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Local and regional climatic constraints of shrub and tree growth near the treeline

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ABSTRACT

Many treeline and shrublines are not responding to climate warming as fast as expected. This lack of responsiveness could be explained by other non-thermal, climate drivers operating at the cold edge of distribution of trees and shrubs. To determine which are the main climate drivers of tree and shrub radial growth near the treeline we measured ring width and related it to climate variables (temperature, precipitation, snow depth) and vegetation greenness (NDVI, Normalized Different Vegetation Index). We compared two dwarf shrub (*Vaccinium uliginosum*, *Dryas octopetala*) and three tree species (*Larix sibirica*, *Picea obovata*, *Pinus uncinata*) sampled in three treeline sites: Polar or Northern Urals, Southern Urals, and Spanish Pyrenees. Dwarf shrubs presented lower first-order autocorrelation (AR1) than trees, excepting in the N. Urals site. In this site, *V. uliginosum* showed a negative growth trend, whereas this tendency was observed in *P. obovata* and *P. uncinata* trees from the S. Urals and Pyrenees sites, respectively. Shrub and tree growth indices correlated with NDVI at different months. Trees showed stronger and positive growth responses to warmer summer conditions and also negative responses to precipitation in the N. and S. Urals. The growth of *D. octopetala* in the Pyrenees was enhanced by prior-winter and current-spring precipitation showing a strong correlation with May snow depth ($r = 0.66$, $p = 0.0006$, period 1998–2020). Dwarf shrubs and trees coexisting near the treeline differently responded to regional climate variability. Our findings indicate a strong dependence of shrubs and trees on local (e.g., snow depth) and regional (e.g., growing-season air temperature) climate conditions, respectively.

1. Introduction

Arctic and alpine regions are experiencing high warming rates with important implications on water provisioning, biodiversity, carbon sequestration, and ecosystem functioning (Rantanen et al., 2022; Marta et al., 2023). These rapid increases in air temperatures are also impacting the growth of arctic and alpine woody plant species. For instance, positive trends in satellite-derived vegetation indices (greening) are linked to shrub expansion and encroachment in tundra sites (Forbes et al., 2010; Myers-Smith et al., 2015a). Polar and alpine treelines and shrublines are also shifting polewards and upwards (Harsch et al., 2009), albeit they have showed lagged or lower-than-expected responses to the increase in air temperature in many sites (Camarero and Gutiérrez, 2004; Camarero et al., 2021; Lu et al., 2021). The mismatches between warmer conditions and reduced responses of treelines and shrublines have been explained by other factors such as soil moisture playing a relevant role. For example, warming-induced drying limited the upward advancement of Himalayan treelines (Sigdel et al., 2018) and constrained the recruitment of juniper shrublines in the Tibetan Plateau (Lu et al., 2018). Recently, it was also shown that atmospheric drought explained the recent responses of many alpine treelines to climate warming (Xie et al., 2024).

Therefore, there may be a paradigm shift from a focus on thermal constraints of growth as major drivers of potential locations of treelines

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and shrublines (Körner, 2012a, 2021; Körner and Paulsen, 2004) to a more complex view where other local climate and non-climate (e.g., soil nutrients) drivers also intervene (McIntire et al., 2016).

To resolve this issue, we need to better understand how functional differences between trees and shrubs, such as the closer aerodynamic coupling of the former, impact on growth in the long term (Körner, 2012b). Comparing climate, snow, and ring-width series of tree and shrub species coexisting near or above the treeline, as has been done under other stressful conditions (García-Cervigón et al., 2012; Gazol and Camarero, 2012a, 2012b; Gazol et al., 2024) or along wide climate gradients (Pellizzari et al., 2016), would advance our understanding on this question. The comparison of the growth responses (correlations) to regional (e.g., temperature) or local (e.g., snow depth) climate factors of coexisting tree and shrub species should be a research priority. Moreover, such correlative approaches should be discussed in light of recent dendrometer or xylogenesis studies which show different patterns in tree and shrub radial growth response to warmer growing-season conditions (Dobbert et al., 2021a, 2021b, 2022a, 2022b, 2022c; Albrecht et al., 2024; Li et al., 2016, 2023).

There is a rich literature on arctic and alpine shrub radial-growth

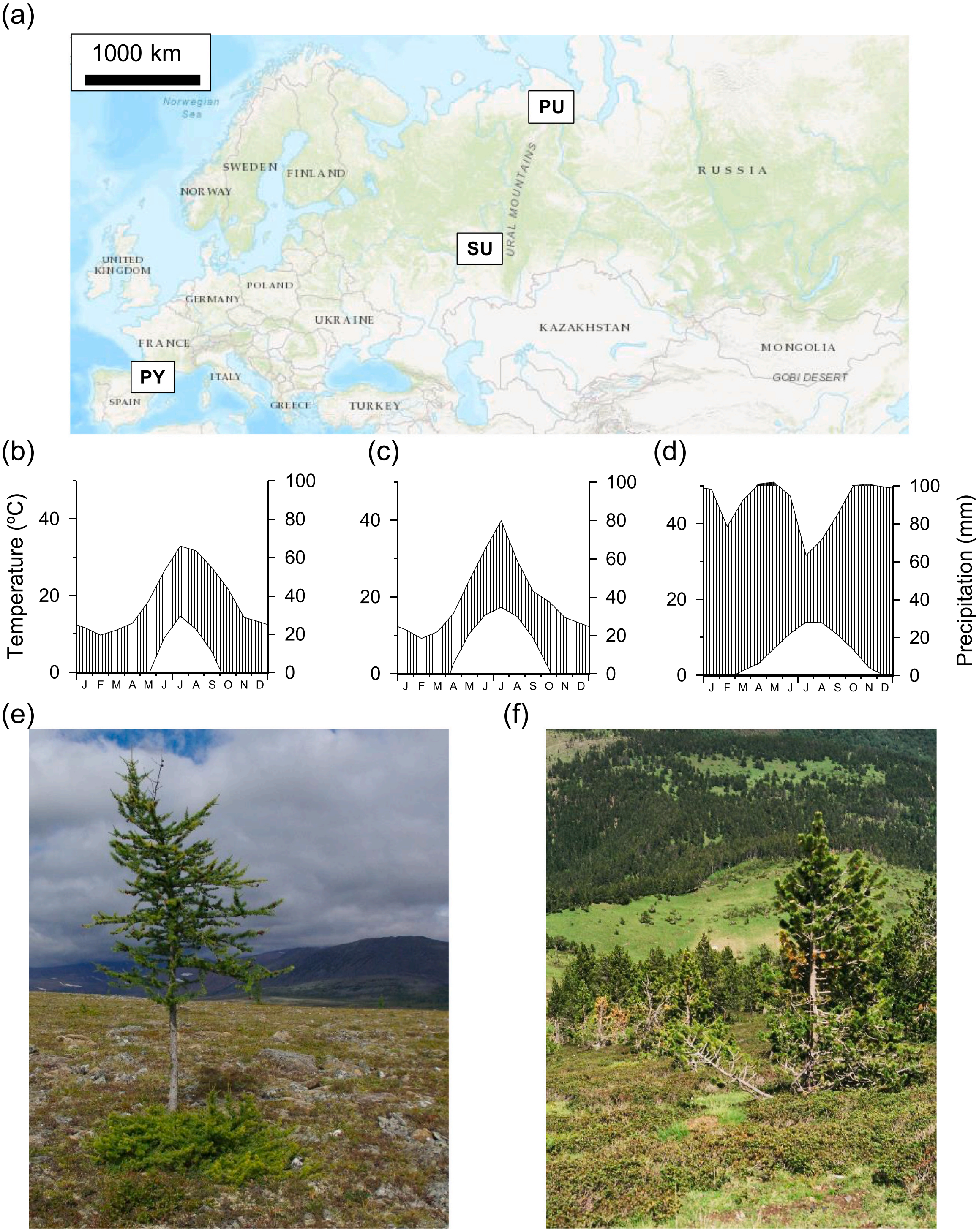

Fig. 1. (a) Location and climatic conditions of the three treeline sites (PY, Pyrenees; PU, Polar Urals; SU, Southern Urals) sampled in the Polar Urals (b), Southern Urals (c) and Spanish Pyrenees (d). Views of treeline sites in the Polar Urals (e) and the Pyrenees (f).

responses to climate, particularly in the case of some gymnosperm (*Juniperus*) and angiosperm (*Salix*, *Betula*, *Alnus*, *Rhododendron*) genera (e.g., Liang and Eckstein, 2009; Hallinger et al., 2010; Blok et al., 2011; Buchwal et al., 2013; Li et al., 2013; Pellizzari et al., 2014; Lu et al., 2015; Francon et al., 2017; Andreu-Hayles et al., 2020; Tumajer et al., 2021; Drew et al., 2023). However, a particular emphasis should be put on dwarf shrubs which are more aerodynamically coupled to soil conditions and represent the dominant woody growth form beyond treelines. In this case, the number of studies on growth of artic and alpine dwarf shrub species is limited but rapidly growing (Lageard et al., 2005; Au and Tardif, 2007; Bär et al., 2007, 2008; Rixen et al., 2010; Liang et al., 2012, 2105; Büntgen et al., 2015; Weijers et al., 2018; Dolezal et al., 2021; Thakur et al., 2024). However, most of this research lacks the comparison with nearby or coexisting trees (but see Francon et al., 2023) which limits our comprehension of growth responses to climate near treeline in these two contrasting life forms.

Therefore, if alpine dwarf shrubs face more variable microclimate conditions than trees, form narrower rings and show a shorter growing season, we would expect that: (i) shrub radial growth would be less coupled to changes in regional climate conditions and vegetation greenness than trees, but more coupled to local snow conditions, (ii) shrubs would respond to climate variables in a shorter narrow temporal window than trees, and (iii) shrubs would be less responsive to regional climate warming. We also expect finding old shrub individuals because harsh climatic conditions and short growing seasons should lead to low growth rates and long lifespans (Shiyatov et al., 2002; Schweingruber and Poschlod, 2005). To test these hypotheses, we quantified changes in radial growth by using dendrochronology in dwarf shrubs (two species) and trees (three species) coexisting near the treeline in three different Eurasian mountain sites (Northern Urals, Southern Urals, and Pyrenees). To assess changes in greenness, we used the Normalized Different Vegetation Index (NDVI), a widely used proxy of canopy activity (greenness) based on remote-sensing information (Tucker and Sellers, 1986).

2. Material and methods

2.1. Study sites and species

We selected three undisturbed treeline sites where previous studies on treeline dynamics and tree growth have been carried out by our teams: Northern or Polar Urals, Southern Urals, and Spanish Pyrenees (Fig. 1a, Table 1). The sites are situated along wide latitudinal (24º, ca. 2400 km) and longitudinal (65º, ca. 6500 km) gradients in Eurasia. These sites provided different climatic conditions characteristic of arctic and alpine areas along a large geographical gradient where several tree and shrub species coexisted.

The N. and S. Urals Russian sites are located near the Rai-Iz and Iremel ranges, respectively. They have been widely studied to characterize long-term, spatio-temporal changes in treeline dynamics (Shiyatov, 2003; Devi et al., 2008; Hagedorn et al., 2014) and their impacts on plant biodiversity (Gazol et al., 2017). The N. and S. Urals sites are dominated by the deciduous Siberian larch (*Larix sibirica* Ledeb.) and the evergreen Siberian spruce (*Picea obovata* Ledeb.), respectively. Bog bilberry (*Vaccinium uliginosum* L., Ericaceae) was the dwarf shrub studied in the two Russian sites. It is a deciduous, short-stature (50−80 cm) species with horizontal rhizomes which usually grows on wet, acid soils and forms the understory in conifer forests across the N. Hemisphere (Jacquemart, 1996). Other species found in the N. and S. Urals sites were *Salix glauca* L., *Juniperus communis* L., and *Betula tortuosa* Ledeb. Mean annual temperature and total precipitation in the N. and S. Urals ranged −6.6−2.0 °C and 800−900 mm, respectively (Hagedorn et al., 2014). The maximum snow depth ranged 150−250 cm in the Russian study sites, but winters are very cold with mean January temperatures up to −24.0 °C low. Soils are rocky and acid, mainly Haplic Cambisols.

The Pyrenean treeline site (Lo Tésol) is located near the Son del Pi village and the “Aigüestortes i Estany de Sant Maurici” National Park (Lleida, NE Spain). It is dominated by Mountain pine (*Pinus uncinata* Ram.), which is an evergreen, shade-intolerant conifer showing a growth peak in May–June (Camarero et al., 1998). Some scattered birch trees (*Betula pendula* Roth.) are also found. The dwarf shrub studied here was the mountain avens (*Dryas octopetala* L., Rosaceae), an evergreen species distributed in mountains of the N. Hemisphere and growing on limestone outcrops. It is a long-lived, dwarf shrub (height 15−30 cm) forming dense, large mats (0.5–1 m in diameter) with short, horizontal rooting branches (Elkington, 1971).

The climate of the Pyrenees is strongly influenced by east–west and north–south gradients, with prevailing Mediterranean conditions (i.e., warm and dry summers) eastwards and southwards, whereas continental conditions (i.e., cold winters, wide thermal amplitude) are dominant in the Central Pyrenees. Mean annual temperature and total precipitation are 2.0 °C and ca. 2000 mm, respectively. Soils are rocky, basic, shallow and well drained. The maximum snow depth ranges 150−350 cm with maximum values in winter but also in early spring (Fig. S1). This is a diffuse treeline with tree height, stand density gradually decreasing upwards as plant understory diversity increases (Camarero and Gutiérrez, 1999, 2002; Pardo et al., 2013).

In the three study sites, treelines are ascending and encroaching as climate warms and tree growth is enhanced, which is particularly evident in the N. Urals (Sánchez-Salguero et al., 2018; Camarero et al., 2021). Furthermore, treeline dynamics are characterized by the positive effects of warmer-snowier and warmer conditions in the prior winter and during the growing season, respectively (Camarero and Gutiérrez, 1999, 2002, 2004; Shiyatov, 2003; Devi et al., 2008; Hagedorn et al., 2014).

2.2. Field sampling

Sampling was done in September 2012 and 2014 in the two Russian sites and in September 2017 and 2020 in the Pyrenees. First, we selected a representative, undisturbed area (50 m x 150 m along the elevational gradient) located above the treeline, which was defined as the highest elevation of 2-m high trees (Körner, 2012a). Second, we sampled 30−35 shrub individuals per species and site, but only used 20 individuals per species and site which were successfully cross-dated (Table 2). Shrubs were sampled in open areas (ca. 50 m x 50 m) where the study species were dominant and located 10−50 m above the treeline. Sampled shrubs were spaced at least 3 m apart from each other. Third, 20−80 mature trees forming the treeline were sampled by taking 5-mm cores at 1.3 m using Pressler increment borers. In the case of N. Urals and Pyrenees sites, the high number of sampled trees is explained by previous studies dealing with treeline responses to climate (Camarero et al., 2021). The mean aspect, slope and elevation of each study sites were recorded (Table 1).

Table 1
Description of study sites, tree and shrub species.

Site	Tree species	Shrub species	Latitude (N)	Longitude (E)	Elevation (m a.s.l.)	Aspect	Slope (º)
Polar Urals	*Larix sibirica*	*Vaccinium uliginosum*	66º 32’	66º 40’	450	SW	15
Southern Urals	*Picea obovata*	*Vaccinium uliginosum*	54º 32’	58º 51’	1400	S	10
Pyrenees	*Pinus uncinata*	*Dryas octopetala*	42º 36’	1º 03’	2360	NE	37

Table 2
Dendrochronological statistics. SD and AR1 are the standard deviation and first-order autocorrelation of ring widths, respectively. MS and rbar are the mean sensitivity and the mean correlation between individual series of ring-width indices, respectively. EPS is the Expressed Population Signal calculated for the 1925–2012 and 1991–2013 periods in the case of trees and shrubs, respectively. Different letters indicate significant ($p < 0.05$) differences in ring width between species of the same site according to Mann-Whitney tests.

Site	Tree (T) or shrub (S) species	No. individuals	No. ring-width series	Best-replicated timespan	Ring width ± SD (mm)	AR1	MS	rbar	EPS
N. Urals	S – *V. uliginosum*	20	39	1991–2013	0.63 ± 0.29	0.56	0.34	0.41	0.82
	T – *L. sibirica*	75	146	1883–2013	0.87 ± 0.42	0.54	0.35	0.76	0.96
S. Urals	S – *V. uliginosum*	20	38	1991–2013	0.72 ± 0.34a	0.30	0.42	0.35	0.80
	T – *P. obovata*	20	39	1925–2012	1.56 ± 0.77b	0.81	0.23	0.52	0.94
Pyrenees	S – *D. octopetala*	20	40	1980–2020	0.11 ± 0.06a	0.38	0.46	0.39	0.81
	T – *P. uncinata*	59	116	1910–2017	1.52 ± 0.73b	0.79	0.20	0.49	0.90

2.3. Preparing and studying wood cores and cross-sections

In the case of trees, cores were air dried in the laboratory, glued to wooden mounts and surfaced with progressively finer sandpapers for visualizing tree-ring boundaries (Fritts, 1976). Then, they were scanned at 2400 dpi resolution and visually cross-dated. Ring widths were measured with a 0.001 mm resolution using scanned images and the CooRecorder-CDendro software (Larsson and Larsson, 2022). The quality of cross-dating was checked using the COFECHA software which calculates moving correlations between individual series of ring-width values and the mean sites series (Holmes, 1983).

In the case of shrubs, there are several studies dedicated to the processing and measuring of radial growth, which is more complicated than in trees due to their multi-stemmed growth form and the formation of rings which can either decrease or increase in width going from the pith to the bark (Fig. 2). Wedging rings, missing rings, eccentricity and asymmetric geometry of the stem challenge the cross-dating of growth curves in wood samples of dwarf shrubs (Bär et al., 2006). Shrub samples taken at different heights also show different responsiveness to climate (Kolishchuk, 1990; Hallinger et al., 2010; Myers-Smith et al., 2015b). *Betula glandulosa* wood samples taken near the root collar were more sensitive to climate than stem samples in NE Canada tundra sites (Ropars et al., 2017). Therefore, we took samples near the root collar in the two studied shrub species. Shrub samples were placed in wet paper towels and dehydrated through immersion within 24–72 h of sampling (Thakur et al., 2024). After dehydration (5 days in 50 % ethanol plus 10 days in 70 % ethanol), samples were air-dried for 2 days and then stored in paper bags until further processing.

To obtain shrub cross-sections we used a sledge microtome (Gärtner et al., 2015). Cross-sections (15–25-µm thick) were mounted on glass slides, stained with a 1:1 mixture of Safranin and Astrablue, staining the lignified parts in red (Safranin) and the non-lignified parts in blue (Astrablue) Then, they were fixed with Eukitt®. High-resolution images of the fixed sections were captured using an Olympus BH2 microscope equipped with an Olympus DP73 camera. The images were stitched with PT-Gui (New House Internet Services BV, Rotterdam, NL) to create one composite image for each sample, and then analysed for growth measurements using again the software CooRecorder and CDendro (Larsson and Larsson, 2022). After carefully visually cross-dating, we measured annual radial growth increments from pith to bark to the nearest micrometre along three radii per cross-section and following the xylem rays (Fontana et al., 2021). Radii were measured in representative stem parts avoiding zones of very wide or very narrow rings. Overall, missing rings were not abundant, and typically ranged from 0 to 2 per radius.

The age of each individual was estimated by determining the maximum number of annual rings observed from bark to pith in each cross-section. To calculate climate– and drought–growth correlations individual ring-width (RW) series were detrended by fitting *x*-year cubic smoothing splines with a 50 % frequency response cut-off, where *x* was 2/3 of the mean series length. The measured ring-width values were divided by fitted values. The resulting series of dimensionless ring-width indices (RWI) were pre-whitened by fitting auto-regressive models, and bi-weight robust means were computed to obtain site series or chronologies preserving annual to decadal variability.

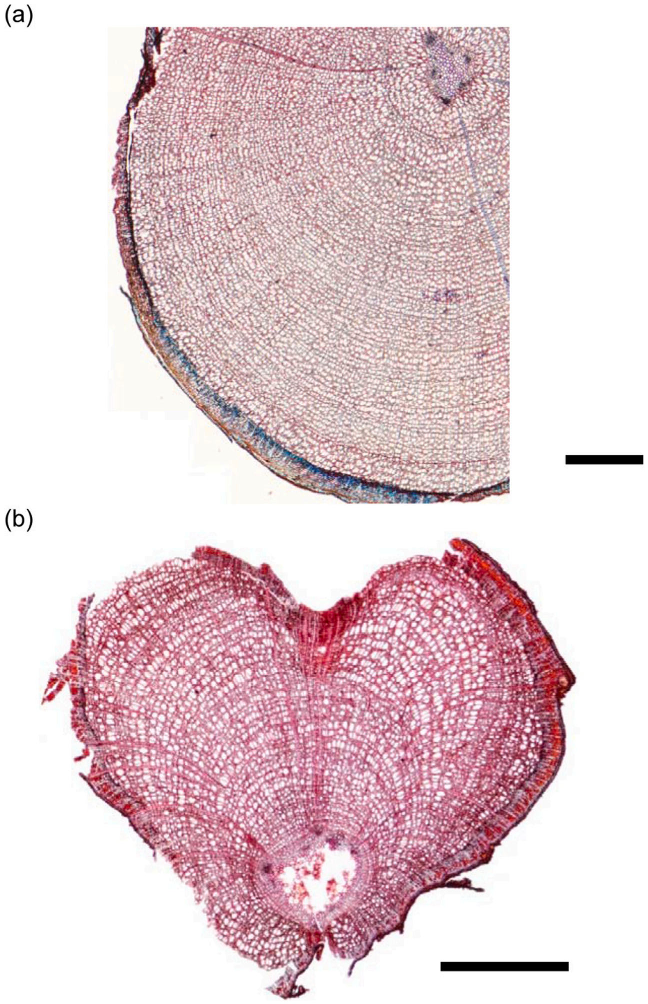

Fig. 2. Cross-sections of (a) *Vaccinium uliginosum* and (b) *Dryas octopetala* shrub individuals sampled in the S. Urals and Spanish Pyrenees treeline sites, respectively. The scale bars measure 1 mm.

To characterize and compare trees' and shrubs' RW and RWI series we calculated several statistics: the mean, standard deviation (SD) and first-order autocorrelation (AR1) of RW series; the mean sensitivity (MS) of standard (not pre-whitened) RWI series to measure the relative changes in RWI between consectuive rings, and the mean correlation (rbar) among individual pre-whitened RWI series. Lastly, calculated over the common 1925–2012 and 1991–2013 periods in the case of trees and shrubs, respectively (Table 2), an Expressed Population Signal (EPS) ≥ 0.80 indicated a high common signal within each of the six study series (Wigley et al., 1984).

2.4. Climate, snow depth, and NDVI data

In the case of the N. and S. Ural sites, historical temperature and precipitation data were taken from the Salekhard (66º 32' N, 66º 32' E, 55 km east of the study site, located at 16 m a. s. l., data for the period 1899–2013) and Zlatoust weather stations (55° 11' N, 59° 41' E, located 90 km north-east of the study area at 475 m a. s. l., data for the period 1837–2013), respectively. In the Pyrenees, we obtained climate data from the Vielha weather station (42º 42' N, 0º 48' E, 22 km north-west of the study site, located at 974 m a. s. l., data for the period 1945–1993). Nevertheless, due to the lack of homogeneous, long-term, updated temperature and precipitation series from stations located near the S. Urals and Pyrenees sites, we used the 0.5° gridded CRU v. 4.07 monthly climate data (mean temperature, total precipitation, period 1901–2022; Harris et al., 2020) to analyse climate-growth relationships. In the N. Urals, local and CRU temperature and precipitation annual data were significantly correlated ($r = 0.95$ and $r = 0.86$, respectively, $p < 0.001$ in both cases; Fig. S1). In the Pyrenees, monthly snow depth data from the Bonaigua climate station (from winter 1997−1998 to winter 2021−2022), located at 7.5 km north from the study site, were obtained (Fig. S2).

To assess how growth indices related to vegetation greenness, we used 0.05º-gridded monthly series of NDVI for the period 1981–2019 (Tucker and Sellers, 1986). NDVI values were obtained from the NOAA climate data record of Advanced Very High-Resolution Radiometer (AVHRR) Surface Reflectance (Vermote, 2019).

2.5. Statistical analyses

Non-parametric Mann-Whitney tests were used to compare ring widths between sites or species to account for the lack of normality in some cases. To assess trends in individual (length ≥ 15 years) and mean RW series we used Kendall *t* tests. Climate−RWI relationship were quantified using Pearson correlations between monthly climate variables (mean temperature, total precipitation, snow depth) and RWI series from prior October to current September and considering the common period 1991–2012. In the case of snow depth, we focused on the period with continuous snowpack in the three sites, i.e. from prior November to current May. Pearson correlations were also used to detect the monthly NDVI series most strongly correlated with RWI series.

Analyses were carried out using the R statistical package (R Core Team, 2023). The dplR package was used to process dendrochronological data including ring-width detrending and the calculation of statistics (Bunn, 2008, 2010; Bunn et al., 2023). Lastly, the "dcc" function from the treeclim package was used to calculate the correlations between climate variables and the mean RWI series (Zang and Biondi, 2015).

3. Results

3.1. Age and growth patterns

We sampled an 86-year-old *D. octopetala* individual, whereas the maximum age of *V. uliginosum* individuals was 36 years. Sampled trees were 88−131 years old. Shrub growth rates were significantly ($p < 0.05$) lower than tree growth rates, excepting for the N. Urals (Table 2). We found a positive correlation between tree and shrub series of ring-width indices in the S. Urals ($r = 0.58$, $p = 0.005$). In the case of shrubs, *V. uliginosum* from N. Urals showed the highest AR1 (0.56), whereas *D. octopetala* from the Pyrenees showed the highest MS (0.46). In the case of trees, *P. obovata* from the S: Urals presented the highest AR1 (0.81), whereas *L. sibirica* from the N. Urals showed the highest MS (0.35). The rbar and EPS values were higher for trees.

3.2. Growth trends

More individual shrub ring-width series showed significant negative than positive trends (Fig. 3). In the N. and S. Urals, 72 % and 50 % of the *V. uliginosum* individual series showed negative trends, respectively, and 0 % and 10 % of individuals showed positive trends, in the same order. In the case of *D. octopetala*, 32 % and 8 % of individual series presented negative and positive trends, respectively.

In the case of trees, 37 % and 22 % of individual ring-width series showed positive and negative trends, respectively, in the N. Urals. In the S. Urals and Pyrenees, 96 % and 42 % of tree series showed negative trends, whilst 0 % and 30 % of series showed positive trends, respectively.

3.3. Relationships between growth and greenness indices

The series of shrub ring-width indices showed significant and positive correlations with NDVI series of growing-season months such as June (*V. uliginosum* in the N. Urals, $r = 0.43$, $p = 0.04$), May (*V. uliginosum* in the S. Urals, $r = 0.47$, $p = 0.03$), and August-September (*D. octopetala* in the Pyrenees, $r = 0.48$, $p = 0.02$) (Fig. 4).

In trees, correlations between growth indices and NDVI were higher than in shrubs in the S. Urals and, particularly, in the Pyrenees. Again, correlations were the highest for growing-season months such as April (*P. obovata* in the S. Urals), July (*L. sibirica* in the N. Urals), and August-September (*P. uncinata* in the Pyrenees).

3.4. Relationships between growth indices and climate variables

Higher temperatures in July correlated with larger growth indices in the shrubs from the N. and S. Urals (Fig. 5). In the N. Urals, shrub growth indices were negatively correlated with the accumulated precipitation from prior October to December ($r = -0.46$, $p = 0.03$), but individual monthly correlations were not significant. In the S. Urals, warm March conditions and dry conditions in the previous autumn-winter (November, January) and current July also improved shrub growth. In contrast, wet conditions in January and May and cool June conditions were related to wider rings in the shrubs from the Pyrenees.

Warm conditions during the growing season enhanced tree growth as shown the positive correlations with June-July and May temperatures in the Urals and Pyrenees sites, respectively (Fig. 5). However, wet conditions in April, May or July were negatively related to tree growth indices in the N. and S. Urals. In the N. Urals, wet September conditions were positively correlated with tree growth indices.

3.5. Relationships between shrub growth indices and snow depth in the Pyrenees

In the Pyrenees, only shrub growth showed positive and significant correlations with monthly snow depth in the previous November and correlations peaked in May ($r = 0.66$, $p = 0.0006$; Fig. 6).

4. Discussion

Dwarf shrubs produced narrower rings than trees, excepting in the N. Urals site where tree growth rates were the lowest. In this site, the shrub *V. uliginosum* showed a negative growth trend, whereas this tendency was observed in trees from the S. Urals (*P. obovata*) and Pyrenees (*P. uncinata*). Shrub growth indices were less coupled to NDVI than trees in the Pyrenees, but trees showed stronger and positive growth responses to warmer summer conditions and also negative responses to precipitation in the two Urals sites. In contrast, prior-winter and current-spring snow precipitation drove growth of the shrub *D. octopetala* in the Pyrenees. Finally, we only found old *D. octopetala* shrubs in the Pyrenees site, suggesting that harsh conditions and short growing seasons near the Urals treelines are too stressful to lead to long lifespans. In the case of.

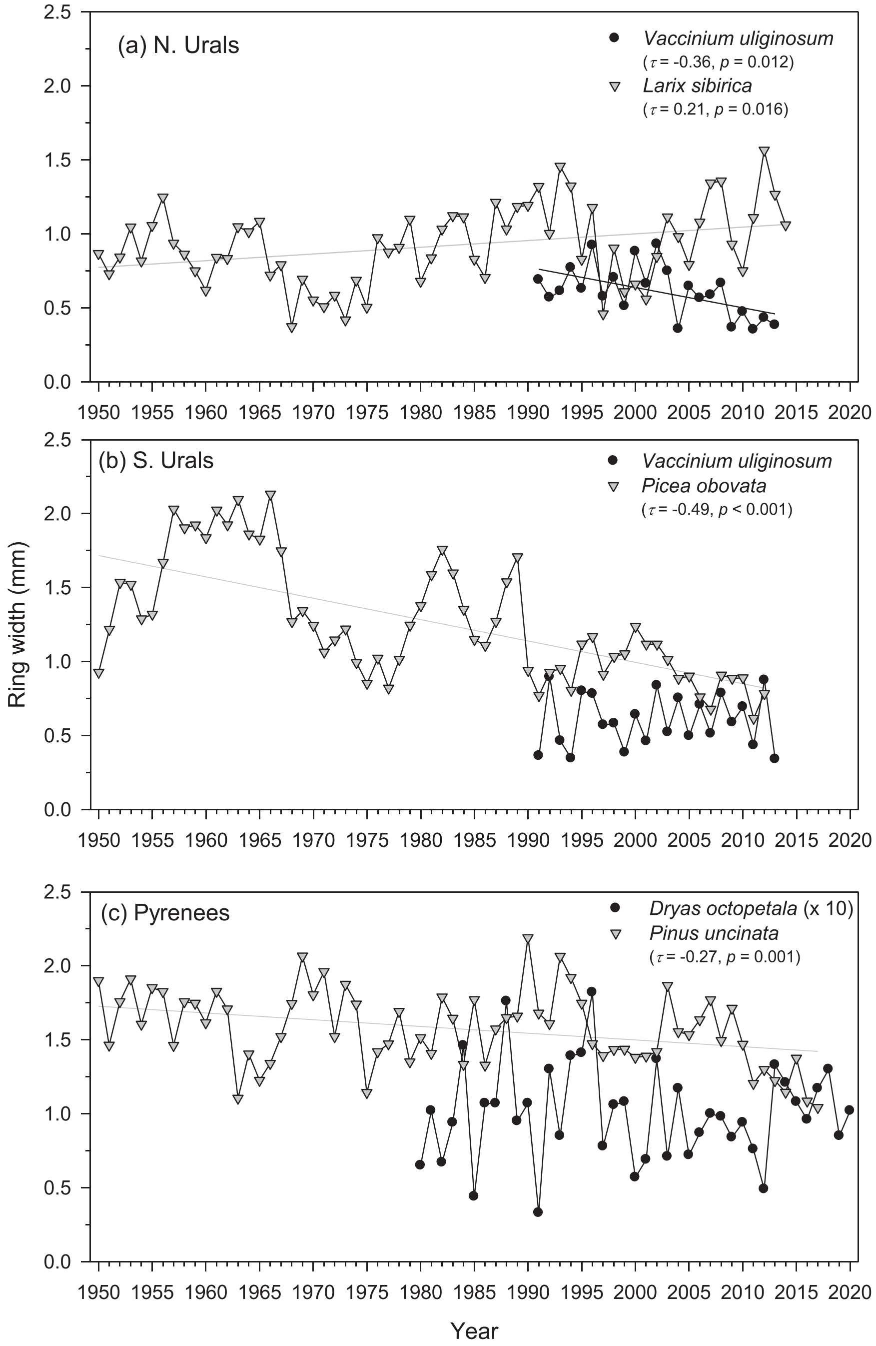

Fig. 3. Site mean series (chronologies) of shrub- and tree-ring width data obtained in the three study treeline sites. Series with significant trends ($p < 0.05$) based on Kendall *t* tests are shown with lines and the corresponding statistics are indicated. In the lowermost plot, *D. octopetala* ring widths were multiplied by 10.

D. octopetala, our estimated maximum age (86 years) was lower than the 116 years found in an individual sampled in a debris fan from the Italian Alps (Fontana et al., 2021). In this and other *Dryas* species, cross-dating is feasible, with or without intra-plant serial sectioning (Kolishchuk, 1990), because missing rings may be present but are not very frequent (Au and Tardif, 2007). In contrast, other shrubs such as *Salix polaris* presented 11 % of missing rings in arctic sites (Buchwal et al., 2013).

4.1. Contrasting growth trends in shrubs and trees among treeline sites

The negative growth trend of *V. uliginosum* in the N. Urals could be explained by its dependence on warm but also wet summer conditions. Warming summer conditions and also warmer-snowier winters are enhancing tree growth and productivity in the N. Urals treeline site (Devi et al., 2008; Hagedorn et al., 2014; Sánchez-Salguero et al., 2018). This could also lead to treeline encroachment and outcompete some understory shrubs due to lower radiation levels, albeit dwarf shrubs were sampled in open areas with rocky soils and low water holding capacity. Thus, warming-induced drought stress could also explain this growth decline as has been postulated in Himalaya treelines (Sigdel et al., 2018) and juniper shrublines in the Tibetan Plateau (Lu et al., 2018).

The negative growth trends observed in trees from S. Urals and Pyrenees could be the effect of ontogenetic changes as stems age and enlarge. The conversion of ring-width into basal area increment (BAI) could solve this issue, but this variable showed again the same ranking of growth trends despite being all positive and significant (Fig. S3). Again, *V. uliginosum* from N. Urals and *P. obovata* from the S. Urals showed the

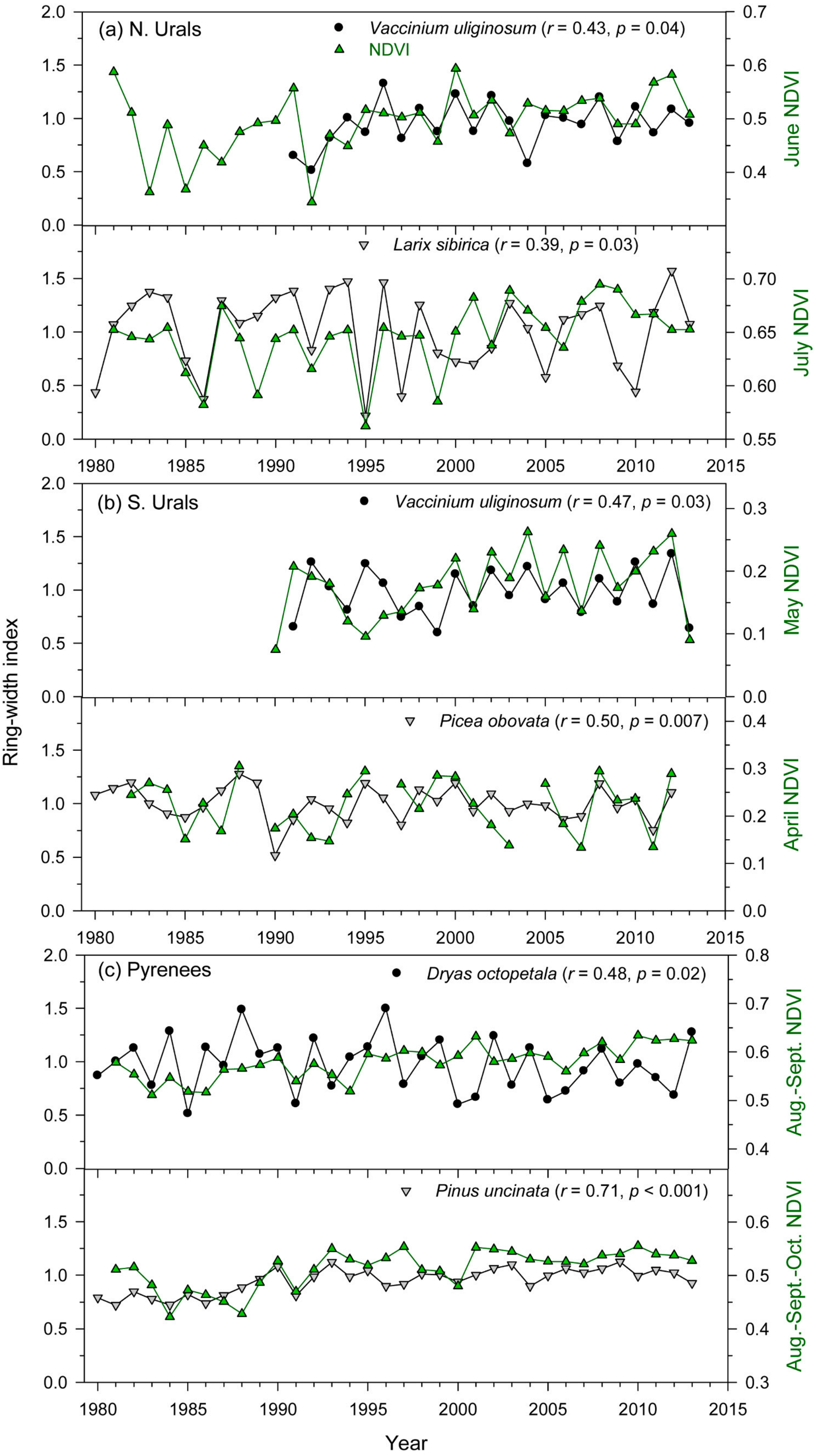

Fig. 4. NDVI-growth relationships in the three study sites (a, b, and c). The statistics shows Pearson correlation coefficients and significance levels of correlations calculated between trees and shrub series of ring-width indices and the corresponding monthly NDVI values. In the Pyrenees (plot c), the maximum correlations were obtained for 2- or 3-month mean NDVI values. All series were cropped until 2013 to make them comparable.

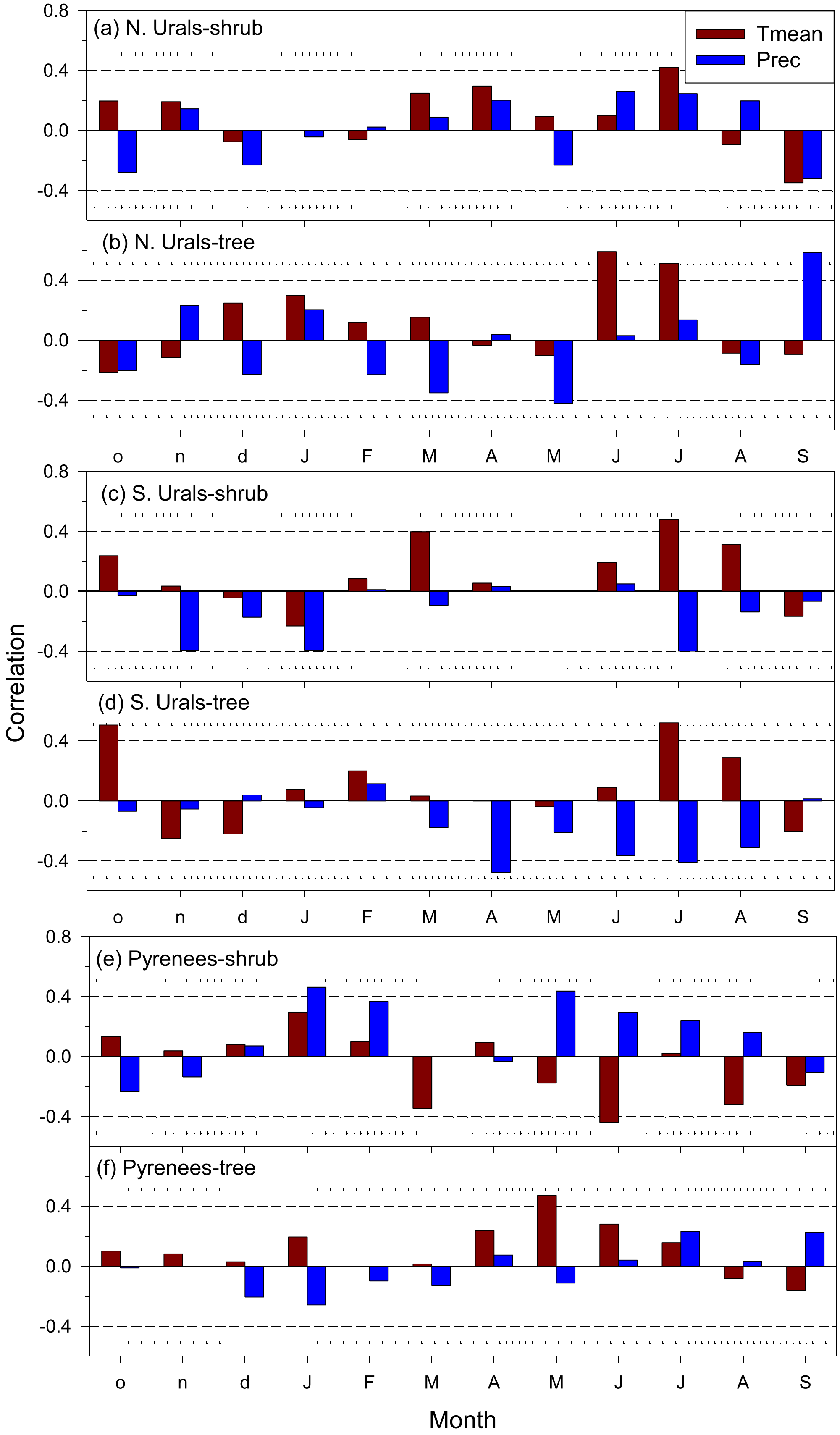

Fig. 5. Climate-growth relationships based on Pearson correlations calculated between monthly climate data (Tmean, mean temperature; Prec, precipitation) and the chronologies of shrub and tree ring-width indices obtained in the three treeline sites. The window of analyses goes from prior October (o) to current September (S). Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively.

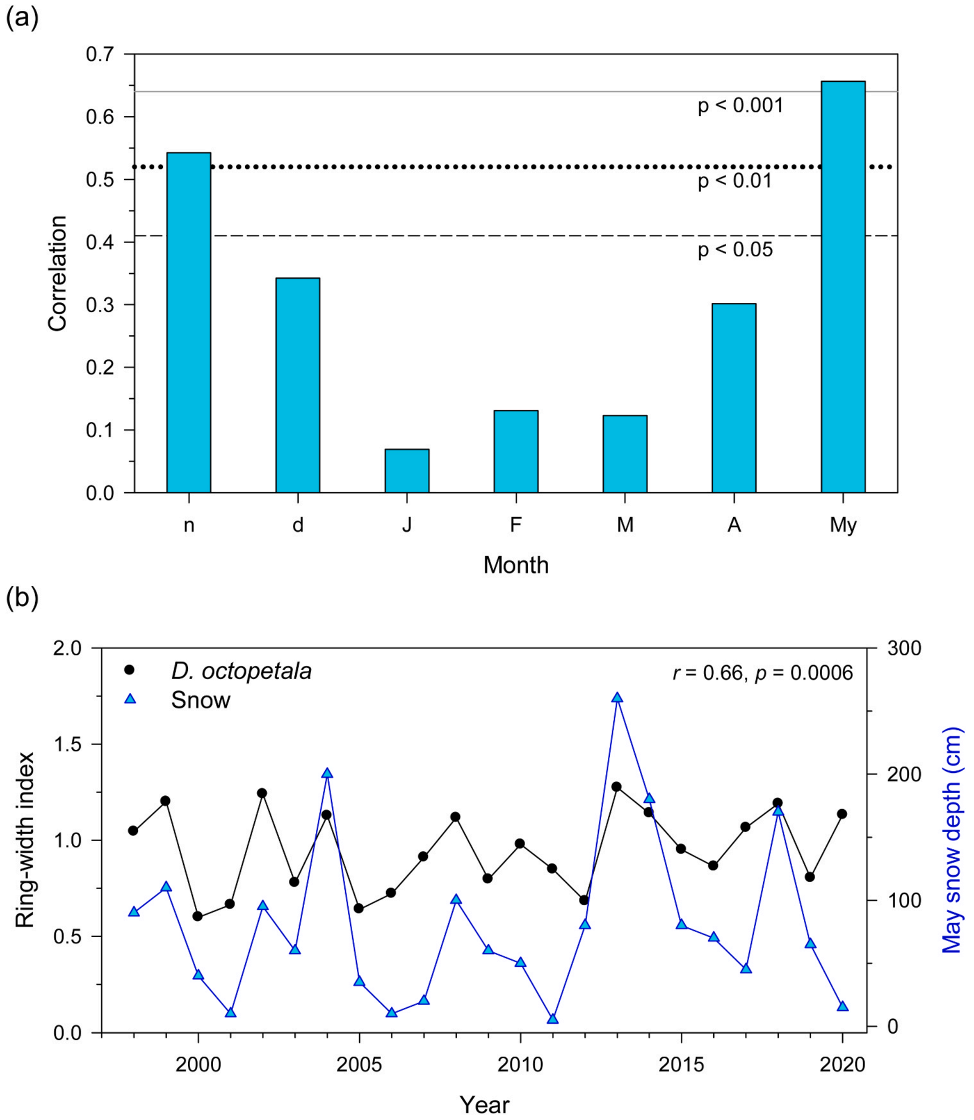

Fig. 6. (a) Correlations (Pearson coefficients) between *D. octopetala* ring-width indices and snow depth from prior November (n) to current May (My) in the Pyrenees treeline site (period 1997−2022). The horizontal lines indicate different significance levels. (b) Common temporal variability of *D. octopetala* ring-width indices and May snow depth measured in the Bonaigua station.

lowest BAI trends, whereas *P. uncinata* and *L. sibirica* showed the highest BAI trend. In general, BAI in the S. Urals was stable, whereas it increased in the other two treeline sites, probably as a response to warmer growing-season conditions (Camarero et al., 2021). Given that the treeline sites are open stands and tree-to-tree competition is still low, the lower growth increase observed in the S. Urals trees could be a response to stronger water shortage due to their dependence on spring and summer precipitation. In the case of shrubs from the S. Urals and Pyrenees, BAI showed increasing trends which are explained by warmer summer conditions and wetter spring conditions, respectively.

4.2. Growth responses to climate, snow depth and NDVI in shrubs and trees

We showed the climatic sensitivity of *D. octopetala* above the treeline, particularly in response to May snow depth variability, which confirms its potential to reconstruct changes in snow depth in sites under stable geomorphological conditions. The ring-width series of other alpine shrubs such as *J. communis* have also shown a strong potential as proxies of snowpack cover in the Italian Alps and the French Pyrenees (Pellizzari et al., 2014; Carrer et al., 2019, 2023; Francon et al., 2023). Moreover, snow cover has been show to influence tree growth in Pyrenean *P. uncinata* forests and *J. communis* shrublands (Sanmiguel-Vallelado et al., 2019; Francon et al., 2023). Links between radial growth and snow cover have been uncovered in several arctic and alpine dwarf shrub (Bär et al., 2006; Rozema et al., 2009; Forbes et al., 2010; Hallinger et al., 2010; Schmidt et al., 2010; Blok et al., 2011; Buchwal et al., 2013) and tree species (Vaganov et al., 1999; Sanmiguel-Vallelado et al., 2019: Francon et al., 2023). These studies illustrated the relevance of winter-spring precipitation, and not only summer temperature, for arctic and alpine shrub and tree growth. We show the growth dependence of dense and prostrated *D. octopetala* mats on snow pack, but not of scattered and more open *V. uliginosum* mats.

A greater snow cover in winter improves the thermal insulation of meristems, enhancing soil microbiota activity and increasing nutrient supply for shrubs in spring (Sturm et al., 2005). Nevertheless, a too deep snowpack may shorten the growing season and reduce shrub growth as found for *Salix arctica* in Greenland (Schmidt et al., 2006). A lasting and deep snow cover could also favor some shrub species which outcompete others. However, genetic variability and phenotypic variability can also affect tree-to-shrub and shrub-to-shrub interactions and impact on treeline and shrubline dynamics (Liang et al., 2016). For instance, *D. octopetala* snowbed ecotypes better tolerated reduced light availability due to increased competition than fellfield ecotypes (McGraw, 1985). Warming could also lead to earlier snowmelt, which could promote shrub growth (Wilcox et al., 2019) or reduce shrub performance by increasing the likelihood of herbivory and fungal damage (Wheeler et al., 2016). A decrease in shoot growth after rapid snowmelt of several dwarf shrub species, including *V. uliginosum*, has been explained by frost exposure (Jonas et al., 2008; Wipf et al., 2009; Gerdol et al., 2013).

Interestingly, tree growth series were more coupled to regional climate and NDVI in the Pyrenees. Tree meristems are more coupled to atmospheric conditions and this would explain their higher sensitivity to regional changes in temperature and greenness. However, in the very open treeline from the N. Urals, cold summers constrain growth of shrubs and trees which could explain why they showed similar couplings with summer NDVI. In the warmer S. Urals and Pyrenees sites, growth covaried with spring and late-summer NDVI, respectively, suggesting longer growing seasons and more complex growth-greenness relationships. When comparing shrub and tree growth-NDVI relationships, biomes, local conditions and temporal scales of responses should be also considered (Vicente-Serrano et al., 2013). Furthermore, xylem phenology and microclimate conditions should be also investigated because they determine growth responses to climate variability (Tumajer et al., 2021). In this sense, microclimate and xylogenesis data have shown that tall shrubs completed wood formation earlier than trees despite experiencing lower soil temperatures (Treml et al., 2019).

4.3. Caveats

Lastly, our analyses and results must be interpreted considering several caveats. First, shrub growth responses to climate depend on site conditions and microclimate variability (Gazol and Camarero, 2012b; Thakur et al., 2024). Therefore, additional factors such as soil nutrient and water availability and shrub-to-shrub interactions, which change through time (García-Cervigón et al., 2013), should be considered in future studies. More finely-resolved (30 m or less) remote-sensing data should be used to obtain vegetation indices. Second, age and size can also influence the shrub responses to climate. For instance, older shrubs (*Alnus viridis* ssp. *fruticosa*) were more sensitive to summer temperatures in the Alaskan Arctic than younger conspecifics (Drew et al., 2023). This could also distort our analyses because the ages of most sampled shrubs (58 %) were lower than 25 years and old trees were also rare in the study treelines (the oldest trees were 205 and 211 years old and they were sampled in the N. Urals and Pyrenees, respectively). On the one hand, this can be explained by the exploratory characteristic of our work without previous knowledge of the growth of the species particularly in the Urals sites. On the other hand, further research should consider larger datasets of shrub individuals growing in the same site but showing a wide range in age and size to account for ontogenetic trends.

4.4. Conclusions

Climate warming is predicted to intensify in cold arctic and alpine regions contributing to greening and vegetation expansion polewards and upwards. Shrubline and treeline dynamics will depend on shrubification and tree encroachment. Our results suggest improved growing conditions in all studied treeline sites but with local differences. In the N. Urals, tree growth is forecasted to increase as temperatures keep rising. In the S. Urals, shrub growth is expected to show higher increases in relative growth rate than trees which could present warming-induced drought stress. In the Spanish Pyrenees, both shrubs and trees will keep high growth rates if spring conditions are wet and warm enough, respectively. Growing-season temperatures drive tree growth near the treeline, but changes in snow depth impact on shrub growth. The mismatches between climate warming and treeline or shrublines shifts could be explained by the spatial and temporal variability of the seasonal snow cover.

CRediT authorship contribution statement

J. Julio Camarero: Writing – original draft, Visualization, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Antonio Gazol:** Writing – review & editing, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Michele Colangelo:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Cristina Valeriano:** Writing – review & editing, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Elisa Tamudo:** Writing – review & editing, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Pavel A. Moiseev:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request. Data generated during this study are available from the corresponding author upon reasonable request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2024.126256.

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