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## Links between climate, drought and minimum wood density in conifers

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### ABSTRACT

As the global climate warms, increased aridity is expected to become a major determinant of forest productivity and tree growth. In gymnosperms, wood density quantified at seasonal to annual scales can be related to changes in tracheid lumen size due to alterations in soil water availability. In this way, minimum wood density (MND) has been shown to respond negatively to early growing-season precipitation in several conifers because dry conditions reduce tracheid lumen size and consequently increase MND. We investigated if this relationship between spring precipitation and MND applies to four conifer species (*Abies alba*, *Pinus sylvestris*, *Pinus nigra*, *Juniperus thurifera*) in NE Spain from mesic (*A. alba*, *P. sylvestris*) to xeric (*P. nigra*, *J. thurifera*) conditions. We further assessed how climate, precipitation, and drought-affected tree-ring width (TRW) and MND at several time scales to test if water shortage in spring increases MND and decreases TRW over time and seasonally. Lastly, we quantified the post-drought MND recovery. We found the strongest negative correlations between MND and spring precipitation in *P. nigra* followed by *J. thurifera*. In these two species, the associations between MND and 9-month long droughts peaked in early spring (*P. nigra*,  $r = -0.73$ ; *J. thurifera*,  $r = -0.50$ ). *Juniperus thurifera* presented a better post-drought recovery (decrease in MND), followed by *P. nigra* and *P. sylvestris*. We conclude that MND is a reliable and accurate proxy of drought severity during spring in conifers subjected to seasonal water shortage. MND can be used as an early-warning indicator of short- and long-term changes in the responses of trees to water shortage.

**Keywords:** conifers; drought stress; earlywood density; growing season; Iberian Peninsula; standardized precipitation–evapotranspiration index (SPEI).

## INTRODUCTION

Droughts are climate extremes that impair tree functioning by reducing photosynthesis and growth rates (Zahner 1968; Eilmann *et al.* 2011). These reductions decrease forest productivity and affect the global carbon cycle (Reichstein *et al.* 2013). Worldwide forests may become increasingly more stressed by droughts in the 21st century (Babst *et al.* 2019). Therefore, understanding how forests respond to water shortage is critical to forecast changes in forest productivity (Anderegg *et al.* 2015) and to develop adaptive forest management strategies (George *et al.* 2015). In particular, global warming is forecasted to increase the severity and duration of droughts in mid-latitudes of the Northern Hemisphere (IPCC 2014), where several conifers reach their southernmost limits of distribution (Camarero *et al.* 2015a, 2015b).

In conifers, most of the annual ring is usually formed by tracheids with wide lumens corresponding to the earlywood, which accounts for most hydraulic conductivity (Domec *et al.* 2009). Dry conditions during the early growing season (spring in the Northern Hemisphere) and before (prior winter) should lead to the formation of fewer tracheids with narrow lumens (Von Wilpert 1991; DeSoto *et al.* 2011). If limited soil water availability reduces tracheid expansion, this should cause the formation of dense earlywood since the tracheid lumen area and earlywood density are negatively correlated (Vaganov *et al.* 2006; Björklund *et al.* 2017). This has been demonstrated by experiments inducing water deficit and increasing wood density in *Picea abies* (Montwé *et al.* 2014). Therefore, the formation of tracheids with narrow lumens in earlywood reflects changes in hydraulic conductivity. However, despite the simplicity of these arguments, earlywood density (EWD) or minimum wood density (MND) are still understudied surrogates of tree responses to drought (Rathgeber 2017). Nevertheless, these variables allow understanding how water availability drives wood formation at intra- and inter-annual scales (Rozenberg *et al.* 2002; Rathgeber *et al.* 2006; Dalla-Salda *et al.* 2011; Rosner *et al.* 2014), but also at inter- and intra-specific levels (Hacke *et al.* 2001; George *et al.* 2015).

There is a lack of research on MND responses to climate and drought as compared with related growth variables such as tree-ring width (TRW) (Björklund *et al.* 2019). However, Björklund *et al.* (2017) showed that conifers growing at mid-latitudes (30–50° N) showed negative responses of MND to precipitation from the prior October up to the current June. This signal was previously found by other researchers and it mainly corresponds to pine and juniper species from drought-prone sites located in the SW USA (Cleveland 1986; Graybill *et al.* 1990), the Mediterranean Basin (Camarero *et al.* 2014; Arzac *et al.* 2018) or Central Asia (Camarero *et al.* 2017). Wood density in Mediterranean tree species explains how TRW responds to climate and drought (Camarero 2019).

Trees adjust their wood density to water availability and this makes them more resilient to drought (Martinez-Meier *et al.* 2008). However, it is unknown how trees change their long-term (decadal) resilience of MND to drought and how this plasticity affects radial growth. Here, we aim to fill that research gap by (i) investigating the relationships between climate, drought, TRW and MND in four conifer species (*Abies alba*, *Pinus sylvestris*, *Pinus nigra*, *Juniperus thurifera*) distributed along a precipitation gradient in NE Spain characterized by different water deficit, and (ii) quantifying their post-drought MND resilience or

1 recovery in mesic and xeric sites. We hypothesize that increasingly drier conditions during 1  
2 spring would lead to lower TRW and higher MND and a reduction of MND resilience, i.e. 2  
3 a failure to recover pre-drought MND values. We also tested if sex influenced the climate- 3  
4 MND relationships in the dioecious *J. thurifera*. 4

## 5 MATERIAL AND METHODS 5

### 6 *Study area and tree species* 6

7 The study sites correspond to undisturbed forests located in the mountains (Pyrenees, 7  
8 Iberian System) of NE Spain (Table 1). Among the four studied species, two have Eurosi- 8  
9 berian distributions and occupy mesic sites (Silver fir, *Abies alba* Mill.; Scots pine, *Pinus* 9  
10 *sylvestris* L.), and the other two are Mediterranean species found in more xeric sites (Black 10  
11 pine, *Pinus nigra* subsp. *salzmannii* (Dunal) Franco; Spanish juniper, *Juniperus thurifera* 11  
12 L.). Sampled sites correspond to open stands with basal area values ranging from 12 to 12  
13 38 m<sup>2</sup>/ha (Camarero *et al.* 2017). *A. alba* was sampled in the Pyrenees, and *P. sylvestris*, *P.* 13  
14 *nigra* and *J. thurifera* were sampled along an altitudinal gradient in the Iberian System. 14  
15 There, *P. sylvestris* is found in high-elevation, cold-wet sites; *P. nigra* tends to occupy mid- 15  
16 elevation, transitional sites, and *J. thurifera* is found in low-elevation sites (Camarero *et al.* 16  
17 2014, 2015b). The sampled stands were not impacted by local anthropogenic disturbances 17  
18 (grazing, fires and logging) since the 1960s. Soils are basic and dominated by clay textures. 18  
19 20

### 21 *Climate and drought data* 21

22 To distinguish between mesic and xeric sites we estimated the water balance at each 22  
23 site using local climate data (Appendix, Fig. A1). We calculated the potential evapotran- 23  
24 spiration (PET) following Hargreaves and Samani (1982). We estimated the annual climate 24  
25 water balance as the sum of the monthly differences between precipitation and PET. These 25  
26 data were used to characterize site climates (Table 1). 26

27 Since local climate data featured missing or heterogeneous data, to analyze associa- 27  
28 tions between climate variables (mean temperature, total precipitation) and TRW or MND 28  
29 we obtained series from a 1.1 km<sup>2</sup>-gridded and homogenized database of Spanish records 29  
30 derived from the entire observational data bank of the Spanish Meteorological Agency 30  
31 (AEMET) for the period 1962–2008 (Vicente-Serrano *et al.* 2017). To quantify the effect 31  
32 of drought we used the Standardized Precipitation–Evapotranspiration Index (SPEI; see 32  
33 Vicente-Serrano *et al.* 2010). The SPEI is a multiscale drought index that considers tem- 33  
34 perature and precipitation effects on the water balance to characterize dry (negative SPEI 34  
35 values) and wet (positive SPEI values) periods. The SPEI was obtained at the same spatial 35  
36 resolution as climate data and at weekly resolution for 1-, 3-, 6-, 9-, 12-, 24- and 48-month- 36  
37 long scales (Vicente-Serrano *et al.* 2017). Note that the SPEI quantifies relative dryness, but 37  
38 not necessarily drought impacts which depend on the studied system (e.g., conifers MND). 38  
39

### 40 *Field sampling* 40

41 We sampled 15–36 dominant individuals per site located at least 5 m apart from each 41  
42 other (Table 2). In *J. thurifera*, the sampling was not random since we selected 17 females 42  
43 and 19 males, and the sex was determined in winter by inspecting the type of produced 43  
44

Table 1.  
Characteristics of the study sites and sampled trees.

Site	Species	Latitude (N)	Longitude (W)	Elevation (m)	Mean annual temperature (°C)	Annual precipitation (mm)	Annual water balance (mm)	Dbh (cm)	Height (m)	Age at 1.3 m (years)
Guara	<i>Abies alba</i> (Silver fir)	42°18'	0°12'	1430	10.6	868	531	52.5 ± 2.6	20.0 ± 0.7	89 ± 9
Gúdar	<i>Pinus sylvestris</i> (Scots pine)	40°19'	0°42'	1615	6.5	669	68	41.0 ± 2.0	10.5 ± 1.0	134 ± 13
Gúdar	<i>Pinus nigra</i> (Black pine)	40°20'	0°48'	1290	8.3	533	-129	35.6 ± 1.4	10.0 ± 0.4	105 ± 8
Corbalán	<i>Juniperus thurifera</i> (Spanish juniper)	40°25'	0°60'	1295	10.8	395	-225	15.6 ± 0.5	6.8 ± 0.2	59 ± 2

The values of tree variables are means ± SE (standard errors). Climate data were obtained from local stations (see Appendix, Fig. A1).

Table 2.

Characteristics of the mean series or chronologies of tree-ring width (TRW) and minimum wood density (MND) (also see Appendix, Table A1).

Species	No. trees (No. cores)	Period	TRW			MND		
			Mean $\pm$ SE (mm)	AR1	Rbt	Mean $\pm$ SE (g/cm <sup>3</sup> )	AR1	Rbt
<i>Abies alba</i> (Silver fir)	15 (23)	1860–2002	3.11 $\pm$ 0.16	0.37	0.63	0.32 $\pm$ 0.01	0.35	0.31
<i>Pinus sylvestris</i> (Scots pine)	15 (22)	1828–2011	1.13 $\pm$ 0.14	0.76	0.66	0.34 $\pm$ 0.01	0.30	0.34
<i>Pinus nigra</i> (Black pine)	17 (34)	1890–2011	1.11 $\pm$ 0.13	0.68	0.75	0.37 $\pm$ 0.02	0.22	0.41
<i>Juniperus thurifera</i> (Spanish juniper)	36 (72)	1938–2015	1.09 $\pm$ 0.10	0.62	0.59	0.49 $\pm$ 0.04	0.45	0.43

Values were calculated for the common period 1962–2002. Abbreviations: SE, standard error; AR1, first-order autocorrelation; Rbt, mean correlation between trees. AR1 and SE were calculated on raw TRW and MND data, whereas Rbt was calculated on TRW and MND indices.

fruits. We measured the diameter at breast height (dbh) and the total height of all sampled trees using tapes and clinometers, respectively. First, two 5-mm-wide cores were taken using Pressler increment borers to cross-date the additional densitometry core and to measure TRW. These two cores were glued onto wooden mounts, sanded with papers of progressively finer grain, visually cross-dated, and checked for dating accuracy by recognising characteristic rings (Fritts 2001). Then, their rings were measured with a 0.01-mm resolution using a Lintab-TSAP system (F. Rinn, Heidelberg, Germany). Lastly, a 10-mm-wide core per tree was extracted at 1.3 m perpendicular to the main stem for densitometry analyses using Pressler increment borers (except 5-mm cores used for *J. thurifera*).

### Tree-ring density data

X-ray density profiles were obtained from each tree using indirect X-ray densitometry. First, the resin was extracted from the wood samples with alcohol in a Soxhlet extractor (excepting *J. thurifera*). Then, each core was cut carefully using a double-bladed saw to obtain 1.2–1.5-mm thin laths, and these samples were then subjected to X-ray exposure for 25 min. Two X-ray techniques were used. Firstly, the DENDRO-2003 X-ray microdensitometer (Walesch Electronics, Illnau-Effretikon, Switzerland) was used for *A. alba*, *P. nigra* and *P. sylvestris*, and secondly, the ITRAX multi scanner was used for *J. thurifera*. In both cases, the wood samples were exposed to controlled air temperature and relative humidity (20°C, 50% RH) to minimize any bias density regarding wood moisture. The resulting X-ray films were scanned with a resolution of 10  $\mu$ m using DENDRO-2003. In the case of the juniper, a Cr tube at 20 kV, 50 mA, with an exposure time of 25 ms, and 20- $\mu$ m step by ITRAX Multiscanner (Cox Analytical Systems, Mölndal, Sweden) was used. The ITRAX X-radiographic images were analyzed using the WinDENDRO software (Regent Instruments, Québec, QC, Canada) to determine wood density values for each point in the wood samples. The grey levels of the images were converted to density values by fitting a light calibration curve derived from a step-wedge sample (Schweingruber 1996). This allowed determining wood

1 density profiles and obtaining TRW and MND values for each annual ring. A final check 1  
2 of the visual cross-dating was again carried out on these samples by using the COFECHA 2  
3 software (Holmes 1983). MND is positively related to EWD, but we only considered MND 3  
4 because it is not dependent on the definition of the earlywood/latewood demarcation, and 4  
5 has shown a stronger response to climate than EWD (Camarero *et al.* 2014, 2017). 5  
6

### 7 *Tree-ring density processing and chronology building* 7

8 The TRW and MND series were individually subjected to trend removal so as to retain 8  
9 the year-to-year variability, and to calculate mean TRW and MND chronologies for each 9  
10 species (Fritts 2001). First, we applied a power transformation to the individual density se- 10  
11 ries for variance stabilization. Second, a smoothing spline with a 50% frequency response 11  
12 at a wavelength of  $2/3$  of the series length was fitted to the individual series. Then, indexed 12  
13 TRW and MND values were obtained by dividing or subtracting, respectively, observed from 13  
14 fitted TRW or MND values. These different standardization procedures used for TRW and 14  
15 MND allowed obtaining dimensionless indices of both variables (Fritts 2001). These were 15  
16 averaged on a yearly basis using a bi-weight robust mean to obtain a series of standard 16  
17 indices for each species. Indexed TRW and MND values were also subjected to autoregres- 17  
18 sive modeling to remove the first-order autocorrelation and averaged to produce a series 18  
19 of residual indices. These procedures were performed using the ARSTAN v 4.4 software 19  
20 (Cook & Krusic 2007). To compare the resulting TRW and MND species chronologies, we 20  
21 calculated two statistics for the common period 1962–2002: first-order autocorrelation of 21  
22 raw data ( $AR_1$ ), which measures the persistence of TRW and MND between consecutive 22  
23 years and mean correlation between trees ( $R_{bt}$ ) of residual series, which quantifies the co- 23  
24 herence of TRW and MND series between trees (Fritts 2001). In the case of *J. thurifera*, we 24  
25 obtained individual MND series for females ( $n = 17$ ) and males ( $n = 19$ ), and also mean se- 25  
26 ries of all ( $n = 36$ ; female and male individuals). 26

27 To calculate MND resilience for the period 1962–2005 and compare it between species 27  
28 from mesic and xeric sites, first, we defined dry years as those showing early-June and 28  
29 9-month SPEI values lower than  $-1.25$ . This month and SPEI temporal scale were chosen 29  
30 because they showed the strongest correlations, in absolute terms, with MND. Second, the 30  
31 difference between standardized and residual MND indices was calculated ( $MND_{STD-RES}$ ) 31  
32 to quantify the legacy effects in the selected droughts (1986, 1994–1995, 2005) following 32  
33 Huang *et al.* (2018). 33  
34

### 35 *Analyses* 35

36 For variables following normal distributions, Student *t*-tests were used to compare them 36  
37 (growth rate, climate-growth correlations) between species and groups as female and male 37  
38 *J. thurifera* trees. In those cases when variables did not fit normal distributions, Mann- 38  
39 Whitney *U*-tests were used in the comparisons. Trends through time in mean series of 39  
40  $MND_{STD-RES}$  were quantified using the Mann–Kendall tau ( $\tau$ ) statistic which was used 40  
41 for exploratory assessments of long-term changes in resilience. Seasonal climate variables 41  
42 were calculated as mean temperature and total precipitation for the previous autumn 42  
43 (September to November, abbreviated as SON) and winter (previous December to current 43  
44

February, abbreviated as DJF), and current spring (March to May, abbreviated as MAM) and summer (June to August, abbreviated as JJA). The associations between climate, drought indices and TRW and MND were assessed by calculating Pearson correlation coefficients between seasonal and monthly climate variables (mean temperature, total precipitation) or weekly SPEI values and residual mean series of TRW and MND indices. In the case of climate variables, the correlations were calculated from prior October to current September based on previous studies (Camarero *et al.* 2014, 2017). The significance threshold was set to  $\alpha = 0.05$ . The correlation coefficients were calculated between selected climate variables or SPEI scales and individual MND series in the case of *J. thurifera* to compare them as a function of sex. The correlations based on individual MND series were compared with correlations based on mean MND series of females and males.

In the case of the SPEI weekly values from current January to October and corresponding to several scales (1-, 3-, 6-, 9-, 12-, 24- and 48-month SPEI values) were used to calculate correlations with residual series of MND. For the sake of simplicity, we only present the two scales with the strongest correlations in absolute terms. The correlations of TRW or MND with climate and the SPEI were calculated for the period 1962–2002 when TRW and MND data were most replicated.

## RESULTS

### *Growth and minimum wood density responses to climate*

The highest and lowest growth rates (TRW) and the lowest and highest MND values corresponded to *A. alba* and *J. thurifera*, respectively (Table 2). Considering all trees, both the first-order autocorrelation ( $AR_1$ ) and the coherence ( $Rbt$ ) between trees were higher in the case of TRW ( $AR_1 = 0.61$ ,  $Rbt = 0.66$ ) than in the case of MND ( $AR_1 = 0.33$ ,  $Rbt = 0.37$ ).

In *A. alba*, stronger correlations were found between climate and TRW than between climate and MND. In this species, high prior-autumn ( $r = -0.40$ ) and current-summer ( $r = -0.42$ ) minimum temperatures negatively related to TRW (Fig. 1). In contrast, *A. alba* growth was enhanced by high maximum temperatures in February ( $r = 0.35$ ) and wet June conditions ( $r = 0.37$ ). In *P. nigra*, *P. sylvestris* and *J. thurifera* TRW increased in response to cool-wet spring and summer conditions. The highest correlations were found between spring precipitation and TRW of *P. nigra* ( $r = 0.47$ ) or *P. sylvestris* ( $r = 0.42$ ). In *J. thurifera*, a prior wet autumn enhanced TRW ( $r = 0.47$ ).

Despite the strongest signal of TRW series as compared to MND series (Table 2), we found highly significant correlations between May precipitation and MND in *J. thurifera* ( $r = -0.55$ ) and *P. nigra* ( $r = -0.47$ ) (Fig. 2). In the other species from mesic sites, May precipitation and MND were also negatively associated (*A. alba*,  $r = -0.37$ ; *P. sylvestris*,  $r = -0.43$ ). April precipitation and MND were negatively correlated in all species except *A. alba*. Consequently, spring precipitation and MND showed negative correlations (*J. thurifera*,  $r = -0.59$ ; *P. nigra*,  $r = -0.55$ ; *P. sylvestris*,  $r = -0.50$ ).

Regarding temperature, mean maximum May temperatures enhanced MND in all species excepting *P. sylvestris*, whereas mean minimum February temperatures were negatively related to MND in all species excepting *P. sylvestris* and *A. alba*. In *J. thurifera* and *A. alba* MND increased in response to warm summer conditions.

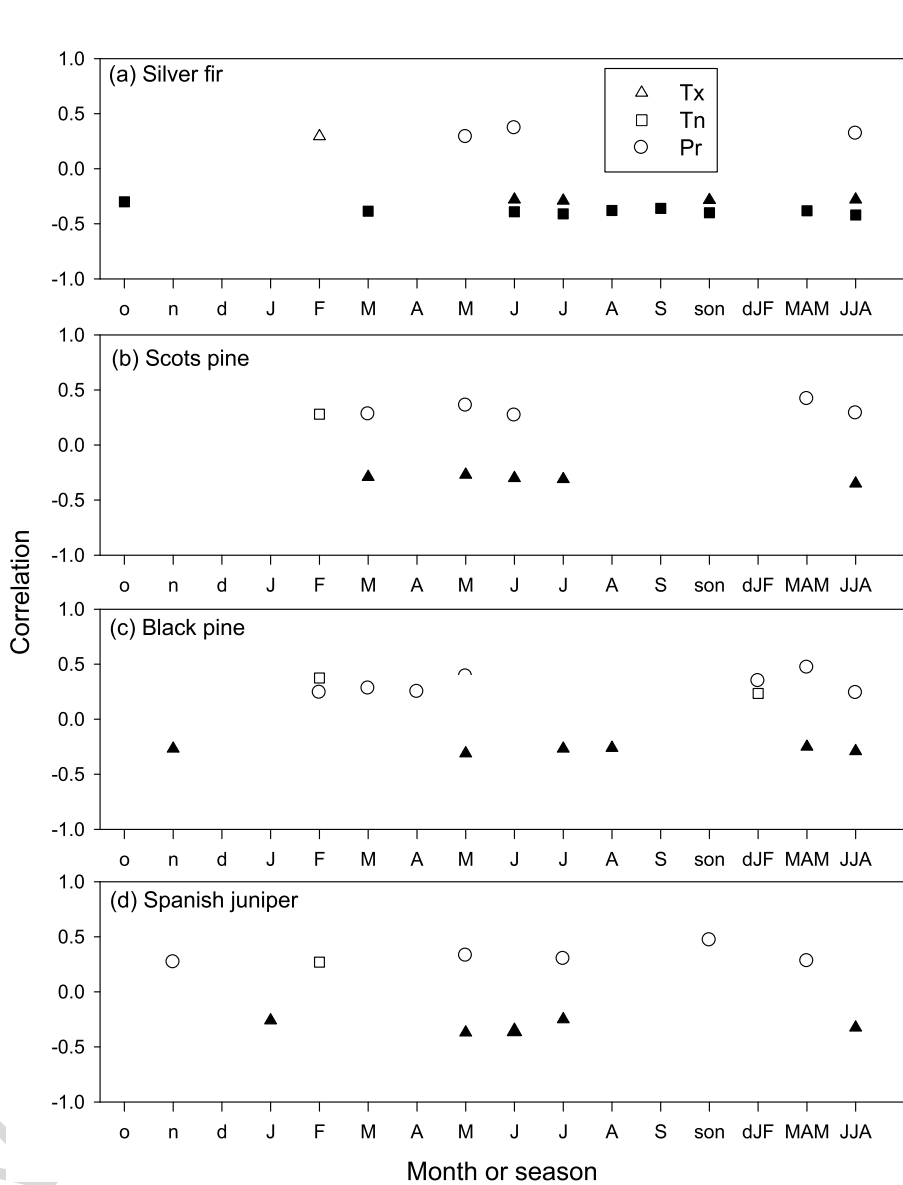


Figure 1. Significant ( $p < 0.05$ ) correlations calculated between monthly and seasonal climate variables (Tx, mean maximum temperature, upward triangles; Tn, mean minimum temperature, squares; Pr, precipitation, circles) and radial growth (ring-width indices) in the four studied species. Filled and empty symbols indicate negative and positive correlations, respectively. Correlations were calculated from the prior October to the current September ( $x$ -axes). Months or seasons corresponding to the prior and current years are abbreviated by lowercase and uppercase letters, respectively.



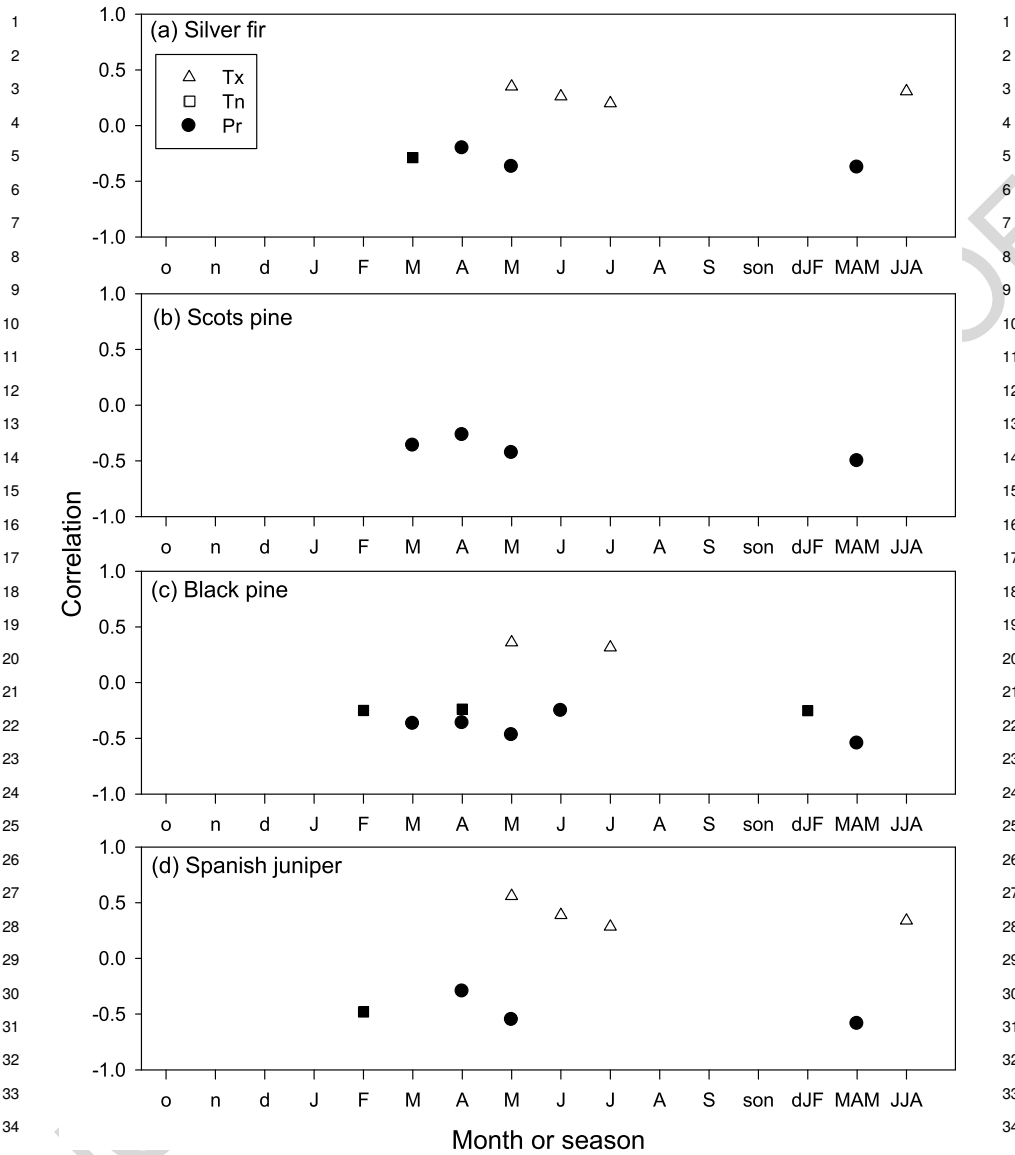


Figure 2. Significant correlations calculated between monthly and seasonal climate variables and minimum wood density (indices) in the four studied species. The rest of the explanations are as in Fig. 1.

In *J. thurifera*, we only found one difference when comparing sexes regarding the climate-MND associations calculated on individual series (Table 3). The MND series of females were more strongly correlated to mean maximum May temperatures than the series

Table 3.

Correlations (means  $\pm$  SE) calculated between individual series of minimum wood density and selected climate variables and drought indices in Spanish juniper (*Juniperus thurifera*) individuals classified as females ( $n = 17$ ) and males ( $n = 19$ ).

	Climate variables or drought index				
	TnFeb	TxMay	PrMay	PrMAM	SPEI
Correlations based on individual series					
Females' series	$-0.23 \pm 0.04$	$0.38 \pm 0.04^*$	$-0.29 \pm 0.05$	$-0.31 \pm 0.04$	$-0.28 \pm 0.05$
Males' series	$-0.24 \pm 0.04$	$0.26 \pm 0.03^*$	$-0.30 \pm 0.05$	$-0.35 \pm 0.04$	$-0.33 \pm 0.06$
Comparisons of the correlations between females and males					
$t(p)$	0.07 (0.94)	2.36 (0.02)	0.18 (0.86)	0.73 (0.46)	0.74 (0.44)
$U(p)$	154 (0.81)	95 (0.04)	158 (0.93)	130 (0.33)	149 (0.70)
Correlations based on mean series					
$r(p)$ -females	$-0.38 (0.004)$	$0.59 (0.00001)$	$-0.54 (0.00002)$	$-0.57 (0.00001)$	$-0.45 (0.0005)$
$r(p)$ -males	$-0.40 (0.003)$	$0.50 (0.0001)$	$-0.56 (0.00001)$	$-0.61 (0.00001)$	$-0.55 (0.00001)$
$r(p)$ -all	$-0.39 (0.003)$	$0.56 (0.00001)$	$-0.55 (0.00001)$	$-0.59 (0.00001)$	$-0.50 (0.0001)$

The statistical comparisons (Student  $t$ - and Mann-Whitney  $U$ -tests) of the correlations are also presented. Finally, the last three rows show the correlations with the mean residual series (chronology) of females, males, and all individuals, respectively. Correlation values are. Significance levels are shown between parentheses and an asterisk indicates values significantly different at the 0.05 level. Climate variables are abbreviated as in Figs. 1 and 2. The SPEI was calculated for a 9-month long scale and corresponds to the second week of June.

of males. In all cases, correlations with climate or SPEI based on mean MND series of females or males were stronger than means of correlations based on individual MND series.

The difference in correlations between MND and May temperatures observed between females and males could not be explained by differences in MND values. Female *J. thurifera* individuals showed a significantly higher ( $t = 2.72$ ,  $p = 0.007$ ) growth rate ( $1.15 \pm 0.04$  mm) than *J. thurifera* males ( $1.00 \pm 0.04$  mm), but MND did not significantly differ between genders ( $t = 0.15$ ,  $p = 0.88$ ; females,  $0.48 \pm 0.01$  g/cm<sup>3</sup>; males,  $0.49 \pm 0.01$  g/cm<sup>3</sup>; see Appendix, Fig. A2).

#### Minimum wood density responses to drought

The pattern of correlations between SPEI and MND was different in *A. alba* from the other species because it presented a minimum correlation ( $r = -0.54$ ) for the 9-month SPEI of the third week of September (Fig. 3). In the case of *P. nigra*, MND was strongly and negatively correlated ( $r = -0.73$ ) with the 9-month SPEI drought index corresponding to the first week of June (Figs. 3 and 4). This was the same temporal scale when the minimum SPEI-MND correlation was observed for *J. thurifera* ( $r = -0.50$ ). In *P. sylvestris*, this negative SPEI-MND association peaked for the 6-month SPEI corresponding to the third week of June ( $r = -0.60$ ).

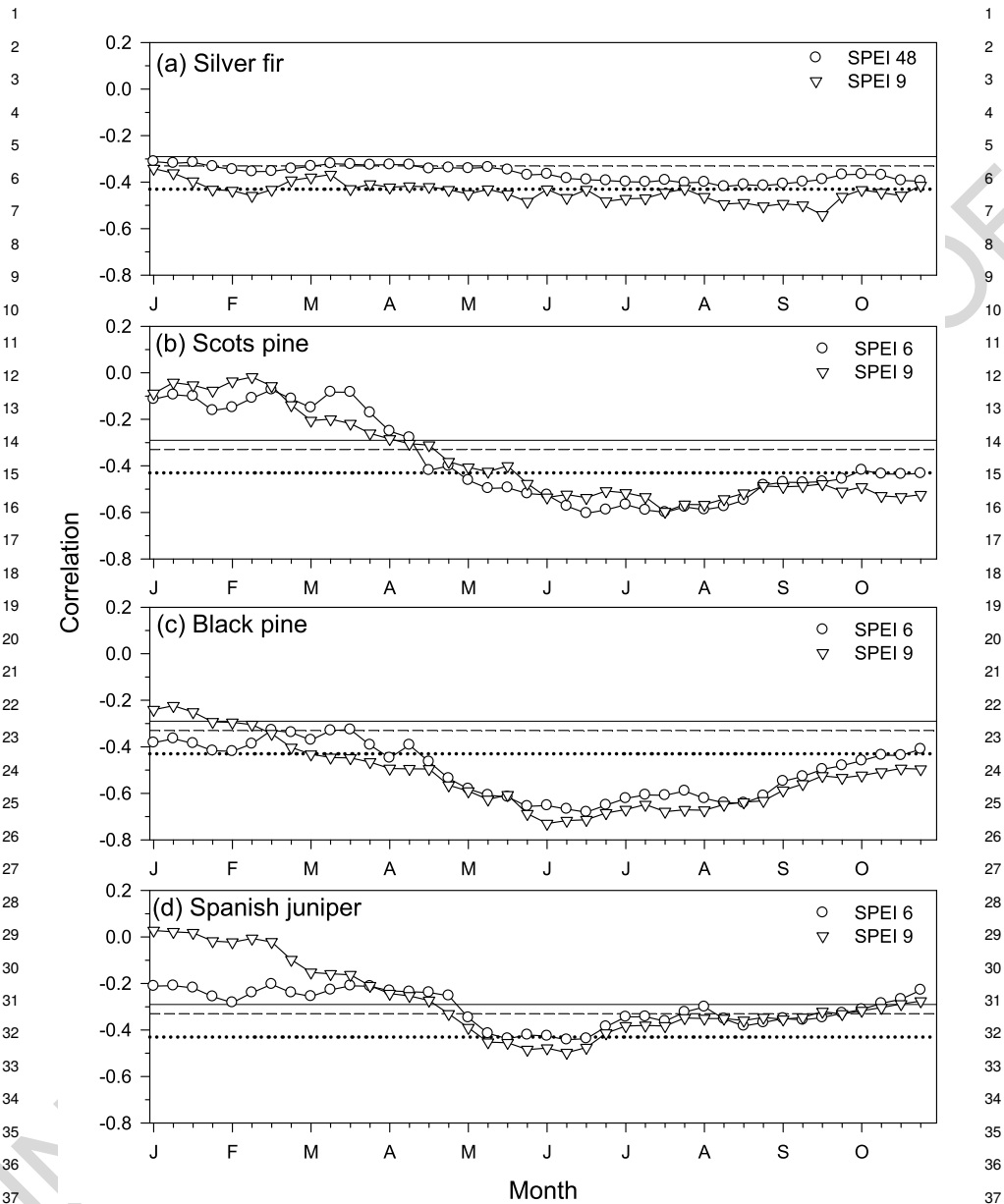


Figure 3. Relationships observed between the SPEI drought index (weekly values, x-axes) and minimum wood density (MND, residual indices) in the four studied species. For each species, the two SPEI scales (number after SPEI in months) showing the maximum Pearson correlations in absolute terms with MND are plotted. The horizontal continuous, dashed and dotted lines show the lower 0.05, 0.01 and 0.001 significance levels, respectively.

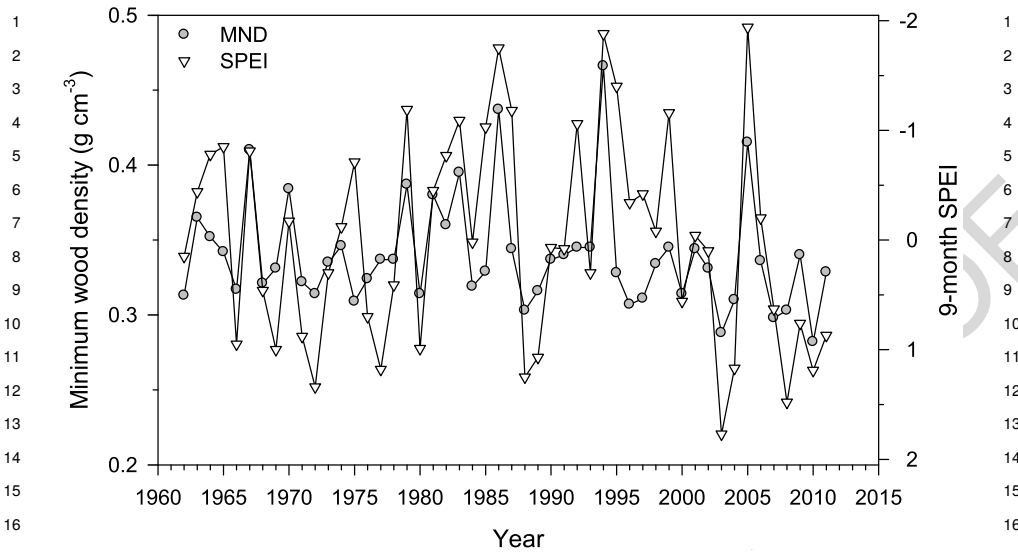


Figure 4. The minimum wood density (MND) of Black pine (*Pinus nigra*) was strongly and negatively related to the 9-month SPEI drought index corresponding to the first week of June. Note the reverse SPEI scale.

#### Minimum wood density resilience

According to the MND resilience index ( $MND_{STD-RES}$ ) the most responsive (increase in  $MND_{STD-RES}$ ) species to the selected droughts (1986, 1994–1995, 2005) was *J. thurifera* (mean  $MND_{STD-RES} \pm SE = 0.029 \pm 0.02$ ), followed by *P. nigra* ( $0.028 \pm 0.01$ ) and *P. sylvestris* ( $0.024 \pm 0.01$ ), albeit there were no significant differences between species ( $F = 0.06$ ,  $p = 0.81$ ). One year after the droughts, there were again no significant  $MND_{STD-RES}$  differences between species ( $F = 1.71$ ,  $p = 0.56$ ), but only *P. sylvestris* showed a drought legacy ( $0.020 \pm 0.01$ ), whilst *P. nigra* ( $-0.020 \pm 0.01$ ) and *J. thurifera* ( $-0.013 \pm 0.01$ ) have recovered. Two years after the droughts, the three species again did not show differences in MND resilience ( $F = 0.56$ ,  $p = 0.20$ ) but *P. nigra* ( $-0.021 \pm 0.01$ ) and *J. thurifera* ( $-0.032 \pm 0.01$ ) presented better recovery (decrease in MND) than *P. sylvestris* ( $-0.001 \pm 0.02$ ).

The 9-month early-June SPEI was negatively related to  $MND_{STD-RES}$  in *P. sylvestris* ( $r = -0.43$ ), *P. nigra* ( $r = -0.67$ ) and *J. thurifera* ( $r = -0.31$ ; see Fig. 5). The most similar series of the MND resilience index were those of *P. nigra* and *J. thurifera* ( $r = 0.54$ ), whereas those of *P. sylvestris* and *J. thurifera* were the least similar ( $r = 0.39$ ). *P. nigra* did not show a significant trend in the MND resilience index, whilst *P. sylvestris* ( $\tau = -0.20$ ,  $p = 0.044$ ) and *J. thurifera* ( $\tau = -0.55$ ) showed significant negative trends.

#### DISCUSSION

We found support to the hypothesis that dry and warm spring conditions reduce growth and increase minimum wood density (MND). The relationship between spring growing conditions and MND was stronger in species from xeric sites (*J. thurifera* and *P. nigra*) than

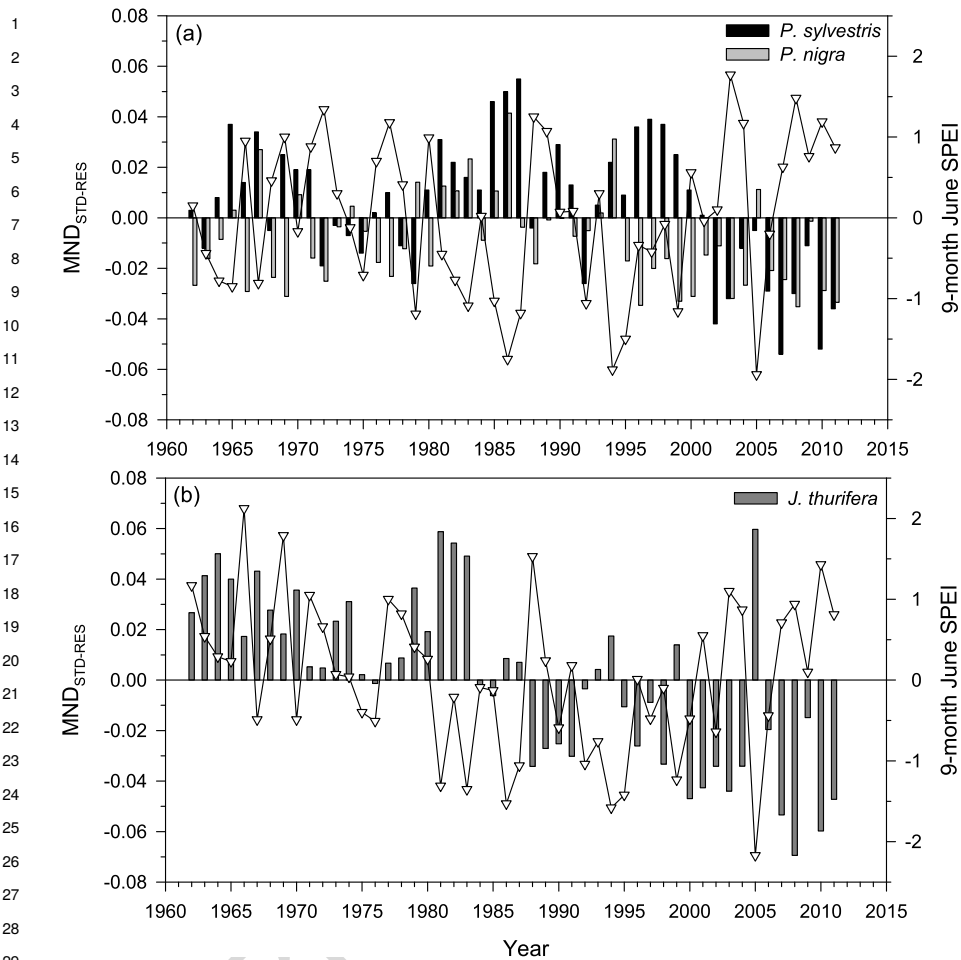


Figure 5. Trends in the resilience index of minimum wood density ( $MND_{STD-RES}$ ) in the three species (a, *P. sylvestris*, black; *P. nigra*, light grey; b, *J. thurifera*, dark grey) showing the strongest responses to drought severity assessed using the 9-month June SPEI.

from mesic sites (*P. sylvestris* and *A. alba*) suggesting that a reduced soil water availability causes an increase in MND by reducing tracheid lumen area in the earlywood (Von Wilpert 1991). This is confirmed by the correlations calculated between SPEI and MND with peaked in early to late June when some of the study species show their maximum growth rates (Camarero *et al.* 2010). This period of active growth coincides with the period when the division and enlargement of tracheids are also very active (Vaganov *et al.* 2006). Furthermore, the link between MND and water shortage was observed for SPEI values over 6 to 9 months, confirming that MND reflects the cumulative water deficit from the prior autumn (October) and winter (January) up to June. This period encompasses the most critical span for recharging soil reserves after the summer drought and includes the main months

1 whose precipitation explains radial growth variability in Mediterranean conifers (Pasho 1  
2 *et al.* 2012). Therefore, MND variability may be used to quantify drought stress during the 2  
3 growing season and before. These findings indicate that low availability of soil moisture in 3  
4 spring reduces cell turgor and the duration of the cell enlargement phase (Cuny *et al.* 2014) 4  
5 decreasing tracheid lumen size and increasing MND. These links explain how a higher MND 5  
6 reflects a loss in hydraulic conductivity (Dalla-Salda *et al.* 2011) and a reduction in growth 6  
7 rate (Rosner *et al.* 2008). Such interpretations agree with observations made by Cleaveland 7  
8 (1986) and Graybill *et al.* (1990) who showed that soil moisture deficit increases MND of 8  
9 conifers growing in semiarid sites. In those works, authors argued that high soil moisture 9  
10 during the previous year (autumn-winter) and during the growing season (spring) triggered 10  
11 the formation of low-density earlywood by prolonging cell maturation (Zahner 1968). In 11  
12 contrast, latewood variables were more responsive to late-summer drought (Griffin *et al.* 12  
13 2013).

14 Since changes in lumen area control earlywood density and have an exponential impact 14  
15 on hydraulic conductivity, MND is a very interesting proxy for year-to-year variations 15  
16 in conductivity at large geographical scales as suggested Dalla-Salda *et al.* (2011) for *Pseudotsuga* 16  
17 *menziesii* or Camarero *et al.* (2014) for *J. thurifera*. Considering the observed strong relationships 17  
18 between MND and spring precipitation in conifer species from xeric sites (e.g., 18  
19 *P. nigra*), future tree-ring networks should include this variable to investigate 19  
20 water transport variability over time following a multiproxy approach including tree-ring 20  
21 width, MND, and isotopes (Camarero *et al.* 2014, 2017; Shestakova *et al.* 2017). Besides the 21  
22 different drought response of tree species, provenances within each species should be considered 22  
23 (Martinez-Meier *et al.* 2008; Eilmann *et al.* 2013) as essential research objectives in 23  
24 the adaptation of forest management to climate change (George *et al.* 2015).

25 The correlations found between MND and spring precipitation in pine (*Pinus nigra*, *Pinus* 25  
26 *sylvestris*) and larch (*Larix sibirica*) species from drought-prone sites were similar to 26  
27 those observed in *J. thurifera* (Camarero *et al.* 2014), explaining on average 32–42% of MND 27  
28 variability. May precipitation was able to explain 22 to 33% of the minimum wood density 28  
29 (MND) variability in *P. nigra* and *J. thurifera*, the two study species inhabiting the driest 29  
30 sites. We advocate the combination of TRW and MND data to get a more comprehensive 30  
31 perspective of post-drought resilience in conifers inhabiting sites subjected to seasonal water 31  
32 shortage. According to TRW data, these species (e.g., Mediterranean pines and junipers) 32  
33 show a high resilience after drought (Gazol *et al.* 2018).

34 The analyses of MND resilience agree with conclusions derived from TRW data because 34  
35 species dominant in xeric sites (*J. thurifera*, *P. nigra*) showed the best post-drought recovery 35  
36 in terms of TRW (Gazol *et al.* 2018) and MND (this study). In contrast, species from mesic 36  
37 sites as *P. sylvestris* showed a post-drought MND legacy which implies a reduced growth 37  
38 and a low MND corresponding to earlywood tracheids with a lumen narrower than expected. 38  
39 The MND resilience index indicated a long-term loss in the ability of *J. thurifera* 39  
40 and *P. sylvestris* to recover MND to pre-drought values which may be related with the dry 40  
41 conditions observed in the study area during the 1990s and 2000s causing dieback in some 41  
42 *P. sylvestris* and juniper stands (Camarero *et al.* 2015a; Gazol *et al.* 2017). In contrast, *P. ni-* 42  
43 *gra* did not show such a loss of resilience. The value of MND as an early-warning signal of 43  
44

1 impending drought-induced dieback should be considered in future studies on similarly 1  
2 vulnerable conifer forests. 2

3 Regarding the use of resilience indices, we opted to follow the approach proposed by 3  
4 Huang *et al.* (2018). We used this framework because other approaches based on calcu- 4  
5 lating differences in growth between periods preceding and following droughts provided 5  
6 indices that were neither independent nor accounted for post-drought climate conditions 6  
7 (Gazol *et al.* 2018). Given that drought legacies usually last from one to two years in conifers 7  
8 (Anderegg *et al.* 2015) and that droughts can be followed by wet or dry conditions (Jiang *et* 8  
9 *al.* 2019), subtracting standardized and residual MND series gives a conservative measure 9  
10 of drought legacies which could be further explored in other tree species. 10

11 Olano *et al.* (2017) found that *J. thurifera* females formed wider tracheids with thinner 11  
12 cell walls than males, whereas males were more responsive to sites dryness and decreased 12  
13 their conductivity by reducing lumen area and increasing tracheid wall thickness in semi- 13  
14 arid sites showing a more conservative strategy. These differences in xylem anatomy were 14  
15 only found in a very dry site (annual precipitation 330 mm) and did not translate into differ- 15  
16 ences in hydraulic functioning indicating that in more mesic sites females may outperform 16  
17 males by growing more and showing an opportunistic behavior. This was found here and 17  
18 also by Rozas *et al.* (2009), who also showed that young *J. thurifera* females were very re- 18  
19 sponsive to summer water deficit. These differences were attributed to higher growth rates 19  
20 and less efficient water use of females potentially related to reproductive costs (DeSoto *et* 20  
21 *al.* 2016). 21

22 Here, *J. thurifera* females showed a stronger positive response of MND to warm May 22  
23 conditions than males but the two groups did not show significantly different responses to 23  
24 water availability. The stronger coupling between MND and May temperatures in females 24  
25 could be interpreted as higher sensitivity to warmer (cooler) conditions leading to the for- 25  
26 mation of tracheids with narrow (wide) lumen area and less (more) potential hydraulic 26  
27 conductivity. This stronger MND plasticity in response to changing maximum May tem- 27  
28 peratures could explain why females grew more than males if the former were better able 28  
29 to prevent drought stress and growth loss by responding to spring warm conditions through 29  
30 changes in tracheid size. Note also that spring temperatures affect water viscosity and this 30  
31 could indirectly affect the radial enlargement of earlywood tracheids and MND in cold, dry 31  
32 biomes forests (Wan *et al.* 2001). The resource-acquisitive strategy of females allows them 32  
33 to grow more if climatic conditions are favorable but, according to MND data, they are also 33  
34 more sensitive to climate warming than coexisting males (Hultine *et al.* 2016). Again, MND 34  
35 could be used as an early-warning indicator of the differential performance of sexes in a 35  
36 warmer world as most climate scenarios forecast. 36

37 To conclude, May precipitation accounted for a remarkable proportion of MND year- 37  
38 to-year variability in *P. nigra* and *J. thurifera*, two Mediterranean conifers dominant in 38  
39 drought-prone sites. Wet spring conditions were associated with a decrease in MND. The 39  
40 MND reflected the cumulative drought stress from the prior 6–9 months up to the growth 40  
41 peak (June). Therefore, MND is a robust proxy of soil moisture availability and precipita- 41  
42 tion during the growing season in conifers (pines, junipers, firs) from seasonally dry biomes 42  
43 located at mid-latitudes. These biomes should be further investigated and include, among 43  
44 44

1 others: Mediterranean forests, semiarid forests from North America, and Eurasian forest- 1  
 2 steppe ecotones. 2

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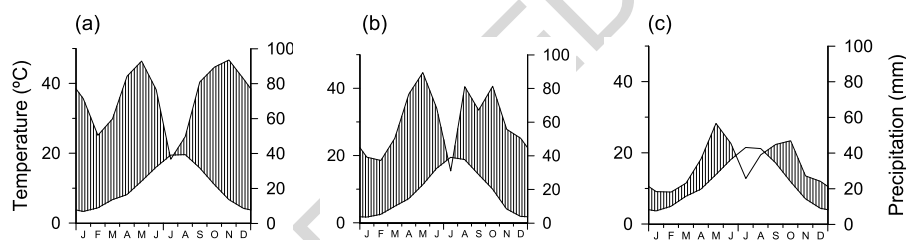
4  
5 APPENDIX

6  
7 Table A1.

8 Correlations ( $r$ , Pearson coefficients) calculated between the mean series of indexed tree-ring width  
9 and minimum wood density values considering the best replicated period.

11 Species	11 Best replicated period	11 $r$ ( $p$ )
12 <i>Abies alba</i>	12 1950–2002	12 –0.09 (0.39)
13 <i>Pinus sylvestris</i>	13 1859–2011	13 –0.56 (<0.0001)
14 <i>Pinus nigra</i>	14 1895–2011	14 –0.75 (<0.0001)
15 <i>Juniperus thurifera</i>	15 1956–2015	15 –0.65 (<0.001)

16 The significance levels ( $p$ ) are shown in parentheses.



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28 Figure A1. Climate diagrams of the study sites: (a) Guara, Silver fir (*Abies alba*) site (data from Nocito  
29 station, 42°12'20" N, 0°015'18" W, 919 m a.s.l.); (b) Gúdar, Black pine (*Pinus nigra*) and Scots pine  
30 (*Pinus sylvestris*) sites (data from Alto de San Rafael station, 40°20'40" N, 0°42'35" W, 1559 m a.s.l.)  
31 and (c) Corbalán, Spanish juniper (*Juniperus thurifera*) site (data from Teruel station, 40°20'38" N,  
01°06'33" W, 915 m a.s.l.).

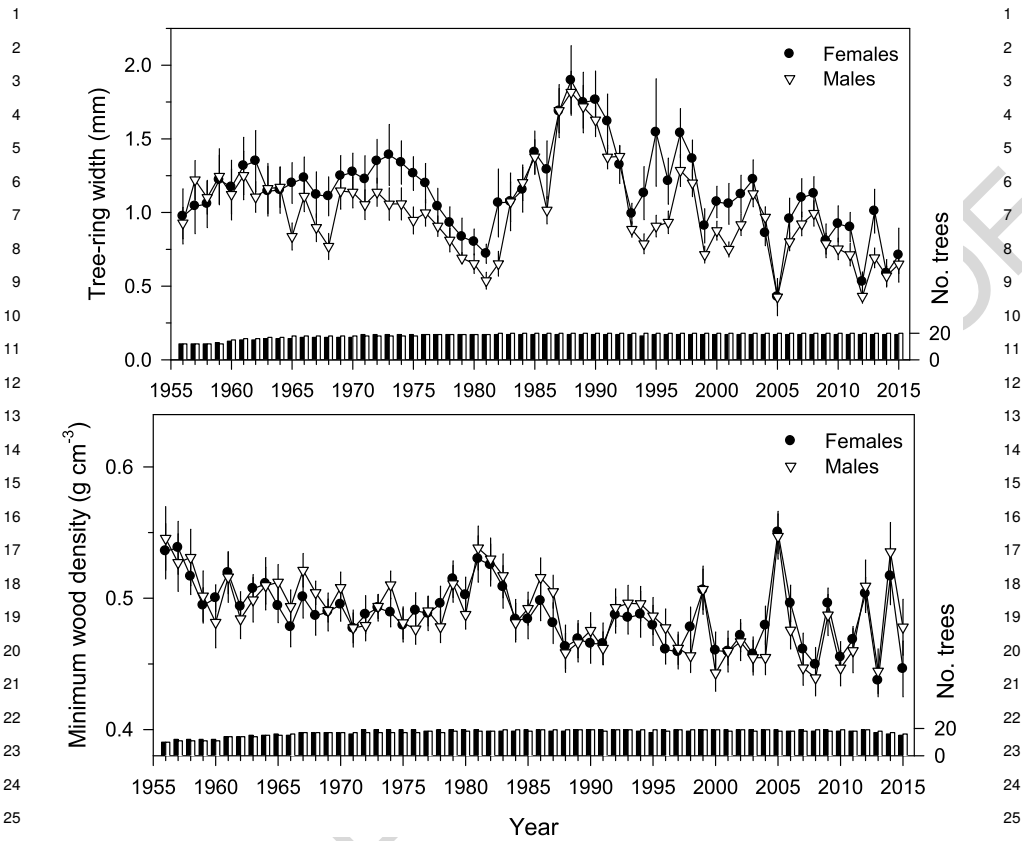


Figure A2. Radial growth (tree-ring width, upper plot) and minimum wood density (lower plot) of the sampled Spanish junipers (*Juniperus thurifera*) classified as female (filled circles) and male (empty triangles) trees. Values are means  $\pm$  SE. The right y-axis shows the annual number of measured trees (bars are filled with the same colors as symbols).