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Monica Turner and Stephen Carpenter
Editors-in-Chief of Ecosystems,

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Dear Editors:

We are pleased to submit an original research article entitled “*Oak resilience to drought and land use show how the ecological and geographical rear edges do not necessarily meet today*” by Antonio J. Pérez-Luque, Guillermo Gea-Izquierdo, Regino Zamora, to be considered for publication in Ecosystems.

This manuscript aims to test if rear-edge populations have a concordance between geographical and ecological marginality, with lower performance, higher vulnerability than do populations at the core of the species' range. We combined dendroecological methods and remote-sensing information to evaluate the impact of drought on radial tree growth and canopy greenness (as proxies for secondary and primary growth) on Mediterranean *Quercus pyrenaica* populations located at the rear-edge of the species distribution. Forest resilience to several extreme drought episodes and to climate change over the long term was also evaluated.

The high values of resilience found for tree growth and canopy greenness suggest that *Q. pyrenaica* populations in Sierra Nevada are located in a geographical but not a climatic, ecological rear edge; with major importance of land-use changes in the current niche. The resilience responses of oak forest to drought events are not spatially homogeneous throughout the mountain range, due to differences in ecological conditions and/or past-management legacies.

Our results suggest that rear edge needs to be redefined, partly because of land-use legacies and their effect on the possible mismatch between the current distribution of species (*i.e.* determining the "available" geographical rear edge) and the ecological (limiting) rear edge of species. We hope you find this research interesting and suitable for publication in Ecosystems because it deals with a traditional paradigm in Ecology (center-periphery hypothesis).

This manuscript has not been published and is not under consideration for publication elsewhere. We have no conflicts of interest to disclose.

Thank you in advance for your consideration

Sincerely,



On behalf of the co-authors,
Antonio J. Pérez-Luque

1 **Land-use legacies and high oak resilience to drought show how the**
2 **ecological and geographical rear edges do not necessarily meet today**

3 **Short title: Relict oak resilience at the rear edge**

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11 **Manuscript highlights**

- 12 • *Quercus pyrenaica* rear-edge forests showed high resilience at tree and stand levels
13 • Resilience and growth response to climate followed a water-stress gradient
14 • Trees and stand expressed high sensitivity to drought and land-use legacies

15 **Abstract**

- 16 • Global change challenges ecosystems in dry locations transformed by intensive human use. Forest
17 resilience to drought of relict Mediterranean *Quercus pyrenaica* Willd. populations in the southern
18 Iberian Peninsula was analyzed in relation to historical records of land use employing

1 Author Contributions. AJPL, GGI and RZ conceived of the study, conducted field work, and collected the data. AJPL and GGI performed the lab work. 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.

19 dendroecological growth of adult trees and greenness (EVI) as proxies for secondary and primary
20 growth.

- 21 • The growth trends reflected a strong influence of land-use legacies (e.g. firewood removal) in the
22 current forest structure. Trees were highly sensitive to moisture availability but both primary and
23 secondary growth expressed high resilience to drought events over the short and the long term.
24 Resilience and response to climate followed a water-stress gradient. Primary and secondary growth
25 were generally less resilient to drought in mesic than in xeric sites, whereas a positive growth trend
26 matching the warming climate since the late 1970s was particularly evident in mesic (i.e. colder and
27 wetter) high-elevation stands, but absent in the most xeric (i.e. warmer and drier) site.
- 28 • Adult oak trees showed high resilience to drought despite being considered relict and at its rear
29 edge. The trees varied in response to the changing climate along a narrow climatic gradient and
30 showed that the ecological and geographical rear edges do not need to meet today in forests with
31 strong land use legacies. Forest resilience including that of regeneration needs to be monitored at
32 xeric of the species under future expected climatic scenarios given that ecological boundaries for
33 species distribution can be narrow and that land-use legacies can play a key role in stand dynamics.

34 **Keywords**

35 extreme drought, resilience, rear edge, *Quercus pyrenaica*, tree growth, dendrochronology, remote
36 sensing

37 **Introduction**

38 The response of species to changing environments is likely to be determined largely by population
39 responses at range margins (Hampe and Petit 2005). Peripheral populations are usually considered more
40 vulnerable compared with populations occurring at the center of a species' range (i.e. center-periphery
41 hypothesis; Sagarin and Gaines 2002; Pironon and others 2016). It has been assumed that rear-edge
42 populations have a concordance between geographical and ecological marginality, with lower
43 performance, higher vulnerability, and thus higher risk of extinction than do populations at the core of the
44 species' range (Pironon and others 2016; Vilà-Cabrera and others 2019). Nonetheless, recent reviews
45 report that species- and population-specific responses do not always support this hypothesis (Sexton and
46 others 2009; Abeli and others 2014). In this respect, to fully understand changes in distribution and
47 abundance of species as a consequence of global-change, we need to determine under what
48 environmental conditions geographical marginality does not correspond with ecological marginality (Vilà-
49 Cabrera and Jump 2019).

50 Climate change is expected to cause major shifts in the distribution and abundance of plant communities,
51 and there are already signs of processes associated with increased intensity and duration of droughts
52 (Allen and others 2010). In fact, the frequency and severity of drought events have increased in recent
53 decades, along with a trend towards drier summers, particularly for Southern Europe (Vicente-Serrano
54 and others 2014; Stagge and others 2017). This is especially critical, since climate-change projections for
55 the Mediterranean area forecast more frequent and severe extreme climate events (Spinoni and others
56 2017). In this climatic-change context, population loss and range retractions are expected in boreal,
57 temperate, and Mediterranean species at the lowest latitudes, elevations, and drought-prone areas of a
58 species' distribution, *i.e.* the rear edge (Hampe and Petit 2005). In a global-change context, the impact of
59 drought on vegetation needs to be evaluated regarding the interactions with other drivers of change
60 (Doblas-Miranda and others 2017). This is especially relevant for areas with a long history of landscape
61 alteration, such as the Mediterranean region, where land-use change plays a major role in current
62 ecosystem ecology (Navarro-González and others 2013), given that the interactions of drought and land-
63 use change are crucial for Mediterranean forests (Doblas-Miranda and others 2017).

64 The effects of drought are also especially relevant for populations considered to be located along the rear
65 edge (either latitudinal or altitudinal along climatic gradients) of their distribution, where climatic conditions
66 mark the species limits, and the populations are likely to be more sensitive to minor climatic and
67 microtopographic variations (Hampe and Petit 2005). The response of rear-edge populations to climate
68 variations could be useful in estimating the adaptation of species to predicted climatic changes (Jump and
69 others 2010). Yet it is crucial to accurately characterize the ecological rear-edge of species. This can be
70 particularly misleading in ecosystems with strong land-use legacies because it is established from current
71 species distribution (Vilà-Cabrera and others 2019). Furthermore, this characterization becomes even
72 more critical for relict populations driven by historical land uses when they harbor high levels of
73 intraspecific genetic diversity (Valbuena-Carabaña and Gil 2013).

74 Understanding the vegetation response to drought requires integrative and multidisciplinary strategies to
75 assess the disturbances of forest at several scales (Hartmann and others 2018). The assessment of
76 resilience to climate disturbances such as droughts provides critical information concerning the capacity
77 of the forests to maintain their structure and render valuable ecosystem services. The drought resilience
78 of species is better assessed when several approaches, such as dendrochronology and remote sensing,
79 are combined. Dendroecological estimates of growth (*i.e.* tree-ring width) are commonly used proxies to
80 characterize tree vitality, and annual tree-ring widths can be used to study changes in growth as a
81 response to drought at the individual-tree scale (Fritts 1976). Remote sensing can be used to study the
82 impact of drought on ecosystems and hence the stand level (*e.g.* Zhang and others 2013). The
83 combination of both approaches (remote sensing and dendroecology) has been used to assess the
84 effects of droughts on vegetation along ecological gradients (*e.g.* Vicente-Serrano and others 2013;
85 Coulthard and others 2017), and also to evaluate growth resilience to drought in several tree species (*e.g.*

86 Gazol and others 2018; Peña-Gallardo and others 2018). Nonetheless, it is crucial to ascertain whether the
87 responses at the tree level differ from those at the ecosystem level and characterize the spatial variability
88 of this response in rear-edge populations.

89 In the present study, we used remote-sensing information and dendroecological methods to evaluate the
90 impact of drought in both canopy greenness (as a proxy to primary growth) and radial tree growth (as a
91 proxy for secondary growth) of *Quercus pyrenaica* Willd. (Pyrenean oak, *melojo*) in southern relict forests
92 at the rear-edge of the species distribution and where species performance is considered to be severely
93 threatened by climate change. We also assessed the resilience of these forests both to several extreme
94 drought episodes and to climate change (*i.e.* warming) over the long term (in the last few decades). Our
95 main hypothesis is that these relict populations driven by historical land use are vulnerable to climate
96 change at their present climatic (either elevational or latitudinal) rear edge, and hence will show low
97 resilience to extreme drought along climatic gradients at a small scale within the rear edge. To test this
98 hypothesis, we: (*i*) quantified how recent extreme drought events influenced primary and secondary
99 growth of *Q. pyrenaica* forests at their present geographical rear edge; (*ii*) analyzed the long-term
100 resilience of these forests to extreme drought events, using time-series of radial growth; (*iii*) and
101 examined differences in the resilience metrics between populations located in contrasting ecological
102 conditions (*i.e.* xeric vs. mesic) along environmental gradients within the rear edge in order to detect
103 vulnerability to climate change at the small spatial scale. For the latter task, we characterized the
104 variability in the forest response to drought within the current geographical rear edge and assessed
105 whether the effect of aspect and environmental conditions expressed in northern and southern
106 populations of *melojo* oak forests differ in their resistance, resilience and recovery to extreme drought
107 events.

108 **Materials and methods**

109 **Tree species and study site**

110 *Quercus pyrenaica* forests extend throughout south-western France and the Iberian Peninsula reaching
111 their southern limit in mountain areas of northern Morocco (Franco 1990). In the Iberian Peninsula, these
112 forests occupy siliceous soils under meso-supramediterranean and mesotemperate areas and subhumid,
113 humid, and hyperhumid ombroclimate. *Q. pyrenaica* is a deciduous species that requires over 650 mm of
114 annual precipitation and some summer precipitation. As a submediterranean species, it has lower drought
115 tolerance than evergreen Mediterranean taxa (Río and others 2007).

116 The forests of this species reach their southernmost European limit in Andalusian mountains such as
117 Sierra Nevada (37°N, 3°W), a high-mountain range with elevations of up to 3482 m a.s.l.. The climate is
118 Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought but

119 with marked variability according to elevation. Sierra Nevada is considered a glacial refuge for deciduous
120 *Quercus* species (Olalde and others 2002). Eight melojo oak patches (2400 ha) have been identified in
121 this mountain range (Figure 1), from 1100 to 2000 m a.s.l. and often associated with major river valleys.
122 Today, *Q. pyrenaica* woodlands in this mountain region represent a rear edge of their habitat distribution
123 (Hampe and Petit 2005). They are the richest forest formation of Sierra Nevada, sheltering several
124 endemic and endangered plant species (Lorite and others 2008). These relict forests have undergone
125 intensive human use throughout history (Camacho-Olmedo and others 2002). Furthermore, the
126 conservation status of this species for southern Spain is considered “Vulnerable” and it is expected to
127 suffer from climate change, reducing its suitable habitats in the near future (Gea-Izquierdo and others
128 2013).

129 **Climatic data and drought episodes**

130 Climate data were obtained from the European Daily High-Resolution Observational Gridded Dataset (E-
131 OBS v16) (Haylock and others 2008). Monthly precipitation and minimum and maximum temperatures
132 had a 0.25 x 0.25 ° resolution for the 1950-2016 period. Grid cells were select to cover each sampled site.
133 The SPEI (Standardized Precipitation-Evapotranspiration Index) (Vicente-Serrano and others 2010) index
134 with a temporal scale of 6 months was used to characterize the drought conditions for the period 1961-
135 2014.

136 The Iberian Peninsula underwent several extreme drought episodes in the last three decades (e.g. 1995,
137 1999, 2005, 2012) (Vicente-Serrano and others 2014). The 2005 and 2012 drought events have been
138 documented as being among the worst in recent decades for the southern Iberian Peninsula (Páscoa and
139 others 2017), and they were characterized as extreme drought in our climatic data (Figure S1; Table S3).
140 We focused on these two drought events because they were included in the period having remote-
141 sensing information of high spatial resolution (MODIS started on 2000; see below). Nevertheless, for
142 radial growth-time series, a greater number of older drought events were also analyzed to contextualize
143 the results for 2005 and 2012 and to evaluate forest resilience to drought over a longer term (see Table
144 S3). A drought event was identified using the SPEI 12-months scale, following a procedure similar to the
145 one proposed by Spinoni and others (2015). We used 0.5° grid cells covering Sierra Nevada taken from
146 the Global SPEI Database (<http://spei.csic.es/database.html>). A severe drought event starts when SPEI
147 falls below the threshold of -1.28 (Páscoa and others 2017; Spinoni and others 2017). A drought event is
148 considered only when SPEI values fall below that threshold for at least two consecutive months. For each
149 drought event, we computed: the *duration* as the number of consecutive months with the SPEI lower than
150 a certain threshold; the *severity* as the sum of the absolute SPEI values during the drought event; the
151 *intensity* and the *Lowest SPEI* refer to the mean and lowest value of SPEI respectively during the drought
152 event.

153 **Greenness data to assess ecosystem resilience**

154 Vegetation greenness of *Q. pyrenaica* was characterized by means of the *Enhanced Vegetation Index*
155 (EVI), derived from MOD13Q1 product of the MODIS sensor. EVI data consists of 16-day maximum value
156 composite images (23 per year) of the EVI value with a spatial resolution of 250 m x 250 m. MODIS EVI
157 data were compiled for the period 2000 - 2016. We selected the pixels covering the distribution of *Q.*
158 *pyrenaica* forests in Sierra Nevada ($n = 928$ pixels). Any values affected by clouds, snow, shadows or
159 high content of aerosols, were filtered out following recommendations for mountain regions (Reyes-Díez
160 and others 2015).

161 The mean Annual EVI (EVI_{mean}) as a surrogate of mean annual primary production was computed for
162 each pixel for the period 2000 - 2016. The EVI standardized anomaly (EVI_{sa}) was computed pixel-by-
163 pixel, in order to minimize bias in the evaluation of anomalies and to provide more information concerning
164 their magnitude (Samanta and others 2012). For each pixel, an annual EVI value was calculated by
165 averaging EVI valid values. Then, the standardized anomaly was computed as: $EVI_{sa,i} = (EVI_{mean,i} -$
166 $EVI_{mean,ref})/\sigma_{ref}$, where $EVI_{sa,i}$ is the EVI standardized anomaly for year i ; $EVI_{mean,i}$ the annual mean
167 value of EVI for year i ; $EVI_{mean,ref}$ the average of the annual EVI values for the period of reference 2000-
168 2016 (all except year i); and σ_{ref} the standard deviation for the reference period. Each pixel was
169 categorized according the EVI standardized anomalies as "greening" ($EVI_{sa} > 1$), "browning" ($EVI_{sa} <$
170 -1) or "no-changes" ($-1 > EVI_{sa} > 1$)(Samanta and others 2012).

171 Rather than other vegetation indices such as the NDVI, EVI_{mean} was chosen because it is highly stable
172 under the use of any filter (Reyes-Díez and others 2015) and because it showed highly significant
173 correlations with annual ($r= 0.81$) and seasonal EVI values ($r_{spring}= 0.76$ and $r_{summer}= 0.88$). For
174 exploratory purposes, temporal trends of EVI_{mean} were examined at the pixel scale, using the Mann-
175 Kendall nonparametric test.

176 **Field sampling and dendrochronological methods to assess individual tree resilience**

177 Trees were sampled during autumn 2016 at two locations in contrasting N-S slopes of Sierra Nevada:
178 San Juan (SJ), a xeric site located at the northern aspect; and Cáñar (CA), a wetter site located at the
179 southern aspect (Figure 1; Table 1). For the southern site, two elevations were sampled: CA-Low (around
180 1700 m) and CA-High (around 1860 m), constituting the current low-elevational limit (CA-Low) and the
181 tree-line (CA-High), respectively, in the sampled aspect. Despite the proximity of these two elevations
182 (less than a 200-m difference) the stands differ markedly in their structure and characteristics (Table 1).
183 The three sampling sites followed a moisture gradient: SJ < CA-Low < Ca-High (Table 1). All the sites
184 were oak monospecific and representative of the population clusters identified for the species in this
185 mountain range (Pérez-Luque and others 2015b). At each site, between 15 and 20 trees from either the

186 single dominant-codominant layer in CA or the open canopy in SJ were randomly sampled. Two cores of
187 5 mm of diameter were taken from each tree at breast height (1.3 m) using an increment borer. Diameter
188 at breast height (DBH) and total height were measured for each tree. In addition, stand competition
189 affecting target trees was assessed by recording distance, azimuth, DBH, species, and total height of all
190 neighboring living trees with DBH > 7.5 cm within a circular plot with a 10-m radius. Several competition
191 indices were calculated: the distance independent indices *density* ($\text{trees} \cdot \text{ha}^{-1}$), and *basal area* (BA, $\text{m}^2 \cdot$
192 ha^{-1}); and the distance dependent index size ratio proportional to distance as $\text{srd} = \sum_{i=1}^n (dbh_j/dbh_i) \cdot$
193 $[1/(dist_{ij} + 1)]$ (see Gea-Izquierdo and Cañellas 2009 for more details). Differences between sites for
194 height, DBH and competition indices were analyzed using non-parametric Kruskal-Wallis rank sum tests.
195 When significant differences were detected, multiple comparisons were run using the Dunn's-test with
196 Bonferroni adjustment to correct for significance.

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

202 The growth trends were analyzed at different time scales. To study the growth response to the inter-
203 annual variability of climate (short-term response), pre-whitened residual chronologies (RWI) were used.
204 These were calculated from ratios between raw growth measurements and individual cubic splines with a
205 50% frequency cutoff at 30 years (Fritts 1976). Tree-ring width series were standardized and detrended
206 using dp1R (Bunn 2010). Mean residual site chronologies were established by computing the biweight
207 robust mean of all prewhitened growth indices for the trees of the same site (Fritts 1976). The statistical
208 quality of each chronology was checked via the expressed population signal (EPS). A threshold value of
209 EPS > 0.85 was used to determine the cutoff year of the time span that could be considered reliable.

210 The long-term growth response was analyzed using basal area increment (hereafter BAI, $\text{cm}^2 \cdot \text{year}^{-1}$). In
211 theory, BAI represents a more accurate indicator of growth than ring width, since it removes variation in
212 growth attributable to increasing stem circumference after 30-40 years of juvenile growth (Biondi and
213 Qeadan 2008). Raw ring widths and measured DBH were used to compute BAI (Piovesan and others
214 2008) with the following equation: $BAI = \pi(r_t^2 - r_{t-1}^2)$ where r is the radius of the tree and t is the year of
215 tree-ring formation. For each individual tree, a mean BAI series was calculated. Then, mean site BAI
216 chronologies were determined by averaging individual tree BAI time series.

217 Disturbance analyses

218 Disturbance chronologies were built using tree-ring width to identify abrupt and sustained increases
219 (release events from competition) or decreases (suppressions) in radial growth (Nowacki and Abrams

1997) as indirect estimates of possible disturbance events (e.g. logging, drought-induced neighbor mortality) in the past. 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: $\%GC = [(M1 - M2)/M2] \times 100$, where $M1$ is the preceding 10-year median and $M2$ is the subsequent 10-year median (Rubino and McCarthy 2004).

Site-disturbance chronologies were constructed by annually averaging the individual disturbance series. To separate growth peaks caused 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 (e.g. Gea-Izquierdo and Cañellas 2014). In addition, the history of the forest and management of our sampling sites was inferred from a detailed analysis of historical land-use changes. For this, existing historical documents were exhaustively reviewed to compile information on socio-economical activities affecting the forests being studied (Table S4). We reviewed several documentary sources: historical documents and maps; detailed mining reports; official information on recent wildfires events and forest-management practices; livestock farming; traditional irrigation channels; and studies concerning the socioeconomic dynamics of forests on Sierra Nevada at different scales (see Table S4 for references).

Assessing ecosystem and tree individual resilience to drought

To evaluate the effects of drought events on ecosystem resilience (using greenness data) and individual tree resilience (using BAI data), we used resilience indices proposed by Lloret and others (2011). The Resistance index estimated as the ratio between performance during and before the disturbance ($Rt = Drought/PreDrought$) quantifies the severity of the impact of the disturbance in the year it occurred. The Recovery index, computed as the ratio between performance after and during disturbance ($Rc = PostDrought/Drought$), represents the ability to recover from disturbance relative to its severity. Finally, the Resilience index ($Rs = PostDrought/PreDrought$) is the capacity to reach pre-disturbance performance levels. The values of these indices were computed for tree growth (BAI) and greenness (EVI mean) during each drought event. The predrought and postdrought values of each target variable (i.e. BAI or EVI) were computed as the mean value over a period of three years before and after the drought event, respectively. A period of three years was chosen because we found similar results on comparing periods of two, three, and four years (Figure S3b), and this time period has been used in other studies (e.g. Gazol and others 2018). Resilience metrics for BAI data were additionally computed for the most severe drought events since 1940 ($n = 8$; Table S3) and compared with drought severity.

251 **Statistical analysis**

252 Relationships between RWI and BAI site chronologies and climatic variables were assessed using
253 bootstrapped Pearson's correlations estimated using `treeclim` (Zang and Biondi 2015). For each of the
254 three resilience indices studied, we used robust two-way ANOVAs to test for differences between drought
255 events (2005 and 2012) and the oak populations studied (northern and southern aspects). These tests
256 were used because original and log-transformed data did not follow the assumptions of normality or
257 homogeneity of variance (Wilcox 2012). Robust measures of central tendency (M-estimator based on
258 Huber's Psi) were used because they were close to the mean value in all cases (Wilcox 2012). When the
259 robust ANOVA test was run, data were bootstrapped 3000 times and trimmed automatically to control the
260 potential influence of outliers. *Post-hoc* differences were assessed pairwise using a similar bootstrap test.
261 All the robust ANOVA and *post-hoc* tests were carried out using the `WRS2` package. The level of
262 significance was set to 0.05 and adjusted for multiple comparisons.

263 **Results**

264 **Time trends in vegetation greenness**

265 The analysis of time trends in greenness showed that 78.9% of the EVI pixels followed a positive trend for
266 the 2000-2016 period. The lowest values of EVI standardized anomalies for the study period were
267 recorded during the 2005 drought, and the minimum EVI values were expressed in the northern (dry)
268 population (Figure 2a). A "browning" episode ($\text{EVI}_{\text{sa}} < -1$) was found during this drought event, whereas
269 no changes in greenness in response to the 2012 drought were detected (Figure 2b).

270 **Analysis of radial-growth trends and disturbances**

271 The trees of the southern population were older than those from the northern one. In addition, trees from
272 the southern population at high elevation were taller and their growth was significantly faster than that of
273 trees from the other two sites, despite the competition measured as plot basal area was greatest in CA-
274 High (Table 1, Figure 3). The growth and height of trees from the northern and the low-elevation southern
275 population proved similar (Figures 3 and S3a). Only trees from the southern sites (*i.e.* the wetter aspect)
276 showed significant positive growth trends since the late 1970s (Figure 3), this trend being far more
277 pronounced for the high elevation, the wetter, colder site (CA-High).

278 Drought events reduced radial growth for all sites (Figure S2a), this negative effect being particularly
279 evident for the 1995 drought (the worst drought spell in our climatic record, Table S3), when the greatest
280 growth reduction was recorded for all chronologies. Tree-growth reduction followed a moisture gradient.
281 The southern sites (CA-High and CA-Low) showed less tree-growth reductions than did the northern site

282 (SJ), especially for 2005 and 2012 (Figure S2a), with the weakest growth reductions being in trees from
283 the wettest site (Figure 3).

284 The northern site (SJ) showed two major release events ($GC > 50\%$ occurring in more than 50% of trees
285 sampled): the first during the 1940s (the most evident) and the second in 1995-2000 (Figure 4). These
286 periods alternated with periods of suppression. By contrast, the two southern sites showed no release
287 events except for CA-High at the beginning of the 1830s and no suppression events in the last 50 years.

288 **Resilience to drought events at the ecosystem and individual-tree levels**

289 Rs and Rt varied in the same direction whereas Rc varied inversely to Rs and Rt . Resilience metrics of
290 tree-growth for drought events since 1950 (*i.e.* shared period among the three chronologies excluding the
291 juvenile years, Table S3) revealed a positive relationship between drought severity and Rc , significant for
292 all oak populations (Figure 5). A similar pattern was found for Rs but proved significant only for SJ.
293 Importantly, non-significant patterns resulted when we excluded 1995, except for Rc in SJ (Figure S5).
294 The trees showed the highest value of tree-growth resilience for 1995, the worst drought event in our
295 study area, particularly SJ where our results suggest a major release event also after 1995 (Figure 4).

296 During the last two drought events, resilience metrics for greenness and tree-growth were significantly
297 different between drought events (Table S1). The 2005 drought event reduced greenness and growth
298 more than that of 2012 (Table S2) but the metrics of resilience generally covaried in the same direction
299 during those two years. Resilience and resistance values were significantly higher for 2012, the most
300 severe event, than for 2005 in both variables (Table S2; Figure 6). Thus, recovery values for greenness
301 were higher for 2005 than for the 2012 drought event. Recovery showed a contrasting pattern for EVI and
302 tree growth.

303 The resilience metrics calculated varied significantly between sites, except for resilience of tree growth (p
304 = 0.534; Table S1), which was similar among the three sites. The two southern populations showed lower
305 recovery values than did the northern site both for greenness and tree growth, but resistance and
306 resilience values were significantly higher for the southern site (Table S2).

307 **Tree-growth response to climate**

308 The response of tree growth to water availability was greater than to temperatures. Cumulative
309 precipitation of the hydrological year and seasonal SPEI values (*i.e.* for the Hydrological year, Spring and
310 Summer) were the climatic variables exhibiting the highest (positive) relationship with growth for all
311 populations (Figure 7a). Nevertheless, differences appeared between northern and southern populations:
312 the positive relationship with SPEI was highest in the more xeric northern population ($r > 0.6$ vs. $r < 0.5$;
313 Figure 7a). In addition, the spring maximum temperature was the most significant limitation for

314 treemgrowth only for the southern populations (Figure 7b and 7c), whereas minimum and maximum
315 temperatures of the current September positively influenced tree growth only in the northern population.

316 **Discussion**

317 By using a combined approach of remote-sensing information and dendrochronology, we have quantified
318 the drought impact on the melojo oak forests of Sierra Nevada and their resilience to several severe
319 drought events in the recent decades. Our results indicated that these relict oak populations driven by
320 historical land use are resilient to climate change at their present rear edge. However, resistance,
321 resilience, and forest recovery to extreme drought events are strongly influenced by mountain aspect,
322 local environmental conditions, and management legacies. This means that the geographical and the
323 ecological rear edges do not necessarily match and, at a small spatial scale, tree performance varies
324 markedly along the rear edge under climate change.

325 **Land-use legacies shape sensitivity to climate change of forests and the present rear edge**

326 The review of historical documents revealed that forest clearings, firewood removal, charcoal making, and
327 mining have strongly affected the forests on Sierra Nevada (Table S4), where an estimated historical loss
328 of broadleaf *Quercus* species approaches 90% of the cover at medium and low elevations (Jiménez-
329 Olivencia and others 2015). Together with the analysis of the disturbance chronologies, the observed
330 notable differences in stand structure, tree size, and age suggest different forest histories and a different
331 management origin (*i.e.* land-use legacy) between northern (coppice) and southern populations (high
332 forest, open woodland). On the northern slopes of Sierra Nevada (*e.g.* SJ site), land uses have been
333 historically distributed along an elevational gradient: grasslands and shrublands for cattle farming at the
334 highest elevations; then forest stands with some croplands; and irrigated terraces with tree crops at the
335 lowest elevations (Jiménez-Olivencia and others 2015). In addition, other activities such as mining must
336 have altered the forest structure, *e.g.* the SJ site has many small mines and quarries that were exploited
337 intermittently throughout history. The release growth event discerned for the 1940s concurs with a period
338 of maximum mining activity in this area (1925 to 1957) (Table S4), during which timbers use increased for
339 mine tunnels and furnaces, these also requiring large amounts of firewood to melt the mineral. This heavy
340 exploitation of the neighboring forest resources must have affected a significant part of this oak woodland,
341 as shown by growth of the remnant trees included in the northern site (Figure S2b). On the other hand,
342 woodlands on the southern slopes (*e.g.* CA site) were mixed with a greater percentage of croplands along
343 the elevational gradient where oaks grow (Jiménez-Olivencia and others 2015). Firewood, charcoal, and
344 acorns have been resources intensively exploited at southern sites, until at least the middle of the 20th-
345 century, when these activities sharply decreased mainly due to rural abandonment and use of gas and
346 fossil fuels (Valbuena-Carabaña and Gil 2013). At the CA-High site, the only positive release event found
347 for the earliest years could be related with conversion from closed forest to an open silvopastoral system,

348 a common management type which has been applied in the past in Iberian oak woodlands (Cañellas and
349 others 2004; Gea-Izquierdo and others 2011) and which has been documented for this site (Valbuena-
350 Carabaña and Gil 2013).

351 The other release event observed for the SJ site during 1995-2000 was lower than during 1940, but also
352 affected most trees (Figures 4, S2b). No records of forest practices in this area over the last 30 years
353 have been found (Bonet and others 2016), and no logging has been recorded during the period 1995 -
354 2000 (F.J. Cano-Manuel *personal communication*). Therefore this release might be related to natural
355 drought-induced mortality after 1995, as has been reported for other Mediterranean tree species after
356 severe drought (e.g. Peñuelas and others 2001; Lloret and others 2004). On the other hand, the strong
357 positive correlations of SPEI with tree growth for this site show high sensitivity to water availability (Gea-
358 Izquierdo and Cañellas 2014).

359 **Sensitivity (resistance) of relict oaks to recent drought events**

360 Severe drought negatively affects both primary and secondary growth of *Q. pyrenaica* forests. This was
361 expressed by the observed reduction in greenness and tree growth in response to the 2005 and 2012
362 drought events as well as by the consistent radial-growth suppression for this oak species during extreme
363 drought events (Corcuera and others 2006; Gea-Izquierdo and Cañellas 2014). Furthermore, the greatest
364 reduction of tree growth was detected during the 1995 drought, a characteristic negative precipitation
365 anomaly that caused severe and extensive damage to the Mediterranean vegetation across the Iberian
366 Peninsula (Peñuelas and others 2001; Gazol and others 2018). Similar to the situation with many other
367 forest species under Mediterranean climates, moisture availability is generally the most limiting factor
368 driving radial growth of *Q. pyrenaica* along its distribution range in the Iberian Peninsula (Gea-Izquierdo
369 and Cañellas 2014). Thus, our results are consistent with previous studies highlighting the influence of
370 precipitation on tree-ring growth in different oak species (e.g. Tessier and others 1994; Di Filippo and
371 others 2010; Gea-Izquierdo and others 2011; García-González and Souto-Herrero 2017).

372 Greenness proved less sensitive to drought than did tree growth, particularly for drier sites. These
373 findings agree with previous works showing tree growth to be a more sensitive metric of forest resilience
374 than is net primary productivity (e.g. Babst and others 2013; Coulthard and others 2017; Gazol and others
375 2018; Peña-Gallardo and others 2018), suggesting that the growth reduction could be mediated by sink more
376 than by source limitations (Körner 2013; Fatichi and others 2014). Tree-ring records complement remote-
377 sensing data in longer time scales by reflecting tree-growth anomalies induced by climate or disturbance
378 over decades to centuries (Babst and others 2017) and provide an accurate measure of growth
379 responses to droughts (Bhuyan and others 2017; Gazol and others 2018).

380 Greenness and tree growth were more affected by drought events in drier northern populations than in
381 wetter southern oak populations. For example, the northern site showed higher browning intensity than

382 did the southern sites during the 2005 drought event, and the stronger correlations of tree-growth with
383 SPEI (hydrological year and summer) in the northern site can be interpreted as higher sensitivity to
384 drought at drier sites (Gea-Izquierdo and Cañellas 2014). It is well known that tree growth and tree
385 responses to drought are site-dependent (e.g. soil features, tree competition, etc.; Babst and others
386 2013), particularly for rear-edge populations (Cavin and Jump 2017; Dorado-Liñán and others 2017b).
387 Trees at CA-High registered higher BAI than those located at lower elevations (CA-Low and SJ; Figure
388 4). This shows the high variability in the response to climate exhibited along a narrow gradient, which is
389 especially noteworthy for southern sites, as these lie very close to each other and overall both are
390 considered to constitute the rear edge for the species.

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

392 Despite the severe drought events in recent decades (Table S3), we found a positive trend for vegetation
393 greenness of *Q. pyrenaica* for the last 16 years, which is consistent with previous findings stressing a
394 recent short-term increase in primary productivity for these forests coinciding with a rather wet decade in
395 the 2000s after a dry decade in the 1990s (Pérez-Luque and others 2015a). For tree growth, positive
396 trends also appeared in the last decade, particularly for the southern high-elevation site (CA-High, Figure
397 4). Similar long-term trends have been described for this species along its distribution range only at high-
398 elevation wet and cold sites (Gea-Izquierdo and Cañellas 2014), which could be related to a non-linear
399 positive effect of warming for the species at cold-limited high-elevation sites (Salzer and others 2009;
400 Gea-Izquierdo and Cañellas 2014). Importantly, for rear edges threatened by climate change, negative
401 growth trends would have been expected, as shown for some temperate and Mediterranean species
402 (Sánchez-Salguero and others 2012; Camarero and others 2015b; Dorado-Liñán and others 2017a).

403 Although the 2012 drought event was more severe and intense than that of 2005 (Table S3), resilience
404 values for greenness and tree-growth were greater for 2012. This could be due to the different timing of
405 the two droughts. The 2012 event was a winter drought (Trigo and others 2013) occurring earlier than the
406 shorter 2005 drought. The latter matched the period of maximum growth for oak forests in late spring
407 (Figure S4). This highlights the importance of the timing of the drought as a key factor determining tree
408 recovery after drought (Camarero and others 2015a; Huang and others 2018). For tree growth, the
409 highest values of resilience were found for the two most severe events (1995 and 1999; Table S3) and
410 tree-growth resilience was positively related to drought severity (Figure 5).

411 The high drought-resilience values reported here, coinciding with high values of genetic resilience for
412 those forests at Sierra Nevada reported elsewhere (Valbuena-Carabaña and Gil 2013, 2017) appear to
413 indicate the strong local adaptation of this oak. Our findings agree with those of studies showing that the
414 assumed higher vulnerability of dry edges does not necessarily hold (e.g. Cavin and Jump 2017).
415 Martínez-Vilalta (2018) pointed out the importance of local adaptation and plasticity, and also of local
416 environmental factors on the vulnerability shown by rear-edge populations. Our results highlight the

417 ample small-scale variability at the ecological boundary and need to better confine the rear-edge limit in
418 our forest. All this, together with the characteristic high resprouting ability of the species, would suggest a
419 long-term persistence of those populations (Bellingham and Sparrow 2000). It should be mentioned that
420 we studied only adult individuals established decades or centuries ago, meaning that it needs to be
421 assessed whether the trees express resilience at the species level or whether we would find vulnerability
422 if we analyzed seedling regeneration, likewise other Mediterranean species at their xeric limit (Castro and
423 others 2004; Vilà-Cabrera and others 2011; Gea-Izquierdo and others 2015).

424 In summary, two main results stand out from this research. First, the high values of resilience observed in
425 our study suggest that *Q. pyrenaica* populations in Sierra Nevada are located in a geographical but not a
426 climatic, ecological rear edge (*sensu* Martínez-Vilalta 2018; Vilà-Cabrera and others 2019). The current
427 niche is a result of land-use changes, which further complicate the definition of potential rear edges. The
428 high resilience values observed could also be related to stabilizing mechanisms promoting community
429 resilience that can buffer the impact of extreme events, as has been described for other species (e.g.
430 *Pinus sylvestris*, Herrero and Zamora 2014).

431 Second, these resilience responses of oak forest to drought events are not spatially homogeneous
432 throughout the mountain range, due to differences in ecological conditions and/or past-management
433 legacies. In fact, there was much small-scale variability in the response to climate within the rear edge
434 that we had *a priori* considered in our study. Furthermore, we even found positive effects of climate
435 change in certain stands, as discussed, in disagreement with our hypothesis of expecting oak
436 vulnerability in the geographical rear edge studied. This suggests that the rear edge therefore needs to be
437 redefined (Vilà-Cabrera and others 2019), partly because of land-use legacies and their effect on the
438 possible mismatch between the current distribution of species (i.e. determining the “available”
439 geographical rear edge) and the ecological (limiting) rear edge of species.

440 Overall, our results show that management history influences tree growth and resilience to climate
441 change of tree species, highlighting the importance of land-use legacies in Mediterranean forests
442 (Navarro-González and others 2013; Doblas-Miranda and others 2017) which, hence, will also strongly
443 determine the current geographical distribution of marginal stands, regardless of the potential extent of
444 ecological marginality of species.

445 **Conclusions**

446 The ecological and geographical read edges did not appear to fully match in our study. Severe drought
447 events provoke major reductions in primary and secondary growth of *Q. pyrenaica* forests in the relict,
448 rear-edge forest studied. However, we found no negative growth trends despite our expectation of
449 vulnerability to climate change for these relict stands. Furthermore, we detected positive trends for
450 primary growth (i.e. greenness) at the ecosystem scale and a steep positive trend of secondary growth at

451 the tree level at the wettest site along the climatic gradient analyzed. The trees exhibited high resilience
452 values in response to drought, particularly in the long-term scale, and resilience was directly related to
453 drought severity. These findings are consistent with other results showing that this mountain region is still
454 acting as a refuge for deciduous species, including *Quercus*. The differences found in tree growth and
455 resilience to drought between sites close together show that responses to drought were site dependent
456 and can drastically vary even in very narrow spatial gradients (*i.e.* following ecological thresholds). This is
457 particularly relevant for rear-edge populations where topographic and biophysical variability facilitates the
458 existence of microrefugia. The analysis of tree-growth dynamics revealed suppression and release events
459 that were consistent with legacies left by land use in local forest dynamics, as inferred from an exhaustive
460 review of historical documents. In this sense, our results highlight the importance of land-use legacies for
461 highly transformed Mediterranean systems. This is relevant for tree species with a high sensitivity to
462 climate change, such as *Q. pyrenaica*, not only for conservation *per se* of the species, but for all
463 ecosystem services that these singular forests offer. As a follow-up to our study, research would be
464 informative to disentangle how forest resistance and resilience might be affected by the combination of
465 climate change and land-use legacies in highly transformed landscapes such as Mediterranean mountain
466 ecosystems.

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683 remote-sensing data: Recent progress and future challenges. *Environmental Reviews* 21:103–15.

1 **Figure 1.** Distribution of *Quercus pyrenaica* forests in the Iberian Peninsula (a) and in Sierra Nevada mountain
2 range (b). Different colors indicate oak-population clusters identified in Sierra Nevada (Pérez-Luque et al. 2015).
3 For each population, a grid with the MODIS pixels is shown (see Material and methods). Detailed location of the
4 dendroecological sampling sites: northern (San Juan, SJ) (c), and southern ones (Cáñar: CA-Low and CA-High)
5 (d). Color orthophotography of 2009 from Regional Ministry of the Environment.

6 **Figure 2. a)** EVI standardized anomaly during the period 2000-2016 for northern and southern populations.
7 Error bars show standard error. See main text for details on EVI calculation. **b)** Percentage of pixels showing
8 browning, greening or no changes during the 2005 and 2012 drought events according to EVI standardized
9 anomalies. See main text for an explanation of greening and browning.

10 **Figure 3.** Basal Area Increment (BAI) chronologies of *Q. pyrenaica* for northern population (SJ; red) and
11 southern ones: low-elevation (CA-Low; green) and high-elevation (CA-High, blue) sites. Shading areas
12 correspond to standard error of the mean. Number of series is displayed in the upper plot. Only years replicated
13 with # series > 5 are shown. Linear trends since 1975 are indicated for all sites (numbers indicate r^2 values;
14 asterisks indicate significant linear trend, $p < 0.001$).

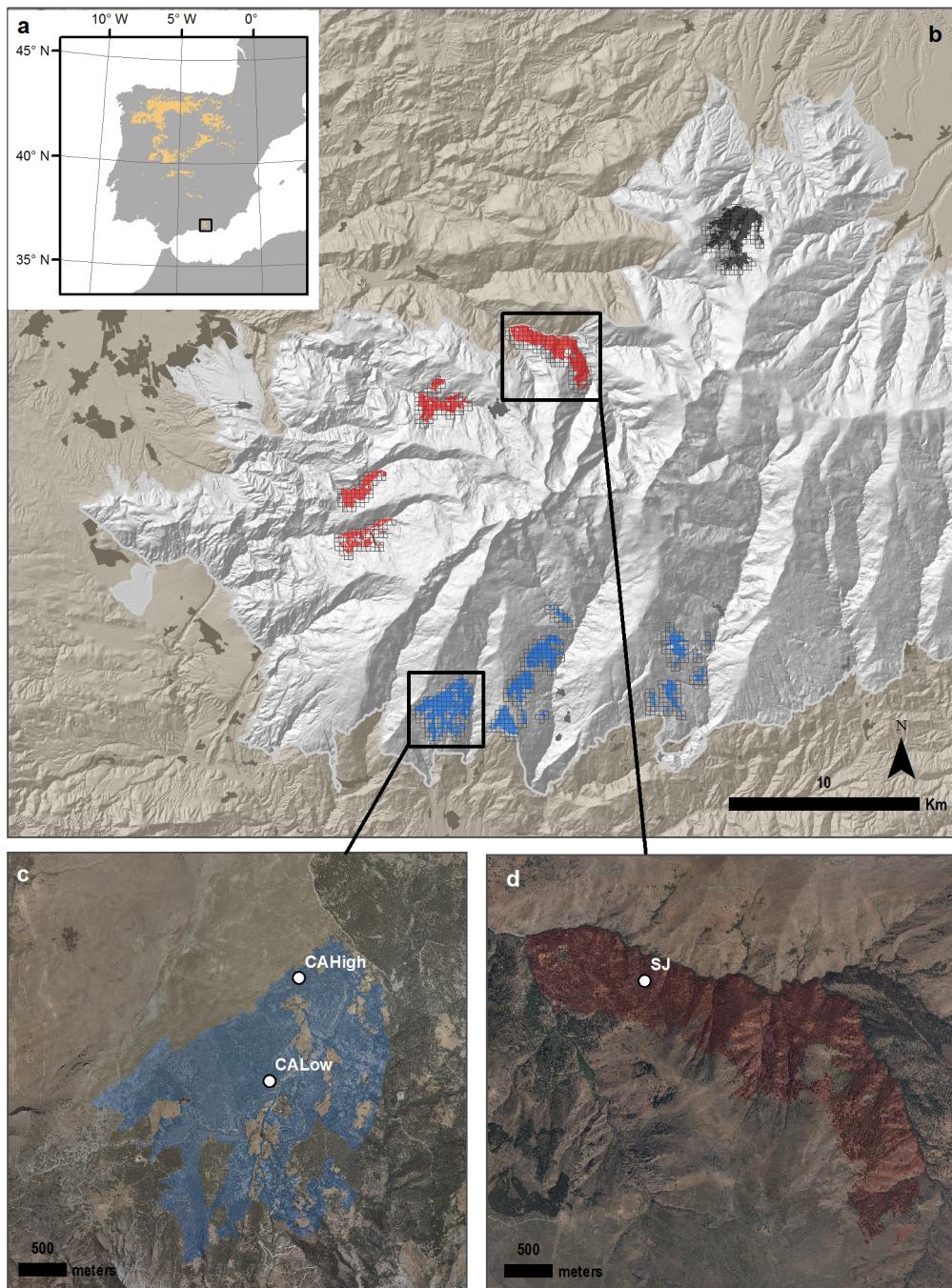
15 **Figure 4.** Comparison of median growth change (GC) following Nowacki and Abrams (1997) for *Q. pyrenaica*
16 sites. Dashed black lines indicate a threshold of 50% of GC (see Material and methods). Note that y-axes do not
17 correspond in all of the three panels for the sake of clarity. Error bars indicate standard error.

18 **Figure 5.** Resilience metrics of tree-growth for eight severe drought events since 1950 (see main text for details)
19 as a function of drought severity. *Left:* Resistance (R_t); *Center:* Recovery (R_c); *Right:* Resilience (R_s). Points
20 indicate resilience metrics for oak populations: SJ (red), CA-High (blue) and CA-Low (green). Resilience metrics
21 were computed for each population (sample depth > 10) and drought event. Gray lines represent overall
22 relationships for each Resilience metrics.

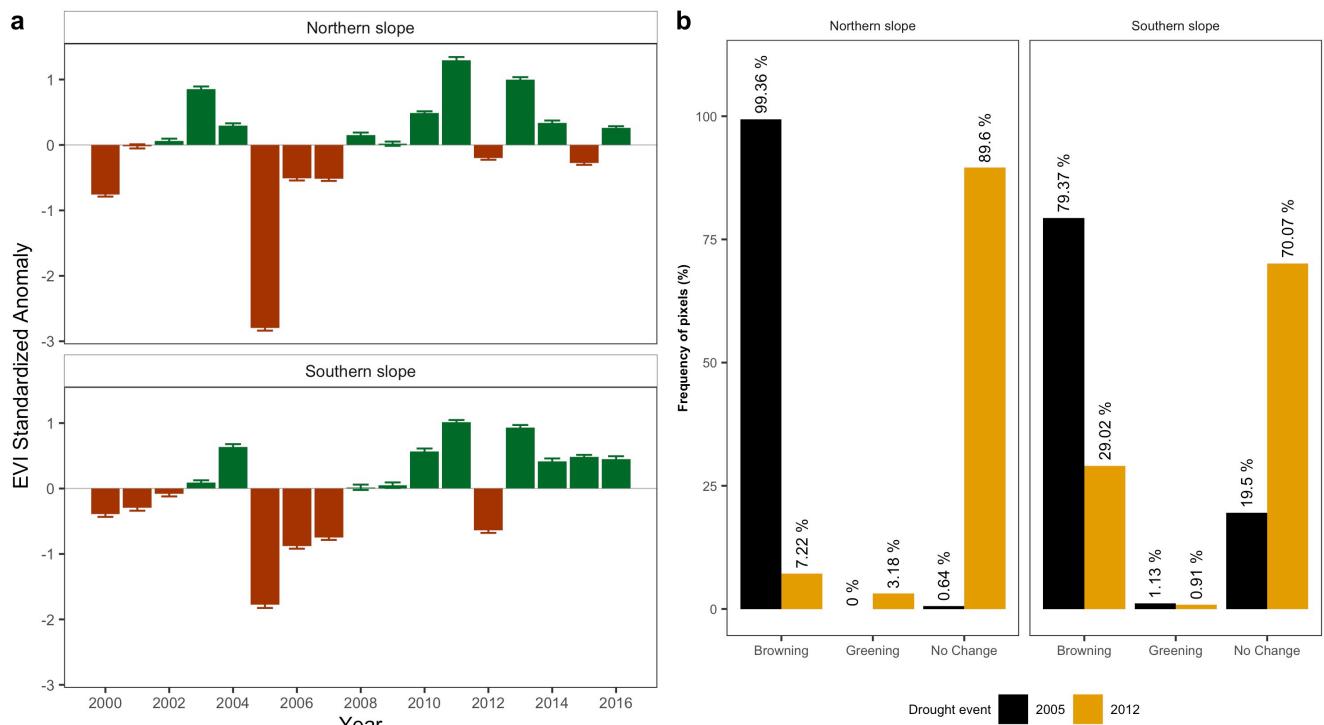
23 **Figure 6.** Comparison of the response of *Q. pyrenaica* forests to drought in terms of resistance, recovery, and
24 resilience of greenness (a) and tree growth (b). For EVI, northern populations (red circle) were compared with
25 southern ones (green circle). For BAI, the more xeric northern population (San Juan, SJ; red circle) was
26 compared with the two southern populations, Cáñar-High (CA-High; blue circle) and Cáñar-Low (CA-Low; green
27 circle). Different letters indicate significant *post hoc* differences between groups (see Material and methods for
28 details).

29 **Figure 7.** Correlation coefficients found by relating tree-ring residual chronologies (RWI) of *Q. pyrenaica* and
30 monthly climatic data: precipitation and 6-month SPEI (a), minimum (b) and maximum (c) temperatures. green
31 bars: northern site (SJ); light blue bars: low-elevation southern site (CA-Low); and dark blue bars: high-elevation
32 southern site (CA-High). Asterisks indicate significant ($P < 0.05$) correlation coefficients.

34 **Figure 1**

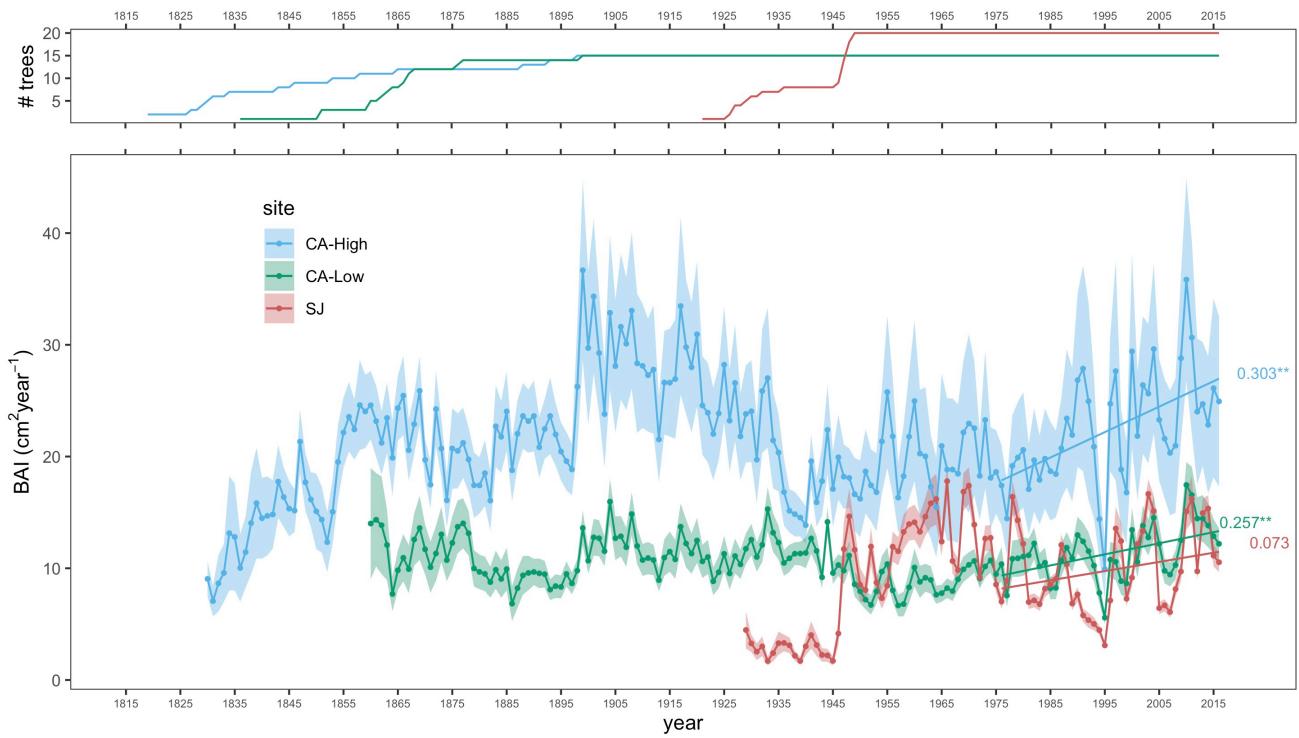


36 **Figure 2**



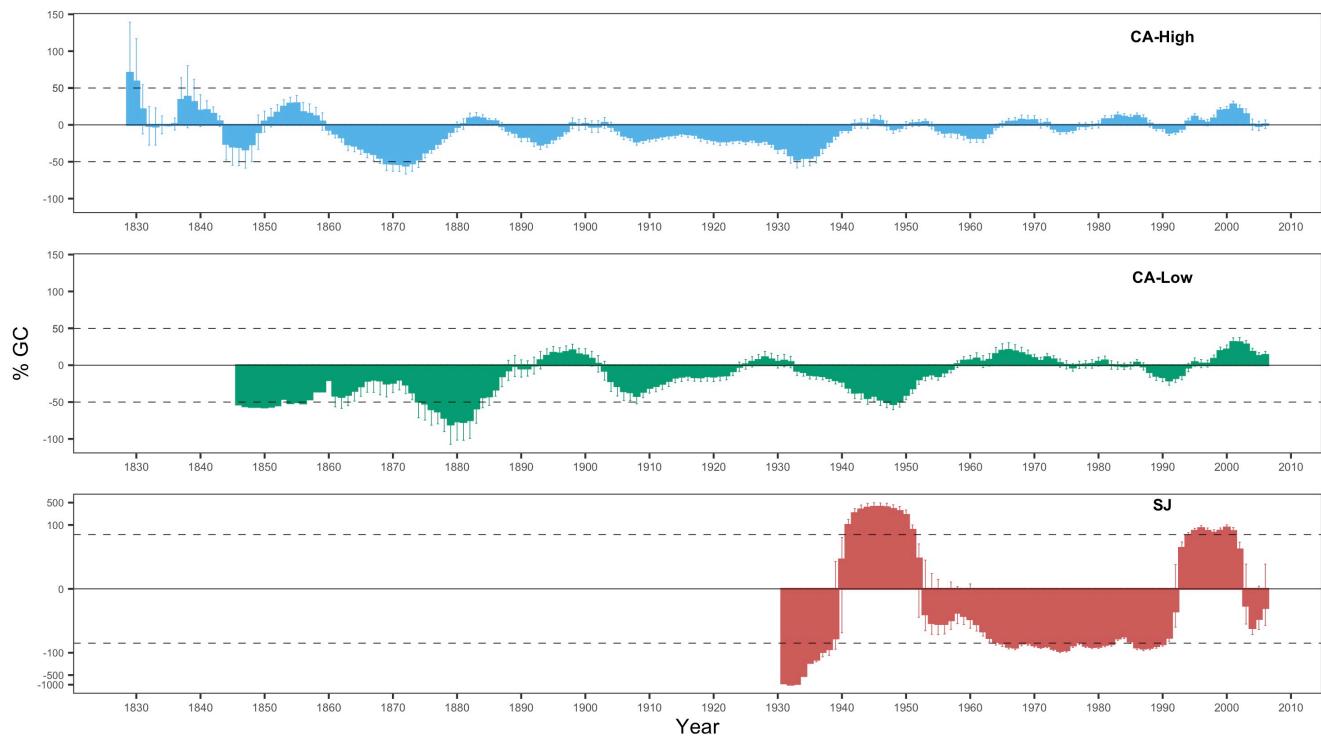
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38 **Figure 3**



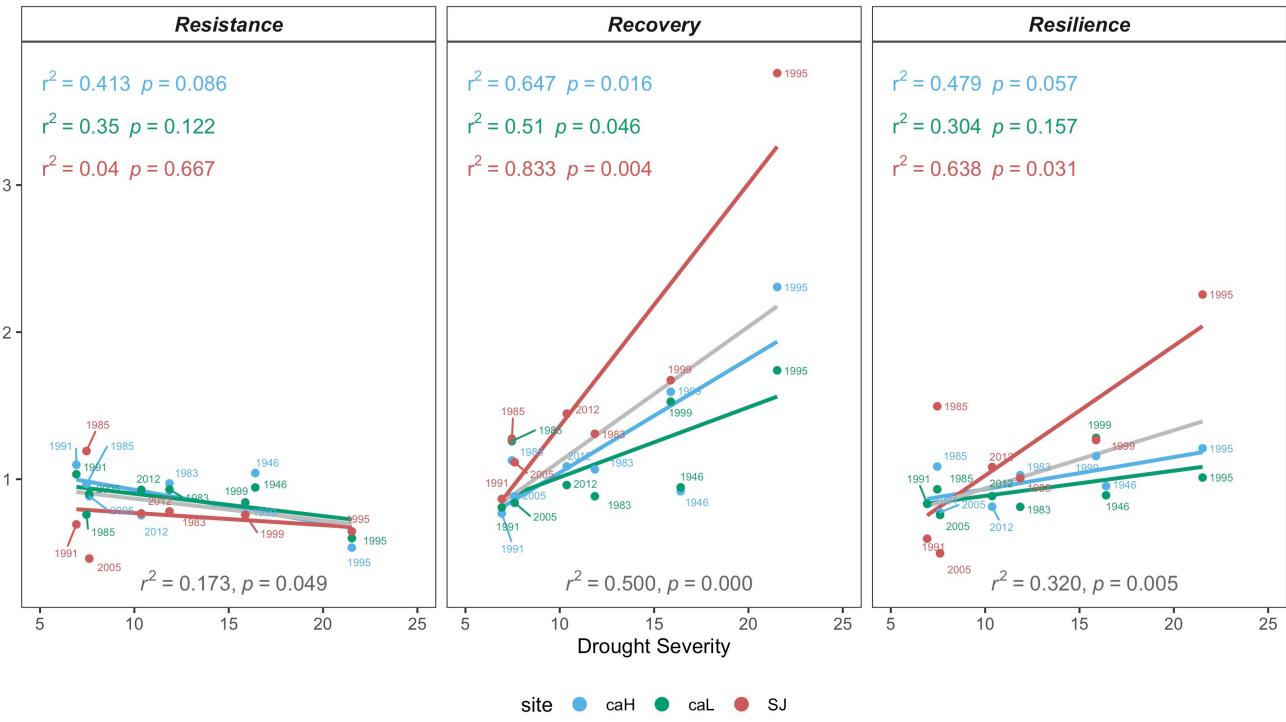
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40 **Figure 4**



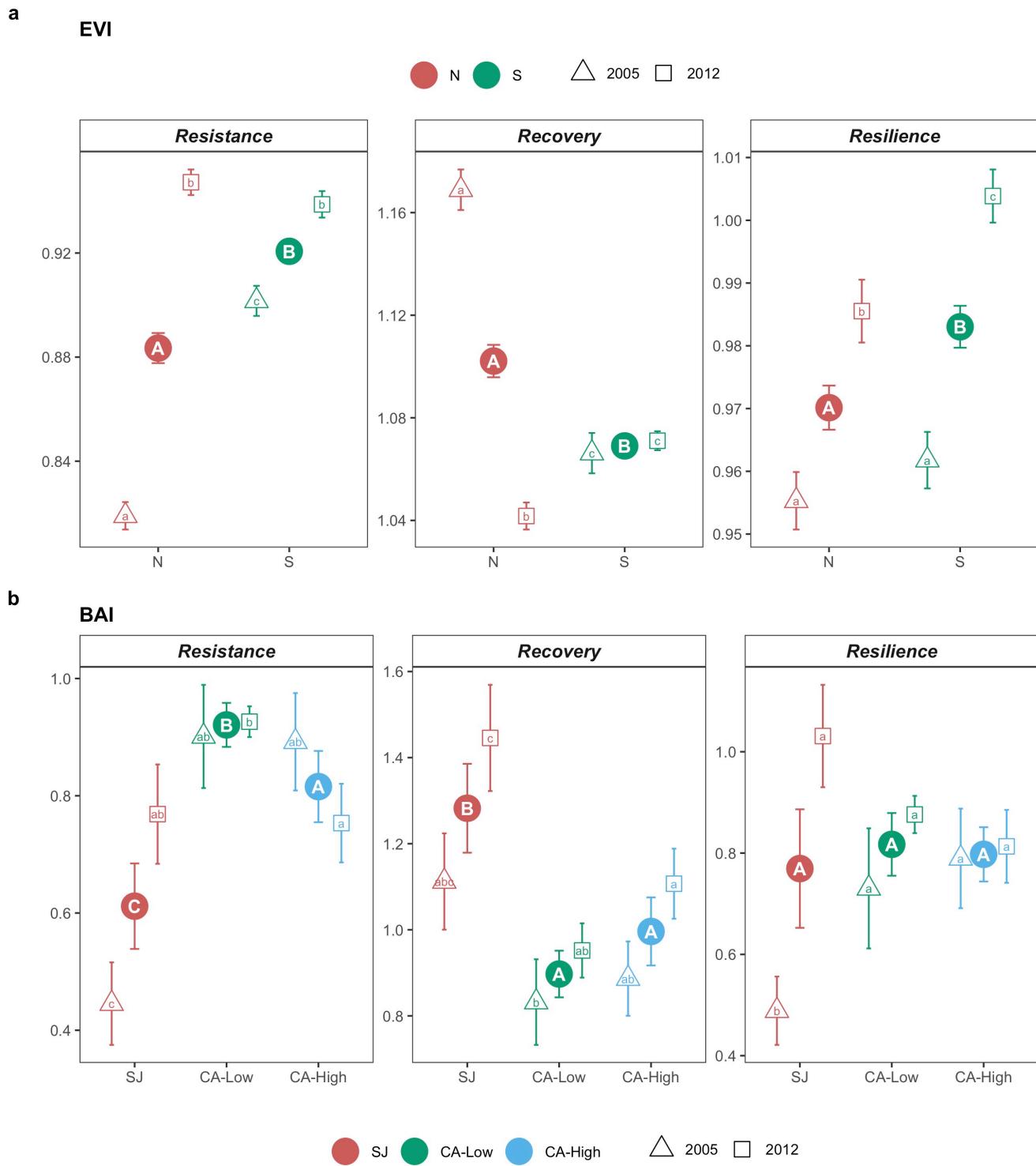
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42 **Figure 5**

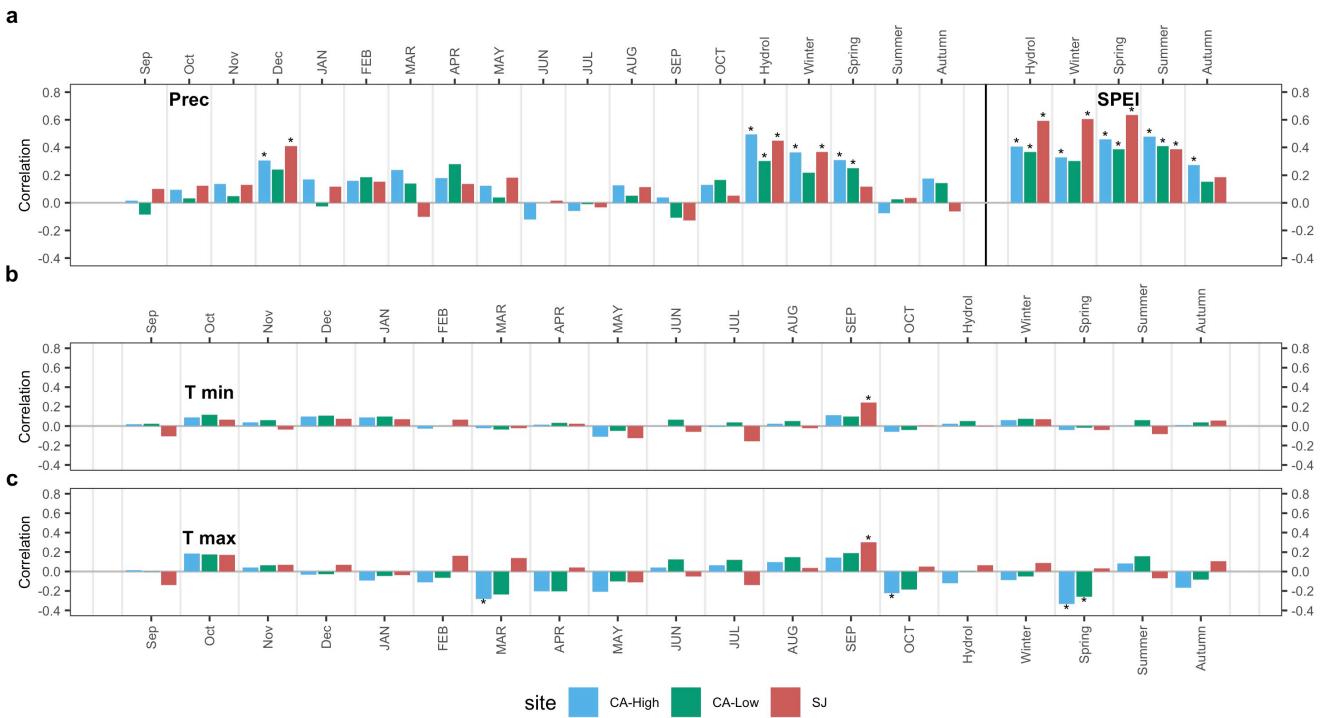


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44 **Figure 6**



46 **Figure 7**



47

1 **Table 1.** Characteristics of sampled plot. Lat = latitude; Long = longitude. Dbh and height of all trees, Basal Area
2 (BA), Density and SRD (size ratio proportional to distance) are computed for all trees within a 10-m radius of focal
3 trees (see Materials and methods). Temp.: annual average of mean monthly minimum and maximum
4 temperatures. Values shown here correspond to site averages. Standard deviations are shown in parentheses.
5 Different letters indicate statistically significant differences between sites (Kruskal-Wallis test followed by Dunn's
6 test, $p < 0.05$). Stands were monospecific, hence all results correspond to oak data.

7 **Table 2.** Characteristics of the mean tree-ring chronologies. Length values in parentheses indicate the number of
8 years replicated with more than five series. RW = mean annual ring width (standard deviation in parenthesis). MS
9 = mean sensitivity. AR(1) = mean autocorrelation of raw series. Rbt = mean correlation between series. EPS =
10 mean expressed population signal. EPS and Rbt were calculated for the mean residual chronologies of growth
11 indices.

12 Table 1

Site							Cored trees				Stand competition				
	Lat (°)	Long (°)	Elevation (m)	Slope (°)	Prec. (mm)	Temp. (° C)	# trees (# cores)	Dbh (cm)	Height (m)	Age (years)	Dbh all (cm)	Height all (m)	BA (m ² ha ⁻¹)	Density (trees ha ⁻¹)	SRD
CA-High	36.97	-3.42	1846 - 1884	12.11 (3.28)	731	3.4-13.8	15 (30)	69.8 (20.5) a	15.4 (1.8) a	161.0 (32.2) a	34.1 (24.3) a	10.8 (4.4) a	39.13 (24.31) a	348.0 (147.1) a	0.91 (0.63) a
CA-Low	36.96	-3.42	1691 - 1751	12.86 (2.98)	658	4.7-15.6	15 (30)	45.9 (8.6) a	12.6 (1.6) b	148.5 (16.5) a	21.7 (14.4) b	9.0 (2.8) b	18.02 (7.11) ab	409.6 (226.0) a	0.89 (0.44) a
SJ	37.13	-3.37	1322 - 1474	27.33 (5.59)	555	4.9-16.35	20 (48)	31.9 (3.7) b	11.8 (2.3) b	72.6 (11.1) b	20.6 (8.1) b	9.7 (3.6) ab	11.64 (5.47) b	339.0 (130.3) a	1.11 (0.52) a

13

14

15 **Table 2**

Site	First year	Last year	Length (years)	# trees	# cores	RW (mm)	MS	AR(1)	Rbt	EPS
CA-Low	1836	2016	181 (164)	15	30	1.253 (0.781)	0.208	0.799	0.520	0.897
CA-High	1819	2016	198 (188)	15	30	1.500 (0.879)	0.203	0.827	0.522	0.907
SJ	1921	2016	96 (90)	20	48	1.725 (1.207)	0.319	0.692	0.637	0.959

16

1 **Supplemental Material**

2 **Table S1.** Robust two-way ANOVAs of the resilience metrics of greenness (EVI) and tree growth (BAI)
3 for the two drought events (in 2005 and 2012) and site.

4 **Table S2.** Robust measures of central tendency of resilience indices for greenness (EVI) and tree growth
5 (BAI), grouped by drought events, site, and interaction. Measures of central tendency are M-estimators
6 based on Huber's Psi (see Materials and methods). In parentheses are the 95% confidence intervals
7 using 3000 bootstraps. *Total* corresponds to the average of 2005 and 2012.

8 **Table S3.** Drought events for the 1901-2016 period for Sierra Nevada ranked according to drought
9 severity calculated from the SPEI index (12 months scale). See Materials and methods for details.

10 **Table S4.** Review of the forest and management history of the sampling sites. Historical documents were
11 exhaustively reviewed to compile information on socio-economical activities affecting forests: historical
12 documents and maps (e.g. Titos 1990); detailed mining reports (e.g. Maestre 1858); official information
13 on recent wildfire events and forest-management practices (e.g. Bonet and others 2016); livestock
14 farming (e.g. Moreno-Llorca and others 2016); traditional irrigation ditches (e.g. Ruiz-Ruiz 2017) and
15 other studies reviewing the socioeconomic dynamics of forest of Sierra Nevada at different scales (e.g.
16 Jiménez-Olivencia and others 2015).

17

18 **Table S1**

Variable	Factor	Resistance		Recovery		Resilience	
		F	p	F	p	F	p
EVI	Drought event	799.9	< 0.001	312.0	< 0.001	207.2	< 0.001
	Site	153.2	< 0.001	105.4	< 0.001	29.8	< 0.001
	Drought event:Site	234.7	< 0.001	364.3	< 0.001	6.1	0.014
BAI	Drought event	6.0	0.019	29.5	< 0.001	44.3	< 0.001
	Site	59.3	< 0.001	53.1	< 0.001	1.3	0.534
	Drought event*Site	32.2	< 0.001	4.4	0.134	30.0	< 0.001

19

20 Table S2

Variable	Sites	2005			2012			Total		
		Resistance	Recovery	Resilience	Resistance	Recovery	Resilience	Resistance	Recovery	Resilience
EVI	Northern slope	0.819 (0.814 - 0.824)	1.169 (1.161 - 1.177)	0.955 (0.951 - 0.960)	0.947 (0.942 - 0.952)	1.042 (1.036 - 1.047)	0.986 (0.980 - 0.990)	0.884 (0.878 - 0.889)	1.102 (1.096 - 1.108)	0.970 (0.967 - 0.974)
	Southern slope	0.902 (0.896 - 0.907)	1.066 (1.058 - 1.074)	0.962 (0.957 - 0.966)	0.939 (0.934 - 0.944)	1.071 (1.067 - 1.075)	1.004 (1.000 - 1.008)	0.921 (0.917 - 0.925)	1.069 (1.065 - 1.073)	0.983 (0.980 - 0.986)
	All	0.858 (0.854 - 0.863)	1.120 (1.113 - 1.126)	0.958 (0.955 - 0.962)	0.943 (0.940 - 0.947)	1.057 (1.054 - 1.060)	0.995 (0.991 - 0.998)			
BAI	CA-High	0.892 (0.809 - 0.975)	0.887 (0.800 - 0.973)	0.790 (0.691 - 0.888)	0.753 (0.686 - 0.820)	1.107 (1.026 - 1.188)	0.813 (0.741 - 0.885)	0.816 (0.755 - 0.876)	0.996 (0.917 - 1.075)	0.798 (0.744 - 0.851)
	CA-Low	0.901 (0.813 - 0.989)	0.832 (0.733 - 0.932)	0.730 (0.612 - 0.849)	0.926 (0.900 - 0.953)	0.952 (0.889 - 1.015)	0.876 (0.839 - 0.913)	0.921 (0.883 - 0.958)	0.897 (0.843 - 0.951)	0.817 (0.755 - 0.879)
	SJ	0.445 (0.375 - 0.516)	1.112 (1.000 - 1.224)	0.489 (0.421 - 0.556)	0.769 (0.684 - 0.853)	1.446 (1.322 - 1.569)	1.031 (0.930 - 1.132)	0.612 (0.539 - 0.685)	1.282 (1.179 - 1.386)	0.769 (0.652 - 0.886)
	All	0.721 (0.644 - 0.798)	0.946 (0.879 - 1.013)	0.653 (0.585 - 0.721)	0.819 (0.776 - 0.863)	1.161 (1.081 - 1.240)	0.911 (0.865 - 0.957)			

21 Table S3

Duration	Intensity	Severity	Lowest	Months	Year
11	-1.957	21.524	-2.585	Jan - Nov	1995
11	-1.581	17.391	-2.024	Nov - Sep	1913-1914
9	-1.823	16.409	-2.42	May - Jan	1945-1946
9	-1.764	15.880	-2.056	Dec - Aug	1998-1999
8	-1.482	11.859	-1.654	Feb - Sep	1983
6	-1.728	10.367	-1.906	Mar - Aug	2012
5	-1.905	9.527	-2.300	Jan - May	1925
5	-1.522	7.611	-1.571	May - Sep	2005
5	-1.493	7.463	-1.537	May - Sep	1985
5	-1.385	6.926	-1.444	Apr - Aug	1991
4	-1.714	6.855	-1.833	May - Aug	1931
4	-1.363	5.453	-1.441	May - Aug	1927

Table S4

Use	Cáñar (CA sites)	Güejar-Sierra (SJ site)	References
Land use	Oak Woodlands mixed with a high percentage of croplands even reached high elevations (mainly barley, rye, and potatoes). Irrigated crops near the village ("regadio de vega")	Grasslands and shrublands for cattle raising located at high elevations. Then forest formations (oak woodlands) with some croplands (mainly herbaceous and potatoes). Irrigated terraces with tree crops (chestnut trees, cherry trees)	Jiménez-Olivencia and others (2015); Zoido and Jiménez Olivencia (2015); Moreno-Llorca and others (2016); Calatrava and Sayadi (2019)
Forest Management Practices	Nearby areas were afforested (pine plantations) to avoid soil erosion in 1925, 1928, 1950, and 1970 Selective thinning during 2007 in a small area near "Casa Forestal" Tree cleaning near trails/trails (2009-2010)	Afforestation of the upper areas of the Genil River basin (1942) Tree cleaning (2006 - 2007) near our study site (<i>La Hortichuela</i>) Scattered afforestation (creation of small, scattered islands of oaks) (2008)	Bonet and others (2016); Moreno-Llorca and others (2016); J. Navarro and F.J. Cano-Manuel <i>personal communications</i> ; Romero-Zurbano (1909)
Forest structure	Inventories of trees made by the Spanish Navy during the second half of 18th century: 2,010,200 new trees; 10,791 growing trees . For the Cáñar site, more than 2,000,000 trees were reported, most of them new, and no old trees were counted, suggesting recent tree felling.	Inventories of trees made by the Spanish Navy during the second half of 18th century: 639 550 new trees; 56 700 growing trees; 220 old trees	Cruz (1991); Wing (2015)
Fires	Several small fires. 1979: 44 Has of Pyrenean oak forests (near "Casa Forestal") 1984: 189 Has of Pine plantations and Holm oak forests ("El Jara") 1994: 65 Has of Pine plantation ("Puente Palo")	Not recorded in the area since 1975	Bonet and others (2014); Moreno-Llorca and others (2016); CMA (2018)
Fruit production (acorns)	Old references have indicated traditional acorn gathering. Auctions of public forests to collect acorns (1927; 1954)		Catastro (1752); Mesa-Torres (2009); Bonet and others (2014)
Wood	Traditional charcoal ("carboneo") making and firewood cutting throughout history. Several references have indicated firewood collection at this site at least since 1572. At the beginning of the last century (1900s), 3 - 4 woodcutters collected firewood from Pyrenean forests daily.	Some references of wood removal for subsistence (1826; 1847). Massive logging during the first decades of 20th century. As a result, several old photos show areas without trees where oak forests stand today (1925; 1932)	Catastro (1752); López (1776); Madoz (1846); Titos Martínez (1997); Ferrer (1999); Jiménez-Serrano and Serrano-Gutiérrez (2004); Mesa-Torres (2009); Bonet and others (2014)
Mining activities	No mining in the area, only scattered private excavations	Intermittent exploitation throughout history. Historical documents indicated two periods of intense mining: the second half of the 19th century after the publication of detailed mineralogical reports and during the first decades of the 20th century until 1960, which is the last year with evidence of mining. Evidence of several furnaces to melt minerals (Cooper)	Maestre (1852); Maestre (1858); Titos (1990); Arnedo (2007); Mesa-Torres (2009)
Quarries		Exploitation of serpentine quarries from the 16th to 19th century (<i>Jaspe Verde</i>)	Navarro and others (2014)
Traditional irrigation channel	An irrigation channel ("Aequia de la Era Alta") is located uphill of the CA-High site (i.e. >2000 m), which functioned from March to June	Several historical irrigation channels, known as <i>acequias de careo</i> , were used since the Middle Ages to cultivate these valleys. Most are abandoned and deteriorated, probably at least since the 1960s.	Martín-Civantos (2014); Martín-Montañés and others (2015); Ruiz-Ruiz (2017)

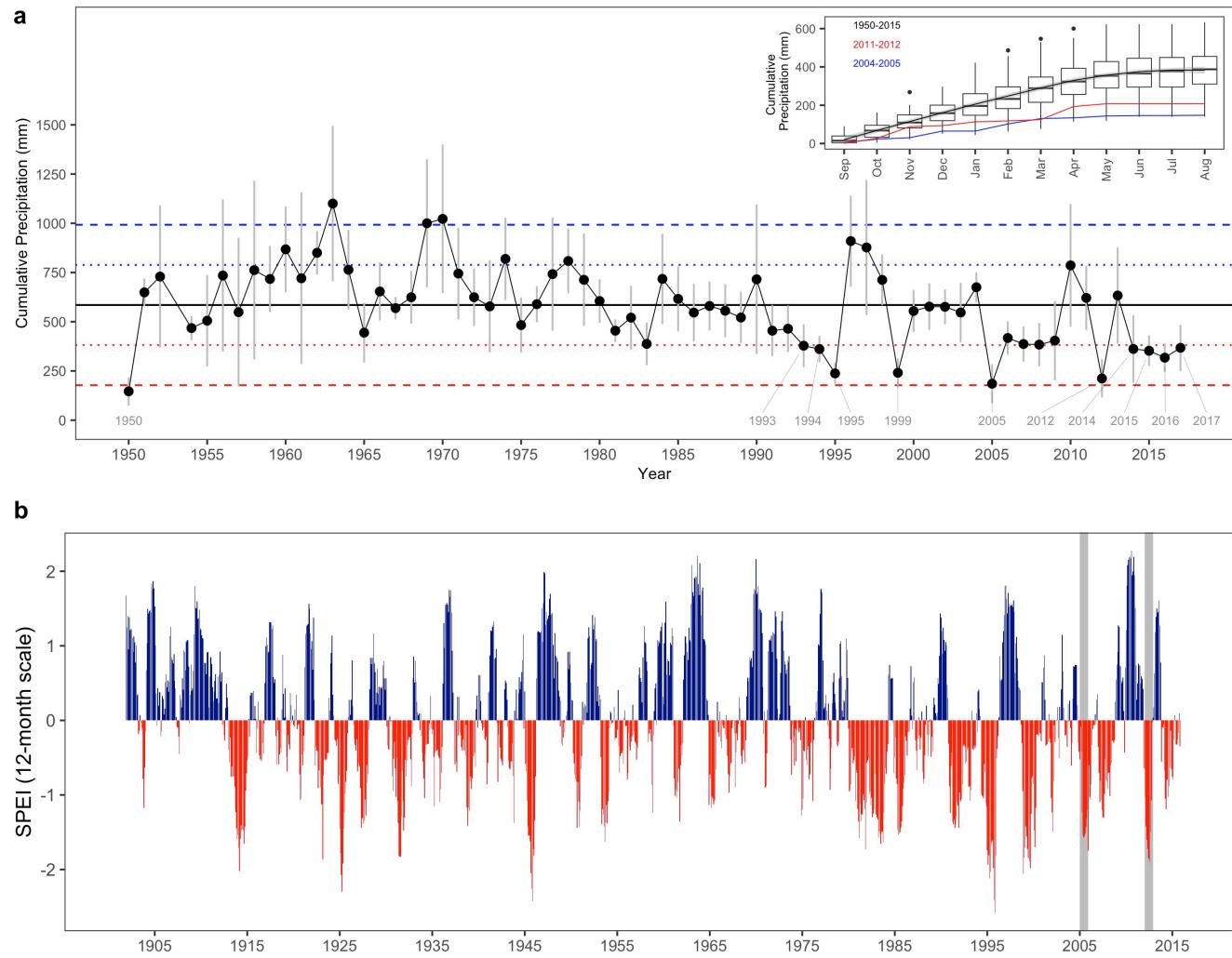
Figure S1. **a)** Temporal evolution of cumulative precipitation (hydrological year) during the period 1950-2017. Points represent the mean, and error bars the standard error. The black line indicates mean for the entire period (585 mm). The red lines represent -1 and -2 standard deviation (dotted and dashed lines, respectively). The blue lines represent +1 and +2 standard deviation (dotted and dashed lines, respectively). Years with average values below -1SD are labeled. Data from 28 meteorological stations distributed around the Sierra Nevada area (from the National Spanish Meteorological Services, AEMET). **Inset plot:** cumulative precipitation during the hydrological years 2004-2005 (blue line) and 2011-2012 (red line). The boxplot representing the average from 1950-2015 period. Data from meteorological station Granada, Base Aérea. **b)** Drought severity in Sierra Nevada for the 1901-2016 period based on the Standardized Precipitation-Evapotranspiration Index (SPEI). Data from Global SPEI database (<http://spei.csic.es/database.html>). We took the SPEI data for a 12-month scale and for all 0.5° grid cells covering Sierra Nevada. Horizontal gray bars indicate the years 2005 and 2012.

Figure S2. **a)** Residual tree-ring chronologies determined for the *Q. pyrenaica* sites. Dashed red lines indicate the start of the reliable period (EPS > 0.85). Dotted black lines show the severe drought years identified in our climatic data (Table S3 and Figure S1). **b)** Percentage of *Q. pyrenaica* trees affected by GC > 50 % by site. Black line shows number of trees (right-axis). Data for number of trees > 2 is shown.

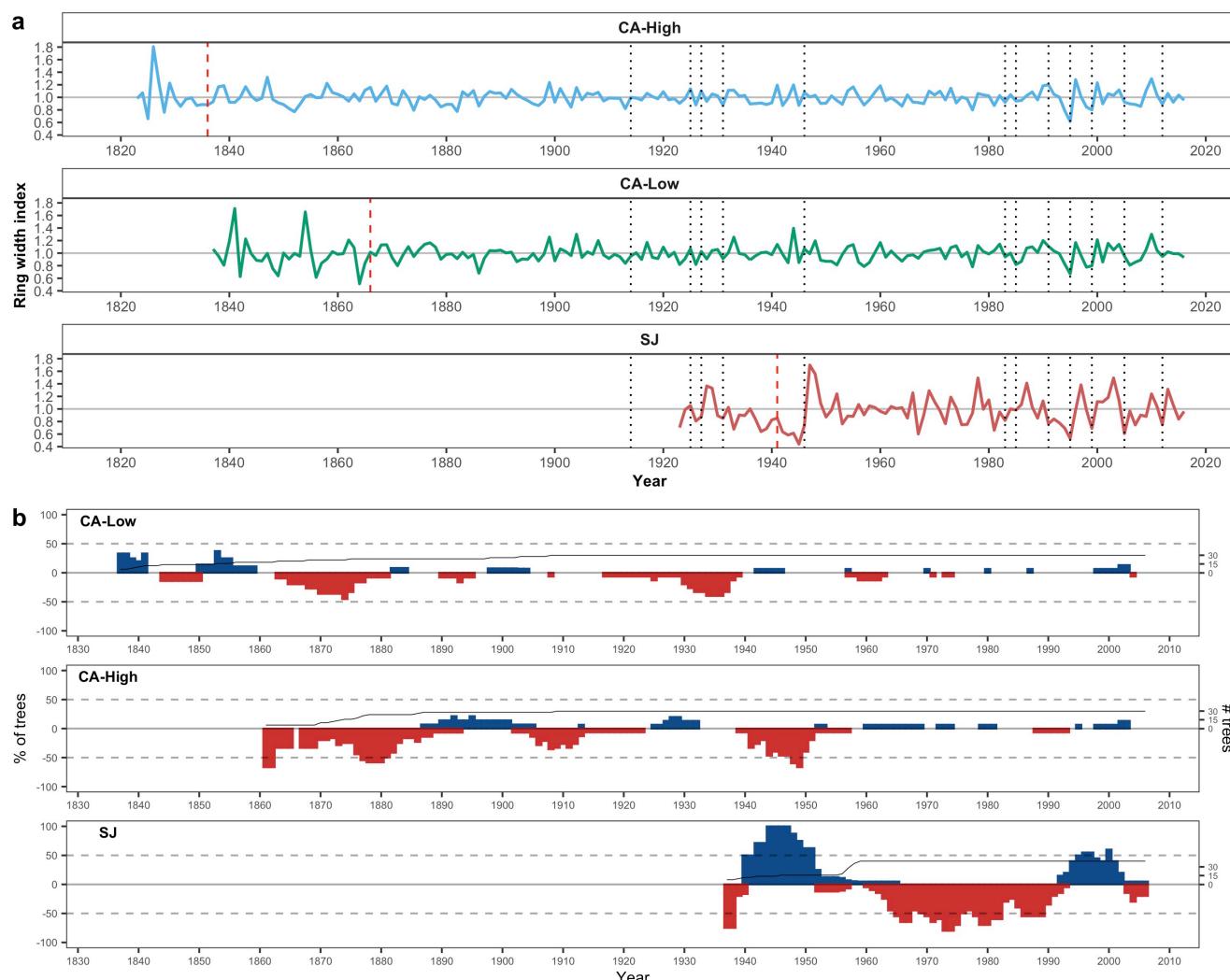
Figure S3. **a)** Correlation among site chronologies (CA-High, CA-Low and SJ) in different time domains after pre-filtering the time series with increasing size of the moving-average window (1 to 40 years). Each site chronology was smoothed using centered moving averages with different window sizes (1 to 40 years), and then Pearson's correlation coefficient between the each pair of chronologies was calculated. Significance was tested using 1000 bootstrap replicates and with 95% confidence intervals built using the R package boot. **b)** Correlation between indices of resilience (*Rt*, resistance; *Rc*, recovery; *Rs*, Resilience) using periods of several lengths (2, 3 and 4 years after a drought).

Figure S4. EVI annual profile (average of the period 2000-2016) for *Q. pyrenaica* forests in Sierra Nevada and drought events. Horizontal bars correspond to the most severe droughts for Sierra Nevada since 1900 (computed as in Table S3). Their position indicates the start and end months of each drought event. Bars lengths show the duration of the drought event (number of consecutive months with SPEI lower than -1.28, see (Páscoa et al. 2017).

Figure S5. Resilience metrics of the tree growth for severe drought events since 1950 (excluding 1995 drought event). *Left:* Resistance (*Rt*); *Center:* Recovery (*Rc*); *Right:* Resilience (*Rs*). Points indicate resilience metrics for oak populations: SJ (blue), CA-High (red) and CA-Low (green). Resilience metrics were computed for each population (sample depth > 10) and drought event. The gray line represents overall relationship for each Resilience metrics.

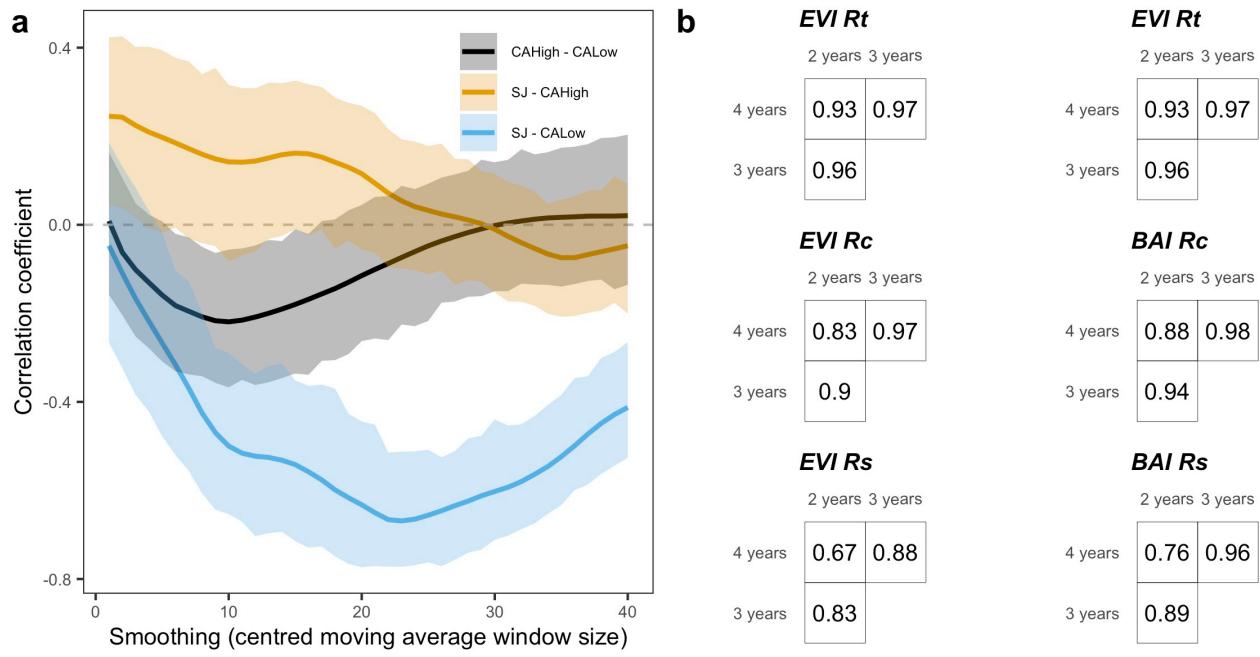
Figure S1

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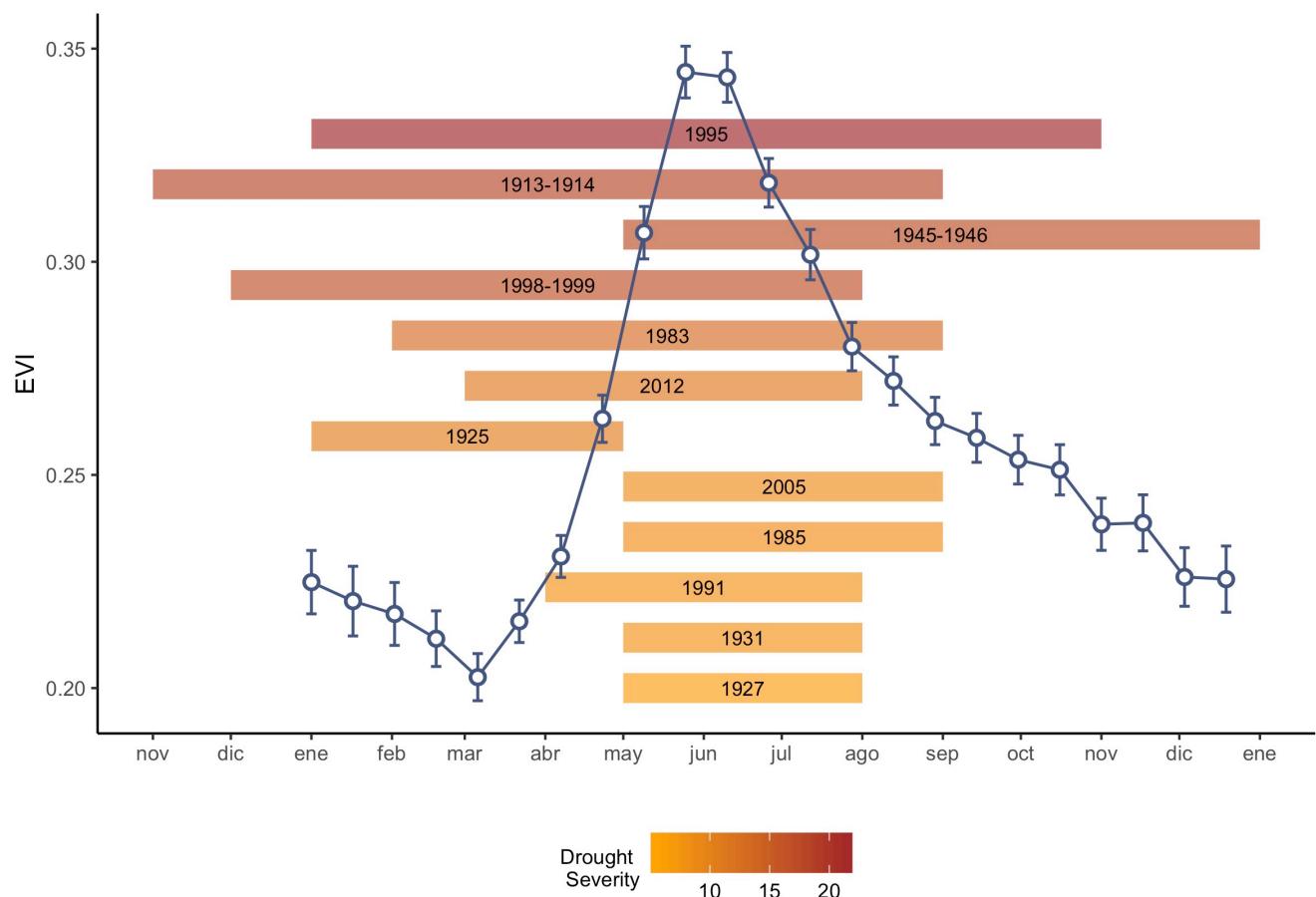
Figure S2

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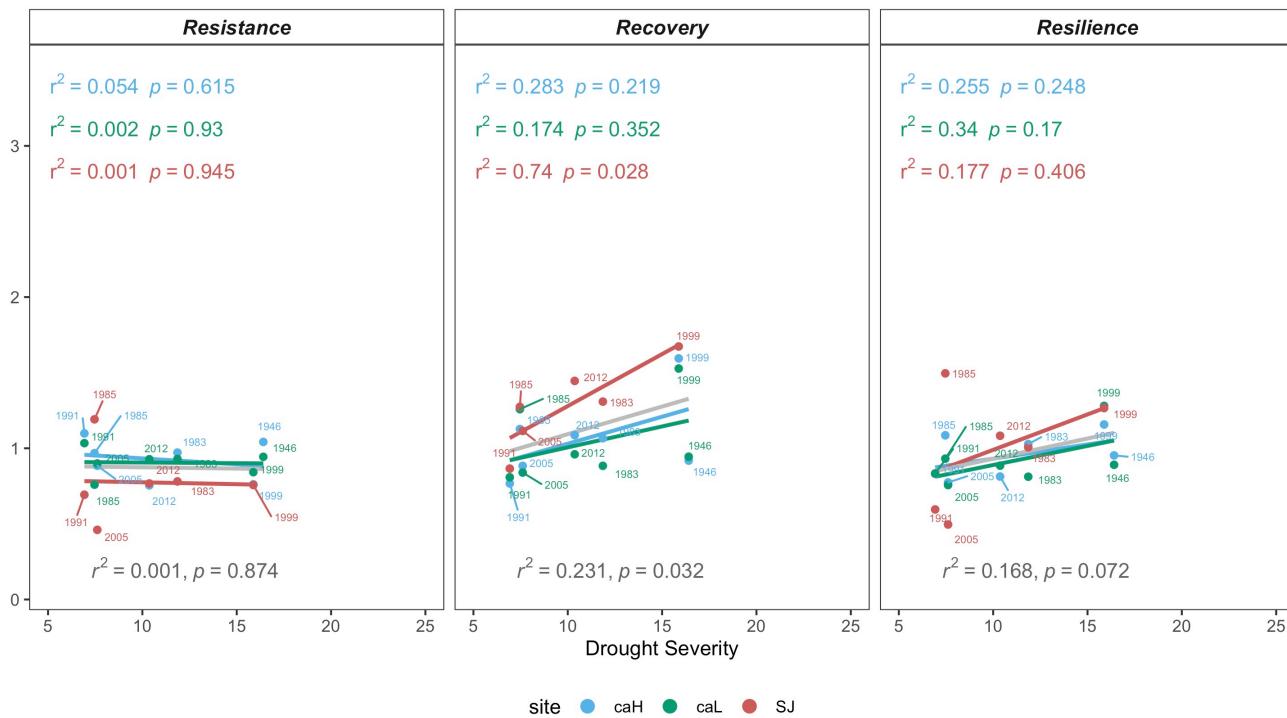
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Figure S3

66 **Figure S4**



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68 **Figure S5**

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