) (Table S3; Figure S3), matching
413 similar declining patterns observed for other species (Sánchez-Salguero and others 2012; Camarero and
414 others 2015b). But, interestingly, the highest values of resilience for tree-growth were obtained for these
415 two drought events. In addition, we observed a positive relation between tree-growth resilience and

Comentado [GG11]: Intenta hacer un ultimo esfuerzo para resumir y organizar perfectamente las ideas en los párrafos. Que fluyan en una estructura coherente y sin repeticiones. 5 páginas de discussion no me parece demasiado largo, aunque si reduces un pelín... siempre mejor.

Comentado [GG12]: Aquí puedes dejar 2 citas y así ahorrarte otra más de la biblio (hay más de 80 aún, creo).

Comentado [GG13]: Esto es muy importante (mira el comentario que te hago abajo donde te inserto la cita en la biblio). Verás que también lo menciono expresamente en el abstract.

Comentado [GG14]: Explica cómo: no entiendo, ¿quieres decir que difiere CA-high? Si es así, haz más hincapié en lo que ya comentas: la variabilidad tan grande dentro del rear-edge (algo hay que poner en abstract, es un resultado muy interesante).

Comentado [GG15]: Esto es general, no creo que haya falta citar solo "el rear-edge" (que es un concepto un poco vago, pero bueno).

416 drought severity. This result seems contradict our initial hypothesis in which we predicted low resilience
417 values for this oak species in their rear-edge after extreme drought events. Yet, the high resilience values
418 obtained for the 1995 drought in the most xeric site (SJ) could be related with drought-induced mortality
419 (*personal communications*), which would show the influence of stand dynamics partly shadowing
420 interpretation of individual resilience estimated from individual growth series.

Comentado [GG16]: Igual decir algo aquí de que puede haber influencia de la dinámica de masa (mortalidad en 1995) en la resiliencia calculada.

Comentado [GG17]: Citar el nombre de la persona que lo ha observado

Comentado [GG18]: Resumir este párrafo.

421 Rear-edge populations live in environmental narrow margins, and small variations in environmental
422 conditions can increase the vulnerability of the species (Hampe and Petit 2005). A high vulnerability to
423 drought is often assumed for populations located at their rear-edge (Martínez-Vilalta 2018). However we
424 obtained positive trends in greenness and tree-growth for the rear-edge of *Q. pyrenaica* and high values
425 of resilience to severe droughts. Our findings are in agreement with those studies that have shown that
426 the assumed higher vulnerability of dry edges does not necessarily hold (Cavin and Jump 2017).
427 Martínez-Vilalta (2018) pointed out the importance of the local adaptation and plasticity, and also of the
428 local environmental factors on the vulnerability showed by rear-edge populations. The high values of
429 resilience to drought reported here together with previously works showing high values of genetic
430 resilience for those forests at Sierra Nevada (cita), seem to be indicative of high local adaptation of this
431 oak. In addition the local environmental conditions of the sites where this species inhabit at Sierra Nevada
432 would explain the low vulnerability to drought showed by this oak. A key consideration for rear-edge
433 populations is the different ways in which marginality can be defined, *i.e.* if it is defined according to
434 geographic, climatic criteria, or according to other ecological factors (Martínez-Vilalta 2018). In this sense,
435 the high values of resilience to the drought events that we have observed, could suggest that the
436 populations of *Q. pyrenaica* in Sierra Nevada are located in a geographical but not a climatic rear-edge.
437 And the current niche is a result of land-use changes, which further complicates the definition of potential
438 rear-edges.

439 Greenness and tree-growth of *Q. pyrenaica* showed different sensitivity to severe droughts. During the
440 last drought events EVI was reduced to 90.3 % (Table 1), whereas BAI was reduced to 70.8 % (Table
441 S2), suggesting a lower sensitivity to drought of greenness than of tree-growth, particularly for drier sites.
442 These findings are in accordance with previously works showing that tree-growth is a more sensitive
443 metric of forest resilience than net primary productivity (*e.g.* Babst and others 2013; Coulthard and others
444 2017; Gazol and others 2018). Besides the different scales of both approaches, *i.e.* tree-based *versus*
445 pixel-based (*i.e.* ecosystem or stand based); the growth reduction seems to be more mediated by sink
446 that by source limitations (Gazol and others 2018). The response of greenness to drought not only
447 reflects the response of trees but from all vegetation within the pixel (Dionisio and others 2012). In this
448 sense, recent results indicate that remote sensing models underestimate the impact of drought on
449 primary production (Stocker and others 2019), as soil moisture is not taken into account by this satellite
450 estimates. This is particularly important for *Q. pyrenaica* forests, as soil moisture is a key growth-related
451 factor for this species (Gea-Izquierdo and Cañellas 2014). On the other hand, tree-ring records allow to

Comentado [GG19]: Si vas a hablar de source-sink....cita a Körner o a otro que no sea Gazol, que eso no es lo suyo. Mira la página 2 del artículo que te adjunto, hay algunas (de las muchísimas) citas para el tema.

452 complement remote sensing data in a longer time scale, by reflecting climate or disturbance induced tree-
453 growth anomalies over decades to centuries (Babst and others 2017) and provide an accurate measure
454 of growth responses to droughts (Bhuyan and others 2017; Gazol and others 2018). A combined
455 analysis, such the approach used in our study, may allow climate-induced variability in forest growth to be
456 disentangled from that driven by community-level ecological processes (Babst and others 2017), since
457 spatio temporal patterns of tree-ring measurement and earth observations (*i.e.* EVI) reflects processes at
458 different spatio-temporal scales (Gea-Izquierdo et al. 2015; Babst et al. 2018).

Comentado [GG20]: Creo que el artículo que te adjunto es muy apropiado para esto: usamos datos de eddy covariance y dendro, que es parecido a lo que habla florin babst.

460 Small-scale environmental variability shapes the sensitivity to climate of trees within the rear-edge

Comentado [GG21]: Este subapartado es muy cortito y el primero muy largo. Si puedes reordenar un poco las ideas... con una última revision lo conseguirás sin problemas.

461 Greenness and tree-growth were more affected by drought events in drier northern populations than in
462 more humid southern oak populations, e.g. the northern site showed higher browning intensity than the
463 southern sites during the 2005 drought event. In addition, the stronger correlations of tree-growth with
464 SPEI (Hydrological and summer) in the northern site, can be interpreted as higher sensitivity to drought in
465 drier sites (Gea-Izquierdo and Cañellas 2014). Similar to many other forest species under Mediterranean
466 climates, moisture availability is generally the most limiting factor driving radial growth of *Q. pyrenaica*
467 along their distribution range in the Iberian Peninsula (Gea-Izquierdo and Cañellas 2014). Thus, our
468 results are consistent with previous studies highlighting the influence of precipitation on tree-ring growth
469 in different oak species (*e.g.* Gea-Izquierdo and Cañellas 2014; González-González and others 2014;
470 García-González and Souto-Herrero 2017)

471 It has been described an effect of elevation on the resistance to drought of several tree-species, where
472 stands located at higher elevations were less drought sensitive, thus high-elevations can be used as local
473 refuge for species in response to climate change (Bhuyan and others 2017). It is well known that tree
474 growth and the tree responses to drought are site-dependent (*e.g.* soil features, tree competence, etc.)
475 (Babst and others 2013; Vicente-Serrano and others 2014a) particularly for rear-edge populations (Cavin
476 and Jump 2017; Dorado-Liñán and others 2017b). Remarkably, the trees at CA-High, which are located
477 around 1900 m. a.s.l. and represent today the upper altitudinal limit (treeline) for the species in this
478 southernmost location, showed higher BAI than those located at lower-elevations (CA-Low and SJ)
479 (Figure 4). This shows the high variability in the response to climate exhibited in a small gradient and is
480 especially interesting for the southern sites, which are very close to each other and overall both constitute
481 the rear-edge for the species. The higher values of tree growth in taller trees that we observed in CA-High
482 site strongly suggest a lower water stress at high-elevation sites (as shown by soil analyses along an
483 elevational gradient in this location, Cobo-Díaz and others 2017). Furthermore, as mentioned, the recent
484 growth increase only at the most humid locations a likely concomitant positive effect of a warming climate
485 (Gea-Izquierdo and Cañellas 2014).. Finally and in a context of global change, in addition to withstanding
486 lower water stress, it is likely that less accessible sites at higher elevations would suffer a lower anthropic

487 impact and the abandonment of traditional uses was earlier, due to their farthest location from human
488 settlements and therefore less access to forest resources (Table S4).

489 **Land-use legacies shape forests and sensitivity to climate change at the rear-edge**

490 The Mediterranean landscapes, even at high elevations, have suffered a strong transformation
491 landscapes driven by human activities throughout history. Multiple evidence from palaeoecological
492 studies indicated an intense human impact on vegetation of Sierra Nevada since 3000 cal year BP
493 (García-Alix and others 2017). From that moment onwards, increases on fire occurrence and both grazing
494 and mining activities, were recorded for this mountain region, with a sharp intensification of the human
495 activities in the last 150 years (García-Alix and others 2017). Mining, forest clearings, firewood extraction
496 and charcoal exploitations (these were strongly suggested in the disturbance chronology in SJ),
497 pastoralism and also wars, have strongly impacted on the forest resources in Sierra Nevada, and on
498 Pyrenean oak forest, as can be derived from the results of the review of historical documents. As a
499 consequence a loss of about 90% of broadleaf *Quercus* species cover from medium and low elevation
500 occurred in this mountain region (Jiménez-Olivencia and others 2015). Therefore, our study sites have
501 been subjected to an intense exploitation of forest resources in history and landscape transformation.
502 Although the estimated age for our sampled trees was lower than 180 years, several documents reported
503 abundant oak presence before that date. For instance, the inventories of trees made by the Spanish Navy
504 during the second half of 18th century, reported for Cáñar and SJ sites more than two millions and 700
505 000 trees respectively, most of them juveniles, suggesting recent wood fellings (Cruz 1991). These
506 numbers are a reflect of the intense exploitation of the forest resources occurring up to the end of
507 nineteenth century (Calatrava and Sayadi 2019) and also concur with the regeneration peaks observed
508 for several Iberian oak woodlands (e.g. Gea-Izquierdo and Cañellas 2014; Gea-Izquierdo and others
509 2015; Dorado-Liñán and others 2017a).

510 Together with the analysis of the disturbance chronologies, the observe strong differences in stand
511 structure, tree size and age suggest different forest history and a different management origin (*i.e.* land-
512 use legacy) between Northern (coppice) and Southern Populations (high forest, open woodland, Jiménez-
513 Olivencia and others 2015). It has been described a sequential distribution of land-uses along the
514 elevational gradient in the northern site (*e.g.* San Juan): grasslands and shrublands for cattle farming are
515 located at high elevations; then forests formation with some croplands; and at lowlands, irrigated terraces
516 with tree crops (Jiménez-Olivencia and others 2015). Other activities like mining should have determined
517 the forest structure at that northern location, since SJ is located in an area with a high concentration of
518 mines and quarries that have been exploited intermitently throughout history [since the 1950s???](#). On the
519 other hand, woodland areas of the southern slopes (Cáñar) are mixed with a greater percentage of
520 croplands along the elevational gradient where oaks occur (Calatrava and Sayadi 2019), being firewood,
521 charcoal and acorns continuously exploited through history (Valbuena-Carabaña and Gil 2013). Charcoal

522 extraction is well known at least since the 15th century up to middle of the 20th century (Jiménez-Serrano
523 and Serrano-Gutiérrez 2004). From this moment to the present, there were a sharp decrease of the wood
524 extraction, mainly due to rural abandonment and use of gas and fossil fuels, similar to other Fagaceae
525 stands across Europe and the Mediterranean (Valbuena-Carabaña and Gil 2013)..

526 Some of the previous historical records of land-use were expressed in our growth chronologies. The
527 release event at 1940s in the northern site concurs with one period of maximum mining activity in this
528 area (1925 to 1957) (Table S4), with an increase on the use of timbers for the mine tunnels and furnaces
529 that additionally required great quantities of fuelwood to melt the mineral (Titos 1990). This heavy
530 exploitation of neighbouring forest resources should have affected a major part of this oak woodland as
531 shown by growth the remnant trees included in the northern site (Figure S4). In addition, paleoecological
532 studies carried out in nearby alpine bogs have recorded increases in the heavy metals concentration
533 since the end of 18th century until mid-20th, which coincides with the maximum activity of the mining in
534 the northern site (García-Alix and others 2017). The other release event observed for SJ site during 1995-
535 2000 was lower than that occurred at 1940, but also affected most trees (Figures 5, S4). There are no
536 records of forest practices carried out in this area in the last 30 years (Bonet and others 2016) and no
537 record for any logging during 1995 - 2000. Therefore, two non-mutually exclusive ways could explain the
538 tree-growth release observed. Firstly it could be related with a natural drought-induced mortality event
539 after 1995 as has been reported for other tree species after severe drought (e.g. Peñuelas and others
540 2001; Lloret and others 2004). On the other hand, the strong positive correlations of SPEI with tree-
541 growth for this site show a high sensitivity to water availability (Gea-Izquierdo and Cañellas 2014).
542 Previous works reported a sharp decline (or non-production) in latewood production during extreme
543 drought events (Corcuera and others 2006). Since smaller latewood vessels are less vulnerable to
544 embolism than earlywood vessels (Corcuera and others 2006), the reduction or even the non-production
545 of former could negatively affect to tree-growth and also enhanced the mortality, particularly for drier sites
546 (Corcuera and others 2006; Gea-Izquierdo and Cañellas 2014).

547 For southern sites, the only positive release event showed at the earliest years for CA-High site could be
548 related with conversion from closed forest to an open silvopastoral system, a common management
549 applied in the past in Iberian oak woodlands (Cañellas et al. 2004; Gea-Izquierdo et al. 2011)
550 documented in this site (Valbuena-Carabaña and Gil 2013).

551 This pattern concurs with a forest expansion into marginal abandoned croplands and an increase in the
552 tree-cover (Camacho-Olmedo and others 2002).

Comentado [GG22]: Esto queda raro aquí. Lo puedes quitar. Habría que redondear el párrafo anterior, queda medio incompleto.

Comentado [GG23]: La frase que te he borrado está muy repetido. Esta última que dejo aquí es interesante, se podría meter por algún sitio (entiendo que hay estudios que muestran que el robledal se está extendiendo?? Si no es así quítala)

553 Conclusions

554 Severe drought events provoke important reductions in primary and secondary growth of *Q. pyrenaica*
555 forests in the studied relict, rear-edge forest. However, we observed no negative growth trends despite
556 we had expected vulnerability to climate change for these relict stands. Furthermore, we observed
557 positive trends for primary growth (i.e. greenness) at the ecosystem scale and a positive steep trend of
558 secondary growth at the tree level at the most humid site along the climatic gradient analyzed. The trees
559 exhibited high resilience values in response to drought, particularly in the long-term scales, and resilience
560 was directly related to drought severity. These results would be consistent with other research showing
561 that this mountain region is still acting as a refuge for deciduous species, including *Quercus*. The
562 differences observed in tree-growth and resilience to drought between very close sites show that
563 responses to drought were site-dependent and can vary in very small gradients (i.e. following ecological
564 thresholds). This is particularly relevant for rear-edge populations where topographic and biophysical
565 variability facilitates the existence of microrefugia. The analysis of tree-growth dynamics revealed
566 suppression and release events that were consistent with legacies left by land-use in local forest
567 dynamics, as inferred from an exhaustive review of historical documents. In this sense our results
568 highlight the importance of land-use legacies for highly transformed Mediterranean systems. This is
569 relevant for tree species with a high sensitivity to climate change, such as *Q. pyrenaica*, not only for
570 conservation per se of the species, but for all ecosystem services that these singular forests offer at
571 Mediterranean mountain. Following our study it is necessary to further disentangle how ecosystem
572 services and stand dynamics are affected by the combination of climate change and land-use legacies in
573 highly transformed landscapes like the one studied here.

574 Acknowledgements

575 We would like to thank Sammy Lucy Behle, M. Suarez-Muñoz and F.J. Bonet-García for their assistance
576 in the field monitoring. A. Reyes and J. Blanco helped in the filtering of satellite data. F.J. Cano-Manuel
577 and F.J. Navarro provided worthwhile information about oak management projects in Sierra Nevada. We
578 also are very thankful to F.J. Bonet-García for his valuable comments in an earlier version of the
579 manuscript. Environment Department of Andalusian Regional Government and Director of Sierra Nevada
580 National and Natural Park provided permission for field work. This research work was conducted in the
581 collaborative framework of the "Sierra Nevada Global Change Observatory" Project from the Environment
582 Department of Andalusian Regional Government (with the support of European Union FEDER Project).
583 We also thank to LIFE-ADAPTAMED (LIFE14 CCA/ES/000612): *Protection of key ecosystem services by*
584 *adaptive management of Climate Change endangered Mediterranean socioecosystems* and H2020
585 project *ECOPOTENTIAL: Improving future ecosystem benefits through earth observations*
586 (<http://www.ecopotential-project.eu/>) (No 641762), for their funding support.

587 **References**

- 588 Alcaraz-Segura D, Cabello J, Paruelo JM, Delibes M. 2009. Use of descriptors of ecosystem functioning
589 for monitoring a national park network: A remote sensing approach. *Environmental Management*
590 43:38–48.
- 591 Alcaraz-Segura D, Reyes A, Cabello J. 2016. Changes in vegetation productivity according to
592 teledetection. In: Zamora R, Pérez-Luque A, Bonet F, Barea-Azcón J, Aspizua R, editors. *Global*
593 *change impacts in Sierra Nevada: Challenges for conservation*. Consejería de Medio Ambiente y
594 Ordenación del Territorio. Junta de Andalucía. pp 142–5.
- 595 Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A,
596 Breshears DD, Hogg E (Ted), Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H,
597 Allard G, Running SW, Semerci A, Cobb N. 2010. A global overview of drought and heat-induced
598 tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*
599 259:660–84.
- 600 Babst F, Poulter B, Bodesheim P, Mahecha M, C Frank D. 2017. Improved tree-ring archives will support
601 earth-system science. *Nature Ecology and Evolution* 1:1–2.
- 602 Babst F, Poulter B, Trouet V, Tan K, Neuwirth B, Wilson R, Carrer M, Grabner M, Tegel W, Levanić T,
603 Panayotov M, Urbinati C, Bouriaud O, Ciais P, Frank D. 2013. Site- and species- specific
604 responses of forest growth to climate across the European continent. *Global Ecology and*
605 *Biogeography* 22:706–17.
- 606 Bhuyan U, Zang C, Menzel A. 2017. Different responses of multispecies tree ring growth to various
607 drought indices across Europe. *Dendrochronologia* 44:1–8.
- 608 Biondi F, Qeadan F. 2008. A theory-driven approach to tree-ring standardization: Defining the biological
609 trend from expected basal area increment. *Tree-Ring Research* 64:81–96.
610 <https://doi.org/10.3959/2008-6.1>
- 611 Bonet F, Aspizua R, Navarro J. 2016. History of Sierra Nevada forest management: Implications for
612 adaptation to global change. In: Zamora R, Pérez-Luque A, Bonet F, Barea-Azcón J, Aspizua R,
613 editors. *Global change impacts in Sierra Nevada: Challenges for conservation*. Consejería de
614 Medio Ambiente y Ordenación del Territorio. Junta de Andalucía. pp 153–6.
- 615 Bunn AG. 2010. Statistical and visual crossdating in r using the dplR library. *Dendrochronologia* 28:251–
616 8.
- 617 Calatrava J, Sayadi S. 2019. Evolution of farming systems in the mediterranean high mountain: The case
618 of the Alpujarra Alta (Spain). *Sustainability* 11:704. <https://doi.org/10.3390/su11030704>

619 Camacho-Olmedo M, García-Martínez P, Jiménez-Olivencia Y, Menor-Toribio J, Paniza-Cabrera A. 2002.
620 Dinámica evolutiva del paisaje vegetal de la Alta Alpujarra granadina en la segunda mitad del s.
621 XX. Cuadernos Geográficos 32:25–42.

622 Camarero J, Franquesa M, Sangüesa-Barreda G. 2015a. Timing of drought triggers distinct growth
623 responses in holm oak: Implications to predict warming-induced forest defoliation and growth
624 decline. *Forests* 6:1576–97.

625 Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM. 2015b. To die or not to die:
626 Early warnings of tree dieback in response to a severe drought. *Journal of Ecology* 103:44–57.

627 Cañellas I, Del Ri'o M, Roig S, Montero G. 2004. Growth response to thinning in *quercus pyrenaica* willd.
628 Coppice stands in spanish central mountain. *Annals of Forest Sciences* 61:243–50.
629 <https://doi.org/10.1051/forest:2004017>

630 Cavin L, Jump AS. 2017. Highest drought sensitivity and lowest resistance to growth suppression are
631 found in the range core of the tree *Fagus sylvatica* L. Not the equatorial range edge. *Global Change*
632 *Biology* 23:362–79. <http://dx.doi.org/10.1111/gcb.13366>

633 Clark JS, Iverson L, Woodall CW, Allen CD, Bell DM, Bragg DC, D'Amato AW, Davis FW, Hersh MH,
634 Ibanez I, Jackson ST, Matthews S, Pederson N, Peters M, Schwartz MW, Waring KM,
635 Zimmermann NE. 2016. The impacts of increasing drought on forest dynamics, structure, and
636 biodiversity in the United States. *Global Change Biology* 22:2329–52.

637 Cobo-Díaz JF, Fernández-González AJ, Villadas PJ, Toro N, Tringe SG, Fernández-López M. 2017.
638 Taxonomic and functional diversity of a *Quercus pyrenaica* Willd. rhizospheric microbiome in the
639 Mediterranean mountains. *Forests* 8:390. <http://www.mdpi.com/1999-4907/8/10/390>

640 Corcuera L, Camarero JJ, Sisó S, Gil-Pelegrín E. 2006. Radial-growth and wood-anatomical changes in
641 overaged *quercus pyrenaica* coppice stands: Functional responses in a new mediterranean
642 landscape. *Trees* 20:91–8.

643 Coulthard BL, Touchan R, Anchukaitis KJ, Meko DM, Sivrikaya F. 2017. Tree growth and vegetation
644 activity at the ecosystem-scale in the eastern Mediterranean. *Environmental Research Letters*
645 12:084008.

646 Cruz M. 1991. Atlas historico-forestal de Andalucía: siglo XVIII. Granada: Universidad de Granada

647 Dai A. 2011. Drought under global warming: A review. *Wiley Interdisciplinary Reviews: Climate Change*
648 2:45–65.

649 Dionisio MA, Alcaraz-Segura D, Cabello J. 2012. Satellite-based monitoring of ecosystem functioning in
650 protected areas: Recent trends in the oak forests (*quercus pyrenaica* willd.) of sierra nevada

Comentado [GG24]: He intentado arañar algunas citas más, como ves.

651 (spain). In: Young SS, Silvern SE, editors. International perspectives on global environmental
652 change. pp 355–74.

653 Doblas-Miranda E, Alonso R, Arnan X, Bermejo V, Brotons L, Heras J de las, Estiarte M, Hódar J, Llorens
654 P, Lloret F, López-Serrano F, Martínez-Vilalta J, Moya D, Penuelas J, Pino J, Rodrigo A, Roura-
655 Pascual N, Valladares F, Vilà M, Zamora R, Retana J. 2017. A review of the combination among
656 global change factors in forests, shrublands and pastures of the Mediterranean region: Beyond
657 drought effects. *Global and Planetary Change* 148:42–54.

658 Dorado-Liñán I, Cañellas I, Valbuena-Carabaña M, Gil L, Gea-Izquierdo G. 2017a. Coexistence in the
659 Mediterranean-temperate transitional border: Multi-century dynamics of a mixed old-growth forest
660 under global change. *Dendrochronologia* 44:48–57.

661 Dorado-Liñán I, Zorita E, Martínez-Sancho E, Gea-Izquierdo G, Filippo AD, Gutiérrez E, Levanic T,
662 Piovesan G, Vacchiano G, Zang C, Zlatanov T, Menzel A. 2017b. Large-scale atmospheric
663 circulation enhances the Mediterranean east-west tree growth contrast at rear-edge deciduous
664 forests. *Agricultural and Forest Meteorology* 239:86–95.

665 Franco A. 1990. *Quercus* L. In: Castroviejo A, Lainz M, López-González G, Montserrat P, Muñoz-
666 Garmendia F, Paiva J, Villar L, editors. *Flora Ibérica*. Vol. 2. Madrid: Real Jardín Botánico, CSIC.
667 pp 15–36.

668 Fritts HC. 1976. *Tree rings and climate*. London: Academic Press

669 García-Herrera R, Hernández E, Barriopedro D, Paredes D, Trigo RM, Trigo IF, Mendes MA. 2007. The
670 outstanding 2004/05 drought in the Iberian Peninsula: Associated atmospheric circulation. *Journal*
671 *of Hydrometeorology* 8:483–98.

672 García-Alix A, Jiménez-Espejo FJ, Toney JL, Jiménez-Moreno G, Ramos-Román MJ, Anderson RS,
673 Ruano P, Queralt I, Delgado Huertas A, Kuroda J. 2017. Alpine bogs of southern Spain show
674 human-induced environmental change superimposed on long-term natural variations. *Scientific*
675 *Reports* 7:7439.

676 García-González I, Souto-Herrero M. 2017. Earlywood vessel area of *Quercus pyrenaica* Willd. is a
677 powerful indicator of soil water excess at growth resumption. *European Journal of Forest Research*
678 136:329–44.

679 Gazol A, Camarero JJ, Vicente-Serrano SM, Sánchez-Salguero R, Gutiérrez E, Luis M de, Sangüesa-
680 Barreda G, Novak K, Rozas V, Tíscar PA, Linares JC, Martín-Hernández N, Martínez del Castillo
681 E, Ribas M, García-González I, Silla F, Camisón A, Génova M, Olano JM, Longares LA, Hevia A,
682 Tomás-Burguera M, Galván JD. 2018. Forest resilience to drought varies across biomes. *Global*
683 *Change Biology*:1–16.

684 Gea-Izquierdo G, Cañellas I. (2009) Analysis of holm oak intraspecific competition using gamma
685 regression. *Forest Science* 55(4), 310-322.

686 Gea-Izquierdo G, Cherubini P, Cañellas I. (2011) Tree-rings reflect the impact of climate change on
687 *Quercus ilex* L. along a temperature gradient in Spain over the last 100 years. *Forest Ecology and*
688 *Management* 262, 1807-1816.

689 Gea-Izquierdo G, Cañellas I. 2014. Local climate forces instability in long-term productivity of a
690 Mediterranean oak along climatic gradients. *Ecosystems* 17:228–41.
691 <http://dx.doi.org/10.1007/s10021-013-9719-3>

692 Gea-Izquierdo G, Fernández-de-Uña L, Cañellas I. 2013. Growth projections reveal local vulnerability of
693 Mediterranean oaks with rising temperatures. *Forest Ecology and Management* 305:282–93.
694 <http://www.sciencedirect.com/science/article/pii/S0378112713003678>

695 Gea-Izquierdo G, Guibal F, Joffre R, Ourcival J-M, Simioni G, Guiot J. (2015) Modelling the climatic
696 drivers determining photosynthesis and carbon allocation in evergreen Mediterranean forests using
697 multiproxy long time series. *Biogeosciences* 12, 3695-3712.

698 Gea-Izquierdo G, Montes F, Gavilán RG, Cañellas I, Rubio A. 2015. Is this the end? Dynamics of a relict
699 stand from pervasively deforested ancient Iberian pine forests. *European Journal of Forest*
700 *Research* 134:525–36.

701 González-González BD, Rozas V, García-González I. 2014. Earlywood vessels of the sub-Mediterranean
702 oak *Quercus pyrenaica* have greater plasticity and sensitivity than those of the temperate *Q.*
703 *Petraea* at the Atlantic–Mediterranean boundary. *Trees* 28:237–52.

704 Gouveia C, Trigo R, Beguería S, Vicente-Serrano S. 2017. Drought impacts on vegetation activity in the
705 Mediterranean region: An assessment using remote sensing data and multi-scale drought
706 indicators. *Global and Planetary Change* 151:15–27.

707 Hampe A, Petit RJ. 2005. Conserving biodiversity under climate change: The rear edge matters. *Ecology*
708 *Letters* 8:461–7.

709 Hartmann H, Moura CF, Anderegg WRL, Ruehr NK, Salmon Y, Allen CD, Arndt SK, Breshears DD, Davi
710 H, Galbraith D, Ruthrof KX, Wunder J, Adams HD, Bloemen J, Cailleret M, Cobb R, Gessler A,
711 Grams TEE, Jansen S, Kautz M, Lloret F, O'Brien M. 2018. Research frontiers for improving our
712 understanding of drought-induced tree and forest mortality. *New Phytologist* 218:15–28.

713 Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, New M. 2008. A European daily high-
714 resolution gridded data set of surface temperature and precipitation for 1950–2006. *Journal of*
715 *Geophysical Research* 113:D20119. <http://dx.doi.org/10.1029/2008JD010201>

Comentado [GG25]: Posiblemente sea demasiadas autocitas, yo las meto por si te son útiles (aunque por otro lado estoy quitando, pero bueno)

Comentado [GG26]: Si te sobra quita éste que solo se cita una vez

716 Herrero A, Zamora R. 2014. Plant responses to extreme climatic events: A field test of resilience capacity
717 at the southern range edge. *PLOS ONE* 9:e87842.

718 Holling CS. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and*
719 *Systematics* 4:1–23.

720 Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring*
721 *Bulletin* 43:69–78.

722 Huang M, Wang X, Keenan TF, Piao S. 2018. Drought timing influences the legacy of tree growth
723 recovery. *Global Change Biology* 24:3546–59.

724 Jiménez-Olivencia Y, Porcel L, Caballero A. 2015. Medio siglo en la evolución de los paisajes naturales y
725 agrarios de Sierra Nevada (España). *Boletín de la Asociación de Geógrafos Españoles* 68:205–32.

726 Jiménez-Serrano B, Serrano-Gutiérrez J. 2004. El Catastro del Marqués de la Ensenada en el antiguo
727 Reino de Granada.

728 Jump AS, Cavin L, Hunter PD. 2010. Monitoring and managing responses to climate change at the
729 retreating range edge of forest trees. *Journal of Environmental Monitoring* 12:1791–8.

730 Lloret F, Keeling EG, Sala A. 2011. Components of tree resilience: Effects of successive low-growth
731 episodes in old ponderosa pine forests. *Oikos* 120:1909–20. [http://dx.doi.org/10.1111/j.1600-](http://dx.doi.org/10.1111/j.1600-0706.2011.19372.x)
732 [0706.2011.19372.x](http://dx.doi.org/10.1111/j.1600-0706.2011.19372.x)

733 Lloret F, Siscart D, Dalmases C. 2004. Canopy recovery after drought dieback in holm-oak mediterranean
734 forests of catalonia (NE spain). *Global Change Biology* 10:2092–9. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2004.00870.x)
735 [2486.2004.00870.x](https://doi.org/10.1111/j.1365-2486.2004.00870.x)

736 Lorite J, Salazar C, Peñas J, Valle F. 2008. Phytosociological review on the forests of quercus pyrenaica
737 willd. *Acta Botanica Gallica* 155:219–33.

738 Martínez-Vilalta J. 2018. The rear window: Structural and functional plasticity in tree responses to climate
739 change inferred from growth rings. *Tree Physiology*.

740 Martínez-Vilalta J, Lloret F. 2016. Drought-induced vegetation shifts in terrestrial ecosystems: The key
741 role of regeneration dynamics. *Global and Planetary Change* 144:94–108.

742 Navarro-González I, Pérez-Luque AJ, Bonet FJ, Zamora R. 2013. The weight of the past: Land-use
743 legacies and recolonization of pine plantations by oak trees. *Ecological Applications* 23:1267–76.

744 Nowacki GJ, Abrams MD. 1997. Radial-growth averaging criteria for reconstructing disturbance histories
745 from presettlement-origing oaks. *Ecological Monographs* 67:225–49.
746 [http://dx.doi.org/10.1890/0012-9615\(1997\)067\[0225:RGACFR\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(1997)067[0225:RGACFR]2.0.CO;2)

Comentado [GG27]: Falta parte de la cita, completar.

747 Olalde M, Herrán A, Espinel S, Goicoechea PG. 2002. White oaks phylogeography in the Iberian
748 Peninsula. *Forest Ecology and Management* 156:89–102.

749 Páscoa P, Gouveia C, Russo A, Trigo R. 2017. Drought trends in the Iberian Peninsula over the last 112
750 years. *Advances in Meteorology*:ID4653126.

751 Peña-Gallardo M, Vicente-Serrano SM, Camarero JJ, Gazol A, Sánchez-Salguero R, Domínguez-Castro
752 F, El Kenawy A, Beguería-Portugés S, Gutiérrez E, De Luis M, Sangüesa-Barreda G, Novak K,
753 Rozas V, Tiscar PA, Linares JC, Martínez del Castillo E, Ribas Matamoros M, García-González I,
754 Silla F, Camisón Á, Génova M, Olano JM, Longares LA, Hevia A, Galván JD. 2018. Drought
755 sensitiveness on forest growth in peninsular Spain and the balearic islands. *Forests*.
756 <https://www.mdpi.com/1999-4907/9/9/524>

757 Peñuelas J, Lloret F, Montoya R. 2001. Severe drought effects on Mediterranean woody flora in Spain.
758 *Forest Science* 47:214–8.

759 Pérez-Luque AJ, Zamora R, Bonet FJ, Pérez-Pérez R. 2015a. Dataset of migrame project (global
760 change, altitudinal range shift and colonization of degraded habitats in Mediterranean mountains).
761 *PhytoKeys* 56:61–81.

762 Pérez-Luque A, Pérez-Pérez R, Bonet-García F, Magaña P. 2015b. An ontological system based on
763 modis images to assess ecosystem functioning of Natura 2000 habitats: A case study for *Quercus*
764 *pyrenaica* forests. *International Journal of Applied Earth Observation and Geoinformation* 37:142–
765 51.

766 Piovesan G, Biondi F, Filippo AD, Alessandrini A, Maugeri M. 2008. Drought-driven growth reduction in
767 old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology*
768 14:1265–81. <http://dx.doi.org/10.1111/j.1365-2486.2008.01570.x>

769 Reyes-Díez A, Alcaraz-Segura D, Cabello-Piñar J. 2015. Implicaciones del filtrado de calidad del índice
770 de vegetación EVI para el seguimiento funcional de ecosistemas. *Revista de Teledetección*
771 2015:11–29.

772 Río S del, Herrero L, Penas Á. 2007. Bioclimatic analysis of the *Quercus pyrenaica* forests in Spain.
773 *Phytocoenologia* 37:541–60.

774 Rubino D, McCarthy B. 2004. Comparative analysis of dendroecological methods used to assess
775 disturbance events. *Dendrochronologia* 21:97–115.

776 Salzer MG, Hughes MK, Bunn AG, Kipfmüller KF. 2009. Recent unprecedented tree-ring growth in
777 bristlecone pine at the highest elevations and possible causes. *PNAS* 106:20348–53.

Comentado [GG28]: Hay algún artículo del tema más moderno (ahora no me viene a la cabeza). Pero al menos hay que citar éste: la tendencia positiva es solo en sitios fríos/altos (y no siempre, por eso pongo no-lineal).

778 Samanta A, Ganguly S, Vermote E, Nemani RR, Myneni RB. 2012. Interpretation of variations in MODIS-
 779 measured greenness levels of amazon forests during 2000 to 2009. Environmental Research
 780 Letters 7:024018.

781 Sánchez-Salguero R, Navarro-Cerrillo RM, Swetnam TW, Zavala MA. 2012. Is drought the main decline
 782 factor at the rear edge of Europe? The case of southern Iberian pine plantations. Forest Ecology
 783 and Management 271:158–69.

784 Spinoni J, Naumann G, Vogt J, Barbosa P. 2015. European drought climatologies and trends based on a
 785 multi-indicator approach. Global and Planetary Change 127:50–7.

786 Spinoni J, Vogt JV, Naumann G, Barbosa P, Dosio A. 2017. Will drought events become more frequent
 787 and severe in Europe? International Journal of Climatology.

788 Stagge JH, Kingston DG, Tallaksen LM, Hannah DM. 2017. Observed drought indices show increasing
 789 divergence across Europe. Scientific Reports 7:14045. <https://doi.org/10.1038/s41598-017-14283-2>

790 Stocker BD, Zscheischler J, Keenan TF, Prentice IC, Seneviratne SI, Peñuelas J. 2019. Drought impacts
 791 on terrestrial primary production underestimated by satellite monitoring. Nature Geoscience
 792 12:264–70. <https://doi.org/10.1038/s41561-019-0318-6>

793 Titos M. 1990. Las minas de la Estrella. In: Titos M, editor. La aventura de Sierra-Nevada 1717-1915.
 794 Editorial Universidad de Granada. pp 226–36.

795 Trigo RM, Añel JA, Barriopedro D, García-Herrera R, Gimeno L, Castillo R, Allen MR, Massey A. 2013.
 796 The record Winter drought of 2011-12 in the Iberian Peninsula. In: Peterson MPH T. C., Herring S,
 797 editors. Explaining extreme events of 2012 from a climate perspective. Vol. 94. pp S41–5.

798 Valbuena-Carabaña M, Gil L. 2013. Genetic resilience in a historically profited root sprouting oak
 799 (*Quercus pyrenaica* Willd.) at its southern boundary. Tree Genetics & Genomes 9:1129–42.

800 Valbuena-Carabaña M, Gil L. 2017. Centenary coppicing maintains high levels of genetic diversity in a
 801 root resprouting oak (*Quercus pyrenaica* Willd.). Tree Genetics & Genomes 13:28.

802 Vicente-Serrano SM, Beguería S, López-Moreno JI. 2010. A multiscalar drought index sensitive to global
 803 warming: The standardized precipitation evapotranspiration index. Journal of Climate 23:1696–718.

804 Vicente-Serrano SM, Camarero JJ, Azorín- Molina C. 2014a. Diverse responses of forest growth to
 805 drought time- scales in the northern hemisphere. Global Ecology and Biogeography 23:1019–30.

806 Vicente-Serrano SM, Gouveia C, Camarero JJ, Beguería S, Trigo R, López-Moreno JI, Azorín-Molina C,
 807 Pasho E, Lorenzo-Lacruz J, Revuelto J, Morán-Tejeda E, Sanchez-Lorenzo A. 2013. Response of
 808 vegetation to drought time-scales across global land biomes. Proc Natl Acad Sci U S A 110:52–7.

Comentado [GG29]: Hay muchas citas de sequía y clima. Puedes quitar un par de ellas.

Comentado [GG30]: Lo mismo si te puedes ahorrar uno de los 4 Vicente-Serranos (a menos que no sean repetidas las citas).

809 Vicente-Serrano SM, López-Moreno JI, Beguería S, Lorenzo-Lacruz J, Sanchez-Lorenzo A, García-Ruiz
 810 JM, Azorín-Molina C, Morán-Tejeda E, Revuelto J, Trigo R, Coelho F, Espejo F. 2014b. Evidence
 811 of increasing drought severity caused by temperature rise in southern Europe. *Environmental*
 812 *Research Letters* 9:044001.

813 Wilcox R. 2012. *Introduction to robust estimation and hypothesis testing* (third edition). Third Edition.
 814 Academic Press

815 Zang C, Biondi F. 2015. Treeclim: An r package for the numerical calibration of proxy-climate
 816 relationships. *Ecography* 38:431–6.

817 Zhang Y, Peng C, Li W, Fang X, Zhang T, Zhu Q, Chen H, Zhao P. 2013. Monitoring and estimating
 818 drought-induced impacts on forest structure, growth, function, and ecosystem services using
 819 remote-sensing data: Recent progress and future challenges. *Environmental Reviews* 21:103–15.

Página 2: [1] Eliminado	Guillermo Gea Izquierdo	29/7/19 15:05
--------------------------------	--------------------------------	----------------------

both [GG1]in primary and secondary growth than Southern populations where lower altitudes were also less resilient than those at high-altitudes

.

Página 2: [2] Comentado	Guillermo Gea Izquierdo	30/7/19 10:30
--------------------------------	--------------------------------	----------------------

¿Es esto verdad? Figs 6 y 7: R_t menor en SJ pero R_s y R_c son (no siempre) mayores. Sería al revés entonces? Más estrés, más resiliencia (en BAI) pero menos resistencia? Revísalo para que quede coherente, creo que ahora mismo no es cierto lo que se pone.

Página 2: [3] Eliminado	Guillermo Gea Izquierdo	30/7/19 12:34
--------------------------------	--------------------------------	----------------------

, the trees showed high resilience in response to drought. Yet, t

.

Página 2: [4] Eliminado	Guillermo Gea Izquierdo	30/7/19 12:38
--------------------------------	--------------------------------	----------------------

s only in the coldest and more humid stands

.