

1 **Drought-induced weakening of growth-temperature associations**
2 **in a high-elevation pine network across the Pyrenees**

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4 J. Diego Galván^{1,2*}, Ulf Büntgen², Christian Ginzler², Håkan Grudd³, Emilia Gutiérrez⁴,
5 Inga Labuhn^{3,5} and J. Julio Camarero^{4,6}

6
7 ¹*Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, Apdo. 202, E-50192 Zaragoza,*
8 *Spain*

9 ²*Swiss Federal Research Institute WSL, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland*

10 ³*Bolin Centre for Climate Research, Department of Physical Geography and Quaternary Geology,*
11 *Stockholm University, 10691 Stockholm, Sweden.*

12 ⁴*Departament d'Ecologia, Universitat de Barcelona, Avda. Diagonal 643, 08028 Barcelona, Spain*

13 ⁵*Laboratoire des Sciences du Climat et de l'Environnement (LSCE), Gif-sur-Yvette, France.*

14 ⁶*ARAID, Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, Apdo. 202, E-50192*
15 *Zaragoza, Spain*

16
17 *Corresponding author at: Instituto Pirenaico de Ecología (IPE-CSIC), Avda.
18 Montañana 1005, Apdo. 202, E-50192 Zaragoza (Spain). Tel. (+34) 695053174 / (+34)
19 976 369 393, fax 974 363 222, e-mail: jgalvan@ipe.csic.es (J. Diego Galván)

22 **ABSTRACT**

23 The growth/climate relationship of theoretically temperature-controlled high-elevation
24 forests has been demonstrated to weaken over recent decades. This is likely due to new
25 tree growth limiting factors, such as an increasing drought risk for ecosystem
26 functioning and productivity across the Mediterranean Basin. In addition, declining tree
27 growth sensitivity to spring temperature may emerge in response to increasing drought
28 stress. Here, we evaluate these ideas by assessing the growth/climate sensitivity of 1500
29 tree-ring width (TRW) and 102 maximum density (MXD) measurement series from 711
30 and 74 *Pinus uncinata* trees, respectively, sampled at 28 high-elevation forest sites
31 across the Pyrenees and two relictic populations of the Iberian System. Different
32 dendroclimatological standardization and split period approaches were used to assess
33 the high- to low-frequency behaviour of 20th century tree growth in response to
34 temperature means, precipitation totals and drought indices. Long-term variations in
35 TRW track summer temperatures until about 1970 but diverge afterwards, whereas
36 MXD captures the recent temperature increase in the low-frequency domain fairly well.
37 On the other hand summer drought has increasingly driven TRW along the 20th century.
38 Our results suggest fading temperature sensitivity of Iberian high-elevation *P. uncinata*
39 forest growth, and reveal the importance of summer drought that is becoming the
40 emergent limiting factor of tree ring width formation in many parts of the
41 Mediterranean Basin.

42

43 *Key-words:* climate change; drought; growth response; high-elevation forest; Pyrenees;
44 summer temperature

45

46 *Highlights:*

- 47 • 1500 TRW and 102 MXD series were collected at 30 sites across the Pyrenees
- 48 • Growth/climate relationships were assessed on high- to low-frequency domains
- 49 • Summer temperatures and MXD increased after the 1970s, whereas TRW decreased
- 50 • Warming-induced drought constrains on TRW formation increased along the 20th
- 51 century

52

53 **1. Introduction**

54 Trees growing in cold-limited environments such as high-latitude forests and the arctic
55 and alpine ecotones can record temperature variations in their annual ring width (TRW)
56 and maximum latewood density (MXD) (Fritts, 2001). In fact, temperature might be the
57 main climatic driver of tree growth and thus it constrains wood formation during overall
58 short growing seasons (Körner, 2012). Old growing treeline species, are therefore
59 regarded as reliable proxy archives that enable annually resolved temperature
60 reconstructions to be continuously developed for several centuries to millennia (Briffa
61 et al., 1990; Esper et al., 2002). At the European-scale, several examples from the high-
62 northern latitudes in Fennoscandia (Briffa et al., 1990; Grudd, 2008), and higher
63 elevations along the Carpathian arc (Büntgen et al., 2007, 2013; Popa and Kern, 2008)
64 and the Alps (Rolland et al., 1998; Büntgen et al., 2005, 2006; Corona et al., 2010) have
65 demonstrated the palaeoclimatic potential of tree rings.

66 Mid-latitude areas are, however, affected by different climatic influences
67 derived from tropical air-masses moving towards the poles and polar air-masses moving
68 towards the equator; this causes most of the mid-latitude areas being alternately
69 influenced by arid and humid conditions, with periodic droughts. Complex
70 growth/climate relationships are therefore known for areas like the Mediterranean Basin
71 or the Sierra Nevada in California (Tardif et al., 2003; Bunn et al., 2005; Carrer et al.,
72 2010; Büntgen et al., 2012). In these ecosystems, daily to seasonal precipitation changes
73 can mediate intra and inter-annual patterns of forest growth, and summer drought can be
74 strong enough to even interrupt cell formation (Nicault et al., 2001; De Luis et al.,
75 2007). It remains unknown if such drought-induced growth responses also occur in
76 high-elevation forests of the Mediterranean mid-latitudes and may even affect water-

77 saturated upper treeline sites. If true, such hydroclimatic stressors would question the
78 consistency of temperature reconstructions based on tree rings from high-elevation areas
79 at mid-latitudes.

80 Spatiotemporal instability in growth/climate relationships, the so-called
81 divergence phenomena (D'Arrigo et al., 2008), may indeed be magnified by predicted
82 future drought across the Mediterranean Basin (Lebourgeois et al., 2012), which would
83 dampen the temperature control of tree growth. Testing the hypothesis of recently more
84 complex growth/climate relationships in Mediterranean mountain forest ecosystems is,
85 however, complicated by the scarcity of high-elevation sites that were temperature-
86 controlled in this area (Körner, 2012). The Pyrenees constitutes the only mountain
87 system where undisturbed temperature-driven upper treelines can be found south of the
88 Alpine arc.

89 Here we seek to assess if the growth/climate relationship in a high-elevation
90 network of *Pinus uncinata* forest sites across the Pyrenees changed over the last century
91 and, if so, to pinpoint the relevant drivers. We compile TRW chronologies from 30 sites
92 and MXD measurements from six of these sites between 1750 and 2451 m asl. Various
93 tree-ring detrending and chronology development techniques, together with split-period
94 approaches and multiple intra-annual intervals are evaluated to assure that the observed
95 associations between tree growth and climate are not artificially induced or
96 spatiotemporally biased.

97

98 **2. Materials and methods**

99 **2.1. Study species and sites**

100 *Pinus uncinata* Ram. is a long-lived, slow-growing and shade-intolerant conifer with a
101 large ecological amplitude concerning topography and soil type (Ceballos and Ruiz de
102 la Torre, 1979). In this species ca. 80% of the annual width is formed during June and
103 July and latewood formation lasts from July up to October (Camarero et al., 1998).
104 Warm autumn and spring temperatures before and during ring formation enhance *P.*
105 *uncinata* radial growth in Pyrenean forests (Tardif et al., 2003). We sampled 30 *P.*
106 *uncinata* sites of which 27 sites are located in the Pyrenees, one site is in the Pre-
107 Pyrenean Sierra de Guara and two southern relict populations are located in the Iberian
108 System (Fig. 1). Data cover the whole geographical range of the species in the Iberian
109 Peninsula and thus capture most of the ecological variability experienced by this species
110 (Table 1). Most of the Pyrenean sites (18 sites) were located within or near protected
111 areas, ensuring that these populations are not likely to have been logged for much of the
112 20th century. Specifically six sites were sampled within or near the Ordesa y Monte
113 Perdido National Park (PNOMP; 42°40'N, 00°03'E; established in 1918), and twelve
114 sites were sampled in the Aigüestortes i Estany de Sant Maurici National Park area
115 (PNAESM; 42°35'N, 00°57'E; established in 1955). Pyrenean *P. uncinata* forests are
116 usually low-density open-canopy stands located in steep and elevated sites forming
117 isolated patches near the alpine treeline. The macroclimate of the Pyrenees is strongly
118 influenced by east–west and north–south gradients with increasing Mediterranean
119 conditions (e.g. warm and dry summers) eastwards and southwards, whereas continental
120 conditions (e.g. cold winters) prevail in the Central Pyrenees. These diverse climatic
121 influences explain the high climatic heterogeneity of this area (López-Moreno et al.,
122 2008). Mediterranean summer drought is more prevalent at PNOMP than at PNAESM
123 sites (Balcells and Gil-Pelegrín, 1992). Mean annual temperature and total precipitation

124 in the studied sites ranged from 2.0 to 4.9 °C and from 1200 to 2000 mm, respectively,
125 with January and July as the coldest (mean -2.0 °C) and warmest (mean 12.5 °C) months
126 respectively (Camarero, 1999). The relict populations of Teruel and Soria and the
127 Prepyrenean site Guara are subjected to typically Mediterranean conditions such as
128 warm and dry summers.

129

130 **2.2. Field sampling and dendrochronological methods**

131 We sampled 711 living trees between 1994 and 2011. At each site, five to 65 dominant
132 (i.e. with crowns above the general level of the canopy) trees (mean \pm SD = 24 ± 14
133 sampled trees per site) were randomly selected. The number of sampled trees per site
134 depended on the availability of suitable trees within each site. All trees were cored with
135 a Pressler increment borer taking two or three cores per tree ($n = 1500$ cores, mean \pm
136 SD = 47 ± 27 sampled cores per site). Each core was mounted and sanded with
137 progressively finer grain until tree rings were clearly visible (Stokes and Smiley, 1968).
138 Samples were then visually cross-dated and measured to a precision of 0.01 mm using a
139 LINTAB measuring device (Rinntech, Germany). Cross-dating was evaluated using the
140 program COFECHA (Holmes 1983), which calculates cross correlations between
141 individual series of each core and a master chronology. For the MXD measurements, we
142 cored a subsample ($n = 74$ trees) by taking cores perpendicular to the stem from 6 sites
143 (4 sites located in PNAESM plus 2 sites from PNOMP) with a thicker Pressler
144 increment borer (10 mm diameter); MXD cores were glued onto wooden supports and
145 thin wooden laths (1.2 mm) were cut with a twin-bladed saw. Density was measured
146 with an Itrax MultiScanner from Cox Analytical Systems (<http://www.coxsys.se>), where
147 laths are scanned using a focused high-energy x-ray beam. The radiographic image is

148 analyzed with the software WinDendro (Regent Instruments, Canada), which performs a
149 light calibration of the grey values using a calibration wedge (Grudd, 2008).

150

151 **2.3. Tree-ring data and detrending**

152 Since we only collected MXD data from the Pyrenees (Tables 1 and 2), we combined all
153 the MXD series in one single chronology set called *Pyrenees*. For its part, TRW was
154 assigned three different chronology subsets depending on the geographical location of
155 the sampled sites: (i) the whole network of 30 sampled sites, (ii) the 27 Pyrenean sites,
156 and (iii) the 15 PNAESM sites; hereafter called *AllSites*, *Pyrenees* and *Aigüestortes*
157 subsets respectively. As explained before, PNOMP is more influenced by
158 Mediterranean and drier conditions than PNAESM; therefore, and in order to assess
159 possible Mediterranean drought influences, we used an additional TRW subset called
160 *Ordesa*, derived from a compilation of the series coming from the six PNOMP sites.
161 Apart from the geographical reason, the *Aigüestortes* subset was taken considering also
162 the relative robust convergence of the principal components scores of the PNAESM
163 sites in the two dimensional space of a principal component analysis, based on the
164 covariance matrix of the chronologies of all sampled sites, and considering their
165 common period 1901-1994 (see yellow symbols in Figure A1). The first and second
166 principal components explained 47.2% and 8.1% of the whole site growth variability,
167 respectively. Sites near the distribution limits of the species (e.g. GU, TE, CN, PA) are
168 arranged at relatively lower altitudes (i.e. PC1 scores). Although the chronologies
169 showed different loadings with the PC1, all of them had positive correlations within it,
170 showing that they shared a common variance.

171

172 To remove tree-age related, non-climatic growth trends from the raw TRW and
173 MXD measurement series (Cook and Kairiukstis, 1990), and to assess the effects of
174 different standardization techniques on the final chronology shape, we applied several
175 detrending methods using the ARSTAN program (Cook and Holmes, 1986).
176 Specifically, we preserved variability at inter-annual to multi-decadal scales detrending
177 each TRW and MXD individual series by means of cubic smoothing splines with 50%
178 frequency-response cutoffs equal to 150 and 300 years (Cook and Peters, 1981). A
179 negative exponential function detrending was also applied together with an alternative
180 linear regression of slope of any sign (detrending called hereafter ‘negative exponential
181 I') or with an alternative linear regression of negative slope (‘negative exponential 2’).
182 We also applied the age-aligned regional curve standardization (RCS; Esper et al.,
183 2003) for preserving inter-annual to centennial-scale variability.

184 For these different detrendings, dimensionless indices were calculated as
185 residuals from the estimated growth curves after power transformation (pt) of the raw
186 measurements (Cook and Peters, 1997), and as ratios after using the raw measurements
187 without any transformation (nt). Summarizing, we applied ten different detrending
188 methods (see table A1). We performed a variance stabilization technique to every
189 chronology for minimizing the putative effects of changing sample size throughout time
190 (Frank et al., 2007). Mean chronologies were then calculated using a bi-weight robust
191 mean (Cook, 1985). We applied the Expressed Population Signal (EPS) calculated over
192 30-year windows lagged by 15 years to estimate signal strength of these records
193 (Wigley et al., 1984). Throughout the paper, unless otherwise stated, we refer to TRW
194 chronologies derived from the whole sampled network (i.e. *AllSites* TRW subset).

195

2.4. Instrumental target data and growth-climate response analyses

Monthly temperature (mean, maximum and minimum) and precipitation data (CRUTS3.10; Harris et al., 2013) were used for growth/climate response analysis. We considered 0.5° resolution grid-box data covering the different sampled sites. We also used the standardized precipitation evapotranspiration drought index (SPEI; Vicente-Serrano et al., 2010), calculated from the CRUTS3.20 dataset. Drought conditions are influenced by factors like temperature, relative humidity, evapotranspiration, wind speed, etc. The Standardized Precipitation Index (SPI) only takes on account the precipitation, thus neglecting the importance of other influential variables. The use of drought indices that include temperature data in their formulation, such as the Palmer Drought Severity Index (PDSI) seems to be preferable to identify warming-related drought impacts on ecological systems (Vicente-Serrano et al. 2010), specially taking on account the global temperature increase of recent decades. However, drought is a multi-scalar phenomenon since the time period from the arrival of water inputs until the water is available differs considerably (McKee et al. 1993). Thus, the time scale over which water deficits accumulate becomes important. The PDSI lacks the multi-scalar character of the SPI; the SPEI, first proposed by Vicente-Serrano et al. (2010) overcomes this limitation, combining in its formulation the sensitivity of PDSI to changes in evaporation demand caused by temperature with the multi-temporal nature of the SPI. Negative (positive) SPEI values correspond to dry (wet) conditions.

All the TRW and MXD chronologies (derived from the different detrendings and subsets) were correlated against monthly and seasonal means of maximum, mean, and minimum temperatures and totals of precipitation. We restricted the analyses to the period 1901-2009, which covers the available CRU data period. We used monthly data

220 from October of the previous year to September of the current year and seasonal means
221 performed from March to September, including therefore the growing season. We also
222 correlated the chronologies to the SPEI index for the 12 months of the year at different
223 time scales from 1 to 24 accumulated months, covering the same period. In order to
224 assess the temporal stability in the growth/climate relationships along the second half of
225 the 20th century, we performed the correlations with climate in two independent 40-year
226 subperiods: 1930-1969 and 1970-2009. We quantified spatial correlation fields between
227 the tree-ring series and monthly and seasonal climatic variables for different periods
228 using the web Climate Explorer (<http://climexp.knmi.nl>). We further evaluated
229 instability in the growth/climate relationship by calculating 31-year moving correlations
230 between growth (TRW, MXD) and climate variables (temperature, SPEI).

231

232 **3. Results**

233 **3.1. Chronology characteristics**

234 TRW (MXD) chronologies span from 1270 to 2010 AD (1407 to 2009 AD), with a
235 mean length of 240 (192) years. TRW (MXD) series have a mean \pm SD annual value of
236 0.66 ± 0.11 mm (0.77 ± 0.39 g cm⁻³) and a series inter-correlation of 0.44 (0.40). In both
237 TRW and MXD, the eight different spline and exponential detrendings showed a very
238 similar shape (Fig. A2); hence we averaged them in a single chronology, hereafter
239 abbreviated as *TRWmean* and *MXDmean*. Raw and RCS TRW chronologies show the
240 typical negative exponential trend until ~1450; from then on, RCS chronologies grow
241 with a long and steady positive trend (Fig. 2a). From the 1950s onwards, all the TRW
242 chronologies decline until the present. Raw and RCS MXD chronologies show a
243 negative trend until ~1700, and then they rise up to the 1950s before decreasing again.

244 Since the 1970s all the MXD chronologies start trending upwards up to the present.
245 (Fig. 2b). These results are essentially the same as the ones observed in the *Pyrenees*
246 and *Aigüestortes* subsets (not shown). This MXD pattern is related to the temperature
247 trends found over the 20th century in Europe: increasing temperatures until the 1950s
248 followed by a decrease until the 1970s and a second increase from the 1970s until
249 nowadays (IPCC 2013). These patterns are consequently observed in series of tree ring
250 proxies (e.g. MXD) of temperature sensitive sites like the Alps, Scandinavia or the
251 Pyrenees, and also in the temperature series of their subsequent climatic reconstructions
252 (Corona et al. 2010; Büntgen et al. 2008a, 2011; Dorado-Liñán et al. 2012). The RCS
253 chronologies highlight the decrease in TRW in the transition between the warm
254 Medieval Climatic Anomaly and the cold Little Ice Age (LIA) starting in 1300 AD and
255 lasting until 1850 AD, where temperatures started to increase again (Moreno et al.,
256 2012). Both TRW and MXD chronologies display a valley shape in 1816 following the
257 eruption of Mount Tambora in 1815, which caused the “year without summer” (Trigo et
258 al., 2009). There is another sharp decrease in TRW and MXD around 1700 AD. The
259 decrease in growth in the last 50 years is not unprecedented and lower growth rates
260 occurred in some periods over the LIA, for instance during the fifteenth century (Fig.
261 2a). Expressed population signal (EPS) and signal-to-noise ratio (SNR) are very
262 consistent among the 10 different detrendings (Table 3). TRW (MXD) chronology stays
263 above the 0.85 EPS threshold since 1500 (1777) AD (Figs. A3 and A4). Mean segment
264 lengths of the TRW site chronologies show how aging trees display a decreasing growth
265 rate (Fig. A5), and proves the existence of a single biological-growth population
266 portrayed by the sampled sites (Esper et al., 2003).

267

268 3.2. Growth-climate responses patterns

269 TRW and MXD are mainly influenced by previous-year November, May and
270 September temperatures (Fig. 3). Similar results were found for the *Pyrenees*,
271 *Aigüestortes* and *Ordesa* subsets (not shown). Among the different detrendings applied,
272 RCS shows a smaller or even negative correlation between TRW chronologies and
273 temperature. This indicates that a divergent behaviour in the recent decades between
274 TRW and temperature is more evident when using RCS chronologies than with the
275 other detrendings.

276 MXD displays higher correlations with temperature than those for the TRW.
277 Monthly correlation analysis highlights the main influences of previous-year November
278 and current-year May, June and September temperatures on MXD, with May being the
279 most prominent month (Fig.3b). Contrary to the TRW, the different MXD detrendings
280 display the same sign and behaviour in their climate correlation functions (Table 3),
281 although RCS detrending brings the highest correlations with temperature for MXD in
282 the second subperiod. This, and the fact that TRW RCS chronologies record a divergent
283 behaviour with temperature more clearly than other detrendings, caused us to focus our
284 analyses mainly on the RCS chronologies.

285 Growth/precipitation correlations are found to be minor compared with those
286 found for temperature, in both TRW and MXD data sets (not shown). Contrastingly,
287 SPEI gives higher correlations than precipitation (Fig. 4). The main drought driver of
288 TRW of Iberian *P. uncinata* forests is the SPEI for June and July accumulated at scales
289 from one to two months, specially for the period 1901-2009 and the sub-period 1930-
290 1969 (Fig. 4). As we pointed out before, PNOMP area has stronger Mediterranean
291 influences than PNAESM area. Correspondingly, TRW from the *Ordesa* subset shows

292 this Mediterranean background in the TRW-SPEI relationship (using SPEI data
293 covering the PNOMP area), where the influence of drought on growth extends until
294 August and, in general, correlation coefficients with summer SPEI are stronger than in
295 the case of *Aigüestortes* and *Pyrenees* subsets, consecutively (Fig. A6). These
296 observations are consistent among the different detrending methods (Fig. A6 and Fig.
297 A7).

298 In the case of MXD for the first subperiod, the highest negative (~ -0.4) and
299 positive ($\sim 0.2-0.3$) correlations occur with the May SPEI for 4 to 5 months, and with
300 July SPEI at 2-month scale, respectively. This greatly changes for the second subperiod,
301 when the highest positive MXD/SPEI correlations (~ 0.4) are found in the period from
302 previous September to current January (Fig. 4). Both TRW and MXD showed higher
303 correlations with SPEI in the second than in the first subperiod, which indicates an
304 increase in drought influence on growth in recent decades.

305 Finally, spatial correlations displayed between MXD values and temperature
306 were stronger and more spatially coherent across SW Europe than those observed with
307 TRW (Fig. A8).

308

309 **3.3. Proxy-temperature divergence**

310 Our results show a temporal instability of the growth/climate relationships of *P.*
311 *uncinata* forests along the 20th century. In the low-frequency domain, divergent trends
312 for TRW and maximum temperature are found since the 1970s (Fig. 5b), while TRW
313 displays a convergent trend with SPEI (Fig. 5e). Similar results are observed for the
314 *Pyrenees* and *Aigüestortes* subsets (not shown). For its part, MXD low-frequency trend

315 parallels with the low-frequency temperature warming, which started in the 1970s (Fig.
316 6b), but it diverges from SPEI (Fig. 6e).

317 A steady negative (positive) trend in the moving correlation record is displayed
318 with temperature (SPEI) in the low-frequency range (Figs. 5b,e). In the high-frequency
319 domain, stronger correlations with temperature are obtained after the 1950's (Fig. 5c),
320 and a negative trend in the moving correlations with SPEI is found (Fig. 5f). MXD
321 moving correlations display an increase with temperature and a decrease with SPEI in
322 low-frequency domains (Fig. 6b,e). Low-frequency moving correlations in TRW seem
323 more stable than in MXD, where we can observe cyclic increases and decreases in the
324 moving correlations along the 20th century (Fig. 6b,e).

325 Focusing on the growing season, May temperature shows a direct correlation
326 with TRW and MXD while summer months usually show a smaller or negative one
327 (Fig. 3). To find out if the divergence phenomenon is due to a loss of temperature
328 sensitivity or to an increase in this negative summer drought effect, we repeated the
329 moving correlation analyses with summer (June-July) and May temperatures. Results
330 are very similar to the ones obtained with the maximum temperature of May-September
331 period (Fig. A9 and A10), again highlighting a TRW-temperature divergence and also a
332 recent increase in the correlation between MXD and temperature.

333 To gain insight into potential differences in the divergence occurrence along the
334 altitude we compared high- (>2150 m, 15 sites, 940 series) and low-elevation (< 2150
335 m, 15 sites, 572 series) TRW chronologies with June-July SPEI and MJJAS maximum
336 temperature series. In both high- and low-elevation chronologies the divergence
337 phenomenon with temperature in the low-frequency range is clear and the convergent
338 trend with MXD in the low-frequency range too (Figures A11 and A12). In the high-

339 elevation chronology the low-frequency divergence with temperature seems to appear
340 shortly delayed compared with the low-elevation chronology.

341

342 **4. Discussion**

343 Our results show low frequency trend offsets between the TRW series and temperature
344 records since the second half of the 20th century (Fig. 5b). This suggests a weakening of
345 the theoretically temperature-sensitive proxies (TRW) to capture recent warming trends
346 such as those observed since the 1970s. Such ‘divergence’ phenomena between climatic
347 and dendrochronological variables have also been displayed in other temperature-
348 constrained high-elevation and boreal forests (Büntgen et al., 2006; Wilmking et al.,
349 2004, 2005; D’Arrigo et al., 2004; Briffa et al., 1998). Nevertheless, this low-frequency
350 offset between growth and temperature is not found in the high-frequency (i.e. year-to-
351 year) climate sensitivity of our TRW series, which increasingly parallels temperature
352 anomalies along the 20th century (Fig. 5c). Hence, the trend offset between the TRW
353 series and temperature records is mainly restricted to the long-term trend, whereas
354 coherency between productivity and temperature persists in the high-frequency (year-to-
355 year) domain.

356 Spring cambial resumption in *P. uncinata* starts in May, and typically the tree
357 growth is faster or slower depending mainly on the temperatures prevailing during this
358 month. The moving correlations between May temperatures and TRW highlight that
359 this spring temperature sensitivity is fading during recent decades (Fig. A9b). Contrary
360 to TRW, MXD low-frequency positive trends follow the warming trend started in the
361 1970s. This is in agreement with data from the European Alps that suggest that the
362 divergent behaviour is expected to occur in TRW more often than in MXD (Büntgen et

363 al., 2006). Furthermore, MXD shows higher correlations with temperature over the
364 growing season compared to TRW, which is in agreement with former observations
365 from the same area and species (Büntgen et al., 2010). This can be explained because
366 TRW is more strongly autocorrelated, incorporating previous-year climatic and
367 ecological conditions, together with ecological carryover effects and temperature
368 forcing over a wider (seasonal or annual) time window (Fritts, 2001). In fact, our results
369 show a significant correlation between TRW and previous November temperatures,
370 which indicates that warmer conditions in late autumn might enhance carbohydrates
371 storage and synthesis used for the formation of earlywood (i.e. increase of TRW) the
372 following growing season.

373 The divergence phenomenon has been attributed to various causes including
374 nonlinear growth-climate thresholds (Loehle, 2009), methodological issues techniques
375 including “end effects” of chronology development (Esper and Frank, 2009; Briffa and
376 Melvin, 2011; Briffa et al. 2013; Melvin et al. 2013), biases in instrumental data or
377 additional anthropogenic influences (see D’Arrigo et al., 2007, and references therein),
378 or temperature-induced drought stress (D’Arrigo et al., 2004) Our sampled sites are
379 located within the drought-prone Mediterranean region, so we hypothesize a possible
380 temperature-induced drought explanation of the TRW-temperature divergence observed.

381 The aforementioned TRW-temperature divergence of the second half of the 20th
382 century is opposite to the relationship between TRW and SPEI trends, with low-
383 frequency moving correlations steadily rising and reaching a maximum level after the
384 1970s (Fig. 5e). Mean temperatures during the growing season have increased during
385 the last century and especially over the last decades, meantime precipitation regimes
386 have not significantly changed (Figure A14). These results suggest that warming-

387 induced summer drought is increasingly influencing TRW in the 20th century in
388 Pyrenean high-elevation forests, which agrees with observations from other Iberian
389 mountain forests (Andreu et al., 2007; Macias et al., 2006). This can be due to a
390 potential loss in the positive thermal response of trees when some temperature
391 functional threshold is exceeded, leading to an increase in the influence of other
392 potential factors like soil moisture or drought (D'Arrigo et al., 2004). This TRW-
393 drought parallelism present in our high-elevation study disagrees with results from low-
394 elevation drought sensitive tree-ring central European sites, where growth/drought or
395 growth/precipitation relationships weaken after the 1970s (Wilson and Elling, 2004).
396 Consequently, emerging elevation-specific factors influencing tree growth can be acting
397 differently between high and low elevation sites or between central and southern
398 European forests, producing these contrasting responses in recent decades.
399 Contrastingly, our comparison between high- and low-elevation chronologies does not
400 show important differences (Figs. A11 and A12).

401 Summer drought is becoming less influential on MXD instead, specifically since
402 the 1970s, when low-frequency moving correlations between SPEI and MXD begin to
403 fall and both trends diverge (Fig. 6e). In any case, the moving correlations of MXD-
404 drought and MXD-temperature relationships show in general more instability than in
405 the case of TRW along time (Fig. 6b,e). When it is too hot or dry for tracheid
406 enlargement to occur, the rate of tracheid production decreases and a denser wood
407 (higher MXD) is formed because of the formation of tracheids with thicker cell walls
408 and narrower lumens (Jyske et al., 2009). This thickening and lignification of the cell
409 walls, illustrated by latewood tracheids, improves the mechanical strength of stems but
410 also allows tracheids to withstand higher xylem tension due to lower water potential

411 (Hacke et al., 2001). Specifically, MXD development is directly linked to climate
412 conditions during spring and mainly during late summer to early autumn, when the
413 latewood is formed (Briffa et al., 1998). During the first part of the growing season,
414 when the earlywood is formed, climatic variations affect radial tracheid enlargement,
415 whereas during the later part of the growing season climate mainly affects the cell wall
416 thickening process of latewood (Camarero et al., 1998) (Fig. A13). For the subperiod
417 1930-1969, the strongest negative correlation (~ -0.4) of MXD with SPEI were found
418 for May SPEI (Fig. 4). This means that wet and cool spring conditions could enhance
419 earlywood formation potentially leading to more and wider tracheids with thinner cell
420 walls and a subsequent delayed summer lignification producing a less dense latewood,
421 i.e. lower MXD values. The strongest positive correlation ($\sim 0.2-0.3$) for the same
422 period corresponds to July SPEI which suggests that wet late summers will entail denser
423 latewood production through enhanced lignification and carbohydrates synthesis at the
424 end of the growing season.

425 In the sub-period 1970-2009 the highest positive MXD-SPEI correlations (~ 0.4)
426 are found in January considering the cumulative drought since the previous September
427 (5-month SPEI scale), which means that wet conditions in the previous autumn and
428 winter of a specific year would imply the production of a dense latewood during the late
429 summer of the next year. This is an unexpected observation since we unveil not only
430 influences of late summer/early autumn conditions of the current year on MXD but also
431 of lagged climatic conditions of the previous year as is usually the case in TRW (Tardif
432 et al., 2003; Fritts, 2001). The interpretation may be the same as in TRW since previous
433 wet conditions might enhance carbohydrates synthesis and storage later used for
434 lignifying and thickening latewood cells the following growing season. Note that these

435 indirect influences of previous winter conditions on latewood production were also
436 observed in xeric *Pinus halepensis* stands, which constitute typical lowland
437 Mediterranean forests (Pasho et al., 2011). Overall, the SPEI drought index provided a
438 superior signal of tree growth than precipitation data in the study forests. Differences in
439 responses between sub-periods could be due to different drought stress intensities from
440 one sub-period to the other, different temperature conditions or climatic variability (e.g.
441 the first half of the 20th century was climatically less variable than the second half) or
442 indirect effects of other global or local drivers like increasing atmospheric
443 concentrations of CO₂ and rising N deposition.

444 Current data support the occurrence of climate warming and its effects on various
445 forest ecosystem services in the Pyrenees during recent decades. From 1880 to 1980 AD
446 at least 94 glaciers disappeared in the whole Pyrenees, 17 of them on the Spanish side
447 since 1980 (Morellón et al., 2012). Camarero and Gutiérrez (2004) observed an increase
448 in tree establishment and density within the treeline ecotone over the 20th century. In a
449 European context there is a positive trend in temperatures (+0.90°C) from the beginning
450 of the 20th century and, although lower than in central and northern Europe, the
451 warming trend in the Mediterranean region has intensified since the 1970s (IPCC 2013).
452 The Pyrenees are more likely to be vulnerable against climate warming and drying
453 trends than other Mediterranean and European ranges (Schröter et al., 2005) due to two
454 main ecological drawbacks. First, the Pyrenees are east-west arranged, i.e.
455 perpendicularly to the expected northern (or upward) migratory routes. Second, they are
456 influenced by Mediterranean climatic conditions characterized by a summer drought.
457 The negative effects on forest growth under the forecasted scenarios of climate change

458 could be even worse than expected if drought stress plays a complementary role
459 together with the rising temperatures.

460 Several dendrochronological studies have focused on growth-climate
461 relationships at Pyrenean high-elevation forests (e.g. Gutiérrez 1991, Rathgeber and
462 Roche 2003, Tardif et al. 2003, Andreu et al. 2007, Büntgen et al. 2008a, Esper et al.
463 2010). Our study constitutes a step forward in the sense that (i) we use a larger dataset
464 covering a broad biogeographical gradient including the southern and western
465 distribution limits of this species and that (ii) we find a weakening in the TRW-
466 temperature relationships possibly connected to an increasingly important role of
467 drought as a growth driver during recent decades. The divergence phenomenon here
468 exposed should be considered in the assessment and performance of Pyrenean climate
469 reconstructions from tree rings, which are based on short calibration periods. Trees are
470 showing increasing drought and decreasing temperature sensitivities in recent decades
471 even in these high-elevation ecosystems where we would expect a strong temperature
472 response. This would imply that a Pyrenean climate reconstruction based on present-day
473 growth-climate relationships should take on account the role of additional climatic
474 factors that could be potentially limiting tree growth in an increasing degree. According
475 to our results, temperature reconstructions performed in the Pyrenean range using MXD
476 (Büntgen et al. 2008a, Dorado-Liñán et al. 2012) are reliable since they are based on
477 MXD/temperature relationships where no divergence was found.

478 This divergence phenomenon has been mainly explained here in terms of
479 temperature-induced drought stress, but we should not ignore additional factors
480 potentially influencing the degree and intensity of the growth/climate offset. For
481 instance, nitrogen fertilization or increasing atmospheric CO₂ concentrations may

482 enhance radial growth thus leading to the formation of a less dense earlywood
483 (Lundgren, 2004). Our next research step would be a site-level study of the low- and
484 high-frequency signals in the growth/climate correlations, which would allow us to
485 draw conclusions for larger scales in a more accurate way (Büntgen et al., 2008b). A
486 more exhaustive MXD sampling of several tree species should be also necessary to
487 make a more accurate comparison between TRW and MXD responses.

488

489 **5. Conclusions**

490 This study comprises 1500 tree-ring width (TRW) and 102 maximum density
491 (MXD) measurement series from 711 and 74 trees, respectively, which were sampled at
492 30 high-elevation *Pinus uncinata* forest sites across the Iberian range of the species.
493 Rising temperatures led to an increase in drought stress of Pyrenean high-elevation
494 forests as has been observed in other Mediterranean mountain forests (Jump et al., 2006;
495 Piovesan et al., 2008). Therefore, these high-elevation forests, growing in typically
496 temperature-limited conditions, are becoming more limited by water availability. This
497 growth limitation driven by the amount of available water could be particularly strong
498 in steep sites with rocky substrates where soil shows a poor water holding capacity. We
499 may be witnessing how tree physiological thresholds in terms of optimal temperature
500 for growth are surpassed, reinforcing the role of drought as a growth-limiting factor of
501 high-elevation forests during recent decades.

502

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514

515

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724

725 **SUPPORTING INFORMATION LEGENDS**

726 **Figure A1.** (a) Principal Components Analysis based on 30 TRW chronologies showing
727 the scores of the first two principal components PC1 and PC2 (sites codes are as in
728 Table 1; analysed period is 1901-1994, covered by chronologies from all sites). PC1 and
729 PC2 scores change as a function of altitude (a) and longitude (b), respectively. Stands
730 with special characteristics or located near the distribution limit of the species are
731 indicated. Different symbols correspond to sites from different geographical areas
732 (PNOMP, black circles; PNASM, yellow circles; western and central Pyrenees,
733 downward blue triangle; Iberian System, red square; eastern Pyrenees, white circle; Pre-
734 Pyrenees, upward white triangle). The continuous line in (c) indicates the regression
735 line without considering the red outlier on the left.

736 **Figure A2.** Upper and lower graphs show the different TRW (blue) and MXD (green)
737 chronologies, respectively, coming from the 10 different detrendings applied. Dark blue
738 and dark green indicate the TRW and MXD RCS chronologies, in that order. Light blue
739 and light green indicate the eight different chronologies coming from exponential and
740 spline detrendings. Continued and dotted lines refer to chronologies derived from non-
741 transformed and power-transformed data, correspondingly.

742

743 **Figure A3.** Temporal distribution of (a) 101 MXD and (b) 1500 TRW core samples of
744 *Pinus uncinata*, ordered by calendar age of their innermost ring, and EPS statistic
745 (calculated over 30 years lagged by 15 years) of the whole set (i.e. 6 MXD sites and 30
746 TRW sites) of raw chronologies. The vertical black lines show the temporal limit of the
747 signal strength acceptance ($EPS > 0.85$): 1777 AD for MXD and 1500 AD for TRW.

748 The grey horizontal dashed lines denote the 0.85 EPS criterion for signal strength
749 acceptance (Wigley et al. 1984).

750

751 **Figure A4.** (a) EPS statistic (calculated over 30 years lagged by 15 years) of each site
752 raw chronology without variance adjustment. (b) Temporal distribution of the 1500
753 *Pinus uncinata* TRW cores, grouped by site (from bottom West to top East) and ordered
754 by calendar age of their innermost ring. Vertical lines show the limit of the signal
755 strength acceptance ($EPS > 0.85$; see Wigley et al. 1984).

756

757 **Figure A5.** Relationships between mean segment length (MSL) vs. mean TRW growth
758 rate (AGR) (a) and MXD (b). Different symbols correspond to sites as in Fig. S1.

759

760 **Figure A6.** Contour plots summarizing the Pearson correlation coefficients (r)
761 calculated between TRW chronologies and June-July SPEI index for the 12 months of
762 the year (y axis) at different time scales from one to 24 accumulated months (x axis),
763 covering the period 1901-2009. For the SPEI index we used averaged data from 0.5°-
764 gridded data covering the sampled sites from *Ordesa*, *Aigüestortes* and *Pyrenees*
765 subsets. *TRW mean* refers to the mean chronology averaging the eight different standard
766 chronologies derived from spline and negative exponential detrendings (from power
767 transformed and non transformed raw data); *TRW RCSpt* and *TRW RCSnt* refer to the
768 TRW standard RCS chronologies from power transformed and non transformed raw
769 data, respectively. Legends in the right side show the correlation coefficients from
770 negative values in blue to positive values in orange and red. Significant values ($p <$
771 0.05) correspond to $r > 0.19$ or $r < -0.19$.

772

773 **Figure A7.** Contour plots summarizing the Pearson correlation coefficients (r)
774 calculated between (a) TRW and (b) MXD standard chronologies and the SPEI index
775 for the 12 months of the year (y axis) at different time scales (1-24 months, x axis),
776 considering the period 1901-2009 and two subperiods: 1930-1969 and 1970-2009. For
777 SPEI index we used averaged data from 0.5° grids covering (a) the 30 TRW sampled
778 sites and (b) the 6 MXD sampled sites. Legends in the right side show the correlation
779 coefficients from negative values in blue to positive values in red. Significant values (p
780 < 0.05) are those with $r > 0.19$ or $r < -0.19$ for the period 1901-2009, and $r > 0.35$ or $r <$
781 -0.35 for both subperiods (1930-1969 and 1970-2009). *TRW/MXDmean* refers to the
782 mean chronology coming from averaging the 8 different standard chronologies derived
783 from spline and exponential detrendings; *RCSpt* and *RCSnt* refer to the RCS
784 chronologies derived from power transformed and non transformed raw data,
785 respectively.

786

787 **Figure A8.** Comparison between the highest spatial field correlations of TRW and
788 MXD RCS chronologies against April-May maximum temperatures for the period
789 1950-2009 (climate data were derived from the CRUTS3.10 dataset). The asterisk
790 indicates the approximate location of the centroid of the study area in NE Spain.

791

792 **Figure A9.** Comparison between May (left column; subfigure a) and June-July (right
793 column; subfigure d) CRUTS3.10 maximum temperature record (red) for the period
794 1901-2009, and TRW RCSnt (dark blue) and TRW RCSpt chronologies (light blue).
795 Upper graphs indicate 31-year moving correlations between the temperature records and

796 the chronologies. Each moving correlation point refers to the central year of a 31-year
797 window. Subfigures (a), (b) and (c) show the standard, 20-year low- and high-pass
798 (anomalies) filtered datasets, respectively, for May temperature. Subfigures (d), (e) and
799 (f) show the same for June-July maximum temperature.

800

801 **Figure A10.** Comparison between May (left column; subfigure a) and June-July (right
802 column; subfigure d) CRUTS3.10 maximum temperature records (red) for the period
803 1901-2009, and MXD RCSnt (dark green) and MXD RCSpt chronologies (light green).
804 The rest of explanations are as in figure A8.

805

806 **Figure A11.** Comparison between low- (left column) and high-elevation (right column)
807 chronologies. In (a) and (b) May-September maximum temperature (red) is compared
808 with the TRW RCSnt chronology (dark blue). Upper graph indicates 31-year moving
809 correlations between the 1901-2009 May-September maximum temperature and the
810 RCSnt chronology. Each moving correlation point refers to the central value of a 31-
811 year window. Subfigures (c, d) and (e, f) show the same for 20-year low-, and high-pass
812 (anomalies) series, respectively.

813

814 **Figure A12.** Comparison between low- (left column) and high-elevation (right column)
815 chronologies. In (a) and (b) June-July SPEI (orange) is compared with TRW RCSnt
816 chronology (dark blue). Upper graph indicates 31-year moving correlations between the
817 1901-2009 May-September maximum temperature and the RCSnt chronology. Each
818 moving correlation point refers to the central value of a 31-year window. Subfigures (c,

819 d) and (e, f) show the same for 20-year low-, and high-pass (anomalies) series,
820 respectively.

821

822 **Figure A13.** Example of a densitometric profile covering seven annual rings (period
823 1927-1933) showing intra-annual MXD and wood-anatomical variability for a *Pinus*
824 *uncinata* tree from Gerber site (PNAESM). MXD reaches the maximum values during
825 the late growing season, usually from August up to September, when cell-walls are
826 thickening.

827

828 Figure A14. CRUTS3.10 mean May-September precipitation (in blue) and mean May-
829 September temperature (in red) trends from 1901 to 2013. We found significant (Mann-
830 Kendall $P < 0.05$) positive mean May-September temperature trends for the period
831 1901-2013 and also for the subperiod 1970-2009 (solid and broken red lines,
832 respectively). Instead, no significant trend was found for the mean May-September
833 precipitation trends.

834

835

836

837 TABLES

838 **Table 1.** Geographical, topographical and ecological characteristics of the sampled *P.*
839 *uncinata* sites. Stands are arranged from East to West. Sites' codes are as in Figure 1.
840 Values are means \pm SD. In bold, sites where samples for maximum density (MXD)
841 were obtained. Superscripts ^o and ^a indicate the sites located in PNOMP and PNAESM
842 respectively. Dbh = diameter at breast height

Site (code)	Latitude (N)	Longitude (E / W)	Altitude (m a.s.l)	Aspect	Slope (°)	Dbh (cm)	Height (m)	Age at 1.3 m (years)
Estans de la Pera (EP)	42° 27'	1° 35' E	2360	SW	30 ± 0	65.2 ± 11.0	7.8 ± 2.0	339 ± 117
Mata de València (MA) ^a	42° 38'	1° 04' E	2019	N-NW	19 ± 10	43.2 ± 3.6	12.0 ± 3.1	237 ± 72
Estany de Lladres (LA) ^a	42° 33'	1° 03' E	2120	NW	35 ± 12	52.1 ± 9.8	8.3 ± 1.6	313 ± 123
Airoto (AI)	42° 42'	1° 02' E	2300	W	37 ± 29	58.5 ± 13.5	7.4 ± 1.6	288 ± 100
Tessó de Son (TS) ^a	42° 35'	1° 02' E	2239	N-NE	42 ± 14	74.5 ± 18.8	9.3 ± 3.8	346 ± 202
Estany Negre (NE)^a	42° 33'	1° 02' E	2451	SE	35 ± 18	71.0 ± 26.0	6.6 ± 1.9	411 ± 182
Estany Gerber (GE)^a	42° 37'	0° 59' E	2268	W	15 ± 15	53.5 ± 14.6	6.9 ± 1.4	426 ± 147
Estany d'Amitges (AM)^a	42° 35'	0° 59' E	2390	S-E	40 ± 21	69.0 ± 26.0	9.3 ± 3.8	355 ± 106
Mirador (MI)^a	42° 35'	0° 59' E	2180	SE	33 ± 18	55.1 ± 25.8	7.6 ± 2.3	401 ± 132
Ratera (RA) ^a	42° 35'	0° 59' E	2170	N	40 ± 5	28.3 ± 8.1	10.4 ± 2.0	380 ± 146
Sant Maurici (SM) ^a	42° 35'	0° 59' E	1933	S-SE	16 ± 15	38.2 ± 5.7	11.5 ± 1.7	204 ± 23
Monestero (MO) ^a	42° 34'	0° 59' E	2280	SE	28 ± 13	64.4 ± 16.1	9.3 ± 2.1	346 ± 110
Cortícels (CO) ^a	42° 34'	0° 56' E	2269	W-NW	24 ± 17	83.1 ± 28.8	10.7 ± 3.8	509 ± 177
Barranc de Llacs (LL) ^a	42° 32'	0° 55' E	2250	N-NW	44 ± 38	71.7 ± 20.0	10.5 ± 2.5	616 ± 175
Atxerito (AT)	42° 53'	0° 45' E	1875	N	57 ± 22	64.7 ± 27.2	7.7 ± 2.4	422 ± 159
Conangles (CG)	42° 37'	0° 44' E	2106	S-SW	43 ± 15	56.0 ± 14.5	6.4 ± 2.7	318 ± 117
Vall de Mulleres (VM)	42° 37'	0° 43' E	1800	N-NE	34 ± 13	69.0 ± 26.0	9.8 ± 1.8	437 ± 184
Bielsa (BI)	42° 42'	0° 11' E	2100	E	60 ± 4	45.1 ± 9.4	7.7 ± 3.0	270 ± 67
Sobrestivo (SB) ^o	42° 40'	0° 06' E	2296	S	38 ± 2	61.7 ± 17.5	7.6 ± 1.7	341 ± 97
Foratarruego (FR)^o	42° 37'	0° 06' E	2031	W	37 ± 11	49.5 ± 18.3	8.3 ± 2.9	433 ± 50
Senda Cazadores (SC)^o	42° 38'	0° 03' W	2247	N	39 ± 12	60.9 ± 16.5	9.4 ± 1.6	357 ± 145
Ordesa-Cara Norte (ON) ^o	42° 38'	0° 03' W	2270	N	40 ± 12	50.2 ± 12.5	9.8 ± 1.7	311 ± 45
Mirador del Rey (MR) ^o	42° 38'	0° 04' W	1980	SW	25 ± 10	53.3 ± 15.3	10.9 ± 4.6	117 ± 18
Las Cutas (CU) ^o	42° 37'	0° 05' W	2150	S-SW	20 ± 5	33.3 ± 8.3	9.9 ± 2.5	129 ± 16
Guara (GU)	42° 17'	0° 15' W	1790	N-NW	35 ± 5	44.5 ± 8.1	9.0 ± 1.7	149 ± 36
Respomuso (RE)	42° 49'	0° 17' W	2350	S	30 ± 19	49.5 ± 15.1	7.6 ± 1.5	280 ± 83
Pic d'Arnousse (PA)	42° 48'	0° 31' W	1940	NW	32 ± 4	65.4 ± 5.1	9.4 ± 0.7	248 ± 83
Valdelinares-Teruel (TE)	40° 23'	0° 38' W	1800	SW-W	10 ± 5	63.8 ± 12.4	10.2 ± 1.8	214 ± 107
Larra-La Contienda (CN)	42° 57'	0° 46' W	1750	SW	38 ± 24	46.4 ± 14.0	7.8 ± 2.2	350 ± 108
Castillo de Vinuesa (VI)	42° 00'	2° 44' W	2050	W	21 ± 1	85.6 ± 23.0	9.4 ± 2.9	368 ± 148

Table 2. Statistical characteristics for each site TRW chronology. Variables of raw tree-ring series for the time span analyzed: SD, standard deviation; AC, first-order autocorrelation. Variables of residual chronologies: ms_x , mean sensitivity, a measure of year-to-year growth variability; r_{bt} , mean correlation between trees which evaluates the similarity in growth among trees; E1, variance explained by the first principal component. The reliable time span was defined as the period with $EPS > 0.85$, where the EPS (Expressed Population Signal) is a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley et al. 1984). $N\ trees$ is the number of trees needed to reach the EPS threshold for each site. The mean length was calculated for the time span, while tree-ring width, AC, ms_x , r_{bt} and E1 are calculated from 1901 to 1994. In bold, sites where MXD sampling was also carried out. Superscripts ^o and ^a indicate the sites located in PNOMP and PNAESM respectively.

Site	No. trees / radii	Time span	Raw data			Residual chronology				
			Mean length (years)	Tree-ring width \pm SD (mm)	AC	Reliable time span (EPS > 0.85)	N trees	ms_x	r_{bt}	E1 (%)
EP	20 / 39	1586-1997	198	0.95 \pm 0.36	0.77	1775-1997	10	0.15	0.35	37.84
MA ^a	10 / 20	1668-1997	175	0.92 \pm 0.51	0.85	1785-1997	9	0.18	0.40	47.19
LA ^a	36 / 74	1390-2009	243	0.80 \pm 0.40	0.85	1390-2009	13	0.13	0.27	32.34
AI	16 / 31	1651-1996	194	1.02 \pm 0.35	0.77	1748-1996	7	0.14	0.45	49.00
TS ^a	10 / 17	1537-1995	252	0.88 \pm 0.38	0.84	1773-1995	13	0.12	0.32	38.43
NE ^a	46 / 86	1393-2009	242	0.74 \pm 0.33	0.79	1652-2009	11	0.14	0.36	38.34
GE ^a	41 / 79	1270-2010	278	0.59 \pm 0.26	0.81	1423-2010	11	0.12	0.43	50.06
AM ^a	25 / 56	1592-2009	229	0.83 \pm 0.33	0.77	1665-2009	7	0.15	0.48	51.79
MI ^a	33 / 85	1390-2009	252	0.59 \pm 0.32	0.83	1596-2009	12	0.16	0.34	37.25
RA ^a	5 / 13	1818-2009	192	1.07 \pm 0.70	0.88	1856-2009	5	0.17	0.40	50.36
SM ^a	20 / 40	1811-1996	164	0.94 \pm 0.68	0.89	1819-1996	9	0.18	0.48	50.57
MO ^a	30 / 76	1481-2009	246	0.92 \pm 0.50	0.87	1691-2009	13	0.12	0.31	34.24
CO ^a	25 / 43	1509-1995	274	0.64 \pm 0.25	0.78	1594-1995	15	0.14	0.34	37.51
LL ^a	17 / 17	1338-1997	435	0.59 \pm 0.29	0.88	1548-1997	17	0.11	0.33	38.51
AT	17 / 43	1317-2010	339	0.59 \pm 0.21	0.75	1474-2010	16	0.13	0.28	31.52
CG	25 / 54	1510-1994	215	0.82 \pm 0.36	0.82	1700-1994	14	0.15	0.26	30.37
VM	12 / 23	1476-1994	234	0.77 \pm 0.37	0.83	1816-1994	12	0.14	0.29	34.34
BI	11 / 20	1707-1996	196	0.80 \pm 0.53	0.82	1766-1996	10	0.21	0.40	46.27

SB ^o	53 / 95	1512-2009	285	0.84 ± 0.51	0.85	1617-2009	16	0.15	0.30	32.1
FR ^o	12 / 25	1438-1947	305	0.50 ± 0.29	0.82	1582-1947	5	0.16	0.30	47.41
SC ^o	65 / 119	1421-2010	256	0.72 ± 0.41	0.85	1571-2010	27	0.12	0.28	29.51
ON ^o	14 / 27	1531-1998	234	0.76 ± 0.36	0.81	1716-1998	6	0.21	0.28	33.43
MR ^o	17 / 34	1795-1998	156	0.77 ± 0.44	0.86	1836-1998	12	0.15	0.31	34.39
CU ^o	10 / 20	1871-1997	98	1.71 ± 0.65	0.74	1892-1997	10	0.22	0.39	47.56
GU	27 / 42	1800-2011	122	1.85 ± 1.00	0.81	1873-2011	11	0.23	0.39	42.26
RE	20 / 47	1572-2010	202	0.84 ± 0.42	0.81	1742-2010	18	0.15	0.26	31.40
PA	8 / 16	1755-1994	170	1.14 ± 0.62	0.84	1778-1994	5	0.18	0.32	40.58
TE	35 / 68	1730-2008	157	1.33 ± 0.74	0.83	1741-2008	13	0.14	0.41	46.57
CN	25 / 57	1364-2010	252	0.68 ± 0.42	0.82	1670-2010	13	0.16	0.33	36.93
VI	24 / 42	1561-2010	238	0.99 ± 0.49	0.81	1731-2010	14	0.18	0.31	42.10

Table 3. Statistical characteristics of TRW and MXD chronologies (from the whole dataset) resulting from the 10 different detrending methods applied. Variables of standard tree-ring series for the period 1901-2009: *corr*, correlation coefficient with the maximum temperature of the period MJJAS; EPS, Expressed Population Signal, a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley et al. 1984); SNR, signal-to-noise ratio, the statistical size of the common variance between the trees; PC1, variance explained by the first principal component; ms_x , mean sensitivity, a measure of year-to-year growth variability.

	Data transformation method	Detrending method	<i>corr</i>	EPS	SNR	PC1 (%)
TRW	non-transformed	neg exp1	0.013	0.995	23.666	28.35
		neg exp2	0.087	0.994	23.365	30.56
		150-yr spline	0.213	0.994	23.365	27.42
		300-yr spline	0.219	0.995	23.366	28.07
		RCS	-0.066	0.995	23.366	22.58
	power-transformed	neg exp1	-0.012	0.995	23.366	27.42
		neg exp2	0.064	0.994	23.365	32.14
		150-yr spline	0.180	0.995	23.366	28.03
		300-yr spline	0.119	0.995	23.366	26.52
		RCS	-0.149	0.996	23.367	25.86
MXD	non-transformed	neg exp1	0.244	0.919	11.381	37.07
		neg exp2	0.277	0.919	11.381	36.16
		150-yr spline	0.336	0.920	11.490	55.31
		300-yr spline	0.301	0.919	11.381	42.59
		RCS	0.247	0.918	11.274	46.27
	power-transformed	neg exp1	0.246	0.921	11.599	33.32
		neg exp2	0.274	0.921	11.599	31.76
		150-yr spline	0.339	0.923	11.820	37.87
		300-yr spline	0.306	0.921	11.599	45.07
		RCS	0.198	0.920	11.490	47.96

FIGURE LEGENDS

Figure 1. Network of the 30 Iberian *Pinus uncinata* sampled sites (white areas indicate high-elevation sites). The left lower 3D graph emphasizes the sampled sites located at high altitudes, mostly in the Spanish Pyrenees. The right lower map shows the location of the study area (red box, NE Spain) within the Mediterranean Basin (blue box).

Figure 2. Comparison between the RCS chronologies (dark lines) and the mean standard chronology derived from the 8 different spline and negative exponential detrendings (light lines), for (a) TRW and (b) MXD. Upper insets show the chronologies comparison for the period 1850-2009 for MXD and 1850-2010 for TRW (areas delimited by the black rectangles). Similar results are displayed in the *Pyrenees* and *Aigüestortes* subsets. Continued and dotted lines refer to chronologies derived from non-transformed and power-transformed data, correspondingly.

Figure 3. Correlation coefficients between maximum temperatures and (a) TRW or (b) MXD RCS chronologies. Monthly correlations are computed from previous-year October (o) to current-year September (Sep), and seasonal correlations are computed from current-year March to September, over the common period 1901-2009 and two subperiods: 1930-1969 and 1970-2009. Significant correlations are indicated with asterisks ($p < 0,05$) and dots ($p < 0,001$).

Figure 4. Contour plots summarizing the Pearson correlation coefficients (r) calculated between (a) TRW and (b) MXD RCS standard chronologies derived from power transformed raw data and the SPEI index for the 12 months of the year (y axis) at different time scales (1-24 months, x axis), considering the period 1901-2009 and two subperiods: 1930-1969 and

1970-2009. For SPEI index we used averaged data from 0.5° grids covering (a) the 30 TRW sampled sites and (b) the 6 MXD sampled sites. Legends in the right side show the correlation coefficients from negative values in blue to positive values in red. Significant values ($p < 0.05$) are those with $r > 0.19$ or $r < -0.19$ for the period 1901-2009, and $r > 0.35$ or $r < -0.35$ for both subperiods (1930-1969 and 1970-2009).

Figure 5. (a) May-September maximum temperature (red lines) and (d) June-July SPEI series (orange lines) compared with TRW RCSnt (dark blue lines) and RCSpt chronologies (light blue lines) for TRW. Upper graph indicates 31-year moving correlations between the climatic series and the RCSnt and RCSpt chronologies, coloured in dark and light blue lines respectively. Each moving correlation point refers to the central value of a 31-year window. For May-September maximum temperature, the same analyses for (b) 20-year low- and (c) high-pass (anomalies) series are displayed. For June-July SPEI, the same analyses are also displayed for (e) 20-year low- and (f) high-pass series.

Figure 6. (a) May-September maximum temperature (red lines) and (b) June-July SPEI series (orange lines) compared with MXD RCSnt (dark green lines) and RCSpt chronologies (light green lines) for MXD. The rest of explanations are as in Figure 5.