



**Land-use legacies and climate change as a double challenge
to oak forest resilience: mismatches of geographical and
ecological rear edges**

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Dear Co-Editor-in-Chief Monica Turner,

Thank you for your correspondence regarding our manuscript entitled “Land-use legacies and climate change as a double challenge to oak forest resilience: mismatches of geographical and ecological rear edges” (ECO19_0444R1).

We appreciate the helpful comments and suggestions from the two reviewers and the subject-matter editor. They have highlighted several points that were not clear in the previous version as well as weak points that needed to be strengthened.

Following their suggestions, we have restructured and rewritten the Introduction and Discussion sections for clarity. Specifically, we have addressed the importance of considering not only climatic or geographical aspects but other dimensions (e.g. land-use legacies) in the definition of the “ecological rear edge.” This has implications for the assessment of resilience in rear-edge populations.

In addition, we have improved our explanation of the different metrics and methods used. Also, we have re-formatted and rewritten the statistical analysis section. We have added a new figure to explain the general outline of our manuscript and the methods used. This new figure will aid the readers in understanding the aims, methods, and the results.

Below, please find our detailed point-by-point responses (indicated with “R”) to the reviewer comments and suggestions (in bold). We have numbered each comment and reply for easy reference and have indicated the line(s) (“L”) where the changes have been made in the manuscript.

A revised version of our manuscript with the new versions of figures and tables has been uploaded through the ECOSYSTEMS MANUSCRIPT CENTRAL.

With these changes, we hope that the manuscript will now be suitable for publication in ECOSYSTEMS.

Sincerely,

Antonio J. Pérez-Luque and co-authors.

Reviewer: 1
Major comments -

A. This work is strongest in its test of the impact of two recent droughts on the growth at the southern edge of a species range. I appreciated the multiple metrics used to quantify these drought responses: resistance, resilience, and recovery. However, I think these metrics needs to be defined in the introduction. They are currently not defined until part way into the methods, which makes the interpretation of the second and third tests of the main hypothesis (L96-103) difficult when they are first introduced. I would also appreciate a discussion of how you might expect the different metrics compare to one another. For example - would you expect resistance but not recovery to be high in edge populations due to

past climate extremes? Would you expect each of these metrics to be equally meaningful for range edge vulnerability?

R.A. We appreciate this comment. We have included definitions of resilience in the Introduction section, explaining their complementary nature (L76-88). We can expect these southernmost populations of Pyrenean oak growing at dry sites to be more vulnerable to drought than similar populations at wetter sites (Gea-Izquierdo et al. 2013; Gea-Izquierdo and Cañellas 2014).

B. The component of the study focused on land-use is very interesting and I agree that historical land-use complicates the assumption of geographic range edges as climate edges and therefore as a metric of climate vulnerability. Despite the focus on the land-use in the introduction and discussion, it is not part of the study objectives. Is there testable question about the growth responses either directly in response to the previous land-use or interactions between previous land-use and drought responses? I realize this may be difficult with only three study sites, but currently the land-use section in the discussion does not seem totally connected to the rest of the study.

R.B. We agree with the reviewer that the land-use component was not explicitly defined in the study. In line with the commentary, we have rewritten the Introduction and Discussion sections, including some sentences concerning the importance of the land-use dimension at the rear-edge of the species (Vilà-Cabrera and others 2019). In addition to the objectives already defined in the manuscript, we examine forest-management history and how it has influenced tree growth and resilience. Thus, we have also explicitly stated this as a specific objective of the study (L110-112).

C. The section on statistical analyses needs to be expanded to explicitly lay out what metrics were put in what models. Please format this section into what models addresses what study objective (i-iii). It would be helpful to walk through each of the climate variables used for these models. Were their separate models for BIA, EVI and RWI metrics of resistance (rt), resilience (rs), and recovery (rc)? Were all three drought metrics used (intensity, duration, lowest) in any models? Were the disturbance response metrics (changes in growth - GC) statistically analyzed? Was the local density of trees included in the models when considering drought responses?

RC. We agree with the reviewer that the use of different metrics can lead to confusion for the reader. We have prepared a figure (Figure 2 in the reviewed version), where we show the different metrics used in our methods and their relation to each of the objectives (numbered from 1 to 4). We also show the main analyses done. As this new figure indicates, resilience metrics were computed for BAI and EVI.

We also have re-formatted the statistical section following to the reviewer's suggestion (L259-286). We indicated the models and the metrics used specifically and their relationships with each of the objectives of the study.

Regarding the drought metrics, our approach was as follows. First, we identified severe drought events since 1901 in our study area following the approach proposed by (Spinoni and others 2015). Secondly, we characterized them using several metrics, i.e. intensity, duration, severity (Table S3). Then, we used this information in two ways. On

the one hand, it served to check whether the droughts of 2005 and 2012 were indeed among the worst drought events in our area of study, as stated in other works (e.g. Páscoa and others 2017). On the other hand, we explored the relationship between drought severity and the resilience metrics used (See Figure 5a).

As stated in L226-243, we used the Growth Changes (GC) in time to indirectly identify possible past disturbance events (e.g. logging, drought-induced neighbor mortality). To separate growth peaks caused by disturbance events from those caused by climate, we considered a threshold of 50% of GC and more than 50% of the individual trees displaying the same growth changes (Gea-Izquierdo and Cañellas 2014). GC was computed at the tree level using tree-ring width (TRW) and then we built site-disturbance chronologies (as stated in the manuscript, L233-236). We do not statistically compare site-disturbance chronologies because we use them only to explore past disturbances.

We are aware that competition interacts with growth responses to climate (Fernández-de-Uña and others 2015, 2016); however it was not possible to determine the local density of trees for each of the past drought events. Like many other studies, we have a picture of competition from a recent sampling. Following this, we computed several competition indices for the present stands (L201-204) and we assumed that current competition is an indicator of past competition.

Line-specific comments-

#1. L38 – Perhaps clarify that this statement holds true for distributional shifts, but potentially not all types of responses

R1. We have clarified this in the text (L35).

#2. L41 – I think the phrasing “It has been often assumed that geographically marginal populations represent ecological marginal populations” may be clearer.

R2. We appreciate this suggestion, as it makes the sentence clearer. We have made the change suggested (L39-40).

#3. L44 – Potentially also reference Oldfather et al 2019 Global Change Biology as a more recent review

R3.. We have included this suggestion in the text (L43 and the references).

#4. P63-72 – This paragraph does not clarify why drought in particular is important at range edges (relative to other climate drivers?). Perhaps I do not fully follow the main take-away from this paragraph. Is it highlighting the importance of studying range edges, or drought? Or considering land-use impacts? This paragraph seems to contradict the first paragraph about how there may be a disconnect between range edges and climate edges.

R4. We agree with the reviewer that the paragraph was somewhat confusing. We have restructured and rewritten part of the Introduction section to present the ideas more clearly, as for example: the importance of the study of the rear-edge populations; the effects of climate change (e.g. droughts) on these rear-edge populations; the effect of

past legacies (land-use legacies) on these populations; and the assessment of resilience by addressing both of the drivers of change in rear-edge populations.

#5. L92 – How is it known that the rear-edge is set by land use? Is there an associated reference for this? I thought this was a question that this paper was addressing. Also, there needs to be a more in-depth introduction on why land-use would limit resilience to drought prior to this.

R5. We agree that this sentence is one of the main issues addressed by our manuscript, and now is highlighted in the Discussion section. We have removed this sentence from the Introduction. As we mentioned in the previous comment, we have included a specific paragraph about how the anthropogenic habitat modification and its legacies are key for rear-edge populations (L60-75). We have also added sentences concerning how the past legacies would limit resilience as they may intensify, confound or delay climate-driven population declines at rear edges (L68-75; L101-104 among others).

#6. L103 – What is the difference between resistance, resilience, and recovery?

R6. We have specifically included the definitions of these terms in a subsection of the Material and Methods (L244-258). Additionally we have included some sentences in the Introduction (L76-96) addressing another comment of Reviewer 1 (see Major Comment A).

Resilience is a key concept in Ecology describing the capacity of an ecosystem to maintain its state and recover from disturbances (Holling 1973; Hodgson and others 2015). There are different metrics that have been used to quantify the ecosystem responses to disturbance events (see Ingrisch and Bahn 2018 for a recent review and references therein). One of the most widely used appears in the approach proposed by Lloret and others (2011), which describes resistance and recovery as different but complementary components of resilience. These authors proposed three indices to quantify the resilience of tree growth to drought based on the differences in growth before, during, and after the drought event. Their approach breaks down resilience to drought into three components: resistance to drought, recovery after drought, and resilience. It has been very widely accepted because it allows a simple, yet highly efficient assessment of short-term responses of trees to drought, although it is not exempt from some criticism (Schwarz and others 2020). Resilience is the capacity of an ecosystem to persist and maintain its state and functions in the face of disturbance. It is determined by the capacity to reduce the impact (resistance) and the capacity to recover from the impact of disturbance (recovery).

#7. L162 – Is it necessary/correct to remove year i from the calculation of $EVI_{mean, ref}$?

R7. We appreciate this comment. As we indicated at L177-180, the computation of the EVI standardized anomaly ($EVI_{sa,i}$) for year i , were done according to: $EVI_{sa,i} = (EVI_{mean,i} - EVI_{mean,ref}) / \sigma_{ref}$, where $EVI_{mean,i}$ is the annual mean value of EVI for year i , and $EVI_{mean,ref}$ the average of the annual EVI values for the period of reference 2000-2016 (all except year i); and σ_{ref} the standard deviation for the reference period.

We had removed the year i for the calculation of the $EVI_{mean,ref}$ because we found that this produces a more sensitive metric than when keeping the year i in the computation. We illustrate this in the Figure R1.

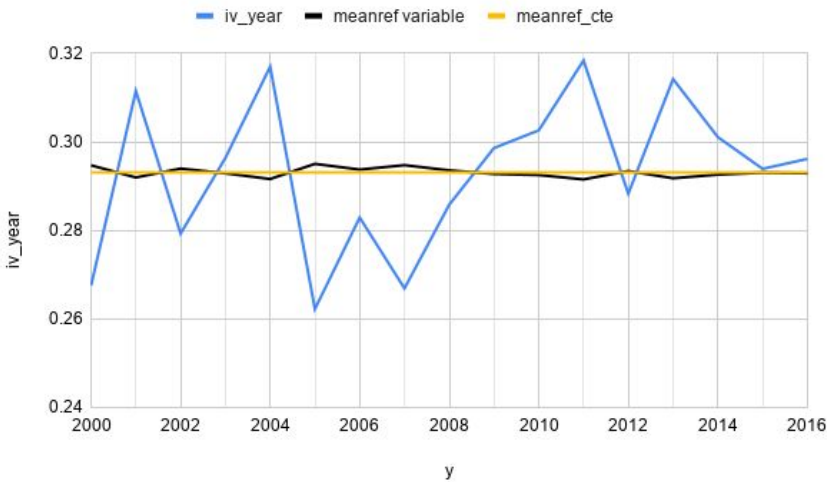


Figure R1. Time-series value of annual mean EVI for a pixel (blue line). Average of the annual EVI values for the study period (2000-2016) by removing the value of year i (black line) and without removing it (yellow line)

We found that both approaches have been frequently used to detect anomalies in the literature (e.g. Saleska and others 2007; Samanta and others 2010, 2012 for examples of removing year; Kuenzer and others 2015; Meroni and others 2019 examples of not removing the year i).

Also, we have calculated the standardized anomalies following the reviewer's suggestion and we have found very small differences in our results, suggesting no alteration in our pattern (Figure R2; Table R1).

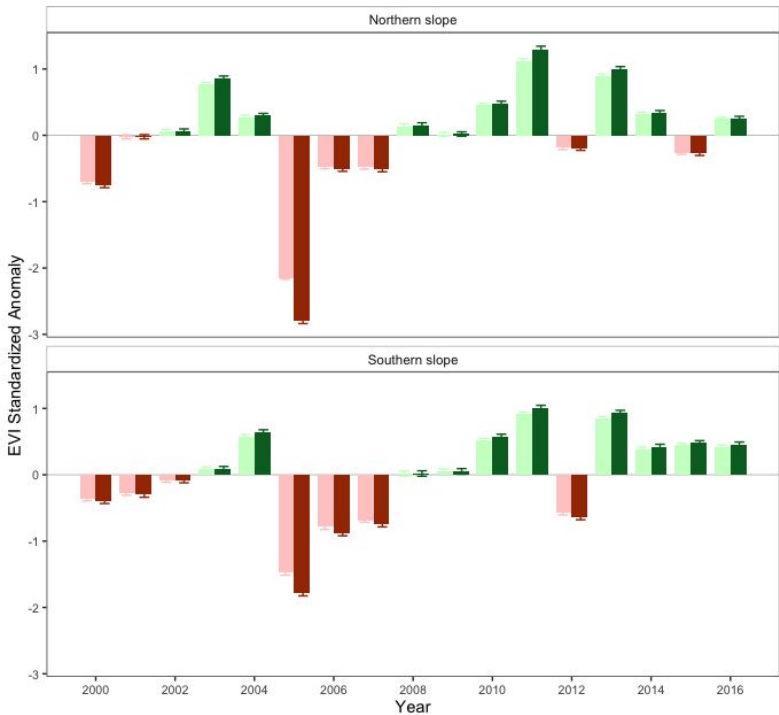


Figure R2. EVI standardized anomaly during the period 2000-2016 for the northern and southern populations. Error bars show standard error. Dark-green and dark-red bars correspond to the values as calculated in the manuscript (see Figure 3a in the

manuscript) and light green and light red correspond to the standardized anomalies calculated according to the reviewer's suggestion.

	type	Year	% pixels Original computation	% pixels new computation
	browning	2005	99.36	99.36
	browning	2012	7.22	5.94
	greening	2005	0	0
Northern slope	greening	2012	3.18	2.55
	no change	2005	0.64	0.64
	no change	2012	89.6	91.51
	browning	2005	79.37	76.87
	browning	2012	29.02	27.44
Southern slope	greening	2005	1.13	1.13
	greening	2012	0.91	0.68
	no change	2005	19.5	22
	no change	2012	70.07	71.88

Table R1. Percentage of pixels showing browning, greening or no changes during the 2005 and 2012 drought events according to EVI standardized anomalies. We show the percentage of pixels calculated following the “original computation” (as in the manuscript) and the “new computation” according to the reviewer’s suggestion.

#8. Line 220 – For tree-ring analyses, are site-level metrics only ever used? This seems to lead a very limited dataset of 3 sites, two of which are much closer together. Is it possible to use the variation of the individual trees? Or why is it best to take a site average?

R8. Please note that we used individual analyses for tree-growth resilience and also calculated indices of individual competition. We combined this analysis with a climate-growth analysis in growth chronologies, which is an widely accepted analysis in dendroecological studies. The fact that we found great variability and differences in the response of trees between sites that are very close is one of the main results of our study: the forest studied is relict and covers a small surface area, and thus is ‘a priori’ considered a rear-edge. Despite the limited size of this forest, we report great variability along the rear edge, and therefore we discuss why it should be redefined in our study area.

We have also included a new figure (see Figure 2) explaining the metrics used and also the analysis carried out.

#9. L233 Why was BAI and not RWI used for individual tree resilience metrics?

R9. We appreciate the question. We used BAI because it represents a more accurate indicator of growth than does ring width, particularly for non-juvenile ages, since it

removes variation in growth attributable to increasing stem circumference after 30-40 years of juvenile growth (Biondi and Qeadan 2008) (L219-221). We specifically tried to avoid possible bias in resilience metrics that could arise from negative exponential biological growth in RWI (i.e. from decreasing RW not related to climate or drought). The use BAI effectively removes the apparent decline in ring-width as a result of increasing stem circumference, and the inverse relationship between radial growth (ring width) and age disappears when analyzed as basal area increments (BAI) (Biondi and Qeadan 2008).

However, despite the widespread use of this approach in dendroecological studies, Schwarz and others (2020), in a recent critical review on the resilience metrics proposed by Lloret and others (2011) (i.e. those that we used in our analysis), noted that resilience metrics are sensitive to the growth variable used. They found that resilience values calculated based on BAI were higher than those calculated for RWI. However, there does not seem to be a clear pattern and it has been pointed out that it also depends on other factors (e.g. period of years considered).

Nonetheless, considering the importance of the point raised by Reviewer #1, and following the recommendation of Schwarz and others (2020), we have computed the resilience metrics using RWI and have made comparisons with the results found when BAI is used. As reflected in the Figure R3, the resilience metrics values were slightly lower with RWI than when resilience metrics were computed using BAI. The difference is minor and, most importantly, the spatio-temporal pattern discussed does not change.

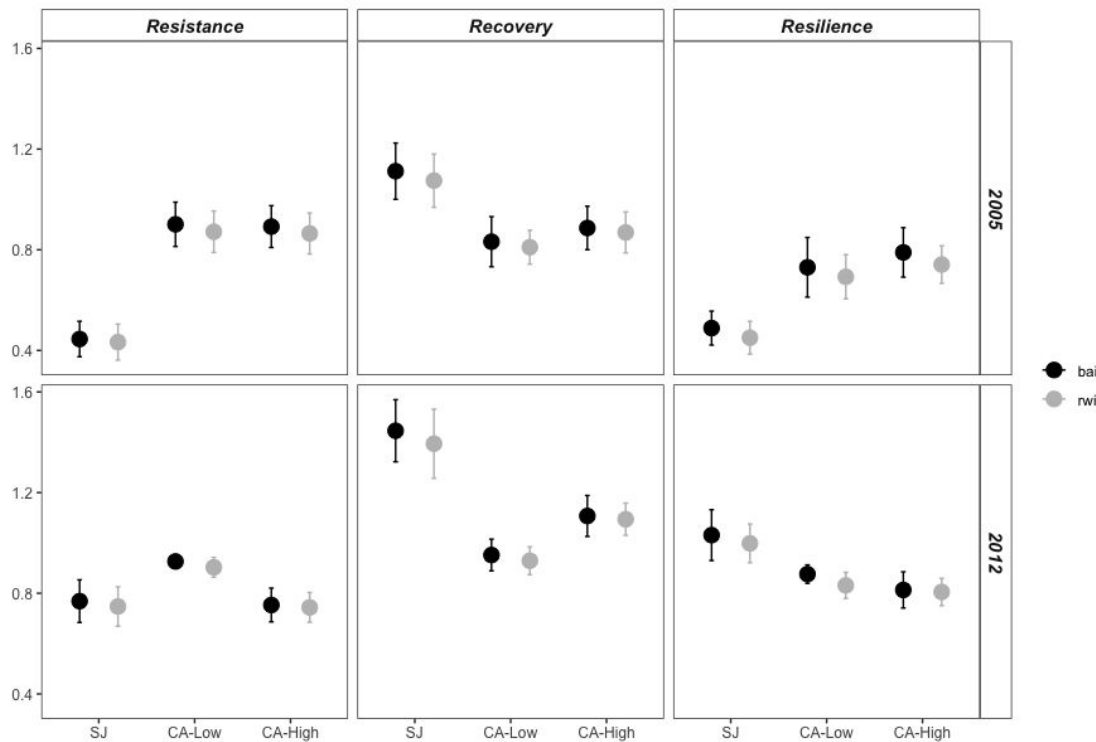


Figure R3. Comparison of the resilience metrics (resilience, recovery, and resistance) computed using BAI (black) and RWI (grey)

#10. Line 283 – These terms are used rarely enough that I think that resistance, resilience, and recovery should be written out fully.

R10. We have removed the abbreviations Rt, Rc, and Rs and have written out those terms (resistance, recovery, and resilience) throughout the manuscript. (e.g. L245-258 and L318-L336).

#11. L 290 _ When stating the resistance, resilience, and recovery results, state the BAI vs EVI results separately. They are currently difficult to follow, and unclear when both metrics are being considered.

R11. As suggested, we have re-written these terms separately for each of the variables (L318-L336).

#12. L300 – Which study aim does growth responses to climate fall under? I am getting mixed up about which question this addresses.

R12. It is a common procedure in dendrochronological studies. The idea is to analyze the relationships between climate and growth. The aim is to explore the effect of climatic variables on growth and then to infer how extreme climatic events could affect the tree growth. We have included this section to show the effect of climate on growth, as is generally done in dendrochronological studies. However, we agree with the reviewer that it could be somewhat confusing if presented as a separate subsection. We have reduced and rewritten this paragraph, including it as part of another section (L308-312).

#13. L319 – 322 – This land-use section fills disconnected currently to the rest of the analyses. See major comment B.

R13. Please see our response to major comment B of the Reviewer #1

#14. L 439 – Did these droughts impact these edge populations more than any central populations? That seems like the central questions to address to test if the geographic edge is ecologically marginal. There could potentially be overall increase in growth across the species range, but the extreme events have a larger impact in the edge populations.

R14. We appreciate the comment. Our work focuses only on the rear edge, and with our data (we did not sample the entire latitudinal gradient of the species) we cannot determine how droughts impacted populations located on the rear edge in comparison with those located in the central area. However, in a previous study, where *Q. pyrenaica* populations were sampled along a latitudinal gradient in the Iberian Peninsula, Gea-Izquierdo and Cañellas (2014) found a stronger effect of the drought-related variables on the populations located in the rear-edge than those in the central area.

In any case, we agree that it would be helpful to assess the resilience of growth variables (e.g. BAI) to the past drought events along climatic gradients across the geographical distribution of the species.

Reviewer: 2

C1.

I have minor suggestions that I think will help clarify the message and resolve some issues I see in the manuscript. The authors focus on precipitation and

drought as a driver of the southern range edge of this species. While I no doubt believe this plays a major role in determining species distributional limits in the Mediterranean region I would like to see some additional thought given to the role of temperature to their southern range limit. Or at least give more details of how drought and precipitation affect other species in this region.

R.C1. We appreciate this suggestion. On this basis, we further discuss the temperature-growth relationships found and highlight the importance of high vapor-pressure deficit and heat waves that should increase with warming and climate change. See L372-387, where we also discuss the importance of temperature on the rear edge of other species.

C2.

The authors use the term ‘ecological edge’ but I think they are really referring to a climatic range-edge. These aren’t necessarily the same thing as an ecological edge could be determined by biotic interactions or other abiotic limits (e.g. soils). But this raises another point, are the authors sure that climate is the true determinate of this range edge? Is it possible human land-use has artificially restricted this species or that biotic interactions (e.g. competition with more southern oaks) limits their distribution? This should be clarified and discussed if possible.

RC2. We appreciate these suggestions, which have served us in writing the new version of the Introduction and Discussion sections, where the different geographical and historical ecological aspects are now explained in more detail (e.g. L42-48, L68-75, L385-387, and L457-483).

C3.

The authors also need to do a better job showing that drought severity was equal at the southern and northern sites, especially during the 2005 drought. This may be difficult to do if there are not site-specific data. The sites appear ~20 km apart and this could mean large differences in drought severity, especially if the northern sites are already known to be drier. If drought severity was higher at the SJ site then this would explain the drop in the EVI at SJ and not such a severe drop at the southern facing sites. At the very least, the authors should acknowledge that the differences in population response to droughts may be related to drought severity rather than just genetic variation of the individuals within the different populations.

The reviewer is correct. The climatic data around each site are not site-specific or continuously recorded. We fully agree with the reviewer on the importance of comparing values in drought severity among sites. We followed two approaches. First, we built a series of precipitation using data coming from several stations close to each of the sites (n= 4 for northern site, SJ; and n=3 for southern sites, CA). As shown in the figure R4, the cumulative precipitation of the hydrological year (a measure of the water stress) was similar from 2005 for both sites, while was slightly lower for SJ sites during the 2012 drought events. Secondly, we explored other nearby stations that had long thermopluviometric data series (temperature, precipitation, and potential evapotranspiration), to evaluate the SPEI index between the two sites since 1990 (Figure R5). We found that the 2005 drought event was similar in intensity and duration at both sites, while the 2012 event was shorter and less intense at the southern sites.

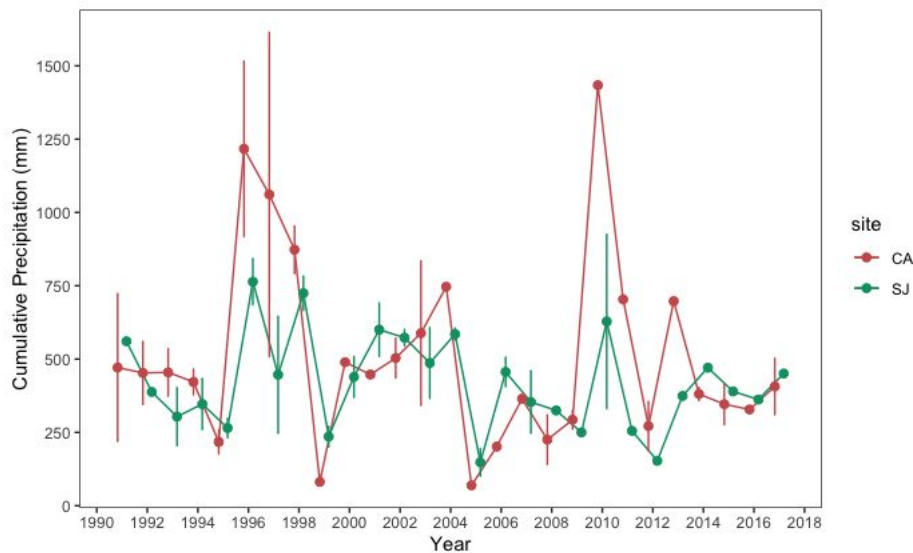


Figure R4. Temporal evolution of cumulative precipitation (hydrological year) during the period 1990-2017. Points represent the mean, and error bars the standard error. Data from meteorological stations distributed around northern (SJ, $n=4$) and southern (CA, $n=4$), sites respectively.

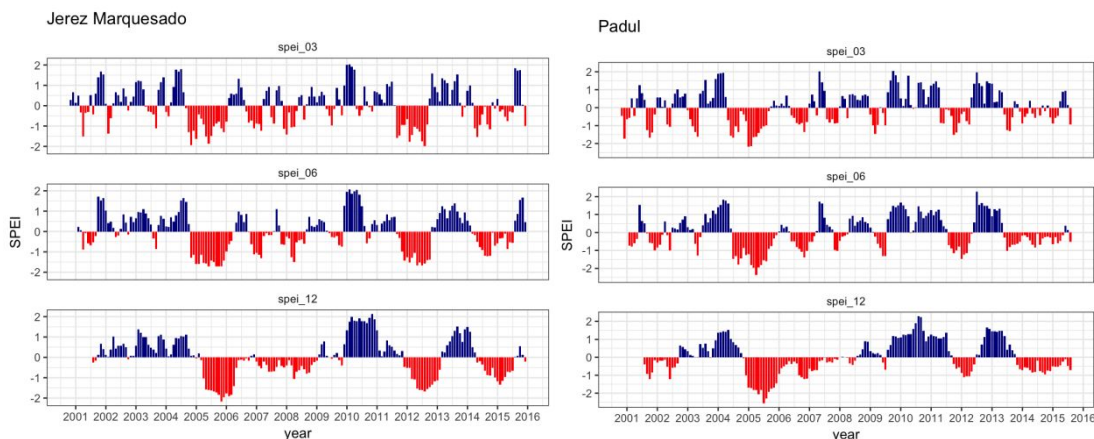


Figure R5. SPEI index for northern (left) and southern (right) population of the Sierra Nevada mountains.

C4.

The manuscript could also use some shortening. Consider moving some of the many figures into the supplement.

We appreciate the suggestion. We have revised the text to remove redundant and unnecessary text. We have combined several figures: the old Figures 3 and 4 were combined into new Figure 3. The old Figures 5 and 6 were combined into new Figure 4. Also, we have moved old Figure 7 into supplementary figures as Figure S6.

More detailed edits:

#15. L44-46 – Should review Rehm et al 2015 Ecology and Evolution for additional references and possible cite.

R15. We appreciate the suggestion. We have included the reference (L41).

#16. L47-48 –A true ecological edge would also account for biotic interactions.

R16. We agree with the reviewer and have included this idea in the new Introduction (L49-50).

#17. L58-62 – the sentence is poorly worded. Consider dropping the second part of the sentence after the Navarro-Gonzalez citation or breaking this into two sentences.

R17. We have removed the second part of the sentence. In any case, as we stated in previous responses (e.g. see response RB) we have restructured and rewritten the Introduction section, removing unnecessary and confounding sentences.

#18. L68 – sentence seems unnecessary

R18. We removed it. See R17.

#19. L69 – sentence starts with “this” but what does “this” refer to? The response of rear-edge populations stated two sentences before?

R19. We have explained this more clearly now, and we have deleted the unnecessary sentences (see last two responses).

#20. L76 – the authors use dendrochronology and then dendroecology. Are they the same thing? If so I suggest just using dendroecology throughout the paper and avoid mixing terms.

R20. The two concepts are closely related. Dendrochronology refers to the science of dating tree rings and studying their structure to interpret information about environmental and historical events and processes (Kaennel and Schweingruber 1995), while dendroecology is a subfield of dendrochronology applied to ecological questions (Fritts and Swetnam 1989). It uses the variation in tree-ring structure and width to determine ecological and environmental variability and its implications for forests. Following the recommendation, we have restricted ourselves to using the term “dendroecology” throughout the manuscript.

#21. L94 – climate change ‘along’ a small-scale gradient?

R21. We appreciate the suggestion and have incorporated the change in the text (L108).

#22. L119 – should be clear on what you mean by ‘richest’. Is this species richness?

R22. Yes, it refers to species richness of plants. We have clarified this in the text (L136).

#23. L142-144 Are severe droughts and drought events different criteria?

R23. A severe drought is a type of drought event. As we stated at L150-L164, a drought event starts when drought index values (SPEI in our case) fall below a certain threshold for at least two consecutive months, and ends when it turns above the mean value of the series (Spinoni and others 2015). The drought events can be classified in the following classes: moderate, severe, and extreme depending on the value of the threshold. We followed the classification proposed by Agnew (2000), which has been used in several works (e.g. Spinoni and others 2015, 2017; Páscoa and others 2017). This approach

uses the following threshold values: moderate if $-0.84 > \text{drought index} \geq -1.28$; severe, if $-1.28 > \text{drought index} \geq -1.65$; and extreme, if $-1.65 > \text{drought index}$.

#24. L173-182 – why weren't multiple elevations sampled at SJ?

R24. Our initial scheme was to sample in each locality at two elevations, but in SJ it is distributed in a narrow altitudinal band (see Figure 1 of the manuscript) located at the bottom of the valley, in contrast to those located in the southern area (CA sites), where they occupy a wider elevational band. We sampled 20 trees at SJ site distributed along the elevational gradient because this was small and we found no ecological heterogeneity to split into two different altitudes. If we split the SJ dataset into two sets (each with 10 trees), i.e. SJ-low and SJ-high elevation, we observe that the difference in elevation between low and high is less than 70 m (SJ-high = 1357 vs. SJ-low = 1288; average values) while in the population of the CA site this difference (between high and low site) is more than 150 m (CA-high = 1894 vs. CA-low = 1742, average values). Furthermore, the stand structure in SJ is homogeneous along the small gradient whereas that in CA differs markedly between the two altitudinal areas sampled (see Table 1 in the main text).

Below, for clarity, we compute separated BAI-chronologies for SJ-High and SJ-Low (had we split data into two), and we find no pattern differences between the two sites (Figure R6). Therefore we did not include two separate elevation groups in the analysis for SJ site.



Figure R6. Basal Area Increment (BAI) chronologies of *Q. pyrenaica* for northern populations at the low elevation (SJ-Low) and the high elevation (SJ-High); and southern ones: low-elevation (CA-Low; and high-elevation (CA-High) sites. Shaded areas correspond to the standard error of the mean.

#25. L267 – consider changing ‘growth was significantly faster’ to “growth was significantly greater”.

R25. We have changed the sentence accordingly (L296).

#26. L330-334 – can the dendroecology work or historical records give an estimate of stand density during these times?

R26. We appreciate the question. We agree that it is important to consider stand density because it greatly affects growth (see references in the main text). Dendroecological methods provide a series of growth data with an annual resolution, which can be used to analyze the forest’s responses to spatio-temporal changes in climate. However, due to a lack of long-term competition series, few studies have been able to profit from the valuable long time span of this type of data in order to investigate the effect of the interaction between competition and climate on tree growth (see Fernández-de-Uña and others 2015 for a revision). Most dendrochronological studies sample only the current stand density, using this as a surrogate for the past stand density (for the 10-20 previous years, maximum) and fewer studies have explicitly modeled growth as a function of both climate and competition (see Fernández-de-Uña and others 2015 for a revision). A way to estimate stand density in the past is to use historical forest inventories and/or permanent plots that provide information on the forest structure and its dynamics. We exhaustively reviewed historical forest inventory and also historical data but found no density estimates that match spatially or temporally with our growth data. In Table S4 summarizes the main data from the review of historical documents.

#27. L430 – can the authors offer a new definition?

R27. We have included some commentary on this issue (L468-483; and also the Concluding Comments section). Our contribution is a case study where we highlight the need to take into account land-use for the definition of rear-edge, which adds more evidence to what other authors suggested (*e.g.* Vilà-Cabrera and others 2019): in order to define the rear edge, at least in the Mediterranean region, it is necessary also to consider other elements such as land legacies.

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1 Land-use legacies and climate change as a double challenge to oak
2 forest resilience: mismatches of geographical and ecological rear
3 edges

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

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12 Manuscript highlights

- 13** • *Quercus pyrenaica* rear-edge forests showed high resilience to drought
- 14** • Resilience and the growth response to climate followed a water-stress gradient
- 15** • Tree growth and vegetation indices were highly sensitive to drought and land-use

16 Abstract

- 17** • Global change challenges ecosystems in xeric locations transformed by intensive human use.
- 18** Resilience to drought of relict Mediterranean *Quercus pyrenaica* populations in the southern Iberian

* 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. All authors contributed in the writing process to the drafts and gave final approval for publication.

Peninsula was analyzed in relation to historical records of land-use, combining dendroecological growth of adult trees and greenness (EVI) as proxies for secondary and primary growth.

- The growth trends reflected a strong influence of old land-use legacies (e.g. firewood removal) in the current forest structure. Trees were highly sensitive to moisture availability but both primary and secondary growth expressed high resilience to drought events over the short and the long term. Resilience and the tree growth response to climate followed a water-stress gradient. A positive growth trend since the late 1970s was particularly evident in mesic (i.e. colder and wetter) high-elevation stands, but absent in the most xeric (i.e. warmer and drier) stands.
- The high values of resilience observed suggest that the studied *Q. pyrenaica* populations are located in a geographical but not a climatic or ecological rear edge. Resilience of oak stands to drought events was not spatially homogeneous across the mountain range, due to differences in ecological conditions and/or past-management legacies. This is particularly relevant for rear-edge populations where topographic and biophysical variability can facilitate the existence of refugia.

Keywords

extreme drought, resilience, rear edge, *Quercus pyrenaica*, tree growth, dendroecology, remote sensing

Introduction

The response of species to changing environments (e.g. distributional shifts) can be determined largely by population responses at range margins (Hampe and Petit 2005). Peripheral populations are usually considered more vulnerable compared with populations at the center of a species' range (i.e. center-periphery hypothesis; Sagarin and Gaines 2002; Pironon and others 2017). Geographically marginal populations have often been assumed to represent ecologically marginal populations. This means lower performance, higher vulnerability, and thus higher risk of extinction than for populations at the core of the species' range (Rehm and others 2015; Pironon and others 2017; Vilà-Cabrera and others 2019). Nonetheless, recent reviews report that species- and population-specific responses do not always support this hypothesis (Sexton and others 2009; Abeli and others 2014; Oldfather and others 2020). This is partly because a rear-edge is a multidimensional concept including an ecological (i.e. climatic and edaphic), a geographical, and a genetic component (Vilà-Cabrera and others 2019), but also an anthropogenic dimension (i.e. land use). In this respect, to fully understand changes in distribution and abundance of species as a consequence of global change, it is crucial to identify and understand mismatches between the geographical and the ecological rear edges (Vilà-Cabrera and Jump 2019).

Limits of species distribution are strongly determined by climatic factors and biotic interactions (Gaston 2009; Sexton and others 2009). Climate change is expected to cause major shifts in the distribution and

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3 51 abundance of plant communities, and signs already indicate that more intense and longer droughts are
4 52 altering forest dynamics (Allen and others 2010). Drought frequency and severity have increased in
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6 53 recent decades, with a trend towards drier summers, particularly for Southern Europe (Vicente-Serrano
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8 54 and others 2014; Stagge and others 2017). In this climatic-change context, population loss and range
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10 55 retractions are expected in boreal, temperate, and Mediterranean species at the lowest latitudes and
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12 56 elevations, as well as in drought-prone areas of a species' distribution, *i.e.* the rear edge. The rear-edge
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14 57 populations are likely to be more sensitive to minor climatic and microtopographic variations and therefore
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16 58 the effects of droughts are expected to be particularly noteworthy (Hampe and Petit 2005; Vilà-Cabrera
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18 59 and others 2019).

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20 60 It is often overlooked that human activity constitutes a driver of change as powerful as natural drivers,
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22 61 such as climate, or even more powerful (Sala and others 2000), particularly for regions with long land-use
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24 62 history such as the Mediterranean Region (*e.g.* Navarro-González and others 2013; Doblas-Miranda and
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26 63 others 2017). In these areas, the susceptibility and response of ecosystems to natural disturbances are
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28 64 conditioned by legacies of historical land-use activity (*e.g.* Munteanu and others 2015; Mausolf and others
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30 65 2018). The past land-use legacies interact with recent natural disturbances and may confound their
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32 66 interpretation (Foster and others 2003). For example, recent works showed that a quarter of current
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34 67 forests in the Iberian Peninsula, the rear edges of several temperate and boreal tree species are growing
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36 68 on former agricultural and grazing land abandoned after the 1950s (Vilà-Cabrera and others 2017).
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38 69 Consequently, anthropogenic habitat modification and its legacies represent a critical dimension of
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40 70 marginality as they may intensify, confound or delay climate-driven population decline at rear edges (Vilà-
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42 71 Cabrera and Jump 2019; Sánchez de Dios and others 2020). In this context, our work seeks to identify
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44 72 the impacts and responses to natural (*e.g.* severe drought) and human disturbances (*e.g.* logging) on oak
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46 73 forests at their southern geographical range. Thus, a historical perspective should help us to interpret the
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48 74 responses of ecosystems to natural disturbances (Foster and others 2003), particularly regarding
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50 75 marginal rear-edge populations (Vilà-Cabrera and others 2019).

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52 76 The assessment of resilience to climate and human disturbances provides critical information concerning
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54 77 the capacity of forests to maintain their structure and render valuable ecosystem services. Resilience is
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56 78 the capacity of an ecosystem to persist and maintain its state and functions in the face of disturbance
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58 79 (Holling 1973; Hodgson and others 2015). Lloret and others (2011) proposed an approach which
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60 80 decomposes resilience into three components: resistance to drought, recovery after drought and
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62 81 resilience. This resilience is determined by the forest's ability to mitigate the disturbance (resistance) and
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64 82 the capacity to recover from the impact (recovery) (Ingrisch and Bahn 2018). This conceptual approach
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66 83 has recently become widely used to assess forest resilience, because it allows a simple, yet highly
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68 84 efficient assessment of short-term responses of trees to drought. Nevertheless, not exempt from criticism,
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70 85 this approach needs to be applied carefully to avoid potential bias at different levels (Schwarz and others
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72 86 2020). In this sense we assessed forest resilience both over the short-term, several recent extreme

drought episodes, as well as over the long-term climate change (*i.e.* warming on the last few decades), using two different proxies to characterize resilience. Dendroecological estimates of growth (*i.e.* tree-ring width) are commonly used proxies to characterize tree vitality, while annual tree-ring widths have commonly been used to study growth changes in response to drought at the individual tree level (Fritts 1976; Dobbertin 2005). Remote sensing can be used to analyze the impact of drought on ecosystems and hence at the stand level (*e.g.* Zhang and others 2013). The combination of remote sensing and dendroecology has been used to assess the effects of droughts on vegetation along ecological gradients (*e.g.* Vicente-Serrano and others 2013; Coulthard and others 2017), and also to evaluate growth resilience to drought in several tree species (*e.g.* Gazol and others 2018; Peña-Gallardo and others 2018).

In the present study, we assess resilience of *Quercus pyrenaica* Willd. (Pyrenean oak) from southern relict forests at the rear edge of the species distribution, where species performance is considered to be threatened by climate change (Gea-Izquierdo and others 2013, 2017). For this, we combined remote-sensing information and dendroecological methods to evaluate the impact of drought both on canopy greenness (as a proxy for primary growth) and radial tree growth (as a proxy for secondary growth). For the analysis of forest resilience to climate, we took into account the land-use history of these transformed forests, reviewing historical documents to reconstruct forest history at the study sites, and analyzing how anthropogenic drivers have shaped the current forest structure. Based on this analysis, we developed a rationale that integrates the ecological and anthropogenic components of marginality to determine the regional and local scale mechanisms shaping the probability of persistence (or extinction) of rear-edge oak populations. Our main hypothesis is that these stands will show low resilience to extreme droughts along a small-scale gradient. To test this hypothesis, we: (i) quantified how recent extreme drought events influenced primary and secondary growth of *Q. pyrenaica* forests at their present geographical rear edge; (ii) reviewed of historical documents to reconstruct forest-management history and to infer how it impacted on tree-growth along time; (iii) analyzed the long-term resilience of these forests to extreme drought events, using time-series of radial growth; (iv) and examined differences in the resilience metrics between populations under contrasting ecological conditions (*i.e.* xeric vs. mesic) along environmental gradients within the rear edge in order to detect vulnerability to climate change at the small spatial scale. For the latter, we characterized variability in the forest response to drought within the current geographical rear-edge and assessed whether the effect of aspect and environmental conditions expressed in northern and southern populations of Pyrenean oak forests differ in their resistance, resilience, and recovery to extreme drought events.

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119 **Materials and methods**

120 **Tree species and study site**

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

127 The forests of this species reach their southernmost European limit in Andalusian mountains such as
128 Sierra Nevada (37°N, 3°W), a high-mountain range with elevations of up to 3482 m a.s.l.. The climate is
129 Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought and
130 increasing aridity with decreasing altitude, and marked variability according to elevation and aspect.
131 Sierra Nevada is considered a glacial refuge for deciduous *Quercus* species (Olalde and others 2002).
132 Eight Pyrenean oak patches (2400 ha) have been identified in this mountain range (Figure 1), from 1100
133 to 2000 m a.s.l. and often associated with major river valleys. Today, *Quercus pyrenaica* woodlands in
134 this mountain region represent a rear edge of their habitat distribution (Hampe and Petit 2005). They are
135 the richest forest formation in vascular plant species of Sierra Nevada, containing several endemic and
136 endangered plant species (Lorite and others 2008). They also harbor high levels of intraspecific genetic
137 diversity (Valbuena-Carabaña and Gil 2013). These relict forests have undergone intensive human use
138 throughout history (Camacho-Olmedo and others 2002). Furthermore, the conservation status of this
139 species for southern Spain is considered “Vulnerable” and it is expected to suffer from climate change,
140 reducing its suitable habitats in the near future (Gea-Izquierdo and others 2013, 2017).

141 **Climatic data and drought episodes**

142 The Iberian Peninsula underwent several extreme drought episodes in the last three decades (e.g. 1995,
143 1999, 2005, 2012; Vicente-Serrano and others 2014). The 2005 and 2012 drought events have been
144 documented as being among the worst in recent decades for the southern Iberian Peninsula (Páscoa and
145 others 2017), appearing as extreme drought in our climatic data (Figure S1; Table S3). We focused on
146 these two drought events because they were included in the period having remote-sensing information of
147 high spatial resolution (MODIS started on 2000; see below). Nevertheless, for radial growth-time series, a
148 greater number of older drought events were also analyzed to contextualize the results for 2005 and 2012
149 and to evaluate forest resilience to drought over a longer term (see Table S3). A drought event was
150 identified using the SPEI (Standardized Precipitation-Evapotranspiration Index) (Vicente-Serrano and
151 others 2010) (SPEI 12-months scale), following a procedure similar to the one proposed by Spinoni and

5

others (2015). We used 0.5° grid cells covering Sierra Nevada taken from the Global SPEI Database (<http://spei.csic.es/database.html>). A severe drought event starts when SPEI falls below the threshold of -1.28 (Páscoa and others 2017; Spinoni and others 2018). A drought event is considered only when SPEI values fall below that threshold for at least two consecutive months. For each drought event, we computed: the *duration* as the number of consecutive months with the SPEI lower than a certain threshold; the *severity* as the sum of the absolute SPEI values during the drought event; the *intensity* and the *Lowest SPEI* refer to the mean and lowest value of SPEI respectively during the drought event.

To explore the relationships between climatic variables and tree-growth variables we used climate data obtained from the European Daily High-Resolution Observational Gridded Dataset (E-OBS v16) (Haylock and others 2008). Monthly precipitation and minimum and maximum temperatures had a 0.25 x 0.25 ° resolution for the 1950-2016 period. Grid cells were selected to cover each sampled site. The SPEI 6-months scale index was used to characterize the drought conditions for the period 1961-2014.

Greenness data to assess ecosystem resilience

Vegetation greenness of *Quercus pyrenaica* was characterized by means of the *Enhanced Vegetation Index* (EVI), derived from MOD13Q1 product of the MODIS sensor. 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. MODIS EVI data were compiled for the period 2000 - 2016. We selected the pixels covering the distribution of *Quercus pyrenaica* forests in Sierra Nevada ($n = 928$ pixels). Any values affected by clouds, snow, shadows or high content aerosols, were filtered out following recommendations for mountain regions (Reyes-Díez and others 2015).

The mean Annual EVI (EVI_{mean}) as a surrogate of mean annual primary production was computed for each pixel for the period 2000 - 2016. The EVI standardized anomaly (EVI_{sa}) was computed pixel-by-pixel, in order to minimize bias in the evaluation of anomalies and to provide more information concerning their magnitude (Samanta and others 2012). For each pixel, an annual EVI value was calculated by averaging EVI valid values. Then, the standardized anomaly was computed as: $EVI_{sa,i} = (EVI_{mean,i} - EVI_{mean,ref}) / \sigma_{ref}$, 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 year i); 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 such as the NDVI, EVI_{mean} was chosen because it is highly stable under the use of any filter (Reyes-Díez and others 2015) and because it showed highly significant correlations with annual ($r = 0.81$) and seasonal EVI values ($r_{spring} = 0.76$ and $r_{summer} = 0.88$).

Field sampling and dendroecological methods to assess individual tree resilience

Trees were sampled during the autumn of 2016 at two locations in contrasting N-S slopes of Sierra Nevada: San Juan (SJ), a xeric site located at the northern aspect (around 1400 m); and Cáñar (CA), a wetter site located at the southern aspect (Figure 1; Table 1). For the southern site, two elevations were sampled: CA-Low (around 1700 m) and CA-High (around 1860 m), constituting the current low-elevational limit for the species (CA-Low) and the maximum altitude currently reached by trees (CA-High), respectively, in the site sampled. Despite the proximity of these two elevations (less than a 200-m difference) the stands differ markedly in their structure and characteristics (Table 1). The three sampling sites followed a moisture gradient: SJ < CA-Low < Ca-High (Table 1). All the sites were oak monospecific and representative of the population clusters identified for the species in this mountain range (Pérez-Luque and others 2015b). At each site, between 15 and 20 trees from either the single dominant-codominant layer in CA or the open canopy in SJ were randomly sampled. Two cores of 5 mm in 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 affecting 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 with a 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 as $srd = \sum_{i=1}^n (dbh_j/dbh_i) \cdot [1/(dist_{ij} + 1)]$ (see Gea-Izquierdo and Cañellas 2009 for more details).

Tree cores were air dried, glued onto wooden mounts, and sanded. Annual radial growth (ring width, RW) was determined with a measuring device coupled to a stereomicroscope, for 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 growth response to the inter-annual variability of climate (short-term response), pre-whitened residual chronologies (RWI) were used. These were calculated from ratios between raw growth measurements and individual cubic splines with a 50% frequency cutoff at 30 years (Fritts 1976). Tree-ring width series were standardized and detrended using dplR (Bunn 2010). Mean residual site chronologies were established by 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 (EPS). A threshold value of EPS > 0.85 was used to determine the cutoff year of the time span that could be considered reliable.

The long-term growth response was analyzed using basal area increment (hereafter BAI, cm² · year⁻¹). In theory, BAI represents a more accurate indicator of growth than ring width, because it removes variation in growth attributable to increasing stem circumference after 30-40 years of juvenile growth (Biondi and

Qeadan 2008). Raw ring widths and measured DBH were used to compute BAI (Piovesan and others 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 tree-ring formation. For each individual tree, a mean BAI series was calculated. Then, mean site BAI chronologies were determined by averaging individual tree BAI time series.

Disturbance analyses and land-use history review

Disturbance chronologies were built using tree-ring width to identify abrupt and sustained increases (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 caused 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 exhaustively reviewed existing 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 spatio-temporal scales (see Table S4 for references).

Assessing resilience to drought at the forest stand and individual-tree levels

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 ($Resistance = Drought:PreDrought$) 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 ($Recovery = PostDrought:Drought$), represents the ability to recover from disturbance relative to its severity. Finally, the Resilience index ($Resilience = PostDrought:PreDrought$) 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.

Statistical analysis

Differences between sites for height, DBH, and competition indices were analyzed using non-parametric Kruskal-Wallis rank sum tests. When significant differences were detected, multiple comparisons were run using the Dunn's-test with Bonferroni adjustment to correct for significance.

The severe drought events since 1901 were identified using SPEI-12. They were characterized in terms of duration, severity and intensity (see Spinoni and others 2015). In a first step, the impact of drought in greenness and growth was explored using the EVI_{sa} and the mean RWI site chronologies (Figure 2). Additionally the relationships between climatic variables and tree-growth variables (RWI and BAI site chronologies) were assessed using bootstrapped Pearson's correlations estimated using treeclim (Zang and Biondi 2015). The non-climatic disturbance impacts on tree-growth were evaluated using site disturbance chronologies (built using growth changes on tree growth).

Responses of vegetation to disturbances were explored in the short- and the long-term using resilience metrics (resilience, resistance and recovery) and temporal trends respectively for both EVI and BAI (Figure 2). Resilience metrics of BAI were computed for the eight most severe drought events since 1950 (including 2005 and 2012), and their relationship with drought severity were explored. Resilience metrics of EVI were computed only for 2005 and 2012 drought events. Temporal trends of EVI_{mean} (pixel scale) and BAI (mean BAI site chronologies) were examined using non-parametric (Mann-Kendall) and parametric test (Pearson) respectively.

For each of the three resilience indices studied, we used robust two-way ANOVAs to test for differences between drought events (2005 and 2012) and the oak populations studied (northern and southern exposures). These tests were used because original and log-transformed data did not follow the assumptions of normality or homogeneity of variance (Wilcox 2012). Robust measures of central tendency (M-estimator based on Huber's Psi) were used because they were close to the mean value in all cases (Wilcox 2012). When the robust ANOVA test was run, data were bootstrapped 3000 times and 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 R package (Mair and others 2017). The level of significance was set to 0.05 and adjusted for multiple comparisons.

286 Results

287 Time trends in vegetation greenness

288 The analysis of time trends in greenness showed that 78.9% of the EVI pixels followed a positive trend for
 289 the 2000-2016 period. The lowest values of EVI standardized anomalies for the study period were
 290 recorded during the 2005 drought, and the minimum EVI values were expressed in the northern (dry)
 291 population (Figure 3a). A “browning” episode ($EVI_{sa} < -1$) was found during this drought event, whereas
 292 no changes in greenness in response to the 2012 drought were detected (Figure 3b).

293 Analysis of radial-growth trends and disturbances

294 The trees of the southern population were older than those from the northern one. In addition, trees from
 295 the southern population at high elevation were taller and their growth was significantly greater than that of
 296 trees from the other two sites, despite stand competition measured as plot basal area was greatest in CA-
 297 High (Table 1, Figure 4a). The growth and height of trees from the northern and the low-elevation
 298 southern population were similar (Figures 4a and S3a). Only trees from the southern sites (*i.e.* the wetter
 299 exposure) showed significant positive growth trends since the late 1970s (Figure 4a), this trend being far
 300 more pronounced for the wetter and colder high elevation site (CA-High).

301 Drought events reduced radial growth for all sites (Figure S2a). The strongest reduction in radial growth
 302 occurred in response to the 1995 drought (the worst drought spell in our climatic record, Table S3) for all
 303 sites. Tree-growth reductions in response to drought followed a moisture gradient. Tree-growth reductions
 304 in response to the studied drought events were lower in the southern sites (CA-High and CA-Low) than in
 305 the northern site (SJ), especially for 2005 and 2012 (Figure S2a). The weakest growth reductions were
 306 found in trees from the wettest site (CA-High).

307 The response of tree growth to water availability was greater than to temperatures. Cumulative
 308 precipitation of the hydrological year and seasonal SPEI values (*i.e.* for the Hydrological year, Spring and
 309 Summer) were the climatic variables exhibiting the highest (positive) relationship with growth for all
 310 populations (Figure S6a). Nevertheless, there were differences between populations: the positive
 311 relationship with SPEI was highest in the more xeric northern population ($r > 0.6$ vs. $r < 0.5$; Figure S6a).

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

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Resilience to drought events at the forest stand and individual-tree levels

Resilience and resistance varied in the same direction whereas recovery varied inversely to resilience and resistance. During the last two drought events, resilience metrics for greenness and tree growth significantly differed between drought events (Table S1). The 2005 drought event reduced greenness and growth more than that of 2012 (Table S2) but the metrics of resilience generally covaried in the same direction during those two years. For EVI, resilience and resistance values were significantly higher for 2012, the most severe event, than for 2005 (Table S2; Figure 5b); whereas recovery values were higher for 2005 than for the 2012 drought event. For BAI, the resilience, resistance and recovery values were higher for 2012 than for 2005 (Table S2, Figure 5c).

The recovery and resistance for greenness and growth varied significantly between sites. Resilience calculated for greenness also differed between sites but not for tree growth ($p = 0.534$; Table S1). The two southern populations showed lower recovery values than did the northern site both for greenness and tree growth, but resistance and resilience values were significantly higher for the southern site (Table S2).

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

Discussion

By using a combined approach of remote-sensing information and dendroecology, we quantified the growth of adult trees and greenness (EVI) as proxies for secondary and primary growth of relict Mediterranean *Quercus pyrenaica* populations in the southern Iberian Peninsula. These relict oak populations, driven by historical land-use, have been resilient to climate change at their present rear edge. However, resistance, resilience, and forest recovery after extreme drought events were strongly influenced by mountain exposure, local environmental conditions, and management legacies. This means that the geographical and the ecological rear edges do not necessarily match and, at a small spatial scale, tree performance can vary markedly along the rear edge under climate change.

High sensitivity and variability in the oak sensitivity to climate at the rear edge

Severe drought negatively affects both primary and secondary growth of *Q. pyrenaica* forests. This was expressed by the observed reduction in greenness and tree growth in response to the 2005 and 2012

drought events as well as by radial-growth suppression during extreme drought events (Corcuera and others 2006; Gea-Izquierdo and Cañellas 2014). Furthermore, the greatest reduction of tree growth was detected during the 1995 drought, a characteristic negative precipitation anomaly that caused severe and extensive damage in the Mediterranean Iberian Peninsula (Peñuelas and others 2001; Gazol and others 2018).

The tree responses to drought are site-dependent (Babst and others 2013), particularly for rear-edge populations (Cavin and Jump 2017; Dorado-Liñán and others 2017c). Greenness and tree growth were more affected by drought events in drier northern populations than in wetter southern oak populations of Sierra Nevada. The northern site showed higher browning intensity than did the southern sites during the 2005 drought event, and stronger correlations of tree-growth with SPEI (hydrological year and summer) at the northern site can be interpreted as higher sensitivity to drought at drier sites (Gea-Izquierdo and Cañellas 2014). Greenness was less sensitive to drought than tree growth, particularly for drier sites. These findings agree with previous works showing tree growth to be a more sensitive metric of forest resilience than is net primary productivity (e.g. Babst and others 2013; Coulthard and others 2017; Gazol and others 2018; Peña-Gallardo and others 2018), suggesting that the growth reduction could be mediated by sink more than by source limitations (Körner 2013; Fatichi and others 2014). Tree-ring records complement remote-sensing data in longer time scales by reflecting tree-growth anomalies induced by climate or disturbance over decades to centuries (Babst and others 2017) and provide an accurate measure of growth responses to droughts (Bhuyan and others 2017; Gazol and others 2018). On the other hand, trees at CA-High registered higher BAI than did those located at lower elevations (CA-Low and SJ; Figure 4). This shows the high variability in the response to climate exhibited along a narrow gradient, which was especially noteworthy for southern sites, as these lie close to each other and both are considered to constitute the rear edge for the species.

As with many other forest species under Mediterranean climates, moisture availability is generally the most limiting factor driving radial growth of *Q. pyrenaica* along its distribution range in the Iberian Peninsula (Gea-Izquierdo and Cañellas 2014). Thus, our results are consistent with those of previous studies highlighting the influence of precipitation on tree-ring growth in different oak species (e.g. Tessier and others 1994; Di Filippo and others 2010; Gea-Izquierdo and others 2011; García-González and Souto-Herrero 2017). A positive effect of moisture availability and negative impact of temperature expressing a limiting effect of high vapor-pressure deficit and potential evapotranspiration can be expected at drought-limited rear-edges. Yet, at the rear edge, the growth of some tree species (e.g. *Abies alba*) has been shown to be more sensitive to moisture-related variables (Martínez-Sancho and Gutiérrez Merino 2019), while others species were more sensitive to temperatures (e.g. *Pinus sylvestris*, Herrero and others 2013), and still other species responded simultaneously to both temperature and moisture-related variables (e.g. *Fagus sylvatica*, Dorado-Liñán and others 2017b, 2017a; *Pinus nigra* subsp. *salzmanii*, Sánchez-Salguero and others 2012). This diversity in the response of tree species to

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precipitation and temperature suggests that vulnerability to climate change is not consistently expressed within the rear edge, therefore evidencing that geographically marginal forests are not necessarily climatically or ecologically marginal (see Dorado-Liñán and others 2019 and references therein).

Relict oaks show high resilience to drought at different spatio-temporal scales: do the geographical an ecological rear-edges match?

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

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

The high drought-resilience values reported here, coinciding with high values of genetic resilience for those forests on Sierra Nevada reported elsewhere (Valbuena-Carabaña and Gil 2013, 2017) appear to indicate the strong local adaptation of this oak species. Our findings agree with those of studies showing that the assumed higher vulnerability of dry edges does not necessarily hold (e.g. Cavin and Jump 2017). In our case, this can be explained by the fact that the current geographical rear-edge does not match with the potential ecological rear edge for the species because this has been determined mostly by human use. Martínez-Vilalta (2018) pointed out the importance of local adaptation and plasticity, and also of local environmental factors on the vulnerability shown by rear-edge populations. Our results highlight the ample small-scale variability at the ecological boundary and thus the rear edges need to be more clearly defined and delineated. All the above points, together with the characteristic high resprouting ability of the

species, show the long-term persistence of these populations (Bellingham and Sparrow 2000). It should be mentioned that we studied only adult individuals established decades or centuries ago, meaning that it needs to be assessed whether the high resilience found is expressed at the species level or only in adult trees. The rear-edge might differ for different ontogenic stages. It is important to assess whether seedling regeneration and recruitment are vulnerable, as in other Mediterranean species at their xeric limit (Castro and others 2004; Vilà-Cabrera and others 2011; Gea-Izquierdo and others 2015).

Land-use legacies in relation to forest response under climate change and to the present rear edge

The review of historical documents revealed that forest clearings, firewood removal, charcoal production, and mining have strongly affected the forests on Sierra Nevada (Table S4), where an estimated historical loss of broadleaf *Quercus* species has approached 90% in tree cover at medium and low elevations (Jiménez-Olivencia and others 2015). Together with the analysis of the disturbance chronologies, the observed notable differences in stand structure, tree size, and age suggest different forest histories and a different management origin (*i.e.* land-use legacy) between northern (coppice) and southern populations (high forest, open woodland). On the northern slopes of Sierra Nevada (*e.g.* the SJ site), land uses have been historically distributed along an elevational gradient: grasslands and shrublands for cattle farming at the highest elevations; next forest stands with some croplands; and, finally, irrigated terraces with tree crops at the lowest elevations (Jiménez-Olivencia and others 2015). In addition, other activities such as mining must have altered the forest structure, *e.g.* the SJ site has many small mines and quarries that were exploited intermittently throughout history. The release growth event expressed in the 1940s concurs with a period of maximum mining activity in this area (1925 to 1957), during which timber use increased for mine tunnels and furnaces, these also requiring large amounts of firewood to melt the mineral (Table S4). This heavy exploitation of the neighboring forest resources must have affected a significant part of this oak woodland, as shown by growth of the remnant trees at the northern site (Figure S2b).

On the other hand, woodlands on the southern slopes (*e.g.* CA site) were mixed with a greater percentage of croplands along the elevational gradient where oaks grow (Jiménez-Olivencia and others 2015). Firewood, charcoal, and acorns were intensively exploited at the southern sites, until at least the mid-20th century, when these activities sharply declined due mainly to rural abandonment and the use of gas and fossil fuels (Valbuena-Carabaña and Gil 2013). At the CA-High site, the only positive release event found for the earliest years could be related to the conversion from closed forest to an open silvopastoral system, a common management practice often applied in the past in many Iberian oak woodlands (Cañellas and others 2004; Gea-Izquierdo and others 2011) and which has been documented for this site (Valbuena-Carabaña and Gil 2013).

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3 452 The other release event observed for the SJ site during the period 1995-2000 was lower than during
4 453 1940, but also affected most trees (Figures 4b, S2b). No records of forest practices in this area over the
5 454 last 30 years have been found (Bonet and others 2016), and no logging was recorded during the period
6 455 1995 - 2000 (F.J. Cano-Manuel *personal communication*). Therefore this release might be related to
7 456 natural drought-induced mortality after 1995, as has been reported for other Mediterranean tree species
8 457 after severe drought (e.g. Peñuelas and others 2001; Lloret and others 2004).

12 458 In summary, this research provides two main results. First, the high values of resilience in our study
13 459 suggest that *Quercus pyrenaica* populations in Sierra Nevada are located in a geographical, but not a
14 460 climatic, ecological rear edge (*sensu* Martínez-Vilalta 2018; Vilà-Cabrera and others 2019). The high
15 461 resilience values observed could also be related to stabilizing mechanisms promoting community
16 462 resilience that can buffer the impact of extreme events, as has been described for other species (e.g.
17 463 *Pinus sylvestris*, Herrero and Zamora 2014). Second, these resilience responses of oak forest to drought
18 464 events are not spatially homogeneous throughout the mountain range, due to differences in ecological
19 465 conditions and/or past management legacies. In fact, there was much small-scale variability in the
20 466 response to climate along the rear edge that we had *a priori* considered in our study. Furthermore, we
21 467 even found positive effects of climate change in certain stands, as discussed, in disagreement with our
22 468 hypothesis of expecting oak vulnerability along the entire geographical rear edge studied. This suggests
23 469 that the rear edge therefore needs to be redefined in space but also in time (Vilà-Cabrera and others
24 470 2019), partly because of land-use legacies and their effect on the possible mismatch between the current
25 471 distribution of species (*i.e.* determining the “available” geographical rear edge) and the potential
26 472 ecological (limiting) rear edge of species. The rear-edge concept should also consider historical aspects
27 473 in addition to the geographic, climatic, and genetic ones (Vilà-Cabrera and others 2019), particularly in
28 474 areas with a long history of human management, such as Mediterranean mountains. Therefore,
29 475 anthropogenic habitat modification and its legacies represent a critical dimension of marginality as they
30 476 may intensify, confound or delay climate-driven population decline at the rear edges (Vilà-Cabrera and
31 477 others 2019). Furthermore, even the geographical dimension of the rear edge is not a continuous, uniform
32 478 space of ecological conditions in mountain landscapes. In other words: in mountains, heterogeneity of
33 479 ecological conditions at fine scales is the rule, enabling the existence of microrefugia and lengthening
34 480 species persistence (Olalde and others 2002; Serra-Diaz and others 2015). In this respect, our results
35 481 showed that the resilience of oak stands to drought events was not spatially homogeneous across the
36 482 mountain range, due to differences in ecological conditions and/or past management legacies. This is
37 483 particularly relevant for rear-edge populations where topographic and biophysical variability can facilitate
38 484 the existence of refugia.

485 Concluding comments

486 The ecological and geographical rear edges did not appear to fully match each other in the forest
 487 ecosystem studied. Severe drought events provoked major reductions in primary and secondary growth
 488 of *Quercus pyrenaica* forests in the *a priori* relict, rear-edge forest studied. Nevertheless, contrary to our
 489 expectations, the trees exhibited high resilience in the response to drought, particularly over the long-
 490 term. The differences found in tree growth, climatic sensitivity and tree resilience between close
 491 neighboring sites showed that responses to drought were site dependent and could drastically vary in
 492 extremely narrow spatial gradients. This is particularly relevant to define the real extent and nature (*i.e.*
 493 geographical and/or ecological) of rear-edge populations where topographic and biophysical variability
 494 facilitates the existence of microrefugia. The analysis of tree-growth dynamics revealed suppression and
 495 release events that were consistent with legacies left by land use in local forest dynamics, as inferred
 496 from an exhaustive review of historical documents. Consequently, the geographical and ecological rear
 497 edges for specific species do not necessarily meet after centuries or millennia of human impact on the
 498 landscape. This is relevant for tree species that are highly sensitive to climate change, such as *Quercus*
 499 *pyrenaica*, not only for conservation *per se* of the species, but for all ecosystem services that these
 500 forests offer.

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For Peer Review

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

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

Table 1

							Cored trees				Stand competition				
Site	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

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

For Peer Review

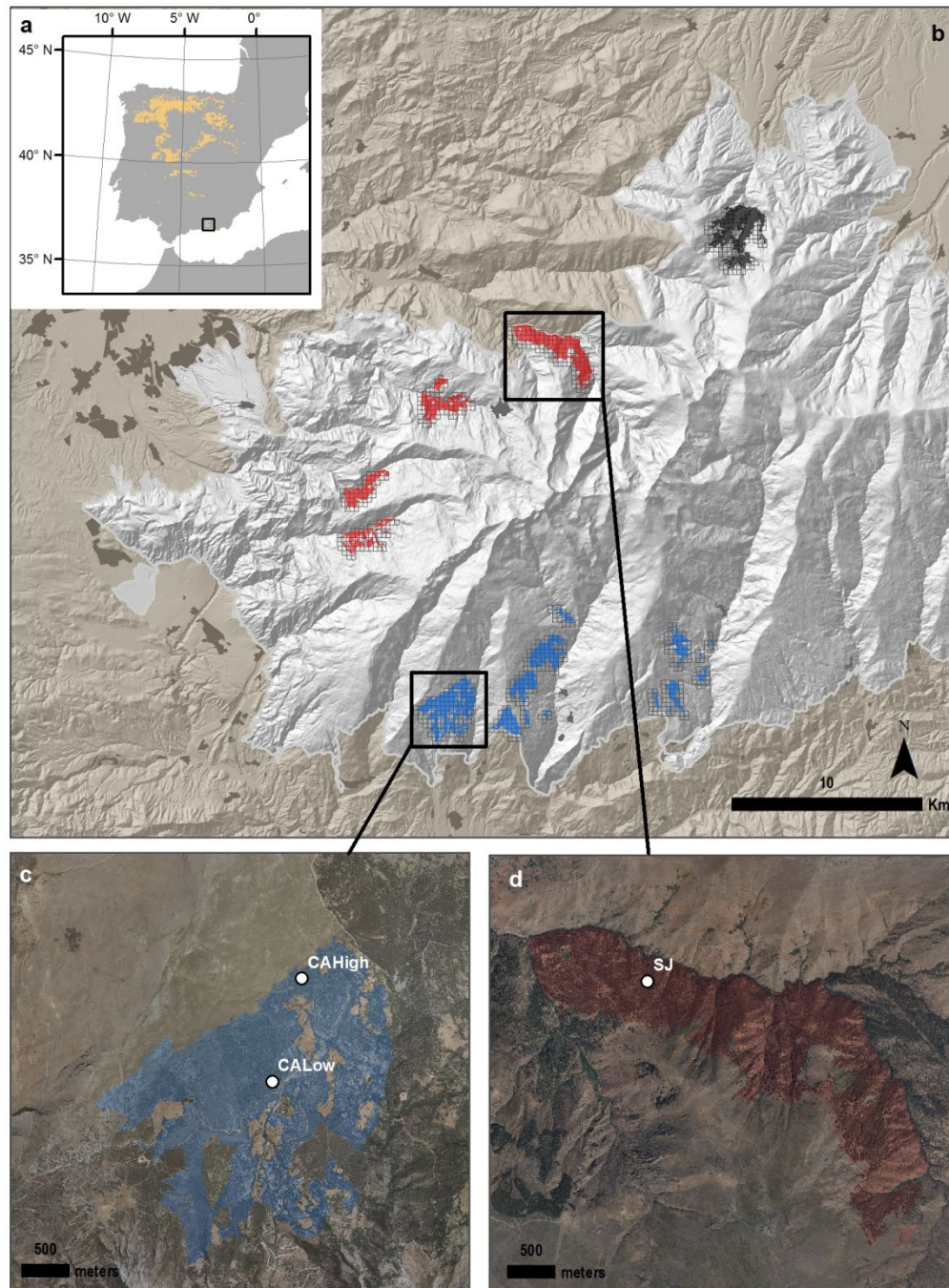
Figure 1. Distribution of *Quercus pyrenaica* forests in the Iberian Peninsula (a) and in Sierra Nevada mountain range (b). Different colors indicate oak-population clusters identified in Sierra Nevada (Pérez-Luque et al. 2015b). For each population, a grid with the MODIS pixels is shown (see Material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

Figure 2. Schema of the different metrics (a) and analyses (b) used in the manuscript (see Material and methods for details). The severe drought events since 1901 were identified using SPEI-12 and characterized in terms of duration, severity and intensity. Climate impacts on vegetation were assessed for greenness and tree-growth. Non climatic disturbances on vegetation were quantified using growth changes on tree growth (% GC) and were also related with anthropogenic alterations inferred from review of historical documents. Responses of vegetation to disturbances were explored in the short- and the long-term using resilience metrics and temporal trends respectively for both EVI and BAI. Resilience metrics of BAI were computed for the eight most severe drought events since 1950, and their relationship with drought severity were explored. For the 2005 and 2012 drought events we also compared EVI and BAI resilience metrics among the three *Q. pyrenaica* populations. Numbers (grey circles) indicate the study aims to which the analyses are related.

Figure 3. a) EVI standardized anomaly during the period 2000-2016 for northern and southern populations. Error bars show standard error. See main text for details on EVI calculation. **b)** Percentage of pixels showing browning, greening or no changes during the 2005 and 2012 drought events according to EVI standardized anomalies. See main text for an explanation of greening and browning.

Figure 4. a) Basal Area Increment (BAI) chronologies of *Q. pyrenaica* for northern population (SJ; red) and southern ones: low-elevation (CA-Low; green) and high-elevation (CA-High, blue) sites. Shading areas correspond to standard error of the mean. Number of series is displayed in the upper plot. Only years replicated with # series > 5 are shown. Linear trends since 1975 are indicated for all sites (numbers indicate r^2 values; asterisks indicate significant linear trend, $p < 0.001$). **b)** Comparison of median growth change (GC) following Nowacki and Abrams (1997) for *Q. pyrenaica* sites. Dashed black lines indicate a threshold of 50% of GC (see Material and methods). Note that y-axes do not correspond in all of the three panels for the sake of clarity. Error bars indicate standard error.

Figure 5. a) Resilience metrics of tree-growth for eight severe drought events since 1950 (see main text for details) as a function of drought severity. Points indicate resilience metrics for oak populations: SJ (red), CA-High (blue) and CA-Low (green). Resilience metrics were computed for each population (sample depth > 10) and drought event. Gray lines represent overall relationships for each Resilience metrics. **b)** Comparison of the response of *Q. pyrenaica* forests to drought in terms of resistance, recovery, and resilience of greenness (b) and tree growth (c). For EVI, northern populations (red circle) were compared with southern ones (green circle). For BAI, the more xeric northern population (San Juan, SJ; red circle) was compared with the two southern populations, Cáñar-High (CA-High; blue circle) and Cáñar-Low (CA-Low; green circle). Different letters indicate significant *post hoc* differences between groups (see Material and methods for details).

37 **Figure 1**

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Figure 2.

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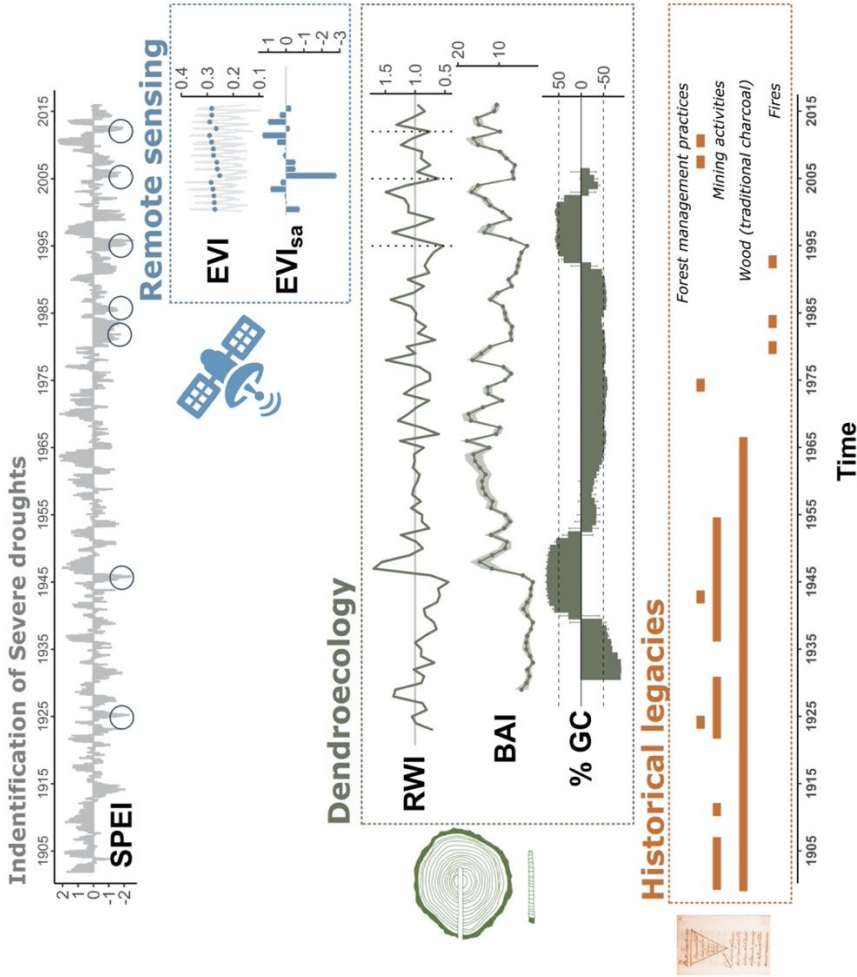
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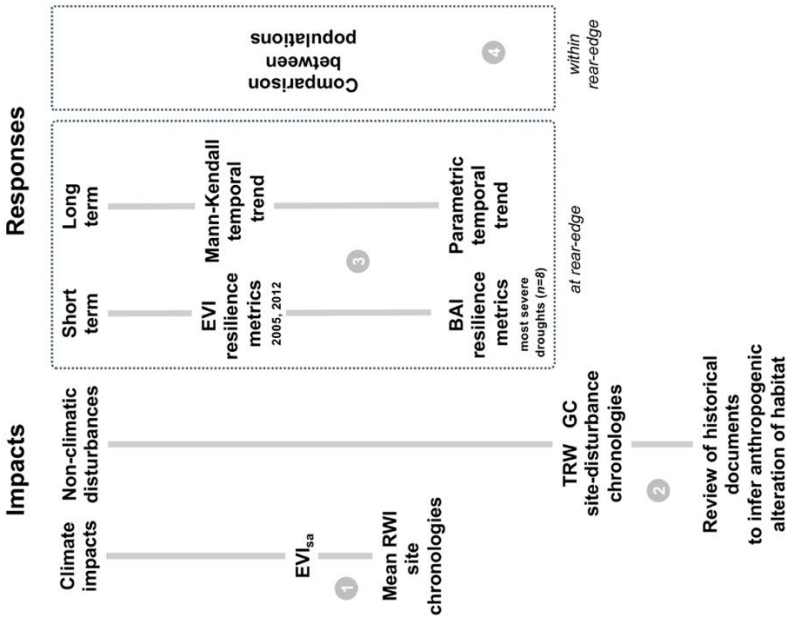


Figure 3.

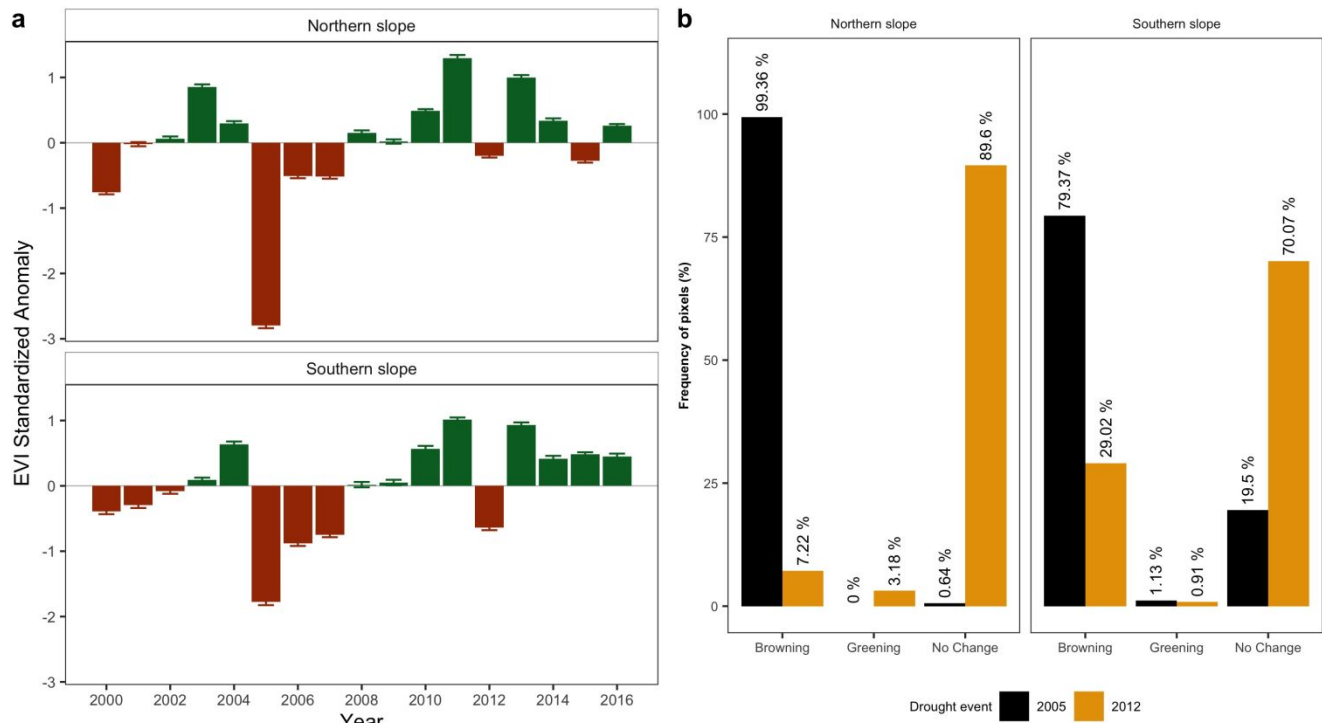
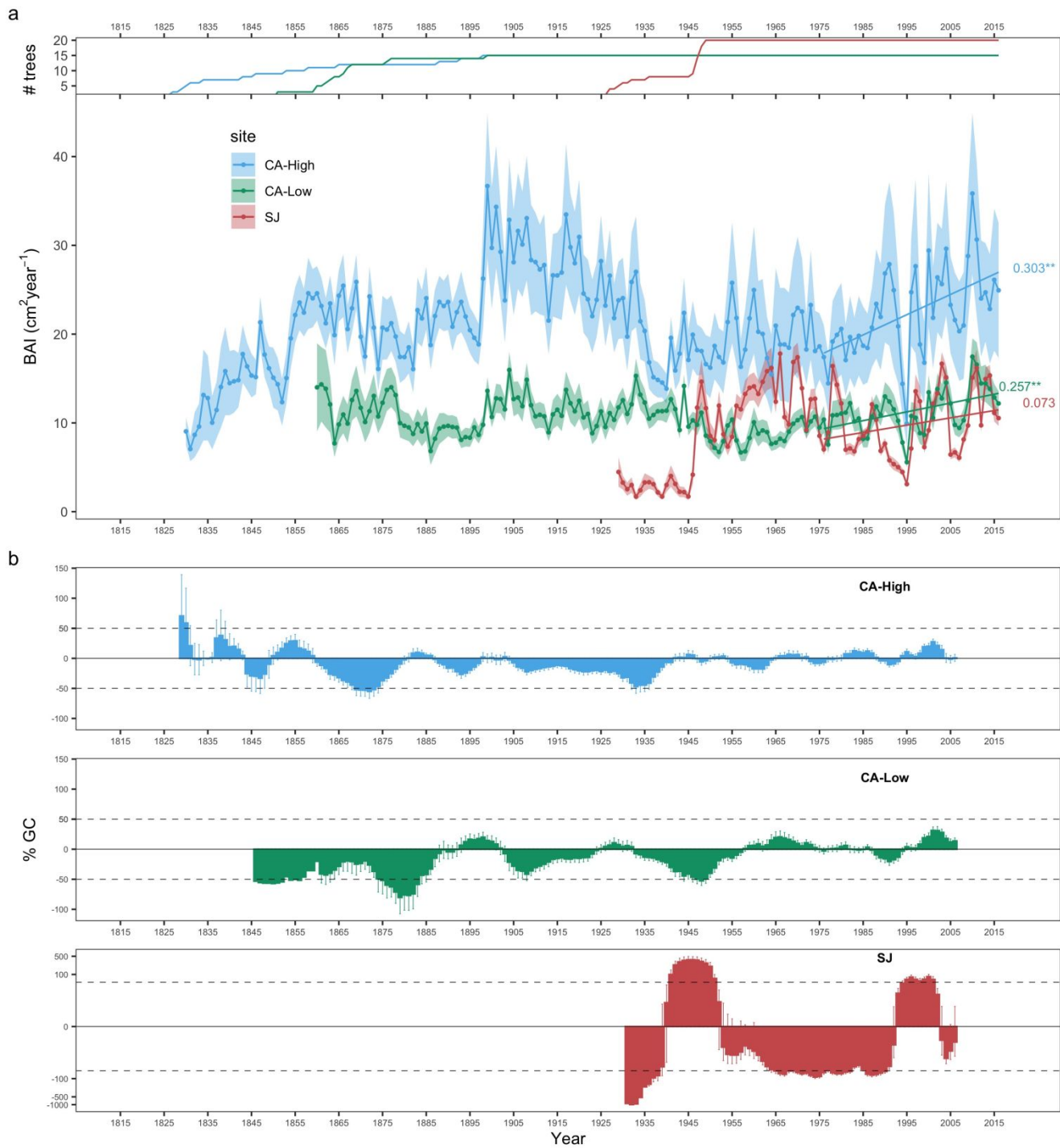
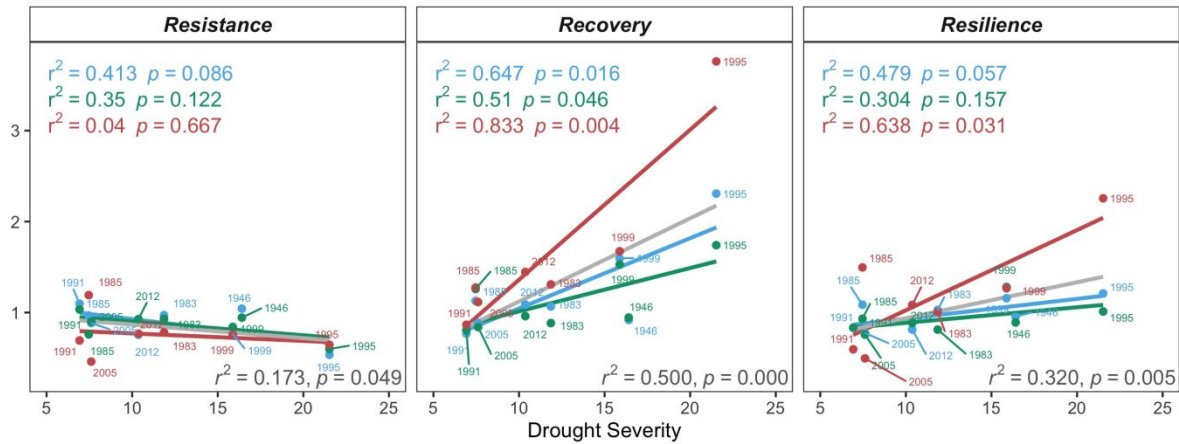


Figure 4



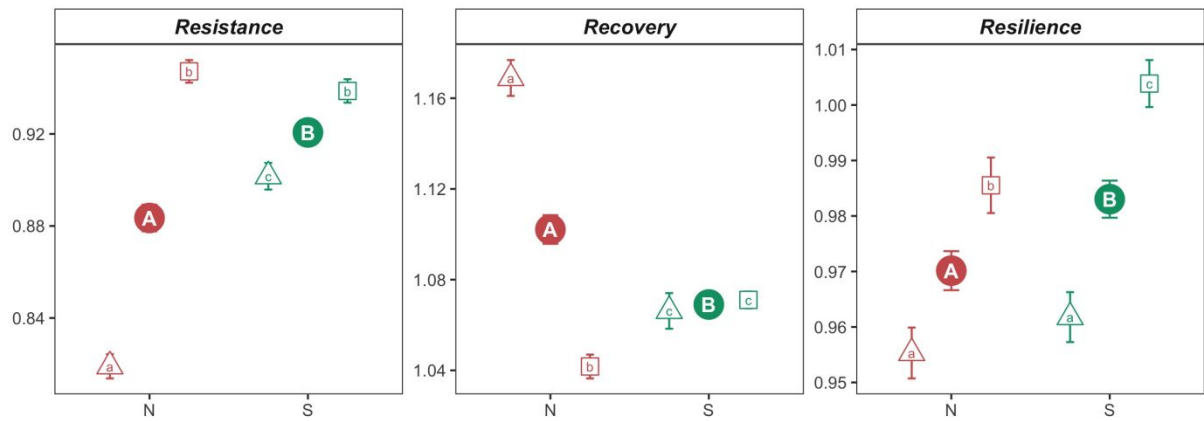
47 **Figure 5**

a)



b) EVI

● N ● S △ 2005 □ 2012



c) BAI

