Detecting snow-related signals in radial growth of *Pinus uncinata* mountain forests

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Abstract

Climate warming is responsible for observed reduction in snowpack depth and an earlier and faster melt-out in many mountains of the Northern Hemisphere. Such changes in mountain hydroclimate could negatively affect productivity and tree growth in high-elevation forests, but few studies have investigated how and where recent warming trends and changes in snow cover influence forest growth. A network comprising 36 high-elevation *Pinus uncinata* forests was sampled in the NE Iberian Peninsula, mainly across the Spanish Pyrenees, using dendrochronology to relate tree radial growth to a detailed air temperature and snow depth data. Radial growth was negatively influenced by a longer winter snow season and a higher late-spring snowpack depth. Notably, the effect of snow on tree growth was found regardless the widely reported positive effect of growing-season air temperatures on *P. uncinata* growth. No positive influence of moisture from spring snowmelt on annual growth of *P. uncinata* was detected in sampled forests. Tall trees showed a lower growth responsiveness to snow than small trees. Decreasing trends in winter and spring snow depths were detected at most Pyrenean forests, suggesting that the growth of high-elevation *P. uncinata* forests can beneficiate for a shallower and of shorter duration snowpack associated with warmer conditions. However, water-limited sites located on steep slopes or on rocky substrates, with poor soil-water holding capacity, could experience drought stress because of early depleted snow-related soil moisture.

Keywords: dendroecology, tree-ring width, snowpack, subalpine forests, Pyrenees.

1. Introduction

Mountain forests are particularly susceptible to climatic variation because low temperatures typically limit radial growth and productivity near the uppermost edge of tree distribution ranges (Körner, 2012). Recent warming trends have induced shifts in tree recruitment (Smithers et al., 2018; Sangüesa-Barreda et al., 2018) and have enhanced radial growth (Innes, 1991; Tardif et al., 2003; Camarero et al., 2015a; Zhuang et al., 2017), excepting few sites were warming have induced some drought stress (Camarero et al., 2015c, Galván et al. 2015). Most studies have focused on the direct effects of rising temperatures on tree growth (e.g. Del Barrio et al., 1990; Gutierrez et al., 1991; Tardif et al., 2003; Andreu et al., 2007; Galván et al., 2014; Camarero et al., 2017; Franke et al., 2017; D'Orangeville et al., 2018; Sanchez-Salguero et al., 2018; Wang et al., 2019). Research focused on the indirect effects of climate warming, such as the influence of snow dynamics on forest productivity, is still scarce (Vaganov et al., 1999; Kirdyanov et al., 2003, Helama et al., 2013, Watson and Luckman 2016; Carlson et al., 2017).

Snow accumulation requires a combination of precipitation and low temperatures to initiate snowfall and persistent below-zero temperatures to sustain the snowpack (Beniston et al., 2011; López-Moreno et al., 2011). Due to the high sensitivity of snow cover to seasonal temperatures (Morán-Tejeda et al., 2013a), a warmer climate can easily impact the process of snow accumulation/melting (Beniston, 2003). An increase in winter temperature leads to a precipitation shift from snow towards rain, and warmer spring conditions induce earlier and faster snowpack melting (Morán-Tejeda et al., 2014). Reduced snowpack depth and duration have been reported in the main mid-latitude mountain ranges (López-Moreno, 2005; Marty, 2008; McCabe and Wolock, 2009; Beniston, 2012; Morán-Tejeda et al., 2013a) including Mediterranean (drought-prone) areas such as the Pyrenees (Morán-Tejeda et al., 2017).

Snow dynamics may influence forest growth (e.g., Kirdyanov et al., 2003). Early snowfalls in the autumn may shorten the growing season and lead to a reduction in the assimilation of carbohydrates, and this can negatively affect growth in the following year (Carlson et al., 2017). A lack of snow cover during the winter can cause premature yellowing and shedding of needles of shrubby krummholz individuals during cold and dry winters and repeated freeze-thaw cycles (winter drought), reducing growth in the following spring (Helama et al., 2013; Camarero et al. 2015b). Larger snow accumulation and a longer snowmelt period may negatively affect tree radial growth by slowing the increase of soil temperature, delaying the growing period, and thus shortening the growing season (Vaganov et al., 1999; Kirdyanov et al., 2003; Watson and Luckman, 2016). On the other hand, snowmelt effects on soil moisture have been reported to positively influence tree growth during the next growing season (St. George, 2014; Watson and Luckman, 2016). All these observations suggest that the radial growth of trees can be related to winter snowpack, melt-out date and spring snow depth.

In the main mountains of the NE Iberian Peninsula (Pyrenees, Pre-Pyrenees, Iberian System), increasing trends in mean temperatures and an increment in precipitation variability have been observed during the second half of the 20th century (López-Moreno et al., 2010; El Kenawy et al., 2011). Such consequent water stress increase may also limit tree growth in high-elevation forests (Tardif et al., 2003; Andreu et al., 2007). Nevertheless, high-elevation mountain pine (*Pinus uncinata*) forests and treelines are forecasted to show enhanced growth during the late 21st century due to a longer and warmer growing season (Sánchez-Salguero et al., 2012, Camarero et al., 2017). Climate warming has also affected mountain hydrology and influences the accumulation, duration and melt-out of snow, leading to a shallow snowpack or a longer snow-free season (Morán-Tejeda et al., 2013a, 2013b). Discerning how and where snow dynamics affects

103 forest growth may help us understand future responses of mountain forests to forecasted
104 hydroclimatic change.

105 The main hypothesis of the present study is that snowpack depth and duration
106 influence radial growth of high-elevation *P. uncinata* forests. It was expected that snow
107 cover affects tree radial growth, in addition to the widely reported temperature effects on
108 growth (Gutiérrez, 1991; Rolland and Schueller, 1994; Camarero et al., 1998). It was also
109 expected that there would be greater impact of snowpack depth and duration on growth
110 in high-elevation forests with a shorter growing season, since elevation indirectly controls
111 the effects of climate on *P. uncinata* growth by modifying growing season air temperature
112 (Tardif et al., 2003; Galván et al., 2014). These hypotheses were tested by analyzing the
113 radial growth of a *P. uncinata* dendrochronological network in the main mountain ranges
114 of NE Iberia in relation to snow cover conditions at site level. The specific objectives of
115 the present study were: (1) to evaluate the associations between snow conditions and
116 radial-growth variability of *P. uncinata* forests; (2) to explore the influence of
117 biogeographical patterns and tree characteristics on tree growth responses to snow depth;
118 and (3) to estimate and compare the temporal evolution of radial growth and snow trends
119 for the 1980-2010 period.

120

121 **2. Materials and methods**

122 *2.1. Study species*

123 The mountain pine (*Pinus uncinata* Ram.) is a long-lasting and light-demanding conifer,
124 which shows a wide ecological tolerance regarding topography (slope, aspect, elevation)
125 and soil type (Cantegrel, 1983) and forms high-elevation forests. The natural habitat of
126 *P. uncinata* includes central and southwest European mountains, while its southern
127 geographical limit is reached in the Iberian System (Spain). It is dominant in the subalpine

belt of the central and eastern Pyrenees (1800-2500 m a.s.l.). Its growing season starts at the end of May and ends in October, with major growth rates occurring from the end of May to July (Camarero et al., 1998). Warm autumn and spring temperatures before and during tree-ring formation enhance *P. uncinata* radial growth, whereas summer precipitation during the growing season is the main positive climate driver of growth in certain xeric sites located in the Pre-Pyrenees and southern Iberian System (Gutiérrez, 1991; Camarero et al., 1998; Tardif et al., 2003; Andreu et al., 2007; Galván et al., 2014). The timing of *P. uncinata* tree-ring formation is schematized in Figure 1.

2.2. Study sites

The 36 studied forests are located in the main mountain ranges of the NE Iberian Peninsula (Figure 2): 33 are located in the Pyrenees, (3 of them in the Pre-Pyrenees, the Pyrenees' foothills), and the other 3 sites are located in the Iberian System. Two of the sites sampled in the southern Iberian system (VATE, VA1U) constitute the southernmost distribution limit of the species in Europe. Sampled sites cover the whole geographical distribution of the species in the Iberian Peninsula. The elevation of the sampled sites ranges from 1750 to 2451 m a.s.l. and the mean slope of the terrain is 35°±16º (see Table S1 in the Supplementary Material). Mean diameter at breast height (dbh) measured at 1.3 m of sampled trees is 66±7 cm, and their age is 334±108 years on average (Table S1).

The location of the Pyrenees, between the Atlantic Ocean on the west side and the Mediterranean Sea in the east, causes a fast climatic transition, while the Central Pyrenees shows a greater continental influence (Del Barrio et al., 1990). In the western areas, most of the annual precipitation falls during the cold winter season, whereas precipitation falls mainly during spring and autumn in the east (Del Barrio et al., 1990). Air temperature changes depend on elevation with -5.17 ºC km^{-1} being the mean temperature lapse rate

across the Pyrenees (Navarro-Serrano et al. 2018). The annual 0 ºC isotherm is located at 2900 m a.s.l. (Del Barrio et al., 1990), whereas it falls to 1600 m a.s.l. between December and April, establishing the lower limit of the seasonal snowpack (López-Moreno et al., 2011). Snow accumulation also shows a correlation to Atlantic–Mediterranean proximity and distance from the main divide of the mountain range (Revuelto et al., 2012). Monthly mean values of temperature, snow depth and melt-out date from1980 to 2009 hydrological years for all sampled sites are presented in Figure 1.

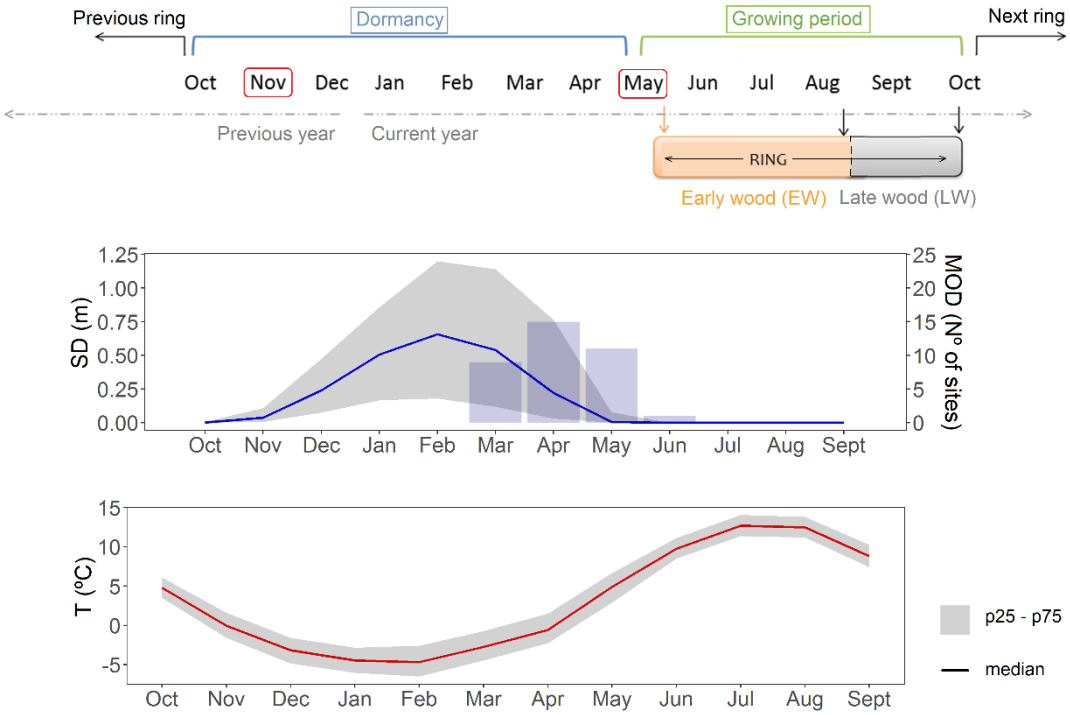
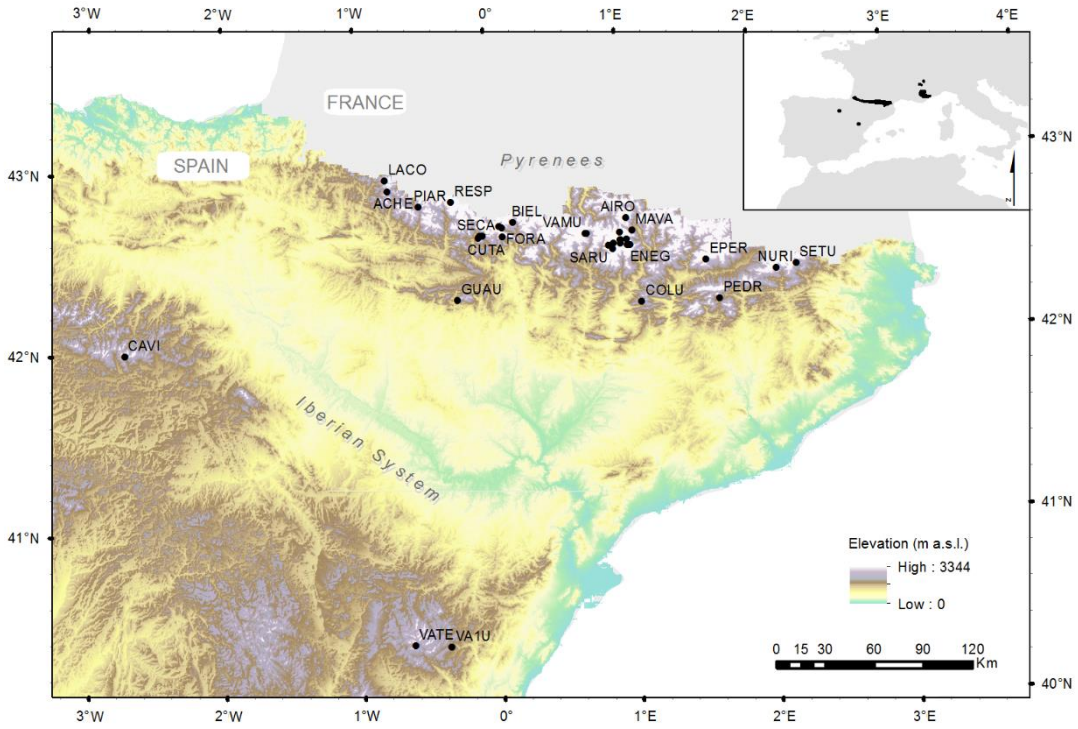


Figure 1. Top panel: Timing of *P. uncinata* tree-ring formation based on Camarero et al. (1998). Red boxes indicate the most influencing months to *P. uncinata* radial growth by temperature (Tardif et al., 2003; Galván et al., 2014). Bottom panels: monthly median snow depth (SD, blue line), melt-out date frequency (MOD, bars) and monthly median temperature (T, red line) of sampled sites in NE Iberian Peninsula from 1980 to 2009 hydrological years. Shaded areas show the 25-75 percentile ranks.



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170 **Figure 2.** Map of sampled mountain *P. uncinata* sites in NE Iberian Peninsula (black
171 dots, see sites' codes in Table S1) and distribution of the study species in Europe (inset,
172 top right).
173

174 *2.3. Dendrochronological data*

175 Dendrochronological data correspond to an updating of data from 36 forests sampled and
176 published by Galván et al. (2012, 2014). Wood samples were collected between 1994 and
177 2010 from 5 to 65 dominant individual trees of different sizes and ages, randomly selected
178 in each site. From each tree, two or three cores were taken at 1.3 m height with Pressler
179 increment borers. The sapwood length was measured in the field, and topographic
180 (elevation, slope and aspect) and biometric (dbh and tree height) variables were also
181 recorded for each individual tree.

182 Wood samples were air dried and sanded until tree-ring boundaries were clearly
183 visible. Then, they were visually cross-dated and measured at 0.01 mm resolution using
184 a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating quality was
185 checked using the program COFECHA (Holmes, 1983) by comparing the individual ring-

width series among coexisting trees of the same species. Finally, cross-dated tree-ring width (RWL) series were obtained.

Dimensionless ring-width indices (RWI) series were obtained by removing age or size trends and temporal autocorrelation to reflect growth response to climate. Residual RWIs were obtained by removing long-term trends of ring-width data fitting negative linear functions, followed by 30-year cubic smoothing splines, and then by eliminating the first-order autocorrelation of the resulting residuals using the software ARSTAN V. 44 (Cook, 1985). A bi-weight robust mean was then computed to obtain residual or pre-whitened chronologies (mean site series) for each site, which were used in subsequent analyses.

2.4. Climatic and snow data

Daily snow depth (SD) and temperature data (T) for the studied sites were extracted from a gridded meteorological dataset obtained by simulation from Weather Research and Forecasting (WRF; Skamarock et al., 2008) model. The WRF model was driven by ERA-Interim (Berrisford et al., 2011) reanalysis and coupled offline with Factorial Snow Model (FSM 1.0; Essery, 2015), a physically based energy and mass balance snow model. WRF outputs were projected to the target elevation, using hygrobarometric formulas and lapse rates and the new projected meteorological information as driving data of FSM. The methodology to develop the snow dataset and its validation is shown in Alonso-González et al. (2018).

Several annual snow indices were created from the daily snow data as indicators of specific snow conditions all year round, based on Figure 1:

- Average November snow depth (Nov SD) as previous autumn snow conditions indicator.
- Average February snow depth (Feb SD) as winter snow conditions indicator.

- Average May snow depth (May SD) as spring snow conditions indicator.

The selection of these monthly SD values for representing snow seasonal conditions is based on the cumulative nature of snow. Thus, the snow depth value at the end of the season will be representative of the accumulated snow and the meteorological conditions of the previous months (e.g. López-Moreno et al., 2005; Morán-Tejeda et al., 2016). Snow indices were not highly correlated with each other, showing an average coefficient of correlation lower than $r_s = 0.55$ (Spearman Rho). Variables were detrended prior to the correlation analyses. Correlation coefficients (r_s) were: 0.48 for Nov SD – Feb SD, 0.33 for Nov SD – May SD and 0.54 for Feb SD – May SD.

Given that snow depth conditions of a given month are highly influenced by the temperature of previous months, the following monthly aggregations (averages) of temperature data were computed for statistical analyses: November mean temperature (Nov T), February mean temperature (Feb T), November-December-January-February mean temperature (Nov-Feb T), December-January-February mean temperature (Dec-Feb T), January-February mean temperature (Jan-Feb T), May mean temperature (May T), March-April-May mean temperature (Mar-May T), April-May mean temperature (Apr-May T).

2.5. Statistical analyses

We searched for snowpack effects on subsequent tree-ring development, considering the period from November (previous to tree-ring formation) to May, based on snow cover presence at the sampled forests (Figure 1).

The growing-season air temperature is a major and widely reported determinant of *P. uncinata* growth (Gutiérrez, 1991; Rolland and Schueller, 1994; Camarero et al., 1998; Tardif et al., 2003; Andreu et al., 2007; Galván et al., 2014). However, temperature also

236 determines the large variability of snowpack among elevations (López-Moreno, 2005;
237 Morán-Tejeda et al., 2013b). Because the aim was to control the temperature effect on
238 growth (RWI) and infer the pure effect of snow, the computed snow indices from the
239 influence of temperature were isolated. This was done by considering the aforementioned
240 snow depth and temperature indices as predictors of RWI by means of stepwise linear
241 regressions. First, Spearman non-parametric correlations (r_s) were computed between the
242 snow depth indices (Nov SD, Feb SD, May SD) and the whole set of temperature monthly
243 aggregations. Temperature aggregations that best correlated with snow indices were
244 November T, Jan-Feb T and Mar-May T for Nov SD, Feb SD and May SD (See
245 Supplementary Material Table S2). These best-correlated temperature aggregations,
246 together with mean May temperature, because its influence on tree growth is widely
247 reported as the most important (e.g., Tardif et al. 2003) and the snow depth indices were
248 then used as predictors in the stepwise linear models (Eq. 1). The stepwise model allows
249 introduction of variables that substantially improve the model by rejecting those that may
250 be redundant. This prevents greatly auto-correlated variables from being included in the
251 model and allowed us to infer whether the snow depth indices or temperature indices were
252 the best predictors of RWI. Linear models were performed individually for each site, as
253 well as a regional model for the whole set of sites. The models can be formulated as
254 follows:

255 $$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n + \varepsilon \qquad \text{(Eq. 1)}$$

256 where y is the response variable (i.e. RWI values), β_0 is the intercept, x_1 to x_n are
257 the predictors (i.e., snow depth and temperature indices), β_1 to β_n are the estimated partial
258 regression coefficients and ε is the error. The models were compared using the Akaike
259 Information Criterion (AIC) value; the smaller the AIC, the better the fit (most
260 parsimonious model) since it penalizes complex models (Burnham and Anderson, 2003).

Only the best model for each site and the one run for the whole set of sites are shown in the results, including the following information: the explained variance (adjusted R^2), the statistical significance (p) and the partial coefficients of the regressions. Automated model selection was performed with the MuMIn package (Barton and Barton, 2018) of the R language version 3.1.0 (R Core Team, 2014).

Additionally, partial correlations using the Spearman coefficient were calculated between RWI and SD indices by partially removing the effects of temperature (Table S2). Non-parametric methods were used, since not all analyzed variables had normal distributions (Shapiro–Wilk test, $p < 0.05$). Snow and temperature variables were previously detrended.

Variations of tree growth responses to snow conditions along biogeographical gradients for a subset of sites where a snow index was the best predictor in the aforementioned stepwise models were investigated. The following variables were considered: latitude, longitude, slope, elevation of the terrain, dbh, tree height, sapwood and tree age (Table S1), and annual maximum snow depth (Max SD) (as an indicator of site differences in snow accumulation). Statistically significant different responses among groups of sites whose models selected the same best predictor using the non-parametric Kruskal-Wallis test were identified along gradients. Non-parametric Spearman correlations were calculated, considering the amount of radial growth variance explained by snow variables (adjusted R^2 from the stepwise models) as the dependent variable and biogeographical gradients as independent variables. Complementary correlation analyses were done using partial correlation coefficients between tree growth and snow depth as dependent variables (in Supplementary Material Figure S3).

Trend analysis for tree-ring width (RWL series) as well as for snow indices was performed using the Mann-Kendall test and Theil-Sen's slope estimator for computing

the magnitude of the trend, considering a subset of sites where any snow – growth significant relationship was previously found. Trend analysis was carried out using the zyp package in R language (Bronaugh et al., 2009), which includes a trend-free pre-whitening method for removing serial autocorrelation.

RWI and RWL series were shorter than the snow series at some sites. Thus, all analyses were performed for the longest common period available, for example, from 1981 to last formed tree-ring measured (number of available years for each one is indicated in Table S1).

3. Results

3.1. Growth responses to snow variables

Stepwise linear models (Table 1) pointed out snow indices as main predictors of *P. uncinata* radial growth in 47% of sites (17 out of 36 sites; with 11 out of the 17 showing a statistically significant model). These 17 sites (Figure 3) were selected and used in later analyses. Average explained variance by models in these sites was 24% (30% for statistically significant models). The site in which predictors explained the larger variance of RWI was CONU (adjusted $R^2 = 0.81$; Table 1). May SD was the best predictor in 64% of sites where snow indices were the most important predictors and their models were statistically significant (Figure 4). It was followed by Feb SD (selected in 27% of these sites) and Nov SD (only selected in one of these 11 sites). All snow indices negatively influenced radial growth (RWI) in all sites, except for Nov SD, which positively influenced tree radial growth in VA1U site.

In total, 17% of statistically significant models (6 out of 36 sites) pointed out temperature indices as main predictors of *P. uncinata* radial growth. Jan-Feb T was

selected as the best predictor of RWI in 5 out of 6 of these sites, and Mar-May T was selected in only one site.

For the regional model, which takes into account all of the 36 site-chronologies combined (Table 1, bottom), Nov SD was selected as the most important predictor (despite it only explained 5% of the total variance). When a subset of statistically significant sites was included in the general model, May SD was the most important predictor again explaining 13% of the total growth variance.

Complementary to stepwise linear models, partial correlations also noted the prevalence of Feb SD, with respect to the other two snow indices, in terms of influencing radial growth of *P. uncinata* (Table S3 and Figure S1, Supplementary Material). Most sites (67%) showed a Feb SD negative influence on radial growth (mean r_s = -0.34; SD = 0.18), being five of them statistically significant. For May SD, one site showed statistically significant partial correlation with radial growth.

Table 1. Statistical parameters of stepwise linear models between radial growth (response variable RWI) and snow and temperature indices (predictors) in each site, for all sites (All sites), and for all statistically significant sites (Sig sites). See sites codes in Table S1 and Figure 2.

Site	N	Coefficients								Adjusted R^2	p
		Intercept	Nov SD	Feb SD	May SD	Nov T	May T	Jan-Feb T	Mar-May T		
ACHE*	30	0.99			**-0.15**					0.11	0.041
AIRO*	16	1.00			**-0.16**			0.04		0.50	0.019
BIEL*	16	1.01			**-4.30**					0.20	0.046
BLLA	30	0.99					0.03	**0.03**		0.25	0.098
CAVI	30	1.01	**-0.36**	-0.07		0.02				0.16	0.090
COLU	30									-	
CONU*	14	0.99	**-0.77**	-0.11	-0.56				-0.08	0.81	0.001
CORT	30	1.00			**-1.80**					0.08	0.072
CUTA	17	1.00				**-0.03**				0.17	0.058
EAMI*	29	1.00			**-0.55**					0.23	0.005
EGER*	30	0.99			**-0.17**			0.02		0.21	0.019
ELLA	29									-	
ENEG*	29	0.99			**-0.32**	-0.02				0.26	0.006
EPER*	17	0.99						**0.07**		0.44	0.002
FORA	29									-	
GUAU	30									-	
LACO	19									-	
LEST	13	1.00		**-0.29**						0.18	0.084

MAVA*	17	1.00						**0.09**		0.29	0.016
MIRA	29	1.00							**0.05**	0.10	0.055
MIRE*	18	0.99		**-0.18**						0.19	0.041
MONE	29	1.00		-0.08	**-1.36**					0.19	0.082
NURI*	21	0.99				-0.03		**0.05**		0.42	0.005
PEDR	26	1.00						**0.03**		0.10	0.063
PIAR	14	1.01						**0.04**		0.21	0.059
RATE	29	0.99	**0.76**							0.06	0.109
RESP	30	1.00			**-0.04**					0.08	0.071
SAMA*	16	0.98						**0.08**		0.20	0.047
SARU*	15	1.00		**-0.27**						0.25	0.034
SECA	29									-	
SETU	19									-	
SOBR	29									-	
TESO*	15	0.97						**0.08**		0.28	0.024
VA1U*	26	1.00	1.77		**-2.83**					0.17	0.030
VAMU*	14	1.02		**-0.23**						0.35	0.015
VATE*	26	0.99							**0.08**	0.15	0.028
All sites	-	0.99	**0.08**		-0.03	-0.01	0.01	0.01	-0.01	0.05	0.00
Sig sites	-	0.99			**-0.13**	-0.01	0.02	0.01	-0.01	0.13	0.00

N: data series length starting from 1981 (years). Statistically significant sites (model $p < 0.05$) are followed by *. The best predictor for each model (site) is indicated in bold characters. Hyphen indicates null models (any significant predictor).

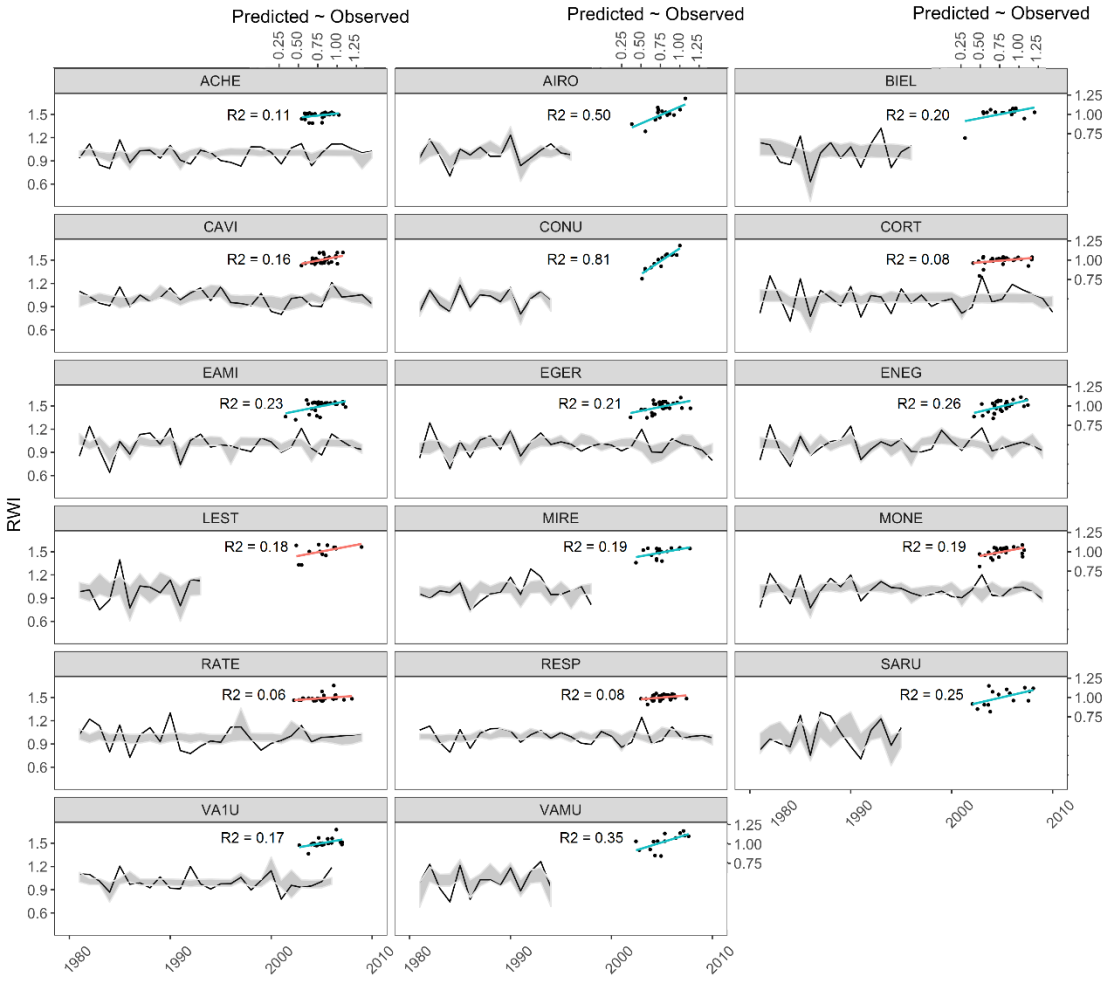

Figure 3. Tree-ring width indices (RWI, lines) and confidence intervals (shaded areas) stepwise linear models for selected sites. Scatter plots show correlatios between observed and RWI values (right y-axes) predicted by the model (adjusted R^2), and its statistical significance (red: not significant; blue: significant, $p < 0.05$).

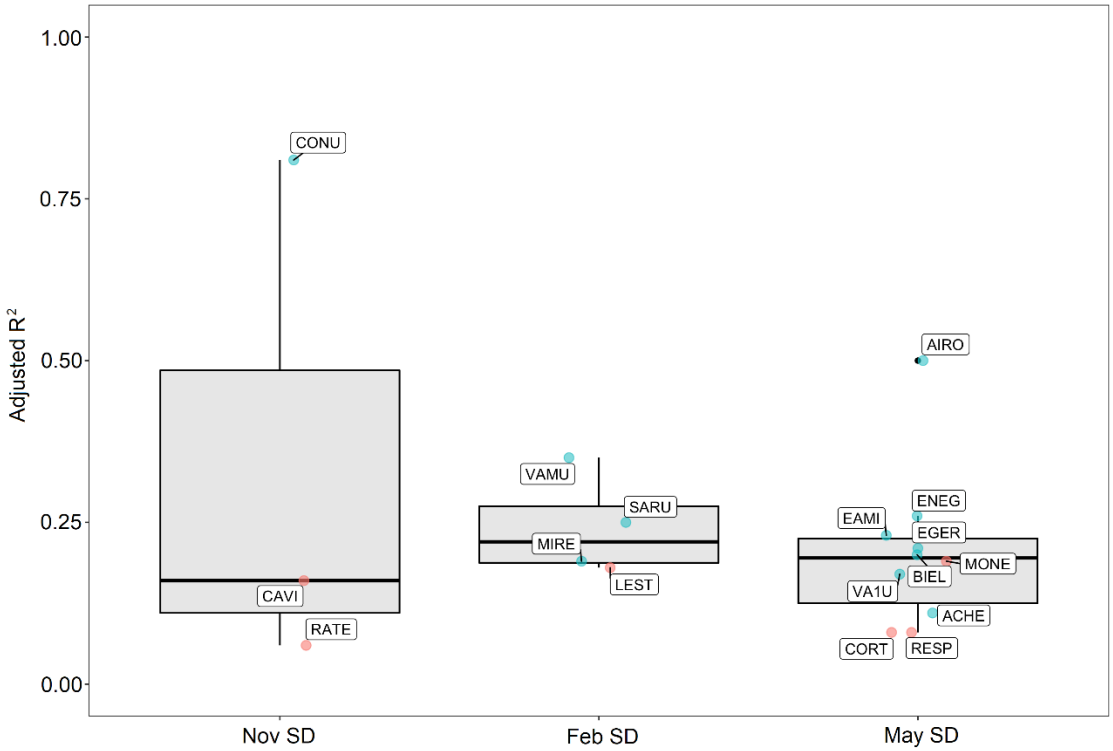

Figure 4. Tree-growth variance (adjusted R^2) explained by stepwise linear models for selected sites. Values are displayed aggregated by best model predictor (snow indices only). Sites related to each model are labelled. Statistical significance of models is represented in red ($p > 0.05$) and blue ($p < 0.05$) colors. See sites codes in Table S1 and Figure 2.

3.2. Influence of biogeographical patterns and tree characteristics on growth responses to snow depth.

Tree characteristics determined the response of growth to snow (Fig 5a). The presence of small trees strengthen the linkage between snow and growth in sites where a snow index was the main driver of RWI (r_s = -0.61, p = 0.03) (Figure 5b). It was observed that sites where a snow index was the statistically significant main driver of *P. uncinata* radial growth were mostly located in the Pyrenees (at western and central area of this mountain range), with the exception of one forest stand located in the southern Iberian System

(VA1U) (Fig S2). May SD was the main RWI predictor across the Pyrenees and also in the southern Iberian System site.

Additional biogeographical analyses based on growth-snow partial correlations showed that greater and statistically significant negative snow influence on tree growth was found in high-elevation sites (Nov SD index) and sites with bigger tree dbh (Feb SD index) (Figure S3).

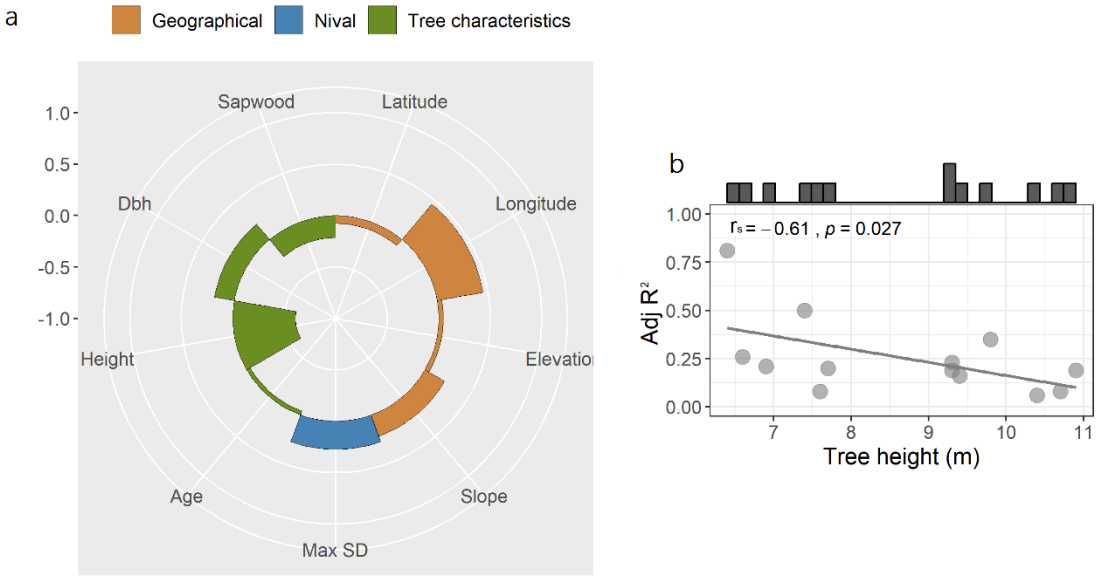

Figure 5. (a) Effects of geographical, nival gradients and tree influences on growth-snow variance (adjusted R^2) established by Spearman correlations (r_s). The southern Iberian System sites were omitted in latitude analyses. (b) Scatterplot of single obtained statistically significant correlation between growth-snow variance and biogeographical gradients (tree height) ($p < 0.05$). Histograms show sites frequency of distribution along this gradient.

3.3. Tree radial growth and snow indices trend analysis

Five of thirteen forests presented statistically significant RWL trends, only one of them showed a positive slope for RWL trend while all the others showed a negative slope (Figure 6b; Figure S4). There were found statistically significant trends for May SD and Feb SD variables, in 35% and 12% of sites where snow index was the main driver of *P.*

uncinata radial growth respectively, but nor for Nov SD. All these statistically significant snow trends show negative slopes.

A statistically significant correlation was found between growth trends (RWL) and snow (Feb SD) trends (r_s = -0.68; p = 0.01) (Figure 6a). From the regional perspective, only in the Pyrenees there were found statistically significant trends in snow variables (all of them with negative coefficients as mentioned above).

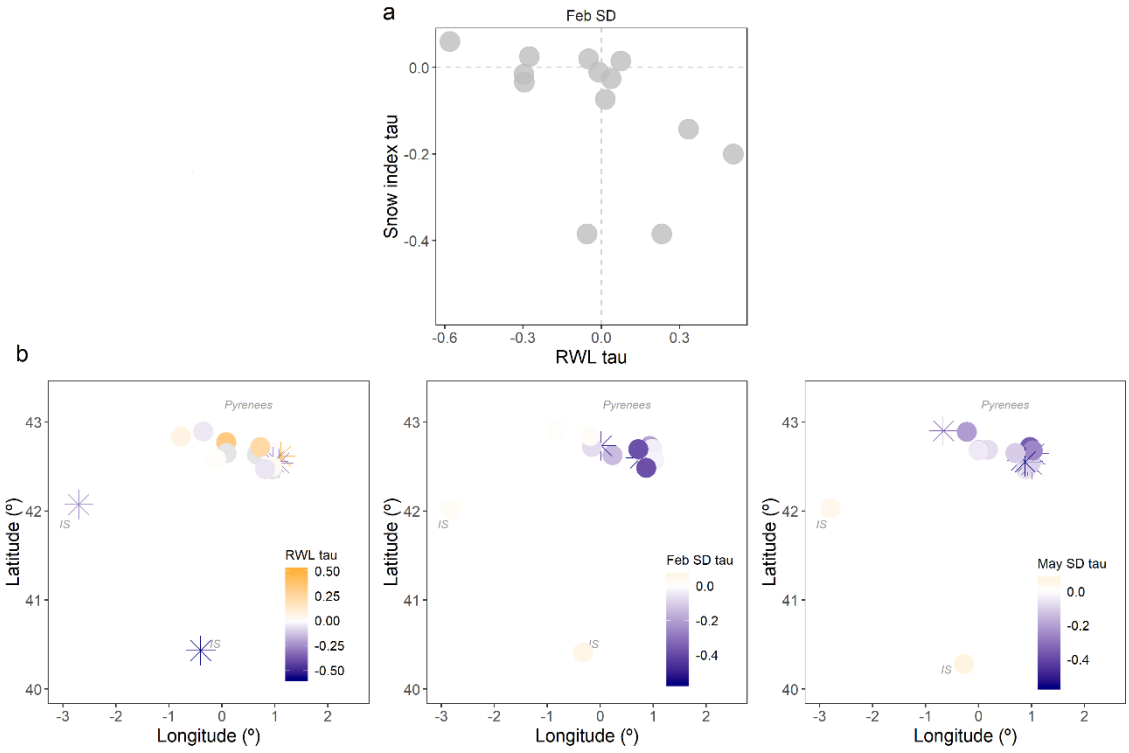

Figure 6. (a) Mann-Kendall linear trends (tau) for tree-ring width (RWL) and Feb SD snow index of selected sites from 1981 to last year with data (see series' lengths in Table S1) and (b) geographical representation of trend analyses results. Pyrenees and Iberian System (IS) locations are indicated.

4. Discussion

There is evidence that previous snow cover conditions influence *P. uncinata* tree-ring formation, in addition to the widely reported growing season air temperature effects, as hypothesized. The used methodology allowed us to infer the pure effect of snow on tree-ring growth by controlling the temperature influence on snowpack evolution. First, the most correlated monthly temperature aggregations to snow indices were detected (Table

S2), including other key temperature indices (May T) for *P. uncinata* growth; second, both temperature and snow indices were taken into account as predictors in radial growth stepwise linear models and by using partial correlations as complementary analyses. Similar procedures were used in Carlson et al. (2017) and Helama et al. (2013). Results provide additional information about the effects of climate on high-elevation *P. uncinata* radial growth. Previous studies showed that radial growth of *P. uncinata* was mainly limited by growing-season air temperature (Rolland and Schueller, 1994; Camarero et al., 1998; Tardif et al., 2003; Andreu et al., 2007; Galván et al., 2014) and, only in certain drought-prone sites, by low early summer precipitation (Andreu et al., 2007; Galván et al., 2014).

The influence of snow cover on radial growth had not been researched for *P. uncinata*, but it has been researched for other species of Pinaceae (Walsh et al., 1994; Kirdyanov et al., 2003; Helama et al., 2013; Watson and Luckman, 2016; Carlson et al., 2017; Franke et al., 2017; Appleton and St. George, 2018; Fkiri et al., 2018; Legendre-Fixx et al., 2018; Truettner et al., 2018). In this study, almost half the sampled forests in the main mountain ranges of the NE Iberian Peninsula showed certain snow-growth interaction (most of them were statistically significant).

The date of cambial initiation is a key factor for climate-growth associations. This date is related to the date when snowmelt occurs (Kirdyanov et al., 2003) and, consequently, with snow accumulation throughout the winter. The presence of abundant snowpack in late spring may induce a late melt-out and, as a result, a delay in the onset of the *P. uncinata* growing season because the persistent snow cover may cool the soil (Kirdyanov et al., 2003; Helama et al., 2013). This would explain the dominant negative spring snow (May SD index) influence on *P. uncinata* annual growth found in this study (Table 1, Figure 4). In this regard, Franke et al. (2017) reported that the average monthly

418 snow cover during the current year's May correlated negatively with *P. sylvestris*
419 chronologies. Likewise, northern conifers showed delayed cambial activity when snow
420 melt was delayed in the beginning of the growing season (Vaganov et al., 1999;
421 Kirdyanov et al., 2003). Previous studies of *P. uncinata* have demonstrated that this pine
422 species is negatively affected by the preceding growing-season low air temperatures
423 because the onset of cambial activity is triggered by a typical rise in temperature during
424 spring (Tardif et al., 2003; Galvan et al., 2014). Since no positive relation was found
425 between May SD snow index and RWI series in the performed models, we cannot report
426 that moisture from spring snowmelt promotes annual growth of *P. uncinata* in sampled
427 forests. The positive influence of snow on tree growth, explained by a moisture-
428 limitation, widely reported in more arid places as well as in large snow accumulation
429 areas (St. George, 2014; Watson and Luckman, 2016; Carlson et al., 2017), was not
430 detected in the few possible drought-prone sites (Pre-Pyrenees and southern Iberian
431 System) sampled in this study. Winter precipitation is less likely to contribute to the soil
432 moisture reservoir used by trees during the following growing season if spring
433 precipitation is abundant and shows low year-to-year variability as is the case. Spring
434 rainfalls would introduce an extra source of water that would sum up to the water from
435 snowmelt, and thus, the positive influence of snow on tree growth based on moisture-
436 limitation was not detected.

437 As discussed above, large winter snow accumulation likely produces larger snow
438 presence in spring and this, in turn, causes a delayed melt-out. It is not easy to isolate the
439 impact of winter snow on radial growth, compared to that of late spring snow, because
440 they both are related; however, we did observe that May SD was selected 60% more than
441 Feb SD as best predictor of RWI in the performed models (Table 1). In this regard,
442 Watson and Luckman (2016) evidenced a relation between larger snow accumulation and

delays in *P. ponderosa* and *Pseudotsuga menziesii* growing seasons in some regions of Canada. Fkiri et al. (2018) also reported that winter snow is a major factor limiting growth of *P. nigra* in NW Tunisia. Other studies, however, pointed to a positive influence of winter snowfall on tree-ring growth due to snowmelt waters may constitute much of the available resource to trees during the beginning of the following growing season (e.g. St. George, 2014).

A possible explanation for the scarce influence of preceding November snow conditions on growth observed in our study is that occasional early-season snowfalls before November did not contribute to overall autumn snow accumulation, thus it was relegated to accumulation occurred in the season last month. As a consequence, small snowpacks were found in November. Furthermore, this late autumn snow depth accumulation has a minor influence on the presence of late spring snow (Nov SD and May SD indices were not correlated, r_s = 0.33), which was pointed out in this study as the most important seasonal snow component influencing *P. uncinata* growth. Contrary to our results, Carlson et al. (2017) in *P. albicaulis* forests and Helama et al. (2013) in *P. sylvestris* forests detected significant negative effects of autumn snowfall and autumn snow depth on radial growth, respectively. The early snowfall in autumn and soil cooling can be related to the cessation and shortening of the growing season (Carlson et al., 2017). In this instance, other physiological tree processes are affected: among others, (1) the reduction of photosynthate storage for the following year growth resumption (Fritts, 1976), (2) the reduction of mycorrhizal activity (Peterson and Peterson, 1994), and (3) the inhibition of carbon transfer into radial growth and later carbon storage for the following year (Hoch and Körner, 2003). Moreover, previous studies have demonstrated that *P. uncinata* is sensitive to previous November low temperatures, when synthesis and

storage of carbohydrates can affect later radial growth (Tardif et al., 2003; Galván et al., 2014).

Evidence of tree characteristics' influence on the snow-radial growth relationship was found. Smaller trees showed to be more sensitive to snow effects (Figure 5b), which could be due to a more efficient hydraulic functioning (Galván et al. 2012) or to a lower influence of snowpack on microclimate and phenology in the case of tall trees. Zhu et al. (2015) reported that large trees have higher recovery rates from snow damage than smaller trees. With regard to geographical distribution of snow-growth interactions, in the Pyrenean sites (central and western areas) occurred almost all of the significant snow-growth correlations, but also the negative snow-growth influence was detected in the drier Iberian System site. Any snow influence on *P. uncinata* growth was found in the Pre-Pyrenees or eastern Pyrenees sampled sites. Previous studies (Tardif et al., 2003; Galván et al., 2014) have demonstrated that elevation plays a major role in *P. uncinata* radial growth-index responses to climate. Galván et al. (2014) observed an elevation pattern regarding temperature: November temperature conditions during the year prior to tree-ring formation influence *P. uncinata* growth mainly in mid-elevation sites, whereas at higher elevations, growth was more dependent on May temperature conditions during the year of tree-ring formation. However, no statistical significant relation was found regarding the elevation gradient determine whether *P. uncinata* radial growth is influenced by a specific snow index. Thought results from partial correlation analyses indicate that the main negative snow influences on tree growth were found at higher elevations (Figure S3), this study did not produce sufficient evidence to confirm our initial hypothesis. We expected that upper and therefore colder forest sites could be the most sensitive to snow-growth influences. The decrease in near-surface air temperature produced by an increase in elevation (Navarro-Serrano et al., 2018) was suggested to limit

the maximum elevation of tree growth due to a short growing season (Körner, 2012). Consequently, snow conditions could be expected to be the most limiting factor for radial growth at high elevations which further reduces *P. uncinata* growth period, especially linked to late spring snow cover. But more detailed information on elevational gradients of snow features are needed to test it.

Significant and decreasing trends were detected in winter and spring snow depths along the Pyrenees (although trend coefficients are very dependent on the selected study period), similar to other main mid-latitude mountain ranges (López-Moreno, 2005; Marty, 2008; McCabe and Wolock, 2009; Beniston, 2012; Morán-Tejeda et al., 2013a; Buisan et al., 2015) (Figure 6b). A significant and negative response of *P. uncinata* growth to the negative trends in winter snow was found (Figure 6a), but it was not ubiquitous. Thus, trends of *P. uncinata* growth were not consistent through all forests, thought almost all the statistically significant coefficients found were negative (only there was one increasing growth trend). This may be related, however, to the length of the radial growth data series. Overall results suggest that *P. uncinata* radial growth could benefit from the predicted shallower snowpack in these mountain ranges (López-Moreno, 2005; Morán-Tejeda et al., 2013a) over the next decades by a prolongation of the growing season, especially in high elevation forests. Likewise, climatic warming is expected to promote forest growth in the Pyrenees in a similar way (Tardif et al., 2003). However, growth could be declined in some dry sites where the amount of soil water available to trees in the growing season relates to the previous months' snowpack (Pederson et al., 2011). Therefore, in xeric sites, a shallower snowpack due to warmer temperatures could lead to limited soil water content in spring and reduce growth (Walsh et al., 1994; Truettner et al., 2018). It has been reported that these thermal stress sites are dependent on early summer precipitation (Richter et al., 1991; Andreu et al., 2007; Galván et al.,

2014), but this has not been observed so far in our studied sites. This may be related to limitation in the data used in this study. The length of the radial growth data series was not consistent throughout the sampled sites, ranging from 30 to 13 years of available data per sampled forest. The temperature and snow depth data were a product of a climate simulation with the WRF model, with a spatial resolution (10 x 10 km) that could be too coarse to represent their real spatial variability on the complex terrains of the forests. The regional nature of this study prevented consideration with finer-scale climatic observations.

This study seeks to further research with higher spatial and temporal resolution data, including in-situ climatic and snow cover records, and other environmental variables (such as soil moisture, wind, and solar radiation) in order to improve understanding of how snow-growth relations occur in *P. uncinata* mountain forests.

5. Conclusions

Radial growth of *P. uncinata* forests is affected by snow cover depth, independent of the widely reported effect of growing season air temperature on their wood formation. *P. uncinata* growth is negatively influenced by a larger winter and late spring snowpack depth. Geographical and topographical gradients and some tree characteristics as height explained differences in snow–growth relationships. This study suggests that a future shallower and more transitory snowpack in the studied mountains may benefit the growth of *P. uncinata* over the next decades, although a few forests could experience warming-induced drought stress.

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774 **Supplementary Material**

775 **Table S1.** *Pinus uncinata* sampled sites and their geographical, topographical, ecological
776 and nival characteristics. Values are means ± standard deviation.
777

Mountain range	Site (code)	Analysed years	Latitude N (º)	Longitude –W, +E (º)	Elevation (m a.s.l.)	Slope (º)	dbh (cm)	Age (years)	Max SD (m)
Pyrenees	Acherito (ACHE)	30	42.89	-0.75	1850	–	–	–	2.31 ± 0.61
	Airoto (AIRO)	16	42.70	1.03	2300	47 ± 29	58.5 ± 13.5	288 ± 100	2.54 ± 0.70
	Bielsa (BIEL)	16	42.70	0.18	2000	88 ± 4	45.1 ± 9.4	270 ± 67	1.14 ± 0.36
	Barranc de Llacs (BLLA)	30	42.53	0.92	2250	44 ± 38	71.7 ± 20.0	616 ± 175	2.65 ± 0.86
	Conangles (CONU)	14	42.62	0.73	2106	43 ± 15	56 ± 14.5	318 ± 117	1.94 ± 0.61
	Corticelles-Delluí (CORT)	30	42.56	0.93	2269	24 ± 17	83.1 ± 28.8	509 ± 177	1.26 ± 0.47
	Las Cutas (CUTA)	17	42.62	-0.08	2150	20 ± 5	33.3 ± 8.3	129 ± 16	1.31 ± 0.49
	Estany d'Amitges (EAMI)	29	42.58	0.98	2390	40 ± 21	69 ± 26.0	355 ± 106	1.51 ± 0.59
	Estany Gerber (EGER)	30	42.62	0.98	2268	15 ± 15	53.5 ± 14.6	426 ± 147	2.24 ± 0.64
	Estany de Lladres (ELLA)	29	42.55	1.05	2120	35 ± 12	52.1 ± 9.8	313 ± 123	1.03 ± 0.54
	Estany Negre (ENEG)	29	42.55	1.03	2451	35 ± 18	71 ± 26.0	411 ± 182	1.68 ± 0.66
	Estanys de la Pera (EPER)	17	42.45	1.61	2360	30 ± 0	65.2 ± 11.0	339 ± 117	0.94 ± 0.39
	Foratarruego (FORA)	29	42.62	0.10	2031	37 ± 11	49.5 ± 18.3	433 ± 50	1.83 ± 0.83
	Larra (LACO)	19	42.95	-0.77	1750	38 ± 24	46.4 ± 14.0	350 ± 108	1.90 ± 0.53
	La Estiva (LEST)	13	42.68	0.08	2000	–	–	–	1.10 ± 0.32
	Mata de València (MAVA)	17	42.63	1.07	2019	19 ± 10	43.2 ± 3.6	237 ± 72	1.65 ± 0.58
	Mirador (MIRA)	29	42.58	0.98	2180	33 ± 18	55.1 ± 25.8	401 ± 132	1.06 ± 0.41
	Mirador del Rey (MIRE)	18	42.63	-0.07	1980	25 ± 10	53.3 ± 15.3	117 ± 18	0.94 ± 0.29
	Monestero (MONE)	29	42.56	0.98	2280	28 ± 13	64.4 ± 16.1	346 ± 110	1.28 ± 0.49
	Vall de Núria (NURI)	21	42.38	2.13	2075	–	–	–	0.49 ± 0.27
	Pic d'Arnousse (PIAR)	14	42.80	-0.52	1940	32 ± 4	65.4 ± 5.1	248 ± 83	2.80 ± 0.67
	Ratera (RATE)	29	42.58	0.98	2170	40 ± 5	28.3 ± 8.1	380 ± 146	1.04 ± 0.40
	Respomuso (RESP)	30	42.82	-0.28	2350	70 ± 19	49.5 ± 15.1	280 ± 83	4.61 ± 1.17
	Sant Maurici (SAMA)	16	42.58	0.98	1933	16 ± 15	38.2 ± 5.7	204 ± 23	0.67 ± 0.22
	Sarradé (SARU)	15	42.55	0.89	1950	–	–	–	1.65 ± 0.51
	Senda de Cazadores (SECA)	29	42.63	-0.05	2247	49 ± 12	60.9 ± 16.5	337 ± 145	1.60 ± 0.76
	Setcases (SETU)	19	42.40	2.28	2080	–	–	–	0.68 ± 0.35
	Sobrestivo (SOBR)	29	42.67	0.10	2296	38 ± 2	61.7 ± 17.5	341 ± 97	2.06 ± 0.88
	Tessó de Son (TESO)	15	42.58	1.03	2239	42 ± 14	74.5 ± 18.8	346 ± 202	1.15 ± 0.37
	Vall de Mulleres (VAMU)	14	42.62	0.72	1800	34 ± 13	69 ± 26.0	437 ± 184	1.27 ± 0.35
Pre-Pyrenees	Cap de Boumort (COLU)	30	42.23	1.12	1915	–	–	–	0.35 ± 0.22
	Guara (GUAU)	30	42.28	-0.25	1790	–	–	–	0.62 ± 0.32
	Pedraforca (PEDR)	26	42.23	1.70	2100	–	–	–	0.69 ± 0.37
Iberian System	Vinuesa (CAVI)	30	42.00	-2.73	2050	21 ± 1	85.6 ± 23.0	368 ± 148	1.31 ± 0.39
	Valdelinares (VATE-VA1U)	26	40.37	-0.37	1955	10 ± 5	63.8 ± 12.4	214 ± 107	0.57 ± 0.32

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Table S2. Coefficients from Spearman correlations (r_s) between snow indices and temperature monthly aggregations. Arrow indicates which monthly aggregation of temperature is best correlated to each snow index and is then used in further analysis.

Temperature indices	Snow indices		
	Nov SD	Feb SD	May SD
Nov T	-0.34** ←		
Feb T		-0.63**	
Nov-Feb T		-0.57**	
Dec-Feb T		-0.63**	
Jan-Feb T		-0.64** ←	
May T			-0.55**
Mar-May T			-0.57** ←
Apr-May T			-0.56**

Values followed by ** are statistically significant at $p < 0.01$.

Table S3. Correlation coefficients from partial correlations calculated between tree-ring width and snow indices.

Site	Nº analysed years	Spearman correlations coefficients (r_s)		
		Nov SD	Feb SD	May SD
ACHE	30	-0.09	-0.27	-0.22
AIRO	16	-0.24	-0.23	-0.41
BIEL	16	0.32	-0.34	-0.12
BLLA	30	0.09	-0.09	-0.13
CAVI	30	-0.23	-0.35	-0.33
COLU	30	0.01	0.14	0.03
CONU	14	-0.06	-0.78**	-0.51
CORT	30	-0.02	-0.26	-0.18
CUTA	17	-0.30	0.01	0.07
EAMI	29	0.14	-0.23	0.03
EGER	30	0.05	-0.29	-0.38*
ELLA	29	0.19	0.21	-0.16
ENEG	29	0.06	-0.23	-0.12
EPER	17	-0.45	-0.56*	0.09
FORA	29	0.15	0.06	0.20
GUAU	30	0.13	0.17	0.06
LACO	19	0.22	-0.25	-0.31
LEST	13	0.14	-0.31	0.31
MAVA	17	0.17	0.08	0.15
MIRA	29	0.06	-0.23	-0.05
MIRE	18	-0.05	-0.47	0.37
MONE	29	0.02	-0.26	-0.21
NURI	21	0.11	-0.13	0.09
PEDR	26	0.04	-0.21	-0.25
PIAR	14	0.32	0.07	0.28
RATE	29	0.33	0.12	-0.24
RESP	30	-0.15	-0.15	-0.27
SAMA	16	0.33	0.05	-0.43
SARU	15	-0.06	-0.54*	-0.12
SECA	29	0.26	0.25	0.10
SETU	19	-0.15	0.07	-0.11
SOBR	29	-0.09	-0.29	-0.08
TESO	15	-0.01	-0.63*	-0.18
VA1U	26	0.34	0.06	0.07
VAMU	14	0.19	-0.71**	0.10
VATE	26	0.18	-0.34	-0.15

Values followed by * and ** are statistically significant at $p < 0.05$ and $p < 0.01$, respectively. Note that data length differs between sites.

Figure S1. Partial correlation coefficients (Spearman, r_s) calculated between tree-ring width and snow indices. Sites where a statistically significant correlation was found are labelled. Statistical significance of models is represented in red ($p > 0.05$) and blue ($p < 0.05$) colors.

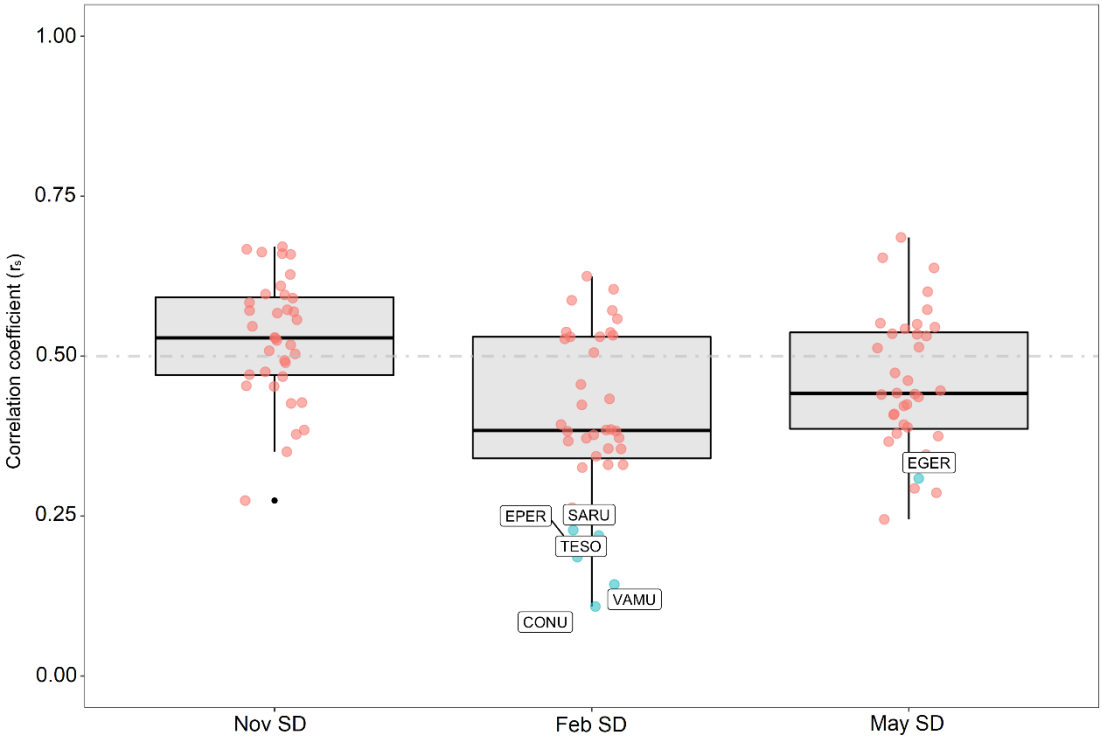

Figure S2. Latitude, longitude and elevation distribution patterns for groups of sites with the same RWI main drivers. Pre-Pyrenees (Pre-Pyr) and Iberian System (IS) locations are indicated where applicable. NA indicates sites whose selected model was null. Stars indicate sites whose selected model was statistically significant ($p < 0.05$).

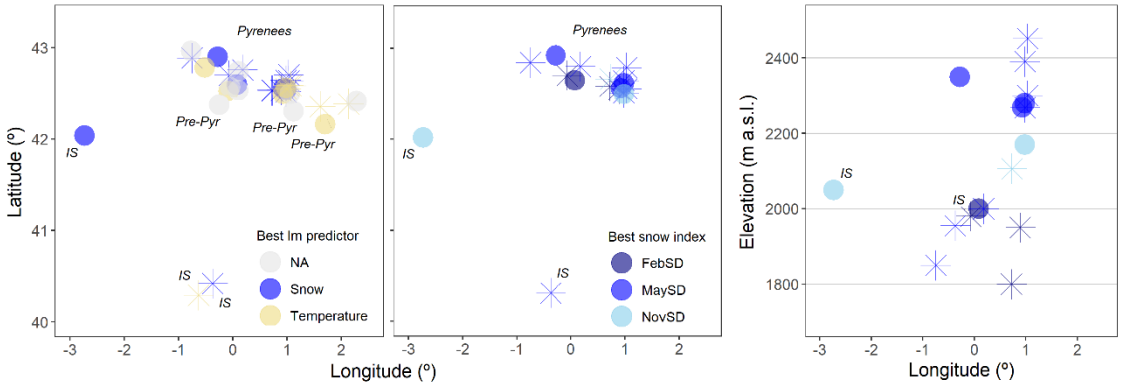

Figure S3. (a) Effect of geographical, nival gradients and tree influences on growth-snow partial correlations (Spearman correlations, r_s). The southern Iberian System sites were omitted in latitude analyses. (b) Scatterplots of statistically significant correlations ($p < 0.05$) obtained between growth-snow partial correlations and biogeographical gradients. Histograms show sites frequency of distribution along gradients.

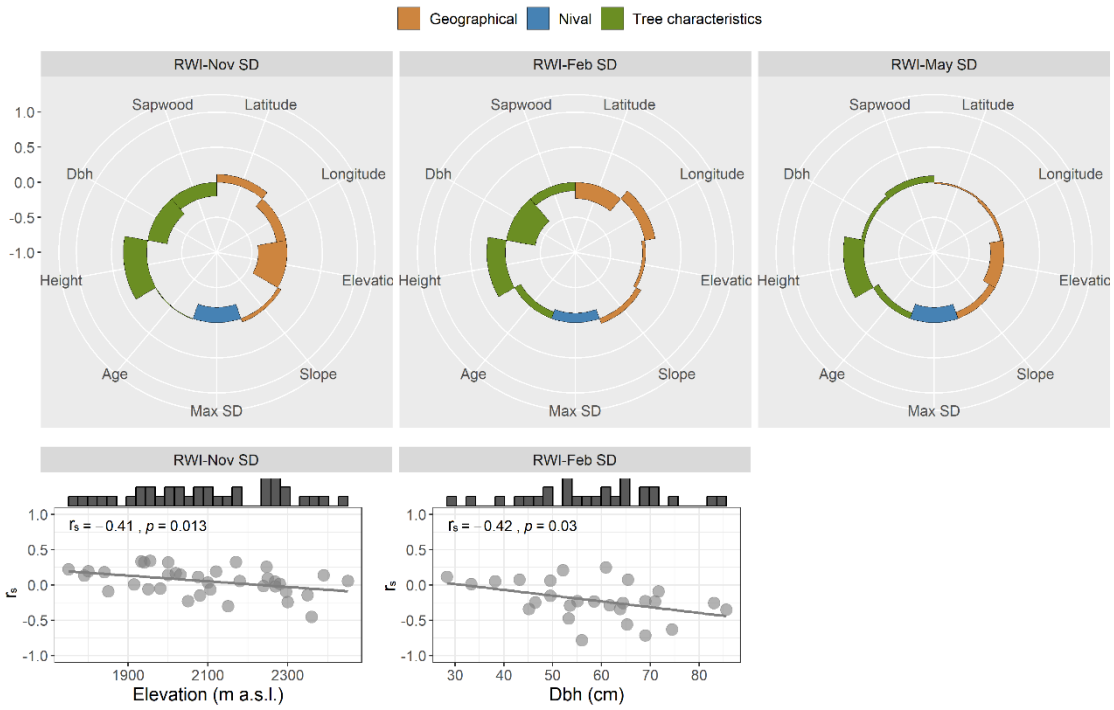

Figure S4. Theil-Sen's slopes (variable's units in mm·year^{-1}) for tree-ring width (RWL) and snow indices trends of selected sites from 1981 to last year with data (series' lengths are shown after site codes). Statistically significant values at $p < 0.05$ are represented with stars. Blank values in RWL mean data is not available for these sites.